Title
Whales of the rainforest: habitat use strategies of sympatric rorqual whales within a fjord system

Permalink
https://escholarship.org/uc/item/52f602q1

Author
Keen, Eric

Publication Date
2017

Supplemental Material
https://escholarship.org/uc/item/52f602q1#supplemental

Peer reviewed|Thesis/dissertation
Whales of the rainforest: habitat use strategies of sympatric rorqual whales within a fjord system

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in

Oceanography

by

Eric Michael Keen

Committee in charge:

Professor Jay Barlow, Chair  
Professor Paul Dayton, Co-Chair  
Professor Lisa Ballance  
Professor David Checkley  
Professor Clark Gibson  
Professor Brice Semmens

2017
The Dissertation of Eric Michael Keen is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2017
DEDICATION

For their friendship throughout this journey, for their heritage and hopes that inspire so many, for their lands and waters worth fighting for, and for all the delicious fish they gifted us, I dedicate this dissertation to the Gitga’at First Nation.
EPIGRAPH

The principles of ecology, if we will take them to heart, should keep us aware that our lives depend upon other lives and upon processes and energies in an interlocking system that, though we can destroy it, we can neither fully understand nor fully control.

Wendell Berry
A Continuous Harmony

And there were days there, as in no other place, as if by accident, beyond any reason I might have had, I was deeply at peace, and happy. And those days that gave me peace suggested to me the possibility of a greater, more substantial peace – a decent, open, generous relation between a man’s life and the world – that I have never achieved; but must have begun to be then, and it has come more and more consciously to be, the hope and the ruling idea of my life.

Wendell Berry
The Long-Legged House
# TABLE OF CONTENTS

Signature Page........................................................................................................... iii

Dedication........................................................................................................ iv

Epigraph........................................................................................................ v

Table of Contents................................................................................................ vi

List of Supplemental Files......................................................................................... viii

List of Tables....................................................................................................... ix

List of Figures..................................................................................................... xi

Acknowledgements............................................................................................ xx

Vita................................................................................................................... xxvi

Abstract of the Dissertation.................................................................................... xxviii

INTRODUCTION................................................................................................. 1

CHAPTER 1: Field methods aboard *RV Bangarang*............................................ 8

CHAPTER 2: Oceanography of the Kitimat Fjord System.................................. 90

CHAPTER 3: “Whale wave”: shifting strategies structure the complex use of critical fjord habitat by humpbacks...................................................... 133

CHAPTER 4: Aggregative and feeding thresholds of sympatric rorqual whales within a fjord system........................................................................ 181

CHAPTER 5: Parsing habitat use strategies of sympatric rorqual whales within a fjord system................................................................................... 256

CHAPTER 6: Novel spatial analytics to identify candidate environmental cues for foraging marine predators........................................................................ 292

CHAPTER 7: From fjord to fins: dive energetics link ocean features to competitive dynamics in sympatric rorqual whales..................................... 309

APPENDIX 1: *RV Bangarang*............................................................................. 349

APPENDIX 2: Excerpt from Observer’s Manual................................................ 352

APPENDIX 3: SBE24plus CTD Configuration and Processing............................ 354
| APPENDIX 4: Comparison of CTD Performance: YSI Castaway and SBE25plus | 357 |
| APPENDIX 5: Echosounder data processing and analysis aboard RV Bangarang | 362 |
| APPENDIX 6: Supplementary materials for “Parsing habitat use strategies…” | 378 |
| APPENDIX 7: Supplementary materials for “Novel spatial analytics” | 385 |
| APPENDIX 8: Supplementary materials for “From fjord to fin…” | 391 |
| APPENDIX 9: Dive and respiratory behavior of humpback and fin whales in the Kitimat Fjord System | 400 |
| REFERENCES | 413 |
LIST OF SUPPLEMENTAL FILES

Research Underway: Bangarang Data Entry Program
LIST OF TABLES

Table 1-1. The eight geographic blocks of the study area. Intensity of Effort (IE) is the percent of the block surveyed with our 300m strip width transects…………………………………...67

Table 1-2. Sampling effort…………………………………………………………………71

Table 1-3. 2013 sampling at oceanographic stations……………………………………..72

Table 1-4. 2014 sampling at oceanographic stations……………………………………..73

Table 1-5. 2015 sampling at oceanographic stations……………………………………..74

Table 1-6. Description of Beaufort sea state categories, adapted from Bowditch (1966)…75

Table 3-1. Explanatory variables used in habitat use models. Model stages are enumerated: I=Prey, 2=Proxy, 3=Prey + Proxy, 4=Habit, 5=Prey + Proxy + Habit………………………………………165

Table 3-2. Monthly oceanographic surveys on the RV Bangarang in 2015……………...166

Table 3-3. Summary of oceanographic properties sampled in each monthly survey of summer 2015 aboard RV Bangarang……………………………………………………………………….167

Table 3-4. Full season model results for each hypothesis explaining the “whale wave”…..169

Table 3-5. Best-fit models for each month (June-September 2015) under each hypothesis of humpback habitat use (Prey, Proxy, etc.).……………………………………………………170

Table 4-1. Whale sightings and focal follows………………………………………………218

Table 4-2. Best-fit models of whale densities as a function of prey-related habitat features, based on transect data……………………………………………………………………..219

Table 4-3. Results of one-sided Kolmogorov-Smirnov tests for differences among prey conditions (mean ± standard deviation reported for all) achieved by whales (measured during focal follows) and available conditions within the study area (measured during systematic transects, first row of table). ……………………………………………………………………………………………221

Table 4-4. Results of Kolmogorov-Smirnov tests for differences among prey conditions achieved by feeding and non-feeding humpbacks and available conditions within the study area (“Area”)…………………………………………………………………………………………223

Table 4-5. Best-fit generalized additive models (GAMs) of the probability that a whale is feeding among krill-like backscatter based on related habitat features sampled during focal follows 2014-2015…. …………………………………………………………………………………………………227

Table 4-6. Aggregative threshold response of humpback and fin whales to increasing total 200 kHz backscatter……………………………………………………………………..229
Table 4-7. Feeding thresholds of humpback and fin whales in response to increasing total 200 kHz backscatter……………………………………………………………………………………230

Table 4-8. Summary of major findings in threshold foraging analysis………………232

Table 5-1. Results of two-tailed Kolmogorov-Smirnov tests for differences among oceanographic conditions (mean ± standard deviation) associated with whales (measured during focal follows) and available conditions within the study area (measured during systematic transects)………………………………………………………………………………………………………283

Table 5-2. Best-fit models of whale aggregation (“Agg.”) and feeding as a function of habitat features of the fjord system. Separate models were built for each species (column Sp.), humpbacks (HW) and fin whales (FW)…………………………………………………………285

Table 5-3. Best-fit generalized additive models (GAMs) of whale aggregation density based solely upon site loyalty……………………………………………………………………………287

Table 7-1. Dive behavior parameters used in models of feeding performance. Parameters were derived by averaging published values listed in Table A8-2. ……………………..332

Table 7-2. Summary statistics of select dive and respiratory behaviors for humpback and fin whales sampled in this study…………………………………………………………………………………………………………………333

Table 7-3. Relative importance of variables (RVI) in prey-based and habitat-based models of dive and respiratory behaviors. Only those variables with RVI above 0.50 are shown. “Feeding” and “Species” are binary factors; all other variables are continuous………………………………335

Table A7-1. Best-fit models of acoustic backscatter characteristics as a function of oceanographic features of the fjord system, using the same systematic dataset used in models of whale density and aggregation (n=140). ………………………………………………………………………………………………………………………………………386

Table A8-1. Dive and respiration measurements of humpback and fin whales from previous studies. Parenthetical numbers are standard deviation……………………………………391

Table A8-2. Best-fit models of whale dive behaviors as functions of metrics of krill-like 200 kHz backscatter………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………...
LIST OF FIGURES

Figure I-1. To achieve the size and mobility needed to find enough prey, the rorqual body frame accommodates two seemingly exclusive designs: the hydrodynamic fusiform of a highly mobile wanderer and the enormous maw and buccal cavity of a lunge-feeder…………………7

Figure 1-1. Study plan. A grid of 24 oceanographic stations (dots) between which environmental and visual transect surveys (lines) were conducted……………………………76

Figure 1-2. Systematic trackline effort during each sampling period of each season. ……..77

Figure 1-3. The research vessel Bangarang………………………………………………………..78

Figure 1-4. Position of the 24 oceanographic stations visited in each sampling period……….79

Figure 1-5. Drop rates of all 2014 SBE25plus CTD casts…………………………………..80

Figure 1-6. The YSI Castaway CTD used in 2013………………………………………………80

Figure 1-7. Trial of observer error in Secchi depth readings (n=25) from 2013 (see text). In this presentation, non-overlapping notches around the means in the neighboring boxplots indicate a strong likelihood that the differences are significant …………………………………………81

Figure 1-8. A-D. The Heron-Bangarang plummet sampler in various stages of stowage, deployment and retrieval. E. The Heron-Bangarang net as rigged in 2013…………..82

Figure 1-9. Calibration of zooplankton net's flowmeter in September 2014………………….83

Figure 1-10. Descent rates of Heron-Bangarang plummet net casts in 2014. Average fall rate was 0.96 ± 0.14 m s⁻¹ (n=40)…………………………………………………………………..83

Figure 1-11. Results of pre-season two calibration of the towed hydrophone array's depth sensor…………………………………………………………………………………84

Figure 1-12. Depth of 100m towed hydrophone array at various payout distances with a variety of weights………………………………………………………………………84

Figure 1-13. Layout of systematic survey tracklines…………………………………………..85

Figure 1-14. Left: Histogram of vessel speed (median=4.7 knots) during systematic transect effort. Right: Box plot of the same data categorized by the eight blocks. …………..86

Figure 1-15. Strip-width zone design. A 300m survey strip was centered about the vessel as it traverses the trackline (dotted line). On each side of the vessel, the strip was split into two distance zones: 0-75m (Zone 1) and 75-150m (Zone 2)………………………………86

Figure 1-16. Histogram of distances to whale sightings from transect surveys in 2014…..87
Figure 1-17. A histogram of Beaufort sea states experienced in 2014. 87

Figure 1-18. Jelly taxa surveyed for during systematic visual transect effort. 88

Figure 1-19. Workflow of nightly data management tasks. 89

Figure 2-1. Detailed map of the study area within the Kitimat Fjord System. 116

Figure 2-2. A) Surface signatures of internal waves on an otherwise calm day within the Kitimat Fjord System at Amy Point (K.B. Watson for scale). B and C) Acoustic backscatter (200 kHz) detections of internal waves from same seafloor sill. 117

Figure 2-3. Sea surface properties in each monthly survey. 117

Figure 2-4. Differences between upper and bottom portions of the water column in each survey month. Some features were not able to be derived from 2013 CTD data. 118

Figure 2-5. Monthly depth distribution of various oceanographic features. Some features were not able to be derived from 2013 CTD data. 119

Figure 2-6. Measurements of marine algae (Chl-a sum, top), krill (inferred from 200 kHz backscatter, middle), and small schooling fish (inferred from 33 kHz backscatter, bottom) from 2014 and 2015 data only. 120

Figure 2-7. Profiles of acoustic backscatter from August 2014. 121

Figure 2-8. Profiles of acoustic backscatter from September 2014. 122

Figure 2-9. Profiles of acoustic backscatter from early June 2015. 123

Figure 2-10. Profiles of acoustic backscatter from late June to early July 2015. 124

Figure 2-11. Profiles of acoustic backscatter from late July 2015. 125

Figure 2-12. Profiles of acoustic backscatter from August 2015. 126

Figure 2-13. Profiles of acoustic backscatter from September 2015. 127

Figure 2-14. The following figures (2-15 to 2-18) present patterns in water properties from inshore to offshore waters along the transect shown here, for 2014 and 2015 data only. 128

Figure 2-15. Monthly cross sections of potential temperature. 129

Figure 2-16. Monthly cross sections of salinity. 130

Figure 2-17. Monthly cross sections of dissolved oxygen. 131

Figure 2-18. Monthly cross sections of chlorophyll-a. 132
Figure 3-1. As summer turns to fall (x-axis), humpbacks sightings occur increasingly deeper into the Kitimat Fjord System (y-axis). .................................................................172

Figure 3-2. Left: Survey effort by Gitga'at (red) and NCCS (blue), 2005 - 2014. Right: Sampling plan for 2015 vessel transects and oceanographic stations...........................................173

Figure 3-3. At peak ebb tide in late August 2015, humpbacks gather at the bottleneck entrance to a large freshwater inlet (Cornwall Inlet) in the study area. Ephemeral but dramatic tidal rapids develop at this site during ebb tides.................................................................174

Figure 3-4. Survey effort (km) by Gitga'at and North Coast Cetacean Society (NCCS) platforms, 2004-2014. Left: Annual survey effort (June through November only). Right: Monthly survey effort.................................................................175

Figure 3-5. The “whale wave” is (a) evident in humpback density estimates and (b) verified by Monte Carlo randomization tests.................................................................176

Figure 3-6. Humpback sightings from the 2015 surveys aboard RV Bangarang. Dots are scaled positively by group size. Black-filled circles are on-transect sightings; empty circles are sightings during "casual" or transit effort.................................................................177

Figure 3-7. Spatial association of humpback density (black line) with prey field in 5 surveys in summer 2015. ..........................................................................................................178

Figure 3-8. Prediction errors of the best-fit models for each hypothesis of humpback habitat use across monthly surveys in summer 2015. Models were fit to each month separately, with unique sets of variable combinations for each hypothesis.................................................................179

Figure 3-9. Smoothing functions of explanatory variables included in the best ............180

Figure 4-1. Study area within the Kitimat Fjord System, Gitga'at First Nation territory, British Columbia, Canada. ..........................................................................................................234

Figure 4-2. Examples of marine mammal associations with debris and detritus. ...............235

Figure 4-3. Examples of “whale webs”, the routine used to calculate shortest-path distances (lines) between focal follows (red dot) and 1-km bins of echosounder data (black dots) collected during systematic transect surveys. ........................................................................236

Figure 4-4. Procedure for constructing and analyzing “position curves.” .........................237

Figure 4-5. Properties used to characterize threshold response to prey conditions. Variables T, K and R correspond to parameters in the logistic regression. Threshold stability (p-value) is determined with Monte Carlo randomization (see Methods). ........................................238

Figure 4-6. Locations of whale sightings (all effort) and focal follows in 2014 (top) and 2015 (bottom) for humpbacks (left) and fin whales (right). ..................................................239
Figure 4-7. Spline functions for best-fit models that predict whale densities based on prey-related habitat variables, both sampled during systematic transect survey effort. ………..240

Figure 4-8. Distributions of prey-related habitat features, displayed vertically as violin plots, sampled during focal follows in both years for fin whales and humpbacks. …………………241

Figure 4-9. Cumulative distribution functions (CDF) of acoustic backscatter conditions available in the study area and those measured during focal follows …………………242

Figure 4-10. Distributions of prey-related habitat features, displayed vertically as violin plots, sampled during focal follows of humpback whales for each survey month in 2015…….243

Figure 4-11. Cumulative distribution functions of total 200 kHz backscatter available in the study area (black line, sampled during systematic transect surveys) and those measured during focal follows (colored lines) of humpbacks. ………………………………………………244

Figure 4-12. Histograms of backscatter measured during follows of feeding whales. ………245

Figure 4-13. Mean positioning of whales with respect to available prey-related habitat features, plotted according to distance (km) from the focal follow… …………………246

Figure 4-14. Mean positioning of humpbacks with respect to available prey-related habitat features (columns, sampled during systematic surveys), plotted according to distance (km) from the focal follow, for each survey month of 2015 (rows). …………………………………247

Figure 4-15. Mean positioning of humpbacks and fin whales with respect to available total 200 kHz backscatter plotted according to distance (km) from the focal follow. ………….248

Figure 4-16. Krill-like backscatter associations achieved by whales as a function of the mean conditions available to them at increasing distances from the focal follow (columns; sampled during systematic transect surveys)……………………………………………………..249

Figure 4-17. Aggregative thresholds of humpback (top) and fin whale (bottom) response to changing totals of krill-like acoustic backscatter (x-axis, total 200 kHz)…….250

Figure 4-18. Aggregative thresholds of humpback response to changing totals of krill-like acoustic backscatter (x-axis, total 200 kHz) for each year (left column, larger panes) then for each survey month within year (smaller panes on right)……………………………………………………………………………………251

Figure 4-19. Feeding thresholds of humpback (left) and fin whale (right) in response to changing totals of krill-like acoustic backscatter (x-axis), located by fitting logistic regressions (red line) that model the probability of a whale (dots) feeding (y=1) or not (y=0) given backscatter present………………………………………………………………………………252

Figure 4-20. Feeding thresholds of humpback whales in response to changing totals of krill-like acoustic backscatter (x-axis), located by fitting logistic regressions (red line) that model the probability of a whale (dots) feeding (y=1) or not (y=0) given backscatter present…..253
Figure 4-21. Summary of humpback response to changes in the best available krill-like conditions

Figure 4-22. Month-to-month patterns in the relationship between humpbacks and krill-like prey conditions (total 200 kHz backscatter) in 2015 (June, July, August, September)

Figure 5-1. Cumulative distribution functions (CDF) of oceanographic conditions available in the study area (black line, measured during systematic transect surveys) and those measured during focal follows (colored lines) for humpbacks (top) and fin whales (bottom)

Figure 5-2. “Position curves” for feeding and non-feeding (“Other”) behavioral states are displayed for each species

Figure 5-3. Mean positioning of humpbacks with respect to select available habitat features (columns, sampled during systematic surveys), plotted according to distance (km) from the focal follow, for each survey month of 2015 (rows)

Figure 5-4. Ranked performance of whale aggregation models. Whale densities were modeled as functions of three types of data: prey-like acoustic backscatter (“Food”), habitat features (“Habitat”) and site loyalty cues (“Site”).

Figure 6-1. Procedure for constructing and analyzing “position curve” correlation

Figure 6-2. Mean position of feeding whales with respect to available prey features as a function of their mean position to various oceanographic features

Figure 7-1. Expected qualitative changes in respiratory behavior and foraging profitability with prey depth for rorqual whales, based on optimal dive theory

Figure 7-2. Depth distribution of mean total krill-like backscatter systematically sampled within the study area, based on data from Chapter 4

Figure 7-3. Key relevant findings demonstrating fin whale associations with deep krill

Figure 7-4. Synopsis of environmental determinants of euphausiid-like 200 kHz backscatter patch depth sampled using systematic surveys of the Kitimat Fjord System

Figure 7-5. Comparison of prey- and habitat-based models of whale dive behavior

Figure 7-6. Dive behavior plotted against mean 200 kHz backscatter depth

Figure 7-7. Durations of dive, surface, and dive cycle as functions of prey patch depth

Figure 7-8. Dive strategy models of each species with increasing prey depth

Figure 7-9. Mean Depth distribution of total 200 kHz backscatter (dashed lines) sampled during (A) systematic acoustic surveys and (B) focal follows of humpback whales (orange) and fin whales (blue)
Figure 7-10. Encounter rate performance of humpbacks and fin whales if each species targeted the same prey patches as the other……………………………………………………………………………346

Figure 7-11. Simulated backscatter encounter rates for humpback (orange) and fin (blue) whales given various depth distributions of the prey field (black dotted line)………………..347

Figure 7-12. Species ratios of backscatter encounter rates as functions of (A) mean and (B) standard distribution of the prey field, based upon simulations (Fig. 7-13)……………….348

Figure A1-1. Speed capabilities of the Bangarang at various RPMs with and against the tide. Trial performed in the Strait of Georgia on 1 August 2014……………………………………351

Figure A1-2. The Jangan Gila Dong II, tender to the Bangarang. Here it is drifting away from the vessel because I forgot to tie its bowline to the swimbridge…………………351

Figure A1-3. The towed hydrophone array stowed on its reel on the aft cabin's topsides deck……………………………………………………………………………………………351

Figure A3-1. Example of nightly visualizations of CTD casts for data check and quality control……………………………………………………………………………………………..356

Figure A4-1. 4 simultaneous casts of the YSI Castaway CTD (solid orange line) and SBE 25plus CTD (dotted blue line)………………………………………………………………………………358

Figure A4-2. Differences in CTD readings by depth (SBE 25plus – YSI castaway) from 2015 trial casts. *Top row: differences in each of the 4 trial casts. Bottom row: Mean difference of the 4 casts…………………………………………………………………………………………359

Figure A4-3. Differences in sound velocity calculations by depth (SBE 25plus – YSI castaway) from 2015 trial casts. *Top row: differences in each of the 4 trial casts. Bottom row: Mean difference of the 4 casts…………………………………………………………………………………………360

Figure A4-4. Multiple casts (n = 10) of the YSI Castaway at the same time and location (S. Douglas Channel) in 2013. All casts occurred within a single hour…………………361

Figure A5-1. Screenshot of raw data output from the echosounder, in .odc format, opened in Text Wrangler…………………………………………………………………………………………364

Figure A5-2. Screenshot of conversion of raw data to hexadecimal format, saved as a .txt file…………………………………………………………………………………………364

Figure A5-3. Hexadecimal data broken into lines, saved as a .txt file……………………………………364

Figure A5-4. Screenshot of conversion to ASCII format, saved as a .csv file, visualized in Text Wrangler:…………………………………………………………………………………………365

Figure A5-5. Screenshot of echodata with assigned survey effort data:……………………………………365
Figure A5-6. Example of echogram of unreduced data from a single day. ..............365

Figure A5-7. Example maps of focal follow tracks. ...........................................366

Figure A5-8. Example of georectified transect data; every row represents approximately the same horizontal distance. .................................................................366

Figure A5-9. Echogram of georectified backscatter from 11 August 2014. Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software.................................................................367

Figure A5-10. Example of a seafloor correction output ......................................367

Figure A5-11. Results of manual seafloor correction. Dark gray is the auto-corrected seafloor, blue is the seafloor after manual correction. Top row is 33 kHz readings, bottom row is 200 kHz...........................................................................368

Figure A5-12. Record of manual selections (grey boxes), made in ImageJ, of "bad areas" in Campania transect (2 June 2015). Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software..................................................369

Figure A5-13. Result of manual filtration, in which “bad areas” are replaced with “NA” entries.............................................................................................................369

Figure A5-14. Result of manual filtration on Campania transect (2 June 2015). Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software..................................................369

Figure A5-15. Backscatter after application of biological noise floor. ...................370

Figure A5-16. Example of annotated map of transect trackline based on echosounder data (from 30 May 2015).................................................................370

Figure A5-17. A combined echogram from 30 May 2015 in Squally channel, with the two frequencies overlayed with translucency (blue = low frequency, red = high frequency).....371

Figure A5-18. 33 kHz backscatter, before (top) and after (bottom) prey patch filtration. From 2 June 2015 in Campania Sound.........................................................371

Figure A5-19. 200 kHz backscatter, before (top) and after (bottom) prey patch filtration. From 30 May 2015 in Squally Channel.........................................................371

Figure A5-20. Before (top) and after (bottom) frequency differencing. From 18 July 2015 in Verney Pass.................................................................372

Figure A5-21. Examples of acoustic backscatter collected during focal follows. ........372

Figure A5-22. Depiction of backscatter metrics..................................................373
Figure A5-23. Maps of the dispersion and intensity of krill-like backscatter (filtered 200 kHz) interpolated from 5km bins of trackline within each monthly survey, summer 2015……..374

Figure A5-24. A) Acoustic backscatter collected during a focal follow of 3 fin whales on 29 July 2015. B) Still-frame of Go-Pro video taken during same focal follow using the Bangarang Krill Imaging and Scrambling System (KISS), displaying dense aggregations of euphausiids at approximately 170m………………………………………………………………………………………….375

Figure A5-25. Photograph of a 2015 zooplankton sample; black dots are the eyes of Euphausiids………………………………………………………………………………………………………………………..376

Figure A5-26. Two zooplankton tows at an oceanographic station in August 2015. Backscatter is presented in two color-scales………………………………………………………………………………………………..377

Figure A5-27. Correlation ($r^2 = 0.18$) between euphausiids sampled at oceanographic stations and filtered acoustic backscatter (Total 200 kHz metric) recorded during zooplankton tows…………………………………………………………………………………………………………………377

Figure A6-1. Violin plots of whale-habitat associations for humpback and fin whales……378

Figure A6-2. Violin plots of humpback-habitat associations in 2015 survey months………379

Figure A6-3. Histograms of habitat features measured during focal follows………………380

Figure A6-4. Spline functions for best-fit GAMs that predict whale aggregative response, based on systematic surveys, and feeding response, based on focal follows, as functions of habitat features. ………………………………………………………………………………………………………………………………………381

Figure A6-5. Patterns in whale density, prey backscatter, and habitat features in the 8 primary channels of the Kitimat Fjord System within our study area………………………………………………………………………………………………………………382

Figure A6-6. Smoothing functions of explanatory variables included in the best-fit models of whale aggregation as a function of site loyalty cues, represented here by spatial coordinates and/or day of year…………………………………………………………………………………………………………………………………………………………………………………………383

Figure A6-7. Smoothing functions of explanatory variables included in the best-fit models of fin whale habitat as a function of prey-related features and habitat features………………384

Figure A7-1. Spline functions for best-fit GAMs that predict acoustic backscatter metrics as functions of habitat features and Julian day of year. ……………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………………388

Figure A7-2. Mean position of feeding humpback whales with respect to available prey features as a function of their mean position to various oceanographic features………………389

Figure A7-3. Mean position of feeding fin whales with respect to available prey features as a function of their mean position to various oceanographic features…………………………390
Figure A8-1. Spline functions for best-fit GAMs that predict whale dive behaviors as functions of 200 kHz backscatter patch depth and habitat features……………………408

Figure A9-1. Distributions of dive and respiratory behaviors, displayed vertically as violin plots, sampled during focal follows for fin whales (grey) and humpbacks (white), from both years, presented in categories of inferred whale behavior. Interior box plots show median, interquartile range and outliers…………………………………………………………..408

Figure A9-2. Distributions of dive and respiratory behaviors, displayed vertically as violin plots, sampled during 2015 focal follows of humpback whales, grouped into each sampling period…………………………………………………………….409

Figure A9-3. Cumulative distribution functions (CDF) of dive and respiratory metrics for each species in feeding and non-feeding behavioral modes……………………410

Figure A9-4. Respiratory metrics plotted against surface time …………………………….411

Figure A9-5. Respiratory metrics plotted against dive time ……………………………….412
ACKNOWLEDGEMENTS

The Great Bears

This dissertation would have been impossible had it not been for the permission, support and guidance of a few key folks. I would first like to thank Cetacealab and the Gitga’at Guardian Watchmen, namely Janie Wray, Hermann Meuter, Chris Picard, Marven Robinson, Bunker Dundas and Nicole Robinson. They introduced me to my field site years ago, welcomed me into their community, and put up with me while I found my footing. Perhaps most importantly, they showed me what can be done with one’s life if one is willing to take risks, trust in others, join in the fight for a larger cause, and stop now and then to listen to the sea and sky. They have been watching over the whales of the Great Bear for many years, and without their support and good faith I would not have had the chance to contribute my small part to their ongoing work.

This project would only have been possible at Scripps; no other institution has the unique combination of resources, people, and supportive culture that could have put it within reach. The graduate office was invariably supportive, professional, and generous: Gilbert Bretado, Denise Darling, Maureen McMormack, Maureen McGreevy, and Adam Petersen all went out of their way to facilitate my work, and sometimes even bail me out of sticky spots. My advisors Jay and Paul offered me undeserved encouragement and unequivocal support at every stage of this journey. I cannot imagine any other faculty member, anywhere, who would give me the trust, independence, adventurous camaraderie, and one-on-one training that these two have. They put up with much from me, including frenetic geography, long absences, long chapters, and bad writing. They gave me the space I needed to not only pursue the dissertation project of my dreams, but also to follow a path that clearly interfered with that of a
conventional PhD career. They have been my friends, first and foremost, and that is why they have been such excellent advisors. I thank Jay specifically for reminding me always to focus on what’s most important in life, even when that is not science. I thank Paul for perpetuating the spirit of natural history at Scripps, and for teaching his students that youthfulness has nothing to do with age.

At the Cetacean Research Program of the Department of Fisheries and Oceans Canada (CRP at DFO), John Ford, James Pilkington, Graeme Ellis, Robin Abernathy, and Jared Towers offered me their collaboration, trust, friendship, patience, and constructive reviews of my chapters. I am grateful to James in particular for inspiring me and demonstrating how to use our love for a place as the fuel and the measure of our work to save it.

This dissertation brought me back to Emily, and I doubt I would have made it to the end of the dissertation without her. Sitting at a dock in Olympia all summer with a seized engine and a brewing lawsuit should have been the lowest point of this project, but thanks to her it was among the highlights. At a critical juncture in this journey, her love gave me the perspective and motivation to carry on, loosen up, and strike a better balance. It ended up being a critical juncture in my life. Her love, support, and silliness have been constant throughout all stages of this PhD: while stuck in Olympia, out on the boat during fieldwork, during the long stretches apart, through the protracted months of frustrating analysis and writing, and in this final stretch. I am so thankful that our life together has begun with memories of the Bangarang, beautiful anchorages and floppy whales.

Finally, I cannot overemphasize the role my dad has played in this journey. Every single aspect of this endeavor was made possible and successful thanks to him. Who knew that a dissertation could become the father-son experience of a lifetime? At every turn, he impressed me with his sense of adventure, generosity, patience, genius, inventiveness, and
endless dedication, motivating me to try to keep up with him and keep at it. Again he has shown me that there is nothing that can replace the encouragement of a parent.

**Crew**

**2013:** During fieldwork at least two other researchers were on board with me at any one time. Most volunteers worked for tours of 6 weeks. These teammates paid their own way to be on board. Nonetheless, they worked harder than anyone could have hoped for. Their tireless high spirits, patience, friendship, hardiness, work ethic, and sense of adventure made all the difference in the world. 2013 crew were Mike Keen, Will Watson, Keri Bryan (Watson), Dylan Padgett, Katie Qualls, Richard Candler, and Matt Irwin.

**2014:** Again the crew volunteered their time and paid their own travel and food costs to participate in the fieldwork. This season’s crew faced inordinate disappointments as a result of the summer debacle of the rebuilt engine’s failure. I would not have endured the summer without their dedication, hard work and friendship. 2014 crew were Emily Ezell, Luke Padgett, Will Watson, Keri Bryan (Watson), Katie Qualls, Sam Watson, Mike Keen, Celia Keen, Matt Irwin, Nelle Pierson, Kelly Beach and Jon Carpenter.

**2015:** This was a full season of non-stop research, and it could not have happened without the tireless, brilliant, and dedicated efforts of Mike Keen, Will Bostwick, Kim-Ly Thompson, Jay Barlow, Barb Taylor, Anne Simonis, Sam Watson, Emily Ezell, Matt Irwin, Nelle Pierson, Luke Padgett, Katie Qualls, Sara Keen, Nick Bruns, and Jeff Garretson.

**2016:** This season I was blessed to have the company and hard work of Mike Keen, Jason and Allison Ipson-Haney, Will and Keri Watson, Emily Ezell, and Celia Keen.

**Funding & Equipment**

The hard work and adventurous spirit of each season’s crew were astounding,
2013: The pilot season was funded by the National Geographic Society Waitt Grant (Grant number 2681-3), the 2013 Mullin Award from the Biological Oceanography curricular group, and the 2012 NSF Graduate Research Fellowship (GRF) video contest. Material support and equipment loans came from SIO's Dayton Lab, the SIO Pelagic Invertebrate Collection (thanks to collection manager Linsey Sala), Barlow's lab at NOAA SWFSC, the DFO Cetacean Research Program (CRP), Andrew Wright, Will Watson, Nicole and Bunker, Don Yeungblat, Shannon Rankin and Cetacealab.

2014: Financial support was provided by the SIO Graduate Office (thanks in particular to Maureen McCormack, Maureen McGreevey, and Denise Darling), DFO CRP, the Explorers Club, Cascadia Research Collective and the SIO Whale Acoustics Lab through a grant from the Office of Naval Research, and the astounding support of private donors including the Watson, Ayres, Cunningham, Barlow and Dobbins families. Support for the lawsuit regarding the failed engine rebuild was provided by the Keen family. Many crew members went above and beyond the agreed terms to support themselves while we were stuck at the Olympia dock without an engine. Material support and equipment loans came from all of the same 2013 sources, as well as Cascadia Research Collective and Luke Padgett.

2015: Our final season was funded by the Gitga'at Guardian Watchmen, DFO Cetacean Research Program, and American Philosophical Society's Lewis and Clark Fund.

Support

The hospitality and support of residents in Hartley Bay, the center of the Gitga'at First Nation, enabled us to endure and enjoy the field seasons. Their good nature and patience were constant, and it made all the difference. Hermann Meuter and Janie Wray of Cetacealab were our primary emergency contacts in the area and our friends and supporters -- as well as the primary inspiration for the inception and realization of this project. Whale Point, Cetacealab
headquarters, was available to us as a shelter in poor weather, a workshop for repairs, a source of drinking water, a place to access email and shower, and a wellspring of fellowship. The maritime community in the study area, upheld by the Gitga'at, Cetacealab, DFO, and the NPO Pacific Wild, provided critical friendship and advice.

None of the above grants would have come through without letters of support from Jay Barlow, Paul Dayton, David Haskell, Trevor Branch and John Calambokidis. Advice from Jay, Barb Taylor, Hermann Meuter, Janie Wray, Mark Ohman, Linsey Sala, Tony Koslow, Jules Jaffe, Shannon Rankin, John Calambokidis, Erin Falcone, Annie Douglas, John Ford, James Pilkington, Graeme Ellis, Linda Nichol, Ian McAllister, Mike Reid, Moira Galbraith, Svein Vagle, Eddy Carmacke, Corinne Pomerleau, Andrew Wright, and Chris Picard substantially improved study design.

In addition to my collaborators, I am particularly indebted to the friendship of Bunker and Nicole and their daughter Kota, Marven Robinson, Cam Hill, Wally, Mike and Sarah Reid, and Karen and Stan of the Hawk Bay. During the fieldwork preparation scrambles in San Diego in 2013 and 2014, the patience and support of Jay, Jenna, Paul, Anne and Emily made everything possible. Chris Elder helped immensely with shipping. Airfare to get back and forth between San Diego and the northwest would be insurmountable without the support of JetBlue Airways. While in Puget Sound the support and friendship of John, Gretchen, Zoe, Alexei, Sue, Erin and Greg were astounding. The encouragement, generosity and hospitality of the Calambokidis, Wright, Schaeffer, Benson and Watson families have been incredible. No aspect of this project would have been possible without the financial, material, and moral support of the Keen family.

Many of those listed above had the power to stop this endeavor in its tracks by simply saying, "No", but chose instead to give the Bangarang Project the benefit of many doubts. I am not sure I can ever justify their grace.
Publications

Chapter 2 is printed here with the permission of coauthors Kim-Ly Thompson and Chris R. Picard. The dissertation author was the primary investigator and author of this paper.

Chapter 3, in part, is a reprint of material as it appears in Marine Ecology Progress Series, 2017: Keen, EM, J Wray, H Meuter, KL Thompson, JP Barlow, CR Picard. (In press) “Whale wave”: shifting strategies structure the complex use of critical fjord habitat by humpbacks. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in part, is a reprint of material as it appears in Ecosphere, 2017: Keen, EM. (In press) “Aggregative and feeding thresholds of sympatric whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.

Chapter 5, in part, is a reprint of material as it appears in PLOS ONE, 2017: Keen, EM, J Wray, J Pilkington, KL Thompson, JP Barlow, CR Picard. (In press) “Parsing habitat use strategies of sympatric rorqual whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.

Chapter 6, in part, has been submitted for publication as it may appear in Proceedings of the Royal Society B, 2017: Keen, EM, J Wray, KM Qualls, CR Picard. (In review) “Novel spatial analytics to identify candidate environmental cues for foraging marine predators.” The dissertation author was the primary investigator and author of this paper.

Chapter 7, in part, has been submitted for publication as it may appear in Marine Ecology Progress Series, 2017: Keen, EM, and KM Qualls. (In review) “From fjord to fins: dive energetics couple habitat features to the competitive dynamics of sympatric rorqual whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.
VITA

2004  Bachelor of Arts, Sewanee: The University of the South
2015  Master of Science, University of California, San Diego
2016  Teaching Assistant, University of California, San Diego
2017  Doctor of Philosophy, University of California, San Diego

PUBLICATIONS


FIELDS OF STUDY

Major Field: Biological Oceanography

    Studies in Marine Tetrapods
    Professors Lisa Ballance and Jay Barlow
Studies in Marine Ecology
Professors Paul K. Dayton, Jim Leichter, Mark Ohman, Lisa Levin, and Lisa Ballance

Studies in Computer-Intensive Statistics
Professors Jay Barlow, Brice Semmens, George Sugihara and Stuart Sandin

Studies in Survey Techniques
Professors Jay Barlow and Lisa Ballance

Studies in Bioacoustics Technology
Professors Jay Barlow and Jules Jaffe
ABSTRACT OF THE DISSERTATION

Whales of the rainforest: habitat use strategies of sympatric rorqual whales within a fjord system

by

Eric Michael Keen

Doctor of Philosophy in Oceanography

University of California, San Diego, 2017

Professor Jay Barlow, Chair
Professor Paul Dayton, Co-Chair

The energy needs of rorqual whales (f. Balaenopteridae) govern their relationship to marine habitats during the foraging season. However, their cryptic foraging strategies and extreme feeding behaviors complicate our ability to identify and protect habitats “critical” for rorquals. What is the relationship between rorquals and their habitat, and how must that shape conservation strategies? I addressed this question in the case of sympatric humpback
(Megaptera novaeangliae) and fin whales (Balaenoptera physalus) in the Kitimat Fjord System of the Great Bear Rainforest (Gitga’at First Nation territory, British Columbia). For three summers (2013-2015) I studied whales, their prey, and their environment aboard the RV Bangarang using oceanographic station sampling, systematic transect surveys, and
opportunistic focal follows of whales (Chapter 1). Ocean sampling demonstrated the strong coupling of water features with offshore patterns in storm forcing and regional meteorology (Chapter 2). By combining these surveys with a long-term Gitga’at dataset, area humpback whales were found to practice a structured and persistent pattern in seasonal habitat use, which demonstrates how complex and habitat-specific a rorqual’s habitat use can be (Chapter 3). Both humpback and fin whales were found to respond to changes in krill supply in aggregative and behavioral thresholds that are set by a combination of intrinsic energetic needs and the context of local prey supply (Chapter 4). Associations with non-prey habitat features were markedly different in the two species (Chapter 5). Humpback distribution was more closely coupled to that of their prey and other habitat features, while fin whale distribution was driven broadly by site fidelity. Novel spatial analytics were used to identify the most probable environmental cues used by foraging whales (Chapter 6). Both species were found to be particularly sensitive to the depth of prey layers, which is governed largely by oceanographic features (Chapter 7). This coupling of feeding performance to habitat features influences the competitive dynamics of rorqual whales. The findings in this case study advance general theories in marine predator ecology and conservation, and have direct implications for the management of Gitga’at territory and the identification of fin whale critical habitat in Pacific Canada.
INTRODUCTION

The marine tetrapods, chiefly marine mammals, sea turtles and seabirds, differ from other marine predators in their evolutionary connection to terrestrial systems and their strong present-day interactions with the air-sea interface (Berta et al. 2006). To persist and compete in their environment, marine tetrapods have converged upon similar natural histories that hinge upon their mobility (Ashmole 1963, Lack 1968, Stearns 1976, Weimerskirch 2001, Gaston 2004). Many are migratory and relatively large, making use of their locomotive prowess and energy reserves to forage upon prey that are patchy in space and time. The most mobile of the marine tetrapods pose the following special problems for ecologists and resource managers alike.

First, mobility is both a problem and a solution in matters of energetics and habitat use. Though generally efficient, mobility requires certain morphologies and activity levels that are energetically intensive to maintain (Tucker 1975, Webb and de Buffrenil 1990, Alexander 2005), particularly for submarine tetrapods facing hydrodynamic forces, such as cetaceans (Croll et al. 2001, Goldbogen et al. 2007, 2008). Mobility increases total foraging area, but its energetic costs reduce the proportion of ocean habitat that can offer sufficient resources. This conundrum further entrenches the importance of mobility to their ways of life, while complicating our ability to infer the habitat needs of a predator based simply upon where it is found.

Second, mobility evolves in balance with feeding behavior, the specifics of which can complicate standards for habitat suitability. The evolution of mobility requires trade-offs in feeding mode and prey specialization. For example, albatrosses (f. Diomedidae) fly with extreme efficiency, but are limited as a result to prey at or just under the surface. Near the other end of the seabird spectrum, auks (f. Alcidae) fly with difficulty but are skilled
pursuit-diving predators (Gaston 2004). Among the whales, the enormous blue whale (*Balaenoptera musculus*) travels with unmatched efficiency (Alexander 2005), but the resulting lack of maneuverability restricts its diet to krill, which are relatively non-evasive, and requires an energetically costly feeding mode known as lunge-feeding, in which swarms of krill are batch-engulfed at once (Fig. I-1). The humpback whale (*Megaptera novaeangliae*) is built instead for maneuvering; at the cost of less efficient travel, it is a generalist predator able to lunge-feed upon many species of plankton and schooling fishes (Woodward et al. 2006). These examples demonstrate that some feeding modes and diets evolve to the detriment of long-range mobility (e.g., pursuit-diving in seabirds), while others may coincide with high mobility but involve their own energy costs (e.g., lunge-feeding in rorqual whales, f. Balaenopteridae). In all cases, feeding mode informs the total energy budget, discussed above, that defines minimum acceptable foraging conditions.

However, feeding mode also determines which conditions other than overall prey supply are also important. Seabirds that consume individuals of prey at a time, for example, can be expected to target different foraging conditions on a different scale than whales that consume entire swarms of prey in a single gulp, as do the lunge-feeding rorquals. Lunge-feeding is an extremely costly behavior (Goldbogen et al. 2017), and its profitability hinges as much upon the patch characteristics of prey in a given area (e.g., swarm density, depth, and catchability) as its total volume (Goldbogen et al. 2011). In turn, patch characteristics are determined to some degree by oceanographic processes, depending on prey type. For plankton such as copepods and krill, upon which many rorquals feed, that habitat-patch formation relationship can be quite strong (see Chapter 7 Introduction). Thus, foraging success for planktivorous rorquals is coupled strongly to their physical habitat through the details not only of their lifestyle of mobility, but also by their diet and feeding mode. The kind and extent of
this coupling should be specific to each marine tetrapod, since the natural history of each
species strikes its own balance between mobility, feeding mode, and trophic niche.

Third, mobility requires habitat use strategies to be sophisticated and complex, and
therefore difficult to study. Mobile marine predators forage by covering vast swaths of ocean
quickly while evaluating habitat features and responding appropriately. Hierarchical habitat
use decisions include 1) which region to travel to in order to forage, 2) where within that
region to allocate time and effort, 3) when to stop searching and attempt to feed, 4) when to
stop feeding in order to search elsewhere, 5) when to continue on to another region, etc.
(Fauchald et al. 2000, Becker and Bessinger 2003). These decisions can be non-strategic (i.e.,
random search), though this is not likely given the energetic needs and brief foraging seasons
generally faced by marine tetrapods. It is more likely that these decisions are highly strategic,
based upon time-tested spatial habits (e.g., migration, philopatry) and/or new information
divined from their environment (Au and Pitman 1988, Piatt et al. 1989, Schneider 1990,
Ballance et al. 1997, Mate et al. 1999, Kot 2005). Habitat use decisions therefore convolve
multiple environmental cues from multiple spatial and temporal scales (Russell et al. 1992,
Observing and disentangling drivers of habitat use can be difficult for biologists, since
apparent mechanisms of predator-habitat associations may only be relevant to processes
occurring at the scale of observation, while the actual mechanisms go unobserved at other
scales (Stommel 1963, Schneider and Piatt 1986, Levin 1992, Logerwell and Hargreaves
1996).

Fourth, large, mobile marine tetrapods have a history of population decimation and
recovery, which complicates their relationships to their habitat. Many were depleted by recent
human exploitation (e.g., whaling), and many face ongoing depletion. Such disturbances have
shifted geographic ranges, altered life histories, stereotyped diets, and reduced the repertoire
of morphologies and behaviors that a species exhibits, such that what we observe today may only be a caricature of what once was (Lockyer et al. 1981, Goddard 1997, Clapham et al. 1999, Branch et al. 2007, Nichol et al. 2002, Hamann et al. 2010). Depletion can also trigger trophic cascades that fundamentally shift the structure of ecosystems (Ballance et al. 2006a, Croll et al. 2006, Paine 2006). Species currently in recovery are doing so in a changed ocean with increasingly changing chemistries, current regimes and fisheries impacts (Hoegh-Guldberg and Bruno 2010 and references therein). Many historical habitats for depleted marine tetrapods now overlap with areas of intense human activity such as fisheries, shipping, point-source pollution, and ecotourism (Berta et al. 2006). As a result, the predator-habitat associations we observe today could be historical, transient, novel, or some murky combination thereof. Disaggregating one from the other is difficult and would arguably be moot, if it were not for the fact that habitat protection is a critical component of species protection in many nations (e.g., United States and Canada).

Given these complications, it is difficult to understand the relationship between recovering marine tetrapods and their habitat. How are we to reconcile their uncanny attunement to their environment with the vagrancy implied by their mobility? Their foraging acumen causes them to seem “faithful” more to a certain set of oceanographic conditions, wherever those may come together, rather to than a certain geographic place (Tershy 1992, Ballance et al. 1997, Bailey et al. 2009, Calambokidis et al. 2009). How “connected” or “dependent” upon a specific habitat can marine tetrapods really be? Furthermore, if a natural history is plastic and incomplete, what conclusions can ecologists draw? And on what basis can they make recommendations to resource and habitat managers? Which version of a natural history should those managers move to restore? And to what extent should they attempt to accommodate both reality and potentiality in their strategic planning?
The marine tetrapod-habitat relationship is the central problem of my thesis, summarized as follows. Given the energetic requirements of their foraging strategies and feeding modes, marine tetrapods require specific, high-quality habitat in order to recover, persist and participate in ecosystems. However, for those same reasons, the needs and strategies of habitat use for marine tetrapods are all the more difficult to identify and protect. What is the connection between mobile marine tetrapods and their habitat, and how does this bear upon efforts to identify certain habitats as “critical”?

This question becomes urgent when habitat is slated for substantial human alteration, such as the introduction of fisheries or shipping lanes. While human activity can directly impact marine tetrapods locally (e.g., ship strikes, entanglement, spills, etc.), other less apparent effects may ultimately prove more consequential to populations and ecosystems. These include non-lethal direct effects that could be referred to as “ecological effects” (e.g., local displacement, range shifts, restricted prey access, prey switching, prey release, etc., all of which can induce trophic cascades) and the cumulative effects of all impacts, which are demographic in nature (e.g., reduced birth rates, increased infant mortality rates, etc.). Neither of these impact categories is well addressed in current policies or impact assessments (e.g., JRP 2013A, 2013B), though cumulative effects are receiving increasing attention (Kerosky et al. 2013).

Population-level demographic effects are best measured with conventional "big survey" techniques, genetic and isotopic studies and stranding programs that span the range of a stock (e.g., Burtenshaw et al. 2004, Oleson et al. 2007). In contrast, ecological effects, which are multi-scale and less readily apparent through the use of classical methods, are more difficult to assess. It is rarely clear whether to evaluate ecological effects from the perspective of a stock or the perspective of an ecosystem. Within a habitat-protection framework, all effects are important regardless of their stock-level consequences (Rhoff 1991), particularly
for the largest predators with the largest trophic footprints such as whales. Within a stock-protection framework, in contrast, local habitat alteration can seem inconsequential when considered in isolation. But it must be recognized first that the aggregate loss of many local habitats will have stock-level effects, and second, that the responses of marine tetrapods to habitat alteration may be obscure to us even when they are severe (Southall et al. 2013). Moreover, species of interest can be impacted by habitat alteration indirectly through ecological pathways. Managers working within either framework must therefore understand the connections between marine tetrapods and their habitat, which includes their prey, their conspecifics, their competitors, their environment, and humans. There must therefore be an ecological component to monitoring marine tetrapods (Croll et al. 1998, Croll et al. 2005, Witteveen et al. 2008b). Our ability to facilitate their recovery depends on how we design and implement those efforts.

Objectives

In this dissertation I address my thesis’ central problem in a habitat that is 1) spatially complex, 2) host to an unconventional assemblage of marine tetrapods, and 3) in need of management solutions given proposed industrial developments. My study area is deep within the Great Bear Rainforest, in the marine territory of the Gitga’at First Nation in the Kitimat Fjord System of British Columbia, which has recently been re-occupied by recovering populations of humpback whales and, most remarkably, fin whales (*Balaenoptera physalus*). This rainforest fjord system has also been proposed as a major shipping lane for bitumen oil and liquid natural gas. Its exceptional circumstances may lend insight into the mechanisms that shape the foraging behavior and habitat use strategies of marine tetrapods in general. I had five primary objectives:
1. Document great whale habitat use in this fjord system.

2. Compare spatial patterns of habitat associations, foraging behavior, and predator-prey interactions in the fjord system's whales using scale-sensitive analyses.

3. Do the same for the area's seabird community.

4. Develop and assess cost-effective, integrative methods that facilitate next-generation ecosystem monitoring by local communities.

5. Establish a baseline against which future ecosystem changes can be evaluated.

While all the necessary data for the seabird component of this study were collected, the chapters that follow are restricted in scope to the whales of the Kitimat Fjord System.

**FIGURE**

Figure I-1. To achieve the size and mobility needed to find enough prey, the rorqual body frame (here a blue whale, *Balaenoptera musculus*) accommodates two seemingly exclusive designs: the hydrodynamic fusiform of a highly mobile wanderer and the enormous maw and buccal cavity of a lunge-feeder.
CHAPTER 1:

Field methods aboard RV Bangarang

Eric M. Keen
INTRODUCTION

Overview

Study Design

Data were collected throughout three summers (2013-5) aboard the RV Bangarang, a 12m motorsailer, with a team of three researchers. Each summer, circuits of the study area were completed at a target rate of one per month. During a circuit we visited a grid of oceanographic stations (n=24) between which we conducted concurrent visual, acoustic and environmental transect surveys (Fig. 1-1, Table 1-1).

In each circuit eight naturally compartmentalized sections of the fjord system, or “blocks”, were surveyed: Two in the outer sounds (Caamano and Estevan Sounds), two protected channels used extensively by both fin and humpback whales (Campania Sound and Squally Channel), two central channels used persistently by humpbacks (Whale Channel and Wright Sound), and two inland fjords encircling Gribbell Island that are visited only by humpbacks only in the late fall (McKay-Ursula Channels and Verney Passage). Most blocks were surveyed within a single day. More days were needed for equal coverage in Campania and Squally such that a single circuit required 12 days of acceptable weather. Between circuits, more focused effort was given to whale focal follows and acoustic recordings in the shared habitat of fin and humpback whales.

Survey data were recorded using a custom data entry program written for a touchscreen laptop at the help, to accommodate the rapid entry and association of position, effort, environmental, and sightings data.

Stations
At each station we performed a Secchi disk reading (8 replicate casts from the same observer) and a water column sample (down to 250m, seafloor permitting) using a SBE25 plus CTD with additional sensors for fluorescence, dissolved oxygen and pH. Three plummet-style zooplankton tows (333μm, 0.7m diameter, OAR 6:1, flowmeter-equipped, dropped to 250m) were taken at the stations within each block. To accommodate variable weather, swell, and whale conditions, these tows could be distributed amongst a block's stations as needed (i.e., all three tows for a block can occur at one station if need be). Samples were preserved in 5% Formalin-seawater solution.

**Passive acoustics**

Non-systematic passive acoustic surveys were conducted with a variety of hydrophone arrays. Options included a towed array (2 hydrophones, 3m separation) custom built for monitoring low- and mid-frequency cetacean vocalizations, an over-the-side hydrophone custom-built with the same specifications, three back-up recording options for these hydrophones, and an autonomous Ocean Instruments SoundTrap recorder.

**Transects**

While underway between stations, three surveys were conducted concurrently.

- *Environmental transects* of meteorology, surface water properties and acoustic backscatter. A weather instrument, mounted approximately 5m above sea level, recorded air temperature, barometric pressure, and wind speed and direction at one-second intervals. Surface water temperature and salinity were sampled at 0.3m depth every two seconds with a Seabird Electronics 45 thermosalinograph. Beaufort sea state and sighting conditions were logged in the data entry program hourly or as they
changed. Hydroacoustic transects were conducted with a down-sounding Syqwest Hydrobox echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of the ambient depth, distribution, and patchiness of backscatter down to 300m. These echo data were automatically synchronized and geo-rectified with sighting and effort data from visual surveys.

- **Visual surveys for cetaceans** using line-transect sampling methodology. Bearing and reticle readings using Fujinon 7x50 binoculars, min-max-best group size estimates, and cue behaviors for each sighting were recorded. At standard intervals observers rotated between three positions, one of which was data entry at the helm. Group size and other information were refined during close approaches to sightings (below).

- **Visual surveys for seabirds, pinnipeds, salmon, jellies and debris** using strip-width methodology. The survey strip was 150m of each side of the vessel (300m total), broken into two zones (0-75m, 75-150m, gauged using handheld rangefinders). Seabird identifications were recorded to species if possible, or conservatively to the lowest taxonomic category that could be determined with certainty. For each sighting min-max-best group size, behavior, estimated flight height and direction, plumage and sex were recorded to the extent possible. Near-surface jellies observed near the boat were noted with estimated distance from beam, species, group size and body size category. Vessel traffic was also tracked and logged.

**Close Approaches**

When whales were seen, transect effort was suspended if possible and focal follows were commenced. Effort was considered “with-whales” when we were within 150m of
groups. During these encounters, the team collected respiration intervals, travel patterns, group composition, identification photographs, behavioral notes, fecal and prey samples where possible, and acoustic backscatter. Seabirds associated with the whales were noted. Special effort was made to observe and document multiple-species feeding events and interactions among predators during the event. We used fine mesh skimmers on long poles, cast nets, and photographs to collect prey, feather, scat and skin. These samples were preserved either in alcohol or formaldehyde, depending on their intended use.

**Extent of data collection**

Over the course of 203 days of fieldwork in 2013-2015, along 2,795 km of trackline, we completed 9 surveys of the study area (Fig. 1-2, Table 1-2). Five of these surveys took place in 2015; effort was limited to two surveys in each of the prior two years due to vessel repair issues. Mean survey length was 21 days. In total, we collected 215 Secchi disk readings, 230 CTD casts, and 164 zooplankton tows. Details of annual oceanographic data collection are provided in Tables 1-3 through 1-5. We collected more than 40 hours of acoustic recordings and more than 90,000 research photographs.

**Design rationale**

In order to achieve my research objectives (*Introduction*) in a single cohesive field effort, study design had to include the following field components:

- Field effort that spanned the majority of the summer foraging season.
- Thorough systematic visual surveys that quantified the density, diversity and distribution of whales and seabirds with high spatial resolution;
• Some form of concurrent, systematic remote sensing of the volume and distribution of these predators' prey;
• Opportunistic focal studies of whale behavior, with simultaneous remote sampling of the immediate prey field;
• Concurrent systematic sampling of the near-surface environment;
• A means of verifying remotely sensed prey with direct prey sampling;
• A means of documenting direct evidence of predator-prey interactions.
• An oceanographic sampling design that could identify gradients and anomalies in the physical and biological properties of the water column throughout the fjord system.
• Opportunistic passive acoustic recordings in the vicinity of whales, with particular focus on fin whale vocalization.
• Methods and equipment that were transferrable to the local community for continued monitoring once my field campaign was complete.
• Close collaboration with local researchers and the area's maritime community.
• Low costs that were affordable with only the aid of small grants, private donations and equipment loans.
• A research vessel with the following features:
  o Highly customizable for this specific project
  o Safe operation in close proximity to whales
  o Able to accommodate a small team as a live-aboard for the entirety of a 4-to-5-month field season
  o Able to be operated and maintained by a relatively inexperienced research crew
  o Affordable to use and maintain in a remote area
Navigable in the study area's narrow, shallow anchorages, and the tiny marina of Hartley Bay.

**Vessel**

This research was conducted on board the SV *Bangarang*, a Cooper Seabird 37' center-cockpit cutter (11.3 m length at waterline, 12m length overall; Fig. 1-3). To make this study feasible financially, logistically and motivationally, I purchased and captained the boat myself. For a detailed description of the vessel and its research instrumentation, see Appendix 1.

Motorsailers are not an uncommon platform for cetacean research (e.g. Papastavrou et al. 1989, Gordon et al. 1999, Dawson et al. 2008), including fin whales studies (Panigada et al. 2005). A 12m vessel like the *Bangarang* is within the ideal size range (10 to 20m) for high quality line transect surveys from smaller vessels (Dawson et al. 2008). Small vessels are good for coastal research because they allow (1) much more survey effort to be expended for the low fuel and operating costs, (2) surveys to be conducted in better sighting conditions (since vessel costs are low, you can afford to wait), and (3) a significant amount of vessel time to be spent on observer training (Dawson et al. 2008). When conditions allow, sailing vessels enable researchers to reduce or eliminate fuel use and collect visual and acoustic data without the disturbance of engine noise. Sailboats are typically designed to minimize visual obstructions and often have ample deck space for handing sails, which is beneficial when working with oceanographic instrumentation on deck. Finally, sails offer a safe alternative in the event of engine trouble.

**Logistics**
Collaboration

Fieldwork in the study area was made possible by research agreements with the Gitga’at First Nation, the North Coast Cetacean Society (NCCS), and the Cetacean Research Program of Canada's Department of Fisheries and Oceans (DFO).

Subsistence

The Metlakatla ferry visited Hartley Bay from Prince Rupert twice a week (an 80 nmi, 3.5 hour trip), upon which fresh vegetables, snacks and supplies were transported. We ordered groceries through NCCS, who had a special relationship with the Overwaitea grocer in Prince Rupert. We would typically get a food order every 14 days. Diesel, engine oil, propane, water, moorage, and cell phone signal (and often gifts of salmon, halibut, and Dungeness crab) were available to us in Hartley Bay.

Permits

In 2013, marine mammal research was conducted under NCCS' permit, DFO MML 043. Zooplankton collection was conducted under DFO license XR 65 2013. In 2014 and 2015, marine mammal research was conducted under NCCS' permit, DFO XMMS 3 2014. Zooplankton collection was conducted under DFO license XR 83 2014.

Emergency response

An EPIRB beacon and SPOT satellite locator were carried on board. The SPOT beacon was used to transmit our location each evening to NCCS, my academic advisor, and my parents. We were always within VHF radio contact of the Prince Rupert Coast Guard office, the Gitga’at Guardian watchmen, and NCCS. We regularly saw pleasure craft and sein-
fishing boats during transects. Most of the crew and I held wilderness medical certifications at the level of WMI Wilderness First Responder (WFR). Mechanisms were in place for how and whom to contact if outsiders needed to contact the *Bangarang* while we were conducting circuits.

**STATIONS**

Stations were spaced in a pseudo-homogeneous distribution (Fig. 1-4, Table 1-1). Their placement was informed to a degree by logistics (e.g., position relative to viable anchorages, protection from prevailing winds, swell, etc.), which is an inevitable feature of working from a small vessel in a remote area. Nevertheless, stations were positioned randomly with respect to oceanography, and as such they occurred at a variety of depths and proximities to shore. This layout was intended to representatively sample both the physical structure of the study area's water column and the diversity and abundance of zooplankton.

**Water column profiles**

In 2014 and 2015 water column properties were sampled at each station using a Seabird Electronics (SBE) 25plus CTD profiler (SBE-1070, temperature sensors SBE-3 and conductivity sensor SBE-4) equipped with WetLABS ECO-FL fluorometry sensor (ECOFL-3486), dissolved oxygen sensor (SBE-43), and pH sensor (SBE-18). This sampler was pump controlled with a maximum depth of 350m and a 16 Hz sampling rate. It featured internal power (12 D Cell batteries, 2 AA batteries and 1 coin cell battery with a battery life of approximately 90 casts) and 2GB internal memory storage (capacity for over 5,000 casts). The profiler was cast to 250m, seafloor permitting, using the same 3/8” double-braided nylon line,
davit and winch system used by the zooplankton net. To achieve a higher resolution sample of
surface waters, the unit was lowered hand-over-hand at roughly 0.3m/s for the first 25m then
allowed to free fall (~1.5 m/s) for the remainder of the cast (Fig. 1-5).

In 2013, a YSI Castaway CTD (rated to 100m) with no additional sensors was used
(Fig. 1-6). The unit was calibrated annually and in 2014 its readings were compared to the
SBE25plus CTD during simultaneous casts (Appendix 4).

Data were downloaded nightly, checked for quality and backed up. During transit the
CTD was lashed to the transom rail and covered with a canvas bib. Between circuits the
conductivity sensor was flushed and the unit was lashed in an interior corner of the aft cabin.

Water clarity

To obtain an index of water clarity, we used a classic 20-cm diameter Secchi disk.
Secchi depth readings can be used to calculate the depth of the euphotic zone and other optical
properties of the water (reviewed in Preisendorfer 1986, Effler 1988, Davies-Colley and Vant
1988, Davies-Colley and Smith 2001, and Hou et al. 2007). In bodies of water where plankton
are the primary cause of turbidity, Secchi depths can provide an estimate of plankton density
(Almazan & Boyd 1978). Seabird distribution (both plunging and pursuit-diving seabirds)
may be influenced by prey visibility/accessibility as a result of turbidity (Ainley 1977, Safina
& Burger 1988; for evidence against this hypothesis see Haney and Stone 1988 and Henkel
2006).

The disk was equipped with a 5 lb. diving weight to combat the effects of strong
currents. The weighted disk was suspended from a tape measure reel that is read from the
same mark on the bow of the vessel (the distance from this mark to the surface is then
subtracted during analysis). The disk was dropped from the bowsprit of the vessel so that
vessel shadow never impeded the readings. The disk was dropped from whichever side was not subject to glare. Viewer boxes are ideal in Secchi readings (Davies-Colley and Vant 1988, Smith and McBride 1990, Smith et al. 1997 and Smith 2001) but were not feasible from my platform. Viewer boxes increase between-observer precision by removing the interfering effects of water surface glare and glitter (Smith 2001). Beaufort sea state (Table 1-6), percent cloud cover and wind speed data were recorded at all stations in order to gauge for their effects on Secchi depth and investigate the development of correction factors.

Eight Secchi depth readings were taken at each station, always by the same observer (EMK). The Secchi depth was defined as the exact depth at which the black and white quadrants cannot be discerned (as in Smith 2001). For odd-numbered readings, the disc was dropped until the Secchi depth was reached. For even-numbered readings, the disc was raised from below the Secchi depth until the quadrants could be discerned. If the drop angle was greater than an estimated 15 degrees it was noted as “slight” in the data entry software. If it was greater than 30 degrees, Secchi readings were not taken at that station.

An alternative sampling design was tested and abandoned in 2013, in which three readings were taken at each station by three different observers. However, it was possible that the variation in Secchi depth observed at stations within and among blocks is less than that among observers at a single station. To address this, a trial was conducted in which three observers made 24 casts each while docked in 30m of water in Barnard Harbor, an cove centrally located in the study area at the southern end of Whale Channel. Throughout the trial, sea state and cloud cover conditions remained constant. Observer differences introduced the most variability to readings (Fig. 1-7; one-way ANOVA, F=58.32, df(2,72), p < 0.0001). Within-observer variability was relatively low. These findings led me to change protocol to that explained in the above paragraph.
**Water color**

Color of seawater was recorded with the numbered Forel-Ule color scale (Sverdrup et al. 1942) using the white background of a Secchi disk (after Haney and Stone 1998, Wernand & Woerd 2010) suspended halfway between the surface and the Secchi depth. The Forel Ule (FU) scale is a color comparator scale with tints varying from indigo-blue to cola brown used to quantify the color of natural waters in marine settings (Wernand & Woerd 2010). The scale is held above the sea surface within a shadow and the operator looks down on the water through the observation windows next to each tube. The best match between the color of the water column and one of the tube-colors is determined and is documented as an integer number representing the FU scale equivalent.

**Zooplankton**

*Daytime plummet casts*

Three tows were taken at the stations within each block. To accommodate variable weather, swell and whale conditions, these tows were distributed amongst a block's stations as needed (i.e., all three tows for a block can occur at one station if they must).

To design for the Bangarang Project's goals within its constraints, I planned for daytime vertical tows with a plummet net (after Bartle 1976, Bradford 1977, Heron 1982, Daly & Macauley 1988 and Hovekamp 1989, among others). A plummet net is a down-fishing zooplankton sampler that has no mouth obstructions and is cinched shut when the desired depth is reached. Because the plummet net falls quickly, vertically, and begins sampling immediately once it hits the water, the problem of drift in strong currents is minimized. The boat may drift in relation to the net, but the net remains relatively stationary with respect to
oceanography. The design was first described in detail by Heron (1982). The elements I contributed to Heron's (1982) original published design were as follows.

- The choke line connected to the tow line at both ends, providing a quicker and more reliable “dual-action” choking motion.
- A fixed-length line ran from the mouth ring to the shackle that joined the choke line to the tow line. This line served as both a safety and as a limit to how tightly the Dacron can be choked, increasing the longevity of the net material.
- A new cod-end design that allowed the net to be dangled and prepared alongside the research platform before a drop.
- Strength-bearing webbing running the length of the net, so that the net could be suspended by the cod end during preparation and sample preservation.
- A mouth ring with eyebolts welded to it at each quadrant, for mounting the flowmeter, adding weight and/or using the net with a bridle as an oblique sampler if needed.

The Heron-Bangarang plummet net (Fig. 1-8) was designed using the principles outlined in Keen (2015) and references therein, and manufactured by Aquatic Systems Designs specifically for this project. The cylindrical portion of the net was non-porous black Dacron cloth, 0.7 m long. An elliptical band of webbing with nine equally spaced stainless steel carabiners ran from the mouth of one side of the Dacron to its opposite cone-ward side; these carabiners acted as leads for the net's choke lines. The conical section was 333 micrometer white Nitex, 2.8 m long, for a total net length of 3.5 m. Three bands of strength-bearing webbing ran the length of the net and extended beyond the 3.5” diameter cod end by 18”. These webbing bands terminated in 1” diameter stainless D-rings, which were held collectively by a large stainless caribener. The net was suspended by this caribener when being staged for a drop.
The 0.70 m-diameter mouth ring (area= 0.38 m$^2$) of solid 3/4” 316 stainless steel was manufactured at the SIO machine shop with 1/2” eye rings welded at each quadrant of the ring (with perpendicular orientation to ring, for hydrodynamics), such that a bridle could be readily attached and used as a classic WP-2 oblique tow net if needed. The ring weighed approximately 30 lbs. To increase drop weight, six 5 lb. diving weights were lashed to the ring next to each eye ring using stainless steel hose clamps. Retrieving the net manually was therefore difficult, especially when a moderate wind opposed a strong current. In 2013 all three researchers on board had to take turns pulling up the line. In 2014, a motorized PowerWinch 300 Pot Hauler with footswitch control was added to the Bangarang’s davit.

