UNIVERSITY OF CALIFORNIA, SAN DIEGO

The co-location of blue whales and their euphausiid prey across multiple spatial scales

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

in

Oceanography

by

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2017

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Chair

University of California, San Diego

2017

DEDICATION

For my parents, who always remind me to try defying gravity.

EPIGRAPH

"We will never fully understand the variability of life in the oceans
But please don't fault us for trying."

Edward Brinton

"Interesting reaction. But what does it mean?!"

Jack Skellington; *The Nightmare Before Christmas*

TABLE OF CONTENTS

SIGNATURE PAGE iii

DEDICATION……iv

EPIGRAPH……..v

TABLE OF CONTENTS..... vi

LIST OF FIGURES xi

LIST OF TABLES..... xvii

ACKNOWLEDGEMENTS..... xviii

VITA……...xxii

ABSTRACT OF THE DISSERTATION xxiii

CHAPTER 1 Introduction to the Dissertation 1

1.1 Introduction..... 2

1.1.1 Basin and California Current System scales..... 5

1.1.2 Regional scale 6

1.1.3 Local scale 7

1.1.4 Vertical distribution 8

1.1.5 Temporal variation..... 9

1.1.6 Approaches 12

1.1.7 Research questions..... 13

1.2 Outline of the Dissertation 14

1.3 References..... 24

CHAPTER 2 Dietary specialization of blue whales in the southern sector of the California Current System..... 29

2.1 Abstract 30
2.2 Introduction 30
2.3 Methods 32
2.3.1 Mandible dissection and identification 32
2.3.2 Mandible to body length regressions 33
2.3.3 Fecal sample collection and enumeration 34
2.3.4 Mandible descriptions 35
2.3.5 Net sample collection and enumeration 36
2.4 Results 37
2.4.1 Mandible descriptions 37
2.4.2 Mandible to body length regressions 40
2.4.3 Species and size composition of ingested euphausiids 40
2.4.4 Comparison of prey digested to prey available 41
2.5 Discussion 42
2.6 Conclusions 44
2.7 Acknowledgements 45
2.8 References 55
CHAPTER 3 Scales of co-occurrence of blue whales and their euphausiid prey in the Northeastern Pacific 57
3.1 Abstract 58
3.2 Introduction 59
3.3 Methods 61
3.3.1 Southern California euphausiid collection and enumeration 61

3.3.2 Southern Vancouver Island euphausiid collection and enumeration 63
3.3.3 Data sources 63
3.3.4 Statistical analysis 64
3.4 Results 65
3.4.1 Basin scale distributions 65
3.4.2 California Current System scale distributions 66
3.4.3 Regional scale distributions 67
3.4.4 Local scale distributions 68
3.4.5 Euphausiid spring/summer abundance co-variation 68
3.4.6 Biomass anomaly trend 69
3.5 Discussion 69
3.5.1 Scales of Co-variation 69
3.5.2 Why did the blue whales head north? 70
3.6 Conclusions 71
3.7 Acknowledgements 72
3.8 References 86
CHAPTER 4 The euphausiid prey field for baleen whales around a steep bathymetric feature in the southern California Current System 90
4.1 Abstract 91
4.2 Introduction 91
4.3 Methods 94
4.3.1 Whale visual survey 95
4.3.2 Acoustic Backscatter 96

4.3.3 Bongo net transects 99
4.3.4 MOCNESS 99
4.3.5 Zooplankton sample analysis 100
4.4 Results 101
4.4.1 Whale distribution 101
4.4.2 Cross-bank prey distribution 102
4.4.3 Vertical prey distribution 104
4.4.4 Effects of strobe light 106
4.4.5 P. planipes gut contents 107
4.5 Discussion 107
4.5.1 Euphausiid association with Nine Mile Bank 107
4.5.2 Whale association with Nine Mile Bank 108
4.5.3 Euphausiid patchiness 110
4.5.4 P. planipes intrusion 112
4.5.5 Implication for interannual variation 113
4.6 Conclusions 114
4.7 Acknowledgements 114
4.8 References 131
CHAPTER 5 Summary of the Dissertation 137
5.1 Introduction 138
5.2 Blue whale diet specificity 138
5.3 Scales of blue whale-euphausiid co-location 139
5.4 Association of predators and prey with steep bathymetric features 140

5.5 Summary 141

5.6 References 141

LIST OF FIGURES

Figure 1.1: (A) Pacific basin distribution of blue whales (from Gilpatrick and Perryman 2008). (B) Residence and population divisions of blue whales as suggested from song types. Type 1 is represents the Northeast Pacific region (from McDonald *et al*. 2006). 16

Figure 1.2: Distribution of the euphausiid *Thysanoessa spinifera* in the North Pacific (Brinton *et al*. 2000). 17

Figure 1.3: Distribution of the euphausiids *Euphausia pacifica* and *Euphausia nana* in the North Pacific (Brinton *et al*. 2000)..... 17

Figure 1.4: The standard CalCOFI 66 station pattern (black circles) plus the 7 coastal SCCOOS stations (red symbols). 18

Figure 1.5: The California Current System distributions of blue whales from systematic line transect surveys (from Calambokidis and Barlow 2004). Light grey lines indicate tracklines. The survey was stratified into : (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, (D) Baja California..... 19

Figure 1.6: The abundance of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* within the CalCOFI region in spring 1969. Data originate from the Brinton Euphausiid Plot Gallery, Scripps Institution of Oceanography 20

Figure 1.7: The distribution of blue whales in the Southern California Bight from commercial whale watching boat records between 2008 and 2012..... 21

Figure 1.8: Daytime vertical distribution of *Nyctiphanes couchi* developmental stages in the Celtic Sea. (Williams and Fragopoulu 1985)..... 22

Figure 1.9: Blue whale dive profile (blue lines) during a 6-hour tag deployment in the Sea of Cortez, Mexico on 1 March 2001. The dark gray shaded krill layer was located based on depth sounder readings (Calambokidis *et al*. 2007)..... 22

Figure 1.10: Comparisons of euphausiid abundances between spring the preceding winter. Winter and spring abundances demonstrate coherence through time (Brinton and Townsend 2003)..... 23

Figure 2.1: Digital images of euphausiid right mandible showing measurement sites for total mandible length (TML), total incisor length (TIL), and total molar width (TMW) Morphological identification regions include: spine pair one (SP1), spine two (S2), cutting edge (C.E.), pars incisiva (PI), pars molaris (PM), root shoulder (SH)..... 47

Figure 2.2: Line drawings of euphausiid right mandibles: (A) *Thysanoessa spinifera*, (B) *Thysanoessa gregaria*, (C) *Euphausia pacifica* (D) *Nyctiphanes simplex* (E) *Euphausia recurva* (F) *Euphausia eximia* (G) *Euphausia gibboides* (H) *Nemoatoscelis diffilis*. Scale bars all indicate 100 µm..... 48

Figure 2.3: Digital images of euphausiid right mandibles (A) *T. spinifera*, (B) *T. gregaria*, (C) *E. pacifica* (D) *N. simplex* (E) *E. recurva* (F) *E. eximia* (G) *E. gibboides* (H) *N. difficilis*. Scale bars all indicate 100 µm. 49

Figure 2.4: Relationship between euphausiid total body length and total mandible length for cool water-associated species (A) *T. spinifera*, (B) *E. pacifica*, (C) *N. difficilis*, and (D) *T gregaria*, and for warm water-associated species (E) *E. eximia*, (F) *E. gibboides*, (G) *E. recurva*, and (H) *N. simplex*. All regressions are significant ($p < 0.01$). 50

Figure 2.5: Euphausiid species % composition reconstructed from mandibles identified from blue whale (*B. musculus*) fecal samples at different collection localities. 51

Figure 2.6: Reconstructed prey euphausiid total body length (mm) distributions from mandible total lengths found in whale fecal samples. 52

Figure 2.7: Prey euphausiid species compositions from mandibles in whale fecal samples compared to ambient available euphausiids collected by bongo or dip nets, at different localities and dates. 53

Figure 2.8: Comparison of reconstructed prey euphausiid total body length distributions from mandibles found in whale fecal samples (solid bars) with ambient available euphausiids collected by bongo (b) or dip (d) nets (open bars).* Denotes statistically significant Kolmogorov-Smirnov test. 54

Figure 3.1: CalCOFI station positions and analytical area quadrant designations. 74

Figure 3.2: The biogeographic distributions of two dominant prey euphausiids for blue whales: (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica* (from Brinton *et al*. 2000)..... 75

Figure 3.3: (A) Pacific basin distribution of blue whales (from Gilpatrick and Perryman 2008). (B) Residence and population divisions of blue whales as suggested from song types. Type 1 is represents the Northeast Pacific region (from McDonald *et al*. 2006). 76

Figure 3.4: The California Current System distributions of two dominant prey euphausiids for blue whales: (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica*. Symbol size represents mean abundance. Gray dashed line separates California Inshore, California Offshore, and Baja California analytical strata. 77

Figure 3.5: The California Current System distributions of blue whales from systematic line transect surveys (from Calambokidis and Barlow 2004). Light grey lines indicate tracklines. The survey was stratified into : (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, (D) Baja California. 78

Figure 3.6: Abundance mean (size of point) +95% (size of ring) of (A) Thysanoessa spinifera and (B) Euphausia pacifica in zones within the southern sector of the California Current System covered by the CalCOFI sampling grid from 2007-2016.. 79

Figure 3.7: (A) Mean (size of point) +95% (size of ring) number of whales encountered per km survey effort in each quadrant. Statistically significant groups denoted with a,b , $p<0.05$. (B) All individual blue whale sightings from CalCOFI summer surveys 2007-2016. 80

Figure 3.8: The distribution of blue whales in the Southern California Bight from commercial whale watching boat records. Nearest CalCOFI station to each aggregation center is marked with an open circle. 81

Figure 3.9: The average abundances of dominant blue whale prey euphausiid species *Thysanoessa spinifera* and *Euphausia pacifica* near local centers of elevated blue whale concentration. 82

Figure 3.10: Comparisons of summer and spring abundances in Southern California of two dominant prey euphausiids for blue whales. 83

3.11: Linear regressions between summer and pre-summer abundances of the same life history phase (A-D), and between spring juveniles and adults the following summer (E,F). 84

3.12: Biomass anomalies of adult and juveniles of *Euphausia pacifica* and *Thysanoessa spinifera* from Southern California (A,C) spring and (E,G) summer, and Southern Vancouver Island (B,D) spring and (F,H) summer. Dashed line marks the reappearance of blue whales off of British Columbia in 1997. 85

Figure 4.1: Nine Mile Bank (NMB) study area near San Diego, CA. The study area was subdivided into 3 regions: inshore, the bank itself, and offshore. Open circles represent

bongo tow locations sampled in 1 year of the study; circles with a dot inside bongo tow locations sampled in 2 or 3 years. 116
Figure 4.2: Tracklines and sightings from the 2015 whale visual survey. 117
Figure 4.3: Echograms of euphausiid-like backscattering (dB) from (A,B,C) July 2014, (D,E) June 2015, and (F) April 2016. Bars above the black lines indicate the area backscattering coefficient (sa, m2 m-2) summed from 0-300 m over 500 m distance bins. Gray shading indicates Nine Mile Bank (contour interval 25 m). 118
Figure 4.4: Mean (±95%) area backscattering coefficients (sa, m^2 m^{-2}) for euphausiid-like backscatter in three regions of Nine Mile Bank: inshore, on the Bank, and offshore. Statistically significant groupings denoted with a, b, c ($p<0.05$)..... 119
Figure 4.5: Mean (±95%) patchiness (Imod) in (A) the vertical and (B) the horizontal dimension from acoustic surveys. Statistically significant groupings denoted with a, b, c ($p<0.05$). 120
Figure 4.6: Mean (±95%) euphausiid abundance by length class from bongo net transects for target prey species (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica*. Statistically significant groupings denoted with a, b; ($p<0.05$). 121
Figure 4.7: Mean (±95%) euphausiid abundance by length class from bongo net transects for incidental prey species (A) *Nematoscelis difficilis*, (B) *Thysanoessa gregaria*, (C) *Euphausia eximia*, (D) *Euphausia gibboides*, and (E) *Nyctiphanes simplex*. Statistically significant groupings denoted with a, b ($p<0.05$). 122
Figure 4.8: Mean (±95%) abundance of *Pleuroncodes planipes* abundance from (A) 2015 and (B) 2016 bongo net transects. Statistically significant groupings denoted with a, b; $P<0.05$. 123

Figure 4.9: Vertical distribution of euphausiids by length class from MOCNESS tows for target prey species (A,C) *T. spinifera* and (B,D) *E. pacifica* from July 2014 along the offshore slope of the bank. (A,B) Daytime tows and (C,D) nighttime tows. Dashed vertical line indicates 10 mm lower size limit of blue whale feeding. 124

Figure 4.10: Vertical distribution of euphausiids by length class from MOCNESS tows for target prey species (A,C) *T. spinifera* and (B,D) *E. pacifica* from June 2015 along inshore of the bank. (A,B) Daytime tows and (C,D) nighttime tows. Dashed vertical line indicates 10 mm lower size limit of blue whale feeding..... 125

Figure 4.11: Vertical distribution of euphausiids by length class from MOCNESS tows for incidental or non-prey species associated with the cold water assemblage (*N. difficilis*, *T. gregaria*) and warm water assemblage (*E. eximia*, *E. gibboides, E. recurva, N. simplex*) from daytime tows. 126

Figure 4.12: Mean abundance of *Pleuroncodes planipes* from June 2015 MOCNESS tows inshore of the bank. (A) Daytime and (B) nighttime tows. 128

Figure 4.13: Echograms of euphausiid-like backscattering concurrent with MOCNESS sampling from July 2014 along the offshore slope of the bank. Gray bars mark the vertical extent of each net through the echogram. (A, B) Daytime and (C,D) nighttime tows. 129

Figure 4.14: Echograms of euphausiid-like backscattering concurrent with MOCNESS sampling from June 2015 inshore of the bank. Gray bars mark the vertical extent of each net through the echogram. 130

LIST OF TABLES

Table 2.1: Collection dates, approximate times, and locations for fecal samples used to assess ingestion by blue whales (*B. musculus*), or for bongo or dip net samples used to assess euphausiid prey available in the water column. CRC = Cascadia Research Collective; OI = Ocean Institute; S1 = SKrillEx I; S2 = SKrillEx II……46

ACKNOWLEDGEMENTS

No one survives a Ph.D. alone. It truly takes a village. First among my supporters has been my advisor, Mark Ohman. I would not have accomplished even half the contents of this dissertation without his guidance, encouragement, and constant push to make the science the best it can be. Mark was able to strike the difficult balance of giving me autonomy as a Chief Scientist while still being unwaveringly on call during the inevitable crises.

The other members of my committee have also played an integral part in this process. Jay Barlow and John Hildebrand helped me keep the whale perspective in mind. Without their expertise and personnel, I would not have been able to carry out the small boat visual survey necessary for Chapter 4. Mike Landry provided many helpful comments along the way and took a detailed eye to the manuscript. Jon Shurin always reminded me to think about both the ecological theory and the meaning of my results.

I was lucky to receive the funding necessary to do the research I envisioned. SKrillEx I was funded by a CCE-LTER shiptime opportunity. SKrillEx II was funded by UC Ship Funds, with additional support from CCE-LTER. SKrillEx III was the result of some available ship time on CCE-P1604, which was generously facilitated by the entire crew and science party for 24 hours. The small boat cetacean visual surveys were funded through the SIO Graduate Department Graduate Student Excellence Research Award.

Everyone at UCSD Ship Operations was exceptionally supportive, especially Bruce Applegate, Elizabeth Brenner, and the Restech group. The crews of the *R/V New Horizon*, *R/V Robert Gordon Sproul*, and *R/V Sikuliaq* were all a privilege to work with. My science parties

made the job of Chief Scientist as easy as it could have been, while keeping up morale from proposal to final report. Everything is awesome!

There may be no crying in baseball, but there is definitely crying in science. The Ohman lab has been an amazing, exceptionally supportive group of people throughout my tenure in it. Miriam Goldstein, Alison Cawood, and Jesse Powell showed me how to manage this whole graduate school thing. Amanda Netburn, Jenni Brandon, Ben Whitmore, Jeff Ellen, and Laura Lilly have been coworkers and friends by land and by sea. My amazing group of undergraduates and volunteers made getting through my mountain of samples remotely possible: Tais Castellano, Han Zhou, Shelbi Richardson, Doris Stumps, and Jui-Yuan Chang. Annie Townsend was a heroically patient teacher as I started learning how to identify euphausiids. Linsey Sala continued my taxonomic education, and has been mentor, teacher, and friend.

Samples and data for this dissertation flowed from many sources. The CalCOFI time-series was invaluable for this project, and I owe many thanks to the CalCOFI team, SWFSC, and their technical staffs. John Hildebrand, Amanda Debitch, and Bruce Thayer let me use the CalCOFI cetacean visual survey data and helped me process it. Josh Jones and Brett Pickering were the small boat survey boat operators, and with the rest of the survey volunteers taught me how to spot and identify whales both large and small. Megan McKenna first brought my attention to whale fecal samples, with the mandible poster that started it all. The Cascadia Research Collective, particularly John Calambokidis, provided most of the whale fecal samples. The Ocean Institute welcomed me onto their whale watching cruises to collect additional whale fecal material. John Hildebrand's lab also collected fecal samples for me while I was at sea collecting undigested krill. Whale watching data was provided by Matt Bissell from the Ocean Institute and Shauna Bingham from the Channel Islands Naturalist Corps. Moira Galbraith of

Fisheries and Oceans Canada provided the euphausiid enumerations from Southern Vancouver Island for comparison with Southern California.

I was able to utilize a wide variety of expertise for technical support. Tony Koslow trusted me with his acoustic equipment and Jian Liu performed the setup and calibration. Jian Liu also began teaching me how to process the data. Pete Davison was very generous with his time to patiently teach me how to extract the information I needed from those data. Alex DeRobertis gave some useful advice to approaching the question of patchiness with acoustic data. Dave Jensen wrote code for both analysis and visualization of the acoustic data.

Finally, I would not have gotten through the last 6 years without my family. My parents and sister, even from the other coast, know by my voice if it's going to be a happy phone call or if I really need a pep talk. Thanks for the puppy pictures. My partner, Nick, has been my steadfast champion. I could not have done this without you. Thank you for embracing the weirdness of this journey with me.

Chapter 2 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M.; Ohman, Mark D. "Dietary specialization of blue whales in the southern sector of the California Current System." It is presented as part of this dissertation with the acknowledgement of the study coauthors Linsey M. Sala and Mark. D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

Chapter 3 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M. "Scales of co-occurrence of blue whales and their euphausiid prey in the Northeastern Pacific." It is presented as part of this dissertation with the acknowledgement of the study coauthor Linsey M. Sala. The dissertation author was the primary investigator and is the primary author of this material.

Chapter 4 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M.; Ohman, Mark D. “The euphausiid prey field for baleen whales around a steep bathymetric feature in the southern California Current System.” It is presented as part of this dissertation with the acknowledgement of the study coauthors Linsey M. Sala and Mark. D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

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ABSTRACT OF THE DISSERTATION

The co-location of blue whales and their euphausiid prey across multiple spatial scales

by

Catherine Frances Nickels

Doctor of Philosophy in Oceanography

University of California, San Diego, 2017

Professor Mark D. Ohman, Chair

Blue whales (*Balaenoptera musculus* Linnaeus) eat almost exclusively euphausiids and must find dense aggregations above the local mean to satisfy their energetic needs. The paradox implied by the predator-prey relationship between these large baleen whales and euphausiids is how the whales can acquire sufficient food from such small, patchily distributed prey. This problem can be conceptualized as interactions on multiple spatial scales. Through analysis of the euphausiid mandible remains in whale fecal samples, I determined that the prey of blue whales from the northeast Pacific population is consistently and overwhelmingly dominated by *Thysanoessa spinifera* Holmes, a large neritic euphausiid. Based on the blue whales' extremely

limited diet, I hypothesized that blue whales and T. spinifera would be consistently co-located across a range of spatial scales. In investigated the spatial relationship between the two species at the scale of the North Pacific Ocean, the California Current System, a regional scale where there is long-term sampling by the CalCOFI program, and a local scale near blue whale aggregation centers. The distributions of blue whales and their *T. spinifera* prey were only related at the two largest scales investigated. The regional and local scales did not capture the scale of interaction between these predators and prey, and a smaller scale of sampling was necessary closer to the ambit of a foraging whale. A reduction in available *T. spinifera* was also not the cause of an apparent northward blue whale range expansion around 1997. Focusing on a single bathymetric feature (Nine Mile Bank near San Diego, California), I tested the hypothesis that both prey euphausiids and baleen whales aggregate at such abrupt topographies. Instead of serving as a point of increased relative abundance, the bank actually represented an offshore limit of feeding habitat for T. spinifera predators, including baleen whales. Large whale prey euphausiids were found deeper in the water than less energetically valuable smaller individuals. This dissertation combined multiple, synoptic sampling techniques to investigate the species specific relationship between large blue whales and their small euphausiid prey.

CHAPTER 1 Introduction to the Dissertation

1.1 Introduction

Plankton in the ocean are patchy at a broad range of scales (Haury *et al.* 1978), and planktivores must co-locate with their prey if they are to feed successfully. Predators with more specialized diets would be expected to have a stronger spatial association with their prey than more generalist predators. Baleen whales have restricted diets, in some cases relying exclusively on euphausiid prey. Three species of baleen whales, blue (*Balaenoptera musculus* Linnaeus), fin (*Balaenoptera physalus* Linnaeus), and humpback (*Megaptera novaeangliae* Borowski) whales, all occur in the southern California Current System and feed to a large extent on euphausiids despite the occurrence of other potential prey taxa with much greater biomass. Blue whales are obligate euphausiid predators (Kawamura 1980; Schoenherr 1991; Croll *et al.* 2005), while fin and humpback whales have more dietary diversity and also consume fish, other crustaceans, or squid (Watkins and Schevill 1979; Kawamura 1980; Kieckhefer 1992; Tershy *et al.* 1993). Some whales may even have preferences for specific species of euphausiids. The narrow diet of blue whales makes it likely that their distributions are tightly associated with those of their euphausiid prey, while humpback and fin whales should show a lower degree of dependence on local euphausiid distribution. The question remains whether the whales co-locate with and consume specific species as the result of the whales' own behavior, or whether the apparent relationship reflects co-occurrence in time and space caused by other factors.

Euphausiids are extremely patchy (Décima *et al.* 2010). Of the thirty-nine euphausiid species present in the California Current System (CCS), eight are numerically dominant: *Euphausia pacifica* Hansen*, Euphausia gibboides* Ortmann, *Euphausia eximia* Hansen, *Euphausia recurva* Hansen, *Nematoscelis difficilis* Hansen, *Nyctiphanes simplex* Hansen, *Thysanoessa gregaria* Sars, and *Thysanoessa spinifera* Holmes (Brinton and Townsend 2003).

In the CCS, patchiness is dependent upon body size in all these species except *Thysanoessa spinifera* (Décima *et al.* 2010). Species with size dependent patchiness demonstrate higher degrees of patchiness at both the smallest and largest body sizes (Décima *et al.* 2010).

Because life as a suspension feeding cetacean is energetically expensive, it requires a large, efficient intake of prey for survival. Baleen whales require exceptionally high prey densities to offset the costs of lunge feeding (Goldbogen *et al.* 2011) and to support migrations through oligotrophic waters (Brodie 1975). The locally high concentrations of euphausiids due to patchiness may be what allow baleen whales to sustain themselves on such small prey. The energetic cost of a feeding lunge is approximately four times that of predicted basal metabolism for the duration of the lunge and includes the energy required to overcome resistance from drag and accelerate the mass of water engulfed (Goldbogen *et al.* 2011). Goldbogen *et al.* (2011) calculated that below a critical prey density of 0.1 kg m^{-3} the energetic demands of blue whales cannot be met, but at typically measured euphausiid patch densities (0.15 kg m^{-3} to 4.5 kg m^{-3}) the energy intake more than offsets the high cost of feeding. The patchiness of euphausiids would lead to discrete areas of density above the critical prey density, which the whales would need to seek out for effective feeding. Whether the distribution of these critical densities can be used to predict the distribution of whales is not yet known. It is also unclear whether whales would respond to critical densities of any euphausiid species or whether species identity is also important.

Some whale species may have preferences for certain species and sizes of euphausiids. The whales may engage in true selective feeding by consuming certain taxa disproportionately to their representation in the water column. Fin whales in the Gulf of California, Mexico fed on *Nyctiphanes simplex* instead of available fish (Tershy *et al.* 1993). In Monterey Bay, blue

whales fed on mostly *Thysanoessa spinifera*, followed by *Euphausia pacifica* Hansen, despite the latter's greater availability (Croll *et al.* 2005). Additionally, the mean size of both euphausiid species was larger in the whale diet than in the water column. In the northern Channel Islands blue whales fed equally on adult *T. spinifera* and *E. pacifica*, despite net tows in the area being strongly dominated by *E. pacifica,* suggesting a preference for the larger *T. spinifera* (Fiedler *et al.* 1998). Near Cordell Bank, California humpback whales fed primarily on *T. spinifera*, which dominated the euphausiid population shallower than 60 m (Kieckhefer 1992). *E. pacifica*, which were consumed in much lower numbers, were numerically dominant below 60 m. This observation suggests that baleen whales are able to target specific species and sizes of euphausiids.

Feeding selectivity is likely to influence the distribution of whales as they track their preferred prey. In November of 1986, an unusually high concentration of blue whales was found in Monterey Bay, California, past the typical blue whale season ending in October. This extended residence was likely due to anomalously extended upwelling in the region which supported unseasonably high abundances of *T. spinifera* (Schoenherr 1991).

The paradox implied by the predator-prey relationship between these large baleen whales and euphausiids is how the whales can acquire sufficient food from such small, patchily distributed prey, especially if the whales focus on only specific species or a restricted size range. This problem can be conceptualized as interactions on multiple spatial scales. In this dissertation, I will start with the basin scale, which includes the entire basin of the North Pacific Ocean. Within the basin scale, I will then address the scale of the California Current System extending from southern British Columbia, Canada to the southern end of Baja California along the west coast of North America. I will next focus on what I will call the "regional" scale. The

regional scale covers the southern sector of the CCS from Point Conception to San Diego, California. The smallest spatial scale is what I will call the "local" scale. The local scale refers to specific bathymetric features around which whales may aggregate in pursuit of prey. Embedded within these other, more horizontal spatial domains is the vertical distribution of organisms in the water column, from the surface to the seafloor. In addition to spatial variability, interactions between predators and prey occur over different scales in time. These temporal scales can include daily, seasonal, interannual, and decadal cycles of both abundance and distribution.

1.1.1 Basin and California Current System scales

On the scale of the North Pacific basin, baleen whales and euphausiids often have similar, coastally associated distributions. Before the whaling moratorium in 1965, blue whales were captured along the entire coastline of the North Pacific, from Japan to Baja California (Fig.1A, Rankin *et al.* 2006; Gilpatrick and Perryman 2008). Blue whales occupy the entire North Pacific Ocean Basin, however there is evidence of two separate populations: one in the central basin and one along the coast in the Northeast Pacific region (Fig.1B, McDonald *et al.* 2006). Euphausiids are found in all parts of the world ocean, but each species occupies a more limited habitat. For example, the range of *Thysanoessa spinifera* extends latitudinally along the west coast of North America from the Gulf of Alaska to 25°N along Baja California (Fig. 2, Brinton 1962; Brinton *et al.* 2000). *Euphausia pacifica* has a similar latitudinal distribution along the North American west coast, but has a wider longitudinal extent across the entire North Pacific Basin and Subarctic Pacific (Fig. 3, Brinton 1962; Brinton *et al.* 2000). Blue whales in all oceans migrate between high latitude wintering habitat and summer feeding habitats at lower latitudes (Burtenshaw *et al.* 2004; McDonald *et al.* 2006; Bailey *et al.* 2009). Humpback and fin whales

occupy the southern sector of the California Current System all year, including winter and spring when blue whales are absent (Campbell *et al.* 2015). Blue whales are thought to travel between seasonally occurring regions of high productivity supporting euphausiids along the eastern Pacific coast (Croll *et al.* 2005), and the seasonally high concentrations of *T. spinifera* and *E. pacifica* near the coast support this inference (Brinton *et al.* 2000).

1.1.2 Regional scale

The southern sector of the California Current System (CCS) is well-suited to the study of baleen whales and euphausiids due to the extensive long term monitoring that has been carried out in the region. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) have conducted research cruises at least quarterly off of Southern California since 1949. Each cruise samples a suite of physical and biological factors at 66 core stations (Fig. 4). Bird and mammal observations were added to the program in 1987. Additional studies of the region are carried out through the California Current Ecosystem-Long Term Ecological Research (CCE-LTER) program.

Baleen whales do not occur in equal abundances throughout their range. Within the Southern CCS, the density of blue whales is higher near the coastline than farther offshore, with 4.94 whales 1000 km^{-2} inshore and only 1.23 whales 1000 km^{-2} offshore (Fig. 5, Calambokidis and Barlow 2004). *T. spinifera* and *E. pacifica* are also concentrated inshore (Fig. 6), but it is not known whether this co-occurrence is due to chance or a causal relationship. If the whales come to the area to feed seasonally, as has been suggested (Croll *et al.* 2005), the whale's distribution pattern could be related to the distribution of the more coastally distributed prey euphausiids. While the information on euphausiid distribution presented in Figure 6 is from spring 1969, it does provide a useful comparison to the blue whale distribution from the 1990's

as it is representative of the long term average distribution (Brinton and Townsend 2003). Brinton and Townsend (2003) have demonstrated that euphausiid abundances vary coherently between winter and spring. It has yet to be determined whether summer euphausiid abundances, when blue whales enter the CCS to feed, are also represented by abundances in the preceding spring.

1.1.3 Local scale

There appears to be a tight association between concentrations of baleen whales and regions of steeply sloped bathymetry near the coast. In a model of blue whale habitat off Southern California, bathymetry had the highest predictive value, and whales were observed at an average seafloor depth of 297 m (Bissell 2013). Blue whales sighted in Monterey Bay between 1992 and 1996 were concentrated along the edge of the Monterey Submarine Canyon (Croll *et al.* 2005). Tagged whales in the study kept within 5 km of the canyon edge and moved parallel to it. In the Channel Islands, blue whales were abundant to the north of San Miguel and Santa Rosa Islands (Fiedler *et al.* 1998). Humpback whales off central California were most numerous near the continental slope (Yen *et al.* 2004). In the Antarctic, humpback and minke whale distributions are related to both distance from the ice edge and bathymetric slope (Friedlaender *et al.* 2006). Humpback and minke whales were also found more often associated with Platts Bank than in the waters surrounding it in the western Gulf of Maine (Stevick *et al.* 2008). In the North Atlantic Ocean, blue whales forage for food along the slope of the Laurentian Channel, the continental shelf edge, some shelf habitats, and may utilize the New England Seamount chain (Lesage *et al.* 2017).

Euphausiid concentration above steep bathymetry may explain the incidence of whales at these submarine features. Mechanisms that may serve to aggregate euphausiids around abrupt

topography include upwelling related increased productivity, physical blockage of zooplankton descent after nighttime surface feeding, behavioral depth retention by swimming against upwelling water flow, and enhanced horizontal flux (Genin 2004). In the St. Lawrence Estuary, euphausiids are aggregated by the interaction of the sloped bathymetry, semidiurnal tidal currents, and the negative-phototactic swimming behavior of the euphausiids (Cotte and Simard 2005). Euphausiids have demonstrated elevated abundances along circulatory features in the ocean such as fronts (Lara-Lopez *et al.* 2012; Ohman *et al.* 2012) and physical features such as the Antarctic ice edge (Murase *et al.* 2002), the continental slope (Fiedler *et al.* 1998; Murase *et al.* 2002), and the edges of submarine canyons (Schoenherr 1991; Croll *et al.* 2005). Whales may use these physical features and oceanographic processes as indicators to help them find dense aggregations of euphausiid prey (Friedlaender *et al.* 2006).

1.1.4 Vertical distribution

Differential consumption of members of the available euphausiid assemblage by baleen whales could be due to active behavioral choice by the predator and/or facilitated by vertical or horizontal organization of the prey. Williams and Fragopoulu (1985), Bollens *et al*. (1992), and Lavaniegos (1996) found older, larger euphausiid developmental stages deeper in the water column than younger, smaller stages (cf. Fig. 8). Smaller euphausiids were also found to migrate up earlier in the evening and return to depth later in the morning than larger euphausiids (De Robertis 2002). This timing gap represents differential behavior by size, which could persist at depth during the day. Euphausiids can form social aggregations (Mauchline 1980), but do not form dense aggregations under all conditions. In Saanich Inlet, British Columbia, *E. pacifica* was not found aggregated in the horizontal plane (DeRobertis 2002). Differential aggregation

may be another explanation for species preference, as adult *T. spinifera* have been documented in dense swarms close to the surface during the day (Smith and Adams 1988; Schoenherr 1991).

Dive data from tagged whales support the idea that whales are targeting specific layers of preferred euphausiids. Blue whales in Monterey Bay were documented "diving consistently and directly down to the 150 to 200 m layer in the water column" (Croll *et al.* 2005). In the Sea of Cortez, Mexico, tagged blue whales have been observed swimming below a layer of krill detected acoustically from a following ship and lunge feeding up into the bottom of the layer (Fig. 9, Calambokidis *et al.* 2007). We do not know why the whales directed their effort at the bottom of the euphausiid layer or how euphausiids are organized with respect to size and species composition within aggregations.

1.1.5 Temporal variation

In addition to spatial variability, the abundance and density of euphausiids and baleen whales has been documented to shift over time scales ranging from daily to decadal. The juvenile and adult stages of many euphausiid species engage in daily vertical migration (DVM) in which they reside below the euphotic zone during the day (possibly to reduce the risk of visual predation) and migrate up to the surface water to feed at night (Brinton 1967). DVM may lead to euphausiids becoming trapped in shallower water during the day if their descent is physically blocked by a steep bathymetric feature such as a bank or the edge of a submarine canyon (Genin 2004). Blue and humpback whales feed at progressively shallower depths to follow the euphausiid ascent in the evening, but cease feeding at night when euphausiids are close to the surface but at lower density than during the day (Fiedler *et al.* 1998; Calambokidis *et al.* 2007; Goldbogen *et al.* 2011; Burrows *et al.* 2016).

Whale and euphausiid distributions can also vary on the seasonal scale. While humpback and fin whales are present in the CCS all year, fin whale density reaches a peak in summer (Campbell *et al.* 2015). Blue whales are rare or absent from the southern CCS in winter and spring, and migrate into the area in summer to feed (Burtenshaw *et al.* 2004; McDonald *et al.* 2006; Bailey *et al.* 2009; Campbell *et al.* 2015). The CalCOFI time series is a rich resource of information on the CCS through time. Of the four quarterly cruises, the spring zooplankton samples are more consistently enumerated by species as the focus of climate change-related studies (e.g., Brinton and Townsend 2003; Lavaniegos and Ohman 2007; Di Lorenzo and Ohman 2013). Euphausiid abundances show a high degree of coherence between winter and spring (Brinton and Townsend 2003), but the assumption of coherence has not been tested between spring and summer. The spring samples may not be an appropriate measure of the prey present when the large whales arrive during the summer.

Climate cycles have been shown to affect the distributions and biology of marine organisms, including euphausiids and whales. The abundance anomalies of *N. simplex* are forced by a double-integration of atmospheric variability, while *E. pacifica* abundance anomalies are the result of a single integration of atmospheric forcing (Di Lorenzo and Ohman 2013). Warm events such as El Niño usually signal a transition from the more typical cold water assemblage of the southern CCS to the intrusion of species with warmer water affinities (Brinton 1981; Brinton and Townsend 2003). In 1998, the warm water associated, generally southern species *N. simplex* was caught off of Vancouver Island, Canada (Tanasichuk and Cooper 2002). This occurrence represents a significant northward extension of the species range (Brinton and Townsend 2003), likely due to the decreased southward transport of the California Current under the influence of the particularly strong 1998 El Niño. During the same El Niño event, a more

diverse assemblage of odontocetes was recorded in Monterey Bay than in surrounding years, owing to an influx of warm water species (Benson *et al.* 2002). A higher concentration of baleen whales was also observed in the bay. The increase of both ondontocete diversity and baleen whale abundance was potentially due to a decrease in offshore zooplankton biomass, bringing the whales closer together and closer to shore as they were tracking the remaining prey resources (Benson *et al.* 2002).

In the CCS, El Niño is characterized by warm surface waters, onshore surface drift in opposition to upwelling, and anomalous poleward flow (Lynn and Bograd 2002). The reduced productivity and altered circulation resulting from these changes can be expected to alter the conditions that determine the growth and position of local euphausiids. Species composition is expected to shift under El Niño conditions as *E. pacifica* has been found to dominate a cold water mass, while *N. difficilis* and *E. gibboides* dominate adjacent warm water in the CCS (Lara-Lopez *et al.* 2012), reflecting the temperature and habitat affinities of each species (Brinton 1962; Brinton and Townsend 2003). Larger euphausiids were also found in the colder water mass (Lara-Lopez *et al.* 2012).

From 1924-1965, catches of blue whales were reported along the entire North Pacific coast from Japan to Mexico (Rankin *et al.* 2006). Since 1997, Calambokidis *et al.* (2009) have documented 15 blue whales off of British Columbia and Alaska, where few had been seen since the end of whaling in 1965. These northern sightings increased from one or two in early surveys to five on one day in 2007. These whales were shown through photo-identification to belong to the California feeding population. The authors postulated several reasons for the apparent re-occupation of this area by California blue whales, one of which was a possible decline in the relative prey abundance in California compared to British Columbia.

1.1.6 Approaches

The occurrence of feeding baleen whales, including blue, fin, and humpback whales, has been documented in the California Current Ecosystem through both opportunistic means and systematic surveys (Campbell *et al.* 2012, 2015; Bissell 2013). Commercial whale watching trips are an opportunistic method of documenting cetaceans and occur more frequently than systematic surveys, resulting in a larger number of whale sightings per year (Bissell 2013). Opportunistic data, however, indicate presence only. Trips focus on areas where whales are routinely spotted and do not establish the absence of whales in other locations. Sightings must be carefully standardized by both the spatial and temporal extent of effort to interpret correctly the results of opportunistic surveys.

In contrast, less frequent, systematic surveys provide both presence and absence data. The CalCOFI program has included bird and mammal observations in their quarterly research cruises off of Southern California since 1987. From 1987 to 2004, a strip-transect protocol was used (Tasker *et al.* 1984), in which all large cetaceans were counted within 1 km of the vessel (Henderson *et al.* 2014). From 2004 to the present, line-transect protocols were implemented wherein the effective strip width is calculated based on the sightings as a consequence of the probability of detecting an animal based on its distance from the trackline (probability density function) and the probability of detecting an animal directly on the trackline (trackline detection probability, Burnham *et al.* 1980; Buckland *et al.* 2001; Soldevilla *et al.* 2006). In addition to CalCOFI, the NOAA Southwest Fisheries Science Center (SWFSC) has been conducting marine mammal abundance surveys off California since 1979, with several in the Southern California Bight (Barlow and Forney 2007).

Acoustic estimates of daytime euphausiid abundance are typically higher than net samples due to net avoidance (Lara-Lopez *et al.*, 2012, Wiebe *et al.*, 2013). Acoustics can resolve the distribution of euphausiids in the water during the day, when nets are most affected by avoidance, and at a much finer spatial resolution. Euphausiid patches can be differentiated from other scatterers in the water using a multifrequency technique called dB differencing. Sound scatterers have characteristic frequency spectra of target strength (TS, the amplitude of the returned echo, Stanton *et al.* 1998). dB differencing takes advantage of the different changes in TS over a range of frequencies for different scatterers. For example, euphausiids and siphonophores have similar TS at 120 kHz, but they differ at 38 kHz (Stanton *et al.* 1998). These differences can be used to identify the groups of scatterers in acoustic echograms (Korneliussen and Ona 2002). These identifications, however, must be sea truthed through comparison with net samples to confirm the composition of the measured assemblage.

1.1.7 Research questions

Baleen whales and euphausiids are both well studied groups; however, bringing information about predators and prey together on the same scales to study their interaction is a challenge. The main goal of this thesis is to determine the specific species and sizes of euphausiid that comprise the diet of blue whales in the California Current System and the spatial and temporal scales at which their interactions occur. The dissertation is organized around three major questions:

1) How limited is the diet of blue whales with respect to size and species?
2) Do blue whales co-locate with their preferred prey species and if so, at what spatial scales?
3) Are baleen whales and prey euphausiids associated with steep bathymetric features?

1.2 Outline of the Dissertation

In Chapter 2, I directly investigate selective feeding by blue whales. I test the hypothesis that Southern California blue whales feed non-randomly on the available euphausiid assemblage. I describe the mandible morphology of the eight numerically dominant California Current euphausiid species and determine regression relationships between mandible length and total euphausiid body length. These identifications are then used to identify the sizes and species of euphausiids consumed by blue whales off Southern California through analysis of fecal samples collected between 1998 and 2015.

Chapter 3 explores the co-location between blue whales and their preferred euphausiid prey species at multiple spatial scales. The distribution of the eastern North Pacific population of blue whales is compared to the distribution of preferred prey species *Thysanoessa spinifera* and secondary prey species *Euphausia pacifica* at the scales of the North Pacific Ocean Basin, the California Current System (CCS), the southern region of the CCS covered by the CalCOFI program, and the local scale near blue whale aggregation centers. Chapter 3 also tests the hypothesis that blue whales re-colonized the waters off British Columbia beginning in 1997 as a result of a reduction in the availability of *T. spinifera* and *E. pacifica* in Southern California waters.

In Chapter 4, I investigate the association of both euphausiids and feeding whales with steep bathymetry. While both groups have been observed in the area of steep bathymetry in the California Current, their absence in adjacent areas has not been established concurrently. To substantiate the association of euphausiids with steep bathymetric features, a series of transects crossed one such feature with both net and acoustic sampling. Visual surveys were also done

over the same feature to document the distribution and behavior of whales, covering areas both on and off the feature. This is the first study of baleen whale and euphausiid co-location at such a focused scale in the Southern California Bight.

Chapter 5 summarizes and draws connections between the preceding chapters. I place the results of this dissertation in the context of the initial guiding questions and suggest future research directions.

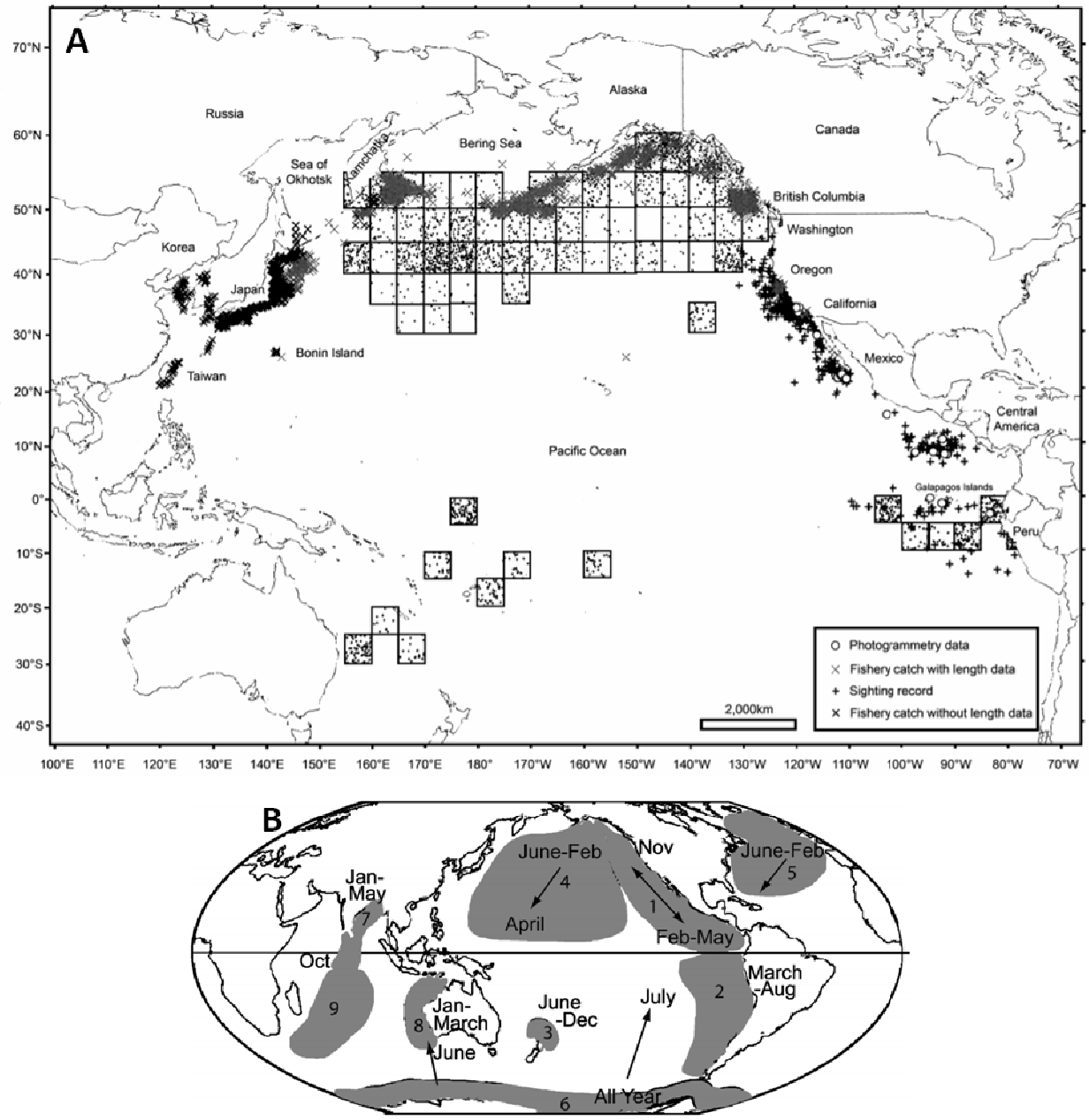

Figure 1.1: (A) Pacific basin distribution of blue whales (from Gilpatrick and Perryman 2008). (B) Residence and population divisions of blue whales as suggested from song types. Type 1 is represents the Northeast Pacific region (from McDonald *et al*. 2006).

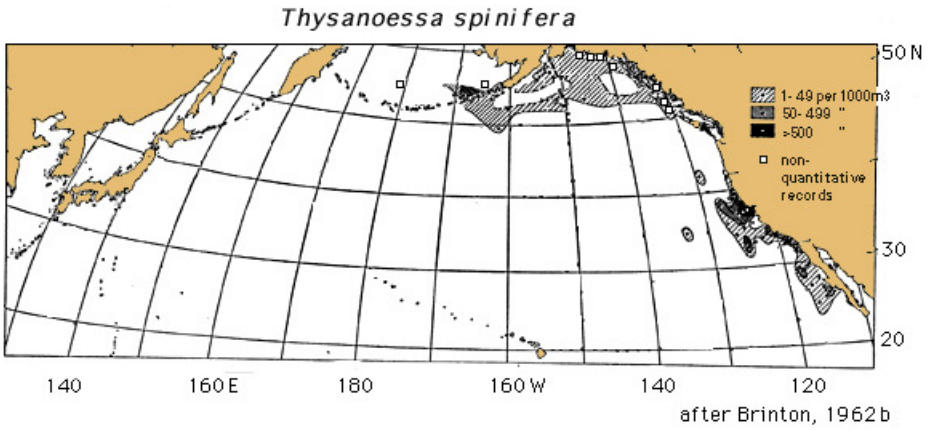

Figure 1.2: Distribution of the euphausiid *Thysanoessa spinifera* in the North Pacific (Brinton *et al*. 2000).

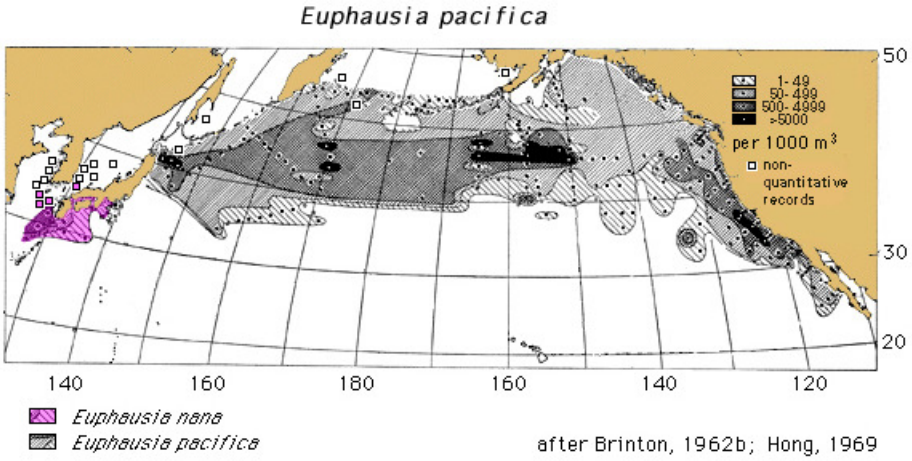

Figure 1.3: Distribution of the euphausiids *Euphausia pacifica* and *Euphausia nana* in the North Pacific (Brinton *et al*. 2000).

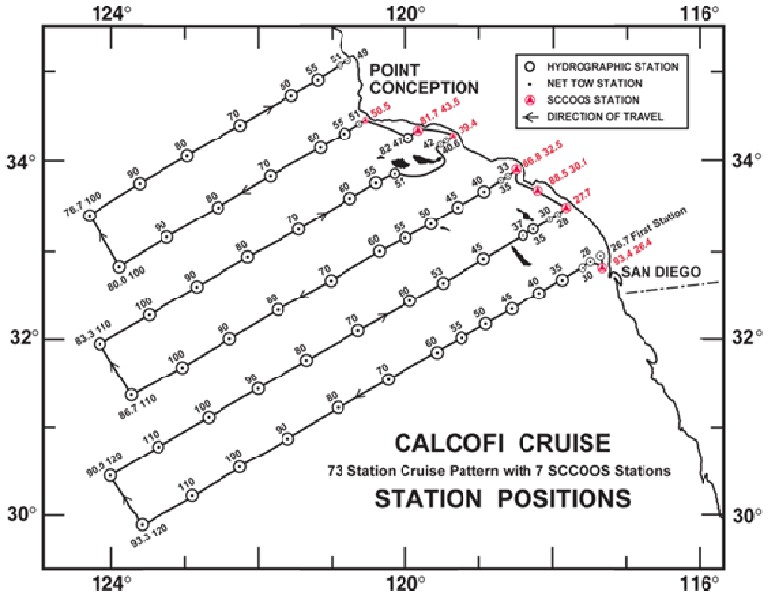

Figure 1.4: The standard CalCOFI 66 station pattern (black circles) plus the 7 coastal SCCOOS stations (red symbols).

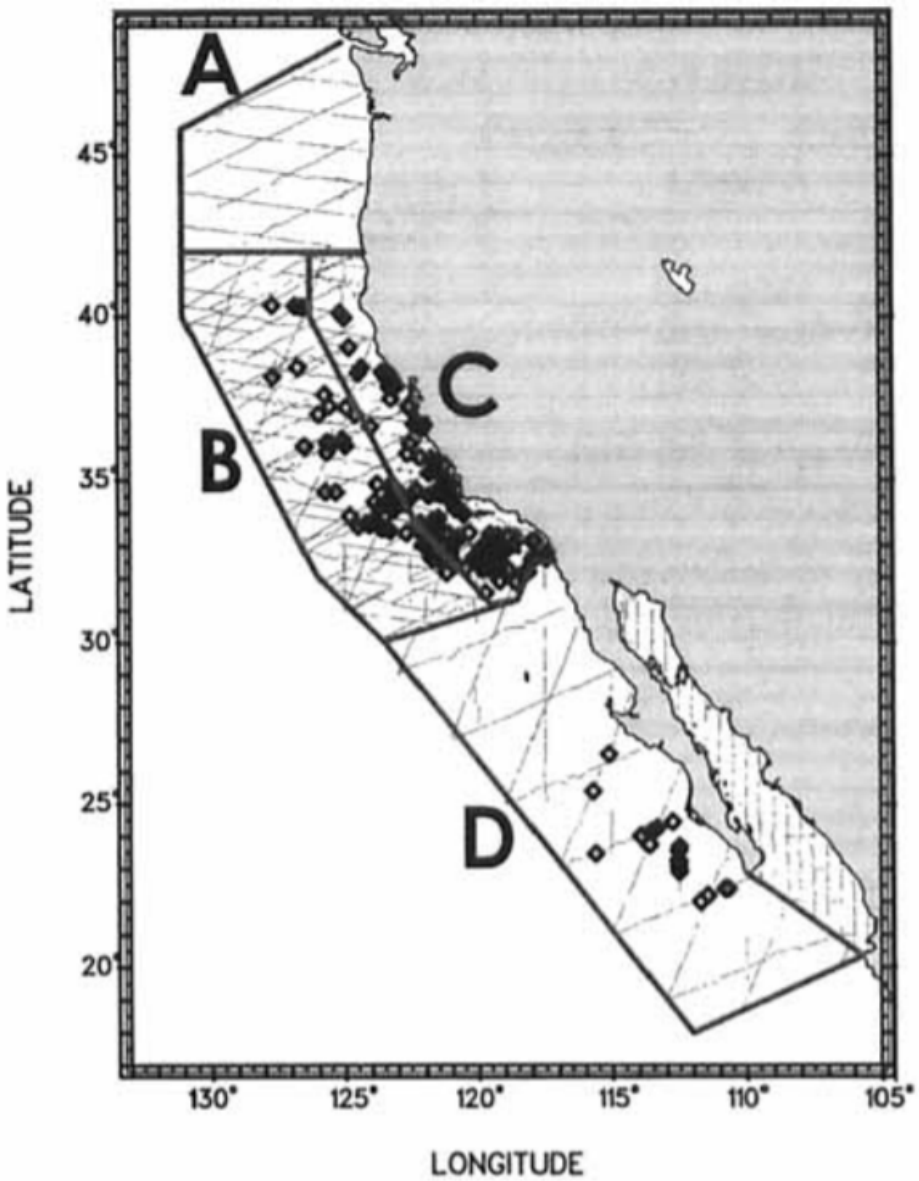

Figure 1.5: The California Current System distributions of blue whales from systematic line transect surveys (from Calambokidis and Barlow 2004). Light grey lines indicate tracklines. The survey was stratified into : (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, (D) Baja California.