The porosity of our 333-micrometer mesh was 66% according to Dynamic Aqua Supply specifications. Assuming a 100% sampling efficiency (which was a conservative estimate for a cylindrical-conical net, Tranter and Smith 1968), and given that the median effective drop depth with our towline was 200m (seafloor depth permitting), the Heron-Bangarang net’s median sample volume was expected to be about 70 m$^3$.

To prevent clogging, a net designed for this tow duration in green waters must have an Open Area Ratio (OAR) of 5.4:1 or greater (Keen 2015). Our net design has an OAR of approx. 6.5:1. Clogging was not observed or suspected in any tows during the study.

The net was equipped with a General Oceanics flowmeter mounted off-center at the entrance of the net (after Tranter & Smith 1968) in order to determine the actual volume of water sampled during each tow. The flowmeter was calibrated in 2014 using protocols adapted from the SIO Pelagics Invertebrates Collection (PIC). The calibration was done with 20 m of dock space on Breakwater A at the marina of Friday Harbor, WA. The flowmeter was mounted to the end of a telescoping pole, placed in the water away from the dock, and paced with and against tidal current for 20m at various target rates (0.75 to 1.25 m s$^{-1}$). The meter was read before and after each trial. Three to four trials were conducted for each speed in each
direction, and a trial was only considered successful if the actual time of the 20 m walk was within 0.5 seconds of the target time. A calibration model was fit to these data (Fig. 1-9).

When mounted on the net, the forward orientation of the flowmeter was maintained with wound elastic. When the net was cinched shut the flowmeter would be turned perpendicular and held by this tension against the Dacron to halt flowmeter spin. This mount was ultimately a difficult design problem, and it was unknown how a flowmeter would perform with a cinching plummet net design. After three seasons of use, it appeared that the cinching action was rough on the flowmeter’s machinery. My conclusion was that tow volume could probably be estimated just as accurately, with less in-field stress and lower costs, via careful measurement of payout (see below).

As the net descended, zooplankton were collected in custom 3.5” outer diameter two-piece cod end bucket whose design was based on that used in the SIO PIC. (In 2013 the buckets were loaned from SIO PIC.) The two pieces were connected with quick-release butterfly shackles with safety latches. Diameter drainage holes (1” diameter) with 333-micron mesh were drilled into the bucket sides. For added security, the removable end was attached with a caribener to a line streaming from the net's webbing tails. This line also prevented the choke line from cinching entirely, minimizing strain on the Dacron and mesh.

Fall rates were measured by noting the timestamp and GPS stamp when 25 m marks on the tow line were submerged during pay out. Descent rates were calculated from this using the time elapsed and the horizontal distance drifted between mark submersion. In 2013, observed fall speeds indicated that the net was not sufficiently weighted and may have contributed to our poor capture rate of adult krill. On average, the net free-fell at 0.785 ± 0.206 m s⁻¹ (n=25, CV=26.18%), which is very close to the recommended speed for vertical tows outlined by UNESCO Working Party No. 2 (0.75 m s⁻¹, Tranter & Smith 1968) and the fall rate used for plummet tows in Hovekamp (1989), but half the recommended fall rate for
capturing euphausiids (Heron 1982). In 2014 the net was weighted with 30 lbs of nylon-coated diving weights, which pushed the descent rate to a more acceptable $0.965 \text{ m s}^{-1}$ (Fig. 1-10). A higher adult euphausiid capture rate was anecdotally observed (and will be quantitatively tested). However, this new configuration strained the vessel's davit to its limits and no more weight was added to the net.

The 250 meters of line for these tows were stuffed into a recycling bin lashed to the stern rail of the vessel; this ensured the line did not foul during payout. The line was marked and color-coded every 25 m with permanent marker and fed through a block suspended from the davit for obstruction-free payout over the stern. When the net was retrieved, the mouth ring was hung from a caribener on the crane so that the crew could work on the cod end and flowmeter without bearing the weight of the net.

**Preservation**

Protocols were developed based on Harris et al. (2000). The nets was rinsed and flushed after each tow with thorough and consistent diligence. An advantage of the Heron-Bangarang design was that the net's contents were washed toward the cod end as it was pulled up. Once out of the water, the cod end was dunked in the water 4 times to wash contents down further into the bucket. Once on deck, the three sections of the net at the cod end were each washed with one thorough rinse from the seawater hose.

The seawater hose was powered by a manual bilge pump fastened to the hydrophone reel that was mounted on the topside deck of the aft cabin. The pump drew water up from a weighted hose that hung from the port transom and could be easily pulled up when not in use and stowed along the inside of the port gunwale.

Upon net retrieval samples were preserved immediately in 16-oz. glass jars in a buffered 5% Formalin-seawater solution with a system modeled after that used by the SIO
PIC. The preservatives were stored on-deck in the Preservation Station, a wooden frame fastened to the side of the hydrophone reel mount on the topsides of the aft cabin. When not in use this station was shielded from rain and sun with a canvas cover.

A 16-oz. squirt bottle containing filtered seawater was also Velcro'd to the floor of the Preservation Station. Sample transfer was expedited using a custom PVC cylinder with 248-micron mesh mounted taut across one end. The cylinder fit securely onto the cod end bucket. The apparatus was then inverted to spill the plankton into the transfer cylinder. When stowed the transfer cylinder was hooked to the inside wall of the Preservation Station. The squirt bottle and hose were used to spray water through the cod end windows to flush the remainder of the sample into the PVC cylinder. Once the cylinder contained the drained sample in full, the cod end bucket was removed and replaced with the sample jar. The apparatus was inverted so that the sample jar sat in the Preservation Station sink, a modified black silicone baking sheet, and the mesh-side of the cylinder pointed skyward. Next the squirt bottle was used to flush the sample into the jar and the jarred sample was then ready for fixative. The baking sheet was equipped with a drain hole that led water through a closed hose system over the side of the vessel.

Lashed inside the Preservation Station was a 10-L Nalgene carboy containing 37% formaldehyde from Dynamic Aqua supply of Vancouver. The carboy was capped with a Nalgene 83B lid with two nozzles that could quickly be sealed shut with a spring-loaded release. Only one nozzle was in use for this setup. Under the cap, a length of Tygon tubing led to the bottom of the carboy. From the top of the lid a length of tubing led to a three-way Luer valve zip-tied to the topsides of the wooden frame. On the opposite side of this valve, a length of tubing led to a 60mL syringe also secured to the frame's topside.
The third end of the valve had tubing that turned down and dangled above a jar holder within the station's sink. When fixative was needed this tubing was inserted into the sample jar and the syringe and valve were used to direct the proper dose of formaldehyde into the jar.

Another 60 mL syringe was secured with Velcro to the inside of the station for transferring super saturated borate (Alta Aecer Sodium tetraborate decahydrate 99+%) from its jar to the sample jar.

The proper dosages for various sample volumes were pre-marked on the syringes with permanent marker so that the correct amount was consistently and easily drawn from the carboy without exposure to the chemicals. A 5% formaldehyde-seawater solution required 1.56 mL of 37% Formaldehyde per total fluid ounce of solution, a mixture derived from the convention of adding 50mL of 37% formaldehyde and 20mL of supersaturated buffer per quart of preserved sample (Linsey Sala, pers. comm. 2013).

If \( V \) is the desired volume (in fluid ounces) of preserved sample, and \( F \) and \( B \) are the mL of Formaldehyde and supersaturated Borate solution, respectively, to add to the solution, the following equations hold.

\[
F = \frac{50mL \cdot V}{32oz}
\]

\[
B = \frac{20mL \cdot V}{32 oz}
\]

For a 25-oz. solution of buffered 5% formaldehyde-seawater solution, add 39.1 mL of 37% formaldehyde and 15.625 mL of supersaturated Borate. For a 20-oz. solution, add 31.3 mL of 37% formaldehyde-seawater and 12.5 mL of super-saturated borate solution.

Once the fixative and buffer had been added to the sample jar, the jar was covered with the transfer cylinder and seawater was poured through the cylinder's mesh to fill the jar up to 16-oz. In this way unfiltered seawater never contaminates the sample. An inner label of
archival paper and an outer adhesive label was then applied to each sample jar, with the same data written on both. The rocking of the boat throughout the day helped to “turn” the preserved samples. They were all turned again manually in the evening and again at the end of the circuit, when they were also photographed.

PASSIVE ACOUSTICS

Non-systematic passive acoustic surveys were conducted intermittently throughout transect effort using a variety of hydrophone arrays. The oil-filled hydrophone array, “Tink”, could be towed 100m behind the vessel during transects or suspended vertically deep in the water column while the vessel drifted. The array itself consisted of 2 HTI-96MIN hydrophones (10 Hz high pass filter with built-in pre-amps) positioned 3 meters apart. I added another pre-amplifier in the array that provides 20dB gain and a soft 480 Hz high pass to both signals. The array is also equipped with a Honeywell PX2 depth sensor that was field calibrated in 2014 in the Strait of Georgia (Fig. 1-11). With this depth sensor it was determined that the array was towed at approximately six meters depth at transect speed when weighted with 10 lbs of lead (Fig. 1-12). When not in use the towed array was stored on deck on a spooling Reel-Core 24” diameter plastic reel. The spool allowed us to perform tangle-free pay out and retrieval of the 100 m of cable in less than two minutes.

The over-the-side hydrophone, “Buzz Bomb”, had the same hydrophone element and pre-amp configuration as the towed array. The array's cable was approximately 15 m in length. For ease of use it was stowed on a smaller reel, mounted on a PVC frame that was hose-clambed to the port transom rail.

An Ocean Instruments SoundTrap (a.k.a. Kiwi SUDAR) was also onboard. It was perennially rigged on a 15 m line for quick over-the-side deployment. This autonomously
recording hydrophone was most often deployed in the presence of fin whales during focal follows.

Two additional acoustic recording packages are onboard: a back-up, hand-deployable towed array built from another Navy-surplus Sonobuoy, courtesy of Don Yeungblat, and an over-the-side backup. With these four recording systems on hand, we maximized the chances of obtaining acoustic data during fin whale focal follows.

The towed and over-the-side arrays were powered by the vessel's 12V AGM research battery, which was isolated from the engine's alternator and house electronics. The array circuitries were also designed such that a 9V battery could be used as a stand-in if needed.

The signal was fed to the aft cabin's Passive Acoustic Listening (PAL) station, which included power control switches and a dedicated passive acoustics laptop stored on a retractable shelf. This laptop was the same make and model as the data entry laptop, such that each served as a backup for each other in the event of computer problems. Sounds were recorded using either PAMGuard or Raven, depending on the sampling frequency. When recorded in Raven, 2-channels were used at either a 32 kHz (2013-4) or 44 kHz (2015) sampling rate. Mid- and low-frequency spectrograms (0.1-16 kHz and 0-100 Hz, respectively) were used to live-monitor recordings, as the laptop screen could be rotated and viewed from the helm. The mid-frequency spectrogram used a Hann window (1050 samples with a 60.4 Hz 3dB Filter Bandwidth), 50% overlap, 525-sample hop size, and DFT size of 2048 samples. The infrasonic spectrogram used a Hann window (15586 samples, 4.07 Hz 3dB filter bandwidth), 50% overlap, 7793-sample hop size, and DFT of 16584 samples.

In 2013, the signal was fed to a interim acoustic station in the main cabin's dinette. That year the towed array was left deployed during station work for convenience, but problems arose when a hydraulic internal wave in Verney Passage caused the hydrophone
cable to knot up and break (the knot took 2 hours to untangle) while conducting oceanographic sampling at a station during a spring tide.

TRANSECT DESIGN

While underway between stations, we conducted full-effort transect surveys to sample surface water conditions and assess the density and distribution of marine mammals, seabirds and their prey (Fig. 1-13). Designing transect surveys in complex coastal habitats is notoriously difficult (Dawson et al. 2008, Thomas et al. 2007).

Layout

According to Thomas et al. (2007), a good design (a) employs randomization in laying out transects such that a sufficiently random sample of all habitats is taken (reiterated in Dawson et al. 2008), (b) is stratified if density is known to vary on a large scale, (c) ensures that each location within a stratum has equal coverage probability, (d) evenly distributes transects (systematic random design), (e) contains 10-20 transects per stratum (if strata are used), and (f) provides for maximum efficiency per unit effort (minimizing off effort time).

Given the logistical constraints of the study area and the research platform, this research was only feasible if practical considerations could inform the study design. This can still qualify as good design as long as the known or suspected distribution of the study's target species played no part in the layout of transects (Dawson et al. 2008). In simulation studies, truly random line placement has been found to have no consistent or clear advantage over pseudo-random placement in reducing bias (DuFresne, Fletcher and Dawson 2006).
In my study design, both station and transects were positioned with the practicalities of swell, wind patterns, and anchorages locations in mind, but the layout still performed as a “design-based” approach: properties of the transect layout were used to make inferences about the populations in question (Thomas et al. 2007). This study's transect lines were (1) spaced randomly with respect to known cetacean and seabird hotspots, but (2) were coerced to pass through stations, while also (3) yielding transect lengths that provided roughly the same intensity of effort (IE) in each block (equal effort per unit area, after Dawson 2008; see below). Most transects had random start points inasmuch as they began at a station, which was placed randomly with respect to oceanography and zoogeography.

Adapting the definition from Dawson et al. (2008), intensity of effort (IE) is defined here as the area scanned as a fraction of the block's total area, i.e., total transect distance (T) multiplied by the strip width (s), divided by the area of the block (A) and expressed as a percentage.

\[ IE = \frac{T \cdot s}{A} \cdot 100 \]

Mean IE for our 300m strip-width surveys was 11% ± 4% (Table 1-1). This variation in IE among blocks can be accounted for in analyses of transect results.

I chose a near-equally spaced zig-zag configuration for most of the study area because such layouts tend to make the most efficient use of boat time on the water. Such designs have been used in surveys for seabirds (e.g., Becker and Beissinger 1997), cetaceans (e.g., Dawson et al. 2008) and forage fish (e.g., Simmonds & MacLennan 2005). Zig-zag designs are also known to produce density estimates with low variance (Strindberg 2001). Due to the highly irregular coastline within our study area, we occasionally had to employ “adjusted-angle” techniques (after Thomas et al. 2007). To maximize near-shore sampling we chose to allow our transect zigzags to rebound at the coast (as opposed to the broken-transect designs used in
Dawson et al. 2008). There are articles that advise against this design (e.g., Dawson et al. 2008), but there are others that report that connected zig-zag legs can be treated as independent samples without problems (Thomas et al., 2007).

It is also important for transect lines to be lain across expected gradients in density or environmental variables (O'Driscoll 1998). In fjords, gradients come at you from all sides but the most influential are likely the overall inshore-offshore gradient and the local shore-to-center gradients within channels. I attempted to design with both gradients in mind.

**Replication and length**

Replication (i.e. multiple discrete transects through the same habitat in the same conditions) is a key to distance sampling analyses (Buckland et al. 2001). Thomas et al. (2007) would not consider their design as good with less than 15 transects in each stratum. Buckland et al. (2001) recommend 10-20. There were many natural breaking points in our design to provide for this: stops at stations, observer rotations, course changes, days of effort, etc. We planned to break up collected data retroactively into smaller, more numerous transects as needed for subsequent analyses.

When defining a transect as a period of full survey effort during which observer positions and vessel heading do not change, our blocks were surveyed using a mean of 10 ± 2 transects each, the outlier being Squally Channel, the size and scientific interest of which called for 23 transects. Mean transect length (n=95) was 4.2 ± 0.52 km (median = 4.085, max = 4.97). Such lengths yield a mean of 49 km effort within each block and 395 km of transects per circuit (Table 1-1). There was considerable variation in mean transect length among blocks, which was a result of attempting to keep both intensity of effort and the number of transects relatively consistent within the confines of pragmatism.
Trackline documentation

The data entry program logged vessel position every 10 seconds. For increased position accuracy, an external antenna was mounted 5m high and clear of obstructions. The echosounder logged position, heading, speed and direction every one second. We allowed ourselves to deviate up to 20 degrees from the planned trackline to avoid swell, glare or rain squalls, and return to the original course once conditions had improved (after Kinzey et al. 2000). Course deviations from the trackline in order to examine “interesting” areas, such as floating debris that may attract cetaceans or other fauna, were prohibited while in on-effort mode. Once such areas were past 90 degrees abeam the observers could elect to enter “off effort” mode, double back and explore the area.

Vessel speed

During transect effort the Bangarang cruises at 1800 RPM at an average of 5.0 ± 0.7 knots (Fig. 1-14). Reasons for our slow pace included the hull speed of the vessel (7.3 knots), the fact that the echosounder and hydrophone signals began to pick up interference at high engine RPM (> 1800), and the fact that lower speeds allowed us to manage the incoming data for four surveys simultaneously - environmental, hydroacoustic, line-transect sampling and strip-transect surveys. Due to the great variability in the strength and direction of tidal currents within the area, we endeavored to maintain a transit speed between 4.5 and 5.5 knots at 1800 RPM, but had to prioritize constant engine RPM for the sake of hydroacoustic data. Peer-reviewed seabird studies have been produced from surveys at 6 knots or below (Brown et al. 1975, Powers et al. 1980, Tasker et al. 1984, Logerwell & Hargreaves 1996, O’Driscoll 1998).
Speeds below 8 knots are atypically slow for cetacean distance sampling surveys. According to convention, survey speed should be at least 2-3 times faster than the typical average speed of the animals (Hiby 1982). We could achieve this for the average slowly traveling humpback whale, but not for any species in the act of directed travel. However, the confined waterways of our study area made it easy to track sightings, predict their movement, and avoid recounting.

Time of day

The optimal dates and times for sampling differed among target seabird species (RIC 1997), and no time window was ideal for all species and study objectives. For example, planktivorous seabirds are often most active at dusk and dawn and may not be associated with prey schools during the day (RIC 1997). The marbled murrelet, threatened under COSEWIC and red-listed in British Columbia (COSEWIC 2012), is an example of a primarily piscivorous species with strong diurnal signature in their behavior and distribution (RIC 2001). This species is unique among North American seabirds in that it nests in old growth conifers (Nelson 1997), to and from which individuals fly every dawn and dusk. As a result marbled murrelets are mostly found directly offshore from nesting flyways at dawn (Ralph et al. 1995). Furthermore, murrelet activity patterns vary throughout the breeding season and among different locations (Hooper 2001, Derocher et al. 1996, Carter 1984).

It is not clear to what extent local whale activity exhibits diurnal patterns, as their behaviors seem influenced largely by foraging conditions and social activities. While I would suggest that fin and humpback whales are mostly diurnal, in this fjord system I've often heard both fin and humpback whales feeding and traveling at night. Equally often I have seen them sleep for hours on end during the day, at which time their probability of detection is reduced. I
have only ever heard humpback feeding calls in the KFS during daylight hours, but social
grunts, whops and song occur at all hours (Janie Wray, pers. comm.). There is, however, a
strong unambiguous effect of time of day upon sighting conditions, e.g., glare, backlighting,
down-lighting (mid-day sun angle during which blows are more difficult to see) and the
general pattern of increasing sea state throughout the day due to afternoon onshore breeze.

The best regime for sampling this diverse community successfully was to aim for
diurnal consistency in effort (RIC 1997, Fauchald et al. 2000). The *Bangarang* aimed to begin
transect effort each day 30 minutes after dawn, which was consistent with recommendations

**Strip-transect sampling**

To count seabirds, pinnipeds, jumping fish and debris I used a fixed-width survey
design (after RIC 1997, Hamer et al. 1997, RIC 2001 and many others). In strip transect
sampling, rectangles are placed randomly in the study area (Buckland et al. 2001). Observers
travel down the centerline of each rectangular strip, counting all objects within the strip as
they go. The rectangles can be any variety of length, but their width must be small enough that
absolutely no sighting is missed by the observers as they travel along.

In a strip-width survey design there are *k* strips, each of width *2w* (*w* is the distance
from the centerline to either side boundary of the strip) and length *l*, The total length *L* is the
summed length of all *k* strips. Therefore the sampled area is *a = 2wL*. If the total number of
objects counted (*n*) is the sum of counts from all *k* strips, then the estimated density *D* of
objects is

\[
D = \frac{n}{a} = \frac{n}{2wL}
\]
This is the simplistic equation for a strip-transect density estimate; the final equation must incorporate parameter uncertainty and variability.

Again, a critical requirement of a strip-width survey is that 100% of events within the strip are observed and noted. To meet this assumption sometimes the strip width has to be very small, which can make this method quite inefficient. But the analysis is intuitive and simple. Another assumption is that the strip width is easily known in the field and that animals are counted accurately as within or outside of the strip. Some rangefinding technique is usually used in fieldwork to ensure this assumption is met.

**Strip width**

To ensure that all birds within the strip are seen, an appropriate strip width must be chosen. A standard fixed-width for seabird surveys is 300 m (Tasker et al. 1984; Gould & Forsell 1989, Russell et al. 1992, Fauchald & Erikstad 2002, Logerwell & Hargreaves 1996, Ballance 2010), often on the non-glare side of the vessel. While some surveys (e.g., Mahon et al. 1992) have used 500m strip-widths for marbled murrelet surveys, it is now known that alcids and other inconspicuous seabirds are not reliably censused from a vessel beyond 150-175 m (Evans et al. 2002). This is true especially for small, low-platform vessels (Dixon 1977, Briggs and Hunt 1981, Wiens et al. 1978, Tasker et al. 1984, Briggs et al. 1985). Ralph et al. (1990) suggested detectability for marbled murrelets may drop off beyond only 100 m. A further consideration is that my study investigated spatial patterns between seabirds and the acoustic backscatter from our hydroacoustic surveys (which is downscanning the water column on both sides of the ship equally), and it was ideal to maximize the overlap of sampled predator and prey fields to the extent possible. To this end Piatt (1990) used only a 50 m radius on each side of the boat.
Because pinnipeds and mustelids are inconspicuous in water and inconsistently at sea, distance sampling is not a reliable method for pinniped abundance estimation (Chapman et al. 2004). Aerial and land-based surveys of haul-out sites are typically used (Loughlin et al. 1992, Bengston et al. 2007). However, the pelagic distribution of British Columbia pinnipeds is a recognized knowledge gap (Williams & Thomas 2007) and such data are needed to ascertain associations with the environment, prey and competitors. To achieve the latter Ribic et al. (1991) used strip-width methodology (300m to one side of the vessel) for pinniped surveys from a large vessel (10 m+ platform height). Other studies have surveyed at-sea pinniped distribution similarly (Ballance 2010). A fixed-width method with the 300 m strip centered over the vessel was determined to be the ideal design for studying pinniped spatial association and at-sea densities on the Bangarang.

To test for reduced strip-widths for inconspicuous species, Ronconi and Burger (2009) recommended that surveyors develop independent estimates of detection probability alongside a strip-width survey to test the assumptions of this transect methodology. A detection function can also be used to determine empirically the actual strip width within which you see 100% of target species occurrences rather than assuming its width (Buckland et al. 2001, Dawson et al. 2008). In my study I trialed a more simplistic but more practical method of transect performance assessment: a split strip-width design.

On the Bangarang we maintained a 300 m strip-width, but we placed the vessel in the center of the strip and recorded sightings on 150 m of both sides of the vessel (as recommended in RIC 1997, Burger and Lawrence 1995, Van Franeker 1994). Further, we divided each side of the vessel into two strips (Fig. 1-15): from the vessel to 75 m (Zone 1) and from 75 m to 150 m (Zone 2; similar to recommendations in RIC 2001). Handheld rangefinders were used to determine which strip each sighting fell into (detailed below). With this set up 4 fixed-strips were surveyed at once. This design allowed for the check of species-
specific patterns in avoidance and reduced visibility as well as comparisons of observer performance. In the event that this split fixed-width method was overwhelming in areas of high density, the observer team could choose to switch to simple 300 m or 150 m strip-width methodology, in which case the change in effort would be noted accordingly.

**Rangefinder**

In order to know whether or not a bird is within Zone 1, Zone 2 or Out (beyond 150 m), *Bangarang* observers used a handheld rangefinder that was customized to their own height and arm length. Handheld, homemade range finders have been used for offshore seabird surveys with unobstructed horizons (Heinemann 1981; Ballance 2010), but we had to develop a rangefinder for coastal studies in which the horizon is usually obscured. See Keen et al. (2016) for full details.

**Seabird issues**

*Bangarang* seabird strip-width methodology was modeled after Tasker et al. (1984), Raphael et al. (2007), RIC (1997), and Ballance (2010), among others. When reporting a bird sighting while on effort, we recorded all factors affecting its visibility: flock size (min-max-best), behavior, flight height, direction of flight, sea state, weather conditions, glare angle, vessel speed and heading, observer, etc. (after RIC 1997, Tasker et al. 1984).

**Continuous counting:** My primary objective in seabird surveys, determining seabird habitat choices based on strategies for acquiring prey, could arguably have been met by only counting sitting or obviously feeding birds. However, my secondary objective of abundance estimation required that flying birds were counted too. My survey plan also had to enable me to address fine scale spatial patterns (after RIC 1997 and Spear et al. 1992, based upon reviews in Schneider and Duffy 1985, Schneider and Piatt 1986, Haney and Solow 1992; as
achieved in O'Driscoll 1998). I therefore opted not to perform snapshot counts at intervals
(after Russell et al. 1992, Fauchald et al. 2000). Instead Bangarang observers recorded seabird
observations continuously while noting the “motion” of each sighting (“flying”, “sitting,
“rafting” or “following”). The 2013 preliminary study demonstrated that densities allowed for
this continuous sampling without overload to observers or the data entry crew. We were also
confident that we could count flying birds without missing stationary birds.

Birds in flight: Continuous counts of flying birds run the risk of “overestimation of
birds caused by flux” (Tasker et al. 1984). “During any one counting period more birds will
fly through the total area surveyed than are present at any one instant in the area. A count of
all flying birds seen to pass through this zone during the 10-minute period would be a measure
of bird flux and would be an overestimate of actual bird density” (Tasker et al. 1984). If
extenuating factors such as molt or feeding conditions cause the ratio of sitting to flying birds
to vary throughout the study period, it would be more difficult to estimate species densities
based on sitting or flying birds alone (Tasker et al. 1984).

It is therefore essential to note whether birds are on the water or in flight (RIC 1997).
This gives researchers the options of including only sitting birds in analyses (after Russell et
al. 1992, Fauchald & Erikstad 2002, Fauchald et al. 2000, Piatt 1990) or comparing results
from on- and off-water birds (after O'Driscoll 1998) to get a sense of foraging preferences.
Birds in flight have often been assumed to be unassociated with underlying prey because they
are commuting between foraging areas (Russell et al. 1992), but this is not always the case.
During flight seabirds are assessing prey fields and making foraging decisions (Gaston 2004).
Furthermore, birds on the water have not necessarily landed only to feed (Grover & Olla
1983).

To counter overestimation due to flux, Spear et al. (1992) re-sighted detected birds,
taking their bearing and distance from the boat at each recording as well as vessel information
(GPS-stamp, time-stamp, heading, and speed of the vessel) at each fix. This proved infeasible for my platform given our other survey objectives. Instead I followed the lead of Spear and Ainley (1997), supplemented by Schnell & Hellack (1979), Pennycuick (1982, 1987), Alerstam and Lindstrom (1990), RIC (1997), and others. For each sighting, we recorded bird direction of flight, height over water, and wind speed and direction. Readings of wind speed and direction were taken at 1-second intervals by the 5m-high weather station (in 2013, in lieu of this automated weather station a handheld anemometer, the Kestrel 2000, was used at every station and course turn). For analyses these wind readings could then be scaled to the bird's altitude using published correction factors (Pennycuick 1982). Seabirds could be grouped in published categories (Spear and Ainley 1997) according to wing loading, flight style and known flight speed response to wind variables. The birds' adjusted flight speeds could then be used to account for bird flux in our density estimations.

Observers were made alert to the problem of following or “leap-frogging” birds and were trained to make a conscientious team effort not to re-count them (such birds were logged as “followers” in the data entry program).

**Line-transect sampling**

Line-transect sampling was used in our surveys of cetaceans, vessel activity and jellies according to the methodologies detailed in Burnham et al. (1980) and Buckland et al. (2001 and 2004). This is a common method to use when estimating absolute abundances of populations (Burnham et al. 1980, Kinzey et al. 2000, Buckland et al. 2001, Williams and Thomas 2007, Zerbini et al. 2007). Unlike strip-width sampling, which limits the area you search and assumes that you see everything within that confined area, distance sampling requires that you record all sightings, regardless of distance, but that you also record the
distance of each sighting from your trackline. This allows a wider strip to be used, providing a larger sample size for the same amount of effort. This is done using some range finding technique. A curve (known as a “detection function”) is then fitted to those detection distances in order to estimate the probability of seeing a certain species at a certain distance. Survey results can then be adjusted according to these probabilities to produce unbiased density estimates for an area. 60-80 sightings are recommended to acquire a good fit to the detection functions of each target species (Buckland et al. 2001), and 20-30 sightings should be considered a minimum.

The three assumptions essential to unbiased density estimation are:

- Objects directly on the line are always detected (i.e., they are detected with a probability of 1).
- Objects are detected at their initial location, prior to any movement in response to the observer.
- Distances (and angles where relevant) are measured accurately (ungrouped data) or objects are correctly counted in the proper distance interval (grouped data).

Other important assumptions include the accurate identification of species and estimates of group sizes.

Similar to strip-width methods, a line transect design comprises a series of randomly placed lines (or a systematically spaced grid). The difference is that density estimation from line transect surveys has to deal with uncertainty since only a proportion of the objects in a surveyed area is detected. This unknown proportion is $P_a$.

$$D = \frac{n}{2wLP_a}$$
Line transect analyses require the following additional data to be collected: (1) the angle between the track line and the sighting and (2) the shortest straight-line, or radial, distance to the sighting (Kinzey et al. 2000). To arrive at these data we recorded compass bearing, binocular reticle and observer for every whale and vessel we saw, as well as the vessel heading and position. The known height of the observer could then be used in the reticle equations to determine the radial distance to the sighting.

For whale and vessel sightings distances were estimated using Fujinon FMTRC-SX 7x50 binoculars, which display reticles and a compass bearing in the left eyepiece. These same 7x50 binoculars were used by all observers on Southwest Fisheries Science Center harbor porpoise surveys and by the data recorder on pelagic surveys for all cetaceans (Kinzey et al. 2000). The binoculars' compass is graduated in 1-degree increments (Kinzey et al. 2000). One eyepiece has reticles of alternating broad and skinny width, but we treated the distance between every line as a full reticle (after Kinzey & Gerrodette 2001). A conversion factor of 0.279 degrees per reticle, which had been determined empirically for this type of binocular by Kinzey & Gerrodette (2001), was used to determine the angle between the observer's vantage of the horizon or shore to her vantage of the sighting.

At the end of a field season, this angle was then used to calculate the season's sightings' true locations by invoking equations outlined in Lerzak & Hobbs (1998) to determine the distance over the earth's (assumed) spherical surface to the sighting (Fig. 1-16). Those equations required the observer's height above water, which was measured for all crew at all positions. Observer name, position, and their reticle and bearing reading was recorded for every sighting during transect effort.

For jellies, observers estimated their distance (in meters, range 0-5m) from the beam of the boat when crossing the beam as well as the depth of the jelly. Area vessel traffic was also tracked using the binocular compass and reticles.
ENVIRONMENTAL TRANSECTS

While surveying along systematic tracklines, instrumentation automatically logged data on meteorology, surface water properties and acoustic backscatter.

Weather and sighting conditions

An AirMar X100 weather station mounted 5m above sea level recorded air temperature, barometric pressure, and apparent wind speed and direction at one-second intervals and transmitted it to the data entry software via NMEA0183. The vessel speed and heading provided by the Garmin GPS allow us to calculate true wind speed and direction. Up-to-the-second wind data were particularly valuable for seabird density analyses.

In addition sighting conditions were recorded at each station as well as whenever any parameter changed between stations. These parameters included the following:

- Sea state using the Beaufort scale (Table 1-6, adapted from Bowditch 1966)
- Swell height using binned height categories
- Estimated percent cloud cover
- Visibility using binned distance categories
- Precipitation status (clear, pouring rain, drizzle, fog, haze)
- The bearing of the left and right extent of glare, if any
- Engine RPM. The ratio of vessel speed to RPM can be used to assess windage and water current speed.

Thermosalinograph
Surface water temperature and salinity were sampled at 30 cm depth every two seconds with a Seabird Electronics 45 thermosalinograph (TSG, not used in 2013). The TSG was calibrated annually. The TSG communicated with the data entry software via NMEA0183.

Installation of a TSG on small vessels is difficult because several conditions must be met: (1) the TSG must be installed very near the source of the water, unless a remote temperature sensor is used, to ensure that temperature readings are not affected by the thermal mass of the ship or friction in the plumbing. (2) For the same reasons the TSG must be mounted as near the front of the vessel as possible. (3) The TSG must be located upstream of its water pump, so that the water pump does not influence temperature either. (4) TSG plumbing must be without high points or low points that could lead to the collection of air bubbles that lose the prime of the pump. (5) Flow through the TSG must be limited to 0.1-0.27 gallons per minute, and (6) most continuous duty water pumps at such low flow rates require “flooded” installation below the waterline. This necessitates that (7) the TSG must also be installed below the waterline. This is difficult and marginally unsafe in a vessel whose draft is only 4 ft, most of that being the 3/4 keel. To meet all these requirements on the Bangaran, the TSG was mounted below the starboard salon settee and was plumbed into hosing for the forward head's sink. A seacock and two ball valves provide emergency shut off in the event of a leak. A March 893-09 12VDC pump, rated to 1 gallon per minute at a head pressure of 6 feet, was installed below the waterline under the sink. From the pump, water was led up through the sink counter to a McMaster-Carr in-line flowmeter (0.1-1.0 gal/min). Above it a throttle valve allowed us to adjust flow rate in the system. Water was then diverted outboard via a dedicated thru-hull fitting. TSG flow was checked throughout the day, more often in heavier swell, to ensure that the pump had not lost its prime. Swell conditions could
sometimes preclude the use of the TSG in the outermost block of Caamano Sound. To regain prime the sink water could be used to backfill and purge air from TSG plumbing.

**Acoustic prey mapping**

Hydroacoustic data were recorded along the trackline with a down-sounding Syqwest Hydrobox echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of the ambient depth, distribution, and patchiness of backscatter down to 300m. The details of this instrumentation, its setup and data processing are provided in Appendix 5.

**VISUAL TRANSECTS**

**Observer positions**

Seabird methodology papers concur that at least two observers are needed to adequately survey a strip of 300m width (Raphael et al. 2007, Tasker et al. 1984, Becker & Beissinger 1999, RIC 1997, Spear et al. 2004). On the Bangarang two observers were stationed atop the visual survey platform (recommended in Dawson et al. 2008) at the mast and a third was at the helm entering data, navigating and monitoring the VHF radio. The helmsman could log missed sightings of any targets for the strip-width survey but was prohibited from alerting the observers to cetaceans until the group had passed the beam of the vessel.

In 2013 a less ideal observer position plan was used. One observer was positioned at the bow and was responsible for surveying one side of the boat, from 90 degrees abeam to 10% beyond dead. Another observer was placed at midships on the other side of the boat; she
and the helmsman shared responsibility for surveying that side. Since the midships observer was responsible for relaying sightings to the helmsman, who was also navigating and entering data, their two efforts combined to ensure that all possible sightings on their side were recorded. Halfway between stations, the two “observer teams” switched sides so that any effects of observer bias would be mitigated and observable (Piatt 1990).

Observers rotated positions at every station, course change, and midway point of transects. Rotations were frequent (target of every 20 minutes) to combat fatigue. If whale activity was particularly dense I could elect to stay at the wheel while the two observers switched sides on the survey platform. If many sightings were currently open and in view, I could decide to forego position rotations so as to track whales as accurately as possible.

All position changes were noted in the data entry program. Station work provided an opportunity for rest and recuperation; often two crew would perform station operations while the third rested. In 2013, the day was found to be so diverse given transect, station and with whales work that fatigue and boredom were not an issue. As a contingency plan the use of a partitioned survey strip (0-75m and 75-150m) allowed me to reduce the strip width used in analysis in the event that fatigue or sighting conditions were thought to be influencing data quality.

Eye heights of 4.5 to 6.0 m are typical of published small boat distance sampling surveys (Dawson et al. 2008). Average eye height for observers on the Bangarang, depending on their height, ranged from 4.5 to 5.0 m.

**Observer training**

In my study design I attempted to achieve both scientific rigor and accessibility, because all of the methods I employ would be passed on in some form to Gitga’at First Nation
for their long-term monitoring efforts. A further constraint was that observers were not professionals but volunteers who supported themselves financially during their 4 to 6-week tour aboard.

Becoming adroit at field identification of the local marine mammal species was easy relative to other study areas given the limited number of species, and seasoned observers helped new crew quickly learn the ropes. The most difficult aspect of joining the observer team was seabird identification. Experience with Pacific Northwest birds was highly encouraged among candidate observers, and at minimum they were required to be enthusiastic birders. Before the season a list of local seabirds was given to each observer as well as *Bangarang*-specific field identification keys, flash cards and an interactive website. While on board several field guides were at hand in the main cabin's research library.

When new observers came on board they were promptly measured and a range finder was built for them. Before a circuit was begun with new observers, several days were spent working on seabird identification, during which the observers also calibrated their sense of strip width, practiced range finding, and familiarized themselves with best practices in distance sampling.

Observers were trained to be taxonomically conservative with seabird identification, reporting only to the level of specificity at which they were confident. I served as the ID specialist on board with final word on difficult sightings. I was on watch at all times during transect effort, ensuring that surveys were conducted correctly and consistently. I also decided when to go on and off effort and whether to pass or close on a sighting.

All observers, new and returning, conducted a rangefinder calibration trial in their first days aboard each season. For the trial a fender was tied to the zooplankton cast line, towed behind the boat while underway (after RIC 1997), and paid out to a set of randomly ordered distances scattered around the two zone boundaries (75m and 150m). The observers first
guessed the distance to the buoy without the aid of the rangefinder, then they decided on the buoy's zone location with the rangefinder, and then they were told the correct distance.

The principles of distance sampling and strip-width surveys were presented to observers in a written manual (the “Bangarang Bible”) prior to the field season, reiterated when they arrived on board, and repeated throughout their tour. The pertinent training paragraphs are provided in Appendix 2.

**Scanning**

The team of observers actively scanned the 180 degrees forward of the ship for new sightings. The two front observers atop the visual survey platform were responsible for scanning 100 degrees on their side of the vessel, from the beam to 10 degrees beyond dead ahead. This provided emphatic coverage of the 20 degrees along the ship's trackline by both observers (after Kinzey et al. 2000; Dawson et al. 2008) while lateral regions were each covered by the equivalent of one observer. In addition to scanning both sides of the vessel for strip-width survey targets, the helmsman entered sightings, weather, navigation, searching effort, observer positions, and other data into the laptop.

Only sightings made by the two forward observers during this “on-transect” mode were used in the line-transect estimates of abundance, but any and all whale sightings during waking hours were noted in the data entry program and “closed on” whenever appropriate. If guests were on board, they were advised not to inform observers of missed whale sightings until after the sighting had passed abeam whereupon I made the appropriate notes for an off-effort sighting (after Kinzey et al. 2000). These sightings, however, were not used in line-transect analyses of abundance. It was important that fourth crew let me know of missed
whale sightings as soon as was appropriate because the decision to “close” on a sighting was time-sensitive.

Transect effort was terminated whenever the sea state reached Beaufort 4, above which inconspicuous seabirds and small cetaceans became very difficult to see (after Ralph and Miller 1995, Raphael et al. 2007, RIC 1997, RIC 2001). For most survey days in 2013 and 2014 we enjoyed BFT sea states 0 to 2 (Fig. 1-17). Transects persisted through drizzle but both visual and hydroacoustic effort stopped during downpours. Transect effort for seabirds would continue through fog if the 300m survey strip was unobstructed, but formal cetacean survey effort would stop if haze or fog reduced visibility to 3km or less. If fog negated all visual effort and we could not afford to repeat the trackline, the vessel would continue hydroacoustic transects while observers casually searched for birds and marine mammals.

Observers scanned their entire jurisdiction in a consistent manner and did not focus on particular regions. Observers were asked to scan primarily without the aid of binoculars. Fujinon 7x50 binoculars were used to identify sightings to species and record bearing and reticle measurements for each sighting (RIC 1997, 2001). However, observers could conduct occasional scans with binoculars especially during midday when lighting conditions or increasing winds diminished sighting conditions. The details of scanning rates and patterns were left to the individual observer's preference (after Barlow 1999).

Debris

Any type of surface debris, anthropogenic or natural, was noted when found within the strip (after Ballance 2010). We logged debris type (e.g., rockweed, log, kelp), extent, orientation with respect to the axis of the channel, and associated fauna (if any). Bands of red tide and other phytoplankton were logged as well.
Fish

Fish breaking the ocean surface were recorded. In the study area jumping salmon (f. Salmonidae) were common. When a jumping salmon was seen, the following information was relayed to the helmsman: survey strip, vessel side, whether the sighting occurred on a strip boundary, and number of jumps. It was the responsibility of each observer not to count the same salmon twice. If it was possible that a jumping salmon could have already been reported, it was not be reported again.

Seabirds

Birds were logged as soon as they were seen within the survey strip, but their zone designation could be Zone 1, Zone 2, “Out”, or “2 to 1”. The latter designation (which did not go into effect until late 2014) meant the bird was first seen in Zone 2 but entered Zone 1 at some point (within 75m of the vessel). Upon detection the following information was relayed to the helmsman: survey zone, vessel side, whether the sighting occurred on a zone boundary, group size estimate (min-max-best), motion (flying, sitting or flushed), behavior, direction of travel, species present (and their percent composition of the entire flock), plumage and sex composition for each species, direction of flight (if flying), elevation of bird (if flying) and feeding behavior (Yes, Maybe or No).

In 2013, flight height was reported in binned elevations: surface to helm-level, eye-level to 5m (top of radar tower), 5m to mid-mast, mid-mast to top of mast, and above mast. In 2014 and 2015, flight height was estimated in meters.
Most sightings were assumed to be “Not feeding”. “Yes” was reserved for undeniable observations like prey in beak (as in RIC 2001) and “Maybe” was reserved for birds exhibiting strong foraging behavior but not providing direct evidence of feeding.

For some species like marbled murrelets, counts of newly fledged juveniles on the water were an important measure of breeding success and productivity, especially mid-June through August in BC (RIC 2001). Plumage composition for each flock was logged for all species. For marbled murrelet plumage classification, what we recorded as “breeding plumage” corresponds to classes 1-3 in Raphael et al. (2007, which were based on Strong 1998) and to the “alternate plumage” designation in RIC (2001). Our “winter plumage” record corresponded to classes 4-7 in the former reference and “basic plumage” in the latter.

A flock was defined as birds that are less than 2m apart (RIC 2001) whose presence was thought to be influencing that of the other (as in Ballance 2010). The behavior of birds that were flushed or dove in reaction to the vessel was noted as “flushed” (RIC 1997). A bird seen as landing or taking off was logged as being on the water, unless flushed (after RIC 1997). Notes were made when any bird was seen holding fish.

In seabird studies, “complete” flock counts (accurate identification of all species and the number of individuals per species) can be difficult to obtain. When faced with overwhelming sightings on the *Bangarang*, observers prioritized data collection using the following hierarchy (after Ballance 2010):

1. Obtain a count of total number of individuals.
2. Obtain a general categorization of taxa and numbers for each (for example: small gulls = 50, large gulls = 150, terns = 75);
3. Look for and document rare species
4. Obtain accurate counts for each taxon.
5. Obtain accurate counts for each species.
If an incomplete count was necessary, the occurrence of the flock was still noted and observers reported as far down the above hierarchy as they could. The helmsman entered the data but also noted that the count is incomplete. Group sizes of diving alcids were estimates of the entire group, including both on- and under-water birds.

When species identification was not possible, sightings were logged identified to the taxon-level of certainty (after Fauchald et al 2000, Fauchald & Erikstad 2002; e.g., an ambiguous large gull could be classified as “T/H/C” for Thayers/Herring/California). Entry forms in the data entry program accommodated those broader categories (Supplemental File 1). Identification and group size counts were a team effort. If other observers were on board they were welcome to aid in species identification and group size counting. Where possible, photographs were taken of large seabird groups for use in retroactive group size corrections (after Gerrodette and Perrin 1991).

Noteworthy sightings (e.g., rare birds and large flocks) that occurred outside of the strip-width were still noted but marked “outside of strip”. In this way a species inventory is kept for each research day regardless of within-strip sightings.

**Pinnipeds and mustelids**

When sea lions, seals or otters were seen the following data were entered: survey zone, vessel side, group size (min-max-best), species, group size, behavior and direction of travel, and comments.

**Jellies**
In the first two seasons jellies were logged in the same fashion as debris and phytoplankton. Beginning in 2015 large scyphozoans and hydrozoans were logged using a modified distance sampling method. When a jelly was seen the following data were reported: side of vessel, estimated distance (integer range 0-5m) from the beam of the boat at the time of passing the beam, estimated depth (taking into account local turbidity from oceanography stations), size class if the species was a moon jelly or lion's mane (categories: golf ball, mug, bowl and plate sized or larger), and number in group. If a group contained multiple size classes the size classes were logged as separate groups.

For this study the following species were counted (Fig. 1-18): sea nettle (*Chrysaora fuscescens*), lion's mane (or sea blubber, *Cyanea capillata*), fried egg (*Phacellophora camtschatica*), moon jelly (*Auralia aurita* and *A. labiata*), crystal jelly (*Hydromedusae*), red-eye (*Polyorchis pencillatus*), hooded nudibranch (*Melibe leonina*), ctenophores, and salp (f. *Salpidae*).

**Cetaceans**

Detections were entered as official sightings when cetaceans had been observed at 0.1 reticles or closer. Any further animals were too difficult to track or localize accurately and were more prone to accidental re-counting, but their blows were still logged as informal sightings that would not contribute to distance sampling analysis. A conscientious effort was made to track distant blows and not recount. If a distant animal came within 0.1 reticles of the vessel it could then be logged as an official detection.

Observers did not report a cue (e.g., a splash) as a sighting but waited until it was an actual confirmed sighting. However, the cue behavior was logged in the sightings form
because certain behaviors changed the likelihood of seeing a whale at a certain distance (e.g., breaches could be seen at much greater distances than blows).

For each sighting, the following data in addition to cue were reported to the helmsman: reticle, bearing, the observer (i.e., whoever was reporting the reticle, not who saw the group first), species, group size (minimum, maximum, and best guess), a general description of its location (to help keep track of various sightings), and the initial behavior of the group (this is typically just “blow”).

Effort was made to locate marine mammals at as great a distance from the research vessel as possible before they may have altered their position or behavior in response to it. However, effort was also made to ensure that no whales on or very near the trackline were missed. If sightings were well away from us, even if they were near the track line and easily visible, observers remained in on-effort searching mode and the helmsman would take responsibility for keeping track of the sighting. If an extra crew member was on board it became her job to track the school.

**Vessels**

Vessel sightings were not entered until the *Bangarang* was as close as it would get to the sighted vessel. This improved our estimate of the vessel's position. If, however, there were too many vessels to keep track of, or if there was a risk that the vessel would soon be out of view, the vessel was entered as a sighting as needed. Commercial vessels were tracked with multiple re-sightings in order to recreate their general route.

It was the responsibility of the observers to collectively keep track of all vessels and marine mammals currently in view, making sure not to recount or let anything fall through the cracks. This was especially important when observers rotate positions; the team briefed each
other on what was currently in their view before rotating. It was also the responsibility of the helmsman to pay attention to the sightings data she was entering. If it seemed that observers might be accidentally reporting the same sighting, the helmsman asked the necessary questions to ensure it got sorted.

CLOSE APPROACHES TO WHALES

When whales were within a reachable distance we broke transect to take photographs, behavioral notes, and samples. All observations were made from a respectful distance in accordance with our research permit and sightings were abandoned if the whales reacted negatively to or avoided the vessel. We strictly adhered to the research etiquette exemplified by our collaborators the North Coast Cetacean Society (NCCS).

“Closing”

The decision to break transect and close on a sighting can be a complicated one (Dawson et al. 2008). Because our transect speed was slow (maximum 6 knots), breaking transect to go “with whales” then returning to the breaking point could be an hours-long endeavor, especially when chasing energetic fin whales. The tidal current direction, current and forecasted wind speed, amount of station and transect work remaining, and the number of sightings at hand all contributed to the decision. It was a hard truth that we were unable to pursue every sighting. Often, seen whales were traveling in a direction that would bring them closer to us further on down the trackline. In such cases we did not break transect until we were as close as we would get.
When multiple sightings were in view the nearest on-effort sighting, rather than the earliest seen, was typically approached first. However, this also depended on the species on offer. Generally speaking, fin whales were highest priority, followed by humpbacks, followed by killer whales.

When I made the decision to leave the transect to approach (or “close”) on a sighting, effort was switched to “casual” until the vessel approached within 150m of the school (determined using our survey rangefinders). During closing, the observers prepared cameras and parameterized acoustic instruments for the encounter. Until the sighting was within range engine speed could increase beyond the 1800 RPM that is maintained during transects.

“With Whales”

Once we were within 150m of the sighting our effort was considered to be “with whales”. This was the distance from which every breath could reliably be recorded, individuals within a group could be tracked, school position updates could accurately be given, subsurface behaviors could be inferred, school size could be accurately estimated, and adequate photographs could be taken. Also, a radius of 150m around a foraging whale was a conservative estimate of the prey field area the whale could “sample” within a single dive. This distance was also easily and accurately determined using the Bangarang rangefinders.

Analyses of echosounder data depended on an accurate record of when we were and were not with foraging whales. So it was essential that this 150 m designation be taken seriously. It was possible that in pursuit of a sighting we would enter in and out of “with whales” range, and our effort was noted accordingly.

Sightings of new schools while already “with whales” were recorded as off-effort sightings. Attention was not focused on these sightings until the current encounter was a
success, but the groups were loosely tracked. If an off-effort school was re-sighted later after returning to search mode, it could be recorded as an on-effort sighting.

When working “with whales”, the following data were collected, usually in this order of priority:

1. Basic data (explained below)
2. Acoustic prey mapping
3. Respiration intervals
4. Travel patterns
5. Photo-ID
6. Passive acoustics
7. Associated seabirds
8. Sample collection

Generally the crew divided responsibilities as follows: the helmsman (always me while with whales) entered data and breath intervals while navigating the vessel; the helmsman also estimates range using a helm-specific range finder. The other two crew had cameras at the ready, tracking the group and scanning for associated seabirds, scat and prey remains.

**Basic data**

*Species identification*

In a close approach, there was never any doubt about which species were present.

*Group size*

A group was defined after Clapham (2000) and Notobartolo-di-Sciara et al. (2003), as “affiliations in which two or more individuals swim side by side within 1-2 body lengths and
generally coordinate at least their surfacing and diving, as well as their speed and direction of movement.” If a number of individuals changed their spacing throughout the focal follow but at one point came within two body lengths of each other, the animals were considered to be a single group.

New sightings were assigned only when there was no doubt that the mammal or group of mammals had not already been assigned a number. If there was any doubt, the animals in question were considered part of the original sighting.

Species and group size (minimum, maximum, and best guess) were identified by consensus, though I had the final word on how sightings were entered into the data entry software. In some circumstances only a low estimate was possible. To estimate group size the observers on watch estimated the number of mammals in the school, all taxa combined. If more than one taxon was present, percent composition of each taxon in the school was also estimated by the observer team. For large cetacean schools or bird flocks, photographs were taken where possible. These were used to more accurately estimate group size and aid in calibrating new observers on group size estimation.

Group attributes

Subgroups: For each close approach, the dispersal (subgroups or even) of individuals was noted. Determining whether two or more groups are subgroups of the same school or separate schools can be difficult in cetacean studies. For the convenience of data entry, a dispersed group consisting of smaller subgroups was counted as a single sighting. Comments were then made to articulate how the group is structured, usually in the syntax “3 + 4 + 2 + 2”, for example. If it became necessary to regard subgroups as distinct groups or sightings, new sighting numbers could be applied post-hoc when the day’s data are reviewed the evening of.
During image processing (detailed below), photographs of individuals were organized into their subgroup associations.

*Spacing:* Spacing was estimated to one decimal place, the unit of measure being the adult length of the sighting's primary species.

*Demographics:* Groups were categorized as all adult, mother calf pair, a mix of juveniles and adults, or all juveniles/subadults. Comments during the close approach gave further specificity to these broad designations.

*Breath synchrony:* Synchrony of breathing was categorized as “Yes”, “Partial”, or “None.” Partial synchrony was when two or more animals consistently breathed, dove and surfaced after a dive within 2 seconds of each other.

*Behavioral Assignments*

Group behavioral state was inferred during the focal follow and recorded along with a confidence level (95%, 66%, or 33%). Behaviors were assigned without knowledge of echosounder backscatter levels. In the data entry software, behaviors could be attributed to the entire group or to specified individuals (arbitrarily designated as individuals A, B, C, etc.).

A humpback was inferred to be “feeding” when most or all of the following behaviors were observed: her travel pattern was circuitous or repetitively back-and-forth; her dives were long; her surface sequence comprised relatively many breaths during which the animal was uncommonly still at the surface, suggesting recovery from feeding activity at depth; her first breath of a surface sequence was inordinately boisterous and subsequent breaths were disproportionately meager; and animal orientation changed before the onset of a dive. There were exceptions. Humpback whales sometimes roved with high energy in large, dispersed groups, performing short dives and traveling in tight circles; in such scenarios it was likely that the whales were coralling a shallow prey school and performing sub-surfaces feeding
lunges. Other times, when humpbacks were feeding in very shallow areas or in the subtidal zone, dives would be very brief and surface sequences consisted of only one or two breaths.

Other behavioral states included traveling, milling, resting and sleeping. A humpback was inferred to be “traveling” when it was moving in a directed, unchanging course with fairly regular and relatively brief dive intervals and surface sequences in a moderate to fast pace. Whales with no directed course and no indication of feeding were classified as “milling”. This category encompassed social behavior and robust actions such as aerial maneuvers and pectoral-slaps. Humpbacks were thought to be “resting” when either still or moving at a very slow, directed pace with relaxed exhalations, uncommon to absent fluking and brief to absent dives. We considered a whale to be “sleeping” if it was absolutely still and completely unresponsive to nearby vessels.

Minor differences in the above rules applied to fin whales, whose behaviors overall were less stereotyped and more difficult to discern based on surface activity. Fin whale travel speeds were overall greater than those for humpbacks, and overall travel pattern was less predictable, particularly during feeding bouts.

**Acoustic prey mapping**

Once “with whales”, engine RPM was kept below 1800 to ensure high quality echosounding (and often much lower, to minimize our disturbance of the group). Hydroacoustic sampling was conducted for a minimum of 150m horizontal distance during close approaches. After (or while) identification photographs and breath intervals were being taken, I navigated the vessel in a “mini-transect” zig-zag that followed behind the whale’s general direction of travel. If the whale was surfacing erratically and its course could not be
predicted, these mini-transects were abandoned and the vessel kept a safer distance. Our target duration was 5-15 minutes of acoustic prey mapping with each large whale.

**Dive Ventilation Metrics**

My objective was to record at least one full ventilation cycle for each individual in each sighting. If the sighting was of a group that was comprehensibly traceable, I monitored the ventilation behavior of up to three whales at a time. If not, I selected a distinct whale that was easy to track in the crowd (often the lead whale at the front of the school, after Jahoda et al. 2003). Following Dolphin (1987), Wursig et al. (1984) and Dorsey et al. (1989), I did not record breath intervals of calves.

Ventilations were logged into the data entry program within 0.01 minutes of their blow. During a close approach the following events were logged in the data entry program with GPS- and time-stamps:

- Start of surface sequence
- Breath
- Terminal surface / dive stroke
- Robust behaviors: aerials, pectoral slaps, face slaps, tail lobs, tonal blows, etc.
- Sharp changes in direction

Other buttons were available in the case of observer error: Missed breath, missed many breaths, missed surfacing after a dive, cancel breath, cancel dive stroke, clear record, or change assignment of behavior to a different individual. These corrections allowed some breath metrics to be salvaged even when others were lost due to distractions or other problems in the field.
For details on the dive-ventilation metrics that can be derived from these field measurements, refer to Chapter 7.

In case Dolphin’s (1987) presence altered the ventilation behavior of the whales he was tracking, he deleted the first 25 minutes of respiration data. I did not have the time to practice this precaution, though I was very attentive to the response of whales to my presence. If I suspected a reaction to our presence I made I note of it and usually abandoned the sighting.

Each night while sightings were still fresh in mind, all breath intervals from the day were reviewed and corrected as needed.

**Photo identification**

The premise of capture-recapture methods is that population parameters can be estimated by visiting the study population, “marking” a random sample from the population, re-releasing them, then repeating the process on subsequent visits. The proportion of marked individuals you find in your subsequent samples can be used to estimate population size, trends and other demographic features of the population. “Marking” can take on various forms, but in cetacean surveys this usually means taking photographs of unique identifiable features on whales (e.g. ventral surface of humpback flukes) so that you can track an individual’s presence in the study area over time.

Photo-identification is a robust and accepted means of capture-recapture analysis for whales (Stevick et al. 2001, Hammond 1990, 1995 and 2001, and Bigg 1982). Mark-recapture can be advantageous for species like humpbacks and fin whales whose individuals are distinctly marked (Dawson et al. 2008) because the method (1) can produce precise abundance estimates relative to distance sampling, (2) generally has fewer vessel requirements (raised
sighting platform not needed), and (3) can also position researchers to collect other
demographic, behavioral, ecological, and health-related data (Dawson et al. 2008).

We took photographs with Canon 7D cameras (f4.5 100-400mm zoom lens) and
Nikon D200 (f4.5 100-300mm zoom lens). A Canon Rebel XT with a Sigma 100-300mm
lens was also on board as back up.

Associated seabirds

All seabirds observed within 150m of the vessel during close approaches with whales
was logged with the same information as during visual transect effort. These bird detections
were marked with the “with-whales” effort designation to allow seabird-whale association
analyses.

Sample collection

Samples of scat, skin, scales, feathers and other remains at the surface were collected
opportunistically using a telescoping (8-23 ft) Mr. Long-Arm pole with a pool skimmer
attachment modified with 333micron Nitex mesh. These samples were preserved in alcohol,
documented similar to the zooplankton samples, and kept in a freezer (12VDC, Engel 14 quart
fridge-freezer) until they could be transferred to a larger freezer at NCCS headquarters or
Hartley Bay. Samples were then provided to DFO for their DNA and isotope analyses.

When balls of forage fish or adult euphausiids were found near the surface, crew used
a dip net or cast net to attempt collection (after Piatt and Arimitsu 2014).

Passive acoustics
Passive acoustic recording was of highest priority with fin whales. If conditions and location allowed us to shut off the engine, at least 10 minutes of acoustic recording were sought during a fin whale close approach. The engine remained running for humpback and orca sightings unless the group was vocally very active.

Returning to the trackline

Upon completion of a focal follow, the Bangarang would return to the trackline to continue transect surveys. If the vessel were less than 1nmi from the trackline, the team could enter “On Transect” effort and meet the trackline at a 20-degree angle or less (after Kinzey et al. 2000 and Dawson et al. 2008). “On Transect” effort was not resumed until the ship had come up to survey speed and there was no chance of mistaking the previous sighting for a new one. Either all individuals from the sightings were left behind the vessel before resuming searching effort or the locations of remaining subgroups forward of 90 degrees were dutifully tracked.

Until the transect line was reached, effort was “casual” and observers used this time to stow the cameras, eat Gribbell sticks, recuperate and brace themselves for the next transect. Once transect effort was resumed, if a school that had been previously seen and entered as an off-effort sighting was seen again a new sighting event was entered for the school. Both the original off-effort and subsequent on-effort sighting events were retained, with comments in the database and on the sighting forms that they were the same school. School size and composition estimates proceeded as usual.

DATA MANAGEMENT
Each evening, after a day of fieldwork and before the next, the *Bangarang* crew teamed up to accomplish a strategic sequence of data management duties (Fig. 1-19).

1. Eric scans raw RUB file for corrections and creates revised RUB file.
2. Crew downloads and backs up raw images.
3. Eric begins echosounder processing sequence.
4. Eric outputs summary spreadsheets of whale sightings and focal follows.
5. Eric applies sighting metadata to research images.
6. Crew continues image workflow, finishing with the best ID shots for every individual of every sighting.
7. Crew processes these best ID shots into the season's fin whale and humpback whale databases.
8. Eric reviews dive-ventilation metrics from focal follow data for quality control.
9. CTD data are downloaded and processed.
10. Eric reviews echosounder data and makes necessary revisions.
12. Eric backs up RUB, echosounder, CTD and passive acoustic recording files.

**Data entry program**

Field data were entered into an app designed specifically for this study. See Supplementl File 1 for details. Each night in the field, the day's output file was reviewed for errors such as faulty GPS readings, mistaken effort designations, flagged regions of the code, and post-hoc sighting data updates. The original output was archived but a copy was amended...
with corrections. The revised output was then backed up on multiple drives. Summary spreadsheets of focal follow and sightings data were output and reviewed for accuracy.

**Echosounder processing**

See Appendix 5.

**CTD configuration & processing**

See Appendix 3.

**Photograph processing**

Downloading and processing images was a nightly task. The software package Photo Mechanic was used to import images, re-name image files, apply the appropriate metadata, and single out the best research images. Photo-ID catalogs for resident orcas, humpbacks, and fin whales were carried on board. An energy-efficient 12VDC 19” LCD monitor was inset in the salon wall for use in photo identification work.

Metadata for all photos included GPS, effort, block, circuit, research mode, photographer and camera settings. These were assigned using R scripts that time-matched photographs to the day’s RUB output file. Metadata for whale photographs were also automatically assigned including sighting number, group size, behavior and percent confidence of that designation, group composition, general location and all comments logged during the sighting. The best fluke and dorsal shots from every whale sighting were saved to a “Cetogram” folder, which were then passed on to NCCS, DFO and the Guardian Watchmen after each circuit (every two weeks or so).
**In-the-Field Image workflow**

- Take Photos
- Download Photos
- Add research metadata (GPS, visual effort, sighting number, demographics, etc.)
  - Automatic, using subroutines in R and code replacement in PhotoMechanic
- Back-Up Photos on external hard drives
- Prepare cameras for next day of research
  - Clean lens, charge battery, format cards
- Categorize photos (whale, bird, people, scenery, etc.)

**Whale sightings**

- Check sighting metadata assigned to images
- Set aside the best photos for ID
- Check against and update season’s photo-ID catalog for each species
- Set aside new arrivals
- Share with NCCS, Gitga’at and DFO

**Seabird images**

- Large flock data corrections: group size, species, and plumage composition.
- Check with and add to photographic database for study area

**Jelly images**

- Check with and add to photographic guide for study area

**Memorable images:**

- Build upon season's photo album and share with project supporters.

Data backup
All data were backed up nightly. Two 1TB external hard drives were stowed in separate caches on the vessel. One was used for nightly data back up while the other was not used until the end of each circuit. Meanwhile the data always existed in at least two places: either their originating laptop and the one external hard drive or both external hard drives. At the end of every circuit, data entry files are also backed up to Dropbox using internet services in Hartley Bay.

Automatic report generation

Using Sweave (Leisch 2002), a language that weaves R code (R Core Team 2013) with LaTeX programming to generate dynamic and reproducible documents, I developed a means of sharing progress updates with my collaborators and supporters on a real-time basis with little to no work in the field. In addition to these research “dailies”, I was able to automatically generate summaries for each circuit and season of the Bangarang Project.
TABLES

Table 1-1. The eight geographic blocks of the study area. Intensity of Effort (IE) is the percent of the block surveyed with our 300m strip width transects.
<table>
<thead>
<tr>
<th>Block</th>
<th>Area $km^2$</th>
<th>Transects $km$</th>
<th>IE $%$</th>
<th>n</th>
<th>Mean $km$</th>
<th>SD $km$</th>
<th>ID</th>
<th>Location</th>
<th>Position</th>
<th>Depth $m$</th>
<th>Long.</th>
<th>Lat.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caamano</td>
<td>289</td>
<td>46.23</td>
<td>4.8</td>
<td>12</td>
<td>3.85</td>
<td>0.367</td>
<td>3</td>
<td>E. Caamano</td>
<td>Center</td>
<td>145</td>
<td>52.8676</td>
<td>129.2017</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
<td></td>
<td></td>
<td>7</td>
<td>C. Caamano</td>
<td>Center</td>
<td>250</td>
<td>52.9131</td>
<td>129.3054</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td></td>
<td></td>
<td>12</td>
<td>W. Caamano</td>
<td>Sill</td>
<td>60</td>
<td>52.9931</td>
<td>129.5015</td>
</tr>
<tr>
<td>Estevan</td>
<td>153</td>
<td>39.011</td>
<td>7.6</td>
<td>11</td>
<td>3.55</td>
<td>0.287</td>
<td>2</td>
<td>S. Estevan</td>
<td>Center</td>
<td>245</td>
<td>52.9580</td>
<td>129.5313</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td></td>
<td></td>
<td>9</td>
<td>S. Principe</td>
<td>Center</td>
<td>380</td>
<td>53.0306</td>
<td>129.6396</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td></td>
<td></td>
<td>12</td>
<td>Otter Ch.</td>
<td>Center</td>
<td>400</td>
<td>53.0888</td>
<td>129.5015</td>
</tr>
<tr>
<td>Campania</td>
<td>112</td>
<td>51.8</td>
<td>13.9</td>
<td>12</td>
<td>4.32</td>
<td>0.303</td>
<td>2</td>
<td>S. Campania</td>
<td>Sill</td>
<td>265</td>
<td>53.0833</td>
<td>129.3333</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td></td>
<td></td>
<td>6</td>
<td>C. Campania</td>
<td>Center</td>
<td>607</td>
<td>53.1490</td>
<td>129.4039</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td></td>
<td></td>
<td>9</td>
<td>Taylor Bight</td>
<td>Center</td>
<td>500</td>
<td>53.2544</td>
<td>129.4329</td>
</tr>
<tr>
<td>Squally</td>
<td>221</td>
<td>99.69</td>
<td>13.5</td>
<td>23</td>
<td>4.33</td>
<td>0.993</td>
<td>1</td>
<td>S. Squally</td>
<td>Sill</td>
<td>265</td>
<td>53.0833</td>
<td>129.3333</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td></td>
<td></td>
<td>5</td>
<td>C. Squally</td>
<td>Center</td>
<td>607</td>
<td>53.1490</td>
<td>129.4039</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td></td>
<td></td>
<td>12</td>
<td>N. Squally</td>
<td>Center</td>
<td>500</td>
<td>53.2544</td>
<td>129.4329</td>
</tr>
<tr>
<td>Whale</td>
<td>143</td>
<td>39.74</td>
<td>8.3</td>
<td>8</td>
<td>4.97</td>
<td>0.694</td>
<td>3</td>
<td>S. Whale</td>
<td>Center</td>
<td>350</td>
<td>53.1427</td>
<td>129.1261</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td></td>
<td></td>
<td>6</td>
<td>Cornwall Inlet</td>
<td>Side</td>
<td>350</td>
<td>53.2235</td>
<td>129.0707</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td></td>
<td>8</td>
<td>S.E. Wright</td>
<td>Center</td>
<td>498</td>
<td>53.3099</td>
<td>129.1681</td>
</tr>
</tbody>
</table>
Table 1-1. The eight geographic blocks of the study area, *continued*. 
<table>
<thead>
<tr>
<th>Block</th>
<th>Area</th>
<th>Transects</th>
<th>IE</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>ID</th>
<th>Location</th>
<th>Position</th>
<th>Depth</th>
<th>Long.</th>
<th>Lat.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wright</td>
<td>147</td>
<td>42.71</td>
<td>8.7</td>
<td>9</td>
<td>4.75</td>
<td>0.7</td>
<td>1</td>
<td>Lewis Pass</td>
<td>Center</td>
<td>543</td>
<td>53.250</td>
<td>129.3152</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>Grenville Ch.</td>
<td>Center</td>
<td>489</td>
<td>53.3585</td>
<td>129.3091</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>S. Douglas</td>
<td>Center</td>
<td>400</td>
<td>53.4422</td>
<td>129.2065</td>
</tr>
<tr>
<td>McKay</td>
<td>77</td>
<td>32.67</td>
<td>12.7</td>
<td>9</td>
<td>3.63</td>
<td>0.613</td>
<td>2</td>
<td>W. McKay</td>
<td>Slope</td>
<td>375</td>
<td>53.3183</td>
<td>129.0659</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>Fraser Reach</td>
<td>Slope</td>
<td>250</td>
<td>53.3154</td>
<td>128.8981</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10</td>
<td>S. Ursula</td>
<td>Center</td>
<td>375</td>
<td>53.4186</td>
<td>128.9188</td>
</tr>
<tr>
<td>Verney</td>
<td>72</td>
<td>41.98</td>
<td>17.5</td>
<td>11</td>
<td>3.82</td>
<td>0.446</td>
<td>3</td>
<td>S. Verney</td>
<td>Center</td>
<td>275</td>
<td>53.4192</td>
<td>129.1222</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>C. Verney</td>
<td>Center</td>
<td>175</td>
<td>53.4960</td>
<td>129.0767</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>N. Ursula</td>
<td>Sill</td>
<td>90</td>
<td>53.5160</td>
<td>128.9812</td>
</tr>
</tbody>
</table>
Table 1-2. Sampling effort. Columns: “Leg” = sampling period of research season. “Days” = duration of leg, in days; “Km” = kilometers of systematic transect surveys conducted during leg; “Avg. Bft.” = Average Beaufort sea state of systematic survey effort (see Table 1-6); “Modes” = Indicates whether systematic “Transects” and/or oceanographic “Stations” were conducted during a given leg.