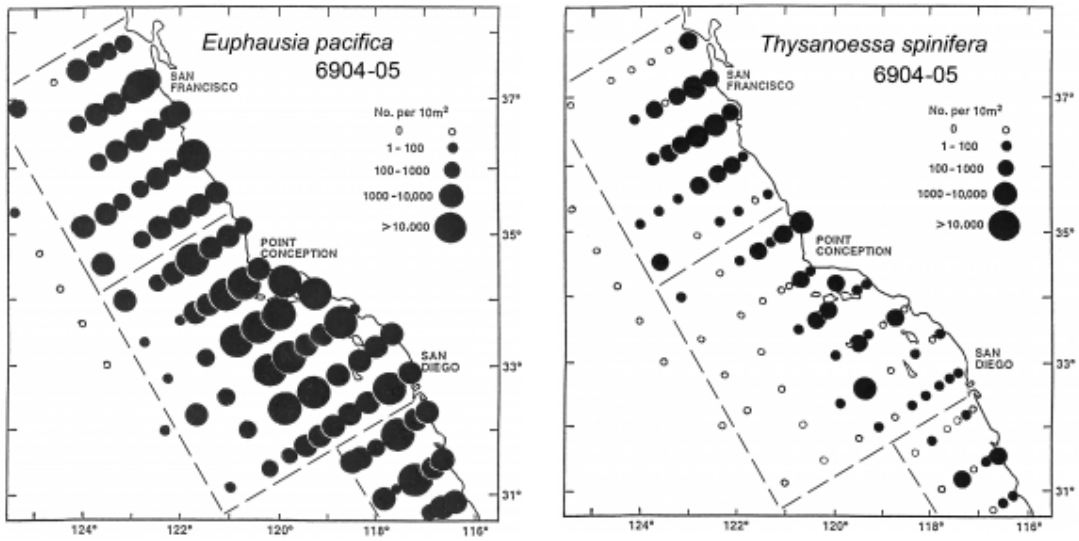

Figure 1.6: The abundance of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* within the CalCOFI region in spring 1969. Data originate from the Brinton Euphausiid Plot Gallery, Scripps Institution of Oceanography

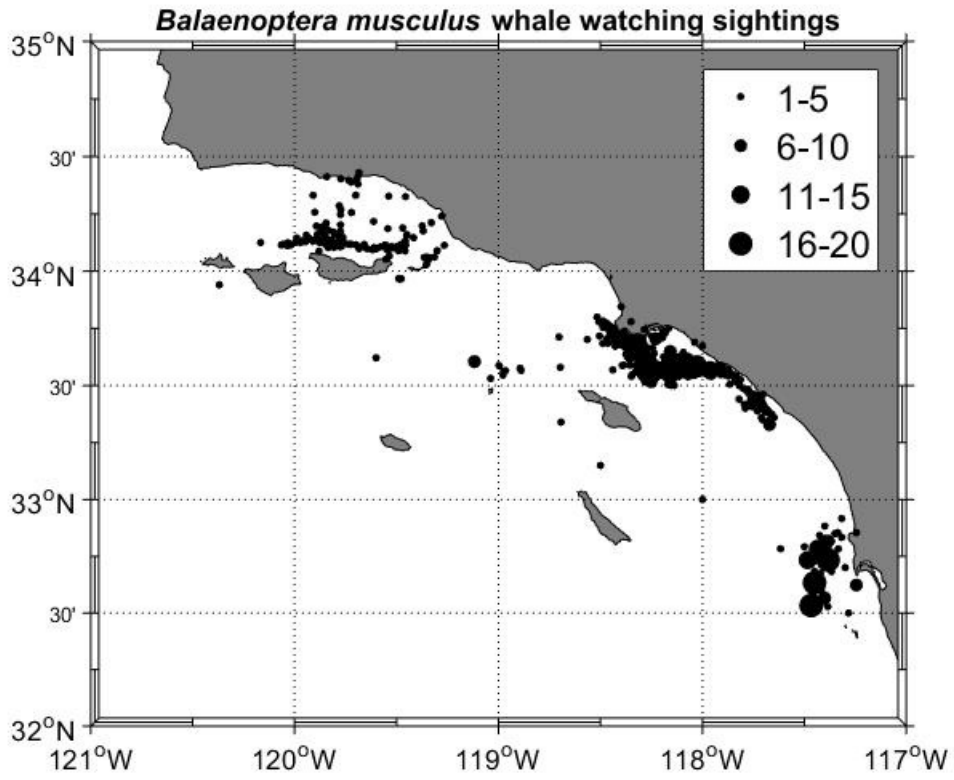

Figure 1.7: The distribution of blue whales in the Southern California Bight from commercial whale watching boat records between 2008 and 2012.

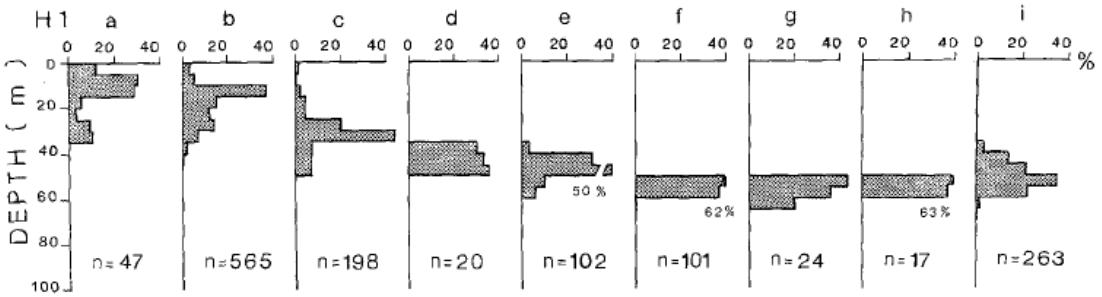

Figure 1.8: Daytime vertical distribution of *Nyctiphanes couchi* developmental stages in the Celtic Sea. (a) furcilia, 2 to 3 mm; (b) furcilia, 3 to 4 mm; (c) early post-larvae, 4 to 5 mm; (d) post-larvae males, 5 to 6 mm; (e) post-larvae males, 6 to 7 mm; (f) post-larvae males, 7 to 8 mm; (g) post-larvae males, 8 to 9 mm; (h) post-larvae males, 9 to 10 mm; (i) total post-larvae males. n=number of individuals m^{-2} (Williams and Fragopoulu 1985).

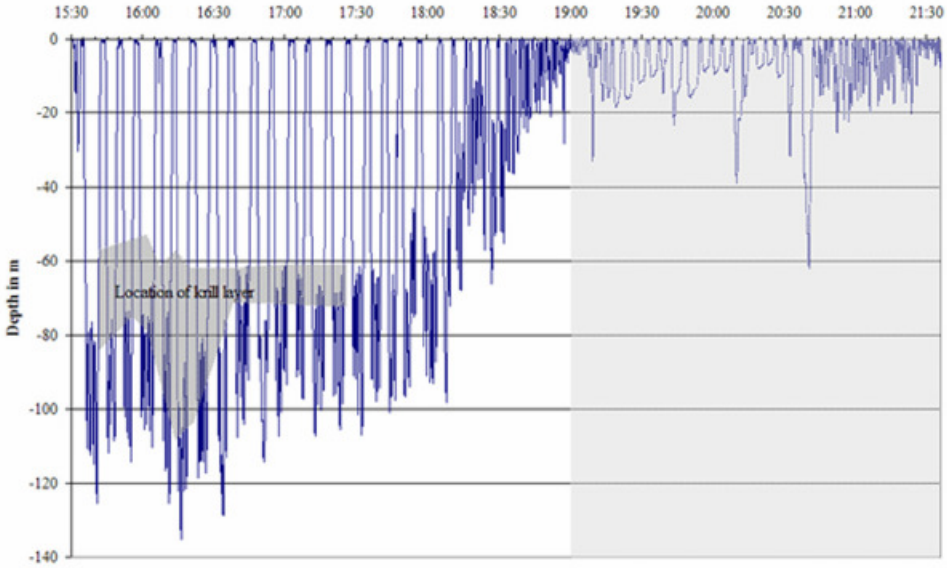

Figure 1.9: Blue whale dive profile (blue lines) during a 6-hour tag deployment in the Sea of Cortez, Mexico on 1 March 2001. The dark gray shaded krill layer was located based on depth sounder readings (Calambokidis *et al*. 2007).

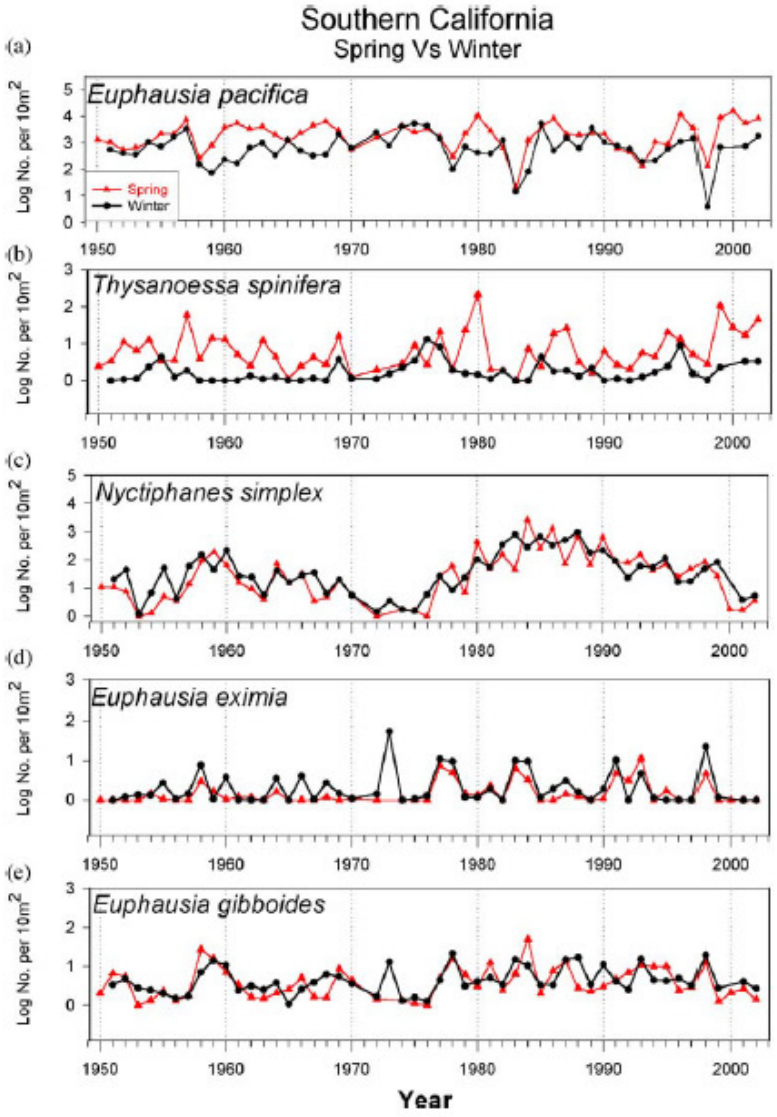

Figure 1.10: Comparisons of euphausiid abundances between spring the preceding winter. Winter and spring abundances demonstrate coherence through time (Brinton and Townsend 2003).

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CHAPTER 2 Dietary specialization of blue whales in the southern sector of the California Current System

2.1 Abstract

Blue whale feeding on euphausiids is thought to be limited to select prey species and size ranges. Here we describe the mandible morphology of the eight numerically abundant California Current euphausiid species and determine regression relationships between mandible size and total body length. We then apply these identifications to the mandibles recovered from blue whale fecal samples collected between 1998 to 2015 off Southern California in order to determine dietary species and size composition. Whale diets in all years were consistently and overwhelmingly dominated by the large, neritic euphausiid *Thysanoessa spinifera*, even when other species were present or dominant in closely collected net samples. More than 99% of ingested euphausiids were longer than 10 mm, indicating that blue whales are dependent upon aggregations of sub-adults or adults of a limited number of coastally associated euphausiid species.

2.2 Introduction

Blue whales (*Balaenoptera musculus*) are the largest animals on earth but may also have one of the most restricted diets, preying entirely on euphausiids (Nemoto 1970; Kawamura 1980; Schoenherr 1991; Croll *et al.* 2005). Like other rorqual whales, blue whales lunge feed, collecting planktonic food from discontinuous volumes of engulfed water during discrete feeding events (Kawamura 1980; Goldbogen *et al.* 2012). Lunge feeding occurs both at the water surface and at depth, and the average blue whale dive depth off the California coast is 190 m (Goldbogen *et al.* 2012). Northeast Pacific blue whales migrate annually between Baja California and an area west of the Costa Rica Dome in winter to as far north as Washington state during the summer, likely tracking their prey (Bailey *et al.* 2009). In the southern sector of the

California Current System, 8 potential prey euphausiid species dominate: *Thysanoessa spinifera* Holmes, *Thysanoessa gregaria* Sars, *Euphausia pacifica* Hansen, *Nyctiphanes simplex* Hansen, *Euphausia recurva* Hansen, *Euphausia eximia* Hansen, *Euphausia gibboides* Ortmann, and *Nematoscelis difficilis* Hansen (Brinton and Townsend 2003).

Researchers working in Monterey Bay and the Channel Islands, California, both found the euphausiid species *Thysanoessa spinifera* over-represented in whale fecal material in comparison with net samples from the water column near where the whales were feeding (Fiedler *et al.* 1998; Croll *et al.* 2005). The more abundant euphausiid *Euphausia pacifica* was consumed at both locations, but in significantly lower proportions than the species' presence in the water column. Additionally, the mean size of both euphausiid species was larger in the whale diet than in the water column in Monterey Bay (Croll *et al.* 2005). However, blue whales occur well beyond the geographic ranges of *Thysanoessa spinifera* and *Eupahausia pacifica*, and are known to consume other euphausiid prey in other locations. In the Southern Ocean, blue whales feed on *Euphausia superba* and *Euphausia crystallorophias* (Kawamura 1980), both of which aggregate near the surface under pack ice (O'Brien 1987). Blue whales have also been observed feeding on surface aggregations of *Nyctiphanes simplex* in the Gulf of California, Mexico (Gendron 1992). Surface swarms may provide accessible aggregations of mature adults (Smith and Adams 1988); however, euphausiid aggregation density is a more important factor in determining the energetic benefit of a particular lunge than the depth of the aggregation (Goldbogen *et al.* 2011). A deeper, but denser aggregation of euphausiids would provide the whale with more net energy gain, despite the added cost of swimming deeper compared to a shallow but sparse aggregation.

Analysis of fecal samples is a non-invasive method of assessing baleen whale diet. Whale fecal plumes contain unassimilated prey remains, including the siliceous mandibles of euphausiids (Kieckhefer 1992; Croll *et al.* 2005). While previous researchers have investigated the feeding specificity of whales through analysis of the mandibles in their fecal material (Kieckhefer 1992; Fiedler *et al.* 1998; Croll *et al.* 2005), there are no published descriptions of the mandible morphology for most of the euphausiid species we describe here, limiting the range of identifiable prey species. In the present study, we compare adult mandible morphologies for the eight numerically dominant species of euphausiid in the California Current System and use those morphologies to assess blue whale feeding specificity in the southern sector of the California Current from San Diego to Cordell Bank.

2.3 Methods

2.3.1 Mandible dissection and identification

We completed mandible dissections with the use of a Nikon SMZ 1500 stereomicroscope. Total body length (tip of the rostrum to the tip of the telson, Boden et *al.* 1955; Brinton 1962; Brinton *et al.* 2000) was measured for each adult euphausiid before mandibles were dissected. Each pair of mandibles was dissected and cleared of the labrum, mandibular palps, 1st and 2nd maxillae, and associated musculature so that accurate measurements could be made. We measured the total mandible length (TML), the total incisor length (TIL), and total molar width (TMW; Fig. 1) so that the mandibular edge index (MEI) could be calculated (Nemoto 1977). Once cleaned, each pair of mandibles was then placed in glycerin on a slide for measurements and closer assessment of morphological characteristics.

Initially, mandibles were dissected from the full adult life history of *E. pacifica* males and females at each mm increment (11-22 mm) to address morphological changes through adult development. This species' adult size range coincides with the size range of euphausiids blue whales have been previously shown to ingest (Croll *et al.* 2005). This analysis revealed similar mandibular morphology across sexes and throughout the adult life history. We then chose specimens at the lower, middle, and high end of the adult size range of each of our 8 species of interest with both sexes represented equally. The adult total body length range for each is as follows: *Thysanoessa spinifera* (15-26 mm), *Thysanoessa gregaria* (7-12 mm), *Euphausia pacifica* (11-22 mm), *Nyctiphanes simplex* (7-17 mm) *Euphausia recurva* (7-16 mm), *Euphausia eximia* (15-30 mm), *Euphausia gibboides* (16-26 mm), *Nematoscelis difficilis* (15-25 mm) (Brinton *et al.* 2000).

Each species generally exhibited consistent morphology throughout their adult size range and between sexes, with only minor variations, making species identifications reliable. A median adult size individual was used for taxonomic descriptions, line drawings (Fig. 2), and digital images (Fig. 3). Mandible drawings were made with Adobe Illustrator CS6 from line drawings made from a camera lucida and a compound microscope at 10X magnification.

2.3.2 Mandible to body length regressions

The relationship between mandible length and total body length for all eight dominant California Current System (CCS) species (Brinton and Townsend 2003) was determined using linear regressions. Regressions with larger sample sizes were calculated for *T. spinifera* and *E. pacifica*, which proved to be the dominant blue whale prey. Three hundred *T. spinifera* individuals, from furcilia to adult stages, were dissected and measured for both right mandible

length and total length. One hundred and thirty six adult *E. pacifica* were dissected and measured in the same way. Statistics were performed in SigmaPlot vers. 10.0 (Systat Software, San Jose, CA).

2.3.3 Fecal sample collection and enumeration

The whale fecal material used in this study came from three sources: the Cascadia Research Collective, the Ocean Institute, and small boat operations associated with the SKrillEx I and II cruises (Nickels *et al*. in prep, see Table 1). The Cascadia Research Collective opportunistically gathers whale fecal samples during cetacean photo ID studies in the waters off California. Clumps of newly discharged, floating fecal material were skimmed off the water's surface using a dip net with approximately 63 µm mesh and either frozen at 20° C or preserved in isopropyl alcohol. Upon receipt, we transferred these samples into buffered 5% Formalin for long term preservation. Fecal samples were also obtained in partnership with the Ocean Institute at Dana Point, California, during public whale watching cruises in 2013. The fecal material was collected with a 183 µm mesh plankton filtering funnel attached to a boat hook and frozen at 20° C before also being transferred to buffered 5% Formalin at room temperature. A dedicated small boat mission for fecal sample collection took place on 31 July 2014 in association with a larger research effort (SKrillEx I) around Nine Mile Bank, near San Diego California. During the second year of that effort (SKrillEx II) in 2015, fecal samples were collected on a dedicated small boat mission and opportunistically during a small boat whale visual survey. The same 183 µm plankton filtering funnel used with the Ocean Institute was used at Nine Mile Bank. Fecal material was immediately preserved in buffered 5% Formalin. For all samples the date of collection and the species of whale whence the sample originated was documented. In most

cases, the location where the sample was collected was also recorded, but some location information is missing from older records.

Fecal material was sorted for euphausiid mandibles and other identifiable prey parts using a dissecting microscope with a calibrated ocular micrometer. To prevent double counting, only right mandibles were identified and measured. Aliquots were removed from well mixed samples and all right mandibles were identified and measured from each aliquot. Sorting continued until at least 300 right mandibles were found or all of the right mandibles from the sample were identified. Mandibles that were too damaged for identification were not included. The length distribution of consumed euphausiids was reconstructed from right-mandible lengths based upon the species-specific linear regressions.

2.3.4 Mandible descriptions

We chose the right mandible as our reference standard for taxonomic identifications, line drawings, descriptions, and digital images as in Nemoto (1977) and Mauchline (1989). The cusp of the mandible is made up of a cutting region referred to as the *pars incisiva*, and the grinding region, the *pars molaris* (Fig. 1). The cusp leads to a root, or basis, which is connected to robust musculature. Within the *pars insiciva,* there are multiple spines and a cutting edge useful for taxonomic identifications. The diagnostic characters described below are the spacing of the anterior spine pair one (SP1), shape and length of spine two (S2), and shape, angle, and length of the cutting edge (CE), proximal to the *pars molaris*. Additionally, there is a shoulder structure (SH) where the main cusp of the mandible connects to the root or posterior leading arced section of the mouthpart (Fig. 1). SP1 is the anterior most process and is typically a combination of two either overlapping or slightly offset spines.

Each *pars incisiva* of the mandible was placed as flat as possible in the same orientation to the observation dish so that the presence or absence of overlapping SP1 could be assessed. This placement leaves the incisor region in the background and the molar region in the foreground. The *pars molaris* from whale fecal samples was often either filled with fecal material or somewhat filed down due to abrasion during digestion and gut passage, thus making the characteristics of the *pars molaris* generally unsuitable for rapid taxonomic identifications. Although the *pars incisiva* possessed enough taxonomic information to serve as the main region for identification of mandibles from whale fecal samples, we also describe a unique character of the *pars molaris* for *E. gibboides, E. recurva,* and *N. difficilis*.

2.3.5 Net sample collection and enumeration

When possible, net samples were also collected to compare the size and species of euphausiids available in the area where the whales were feeding with those consumed by the whales, as inferred from fecal analysis. Cascadia Research Collective sampled ambient euphausiids near the Channel Islands on 21 Sept. 2009 at 16:41with a 333 µm mesh bongo net towed obliquely from ~300 m to the surface. On 15, 16, and 26 Aug. 2010, during daylight, surface swarming euphausiids near Long Beach CA were collected with an dip net (approximately 63 µm mesh). These euphausiids were initially preserved in ethanol but then transferred to buffered 5% Formalin. Additional euphausiid sampling was conducted near San Diego, CA in 2014 and 2015 as part of SKrillEx I and II (Nickels *et al*., in prep). On each cruise, bongo net transects with calibrated flowmeters were performed across a steep bathymetric feature thought to be a blue whale aggregation center. The 202 µm mesh bongo nets were lowered to 200 m depth or 10 m above the sea floor and towed obliquely as the ship moved at 1-

2 kts (0.5-1 m s^{-1}) to preserve a 45° degree wire angle. These samples were immediately preserved in buffered 5% Formalin.

Net samples were enumerated under a dissecting microscope with a calibrated ocular micrometer. From each sample, either all euphausiids were identified to species and life history phase (furcilia, juvenile, adult) or they were subsampled with a Folsom splitter so that approximately 200 individuals were identified. The identified euphausiids were measured for total length from the tip of the rostrum to the end of the telson (Boden *et al.* 1955; Brinton 1962; Brinton *et al.* 2000). For fecal samples paired with net samples from the same time period and region, we compared the size distribution of euphausiid prey consumed (reconstructed from fecal samples) with the size distribution of euphausiid prey available (determined by net samples) using a Kolmogorov-Smirnov test. The mean size distribution was used for comparison where multiple fecal or net samples were collected from similar dates and locations. Species proportions were compared between fecal and net samples with pairwise G-tests. Statistics were performed in R vers. 3.1.2 (R Core Team, 2014).

2.4 Results

2.4.1 Mandible descriptions

We found all eight common euphausiid species to have distinctive mandibular morphology, making it possible to identify the species of origin.

T. spinifera – pars incisiva spines of SP1 overlap one another. S2 large and acute extends fully out to and sometimes beyond terminal end of SP1. Deep acute groove between SP1 and S2. CE is a 3 acutely pointed process descending in height as it

approaches margin of the *pars molaris*. The CE varies and in some cases can possess only 1-2 processes with longest process reaching approximately half the length of S2 (Fig. 2A, 3A).

T. gregaria – pars incisiva spines of SP1 are offset; this is the primary difference between *T. gregaria* and *T. spinifera,* besides overall size of right mandible. S2 large and acute and extends fully to and sometimes beyond the terminal end of SP1. CE is a 3 acutely pointed process descending in height as it approaches the margin of the *pars molaris*. The CE varies and in some cases can possess only 1-2 processes with longest process reaching approximately half the length of S2 (Fig. 2B, 3B).

E. pacifica – pars incisiva has a slightly offset SP1. Acute S2 located tightly to SP1 extending to just before or to terminal end of SP1 but not extending beyond it. The CE is typically a diagnostic wide plateau or slightly corrugated ridge. The CE in some cases may lack this character or possess a low-lying ridge with two small peaks as S2. An additional diagnostic character is the swollen shoulder (SH) present forming a convexity and noticeable protrusion of chitinous material toward the lateral margin. The SH forms from the anterior most end of the *pars incisiva* leading to the posterior end of the animal. The specimen must be rotated to see this 3 dimensional characteristic. In addition to the presence of the flat ridge of the CE, the SH sets *E. pacifica* apart from the similar mandible of *N. simplex* (Fig. 2C, 3C).

N. simplex – pars incisiva spines of SP1 slightly offset. Very acutely pointed S2 that does not extend fully to the terminal end of SP1. CE is a series of 2 processes 2/3 the length of S2. No SH protrusion present. Anterior edge of *pars incisiva* continuous more gradual approach towards the SH of the basis of the mouthpart (Fig. 2D, 3D).

E. recurva – pars incisiva spines of SP1 fully overlap one another. Acute S2 located tightly to SP1 and terminal end extends fully out to and even slightly beyond SP1. A deep, wide trough between S2 and CE. Obtuse process CE approximately 1/3 the length of S2. Lateral approach from cusp to basis more gradual and rounded than *E. eximia*. (Fig. 2E, 3E).

E. eximia – pars incisiva spines of SP1 fully overlap one another. Acute S2 located tightly to SP1 and terminal end extends fully out to and even slightly beyond SP1. CE is widely separated from S2 and an obtuse blunt curved process. Deep, wide trough between S2 and CE. Obtuse process CE approximately 1/3 length of S2. Lateral approach from cusp to basis more angular than rounded (Fig. 2F, 3F).

E. gibboides – pars incisiva spines of SP1 fully overlap one another. S2 located closely to SP1 and terminal end forming a less acute more blunted end when compared with other *Euphausia* species and similarly sized *T. spinifera* mandibles. CE forms single or double rounded process widely separated from S2. *Pars molaris* ornamented with highly serrated marginal edge (Fig. 2G, 3G).

N. difficilis – pars incisiva spines of SP1 overlap but length of dorsal spine does not extend fully out to ventral spine. Each spine of SP1 is very elongate and acute. S2 is acute and much wider than SP1, does not fully extend out to terminal end of SP1. CE is 3rd large, acute process and does not fully extend to terminal end of S2. Overall length and shape of main mandible cusp structure leading to the SH1 and root is more elongate than all others described here. SH1 forms sharp 160° angle. *Pars molaris* ornamented with highly serrated marginal edge (Fig. 2H, 3H).

2.4.2 Mandible to body length regressions

All 8 species showed significant ($p<0.01$), positive linear regressions between right mandible total length and total body length for the adult reference individuals (Fig. 4). The r^2 values were all above 0.85. *T. spinifera*, *E. pacifica*, *E. eximia*, and *N. simplex* r^2 values were above 0.90.

2.4.3 Species and size composition of ingested euphausiids

All blue whale fecal samples were dominated by mandibles positively identified as those of *T. spinifera* (Fig. 5). Of the 18 fecal samples analyzed, 2/3 of them were composed of 100% *T. spinifera* prey. The other third contained between 1 and 19% *E. pacifica*. One sample from near San Diego in 2015 contained two *N. difficilis* mandibles. A single *N. simplex* mandible was found in the sample from an unknown location in 1998.

Some fecal samples also contained identifiable material other than euphausiid mandibles. The fecal sample from near Long Beach on 14 Sept. 2010 contained a single *N. difficilis* carapace. A *Pyrosoma atlantica* was found in the fecal sample from near Dana point on 18 July

2013. The sample from 26 June 1999 had an antenna from the pelagic red crab, *Pleuroncodes planipes*. More substantial crustacean remains were found in the sample from 23 June 2015 near San Diego, including *P. planipes* limbs and chelipeds as well as appendages of another decapod.

The reconstructed body lengths of ingested euphausiids (Fig. 6) ranged from 7.1 mm to 29.6 mm. Both the smallest and largest individuals were *T. spinifera*, with a median of 17.46 mm. The modal size of ingested euphausiids varied considerably by collection date (Fig. 6). Of all euphausiid sizes reconstructed from mandible measurements, less than 0.01% were smaller than 10 mm total body length. Size distributions varied by sampling date and location.

2.4.4 Comparison of prey digested to prey available

When blue whales were feeding in surface swarms composed of 100% *T. spinifera*, the whales did not ingest other species not represented in dip net samples (Aug. 2010, Fig. 7). When bongo nets were used to sample prey at depth, the species composition of ingested prey euphausiids was less diverse than the available euphausiids. In all cases when other euphausiid species were also present, *T. spinifera* was over-represented in the diet compared to its availability in the water column ($p \leq 0.05$, pairwise G-test). Notably, *E. pacifica* was the most abundant euphausiid in the water column in July 2014 and June 2015, but was under-represented in the whale diet on both occasions ($p < 0.001$, pairwise G-test)

There were often differences in size distributions between ingested euphausiids and ambient euphausiids available in the water column (Fig. 8). In all three comparisons between fecal samples and deeper bongo tows, whales consumed significantly larger euphausiids than were available ($p < 0.05$, Kolmogorov-Smirnov test, Fig. 8 A, D, E). Of the two instances when surface euphausiid aggregations were sampled by dip nets, in one case there was no difference in size distributions ($p > 0.05$, Kolmogorov-Smirnov test, Fig. 8C), and the other was the only

instance where larger euphausiids were available than ingested ($p<0.05$, Kolmogorov-Smirnov test, Fig 8B).

2.5 Discussion

Prey euphausiid sizes were estimated by Croll *et al.* (2005) using linear regressions for *T. spinifera* and *E. pacifica* developed by Kieckhefer (1992). For *T. spinifera*, our slope is slightly steeper (12.6 compared to 11.3) and y-intercept slightly lower (-1.25 compared to 1.30). Our T. *spinifera* equation is the result of a larger body size range (3-25 mm compared to 10-29 mm) and a larger N (300 compared to 166). For *E. pacifica*, both regressions have the same slope (12.95), although we have a slightly smaller y-intercept (1.76 compared to 2.84). The two *E. pacifica* regressions are the result of similar body size range coverage (9-21 mm compared to 10-22 mm) and similar N (136 compared to 144).

Our results agree with previous studies (Fiedler *et al.* 1998; Croll *et al.* 2005) that blue whales appear to target large *T. spinifera* as prey in the southern and central sectors of the California Current System. When surface swarms were present, blue whales fed on surface swarms composed of entirely *T. spinifera.* *T. spinifera* have been documented to form dense daytime surface swarms (Brinton 1981; Smith and Adams 1988) and grow to a relatively large size for the southern CCS, which likely leads them to be high value, low cost prey for lunge feeding whales. Even when *E. pacifica* dominated deep net samples numerically, *T. spinifera* was over-represented in fecal material. The smallest previously reported prey size was estimated at approximately 10 mm (Croll *et al.* 2005). While we did find several mandibles from euphausiids between 7 and 10 mm, these accounted for less than 0.01% of the total euphausiid

prey. Smaller sizes may be occasionally ingested, but are relatively unimportant both numerically and energetically and are not targeted as prey by blue whales.

Other than *T. spinifera* and *E. pacifica*, we occasionally identified mandibles of *N. simplex* and *N. difficilis* in blue whale fecal material. It is of note that the single *N. simplex* consumed was found in the 1998 fecal sample. *N. simplex* is a warm water associated sub-tropical to marginally tropical species, and typically in greater abundance off California during warm El Niño events such as 1998 (Brinton and Townsend 2003) and during positive phases of the Pacific Decadal Oscillation (Brinton and Townsend 2003; Di Lorenzo and Ohman 2013). While we unfortunately do not know where the sample containing *N. simplex* was collected, *N. simplex* was found as far north as Barkley Sound, Canada during the 1998 event (Tanasichuk and Cooper 2002). The small percentage of *N. difficilis* consumed near San Diego in 2015 may have been engulfed incidentally when *T. spinifera* were the whale's target. Adult *E. pacifica*, *T. spinifera*, and *N. difficilis*, in order of descending abundance, all co-occurred in the same deep, daytime layer in 2015 (Nickels *et al*. in prep).

Some non-euphausiid prey remains were found in the fecal samples. We interpret these as incidental ingestions rather than alternative target prey. Pyrosomes are passive drifters in the ocean, and would neither have been able to avoid engulfment by a whale nor provided significant nutritional value. *Pleuroncodes planipes* occurs off Southern California during El Niños (Boyd 1962; McClatchie *et al.* 2016). The presence of *P. planipes* in the area as evidenced by blue whale diet is therefore not surprising. This would, however, be the first observation of blue whale feeding on *P. planipes* to be confirmed by fecal contents. If the *P. planipes* had been the targets of whale feeding, we would not have expected to see as many euphausiid mandibles, as these two taxa occupy different depths during the day when whales feed (Nickels *et al*. in prep).

When comparing the prey ingested by a whale to the prey available, we have here chosen to pair the samples that are closest in space and time. However, these comparisons assume that the patches of euphausiids around the area where a whale was feeding are a good representation of the prey field at the time the material in the feces was ingested. The gut passage time for blue whales has not been estimated, and our closest approximation is an 18 hour time period estimated for their smaller relative fin whales (*Balaenoptera physalus*, Vikingsson 1997). The larger blue whale is likely to have a longer digestive tract, and therefore may have a longer passage time, or the time may vary depending on the quantity and rate of prey engulfed. Gut passage times longer than 24-48 hours or high variability in the composition of available euphausiids on a shorter timescale than gut passage would decrease the likelihood that the net samples represent the prey available when the whale was feeding.

2.6 Conclusions

Euphausiid mandible morphology varies by species and can be used for taxonomic identification of size reconstruction of consumed prey from whale fecal material. Using this method, we determined that blue whales in the southern California Current System focus their feeding primarily on the euphausiid species *T. spinifera*, and secondarily on *E. pacifica*, over other available species. Blue whales usually consumed individuals longer than 10 mm total body length. Smaller individuals, other species and taxa, as well as presumably *E. pacifica*, are all likely consumed incidentally when whales target their lunge feeding on patches of large *T. spinifera*.

2.7 Acknowledgements

We would like to thank the Cascadia Research Collective, in particular John Calambokidis, the Ocean Institute, and John Hildebrand and his lab members for collection of the fecal samples for this study. Megan McKenna began the investigation of the diet of CCS blue whales that grew into this paper. Mike Landry, Jay Barlow, Jon Shurin, and John Hildebrand provided valuable comments as the project developed. Annie Townsend instructed us in identification of the adult euphausiids. Additional laboratory assistance was provided by Tais Castellano and Shelbi Richardson. We thank the Pelagic Invertebrate Collection of Scripps Institution of Oceanography for use of samples, lab space, and equipment. This work was supported by the U.S. National Science Foundation via the California Current Ecosystem LTER site (OCE-10-26607 and OCE-16-37632), UC Ship Funds, and the Scripps Institution of Oceanography Graduate Department.

Chapter 2 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M.; Ohman, Mark D. "Dietary specialization of blue whales in the southern sector of the California Current System." It is presented as part of this dissertation with the acknowledgement of the study coauthors Linsey M. Sala and Mark. D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

Table 2.1: Collection dates, approximate times, and locations for fecal samples used to assess ingestion by blue whales (*B. musculus*), or for bongo or dip net samples used to assess euphausiid prey available in the water column. CRC = Cascadia Research Collective; OI = Ocean Institute; S1 = SKrillEx I; S2 = SKrillEx II.

Sample Type	**Date**	**Time**	**Location**	**source**
Fecal	19 July 1998	Daylight	unknown	CRC
Fecal	26 June 1999	11:20	Channel Islands	CRC
Fecal	26 June 1999	14:30	Channel Islands	CRC
Fecal	28 June 1999	11:48	Channel Islands	CRC
Fecal	17 Sep. 1999	17:02	Cordell Bank	CRC
Fecal	21 Sep. 2009	16:45	Channel Islands	CRC
Fecal	17 Aug. 2010	Daylight	Long Beach	CRC
Fecal	28 Aug. 2010	Daylight	Long Beach	CRC
Fecal	14 Sep. 2010	Daylight	Long Beach	CRC
Fecal	18 July 2013	10:00-15:30	Dana Point	OI
Fecal	11 Aug. 2013	10:00-15:30	Dana Point	OI
Fecal	4 Sep. 2013	10:00-15:30	Dana Point	OI
Fecal	31 July 2014	12:20	San Diego	S1
Fecal	31 July 2014	14:05	San Diego	S1
Fecal	20 June 2015	14:29	San Diego	S2
Fecal	23 June 2015	09:51	San Diego	S2
Fecal	23 June 2015	14:10	San Diego	S2
Fecal	25 June 2015	13:20	San Diego	S2
Bongo Net	21 Sep. 2009	16:41	Channel Islands	CRC
Dip Net	15 Aug. 2010	Daylight	Long Beach	CRC
Dip Net	16 Aug. 2010	Daylight	Long Beach	CRC
Dip Net	26 Aug. 2010	Daylight	Long Beach	CRC
Dip Net	28 Aug. 2010	Daylight	Long Beach	CRC
Bongo Net	26-31 July 2014	2000-0500	San Diego	S1
Bongo Net	11-17 June 2015	2000-0500	San Diego	S2

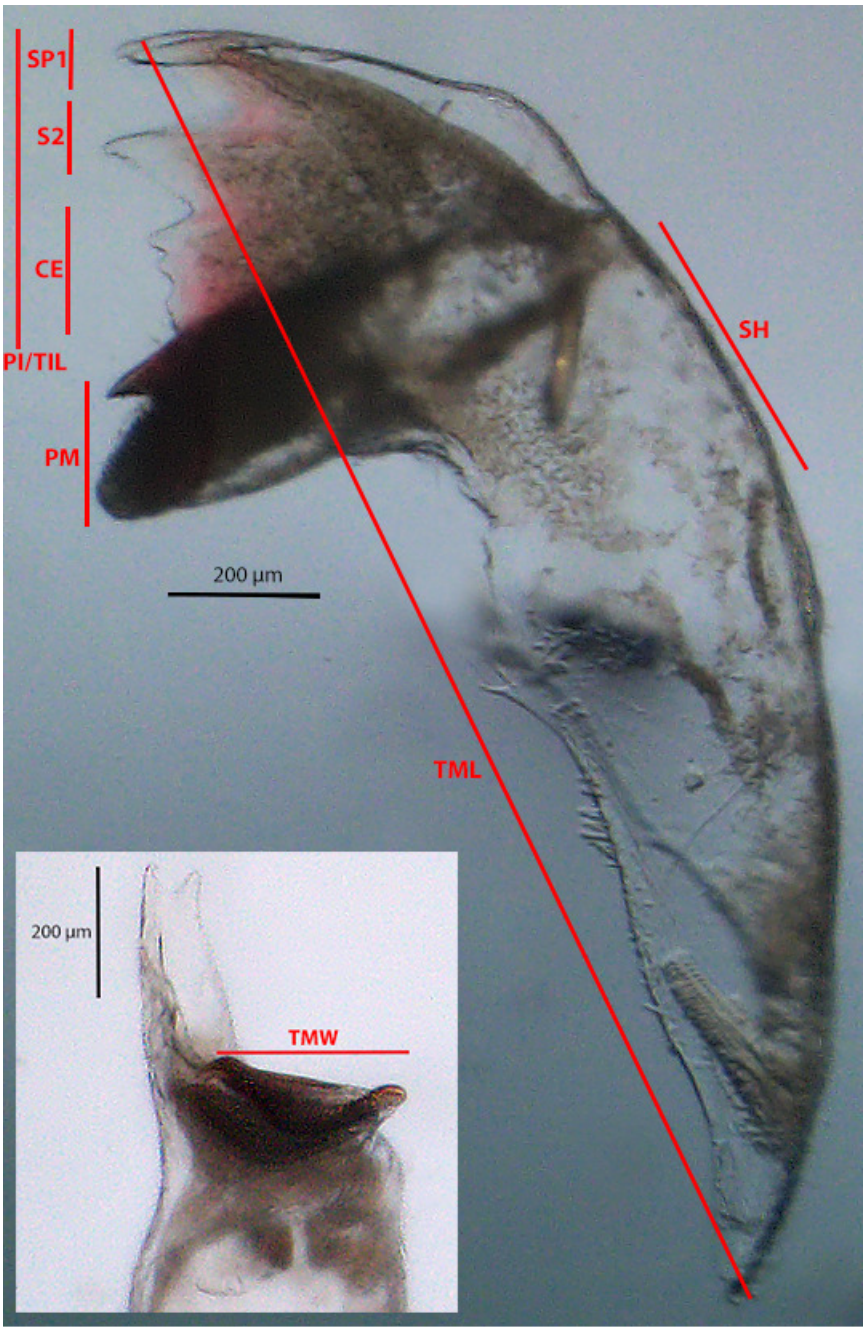

Figure 2.1: Digital images of euphausiid right mandible showing measurement sites for total mandible length (TML), total incisor length (TIL), and total molar width (TMW) Morphological identification regions include: spine pair one (SP1), spine two (S2), cutting edge (C.E.), pars incisiva (PI), pars molaris (PM), root shoulder (SH).

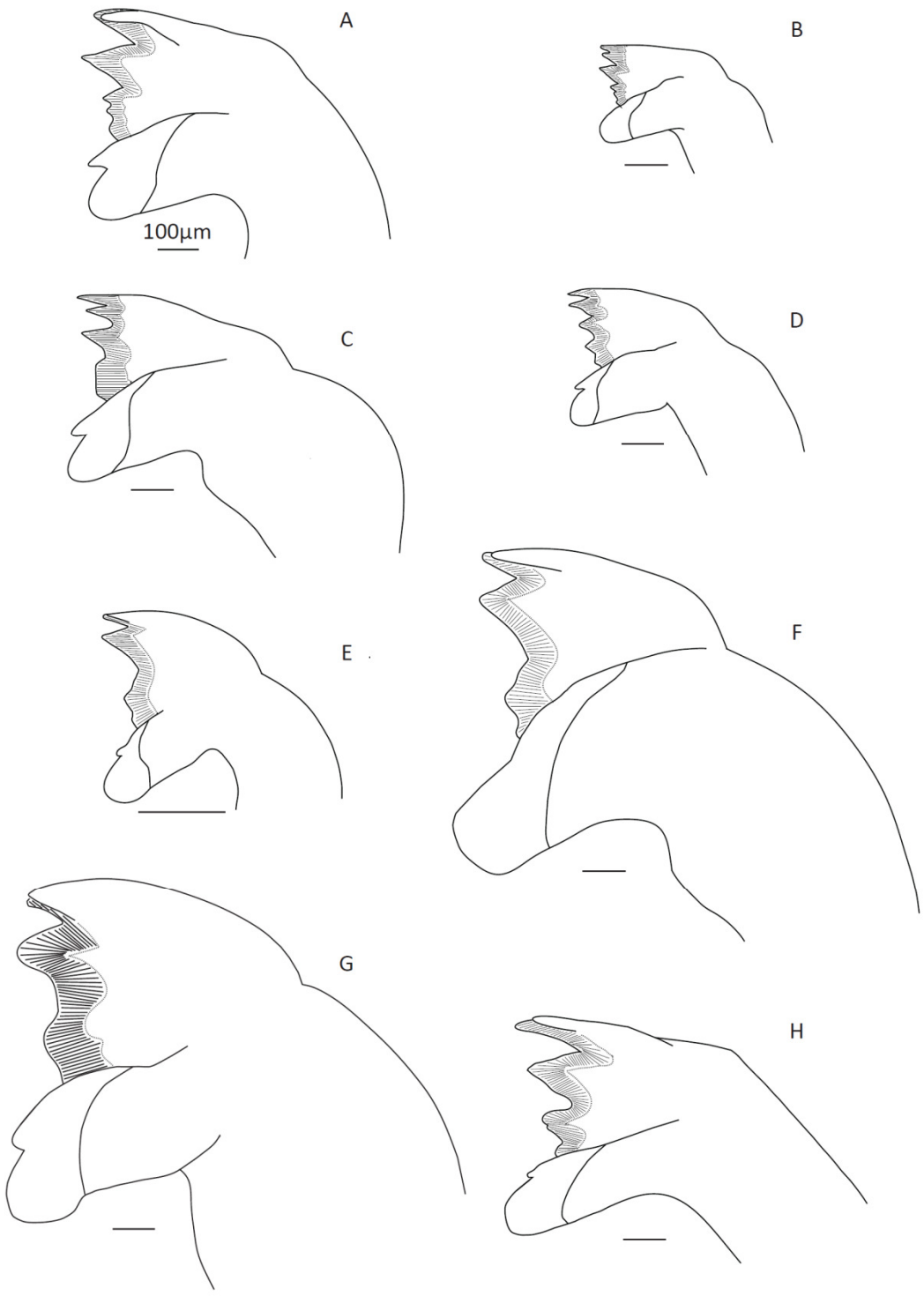

Figure 2.2: Line drawings of euphausiid right mandibles: (A) *Thysanoessa spinifera*, (B) *Thysanoessa gregaria*, (C) *Euphausia pacifica* (D) *Nyctiphanes simplex* (E) *Euphausia recurva* (F) *Euphausia eximia* (G) *Euphausia gibboides* (H) *Nemoatoscelis diffilis*. Scale bars all indicate 100 µm.

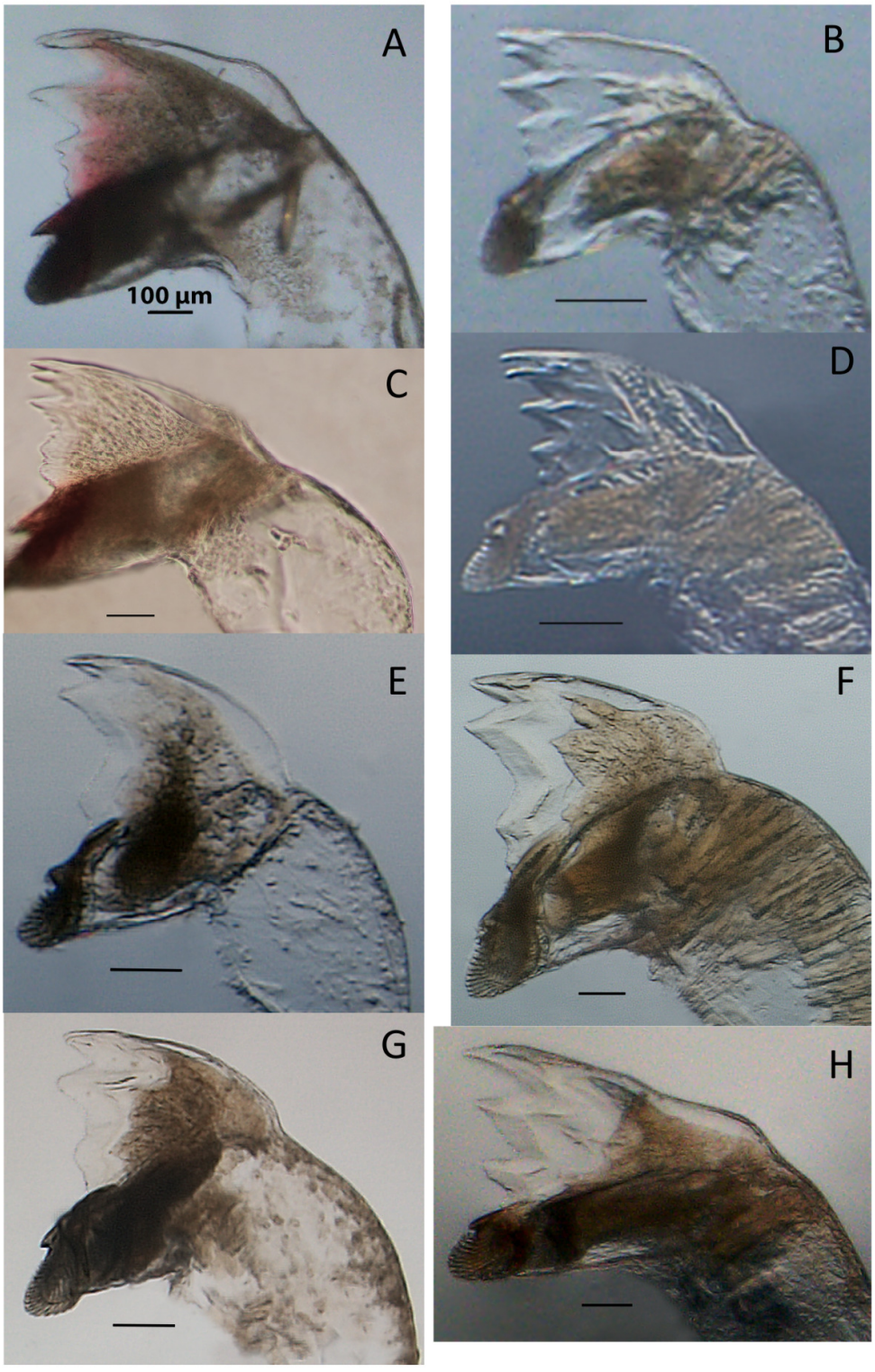

Figure 2.3: Digital images of euphausiid right mandibles (A) *T. spinifera*, (B) *T. gregaria*, (C) *E. pacifica* (D) *N. simplex* (E) *E. recurva* (F) *E. eximia* (G) *E. gibboides* (H) *N. difficilis*. Scale bars all indicate 100 µm.

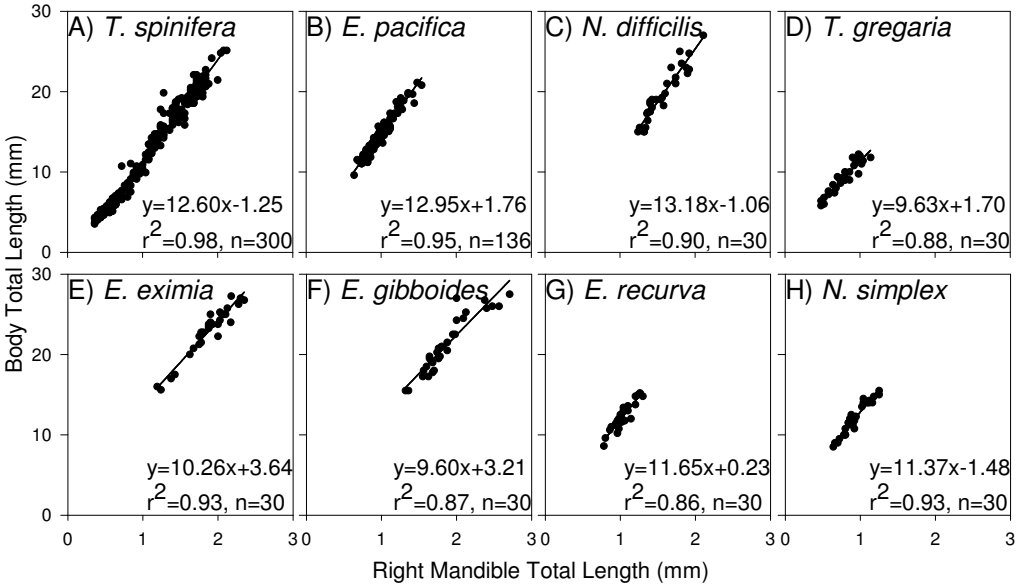

Figure 2.4: Relationship between euphausiid total body length and total mandible length for cool water-associated species (A) *T. spinifera*, (B) *E. pacifica*, (C) *N. difficilis*, and (D) *T gregaria*, and for warm water-associated species (E) *E. eximia*, (F) *E. gibboides*, (G) *E. recurva*, and (H) *N. simplex*. All regressions are significant ($p < 0.01$).