<table>
<thead>
<tr>
<th>Year</th>
<th>Leg</th>
<th>Month</th>
<th>Dates</th>
<th>Days</th>
<th>Km</th>
<th>Avg. Bft.</th>
<th>Transect</th>
<th>Stations</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>1</td>
<td>July</td>
<td>7/06 – 7/27</td>
<td>22</td>
<td>245</td>
<td>N/A</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Aug.-Sept.</td>
<td>8/10 – 9/04</td>
<td>24</td>
<td>259</td>
<td>N/A</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>46</td>
<td>504</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2014</td>
<td>1</td>
<td>August</td>
<td>8/11 – 8/28</td>
<td>17</td>
<td>366</td>
<td>1.38</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>September</td>
<td>8/29 – 9/14</td>
<td>17</td>
<td>273</td>
<td>1.15</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>34</td>
<td>639</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>1</td>
<td>May – June</td>
<td>5/24 – 6/14</td>
<td>22</td>
<td>320</td>
<td>1.6</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>June – July</td>
<td>6/15 – 7/10</td>
<td>26</td>
<td>335</td>
<td>1.3</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Late July</td>
<td>7/11 – 7/31</td>
<td>21</td>
<td>346</td>
<td>1.4</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>August</td>
<td>8/01 – 8/26</td>
<td>27</td>
<td>322</td>
<td>1.4</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>September</td>
<td>8/27 – 9/22</td>
<td>27</td>
<td>330</td>
<td>1.4</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>123</td>
<td>1,653</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grand</td>
<td></td>
<td></td>
<td></td>
<td>203</td>
<td>2,796</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1-3. 2013 sampling at oceanographic stations. The number of samples at the station are indicated; this differs from effort tables for the subsequent years because my initial goal in 2013 was to take oceanographic samples at every single trackline turn. This quickly proved unsustainable. Abbreviations: Tot = Number of samples taken within geographic block for a given sampling period ("Leg"). S=South station of geographic block, Ctr= Central station, N=North station. Blocks: CAA = Caamano Sound; CMP = Campania Sound; EST = Estevan Sound; MCK = McKay Reach and south Usula Channel; SQU = Squally Channel; VER = Verney Passage and north Ursula Channel; WHA = Whale Channel; WRI = Wright Sound. * In 2013, a YSI Castaway CTD was used instead of a SBE2plus.

<table>
<thead>
<tr>
<th>Station</th>
<th>CTD*</th>
<th>Secchi</th>
<th>Zooplankton Tows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leg</td>
<td>Block</td>
<td>Tot</td>
</tr>
<tr>
<td>1</td>
<td>CAA</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>CMP</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>EST</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>MCK</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>SQU</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>VER</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>WHA</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>WRI</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>66</td>
<td></td>
<td>62</td>
</tr>
</tbody>
</table>

|         | Leg  | Block  | Tot  | S | Ctr | N | Tot  | S | Ctr | N | Tot  | S | Ctr | N |
| 2       | CAA  | 2      | 1    | 1 | 0   |   | 2    | 1 | 1   | 0 | 1    | 0 | 1   | 0 |
|         | CMP  | 4      | 1    | 1 | 2   |   | 3    | 1 | 1   | 1 | 1    | 0 | 1   | 0 |
|         | EST  | 0      | 0    | 0 | 0   |   | 0    | 0 | 0   | 0 | 0    | 0 | 0   | 0 |
|         | MCK  | 3      | 1    | 1 | 1   |   | 4    | 1 | 1   | 2 | 2    | 0 | 1   | 1 |
|         | SQU  | 3      | 1    | 1 | 1   |   | 4    | 2 | 1   | 1 | 1    | 0 | 1   | 0 |
|         | VER  | 3      | 0    | 2 | 1   |   | 3    | 1 | 1   | 1 | 1    | 0 | 1   | 0 |
|         | WHA  | 3      | 1    | 1 | 1   |   | 1    | 1 | 0   | 0 | 1    | 0 | 1   | 0 |
|         | WRI  | 3      | 1    | 1 | 1   |   | 1    | 1 | 2   | 1 | 1    | 1 | 0   | 0 |
| Total   | 21   |        | 21   | 8 |
| GRAND   | 87   |        | 83   | 27 |
Table 1-4. 2014 sampling at oceanographic stations. See Table 1-3 for abbreviations key. ✓ = Sampling occurred; for zooplankton tows, the number of tows at the station are indicated.

<table>
<thead>
<tr>
<th>Station</th>
<th>CTD</th>
<th>Secchi</th>
<th>Zooplankton Tows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leg</td>
<td>Block</td>
<td>Tot</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>CAA</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>CMP</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>EST</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>MCK</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>SQU</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>VER</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>WHA</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>WRI</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: ✓ indicates sampling occurred; S, Ctr, and N represent the number of tows.
Table 1-5. 2015 sampling at oceanographic stations. See Table 1-3 for abbreviations key. ✓ = Sampling occurred; for zooplankton tows, the number of tows at the station are indicated.

<table>
<thead>
<tr>
<th>Station</th>
<th>CTD</th>
<th>Secchi</th>
<th>Zooplankton Tows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leg</td>
<td>Block</td>
<td>Tot</td>
</tr>
<tr>
<td>1</td>
<td>CAA</td>
<td>2</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>CMP</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>EST</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>MCK</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>SQU</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>VER</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WHA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WRI</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>21</td>
<td>22</td>
</tr>
<tr>
<td>2</td>
<td>CAA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>CMP</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>EST</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>MCK</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>SQU</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>VER</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WHA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WRI</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>4</td>
<td>CAA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>CMP</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>EST</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>MCK</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>SQU</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>VER</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WHA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WRI</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>23</td>
<td>24</td>
</tr>
<tr>
<td>5</td>
<td>CAA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>CMP</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>EST</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>MCK</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>SQU</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>VER</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WHA</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td></td>
<td>WRI</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>GRAND</td>
<td>95</td>
<td>92</td>
<td>94</td>
</tr>
</tbody>
</table>
Table 1-6. Description of Beaufort sea state categories, adapted from Bowditch (1966).

<table>
<thead>
<tr>
<th>Beaufort Sea State</th>
<th>Knots</th>
<th>Breeze description</th>
<th>Sea conditions</th>
<th>Probable wave height (ft)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0-1</td>
<td>Calm</td>
<td>Sea smooth and mirror-like</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>1-3</td>
<td>Light air</td>
<td>Scale-like ripples without foam crests</td>
<td>¼</td>
</tr>
<tr>
<td>2</td>
<td>4-6</td>
<td>Light breeze</td>
<td>Small short waves; crests have a glassy appearance and do not break.</td>
<td>½</td>
</tr>
<tr>
<td>3</td>
<td>7-10</td>
<td>Gentle breeze</td>
<td>Large wavelets; some crests begin to break; foam of glassy appearance. Occasional white foam crests.</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>11-15</td>
<td>Moderate breeze</td>
<td>Small waves, becoming longer; fairly frequent white foam crests.</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>17-21</td>
<td>Fresh breeze</td>
<td>Moderate waves, taking a more pronounced long form; many white foam crests; there may be some spray.</td>
<td>6</td>
</tr>
<tr>
<td>6</td>
<td>22-27</td>
<td>Strong breeze</td>
<td>Large waves begin to form; white foam crests are more extensive everywhere; there may be some spray.</td>
<td>10</td>
</tr>
</tbody>
</table>
Figure 1-1. Study plan. A grid of 24 oceanographic stations (dots) between which environmental and visual transect surveys (lines) were conducted.
Figure 1-2. Systematic trackline effort during each sampling period of each field season.
Figure 1-3. The research vessel Bangarang.
Figure 1-4. Position of the 24 oceanographic stations visited in each sampling period.
Figure 1-5. Drop rates of all 2014 SBE25plus CTD casts.

Figure 1-6. The YSI Castaway CTD used in 2013, here wielded by Bangaranger Will Watson.
Figure 1-7. Trial of observer error in Secchi depth readings (n=25) from 2013 (see text). In this presentation, non-overlapping notches around the means in the neighboring boxplots indicate a strong likelihood that the differences are significant (One-way ANOVA, F=53.82 df(2,72), p < 0.0001)
Figure 1-8. A-D. The Heron-Bangarang plummet sampler in various stages of stowage, deployment and retrieval. E. The Heron-Bangarang net as rigged in 2013.
Figure 1-9. Calibration of zooplankton net’s flowmeter in September 2014.

Figure 1-10. Descent rates of Heron-Bangarang plummet net casts in 2014. Average fall rate was $0.96 \pm 0.14 \text{ m s}^{-1}$ (n=40).
Figure 1-11. Results of pre-season two calibration of the towed hydrophone array's depth sensor.

\[ y = 0.1379x + 3.8410 \]
\[ r^2 = 0.9965 \quad p < 0.0001 \]

Figure 1-12. Depth of 100m towed hydrophone array at various payout distances with a variety of weights.
Figure 1-13. Layout of systematic survey tracklines.
Figure 1-14. Left: Histogram of vessel speed (median=4.7 knots) during systematic transect effort. Right: Box plot of the same data categorized by the eight geographic blocks of the study area, each of which have distinct tidal current regimes and wave heights that influence the mean and variance of transect speed.

Figure 1-15. Strip-width zone design. A 300m survey strip was centered about the vessel as it traverses the trackline (dotted line). On each side of the vessel, the strip was split into two distance zones: 0-75m (Zone 1) and 75-150m (Zone 2).
Figure 1-16. Histogram of distances to whale sightings from transect surveys in 2014.

Figure 1-17. A histogram of Beaufort sea states experienced in 2014, logged every 10 seconds during transect effort.
Figure 1-18. Jelly taxa surveyed for during systematic visual transect effort.
Figure 1-19. Workflow of nightly data management tasks.
CHAPTER 2:

Oceanography of the Kitimat Fjord System

Eric M. Keen, Kim-Ly Thompson, Chris R. Picard
ABSTRACT

The Kitimat Fjord System (KFS), centered at 53°N and 129°W, contains the marine territories of the Gitga’at and Haisla First Nations, the confined channel portion of several proposed shipping lanes and proposed critical habitat for several endangered or threatened marine species. This fjord complex is nested within the Kitimat Ranges of the Great Bear Rainforest, part of the largest temperate coastal rainforest in the world. An uncommon attribute of this fjord system is its large islands that compartmentalize the fjord into a network of channels. Spanning the coastal boundary between ocean and the coastal ranges, the KFS houses strong, seasonally mediated offshore-inshore gradients in climate and oceanography. Water movements are influenced by seasonal climate patterns and punctuated storm events on the adjacent shelf, which are strongest in autumn. I use three summers of oceanographic sampling (2013 – 2015) to describe recent summertime oceanographic conditions and place them within the context of previous literature and region-scale patterns in climate. Results emphasize the coupling between the distribution of water features within the fjord system, such as thermocline depth, and offshore patterns in storm forcing. The effect of the “warm blob” temperature anomaly is seen in 2014 and 2015 temperature and oxygen data.

INTRODUCTION

My study area, the Kitimat Fjord System (KFS, Fig. 2-1) is among the better studied systems of British Columbia’s fjordland, but the only oceanographic publications date to the late 1970s and early 1980s. In this chapter I first review the literature regarding the KFS my study area, the Kitimat Fjord System, within its regional context of geology, meteorology and oceanography. Second, I report on three summers of oceanographic samplings (2013 – 2015)
within the KFS. When interpreted within the contexts of the historical records and contemporary patterns in regional climate, our data portray a fjord system whose habitat features are broadly predictable with classic principles in fjord oceanography but whose details are functions of local stochastic processes and regional patterns in climate.

STUDY AREA

Regional Context

The coastal corridor of British Columbia (BC) is a broad zone of protected waters and labyrinthine inland passages. Contiguous with the fjord-gouged shoreline of the Gulf of Alaska (GOA), it is a productive ecosystem of more than 27,300 km in shoreline length (Sebert and Munro 1972, Thomson 1981). It contains the largest coastal rainforest in the temperate world, supports multi-million-dollar fishing and ecotourism industries, and provides subsistence for many coastal First Nations (Turner 2000).

Geography

The orientation and bifurcation of British Columbia fjords, including that of the study area, are a result of the province's geologic history. During the last glacial maximum, ice flowed from the coastal range to the sea along faultlines and other weaknesses in the bedrock (Syvitski et al. 1987). Like most of western North America, the British Columbia coast has been an active continental margin for ~700 million years (Cannings et al. 2011). Varying relative plate vectors throughout this time have created a complex provincial geology of thrust belts, volcanoes, granitic batholiths and mountain ranges. In the Cenozoic, BC's margin changed from an area of consistent subduction to one of transcurrent faulting and the periodic
subduction of bands of ancient archipelagos. The juxtaposition of oceanic and intra-oceanic island arc terranes, separated by faultlines trending both parallel and perpendicular to the continental margin, characterize the geology currently manifest throughout the BC coast (Cannings et al. 2011).

Most recently (approx. 38 mya), motion between the North American and Pacific plates shifted, instigating crustal extension in much of western North America. The decompression resulted in expansive graben basins and fault zones ranging from San Andreas to Denali and including BC’s Queen Charlotte region (Cannings et al. 2011).

British Columbia's south coast stretches from the Strait of Juan de Fuca to the tip of Vancouver Island, the region's most prominent feature. Between this island and the coastal ranges of the mainland lay a maze of passages gated throughout by tidal rapids. These tight corridors open up to the north into Queen Charlotte Strait then into Queen Charlotte Sound, which in turn opens north of Vancouver Island to the north Pacific.

The central coast is a densely packed archipelago with a continuous waterway (the Inside Passage) that separates outer islands from the mainland. This otherwise closed coastline is divided into discrete regions by several broad entrances (Fitz Hugh, Milbanke, and Laredo Sounds), each of which has branching fjord inlets cutting deep into the mainland. Offshore of this fjordland, the broad and shallow continental shelf splays westward to the Haida Gwaii archipelago, creating a bounded but stormy area known as Hecate Strait.

North of Princess Royal Island, an enormous island encircled by deep fjord channels, two parallel bands of nearshore islands create two protected passageways north to the Prince Rupert area (and onward to the Alaska border), with some large entrances intermittently uniting the passages. Just north of Princess Royal Island are the Douglas and Gardner fjord systems, known collectively as the Kitimat Fjord System. These fjords open to Hecate Strait in the broad amphitheater of Caamano Sound. This area's intracoastal zone, from Caamano to the
mouths of Douglas and Gardner fjords, comprises the marine territory of the Gitga'at First Nation and this project's study area.

The central and north coasts are fjordlands, and as such their coastal boundaries consist of three subregions (Mackas 1992): the inner shelf (including the fjords), the shelf break and slope, and the blue waters offshore. As fjords, the coastal inlets are semi-enclosed systems restricted from interactions with open waters by shallow sills and narrow entrances. The BC shelf's shallow basins represent a hybrid of oceanic and neritic environments (Thomson 1981). Water properties within these inlets are quite distinct from more open shelf waters because of their isolation (Burrell 1986, Crawford et al. 2007; see below).

*Meteorology*

In BC waters the strongest environmental signal is the annual seasonal cycle, governed by the interaction of stacked oceanographic and atmospheric systems (Mackas 1992). Over the offshore waters of BC there are two juxtaposed atmospheric systems: the subtropical North Pacific High and, to the north, the subpolar Aleutian Low. The North Pacific high is dry, stable and fair weather. Clockwise winds surround the North Pacific High, deflected to the right by Coriolis forces. Counter-clockwise winds surround the wet and stormy Aleutian Low.

Stormy weather occurs at the transition zone between these two systems, which is generally a latitudinal front located somewhere along the BC coast. The front drifts north and south throughout the year, orchestrating patterns in coastal winds, storms and temperature. These winds influence oceanic gyres and currents.

*Coastal oceanography*
Related to the meteorological boundary between the Aleutian Low and North Pacific High is an oceanographic transition zone between two gyres, the southern East Pacific Gyre and the northern Alaska Gyre. This gyre boundary oscillates north and south according to seasonal changes in climate and basin-scale circulatory processes (Crawford et al. 2007). At the boundary is the slow (5-10 cm s\(^{-1}\)), east-flowing North Pacific Current (also called the Subarctic Current). When this current reaches the BC coast it splits to contribute to both the equatorward California Current upwelling system and the poleward Alaska Current downwelling system, which itself is an extension of the California Countercurrent (Mackas et al. 2000). At the split waters meander and eddy.

When these two gyres shift north or south, the location of their split will change, and in turn the direction of current flow at a point on the coast may change. This is significant to regional patterns in productivity, since current direction determines upwelling rates, which in turn determines nutrient availability for phytoplankton communities.

Over large scales in space and time, BC coastal currents are dictated by regional oscillations in oceanic gyres and atmospheric systems. On the mesoscale these larger processes are interrupted by both terrigenous freshwater inputs and also episodic anticyclonic eddies, which are induced by strong currents flowing around topography offshore. On smaller spatial scales, currents are governed by coastal morphology and the bathymetry of the continental shelf (Crawford et al. 2007). On the BC coast, large tidal currents tend to dominate the water movement over time scales of hours, though the oscillatory motion of the ebb/flood cycle can result in little net movement (Crawford et al. 2007).

Regional upwelling cycles determine across-shore patterns in salinity and temperature. A cross-shelf salinity gradient is present most of the year (Royer 1998), strongest just before the onset of the upwelling season (April-May). In the late winter onshore-flowing currents confine freshwater discharge to coastal inlets and create the lowest salinities of the
year (Freeland et al. 1980, Mackas 1992). The lowest surface nutrient concentrations on the shelf occur at the end of the winter current regime, in March or April in Juan de Fuca Strait (a rainwater-driven system) and May-June in all snow-melt-driven regions to the north and on the mainland (Mackas 1992, Thomson 1981).

In late spring upwelling signals begin on the continental shelf, where they remain strongest throughout the summer season. After the transition to upwelling, freshwater discharge is pulled out to sea and high-salinity water is entrained with it from below, reducing overall coastal salinity (Mackas 1992) but increasing salinity within inlets. As upwelling establishes, surface temperatures decrease. In late fall upwelling weakens and freshwater discharge abates, slowly returning the coast to winter conditions of higher salinities over the shelf and lowest salinities within fjords.

Freshwater drainage integrated along the fjordland coast creates an inshore-offshore salinity gradient analogous to those found within individual fjords. As upwelling pulls this freshwater lens to sea, bottom water flows shoreward in compensation. The resulting hydraulic gradient is a large-scale analog to the estuarine circulation occurring within the individual fjords that feed the coast. This hints at the fractal nature of geography and oceanography found on the BC coast as one scales up from fjord to fjordland to coastline (Thomson 1981).

**Fjord oceanography**

**General**

Syvitski et al. (1987) defined a fjord as "a deep, high-latitude estuary which has been (or is presently being) excavated or modified by land-based ice." Fjords are estuaries according to the definition of Cameron and Pritchard (1963): a "semi-enclosed body of water
having a free connection with the open sea and containing a measurable quantity of sea salt”.

A typical temperate fjord is a deep U-shaped basin, the vestige of scouring from seaward-flowing glaciers in the late Pleistocene, with a seafloor of fine sediment and mud, a glacier or snow-driven river at its head, and an underwater ridge or sill across the mouth created by sediment deposition at the glacier’s terminal moraine (Pickard 1967, Pickard and Stanton 1980).

Sills are barriers to the exchange of nutrients, salinity and oxygen in the deep waters of fjords. Sills also contribute to the retention and concentration of river-borne nutrients within fjords, which is a primary cause of their high productivity (Thomson 1981) and disproportionately large role in global organic carbon sequestration (Smith et al., 2015). Sills can cause sharp gradients in water properties at fjord mouths (e.g., 2 psu differences in salinity at 100m are not uncommon at the sills of BC’s fjords; Thomson 1981).

Silled fjords are a phenomenon of mid-to high-latitude coastlines worldwide, occurring at temperate and subpolar latitudes in both the Atlantic and Pacific oceans (Mann and Lazier 1996). Due to their crenellated and complex topography, fjords comprise a major percentage of the world's coastline (Syvitski et al. 1987) and play a governing role in the seasonal productivity of nearshore boreal waters (Pearson 1989). As geologically young land features, fjords remain in a state of fundamental upheaval, subject to interglacial rebound, glacial scouring and massive sediment loading (Miller et al. 1982). Strong tidal, diurnal and seasonal environmental cycles induce further variability in water mixing, terrigenous inputs and precipitation (Hoskin and Burrell 1972). The inordinate heterogeneity of all aspects of fjord ecosystems is thought to yield unique patterns in ecology, diversity, and productivity (Matthews and Heimdal 1980).

Estuarine circulation is an ecologically important process in fjord estuaries. Bouyant freshwater discharge enters the fjord from the glacier or river at its head and exits in a shallow
surface layer. As this fresh lens progresses seaward along the surface it entrains the saline water underlying it. A slow, deep inflow of water must compensate for this upward entrainment of seawater. A two-way flow is therefore established: a seaward surface flow and its landward bottom countercurrent. This process can establish stark gradients in water column density, salinity, oxygenation, and nutrient load (Carstens 1970).

Estuarine flow is strongest during periods of high runoff, but can be also be modulated by tides (Masson and Cummins 2000), winds and oceanographic conditions offshore over short time periods (Pickard and Stanton 1980). For example, estuarine-driven surface currents in Burke Channel, BC, can reach speeds of 100-200 cm s\(^{-1}\), with a significant reverse flow below the halocline (Crawford et al. 2007).

Tidally accelerated flows of stratified estuarine waters over sills and other channel constrictions and seafloor features can produce internal waves (Cummins et al. 2003). Internal waves of both short period (minutes) and longer period (hours) are common features of Pacific fjords (Pickard and Stanton 1980). Vigorous tidally induced mixing occurs in the bottlenecks within coastal inlets, where waterways are constricted either vertically by sills or laterally by narrowing channel walls, or both. As waters are pulled over them and into the inland basin by estuarine circulation, displacing deeper water upwards, extensive mixing and upwelling can occur.

Phenomenal motionless internal wave trains can develop over some fjord sills, such as those in BC's Knight Inlet (Cummins et al. 2003) and Verney Channel (study area, pers. obs.). Such waves are most conspicuous in the oscillating position of the halocline (Pickard and Stanton 1980), but they sometimes develop surface signatures too (Fig. 2-2; Crawford et al. 2007, Cummins et al. 2003). All of these tidally induced features mix waters, accumulate nutrients, aggregate plankton, and attract a cadre of predators (Gilmartin 1964, Crawford et al. 2007).
Their remoteness and ruggedness aside, Syvitski et al. (1987) remarked that fjords are "perfect natural oceanographic and geologic laboratories. Source inputs are easily identified and their resulting gradients are well developed". Isolated from the continental shelf by narrow entrances and shallow sills (Crawford et al. 2007), these isolated environments allow marine scientists to approach systemic questions pseudo-experimentally in a natural setting. This offers the same conveniences that islands afford terrestrial ecologists, bequeaths similar insights into the ecological rules that govern isolated communities, and brings the need to assess human impacts in marine systems within reach of limited scientific resources. However, due to their remote and rugged location, fjord systems are considered one of the least understood coastal habitats on earth (Pearson 1989).

*British Columbia's fjordland*

North America's northwest coast, including Washington, British Columbia, and southeast Alaska, is one of the earth's 9 fjordlands, containing approximately 390 of its 1900 identified fjords (Syvitski et al. 1987). British Columbia's coast extends 850km from Washington to Alaska (Pickard and Stanton 1980), but the fjordland's complexity results in a shoreline length of over 27,000 km (Thomson 1981). Forty-two of the province's mainland inlets are 16km or more in length (Pickard 1961). The mean width of these fjords ranges from 0.6 to 15 km (Pickard and Stanton 1980).

The BC fjords can be categorized as mainland or insular fjords (Syvitski et al. 1987) and further as high, intermediate or low discharge (or runoff) inlets (Crawford et al. 2007). The amount of freshwater that flows into an inlet from its rivers depends on the drainage area, the time of year, and whether the rivers are fed primarily by rainfall or snow-melt (Thomson 1981). Rain-fed inlets on islands further south (e.g. Vancouver Island) reach their maximum discharge volume in late-winter, at the peak of the winter storms. In contrast, large mainland
inlets further north, which drain the coastal ranges, reach their discharge peak at the height of the snowmelt season, beginning in May. Summer snow-melt runoff can be an order of magnitude greater than winter rain-fed volume (Thomson 1981). The largest discharge of meltwater will not arrive until the summer long after the spring rains have grown rare (Freeland et al. 1980, Mackas 1992).

Within fjord inlets the variability of water temperatures depends on the intensity of solar heating as well as the degree of vertical mixing by wind, tide and convection. Surface salinities are more governed by variability in the estuarine circulation: low during periods of comparatively large runoff and high during periods of relatively low runoff (Thomson 1981).

Salinity and temperature in fjords are thought to exhibit an annual cycle: In February, after a winter of extensive and deep mixing by storms, winds and convection, surface waters are found to be highly saline and very cold while bottom waters are at their freshest and warmest (MacDonald et al. 1982). All properties are more homogenous throughout the water column. In spring, as the water column becomes more stratified and estuarine circulation is reestablished, surface salinities decrease and deepwater salinities increase. Estuarine circulation is well established by early summer, at the height of snow-melt (Thomson 1981, Freeland and Farmer 1980). The summer peak in estuarine circulation brings about annual minima in surface salinities and maxima in deepwater salinities. In late autumn, there is strong near-surface stratification: a shallow, brackish (< 26 psu) upper layer and a deep, cold, near-oceanic (> 32 psu) bottom layer. Iso-, thermo-, and haloclines are sharp (e.g., in Knight Inlet, the thermocline is typically 2-5m thick; Trevorrow et al. 2005), thought not always overlapping (Coyle and Pinchuk 2005). As winter sets in and mixing intensifies, the pattern reverses back to February conditions.

In BC fjords, surface DO values are usually at or above saturation (especially during spring plankton blooms; Crawford et al. 2007). Oxygen levels tend to decrease with depth
(Crawford et al. 2007) but the regularly renewed bottom waters are rarely, if ever, anoxic (Pickard and Stanton 1980; unlike other fjordlands where bottom anoxia can be common, Syvitski et al. 1987). Vertical maxima and minima in dissolved oxygen are common but do not show any strong pattern (Pickard 1961).

Despite large amounts of suspended sediments and tannins in the freshwater discharge that restricts light penetration in fjord waters, high phytoplankton levels can be maintained throughout an inlet (Gilmartin 1964, Hooge and Hooge 2002). High average chlorophyll concentrations occur through the spring, summer, and early autumn on the inner shelf (Mackas 1992).

**Kitimat Fjord System**

*Morphology*

Like all of British Columbia's fjords, the Kitimat Fjord System (Fig. 2-1) was born during the ice retreat following the most recent glacial maximum. This system's glacier began to withdraw up Douglas Channel approximately 13,000 years before present (Bornhold 1983). Two thousand years later, after a series of minor advances and retreats, the ice had withdrawn past Kitimat, the town now located at the inland-most extent of Douglas Channel. In the millennia since, sediment deposition has continuously been filling the basins of Douglas Channel and Gil Basin (Bornhold 1983).

Fjords of the Kitimat system have a typical morphology, with steep bedrock walls and relatively smooth sediment-floored basins separated by high-relief sills (Pickard 1961, Pickard 1967, MacDonald et al. 1983). Douglas Channel, Gardner Canal, and Surf Inlet are the primary fjords that feed the system (Pickard 1961). Douglas is 45 nmi long, 1.9 nmi mean width, 330 m mean depth, 455 m max depth, 210 m sill depth (Pickard 1961). Gardner is 70
nmi long, 1.0 nmi mean width, 275 m mean depth, 500 m max depth, with a outer sill depth of 67 m (Pickard 1961).

Mean channel depth is highly variable but all are deeper than the adjacent continental shelf in Hecate Strait. The channels of Gil Basin (Squally, Wright and Whale) are among the deepest inlets on the coast (MacDonald et al. 1983; maximum depth is 700 m). Each of the fjord system's channels is bookended and/or interrupted by dramatic bottlenecks and seafloor sills. Sills divide the system into 3 major marine basins (MacDonald et al. 1983): (1) Gardner Basin within Gardner Canal, a side channel of the Kitimat-Douglas Channel fjord separated by a 100 m sill. (2) Maitland Basin, the northern half of Douglas Channel including Kitimat Arm and Devastation Channel, and (3) Gil Basin, separated from the outermost waterways by a 200 m sill at Otter Channel and a broad 170 m sill at the entrance to Caamano. Gil Basin is the deepest and most complex of these three basins. Two of the system's shallowest sills occur on the east and north corners of Gribbell Island: 31 m and 35 m sills crossing Verney Passage and Ursula Channel, respectively, and a 130 m sill at the entrance to Fraser Reach/Princess Royal Channel.

These seafloor features, when combined with large tidal changes, set the stage for a highly stratified but highly dynamic water column continuously disturbed by internal tidal waves, which in turn flush deepwater nutrients and biota into the upper water column.

Oceanography

The Kitimat Fjord System connects oceanographically to the rest of the Pacific coast at four points, the broadest and most important being the entrances at Campania Sound and Otter Channel. The other two connections, Grenville Channel and Fraser Reach/Princess Royal Channel, are narrow and long connections to adjacent fjord systems (MacDonald et al. 1983).
Pickard (1961) classified Douglas Channel and Gardner Canal, the two main fjords feeding the KFS, as "A-1" inlets, which is a fjord classification characterized by particularly low surface salinities at the head (MacDonald et al. 1983). The seven drainage basins of the KFS (comprised of 29 watersheds, Fissel et al. 2010) result in its classification as a high-discharge system, a designation that suggest strong oceanographic gradients from inshore to off and from surface to seafloor (Freeland et al. 1980, MacDonald et al. 1983, Crawford et al. 2007). Gardner Canal discharge is among the highest of BC's fjords (second to Portland Inlet of the Nass River; Pickard 1961). The freshwater lens reaches depths of 9.6 m in Gardner Canal and 3.6 m in Kitimat Arm (Fissel et al. 2010). This lens thins to less than 1 m in the system's outer channels.

KFS waters are circulated by a combination of three processes: estuarine circulation (forced by freshwater discharge), wind stress (e.g., katabatic outflows) and tides (MacDonald et al. 1983). The relative importance of each varies according to location and time. The former two are responsible for a vast majority of fjord water communication with outer waters. Tidal oscillations do not function as a strong advective agent (MacDonald et al. 1983). Water movements are further influenced by seasonal patterns and punctuated storm events on the adjacent shelf (MacDonald et al. 1983).

Regardless of the local prevailing force, currents tend to be aligned with the axes of the channels themselves; cross-channel currents are relatively negligible (Fissel et al. 2010). This is less true in the outer, broader channels of fjord systems such as Caamaño Sound where currents can exhibit a much greater range of directions (Fissel et al. 2010).

As a high-runoff system, the KFS is expected to have well-developed estuarine circulation (MacDonald et al. 1983). Average net flows are observed to be seaward near the surface and generally landward at depth (Fissel et al. 2010). Typical surface currents are 15-30 cm s⁻¹ (Fissel et al. 2010). The highest surface currents, over 1 m s⁻¹, occur in seaward
portions, including Campania and Caaamano Sounds (Fissel et al. 2010). Bottom currents in
the system appear to be consistently vigorous, so much that side-channel sediment deposition
is dramatically reduced in the waterways connected to Gil Basin (Bornhold 1983).

Due to the height of surrounding hills, winds tend to be directed up or down channels
rather than across (MacDonald et al. 1983). Depending on their orientation winds in fjords can
serve to temporarily slow, stop, or exacerbate estuarine circulation. When freshwater
discharge is minimal, strong down-inlet winds can maintain a two-way flow similar to
estuarine circulation (Dodimead and Herlinveaux 1968; Herlinveaux 1973). Such winds,
which are especially common in winter, can also deepen the mixed layer (Thomson 1981,
Freeland and Farmer 1980). The katabatic winds of winter can drive surface waters seaward at
such rates that both bottom and intermediate waters are pulled into BC inlets (MacDonald et
al. 1983).

As a result of the system’s relatively deep sills and vigorous estuarine and wind-drive
circulation, bottom waters in the three basins of the KFS undergo regular renewals (perhaps
two replacements per year) and there are no records of anoxic conditions being observed
(MacDonald et al. 1983). In Gil Basin, the strong estuarine circulation and northwest winds of
June – October completely flush bottom waters (MacDonald et al. 1983).

Tides and internal waves

Tidal currents and sea level changes in fjords can be dramatic, with a normal tidal
range of 4-6m (Chyna Sea Ventures 2014). A 6.2 m tide has been observed in the Gitga’at
Territory (Fissel et al. 2010). An 8.0 m tide was observed nearby in Principe Channel (Fissel
et al. 2010).

Steep seafloor sills within the KFS can be very shallow; the sill at Amy Point at the
north tip of Gribbell Island is less than 30m deep. Flooding and ebbing tides pump water over
these sills, creating underwater turbulence that often sorts into internal waves. Gitga’at waters have particularly excellent examples of internal wave processes (Fig. 2-2). These features are of great interest to oceanographers and ecologists because they contribute to mixing that brings nutrients to the surface, thus driving productivity, and aggregate phytoplankton and zooplankton which are then exploited by predators.

**Previous Research**

Few of BC’s fjords have been studied in any detail, the exceptions being Knight Inlet, the Bella Coola estuary (Fitz Hugh Sound/Burke Channel), Rivers Inlet (Whitney 2002), Rupert-Neroutsos Inlets, and to a lesser extent the Kitimat system (Webster 1980, Narayana 1980, MacDonald et al., 1982, MacDonald et al., 1983). Knight Inlet, particularly the hydraulic flow over its sill, has been particularly well studied (Crawford et al. 2007, Cummins et al. 2003, and others).

Most existing literature on the KFS is a result of human use assessment. Kitimat, the port at the head of the fjord system, has been targeted for industrial development since the 1970s (Narayanan 1980). As a result physical oceanographic surveys have occurred in the area with emphasis in Douglas Channel (Narayanan 1980, Bornhold 1983, MacDonald et al. 1983, Fissel et al. 2010).

Several literature reviews and unpublished data from the KFS were compiled during recent environmental impact assessments for petroleum product trafficking proposals and climate change (Simpson 1997, Clarke et al. 2006, Crawford et al. 2007, Enbridge 2010a and b, Fissel et al. 2010, Jacques Whitford 2010, Joint Review Panel 2013a and b, Okey et al. 2012, Thomson et al. 2012, Watson et al. 2010, Wheeler et al. 2010). These include reports specific to cetacean activity in the area (Pilkington et al. 2011a and b, Wray et al. 2011). Nearly all local bird studies have been focused on the port of Kitimat (Norecol 1991) and the
Kitimat Valley area (Hay 1976, Horwood 1992). The only pelagic bird survey of the Kitimat Fjord System, to my knowledge is Jacques Whitford (2010). Mather et al. (2010) modeled marbled murrelet (*Brachyramphus marmoratus*) habitat suitability on the BC coast, including the Kitimat Fjord System. Seabird abundance reports for nearby offshore nesting sites provide some context for probable seabird use of the KFS (e.g., Reimchen and Douglas 1987, Mazur and Wilkin 2003)


In the last decade, the KFS has been discussed in several critical habitat evaluation papers for threatened cetacean species (e.g., Ford 2006; Fisheries and Oceans Canada (FOC) 2008 and 2013; Nichol and Ford 2011; Ford et al., 2013). Ashe et al. (2013), an abundance estimate of the "summer resident" humpback population, is the most recent publication regarding cetacean activity in the study area. Other marine mammal papers that specifically discuss populations in the KFS include Williams and Thomas (2007), Williams and O’Hara (2010), Williams et al. (2011), and Williams et al. (2013).

**METHODS**

Details of data collection methods are provided in Chapter 1. In summary, in the summers of 2013 - 2015, whale and ecosystem surveys were conducted aboard the *RV*
**Bangarang**, a 12 m motorsailer, with a team of three researchers. 2,795 km of transect effort were logged over the course of 9 monthly surveys. In each survey we visited a grid of oceanographic stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys.

During transects, surface water temperature and salinity were sampled at 0.3m depth every two seconds with a Seabird Electronics (SBE) 45 thermostalinograph (TSG). At each station we performed a Secchi disk reading (8 replicate casts from the same observer) and a water column sample (down to 250m, seafloor permitting) with a SBE 25plus CTD with additional fluorometer and dissolved oxygen sensors.

Field methods were largely identical across years with the following relevant exceptions. These are explained fully in Chapter 1:

- In the July leg of 2013, CTD and secchi casts were made at approximately 9 stations within each block (total of 72). This was found to be unsustainable, so in the August leg a minimal sampling scheme was tested, with 1 to 3 casts in each block. By the start of the 2014 season, the grid of 24 oceanographic stations had been determined.
- In 2013, a slightly different method was used for Secchi disk readings. Rather than have a single observer take all 8 readings as in 2014 and 2015, three to four crewmembers would each provide a single reading.
- In 2013 we used a YSI Castaway CTD rated to 100m, with no additional sensors. In 2014 and 2015 we used the SBE 25plus with additional sensors (see below). The performance of these two CTDs was compared in side-by-side trials (Appendix 4).
- 2013 was a test season for acoustic backscatter collection, and those data will not be reported on here.

The SBE 25plus CTD and its additional sensors measured temperature, salinity, density, chlorophyll-a, and dissolved oxygen concentration. From these measurements the
following variables were calculated: mixed layer depth, which indicates the degree of near-surface mixing due to waves and runoff, was calculated as SST - 0.8°C (Fiedler 2010); thermocline was calculated with the differencing technique used in Reilly & Fiedler (1994) and Fiedler & Talley (2006) and outlined in Fiedler (2010); stratification was calculated as the density difference between the surface and a standard depth (Behrenfield et al., 2006), in our case 50m due to regions of shallow seafloor within the study area. For temperature and salinity, mean values were calculated for the “upper” water column (depths above the thermocline) and the “bottom” water column (depths below thermocline).

Backscatter and oceanography variables were interpolated to a 0.25 km² grid of the study area’s marine habitat. Interpolation was performed using inverse path-weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell, accounting for land obstruction (R package ipdw, Stachelek 2015).

RESULTS

Note: due to different sampling protocols, data from 2013 were excluded from all summary statistics. Where appropriate, qualitative descriptions of 2013 dynamics are included. Otherwise, these results primarily detail the field efforts of 2014 and 2015.

Seafloor

Mean seafloor depth within the surveyed area is 329 ± 164 m (max. 674), and mean seafloor slope is 143 ± 140 m km⁻² (min. 4, max. 648).

Salinity
Mean surface salinity was 26.56 ± 2.79 psu (min. 13.08, max. 31.73; Fig. 2-3). In all sampling periods, the most saline waters were in the outer channels of Estevan and Caamano Sounds. Cross-sections (Figs. 2-14 and 2-16) demonstrate that the fjord system’s freshwater lens thins out as it flows to sea. In most sampling periods, this lens (defined here as < 28 psu) is not detected further out than the confluence of Squally Channel and Campania Sound (though in August 2014 it reached all the way out to Caamano Sound).

Mean surface salinity gradient was 0.94 ± 1.17 delta psu km⁻² (min. 0.00, max. 8.96). The widest range of measurements within the study area were taken in July 2013 (8.87 – 31.58 psu) and August 2015 (11.59 – 31.36 psu). Offshore-inshore gradients were only weakly apparent in June and July 2015 and not evident in other months of the study (Fig. 2-3). The front between high salinity outside and relatively low salinity inside typically occurred at the southeast and northwest tips of Gil Island, where Gil Basin restricts at Whale Channels’ south entrance and Lewis Passage, respectively. Vast, turbulent tidal mixing was commonly observed at these locations.

Subsurface salinity (between thermocline and surface, measured with the CTD) exhibited a more persistent offshore-inshore gradient than surface measurements with the thermosalinograph (TSG), but otherwise reflected an exacerbated version of the surface conditions described above (Fig. 2-4). Bottom (sub-thermocline) salinity exhibited a noticeable gradient in some but not all sampling periods; bottom gradient was weak in August 2015, when it was strongest at the surface. Interestingly, the least saline waters were found in south Douglas Channel for subsurface waters but in Verney Passage for bottom waters. Verney drains Gardner Canal, the other major fjord in the system. Also noteworthy is that bottom water salinity is highest not in the outermost channels (as was the case in surface waters) but in the Gil Basin channels of Squally and Campania. This may be a function of
depth; Squally is the deepest channel in the fjord system while the outer sounds of Estevan and Caamano are the shallowest.

In both upper and bottom waters, fjord system salinity increased substantially from August to September 2015. September 2015 was the month with the highest and most homogenous surface salinity (mean 26.92 psu, max. 31.73), perhaps due to mixing by the early onset of autumn storms. In 2014 and 2015, September surface salinity was minimal not in the innermost channels, but in Whale Channel and Wright Sound (which communicate directly with Douglas Channel, the largest fjord of the system).

Temperature

Mean surface temperature was 13.18 ± 1.29 °C (min. 9.5, max. 19.05; Fig. 2-3). September 2015 was the month with lowest surface temperatures (mean 12.37 °C). The highest surface temperatures occurred in July 2015 (mean 14.67°C), with hotspots in Squally Channel, Wright Sound and McKay Reach. This was also the month with the widest range of measurements (11.41 – 19.05 °C).

Surface temperatures exhibited no apparent gradients, but instead peaked in isolated hotspots that are likely the result of local insolation of stagnant waters trapped by tidal fronts. Highest surface temperatures were typically found in Gil Basin waters, particularly Wright and Whale Channel. Subsurface (above thermocline) temperatures were also patchily variable, with warmest waters generally within Gil Basin. Subsurface temperatures generally mirrored sea surface temperatures: isolated hotspots with overall temperature peaking in July 2015 (Fig. 2-4), though a gradient from cool waters offshore to warm waters inshore was found in July 2013 and July 2015. Bottom water temperatures, however, increased throughout summer 2015 to peak in September. This warming was most dramatic in the outer channels of Caamano and Campania Sounds (Fig. 2-15). Bottom temperatures were much more homogenous, peaking
where seafloor depth is shallowest (Estevan Sound, south Campania Sound and north Verney Passage). Bottom temperatures were consistently lowest in the deep inland channels: south Douglas, Whale Channel and McKay Reach.

Temperature cross sections demonstrated that in August and September of both years the outer-water column is generally warmer than that of the inner fjords (Fig. 2-15). This gradient was strongest in September 2015, in which warming occurred throughout the study area but was most dramatic in the outer sounds of Caamano and Campania.

The thermocline was typically strongest in the central waters of the study area, particularly Whale Channel, and consistently weakest in the outer channels (Fig. 2-4). The thermocline was highly variable around the inner channels around Gribbell Island but was consistently weak relative to other channels. Area thermocline was strongest overall in July 2013, August 2014 and July 2015. In all years, the thermocline weakened in late summer; for example, by September 2015 (the sampling period with the lowest temperatures and strongest winds), the thermocline in the study area was uniformly weak.

Mean thermocline depth was $15.83 \pm 12.02$ m (min. 2.69, max. 62.81) and was relatively deep in outer channels (Fig. 2-5). Elsewhere it remained uniformly shallow until the cold and storms of September 2015, when it abruptly dropped tens of meters in all but the innermost channels.

**Stratification**

Mean stratification strength (referenced to 50m depth) was $4.79 \pm 1.71$ kg m$^{-3}$ (min. 0.87, max. 11.59; Fig. 2-4). It exhibited a stark offshore-inshore gradient (increased stratification occurs deeper inland), very similar to and a function of subsurface salinity. In the central waters surrounding Gil Island, the western side (Squally Channel) was consistently
less stratified than the eastern side (Whale Channel), except in September 2015 when this pattern flipped.

Mixed layer depth

Mean mixed layer depth was 7.33 ± 6.64 m (min. 1.36, max. 46.91; Fig. 2-5). Like the thermocline, the mixed layer was deepest in outer channels, while inside the mixed layer was uniformly shallow; this changed in September 2015, when the outer and central mixed layer deepened substantially. These patterns reflect the areas exposed to the strongest winds, be it from southeast storms or northeasterly outflows, both of which are typically strong in the early fall.

Turbidity

Mean euphotic depth, a function of surface water turbidity mediated by phytoplankton productivity and suspended particulate load, was 18.49 ± 6.17 m (min. 7.62, max. 43.91). In general, the interior channels to the east and north of Gil Island were the most turbid (Fig. 2-5); this pattern was most stark in 2014 and in August 2015, and least apparent in September 2015, during which Squally and south Douglas had the highest turbidity. Waters were much clearer in 2013 than in the following two years. In 2015, June was by far the most turbid month sampled, and July was by far the least, particularly in Squally Channel.

Dissolved oxygen

Mean dissolved oxygen maxima were 6.68 ± 1.15 ml l⁻¹ (min. 4.60, max. 9.75). These maxima occurred at a mean depth of 3.95 ± 3.38 m (min. 1.01, max. 23.24). Mean minima were 2.88 ± 0.42 ml l⁻¹ (min. 2.15, max. 4.15). In most sampled months there was no clear offshore-inshore gradient in this property, the exception being September 2015 when outer
ways were more oxygenated (Fig. 2-17). In general, the depth and concentration of dissolved oxygen were functions and reflections of chlorophyll-a (below). Sub-thermocline waters were more oxygenated in 2014 than in 2015, and throughout 2015 dissolved oxygen levels declined in both surface and bottom waters.

Chlorophyll-a

Mean integrated chlorophyll-a was $81.95 \pm 53.69 \, \mu g \, l^{-1}$ (min. 20.92, 444.66). Chlorophyll-a concentrations declined throughout the 2015 season (Figs. 2-6 and 2-18). June concentrations were much higher in the southwest channels (chlorophyll maximum = 28.5 \, \mu g \, l^{-1}). In July, high integrated levels remained only in Estevan Sound, after which they only persisted in isolated hotspots elsewhere. The largest hotspots were in north Squally in June (above value) and in Douglas Channel in September (27.02 \, \mu g \, ml^{-1}). 2014 sampling revealed higher concentrations within the interior half of the study area, but 2015 sampling from the same months revealed the opposite.

Acoustic backscatter

For backscatter exploration we visualized data as maps (Fig. 2-6) and as cross-sections (Figs. 2-7 through 2-13). Backscatter distribution on both frequencies shifted throughout the summer, but these shifts were neither unidirectional nor simple. Some channels consistently contained krill-like patches (e.g., Squally, SQU), while others were entirely empty in some months and full in others (e.g., compare Whale Channel month to month).

Krill-like backscatter (200kHz) was prevalent throughout the season. Total backscatter was highest in the outer channels during June. In other months it remained stable overall, but distribution was patchy and variable. In early June most backscatter was confined to the western half of the study area; by July it was found almost exclusively in the central
waters of north Squally Channel and western Wright Sound. By late summer areas of high total 200kHz backscatter had dispersed into multiple channels, including those further inland. Total fish-like backscatter (33kHz) declined throughout the summer. The highest readings were in June, also in the outer channels. As total backscatter declined in general, isolated areas of high total backscatter developed in all channels with no clear offshore-inshore pattern. One noteworthy exception was a late-season hotspot in the furthest inland channels of the study area (north tip of Verney Pass). Total backscatter was consistently high in the offshore sounds of Estevan and Caamano. Both of these areas have to relatively shallow seafloors and experience strong mixing by both tides and winds.

Patterns were less obvious in the vertical dispersion and intensity of backscatter (maps not shown). Mean intensity was highest overall in June and September, for both frequencies. The only noteworthy pattern in dispersion was for 200kHz in September: lower values in the inland channels (i.e., tighter scattering layers) than in outer channels, although both areas contained relatively high total backscatter for the month.

Annual differences: 2014 vs. 2015

The three substantial differences between years were: 1) surface property gradients were relatively weak in 2014; 2) deep water temperatures were warmer in 2015; and 3) oxygen levels were higher in 2014. Due to limited sampling in 2014, further comparisons between survey years cannot be made meaningfully. However, it is interesting that conditions in August and September 2014 were generally quite different from the same months in 2015; to the extent that a “typical” oceanographic pattern exists for this fjord system, the timing of the pattern, or perhaps the pattern itself, was different for these two years.

The most probable explanation for these differences is the “warm blob”, a remarkably persistent ridge of high pressure over the north Pacific that caused anomalously warm waters
to develop in December 2013 and did not dissipate until November 2015 (Bond et al., 2015, CPC 2016, Dewey 2016). Warm waters typically hold less dissolved oxygen than colder waters, which may account for the oxygen decline in 2015.

*Role of the warm blob*

The warm blob was documented by Fisheries and Oceans Canada Weather Buoys stationed within and adjacent to the Kitimat Fjord system. Sea surface temperature data recorded at Buoy 46185 [52°24.4’N, 129°47.0 W] (South Hecate Strait) and Buoy 46181 [53°50.0 N, 128°49.9W] (Nanakwa Shoal), recorded annual mean temperatures peaking at approximately 1.8°C above the annual mean sea surface temperature (SST) in 2015, compared to the previous decade. 2015 winter SST recorded in South Hecate Strait were most dramatically higher than previous winters, with temperatures 1.8°C warmer than previous winters. Meanwhile, summer SST recorded at Nanakwa shoal in 2015 was nearly 2°C than previous summers. In addition to trophic effects caused by less dissolved oxygen in warm water, the warm blob may have allowed for a temporary northward range expansion of typically warmer-water species. These include the Pacific pompano (*Peprilus simillimus*), *Mola mola*, and *Vellela vellela* that were each reported on several occasions within the study area in 2014 and 2015 (pers. comm. T. Robinson, A. Clifton, & D. Reece). Warm waters may have also contributed to a mass mortality event that affected numerous asteroid species between 2014 - 2015 (Eisenlord et al. 2016).

**ACKNOWLEDGMENTS**

This chapter is included with the permission of coauthors Kim-Ly Thompson and Chris R. Picard. The dissertation author was the primary investigator and author of this paper.
Figure 2-1. Detailed map of the study area within the Kitimat Fjord System.
Figure 2-2. A) Surface signatures of internal waves on an otherwise calm day within the Kitimat Fjord System at Amy Point (K.B. Watson for scale). B and C) Acoustic backscatter (200 kHz) detections of internal waves from same seafloor sill (large red bands at bottom of each pane are seafloor reflections).

Figure 2-3. Sea surface properties in each monthly survey.
Figure 2-4. Differences between upper and bottom portions of the water column in each survey month. Some features were not able to be derived from 2013 CTD data.
**Figure 2-5.** Monthly depth distribution of various oceanographic features. Some features were not able to be derived from 2013 CTD data.
Figure 2-6. Measurements of marine algae (Chl-a sum, top), krill (inferred from 200 kHz backscatter, middle), and small schooling fish (inferred from 33 kHz backscatter, bottom) from 2014 and 2015 data only.
Figure 2-7. Profiles of acoustic backscatter from August 2014. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor or manually removed noise. Extensive grey below 150m in Whale and Squally Channels is the result of accidentally setting depth range on echosounder to 150m during this month.
Figure 2-8. Profiles of acoustic backscatter from September 2014. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-9. Profiles of acoustic backscatter from early June 2015. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-10. Profiles of acoustic backscatter from late June to early July 2015. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-11. Profiles of acoustic backscatter from late July 2015. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-12. Profiles of acoustic backscatter from August 2015. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-13. Profiles of acoustic backscatter from September 2015. Each row displays transects within a single channel of the Kitimat Fjord System, from south (left) to north (right), and from sea surface (top of row) to 300m depth (bottom of row). Channels are arranged from offshore (bottom) to inshore (top). Prey-like backscatter is presented in two color-scales: red scale = 200 kHz, blue scale = 33 kHz, grey = seafloor.
Figure 2-14. The following figures (2-15 through 2-18) present patterns in water properties from inshore waters to offshore waters along the transect shown below, for 2014 and 2015 data only. Each figure shows monthly water column cross-sections of a single property, such as temperature. The transect begins in Caamaño Sound (left side of page) and travels through the fjord system to north Verney Pass (right side of page). Each row is a single survey month, displaying a cross-section of the water column from the sea surface to 150m. Plots were made by interpolating CTD measurements taken at approximately 12 stations along the transect (number of stations varies by one to three by monthly sampling period).
Figure 2-15. Monthly cross sections of potential temperature in the Kitimat Fjord System. Each row is a monthly survey. Cross-section travels from offshore waters (left) to inshore waters (right; see Fig. 2-14 for detailed route).
Figure 2-16. Monthly cross sections of salinity in the Kitimat Fjord System. Each row is a monthly survey. Cross-section travels from offshore waters (left) to inshore waters (right; see Fig. 2-14 for detailed route).
Figure 2-17. Monthly cross sections of dissolved oxygen in the Kitimat Fjord System. Each row is a monthly survey. Cross-section travels from offshore waters (left) to inshore waters (right; see Fig. 2-14 for detailed route).
Figure 2-18. Monthly cross sections of chlorophyll-a concentrations in the Kitimat Fjord System. Each row is a monthly survey. Cross-section travels from offshore waters (left) to inshore waters (right; see Fig. 2-14 for detailed route).
CHAPTER 3:

“Whale wave”: shifting strategies structure the complex use of critical fjord habitat by humpbacks

Eric M. Keen, Janie Wray, Hermann Meuter, Kim-Ly Thompson, Jay P. Barlow, Chris R. Picard
ABSTRACT

A decade of visual surveys (2005-2014) found that humpbacks (*Megaptera novaeangliae*) occupy a temperate fjord system in British Columbia, Canada, in a wave that propagates from outer channels in the summer to deep inland channels in late fall. Monte Carlo randomization confirmed this apparent pattern statistically. “Before” and “after” shift phases were most evident in July and October, respectively. We hypothesized that the “whale wave” was being driven by 1) prey following, 2) the tracking of environmental proxies, 3) fine-scale philopatry, or some combination of the three. To evaluate these hypotheses we collected new data in 2015, including visual and hydroacoustic surveys and oceanographic sampling. To both full-season and monthly datasets we fit generalized additive models (GAMs) in a stepwise procedure, using variable sets that represent our hypotheses. Prey models were generally the worst predictors of humpback distribution, while the most complex habitat models were the best. The Prey model performed best in June but increasingly poorly in remaining months. All models’ performance declined throughout the season, suggesting not only that this “whale wave” is being driven by needs other than food, but also that untested variable(s) inform late-season distribution. Alternative explanations of the wave include physiological maintenance and social habitat partitioning. Our findings demonstrate that marine predators can use complex spatial strategies not only to navigate vast areas of ocean but also to exploit specific habitats thoroughly. Though annually persistent and specific in structure, the whale wave would go (and has gone) unnoticed in typical marine mammal surveys.
INTRODUCTION

As the world’s largest predators, the great whales must satisfy superlative energetic needs (Alexander 2005) during brief foraging seasons in which ephemeral prey patches are dispersed across vast areas. Foraging efficacy must be optimized, meaning habitat use must be strategic; cues about prey conditions must be tracked at nested spatial and temporal scales, from transoceanic migration to a single foraging excursion (Ballance et al., 2006b, Hazen et al., 2009, Benoit-Bird et al., 2013, Bailey et al., 2009). But whales are more than mouths; foraging must be balanced by other needs (e.g., reproductive, social, health), and resource space must be navigated based on a combination of continuous habitat sampling (either directly or indirectly through proxies), recent experience (Mayo and Marx 1990, Fauchald 1999), and sheer habit (time-tested heuristics in behavior and distribution that maximize chances of resource access; e.g., philopatry). The balance of these strategies is likely species-, context-, and scale-specific (Fauchald 1999, Jacquet and Whitehead 1996, Anderwald et al., 2012). Habitat use is thus a dynamic amalgam of motivations (Manly et al., 2002) that is difficult but necessary to parse in order to identify and protect critical habitats (Bjorge 2001, Guisan & Thuillier 2005, Cañadas et al., 2005). Without an understanding of underlying causes, researchers cannot advance beyond descriptions of spatial pattern to tractable accounts of habitat use that describe why a given habitat is important to a predator (Redfern et al., 2006).

The high dimensionality of habitat use is reflected in the prevalence of multivariate cetacean-habitat models. While prey metrics alone can strongly predict whale densities (e.g., Piatt and Methven 1992), many published models are improved by the inclusion of non-prey variables, such as fixed hydrographic data (e.g., seafloor depth) and variable water column data (e.g., chlorophyll-a; Friedlaender et al., 2006, Benoit-Bird et al., 2013). Meanwhile, many
have found significant results without including prey variables at all (e.g., Ferguson et al., 2006, Rosa et al., 2012, Bombosch et al., 2014). Environmental variables in these models are often assumed to serve as proxies for prey abundance and availability (Redfern et al., 2006), the underlying premise being that the processes and resources that govern prey distribution in turn govern that of whales (Croll et al., 2005). However, the relationships between explanatory variables in a system cannot be disaggregated when only some are sampled, and many variable relationships remain poorly understood (Pershing et al., 2009). Alternative explanations for the importance of non-prey variables, such as the thermal maintenance of epicutaneous algal growth (Boily 1995, Durban and Pitman 2011), are receiving increased attention for certain species. Ultimately, knowledge of which variables to include in a habitat model relies upon hypotheses about variable relationships that can only be inspired by close familiarity with the specifics of a system, including the prevalence and persistence of the spatial pattern in question.

Mobile predator habitat use is notoriously difficult to study amid the subtle expanse of the open ocean (Block et al., 2011), but equal and unique challenges are present in complex coastal habitats such as fjords. Compared to other coastal zones, fjords are seasonally productive, spatially complex, oceanographically dynamic, and economically valuable (Syvitski et al., 1987). As semi-closed systems in which oceanographic processes are relatively self-contained, fjords are also exciting venues for ecosystem research (Pearson 1989). Overall they serve as intriguing foraging grounds for large whales (Ware et al., 2011), but the opportunity to study feeding whales in such habitats has only recently become possible as recovering populations in some areas return to pre-whaling coastal habitats (citations below).

Industrial whaling severely depleted humpbacks in the coastal fjords of British Columbia, Canada (Ford 2014), but as the North Pacific population recovered they began
returning en force in the last two decades (Ashe et al., 2013). Here we report on a decade of cetacean research within a northern BC fjord system (Fig. 2-1) proposed as critical habitat for humpback whales (*Megaptera novaeangliae*) and other marine mammal species (Ashe et al., 2013). Collectively, our sightings suggest that humpbacks occupy this fjord system in a kind of “wave”, in which high whale densities propagate from outer channels in summer to deep inner channels in the fall (Fig. 3-1). If this apparent pattern is real, the “whale wave” would be a rare example of persistent, structured and complex habitat use that would a) be an exception to paradigms in the conservation of large marine predators and b) likely go unnoticed and/or unvetted at the spatio-temporal coverage of typical marine mammal surveys which, given finite resources, tend to prioritize greater spatial range instead of repeated coverage of a restricted site. Furthermore, this novel habitat use strategy may lend insight into the importance of fjord systems to recovering whale populations in B.C. and elsewhere, as well as the converse: the whales’ ecological importance to fjords, both historical and potential.

Our objective in this study was first to verify the apparent spatial pattern statistically, then to determine the underlying driver(s) of the “whale wave”. To do so, we designed and launched a new oceanographic survey in 2015 designed to evaluate the following hypotheses of increasing habitat use complexity:

1. **Prey**: Humpbacks are strictly following their prey.

2. **Proxy**: Humpbacks are tracking environmental indicators of prey conditions or other habitat needs.

3. **Habit**: Humpbacks are practicing a habit of habitat use, concentrating in certain portions of the fjord system at certain stages of the summer, akin to a fine-scale and timed philopatry.

4. **Prey + Proxy**: Distribution is informed by both direct interactions with prey and the tracking of environmental indicators.
5. **Prey + Proxy + Habit:** Distribution is informed by all three strategies.

**METHODS**

**Study Area**

The study area (1,961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland British Columbia (BC), centered at 53°N and 129°W (Fig. 2-1). The KFS contains the marine territory of the Gitga'at First Nation, the confined channel portion of several proposed shipping lanes (e.g., Enbridge 2010), critical habitat for several endangered or threatened species and Fisheries Management Area (FMA) 6 for the BC coast (Ashe et al., 2013).

This fjord complex extends 140km inland from the Pacific Coast (MacDonald et al., 1983), nested within the Kitimat Ranges of the Great Bear Rainforest, the largest temperate coastal rainforest in the world (Thompson 1981). An uncommon attribute to this fjord system is its large islands that compartmentalize the fjord into a network of channels. These channels have a typical fjord morphology, with steep bedrock walls and relatively smooth sediment-floored basins separated by high-relief sills (Pickard 1961, MacDonald et al. 1983). Douglas Channel, Gardner Canal, and to a lesser extent Surf and Cornwall Inlets, are the primary fjords that feed the system (Pickard 1961).

Spanning the coastal boundary between ocean and the coastal ranges, the KFS is characterized by strong offshore-inshore gradients in climate (Fissel et al., 2010), oceanographic properties (MacDonald et al., 1983) and intertidal ecology (Turner 2003). KFS waters are circulated by a combination of three processes: estuarine circulation (forced by freshwater discharge), wind forcing (e.g., katabatic outflows) and tides (MacDonald et al., 1983). The relative importance of each varies according to location, season and timescale.
Water movements are further influenced by seasonal patterns and punctuated storm events on the adjacent shelf, which are strongest in autumn (MacDonald et al., 1983).

In the spring, seasonally resident humpbacks migrate to the KFS from tropical Pacific breeding grounds, primarily Hawaii (Ashe et al., 2013). Most leave the KFS by late fall, though our field observations suggest that some individuals may overwinter in protected coastal waters of northern BC. During the summer, these humpbacks feed opportunistically upon euphausiids and small schooling fish. Local net tows indicate that dominant euphausiid species include *Euphausica pacifica*, *Thysanoessa spinifera*, *T. longipes*, and *Tessarabrachion oculatum*, and data on community dynamics are currently being prepared for publication (Katelyn Qualls, pers. comm.). Based on field observations and local traditional knowledge, fish prey include herring (*Clupea harengus pacifica*), sand lance (*Ammodytes hexapterus*), and various species of smelt (f. Osmeridae). In rare years, KFS humpbacks have been observed feeding upon sardine (*Sardinops sagaz caerulea*; authors, unpublished data).

**Visual surveys 2005-2014**

Over the course of a decade, whale surveys were conducted an average of once per month by two collaborative research efforts: the Gitga’at Cetacean Monitoring Program and North Coast Cetacean Society (NCCS) study (Fig. 3-2), with some differences in methodology and spatial coverage.

Gitga’at surveys were conducted from either a 7 m or 9 m vessel (Fig. 3-2). Nearly all surveys began in Hartley Bay and included the circumnavigation of Gribbell and Gil Islands. The remainder of the survey route varied according to weather conditions and available daylight. Beginning in 2013 additional surveys focused on the outer channels (primarily
Caamano Sound), launching from and ending at a remote outcamp (GW in Fig. 1). Survey routes were recorded manually using GPS. Average survey speed was 38 km hr\(^{-1}\).

NCCS surveys were conducted in non-winter months during good weather conditions with visibility greater than 3 nautical miles and sea state no greater than Beaufort 3. All surveys began from the south end of Gil Island (Fig. 3-2). Surveys were conducted aboard a 7 m vessel at an average speed of 28 km hr\(^{-1}\) (in 2006, a 8 m vessel was used, 12 km hr\(^{-1}\)). Regular stops were made to listen for blows with the engine off.

On both platforms, 2-3 observers scanned for cues of whale presence including blows, splashes, flukes, fins, or breaches. Groups were approached slowly in order to estimate group size and record behavior, and GPS location was recorded manually from the vessel’s chartplotter. During each encounter one observer would continue scanning for the presence of other whales. An encounter ended when notes on group size and behavior were complete, or within 30 minutes, at which point the survey would continue along the pre-determined route.

**2015 survey efforts**

May through September 2015, concurrent visual and oceanographic surveys were conducted aboard the *RV Bangarang*, a 12 m motorsailer with a survey speed of 5 knots, with a team of three researchers. Monthly surveys of the study area were completed within a target duration of 20 days, during which we visited a grid of stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys (Fig. 3-2).

**Visual whale surveys**

Monthly surveys were conducted using line-transect sampling methodology (Buckland et al., 2001). Bearing and reticle readings using Fujinon 7x50 binoculars, min-max-
best group size estimates, and cue behaviors for each sighting were recorded by an observation
team from a platform 2 m above sea level. At standard intervals observers rotated between
three positions, one of which was data entry at the helm. Survey routes were recorded in a data
entry software interfaced to a Garmin 441s GPS unit with an external antenna mounted atop
the radar tower.

**Hydroacoustic data**

Hydroacoustic data were collected along survey tracklines with a down-sounding
Syqwest Hydrobox echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of
the depth, distribution, and patchiness of backscatter down to 300m, a range that encompasses
the maximum dive recorded for humpback whales (Hamilton et al., 1997). Appendix 5
provides details of echosounder data collection and processing. When odontocetes were seen
the echosounder was turned off to minimize disturbance.