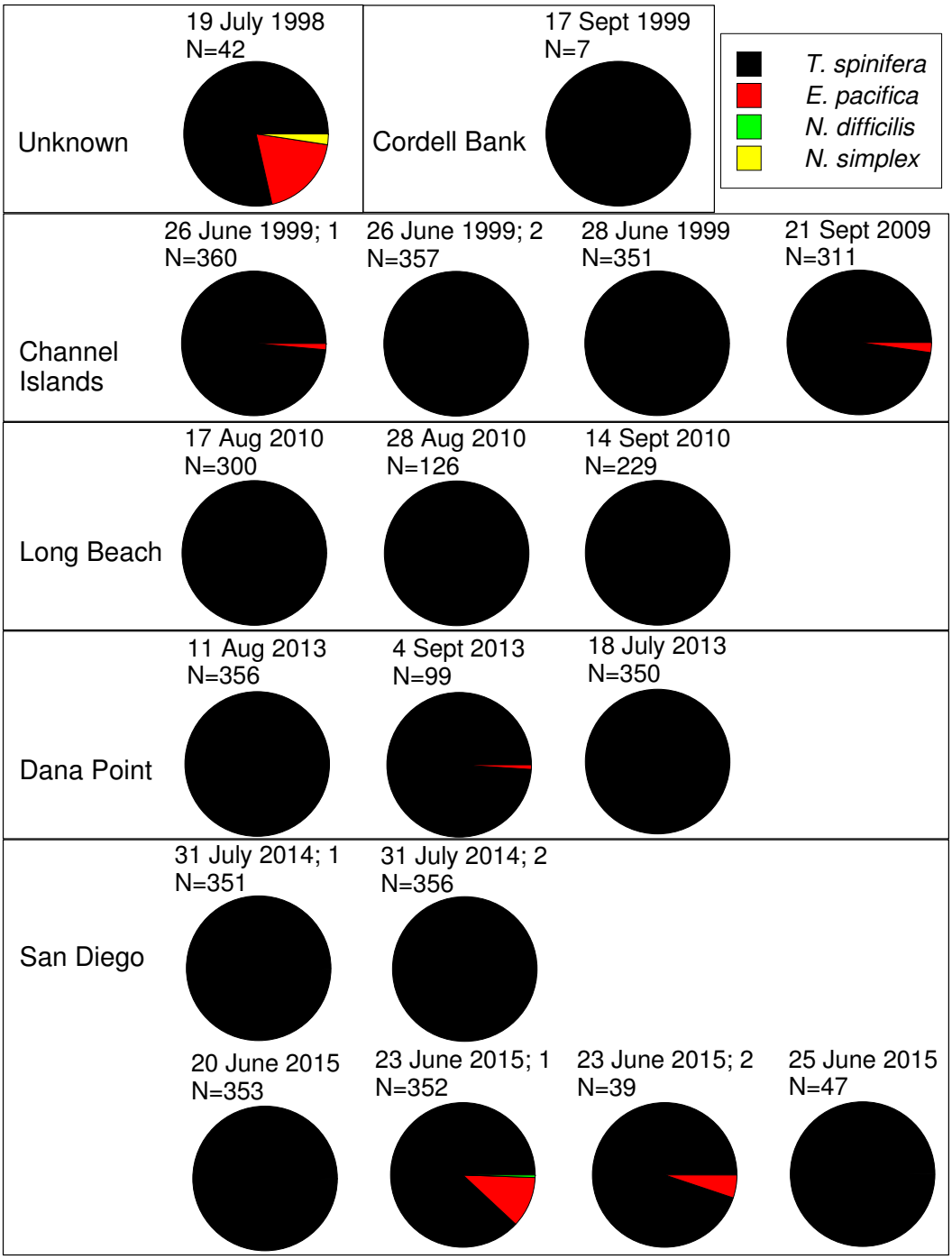

Figure 2.5: Euphausiid species % composition reconstructed from mandibles identified from blue whale (*B. musculus*) fecal samples at different collection localities.

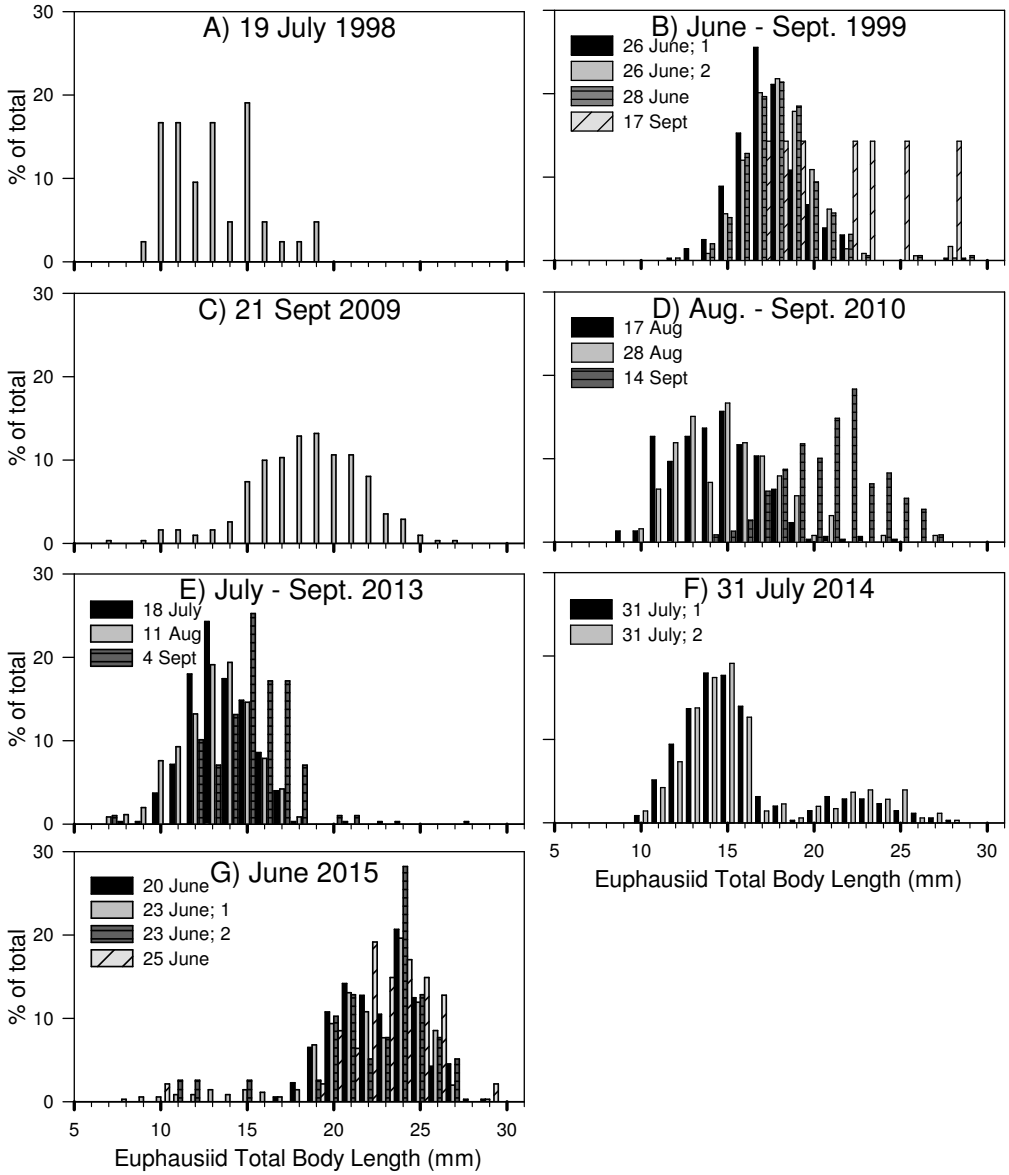

Figure 2.6: Reconstructed prey euphausiid total body length (mm) distributions from mandible total lengths found in whale fecal samples.

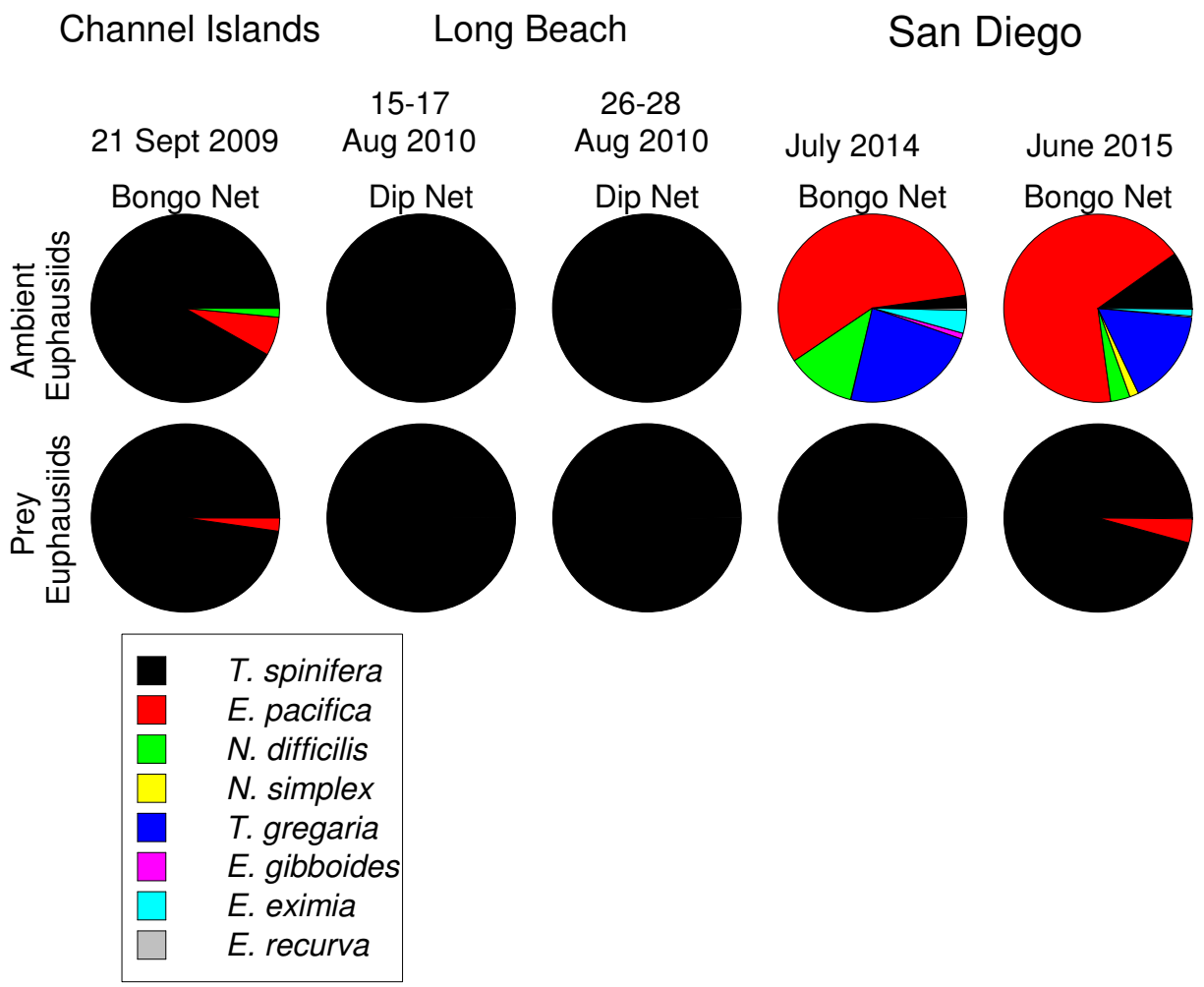

Figure 2.7: Prey euphausiid species compositions from mandibles in whale fecal samples compared to ambient available euphausiids collected by bongo or dip nets, at different localities and dates.

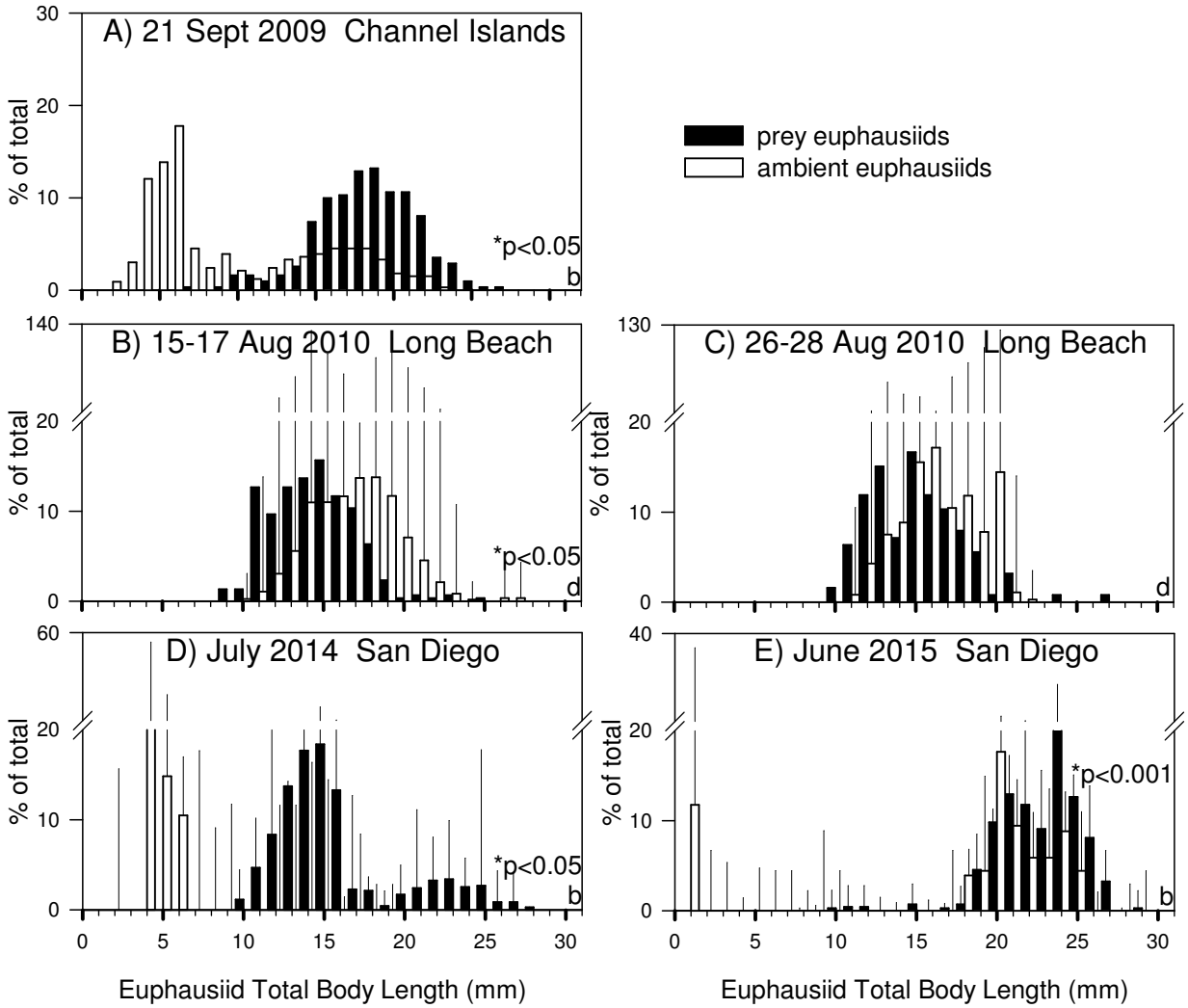

Figure 2.8: Comparison of reconstructed prey euphausiid total body length distributions from mandibles found in whale fecal samples (solid bars) with ambient available euphausiids collected by bongo (b) or dip (d) nets (open bars).* Denotes statistically significant Kolmogorov-Smirnov test.

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CHAPTER 3 Scales of co-occurrence of blue whales and their euphausiid prey in the Northeastern Pacific

3.1 Abstract

Blue whales (*Balaenoptera musculus*) are obligate euphausiid predators, and those in the eastern North Pacific population feed primarily on *Thysanoessa spinifera* and only secondarily on the more abundant *Euphausia pacifica*. We investigate the relevant scales of co-location between blue whale predators and these preferred prey. The distributions of blue whales and prey euphausiids are compared at the scale of the North Pacific Ocean basin, the California Current System, the region from Northern California to Baja California covered by the CalCOFI program, and a local scale near blue whale aggregation centers. A relationship between blue whales and *T. spinifera* distributions was observed only at the ocean basin and California Current System scales. Analyses at even smaller scales, corresponding to the daily ambit of feeding whales, will be necessary to understand the interaction between blue whales and their prey. We also investigate whether reduction in the availability of key euphausiid species in Southern California waters could have been the cause of the blue whale range expansion to the waters off of British Columbia beginning in 1997. We analyzed euphausiid abundances and biomass anomalies from spring and summer CalCOFI cruises to determine whether there had been a shift in the availability of *T. spinifera* and *E. pacifica* in comparison to Southern Vancouver Island. Instead of a reduction in Southern California prey availability, we found a positive trend in biomass anomalies current-wide in both spring and summer, suggesting the northward expansion of blue whales must be explained by other factors.

3.2 Introduction

Like other baleen whales, blue whales (*Balaenoptera musculus*) migrate seasonally between low-latitude feeding grounds in the summer and high latitude wintering habitats (Bailey *et al.* 2009). The southern sector of the California Current System (CCS) is a feeding ground in the Northeastern Pacific where blue whale density peaks during the summer months (Campbell *et al.* 2015). Blue whales are "swallowing type" feeders that engulf prey in discrete lunges rather than continuously straining prey from the water as they swim (Nemoto 1970). This lunge feeding behavior requires that prey can be found in sufficient densities that the energy expended in the lunge can be compensated, plus a surfeit to provision the whale when not actively feeding (Goldbogen *et al.* 2011). Blue whales appear extremely limited in their prey selection in the southern sector of the CCS, feeding essentially exclusively on euphausiids, and primarily on the euphausiid *Thysanoessa spinifera* Holmes and only secondarily on the more abundant *Euphausia pacifica* Hansen, despite the presence of multiple additional euphausiid species (Nickels *et al*. in prep). Prey euphausiids are limited in size as well as species. Blue whales mostly consume euphausiids larger than 10 mm (Croll *et al.* 2005; Nickels *et al*. in prep), which includes adult and juvenile *T. spinifera*, but only adult *E. pacifica* (Brinton *et al.* 2000). The dependence of blue whales on utilization of dense aggregations of larger body sizes of specific euphausiid species suggests that blue whale spatial distributions should be responsive to changes in prey availability.

Despite the importance of high euphausiid densities to blue whale survival, direct measures of prey availability are not typically included in blue whale habitat models (Gregr and Trites 2001; Stafford *et al.* 2009; Gill *et al.* 2011). Euphausiids are extremely patchy prey that must be directly sampled to obtain species and life history phase identification (Kramer *et al*.

1972; Ohman and Smith 1995; Brinton and Townsend 2003). Blue whales are patchy as well, but must be documented through visual or acoustic surveys that are rarely synoptic with prey field sampling (Soldevilla *et al.* 2006; Barlow and Forney 2007). Tying predator distribution directly to prey seems ecologically reasonable, yet has not been useful in practice for these large cetaceans and their small invertebrate food. The different scales at which these organisms live and are observed by scientists is a likely barrier to understanding the relationship between them. In this paper, we investigate the spatial distributions of blue whales and key prey euphausiids at a hierarchy of scales: the North Pacific Basin, the California Current System, a "regional" scale offshore of Southern California, and a "local" scale at individual blue whale hotspots. Identifying which of these scales are relevant in describing the spatial relationship of blue whales to their prey is necessary to discover how such patterns occur and what their consequences may be (Levin 1992). We hypothesize that blue whale distribution will be related to the distribution of preferred prey *T. spinifera* at all four scales.

North Pacific blue whales were hunted from the early 1900's until they were protected by the International Whaling Commission (IWC) in 1966 (Reeves *et al.* 1998; Clapham and Baker 2002). Currently, blue whales are classified by the IUCN as endangered and legally protected worldwide, but are increasing in population size (Reilly *et al.* 2008). After the end of whaling, there was an apparent lack of blue whale recovery off of British Columbia and in the Gulf of Alaska, with few documented sightings since the 1970's (Stewart *et al.* 1987). At the same time, large concentrations were still documented off California and Baja California and in the Eastern Tropical Pacific since the 1970's (Calambokidis *et al.* 1990; Calambokidis and Barlow 2004). Beginning in 1997, Calambokidis *et al.* (2009) again discovered whales from the California feeding population off of British Columbia and the Gulf of Alaska. A decline in estimated blue

whale abundance off of California in the early 2000's compared to the 1990's was interpreted as a redistribution of individuals away from California waters rather than a true population decline (Barlow and Forney 2007). The cause of this range expansion of the California feeding population is unclear. Here we test the hypothesis that there was a reduction in available euphausiid prey in the southern sector of the California Current System relative to waters off British Columbia, which motivated the whales to seek prey further north.

The southern sector of the California Current System has been systematically monitored by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1949 (Fig. 1). Hydrographic and biological data are collected on quarterly cruises. To date, the zooplankton samples from spring have been the focus of climate change-related studies (e.g., Brinton and Townsend 2003; Lavaniegos and Ohman 2007; Di Lorenzo and Ohman 2013) due to spring-related phytoplankton blooms and abundance maxima. However, this single season time point does not align with the summer presence of blue whales in the area and may not accurately represent the prey field available when blue whales arrive to feed. Here we investigate the coherence between spring and summer abundances for key whale prey euphausiid species during a critical whale feeding period in the region to determine the utility of the larger spring dataset in testing prey-predator relationships in summer.

3.3 Methods

3.3.1 Southern California euphausiid collection and enumeration

Zooplankton samples were collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). From 1949-1969, a 505 µm mesh, 1 m diameter ring net was used to a sampling depth of 140 m (Ohman and Smith 1995). The sampling depth was increased to 210

m in 1969. In December 1977, sampling transitioned to a 505 µm mesh 0.71 m diameter bridle-less bongo net with a flowmeter (General Oceanics model 2030R) installed in the starboard side, sampled to 210 m. While recognizing the species-specific corrections presented in Brinton and Townsend (1981), we follow Brinton and Townsend (2003), and do not attempt to correct for the changes in tow depth or net type. In the early years of the time series, cruises were conducted at approximately monthly intervals. Beginning in 1984, quarterly cruises occupy a standard suite of 66 stations in summer and autumn, with additional coverage in central California waters in spring (Fig. 1). Samples were preserved in sodium borate-buffered 5% formalin (Kramer *et al.* 1972; Ohman and Smith 1995).

Due to strong diel vertical migration behaviors and daytime avoidance responses of adult euphausiids (Brinton 1967), only night time net tows -- defined between about an hour after sunset and an hour before sunrise -- were used in the plankton sample analysis. A Folsom plankton splitter was used to subsample. Samples were enumerated until at least 200 individuals or 1/8 of the sample was identified. Counts were then converted into individuals 1000 m^{-3} using the volume of water filtered. Enumerations were converted into mg carbon biomass m^{-3} using the equation from Ross (1982) and the median size within life history phase for each species (Brinton *et al.* 2000). Yearly mg carbon biomass m^{-3} was then converted to anomalies by subtracting the mean value of the timeseries from the value of each year. To evaluate the subregional distribution of euphuausiids within the southern sector of the California Current system, the CalCOFI grid (Fig. 1) was separated into north (lines 76.7 to 83.3) and south (lines 86.7 to 93.3), and inshore (stations 26.4 to 60) and offshore (stations 70 to 120) regions.

3.3.2 Southern Vancouver Island euphausiid collection and enumeration

To assess available prey off of British Columbia, Fisheries and Oceans, Canada provided data from the Southern Vancouver Island time series (M. Galbraith, pers. commun.). Detailed methods are described in Mackas *et al.* (2001). Briefly, vertically integrated bongo tows were performed during four or five seasonally spaced surveys each year from 1985 to the present. A 0.25 m^2 mouth area bongo net fitted with 230 µm black nylon mesh and a TSK flowmeter was used for almost all tows. To maintain sample size both day and night tows were collected and used in analysis, with a correction factor applied to reconcile the difference in capture efficiency. Subsamples were enumerated to species and stage with the sample fraction adjusted so that 30-50 individuals were counted within each major zooplankton taxon. Local abundances were converted to dry weight biomass estimates for summed stages within species, then averaged and summed to produce regional averages of biomass. Within-sampling-period averages were converted into log-scale anomalies averaged within each year.

3.3.3 Data sources

Data were compiled from several sources over a hierarchy of spatial scales. On the largest scale considered, that of the North Pacific Ocean Basin, data on euphausiid distributions are included from Brinton (1962) and Brinton *et al*. (2000). Basin scale blue whale distributions are from Gilpatrick and Perryman (2008) and sources therein, and McDonald *et al.* (2006). On the scale of the California Current System (CCS), data were obtained from the Brinton and Townsend Euphausiid Database (http://oceaninformatics.ucsd.edu/euphausiid/) for summer CalCOFI cruises in years when Central California, Southern California, and Baja California were all sampled. Station averages are included if they were analyzed for at least 2 of the 5 years of available data (1958, 1968, 1969, 1978, and 1984). The CCS blue whale distribution was

obtained from the systematic visual surveys of Calambokidis and Barlow (2004) from 1991-1996. Data from just the Southern California sector of the CalCOFI surveys from summer cruises between 2007 and 2016 were used as a regional scale. The euphausiid abundances were averaged over all stations analyzed within a quadrant and the mean taken over all years for that quadrant. Blue whale survey data at the regional scale came from the same CalCOFI cruises as the euphausiid data (A. Debitch and B. Thayer, pers. commun., http://oceaninformatics.ucsd.edu/datazoo/catalogs/ccelter/datasets). We calculated the blue whale encounter rate for each quadrant by dividing the total number of whales observed by the survey effort in km within each quadrant. At the local scale, areas of reliably high blue whale presence (blue whale "hotspots") were identified from opportunistic whale watching data (M. Bissell and S. Bingham, per commun.). For the nearest representative CalCOFI station to each hotspot, the mean euphausiid abundances were calculated from enumerated night tows from 1951-2016.