**Oceanography**

We limited oceanographic variables for our habitat models to surface temperature,
surface salinity, and maximum chlorophyll-a concentrations between surface and 250m depth.
During transects, surface water temperature and salinity were sampled at 0.3m depth every
two seconds with a Seabird Electronics 45 thermsalinograph (TSG). At each station, we
sampled chlorophyll-a with a WetLabs ECO-FL fluorometer mounted to a SBE25plus CTD.

**Analysis**

*Seasonal spatial pattern*
A seasonal distribution shift is a pattern in both space and time. Observing it requires 1) the division of the study area into small geographic strata and 2) the division of the year into small temporal blocks. The fjord system is compartmentalized by islands and underwater sills that divide the fjord into discrete channels. We pooled survey effort within these channels into a total of 26 geographic strata in a scheme that balanced spatial resolution against the loss of statistical power with increased strata, making sure to compartmentalize high effort areas (e.g., thoroughfares, entries to headquarters, etc.) from low effort areas. We aimed for 2 - 4 strata per channel.

The area of viable humpback habitat within each stratum was calculated with a GIS (www.geojson.io) using local knowledge and our combined field experience. As a steep-walled fjord system, humpbacks are commonly seen accessing habitat up to and within the intertidal zones of the area's shoreline. We therefore defined the study area as the waters that humpbacks could easily access at all tides.

Tracks from Gitga'at and NCCS surveys were drawn in a GIS (same as above) based on waypoints and notes taken during the surveys. For each survey, effort (kilometers of trackline surveyed) and humpbacks seen were then totaled within each geographic stratum. Effort and whales were further pooled into monthly bins. From these datasets humpback density in each month-stratum was calculated as the number of whales seen per kilometer of effort.

We used Monte Carlo randomization in R (R Core Team 2013) to test the null hypothesis that, within each geographic stratum, month-to-month differences in observed humpback density were due only to random chance. In effect we ran 26 randomization tests, one per stratum. Randomization tests are a versatile, valid and relatively intuitive alternative to classical tests when data may not meet parametric assumptions (Manly 1991). Each stratum's randomization entailed 10,000 iterations of the following procedure. All humpbacks seen
within a given stratum were totaled across all months and years. These whales were then randomly redistributed amongst the months during which effort occurred. Redistributed sightings were divided by actual tracklength covered to arrive at a simulated null density for each month. After all iterations were complete, a distribution of null densities were available for each month-stratum. The observed density was then compared to the null distribution to infer statistical significance. The quantile of the null densities that corresponded to the observed density was interpreted as the likelihood that observed density equaled or surpassed that which would be expected by random chance.

*Acoustic backscatter*

Acoustic backscatter processing is detailed in Appendix 5. In summary, the Syqwest Hydrobox outputs a pixelated representation of water column backscatter where the larger the pixel value the greater the backscatter. These pixel data were georectified to account for variable vessel speed and were visually scrutinized to ensure all reflections attributable to seafloor, near-surface water bubbles, engine cavitation, sonars of passing ships, and whales were removed. In order to reduce each frequency further to display only backscatter of probable whale prey, we filtered data based on patch characteristics and overlapping frequencies so that, to the extent possible, 33kHz backscatter represents small schooling fish while 200kHz backscatter represents euphausiids. Deepwater krill imaging and zooplankton tows were used to verify the efficacy of 200kHz backscatter processing methods.

Middle-priced echosounders like that used in this study can characterize prey-like backscatter but cannot quantify the biomass of constituent taxa. We developed 3 simple metrics for each filtered frequency, described below and depicted in Fig. A5-22. These metrics were cross-checked pairwise for collinearity.
1. Total backscatter (T): The mean sum of pixel values of prey-like backscatter; this is a proxy for the quantity of potential prey available.

2. Backscatter intensity (I): The mean pixel value of prey-like backscatter; this is a proxy that can represent the school density, body size and composition, and/or patch characteristics of potential prey swarms.

3. Vertical dispersion (D): The standard deviation of the depth distribution of prey-like backscatter; this is a proxy for the vertical extent of prey swarms; highly dispersed backscatter may be less ideal for batch-feeding predators such as rorqual whales.

**Station interpolation**

Within each survey month, chlorophyll-a values from stations were interpolated for each transect centroid using inverse path weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell, accounting for land obstruction (R package *ipdw*, Stachelek 2015). Interpolation was also used to fill the few gaps in TSG data that were the result of rare priming issues caused by air entering the plumbing during large swells.

**Habitat modeling**

We used generalized additive models (GAMs) to test for and elucidate relationships between humpbacks, potential prey metrics, and other environmental variables. The GAM is a modeling approach that relates observations (in our case, humpback counts) to predictor variables using non-linear link functions (smoothing or "spline" functions) without imposing parametric limits on the data (Hastie and Tibshirani 1990). GAMs can accommodate highly nonlinear functional relationships (Zuur et al., 2009). GAMS were built using R package *mgcv*
Poisson, quasi-Poisson, and negative binomial models were explored (with their default link functions) for modeling humpback counts along transects.

Monthly surveys were split into transects of approximately 5km length (n=216; after Hedley et al., 1999). This scale was sufficient to minimize autocorrelation between adjacent transects, include a sufficient percentage of humpback sightings (below), and maintain adequate sample size for modeling. Because the model families tested required us to model whale counts and not densities, the logarithm of transect length was included in models as an offset. An example model, in which humpback counts are modeled by total 200 kHz backscatter and dispersion, would appear as follows in R: \texttt{gam(formula= hw \sim offset(log(effort)) + s(T.hi) + s(I.hi), data=data, family=nb, gamma=1.4)}.

We excluded our third survey (late July) because oceanographic data were not collected, and redundant transects in Squally (SQU) and Campania (CMP) were removed to equalize effort among all geographic blocks (Fig. 2-1). For each 5km transect, TSG readings were averaged, backscatter metrics were derived, and chlorophyll-a maxima (calculated from fluorescence using SBE laboratory calibrations) were taken from the interpolation cell containing the transect centroid. Whale positions were geo-located using binocular bearing and reticle readings from the observation platform (using R package \texttt{bangarang}, Keen 2016; which accounts for horizon obstruction in confined North Pacific channels) and their Euclidean distances to transect centroids were calculated (\texttt{swfscMisc}, Archer 2014). Humpbacks and effort (km trackline surveyed) were totaled in a 2.5km radius from the centroid of each transect.

We developed sets of candidate models that correspond to our five hypotheses (see Introduction). Prey, Proxy and Habit model candidates were based on non-overlapping sets of explanatory variables (Table 3-1) that are regularly included within cetacean-habitat models (Reilly 1990, Reilly and Fiedler 1994, Redfern et al., 2006). We did develop one novel metric,
Distance to Nearest Inlet (abbreviated as Inlet), inspired by observations across years of humpback association with the fjord system’s three major freshwater inlets (Surf Inlet, Cornwall Inlet, and Gardner Canal, Fig. 2-1). These waters enter the fjord in tidally mediated flows that can become rapids at peak ebb. In late summer humpbacks are regularly seen near or among these rapids (Fig. 3-3). Both Inlet and Distance into Fjord (Dist) were calculated in R as shortest-path travel routes between points in the Kitimat Fjord System, accounting for winding channels and island obstruction (Keen 2016).

Models for Prey+Proxy and Prey+Proxy+Habit hypotheses were built by pooling their constituent variable sets and adding bivariate interactions that combined variables from separate sets. For models that required position variables, both continuous and categorical versions were trialed (Table 3-1). Categorical variables and bivariate interactions (e.g., Lat. x Long.) are penalized during model selection due to the degrees of freedom they require, but they may best capture the spatiotemporal trend of the wave. All continuous variables were tested for pairwise collinearity with a Pearson’s correlation coefficient cutoff of 0.5 (Zuur et al., 2009). We found that sea surface salinity (SSS) was correlated to Distance into Fjord and latitude (Pearson’s $r^2 = 0.71$). This reflects the inshore-offshore salinity gradient typical of fjord oceanography. Given the different motivations each variable represents, we kept both variables and explored results with caution.

Models were evaluated based on the second-order Akaike Information Criterion (AICc), a metric for model comparison that, like its predecessor AIC, weighs negative-log Likelihood against the number of parameters it invokes (Akaike 1974) but more heavily penalizes overfitting and provides bias correction for small sample sizes (Burnham and Anderson 2002). In doing so, AICc selects for models that capture central tendencies most parsimoniously and thus are more predictive than descriptive. Since AICc is a relative measure of fit with no standard scale, Akaike weights ($w$) were also calculated within each
model set to compare evidence ratios on a scale from 0 to 1, such that all \( w \) for a model set sum to 1 (Burnham and Anderson 2002). When ranked in decreasing order of \( w \), the subset of models whose cumulative \( w \) is 0.95 is called the 95% confidence set. A large 95% set suggests that many variable combinations achieve the same level of parsimony and that there is no clear model choice (Symmonds and Moussalli 2011). When no single model is clearly the best fit, 95% confidence set is the most transparent way to report results (Symmonds and Moussalli 2011).

Where possible, we kept candidate model sets “balanced”, such that each variable within a set is used an equal number of times. Given equal representation, each variable’s cumulative Akaike weight, summed across all models that include it, can be used as a metric of relative variable importance (RVI; Burnham and Anderson 2002). Interaction terms were not included in balanced sets.

Models were first fit to the full season dataset. Explanatory variables were normalized to a mean of zero, a transformation that preserves variable spread but improves model convergence and facilitates the comparison of effect sizes (Zuur et al., 2009). Proxy variables (\( SST, SSS, Chl, Inlet \)) were normalized across the season, but we opted to normalize backscatter metrics within each month separately. Our rationale was that doing so would a) reflect the fact that humpbacks are orientating themselves to the best prey conditions available, and b) clarify interpretation of results. We wished for our models to elucidate patterns in humpback habitat use rather than account for trends in explanatory variables.

Models were fit to individual months using the same sets of model candidates. Before fitting, all explanatory variables were normalized within each survey subset. Interaction terms were not used due to reduced sample size, and Julian day was excluded from the Habit variable set. Prey, Proxy, and Prey+Proxy sets were balanced, and for these stages we calculated RVI as above. In order to facilitate results exploration, RVI’s were also scaled by
the most important variable, so that all RVIs ranged between 0 and 1. AICc scores were calculated to determine these variable weights but were not used for model selection, since AICc could not be compared across models based on different datasets (Burnham and Anderson 2002). Instead, we selected best models based upon minimum prediction error from leave-one-out cross validation, an iterative routine in which each datum (“test set”) is excluded from the data used for model fitting (“training set”); its humpback count is then predicted with the training model (Hastie et al., 2009). The mean squared error (MSE) of predictions, scaled by the mean observation value to account for changes in local humpback abundance and/or group size, provides a metric of model performance across similar datasets (here, survey month), lower MSE being better.

RESULTS

2005-2014 Surveys

Gitga’at effort comprised 182 days spanning all 10 years of the survey period. NCCS effort (beginning in 2006) comprised a total of 252 days. Effort was concentrated April to November, but occasional opportunistic trips occurred from December to March. In general, survey lengths for both platforms increased during summer months and in the latter years of the study decade (Fig. 3-4).

Between 2005 and 2014, NCCS and Gitga’at surveys found a total of 4,783 humpbacks. Pooled sightings from all years confirmed that, even after effort-corrected density estimation, the whale wave was strongly apparent (Fig. 3-5, top). Sightings and effort were also pooled into pairs of years and spatially stratified density was mapped, confirming that the wave was an annually persistent phenomenon.
The Monte Carlo test found that results were nonrandom at the 5% significance level in most strata in most months (Fig. 3-5, bottom). The pattern was most evident in July and October. The test suggested that the move inland actually happens fairly abruptly between August and September. In general the pattern was more uniformly significant in the interior channels to the northeast of Gil Island. In May, 13 out of 14 geographic strata inland of Gil Island had lower observed humpback densities than was expected by random chance, 11 of which were lower than 95% of simulated densities. By September, all 14 strata had higher observed densities than 95% of random trials. The pattern was reversed in the outer channels: in July, 12 out of 13 outer strata had higher humpback densities than 95% of simulated densities, but by October this number dropped to 3. Of the remaining outer strata, 9 had lower densities than expected by chance and 5 of these were lower than 95% of simulated densities.

Statistical results broadly supported the existence of a wave of humpback density that propagates from outside to inside waters, but not uniformly so. Notable exceptions to the pattern include certain strata in central and outer waters. The strata at the bottom of Gil Island seemed to have unexpectedly high humpback densities in May, before other outer channels were populated, and onward into the fall when the other adjacent strata had already been cleared out. Based on our field experience, this area appears to be of special importance to resident humpbacks across seasons. Another stratum of interest is the most southeastern in the study area, the sector of Caamano Sound that abuts Loredo Sound and Surf Inlet (one of the three large inlets feeding the fjord system). In all months this stratum was exceptional, and coincides with local knowledge about late-fall cetacean activity at the mouth of Surf Inlet.

**2015 Survey**

*Visual survey*
In 2015, the five vessel surveys covered a total of 1,653km of trackline in 5 surveys over 117 days (Table 3-2). On average, each survey covered 331km (min. 320, max. 346) in 23 days (min. 16, max. 28). 968 humpbacks were observed, 430 of which were seen during transect effort (in 268 sightings, mean 54 per survey, min. 39, max. 89). Mean group size was 1.6 individuals. While humpbacks were abundant in all survey months, the highest numbers were observed in August. The monthly distribution of these sightings confirms that the “whale wave” occurred again in 2015 (Fig. 3-6). As the wave propagated inland, humpback densities also became less concentrated. The most dispersed humpback distribution was observed in September.

**Backscatter**

For backscatter exploration we developed both map and profile views (Figs. 2-6 and 3-7). Backscatter distribution on both frequencies shifted throughout the summer, but these shifts were neither unidirectional nor simple. Some channels consistently contained krill-like patches (e.g., Squally, SQU), while others were entirely empty in some months and full in others (e.g., compare Whale Channel, WHA, month to month in Fig. 3-7).

Krill-like backscatter (200kHz) was prevalent throughout the season. Total backscatter was highest in the outer channels during June. In other months total backscatter remained stable overall, but distribution was patchy and variable. In early summer most total backscatter was generally confined to the western half of the study area; in July almost exclusively in north Squally Channel (SQU) and western Wright Sound (WRI). By late summer areas of high total backscatter had dispersed into multiple channels, including those further inland.

Total fish-like backscatter (33kHz) declined throughout the summer. The highest readings were in June, also in the outer channels. As total backscatter declined, isolated
aggregations of backscatter developed in all channels with no clear offshore-inshore pattern. One noteworthy exception was a late-season area of high total backscatter in the furthest inland channels of the study area (see Fig. 3-7, VER block during Sept). Total backscatter was consistently high in the offshore channel of Caamano Sound (CAA).

Patterns were less obvious in the dispersion and intensity metrics (Fig. A5-23). Mean intensity was highest overall in June and September, for both frequencies. The only noteworthy pattern in dispersion was for 200kHz in September: lower values in the inland channels (i.e., tighter scattering layers) than in outer channels, although both areas contained relatively high total 200kHz backscatter for the month.

*Oceanography*

Month-to-month sea surface conditions were highly variable (Fig. 2-3, Table 3-3). Outer channels were consistently the coolest and most saline; inner channels were typically the freshest but with variable temperatures (SST). Property ranges were widest in July and August for SST (11.41 – 19.05°C) and salinity (SSS, 11.59 – 31.36psu), respectively. Waters were warmest in July (mean 14.67°C, max 19.05°C), with isolated areas of warmer surface waters in SQU, WRI and MCK. Offshore-inshore salinity gradient was strongest in August and June, but relatively negligible in July and September. The most homogenous surface conditions occurred in September, perhaps due to mixing by the early onset of autumn storms, as did the coolest (mean 12.37 °C, min 10.48 °C) and most saline measurements (mean 26.92 psu, max. 31.73 psu).

Chlorophyll-a (Chl) maxima declined throughout the season (Fig. 2-6, Table 3-3). June Chl concentrations were much higher in the southwest channels (max. 28.5 μg l⁻¹). After June, strong maxima only persisted in isolated hotspots occurring increasingly inland. The
largest maxima were found in north Squally (SQU) in June (above value) and in Douglas Channel (DOU) in September (27.02 μg ml⁻¹).

**Habitat Models**

*Full season*

Superimposing humpback counts upon backscatter data was an important means of visually ground-truthing the modeling process (Fig. 3-7). We found overdispersion in humpback whale count data, and the negative binomial model was selected over the Poisson and quasi-Poisson models based on visual inspection of quantile-quantile plots. Because residual distributions in negative binomial models are typically non-Gaussian (Hilbe et al., 2009, Zuur et al., 2009), the Anscombe correction was applied to survey cross-validation residuals (Anscombe 1953). There were two accepted algorithms within the literature (McCullagh & Nelder 1989, Choi et al., 2005), so we calculated both. Results were practically identical; those based on the Choi et al. (2005) algorithm are presented here.

The “Prey” model gave the poorest explanation of humpback distribution (min. AICc = 601; Table 3-4). All other model stages yielded model fits with lower AICc values and higher proportions of null deviance explained (hereafter represented as r², after Friedlaender et al., 2006), culminating in the Prey+Proxy+Habit model (min. AICc = 554, r² = 0.62). The best Prey models explained only 16% of the dataset’s null deviance.

Of the 95 candidate Prey models, 41 remained in the 95% confidence set, all of which were AICc equivalent (i.e., within 6 AICc units for datasets of n < 256, Hilbe 2011): a sign of high uncertainty in model selection. Out of the 39 “Proxy” models fitted, 4 AICc-equivalent models remained in the 95% set (min. AICc = 587, r² = 0.35). The Prey+Proxy model set, which fit 30 candidates, yielded a 95% confidence set of 7 models, 3 of which were AICc
equivalent (min. AICc = 580, r² = 0.39). Of 16 candidate models, the 95% Habit set kept only one (AIC = 560, r² = 0.42): a good sign of strong support. While the second-best model had considerably worse parsimony (AICc = 571), it is worth noting that this model contained the categorical variable Block, whose 8 levels would have been heavily penalized in an AICc framework. Its low AICc suggests the potential importance of channel-specific patterns in variables and/or humpback distribution. 55 candidate models were passed to the Prey+Proxy+Habit step. The 95% set contained 8 models, all AICc-equivalent (min. AICc = 553, r² = 0.62).

**Monthly surveys**

Based on low importance in full-season fits, backscatter metrics 33 kHz dispersion and 200 kHz intensity were left out of monthly variable sets. Prediction error generally increased throughout the summer (Fig. 3-8). Prey model performance was relatively poor, but it was not always the worst; in fact the June Prey model tied for overall lowest prediction error, but its error increased steeply from thereon. In all months but June, the best-fit Prey+Proxy model was the same as the Proxy model (i.e., no backscatter variables were used; Table 3-5). Habit model performance was sporadic, declining most sharply from August to September. The Prey+Proxy+Habit model was always the best fit. Its prediction error was lowest in July.

**Variable Importance**

Based on the variables present in the full-season 95% confidence sets (Table 3-4), Total 200 kHz was the most important backscatter metric, though 200 kHz dispersion and total 33 kHz were also used within interaction terms. Total 200 kHz was the only variable to persist in the Prey+Proxy 95% set, but 200 kHz dispersion returned in interaction with total
200 kHz within the overall best-fit model. All four oceanographic variables remained in the 95% Proxy set. SST and SSS only appeared important when in interaction with each other; the best-fit Proxy model included SST x SSS only. The best available Habit model included Julian and the bivariate interaction Lat x Lon. Similar results were found in RVI weights calculated from balanced subsets of the Prey and Proxy candidates. With interaction terms removed, SSS arose as the most important oceanographic variable by far. This may be more related to its collinearity with latitude (see Methods) than its indication of proximity to the fjord’s freshwater source. Interestingly, Inlet was the second most important variable in the Proxy models.

Results differed slightly within the best-fit monthly models, in which importance, when inferred from both 95% sets and RVI, shifted month-to-month (Table 3-5). Total 200kHz and dispersion remained the most important backscatter variables, but all months were best-fit by multivariate Prey models. One notable finding was that total 200kHz was the most important backscatter metric in June and July, but in the second half of the summer 200kHz dispersion became the most important, possibly suggesting increasing importance of patch characteristics in late season foraging strategy. Except for June, backscatter was entirely absent from Prey+Proxy models, suggesting that oceanographic and position variables held much more explanatory power at the timescale (and sample size) of a single month. One notable discrepancy is that total 200kHz was the most important variable in the July Prey+Proxy model according to Akaike-based RVI, but residual-based prediction error selected a model with no backscatter metrics whatsoever. On a monthly basis, Chl and SSS were regularly the most important oceanographic variables. Again, geospatial coordinates outperformed Distance into Fjord as a position metric.

*Functional relationships*
Inspection of smoothing functions for the variables in the top season models revealed complex interactions between explanatory variables and the linear predictor in some cases (e.g., $SST \times SSS$, Fig. 3-9b), but near-linear relationships in others (e.g., $Chl$, Fig. 3-9a,e). The large central bulge in the $Lat \times Long$ perspective plot corresponds to the position of Squally Channel (SQU), which sustained the highest humpback densities throughout the season (Fig. 3-9c). The Julian day smoothing function captured the increase in humpback abundance in August (Fig. 3-9d). The smoothing function for integrated 200kHz backscatter was a near-sigmoidal curve (Fig. 3-9f), reminiscent of a Type III functional response (Holling 1965; see Discussion).

DISCUSSION

Documenting the Wave

Ten years of research demonstrated that humpback densities propagate throughout the Kitimat Fjord System in an offshore-inshore wave as summer turns to fall. Results of our stratified Monte Carlo procedure were strongly nonrandom but not absolute. The persistent high-density areas to the southwest of Gil Island (Fig. 3-5) demonstrate that there are fine-scale deviations from the mesoscale pattern of the wave. Interestingly, another persistent exception to the pattern was the late season hotspot at the entrance of Surf Inlet, one of the three major freshwater sources to the outer fjord system (Fig. 2-1; more on these inlets below).

Habitat Models
This study involved 1) long-term, four-season monitoring that identified spatial pattern and developed hypotheses, followed by 2) new fieldwork dedicated to hypothesis testing. While we recommend this research procedure in general, we acknowledge the limitations of using a single summer to explain a long-standing pattern. 2015 may have been an exceptional year in terms of oceanography that decoupled humpbacks from their typical associations. Indeed, it was in the aftermath of the “warm blob” and at the onset of an El Niño (Bond et al., 2015, CPC 2016). It is particularly difficult to discount philopatric behavior, which would have been acquired and refined over many years, as any one year may not be optimal.

Nevertheless, our analysis allowed us to compare conventional theories of habitat use strategy against each other, weighing their relative explanatory power on the scale of the full season and from month-to-month. Similar to previous studies (e.g., Friedlaender et al., 2006; Ferguson et al., 2006; Rosa et al., 2012), the most complex models of habitat use (including both prey, proxy, and habit variables) tended to best explain humpback distributions. Also similar to past findings (e.g., Benoit-Bird et al., 2013) was the importance of multiple prey metrics rather than just backscatter quantity, and there was some indication that as volume declined, the vertical dispersion of remaining backscatter became an increasingly important predictor.

Our most curious results were a) the generally low importance of prey metrics relative to environment variables, b) the decline in Prey model rank from first in June to among the worst in remaining months, and c) the general decline in performance of all models as the season wore on.

*Low Prey Importance*
Certain backscatter metrics (particularly total 200 kHz) were included in many of the best-fit models, but in monthly surveys their importance was quite low compared to environmental variables. This may reflect reliance upon environmental proxies instead of direct prey sampling at the spatiotemporal scales of our data collection. However, apparently weak whale-prey coupling may also be an artifact of our sampling design. Our study attempted to capture a pattern in both space and time, and it may be that our surveys of the study area were not sufficiently synoptic to capture whale-prey associations. Our instrumentation or backscatter metrics may have inadequately characterized humpback prey, or the measurement scales of our backscatter bins and humpback count radii may have been mismatched; weak results could speak more to analysis design than to ecological patterns (Levin 1992). Many predator-prey association studies have found mixed, highly scale-sensitive results when relying on prey quantity metrics alone (Faucald 2013). Benoit-Bird et al. (2013) emphasized that observed spatial pattern (or lack thereof) depends entirely upon what is measured, which is why we included several backscatter metrics. While we were able to use frequency differencing and patch characteristics to roughly distinguish prey type within backscatter patches, our prey metrics may have failed to capture a dimension of prey association related to nutritional differences, if any, in available prey. This has been an important distinction in seabird foraging studies (Hunt et al., 1993).

An issue with an automated approach to backscatter metric calculation approach is that our results depend upon the level of refinement and biological relevance of the metrics and filters we developed. However, we stand by our automated analysis on the grounds that a) manual approaches are subject to human error and not reproducible, and b) underestimation is more likely than overestimation in automated methods, while manually selected patches can incorporate subjective knowledge that increases the risk of positively biased results.
Decline in prey model performance

We offer four hypotheses to explain the disproportionate decline in prey model performance throughout the season:

1. **Prey switching**: to a prey type that was inadequately detected by our echosounder or backscatter metrics, though we cannot guess what that prey type would be, nor did we ever observe any major shifts in foraging style.

2. **Inadequate coverage**: Our sampling plan may have been inadequate to detect locally rich but generally sparse backscatter patches of early fall. Indeed, when we broke transect in fall 2015 to approach the whales within inland channels, groups generally behaved as if they were feeding deep and the echosounder detected isolated but dense backscatter patches (Chapter 4).

3. **Satiation**: After a winter of fasting, early summer habitat use was one-dimensional and food-focused. As blubber stores were replenished, whales no longer needed to track the best prey conditions available. Search effort could have relaxed, perhaps falling back on the heuristics of proxies and habit, and other priorities were allowed to inform habitat use (see next section).

4. **Competition**: Overall backscatter volume decreased while humpback densities increased, peaking in August. At this time of year a community of other euphausivorous predators descends upon the fjord system, including fin whales (*Balaenoptera physalus*; Ford 2014; authors, unpubl. data), a variety of seabirds and salmon. Most of these exhibit preference for outer and central channels (authors, unpublished data). Intra- and inter-specific competition may have pushed humpbacks deeper inland and compromised their spatial overlap with prey.

5. **Search shift**: While spatial overlap with prey must occur on the smallest scale in order for feeding to occur, mobile oceanic predators must seek out and position themselves
for that opportunity by navigating and assessing prey conditions at multiple nested scales in space and time. The scale of apparent spatial association, therefore, may be a moving target. In the abundance of early summer, humpbacks may have been able to find sufficient prey patches without much searching (once they had arrived in the most productive channels). But in the scarcity of autumn, the best foraging strategy may have been to allocate more time and effort to searching, remaining mobile until adequate patches are found. If so, from our trackline perspective the average humpback would be spatially decoupled from prey-rich areas but all could still have been engaged in food-driven behavior.

**Decline in all models’ performance**

The growing prediction error in all models throughout the summer suggests that we failed to sample some habitat component that became increasingly important into the fall. Two possible needs that were poorly included in this study are as follows.

1. **Physiological maintenance**: “Nearest inlet” was our only health-related variable, inspired by curious field observations (Fig. 3-3) and hypotheses from the literature (Boily 1995, Durban and Pitman 2011). Durban and Pitman (2011) hypothesized that physiological maintenance was a driver of baleen whale migration. It seemed possible to us that turbulent mixing zones of fresh, warm water within fjord systems may provide a similar service that prolongs the foraging season; this could also explain why many humpbacks are able to remain in the deep channels of this fjord system long into the fall, possibly overwintering here (authors, unpublished data). However, inlet importance was mixed according to 95% model sets and RVI. This hypothesis merits further investigation, given that such inlets are a feature unique to fjord
foraging habitats and may suggest the unsung importance of fjords, both historically and into the future, for whale populations.

2. **Social habitat needs:** Humpbacks are often philopatric to reliably productive feeding grounds (Fleming and Jackson 2013). But the foraging season also has a strong social component. Foraging regions tend to correspond to distinct breeding populations (Baker et al. 2013). Field biologists in these feeding grounds often observe complex behavioral transmission (Weinrich et al., 1992), annually persistent social bonds (Ramp et al., 2010) and even song (Vu et al., 2013). Social interests may gain precedence over foraging as migration and breeding season nears, and the interior channels of the fjord system may be better for socializing in some way. If so, acoustics may be a driving concern for this exceptionally vocal species in this habitat. The steeper walls of bare bedrock and narrow channels of the interior fjords, secluded as they are from major shipping lanes may offer an attractive acoustic space (Williams et al., 2013). Both social calls and song are common within this fjord system during the late fall (Meuter and Wray, unpublished data), but further data are needed to test for differences in call rates among channels. An alternative is that the whales found further inland belong to a social network distinct from those loyal to the outer channels, and the apparent wave is in fact a turnover in the resident population with different habitat preferences. Territoriality or inter-group competition may even exacerbate the pattern. Social association analyses based on photo-identification data from our decade of research are forthcoming.

**Whale-climate coupling**
If the “whale wave” is a response to changes in prey or their environmental proxies, then its ultimate mechanism is oceanographic. As in most fjord systems, the KFS experiences strong offshore-inshore gradients in oceanography and meteorology driven by seasonal signals in climate and water mixing (MacDonald et al., 1983, Fig. 2-6). These midsummer gradients may serve as aids to orientation or cues to habitat needs. Gradients are maintained by estuarine circulation, a seaward surface flow of relatively freshwater atop a landward countercurrent at depth (Syvitski et al., 1987). Estuarine flow is governed by snowmelt and, to a lesser degree, seasonal rains (Masson and Cummins 2000). Gradients are disrupted with the onset of fall storms, whose sea waves and strong winds overwhelm estuarine flow and collide with katabatic outflows, inducing vigorous mixing (Thomson 1981, Freeland and Farmer 1980). By wintertime KFS waters are relatively homogenous (MacDonald et al., 1983). The breakdown of cue gradients could disperse prey and/or instigate in situ prey production deeper inland. In this way, the timing of the “whale wave” may be coupled to the shifting balance between estuarine circulation and autumn mixing by storms. Both of these processes are governed by climate, including interannual oscillations and long-term trends. If so, whale use of fjord habitats could be particularly sensitive to global trends in climate.

**Threshold foraging and ecological role**

The season’s relationship between humpbacks and krill-like backscatter was muted but sigmoidal (Fig. 3-9f), suggesting a threshold functional response to prey conditions (Holling 1965). Metabolic and kinematic theory predicts that foraging thresholds are high in large marine predators and have implications for habitat use (Goldbogen et al., 2011). Piatt & Methven (1992) was the first study to document a threshold response in cetaceans (between humpback whales and capelin, *Mallotus villosus*). Piatt (1990) observed a similar response to
the same prey in common murres (Uria aalge). Friedlaender et al. (2006), using a GAM framework similar to ours, found a functional relationship between humpbacks and backscatter that was nonlinear but more reminiscent of a saturation response than a sigmoid. Energetic costs of mobility and associated threshold foraging have ecological consequences by reducing the proportion of accessible habitat that is usable, which decouples a predator’s trophic impact from its geographic distribution.

Interestingly, the functional relationship with chlorophyll-a, the strongest environmental predictor, was practically linear (Fig. 3-9e). Its difference from the backscatter sigmoid may reflect nested strategies, in which proxies are used to position for the best probability of prey interactions (higher is always better), while their prey association within those high-probability areas is more discriminating (Fauchald et al., 2000).

As the whales propagate inland, so too does their ecological footprint. Although humpbacks are abundant within the Kitimat Fjord System, their trophic impact at any one time is highly localized. Beyond predation and competition, this includes the facilitation of other predators and nutrient redistribution (Roman et al., 2014). Other species may come to coordinate their use of this fjord system accordingly. Habitat use patterns like the whale wave may be a significant medium of “ecosystem engineering” among large marine predators.

**Implications for management**

Habitat use inevitably manifests itself as a pattern in both space and time. Like all spatial patterns, it may only be strong, stable, and/or apparent at certain scales (Levin 1992). Others have studied humpbacks in this area without detecting the whale wave (Williams and Thomas 2007, Wheeler et al., 2010, Gribba and Bailey 2015), and their findings have become the basis for the impact assessment of proposed industrial activities in this fjord system.
Long-lived, mobile predators must be observed across seasons and for many years before strategies and motivations of habitat use can be understood. Where available, research is greatly enhanced by the involvement of local residents who have the familiarity with their home system to interpret observations with unique insight. Our study highlights the value of long-term, local monitoring by indigenous communities and their partnership with non-profit and academic research organizations.

Our findings suggest humpback foraging needs within this fjord system are balanced against interests other than food, and that balance shifts within the foraging season. The annual persistence and statistical strength of the whale wave demonstrate that humpback habitat use can be structured and strategic. It may facilitate the most thorough possible use of a fjord system's resources, provide similar access to other complex systems of BC’s fjordland, and accommodate higher densities of humpbacks in the dwindling number of relatively undisturbed coastal foraging grounds of the northeast Pacific than would otherwise be possible. It is likely coordinated to the specific oceanography of the study system, suggesting that local displacement by human impacts may have more consequences than previously supposed. Industrial projects that disrupt habitat continuity, such as shipping lanes, may be particularly detrimental to the integrity of this and other critical habitats. Until sufficiently thorough habitat use studies have been carried out, irrevocable management decisions should be treated with caution.

Protecting entire species ranges is typically impossible, particularly in the case of mobile oceanic predators such as whales, so we must ask which portions are most important. It is here that the common depiction of mobile predators as masters of foraging improvisation and environmental forensics can be counterproductive for conservation. Though accurate, this picture can be misconstrued as an argument against the protection of specific sites, given that an entire ocean remains available. This outlook ignores the fact, demonstrated by our findings,
that mobile marine predators can use complex strategies not only to navigate vast swaths of marine habitat but also to tune into the specific features and attributes of certain areas and develop spatial strategies that enable its most thorough and efficient use.

ACKNOWLEDGMENTS

This chapter, in part, is a reprint of material as it appears in *Marine Ecology Progress Series*, 2017: Keen, EM, J Wray, H Meuter, KL Thompson, JP Barlow, CR Picard. (In press) “Whale wave”: shifting strategies structure the complex use of critical fjord habitat by humpbacks. The dissertation author was the primary investigator and author of this paper.

In addition to front matter acknowledgments, NCCS fieldwork was funded in part by the Save Ours Seas Foundation and Willow Gove Foundation, with special thanks to Andy Wright, the Zumwalt family, Julie Walters and Sam Rose. 2015. The authors thank Katie Qualls for her work on euphausiid counts, World Wildlife Fund for providing GIS coordinates for NCCS 2008-2012 survey tracks, B.L. Padgett for providing inlet footage, Megan Ferguson for analytical guidance.
**Tables**

**Table 3-1.** Explanatory variables used in habitat use models. Model stages are enumerated: 1=Prey, 2=Proxy, 3=Prey + Proxy, 4=Habit, 5=Prey + Proxy + Habit. Each backscatter variable is actually two; one for each frequency (H=200kHz, L=33kHz). Variable type: Cont.=Continuous, Nom.=Categorical.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Type</th>
<th>Models</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acoustic backscatter</td>
<td>Total</td>
<td>$T_H$</td>
<td>Cont. 1,3,5</td>
<td>Mean sum of water column pixel values..</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$T_L$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intensity</td>
<td>$I_H$</td>
<td>Cont.1,3,5</td>
<td>Mean pixel value.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$I_L$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dispersion</td>
<td>$D_H$</td>
<td>Cont.1,3,5</td>
<td>Standard deviation of backscatter depth distribution (m).</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$D_L$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oceano-</td>
<td>Nearest inlet</td>
<td>Inlet</td>
<td>Cont.2,3,5</td>
<td>Swimming distance (km) to nearest major inlet.</td>
</tr>
<tr>
<td>graphy</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea Surface Temperature</td>
<td>SST</td>
<td>Cont.2,3,5</td>
<td>Degrees (°C)</td>
<td></td>
</tr>
<tr>
<td>Sea Surface Salinity</td>
<td>SSS</td>
<td>Cont.2,3,5</td>
<td>Practical salinity units (psu)</td>
<td></td>
</tr>
<tr>
<td>Chlorophyll-a maximum</td>
<td>Chl</td>
<td>Cont.2,3,5</td>
<td>Peak interpolated water column chlorophyll-a concentration (µg ml$^{-1}$)</td>
<td></td>
</tr>
<tr>
<td>Position</td>
<td>Survey month</td>
<td>Month</td>
<td>Cat.4,5</td>
<td>4 levels: June, July, Aug, Sept.</td>
</tr>
<tr>
<td></td>
<td>Block</td>
<td>Blk</td>
<td>Cat.4,5</td>
<td>8 levels (see Fig. 2-1).</td>
</tr>
<tr>
<td></td>
<td>Julian day</td>
<td>Jul</td>
<td>Cont.4,5</td>
<td>Geospatial coordinates (dec.deg.)</td>
</tr>
<tr>
<td></td>
<td>Position</td>
<td>Lat</td>
<td>Cont.4,5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Long</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance into Fjord</td>
<td>Dist</td>
<td>Cont.4,5</td>
<td>Swimming distance (km) from the furthest point inland</td>
<td></td>
</tr>
</tbody>
</table>
Table 3-2. Monthly oceanographic surveys on the *RV Bangarang* in 2015, detailing the days of fieldwork within each survey month (*Days*), the kilometers of formal transect effort (*km*), the number (*n*) of 5km transect bins used in habitat models (Late July was excluded from modeling), the average Beaufort sea state conditions during the formal effort (*Bft*), the number (*n*) of humpbacks (*HWs*) seen, the average group size during the month (*Grp*), the mean ± standard deviation of humpback count within 5km transect bins (*Mean Count*), and the percent of bins with a count of 0 (% 0).

<table>
<thead>
<tr>
<th>Month</th>
<th>Days</th>
<th>km</th>
<th>n</th>
<th>Bft</th>
<th><em>n</em></th>
<th><em>Grp</em></th>
<th>Mean Count</th>
<th>% 0</th>
</tr>
</thead>
<tbody>
<tr>
<td>May – June</td>
<td>16</td>
<td>320</td>
<td>47</td>
<td>1.6</td>
<td>39</td>
<td>1.538</td>
<td>0.705 ±1.425</td>
<td>75</td>
</tr>
<tr>
<td>June – July</td>
<td>26</td>
<td>335</td>
<td>57</td>
<td>1.3</td>
<td>39</td>
<td>1.744</td>
<td>1.143 ± 2.422</td>
<td>71</td>
</tr>
<tr>
<td>Late July</td>
<td>21</td>
<td>346</td>
<td>-</td>
<td>1.4</td>
<td>49</td>
<td>1.714</td>
<td>1.114 ± 1.806</td>
<td>60</td>
</tr>
<tr>
<td>August</td>
<td>26</td>
<td>322</td>
<td>59</td>
<td>1.4</td>
<td>89</td>
<td>1.416</td>
<td>1.681 ± 2.587</td>
<td>48</td>
</tr>
<tr>
<td>September</td>
<td>28</td>
<td>330</td>
<td>56</td>
<td>1.4</td>
<td>52</td>
<td>1.558</td>
<td>0.853 ± 1.417</td>
<td>62</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>117</td>
<td>1653</td>
<td>219</td>
<td>-</td>
<td>268</td>
<td>-</td>
<td>1.101 ± 2.005</td>
<td>63</td>
</tr>
</tbody>
</table>
Table 3-3. Summary of oceanographic properties sampled in each monthly survey of summer 2015 aboard RV Bangarang. SSS=Sea surface salinity (psu=practical salinity units); SST=Sea surface temperature (° Celsius); Chl-a=Chlorophyll-a (µg ml⁻¹). Metrics include the mean, standard deviation (SD), minimum (Min.) and maximum (Max.). Chlorophyll-a was not sampled in July.
<table>
<thead>
<tr>
<th>Month</th>
<th>SSS (psu)</th>
<th>SST (°C)</th>
<th>Chl-a (µg ml⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Min.</td>
</tr>
<tr>
<td>M - J</td>
<td>25.70</td>
<td>2.48</td>
<td>15.60</td>
</tr>
<tr>
<td>J – J</td>
<td>26.72</td>
<td>2.47</td>
<td>17.75</td>
</tr>
<tr>
<td>Jul.</td>
<td>27.84</td>
<td>2.84</td>
<td>17.46</td>
</tr>
<tr>
<td>Aug.</td>
<td>25.51</td>
<td>4.02</td>
<td>11.59</td>
</tr>
<tr>
<td>Sept.</td>
<td>26.92</td>
<td>2.43</td>
<td>19.21</td>
</tr>
</tbody>
</table>
Table 3-4. Full season model results for each hypothesis. *Data* rows summarize the datasets, including sample size ($n$) and the number of explanatory variables (Vars.) in each stage. *Model set* summarizes the number of variable combinations fit to the data (Combos), and the subset of those models that are *Balanced* (equal variable representation). Balanced model sets were used to calculate relative variable importance (*RVI*) for Prey and Proxy models. 95% *Models* rows summarize the resulting 95% confidence sets based on Akaike weights: the number of models in each set ($n$), the number of those models that are AICc equivalent (=AICc; within 6 AICc units of the set’s minimum AICc, after Hilbe 2009), the minimum AICc in the 95% set (minAIC), and the proportion of null deviance explained by the model ($r^2$). 95% *vars* list the explanatory variables within 95% sets; variables with a “-“ were among the candidates; those with ✓ were included (*Incl.*). Variables used in the model with the lowest AICc are denoted instead with the significance level (p-value) of their smoothing function. When balanced subsets were available, *RVI* is reported. Bivariate interactions are given their own rows, joined by an “x”.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Prey</th>
<th>Proxy</th>
<th>Habit</th>
<th>Prey + Proxy</th>
<th>Prey + Proxy + Habit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>216</td>
<td>216</td>
<td>216</td>
<td>216</td>
<td>216</td>
</tr>
<tr>
<td>Vars</td>
<td>6</td>
<td>4</td>
<td>7</td>
<td>5</td>
<td>12</td>
</tr>
<tr>
<td><strong>Model set</strong></td>
<td>Combos</td>
<td>95</td>
<td>39</td>
<td>22</td>
<td>30</td>
</tr>
<tr>
<td>$n$</td>
<td>51</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>95% Models</strong></td>
<td>= AICc</td>
<td>41</td>
<td>4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.16</td>
<td>0.35</td>
<td>0.41</td>
<td>0.39</td>
<td>0.62</td>
</tr>
<tr>
<td><strong>Incl.</strong></td>
<td>RVI</td>
<td>Incl.</td>
<td>RVI</td>
<td>Incl.</td>
<td>Incl.</td>
</tr>
<tr>
<td><strong>95%</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_H$</td>
<td>✓</td>
<td>1.00</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>$T_L$</td>
<td>✓</td>
<td>0.76</td>
<td>✓</td>
<td>✓</td>
<td>-</td>
</tr>
<tr>
<td>$D_H$</td>
<td>✓</td>
<td>0.61</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$D_L$</td>
<td>✓</td>
<td>0.37</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$I_H$</td>
<td>✓</td>
<td>0.32</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$I_L$</td>
<td>0.1</td>
<td>0.41</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$T_H \times D_H$</td>
<td>.001</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>$T_H \times I_H$</td>
<td>✓</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$T_H \times V_L$</td>
<td>✓</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$D_H \times D_L$</td>
<td>✓</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SSS</td>
<td>-</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SST</td>
<td>-</td>
<td>0.16</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Chl</td>
<td>✓</td>
<td>0.27</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Inlet</td>
<td>✓</td>
<td>0.40</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>SSS $\times$ SST</td>
<td>.001</td>
<td>.001</td>
<td>.01</td>
<td>.01</td>
<td>.01</td>
</tr>
<tr>
<td>Chl $\times$ Inlet</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>$T_H$ $\times$ Chl</td>
<td>.01</td>
<td>.05</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$T_H$ $\times$ Inlet</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Lat $\times$ Lon</td>
<td>.001</td>
<td>.01</td>
<td>.01</td>
<td>.01</td>
<td>.01</td>
</tr>
<tr>
<td>Julian day</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3-5. Best-fit models for each month (June-September 2015) under each hypothesis of humpback habitat use (Prey, Proxy, etc.). For each model-month, the following performance metrics are reported: Mean square prediction error (Adj. MSE) based on Anscombe residuals (Choi et al., 2005) and scaled by mean humpback count; Proportion of null deviance in humpback counts explained by model ($r^2$); explanatory variables used in candidate models (symbols are keyed in Table 3-1). Variables included in the best-fit model are denoted with the significance level ($\alpha$) of their smoothing function ($ns = p > 0.05$). Variables that were tested but not included in a best-fit model are denoted with an “-”. For the first three model stages, whose model sets were balanced (equal variable representation), relative variable importance (RVI) is also reported, calculated from Akaike weights and scaled within month-models between 0 and 1. Note that RVI metrics can only be quantitatively compared within model-months.
<table>
<thead>
<tr>
<th>Model</th>
<th>Month</th>
<th>Adj. MSE</th>
<th>( r^2 )</th>
<th>Backscatter</th>
<th>Oceanography</th>
<th>Position</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( T_H )</td>
<td>( T_L )</td>
<td>( D_H )</td>
</tr>
<tr>
<td>Prey</td>
<td>J</td>
<td>0.81</td>
<td>.16</td>
<td>( a )</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>1.00</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>1.50</td>
<td>.38</td>
<td>( a )</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>1.00</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>2.10</td>
<td>.19</td>
<td>( a )</td>
<td>-</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.47</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>2.38</td>
<td>.17</td>
<td>( a )</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.89</td>
<td>0.60</td>
</tr>
<tr>
<td>Proxy</td>
<td>J</td>
<td>1.65</td>
<td>.39</td>
<td>( a )</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.31</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>0.92</td>
<td>.56</td>
<td>( a )</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.08</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>1.41</td>
<td>.68</td>
<td>( a )</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>1.00</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>2.21</td>
<td>.16</td>
<td>( a )</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.53</td>
<td>0.63</td>
</tr>
<tr>
<td>Prey</td>
<td>J</td>
<td>0.81</td>
<td>.16</td>
<td>( a )</td>
<td>ns</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Proxy</td>
<td>J</td>
<td>0.92</td>
<td>.56</td>
<td>( a )</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>1.00</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>1.41</td>
<td>.68</td>
<td>( a )</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>2.21</td>
<td>.16</td>
<td>( a )</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td>0.43</td>
<td>0.29</td>
</tr>
<tr>
<td>Habit</td>
<td>J</td>
<td>1.36</td>
<td>.41</td>
<td>-</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>1.48</td>
<td>.37</td>
<td>-</td>
<td>-</td>
<td>.05</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>1.39</td>
<td>.69</td>
<td>-</td>
<td>-</td>
<td>.001</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>3.04</td>
<td>.12</td>
<td>-</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td>Prey</td>
<td>J</td>
<td>0.76</td>
<td>.52</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>0.54</td>
<td>.48</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Proxy</td>
<td>A</td>
<td>1.34</td>
<td>.69</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>( R^2 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>S</td>
<td>1.64</td>
<td>.18</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 3-1. As summer turns to fall (x-axis), humpbacks sightings occur increasingly deeper into the Kitimat Fjord System (y-axis). Black line is running 10-day mean of raw sightings (gray dots, n=2,527) from Gitga’at and North Coast Cetacean Society surveys 2004 - 2014.
Figure 3-2. Left: Survey effort by Gitga’at (red) and NCCS (blue), 2005 - 2014. Right: Sampling plan for 2015 vessel transects (lines) and oceanographic stations (filled circles) aboard RV Bangarang.
Figure 3.3. A) At peak ebb tide in late August 2015, humpbacks gather at the bottleneck entrance to a large freshwater inlet (Cornwall Inlet) in the study area. Ephemeral but dramatic tidal rapids develop at this site during ebb tides. Coincidentally moored in an adjacent cove just out of the tidal stream, we were able to document this pair and their associated Stellar’s sea lions (*Eumetopias jubatus*) rollicking in the rapids (B) for more than an hour, repeatedly practicing contortion maneuvers (C-D). Stills pulled from footage by Luke Padgett, available online here: https://vimeo.com/154083846 (password: baleen).
Figure 3-4. Survey effort (km) by Gitga’at and North Coast Cetacean Society (NCCS) platforms, 2004-2014. Left: Annual survey effort (June through November only). Right: Monthly survey effort.
Figure 3-5. The “whale wave” is (a) evident in humpback density estimates and (b) verified by Monte Carlo randomization tests. 2004 - 2014 surveys from Gitga’at and North Coast Cetacean Society (NCCS) platforms were pooled then spatially stratified (n = 26 strata). Randomization results (b) are color-graded for each stratum as follows: Dark red = observed whale density was lower than at least 95% of the random trials; pink = observed density was lower than the randomization median; light blue = observed was higher than randomization median; dark blue = observed was higher than 95% of random trials.
Figure 3-6. Humpback sightings from the 2015 surveys aboard RV Bangarang. Dots are scaled positively by group size. Black-filled circles are on-transect sightings; empty circles are sightings during "casual" or transit effort.
Figure 3-7. Spatial association of humpback density (black line) with prey field in 5 surveys in summer 2015. Profiles are transects of discrete waterways arranged roughly from offshore (left) to inshore (right). Profile background is acoustic backscatter (blue = fish-like, 33 kHz; red = krill-like, 200 kHz) from the surface (profile top) down to 300m. Color intensity indicates backscatter strength (deeper/darker colors = stronger backscatter). White is backscatter that did not register above a threshold level. Grey is seafloor and manually removed self-noise. Humpback line is a running mean (approx. 500 m window size) of whales seen within 2.5 km of trackline.
Figure 3-8. Prediction errors of the best-fit models for each hypothesis of humpback habitat use across monthly surveys in summer 2015. Models were fit to each month separately, with unique sets of variable combinations for each hypothesis (see Table 3-1). For each survey, prediction error is calculated as the mean square of Anscombe residuals (Choi et al. 2005), scaled by the month’s mean humpback count.
Figure 3-9. Smoothing functions of explanatory variables included in the best models fit to the full 2015 dataset. a - c) Bivariate smoothing functions from the all-around best-fit model (Prey + Proxy + Habit model in Table 3-4); d - f) smoothing functions from two AICc-equivalent models (within 6 AICc of the minimum AICc; Hilbe 2011) that contained Chl and 200 kHz integrated backscatter in univariate terms, whose plots offer a simpler but related perspective on functional relationships between normalized explanatory variables and the linear predictor of humpback counts (z-axis in 3-D graphs, y-axis in 2-D plots). Plots d - f feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading).
CHAPTER 4:

Aggregative and feeding thresholds of sympatric rorqual whales within a fjord system

Eric M. Keen
ABSTRACT

Rorqual whales supposedly respond to increases in prey supply according to aggregative thresholds, gathering in areas above a minimum prey density set by their basal metabolic needs, as well as to feeding thresholds, initiating feeding behavior at a prey density set by the energetic cost of lunge feeding. Dual systematic and focal follow surveys were conducted in a British Columbia fjord system to compare prey preferences and thresholds in two sympatric rorquals, humpbacks (Megaptera novaengliae) and fin whales (Balaenoptera physalus). While multiple prey-related habitat features were found to influence whale aggregation and feeding, both threshold types were observed in each species’ response to total 200 kHz backscatter. Humpback response to prey features was less predictable and influenced by more factors than that of fin whales, who appeared to be exclusively euphausivorous and interested predominantly in the deepest high-volume krill-like backscatter patches within the deepest channels. Compared to fin whales, humpbacks found higher integrated backscatter and had higher aggregative thresholds, but had lower feeding thresholds. Findings aligned overall with the expectations that aggregative behavior is responsive to local prey supply while feeding thresholds are governed by the less mutable energetic constraints imposed by body size and feeding mode. For both threshold types, their response curve appeared to be a function of local conditions: as total krill-like backscatter increased, feeding thresholds stabilized (became more nonlinear and more nonrandom), while aggregative thresholds destabilized. All results emphasized the importance of incorporating observations of feeding effort in studies of prey preference and habitat use.
INTRODUCTION

Organisms respond to changes in resource supply first functionally (changes in behavior or distribution, Solomon 1949), then possibly developmentally (changes in growth rates, Murdoch & Oaten 1975), and ultimately numerically (changes in demographic rates, Solomon 1949). The modes of response that are most ecologically relevant to foraging success and population stability depends on the details of a species’ natural history. For long-lived, mobile predators such as baleen whales (Cetacea: Mysticeti), whose prey resources are patchy in space and ephemeral in time, the predominant mode of response is functional.

Hollings (1965) provided a formal framework for the varieties of functional response. His Type III S-curve represents a density-dependent “threshold” response, in which the proportion of prey destroyed initially increases nonlinearly with prey density until an inflection point, above which the proportion destroyed declines asymptotically. Parker & Boseman (1954) proposed an energetic mechanism for threshold response, suggesting that the basking shark (Cetorhinus maximus) would be “feeding at a loss” (Sims 1999) unless it maintained a close association to areas with anomalously high zooplankton density. Energetic thresholds are expected to be high for sharks, whales, and other pelagic predators because the metabolism and mobility essential to their life strategies in water require activity levels and body plans that are energy-intensive to maintain (Alexander 2005). Mobility is thus double-edged, conferring access to a larger foraging area but reducing the proportion of usable area above the profitability threshold.

Aggregative thresholds
Aggregative thresholds, in which predator densities respond to plant/prey densities in a Type III curve, have been documented in several taxa and systems: waterfowl (van Eerden 1984, Mitchell et al., 1994, De Leeuw 1999, Lovvorn et al., 2013), coastal benthic systems (Hines et al., 1997, Stillman et al., 2005, Seitz et al., 2008), terrestrial systems (Forcardi et al., 1996), sharks (Parker & Boseman 1954, Sims 1999) and seabirds (Piatt 1990). Many studies of aggregative response have aligned well with the predictions of energetic models (Lovvorn and Gillingham 1996, Sims 1999, Sponberg & Lodge 2005, Nolet et al., 2006, but see Lovvorn et al., 2013). Predators can aggregate for reasons unrelated to foraging, such as reproduction or safety from other predators, but here our scope is restricted to aggregative foraging response.

That baleen whales associate with very dense prey patches is a common finding (Dolphin 1987, Mayo and Marx 1990, Croll et al., 2001, Croll et al., 2005, Friedlaender et al., 2006, Witteveen et al., 2008, Goldbogen et al., 2011), but Piatt and Methven (1992) was the first of only two studies to observe threshold aggregative response in a whale species (in their case: the humpback, *Megaptera novaengliae*) to increasing prey (capelin, *Mallotus villosus*) within a defined area (Witless Bay, Newfoundland). The other study is Feyrer & Duffus (2015; gray whales, *Eschrichtius robustus*, feeding upon mysids, f. Mysidae, off west Vancouver Island). Recent models of whale-prey association have found nonlinear relationships in their model output that are suggestive of nonlinear and sigmoid- or Hollings-type responses (Friedlaender et al., 2006).

**Feeding thresholds**

Aggregative thresholds govern predator position with respect to available prey, at which point a predator must decide whether or not to feed. Thresholds of feeding response
may also exist for certain species, but published examples are few for marine predators. Mayo and Marx (1990) documented a possible feeding threshold in North Atlantic right whales (*Eubalaena glacialis*), and Feyrer and Duffus (2015) observed a feeding threshold in gray whales.

The lunge feeding mode of rorqual whales (f. Balaenopteridae) distinguishes these predators, the ocean’s largest, from other filter feeders such as right whales and from other marine homeotherms such as seabirds. The energetic costs of lunge feeding are extreme (Goldbogen et al., 2007), and combine with the inherently high metabolic needs of rorquals to prescribe superlative feeding thresholds that have been predicted by modeling (Goldbogen et al., 2010) but rarely observed.

The paucity of feeding threshold examples could be due either to the complex study design needed to identify them or to the conflation of the two threshold types in the literature. Comparing the two types is even more difficult, since prey sampling near feeding predators must occur during systematic, scale-appropriate surveys of predator and prey within a defined area. Feyrer and Duffus (2015) were the first to attempt this comparison. They found that the feeding threshold for gray whales, which are not true lunge feeders, in response to increasing densities of benthic mysids was lower than the aggregative threshold (by roughly half).

The two threshold types need not occur at the same prey densities, though they may be related. If the energetic cost of feeding is negligible (e.g., passive filter feeding while traveling), energy deficits can be partially offset even in areas with sub-threshold prey densities, thus increasing the chances of satiation once adequate patches are found. But when the act of feeding is costly, as in the case of rorquals, starving may be more energy-conserving than feeding. It follows that feeding thresholds should occur at different prey densities than aggregative thresholds in certain taxa, with potentially profound ecological implications (see below).
Threshold ecology

Both types of threshold response are expected to influence ecosystem stability and resilience. In a “concurrent” density-dependent interaction (in which enemy/predator increases with host/prey density), Solomon (1949) hypothesized that the predator’s regulation of prey would “relax” at low prey density, resulting in prey “conservation”. Referencing that study as well as Tinbergen & Klomp (1959), Hollings (1965) posited that Type III responses dampen the oscillations typical of predator-prey dynamics and would be more effective than other response types at returning prey to an equilibrium density, thus lowering the prey population’s extinction threshold. Hollings also predicted species-specific thresholds, which may promote the coexistence of predator species sharing a single prey resource (Abrams 1983). Hassell & May (1974) emphasized that in a spatially heterogeneous prey field, functional response has a strong spatial (aggregative) component that could serve to stabilize prey. These expectations are largely based in simulation and theory, difficult to document in real systems.

The ecological implications of aggregative and feeding thresholds may also differ in important ways. The former governs the geographic distribution of predators and their ecological impact, both trophic and otherwise (e.g., the facilitation or displacement of other predators; nutrient redistribution through defecation; parasite transmission, etc.; Roman et al., 2014). Strong aggregative response can concentrate and intensify such impacts within small portions of available habitat, exacerbating local top-down regulation. Aggregative thresholds may also be context-dependent, such that threshold height changes as a function of prey supply and ecosystem state (Piatt 1990, Piatt and Methven 1992, Feyrer and Duffus 2015).

In contrast, a feeding threshold response is a binary behavioral shift (feeding or not) defined by inherent energetic constraints that should not be context-dependent (though this has
never been shown). A high feeding threshold implies high trophic impact in terms of the quantity and rate of biomass removal. If the two threshold types occur at different prey densities, a predator’s trophic impact (i.e., feeding) would be spatially decoupled from its non-trophic contributions to a system (e.g., nutrient redistribution through defecation, parasite transport, etc.; Roman et al., 2014). The potential difference in the impact of the two types, therefore, may depend upon their difference in “height” (prey density at threshold). These hypotheses highlight the need for studies that observe both threshold types simultaneously.

Aggregative and feeding thresholds also have consequences for the conservation and monitoring of marine predators, since predators may appear spatially and behaviorally decoupled to prey and the habitat drivers of prey when prey densities are far below or far above the vicinity of the threshold. In efforts to identify habitats critical to the recovery of threatened marine predators, it is paramount to understand the dynamics of threshold foraging behavior in a given study site.

Objectives

The recent return of recovering humpback and fin whale (*Balaenoptera physalus*) populations to a fjord system in northern British Columbia, where they had been removed by industrial whaling (Ford 2014), presents an opportunity to compare the relationship between aggregative and feeding thresholds in two rorqual species simultaneously within a relatively confined and unique marine habitat. Using an ecosystem sampling design that combines systematic surveys with close observations of whales, I first sought to understand which prey-related habitat features govern the spatial pattern and feeding effort of each species. Second, within this broad context of whale-prey interactions, I sought to identify, characterize and compare aggregative and feeding thresholds. Third, I sought to ascertain the context-
dependence of whale-prey associations and both threshold types. Finally, I sought to meet these objectives using analytical approaches that were sensitive to the multiple spatial and temporal scales involved.

METHOIDS

Study Area

Geography

The study area (1,961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland British Columbia (BC), centered at 53°N and 129°W (Fig. 4-1). The KFS contains the marine territory of the Gitga’at and Haisla First Nations, the confined channel portion of several proposed shipping lanes (e.g., Enbridge 2010), critical habitat for several endangered or threatened species and Fisheries Management Area (FMA) 6 for the BC coast (e.g., Ford 2006, FOC 2013, Ford et al., 2013, Linda Nichol, pers. comm.).

This fjord complex extends 140km inland from the Pacific Coast (MacDonald et al., 1983), nested within the Kitimat Ranges of the Great Bear Rainforest, a segment of the largest temperate coastal rainforest in the world (Thompson 1981). An uncommon attribute of this fjord system is its large islands that compartmentalize the fjord into a network of channels. These channels have a typical fjord morphology, with steep bedrock walls and relatively smooth sediment-floored basins separated by high-relief sills (Pickard 1961, MacDonald et al. 1983), though outer channels grade into shallower shelf-type sounds. Douglas Channel, Gardner Canal, and to a lesser extent Surf and Cornwall Inlets, are the primary fjords that feed the system (Pickard 1961).
Oceanography

Spanning the coastal boundary between ocean and the coastal ranges, the KFS is characterized by strong offshore-inshore gradients in climate, oceanographic properties (MacDonald et al., 1983), terrestrial botany and intertidal ecology (Turner 2003). KFS waters are circulated by a combination of three processes: estuarine circulation (forced by freshwater discharge), wind forcing (e.g., katabatic outflows) and tides (MacDonald et al., 1983). The relative importance of each varies according to location, season and timescale. Water movements are further influenced by seasonal patterns and punctuated storm events on the adjacent shelf, which are strongest in autumn (MacDonald et al., 1983).

Whales and diet

Industrial whaling severely depleted humpbacks and fin whales from the coastal fjords of British Columbia, Canada (Ford 2014), but as the North Pacific population recovered they began returning en force in the last two decades (Gregr et al., 2006, Ashe et al., 2013, FOC 2013, Ford 2014, Linda Nichol, pers. comm.). In the spring, seasonally resident humpbacks migrate to the KFS from tropical Pacific breeding grounds, primarily Hawaii (Barlow et al., 2011, Ashe et al., 2013). Most leave the KFS by late fall. During the summer, these humpbacks feed opportunistically upon euphausiids and small schooling fish. Based on field observations and local traditional knowledge, fish prey include herring (Clupea harengus pacifica), sand lance (Ammodytes hexapterus), sardine (Sardinops sagax caerulea) and various species of smelt (f. Osmeridae).

During BC’s commercial whaling period, fin whales were predominantly hunted in BC’s offshore waters past the continental shelf, though 17% of BC fin whale kills between 1908 and 1967 (for which location information is available) took place on the continental shelf in exposed coastal areas (e.g., Hecate Strait and Queen Charlotte Sound) and several
confined waterways along the north-central mainland BC coast (Gregr et al., 2006; COSEWIC 2005). Of these confined water, none were more frequented by fin whales than the waters of the KFS (DFO Cetacean Research Program, unpubl. data). Along with fin whales elsewhere in BC, the species was decimated in the KFS by whaling, and only a handful of alleged sightings occurred in KFS waters between 1968 and 2006, after which fin whales began occurring regularly within the KFS once again (Ford 2014). They have been increasing steadily there ever since (Linda Nichol, pers. comm.).

The majority of North Pacific fin whale diet studies are based on stomach analyses of flensed whales and pertain to regions further offshore or north of BC (Pike 1950). Stomachs contained mainly (sometimes exclusively) euphausiids in these studies, but the proportion of diet components could change significantly between years (Flinn et al., 2002). Other prey species include copepods, fish and cephalopods. The euphausiids preyed upon by fin whales included *Euphausia pacifica*, *Thysanoessa spinifera*, *T. longipes*, and *T. inermis* (Flinn et al., 2002).

**Data collection**

In the summers of 2014 and 2015, whale and ecosystem surveys were conducted aboard the *RV Bangarang*, a 12 m motorsailer, with a team of three researchers. Circuits of the study area were completed within a target duration of 20 days, during which we visited a grid of oceanographic stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys (Table 1-2).

*Visual surveys for whales and debris*
Whale surveys were carried out using line-transect sampling methodology (Buckland et al., 2001). Bearing and reticle readings using Fujinon 7x50 binoculars, min-max-best group size estimates, and cue behaviors for each sighting were recorded by an observation team from a platform 2 m above sea level. At standard intervals observers rotated between three positions, one of which was data entry at the helm. Survey routes were recorded in data entry software interfaced to a Garmin 441s GPS unit with an external antenna mounted atop the radar tower. Whale positions were geo-located using binocular bearing and reticle readings from the observation platform (using R package bangarang, which accounts for horizon obstruction in confined North Pacific channels).

Aggregations of surface debris are a ubiquitous hazard to navigation within fjord systems, but they serve as indicators of tidal mixing and internal wave activity that can aggregate nutrients and plankton and attract nekton (Wolanski & Hamner 1988). Rorquals are known to forage within tidally induced oceanographic features in coastal areas (Chenoweth et al., 2011). During fieldwork we found whales, other marine mammals and seabirds to be regularly associated with areas of dense debris (Fig. 4-2). To quantify debris densities we conducted concurrent strip-width surveys using standard strip-transect methodology typical of seabird surveys (Buckland et al., 2001). The survey strip was 150m on each side of the vessel (300m total), broken into two zones (0-75m, 75-150m) gauged using handheld rangefinders designed for confined channels (Keen et al., 2016). Any type of surface debris, anthropogenic or natural, was noted when it entered the strip. We logged debris type (e.g., rockweed, small and large logs, kelp, etc.), extent, orientation with respect to the axis of the channel, and any associated fauna. Bands of algae (e.g., red tide) were logged as well. Zones of water mixing and surface signatures of internal waves were also noted, collectively referred to as “Beaufort belts” (BFT belts; Fig. 2-2).
**Acoustic backscatter**

Hydroacoustic data were collected with a down-sounding *Syqwest Hydrobox* echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of the ambient depth, distribution, and patchiness of backscatter down to 300m, a range that encompasses the maximum dive recorded for humpback whales (Hamilton et al., 1997) and the common dive range for fin whales (100-230m, Leatherwood and reeves 1983; the maximum recorded dive depths, 470 - 565 were observed in Mediterranean fin whales; Notobartolo-di-Sciara et al., 2003, Panigada et al., 2003). A preliminary study in 2013, with a 500m backscatter range, did not detect any euphausiid-like backscatter below 250m (author, unpubl. data). Details of echosounder data collection and processing are provided in Appendix 5. When odontocetes were seen the echosounder was turned off to minimize disturbance.

**Zooplankton tows**

Three daytime, plummet-style zooplankton tows (333u, 0.7m diameter, OAR 6:1, flowmeter-equipped, dropped to 250m; designed according to Keen 2015) were taken at the stations within each channel. A plummet net is a down-fishing zooplankton sampler that has no mouth obstructions and is cinched shut when the desired depth is reached (Heron 1982). Samples were immediately preserved in 5% Formalin-seawater solution. Euphausiids were identified to species level by collaborators at Oregon State University (Bernard lab).

**Focal follows**

When whales were seen, transect effort was suspended if possible and focal follows were attempted. Focal follow effort commenced once the vessel was within 150m of the animals. Target duration was 5-15 minutes (1–3 km). During these encounters, the team
collected respiration intervals, travel patterns, group composition, identification photographs, behavioral notes, acoustic backscatter (see below), and fecal and prey samples where possible.

While observations were being recorded, the vessel collected acoustic backscatter by tracing the whales’ track at a distance of 100-150m, moving from fluke footprint to footprint in a "mini-zigzag" pattern to achieve a broad sample of the prey field below the group. This zigzag pattern was adjusted as needed to minimize disturbance to the animals, position the observers for identification photographs, and avoid obstacles such as debris and the shore.

Group behavioral state was inferred during the focal follow and recorded along with a confidence level (95%, 66%, or 33%). Behaviors were assigned without knowledge of echosounder backscatter levels. A humpback was inferred to be "feeding" when most or all of the following behaviors were observed: her travel pattern was circuitous or repetitively back-and-forth; her dives were long; her surface sequence comprised relatively many breaths during which the animal was uncommonly still at the surface, suggesting recovery from feeding activity at depth; her first breath of a surface sequence was inordinately boisterous and subsequent breaths were disproportionately meager; and animal orientation changed before the onset of a dive. There were exceptions. Humpback whales sometimes roved with high energy in large, dispersed groups, performing short dives and traveling in tight circles; in such scenarios it was likely that the whales were coralling a shallow prey school and performing sub-surfaces feeding lunges. Other times, when humpbacks were feeding in very shallow areas or in the subtidal zone, dives would be very brief and surface sequences consisted of only one or two breaths.

Other behavioral states included traveling, milling, resting and sleeping. A humpback was inferred to be "traveling" when it was moving in a directed, unchanging course with fairly regular and relatively brief dive intervals and surface sequences in a moderate to fast pace. Whales with no directed course and no indication of feeding were classified as “milling”. This
category was a catch-all that encompassed social behavior and robust actions such as aerial maneuvers and pectoral-slaps. Humpbacks were thought to be "resting" when either still or moving at a very slow, directed pace with relaxed exhalations, uncommon to absent fluking and brief to absent dives. We considered a whale to be "sleeping" if it was absolutely still and completely unresponsive to nearby vessels.

Minor differences in the above rules applied to fin whales, whose behaviors overall were less stereotyped and more difficult to discern based on surface activity. Fin whale travel speeds were overall greater than those for humpbacks, and overall travel pattern was less predictable, particularly during feeding bouts.

Data Preparation

Acoustic backscatter

Acoustic backscatter processing is detailed in Appendix 5. In summary, the Sygwest Hydrobox outputs a pixelated representation of water column backscatter. These pixel data were georectified to account for variable vessel speed and were visually scrutinized to ensure all reflections attributable to seafloor, near-surface water bubbles, propeller cavitation, sonars of passing ships, and whales were removed. In order to reduce each frequency further to display only backscatter of probable whale prey, we filtered data based on patch characteristics and overlapping frequencies so that, to the extent possible, 33kHz backscatter represents small schooling fish while 200kHz backscatter represents euphausiids (Fig. A5-21; see details in Appendix 5 for justification). Deepwater krill imaging and zooplankton tows were used to verify the efficacy of 200kHz backscatter processing methods (Appendix 5).

Middle-priced echosounders like that used in this study can characterize prey-like backscatter but cannot quantify the biomass of constituent taxa. We developed four simple
metrics for each filtered frequency, described below and depicted in Fig. A5-22. These metrics were cross-checked pairwise for collinearity.

4. Total backscatter (T): The mean sum of pixel values of prey-like backscatter; this is a proxy for the quantity of potential prey available. Total backscatter was log-transformed for all analyses; values that were originally 0 were assigned a post-transform value of -1.

5. Backscatter intensity (I): The mean pixel value of prey-like backscatter; this is a proxy that can represent the school density, body size and composition, and/or patch characteristics of potential prey swarms.

6. Mean depth (Z): The mean of the depth distribution of prey-like backscatter.

7. Vertical dispersion (D): The standard deviation of the depth distribution of prey-like backscatter; this is a proxy for the vertical extent of prey swarms; highly dispersed backscatter may be less ideal for batch-feeding predators such as rorqual whales.

Systematic echosounder transects were binned into segments (Fig. 1-2) of approximately 1.2 km (the average distance covered during echosounder sampling in focal follows; Table 4-1). Backscatter metrics were computed for each transect bin.

Behavior designation

For analyses the behavioral states recorded during focal follows were pooled into two categories: Feeding (those inferred to be feeding with confidence 66% or higher) and Other (all other behaviors and confidence levels). Focal follow echograms were reviewed and the apparent predominant prey-type present was recorded as “none”, “krill”, “fish”, or “both”. If classified as “none”, the behavior for the followed whale was changed to “Other”; this step was taken to ensure that results reflected whale-prey interactions rather than data entry prowess. Prey-type designations were also used to modulate behavioral designations according
to the backscatter frequency of interest in prey preference analyses; feeding whales whose backscatter was prey type “fish” were designated as behavioral state “Other” for analyses of 200 kHz backscatter metrics, and vice versa. Behavior for focal follows with prey type “both” remained unchanged. This modulation was not done for spatial distribution analyses such as aggregation GAMs and “condition curves” (below).

Analysis

Analysis was driven by the following sequence of questions, which reflect the study’s three objectives (see Introduction).

1. Which prey conditions are whales targeting?
   a. Which prey-related habitat features are whales associating with, based on systematic surveys?
   b. Are whales aggregating according to the absolute or relative quality of these features?
   c. How do these associations with prey compare to those sampled during focal follows?
   d. To what extent does knowledge about behavioral state improve inferences into prey preferences?
   e. How anomalous, compared to available conditions, are the prey conditions achieved by feeding whales?

2. Do whales exhibit threshold responses to changing prey conditions?
   a. Do whales respond to changing prey conditions in an aggregative threshold response?
   b. Do whales exhibit a threshold feeding response to changing prey conditions?
   c. What is the relationship between aggregative and feeding threshold response?
d. Are thresholds a function of available conditions?

1. Targeted prey conditions

1a. Aggregative relationship to prey conditions

We used generalized additive models (GAMs) to elucidate associations between whale aggregations and prey-related habitat features sampled during systematic transect surveys. The GAM is a modeling approach that relates observations (in our case, whale counts) to predictor variables using non-linear link functions (smoothing or “spline” functions) without imposing parametric limits on the data (Hastie and Tibshirani 1990). GAMs can accommodate highly nonlinear functional relationships (Zuur et al., 2009). GAMS were built using package mgcv (Wood 2011) in R (R Core Team 2013) with gamma set to 1.4 to prevent overspecification (Wood 2011). Poisson, quasi-Poisson, and negative binomial models were explored (with their default link functions) for modeling whale counts on each effort segment.

The study area was split into 26 strata (sensu Chapter 3), such that there were 26 data points for each of 7 surveys (2 in 2014, 5 in 2015; n=159). “Prey conditions” were represented using acoustic backscatter metrics and physiographic variables that may influence prey aggregation (seafloor depth and slope and evidence of tidal fronts). For each datum, the following values were calculated: km of transect effort; number of whales seen for each species; backscatter metrics (Fig. A5-22); mean seafloor depth; and densities of debris and BFT belts (records per km trackline).

Models were built by adding single explanatory variables at a time, building off variable combinations that yielded the lowest AICc (Akaike 1974, Burnham and Anderson 2002) and repeating until AICc no longer improved. Due to our sample size, models that were within 6 AICc of the lowest AICc were considered to be of equivalent fit (Hilbe 2011).
1b. Context-specificity of aggregative response

To determine whether whales are aggregating according to the absolute or relative quality of these features, three versions of the data were fitted to whale counts: absolute conditions (no scaling), conditions scaled by the median of conditions (50th quantile) available during their respective survey months, and conditions scaled by the “best” available conditions (defined here as the 95th quantile for a given survey). AICc was used to determine which data scaling yielded the most explanatory model.

1c. Achieved prey conditions

Environmental sampling during focal follows allowed us to determine the prey-related habitat features achieved by the aggregative behavior surveyed from transects. In addition to visual comparison of sample distributions, the Kolmogorov-Smirnov test (K-S test, Chakravarti and Roy 1967) was used to identify significant differences between prey-related conditions sampled near humpbacks and those near fin whales. K-S tests were used to compare behavioral states, “Feeding” and “Other”, in each species and between species. Species were also compared without distinguishing behavioral states. One-sided tests evaluated the hypotheses that fin whales, being the larger of the two species with greater overall metabolic needs, were found among backscatter with higher total backscatter and higher intensity, concentrated in vertically compact patches (i.e., lower dispersion), at greater depths (based on the pattern that larger species target deeper patches; Friedlaender et al., 2009a, Ryan et al., 2013, and Friedlaender et al and 2015). For each species, feeding whales were hypothesized to achieve higher total backscatter, higher intensity, lower dispersion, at shallower depths (based on optimal foraging theory, Doniol-Valcroze et al., 2011) than non-feeding whales.
**1d. Conditions targeted by feeding whales**

To constrain further the prey conditions that most influence feeding behavior, we used focal follow data to build binomial GAMs of the probability that a whale is feeding or not given local prey-related conditions. Akin to the above procedure for aggregative GAMs, models were built in a stepwise manner and evaluated using AICc. To prevent over-specification, “gamma” input was set to 1.4 (Wood 2011).

To allow interspecific comparison the focus of this analysis was on euphausivory, so focal follows of humpbacks in which the predominant prey was fish were assigned behavior “Other”. BFT belt density was replaced by a variable for tidal state (hours since the previous slack tide, calculated based on publicly available tidal predictions provided by the Canadian Hydrographic Service; Beauchemin Channel station). This was done because the interpolated dataset of BFT belt density was appropriate for spatial modeling but lacks the time-resolution to be relevant to feeding behavior.

**1e. Achieved vs. available prey conditions**

In addition to visual review of sample distributions, K-S tests were used to compare the prey conditions achieved by whales (sampled during focal follows) to those available within the fjord system within the same survey month (sampled during systematic transects). One-sided tests evaluated the hypotheses that whales, in all behavioral states, were found among backscatter with anomalously high total sum, high intensity, low dispersion, and shallow depth (after Doniol-Valcroze et al., 2011). In channels with double-effort (see Fig. 1-2), only half of the transect data were used to build distributions of available conditions that represented the study area accurately.
A second, scale-sensitive approach compared achieved conditions to available conditions at increasing distances from focal follows, the underlying premise being that positioning within the prey field is a central component to foraging strategy. To accomplish this, shortest-path distances were calculated between each focal follow and the centroids of all 1-km transect bins from the same survey month (examples in Fig. 4-3). Transect condition values were averaged such that each focal follow contributed no more than one datum regarding “available” conditions to each kilometer-wide bin from 0 km out to 80 km from the whale. Condition-distance datasets were then pooled from all focal follows for each species and the mean and standard deviation of conditions within each kilometer bin were calculated. This process yielded a “position curve” depicting the mean position of whales with respect to available prey conditions within the fjord system (Fig. 4-4). Position curves were calculated with raw data as well as with data scaled by median available conditions and best available conditions (95th quantile). Scaling was applied for each focal follow before pooling.

Position curve datasets were also used to test the spatial scale of context-dependent feeding behavior. The total 200 kHz backscatter in which whales were and were not feeding were modeled as a simple linear function of available conditions averaged at increasing radii from focal follows (2.5, 5, 10 and 20 km). The slope, regression coefficient and F-statistic p-value of fit models were used to gauge the extent to which patterns in feeding decisions reflect patterns in nearby conditions.

2. Threshold functional response

2a. Aggregative thresholds

To locate thresholds of aggregative response to total 200 kHz backscatter, I adapted the iterative step-function analysis used by Piatt (1990) and Piatt & Methven (1992) for
application within a Likelihood framework. This allowed the same approach to be used for both aggregative and feeding threshold analyses (see below).

A threshold response is a sigmoidal curve best modeled with a binomial regression with logit link function, which contains parameters that determine the inflection point of the curve (threshold, T), the maximum slope of the curve or growth rate (R) and the upper asymptote (K; Fig. 4-5):

\[
f(x) = \frac{K}{1 + e^{-R(x-T)}}
\]

Regression was performed in two stages. Stage 1 was to locate the threshold “height” (prey value at the sigmoid’s inflection point). I fit a binomial regression to 100 possible values spanning the range of sampled backscatter values (removing the 1st and 99th quantiles to avoid boundary issues). During this fit, the sigmoid was forced into a step function (with R equal to the sample size of the dataset) such that K was the only parameter to be constrained using unweighted nonlinear least squares optimization in R (function “nls” in R). The “port” algorithm was used in order to create a lower bound of 0 for the growth rate. The test threshold whose regression returned the minimum AICc value was designated as the threshold.

In stage 2, the model was re-fit to the data allowing both K and R to be optimized. Their optimized values provided a measure of the “strength” and “steepness” of the threshold, respectively (Fig. 4-5). Higher values for K and R indicate a stronger and steeper threshold, respectively.

This process was first applied to unscaled data then repeated for conditions when scaled by median and best (95th quantile) conditions available.
Monte Carlo randomization (Manly 1991) was then used to ascertain the probability that threshold responses apparent in the data could have occurred by chance alone (sensu Piatt 1990). For 1,000 iterations, observed whale densities were randomized with respect to prey observations and AICc of the best-fit model (parameterized using actual observations) was recalculated using the simulated data. The only constraint on randomized data was that the mean density above the threshold had to be greater than that below. The proportion of simulated AICc found to be lower than the observed AICc was interpreted as the probability that the location and shape of the observed response could be the result of random chance. This was taken as a measure of threshold “stability” (Fig. 4-5).

2b. Feeding thresholds

Feeding thresholds were located and tested using the same procedure as above for aggregative thresholds, but whale behavior rather than whale densities were treated as a function of prey-related variables. During model fitting parameter constraints were used to ensure that regions of zero probability predicted by models did not conflict with non-zero data. Due to small sample size of fin whale focal follows (n=33), only a single threshold was calculated for all years pooled.

2c-d. Context-dependence of thresholds

To determine whether aggregative and feeding thresholds are a function of available conditions in general, humpback thresholds for each survey month were plotted against best available conditions. Low sample size (n=6) precluded statistical analysis.
RESULTS

Surveys

Data were collected over 155 days throughout the summers of 2014 and 2015 (Table 1-2), during which 2,291 km of transect surveys were completed (Fig. 1-2). Mean survey duration was 22 days. Two surveys were completed in August – September 2014, and five surveys were completed in June – September 2015.

Sightings

Visual effort yielded 1,688 whale sightings (1,529 humpbacks and 159 fins) and 388 focal follows (338 humpbacks, 50 fins; Table 4-1). Mean focal follow track length was 1.20 km (1.03 km for humpbacks, 2.39 km for fins). 49% of focal follows were of feeding whales (47% for humpback, 62% for fins). Focal follow locations were a representative sample of whale distribution found during surveys (Fig. 4-6).

Euphausiids

Preliminary analysis of local net tows indicate that euphausiid species present include, in descending rank of abundance, *Euphausia pacifica* (by far), followed by *Thysanoessa*, then *T. gregaria* and *T. longipes* (Katelyn Qualls, pers. comm.). *Tessarabrachion oculatum* is also present but extremely rare. Other zooplankton taxa dominated samples numerically, particularly copepods, amphipods and chaetognaths. Detailed results will be published separately.
Targeted prey conditions

Aggregative patterns

Models of whale aggregation as functions of systematically sampled prey condition are summarized in Table 4-2. We found overdispersion in whale count data, and the negative binomial model was selected over the Poisson and quasi-Poisson models based on visual inspection of quantile-quantile plots. For humpback whales, 5 of the 27 model fits were AICc-equivalent. These best-fit models included the variables seafloor depth, total backscatter (both frequencies), 200 kHz dispersion and 200 kHz patch depth. Context-agnostic models explain humpback aggregation as fully as context-scaled models (AICc difference between rank 1 and 2 models, or \( \Delta \text{AICc} = 2.9; r^2 \) of best fit = 0.42).

For fin whales, 2 of the 30 models fit were AICc-equivalent. These best-fit models included the variables seafloor depth, total backscatter (both frequencies), 200 kHz dispersion, and BFT belt density. Julian day was a significant variable for both species, reflecting seasonal changes in density. Fin whale aggregation is most explicable when using prey variables that are scaled by the best available conditions (95\(^{\text{th}}\) quantile; \( \Delta \text{AICc} = 15.1; r^2 = 0.87 \)).

Spline functions provided insight into the relationships between prey variables and whale densities (Fig. 4-7). They indicate that humpbacks were more associated with moderate seafloor depths with high-total 200 kHz backscatter that is relatively dispersed at an optimum depth of 95-115m. Humpback distribution is governed more by krill-like backscatter than by fish-like backscatter, but at very high concentrations the 33 kHz backscatter gains some influence. Humpbacks exhibit no significant relationships to the density of BFT belts or debris.
Spline functions indicate that fin whales were more associated with the deepest available waters with high-total patches of 200 kHz backscatter that, contrary to what might be expected, are vertically dispersed. Also surprising is that total backscatter influences aggregative response only up to a relatively low value, beyond which the response curve flattens. Fins exhibit a negative relationship with areas of high densities of debris and tidal features.

Achieved prey conditions

Violin plots (Fig. 4-8) and cumulative distribution functions (Fig. 4-9) of the prey conditions sampled during focal follows revealed the importance of incorporating behavioral observations in prey preference studies, particularly when comparing two predator species. Strong differences in achieved conditions between feeding and non-feeding whales were evident for some prey conditions (particularly total backscatter) but not all (e.g., debris density, 200 kHz intensity and dispersion, etc.). In general, feeding whales were found within a more restricted range of conditions than non-feeding whales. Kolmogorov-Smirnov (K-S) tests corroborated these findings (Table 4-3).

Interspecific differences: Humpbacks of all behavioral states were found in a greater range of conditions than fin whales. Without behavioral resolution, the only significant preference differences between species were that humpbacks were found in higher 200 kHz intensity (p = 0.997) and fin whales were found among deeper patches (p = 0.032). For feeding whales, humpbacks were found in greater 200 kHz intensity (p=0.998) and fins again were found among deeper patches (p = 0.007). Non-feeding humpbacks were also found among significantly higher 200 kHz intensity than non-feeding fins (p = 0.962), with no difference in patch depth (p=0.244).
**Intraspecific differences:** Humpbacks that were feeding achieved higher backscatter total and intensity than non-feeding humpbacks (p < 0.0001 for both frequencies), but there was no difference in dispersion (p = 0.387) or patch depth (p = 0.115). Feeding fin whales were found in higher 200 kHz backscatter totals (p < 0.001) and lower dispersion (p = 0.014) than non-feeding fins, suggesting (contrary to aggregative GAM results) that fins were also targeting vertically compact prey layers.

**2015 monthly differences:** A large sample size in 2015 allowed humpback focal follows to be examined by survey month. Violin plots demonstrate that feeding humpbacks generally occurred in a more restricted range of conditions than non-feeding animals (Fig. 4-10). Feeding whales were found in higher total backscatter with slightly higher intensity and slightly less dispersion. No strong inter-behavioral differences were evident for patch depth, seafloor depth, or debris densities. Throughout the summer, the discrepancy between behavioral states increased for total backscatter; non-feeding conditions declined while feeding conditions remained consistent. Achieved 200 kHz patch depth and dispersion increased throughout summer for both behavioral states. Whale distribution also became more dispersed and trended further inland (measured as distance from the fjord source; see Chapter 3).

K-S test results for the comparison of monthly condition distributions (Fig. 4-11) are reported in Table 4-4. Feeding humpbacks achieved significantly different total 200 kHz backscatter than non-feeders in all months except June 2015 (p=0.4483; this was the month with highest overall total backscatter in the study area). Feeding whales targeted higher intensity prey patches in most but not all months. In 2014 achieved patch depth was shallower in feeding whales, but there was no difference between behavioral states in any month of 2015; dispersion was lower for feeding humpbacks in September 2015 only (p = 0.0242).
Sample size for humpbacks feeding upon fish-like backscatter was too low for month-resolved analysis.

**Conditions targeted by feeding whales**

Based on focal follow GAMs, prey conditions were better predictors of whale behavioral state for fin whales ($r^2=0.48$) than for humpbacks ($r^2=0.18$), and humpbacks appear to toggle feeding behavior according to a more complex suite of patch characteristics (Table 4-5). For humpbacks 30 models were fit and 4 were AICc-equivalent. All variables but 200 kHz patch depth were included in one or more of these best-fit models, of which the following were significant at conventional levels: total 200 kHz ($p < 0.0001$), intensity ($p < 0.01$), seafloor depth and tidal state ($p < 0.05$). For fin whales 15 models were fit, of which 8 were AICc-equivalent (discerning model fit was impaired by low sample size, n=45). All variables were included in at least one best-fit model, but total 200 kHz was the only significant predictor ($p < 0.05$).

**Achieved vs. available prey conditions**

Histograms (Fig. 4-12) and cumulative distributions (Figs. 4-9 and 4-11) reveal the ability of whales to locate anomalous prey conditions for certain variables, particularly for total backscatter metrics. K-S tests corroborate this and again demonstrate the importance of behavioral resolution in discerning prey preferences (Tables 4-3 and 4-4).

Ignoring behavioral state, humpbacks targeted areas with exceptionally high total 200 kHz backscatter ($p < 0.0001$) of high intensities ($p < 0.0001$) and great depth ($p = 0.996$). Fin whales targeted relatively high total backscatter ($p < 0.0001$) of great depth (both $p < 0.001$), but not of particularly high intensity ($p = 0.386$). Non-feeding humpbacks were found among higher total 200 kHz and patch depth ($p < 0.001$ and $p = 0.997$, respectively), but no
differences were found between achieved and available conditions for non-feeding fins. Feeding humpbacks achieved significantly different conditions than those available for all variables except dispersion, while feeding fins achieved higher total backscatter and greater patch depths only.

Feeding humpbacks found anomalously intense 200 kHz backscatter in 4 of the 6 survey months (exceptions were August 2014 and September 2015). Achieved dispersion was exceptional in September 2015 only (p < 0.001), and achieved patch depth was exceptional only in August and September 2015 (p = 0.977 and p = 0.998, respectively). In 2015, feeding humpbacks found anomalously high total 200 kHz in all months (p < 0.0001 except June 2015, p = 0.0036).

**Achieved positioning**

Position curves demonstrate that species are achieving strategic positioning with respect to the available spatial distribution of some but not all prey-related habitat features (Fig. 4-13). The most salient patterns were found for total 200 kHz, patch depth and seafloor depth. Both humpback and fins, of both behavioral states, are positioned in the greatest 200 kHz patch depths. There was no obvious positioning pattern for 200 kHz dispersion or total 33 kHz curves. These findings corroborate those of transect GAMs and focal follow GAMs that, on average, neither humpbacks nor fin whales are positioning themselves within prey space according to fish-like backscatter conditions. The jaggedness of fin whale position curves is a product of low sample size.

Position curves were notably different between behavioral states for total 200 kHz backscatter for both species, 200 kHz patch depth for fin whales (feeding whales were positioned in the deepest patches available in the study area) and 200 kHz intensity for humpbacks (which spiked within 5km of feeding whales).
Feeding whales were positioned in better conditions than non-feeding whales at both immediate scales and beyond. Feeding humpbacks, for example, remained on average among the highest total 200 kHz backscatter available within the study area; their position curve rises monotonically to the whales’ mouths from more than 30 km away. The non-feeding curve begins similarly but levels off after only 15 km.

Position curves resolved prey associations that were unclear or contradictory in other analyses. Fin whales feed in broad areas of high dispersion, but dispersion appeared to decline within 5 km of the fin whales sampled. This may explain the discrepancy between their aggregative relationship with high dispersion (found in transect GAMs) and their feeding relationship with low dispersion (found in behavior modeling based on focal follow data).

Position curves of 2015 humpbacks elucidate how dynamic spatial relationships between whales and prey-related habitat features can be from month to month (Fig. 4-14). Two notable findings are that 1) contrary to the 200 kHz patch depth curve in Fig. 4-13, patch depth is not maximized in every month, and 2) that, for total 200 kHz, the spatial radius of condition optimization declines month to month; in the prey-rich month of June humpbacks are at the summit of a broad, tall position curve that begins ascending monotonically 40 km away. By the prey-poor month of September, the monotonic increase begins only 5 km away, beyond which the position curve flat-lines. This pattern suggests that the spatial scale of whale-prey spatial association is a function of prey supply, and could explain instances of weak prey association found in studies using systematic survey methods (e.g., Logerwell & Hargreaves 1996; this dissertation, Chapter 3).

Scaled position curves (Fig. 4-15) indicate that feeding humpbacks and fins are positioning themselves on average among total 200 kHz conditions that are nearly twice the median available in the study area. Conditions are above-median approximately 25 km out
from humpbacks but only 10km out from fin whales. Their mean achieved condition is just less than the 95\textsuperscript{th} quantile of available conditions in the study area.

\textit{Spatial scale of context-dependence}

As expected for both species, correlation between achieved and available conditions decreased with increasing spatial scale used to measure available conditions (Fig. 4-16). Available conditions were strongly correlated to conditions achieved by non-feeding whales out to moderate spatial scales (out to 20 km from the focal follow), but correlations with feeding conditions were weaker and more spatially confined. For humpbacks, feeding conditions were correlated to available conditions at radii 2.5 km (\(p < 0.001, r^2=0.17\)) and 5 km (\(p < 0.001, r^2=0.01\)), but not beyond. Non-feeding conditions were correlated to those available at all radii tested (\(p < 0.001\) for all models). For fins, conditions amid feeding whales were correlated to available conditions only at radius 2.5km (\(p < 0.001, r^2=0.45\)). Correlation for non-feeders was found out to 5km only.

These differences signify that non-feeding conditions will reflect patterns of aggregation, while feeding conditions should only reflect the conditions in which it is energetically appropriate to feed. The spatially limited relationship found in feeding whales indicates that feeding decisions are in fact informed to some extent by nearby available conditions. This may explain the low predictive power of feeding GAMs, which did not account for local context. Interestingly, feeding focal follows appeared more strongly correlated to available conditions only when available conditions were high (see feeding humpbacks at radius 2.5 km, Fig. 4-16), implying that feeding decisions are context-dependent only above a minimum threshold value.
Threshold functional response

Aggregative thresholds

There was stronger evidence for threshold aggregative response in humpbacks than fin whales (Table 4-6, Figs. 4-17). Humpbacks also had a higher threshold than fins overall (3.28 vs. 2.54 total 200 kHz) and in each year (2014: 5.08 vs. 3.28; 2015: 3.16 vs. 2.58). For humpbacks, the aggregative threshold was placed at 75% of median available conditions and 53% of best available conditions (for fin whales, 59% and 42%, respectively).

Monte Carlo randomization indicated that the thresholds fit to fin whale aggregation were not significantly non-random (p = 0.076 for pooled dataset). Thresholds were much more stable for humpbacks in general (p < 0.0001 for pooled dataset), though evidence was weak in some months (August 2014, p=0.074; September 2015, p = 0.808). In 2015, threshold height and stability generally decreased from month to month (Fig. 4-18). Thresholds found in raw data had higher stability than those regressed to context-scaled data.

Feeding thresholds

For both species there was strong evidence for feeding thresholds in response to increasing total 200 kHz backscatter (Table 4-7, Fig. 4-19). Based on the entire dataset, the fin whale feeding threshold was higher than that of humpbacks (5.02 at p < 0.001 compared to 4.78 at p < 0.001), but humpbacks did achieve a higher threshold in July 2015 (6.17, p = 0.078). Feeding threshold stability for humpbacks was low in June and July 2015 (Fig. 4-20), the two months with the highest best available conditions of the study. Throughout the 2015 summer humpback feeding threshold stability and steepness increased, but threshold height was variable.
Context-dependence

To explore the context-dependence of foraging strategy overall, available conditions in each survey month were plotted against mean achieved conditions and threshold heights (Table 4-8, Fig. 4-21). With only 6 surveys to compare, statistical tests were not possible. Mean conditions achieved by feeding whales do not appear related to available conditions (Fig. 4-21A), but those achieved by non-feeding do (Fig. 4-21B), causing their ratio (the “feeding ratio”) to decrease with increasing available conditions (Fig. 4-21C). Similarly, feeding thresholds do not appear related to available conditions (Fig. 4-21D), but aggregation thresholds do (Fig. 4-21E), causing their ratio (the “threshold ratio”) to decrease with increasing available conditions (Fig. 4-21F).

Intriguing patterns in these relationships were also found in 2015 humpback data (Fig. 4-22). Best available conditions declined throughout the summer (Fig. 4-22A); this decline is reflected in the mean conditions sampled when with non-feeding whales (Fig. 4-22B). However, the mean conditions in which whales were feeding remained constant (Fig. 4-22C), causing the feeding ratio to increase throughout summer (Fig. 4-22D). Aggregation and feeding thresholds followed similar trajectories, peaking in July then declining through September (Fig. 4-22E and F). This pattern was less dramatic in feeding thresholds, causing the threshold ratio to increase throughout the summer as well (Fig. 4-22G). As best available conditions and the height of aggregation thresholds declined, so too did aggregation threshold stability (reflected in the increasing p-value of Monte Carlo randomization test; Fig. 4-22H). Conversely, feeding threshold stability and steepness increased (Fig. 4-22I and J).
DISCUSSION

Within the context of a complex coastal habitat, in which multiple prey-related habitat features were found to influence whale aggregation and feeding effort, both aggregative and feeding threshold responses to increasing krill supply were observed in two species of rorqual: humpback and fin whale. Overall, findings align with the expectations that aggregative behavior is responsive to local context while feeding thresholds are governed by the less mutable energetic constraints imposed by feeding mode. As a result, the height difference of the two thresholds appears to be context-dependent, as would be the expected ecological implications of their difference (see Introduction). For both threshold types in humpbacks, threshold stability appeared to be a function of local conditions: as total krill-like backscatter increased, aggregative thresholds stabilized and feeding thresholds destabilized (Fig. 4-22). In prey-poor areas, aggregative response seems to degrade to another response type or even into no response at all, while feeding response steepens and stabilizes.

This study explored whale-prey associations from three vantages: systematic distribution surveys, behavioral focal follows, and “position curves”, a novel technique that fuses the first two. While all vantages seem indispensable, I cannot overstate the importance of behavioral observations alongside prey sampling in my objective of identifying the prey-related habitat features that each species is targeting. Results of spatial association modeling based upon systematic surveys were incomplete and, in some cases, misleading. Position curves were particularly useful in explaining the discrepancies between systematic and focal follow findings (see Results).

From all vantages, humpback association with and behavioral response to prey-related habitat features were less predictable and affected by more factors than that of the fin whale, who appeared to be exclusively euphausivorous and interested predominantly in the total
amount and depth of krill-like backscatter within the deepest channels. Humpbacks used more of the study area (Fig. 4-6), fed in a wider range of conditions (Fig. 4-8), fed upon both euphausiids and small schooling fish (Fig. 4-12), toggled feeding effort according to a more complex suite of patch characteristics (Table 4-5), positioned itself more consistently within the best feeding conditions available within the entire study area (Figs. 4-13 and 4-15), adjusted aggregation and feeding decisions based on a larger context radius (Fig. 4-16), found larger prey patches (in both feeding and non-feeding behavioral states, Table 4-8), and exhibited higher aggregative thresholds (Fig. 4-17). And yet, despite all this evidence that humpbacks are “better” foragers within the Kitimat Fjord System than fin whales, the feeding threshold for fin whales was higher than that of humpbacks. These findings, which are in alignment with the expectations of energetics (Goldbogen et al., 2007, 2008), further support the energetic, context-independent basis for feeding threshold height. They also suggest that aggregative thresholds can be a function not only of energetic requirements, but also foraging strategy and habitat familiarity. While humpbacks may benefit from prey patches within this fjord system that far surpass their feeding threshold, they also benefit from being able to feed profitably at lower prey densities than a larger close relative.

The finding that feeding thresholds were generally higher than aggregative thresholds is the opposite of that in the only other whale-focused study that has compared the two threshold types, Feyrer and Duffus (2015). Their disagreement may reflect the energetic differences between gray whale feeding upon benthic and epibenthic prey, in their study, and the rorqual lunge feeding studied here.

That humpbacks were better positioned within prey-rich regions alongside prey-like backscatter that had higher totals, higher intensity and lower vertical dispersion than were fin whales, begs the question of how. It seems key that humpbacks are willing to explore the entirety of the fjord system, rather than just a few of its channels as fin whales do. Beyond
that, however, I hypothesize 1) that humpbacks are more attuned and responsive than fin whales are to oceanographic indicators of foraging opportunities within the fjord system (as suggested by the importance of tidal state in humpback behavioral state, Table 4-6); 2) that humpbacks achieve their intimacy with prey and environmental cues via more thorough strategies of travel and exploratory diving; 3) that the much higher density of humpbacks within the fjord system increases the chances of encountering better prey patches, to which other humpbacks can then be alerted via some acoustic, visual, or otherwise social cue, and 4) that the euphausivorous fish targeted by humpbacks when not feeding upon krill serve to maintain and perhaps even enhance humpback-krill spatial association (J. Pilkington, pers. comm.). Hypotheses 1 and 2 are testable with data from the same fieldwork conducted for this study, and these analyses are forthcoming.

The most curious finding revealed by focal follow sampling and condition curve analysis was that whales were positioning themselves amid the deepest prey patches available (Fig. 4-13), which seems to go against current paradigms of optimal foraging theory (OFT) for rorqual whales (Doniol-Valcroze et al., 2011). This was true for both species, but the pattern was particularly strong for fin whales. Dive-ventilation metrics, collected during the fieldwork for this study, may offer insight into the foraging effort strategies employed by each species within various prey contexts. These analyses are also forthcoming.

Laidre et al. (2010) found a similar preference for deeper krill patches in Greenland whales, but they suspected that it was due to the low krill volume typical of shallow shelf waters. This is not a viable explanation in the present study. Friedlaender et al. (2015) found that blue whales feed deeper for longer dives than sympatric fin whales, proposing that competition may have compelled the two species to partition the prey field. Prey or habitat partitioning has been offered as explanations of prey preference differences in other studies (Friedlaender et al., 2009a, Ryan et al., 2013), which have noted the potential implications for
ecosystem diversity and stability. Humpbacks and fins in the present study system can be said to be competing for the same prey resource, and certain of their prey-related habitat preferences do differ. However, to the extent that “partitioning” also implies a response of predators to their co-occurrence, the findings presented here are compatible with but not suggestive of it. An alternative hypothesis is that euphausiids within the fjord systems are vertically structured by taxon or demography and thus by nutrient content (Decima et al., 2010), which may differentially suit the capture abilities and/or energetic needs of humpbacks and fins.

Fin whales seem to prefer only a few waterways within the Kitimat Fjord System but are consistently positioned among the deepest krill-like backscatter in the deepest waters, and this backscatter is consistently among the highest-total available in any given summer month. These facts may reflect underlying mechanisms, likely oceanographic in nature, that render these fjord channels specifically suitable for fin whales. This in turn may explain the historical importance of this fjord system to fin whales relative to apparently similar systems to the north and south which fin whales rarely use (Ford 2014, Nichol and Ford 2011), and invites particular caution in the assessment of proposed industrial developments within this fjord system.

Like all spatial patterns, that of predator-prey interactions may only be strong, stable, and/or apparent at certain scales (Levin 1992). While overlap with prey must occur on the smallest scale in order for feeding to occur, predators must seek out and position themselves for that opportunity by navigating and assessing prey conditions at multiple nested spatial scales. Position curve analysis proved a particularly enriching means of exploring the spatial scale of interactions between whales and prey-related habitat features, and there is much room for further refinement and application of this tool. Care should be taken with its application, however, as its value is contingent upon the appropriate balance of scales in survey design;
spatial coverage must sufficiently comprehend available habitat and temporal coverage must be sufficiently synoptic. The multiple perspectives used in this study, and the emergent insight they yielded, was made possible by the dual design of systematic surveys punctuated by focal follows, with oceanographic sampling during both research modes. Further implementation of this dual design in coastal systems would be of great value as we strive to understand, appreciate and restore the role of large pelagic predators in marine systems.

ACKNOWLEDGEMENTS

This chapter, in part, is a reprint of material as it appears in *Ecosphere*, 2017: Keen, EM. (In press) “Aggregative and feeding thresholds of sympatric whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.

In addition to front matter acknowledgments, Katie Qualls provided preliminary analyses on euphausiid data.
Table 4-1. Whale sightings and focal follows. Sightings are number of individuals seen, reported according to observation effort at time of sighting (Transect or Other). Focal follows are reported according to the whale’s inferred behavioral state. Column km reports kilometers covered by vessel during focal follows.

<table>
<thead>
<tr>
<th>Year</th>
<th>Leg</th>
<th>Species</th>
<th>Effort</th>
<th>Total</th>
<th>Feed</th>
<th>Behavior</th>
<th>All</th>
<th>km</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Transect</td>
<td>Other</td>
<td></td>
<td>Transect</td>
<td>Other</td>
<td></td>
</tr>
<tr>
<td>2014</td>
<td>All</td>
<td>Humpback</td>
<td>212</td>
<td>283</td>
<td>495</td>
<td>56</td>
<td>60</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>34</td>
<td>35</td>
<td>69</td>
<td>12</td>
<td>12</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Humpback</td>
<td>121</td>
<td>194</td>
<td>315</td>
<td>37</td>
<td>35</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>26</td>
<td>24</td>
<td>50</td>
<td>8</td>
<td>9</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Humpback</td>
<td>91</td>
<td>89</td>
<td>180</td>
<td>19</td>
<td>25</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>8</td>
<td>11</td>
<td>19</td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>2015</td>
<td>All</td>
<td>Humpback</td>
<td>416</td>
<td>618</td>
<td>1034</td>
<td>104</td>
<td>118</td>
<td>222</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>42</td>
<td>48</td>
<td>90</td>
<td>19</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>Humpback</td>
<td>61</td>
<td>89</td>
<td>150</td>
<td>21</td>
<td>24</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>3</td>
<td>8</td>
<td>11</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Humpback</td>
<td>69</td>
<td>108</td>
<td>177</td>
<td>26</td>
<td>25</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>0</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Humpback</td>
<td>78</td>
<td>70</td>
<td>148</td>
<td>16</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>5</td>
<td>13</td>
<td>18</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Humpback</td>
<td>127</td>
<td>214</td>
<td>341</td>
<td>21</td>
<td>36</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>17</td>
<td>8</td>
<td>25</td>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Humpback</td>
<td>81</td>
<td>137</td>
<td>218</td>
<td>20</td>
<td>17</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>17</td>
<td>12</td>
<td>29</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Grand Total</td>
<td>Humpback</td>
<td>628</td>
<td>901</td>
<td>1,529</td>
<td>160</td>
<td>178</td>
<td>338</td>
<td>1.03</td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td>76</td>
<td>83</td>
<td>159</td>
<td>31</td>
<td>19</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td></td>
<td>704</td>
<td>984</td>
<td>1,688</td>
<td>191</td>
<td>197</td>
<td>386</td>
</tr>
</tbody>
</table>
Table 4-2. Best-fit models of whale densities as a function of prey-related habitat features, based on transect data. Models were fit to three versions of the data (column q): raw data, data scaled by the median available conditions during the same survey month (50th quantile), and data scaled by the “best” available conditions (95th quantile). Model fit is described by number of variable combinations tested ($n_{fit}$), the number of AICc-equivalent best-fit models ($n =$), the minimum AICc within that group (Min. AICc), and its $r^2$ (proportion of deviance explained by the model). Backscatter metric abbreviations follow those within Fig. A5-22. The variables included in best-fit models are denoted by their significance level (the highest found within best-fit set).

Significance keys for spline functions of predictors: $ns = p > 0.05$; $* = p \leq 0.05$; $** = p \leq 0.01$; $*** = p \leq 0.001$. Underlined significance level indicates variables included in model with minimum AICc.
<table>
<thead>
<tr>
<th>Model</th>
<th>Species</th>
<th>Fit</th>
<th>Explanatory Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>200 kHz</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humpback</td>
<td>Raw</td>
<td></td>
<td>T</td>
</tr>
<tr>
<td>n=159</td>
<td></td>
<td></td>
<td>27</td>
</tr>
<tr>
<td>50th</td>
<td></td>
<td></td>
<td>26</td>
</tr>
<tr>
<td>95th</td>
<td></td>
<td></td>
<td>26</td>
</tr>
<tr>
<td>Fin</td>
<td>Raw</td>
<td></td>
<td>n=159</td>
</tr>
<tr>
<td></td>
<td>50th</td>
<td></td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>95th</td>
<td></td>
<td>30</td>
</tr>
</tbody>
</table>

- * indicates significance at the 0.05 level.
- ** indicates significance at the 0.01 level.
- *** indicates significance at the 0.001 level.
- ns indicates nonsignificance.
Table 4-3. Results of one-sided Kolmogorov-Smirnov tests for differences among prey conditions (mean ± standard deviation reported for all) achieved by whales (measured during focal follows) and available conditions within the study area (measured during systematic transects, first row of table). Side of test is reported as subscript of p-value; for “p$$^l$$”, $$H_0 = \text{case 1} < \text{case 2}$$; “p$$^g$$”, $$H_0 = \text{case 1} > \text{case 2}$$. Top section compares conditions achieved during behavioral states to those available in study area; middle section compares conditions measured near feeding whales of same species to those near other behavioral states; bottom section compares conditions by humpbacks to those achieved by fin whales. Column $$n$$ reports the sample size used to calculate results (number of focal follows for each behavioral state, Bhr; for Study Area, number of 1-km transect bins). When two sample sizes are reported, the first is for the total 200 kHz test, the second for total 33 kHz. Sample size was too low for 33 kHz tests for fin whales.
<table>
<thead>
<tr>
<th>Species</th>
<th>Bhr</th>
<th>n</th>
<th>200 kHz</th>
<th></th>
<th>33 kHz</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Intensity</td>
<td>Dispersion</td>
<td>Patch Depth</td>
<td>Total</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Study Area</td>
<td>1,739</td>
<td>3.36 ± 2.49</td>
<td>144.13 ± 17.87</td>
<td>10.89 ± 9.72</td>
<td>93.2 ± 38.44</td>
<td>2.33 ± 2.39</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humback</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>350</td>
<td>4.85 ± 2.67</td>
<td>147.95 ± 20.21</td>
<td>10.50 ± 8.76</td>
<td>103.99 ± 31.83</td>
<td>0.49 ± 2.72</td>
<td>p_l &lt; 0.000</td>
<td>p_h &lt; 0.000</td>
<td>p_g = 0.007</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed</td>
<td>136 /</td>
<td>6.43 ± 1.41</td>
<td>150.88 ± 19.46</td>
<td>10.46 ± 8.95</td>
<td>101.21 ± 31.57</td>
<td>5.73 ± 1.12</td>
<td>p_l &lt; 0.000</td>
<td>p_h &lt; 0.000</td>
<td>p_g &lt; 0.000</td>
</tr>
<tr>
<td>40</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>214 /</td>
<td>3.84 ± 2.8</td>
<td>145.76 ± 20.54</td>
<td>10.53 ± 8.64</td>
<td>106.22 ± 31.95</td>
<td>-0.18 ± 2.05</td>
<td>p_l &lt; 0.001</td>
<td>p_h = 0.039</td>
<td>p_g = 0.997</td>
</tr>
<tr>
<td>310</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>47</td>
<td>5.15 ± 2.11</td>
<td>140.92 ± 14.97</td>
<td>11.58 ± 6.87</td>
<td>116.25 ± 26.44</td>
<td>-</td>
<td>p_l &lt; 0.000</td>
<td>p_h = 0.386</td>
<td>p_g = 0.979</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed</td>
<td>27</td>
<td>6.13 ± 1.17</td>
<td>140.33 ± 14.73</td>
<td>9.76 ± 5.16</td>
<td>118.11 ± 23.9</td>
<td>-</td>
<td>p_l &lt; 0.000</td>
<td>p_h = 0.229</td>
<td>p_g = 0.972</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>20</td>
<td>3.78 ± 2.37</td>
<td>141.74 ± 15.63</td>
<td>14.27 ± 8.25</td>
<td>113.52 ± 30.26</td>
<td>-</td>
<td>p_l &lt; 0.001</td>
<td>p_h = 0.928</td>
<td>p_g = 0.993</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humpback Feeding vs Other</td>
<td>p_l &lt; 0.000</td>
<td>p_h &lt; 0.000</td>
<td>p_g = 0.387</td>
<td>p_g = 0.115</td>
<td>p_l &lt; 0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin      Feeding vs Other</td>
<td>p_l &lt; 0.000</td>
<td>p_h = 0.393</td>
<td>p_g = 0.014</td>
<td>p_g = 0.792</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humpback All vs Fin</td>
<td>p_g = 0.412</td>
<td>p_g = 0.997</td>
<td>p_l = 0.832</td>
<td>p_g = 0.032</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed     Humpback vs Fin</td>
<td>p_g = 0.940</td>
<td>p_g = 0.998</td>
<td>p_l = 0.679</td>
<td>p_g = 0.007</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other    Humpback vs Fin</td>
<td>p_g = 0.441</td>
<td>p_g = 0.962</td>
<td>p_l = 0.945</td>
<td>p_g = 0.244</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4-4. Results of Kolmogorov-Smirnov tests for differences among prey conditions (mean ± standard deviation) achieved by feeding and non-feeding humpbacks (“Feed” and “Other” in “Bhvr” column, respectively; measured during focal follows) and available conditions within the study area (“Area”). Data are reported for each year, then for each survey month (Mo.) within each year. Column n reports the sample size used to calculate results (number of focal follows for each behavioral state, Bhvr; for Study Area, number of 1-km transect bins). When two sample sizes are reported, the first is for the total 200 kHz test, the second for total 33 kHz. For each time period, two p-values are given: the first from a one-sided K-S test comparing Feed samples to Area samples (subscript denotes side of test, e.g., $p_{F<A}$ reports probability of $H_0 = $ Feeding < Area), the second from a two-sided K-S test comparing Feed samples to Other samples ($p_{FO}$). Sample size was too low for 33 kHz tests in single months.
## Backscatter Metrics

<table>
<thead>
<tr>
<th>Year</th>
<th>Mo.</th>
<th>Bhr</th>
<th>n</th>
<th>200 kHz</th>
<th>33 kHz</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>Dispersion</td>
</tr>
<tr>
<td><strong>2014</strong></td>
<td>All</td>
<td>Area</td>
<td>457</td>
<td>3.03 ± 2.52</td>
<td>141.99 ± 15.71</td>
</tr>
<tr>
<td></td>
<td>Feed</td>
<td>50/10</td>
<td>6.47 ± 1.41</td>
<td>146.9 ± 20.09</td>
<td>12.64 ± 11.97</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>68/114</td>
<td>4.20 ± 2.55</td>
<td>140.14 ± 15.10</td>
<td>11 ± 9.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>p_{F\leq A} &lt; 0.000</td>
<td>p_{F\leq A} &lt; 0.001</td>
<td>p_{F&gt; A} = 0.862</td>
</tr>
<tr>
<td>Aug</td>
<td>Area</td>
<td>222</td>
<td>3.38 ± 2.63</td>
<td>144.87 ± 17.33</td>
<td>8.03 ± 6.70</td>
</tr>
<tr>
<td></td>
<td>Feed</td>
<td>33</td>
<td>6.46 ± 1.48</td>
<td>141.88 ± 17.28</td>
<td>13.1 ± 13.53</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>39</td>
<td>4.22 ± 2.76</td>
<td>138.67 ± 16.34</td>
<td>10.99 ± 8.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>p_{F\leq A} &lt; 0.000</td>
<td>p_{F\leq A} = 0.134</td>
<td>p_{F&gt; A} = 1.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>p_{F\leq O} &lt; 0.001</td>
<td>p_{F\leq O} = 0.161</td>
<td>p_{F&gt; O} = 0.698</td>
</tr>
<tr>
<td>Sep</td>
<td>Area</td>
<td>235</td>
<td>2.69 ± 2.36</td>
<td>139.17 ± 13.39</td>
<td>11.77 ± 12.14</td>
</tr>
<tr>
<td></td>
<td>Feed</td>
<td>17</td>
<td>6.50 ± 1.29</td>
<td>156.66 ± 22.03</td>
<td>11.76 ± 8.45</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>29</td>
<td>4.16 ± 2.23</td>
<td>142.11 ± 13.30</td>
<td>11.02 ± 10.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>p_{F\leq A} &lt; 0.000</td>
<td>p_{F\leq A} &lt; 0.000</td>
<td>p_{F&gt; A} = 0.632</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>p_{F\leq O} &lt; 0.001</td>
<td>p_{F\leq O} &lt; 0.001</td>
<td>p_{F&gt; O} = 0.702</td>
</tr>
</tbody>
</table>
Table 4. Results of Kolmogorov-Smirnov tests for differences among prey conditions (mean ± standard deviation) achieved by feeding and non-feeding humpbacks ("Feed" and "Other" in "Bhvr" column, respectively; measured during focal follows) and available conditions within the study area ("Area"), continued.
<table>
<thead>
<tr>
<th>Year</th>
<th>Mo.</th>
<th>Bhvr</th>
<th>n</th>
<th>200 kHz</th>
<th>33 kHz</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>Dispersion</td>
</tr>
<tr>
<td>2015</td>
<td></td>
<td>All</td>
<td>1,282</td>
<td>3.48 ± 2.47</td>
<td>44.84 ± 18.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feed</td>
<td>86/30</td>
<td>6.40 ± 1.41</td>
<td>153.19 ± 18.81</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>114/197</td>
<td>3.65 ± 2.92</td>
<td>149.11 ± 22.59</td>
</tr>
<tr>
<td></td>
<td>Jun</td>
<td>Area</td>
<td>262</td>
<td>4.64 ± 2.61</td>
<td>149.9 ± 23.41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feed</td>
<td>20</td>
<td>6.41 ± 1.18</td>
<td>165.98 ± 20.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>25</td>
<td>5.96 ± 1.67</td>
<td>150.01 ± 19.44</td>
</tr>
<tr>
<td></td>
<td>Jul</td>
<td>Area</td>
<td>264</td>
<td>2.14 ± 2.65</td>
<td>144.39 ± 21.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feed</td>
<td>21</td>
<td>6.49 ± 1.99</td>
<td>154.64 ± 16.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>30</td>
<td>3.86 ± 3.03</td>
<td>152.9 ± 20.99</td>
</tr>
<tr>
<td></td>
<td>Aug</td>
<td>Area</td>
<td>243</td>
<td>3.60 ± 2.22</td>
<td>142.88 ± 15.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feed</td>
<td>15</td>
<td>6.80 ± 1.14</td>
<td>155.27 ± 20.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>31</td>
<td>3.14 ± 3.16</td>
<td>145.32 ± 18.46</td>
</tr>
<tr>
<td></td>
<td>Sep</td>
<td>Area</td>
<td>246</td>
<td>4.07 ± 1.82</td>
<td>144.73 ± 10.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Feed</td>
<td>19</td>
<td>6.39 ± 1.30</td>
<td>143.8 ± 13.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Other</td>
<td>15</td>
<td>2.13 ± 2.33</td>
<td>144.65 ± 22.40</td>
</tr>
</tbody>
</table>
**Table 4-5.** Best-fit generalized additive models (GAMs) of the probability that a whale is feeding among krill-like backscatter based on related habitat features sampled during focal follows 2014-2015. \( n = \) total number of focal follows used in each species model; \( n Fe \) = number of \( n \) that were with feeding whales. Model fit is described by number of variable combinations tested (\( n \) fit), the number of AICc-equivalent best-fit models (\( n = \)), the minimum AICc within that group (Min. AICc), and its \( r^2 \) (proportion of deviance explained by model). Explanatory variables included in best-fit model set are denoted by their significance level (the highest found within best-fit models). Backscatter variable abbreviations follow those in Fig. A5-22. Other variables: \( z \) = mean seafloor within 1 km\(^2\) of the geographic centroid of the focal follow; \( \Delta z \) = maximum slope within that same radius; \( \text{tide} \) = hours since the previous slack tide; \( \text{debris} \) = debris sightings per km surveyed. Significance key: ns = \( p > 0.05 \); * = \( p \leq 0.05 \); ** = \( p \leq 0.01 \); *** = \( p \leq 0.001 \). Underlined significance level indicates variables included in model with minimum AICc. Variables not included in a best-fit model are given a dash (-).
<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Fe</th>
<th>n fit</th>
<th>n</th>
<th>Min. AICc</th>
<th>r²</th>
<th>200 kHz backscatter</th>
<th>z</th>
<th>Δz</th>
<th>tide</th>
<th>debris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humpback</td>
<td>277</td>
<td>135</td>
<td>30</td>
<td>4</td>
<td>332.7</td>
<td>.18</td>
<td>*** ** ns</td>
<td>-</td>
<td>** ns</td>
<td>*</td>
<td>ns</td>
</tr>
<tr>
<td>Fin</td>
<td>45</td>
<td>26</td>
<td>15</td>
<td>8</td>
<td>44.6</td>
<td>.48</td>
<td>* ns ns ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>
Table 4-6. Aggregative threshold response of humpback and fin whales to increasing total 200 kHz backscatter. Parameters and fit metrics of regression analyses used to locate thresholds are reported for various temporal subsets (columns Yr, year, and Mo, month) and three versions of scaled data (column $q$): raw data, data scaled by the median available conditions during the same year-month (50th quantile), and data scaled by the “best” available conditions (95th quantile). Parameters correspond to threshold height ($T$), strength ($K$), and steepness, with associated p-values (R; see Fig. 4-5). The p-value of $T$ was determined with Monte Carlo randomization (see Methods). Reported AICc pertains to the second stage of model fitting.

<table>
<thead>
<tr>
<th>Species</th>
<th>Yr</th>
<th>Mo.</th>
<th>$q$</th>
<th>AICc</th>
<th>Threshold</th>
<th>Asymptote</th>
<th>Growth rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$T$</td>
<td>$p$</td>
<td>$K$</td>
</tr>
<tr>
<td>Humpback</td>
<td>All</td>
<td>All</td>
<td>-</td>
<td>-324</td>
<td>2.54</td>
<td>0.076</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>-324</td>
<td>0.59</td>
<td>0.066</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>-322</td>
<td>0.42</td>
<td>0.574</td>
<td>0.05</td>
</tr>
<tr>
<td>'14 All</td>
<td>-</td>
<td></td>
<td></td>
<td>-73</td>
<td>3.28</td>
<td>0.137</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>-72</td>
<td>0.69</td>
<td>0.145</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>-73</td>
<td>0.48</td>
<td>0.152</td>
<td>0.05</td>
</tr>
<tr>
<td>'15 All</td>
<td>-</td>
<td></td>
<td></td>
<td>-247</td>
<td>2.58</td>
<td>0.243</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>-246</td>
<td>0.59</td>
<td>1.000</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>-246</td>
<td>0.40</td>
<td>0.627</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>All</td>
<td>-</td>
<td>240</td>
<td>3.28</td>
<td>$&lt; 0.001$</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>236</td>
<td>0.75</td>
<td>$&lt; 0.001$</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>237</td>
<td>0.53</td>
<td>$&lt; 0.001$</td>
<td>0.52</td>
</tr>
<tr>
<td>'14 All</td>
<td>-</td>
<td></td>
<td></td>
<td>63</td>
<td>5.08</td>
<td>$&lt; 0.001$</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>64</td>
<td>1.16</td>
<td>$&lt; 0.001$</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>63</td>
<td>0.75</td>
<td>$&lt; 0.001$</td>
<td>1.01</td>
</tr>
<tr>
<td>Aug</td>
<td>-</td>
<td></td>
<td></td>
<td>20</td>
<td>3.30</td>
<td>0.074</td>
<td>0.41</td>
</tr>
<tr>
<td>Sep</td>
<td>-</td>
<td></td>
<td></td>
<td>15</td>
<td>5.06</td>
<td>$&lt; 0.001$</td>
<td>0.73</td>
</tr>
<tr>
<td>'15 All</td>
<td>-</td>
<td></td>
<td></td>
<td>172</td>
<td>3.16</td>
<td>0.018</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td></td>
<td></td>
<td>170</td>
<td>0.73</td>
<td>0.011</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>.95</td>
<td></td>
<td></td>
<td>171</td>
<td>0.51</td>
<td>0.036</td>
<td>0.49</td>
</tr>
<tr>
<td>Jun</td>
<td>-</td>
<td></td>
<td></td>
<td>4</td>
<td>5.28</td>
<td>0.002</td>
<td>0.30</td>
</tr>
<tr>
<td>Jul</td>
<td>-</td>
<td></td>
<td></td>
<td>13</td>
<td>6.17</td>
<td>0.006</td>
<td>1.43</td>
</tr>
<tr>
<td>Aug</td>
<td>-</td>
<td></td>
<td></td>
<td>26</td>
<td>3.44</td>
<td>0.028</td>
<td>0.34</td>
</tr>
<tr>
<td>Sep</td>
<td>-</td>
<td></td>
<td></td>
<td>64</td>
<td>1.91</td>
<td>0.808</td>
<td>0.66</td>
</tr>
</tbody>
</table>
Table 4-7. Feeding thresholds of humpback and fin whales in response to increasing total 200 kHz backscatter. Parameters and fit metrics of regression analyses used to locate thresholds are reported for various temporal subsets (columns Yr, year, and Mo, month). Sample size All is the total number of focal follows used, Feed is those of n that were feeding. Parameters correspond to threshold height (T), strength (K), and steepness, with associated p-values (R; see Fig. 4-5). $k_2 - k_1 =$ the difference of mean prey conditions above and below the threshold. The p-value of T was determined with Monte Carlo randomization (see Methods). Reported AICc pertains to the second stage of model fitting.
<table>
<thead>
<tr>
<th>Species</th>
<th>Yr</th>
<th>Mo.</th>
<th>Sample size</th>
<th>Threshold</th>
<th>Asymptote</th>
<th>Growth rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$T$</td>
<td>$k_2 - k_1$</td>
<td>$K$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$p$</td>
<td></td>
<td>$R$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$p$</td>
</tr>
<tr>
<td>Fin</td>
<td>All</td>
<td>All</td>
<td>45</td>
<td>5.02</td>
<td>3.50</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>All</td>
<td>19</td>
<td>$&lt; 0.001$</td>
<td></td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>Hump-back</td>
<td>All</td>
<td>All</td>
<td>276</td>
<td>4.78</td>
<td>3.12</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>All</td>
<td>117</td>
<td>$&lt; 0.001$</td>
<td></td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>‘14</td>
<td>All</td>
<td>103</td>
<td>55</td>
<td>4.80</td>
<td>3.49</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>Aug</td>
<td>62</td>
<td>31</td>
<td>3.39</td>
<td>3.97</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Sep</td>
<td>41</td>
<td>17</td>
<td>4.94</td>
<td>3.37</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>173</td>
<td>87</td>
<td>4.77</td>
<td>3.02</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Jun</td>
<td>43</td>
<td>23</td>
<td>4.69</td>
<td>2.72</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Jul</td>
<td>35</td>
<td>15</td>
<td>6.17</td>
<td>2.73</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Aug</td>
<td>44</td>
<td>28</td>
<td>4.84</td>
<td>2.93</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>Sep</td>
<td>28</td>
<td>10</td>
<td>3.5</td>
<td>3.68</td>
<td>0.78</td>
</tr>
</tbody>
</table>

Sigmoidal Regression
Table 4-8. Summary of major findings. Median and best available conditions are reported (50th and 95th quantiles, respectively, of total 200 kHz backscatter sampled during systematic transects) for various subsets of the 2014-2015 dataset (columns Yr, year, and Mo, month). Mean conditions achieved by each species (Sp; H = humpbacks, F = fins) are reported for feeding whales (Fe) and those in some other behavioral state (Oth), followed by their difference (Δ). Threshold responses are characterized by height (T, in backscatter units), strength (K) and steepness (R) parameters for aggregative and feeding threshold types, and their difference (T_{FE} – T_{AG}). Fin whale summaries were only possible for the total combined dataset due to low sample size.
<table>
<thead>
<tr>
<th>Yr</th>
<th>Mo</th>
<th>50&lt;sup&gt;th&lt;/sup&gt;</th>
<th>95&lt;sup&gt;th&lt;/sup&gt;</th>
<th>Sp</th>
<th>Aggregative</th>
<th>Feeding</th>
<th>T</th>
<th>K</th>
<th>R</th>
<th>T</th>
<th>K</th>
<th>R</th>
<th>$T_{FE} - T_{AG}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>All</td>
<td>3.64</td>
<td>7.02</td>
<td>H</td>
<td>6.43</td>
<td>3.84</td>
<td>2.59</td>
<td>3.28</td>
<td>0.39</td>
<td>20.0</td>
<td>4.78</td>
<td>0.72</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>6.13</td>
<td>3.78</td>
<td>2.35</td>
<td>2.54</td>
<td>0.03</td>
<td>21.7</td>
<td>5.02</td>
<td>0.86</td>
<td>2.50</td>
<td>2.48</td>
<td></td>
</tr>
<tr>
<td>‘14 All</td>
<td>3.29</td>
<td>6.75</td>
<td>H</td>
<td>6.47</td>
<td>4.20</td>
<td>2.27</td>
<td>5.08</td>
<td>1.04</td>
<td>1.3</td>
<td>5.05</td>
<td>0.63</td>
<td>2.0</td>
<td>-0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.28</td>
<td>0.05</td>
<td>245</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>‘15 All</td>
<td>3.84</td>
<td>7.13</td>
<td>H</td>
<td>6.40</td>
<td>3.65</td>
<td>2.75</td>
<td>3.16</td>
<td>0.35</td>
<td>16.5</td>
<td>4.77</td>
<td>0.75</td>
<td>0.7</td>
<td>1.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.58</td>
<td>0.03</td>
<td>131</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

*Each survey*

| ‘14 Aug | 3.71 | 7.02 | H | 6.46 | 4.22 | 2.24 | 3.30 | 0.41 | 94.6 | 3.39 | 0.71 | 10.0 | 0.09 |
| Sep | 2.88 | 6.51 | 6.50 | 4.16 | 2.34 | 5.06 | 0.73 | 311 | 4.94 | 0.65 | 2.5 | -0.12 |
| ‘15 Jun | 5.29 | 7.83 | 6.41 | 5.96 | 0.45 | 5.28 | 0.30 | 232 | 4.69 | 0.86 | 0.1 | -0.59 |
| Jul | 1.85 | 6.87 | 6.49 | 3.86 | 2.63 | 6.17 | 1.43 | 3.0 | 6.17 | 1.00 | 0.4 | 0.00 |
| Aug | 3.85 | 6.78 | 6.80 | 3.14 | 3.66 | 3.44 | 0.34 | 119 | 4.84 | 0.50 | 3.9 | 1.40 |
| Sep | 4.28 | 6.56 | 6.39 | 2.13 | 4.26 | 1.91 | 0.66 | 2.7 | 3.5 | 0.78 | 78.4 | 1.59 |
Figure 4-1. Study area within the Kitimat Fjord System, Gitga’at First Nation territory, British Columbia, Canada. Asterisk (*bottom left*) is treated as the reference point for Ocean Distance measurements.
Figure 4-2. Examples of marine mammal associations with debris and detritus within the Kitimat Fjord System. A. Fin whales feeding within a broad field of logs and smaller debris aggregated by converging tides. B. Another fin whale sighting foraging within debris. C. A humpback whale mother and calf roll in the kelp of the fjord system’s subtidal zone. D. Harbor seals (*Phoca vitulina*) haul out upon large tree falls that are carried into the fjord channels during spring tides.
Figure 4-3. Examples of “whale webs”, the routine used to calculate shortest-path distances (lines) between focal follows (red dot) and 1-km bins of echosounder data (black dots) collected during systematic transect surveys. Panels display examples of the routine for whales occurring in outer (left), central (center) and inner (right) channels of the Kitimat Fjord System.
**Fig 4-4.** Procedure for constructing and analyzing “position curves.” A. In a dual-dual survey design, opportunistic focal follows are conducted within a network of systematic transects, and in both effort modes visual whale data and acoustic backscatter are collected. Transect data can be binned into small lengths (here, 1 km). B. Swimming distances (shortest path) are calculated from the focal follow to each transect bin, placing the whale at the center of a “web” of samples of its habitat. C. For a given habitat variable, its value can be plotted according to its swimming distance from the whale. Curve examples are presented from four focal follows. D. Curves are averaged for all focal follows of a species in a certain behavioral state to produce a “position curve”; black line tracks the mean variable value at increasing distance from the whale, gray bars represent standard deviations.
Figure 4-5. Properties used to characterize threshold response to prey conditions. Variables T, K and R correspond to parameters in the logistic regression. Threshold stability (p-value) is determined with Monte Carlo randomization (see Methods). Example data are behavioral modes (Feed = 1, Other = 0) from August 2015 as a function of total 200 kHz backscatter.
Figure 4-6. Locations of whale sightings (all effort) and focal follows in 2014 (top) and 2015 (bottom) for humpbacks (left) and fin whales (right).
Figure 4-7. Spline functions for best-fit models that predict whale densities based on prey-related habitat variables, both sampled during systematic transect survey effort. Humpback densities were best predicted by absolute measurements (“Abs”, i.e., no scaling). Fin densities were best predicted when prey variables were scaled by “best” available conditions (95th quantile, q=0.95). Gaps occur where variables were not included in any of the AICc-equivalent best-fit models. Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading). See Table 4-2 for detailed results.
Figure 4-8. Distributions of prey-related habitat features, displayed vertically as violin plots, sampled during focal follows in both years for fin whales (grey) and humpbacks (white). Interior box plots show median, interquartile range and outliers. For each species, the distribution of achieved conditions is given for ALL focal follows, for feeding whales (FEED), and all OTHER behaviors. Bottom right: A final metric was included here, the shortest-path distance of whales from the fjord’s “source”, located for this study’s purposes as the asterisk in Fig. 4-1.
Figure 4-9. Cumulative distribution functions (CDF) of acoustic backscatter conditions available in the study area (black line, measured during systematic transect surveys) and those measured during focal follows (colored lines) for humpbacks (top) and fin whales (bottom). Focal follows are displayed by behavioral category. Gray line = all behaviors; Red line = feeding whales; Blue line = other behavioral states. Colored asterisks along x-axis are the mean of their respective distributions.
Figure 4.10. Distributions of prey-related habitat features, displayed vertically as violin plots, sampled during focal follows of humpback whales for each survey month in 2015. For each month, achieved conditions are displayed for whales inferred to be feeding (grey) and all other behavioral states (white). Interior box plots show median, interquartile range and outliers. 