3.3.4 Statistical analysis

Sub-regional euphausiid abundances and blue whale encounter rates were compared using a Wilcoxon Rank Sum test in R vers. 3.1.2 (R Core Team, 2014). Spring and summer euphausiid abundances were compared using linear regressions in SigmaPlot vers. 10.0 (Systat Software, San Jose, CA). We compared the same life history stages of the same species from the same year with one another. We also compared the adult summer abundances with the juvenile abundances from the spring of the same year to determine whether the maturing cohort could explain the adult abundances. To determine whether there was a temporal change in abundances, we compared the combined adult and juvenile biomass of each species before 1996 and after 1997 using a Wilcoxon rank-sum test in R vers. 3.1.2 (R Core Team, 2014).

3.4 Results

3.4.1 Basin scale distributions

On the scale of the North Pacific Ocean basin, the two primary prey species have different distributions (Fig. 2, Brinton 1962; Brinton *et al.* 2000). *Thysanoessa spinifera* (Fig. 2A) is confined to the eastern side of the basin. The westernmost edge of the *T. spinifera* habitat is approximately 170°W along the Aleutian Islands north of 50°N. The range extends latitudinaly from the Gulf of Alaska in the north to 25°N to the south along Baja California. The highest *T. spinifera* densities occur near the coast offshore of Oregon and in the Southern California Bight. *Euphausia pacifica*, by contrast, spans the entire North Pacific Ocean Basin from the Sea of Japan to the west coast of North America. Along the North American west coast, *E. pacifica* occupies the same latitudinal range as *T. spinifera* from the Gulf of Alaska to 25°N along Baja California. *E. pacifica* peak densities are off Point Conception, California, several places in the subarctic Pacific, and off the northern edge of Japan. *E. pacifica* occurs in higher average densities than *T. spinifera*.

Like *E. pacifica*, blue whales occupy the entire North Pacific Basin, from the Sea of Japan to the west coast of North America (Fig. 3A, Gilpatrick and Perryman 2008). The whales appear to occur in the highest densities near the coast, but this may be due to sampling bias because these observations are from shore-based fishery and research sources. However, there are thought to be two separate populations of blue whales in the North Pacific: one occupying the central North Pacific and another in the eastern North Pacific, with some spatial overlap in the Gulf of Alaska (Fig. 3B, McDonald *et al.* 2006). These two populations have been suggested from body morphology (Gilpatrick and Perryman 2008) and song type (Stafford *et al.* 2001; McDonald *et al.* 2006). The eastern North Pacific population migrates from warmer waters near

Central America and Mexico to summer feeding grounds along the west coast of North America (McDonald *et al.* 2006). The habitat of the central North Pacific population extends over much of the *E. pacifica* distribution, while the eastern North Pacific population occupies a more limited region, though not as limited as the range of *T. spinifera*. The central population must either consume a higher proportion of *E. pacifica* or have a different primary prey species altogether because their distribution does not overlap with that of *T. spinifera*.

3.4.2 California Current System scale distributions

The California Current System (CCS) contains much of the habitat of the eastern North Pacific blue whale population. Similar to the basin scale, *T. spinifera* is much less abundant overall than *E. pacifica* on the scale of the CCS (Fig. 4). The highest *T. spinifera* abundances are inshore off California, followed by California offshore, and the lowest abundances are offshore of Baja California (Fig. 4A). *E. pacifica* occurs throughout almost the entire sampled area. The densities of *E. pacifica* are not significantly different between inshore and offshore of California, but are significantly lower off Baja California.

The distribution of blue whales appears to be most concentrated near the Southern California Bight and around Point Conception (Fig. 5, Calambokidis and Barlow 2004). Calambokidis and Barlow (2004) found blue whale density to be 4.94 whales 1000 km^{-2} in the California Inshore stratum, 1.23 whales 1000 km^{-2} in the California Offshore stratum, and 1.06 whales 1000 km^{-2} in the Baja stratum. The descending abundance of blue whales from inshore to offshore California matches the abundance pattern of *T. spinifera*. The blue whales sighted near southern Baja California may have remained on wintering grounds instead of following food resources north (Calambokidis and Barlow 2004; McDonald *et al.* 2006).

3.4.3 Regional scale distributions

We have divided the Southern California CalCOFI grid into four quadrants: north offshore, north inshore, south offshore, and south inshore. Euphausiid distributions are presented as the mean abundance within each quadrant, averaged over all the stations within each year, then averaged over all years from 2007-2016 (Fig 6). *T. spinifera* was more abundant in the northern inshore quadrant than the other three ($p < 0.05$, Fig. 6A). *E. pacifica* was more abundant in the north offshore, north inshore, and south inshore quadrants than in the south offshore quadrant ($p < 0.05$, Fig. 6B).

The distribution of blue whales is presented as the mean encounter rate standardized by the effort in km within each quadrant (Fig. 7A) along with the locations of all individual or groups of whales observed (Fig. 7B) from summer CalCOFI cruises between 2007-2016. The encounter rate for blue whales was higher in the south inshore quadrant compared to the other three ($p < 0.05$). Blue whale encounter rate and *T. spinifera* abundance were each significantly elevated in a single inshore quadrant, but blue whales peaked in the south and *T. spinifera* peaked in the north. The trio of quadrants where *E. pacifica* were at their highest abundance did include the quadrant with the blue whale peak, but the lack of blue whale encounters in two of those quadrants makes it unlikely that the euphausiids are the reason for the increased whale presence. An attempt at constructing a generalized additive model (GAM) to explain blue whale encounter rate by quadrant utilizing prey euphausiid abundance as a potential explanatory variable in addition to environmental variables including water temperature and salinity failed to indicate ecologically sensible relationships. At the regional scale, euphausiid abundance and blue whale encounters are not related.

3.4.4 Local scale distributions

While the eastern North Pacific population of blue whales appears to co-occur with primary prey euphausiid *T. spinifera* on the scale of the North Pacific basin, the distribution of these whales does not appear to mimic their prey distribution at the CCS or regional scales. To test for blue whale-euphausiid co-occurrence at the local scale, from commercial whale watching data, we identified three places of recurrently elevated blue whale concentration. These "hotspots" are north of Santa Cruz Island, offshore of San Pedro, CA, and Nine Mile Bank (Fig. 8). For each hotspot, we enumerated the prey euphausiids at the nearest representative CalCOFI station (Fig. 9). At all three blue whale hotspots, the abundance of less preferred prey *E. pacifica* was much greater than the abundance of *T. spinifera* adults and juveniles combined ($p<0.05$, Kruskal-Wallis). At the identified blue whale hotspots, primary prey euphausiids were not especially abundant and were not more abundant than secondary prey.

3.4.5 Euphausiid spring/summer abundance co-variation

The sequence of maxima and minima of abundance were similar for *Euphausia pacifica* adults (Fig. 10A), *E. pacifica* juveniles (Fig. 10B), *Thysanoessa spinifera* adults (Fig. 10C), and *T. spinifera* juveniles (Fig. 10D) in both spring and summer. There are minima corresponding to the strong El Niños of 1957-1958, 1997-1998, and 2015-2016. Maxima correspond to the La Niña conditions of 1955-1956 and 1999-2000. The amplitudes of variation were similar between spring and summer, but abundances were usually higher in summer than spring for both stages of both species.

Linear regressions were significant ($p \leq 0.05$) between spring and summer abundances of the same year for *E. pacifica* adults (Fig. 11A), *E. pacifica* juveniles (Fig. 11C), and *T. spinifera* adults (Fig. 11B). Only *T. spinifera* juveniles did not show a significant relationship between

spring abundance and the following summer abundance ($p > 0.05$). Both *E. pacifica* and *T. spinifera* had a significant relationship between spring juvenile abundance and the abundance of adults the following summer ($p \leq 0.05$, Fig. 11 E, F).

3.4.6 Biomass anomaly trend

Biomass anomalies for adults and juveniles combined of *E. pacifica* and *T. spinifera* in spring and summer showed higher values post-1996 in both Southern California and Southern Vancouver Island (Fig. 12, $p \leq 0.05$, Wilcoxon). In spring, both *E. pacifica* and *T. spinifera* had significantly more positive anomalies after 1997 in both Southern California and Southern Vancouver Island ($p \leq 0.05$, Fig. 12A-D). In summer, *T. spinifera* had significantly more positive anomalies after 1997 off Southern California ($p < 0.05$, Fig. 12G), and both *E. pacifica* and *T. spinifera* had significantly more positive anomalies after 1997 off of Southern Vancouver Island ($p < 0.001$, Fig 12 F, H). Only *E. pacifica* off Southern California in summer showed no significant difference in biomass anomalies before and after 1997 ($p < 0.05$, Fig. 12E).

3.5 Discussion

3.5.1 Scales of Co-variation

One of the goals of ecology is to determine the mechanism underlying patterns, but patterns are influenced by the observation scales (Levin 1992). While we have demonstrated co-location between blue whales and their preferred prey species, *T. spinifera*, at the basin and California Current System (CCS) scales, there is no apparent spatial relationship between the two at the regional or local scales. Pattern at the broadest scales should result from the aggregation of the behaviors of smaller units (Levin 1992). The lack of relationship between the distributions

of blue whales and *T. spinifera* (or *E. pacifica*) at sub-CCS scales indicates that the mechanism of interaction between the two taxa has not been measured at the scale at which it occurs.

Despite the benefit of their long-term occupation, the CalCOFI stations appear to be spaced too far apart to capture the necessary details of euphausiid distributions at scales relevant to blue whales. We suggest that, due to the patchiness of both the whales (Soldevilla *et al.* 2006; Barlow and Forney 2007) and the euphausiids (Décima *et al.* 2010), a smaller scale and more synoptic sampling strategy is necessary. This will likely involve an exploration of the ambit at which the whales locate their prey as well as the fine-scale structure of euphausiid patches and the species and size distributions within.

The mean euphausiid abundances within our sub-regions likely obscure smaller scale variability. Gomez-Gutierrez *et al*. (2005) found significant differences in the distribution of *T. spinifera* and *E. pacifica* along the Newport Line off central Oregon, the entirety of which is closer to the coast than the westward limit of our "inshore" quadrants. They found *T. spinifera* adults and juveniles to be associated with stations near the shelf break (~28-56 km from shore), while *E. pacifica* was associated with stations offshore of the shelf break (~65-110 km from shore). On even smaller scales, spatially distinct euphausiid schools can differ in species composition, size distribution, and density (Schoenherr 1991; Croll *et al.* 2005). Blue whales may concentrate their foraging on certain types of euphausiid patches for reasons that are not apparent at the current scales of measurement.

3.5.2 Why did the blue whales head north?

Blue whales may have redistributed their population between Californian and British Columbian waters beginning around 1997 (Barlow and Forney 2007; Calambokidis *et al.* 2009), but it was likely not due to a prolonged decrease in available prey off California. Instead of a

decreased availability of *T. spinifera* and *E. pacifica* in the south, we found a system-wide increase in biomass anomalies in both spring and summer. The only exception to the positive trend was southern California *E. pacifica* in the summer, which showed no significant difference before and after 1997.

Variations in the abundance and distribution of species in the ocean are often related to climate variability. Two main climate perturbations that could affect California Current System euphausiids and blue whales are the Pacific Decadal Oscillation (PDO) (Mantua and Hare 2002) and the El Niño Southern Oscillation (ENSO) (Bograd and Lynn 2001). *E. pacifica* has a weak but significant negative association with the PDO in Southern California spring, while *T. spinifera* has no significant relationship in Southern California spring (Brinton and Townsend 2003). In the late 1990's, the PDO shifted to a cool phase after remaining warm for much of the preceding decade, which would have favored the availability of *E. pacifica* for blue whale feeding off of Southern California. Both euphausiid species showed negative biomass anomalies off Southern California during the 1998 El Niño, but recovered during the 1999 La Niña and mostly positive anomalies until the 2014 "warm blob" (Leising *et al.* 2015) and 2015-2016 El Niño (McClatchie *et al.* 2016) events.

3.6 Conclusions

Eastern North Pacific blue whales are co-located with their primary prey species *Thysanoessa spinifera* on the scales of the North Pacific Ocean basin and California Current System, but not at the regional or local hotspot scales. A smaller scale, defined by the daily ambit of the predators, will need to be invoked to understand the spatial relationship between blue whale predators and their preferred euphausiid prey. The abundances of *Euphausia pacifica*

adults and juveniles and *T. spinifera* adults vary concurrently between spring and summer in the southern sector of the California Current System. Despite the renewed presence of blue whales farther north off British Columbia and an apparent decline in the California feeding population, reduced prey availability in the southern sector of the California Current System was not the cause. There was instead an increase in biomass anomalies off both Southern California and Southern Vancouver Island after the whales began their move north in 1997.

3.7 Acknowledgements

We dedicate this paper to Ed Brinton and Annie Townsend, without whose years of dedication to the biogeography and taxonomy of the euphausiids of the CCS the present work would not have been possible. We particularly thank Annie Townsend for a life-time of dedication and passing down her invaluable taxonomic expertise to us so that this work and time-series could be carried forward into the next generation. We thank the Ohman Lab's efforts to maintain the Cooperative Zooplankton Dataspace: Brinton Townsend Euphausiid Database for the generation of continued CalCOFI euphausiid enumeration data and the Pelagic Invertebrate Collection for maintaining the samples and providing research support. We thank the Pelagic Invertebrate Collection of Scripps Institution of Oceanography for use of samples, lab space, and equipment. Moira Galbraith of Fisheries and Oceans, Canada (Pacific Region) provided the Southern Vancouver Island biomass anomaly data. We thank Amanda Debitch, Bruce Thayer, and John Hildebrand for providing the CalCOFI marine mammal observations. We also thank the scientists and crew of the CalCOFI program over the years.

Chapter 3 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M. "Scales of co-occurrence of blue whales and their euphausiid prey in the Northeastern

Pacific." It is presented as part of this dissertation with the acknowledgement of the study coauthor Linsey M. Sala. The dissertation author was the primary investigator and is the primary author of this material.

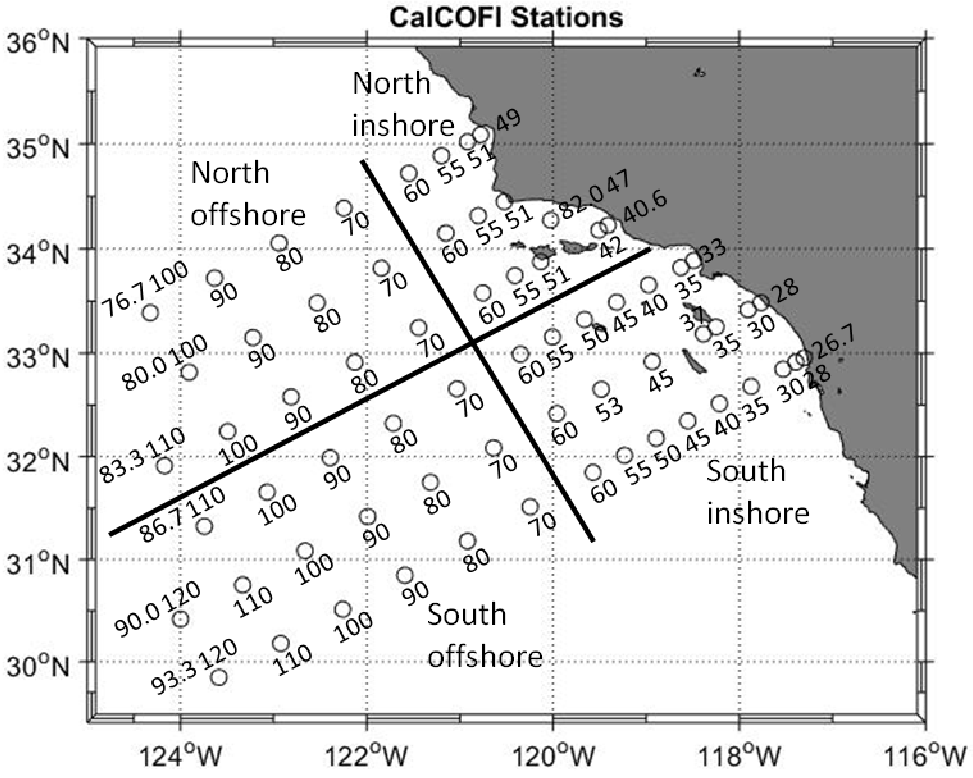


Figure 3.1: CalCOFI station positions and analytical area quadrant designations.

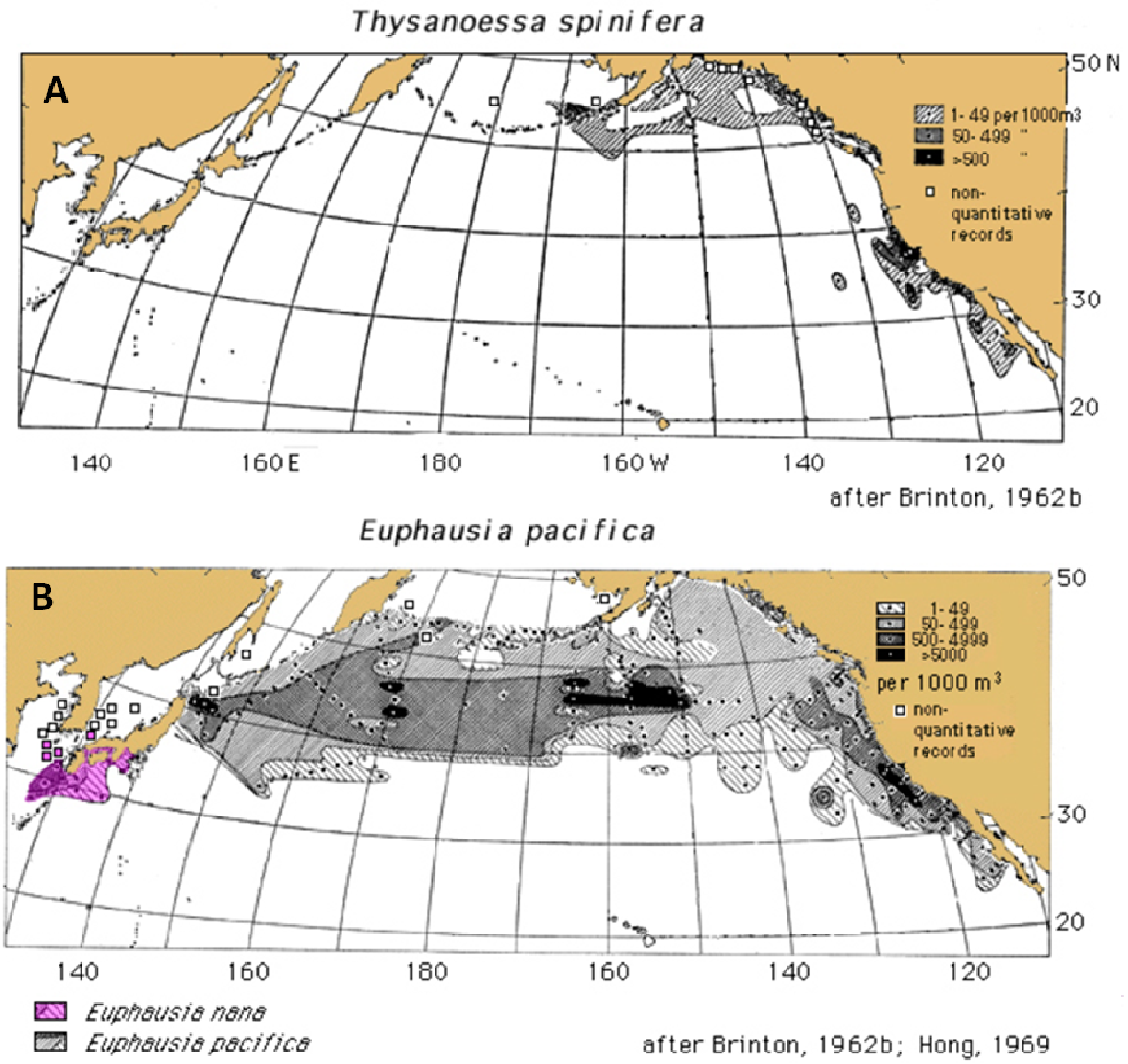


Figure 3.2: The biogeographic distributions of two dominant prey euphausiids for blue whales: (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica* (from Brinton *et al*. 2000).

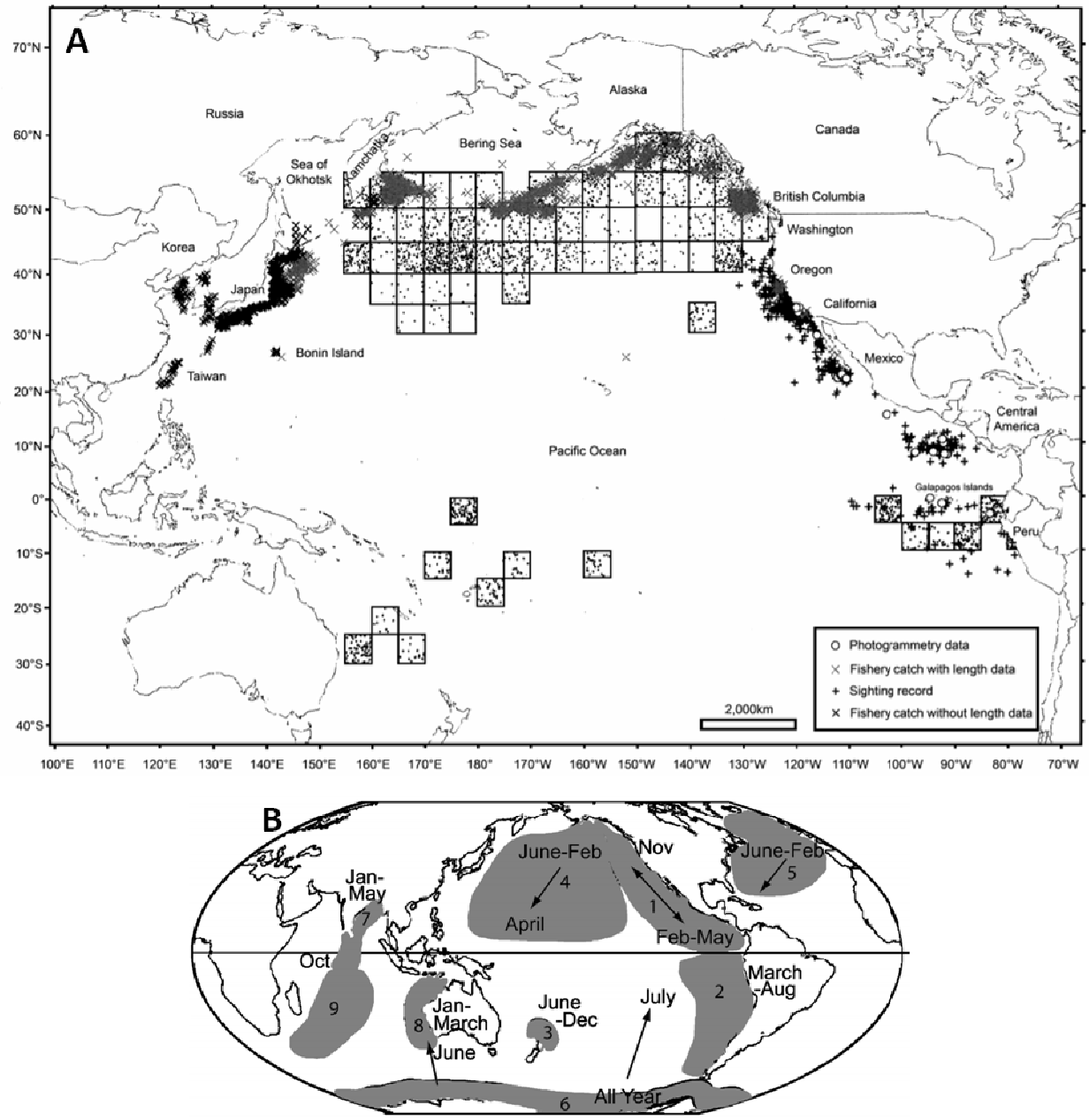


Figure 3.3: (A) Pacific basin distribution of blue whales (from Gilpatrick and Perryman 2008). (B) Residence and population divisions of blue whales as suggested from song types. Type 1 is represents the Northeast Pacific region (from McDonald *et al*. 2006).

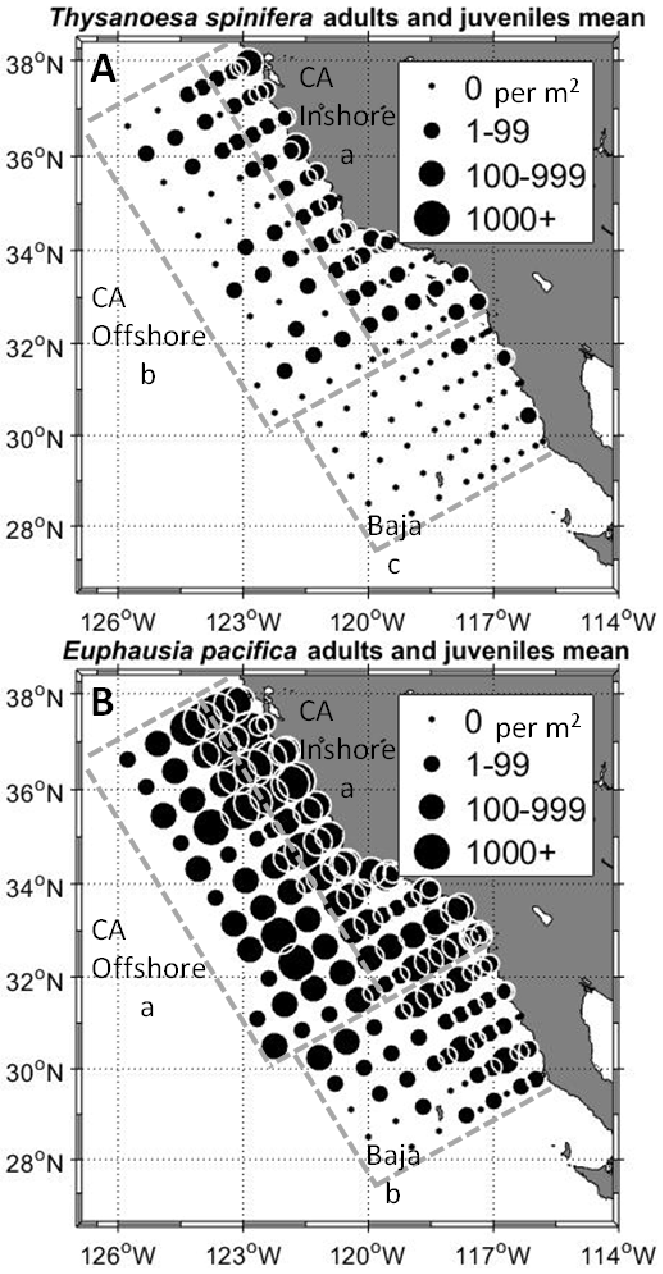


Figure 3.4: The California Current System distributions of two dominant prey euphausiids for blue whales: (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica*. Symbol size represents mean abundance. Gray dashed line separates California Inshore, California Offshore, and Baja California analytical strata. Statistically significant groups denoted with a,b,c, $p<0.01$.