Bottom right: A final metric was included here, the shortest-path distance of whales from the fjord’s “source”, located for this study’s purposes as the asterisk in Fig. 4-1.
Figure 4-11. Cumulative distribution functions of total 200 kHz backscatter available in the study area (black line, sampled during systematic transect surveys) and those measured during focal follows (colored lines) of humpbacks. Data are subset by year (left column, larger panes) then by month within year (smaller panes on right). Focal follows are subset by behavioral category. Gray line = all behaviors; Red line = feeding whales; Blue line = not feeding. Colored asterisks along x-axis are the mean of their respective distributions.
Figure 4-12. Histograms of acoustic backscatter measured during focal follows of feeding whales. Distributions for fin whales (orange) and humpbacks (blue) can be compared to the distribution of “available conditions” (gray) sampled during systematic transect surveys. No feeding fin whales were found among non-zero 33 kHz backscatter levels.
Figure 4-13. Mean positioning of whales with respect to available prey-related habitat features (columns, sampled during systematic surveys), plotted according to distance (km) from the focal follow. “Position curves” for feeding and non-feeding (“Other”) behavioral states are displayed for each species. Black line tracks the mean value within each 1-km distance window of all focal follows; vertical bars represent standard deviation.
Figure 4-14. Mean positioning of humpbacks with respect to available prey-related habitat features (*columns*, sampled during systematic surveys), plotted according to distance (km) from the focal follow, for each survey month of 2015 (*rows*). Black line tracks the mean value within each 1-km distance window of all focal follows; vertical bars represent standard deviation.
Figure 4-15. Mean positioning of humpbacks (left) and fin whales (right) with respect to available total 200 kHz backscatter plotted according to distance (km) from the focal follow. Backscatter were sampled during systematic surveys then scaled by median (top row) and best (95th quantile; bottom row) conditions within the same survey month, such that values occurring above 1.0 are “above-quantile” conditions, and values at 0 km distance are the mean ratio of focal follow conditions to the quantile of available conditions. Black line tracks the mean value within each 1-km distance window of all focal follows; vertical bars represent standard deviation.
Figure 4-16. Krill-like backscatter associations achieved by whales as a function of the mean conditions available to them at increasing distances from the focal follow (columns; sampled during systematic transect surveys). Focal follows (dots) are separated by species then by behavioral state (rows). For each scatterplot, fit of the linear regression (black line) is characterized by correlation coefficient ($r^2$) and p-value of the F-statistic.
Figure 4-17. Aggregative thresholds of humpback (top) and fin whale (bottom) response to changing totals of krill-like acoustic backscatter (x-axis, total 200 kHz). Models were fit to three versions of the data: raw (no scaling, left column), scaled by the median available conditions during the same year-month (50th quantile, center column), and scaled by the “best” available conditions (95th quantile, right column). Thresholds were located by iterative model fitting of sigmoidal regressions (red line) to prey conditions and associated whale densities (dots) sampled during systematic transect surveys. Line graphs atop each scatter plot display AICc scores for each tested threshold; the value corresponding to the minimum AICc was deemed the threshold height. The p-value of the threshold, displayed in each scatterplot, was determined with Monte Carlo randomization (see Methods).
Figure 4-18. Aggregative thresholds of humpback response to changing totals of krill-like acoustic backscatter (x-axis, total 200 kHz) for each year (left column, larger panes) then for each survey month within year (smaller panes on right). Thresholds were located by iterative model fitting of sigmoidal regressions (red line) to prey conditions and associated whale densities (dots) sampled during systematic transect surveys. The p-value of the threshold, displayed in each scatterplot, was determined with Monte Carlo randomization (see Methods).
Figure 4-19. Feeding thresholds of humpback (left) and fin whale (right) in response to changing totals of krill-like acoustic backscatter (x-axis), located by fitting logistic regressions (red line) that model the probability of a whale (dots) feeding (y=1) or not (y=0) given backscatter present. Regressions were fit to each backscatter value within the dataset range; the value whose regression yielded the minimum AICc value was designated as the threshold (line graph atop each scatter plot displays AICc scores for tested thresholds). The p-value of the threshold, displayed in each scatterplot, was determined with Monte Carlo randomization (see Methods).
Figure 4-20. Feeding thresholds of humpback whales in response to changing totals of krill-like acoustic backscatter (x-axis), located by fitting logistic regressions (red line) that model the probability of a whale (dots) feeding (y=1) or not (y=0) given backscatter present. Thresholds were found for each year of data, (left column, larger panes) then for each survey month within year (smaller panes on right). The p-value of the threshold, displayed in each scatterplot, was determined with Monte Carlo randomization (see Methods).
Figure 4-21. Summary of humpback response to changes in the best available krill-like conditions (the 95th quantile of total 200 kHz backscatter sampled during systematic surveys, x-axes). Each dot represents a survey month (n=6, 2 from 2014 and 4 from 2015). A. Mean conditions achieved by feeding whales do not appear related to available conditions, but (B.) those achieved by non-feeding do, causing (C.) their ratio (the “feeding ratio”) to decrease with increasing available conditions. D. Feeding thresholds do not appear related to available conditions, but (E.) aggregation thresholds do, causing (F.) their ratio (the “threshold ratio”) to decrease with increasing available conditions. Far right dot is June 2015. Superimposed lines are simple linear models fit to the 6 data.
Figure 4-22. Month-to-month patterns in the relationship between humpbacks and krill-like prey conditions (total 200 kHz backscatter) in 2015 (June, July, August, September). A. The best-available conditions (95% quantile of backscatter sampled on systematic transects) decline throughout the summer. B. Humpbacks in non-feeding behavioral states are found in declining prey conditions. C. Feeding humpbacks achieve consistent prey conditions throughout the season, causing (D) the ratio between feeding and non-feeding conditions to increase. E. Aggregative thresholds peak then decline, as do (F) feeding thresholds though more slowly, causing their ratio (G) to increase similar to the feeding ratio. H. The p-value of the aggregative threshold (determine by Monte Carlo randomization) increases throughout the summer, but (I) that of the feeding threshold declines. J. The steepness (growth parameter R) of feeding thresholds increases throughout the summer.
CHAPTER 5:

Parsing habitat use strategies of sympatric rorqual whales within a fjord system

*Eric M. Keen, Janie Wray, James F. Pilkington, Kim-Ly Thompson, Chris R. Picard*
ABSTRACT

Evaluating the importance of marine areas for highly mobile predators requires parsing the contributions of prey distribution (food), physical environment (habitat), and time-tested spatial habits (site loyalty) to their strategies of habitat use. To understand the use of British Columbia’s Kitimat Fjord System by sympatric humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*), we sampled whale distribution and feeding effort, oceanography, and prey distribution using systematic surveys and focal follows that spanned two summers (2014 & 2015). Habitat features were found to be strongly associated with whale distribution but not with their feeding effort. Models of whale density based only on habitat features generally performed worse than models based upon food and site loyalty, especially for fin whales. Model comparison suggested that humpback whales were more responsive to prey distribution as well as oceanographic dynamics. Fin whale habitat use appears driven broadly by site loyalty to a select few of the fjord system’s waterways, though within those channels they may be tracking down preferred prey conditions. When interpreted within broader contexts, findings such as these can help identify and manage critical habitat for fin whales in Pacific Canada.

INTRODUCTION

Strong correlations are often found between features of marine habitat and the distribution of mobile predators such as whales and seabirds (Redfern et al., 2006; Ferguson et al., 2006, Panigada et al., 2008; Cotte et al., 2009; Rosa et al., 2012; Bombosch et al., 2014). Such correlations may be expected and can be used to predict distributions, since habitats and strategies of their use are based ultimately in the details of their environment (Guissan and
Thuller 2005). Alone, however, associations do not help us understand how or why a given habitat is used, or whether that habitat is important relative to others in use (Canadas et al., 2005).

In the case of cetaceans, oceanographic and physiographic associations are often assumed to reflect associations with prey (Redfern et al., 2006). Indeed, many studies demonstrate that whale distribution and behavior can be explained largely by their sophisticated attunement to that of their prey (e.g., Piatt and Methven 1992; Friedlaender et al., 2006; Hazen et al., 2009; Benoit-Bird et al., 2013). But such associations with non-prey aspects of their habitat can certainly have non-trophic motivations (e.g., maintenance migrations; Durban and Pitman 2011), or it could be that they are the cause or effect of site loyal behavior, by which whales orient towards or stay within preferred habitat for reasons that may or may not be prey-related. Even if habitat use is motivated by food during the foraging season, it may be that whales achieve sufficient associations with prey by positioning themselves using environmental information other than prey distribution, such as habitat gradients that are more easily tracked than patchy and isolated prey swarms, or strategies based instead upon previous success in an area, such as site loyalty. This may be why the inclusion of prey-related metrics in cetacean habitat models does not always increase model performance (Torres et al., 2008; Barlow et al., 2009; this dissertation, Chapter 3).

Despite these complexities, efforts must be made to understand the balance of strategies governing habitat use in addition to the motivation(s) behind those strategies, since both matters will determine the importance of a habitat for a species and how they might respond to its alteration. For these reasons such information is a typical requirement of critical habitat designation (e.g., U.S. Endangered Species Act, Canada Species At Risk Act). Accounts of habitat use must go beyond the “what” and account for the “how” and the “why”.
Parsing the relationships among whales, their prey, a place and its environment is important in understanding how habitat is used, but the synoptic, scale-appropriate collection of the necessary data for such comparative analyses is challenging and may not be feasible for all species in all habitats. The recent return of recovering humpback whale (*Megaptera novaeangliae*) and fin whale (*Balaenoptera physalus*) populations to a British Columbia fjord system (Ashe et al., 2013; Ford 2014) provides an opportunity to conduct an appropriate study within a relatively compartmentalized and oceanographically dynamic habitat. Chapter 4 reports on the prey types and patch characteristics that govern each species’ aggregation and feeding effort within this fjord system. That same field effort involved oceanographic sampling, enabling us here to compare habitat use strategies employed by the two rorqual species (f. Balaenopteridae) in a synergistic study.

Studies that compare the foraging strategies and habitat use of sympatric whale species were once rare but are increasingly common (e.g., Chapter 4, this dissertation; Friedlaender et al., 2009; Friedlaender et al., 2015; Witteveen et al., 2015; Witteveen and Wynne, 2016). Other than Chapter 4, of most relevance are studies in the nearby Gulf of Alaska that investigated habitat use by sympatric humpback and fin whales (Witteveen et al., 2015; Witteveen and Wynne, 2016), which found that niche partitioning occurred between the two species in some but not all regions studied, suggesting their sympatric relationship was context-dependent. This rich literature can be best augmented with studies that investigate both prey and habitat associations simultaneously, as we endeavor to do here. To do so, we compare habitat preferences based on focal follow sampling. Second, we identify the habitat features that most strongly predict whale distribution, based upon systematic transect surveys, and feeding effort. Third, we evaluate the potential influence of site loyalty in each species’ distribution, also using modeling. Finally, we compare model results to those of prey
association models in Chapter 4 in an effort to parse and rank habitat use strategies in each species.

For our purposes here, we refer to the three habitat use strategies we evaluate simply as *food, habitat, and site loyalty*. Each strategy has an associated statistical model with the same name. The *food* model of habitat use posits that patterns of whale distribution and behavior are best explained by their association with certain qualities of the fjord’s prey field, including prey type, supply (volume), and patch characteristics (e.g., swarm density and vertical distribution). The *habitat* model posits that those patterns are best explained by their association with measurable qualities of the marine environment other than their prey. These are referred to collectively as habitat features, and include bathymetry (fixed habitat features) and oceanography (dynamic habitat features) such as the distributions of salinity, temperature, turbidity and phytoplankton. The *site loyalty* model (abbreviated in tables and figures as “Site”) posits that spatiotemporal patterns are best explained by spatial metrics such as latitude, and longitude, the premise being that habitat use may be driven by simple spatial habits based not upon new information sensed from the environment but instead upon previous experience in the same area. This is a slightly unconventional use of the phrase “site loyalty”, which typically refers to the recurrence of individual whales in the same region across multiple sampling periods, but we felt the terminology was apt given that both uses of the phrase imply 1) that previous success is a driver of current habitat use and 2) that whales are orienting to the site itself, rather than transient conditions of the site, to maximize their chances of meeting their needs (explored further in the Discussion).

METHODS

Study Area
The study area (1,961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland British Columbia (BC), centered at 53°N and 129°W (Fig 3-1). The regional context, fjord morphology and oceanography of the KFS are reviewed in Chapter 2.

In the Chapter 4 study of whale prey preferences and foraging strategy within the KFS, both humpback and fin whales were found to be primarily euphausivorous, positioning themselves within the fjord system in regions of the highest available total krill-like backscatter. Humpback whales were found to feed opportunistically on fish, but not structure their distribution according to fish-like backscatter. Both species, but particularly fin whales, targeted deeper layers of krill-like backscatter, and responded to total backscatter (a proxy for krill volume) with threshold foraging behavior.

Data collection

In the summers of 2014 and 2015, whale and ecosystem surveys were conducted aboard the *RV Bangarang*, a 12 m motorsailer, with a team of three researchers. 2,291 km of transect effort were logged. Surveys of the study area were completed within a mean duration of 22 days, during which we visited a grid of oceanographic stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys. Two surveys were completed in August – September 2014, and 5 surveys were completed in June – September 2015.

Detailed field methods are provided in Chapter 1. Systematic surveys were punctuated by focal follows of encountered whales (field permit DFO XR 83 2014), during which behaviors and acoustic backscatter were recorded. Detailed methods are provided in Chapter 4 for visual surveys and in Appendix 5 for hydroacoustic survey methods. Surveys yielded
1,688 whale sightings (1,529 humpback whales and 159 fin whales) and 388 focal follows
(338 humpback whales, 50 fin whales; Fig 4-5).

During transects, surface water temperature and salinity were sampled at 0.3m depth
every two seconds with a Seabird Electronics (SBE) 45 thermosalinograph. At each station we
performed a Secchi disk reading (8 replicate casts from the same observer) and a water
column sample (down to 250m, seafloor permitting) with a SBE 25plus CTD.

The CTD and its additional sensors measured temperature, salinity, density,
chlorophyll-a, and dissolved oxygen concentration. From these measurements the following
variables were calculated: mixed layer depth, which indicates the degree of near-surface
mixing due to waves and runoff, was calculated as SST - 0.8C (Fiedler 2010); thermocline
was calculated with the differencing technique used in Reilly et al. (1994) and Fiedler and
Talley (2006) and outlined in Fiedler (2010); stratification was calculated as the density
difference between the surface and a standard depth (Behrenfield et al., 2006), in our case 50m
due to regions of shallow seafloor within the study area. For temperature and salinity, mean
values were calculated for the “upper” water column (depths above the thermocline) and the
“bottom” water column (depths below thermocline).

Backscatter and oceanography variables were interpolated to a 0.25 km$^2$ grid of the
study area’s marine habitat. Interpolation was performed using inverse path-weighted
distance, a function that linearly weights combinations of sampled points based on their
distance from the interpolation cell, accounting for land obstruction [16].

Analysis

*Habitat preference comparison*
Surface water sampling during focal follows and interpolated station data allowed us to determine the habitat feature associations achieved by the aggregative whale behavior surveyed from transects. In addition to visual comparison of sample distributions, the Kolmogorov-Smirnov test (K-S test [18]) was used to identify significant differences between conditions sampled near humpback whales and those near fin whales. Two-sided K-S tests were used to compare behavioral states, “Feeding” and “Other”, in each species and between species. Species were also compared without distinguishing behavioral states. K-S tests were also used to compare the habitat features associated with whales (sampled during focal follows) to those available within the fjord system within the same survey month (sampled during systematic transects). The K-S test is suitable here because it is robust to differences in sample size and relatively low sample size. “Position curves”, which depict the mean position of whales with respect to available conditions within the fjord system, were also used to investigate the spatial scale of environmental associations. An explanation of position curves is summarized in Fig 4-4 and detailed in Chapter 4.

**Habitat models**

Chapter 4 elucidates whale associations with prey-related habitat features (i.e., acoustic backscatter, bathymetry and tidal fronts) using generalized additive models (GAMs), and details of acoustic backscatter processing are provided in Appendix 5. Backscatter was characterized using simple metrics: total, or integrated, backscatter; mean pixel intensity; vertical dispersion (the standard deviation of backscatter depth distribution), and the mean backscatter patch depth. GAMs were built using package mgcv (Wood 2011) in R (R Core Team 2013)] with gamma set to 1.4 to prevent overspecification (Wood 2011). GAMs were used to model whale aggregation as a function of prey based on systematic transect data, as well as whale feeding behavior as a function of prey based on focal follows; the negative
binomial and binomial distribution families, respectively, were used to model the two datasets. These findings are summarized in Tables 4-2 and 4-5 and Fig. 4-6.

Mirroring the methodology for whale-prey GAMs (Chapter 4), whale aggregation and feeding effort were modeled as functions of habitat features (fixed bathymetric features and dynamic oceanographic features). Aggregation GAMs (negative binomial, gamma=1.4) predicted whale density using habitat features based on systematic surveys; feeding GAMs (binomial, gamma=1.4) predicted the probability that a whale is feeding using data collected during focal follows.

For aggregation GAMs, the study area was split into 26 strata (Fig 3-6), such that there were 26 measures for each of 7 surveys (2 in 2014, 5 in 2015; n=159). Interpolated habitat variables were averaged within each survey-stratum. Surface salinity and temperature gradients were calculated as the mean range of measurements within 1-km bins of survey effort. For feeding GAMs, variables were calculated by taking the mean of measured and interpolated variables within 1 km² of the geographic centroid of the focal follow.

All candidate variables were tested for pairwise collinearity with a Pearson’s correlation coefficient cutoff of 0.6, which is slightly higher than that used elsewhere (e.g., 0.5 in Zuur et al., 2009). A higher cutoff was necessary given the coupled nature of oceanographic gradients within the fjord system. Variable pairs whose correlation coefficient fell between 0.5 and 0.6 included Julian day ~ surface temperature (Pearson’s $r^2 = -0.52$), Julian day ~ thermocline depth ($r^2 = 0.53$), surface temperature ~ thermocline depth ($r^2 = 0.54$), surface temperature gradient ~ surface salinity gradient ($r^2 = 0.54$), surface salinity ~ euphotic depth ($r^2 = 0.51$), thermocline depth ~ integrated chlorophyll ($r^2 = -0.54$), and euphotic depth ~ integrated chlorophyll ($r^2 = -0.53$). Variable pairs whose correlation exceeded our 0.6 cutoff included distance into fjord ~ stratification ($r^2 = 0.67$), surface salinity ~ stratification ($r^2 = -$
0.86), mixed layer depth ~ thermocline depth ($r^2 = 0.89$), mixed layer depth ~ stratification ($r^2 = 0.61$), thermocline depth ~ stratification ($r^2 = -0.66$).

Given these correlations, we subset our dataset to the following variables: Julian day, seafloor depth, integrated chlorophyll-a, euphotic depth, surface temperature, surface salinity gradient, mixed layer depth, and stratification. Surface salinity gradient was chosen over temperature gradient because 1) surface salinity lacked direct representation within the variable set after its removal due to collinearity with several variables, and 2) because salinity gradients would be more reflective of oceanographic fronts than would surface temperature, which is influenced by local insolation.

Models were built by adding single explanatory variables at a time, building off variable combinations that yielded the lowest AICc (Akaike 1974; Burnham and Anderson 2002) and repeating until AICc no longer improved. Due to our sample size, models that were within 6 AICc of the lowest AICc were considered to be of equivalent fit (Hilbe 2011). Given the low number of fin whale focal follows ($n = 26$), feeding models were only built for humpback whales ($n = 202$). The significance of spline functions was evaluated based on an F-test and output in mgcv result summary.

Site loyalty models

To determine the degree to which whale aggregation could be explained by site loyalty alone, whale density was modeled as a function spatial coordinates, Julian day, or bivariate interactions thereof. GAMs representing 11 combinations of these variables were fit for each species (gamma=1.4).

Because fin whale sightings were confined to a geographically limited subset of the study area (Fig 4-5), it was possible to ask further whether waters in which fin whales are known to occur share any diagnostic oceanographic or prey-related features. To model fin
whale habitat, strata in which a fin whale had been seen at any point during our study (n=10 of 26) was assigned a dummy variable value of 1; all other strata were assigned a 0. GAMs were then built upon food and habitat variable sets to predict the probability that a stratum was known fin whale habitat (binomial distribution family, gamma=1.4). This analysis was not possible for humpback whales, which were seen in all strata of the study area repeatedly throughout fieldwork.

Model comparison

The analyses above and in Chapter 4 resulted in three models of whale aggregation: whale density as functions of food, habitat features, and site loyalty cues. We compared the performance of these models in an effort to parse the strategies underlying whale habitat use. Before comparison, whale~food models from Chapter 4 were re-fit using the reduced dataset of the present study (n=159 and n=140, respectively), in which one of the 7 surveys (Late July 2015) was removed due to lack of oceanographic sampling effort.

Seafloor depth was a complicating variable in this analysis, because it can arguably serve as a variable for any of the three model types: it influences prey patch characteristics and can be used as an aid in feeding (particularly in protected channels such as fjords), it mediates oceanographic processes that determine habitat features, and it can be used for spatial orientation in site-loyal behavior. Rather than constrain this variable arbitrarily to a single model type or generate a fourth model type, all model types were fit twice, once without including seafloor depth as a candidate variable and again including it. The 6 model types for each species were ranked by AICc to compare model fit.

RESULTS
Habitat association comparison

Cumulative distributions (Fig 5-1), and histograms (Figs. A6-1 through A6-3) indicate certain distinct differences in habitat associations between humpback and fin whales, the most apparent being chlorophyll-a (higher in humpback whales), surface salinity (lower in humpback whales), thermocline depth (shallower in humpback whales), and stratification (higher in humpback whales).

In general, humpback whales were found in a greater range of conditions for each habitat feature. Inspection of monthly surveys for humpback whale focal follows (Fig. A6-2) indicate that associated conditions reflect both the state of the fjord system (figures in Chapter 2) and the distribution of humpback whales in a given month (Fig. 4-5). Based on visual exploration, no difference in associated oceanographic features was apparent between feeding and non-feeding whales. Two-sided Kolmogorov-Smirnov (K-S) tests corroborate these findings (Table 5-1 and below). All p-values within this subsection refer to two-sided K-S tests.

Interspecific differences

Humpback and fin whales were found in waters with different seafloor depth (p < 0.01, all behaviors) and slope (p < 0.05 for “All” behaviors only), surface salinity (p < 0.05, all behaviors), euphotic depth (p < 0.05, all behavior) and stratification (p < 0.05 for “All” and “Feed” behaviors only). Based upon distributions (Fig 5-1) and means (Table 5-1), fin whales were found in deeper waters (446 ± 132 m) than were humpback whales (355 ± 158m), with less seafloor slope, higher salinity, deeper euphotic zone, and less stratification. There was no
significant difference for chlorophyll-a concentration, surface temperature, salinity gradient, mixed layer depth, or thermocline depth.

**Behavioral differences**

The only significant difference between feeding and non-feeding whales was found in humpback whales regarding surface salinity gradient ($p = 0.022$); feeding humpback whales were associated with steeper gradients. There was no significant difference in oceanographic features between feeding and non-feeding fin whales. These findings corroborate those of feeding GAMs, that habitat features are better predictors of whale distribution than of feeding effort.

**Associated vs. available environment features**

Differences between habitat features measured with whales and those available in the study area were found visually (Fig 5-1) and with two-sided K-S tests (Table 5-1). With all behaviors pooled, the only humpback whale associations with habitat whose distribution did not differ significantly (i.e., $p > 0.05$) from the distribution of available conditions were chlorophyll-a concentration and euphotic depth; all other variable associations were significant at $p < 0.0001$. The only notable distinction when accounting for behavior was that feeding humpback whales were not found above significantly deep seafloor ($p < 0.099$). Cumulative distributions (Fig 5-1) and means (Table 5-1) indicate that humpback whales fed in waters of relatively high seafloor slope, slightly high temperatures, low salinity, high salinity gradient, low mixed layer and thermocline depths, and high stratification.

Fin whales were associated with relatively deep and steep seafloor ($p < 0.05$, both tests), chlorophyll-a concentration (only when feeding), surface salinity and salinity gradient (only when feeding), euphotic depth and thermocline depth. Cumulative distributions (Fig 5-
1) and means (Table 5-1) indicate that fin whales feed in waters of relatively great depth, low chlorophyll-a levels, high salinity and low salinity gradient and deep euphotic zone.

Position curves (Fig 5-2) confirmed the findings of above analyses that differences in habitat associations between feeding and non-feeding whales were mostly negligible. For humpback whales, many position curves were flat or nearly so, indicating no clear pattern or strategy in positioning; this was the case for chlorophyll-a, surface temperature, and euphotic depth. Position curves for surface salinity and stratification positioning were nearly flat, though their distant spikes indicate that humpback whales consistently concentrate far from the most saline and least-stratified waters of the fjord system (i.e., the outermost channels). A steep curve was found for thermocline depth, suggesting that humpback whales are consistently in the waters with the shallowest available thermocline; this curve appeared steeper for feeding humpback whales. Fin whale position curves demonstrate the species’ preference for waters with the lowest chlorophyll-a levels, highest salinity, deepest euphotic zone and least stratification available. Position curves were nearly flat for surface temperature and thermocline depth.

Position curves of humpback whales from 2015 show how much spatial relationships between whales and habitat features can vary from month to month (Fig 5-3), and afford unique insights into the stability of associations. Positioning patterns with respect to surface salinity and stratification seemed to invert over the course of the summer; while curves were steep from month to month, when averaged together they would cancel each other out to suggest no spatial association whatsoever (Fig 5-2). However, note that while the “tails” of the curves (greater distances) varied strongly from month to month for these two variables, the association at close range varied little; humpback whales remained within surface salinities of approx. 25 – 27 ‰ and within stratification of approx. 5 kg m$^{-3}$ (except August, approx. 6 kg m$^{-3}$). The fact that near-whale conditions were fairly constant while distant conditions varied
greatly suggests that associations with these conditions were being optimized. In contrast, near-whale thermocline depth varied greatly (approx. 8 – 28 m) but was always near the minimum available value, which suggests that this association was seeking a minimum, not an optimum. The third case, in which both near-whale and curve-tail conditions vary widely from month to month such as chlorophyll-a, surface temperature and euphotic depth, suggests an association strategy is either non-existent or seasonally dynamic.

**Habitat models**

**Aggregation models**

Models of whale aggregation as functions of systematically sampled habitat features returned low explanatory power for humpback whales but moderate power for fin whales (Table 5-2). For humpback whales, 7 of the 13 model fits were AICc-equivalent (lowest AICc = 639.9, r² = .23, n = 140; here we define r² as the proportion of null deviance explained). Due to poor overall fit, all variables were used in one or more of the best-fit models; those with the highest significance levels were Julian day (p < 0.05), seafloor depth (p < 0.001), surface salinity gradient (p < 0.05) and mixed layer depth (p < 0.05). The model with lowest AICc included only Julian day, seafloor depth, and mixed-layer depth.

For fin whales, 4 of the 25 model fits were AICc-equivalent (lowest AICc = 167.8, r² = .74, n = 140). Non-significant (p > 0.05) variables included in best-fit models were surface temperature and stratification; significant variables were Julian day (p < 0.05), seafloor depth (p < 0.01), chlorophyll-a (p < 0.05), euphotic depth (p < 0.01) and mixed layer depth (p < 0.01).

Spline functions provided insight into the relationships between significant habitat features and whale densities (Fig. A6-7). They indicate that humpback whales prefer waters
within the Kitimat Fjord System (KFS) that are deep and moderately stratified with strong
gradients in surface salinity and shallow mixed layer. Fin whales prefer KFS waters with deep
seafloor, deep euphotic zone, low chlorophyll-a concentrations, and moderate sea surface
temperatures. There was also a moderate preference for relatively deep mixed layer. For both
species there was little evidence of strongly nonlinear relationships.

*Feeding models*

Based on focal follow GAMs (Table 5-2), habitat features play almost no role in
humpback whale behavioral state (AICc = 277.5, \( r^2 = .06, n=202 \); sample size was too low to
model fin whales conclusively, \( n=26 \)). Of the 23 models fit, 16 were AICc-equivalent, and all
variables occurred in one or more of these best-fit models. No variable spline function
significance was below \( p = 0.05 \) (Table 5-2). Spline functions weakly suggested that
humpback whales are more likely to feed in areas of higher chlorophyll-a concentrations and
shallower seafloor depth (Fig A6-4). The latter association may reflect their common practice
of employing the steep shoreline of the fjord system to corral their prey.

*Site loyalty models*

A general depiction of channel-to-channel differences in food, habitat features, and
whale density within the Kitimat Fjord System is provided in Fig A6-5. Overall, the fit of site
loyalty models were comparable to that of other model types, and fin whale models performed
better than humpback whale models. For humpback whales, of the 11 models fit, 5 were
AICc-equivalent (min. AICc = 640.7, \( r^2 = .25 \); Table 5-3). Spatial variables included in best-fit
models were longitude alone (\( p < 0.001 \)) and the latitude-longitude interaction term (\( p <
0.001 \)). Latitude was included in an interaction term with Julian day (\( p < 0.05 \)) in one best-fit
model. Spline functions (Fig A6-9) indicate that the effect of latitude on the linear predictor
depended on the other term in the interaction; when coupled with Julian day latitude increased the predictor monotonically, but when coupled with longitude the relationship was nonlinear and complex, peaking in central western coordinates (corresponding to Squally Channel, a known hotspot within the fjord system; Fig. 2-1), flattening to the northeast (Gribbell Island waters) and dropping in the northwest region corresponding to the mainland.

For fin whales, of the 11 models fit, 3 were AICc-equivalent (min. AICc=149.2, $r^2 = .78$). The same spatial variables as those listed for humpback whales above were included in best-fit fin whale site loyalty models, but only latitude-longitude and longitude-Julian day were significant ($p < 0.05$ for both). The longitude-latitude spline functions exhibited a peak in the linear predictor in central western waters, similar to humpback whale results, a flat response to the south, and a precipitous decline to the north (the inland channels).

Julian day was included in both species’ sets of best-fit models, but spline functions indicated that it reflected monthly changes in area abundance and apparently did not interact with other variables.

**Fin whale habitat model**

Known fin whale habitat was modeled better by habitat features than by food. Of the 35 prey-related models fit, 12 were AICc-equivalent (min. AICc = 114.1, $r^2 = .48$). All explanatory variables were included in at least one of the best-fit models but only a few had significant spline functions: seafloor depth ($p < 0.01$), total 200 kHz ($p < 0.001$), dispersion ($p < 0.01$), and patch depth ($p < 0.05$). Of the 26 oceanographic models fit, the best model included seafloor depth, mixed layer depth, stratification, and Julian day, but not of these spline functions were significant (AICc = 107.9, $r^2 = .77$). Spline functions (Fig. A6-7) indicate that fin whale habitat is characterized by seafloor depths of at least 200m featuring 200 kHz backscatter that is high in total 200 kHz backscatter, dispersion and patch depth.
These waters have variable mixed layer depth throughout the summer and moderate stratification.

Model comparison

The comparison of models based upon food features (Food), habitat features (Habitat) and site loyalty proxies (Site) revealed the strong influence of seafloor depth on model results (Fig 5-4). When including seafloor depth as a candidate variable, fin whale models were AICc-ranked Food ($r^2 = .92$) < Site ($r^2 = .78$) < Habitat ($r^2 = .74$); without depth, fin models ranked Site ($r^2 = .78$) < Food ($r^2 = .69$) < Habitat ($r^2 = .77$). Seafloor depth did not significantly improve Site model fit ($\Delta$AICc = 1.88; fit equivalence cutoff is $\Delta$AICc = 6 at our sample size of n = 140). When ranked altogether, Food + depth still ranked first but was nearly AIC-equivalent to the Site model without depth ($\Delta$AICc = 6.62). The high $r^2$ value of all models probably reflects the geographically confined use of only a few channels within the study area; the less variable the habitats in use compared to available habitat, the easier it should be to characterize and predict their use. Taken together, these findings suggest that site loyal behavior explains fin whale aggregation nearly as well as the distribution of its prey.

For humpback whales, Food models were top-ranked regardless of the inclusion of depth. When depth was included, models ranked Food ($r^2 = .41$) < Site ($r^2 = .24$) < Habitat ($r^2 = .23$). Without depth, models ranked Food ($r^2 = .30$) < Site ($r^2 = .25$) < Habitat ($r^2 = .18$). When all ranked together, rank 2-5 models were all AICc-equivalent (these were Food, Site + depth, Habitat + depth, and Site). The generally poor fit of humpback models likely reflects 1) the diversity of waters within the fjord system that humpback whales use, 2) temporally dynamic distribution and the possibility that habitat use strategies change throughout the season (see Chapter 3) the relatively diverse diet of area humpbacks, who are known to feed a
minority of the time upon schooling fish (Chapter 4). For both species, Habitat models without depth were ranked last.

**DISCUSSION**

Ecosystem sampling during systematic surveys and opportunistic focal follows of whales within the Kitimat Fjord System (KFS) support several main findings: 1) Habitat features (oceanography and physiography) were strongly associated with the spatial pattern of whale aggregation but not with feeding effort, suggesting that habitat features are more important as cues on all but the smallest scales of the foraging strategies of fin and humpback whales. Despite these strong associations, 2) models of whale density based on habitat features alone generally performed worse than those based on prey distribution and site loyalty proxies, especially for fin whales. 3) Taken together, our findings indicate that humpback whales are more responsive than fin whales to the spatial dynamics of their prey as well as several habitat features, particularly thermocline depth. 4) Fin whale habitat use appears driven broadly by site loyalty to a select few of the fjord system’s waterways, though within those channels they may be seeking preferred prey conditions. Note that the scope of these conclusions are limited to these species’ behavior within the KFS for the years sampled, and may of course change as functions of whale and prey densities, trends in dynamic habitat features (i.e., oceanography), or anthropogenic effects.

In attempting to parse and compare competing strategies of habitat use in two rorquals, our goal was not to identify a single driving strategy for each species, but rather to rank strategies by their relative importance and assess the dimensionality of its overarching strategy. Therefore, our finding that food following was the top ranked strategy for humpbacks is not in conflict with previous work on humpbacks in this area (Chapter 3) that concluded that
food following alone cannot explain their seasonal distribution. Rather, that conclusion is reinforced by the performance of our site loyalty and habitat models.

This study’s design enabled the use of position curves, a technique introduced in Chapter 4, as a new means of examining the spatial scale of whale association with environmental features. We found position curves to be a valuable supplement to traditional modeling approaches when interpreted with caution. Given the spatiotemporal confines of studies such as ours, depictions of habitat use must be interpreted with restraint within broader contexts of knowledge about the region and the species in question. Fjord systems are naturally compartmentalized marine habitats that are tempting to consider in isolation, but the spatial scale of whale habitat use strategy within a given time period may be much larger than the KFS. This is particularly true for fin whales; despite high rates of site loyalty to this system, individuals likely leave to visit other foraging areas regularly throughout the summer (Linda Nichol, pers. comm.). While many humpback whale individuals are known to be resident to the KFS for much of the summer, others are seen here only briefly each year and some are rarely seen again (Ashe et al., 2013).

Whale strategies of habitat use govern their ecological interactions within a system, as well as their responses to system changes. Chapter 4 discussed the degree to which the spatial overlap of humpback and fin whales in fjord system was evidence, along with their shared prey preferences, of habitat partitioning, a tool for co-occurrence that has been proposed for rorquals elsewhere (Friedlaender et al., 2015; Witteveen et al., 2015; Witteveen and Wynne, 2016). The confined range of fin whales in the KFS makes the area of overlap quite limited, which could be either a means of partitioning or a reason it is not necessary. Though sympatric, and though both species are primarily euphausivorous here (Chapter 4), we have found that they appear attuned to different aspects of the area and its habitat. Therefore, their
responses to habitat changes, including anthropogenic impacts, would likely be different in both nature and degree.

**Causes of habitat association**

The relatively weak performance of our habitat-based models may be reflective of weak or confounding reasons for cetacean-habitat associations. In cetacean habitat models, oceanographic and physiographic associations are generally assumed to be an indirect result of associations with prey whose distributions are strongly coupled to oceanography (Redfern et al., 2006). But in other marine tetrapods such as seabirds (Gaston 2004), habitat associations can be used strategically to track environmental indicators that will lead to profitable foraging areas. While examples of this strategy within the Cetacea are few, it may be that whale-habitat associations within the KFS are both the cause and effect of foraging. For example, the diversity of habitat associations we found for humpbacks mirrors the diversity of prey patch features they are associated with (Chapter 4), but the direction of that causal relationship, if one exists, remains elusive. Our analysis did not allow us to parse whale habitat use to this level of detail, and we are not aware of any published study that has. We believe doing so would require a sampling design similar to ours, but analytical techniques require further development.

**Humpback whales**

Our findings can explain those from previous studies in this fjord system, particularly 1) that humpback whales, though a smaller species, find higher-volume prey patches than fin whales and exhibit a higher aggregative threshold response to prey patch volume (Chapter 4);
and 2) that humpback whale habitat use strategies shift throughout the foraging season (Chapter 3). In the present study we found that humpback whales in our study area rely more upon food association and/or a complex, seasonally dynamic site loyalty, both of which would enable association with better food supply during a higher percentage of the foraging season. Furthermore, our finding that humpback whales prefer strong salinity gradients aligns with other studies about the importance of tidal fronts and island wake systems to foraging humpback whales and their congenics ([26] and references therein).

**Low explanatory power**

Overall, oceanographic associations were better modeled for fin whales than for humpback whales. For all three humpback whale modeling exercises (food, habitat, and site loyalty), explanatory power was quite poor relative to fin whales and to humpback-habitat models published elsewhere ([e.g., Rose et al., 2012; Friedlaender et al., 2006]; models were compared anecdotally based upon proportion of deviance explained). This is likely due to the fact that humpbacks used the entirety of our study area, spanning wide ranges in a variety of habitat features. Explanatory power for humpback whale models would likely have been higher if the study included areas where humpback whales are not common. It is possible that our ability to model humpback whale habitat preferences is impaired by their high density within this habitat. Furthermore, humpback whale distribution is known to shift substantially within this fjord system from month to month, such that monthly humpback-habitat associations are more easily modeled (Chapter 3). Fin whales, in contrast, practiced a spatially confined and seasonally stable use of certain channels within the fjord system. Interestingly, this appeared to be a much more significant impairment than sample size; despite nearly an
order of magnitude fewer focal follows of fin whales, the effect size and significance of their distribution models were much better.

**Importance of thermocline / mixed layer depth**

Despite the overall weak habitat model performance, correlation of humpback whale distribution to certain habitat features was unexpectedly strong, in particular the depths of the thermocline and mixed layer. There was also a consistent but weaker relationship with seafloor depth. The humpback–thermocline depth relationship may be instrumental and/or incidental in the species’ foraging strategy within this fjord system, and may couple the species’ use of this fjord habitat to region- and basin-scale trends in climate (Chapter 3 Discussion).

**Fin whales**

**Site loyalty**

In fjord systems, in which oceanographic structure so closely mirrors geography, disaggregating spatial habit from other habitat use strategies is difficult but made easier when whales use only a subset of available habitat. We found fin whale habitat to be distinguishable from the remainder of the fjord system by high total backscatter, deep backscatter depth, deep seafloor and moderate stratification (Fig A6-7), and simple visual review suggests that the channels used by fin whales also have relatively deep euphotic zones and low chlorophyll-a levels (Fig A6-5). The alignment of these findings with our model comparison emphasizes the viability of site loyalty as a habitat use strategy for fin whales within this fjord system and
explains the high rank of site loyalty models over those based upon prey distribution and habitat features alone.

Our findings begin to explain why fin whales use only a subset of channels within the KFS, but there remains evidence that within those channels, fin whales are excellent at associating in areas with deep backscatter (Chapter 4). That is, site loyalty explains fin whale habitat use on the scale of the fjord system, but on the smaller scale of fin whale habitat within it, the species exhibits impressive prey associations.

Throughout this chapter we have used the term “site loyalty” to describe recurring fin whale presence in a habitat that has no strong apparent advantage over adjacent habitat. As mentioned in this chapter’s Introduction, the term more conventionally refers to the recurrence of individuals in the same area explained by previous success there, and forthcoming analyses based on photo-identification from this field effort will demonstrate high return rates of fin whale individuals to the KFS (Linda Nichol, pers. comm.). It should be acknowledged that in both usages, “site loyalty” is itself a proxy for habitat features that can be sensed by whales but which are not accounted for in our measured parameters or modeling techniques. For example, it is possible that fin whales may restrict their KFS distribution to outer channels to preserve escape routes in the case of attack by Bigg’s killer whales, as their flight response requires open and unobstructed waters (Ford and Reeves 2009). Humpback whales are more likely to fight off killer whale attack, and need not avoid inner channels. Flight and fight responses in these respective species have been observed in this fjord system before (authors, field observations), but they are difficult to quantify and include in habitat modeling.

It must also be noted that animals do not orient using a GPS but rather with geographic, meteorological and in some cases astrological landmarks or signs. The means of site loyalty can therefore involve certain environmental features that here we grouped into our habitat models, such as seafloor depth and slope. The implication is that on certain spatial
scales, it may not be possible for us to fully disentangle site loyalty from habitat association using the comparative modeling approach that we invoked. This points back to the complication, mentioned above, that after our analysis it remains unclear whether habitat associations are an end in themselves or a means to stronger associations with a place or its prey.

Ultimately, it could be that all of these strategies are as inextricable in models as they are in nature, given that site loyalty is a time-tested habit shaped recursively by past experiences with a place’s food and habitat features. Our efforts to reduce a habitat use strategy to its constituent parts run the risk of blinding us to the prolonged, dialectical ecological processes that shape them and make them such a rich matter of study.

**Implications for management**

On the larger scale of the entire BC fjordland, it is unclear the extent to which these findings explain why this fjord system is the only one used heavily by fin whales before whaling (citations below) and the only one they have begun to use heavily since the end of whaling (Ford 2014). A considerable concentration of fin whale catches were made in the KFS during 20th century whaling in BC (Gregr et al., 2000; Gregr et al., 2006; COSEWIC 2006), suggesting that fin whales historically used this area as a foraging ground more heavily than any other fjord system on the BC coast. Since the end of whaling, fin whales were not seen regularly within the KFS until 2006 (authors, unpublished data); in the years since, the number of individuals identified here has increased annually, possibly reflecting the recovery of the BC population (Linda Nichol, pers. comm.). To our knowledge this is currently the only habitat in which fin whales can be regularly photo-identified from land. As of 2005 the northeast Pacific fin whale population was an estimated 50% of numbers 60-90 years ago
(COSEWIC 2005), and has been assessed as ‘Threatened’ by COSEWIC (2005) and under the Species at Risk Act (SARA; Gregr et al., 2006). This listing requires critical habitat to be designated, and the KFS’s outer channels have been identified as a potential site (Nichol and Ford 2011; Linda Nichol, pers. comm.).

We are not aware of similar studies in fin whale habitat elsewhere that would allow direct comparison to their use of the KFS. It should be relevant that the Kitimat Fjord System is among the deepest of the British Columbia fjordland (MacDonald et al., 1983), and Squally Channel, the primary area of fin whale use within the KFS, is among the deepest of all mainland channels at 700+ m (NOAA 2013). The area’s low wave energy relative to the exposed coastal zone may contribute to the acoustic quality of KFS habitat (Williams et al., 2013), which may be advantageous for fin whales that rely on vocalization or passive acoustic orientation for summertime habitat use. The northern confined channels are exposed to less shipping noise than those to the south (Erbe et al., 2014), and fin whale habitat within the KFS includes channels that are currently not used by deep-sea shipping (i.e., Squally Channel), but that does not explain the historical importance of these waters. Regional geography might suggest that the KFS serves as a foraging corridor that connects productive areas to the north and south, but that idea lacks support given the paucity of sightings in Estevan Sound (this study; Fig. A6-5) and Principe Channel (Linda Nichol, pers. comm.). Perhaps the most apparent unique attribute of the KFS is that it abuts Moresby Trough, a prominent feature that extends from the KFS entrance across southern Hecate Strait. Moresby Trough is an area of heavy fin whale use (Linda Nichol, pers. comm.); this feature may lead fin whales into the productive waters of the KFS. We emphasize our earlier caution that habitat use within the KFS is a part of a much larger habitat use strategy of the northern BC coastal zone. Regardless of the factors that bring fin whales into the KFS, it remains noteworthy that this fjord system is the only one, out of many within the species’ range in British Columbia and elsewhere, for
which we have record of both their historical use and their recent return. These facts, and the opportunities for further study in this unique setting, compound the potential value of habitat protection in the KFS.

ACKNOWLEDGMENTS

This chapter, in part, is a reprint of material as it appears in PLOS ONE, 2017: Keen, EM, J Wray, JF Pilkington, KL Thompson, JP Barlow, CR Picard. (In press) “Parsing habitat use strategies of sympatric rorqual whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.

In addition to front matter acknowledgments, JW wishes to thank Andy Wright, the Zumwalt family, Julie Walters and Sam Rose.
TABLES

Table 5-1. Results of two-tailed Kolmogorov-Smirnov tests for differences among habitat features (mean ± standard deviation) associated with whales (measured during focal follows) and those available within the study area (measured during systematic transects, first row of table). For study area and species totals, parenthetical displays minimum and maximum recorded values. Top section compares conditions associated with behavioral states to those available in study area; middle section compares conditions measured near feeding whales of same species to those near whales of other behavioral states; bottom section compares humpbacks to fin whales in all behavioral states. \( n \) reports the sample size used to calculate results (number of focal follows for each behavioral state, \( Bhvr \); for Study Area, number of 1-km transect bins). \( \Delta \) seafloor and \( \Delta \) salinity represent gradients in seafloor depth and surface salinity, respectively, in a 1 km\(^2\) radius about transect centroids.
<table>
<thead>
<tr>
<th>Sp.</th>
<th>Bhr</th>
<th>n</th>
<th>Seafloor depth</th>
<th>Surface Temp</th>
<th>Surface Salinity</th>
<th>Δ Salinity</th>
<th>Euphotic Depth</th>
<th>Mixed Layer Depth</th>
<th>Thermocline Depth</th>
<th>Stratification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study Area</td>
<td>1,472</td>
<td>329 ± 164 (0.674)</td>
<td>143 ± 140 (4.48)</td>
<td>81.95 ± 53.69 (20.92, 444.66)</td>
<td>13.18 ± 1.29 (9.5, 19.05)</td>
<td>26.56 ± 2.79 (13.08, 31.73)</td>
<td>0.94 ± 1.17 (0, 8.96)</td>
<td>18.49 ± 6.17 (7.62, 43.91)</td>
<td>7.33 ± 6.64 (1.36, 46.43)</td>
<td>15.83 ± 12.02 (2.69, 62.81)</td>
</tr>
<tr>
<td>Humpback</td>
<td>All</td>
<td>446</td>
<td>355 ± 158 (19.639)</td>
<td>235 ± 165 (9.39)</td>
<td>77.02 ± 42.42 (26.49, 237.33)</td>
<td>13.41 ± 1.17 (10.66, 18.17)</td>
<td>25.88 ± 2.22 (17.47, 31.31)</td>
<td>1.01 ± 1.2 (0.01, 6.01)</td>
<td>18.78 ± 6.59 (8.18, 44.15)</td>
<td>5.55 ± 5.81 (1.51, 44.11)</td>
</tr>
<tr>
<td>Feed</td>
<td>163</td>
<td>340 ± 162 (p &lt; .000)</td>
<td>233 ± 164 (p &lt; .000)</td>
<td>80.39 ± 45.07 (p &lt; .005)</td>
<td>13.37 ± 1.16 (p &lt; .000)</td>
<td>26.69 ± 2.17 (p &lt; .000)</td>
<td>1.04 ± 1.33 (p &lt; .000)</td>
<td>19.06 ± 6.98 (p &lt; .000)</td>
<td>5.41 ± 5.15 (p &lt; .000)</td>
<td>11.38 ± 7.61 (p &lt; .000)</td>
</tr>
<tr>
<td>Other</td>
<td>265</td>
<td>365 ± 154 (p &lt; .000)</td>
<td>236 ± 165 (p &lt; .000)</td>
<td>74.79 ± 40.5 (p &lt; .000)</td>
<td>13.44 ± 1.17 (p &lt; .000)</td>
<td>25.74 ± 2.24 (p &lt; .000)</td>
<td>0.99 ± 1.1 (p &lt; .000)</td>
<td>18.6 ± 6.33 (p &lt; .000)</td>
<td>5.64 ± 6.22 (p &lt; .000)</td>
<td>11.74 ± 9.37 (p &lt; .000)</td>
</tr>
<tr>
<td>Fin</td>
<td>All</td>
<td>57</td>
<td>446 ± 132 (199.675)</td>
<td>194 ± 175 (11.556)</td>
<td>62.66 ± 33.4 (31.32, 172.22)</td>
<td>13.26 ± 1.27 (10.24, 16.26)</td>
<td>27.36 ± 1.55 (22.20, 31.22)</td>
<td>0.87 ± 1.21 (0.02, 5.22)</td>
<td>20.92 ± 5.91 (10.99, 41.65)</td>
<td>6.68 ± 7.19 (2.41, 33.59)</td>
</tr>
<tr>
<td>Feed</td>
<td>30</td>
<td>455 ± 116 (p &lt; .000)</td>
<td>192 ± 166 (p &lt; .000)</td>
<td>60.5 ± 39.56 (p &lt; .000)</td>
<td>13.26 ± 1.2 (p &lt; .000)</td>
<td>27.29 ± 1.5 (p &lt; .000)</td>
<td>0.82 ± 1.3 (p &lt; .000)</td>
<td>21.26 ± 6.77 (p &lt; .000)</td>
<td>6.76 ± 7.3 (p &lt; .000)</td>
<td>13.68 ± 10.56 (p &lt; .000)</td>
</tr>
<tr>
<td>Other</td>
<td>21</td>
<td>433 ± 155 (p &lt; .002)</td>
<td>196 ± 191 (p &lt; .002)</td>
<td>65.74 ± 37.66 (p &lt; .002)</td>
<td>13.27 ± 1.39 (p &lt; .002)</td>
<td>27.46 ± 1.65 (p &lt; .002)</td>
<td>0.94 ± 1.08 (p &lt; .002)</td>
<td>20.43 ± 4.52 (p &lt; .002)</td>
<td>6.57 ± 7.21 (p &lt; .002)</td>
<td>12.32 ± 9.81 (p &lt; .002)</td>
</tr>
<tr>
<td>Humpback v Other</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed v Other</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin v Other</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humpback v Fin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin v Other</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5-2. Best-fit models of whale aggregation (“Agg.”) and feeding as a function of habitat features of the fjord system. Separate models were built for each species (column Sp.), humpbacks (HW) and fin whales (FW). Aggregation models, which predict whale density (individuals per km trackline), were based on systematic transect data. Feeding models, which predict feeding behavior amid krill-like patches of backscatter, were based on focal follow data. A fin whale feeding model was not possible due to low sample size. Model fit is described by number of variable combinations tested ($n_{fit}$), the number of AICc-equivalent best-fit models ($n = -$), the minimum AICc within that group ($Min. AICc$), and its $r^2$ (proportion of deviance explained by the model). All variables, unless otherwise noted below, were calculated by averaging interpolated values within a 1-km² radius of focal follow centroid. Variable abbreviations: $z =$ mean seafloor; $\Delta z =$ maximum seafloor slope; Chl-a = integrated chlorophyll-a; $Z_{eu} =$ euphotic depth; $SST =$ Sea surface temperature; $\Delta SSS =$ sea surface salinity gradient; $MLD =$ mixed layer depth; $strat =$ stratification; $tide =$ hours since slack tide. The variables included in best-fit models are denoted by their significance level (the highest found within best-fit set). Significance keys for spline functions of predictors: $x =$ not tested; $ -$ = not included in best-fit model set; $ns =$ $p > 0.05$; $* =$ $p \leq 0.05$; $** =$ $p \leq 0.01$; $*** =$ $p \leq 0.001$. Underlined significance level indicates variables included in model with minimum AICc.
<table>
<thead>
<tr>
<th>Model</th>
<th>Fit</th>
<th>Explanatory Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sp.</td>
<td>Predict</td>
<td>n</td>
</tr>
<tr>
<td>HW</td>
<td>Agg. 140</td>
<td>13</td>
</tr>
<tr>
<td>Feed 202</td>
<td>23</td>
<td>16</td>
</tr>
<tr>
<td>FW</td>
<td>Agg. 140</td>
<td>25</td>
</tr>
<tr>
<td>Feed 26</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 5-3. Best-fit generalized additive models (GAMs) of whale aggregation density based solely upon site loyalty, represented here by spatial coordinates and/or day of year (n=140). 11 models of different variable combinations were fit. Model performance is described by number of AICc-equivalent best-fit models (n =), the minimum AICc within that group (Min. AICc), and its $r^2$ (proportion of deviance explained by model). Explanatory variables included in best-fit model set are denoted by their significance level (the highest found within best-fit models). Variable abbreviations: Jul = Julian day; X = Longitude; Y = Latitude; z = Seafloor depth. Interaction terms are treated as separate variables and are denoted with a dot (e.g., X·Y).

Significance key: $ns = p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Underlined significance level indicates variables included in model with minimum AICc. Variables not included in a best-fit model are given a dash (-).

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>n</th>
<th>Min. AICc</th>
<th>$r^2$</th>
<th>Explanatory variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Humpback</td>
<td>5</td>
<td>640.7</td>
<td>.25</td>
<td>ns</td>
<td>*** - *** * -</td>
</tr>
<tr>
<td>Fin</td>
<td>3</td>
<td>149.2</td>
<td>.78</td>
<td>ns</td>
<td>ns - * * -</td>
</tr>
</tbody>
</table>
Figure 5-1. Whale-habitat associations. Cumulative distribution functions (CDF) of habitat features available in the study area (black line, measured during systematic transect surveys) and those measured during focal follows (colored lines) for humpbacks (top) and fin whales (bottom). Focal follows are displayed by behavioral category. Gray line = all behaviors; Red line = feeding whales; Blue line = other behavioral states. Colored asterisks along x-axis are the mean of their respective distributions.
Figure 5-2. Position curves for humpback and fin whales. “Position curves” for feeding and non-feeding ("Other") behavioral states are displayed for each species. These display the mean positioning of whales with respect to select available habitat features (*columns*, sampled during systematic surveys), plotted according to distance (km) from the focal follow. Black line tracks the mean value within each 1-km distance window of all focal follows; vertical bars represent standard deviation.
2015 Humpbacks

Figure 5.3. Position curves for humpbacks in 2015 survey months. Mean positioning of humpbacks with respect to select available habitat features (*columns*, sampled during systematic surveys), plotted according to distance (km) from the focal follow, for each survey month of 2015 (*rows*). Black line tracks the mean value within each 1-km distance window of all focal follows; vertical bars represent standard deviation.
Figure 5-4. Comparison of models of habitat use strategy. Ranked performance of whale aggregation models. Whale densities were modeled as functions of three types of data: prey-like acoustic backscatter (“Food”), habitat features (“Habitat”) and site loyalty cues (“Site”). Each model type was fit twice: once without including seafloor depth (“z”) as a candidate variable (e.g., “Food”) and again including it (e.g., “Food + z”). Dotted line demarcates AICc-equivalence boundary with lowest-AICc model. Note that lower AICc = better model fit.
CHAPTER 6:

Novel spatial analytics to identify candidate environmental cues for foraging marine whales

*Eric M. Keen, Katelyn M. Qualls, Kim-Ly Thompson, Janie Wray, Chris R. Picard*
ABSTRACT

To understand associations between marine predators and their habitat, scientists must also study predator-prey and prey-habitat interactions. With these data, however, it is difficult to identify which habitat features have potential as foraging cues for a given predator with conventional modeling techniques. We developed a new statistical tool, position curve correlation analysis (PCCA), that synthesizes rorqual whale data collected during systematic transects and opportunistic focal follows and tests the potential utility of habitat features as cues in whale foraging strategy. Using data collected in a the Kitimat Fjord System of British Columbia, PCCA identified thermocline depth as a potentially important cue to aid humpback whales (Megaptera novaeangliae) in finding high-volume patches of krill-like backscatter. For fin whales (Balaenoptera physalus), several oceanic cues are available for tracking deep layers of krill-like backscatter, but few were correlated with high-volume layers. We used conventional additive modeling of whale, prey and habitat interactions to verify and augment PCCA interpretation. This tool is applicable for other marine predators in other systems, provided the relevant data are collected synoptically at appropriate scales.

INTRODUCTION

Do marine predators such as whales find food simply by blundering into it, or do they use other habitat features to concentrate their search in areas that are likely to have high prey concentrations? The strong correlations that are often found between ocean features and mobile marine predators (e.g., Ferguson et al., 2006, Redfern et al., 2006, Torres et al., 2008, Rosa et al., 2012) can be a cause or effect of foraging for prey. Predators that feed upon taxa whose distribution is strongly coupled to oceanographic dynamics, e.g. zooplankton, can be
unintentionally correlated to those same habitat features. Predators can also track those habitat features as part of a foraging strategy, using indirect indicators to position themselves within profitable feeding areas (Gaston 2004). However, marine predators likely use an ensemble of sensory modalities to locate prey (Gaston 2004; Goldbogen et al., 2012a). Some predator taxa may rely more than others upon habitat cues, and such cues may be important to a given taxon only at certain spatial scales. Despite these complexities, understanding the mechanisms of habitat associations is necessary to evaluate the importance of habitats for threatened species (Redfern et al., 2006). Throughout this chapter, we will use the term ‘habitat’ to refer to the non-prey aspects of a whale’s environment.

Prey-habitat relationships must be understood in order to parse the predator-habitat relationship, meaning studies must concurrently sample at least three levels of a given ecosystem: relevant habitat features, potential prey, and the predator(s) of interest. This may not be feasible for all species in all habitats, particularly for those at sea, and even in opportune circumstances it is unclear how to analyze those data streams satisfactorily. Dialectic models can be built that predict predator, prey and habitat as functions of each other, but those models’ outputs need to be synthesized in an intelligible way, preferably quantitatively, in order to evaluate habitat features as candidate foraging cues.

Modeling cannot determine whether habitat features are being used as foraging cues, but quantitative methods can identify which habitat features would be *useful as such*, when given an appropriate study design in an appropriate system. Here we introduce a novel spatial tool that was built upon the “position curve” technique developed in Chapters 4 and 5, and demonstrate its ability to augment conventional modeling techniques using a study of sympatric rorqual whales within a British Columbia fjord system.
METHODS

Study Area

The study area (1,961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland British Columbia (BC), centered at 53°N and 129°W (Fig. 3-1). The regional context, fjord morphology and oceanography of the KFS are reviewed in Chapter 2.

In the Chapter 4 study of whale prey preferences within the KFS, both humpback and fin whales were found to be primarily euphausivorous, positioning themselves within the fjord system among the highest available total krill-like backscatter. Humpback whales were found to feed opportunistically on fish, but did not structure their distribution according to that of fish-like backscatter. Both species, particularly fin whales, targeted deeper kill patches and responded to krill volume with threshold foraging behavior.

Chapter 5 compared habitat associations in the two species. Habitat features were found to be strongly associated with whale distribution but not with their feeding effort. Humpback whales fed in waters with variable seafloor depths, high seafloor slope, moderate-to-high temperatures, low salinity, high salinity gradients, high stratification, and, most notably, low thermocline depth. Fin whales fed in deep waters with low chlorophyll-a levels, high salinity and low salinity gradients, low stratification, and deep euphotic zone.

Data collection

In the summers of 2014 and 2015, whale and ecosystem surveys were conducted aboard the RV Bangorang, a 12 m motorsailer, with a team of three researchers. Over the course of 7 monthly surveys, 2,291 km of transect effort were logged. In each survey we
visited a grid of oceanographic stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys. Surveys yielded 1,688 whale sightings (1,529 humpbacks and 159 fins) and 388 focal follows (338 humpbacks, 50 fins). Systematic surveys were punctuated by focal follows of encountered whales, during which behaviors and acoustic backscatter were recorded. Details can be found in Chapter 1 for survey design, Chapter 4 for whale survey and focal follow protocol, Appendix 5 for echosounder processing protocols, and Chapter 5 for oceanographic sampling and analysis. Acoustic backscatter at 200kHz and 33kHz were processed to represent krill patches and schooling forage fish, respectively, and were characterized using simple metrics: total, or integrated, backscatter; mean backscatter intensity; vertical dispersion (the standard deviation of backscatter depth distribution), and the mean backscatter patch depth.

Analysis

Backscatter and oceanography variables were interpolated to a 0.25 km² grid of the study area’s marine habitat. Interpolation was performed using inverse path-weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell and accounts for land obstruction (R package ipdw, Stachelek 2015).

Backscatter – Habitat models

Metrics of prey-like acoustic backscatter were modeled as functions of habitat features. These model results were interpreted in light of whale ~ backscatter models in Chapter 4 and whale ~ habitat models in Chapter 5, which were built using the same
systematic transect dataset, to verify and compare results from the position curve analyses that follow.

The study area was split into 26 strata (Fig. 3-6) to give 26 measures for each of 7 surveys (2 in 2014, 5 in 2015; n=159; sensu Chapters 3, 4 and 5). Interpolated acoustic backscatter and ocean variables were averaged within each survey-stratum. Surface salinity and temperature gradients were calculated as the mean range of measurements within 1-km bins of survey effort.

Models were built for each of the 5 backscatter metrics with the same stepwise fitting procedure used in Chapters 4 and 5. GAMs were built using package mgcv (Wood 2011) in R (R Core Team 2013) with the Gaussian distribution family and gamma set to 1.4 to prevent overspecification (Wood 2011). Models were built by adding single explanatory variables at a time, building off variable combinations that yielded the lowest AICc (Akaike 1974, Burnham and Anderson 2002) and repeating until AICc no longer improved. Due to our sample size, models that were within 6 AICc of the lowest AICc were considered to be of equivalent fit (after Hilbe 2011). The significance of spline functions was evaluated based on an F-test calculated by mgcv.

**Position Curves**

Position curves depict the mean position of whales with respect to available prey and habitat features within the fjord system, and provide data on the spatial scale for those associations. The premise of this technique is that the central task of a predator’s foraging strategy is positioning itself strategically within prey- and habitat-space. Position curves are possible when a study investigates predator-environment associations from the two vantages of systematic distribution surveys and behavioral focal follows. Position curves are built using
the procedure in Fig. 6-1A-D and detailed in Chapter 4. Prey position curves are presented in the same chapter. Habitat feature position curves are presented in Chapter 5.

**Position Curve Correlation Analysis**

To directly test the viability of habitat features as cues for associating with preferred prey patch characteristics, we tested for correlation between prey position curves and habitat position curves of feeding whales (Fig. 6-1E). Each backscatter metric’s position curve was modeled as a function of each habitat feature’s position curve in a univariate GAM (gamma=1.4, k=3 for smoothing spline to constrain complexity of functional relationship). To control for different effect sizes, variables were normalized before modeling to a mean of 0 and standard deviation of 1. Model fit was assessed using AICc. The stronger the correlation between prey and habitat position curves, the more feasible it is that a given habitat feature facilitates a whale’s association with preferred attributes of the prey field. This interpretation assumes that whales are successfully associating with preferred prey patch characteristics.

**RESULTS**

**Backscatter ~ Habitat models**

Backscatter metrics are predicted by environmental variables with mixed success, and many backscatter-habitat feature relationships are strongly non-linear. Details of model results are provided in Appendix 7.

**Position Curve Correlation Analysis**
Position curves for each backscatter metric were modeled as functions of position curves for each oceanographic variable, and full results are visualized in Figures A7-3 and A7-4. Here we restrict our focus to curve analyses for 200kHz patch depth and total 200kHz (Fig. 6-2), which were the two most influential backscatter metrics for whale distribution and feeding effort (Chapter 4). In general, correlations are nonlinear for total backscatter and near-linear for patch depth. The humpback whale position curve for total backscatter is correlated most strongly with that for thermocline depth (AICc = 164, r² = 0.55), though model fit is also good using euphotic depth (AICc = 204, r² = 0.22) and seafloor depth (AICc = 185, r² = 0.42). The species’ position curve for patch depth is closely correlated to that for thermocline depth as well (AICc = 32, r² = .92), and also to seafloor depth (AICc = 47, r² = 0.90).

The fin whale position curve for total 200 kHz backscatter is poorly modeled by habitat position curves. Four models are AICc-equivalent: chlorophyll-a (AICc = 197, r² = .30), surface salinity (AICc = 199, r² = .29), euphotic depth (AICc = 188, r² = 0.39) and seafloor depth (AIC = 192, r² = 0.35). Correlation to patch depth position curve, however, is high for most habitat position curves, the best fit being with that of seafloor depth (AICc = 79, r² = .85).

DISCUSSION

We used position curve correlation analysis (PCCA) to quantitatively compare the potential habitat cues available to humpback and fin whales within the Kitimat Fjord System (KFS). The differences between the two species were stark. We identified thermocline depth as a potentially important cue for humpbacks tracking high-volume patches of krill-like backscatter. We found several oceanic cues available for fin whales tracking deep layers of krill-like backscatter, but few cues seem helpful to fin whales for tracking down high-volume
layers. Here and elsewhere (Chapters 4 and 5), we used conventional GAMs to build models of whale, prey and habitat interactions that verified and augmented PCCA results (see below).

PCCA is a simple and direct analysis whose results can be visualized more intuitively than those of conventional modeling methods such as GAMs. As a single model based upon the spatial association of predators to prey and habitat features, PCCA does not require the meta-analysis of multiple model outputs. Large predator associations with prey and habitat features are often nonlinear (Hollings 1965), as can be prey associations with habitat (Fig. A7-1), and the spline functions output by GAM routines are typically difficult to interpret one at a time. Deriving foraging cue potential from the multiple spline functions generated by the three required models (whale ~ prey, whale ~ habitat, and prey ~ habitat) would be exceedingly difficult to quantify and communicate efficiently. In contrast, PCCA provides a single correlation metric and is easily graphed, albeit after considerable data processing. We believe that this tool is applicable for other marine predators in other systems, provided the appropriate data are collected synoptically at an appropriate spatiotemporal scale within a study area that can be considered in relative isolation from surrounding waters.

While PCCA can be a direct and effective means of exploring predator-prey-habitat relationships, this tool does not eliminate the ambiguity between correlation and causation in predator-habitat associations. For example, the humpback ~ thermocline depth relationship discussed below can be either instrumental or incidental in the species’ foraging strategy within this fjord system. We found that PCCA highlights this habitat feature and statistically tests its utility as a foraging cue better than other available analyses. However, as with conventional models, determining its importance requires cautious consideration of the natural histories of the predators, prey, and ecosystem involved.

If there is no conceivable way in which a predator can sense a certain habitat feature, it is not prudent to consider that feature as a candidate cue, regardless of model/PCCA results.
All of the potential cues discussed below can be feasibly sensed by our study species. For example, thermocline depth may be sensed along the whale’s body during a dive, and other readily sensed habitat features, such as wave energy, are often related to thermocline depth; euphotic depth may be gauged visually via surface water turbidity; and seafloor depth may be inferred based upon the acoustic qualities of a space (Payne and Webb 1971).

**Viability of foraging cues**

Overlap between predator and prey must occur on the smallest scale in order for feeding to occur, but marine predators must seek out and position themselves for that opportunity by navigating and assessing prey conditions on multiple nested spatial scales. The extent to which large whales rely on habitat indicators to track down prey or promising foraging areas is unknown. It may be that whales are able to directly sense prey as easily as they can sense habitat proxies thereof. Large rorquals probably use a medley of sensory modalities to locate, assess and capture prey. They are thought to sample the prey field during the deeper dives they intersperse throughout the series of shallow dives they execute while traveling. One-lunge dives have been observed in tagged blue whales (Croll et al. 2001).

At very close range, prey patches can be detected tactiley, using the enervated vibrissae lining the rostrum (Goldbogen et al. 2012a). Depending on depth and water turbidity, prey can also be detected visually: daytime foraging dives by blue and fin whales often involve steep upward pitch angles, during which the krill patch is backlit by downwelling sunlight and the whale’s form is lost in the abyssal shadow (Calambokidis et al. 2007, Goldbogen et al. 2012a). However, these tactics may be less effective in turbid habitats such as fjords. The usefulness of such habitat cues are clearly context-dependent.
Habitat cues may be particularly important for threshold-foraging predators, such as the rorquals of this fjord system (Chapter 4), because above-threshold prey volumes must be located to meet high energetic demands. The quality of prey patches within the immediate vicinity of a whale may be less informative for navigating to profitable foraging areas than equally accessible oceanographic features. This is particularly true for predators practicing site-loyal behavior, as humpback and fin whales of this fjord system are known to do (Ashe et al., 2013; Linda Nichol, pers. comm.; this dissertation, Chapters 3 and 5). Site loyalty to an area may be prey-driven – a spatial habit designed to lead, on average, to reliable overlap with prey – but it can still be practiced via attendance not to prey but to habitat cues. These habitat cues may provide more spatiotemporally stable and contiguous gradients than the patchy and ephemeral plankton targeted by large rorquals. Therefore it is not out of the question that the whales of the Kitimat Fjord System rely to some extent upon habitat cues as part of their foraging and/or site loyalty strategies.

Humpback whales

Importance of shallow thermocline

Of all features sampled, thermocline depth may have the greatest potential for humpback whales as an oceanographic cue for euphausiid prey. The strong relationship between the species’ association with those variables and its association with preferred prey patch features aligns with similar findings in the whale ~ habitat models of Chapter 5. Backscatter ~ habitat GAMs (Appendix 7) detected a weak nonlinear relationship between backscatter volume and the related variable mixed layer depth (MLD). A similarly weak relationship was found between backscatter patch depth and MLD, but the relationships among these variables appeared much stronger in PCCA. The spatial association between
humpback whales and shallow thermocline also appears to be of potential use in explaining humpback association with low prey patch dispersion (Fig. A7-2).

_Humpback – climate coupling_

This whale-thermocline-prey relationship, in turn, offers a reasonable explanation of the “whale wave”, a curious pattern practiced by this fjord system’s humpback whales in which their distribution shifts from outer channels to inner channels as summer turns to fall (Chapter 3). As storm energy and katabatic winds strengthen during late summer within the KFS, mixing begins in the exposed outer channels and progressively encroaches into the protected channels (Chapter 2). That the timing of this process aligns with the shift in humpback habitat use may be a coincidence, but this is unlikely given the results of our backscatter ~ habitat GAMs, which found a relationship between thermocline depth and krill volume (A7-1). It is likely that the onset of autumn weather influences the volume and depth of krill patches, which in turn informs humpback whale distribution, as well as the amount of daylight foraging hours available to the whales. In this scenario, the whale-thermocline-prey relationship would be further coupled to regional meteorology and fjord circulation processes (Chapter 3), both of which are susceptible to the inter-annual, decadal and longer-term dynamics of global climate.

_Fin whales_

Chapter 4 showed that within the subset of the KFS used by fin whales, the species is generally able to associate with anomalously high-volume krill-like backscatter compared to that available in the studied area of the fjord system. Chapter 5 showed that fin whale habitat has diagnostic environmental and prey-related properties. Here we have shown that, in
addition to direct prey sensing, several ocean features within that habitat are available as cues to facilitate fin whale associations the species’ preferred prey patch characteristics.

**Importance of patch depth**

Chapter 4 found that fin whales associate more strongly with deep prey patches than with high total 200 kHz backscatter within this fjord system, and I related this unexpected pattern to current optimal foraging theory. Position curve correlation analysis (PCCA) showed that fin whale association with high volume prey patches was poorly correlated to their habitat associations, with the weak exception of seafloor depth. In stark contrast were PCCA results for association with deep prey patches, which were strongly correlated to their associations with nearly all habitat features, with the exception of thermocline depth. This differs diametrically from the humpback PCCA for patch depth. All of these patterns are verified by the spline relationships in the patch depth ~ habitat GAM (Fig. A7-1; discussed below), with the possible exception of surface temperature. To the extent that deep patches are a preferred prey feature for fin whales, several ocean cues are available to facilitate that association.

Fin whales may be targeting the deepest patches within the fjord channels they use, or it may be that deep patches are an indirect cost of site loyalty to a quiet foraging corridor that happens to have deep krill patches (discussed in Chapter 5). Either way, this whale-prey-habitat interaction couples this species’ habitat use strongly to oceanographic dynamics, and it should have implications for the energetic profitability of foraging within this historically important habitat.

**Oceanographic determinants of backscatter metrics**
The dominant euphausiids present in the study area, *Euphausia pacifica* (82%) and *Thysanoessa spinifera* (14%), make up 96% of adult euphausiids captured in net samples (authors, forthcoming publication). Drivers of their patch formation are known to be complex and multifarious on vertical, horizontal, and temporal scales. The location and density of euphausiid patches depends not only upon a species' environmental preferences (e.g., light, temperature, salinity, etc.; Iguchi et al., 1993; Taki, 1998; Taki, 2008) but food availability and patchiness (e.g., Chl-a distribution; Endo and Yamano, 2006; Sogawa et al., 2016; Ressler et al., 2004) and the interaction between advective processes (currents, upwelling, fronts, etc.; Mackas et al., 1997; Marinovic et al., 2002) and benthic topography (which often create advection and/or define the lower bound for vertical migration; Ianson et al., 2011). In our study, GAMs of the mean depth of krill-like backscatter as a function of habitat features revealed strong nonlinear interactions with depths of the euphotic zone, seafloor, and mixed layer (Fig. A7-1). Chapter 2 presented striking patterns among patch depth and these ocean features across survey months: waters in July 2015 were markedly less turbid (deeper euphotic zone) than all other months, and this was also the month with the deepest 200 kHz patch depth by far (Fig. 2-5). In September 2015, the depth of the thermocline and mixed layer increased dramatically with no apparent change in patch depth. These coincidences point to the potential influence of water turbidity upon daytime krill patch depths and may lend support to the contested “isolume hypothesis”, the concept that some zooplankton guilds mediate diel vertical migration depths by following a certain light level up and down the water column throughout a 24-hour period (Lampert 1993).

Our model of total 200 kHz backscatter as a function of environmental features performed unexpectedly poorly. Some unsampled aspect of the fjord environment, such as currents and nutrient distributions, may have been an important determinant in the distribution of this backscatter metric. Gil Basin (Squally Channel, Wright Sound, Whale Channel)
consistently housed the highest total 200 kHz in the study area, and it is deep relative to surrounding waterways; tidally mediated currents flowing over the sills of its boundaries may have served to retain nutrients and euphausiids within.

ACKNOWLEDGMENTS

This chapter, in part, has been submitted for publication as it may appear in Proceedings of the Royal Society B, 2017: Keen, EM, J Wray, KM Qualls, CR Picard. (In review) “Novel spatial analytics to identify candidate environmental cues for foraging marine predators.” The dissertation author was the primary investigator and author of this paper.

In addition to front matter acknowledgments, JW wishes to thank the Save Our Seas Foundation, Willow Grove Foundation, and the Wright and Zumwalt families for their support of ongoing research in the study area.
**FIGURES**

**A. Dual design**
Systematic transects + focal follows

**B. “Whale web”**
Measure swim-distance to transect bins

**C. Plot variable against distance**
One curve for each focal follow

**D. “Position curve”**
Average curves together.
One curve per Species + Behavior + Variable

**E. Correlation analysis**
Model prey positioning as function of oceanographic positioning

**Figure 6-1.** Procedure for constructing and analyzing “position curves.” A. In a dual survey design, focal follows are conducted amid a network of systematic transects, which can be binned into small lengths (here, 1 km). B. Swimming distances (shortest path) are calculated from the focal follow to each transect bin, placing the whale at the center of a “web” of samples of its habitat. C. For a given habitat variable, values are calculated for each 1-km bin, then each bin’s value is plotted against the whale’s swimming distance to it. Variable-distance plot examples are presented from four focal follows. D. These plots are averaged for all focal follows of a species in a certain behavioral state to produce a “position curve”; black line tracks the mean variable value (left: 200 kHz patch depth; right: thermocline depth) at increasing distance from the whale, gray bars represent standard deviations within each distance bin. E. To ascertain the potential role of an oceanographic feature in facilitating prey association we carried out position curve correlation analysis (PCCA), in which a prey position curve is modeled as a function of an oceanographic position curve. Each dot is the oceanography value (x-axis) and backscatter value (y-axis) for a certain distance from the whale (color-coded by its distance).
Figure 6-2. Mean position of feeding whales with respect to available prey features as a function of their mean position to various oceanographic features. Only two prey features are displayed, 200 kHz integrated volume and patch depth, chosen for their stark position curves. Dots are color-coded by distance from whale, 0-76 km. Correlation was tested using GAMs, and the best-fit models are signified by fit metrics (AICc and $r^2$, i.e., proportion of deviance explained). All variables were normalized to mean of zero and standard deviation of 1 (hence no units).
CHAPTER 7:

From fjord to fins: dive energetics link ocean features to competitive dynamics in sympatric rorqual whales

*Eric M. Keen and Katelyn M. Qualls*
ABSTRACT

Energetically costly lunge feeding renders rorqual whales (f. Balaenopteridae) sensitive to prey patch depth for foraging success. For planktivorous species, feeding performance should be closely coupled to features of marine habitat that influence prey patch formation. In a two-year study of sympatric euphausivorous rorquals in a British Columbia fjord system, we tested whether dive behaviors of humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) could be predicted by habitat features, and that interspecific differences in dive ability interact with local prey depth distribution to determine their competitive dynamics. Both prey- and habitat-based models predict dive behaviors equally well in general, though explanatory power was low (max. $r^2 = 0.30$). Humpback whale dive duration appeared limited at prey depths beyond 150m, while fin whale dive time increased steadily with prey depth. Based upon depth distribution of acoustic backscatter within the fjord system, fin whales can encounter nearly double the prey a humpback whale can in an hour of non-selective, random search. Encounter rates peak at prey depths of 94.4m for fin whales and 78.3m for humpback whales. Selective foraging, however, allows humpback whales to attain near-equal prey encounter rates. Simulations based on findings indicate that fin whales gain an increasing foraging advantage with increasing prey patch depth. Our results highlight the unique coupling of rorquals to habitat features due to their sensitivity to prey patch depth; the importance of swim speed in their foraging strategy; and the influence of prey depth distribution upon their dive energetics, competitive interactions, and habitat use.

INTRODUCTION
Vast trophic webs couple the ocean’s largest predators to fundamental ocean processes such as seasonal upwelling (Croll et al., 2005), which determine levels of production and hence the composition and abundance of prey. The great rorqual whales (f. Balaenopteridae) feed primarily upon plankton, coupling them more directly than top predators to oceanographic dynamics. But prey type and volume are not the only keys to foraging success. Prey patch characteristics, such as patch density and depth, are critical to the energetic profitability of feeding for many predator taxa (Doniol-Valcroze et al., 2011; Goldbogen et al., 2011; Benoit-Bird et al., 2013), particularly for those tied to the ocean surface for respiration.

Of the air-breathing divers, rorquals are particularly sensitive to prey patch features because of their energy-intensive practice of lunge feeding (Krutzikowsky and Mate, 2000; Goldbogen et al., 2006; 2007; 2008; 2011). Lunge energetics requires prey patches to be dense and accessible, maximizing food intake per hour and also per lunge while minimizing energetic costs (Dolphin 1988; Goldbogen et al. 2011; Doniol-Valcroze et al., 2011). Allometric scaling of dive energetics enhances these requirements in the largest rorquals, the blue (Balaenoptera musculus) and fin whales (B. physalus; Goldbogen et al., 2012b). Optimal dive theory states that, all else being equal, shallower prey patches increase hourly feeding rates by reducing transit time and keeping dive times well below aerobic limits so as to minimize surface recovery (Fig. 7-1; Houston and Carbone 1992; Doniol-Volcroze et al., 2011). According to this theory, the rate at which time with prey diminishes with increasing prey depth differs among competing predators as functions of their aerobic capacity, locomotive ability, metabolic rate and behavioral repertoire. Therefore, discrepant dive ability should play some role in the competitive interactions of sympatric predators, but that role is not well understood.
The prey-depth dependence of dive strategy has been studied in sympatric seabirds (e.g., Mori 2002, Halsey et al. 2003, Cook et al., 2008), but no published study tests these ideas for sympatric whales. Dolphin’s (1987 and 1988) work with humpback whales (Megaptera novaeangliae) is the first and most extensive study of dive behavior as a function of prey depth for a single rorqual species. He concluded, “The influence of prey distribution on the ventilator behavior of humpbacks could, therefore, be substantial” (Dolphin 1987).

Friedlaender et al. (2015) is a limited study of dive behavior in a blue whale and a fin whale foraging upon a common prey resource, but the scale of their study did not allow prey depth effects to be tested.

Chapter 4 was a study of prey association in sympatric humpback and fin whales within a fjord system in northern British Columbia (Fig. 3-1). There we found that both species feed primarily upon high-volume swarms of euphausiids that were vertically condensed relative to mean available prey distribution in the fjord system. Surprisingly, fin whales were associated with krill patches that were significantly deeper than the fjord system’s mean (Fig. 7-2). This trend was exacerbated in feeding fin whales compared to non-feeders, suggesting deeper patches were preferred (Fig. 7-3). Humpback whales were also associated with deeper-than-average prey layers, but the association was weak and there was no evidence that feeding humpbacks preferred deeper prey patches than non-feeders did. A final puzzle was that fin whales, despite being larger, were associated with lower-volume krill patches. These findings do not align with current dive theory, but they do underline the relevance of prey patch features in interspecific rorqual competition.

Plankton patch characteristics are a function of oceanographic and physiographic features, but the relationships are species-specific and complex on horizontal, vertical and temporal scales. In Chapter 4 above, the dominant euphausiids present, Euphausia pacifica and Thysanoessa spinifera (82% and 14% of net samples, respectively), are common prey for
northeast Pacific rorquals (e.g., Croll et al. 2001, Fiedler et al., 2010, Friedlaender et al., 2015). These species are known to have regionally and temporally dependent vertical distributions that are influenced by water temperature (Iguchi et al., 1993; Taki, 1998; Taki, 2008), salinity (Taki et al., 1996; Yoon et al., 2000), and the distribution of chlorophyll-a (Endo and Yamano, 2006; Sogawa et al., 2016; Ressler et al., 2004). *E. pacifica* exhibits strong diel vertical migration (DVM), which may be coupled to light levels (discussed in Lampert 1993) and therefore to local water turbidity (Chapter 6), while *T. spinifera* does not (Taniguchi, 1969; Brinton, 1962). The vertical distribution of *E. pacifica* is also known to be affected by abundance of zooplanktivorous fish (Bollens et al., 1992), maturity stage (Yoon et al., 2000), and molting status (Endo and Yamano, 2006). Circulation is also important in euphausiid patch formation and persistence. Features such as upwelling, eddies, and hydrographic fronts promote the formation of dense patches of euphausiids, as does the interaction of bottom topography and currents (Janson et al., 2011). Areas in which hydrographic and topographic discontinuities co-occur are particularly suitable for krill patch formation (Mackas et al., 1997; Marinovic et al., 2002). In Chapter 6, we assessed the oceanographic basis for rorqual-krill associations using additive modeling. We found that euphausiid patch depth was well predicted (67% deviance explained) using several oceanographic variables, most prominently water turbidity, thermocline depth and (in shallow areas) seafloor depth (Fig. 7-4).

Rorquals are clearly coupled to prey patch features, which are clearly coupled to habitat features. Therefore we hypothesize that rorqual dive behavior is also coupled predictably to habitat features. Such coupling would also link habitat features to the competitive dynamics of sympatric rorquals, since interspecific differences in dive behavior may render certain prey depth distributions – and therefore certain marine habitats – more suitable and advantageous for certain rorqual species. Correlations have been found previously
in baleen whale dive behavior and seafloor depth (Würsig et al., 1984; Dolphin 1987; Dorsey et al., 1989), but to our knowledge no other habitat variable has been tested.

Dive behavior was recorded during whale observations in fieldwork for Chapters 4, 5 and 6, allowing us here to compare the relationships among respiratory behavior, prey patch characteristics, and habitat features in two sympatric rorqual species within a relatively confined and unique marine habitat. We identify 1) significant coupling between whale respiratory behavior and habitat features, comparable to the coupling of measured prey patch features and habitat features; and 2) interspecific differences in dive performance with increasing prey patch depth. By exploring optimum diving theory in these two species via modeling simulations, we explore the implications of prey patch depth on rorqual competitive dynamics, habitat choice, and recovery in a changing ocean.

METHODS

Study Area

The study area (1,961 km² of water) is located within the Kitimat Fjord System (KFS) of northern mainland British Columbia (BC), centered at 53°N and 129°W in Gitga’at First Nation territory (Fig. 3-1). The regional context, fjord morphology and oceanography of the KFS are reviewed in Chapter 2.

Data collection

In the summers of 2014 and 2015, whale and ecosystem surveys were conducted aboard the RV Bangarang, a 12 m motorsailer, with a team of three researchers. In each
monthly survey we visited a grid of oceanographic stations (n = 24), between which we conducted concurrent visual and acoustic transect surveys while sampling surface properties with a thermostalinograph (TSG; Fig. 1-1). At stations we conducted CTD casts, zooplankton tows and water turbidity samples with a Secchi disk. 2,291 km of transect effort were logged over the course of seven monthly surveys, which yielded 1,688 whale sightings (1,529 humpback; 159 fin; Table 1-2).

Systematic surveys were punctuated by focal follows of encountered whales (338 humpback; 48 fin; Fig. 6), during which behaviors and acoustic backscatter were recorded. Group behavioral state was inferred during the focal follow and recorded, without knowledge of backscatter levels, along with a confidence level (95%, 66%, or 33%). Potential behavioral states included “Feeding at depth”, “feeding at or near surface”, “traveling”, “milling” and “resting”.

Details can be found in Chapter 1 for survey design, Chapter 4 for whale survey and focal follow protocol, Appendix 5 for echosounder processing protocols, and Chapter 5 for oceanographic sampling and analysis. In short, 200kHz and 33kHz acoustic backscatter were processed to represent krill patches and schooling forage fish, respectively, and were characterized using simple metrics: total, or integrated, backscatter; mean backscatter intensity; vertical dispersion (the standard deviation of backscatter depth distribution), and mean backscatter patch depth.

Focal follow effort commenced once the vessel was within 150m of whale groups. During these encounters, the team collected respiration intervals, travel patterns, group composition, identification photographs, behavioral notes, and acoustic backscatter. All focal follows occurred during daylight hours.

Blows and other surface behavior were logged within a second of their occurrence. The following events were logged: start of surface sequence, blow, terminal blow before a
dive, aerial and other robust behaviors, and abrupt changes in direction. Missed blows were noted and addressed in nightly reviews of focal follow data. Our field objective was to record at least one full ventilation cycle for as many individuals in the group as possible. A ventilation cycle is defined by Dolphin (1987) as the duration from the dive stroke of a whale, through the dive, through its surface period and up to the initiation of the subsequent dive. If whales were too numerous to track reliably, I selected one or two individuals that were distinguishable either by their size or their position within the school, often the lead whale at the front of the school (after Jahoda et al., 2003). If we suspected a reaction to our presence the focal follow was abandoned.

Analysis

Backscatter metrics were calculated for each focal follow. Habitat features at focal follow sites were drawn from interpolated station data with 0.25 km² resolution, with the exception of surface temperature and salinity which were sampled during focal follows with a TSG. Interpolation was performed using inverse path-weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell and thus accounts for land obstruction (R package ipdw, Stachelek 2015).

Dive metrics

Rather than treat ventilation cycles as units of replications (sensu Dolphin 1987), we treated each closely observed group as a single data point, since individuals within a group are likely to influence one another’s respiration behavior. If we observed multiple ventilation cycles in a single whale, measurements for those cycles were averaged to produce a single datum. Metrics for individuals were then averaged to arrive at a single set of dive and
respiration metrics for the group. Following Dolphin (1987) and Dorsey et al. (1989), calves were excluded from the analysis. When a surface period included only one blow the group’s mean blow interval was given the value 0.1 (after Dolphin 1987). Any blow interval of greater than 1.5 minutes was revised to be a dive, unless the whale was visible near the surface (e.g., sleeping; after Dolphin 1987).

Measured dive cycle metrics were mean blow interval, mean number of blows, mean dive time, mean surface time, and mean cycle time (dive + surface). These metrics are defined formally in Appendix 9. The proportion of cycle at surface was calculated using these metrics (surface / cycle).

For whales thought to be feeding at depth, three further metrics were inferred based upon species-specific parameters drawn from recent literature (Table A8-2) and the mean backscatter depth sampled during focal follows: transit time to prey patch is calculated using published transit rates of descent and ascent ($r_d$ and $r_a$, respectively) as well as their angle of travel ($\theta_d$ and $\theta_a$; Table 7-1). Assuming these rates and angles are constant regardless of prey depth, the following equation may approximate transit time:

\[
\text{Transit time} = \text{Descent time} + \text{Ascent time} = \frac{z}{r_d \sin \theta_d} + \frac{z}{r_a \sin \theta_a}
\]

Time at prey depth dive$^{-1}$ (shorthand: feed time) is calculated as dive time – transit time.

Proportion of cycle at prey depth is calculated as feed time / cycle time.

*Dive behavior models*

Dive behavior metrics (Table 7-2) were modeled as functions of prey backscatter characteristics then as functions of habitat features using generalized additive models (GAM)
with a Gaussian distribution family in the R package mgcv (Wood 2011). Separate models were fit to krill and fish feeding events. In krill feeding events, only 200 kHz backscatter metrics were used as predictors; in fish feeding events, only 33 kHz backscatter was used.

After removing correlated predictors based on a Pearson’s correlation coefficient cutoff of 0.5 (Zuur et al., 2009), our final habitat variable set included sea surface temperature, density stratification of the water column from 0-50m, thermocline depth (calculated using the differencing technique in Reilly & Fiedler 1994), integrated chlorophyll-a concentrations, euphotic depth, seafloor depth and seafloor slope (m km⁻¹).

For both prey and habitat models, species was included in the set of candidate explanatory variables as factors. Inferred feeding behavior was also included as a factor because when whales are not feeding their respiratory behavior may be decoupled from local conditions. Before modeling, numerical explanatory variables were normalized to a mean of zero, a transformation that preserves variable spread but improves model convergence and facilitates the comparison of effect sizes (Zuur et al., 2009). Twelve outliers were removed, yielding a maximum sample size of n = 315 for krill models and n = 66 for fish models. Actual sample size differed for each dive behavior modeled, since the necessary data for all metrics were not collected for every focal follow.

Models were built and evaluated using multimodel inference (Burnham and Anderson 2002) with second-order AIC (Akaike 1974) or AICc as the fit metric. The “gamma” input in mgcv was set to 1.4 to prevent overspecification (Wood 2011). To fit models using the Gaussian distribution family, blow interval was log-transformed.

Since AICc is a relative measure of fit with no standard scale, Akaike weights (w) were also calculated within each model set to compare evidence ratios on a scale from 0 to 1, such that all w for a model set sum to 1 (Burnham and Anderson 2002). When ranked in decreasing order of w, the subset of models whose cumulative w is 0.95 is called the 95%
confidence set. A large 95% set suggests that many variable combinations achieve the same level of parsimony and that there is no clear model choice (Symmonds and Moussalli 2011). When no single model is clearly the best fit, 95% confidence set is the most transparent way to report results (Symmonds and Moussalli 2011). Prey- and habitat-based models of each dive behavior were compared using the minimum AICc in the two 95% confidence sets.

We kept variables “balanced” within the set of candidate models, such that each variable within a set is used an equal number of times. Given equal representation, each variable’s cumulative Akaike weight, summed across all models that include it, is used as a metric of relative variable importance (RVI; Burnham and Anderson 2002). In order to facilitate results exploration, RVIs were scaled by the most important variable, so that all RVIs ranged between 0 and 1.

**Dive behavior as function of prey depth**

To explore the influence of prey depth upon dive behavior, focal follows were grouped into 20m bins according to mean backscatter depth (after Dolphin 1988) and dive metrics were averaged for each depth bin. While whales may not be targeting prey only at their mean depth, this simplification was sufficient to capture broad trends. Depth bins ranged from 0-20m to 200-220m because whales were not observed in other mean backscatter depths. To model time at prey depth per dive as a function of depth, the depth curves for dive time and surface time were fit by univariate GAMs (gamma=1.4, k=3 for smoothing spline to constrain complexity of functional relationship). Time at prey depth dive$^{-1}$ was calculated as above, then multiplied by the mean number of dive cycles hr$^{-1}$ to estimate the maximum time at prey depth hr$^{-1}$.

**Backscatter encounter rates (BER)**
The depth distribution of potential time at prey depth hr\(^{-1}\) interacts with the actual depth distribution of prey to determine how much prey a whale is able to encounter during an hour of foraging. We approximated this with backscatter encounter rates (BERs), based first upon backscatter depth distributions sampled during systematic transect surveys of the study area and then upon that sampled during focal follows of whales. For each depth, encounter rates were calculated as the product of hourly foraging time possible and mean backscatter value surveyed (pixel value, 0 – 255). Because our backscatter metrics are only proxies for prey biomass, we used ratios to compare species foraging performance (fin / humpback). Two ratios were calculated: integrated encounter rate (the sum of encounter rates across all depths, 20 – 220 m) and maximum encounter rate.

To further explore the competitive implications of dive strategy difference in humpback and fin whales, BERs were calculated using simulated prey depth distributions generated with a normal distribution with various permutations of mean and standard deviation. For simulations, we only considered depths of 20 to 220 m.

**RESULTS**

Select metrics of dive behavior are provided in Table 7-2; further details are provided in Appendix 9.

**Dive behavior models**

Prey models of dive behavior using krill-like (200 kHz) backscatter metrics (Table A8-3) perform much better than those based on fish-like (33 kHz) backscatter, which have almost no predictive power at all (\(r^2\) range 0.00 to 0.06; Table A8-3). This was expected, given
that both species fed primarily upon krill in this fjord system (fin whales exclusively) during the years of this study (Chapter 4). Hereafter, “prey-based models” refers to those using krill-like 200 kHz backscatter.

In general, prey- and habitat-based models predict dive and respiration behaviors equally well (Fig. 7-5). Models are AICc-equivalent for all behaviors other than surface time and cycle time, which are better modeled by prey-based metrics. Both model types explain a low to moderate proportion of variance ($r^2$ range of 0.11 to 0.30), which we believe results from high inherent variability of behaviors rather than from missing important predictors. Based on proportion of null deviance explained ($r^2$), models of blow interval and time spent at prey depth perform best ($r^2=0.30$, habitat-based; and $r^2=0.24$, prey-based; respectively), while models of dive time and surface time perform worst ($r^2=0.14$, prey-based; for both).

Species and inferred feeding behavior are among the most important variables in both prey- and habitat-based models (Table 7-3). In prey-based models, feeding behavior has a higher mean relative variable importance (RVI = 0.88) than species (RVI = 0.80) across all behaviors. The most important backscatter metric is 200 kHz patch depth (mean RVI = 0.79; Table A8-2). The second-highest RVI of 0.45 is total 200 kHz backscatter. In habitat-based models, the predictors with top RVIs are species (mean RVI = 0.75), stratification (0.71), feeding behavior (0.70), seafloor slope (0.60), chlorophyll-a (0.53), and euphotic depth (0.52: Table A8-4). GAM spline function plots are provided in Figure A8-1.

**Dive behavior and foraging time as functions of depth**

Humpback whales were found foraging on presumed krill (200 kHz backscatter) with mean depths ranging from 19.01 to 218.23 m. Fin whales were found among mean backscatter depths of 60.30 to 167.75 m. The relationship between prey depth and dive metrics range from
weak to strong, and appears to depend upon species and behavioral state (Table A9-1, Fig. 7-6). For both species, dive, surface, and cycle durations increase with increasing prey depth down to 150 m (Fig. 7-7), aligning with optimal dive theory. However, humpback whale dive and surface durations level off and then decline beyond 150 m depth, while fin whale durations continue to increase steadily. As prey depth increases, transit time increases more rapidly for humpbacks than for fin whales due to their different speeds of descent and ascent (transit angles are negligibly similar; Table A8-1). In fact, humpback whale transit time increases more rapidly with depth than dive and surface times do, and these discrepancies increase at greater depths; in contrast, fin whale transit time increases less rapidly than dive time and only slightly more rapidly than surface time.

Dive models (Fig. 7-8) indicate that as a result of these depth-specific patterns, humpback time with prey dive\(^{-1}\) peaks at 71 m then decreases with deeper prey. Time at prey depth hr\(^{-1}\) is highest in the shallowest prey depths and drops precipitously with increasing prey depth, suggesting that the feeding performance of humpback whales hinges critically upon depth of prey. For fin whales, in contrast, time with prey dive\(^{-1}\) increases with depth steadily, though more slowly than dive time. As a result, fin whale time at prey depth hr\(^{-1}\) is maximized with the shallowest prey and declines with increasing prey depth, but the rate of decline slows with depth and is nearly zero between 150 and 220 m. These patterns suggest that, while shallower prey still affords more foraging time at prey depth, prey depth is a less critical variable for fin whale feeding performance within the depth range considered.

**Backscatter encounter rates (BER)**

The fin whale’s greater time at prey depth hr\(^{-1}\) leads to higher potential rates of prey encountered hr\(^{-1}\). Based upon the backscatter depth distribution sampled during systematic
surveys of the fjord system, which reflects the prey distribution whales would encounter if they were randomly searching the area without tracking preferred patch features, the integrated backscatter encounter rate (BER) for fin whales is 1.66 times that of humpbacks whales (Fig. 7-9A). The species ratio for maximum BER is 1.85. Fin whales achieve their maximum BER at 94.4 m, while humpback whales achieve theirs at 78.3 m.

When BERs are calculated based instead upon the backscatter depth distribution sampled during focal follows, fin whales still hold a higher integrated BER than humpbacks, but the ratio is closer to 1 (1.16; Fig. 7-9B). Species ratio for maximum BER is 1.14. Shallower than their shared maximum BER depth of 79.8 m, humpbacks have equal or higher BER. Below 79.8 m, fin whale BER is greater. By targeting the prey patch features they do, fin whales attain integrated and maximum BERs that are 1.99 and 2.38 times, respectively, their BERs based upon systematic random sampling. For humpbacks these ratios are higher (integrated BER = 2.86; maximum BER ratio = 2.95). These ratios serve as rough metrics of the payoff of selective foraging.

If fin whales were associated with the same prey patch characteristics as humpback whales, their integrated and maximum BERs would increase by factors of 1.39 and 1.29, respectively (Fig. 7-10A). If humpback whales associated with the same prey features as fin whales, their BER ratios would drop to 0.69 and 0.77 of what they currently attain (Fig. 7-10B). These findings point to the influence of species-specific prey patch preferences and the importance of selective foraging.

To explore the prey depth contingency of foraging advantage, integrated and maximum BERs for each species were calculated for simulated prey distributions of varying mean depth and dispersion (i.e., standard deviation; Fig. 7-11). Mean patch depth (simulated with SD = 20 m) has a much larger effect on species BER ratios (Fig. 7-12). Deeper prey exacerbates species ratios for both integrated and maximum BER; beyond 150 m, ratios
increase abruptly such that at 200 m the integrated ratio is almost 15 and the maximum ratio is more than 5. The effects of prey dispersion are less extreme and more complicated. When prey become increasingly dispersed about a mean depth of 100 m, the integrated BER ratio climbs from its starting point at 1.62 to 1.80 once standard deviation reached 100 m, but then it plateaus. Conversely, in that same depth window the maximum BER ratio drops from 1.62 to 1.25, then slowly diminishes to 1.10 by the time a prey depth of 220 m is reached. Collectively these simulations suggest that, within the depth range considered, the fin whale’s competitive advantage over humpback whales increases along with prey depth. The vertical dispersion of prey has a relatively negligible impact on performance ratios, but it does control the intensity of interspecific competition by governing the degree of necessary overlap in foraging depths (i.e., competition intensity will increase in less vertically dispersed prey fields).

**DISCUSSION**

In general, whale dive metrics were predicted equally well with prey- and habitat-based models, demonstrating the connection between the energetics of foraging rorquals and their habitat. These dive behaviors, when pitted against the depth distribution of krill within the Kitimat Fjord System (KFS), determined the relative feeding success of co-occurring humpback and fin whales and explained prey patch associations. Simulations based on findings indicate that fin whales gain an increasing foraging advantage with increasing prey patch depth. Our results emphasized the importance of swim speed in rorqual foraging strategy and the influence of prey depth distribution upon rorqual dive energetics, competitive interactions, and habitat use.
As the first extensive comparison of dive strategy in sympatric rorqual whales to include prey distribution data, this study would have benefited from quantitative prey biomass measurement and the concurrent deployment of archival multi-sensor tags, which would have provided several key variables needed for full-fledged energetics analysis (e.g., actual dive depth, time spent in prey patch, locomotive actions, and number of lunges dive⁻¹). However, by employing affordable, remote techniques of sampling whales and their habitat, we were able to place a large behavioral dataset within a well-sampled ecological and oceanographic context, and so broach the question of how prey-mediated dive energetics can couple whales to the dynamics of their marine habitat. Our findings highlight this important link and point to its potential role in the habitat choices of foraging whales.

Dive models highlighted the role of swim speed in determining depth-specific prey encounter rates. The relative rates of dive time, surface time, and transit time, and the changes of those rates with prey depth, determine feeding performance in humpback and fin whales of the KFS. According to published speeds of ascent and descent, every 10 m increase in patch depth is a 13.1- and 7.6-second increase in transit time for humpback and fin whales, respectively. Round-trip transit times to the mean backscatter depths of focal follows are 132.0 and 89.4 seconds, respectively, which is a significant portion of dives for both species; but fin whales, the “greyhounds of the sea”, clearly hold a significant advantage, particularly when considering their capacity for longer dives. The locomotive advantage of large body size is well established for the rorqual body plan (Tucker 1975; Williams 2006), but its importance in dive energetics and the competitive dynamics of foraging rorquals appears to be underestimated.

Our findings help explain puzzles about the rorquals of this fjord system discussed in Chapter 4 and this chapter’s Introduction. Although fin whales are associated with lower volume krill patches than humpback whales, their dive behavior nevertheless enables higher
hourly prey encounter rates. Furthermore, fin whale dive behavior aligns with this fjord system’s average prey distribution such that deeper prey patches, when foraged upon in a mode of random search, actually yield higher encounter rates than shallow patches. Focal follows show that selective foraging can improve upon random-search encounter rates when fin whales target relatively deep prey patches, in which maximum encounter rates are nearly equal from 75 to 125 m depth (Fig. 7-9B). Therefore, in both selective and unselective foraging modes, relatively deep prey patches can be maximally profitable for the fin whales of this fjord system. This may further explain the viability of prey-agnostic site loyalty behavior practiced by the fin whales of this fjord system (Chapter 5), and emphasizes the potential importance of this habitat as a foraging corridor for recovering BC fin whales (discussed in Chapter 5).

Humpback whales in the KFS outperform fin whales in one important metric: their selective foraging strategy, which has been shown to be more attuned to environmental indicators of prey volume (Chapters 5 and 6), increases prey encounter rate above that expected from random search by a greater factor; i.e., the energetic payoff of foraging selectivity is higher in humpback whales. Despite this higher payoff, however, humpback-prey encounter rates are low relative to fin whales, apparently because of the loss of foraging efficiency with increasing prey depth. This aligns with previous findings elsewhere; humpback whales have been observed feeding shallower than the prey maximum (Dolphin 1987; Goldbogen et al., 2008), and the species is known to feed at night when vertically migrating prey are closer to the surface but more dispersed (Ware et al., 2010). Fin whales are known to practice similar measures in habitats with deeper euphausiid distribution, such as the Ligurian Sea where fin whales conduct crepuscular feeding upon moderately deep swarms of *Meganyctiphanes norvegica* that have not yet dispersed to feed in shallow waters (Panigada et al., 2003). Our dive models suggest that the depth distribution of prey in the KFS, which falls
just below the humpback whale’s energetic “comfort zone” but well within that of the larger fin whale, defines the foraging strategies of these sympatric rorquals. While the humpback whale’s dive behavior is constrained by the need to minimize energetic loss, the fin whale’s dive behavior is relatively free to target optimal prey patches at optimal depths.

Earlier studies in rorqual dive strategy proposed that the high cost of lunge feeding limited dive time and therefore prey access (e.g., Croll et al., 2001; Acevedo-Guiterrez et al., 2002). The past decade was one of considerable progress in understanding the allometry of dive and lunge energetics (Goldbogen et al., 2006; 2010; 2012b; Potvin et al., 2012). Doniol-Valcroze et al. (2011) and Friedlaender et al. (2015) emphasized instead that optimal foraging theory, when combined with allometric dive energetics, best explains rorquals’ behavior of diving well below their theoretical aerobic limit and their preference for shallower prey, since brief dives require less recovery time at the surface and thereby maximize hourly feeding rates. We suggest that species-specific aerobic and locomotive abilities, combined with the specifics of prey distribution, defines the balance of gain optimization and loss mitigation in rorqual dive strategy. Our findings highlight the importance of prey distribution in these energetic dynamics; optimal behaviors cannot be understood without knowledge of the prey field, nor can prey preferences be understood without knowledge of the interaction between prey field and dive strategy.

Prey depth distribution and depth-specific feeding abilities interact to determine the competitive advantages and disadvantages for sympatric rorquals feeding upon a common prey source. The location and persistence of mean prey depth determines differences in foraging opportunities for competing species, defined by differences in their aerobic and locomotive capacities. The vertical dispersion of prey sets the spatial overlap of competitive interactions and therefore their intensity. To the extent that these dynamics impact a species’ cumulative energy gain over the course of a foraging season, they may contribute to patterns
in habitat use and site loyalty. They may also impact dive strategy itself; in areas with limited prey supply in which the competitors’ primary interest is securing sufficient net energy gain on the timescale of a season, rorquals could conceivably concentrate feeding effort at depths that maximize competitive advantage rather than food intake. Alternatively, it is also conceivable that rorquals partition the prey field according to differences in depth-specific feeding performance in order to minimize lost feeding opportunities due to competition (Friedlaender et al., 2015). This scenario is a plausible explanation for our observations in the KFS, in which fin whales are found among deeper prey patches than humpback whales but apparently not to their significant disadvantage. Further studies of sympatric rorqual feeding behaviors are clearly needed in a variety of marine habitats and prey communities.

Although our data clearly show that fin whales, and to a lesser extent humpback whales, feed in association with deeper-than-average prey layers, we cannot say why. Our dive data and model show that the relative cost of deep feeding is lower for fin whales, which agrees with our observation that they feed on deeper prey layers than humpback whales. But, for some reason, both appear to be feeding towards the bottom of their energetically feasible depth range. All other things being equal, they should be feeding on the shallowest prey layers to optimize their net energy gain. Some unmeasured attribute of krill (e.g., size or energy density) or their behavior (avoidance or schooling) may make deep krill more desirable.

As our dive-habitat models and related prey-habitat models (Chapter 6) show, habitat features can facilitate or complicate the rorqual’s task of diving strategically to maximize net energy gain. Rorqual habitat use is a matter of optimal foraging strategy on many levels, including that of dive energetics. This raises the question of which marine habitat types are inherently more advantageous for foraging rorquals. Fjord systems, for example, are oceanographically dynamic estuarine habitats known for high rates of production (Syvitski et al., 1987), in part because they receive high nutrient input from offshore waters as well as
terrigenous sources. These processes create seasonally turbid conditions within fjords, which would increase rates of light attenuation with depth. Fjord systems are also subject to isolated warming events due to summertime insolation (Thomson 1981) and, in the northeast Pacific, to differential mixing from outer to inner channels caused by the onset of autumnal storms and katabatic winds (reviewed in Chapter 2). All of these processes are known to affect krill patch formation (see chapter’s Introduction), all processes have been observed in the KFS, and monthly patterns in these fjord conditions align strikingly well with monthly patterns in system-wide patterns in 200 kHz backscatter depth (Fig. 2-5). Within-month variability in KFS backscatter depth is well predicted by habitat features (Chapter 6), further emphasizing the strong coupling between habitat, prey patch formation, and whale feeding performance within this fjord system.

However, it is unclear whether KFS krill depth distribution lends any unique advantage compared to other northeast Pacific foraging grounds, since it does not appear to be notably different from that of other north Pacific systems. Daytime patches of krill found in this study are found at a mean depth of 93 m ± 38.44 (Chapter 4) but occur from the sea surface to below 220 m. This is similar to the 80-100 m mean daytime depth range for *E. pacifica* sampled within Saanich Inlet, BC (Boden and Kampa, 1965; Robertis, 2002), their 50-125 m range in another Washington fjord (Bollens et al., 1992), and depth ranges reported in studies elsewhere in the north Pacific (Taniguchi, 1969; Brinton, 1962; Nakagawa et al., 2003; Taki, 2008; Sogawa et al., 2016). There is some evidence that krill patches are relatively deep in the southern California Current: published whale dive depths from southern and central California are notably deeper than the mean prey patch depths of our study area and the other fjord systems referenced above, for both humpback whales (189 m) and fin whales (97 – 248 m; see references in Table A8-1).
These uncertainties aside, previous studies in the KFS have established its suitability in many respects for foraging rorquals relative to other habitats in the northeast Pacific. The unique position and morphology of the KFS within northwest North America’s fjordland may render it uniquely suitable to foraging whales (discussed in Chapter 5). It and other fjord systems house unmatched spatiotemporal habitat variability within a small compartmentalized area (Macdonald et al., 1983; Thomson 1981), establishing steep environmental gradients that can facilitate the location of preferred prey features (discussed in Chapter 6) and provide foraging space of sufficient heterogeneity to accommodate euphausivorous competitors with divergent prey patch preferences (discussed in Chapter 4). Fjords are also remote, relatively undeveloped, and relatively quiet marine habitats with unique acoustic properties due to their steep-walled channel enclosures (Williams et al., 2013; 2015). It should be expected that fjord systems and other complex coastal areas are important foraging grounds for whales. Fjords are also exciting venues for research for many of the same reasons. However, due to the worldwide depletion of coastal whale populations by industrial whaling and the subsequent rise of ecological cetology in the nadir that followed, the historical and potential importance of fjord systems to whale populations may be underappreciated. Hopefully this will change as recovering populations restore their use of historical foraging grounds and receive further study.

**Suggestions for further research**

We encourage further dedicated field studies in a variety of marine habitats that combine behavioral focal follows and multi-sensor tagging efforts with prey and habitat sampling within well-defined marine areas. Such efforts would add important complexity to this paper’s simplified models, which (1) consider dive strategies only within a limited depth
range; (2) are limited by low sample size in the tails of prey depth distribution; (3) assume uniform depth distribution of the energy content and capturability of prey, which is highly unlikely given the discrepant depth preferences of the two main euphausiid species in the fjord system, *E. pacifica* and *T. spinifera* (Brinton, 1962; Coyle and Pinchuk, 2005); (4) ignore the contributions of crepuscular and nighttime foraging (which have been observed in these species elsewhere: Panigada et al., 1999; Panigada et al., 2006; Friedlaender et al., 2009b; Friedlaender et al., 2015; and in humpback whales of this study: authors, unpublished data); and (5) assume that key behavioral rates, such as lunge frequency dive$^{-1}$ and aerobic dive limits, are not functions of prey patch qualities although they are known to be (Goldbogen et al., 2008; Doniol-Valcroze et al., 2011).

**ACKNOWLEDGMENTS**

This chapter, in part, has been submitted for publication as it may appear in *Marine Ecology Progress Series*, 2017: Keen, EM, and KM Qualls. (In review) “From fjord to fin: dive energetics couple habitat features to the competitive dynamics of sympatric rorqual whales within a fjord system.” The dissertation author was the primary investigator and author of this paper.
Table 7-1. Dive behavior parameters used in models of feeding performance. Parameters were derived by averaging published values listed in Table A8-1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Humpback</th>
<th>Fin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate of descent m s(^{-1})</td>
<td>1.60</td>
<td>3.25</td>
</tr>
<tr>
<td>Angle of descent</td>
<td>58.50</td>
<td>53.00</td>
</tr>
<tr>
<td>Rate of ascent m s(^{-1})</td>
<td>1.45</td>
<td>2.03</td>
</tr>
<tr>
<td>Angle of ascent</td>
<td>55.50</td>
<td>64.00</td>
</tr>
</tbody>
</table>
Table 7-2. Summary statistics of select dive and respiratory behaviors for humpback and fin whales sampled in this study. Further dive metrics are provided in Table A9-1. $n =$ number of groups followed. $p$-value = significance of two-sided KS-test between species. * Metric calculated only for whales inferred to be deep-feeding.
<table>
<thead>
<tr>
<th>Dive behavior metric</th>
<th>Humpback</th>
<th>Fin</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td>n</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td>p</td>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td></td>
<td>n</td>
</tr>
<tr>
<td>Observed</td>
<td>275</td>
<td>24.62</td>
<td>11.20</td>
<td>67.60</td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
<td>250</td>
<td>5.94</td>
<td>3.32</td>
<td>17.00</td>
<td>0.022</td>
<td></td>
<td>38</td>
<td>7.06</td>
<td>3.09</td>
<td>13.00</td>
<td>&lt; 0.0001</td>
<td>37</td>
<td>6.62</td>
<td>2.55</td>
<td>16.12</td>
<td></td>
</tr>
<tr>
<td>Blowing interval (sec)</td>
<td>250</td>
<td>5.94</td>
<td>3.32</td>
<td>17.00</td>
<td>38</td>
<td>7.06</td>
<td>3.09</td>
<td>13.00</td>
<td>0.022</td>
<td></td>
<td>37</td>
<td>6.62</td>
<td>2.55</td>
<td>16.12</td>
<td>&lt; 0.0001</td>
<td>37</td>
<td>6.62</td>
<td>2.55</td>
<td>16.12</td>
<td></td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Number of blows</td>
<td>232</td>
<td>4.77</td>
<td>2.38</td>
<td>17.63</td>
<td>39</td>
<td>2.06</td>
<td>0.92</td>
<td>3.95</td>
<td>0.3171</td>
<td></td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td>&lt; 0.0001</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td></td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Dive time (min)</td>
<td>244</td>
<td>1.89</td>
<td>1.09</td>
<td>6.36</td>
<td>39</td>
<td>2.06</td>
<td>0.92</td>
<td>3.95</td>
<td>0.3171</td>
<td></td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td>&lt; 0.0001</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td></td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Surface time (min)</td>
<td>244</td>
<td>1.89</td>
<td>1.09</td>
<td>6.36</td>
<td>39</td>
<td>2.06</td>
<td>0.92</td>
<td>3.95</td>
<td>0.3171</td>
<td></td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td>&lt; 0.0001</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td></td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Cycle time (min)</td>
<td>211</td>
<td>6.63</td>
<td>3.00</td>
<td>19.20</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td>&lt; 0.0001</td>
<td></td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td>&lt; 0.0001</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
<td>18.13</td>
<td></td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Inferred</td>
<td>70</td>
<td>3.54</td>
<td>2.20</td>
<td>14.78</td>
<td>23</td>
<td>5.36</td>
<td>2.32</td>
<td>14.23</td>
<td>&lt; 0.0001</td>
<td></td>
<td>23</td>
<td>5.36</td>
<td>2.32</td>
<td>14.23</td>
<td>&lt; 0.0001</td>
<td>23</td>
<td>5.36</td>
<td>2.32</td>
<td>14.23</td>
<td>&lt; 0.0001</td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Time at depth (min)*</td>
<td>70</td>
<td>0.41</td>
<td>0.15</td>
<td>0.77</td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td></td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
<tr>
<td>Proportion of cycle at depth*</td>
<td>70</td>
<td>0.41</td>
<td>0.15</td>
<td>0.77</td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td></td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
<td>0.78</td>
<td>&lt; 0.0001</td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
<td>86.44</td>
<td>0.0554</td>
<td></td>
</tr>
</tbody>
</table>
Table 7-3. Relative importance of variables (RVI) in prey-based and habitat-based models of dive and respiratory behaviors. Only those variables with RVI above 0.50 are shown. “Feeding” and “Species” are binary factors; all other variables are continuous.
<table>
<thead>
<tr>
<th>Model set</th>
<th>Predictor</th>
<th>Mean RVI</th>
<th>Number of blows</th>
<th>Blow interval</th>
<th>Dive time</th>
<th>Surface time</th>
<th>Cycle time</th>
<th>Time at prey depth</th>
<th>Prop. time at prey depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey-based</td>
<td>Feeding</td>
<td>0.88</td>
<td>1.00</td>
<td>1.00</td>
<td>0.77</td>
<td>0.63</td>
<td>0.99</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>0.81</td>
<td>0.52</td>
<td>0.89</td>
<td>1.00</td>
<td>0.26</td>
<td>0.99</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Patch depth</td>
<td>0.79</td>
<td>0.98</td>
<td>0.73</td>
<td>0.96</td>
<td>1.00</td>
<td>1.00</td>
<td>0.26</td>
<td>0.65</td>
</tr>
<tr>
<td>Habitat-based</td>
<td>Species</td>
<td>0.75</td>
<td>0.62</td>
<td>0.31</td>
<td>1.00</td>
<td>0.32</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Stratification</td>
<td>0.71</td>
<td>0.87</td>
<td>1.00</td>
<td>0.64</td>
<td>0.29</td>
<td>0.82</td>
<td>0.62</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Feeding</td>
<td>0.70</td>
<td>1.00</td>
<td>1.00</td>
<td>0.51</td>
<td>0.32</td>
<td>0.67</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Seafloor slope</td>
<td>0.60</td>
<td>0.92</td>
<td>0.30</td>
<td>0.37</td>
<td>1.00</td>
<td>0.58</td>
<td>0.33</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Chlorophyll - a</td>
<td>0.53</td>
<td>0.35</td>
<td>0.98</td>
<td>0.30</td>
<td>0.95</td>
<td>0.35</td>
<td>0.35</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Euphotic depth</td>
<td>0.52</td>
<td>0.81</td>
<td>1.00</td>
<td>0.30</td>
<td>0.27</td>
<td>0.45</td>
<td>0.35</td>
<td>0.43</td>
</tr>
</tbody>
</table>
Figure 7.1. Expected qualitative changes in respiratory behavior and foraging profitability with prey depth for rorqual whales, based on optimal dive theory. In this simplistic representation, depth curves are assumed to be linear. As prey depth increases, transit time from the surface increases. To maintain time at prey depth per dive, dive time must increase, depleting oxygen stores and thus requiring greater time at the surface for recovery between dives. Thus cycle time increases faster than dive time, reducing the proportion (dotted line) of each dive cycle and foraging hour spent with prey.
Figure 7-2. Depth distribution of mean total krill-like backscatter systematically sampled within the study area, based on data from Chapter 4. Lines are mean backscatter depths sampled during focal follows of humpback whales (solid grey) and fin whales (dotted grey).
Figure 7-3. Key relevant findings from Chapter 4 demonstrating fin whale associations with deep krill patches. A. “Position curves” portray the 200 kHz backscatter patch depth (mean = black line; SD = grey bars) sampled at increasing distances from whales (x axis) during systematic transects. Both species are associated on average with the deepest available backscatter, but this pattern is particularly dramatic for feeding fin whales. B. Histograms of 200 kHz backscatter depth sampled near fin whales (orange) and humpback whales (blue), superimposed upon that sampled systematically within the study area (grey).
Figure 7-4. Synopsis of environmental determinants of euphausiid-like 200 kHz backscatter patch depth sampled using systematic surveys of the Kitimat Fjord System, adapted from Appendix 8. Backscatter depth was modeled using generalized additive modeling (n=140; proportion of null deviance explained: $r^2 = 0.67$). Each pane is the spline function for a given habitat feature. Panes feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading). The significance of spline functions (p value) was evaluated based on an F-test and output in R package mgcv result summary.
Figure 7-5. Comparison of prey- and habitat-based models of whale dive behavior. Due to limited sample size \( (n < 264) \), models were considered equally parsimonious if within 9 AICc points of each other (“Zone of AICc equivalence”; Zuur et al., 2009).
Figure 7-6. Dive behavior plotted against mean 200 kHz backscatter depth sampled during each focal follow. Points are colored by inferred behavioral state (black = feeding; white = other behaviors). Simple linear models were fit to each behavioral state (solid line = feeding; dotted line = other); model fits are reported in Table A9-1.
Figure 7.7. Durations of dive, surface, and dive cycle as functions of prey patch depth. Focal follows were grouped in 20m bins of mean backscatter depth and their dive measurements were averaged.
Figure 7-8. Dive strategy models of each species with increasing prey depth. Cycle time, dive time and surface time were modeled from the observations reported in Fig. 7-7. Transit time was modeled using published dive metrics (Table A8-1). Time at prey depth dive was derived from these curves, then proportion of foraging hour at prey depth (orange line) from that.
Figure 7-9. Mean Depth distribution of total 200 kHz backscatter (dashed lines) sampled during (A) systematic acoustic surveys and (B) focal follows of humpback whales (orange) and fin whales (blue). With this prey distribution and the depth-specific dive strategies modeled in Fig. 7-8, we calculated the depth distribution of backscatter encountered per foraging hour (thick lines).
Figure 7-10. Encounter rate performance of humpbacks and fin whales if each species targeted the same prey patches as the other. A. Encounter rates when targeting prey patches sampled during humpback focal follows. B. Encounter rates when targeting prey patches sampled during fin whale focal follows.
Figure 7-11. Simulated backscatter encounter rates for humpback (orange) and fin (blue) whales given various depth distributions of the prey field (black dotted line). Top row explores effect of mean prey depth (SD = 20 m); bottom row explores effect of increasing vertical dispersion (about mean 100 m).
Figure 7-12. Species ratios of backscatter encounter rates as functions of (A) mean and (B) standard distribution of the prey field, based upon simulations (Fig. 7-11). Two ratios are calculated: that of the integrated backscatter encounter rate for the water column (0-220m; black line) and the maximum encounter rate modeled within that range (grey line).
APPENDIX 1

RV Bangarang

The Bangarang was built in 1980 in Port Coquitlam, British Columbia. Her 3/4 keel draws 4.0 ft and her displacement is 18,000 lbs with a cruising speed of 6.1 knots and a hull speed of approximately 7.3 knots (Fig. A1-1). Both her diesel and water tanks are 120 gallons. Her 3-blade (12-17) prop, which is enclosed by the keel and a keg-hung rudder, provides protection against fouling in kelp and renders her a relatively safe vessel for close whale interactions. Her sail inventory includes a mainsail (original), staysail (original), yankee jib (2007) on a roller furler (2015), and a spare genoa (original). For quick and safe dousing, the mainsail is contained by a Doyle Cradle Cover and lazy jacks system (2014) and a reeling system (2014).

The Bangarang’s layout includes a center cockpit with wheel helm (Wagner hydraulic steering); aft stateroom with a queen bed and a head with shower; and a main cabin with kitchen, dinette, salon with two settee berths, and a forward head. Bangarang sleeps 3 quite comfortably, 4 comfortably if two are a couple, and up to 6 if needed. Hot water flows to all faucets. The water heater can use either passive heating by the running engine or 30-Amp AC shorepower to function. The kitchen has an icebox and a gimbaled propane stove. Propane is stored under the helm seat in the cockpit and spare tanks are kept under the visual survey platform around the mast. An Espar heater provides forced-air ventilation for all cabin areas.

With the boat being 34 years old and in considerable disrepair at the onset of the project, many improvements had to be made in order for the Bangarang to perform as a liveaboard research vessel. The first season (2013) was carried out with many of the original systems still in place, resulting in the loss of 34 field days to repairs. Culprits include a failed potable water system, alternator, shorepower battery charger, raw water pump, and leaking engine gasket. Before season two, her original Perkins 4-108 45 horsepower diesel (3000+ hours) was therefore replaced with a 2014 Yanmar 3JH5 3-cylinder 39 horsepower diesel, including a new propeller shaft, coupler, packing gland and stringer mounts. At cruising speed this engine uses 0.68 gallons per hour.

The Bangarang’s anchor system was replaced in 2013 with 89’ of high-test G4 3/8” chain, 200’ of 7/16” double-braided nylon, and a 54 lb. Bruce-type anchor retrievable with a manual windlass at the bow. Potable water hosing, water pump, toilets and toilet plumbing were also replaced. Her tender, a 2013 8ft West Marine rowing inflatable christened the Jangan Gila Dong II, was stowed onboard the aft swimbridge (Fig. A1-2). The cockpit's beautiful dodger and bimini (new 2014) provided full protection of cockpit electronics during rain.

The battery bank (new 2014) included two Dyno 6V flooded-lead-acid 245 Amp-hr batteries in series for the house bank and a Dyno Group 31 12V flooded-lead-acid 1600 Cold-Cranking-Amps starter battery. The bank was charged with the engine's 80-Amp alternator. At the dock the battery bank could be charged through shorepower with a new battery charger. Battery voltage was monitored using a Xantrex LinkLite-Pro. The new inverter bank, which could be switched between shorepower to supply the vessel's AC outlets, included a 1200-Watt pure sine wave inverter and a 1550-Watt square wave inverter. The vessel was almost fully re-wired with a new DC switch panel and fuse block. Upgraded navigation electronics included a Garmin 441s chartplotter/depthsounder and a Furuno 1623 radar. There were three new VHF radios on board, an iCom 2200H, a Standard Horizon unit, and a handheld iCom.
The *Bangarang* had a top-knotch library of regional natural history field guides, whale-oriented literature, adventure classics, sailboat maintenance manuals, regional identification catalogs and scientific publications. Her chart drawer covered the entirety of the southern Inside Passage in detail from Olympia, WA, to Prince Rupert, CA. The 4-speaker JVC KD-X200 stereo was new in 2013, and was used for live-listening and playback of hydrophone recordings. Songbooks are also on board. Epiphytic ukelele, guitar, and banjo were stowed on the walls and ceiling of the salon with quick-release lashings. Harmonicas (keys G, C, F, D, and A) were also in arm’s reach, along with several other small hand instruments. The season’s supply of box wine and 20lbs of dark chocolate were stored under the salon's settees.

For research, the *Bangarang* had a dedicated 12V Group 31 AGM research battery capable of isolation from other electronics and the engine to ensure clean signals for sensitive acoustic instrumentation. This battery powered the data entry laptop at the helm as well as the echosounder, whose processor was mounted in an “acoustics cubby” aside the dinette. The towed and over-the-side hydrophones were also powered by this battery. Hydrophone recording was controlled in the aft stateroom's Passive Acoustics Listening (PAL) station. Weather station and VHF antenna were mounted on the 10-ft radar tower at the port transom. Weather, echosounder and GPS data were sent to an 8-port Moxa U-Port serial port hub in the dinette then to the helm's data entry laptop through a single USB cable. The forward head was converted to a laboratory for zooplankton imaging and analysis. While in the seated position, one could pull out a Wild Mark-5 stereo dissecting microscope replete with LED lights and tools on a sliding desk. The counter held a live-well and provided storage space for sample jars and notebooks. A Celestron USB-imager was installed in place of one of the microscope's eyepieces for image and video capture of samples.

On deck a visual survey platform was built around the mast with hatches to stow equipment. While on effort the observers lashed themselves to the mast with webbing secured with quick-release caribeners. Telescoping poles used in fecal and prey sampling were rail-mounted around the deck for quick access. Pelican cases were secured to the topside deck under the dodger for easy access to research cameras and passive acoustic recording packages. On the topsides of the aft cabin, a wooden frame was installed to mount the hydrophone reel (24” flange Reel-Core, Fig. A1-3). The hydrophone cable was routed through a yoke with rollers on a PVC crane that kept the cable high and aft of the propeller's turbulence. To the hydrophone reel's frame the zooplankton preservation station was mounted and both were covered with protective canvas. At the starboard transom an Ocean Marine Systems stainless steel 7-ft rotating davit was installed with an electric Power-Winch 300 pot hauler (150’ per minute) for CTD and zooplankton casts (2014). The echosounder transducer was mounted on a stainless steel arm that swiveled in and out of deployed position on a transom-mounted hinge. For winter storage the transducer cable could be disconnected from a weatherproof plug on the transom and the swivel arm could be removed.
Figure A1-1. Speed capabilities of the Bangarang at various RPMs with and against the tide. Trial performed in the Strait of Georgia on 1 August 2014.

Figure A1-2. The Jangan Gila Dong II, tender to the Bangarang. Here it is drifting away from the vessel because I forgot to tie its bowline to the swimbridge.

Figure A1-3. The towed hydrophone array stowed on its reel on the aft cabin's topsides deck.
APPENDIX 2:
Excerpt from Observer Manual

Seeing things. This is the crew's primary duty on board, the bread and butter of the science we are doing. During Bangarang transects, we are conducting two modes of visual survey simultaneously: (1) distance sampling for marine mammals and vessels, and (2) strip-width sampling for seabirds, jumping salmon, and debris.

Each mode demands certain things of observers, and most of these demands overlap. For distance sampling to produce reliable results, the key assumptions of an observer's performance are that:

- The probability of detecting an animal of interest on the track line is 1 (or can be estimated). This means we don't miss anything right in front of us.
- The animals of interest do not move in response to the survey platform before detection (or the extent to which they do can be estimated). This means seeing them an adequate distance away, before they respond to our presence.
- The species are identified correctly. This means knowing your blows and knowing your birds.
- Distance to sighting is estimated accurately. This means knowing how to read compass and reticle with your binoculars, and, most importantly, reporting their readings as accurately as possible to the helmsman - no rounding, no lazy looks, no fabrication.
- Group size is also estimated accurately. This means taking pains to estimate accurately and honestly.

For strip-width sampling to produce reliable results, the observers are expected to accomplish the following.

- Accurately determine what is within their viewing strip and what is not from any particular vantage. This means knowing how to use your rangefinder and using it consistently.
- Not overlook any target species that occurs within the viewing strip.
- Give equal and adequate coverage to their viewing strip.
- Identify species and their behavior correctly. Again, this means knowing your blows and birds well.
- Again, estimate group size accurately.
- Report any changes in behavior as a result of the vessel to the helmsman.

Although there is obviously overlap in the two directives, combining the two survey modes is no small task. Conducting each type of survey adequately requires special mindfulness on the part of observers. This is something that we must learn and remind ourselves of throughout the season.

Good observers have long attention spans, can tolerate long periods of discomfort and are not prone to motion sickness. However, no observer can be expected to be perfect. The key is being consistently imperfect in your observer performance.

To explain: The quantitative analyses Eric will apply to field observations will rely on a standardized, recordable, consistent effort to be made during transects. By standardized, I
mean that effort among observers must be equally rigorous and that the viewing area must be covered in the same strategic manner by all observers, all season long. It is impossible to expect that effort is equally effective among observers - this is why we rotate positions between transects. By recordable, or transferable, I mean that the effort made by one observer can be described and replicated by other observers. By consistent, I mean that effort must remain the same within the work of individual observers.

Each observer must take ultimate responsibility in conducting each transect with equal, sustainable, unchanging effort. Eric is trusting you, the observer, to be intellectually honest with yourself and with him about your performance. To observe sustainably means to strike a balance between intense focus and comfort. Begin each transect with the same effort you can sustain until the end of the transect, until the end of the day, and until the end of the season.

Clearly, to be a good observer is to be rigorous but balanced. Some concrete instructions are as follows.

**Rules for good observing**

- Look hard, but not so hard that you burn out near the end of the transect, day, and season.
- Do not just look - look for. Do not just go through the motions of scanning your eyes over the water. It is easy to fall into the trap of just going through the motions. We need effort to be consistent, purposeful, meaningful and sustainable.
- Take responsibility for seeing everything within your strip, but always check the distances for blows and vessels.
- Keep an eye on open sightings, but pay adequate attention to your entire viewing strip.
- Pay particular attention to your viewing strip directly ahead of the vessel, but do not neglect the rest of your strip. If one observer is used on each side, each should spend approximately 1.5 times as much energy scanning from dead ahead to 45 degrees than from 45 degrees to 90 degrees. It is good practice for the two observers to overlap their scans slightly on the track line.
- A good observer sees everything immediately in front of her, most things at a moderate distance away, and some things at a great distance. Do not try to compete for seeing the most distant blows at the cost of missing the murrelets swimming right under your nose.
- To reiterate, be certain that you are seeing everything within your 150m viewing strip!
- This cannot be emphasized enough: provide absurdly accurate reticle and bearing readings to the helmsman. In our confined study area, readings rounded to the nearest tenth or to 0.0 are obviously false (vessels cannot be on the shore unless they are amphibious or run aground). Be over the top about it. Do not take shortcuts here!
- Practice using your range finder and your compassed binoculars as much as possible before your first transects.
- Re-read this observers manual regularly throughout survey.
APPENDIX 3:  
SBE25plus CTD Configuration and Processing

Configuration

The following configuration was set in July 2014.

- Pump delay is set to 120 seconds.
- Minimum conductivity frequency: 2.9 kHz. This default factory setting for this parameter is set to 3.0 kHz. The manual says to calculate this parameter for yourself using Equations condsal and condfresh.

\[
\text{Min Conductivity Frequency} = \text{Zero Raw Conductivity Frequency} + 500 \text{ Hz}
\]

Nearly freshwater applications:
\[
\text{Min Conductivity Frequency} = \text{Zero Raw Conductivity Frequency} + 5 \text{ Hz}
\]

- Our specific sampler's Zero Conductivity Frequency is provided on the conductivity sensor's calibration sheet. According to it, the sensor registers a frequency of 2.78557 kHz at 0 salinity units. Because our study area can have nearly fresh water water at the surface and it is important for the CTD to be triggered and logging near the surface, I have set our minimum conductivity frequency to roughly 100 Hz higher than our sensor's minimum frequency. That is, I have set this parameter to 2.9 kHz.

- Voltage Delays:
  - SetVAuxDelay0 = 1 second
  - SetVAuxDelay1 = 2 s
  - SetVAuxDelay2 = 3 s
  - SetVAuxDelay3 = 4 s
  - SetOutputFormat = 0 (the format readable by SeaSave V7)

Processing

CTD data were downloaded nightly via USB to the data laptop. The cast files were then converted and processed in “SBE Data Processing” software according to the procedure recommended in the Seabird Electronics 25plus manual.

Data conversion

Convert raw .xml data file into another file format, “.cnv”, formatted according to user-defined syntax. This steps creates a NEW file. It does not replace the original raw data. Our converted files include the following data columns, in this order:

- Time (seconds)
- Acceleration (m/s2)
- Depth (saltwater, m)
- Pressure (db)
- Conductivity (Siemens)
- Dissolved oxygen (mL/L)
- pH
- Fluorescence

Filter
Low-pass filter pressure to increase pressure resolution for Loop Edit and low-pass filter temperature and conductivity to smooth high frequency data. According to SBE Data Processing, I set time constant A to 0.1 to apply to Temperature and Conductivity, and constant B to 0.5 to apply to pressure.

**Align CTD**
Advance conductivity, temperature and oxygen relative to pressure, to align parameters in time. This ensures that calculations of salinity, DO and other parameters are made using measurements from the same parcel of water. According to the SBE25plus help manual, I have entered the following advance values:
- Acceleration: 0
- Pressure: 0
- Temp: 0
- Conductivity: +0.1
- Oxygen: +3.5
- pH: 0
- Fluorescence: 0

**Cell thermal mass**
To obtain higher resolution and more accurate conductivity values, I adjusted the following parameters in Data Set Up:
- Temperature sensor to use: 0.04
- Therma anomaly time constant: 8.0

**Loop edit**
Removes “bad” parts of data. Setup parameters:
- Minimum CTD velocity: 0.25 m/s
- Window size: 300s
- Percent of mean speed: 20
- Remove surface soak: checked
- Minimum soak depth: 0.1m
- Max soak depth: 0.5m
- Use deck pressure as pressure offset: checked
- Exclude scans marked bad: Checked

**Derive**
Add the following derived variables, in this order:
- Descent rate (m/s)
  - Potential temperature (ITS-90, deg C)
  - Salinity (psu)
  - Density (sigma-theta, kg/m3)
- Sound velocity (Wilson, m/s)
- Setup file: “Derive.psa”

**ASCII Out**
Convert to ASCII .txt file
Data check
The output ASCII file is then backed up and visualized in R (Fig. A3-1) for quality control each field night.