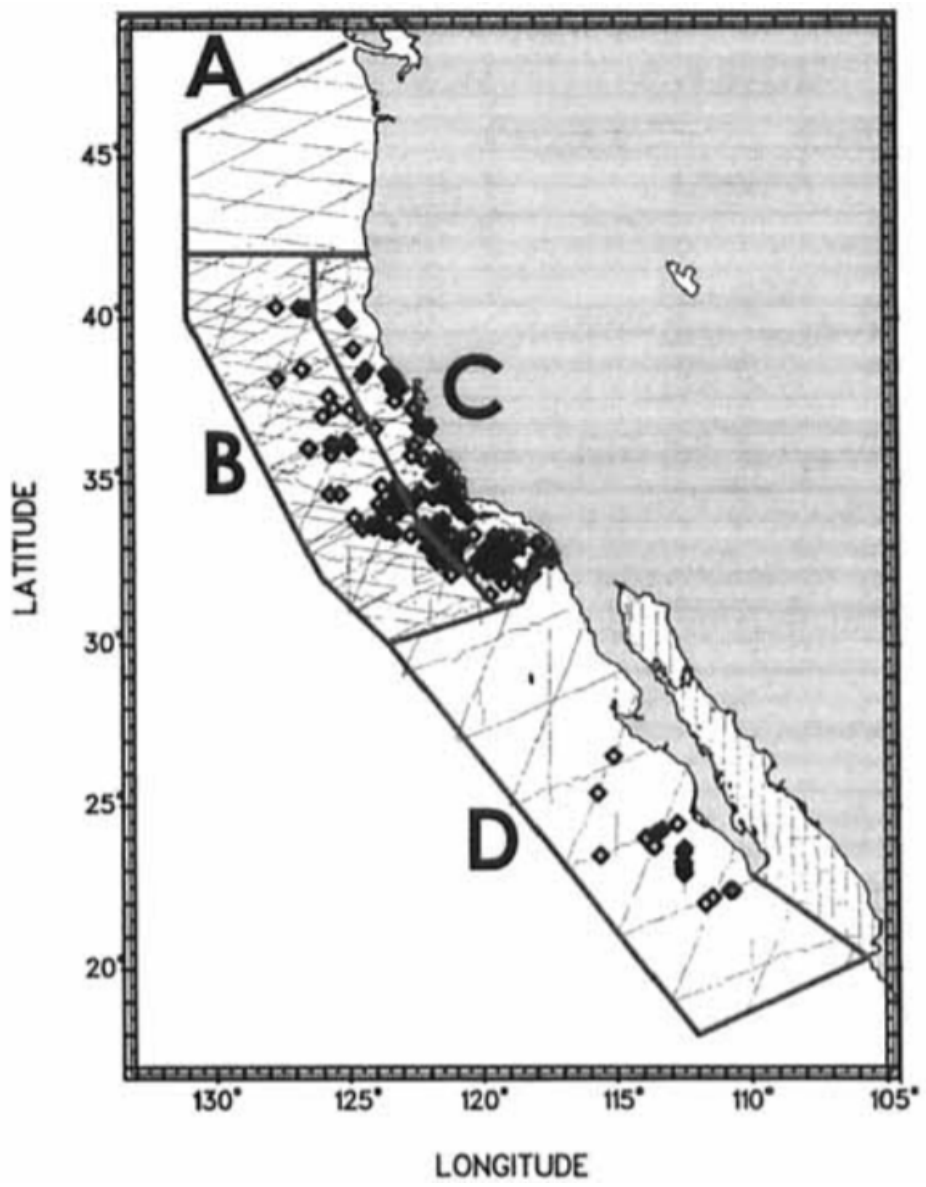


Figure 3.5: The California Current System distributions of blue whales from systematic line transect surveys (from Calambokidis and Barlow 2004). Light grey lines indicate tracklines. The survey was stratified into : (A) Oregon and Washington, (B) California Offshore, (C) California Inshore, (D) Baja California.

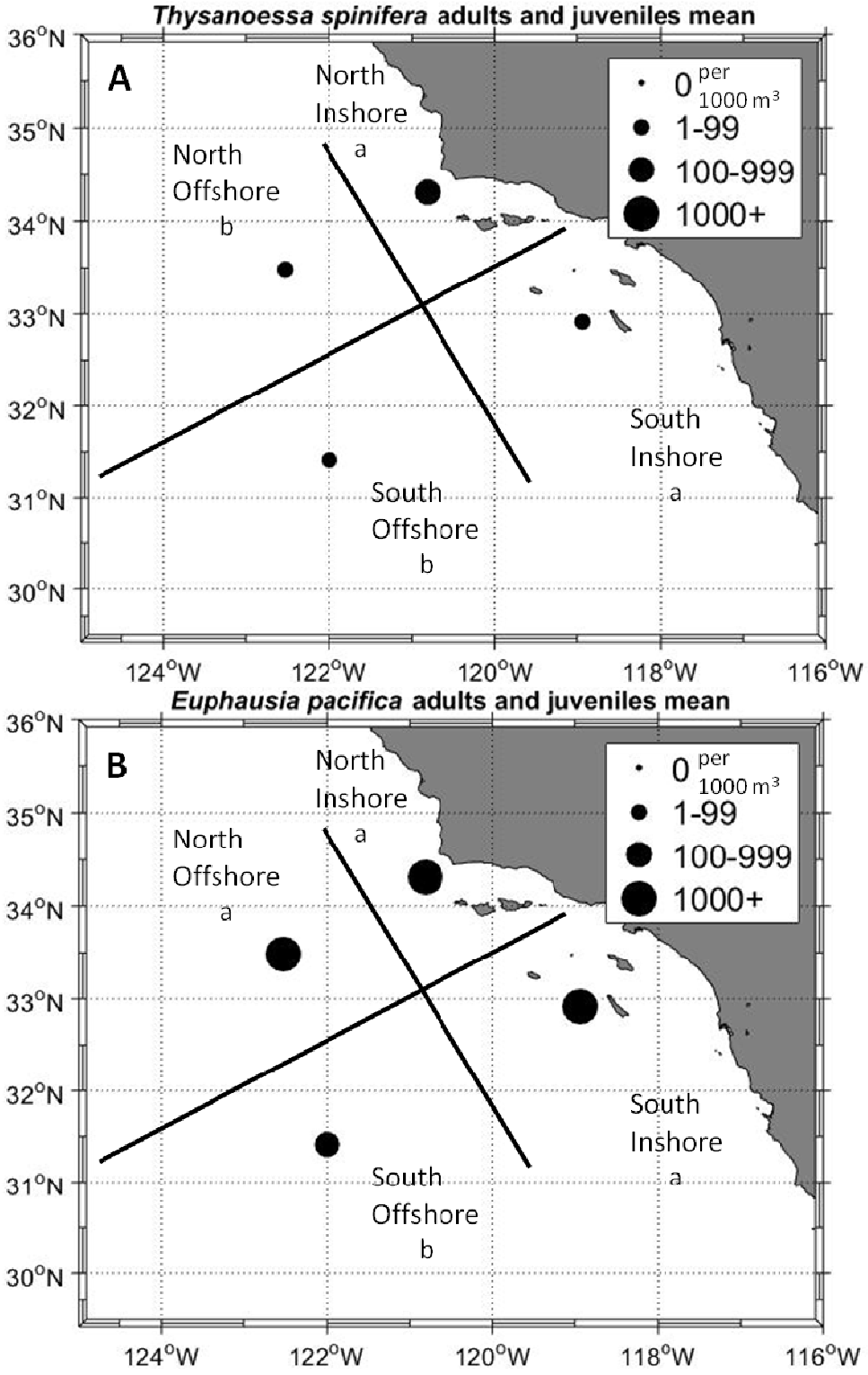


Figure 3.6: Abundance mean (size of point) +95% (size of ring) of (A) Thysanoessa spinifera and (B) Euphausia pacifica in zones within the southern sector of the California Current System covered by the CalCOFI sampling grid from 2007-2016. North: lines 76.7 to 83.3; South lines 86.7 to 93.3; Inshore stations 26.4 to 60; Offshore stations 70 to 120. Statistically significant groups denoted with a,b, $p<0.05$.

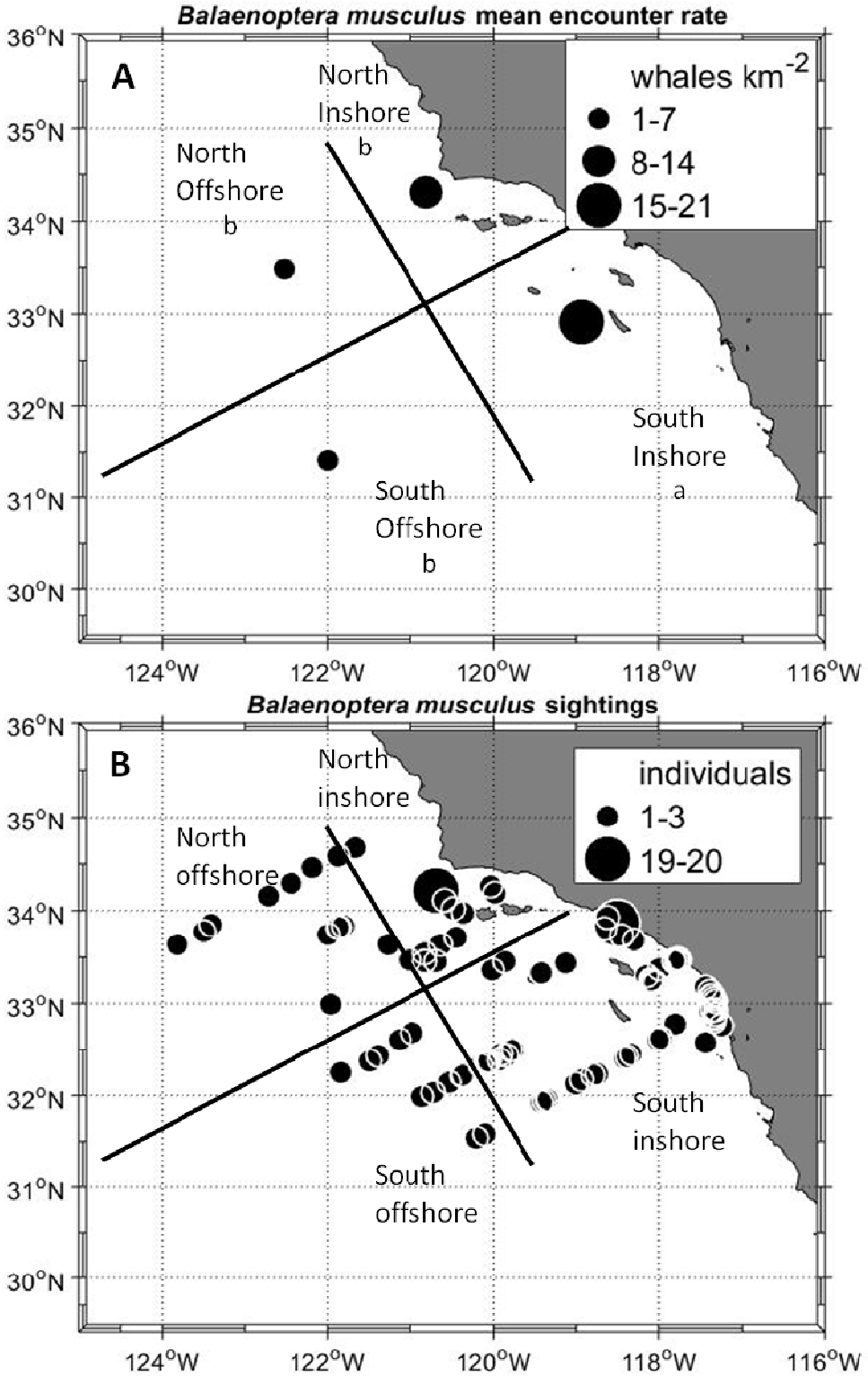


Figure 3.7: (A) Mean (size of point) +95% (size of ring) number of whales encountered per km survey effort in each quadrant. Statistically significant groups denoted with a,b , $p<0.05$. (B) All individual blue whale sightings from CalCOFI summer surveys 2007-2016.

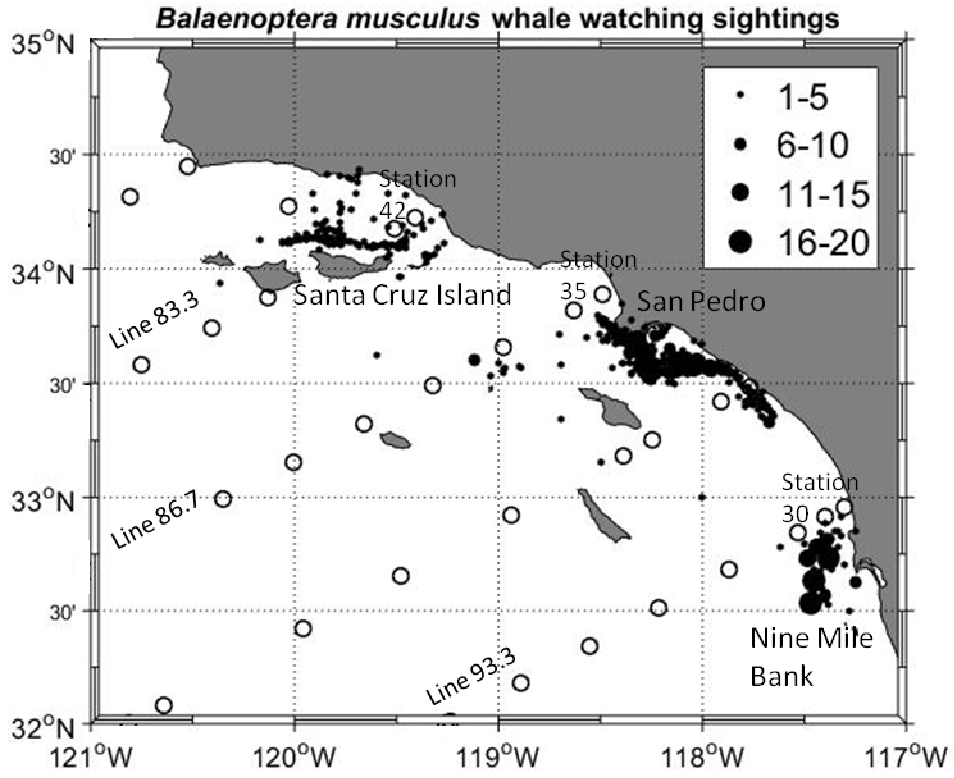


Figure 3.8: The distribution of blue whales in the Southern California Bight from commercial whale watching boat records. Nearest CalCOFI station to each aggregation center is marked with an open circle.

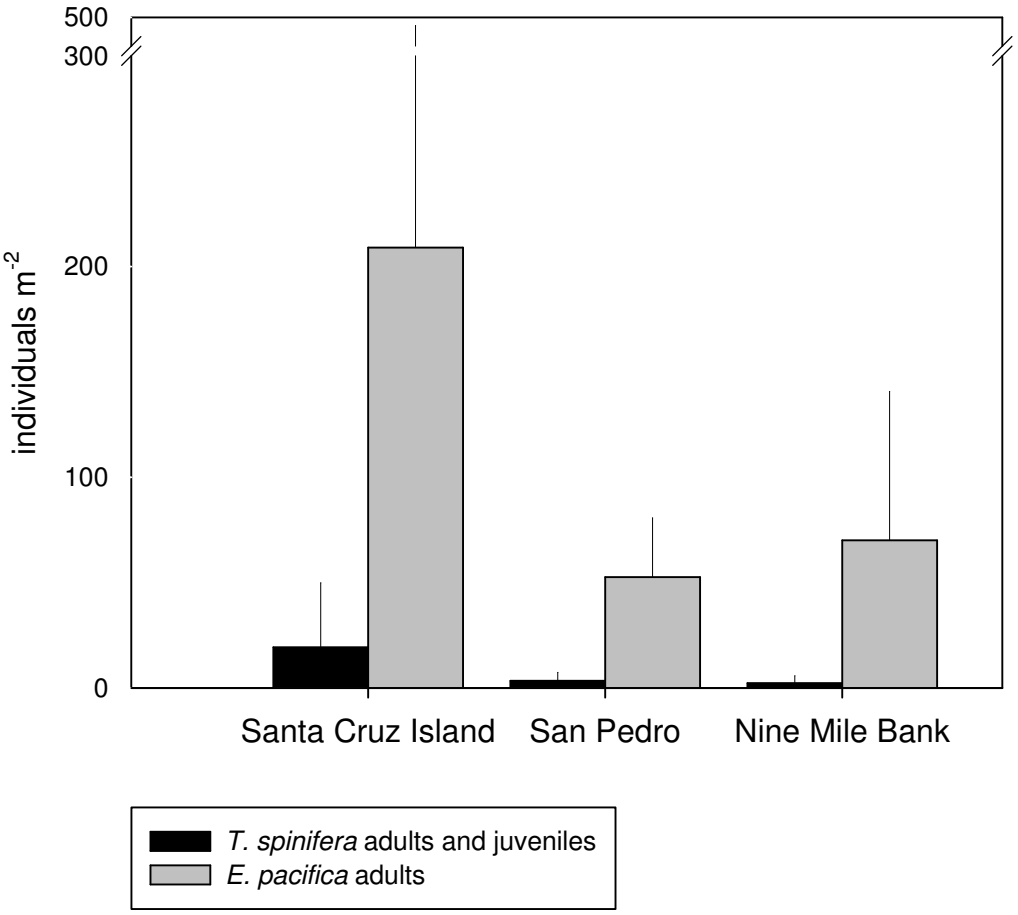


Figure 3.9: The average abundances of dominant blue whale prey euphausiid species *Thysanoessa spinifera* and *Euphausia pacifica* near local centers of elevated blue whale concentration.

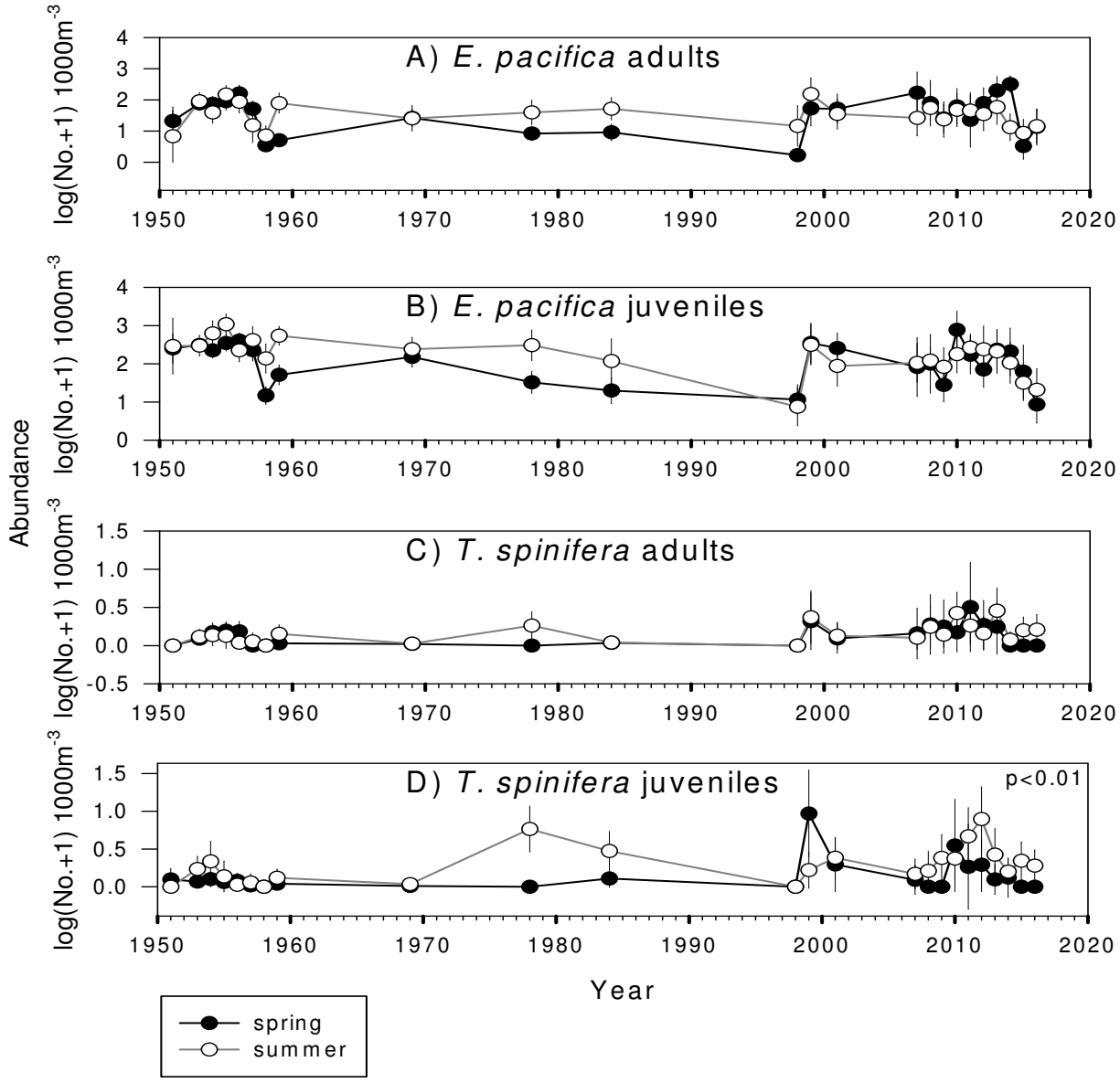
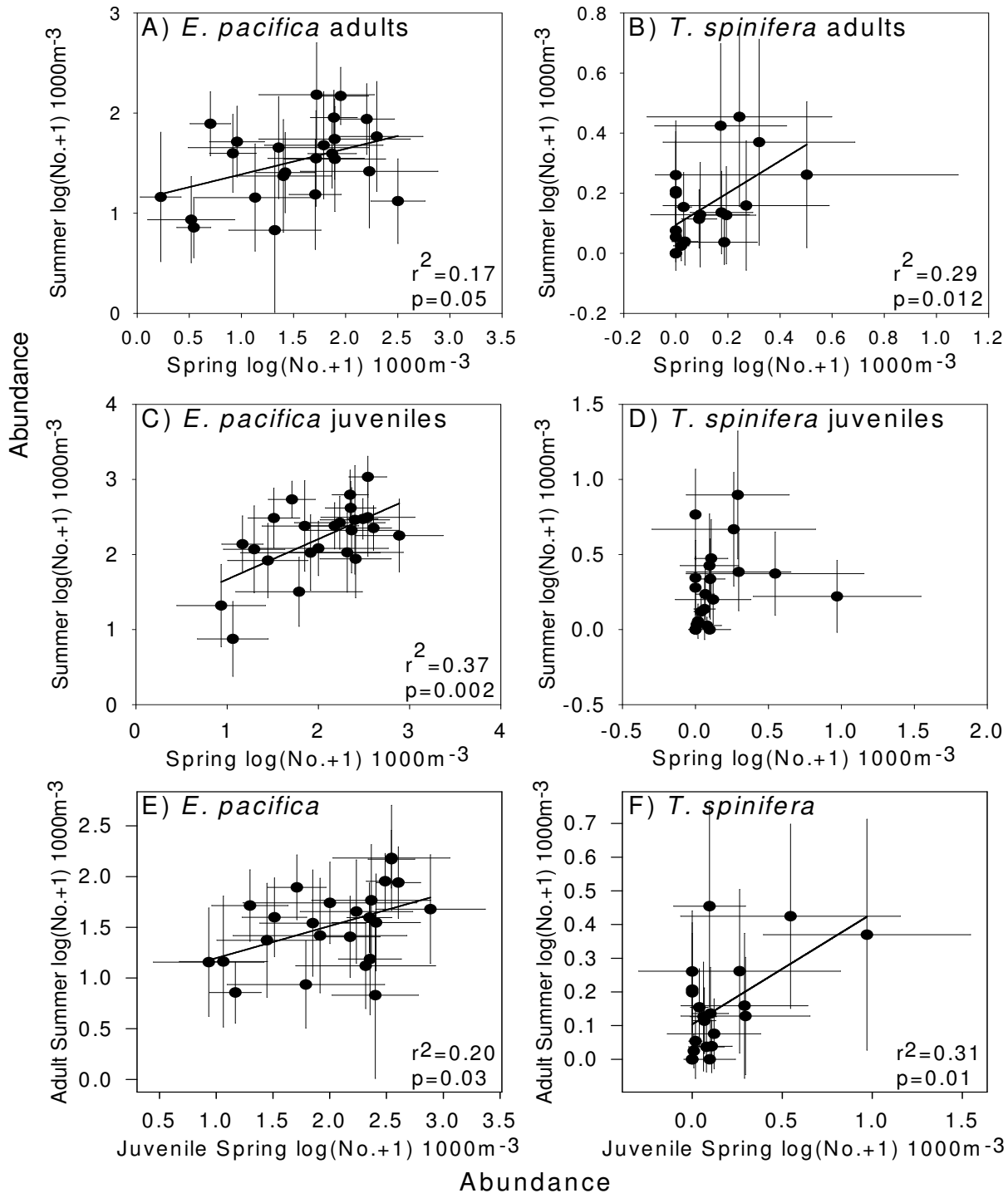
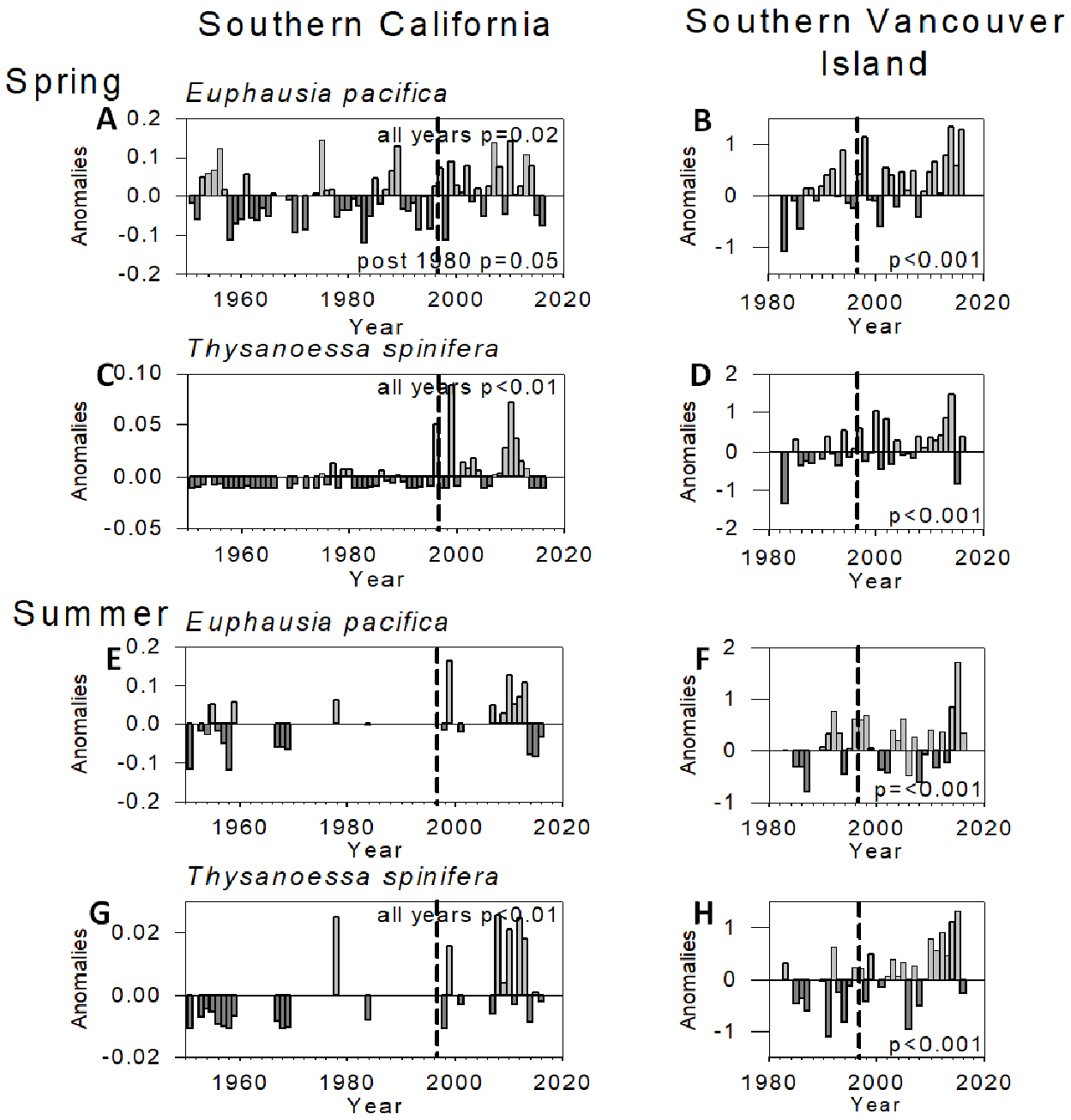


Figure 3.10: Comparisons of summer and spring abundances in Southern California of two dominant prey euphausiids for blue whales.