Figure A3-1. Example of nightly visualizations of CTD casts for data check and quality control.
Two CTDs were used in this study. In 2013, we used a YSI Castaway, provided by the Cetacean Research Program at Canada Department of Fisheries and Oceans (DFO). In 2014 and 2015, we used a SBE 25plus provided by the Gitga’at First Nation. The YSI is a relatively affordable unit (~$5,000 USD) whose use is uncommon in rigorous oceanographic studies, but its affordability is attractive to users for whom accuracy and precision need not be perfect. Studies are needed that compare the YSI to expensive industry-standard instruments, such as the SBE 25plus (~$25,000+ with additional sensors), in order to assess YSI performance and determine the scenarios in which it can suffice.

In summer 2015, we conducted four simultaneous casts of the two CTDs aboard the RV Bangarang. We performed casts in distinct oceanographic conditions: one trial occurred in outer waters of the fjord system where water column salinity was high throughout, two occurred in central waters with variable water column structure, and the fourth occurred in inner channels with relatively low surface salinity and consequently high stratification. The two CTDs were last calibrated in spring 2014. Due to the YSI’s limited depth range (100 m max), this comparison can only speak to differences in CTD performance in the upper water column. Details of CTD deployment are provided in Chapter 2.

Figure A4-1 presents depth profiles of temperature and salinity for each cast. Figure A4-2 presents difference in readings at each depth between the two CTDs. Figure A4-3 presents differences in calculated sound velocity, of interest in parameterization of acoustic instruments. In general, YSI samples were warmer and more saline (by means of ~0.5 C and ~0.75 psu, respectively), with the exception of colder and less saline readings at approximately 10 m depth (means of ~1.0 C and ~1.5 psu, respectively). Differences in readings were more variable above 20m depth, below which YSI readings were consistently warmer and more saline. These discrepancies resulted in sound velocity differences of a stable mean of +1.75 m s⁻¹ below 20 m and a more variable mean above 20m, reaching an extreme of -3.0 m s⁻¹ at 10 m depth.

In 2013, the YSI was deployed multiple times (n = 10) in immediate succession at a single location (S. Douglas Channel) to assess variability of readings in constant conditions. All casts were conducted within a single hour. Results indicated low variability at all depths (Fig. A4-4); the differences observed are likely the result of internal wave activity at the sample site.

This trial would have been improved by conducting trials immediately following instrument calibration. As more trials of this nature are conducted in a variety of marine habitats, we will better understand the circumstances in which the YSI, which is much more affordable and easier to deploy, is an appropriate choice for oceanographic monitoring initiatives.
Figure A4-1. 4 simultaneous casts of the YSI Castaway CTD (solid orange line) and SBE 25plus CTD (dotted blue line).
Figure A4-2. Differences in CTD readings by depth (SBE 25plus – YSI castaway) from 2015 trial casts. *Top row:* differences in each of the 4 trial casts. *Bottom row:* Mean difference of the 4 casts.
Figure A4-3. Differences in sound velocity calculations by depth (SBE 25plus – YSI castaway) from 2015 trial casts. *Top row:* differences in each of the 4 trial casts. *Bottom row:* Mean difference of the 4 casts.
Figure A4-4. Multiple casts (n = 10) of the YSI Castaway at the same time and location (S. Douglas Channel) in 2013. All casts occurred within a single hour.
APPENDIX 5:

Echosounder data processing and analysis aboard RV Bangarang

INTRODUCTION

This document outlines the steps taken in the preparation of echosounder data collected aboard the RV Bangarang for use in analyses of whale-prey interactions in the Kitimat Fjord System, northern British Columbia. All of these steps take place within open-source software including Visual Basic, ImageJ, Fhred, TextWrangler and R (R Core Team 2013), with routines written by EMK. Visual Basic code is available on EMK’s research website, www.rvbangarang.org, and scripts of R and ImageJ code are available upon request.

Instrumentation

Aboard the Bangarang, hydroacoustic data were recorded along survey tracklines with a down-sounding Syqwest Hydrobox echosounder (33 and 200 kHz dual-frequency) to obtain a profile map of the depth, distribution, and patchiness of backscatter down to 300m.

The Hydrobox performs some preliminary processing before making data available to users. This includes the implementation of a 20logR time-varied gain and the conversion of acoustic backscatter into color pixels based on gain and threshold parameters set by the user. These parameters are locked; they do not change in response to seafloor depth or overall noise levels. Each transmission is reported in the form of 200 pixels representing backscatter from the sea surface to 300m depth, such that each pixel is a bin representing 1.5 vertical meters of water. Pixels are given as integers, ranging from 0 to 255.

The use of similar low-cost echosounders has been common in studies of cetacean and seabird foraging strategy (e.g., Dolphin 1988; Piatt 1987, 1990; Piatt et al. 1989; Burger & Piatt 1990; Piatt & Methven 1992; O'Driscoll 1998; Benoit-Bird et al. 2001; Benoit-Bird & Au 2003). Because of the Hydrobox’s in-house processing, the data cannot be analyzed or described in the standard terminology of scientific echosounders as outlined in MacLennan et al. (2002). As it is not possible to conform our data to conventional units and definitions, we were careful to develop backscatter metrics that were similar to but clearly different from the standard in both unit and name.

The Bangaranag's Hydrobox transmitted at 600 Watts. Each frequency transducer was housed within the same hydrodynamic moulding. Each frequency was transmitted at a rate of 1 Hz. The frequencies were offset from each other by 0.5 sec. Gain settings within Hydrobox software were set to 27 dB for 33 kHz and 60 dB for 200 kHz. Beam widths were 18 degree for 33 kHz and 10 degree for 200 kHz. Within Hydrobox software, the detection threshold was set to 0 for both frequencies, and a sound speed 1500 m/s was used.

The transducer body was mounted 0.5m deep (within the range of depths in Rowe 1993, Yule 2000, Benoit-Bird et al., 2001), deployed at the most stable point on the vessel at the port transom by a stainless steel pipe that was secured to the vessel's swimbridge. When not in use the transducer swings up on a hinge for safe stowage. The transducer's signal was passed via weather-proof cable to a serial hub within the vessel’s dinette, then on to the data entry laptop at the helm. On this laptop the echosounder data were saved and displayed in real-time. The
echosounder was powered by the ship’s dedicated research battery, which was isolated from house and engine battery circuits, to eliminate electrical interference.

**Frequency choice**
The backscatter properties of an organism can be frequency-dependent, the details of which are primarily a function of the organism’s overall size and its material properties (Romaine et al. 2002). Echograms from 38kHz sounds or lower detect mainly air-bladdered fish (Cochrane et al. 2000) or physonectid siphonophores (Farquar, 1971; Andersen and Zahuranec, 1977). Fish with air-filled swim-bladders cause backscatter in a wide-range of frequencies, from 12 kHz to above 200 kHz (Foote 1980). Herring and young hake are the principal species associated with scattering layers in BC mainland inlets (Bary 1966, Sato et al. 2013).

Unlike air-bladdered fish, zooplankton that are iso-osmotic and only centimeters in size have much higher frequency dependence (Stanton et al. 1996, Kang et al., 2002). Many studies have used a 200kHz echosounder for detecting euphausiid swarms (e.g., Coyle and Cooney 1992, Rowe 1993, Cochrane et al., 2000, Benoît-Bird et al. 2001, Romaine et al. 2002, Sato et al. 2013).

A 38kHz and 200kHz dual-beam setup is among the most common in surveys for both fish and euphausiids (e.g., Coyle and Cooney 1992, Wiebe et al. 1997). A 38kHz transducer was not available for my system so the closest available frequency was used, 33 kHz.

**Processing summary**
Raw output from the Hydrobox software was converted to ASCII and timestamp-matched to visuals data. Systematic transect effort and focal follows were extracted from each day of acoustic data. GPS-stamps were used to account for variable vessel speed by pooling pings into bins representing 6m of trackline, such that each pixel value in a section of echosounder data represented a volume of water approximately 6 m x 6 m x 1.5 vertical meters.

Seafloor detections were verified by visual review and corrected using hydrographic data. Backscatter within 6m of the surface and seafloor were removed. Each day’s backscatter was visually reviewed for manual removal of regions of noise caused by engine cavitation or depth sounders from passing ships. All pixel values below a chosen "biological noise floor" were then removed.

Each frequency was then inspected visually, and filters were applied that removed backscatter that did not seem attributable to potential humpback prey, which we limited for our purposes to schooling “forage” fish and euphausiids. As a simplistic kind of “frequency differencing” technique, 200 kHz backscatter that overlapped with 33 kHz backscatter was removed such that the former represented krill-like backscatter and the latter represented schooling-fish-like backscatter. These scrutinization steps were verified using deepwater imaging and zooplankton tows.

**BASIC FORMATTING**
The raw data provided by Hydrobox software has two types of NMEA strings: a pixel row (one row for each frequency) and a context row (depth, lat, long, speed, heading, etc.) These strings were saved in a single playback file in a format that requires conversion to hexadecimal characters then to ASCII.
The first step is converting the file to pure hexadecimal format then breaking it into lines of text. The former is done in the open-source software Frhed and the latter is done with a custom routine written in Visual Basic.

The remaining processing steps are conducted in R. Lined text files of hexadecimal characters are translated into ASCII using an ASCII conversion table. The ASCII translation is output to comma-separated text files.
Each line of these text files is then assigned visual effort designations using timestamp-matching from the day's RUB output file. Effort-synched comma-separated files for each frequency (33kHz and 200kHz) of each date of field effort are generated and stored.

The echosounder software stores long recording sessions in small contiguous files of 1 MB file size. As the final step in basic formatting, all files from a single day are combined into a single file. In the same R routine EMK also standardized depth output (which is stored with variable significant figures in the raw echosounder output, depending on depth). The full-day's echo file is then visualized for quality control. Because about 55,000 pings are recorded in the average field day, the full-day files are quite large (10s of MBs).
DATA REDUCTION

Subset to transects and focal follows
Using the effort codes now associated with the data, pings corresponding to periods of transect effort and focal follows are isolated and saved separately. For focal follow echograms sighting and survey information were also included as a reference. As an aid in the interpretation and processing of focal follow echograms, maps of vessel tracks during focal follows are also produced.

Figure A5-7. Example maps of focal follow tracks.

Georectify
To ensure that changes in vessel speed did not falsely represent the extent of backscatter along a trackline, echo data are "georectified" by averaging pings into bins of equal lateral distance of approximately 6m according to their GPS-stamps. The result is reduced backscatter whose pixels represent a volume of the water 6m x 6m wide x 1.5m deep (54 m³), each calculated from the average of 1 to 10 horizontal raw pixels depending on vessel speed. Georectification is performed on both transect and focal follow data. At our average transect speed (4.5 knots, 2.3 m s⁻¹), 2 to 3 pixels are averaged together to yield a single pixel value in the georectified file. At focal follow speed, which is highly variable but a safe average is 2 knots or approximately 1 m s⁻¹), 5 to 7 pixels are averaged together for a single horizontal bin.

Figure A5-8. Example of georectified transect data; every row represents approximately the same horizontal distance.
Figure A5-9. Echogram of georectified backscatter from 11 August 2014. Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software.

NOISE PROCESSING

Automated seafloor correction
As a first step in ridding data of non-biological backscatter, seafloor echoes are removed. With every ping the echosounder stores an estimate of the seafloor depth, but these estimates differ slightly between frequencies and can be "tricked" by engine cavitation or inordinately thick prey layers. Moreover, the echosounder does not estimate depth below the prescribed depth range of 300m, but an accurate local depth was needed for habitat use and prey patch analyses.

To ground-truth, correct and gap-fill the echosounder's seafloor readings, they are compared to a publicly available 3-arc-second bathymetric dataset (NOAA 2013). Because the low-frequency can reflect the seafloor more accurately at greater depths, every high-frequency seafloor reading is replaced with that of the low-frequency ping that is closest in time. Then, for each ping regardless of frequency, the perceived seafloor is GPS-matched to the closest NOAA datum using the Vincenty method of the great-sphere distance algorithm (function "distance" in R package "swfscMisc" by Eric Archer). Only matches within a maximum distance (0.005 degrees latitude) are accepted, so that distant NOAA data would not be mistakenly used. Because our echosounder data have much greater resolution than the 3-arc-second dataset, the NOAA data are interpolated between adjacent readings to make seafloor slopes less jagged.

The NOAA datum is kept as the correct depth 1) if the NOAA data show that the vessel was in greater than 300m of water, or 2) if the echosounder's reading reads "NA". The echosounder reading was kept 1) if both the NOAA match and echosounder reading reported a depth less than 300m, and 2) when no NOAA datum occurred within 0.005 degrees of the vessel at the time of the ping. The seafloor correction routine outputs a graph that displays the decisions made datum by datum. Depth-corrected data files are output along with an echogram that displays the corrected seafloor superimposed. These same seafloor correction processes are also applied to focal follow echo data.

Figure A5-10. Example of a seafloor correction output. Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software. The "fixed" seafloor is
superimposed on the transect's georectified echogram. Obvious imperfections remain, hence the next step of manual seafloor correction.

**Manual seafloor correction**
The automated seafloor correction process is imperfect. For those pings where the "fixed" seafloor is still obviously erroneous (evidenced by the echogram of the corrected seafloor), the NOAA data were used as the best estimate of local depth. If there is no NOAA data within 0.005 degrees of the ping, the depth has to be updated to “NA”.

A JPEG of the echogram with automatic seafloor correction is reviewed in ImageJ, in which EMK drew rectangles around erroneous segments of seafloor and save those rectangle's measurements to a .CSV. Those measurements correspond to the start and end rows of problematic stretches of seafloor in the echo .CSV files. The conversion from JPEG pixel measurements to dataframe coordinates is not perfect due to margins that scale along with the length of the echo file, so a conversion routine was developed in R. To do so EMK manually converted measurements from 39 echogram JPEG's from 2014 echodata to the coordinates in their corresponding .CSV. Based on these manual conversions a linear model was defined that enabled EMK to automate the conversion. For each JPEG, the problematic segments of seafloor are isolated and replaced with GPS-matched CHS bathymetric data. New .CSVs, echograms, and seafloor correction plots are saved to file.

![Figure A5-11. Results of manual seafloor correction. Dark gray is the auto-corrected seafloor, blue is the seafloor after manual correction. Top row is 33kHz readings, bottom row is 200kHz.](image)

**Manual noise removal**
Each day’s backscatter were then visually reviewed for manual removal of regions of noise caused by engine cavitation, depth sounders from passing vessels, tracks of diving whales, and kelp. EMK reviewed each JPEG in ImageJ, drew rectangles around noise, saved those measurements to a text file, then ran a script in R that replaces that noisy data with NA values in the corresponding .CSV.
369

Figure A5-12. Record of manual selections (grey boxes), made in ImageJ, of “bad areas” in Campania transect (2 June 2015). Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software.

Figure A5-13. Result of manual filtration, in which “bad areas” are replaced with “NA” entries.

Figure A5-14. Result of manual filtration on Campania transect (2 June 2015). Top row is 33 kHz output, bottom row is 200 kHz. Color palette is same as that used in Hydrobox echogram display software.

Noise floor filter
Next, weak backscatter whose intensity registers below a background noise floor are removed using a filter. Values below this floor are assumed to be noise, values above are considered biological and potentially qualify as whale prey. Based on visual examination of multi-season echograms, noise floors are set to pixel values of 135 and 125 for 33kHz and 200kHz backscatter, respectively.
In this step, surface and seafloor buffers are also applied, in which the top 6m of the water column are removed as well as the 6m of backscatter above the seafloor.

Figure A5-15. Backscatter after application of biological noise floor. White areas are backscatter that did not register above noise floor threshold. Grey areas are seafloor or manually removed noise. Color palette for “biological” backscatter is same as that used in Hydrobox echogram display software. Top row is 33 kHz output, bottom row is 200 kHz.

FINALIZE DATASETS

Package into transect blocks
On rare occasions, transect effort within a single waterway had to span more than one day due to inclement weather. Such days were concatenated into a single file so that effort in each waterway during a sampling period was represented by a single file. Also, data in each file were sequenced to progress from south to north. To make sure that the transect was packaged correctly, annotated maps of each packaged file were produced.

Figure A5-16. Example of annotated map of transect trackline based on echosounder data (from 30 May 2015).

Echogram visualization scheme
To simplify visualizations of echodata and verify subsequent scrutinization procedures, echograms were created in which the two frequencies are overlaid. The colors for each
frequency are graded monochromatically and made translucent, so that areas of overlap can be seen. The width of the JPEG was set to a standard 5:1 ratio.

![Figure A5-17. A combined echogram from 30 May 2015 in Squally channel, with the two frequencies overlaid with translucency (blue = low frequency, red = high frequency).](image)

**Scrubinization: prey patch filtration**

In order to reduce each backscatter frequency further to display only patches that are probable whale prey, semi-automatic filters were applied based on patch characteristics so that, to the extent possible, 33kHz backscatter represents only small schooling fish while 200kHz backscatter represents euphausiids. Filter parameters were adjusted broadly for each month, and, in the case of anomalous noise levels, each day. This step was necessary because the biological noise floor threshold may have missed strongly backscattering water features such as particulate debris, inordinately dense mats of phytoplankton, and strong haloclines, all of which can be prominent within this fjord system. Moreover, each frequency reflects organisms that were not likely whale prey (e.g., fry and siphonophores at 33 kHz and copepods at 200 kHz; Macaulay et al. 1995, Barraclough et al. 1969).

![Figure A5-18. 33kHz backscatter, before (top) and after (bottom) prey patch filtration. From 2 June 2015 in Campania Sound.](image)

![Figure A5-19. 200kHz backscatter, before (top) and after (bottom) prey patch filtration. From 30 May 2015 in Squally Channel.](image)

Because air-bladdered fish can induce backscatter on both 33kHz and 200kHz frequencies (Foote 1980, Coyle and Cooney 1992, Kang et al., 2002, Jech et al., 2006), a simplified version of “frequency-differencing” was then implemented, in which 200 kHz backscatter that overlapped with 33 kHz was removed.
Fig. A5-20. Before (top) and after (bottom) frequency differencing. From 18 July 2015 in Verney Pass.

Fig. A5-21 provides examples of finalized acoustic datasets for focal follows. Those for each sampling period are provided in Chapter 2 (2-9 through 2-13).

Figure A5-21. Examples of acoustic backscatter collected during focal follows. Each pane is a separate focal follow, designated with its date, sighting number, species (HW=humpback), and uncommon behaviors, if any. Top row: focal follows containing backscatter that is likely attributable to small schooling fish; the top left focal follow is an example of both fish- and euphausiid-like backscatter occurring in close proximity. Bottom row: Focal follows with backscatter attributable to euphausiids only. Y-axis is depth (m), X-axis is chronological order of echosounder pings geo-rectified into 10m horizontal bins, and backscatter is represented in color gradients representing backscatter intensity (red = 200 kHz, blue = 33 kHz, grey = seafloor or manually removed self-noise).
BACKSCATTER METRICS

Middle-priced echosounders like that used in this study can characterize prey-like backscatter but cannot quantify the biomass of constituent taxa. We developed 4 simple metrics for each filtered frequency, described below and depicted in Fig. A5-22.

1. **Total backscatter (T):** The mean sum of pixel values of prey-like backscatter; this is a proxy for the quantity of potential prey available.

2. **Backscatter intensity (I):** The mean pixel value of prey-like backscatter; this is a proxy that can represent the density, body size, and/or swarm characteristics of potential prey swarms.

3. **Mean depth (Z):** The mean of the depth distribution of prey-like backscatter. This metric was not used in the present paper but we include it here nonetheless as a candidate that we considered.

4. **Vertical dispersion (D):** The standard deviation of the depth distribution of prey-like backscatter; this is a proxy for the vertical extent of prey swarms; highly dispersed backscatter may be less ideal for batch-feeding predators such as rorqual whales.

**Figure A5-22.** Depiction of backscatter metrics, explained in text above. Y-axis is depth (m), X-axis is chronological order of echosounder pings geo-rectified into 10m horizontal bins, and backscatter is displayed on a red color gradient (deeper red = higher backscatter return; grey = seafloor or manually removed self-noise). Backscatter is stored at rows (pings) of 200 columns of pixel values (each pixel representing backscatter within a 1.5m vertical bin; box inset). Example shown is from a focal follow of a humpback (Sighting 03 on 6 June 2015).

These metrics were cross-checked pairwise for collinearity. Figure 2-6 displays interpolated maps for total backscatter, while Figure A5-23 below displays interpolated maps for 200 kHz backscatter intensity and vertical dispersion:
Figure A5-23. Maps of the dispersion and intensity of krill-like backscatter (filtered 200 kHz) interpolated from 5km bins of trackline within each monthly survey, summer 2015. Color scales range from noise floor to the season’s maximum reading. Interpolation was performed using inverse path weighted distance, a function that linearly weights combinations of sampled points based on their distance from the interpolation cell, accounting for land obstruction.

VERIFICATION

To visually ground-truth the objects causing krill-like backscatter on echograms, we developed the Krill Imaging and Scrambling System (KISS), a weight-balanced deepwater imaging towfish apparatus with mounted Go-Pro and 2,000-lumen LED spotlight in pressure-rated housing (Group B Inc.). KISS casts were conducted regularly throughout the season in various backscatter conditions. The KISS was deployed on 250 meters of line marked every 25m so that KISS depth could be recorded throughout a cast. Recorded video was retrieved and frames were assigned depths using timestamp matching with data entry software output. By comparing recorded video to backscatter collected during the cast, we were able to confirm that our processed 200 kHz backscatter represented swarming euphausiids (example in Fig. A5-24)
Figure A5-24. Below: A) Acoustic backscatter collected during a focal follow of 3 fin whales on 29 July 2015. Y-axis is depth (m), X-axis is chronological order of echosounder pings geo-rectified into 6m horizontal bins. Greyed-out sections are periods of high engine RPM that compromised 33 kHz readings and were manually removed. B) Still-frame of Go-Pro video taken during same focal follow using the Bangarang Krill Imaging and Scrambling System (KISS), displaying dense aggregations of euphausiids at approximately 170m. Black bracketed line in panel A displays the time window in which KISS cast descended from 150m to 200m. Full video at: http://www.rvbangarang.org/moments
Zooplankton tows
Three daytime, plummet-style zooplankton tows (333μ, 0.7m diameter, OAR 6:1, dropped to 250m seafloor permitting; designed according to Keen 2015) were taken at the stations within each channel. A plummet net is a down-fishing zooplankton sampler that has no mouth obstructions and is cinched shut when the desired depth is reached (Heron 1982). Samples were immediately preserved in 5% formaldehyde-seawater solution.

Figure A5-25. Photograph of a 2015 zooplankton sample; black dots are the eyes of euphausiids.

Acoustic backscatter was recorded during work at oceanographic stations, affording the opportunity to ground-truth our backscatter processing routine. Noise and patch filtration steps were conducted with the same parameterization and scrutiny described above, the only difference being that station data were subset to only the pings recorded during the net’s descent (sampling) phase. Backscatter caused by the net (e.g., Fig. A5-26) was manually removed as well. Backscatter metrics were then calculated. Euphausiid individuals in each sample were counted by collaborators at Oregon State University (Katie Qualls, Bernard lab, pers. comm.). The numbers of other major zooplankton taxa were also approximated, including copepods, amphipods, chaetognaths, and other gelatinous taxa. Krill counts were found to be correlated with our total 200 kHz backscatter metric (n = 40, p = 0.006, r² = 0.18; Fig. A32), while other taxa were not correlated (copepods: p = 0.81; amphipods: p = 0.895; chaetognaths: p = 0.50; other gelatinous: p = 0.298). This verified the sufficiency of our backscatter processing techniques for our purposes here.
Figure A5-26. Two zooplankton tows at an oceanographic station in August 2015. Backscatter is presented in two color-scales: red scale = 200 kHz backscatter, blue scale = 33 kHz.

Figure A5-27. Correlation ($r^2 = 0.18$) between euphausiids sampled at oceanographic stations and filtered acoustic backscatter (Total 200 kHz metric) recorded during zooplankton tows.
Figure A6-1. Distributions of habitat features, displayed vertically as violin plots, sampled during focal follows for fin whales (grey) and humpbacks (white), from both years. Interior box plots show median, interquartile range and outliers. For each species, the distribution of associated conditions is given for ALL focal follows, for feeding whales (FEED), and all OTHER behaviors.
Figure A6-2. Distributions of habitat features, displayed vertically as violin plots, sampled during focal follows of humpback whales for each survey month in 2015. For each month, associated conditions are displayed for whales inferred to be feeding (grey) and all other behavioral states (white). Interior box plots show median, interquartile range and outliers.
Figure A6-3. Histograms of select habitat features measured during focal follows of feeding whales. SSS = Sea Surface Salinity; SST = Sea Surface Temperature. Distributions for fin whales (orange) and humpbacks (blue) can be compared to the distribution of “available conditions” (gray) sampled during systematic transect surveys.
Figure A6-4. Spline functions for best-fit GAMs that predict whale aggregative response, based on systematic surveys, and feeding response, based on focal follows, as functions of habitat features. Sample size was too low for fin whales to model feeding response. Gaps occur where variables were not included in any of the AICc-equivalent best-fit models. Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading).
Figure A6.5. Patterns in whale density, prey backscatter, and habitat features in the 8 primary channels of the Kitimat Fjord System within our study area. Channels are arranged roughly from most offshore (left) to most inshore (right), though all occur within the fjord system. Distributions of variables are represented as violin plots, i.e., vertical and symmetrical histograms, with inset box-and-quartile plots. Whale density is calculated as individuals per kilometer trackline surveyed. Channel abbreviations: CAA = Caamano Sound, EST = Estevan Sound, CMP = Campania Sound, SQU = Squally Channel, WHA = Whale Channel, MCK = McKay Reach and S. Ursula Channel, VER = Verney Passage and N. Ursula Channel.
Figure A6-6. Smoothing functions of explanatory variables included in the best-fit models of whale aggregation as a function of site loyalty cues, represented here by spatial coordinates and/or day of year. 3D surface plots are presented for bivariate smoothing functions (z axis is linear predictor, which corresponds to y axis in 2D graphs). Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading).
Figure A6-7. Smoothing functions of explanatory variables included in the best-fit models of fin whale habitat as a function of prey-related features and habitat features. Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading). Seafloor was included in both model exercises (hence the two spline functions presented here).
APPENDIX 7:
Supplementary materials for “Novel spatial analytics...”

CONTENTS:
I. Results of habitat-based models of acoustic backscatter
II. Detailed PCCA results for each species

I. Results of habitat-based models of acoustic backscatter

Backscatter metrics were predicted by environmental variables with mixed success (Table A7-1, Fig. A7-1). For total 200 kHz backscatter, 6 of 16 models fit were AICc-equivalent (min. AICc = 519.9, \( r^2 = .24 \)). Julian day (p < 0.01) and seafloor depth (p < 0.05) were the only significant predictors, but best-fit models also included surface temperature, salinity gradient, mixed layer depth and stratification. Spline functions were poorly constrained in general; higher total backscatter corresponds directly to deeper waters and strongly nonlinearly, but generally inversely, with Julian day.

For backscatter intensity, 7 of 26 models fit were AICc-equivalent (min. AICc = 1056.9, \( r^2 = .33 \)). All variables were included in at least one of the best-fit models; significant predictors were seafloor depth (p < 0.05), chlorophyll-a (p < 0.001), and salinity gradient (p < 0.01). Spline functions show that higher backscatter intensity is expected in waters with relatively high chlorophyll-a levels, cool temperatures, high salinity gradient and shallow seafloor.

For backscatter dispersion, 6 of 26 models fit were AICc-equivalent (min. AICc = 1008.7, \( r^2 = .36 \)). All variables were included in at least one of the best-fit models; significant predictors were Julian day (p < 0.05), seafloor depth (p < 0.01), chlorophyll-a (p < 0.01) and stratification (p < 0.01). The only spline functions that were well-constrained and clear were with seafloor depth (dispersion peaks at ~200 m) and Julian day (dispersion increases throughout summer).

Patch depth models performed highest. 4 of 33 models fit were AICc-equivalent (min. AICc = 1251.9, \( r^2 = .67 \)). All variables were included in at least one of the best-fit models, and all but chlorophyll-a and salinity gradient were significant (p < 0.05). Higher patch depths were found in waters with relatively low chlorophyll-a levels, low salinity gradient and low stratification, but the most constrained relationships were nonlinear: patch depth peaked in midsummer; seafloor depth increases with patch depth until ~225m, beyond which the two are not collinear; euphotic depths below 25m do not correlate to patch depth, but beyond 25m euphotic depth the two are collinear; shallow mixed layers do not correlate to patch depth, but mixed layers deeper than 20m correlate inversely to path depth.

For total 33 kHz, 5 of 30 models fit were AICc-equivalent (min. AICc = 517.1, \( r^2 = .58 \)). All variables were included in at least one of the best-fit models, and all of them were significant (p < 0.05) except salinity gradient and mixed layer depth. Total backscatter was highest early in the summer and in waters with low chlorophyll-a, high temperatures, low salinity gradient, shallow euphotic zone, low stratification, shallow mixed layer and shallow seafloor.
Table A7-1. Best-fit models of acoustic backscatter characteristics as a function of oceanographic features of the fjord system, using the same systematic dataset used in models of whale density and aggregation (n=140). Model fit is described by number of variable combinations tested (n fit), the number of AICc-equivalent best-fit models (n = ), the minimum AICc within that group (Min. AICc), and its r² (proportion of deviance explained by the model). Variable abbreviations: z = mean seafloor; Chl-a = integrated chlorophyll-a; Zeu = euphotic depth; SST = Sea surface temperature; ΔSSS = sea surface salinity gradient; MLD = mixed layer depth; strat = stratification. The variables included in best-fit models are denoted by their significance level (the highest found within best-fit set). Significance keys for spline functions of predictors: - = not included in best-fit model set; ns = p > 0.05; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001. Underlined significance level indicates those variables included in the model with minimum AICc.
<table>
<thead>
<tr>
<th>Backscatter</th>
<th>Model fit</th>
<th>Oceanographic predictors</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Frequency</strong></td>
<td><strong>Metric</strong></td>
<td><strong>n fit</strong></td>
</tr>
<tr>
<td>200 kHz</td>
<td>Total</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Intensity</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Dispersion</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Patch depth</td>
<td>33</td>
</tr>
<tr>
<td>33 kHz</td>
<td>Total</td>
<td>30</td>
</tr>
</tbody>
</table>
Figure A7-1. Spline functions for best-fit GAMs that predict acoustic backscatter metrics as functions of habitat features and Julian day of year. Gaps occur where variables were not included in any of the AICc-equivalent best-fit models. Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading).
II. Detailed PCCA Results for each species

Figures A7-2 and A7-3 are results of all position curve correlation analyses (PCCA) run for each species. The main manuscript reports only results for total 200kHz backscatter and 200kHz patch depth.

**Figure A7-2.** Mean position of feeding humpback whales with respect to available prey features as a function of their mean position to various oceanographic features. Dots are color-coded by distance from whale, 0-76 km. Correlation is tested using GAMs, and the best-fit models are signified by fit metrics (AICc and $r^2$, i.e., proportion of deviance explained). All variables are normalized to unitless measures with a mean of zero and standard deviation of 1.
Figure A7-3. Mean position of feeding fin whales with respect to available prey features as a function of their mean position to various oceanographic features. Dots are color-coded by distance from whale, 0-76 km. Correlation is tested using GAMs, and the best-fit models are signified by fit metrics (AICc and $r^2$, i.e., proportion of deviance explained). All variables are normalized to unitless measures with a mean of zero and standard deviation of 1.
APPENDIX 8:  
Supplementary materials for “From fjord to fin…”

Table A8-1. Dive and respiration measurements of humpback and fin whales from previous studies. Parenthetical numbers are standard deviation.

<table>
<thead>
<tr>
<th>Dive metric</th>
<th>Humpback</th>
<th>Fin</th>
<th>Behavior</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blow interval (sec)</td>
<td>17.5 (1.7)</td>
<td></td>
<td></td>
<td>Ligurian Sea</td>
<td>Jahoda et al 2003</td>
</tr>
<tr>
<td>Number of blows</td>
<td>4.4 (2.8)</td>
<td>5.1 (3.7)</td>
<td>Foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td>4.2 (1.7)</td>
<td></td>
<td></td>
<td>Ligurian Sea</td>
<td>Jahoda et al 2003</td>
</tr>
<tr>
<td></td>
<td>4.6 (1.8)</td>
<td></td>
<td></td>
<td>Ligurian Sea</td>
<td>Lafortuna et al. 2003</td>
</tr>
<tr>
<td>Mean dive time (min)</td>
<td>7.7 (2.0)</td>
<td>7.9 (1.5)</td>
<td>Foraging</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td>4.8 (3.4)</td>
<td>4.2 (3.0)</td>
<td>Non-foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td>9.2 (2.1)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td>7.0 (1.4)</td>
<td>6.3 (1.53)</td>
<td>Foraging</td>
<td>Monterey Bay, CA</td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td></td>
<td>4.2 (1.67)</td>
<td>3.75 (1.52)</td>
<td>Non-foraging</td>
<td>Monterey Bay, CA</td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td></td>
<td>4.23 (2.63)</td>
<td>8.3 (1.5)</td>
<td></td>
<td>Ligurian Sea</td>
<td>Lafortuna et al. 2003</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SCB</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7.0 (1.0)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
<tr>
<td>Maximum dive time (min)</td>
<td>139 (29)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td>156 (25)</td>
<td>11.3 (1.5)</td>
<td>Foraging</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.3 (3.1)</td>
<td>Non-foraging</td>
<td>California</td>
<td>Goldbogen et al., 2011</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16.9</td>
<td></td>
<td>Monterey Bay, CA</td>
<td>Strong 1990</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.6</td>
<td></td>
<td>Ligurian Sea</td>
<td>Panigada et al 1999</td>
</tr>
<tr>
<td>Surface time (min)</td>
<td>1.4 (1.2)</td>
<td>2.6 (4.3)</td>
<td>Foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.03 (0.47)</td>
<td>Non-foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.27 (0.44)</td>
<td></td>
<td>Ligurian Sea</td>
<td>Lafortuna et al. 2003</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ligurian Sea</td>
<td>Jahoda et al 2003</td>
</tr>
<tr>
<td>Blow rate</td>
<td>0.9 (0.6)</td>
<td>1.1 (0.8)</td>
<td></td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td>% Surface time</td>
<td>26.4 (21.5)</td>
<td>35.1 (24.3)</td>
<td>Foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td>18.9 (8.4)</td>
<td>Non-foraging</td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ligurian Sea</td>
<td>Jahoda et al 2003</td>
</tr>
<tr>
<td>% Bottom time</td>
<td>72.43 (26.31)</td>
<td></td>
<td></td>
<td>Frederick Sd, AK</td>
<td>Dolphin 1988</td>
</tr>
<tr>
<td>TADL (min)</td>
<td>22.1</td>
<td>27.6</td>
<td>California</td>
<td>Monterey Bay, CA</td>
<td>Goldbogen et al., 2011</td>
</tr>
<tr>
<td></td>
<td></td>
<td>28.6</td>
<td></td>
<td></td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td>Descent speed (m s⁻¹)</td>
<td>1.7 (0.2)</td>
<td>1.5 (0.4)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.0 (0.17)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.8 (0.3)</td>
<td>Monterey Bay, CA</td>
<td>Croll et al. 2001</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.7 (0.4)</td>
<td>S. California Bight</td>
<td>Friedlaender et al. 2015</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
</tbody>
</table>
Table A8-1. Dive and respiration measurements of humpback and fin whales from previous studies, continued.

<table>
<thead>
<tr>
<th>Dive metric</th>
<th>Humpback</th>
<th>Fin</th>
<th>Behavior</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ascent speed (m s⁻¹)</td>
<td>1.4 (0.2)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td>1.5 (0.3)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td>1.7 (0.37)</td>
<td></td>
<td></td>
<td>Monterey Bay, CA</td>
<td>Friedlaender et al. 2001</td>
</tr>
<tr>
<td></td>
<td>2.0 (0.2)</td>
<td></td>
<td></td>
<td>S. California Bight</td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td></td>
<td>2.4 (0.3)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
<tr>
<td>Descent angle</td>
<td></td>
<td></td>
<td>- 57 (8)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>- 60 (8)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>- 53 (8)</td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
<tr>
<td>Ascent angle</td>
<td></td>
<td></td>
<td>56 (11)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>55 (19)</td>
<td>California</td>
<td>Goldbogen et al., 2008</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>64 (7)</td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
<tr>
<td>Mean dive depth</td>
<td>189 (74)</td>
<td>170 (70)</td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2011</td>
</tr>
<tr>
<td></td>
<td>97.9 (32.59)</td>
<td></td>
<td></td>
<td>Monterey Bay, CA</td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td></td>
<td>59.3 (29.67)</td>
<td></td>
<td></td>
<td>Monterey Bay, CA</td>
<td>Croll et al. 2001</td>
</tr>
<tr>
<td></td>
<td>231 (49)</td>
<td></td>
<td></td>
<td>S. California Bight</td>
<td>Friedlaender et al. 2015</td>
</tr>
<tr>
<td></td>
<td>248 (18)</td>
<td></td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2006</td>
</tr>
<tr>
<td>Maximum dive depth</td>
<td>214 (76)</td>
<td>211 (58)</td>
<td></td>
<td>California</td>
<td>Goldbogen et al., 2011</td>
</tr>
</tbody>
</table>
Table A8-2. Best-fit models of whale dive behaviors as functions of metrics of krill-like 200 kHz backscatter. n = sample size for model; n fit = number of models (i.e., variable combinations) fit in the multimodel inference approach; n 95% = number of models in the 95% confidence set; min. AICc = minimum AICc value within 95% set; $r^2$ = proportion of null deviance explained by the model with minimum AICc; p = minimum p-value of F-test for predictor’s spline function in 95% confidence set models; RVI = Relative variable importance, calculated using Akaike weights, 1.00 being the most important; Mean RVI = A predictor’s mean relative variable importance for all behaviors. Significance keys for spline functions of predictors: ---- = not tested; - = p > 0.05; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.
### Dive behaviors

<table>
<thead>
<tr>
<th></th>
<th>Number of blows</th>
<th>Blow interval</th>
<th>Dive time</th>
<th>Surface time</th>
<th>Cycle time</th>
<th>Time at prey depth</th>
<th>Prop. time at prey depth</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>n</strong></td>
<td>206</td>
<td>243</td>
<td>196</td>
<td>209</td>
<td>185</td>
<td>78</td>
<td>73</td>
</tr>
<tr>
<td><strong>Model process</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>n fit</strong></td>
<td>63</td>
<td>63</td>
<td>63</td>
<td>63</td>
<td>63</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td><strong>n</strong></td>
<td>15</td>
<td>15</td>
<td>19</td>
<td>24</td>
<td>8</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td><strong>95% min. AICc</strong></td>
<td>1038.5</td>
<td>168.7</td>
<td>2469.7</td>
<td>2291.7</td>
<td>2404.0</td>
<td>948.4</td>
<td>75.9</td>
</tr>
<tr>
<td><strong>r²</strong></td>
<td>0.16</td>
<td>0.27</td>
<td>0.14</td>
<td>0.14</td>
<td>0.21</td>
<td>0.24</td>
<td>0.13</td>
</tr>
</tbody>
</table>

**Predictors**

<table>
<thead>
<tr>
<th></th>
<th>Species</th>
<th>RVI</th>
<th>Feeding</th>
<th>RVI</th>
<th>200 kHz backscatter</th>
<th>Intensity</th>
<th>RVI</th>
<th>Dispersion</th>
<th>RVI</th>
<th>Patch depth</th>
<th>RVI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>p</strong></td>
<td>-</td>
<td>**</td>
<td>***</td>
<td>**</td>
<td>***</td>
<td>-</td>
<td>***</td>
<td>-</td>
<td>***</td>
<td>***</td>
<td>**</td>
</tr>
<tr>
<td><strong>RVI</strong></td>
<td>0.52</td>
<td>0.89</td>
<td>1.00</td>
<td>0.26</td>
<td>0.99</td>
<td>1.00</td>
<td>1.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>p</strong></td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>**</td>
<td>***</td>
<td>***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>RVI</strong></td>
<td>1.00</td>
<td>1.00</td>
<td>0.77</td>
<td>0.63</td>
<td>0.99</td>
<td>-----</td>
<td>-----</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>p</strong></td>
<td>0.71</td>
<td>0.86</td>
<td>0.31</td>
<td>0.27</td>
<td>0.31</td>
<td>0.32</td>
<td>0.34</td>
<td>0.45</td>
<td></td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><strong>RVI</strong></td>
<td>0.40</td>
<td>0.76</td>
<td>0.32</td>
<td>0.26</td>
<td>0.26</td>
<td>0.72</td>
<td>0.28</td>
<td>0.43</td>
<td></td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><strong>p</strong></td>
<td>0.28</td>
<td>0.38</td>
<td>0.26</td>
<td>0.29</td>
<td>0.32</td>
<td>0.25</td>
<td>0.25</td>
<td>0.29</td>
<td></td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><strong>RVI</strong></td>
<td>0.98</td>
<td>0.73</td>
<td>0.96</td>
<td>1.00</td>
<td>1.00</td>
<td>0.26</td>
<td>0.65</td>
<td>0.79</td>
<td></td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

**Mean RVI**

- **0.81**
- **0.88**
- **0.45**
- **0.43**
- **0.29**
- **0.79**
Table A8-3. Best-fit models of whale dive behaviors as functions of metrics of fish-like backscatter. n = sample size for model; n fit = number of models (i.e., variable combinations) fit in the multimodel inference approach; n 95% = number of models in the 95% confidence set; min. AICc = minimum AICc value within 95% set; $r^2$ = proportion of null deviance explained by the model with minimum AICc; p = minimum p-value of F-test for predictor’s spline function in 95% confidence set models; Significance keys for F-tests of spline functions of predictors: ---- = not tested; - = p > 0.05; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.
### Dive behavior

<table>
<thead>
<tr>
<th></th>
<th>Blow interval</th>
<th>Number of blows</th>
<th>Dive time</th>
<th>Surface time</th>
<th>Cycle time</th>
<th>Blow rate</th>
<th>Surface blow rate</th>
<th>MBCI</th>
<th>PCST</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>66</td>
<td>60</td>
<td>53</td>
<td>60</td>
<td>53</td>
<td>52</td>
<td>60</td>
<td>60</td>
<td>52</td>
</tr>
<tr>
<td>Model process</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n fit</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>95%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>min. AICc</td>
<td>78.3</td>
<td>309.7</td>
<td>685.3</td>
<td>669.6</td>
<td>694.5</td>
<td>-384.2</td>
<td>-282.0</td>
<td>78.7</td>
<td>-52.0</td>
</tr>
<tr>
<td>r²</td>
<td>0.03</td>
<td>0.01</td>
<td>0.04</td>
<td>0.00</td>
<td>0.04</td>
<td>0.06</td>
<td>0.04</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Predictors</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>33 kHz</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table A8-4. Best-fit models of whale dive behaviors as functions of habitat features. n = sample size for model; n fit = number of models (i.e., variable combinations) fit in the multimodel inference approach; n 95% = number of models in the 95% confidence set; min. AICc = minimum AICc value within 95% set; $r^2$ = proportion of null deviance explained by the model with minimum AICc; p = minimum p-value of F-test for predictor’s spline function in 95% confidence set models; RVI = Relative variable importance, calculated using Akaike weights, 1.00 being the most important; Mean RVI = A predictor’s mean relative variable importance for all behaviors. Significance keys for F-tests of spline functions of predictors: ---- = not tested; - = p > 0.05; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.
<table>
<thead>
<tr>
<th>Predictors</th>
<th>Species</th>
<th>RVI</th>
<th>&quot;p&quot;</th>
<th>***</th>
<th>-</th>
<th>***</th>
<th>***</th>
<th>***</th>
<th>*</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>p</td>
<td>0.62</td>
<td>0.31</td>
<td>1.00</td>
<td>0.32</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Feeding</td>
<td>RVI</td>
<td>1.00</td>
<td>1.00</td>
<td>0.51</td>
<td>0.32</td>
<td>0.67</td>
<td>-----</td>
<td>-----</td>
<td>0.70</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>SST</td>
<td>p</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>features</td>
<td>RVI</td>
<td>0.43</td>
<td>0.25</td>
<td>0.60</td>
<td>0.36</td>
<td>0.34</td>
<td>0.31</td>
<td>0.30</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>Strat</td>
<td>p</td>
<td>*</td>
<td>**</td>
<td>-</td>
<td>-</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.87</td>
<td>1.00</td>
<td>0.64</td>
<td>0.29</td>
<td>0.82</td>
<td>0.62</td>
<td>0.72</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>Chl-a</td>
<td>p</td>
<td>-</td>
<td>***</td>
<td>-</td>
<td>**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.35</td>
<td>0.98</td>
<td>0.30</td>
<td>0.95</td>
<td>0.35</td>
<td>0.35</td>
<td>0.41</td>
<td>0.53</td>
<td></td>
</tr>
<tr>
<td>Z\text{HC}</td>
<td>p</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.26</td>
<td>0.52</td>
<td>0.29</td>
<td>0.29</td>
<td>0.25</td>
<td>0.26</td>
<td>0.29</td>
<td>0.31</td>
<td></td>
</tr>
<tr>
<td>Z\text{EU}</td>
<td>p</td>
<td>*</td>
<td>**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.81</td>
<td>1.00</td>
<td>0.30</td>
<td>0.27</td>
<td>0.45</td>
<td>0.35</td>
<td>0.43</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>Z\text{SEA}</td>
<td>p</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.46</td>
<td>0.28</td>
<td>0.32</td>
<td>0.44</td>
<td>0.42</td>
<td>0.37</td>
<td>0.41</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td>\Delta Z\text{SEA}</td>
<td>p</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RVI</td>
<td>0.92</td>
<td>0.30</td>
<td>0.37</td>
<td>1.00</td>
<td>0.58</td>
<td>0.33</td>
<td>0.71</td>
<td>0.60</td>
<td></td>
</tr>
</tbody>
</table>

**Dive behavior**

<table>
<thead>
<tr>
<th>Number of blows</th>
<th>Blow interval</th>
<th>Dive time</th>
<th>Surface time</th>
<th>Cycle time</th>
<th>Time at prey depth</th>
<th>Prop. time at prey depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>206</td>
<td>243</td>
<td>196</td>
<td>209</td>
<td>185</td>
<td>78</td>
</tr>
<tr>
<td>n fit</td>
<td>511</td>
<td>511</td>
<td>511</td>
<td>511</td>
<td>255</td>
<td>255</td>
</tr>
<tr>
<td>n</td>
<td>120</td>
<td>27</td>
<td>204</td>
<td>152</td>
<td>166</td>
<td>108</td>
</tr>
<tr>
<td>min. AICc</td>
<td>1035.8</td>
<td>172.7</td>
<td>2475.9</td>
<td>2303.7</td>
<td>2418.9</td>
<td>949.1</td>
</tr>
<tr>
<td>(r^2)</td>
<td>0.23</td>
<td>0.30</td>
<td>0.11</td>
<td>0.11</td>
<td>0.18</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Mean RVI
Figure A8-1. Spline functions for best-fit GAMs that predict whale dive behaviors as functions of 200 kHz backscatter patch depth (top row) and habitat features (remaining rows). Plots feature superimposed residuals (dots) and ±1 Standard Error bounds (gray shading).
APPENDIX 9:

Dive and respiratory behavior of humpback and fin whales in the Kitimat Fjord System

[Because it must interrupt feeding and social activities,]
“breathing may thus exert a greater influence on behavior of
whales than on behavior of most terrestrial mammals.
Breathing patterns may differ during different behaviors and
activity levels and may be useful in characterizing such
behavioral states. Number of exhalations (blows) per unit time
can be used to estimate energetic costs (Sumich 1983), and
relative time spent at and below the surface can be used in
calibrating counts of whales during aerial and shipboard
surveys (eg Davis et al. 1982). Thus, a quantitative description
of surfacing, respiration, and dive behaviour is needed as the
basis for any detailed ecological study or census of whales.
Such a study is also needed as part of any evaluation of the
effects of industrial disturbance, e.g., shipping or oil
exploration, on whale behavior.”
(Wursig et al. 1984)

“Whales are tied to the surface by the necessity to breathe: all
activities are consequently subjugated to ventilatory patterning
in a manner more profound than for any terrestrial mammal.”
(Dolphin 1987)

METHODS

Dive metrics

From the field observations of whales detailed in the main text, the following dive-respiration
metrics were derived:
1. **Dive time** begun with a “dive stroke” or “terminal breath” (for humpback adults this
   was usually followed by display of a fluke) and ends with its next appearance at the
   surface (be it a breath or a breach or some other robust behavior).
2. **Surface time** began upon the first blow upon return from a dive, and ended upon the
   final blow before the subsequent dive.
3. **Number of blows** during the surface period.
4. **Mean blow interval** between consecutive blows during a surface period.

From these, the following metrics were calculated, to allow comparison to previous literature
such as Wursig et al. (1984), Dolphin (1987), and Dorsey et al. (1989).

1. **Mean blow count intervals**: Surface time / number of blows.
2. **Overall blow rate**: Number of blows / total ventilation cycle.
3. **Surface blow rate**: blow rate as a function only of the time spent at surface (inverse of mean blow count interval).
4. **Proportion of cycle at surface**: surface time / cycle time.

Using parameters from published literature (Table S1.2), the following metrics were calculated as detailed in the main text:

1. **Time at prey depth per dive**.
2. **Proportion of cycle at prey depth**.
3. **Proportion of foraging hour at prey depth**.
4. **Percent of Theoretical Aerobic Dive Limit (TADL)**: dive time as a percent of species-specific aerobic dive limit.

**Species Comparison**

In addition to visual comparison of sample distributions, the two-sided Kolmogorov-Smirnov test (K-S test, Chakravarti and Roy 1967) was used to identify significant differences in dive and respiratory metrics between humpback and fin whales. Due to restricted sample size for fin whales, all behaviors were pooled for these comparisons. However, sample size did allow us to test separately for interspecific behavioral differences in deep-feeding whales.

Results are presented in the following tables and figures.
Table A9-1. Collinearity of dive behavior observations and correlation of dive behaviors with backscatter depth. Regressions were fit separately to feeding and other behavioral states. See Fig. 7-6, A9-4 and A9-5 for visualizations of fits. Significance keys for p-value of slope parameter reported in linear model output in R: - = p > 0.05; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.
<table>
<thead>
<tr>
<th>Relationship</th>
<th>Humpback whale</th>
<th></th>
<th>Fin whale</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Feeding</td>
<td>Other</td>
<td>Feeding</td>
<td>Other</td>
</tr>
<tr>
<td>Blow number – blow interval</td>
<td>df 135, r² 0.12, p .0000</td>
<td>df 124, r² 0.08, p .0002</td>
<td>df 25, r² 0.09, p .12</td>
<td>df 12, r² 0.16, p .0009</td>
</tr>
<tr>
<td>Surface time – blow interval</td>
<td>df 132, r² 0.00, p –</td>
<td>df 120, r² 0.09, p ***</td>
<td>df 25, r² 0.13, p *</td>
<td>df 12, r² 0.00, p –</td>
</tr>
<tr>
<td>Surface time – blow number</td>
<td>df 135, r² 0.64, p ***</td>
<td>df 120, r² 0.40, p ***</td>
<td>df 25, r² 0.40, p ***</td>
<td>df 12, r² 0.83, p ***</td>
</tr>
<tr>
<td>Dive time – blow interval</td>
<td>df 124, r² 0.04, p .0001</td>
<td>df 104, r² 0.02, p –</td>
<td>df 23, r² 0.00, p –</td>
<td>df 13, r² 0.13, p –</td>
</tr>
<tr>
<td>Dive time – blow number</td>
<td>df 122, r² 0.40, p ***</td>
<td>df 90, r² 0.11, p ***</td>
<td>df 23, r² 0.29, p *</td>
<td>df 12, r² 0.32, p *</td>
</tr>
<tr>
<td>Dive time – surface time</td>
<td>df 122, r² 0.19, p ***</td>
<td>df 90, r² 0.05, p *</td>
<td>df 24, r² 0.13, p *</td>
<td>df 12, r² 0.34, p *</td>
</tr>
<tr>
<td>Dive time – time at prey depth</td>
<td>df 67, r² 0.85, p ***</td>
<td>df –, r² –, p –</td>
<td>df 20, r² 0.96, p ***</td>
<td>df –, r² –, p –</td>
</tr>
<tr>
<td>Dive time – dive blow rate</td>
<td>df 122, r² 0.10, p ***</td>
<td>df 87, r² 0.17, p ***</td>
<td>df 23, r² 0.10, p .0001</td>
<td>df 12, r² 0.00, p –</td>
</tr>
<tr>
<td>Dive time – prop. cycle at surface</td>
<td>df 122, r² 0.09, p ***</td>
<td>df 90, r² 0.18, p ***</td>
<td>df 24, r² 0.00, p –</td>
<td>df 12, r² 0.00, p –</td>
</tr>
<tr>
<td>Dive time – prop. cycle at prey depth</td>
<td>df 61, r² 0.43, p ***</td>
<td>df –, r² –, p –</td>
<td>df 20, r² 0.33, p *</td>
<td>df –, r² –, p –</td>
</tr>
<tr>
<td>Prey depth – blow interval</td>
<td>df 128, r² 0.01, p –</td>
<td>df 121, r² 0.06, p ***</td>
<td>df 22, r² 0.00, p –</td>
<td>df 14, r² 0.03, p –</td>
</tr>
<tr>
<td>Prey depth – blow number</td>
<td>df 119, r² 0.11, p ***</td>
<td>df 93, r² 0.00, p –</td>
<td>df 20, r² 0.13, p .0001</td>
<td>df 11, r² 0.50, p **</td>
</tr>
<tr>
<td>Prey depth – surface time</td>
<td>df 121, r² 0.12, p ***</td>
<td>df 92, r² 0.01, p –</td>
<td>df 21, r² 0.13, p *</td>
<td>df 11, r² 0.52, p **</td>
</tr>
<tr>
<td>Prey depth – time at prey depth</td>
<td>df 67, r² 0.00, p –</td>
<td>df –, r² –, p –</td>
<td>df 20, r² 0.21, p *</td>
<td>df –, r² –, p –</td>
</tr>
<tr>
<td>Prey depth – dive time</td>
<td>df 112, r² 0.11, p ***</td>
<td>df 81, r² 0.01, p –</td>
<td>df 22, r² 0.33, p *</td>
<td>df 12, r² 0.10, p –</td>
</tr>
<tr>
<td>Prey depth – dive blow rate</td>
<td>df 104, r² 0.00, p –</td>
<td>df 63, r² 0.00, p –</td>
<td>df 20, r² 0.00, p –</td>
<td>df 11, r² 0.13, p –</td>
</tr>
<tr>
<td>Prey depth – prop. cycle at surface</td>
<td>df 108, r² 0.00, p –</td>
<td>df 69, r² 0.00, p –</td>
<td>df 21, r² 0.00, p –</td>
<td>df 11, r² 0.13, p –</td>
</tr>
<tr>
<td>Prey depth – prop. cycle at prey depth</td>
<td>df 61, r² 0.13, p **</td>
<td>df –, r² –, p –</td>
<td>df 20, r² 0.00, p –</td>
<td>df –, r² –, p –</td>
</tr>
</tbody>
</table>
Table A9-2. Summary of dive behaviors for humpback and fin whales. \( n = \) number of groups followed. \% TADL, percent of theoretical aerobic dive limit, is based on published TADL values (Table SA8-1). \( p \)-value = significance of two-sided KS-test between species. * Metric calculated only for whales inferred to be deep-feeding.
<table>
<thead>
<tr>
<th>Dive behavior metric</th>
<th>Humpback</th>
<th></th>
<th></th>
<th>Fin</th>
<th></th>
<th></th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$n$</td>
<td>Mean</td>
<td>SD</td>
<td>Max.</td>
<td>$n$</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td><strong>Observed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blow interval (sec)</td>
<td>275</td>
<td>24.62</td>
<td>11.20</td>
<td>67.60</td>
<td>46</td>
<td>21.93</td>
<td>12.19</td>
</tr>
<tr>
<td>Number of blows</td>
<td>250</td>
<td>5.94</td>
<td>3.32</td>
<td>17.00</td>
<td>38</td>
<td>7.06</td>
<td>3.09</td>
</tr>
<tr>
<td>Dive time (min)</td>
<td>232</td>
<td>4.77</td>
<td>2.38</td>
<td>17.63</td>
<td>37</td>
<td>6.62</td>
<td>2.55</td>
</tr>
<tr>
<td>Surface time (min)</td>
<td>244</td>
<td>1.89</td>
<td>1.09</td>
<td>6.36</td>
<td>39</td>
<td>2.06</td>
<td>0.92</td>
</tr>
<tr>
<td>Cycle time (min)</td>
<td>211</td>
<td>6.63</td>
<td>3.00</td>
<td>19.20</td>
<td>39</td>
<td>9.05</td>
<td>3.10</td>
</tr>
<tr>
<td><strong>Calculated</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blow rate</td>
<td>222</td>
<td>0.8829</td>
<td>0.3536</td>
<td>2.0455</td>
<td>41</td>
<td>0.8311</td>
<td>0.2665</td>
</tr>
<tr>
<td>Dive blow rate</td>
<td>216</td>
<td>1.3013</td>
<td>0.7326</td>
<td>5.4244</td>
<td>41</td>
<td>1.192</td>
<td>0.5023</td>
</tr>
<tr>
<td>Surface blow rate</td>
<td>261</td>
<td>0.0604</td>
<td>0.0332</td>
<td>0.375</td>
<td>43</td>
<td>0.0615</td>
<td>0.017</td>
</tr>
<tr>
<td>Mean blow count interval</td>
<td>262</td>
<td>21.50</td>
<td>14.62</td>
<td>132.00</td>
<td>43</td>
<td>18.09</td>
<td>7.43</td>
</tr>
<tr>
<td>Proportion of cycle at surface</td>
<td>225</td>
<td>0.278</td>
<td>0.133</td>
<td>0.843</td>
<td>42</td>
<td>0.2341</td>
<td>0.0809</td>
</tr>
<tr>
<td><strong>Inferred</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% TADL</td>
<td>250</td>
<td>21.38</td>
<td>10.37</td>
<td>58.67</td>
<td>44</td>
<td>23.97</td>
<td>9.03</td>
</tr>
<tr>
<td>Time at depth (min)*</td>
<td>70</td>
<td>3.54</td>
<td>2.20</td>
<td>14.78</td>
<td>23</td>
<td>5.36</td>
<td>2.32</td>
</tr>
<tr>
<td>Proportion of cycle at depth*</td>
<td>70</td>
<td>0.41</td>
<td>0.15</td>
<td>0.77</td>
<td>23</td>
<td>0.53</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Table A9-3. Respiratory metrics of humpback and fin whales, separated by inferred behavior. Mean ± SD (sample size) is reported for measurements Blow interval – Cycle duration, and Blow rate - %TADL are calculated from those measurements (hence no sample size provided). See methods in Appendix 9 for derivation of calculated metrics. p-value under Humpback Feed Deep is a two-sided K-S test of the humpback and fin deep-feed dive-ventilation metrics.
<table>
<thead>
<tr>
<th>Respiratory metric</th>
<th>Feed/Deep</th>
<th>Feed/Surf</th>
<th>Travel</th>
<th>Mill</th>
<th>Rest/Sleep</th>
<th>Feed/Deep</th>
<th>Feed/Surf</th>
<th>Travel</th>
<th>Mill</th>
<th>Rest/Sleep</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blow interval (sec)</td>
<td>19.25 ± 5.31 (97)</td>
<td>22.79 ± 10.79 (43)</td>
<td>26.42 ± 10.62 (62)</td>
<td>30.12 ± 12.93 (19)</td>
<td>40.55 ± 10.63 (26)</td>
<td>22.52 ± 15.49 (26)</td>
<td>22.20 ± 8.83 (3)</td>
<td>21.40 ± 3.75 (9)</td>
<td>21.40 ± 3.75 (9)</td>
<td></td>
</tr>
<tr>
<td>Number of blows</td>
<td>8.19 ± 3.20 (84)</td>
<td>4.35 ± 4.13 (48)</td>
<td>5.44 ± 5.04 (54)</td>
<td>3.83 ± 3.04 (18)</td>
<td>4.56 ± 3.04 (16)</td>
<td>7.86 ± 4.44 (23)</td>
<td>4.44 ± 0.66 (2)</td>
<td>7.00 ± 3.58 (6)</td>
<td>7.00 ± 3.58 (6)</td>
<td></td>
</tr>
<tr>
<td>Dive duration (min)</td>
<td>6.09 ± 2.29 (76)</td>
<td>3.41 ± 1.27 (49)</td>
<td>4.64 ± 2.29 (54)</td>
<td>3.08 ± 2.24 (13)</td>
<td>4.93 ± 1.55 (20)</td>
<td>7.53 ± 2.58 (20)</td>
<td>5.07 ± 1.66 (3)</td>
<td>7.04 ± 2.37 (7)</td>
<td>7.04 ± 2.37 (7)</td>
<td></td>
</tr>
<tr>
<td>Time at surface (min)</td>
<td>2.23 ± 0.97 (81)</td>
<td>1.43 ± 0.97 (49)</td>
<td>2.13 ± 1.27 (54)</td>
<td>1.66 ± 1.99 (17)</td>
<td>2.01 ± 0.92 (16)</td>
<td>2.29 ± 0.83 (24)</td>
<td>1.23 ± 0.49 (2)</td>
<td>2.06 ± 1.28 (6)</td>
<td>2.06 ± 1.28 (6)</td>
<td></td>
</tr>
<tr>
<td>Cycle duration (min)</td>
<td>8.48 ± 2.73 (73)</td>
<td>4.87 ± 2.57 (49)</td>
<td>6.45 ± 2.57 (45)</td>
<td>4.93 ± 2.57 (13)</td>
<td>7.01 ± 2.57 (12)</td>
<td>10.12 ± 2.67 (23)</td>
<td>6.04 ± 2.83 (2)</td>
<td>9.49 ± 3.40 (7)</td>
<td>9.49 ± 3.40 (7)</td>
<td></td>
</tr>
<tr>
<td>Blow rate</td>
<td>0.9653 ± 0.3051</td>
<td>0.916 pm 0.3397</td>
<td>0.834 pm 0.376</td>
<td>0.904 pm 0.5703</td>
<td>0.678 pm 0.2562</td>
<td>0.849 pm 0.2163</td>
<td>0.781 pm 0.1932</td>
<td>0.7098</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Dive blow rate</td>
<td>1.3085 ± 0.5604</td>
<td>1.562 pm 0.9629</td>
<td>1.269 pm 0.6853</td>
<td>1.659 pm 1.2343</td>
<td>0.961 pm 0.3903</td>
<td>1.208 pm 0.4309</td>
<td>1.143 pm 0.2949</td>
<td>0.9212</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Surface blow rate</td>
<td>0.0629 ± 0.0172</td>
<td>0.070 pm 0.0521</td>
<td>0.053 pm 0.0295</td>
<td>0.056 pm 0.0537</td>
<td>0.039 pm 0.0123</td>
<td>0.0615 pm 0.0154</td>
<td>0.057 pm 0.0190</td>
<td>0.0667</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Proportion of cycle at surface</td>
<td>0.2668 ± 0.0919</td>
<td>0.283 ± 0.1399</td>
<td>0.301 ± 0.1501</td>
<td>0.342 ± 0.2196</td>
<td>0.257 ± 0.0871</td>
<td>0.229 ± 0.0637</td>
<td>0.287 ± 0.1411</td>
<td>0.0160 ± 0.0756</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>% TADL</td>
<td>0.2739 ± 0.092</td>
<td>0.1506 pm 0.0795</td>
<td>0.2089 pm 0.1014</td>
<td>0.1444 pm 0.0991</td>
<td>0.2157 pm 0.073</td>
<td>0.2625 pm 0.0879</td>
<td>0.1979 pm 0.0566</td>
<td>0.2552</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Figure A9-1. Distributions of dive and respiratory behaviors, displayed vertically as violin plots, sampled during focal follows for fin whales (grey) and humpbacks (white), from both years, presented in categories of inferred whale behavior. Interior box plots show median, interquartile range and outliers.
Figure A9-2. Distributions of dive and respiratory behaviors, displayed vertically as violin plots, sampled during 2015 focal follows of humpback whales, grouped into each sampling period: J = June, J-J = Late June through early July, LJ = Early July; A = August; S = September.
Figure A9-3. Cumulative distribution functions (CDF) of dive and respiratory metrics for each species in feeding and non-feeding behavioral modes.
Figure A9-4. Respiratory metrics plotted against surface time sampled during each focal follow. Points are colored by inferred behavioral state (black = feeding; white = other behavior). Simple linear models were fit to each behavioral state (solid line = feeding; dotted line = other); model fits are reported in Table A9-1.
Figure A9-5. Respiratory metrics plotted against dive time sampled during each focal follow. Points are colored by inferred behavioral state (black = feeding; white = other behavior). Simple linear models were fit to each behavioral state (solid line = feeding; dotted line = other); model fits are reported in Table A9-1.
REFERENCES


Coyle KO, Cooney RT (1992) Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea.


Dixon TJ (1977) The distance at which sitting birds can be seen at sea. Ibis 119:372-375.


Hays RB (1976) An Environmental Study on the Kitimat Region with Special Reference to the Kitimat River Estuary. Prepared for The Canadian Wildlife Service. Delta, BC.


NGP (Enbridge Northern Gateway Project) (2010a) Sec. 52 Application, Volume 8B: Environmental and Socio-Economic Assessment (ESA) - Marine Transportation. May 2010.


Okey TA, Alldina HM, Lo V, Montenegro A, Jessen S (2012) Climate change impacts and vulnerabilities in Canada’s Pacific Marine Ecosystems. CPAWS BC and WWF-Canada, Vancouver, BC.


Pennycuick CJ (1982) The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity.


Piatt JF (1987) The behavioural ecology of common murre and Atlantic puffin predation on capelin: implications for population biology. PhD, Memorial Univ. of Neufoundland, St. John's.


Pilkington JF, Meuter H, Wray J (2011a) Occurrence of Northern Resident Killer Whales (Orcinus orca) in the Confined Channel Assessment Area between Wright Sound and Caamaño Sound from North Coast Cetacean Society Observations for the Period 2006 to


Wray J, Meuter H, Pilkington JF, Ballert C (2011) Occurrence of humpback whales (Megaptera novaeangliae) in the Confined Channel Assessment Area between Wright Sound and Caamaño Sound from North Coast Cetacea Society observations for the period 2004 to 2011. Written evidence, JRP for Northern Gateway Pipeline.