3.11: Linear regressions between summer and pre-summer abundances of the same life history phase (A-D), and between spring juveniles and adults the following summer (E,F).



3.12: Biomass anomalies of adult and juveniles of *Euphausia pacifica* and *Thysanoessa spinifera* from Southern California (A,C) spring and (E,G) summer, and Southern Vancouver Island (B,D) spring and (F,H) summer. Dashed line marks the reappearance of blue whales off of British Columbia in 1997. Anomalies calculated as the mean of the timeseries subtracted from each year's value.

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CHAPTER 4 The euphausiid prey field for baleen whales around a steep bathymetric feature in the southern California Current System

4.1 Abstract

Euphausiids are important prey for many marine organisms and often occur in patchy aggregations. Euphausiid predators, such as blue, fin, and humpback whales, may be drawn into observable "hot spots" by the distribution of these aggregations. We investigated a blue whale hot spot called Nine Mile Bank near San Diego, California, defined by an area of steep bathymetry, to determine whether the frequent whale sightings in that locality can be explained by the distribution of euphausiids across the bank. The preferred prey euphausiid *Thysanoessa spinifera* was consistently less abundant offshore of the bank that on or inshore of it. In contrast, *Euphausia pacifica,* a minor secondary prey species, was abundant throughout the study area. A series of whale visual surveys in 2015 found a higher whale encounter rate associated with higher *T. spinifera* abundance, suggesting that the whales may follow the movements of specific prey species, often in association with bathymetric features.

4.2 Introduction

The three most frequently encountered baleen whales in the southern sector of the California Current System (CCS) are blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and humpback (*Megaptera norvegica*) whales (Campbell *et al.* 2015). The three species differ in their seasonal timing of appearance. Humpback and fin whales are present year round and fin whale density peaks in summer (Campbell *et al.* 2015). The density of blue whales also peaks in summer and decreases in fall, but blue whales rare or absent from the southern CCS in winter and spring (Campbell *et al.* 2015). Blue whales migrate into the area to feed in summer and return to higher latitudes during the winter months (Burtenshaw *et al.* 2004; McDonald *et al.* 2006; Bailey *et al.* 2009). Blue, fin, and humpback whales all lunge feed, a

behavior where food is captured in discrete events instead of continuous filtration (Goldbogen *et al.* 2012; Kawamura 1980). Lunge feeding can occur at the surface or at depth. The average dive depth off the California coast is 190 m for blue whales, 170 m for fin whales, and 189 m for humpback whales (Goldbogen *et al.* 2012).

Lunge feeding baleen whales require exceptionally high prey densities to offset their high energetic costs (Goldbogen *et al.* 2011), far above the average densities measured over large spatial scales (Croll *et al.* 2005). In the southern sector of the California Current, blue, fin, and humpback whales appear from whale watching data to associate with steep bathymetric features (Bissell 2013), although whale watching data report only positive records and can be further biased by recurrent trips to the same sites. The association of whales with abrupt bathymetry has, however, also been reported in other locations. Blue whales sighted in Monterey Bay between 1992 and 1996 were concentrated along the edge of the Monterey submarine canyon (Croll *et al.* 2005). In 1995 and 1996, Fiedler *et al.* (1998) found abundant blue whales to the north of San Miguel and Santa Rosa Islands in the Channel Islands. Yen *et al.* (2004) found humpback whales to be most numerous near the continental slope (identified by the 1000 m isobath) off central California. The distribution of Antarctic humpback and minke whales is related to bathymetric slope and distance from the ice edge (Friedlaender *et al.* 2006). North Atlantic blue whales forage along the slope of the Laurentian Channel, the continental shelf edge, some shelf habitats, and may utilize the New England Seamount chain (Lesage *et al.* 2017). Humpback and minke whales were associated with Platts Bank compared to surrounding waters in the western Gulf of Maine (Stevick *et al.* 2008).

The likely explanation for this bathymetric association is increased productivity or aggregation of prey around abrupt features. Friedlaender *et al*. (2006) found the distribution of

humpback and minke whales in Western Antarctic Peninsula shelf waters to be strongly linked to euphausiid abundance (inferred from acoustic backscatter) and two features thought to aggregate prey: distance from the ice edge and bathymetric slope. In the St. Lawrence Estuary, Cotté and Simard (2005) found euphausiids aggregated by the interaction of sloped bathymetry, semidiurnal tidal currents, and euphausiid negative-phototactic swimming behavior. Fin whales around the Davidson Seamount off central California were above and to the west of the seamount, where euphausiid abundance was higher than other surveyed areas (Newton and DeVogelaere 2013). Euphausiids have demonstrated elevated abundances along ocean circulation features such as fronts (Lara-Lopez *et al.* 2012; Ohman *et al.* 2012) and physical features such as the Antarctic ice edge (Murase *et al.* 2002), the continental slope (Fiedler *et al.* 1998; Murase *et al*. 2002), and the edges of submarine canyons (Schoenherr 1991; Croll *et al.* 2005). Euphausiid aggregation where upwelling takes place along sloping topography may help maintain them in regions with high potential productivity (Cotté and Simard 2005). Potential mechanisms for the formation of zooplankton aggregations around abrupt topography are reviewed by Genin (2004) and include upwelling-related increased productivity, physical blockage of zooplankton descent, behavioral depth retention by swimming against upwelling water flow, and enhanced horizontal flux. These physical features and oceanographic processes may also help whales locate dense prey aggregations (Friedlaender *et al.* 2006).

Blue whales are typically obligate predators on euphausiids (Schoenherr 1991; Croll *et al.* 2005; Nickels *et al.* in prep), while fin and humpback whales have more dietary diversity and also consume fish (Watkins and Schevill 1979; Kieckhefer 1992; Tershy *et al.* 1993; Fossette *et al.* 2017). Blue whales in the central California region feed mostly on *Thysanoessa spinifera* and to a lesser extent *Euphausia pacifica* to a lower size limit of approximately 10 mm (Croll *et al.*

1998; Nickels *et al.* in prep). Humpback whales also appear to target mature euphausiids (Kieckhefer 1992; Szabo 2015). Both *T. spinifera* and *E. pacifica* adults can form dense surface aggregations (Brinton 1981; Endo 1984; Smith and Adams 1988), allowing whales to capture more individuals in a single lunge than if the prey were more dispersed (Schoenherr 1991; Fiedler *et al.* 1998). However, the whales' restricted choice of prey items limits the food resources available to baleen whales and may serve to structure whale distributions.

This study addresses two related questions: (1) Are baleen whales (blue, humpback, and fin) in the southern sector of the California Current associated with steep bathymetric features? (2) Are prey euphausiids associated with steep bathymetric features, and can they explain the whale distribution? We hypothesized that baleen whales would be found associated with Nine Mile Bank more often than on either side of it. We also hypothesized that large individuals of the primary prey *T. spinifera* would be found associated with the bank more than on either side.

4.3 Methods

The study area is a locally recognized blue whale aggregation center near La Jolla, California, USA, called Nine Mile Bank (NMB, Fig. 1). NMB is situated 9 nautical miles from San Diego, between the San Diego Trough to the west and the Loma Canyon to the east. Here the bank is defined as the region between points where the bathymetry changes abruptly from steep decline to flat, proceeding away from the center of the bank. The region to the east will be referred to as inshore, and to the west as offshore. Sampling was conducted on three successive cruises: 26-31 July 2014 aboard the *R/V New Horizon*, 11-17 June 2015 aboard the *R/V Robert Gordon Sproul*, and 24-25 April 2016 aboard the *R/V Sikuliaq*. The cruises in June and July sampled the euphausiid prey field when blue whales are expected to be present, while April

represents contrasting conditions before the whales arrive for the summer season (Burtenshaw *et al*. 2004; Bissell 2013; Campbell *et al.* 2015). Sampling in all three years included active acoustic methods and bongo net collection. Sampling in 2014 and 2015 also included vertically stratified MOCNESS tows and collection of whale fecal material. A series of repeated whale visual surveys was conducted in 2015. Statistics were performed in R ver. 3.1.2 (R Core Team, 2014), Matlab ver. 2016b (Mathworks, Natick, MA), and SigmaPlot ver. 10.0 (Systat Software, San Jose, CA).

4.3.1 Whale visual survey

In conjunction with the 2015 cruise, ten whale visual surveys were completed from 11 June -31 July 2015, using a standard line-transect protocol (Burnham *et al.* 1980; Barlow and Forney 2007; Buckland *et al.* 2015). Surveys were conducted from a rigid hulled inflatable boat (RHIB) travelling at 10 kts (~5 m s^{-1}) while on effort. Each survey repeated the same tracklines (Fig. 2) and included 3-4 observers, including the boat operator and a dedicated record keeper when personnel allowed. One primary observer on each side of the vessel monitored a 90° field of view from the bow to abeam; sightings were also included when first observed by either the boat operator or record keeper. When a whale was spotted, we went off effort in closing mode to confirm species and group size (Barlow 1997). Survey effort was calculated as distance in km on effort along the trackline. All effort was conducted in sea state conditions of Beaufort 3 or less (average 2.1) during daylight.

Three species of large baleen whale are included in this analysis: blue (*Balaenoptera musculus*), humpback (*Megaptera novaeangliae*), and fin (*Balaenoptera physalus*). Due to small sample size all 10 survey days and 3 whale species are pooled for analysis. Whales for which we could not confirm species identity but were consistent in blow and behavior with large baleen

whales were recorded as "unidentified large whale" and included in the density and encounter rate calculations. Density was estimated using the software Distance 6.2 (Thomas *et al.* 2010). We used the detection track probability (g(0)) of blue whales in an average Beaufort state of 2 estimated by Barlow (2015) of 0.748. The detection function model was selected that minimized the value of the Akaike Information Criterion and maximized the goodness of fit. Some encounters were missing information on the distance and/or angle of the sighting. To correct for this deficiency, the effective strip width was calculated without these sightings, the distances were estimated based on the probability density function, and then density of whales was calculated with the full suite of sightings. To compare regions, we calculated a comparative encounter rate as:

$$\frac{\text{number of sightings} \times \text{average group size}}{\text{length of transect}}$$

Heterogeneity among these encounter rates was then tested with a Kruskal-Wallis nonparametric ANOVA.

4.3.2 Acoustic Backscatter

Acoustic backscatter was measured at 38, 120, and 200 kHz with a hull mounted Simrad EK60 in 2014 on the *R/V New Horizon*, a pole mounted Simrad EK60 in 2015 on the *R/V Robert Gordon Sproul*, and a hull mounted Simrad EK80 in 2016 on the *R/V Sikuliaq*. The echosounders were calibrated before the start of each cruise using the standard sphere method (Foote *et al.* 1987). All frequencies were transmitted simultaneously every 2 s with a 1.024 ms pulse length. Acoustic surveys were conducted between one hour after sunrise and one hour before sunset so that euphausiid distributions would reflect the daytime feeding period of blue

whales (Croll *et al.* 1998; Fiedler *et al.* 1998; Calambokidis *et al.* 2007; Oleson *et al.* 2007). Each survey crossed the bank between 2 and 8 times at ship speeds of 5-8 kts (~2.6-4 m s^{-1}).

Acoustic backscatter was analyzed in Myriax's Echoview 4 software. Background noise was removed following De Robertis and Higginbottom (2007), with a signal-to-noise threshold of 5 dB. Data were thresholded at -70 dB to remove weak scattering. Euphausiid-like backscattering was identified utilizing the empirical multifrequency classification Z-score method and characteristic euphausiid values of De Robertis *et al*. (2010). While the size distribution of euphausiids is smaller at NMB, values from De Robertis *et al*. (2010) were the closest match from the literature and are used as a reasonable approximation in the absence of sufficient direct measurements in this study. Acoustic targets were identified based on the difference in volume backscattering strength (ΔS_v) between frequencies. Values were allowed to vary 2 standard deviations from the mean expected ΔS_v of De Robertis *et al*. (2010). Backscatter was classified as euphausiid-like if $\Delta S_{v,\ 120\text{-}38}$ was between 8 and 19.6 dB, $\Delta S_{v,\ 200\text{-}38}$ was between 10.5 and 22.1 dB, and $\Delta S_{v,\ 200\text{-}120}$ was between -0.5 and 5.1 dB. The Z-score, or normal deviate, was used to estimate confidence in the identification by summarizing the deviations of the observed from expected ΔS_v.

Analysis of concurrent acoustic backscatter and MOCNESS sampling (described below) revealed that the dB differencing failed to distinguish the backscattering caused by euphausiids from that of pelagic red crabs (*Pleuroncodes planpipes*), which first reappeared in this region in 2014 and were abundant in 2015 and 2016. Despite its success in separating *P. planipes* from *N. simplex* off Mexico, the difference in scattering intensity at 120 kHz (Gomez-Gutierrez and Robinson 2006) was also ineffective. To solve this problem, the Echoview 4 school detection module was used to isolate *P. planipes* in masked echograms passed through a 5x5 dilation filter

to make the aggregations more contiguous for detection. Schools must have been greater than -70 dB re 1 m^{-1} for at least 40 m along the track and 20 m vertically. These parameters identified *P. planipes* layers, but not euphausiid layers as determined from the MOCNESS samples. The school detection was then applied to all acoustic echograms. Differentiation was possible during the day, when the two taxa occupied different vertical layers, but not at night when both migrated vertically to the surface and the layers merged.

Further analyses were performed on the 200 kHz echogram with all non-euphausiid-like data removed. We use euphausiid-like backscattering (ELB) as an index of euphausiid density because our limited direct sampling of acoustically detected layers would make biomass calculations questionable. The area backscattering coefficient (s_a) was integrated over the upper 300 m in 500 m segments along the track. The s_a was then compared between regions within each survey using a Kruskal-Wallis test. To evaluate the patchiness of euphausiid-like scattering, we used the modified Bez's index of Decima *et al*. (2010) I_{mod}:

$$I_{mod} = \left[\frac{\sum_i z_i^2}{s(\sum_i z_i)^2}\right] N$$

The volume backscattering coefficient (s_v) was used as an index of density (z). The sampling area (s) was 25 m depth by 500 m distance bins and the number of bins (N) varied by depth or distance included. Vertical patchiness was calculated as I_{mod} for each 500 m wide vertical slice of the echogram, and horizontal patchiness for each 25 m high horizontal slice within a region. This allowed a mean and standard deviation of I_{mod} to be calculated for each region within a survey, as well as for each year of the study. The indexes were then compared using a Kruskal-Wallis test.

4.3.3 Bongo net transects

To assess the distributions of individual euphausiid species with respect to the bank, zooplankton were sampled in a series of bongo net transects on each cruise for summer 2014, 2015, and spring 2016 (Fig. 1). Transects included tows in the inshore, bank, and offshore regions and proceeded in the offshore (westerly) direction, perpendicular to the long axis of the bank. A 71 cm diameter, 202 µm mesh bongo net was lowered at 50 m min^{-1} to obtain a tow depth of approximately 200 m and retrieved at 20 m min^{-1}, towing obliquely while the ship speed varied between 1-2 kts (0.5-1 m s^{-1}) to preserve a 45° wire angle. All tows were conducted between an hour after sunset and an hour before sunrise to minimize net avoidance by larger individuals. A calibrated General Oceanics flow meter was used to record the volume water filtered. Zooplankton were immediately preserved in sodium borate buffered 5% Formalin after collection.

4.3.4 MOCNESS

To determine the vertical distributions of the individual euphausiid species, we used a Multiple Opening/Closing Net and Environmental Sensing System (Wiebe *et al.* 1985) with a 1 m^2 opening and 202 µm mesh in July 2014 and June 2015. Two day and two night tows were performed each year with the start and end locations constant within a year. For all tows, the MOCNESS was lowered into the water to below approximately 350 m at before being brought back up to the surface at 10-20 m min^{-1} towing obliquely. The first five nets in the deeper depth strata each sampled 50 m of the water column, and the last four nets in the shallower strata each sampled 25 m. In June 2014, we towed along the offshore downslope of the bank, and in 2015 we moved inshore where *T. spinifera* had been most abundant in 2014.

The species of interest are strong daytime net avoiders (Brinton 1967), so we tested whether a strobe light system (Sameoto *et al.* 1993; Wiebe *et al.* 2013) would mitigate the effect. A set of three additional day and night MOCNESS pairs of strobe light testing was performed on the R/V *Melville* in August 2014 off Point Conception, California. Separate day and night tows were conducted in June 2015, towing in a 1 nm (1.85 km) diameter circle in the same location as the other MOCNESS tows near NMB. The 490-515 nm wavelength strobe lights flashed regularly at 1Hz with a pulse width of 40 ms (Wiebe *et al.* 2013). We did not have remote control of the strobe lights, and therefore had to recover the MOCNESS to turn the lights on or off. During the day tows, the MOCNESS was lowered to the euphausiid layer identified in acoustic records and previous tows, with the strobe on or off depending on randomized assignment. Nets towed obliquely up and down in tow-yo mode through the euphausiid layer for nets 1-4. After net 5 was opened, the MOCNESS was recovered and the strobe switched to the opposite setting (off or on). The MOCNESS was then re-deployed to tow-yo nets 6-8 through the layer and recovered. At night, the euphausiid layer migrated to the surface allowing all 10 nets to sample the layer. Six successive nets sampled with the lights on or off, and four nets sampled with the opposite setting. Only adults and juveniles were enumerated for investigation of the effect of the strobe light, as furciliae and calyptopes are well sampled both day and night (Brinton 1967).

4.3.5 Zooplankton sample analysis

The starboard side of each bongo tow was enumerated for euphausiids. Sub-sampling was conducted with the use of a Folsom plankton splitter for identification of approximately 200 individuals per tow. Identifications were limited to the top 8 most abundant euphausiid species in the Southern California sector of the California Current: *Euphausia pacifica* Hansen,

Thysanoessa spinifera Holmes, *Nematoscelis difficilis* Hansen, *Thysanoessa gregaria* Sars, *Euphausia recurva* Hansen, *Euphausia gibboides* Ortmann, *Euphausia eximia* Hansen, and *Nyctiphanes simplex* Hansen (Brinton and Townsend 2003). The first 4 species are cool-water associated, while the latter four are warm-water associated. Each individual was identified to species and life history phase, and total length was measured from the tip of the rostrum to the tip of the telson (Boden *et al.* 1955; Brinton 1962; Brinton *et al.* 2000). Only the results for euphausiids larger than the blue whale lower feeding limit of 10 mm are presented here. Adult and juvenile pelagic *Pleuroncodes planipes* Stimpson were also enumerated. Counts were standardized to individuals 1000 m^{-3}. A subset of *P. planipes* guts was dissected and analyzed with the use of a stereomicroscope. The gut contents were identified to lowest taxonomic level possible to assess if there was predation on zooplankton, specifically euphausiids. Abundances were compared among regions within each year using a Kruskal-Wallis test.

4.4 Results

4.4.1 Whale distribution

A total of 26 blue, 6 fin, 2 humpback, and 2 unidentified large whales was encountered over the 10 surveys (Fig. 2). While we did not achieve the recommended minimum sample size of 60 detections (Burnham *et al.* 1980; Buckland *et al.* 2015), our total sample size for all species of large baleen whales was 36, and we use this pooled number for all analysis. This led to a coefficient of variation (CV) of 0.28, which is relatively large but acceptable for our comparative purposes. The sample size also limited us to conventional distance sampling because there were not enough data for multiple covariates to be accurate. Models with half normal-cosine and hazard rate-cosine detection functions were indistinguishable. For the total survey area, the

density was 30 whales 1000 km^{-2} (95% CI 17-52). Zero whales were encountered offshore. While 1.8 times as many whales were encountered per km surveyed on the bank compared with inshore, the difference was not statistically significant ($p>0.05$, Kruskal-Wallis); however, both the bank and inshore showed higher whale encounters than offshore ($p<0.05$).

4.4.2 Cross-bank prey distribution

The acoustic echograms provide a high-resolution picture of the distribution of euphausiid-like backscattering (ELB) in the water during the daytime feeding period of blue whales (Fig. 3). Figure 3 depicts vertically resolved ELB (point clouds) and vertically integrated (0 to 300 m) area backscattering coefficient (s_a, black bars over echograms) in relation to Nine Mile Bank (grey contours). On both dates in July 2014 (Fig. 3 A, B), ELB was diffuse throughout the upper 300 m without well-defined vertical layers of elevated concentration. On three successive days in June 2015, (Fig. 3 C-E), ELB occurred in two distinct layers. Lower intensity backscattering was present from approximately 0-150 m, while a higher intensity layer occurred deeper than approximately 200 m (two portions of which can be seen offset from one another in the echograms). Some of the higher intensity backscattering occurred above the Nine Mile Bank plateau at depths shallower than 200 m. The distribution of ELB in April 2016 (Fig. 3 F) resembled the vertical layering pattern of June 2015, but without clear association with the shallow water bank region.

The area backscattering coefficient (s_a) represented by the histogram in figure 3 is summarized in figure 4. In all surveys, s_a was significantly lower offshore than on the bank or inshore ($p<0.05$). In both July 2014 surveys, ELB was significantly elevated on the bank compared to offshore ($p<0.05$), and inshore was not significantly different from either (Fig. 4 A, B). On 14 and 16 June 2015, ELB was significantly elevated on the bank and inshore compared

to offshore (Fig. 4 C, E; $p<0.05$). On 15 June 2015, ELB was significantly different among all three regions with the highest value on the bank, inshore intermediate, and offshore lowest (Fig. 4 D, $p<0.05$). In April 2016, ELB was significantly enhanced inshore compared to both the bank and offshore (Fig. 4 F, $p<0.05$).

A test for differences in patchiness among these same three regions indicated inconsistent regional differences that did not prove to be informative. Comparison of vertical and horizontal patchiness among years, however, showed that vertical patchiness was significantly lower in 2014 than both 2015 and 2016 (Fig. 5A, $p<0.05$). Horizontal patchiness was significantly different among all 3 years (Fig. 5B, $p<0.05$), with the lowest patchiness in 2014 and the highest in 2016.

The bongo transects evaluate the spatial distributions of individual euphausiid species in relation to Nine Mile Bank (Fig. 6-7). *T. spinifera* is the preferred prey of blue whales, followed by a minor contribution of *E. pacifica* (Schoenherr 1991; Croll *et al.* 1998; Fiedler *et al.* 1998; Croll *et al.* 2005; Nickels *et al.* in prep). When differences were significant (i.e., *T. spinifera* in 2014 and 2015, *E. pacifica* in 2014), the abundances of these species were significantly lower offshore than either on the bank or inshore ($p<0.05$). *T. spinifera* (Fig. 6A) was most abundant inshore in July 2014 compared to both the bank and offshore. In June 2015, *T. spinifera* was more abundant on the bank compared to offshore, with inshore not significantly different from either. *T. spinifera* was virtually absent in April 2016, when only a few specimens were found on the bank. *E. pacifica* (Fig. 6B) was the most abundant species in July 2014 and June 2015. Like *T. spinifera*, *E. pacifica* was more abundant inshore than on the bank or offshore in July 2014. There were no significant differences among regions in the abundance of *E. pacifica* in June 2015 or April 2016 (low and variable densities found).

Species that make up only a small portion of blue whale diet include cool water-associated species *N. difficilis* and *T. gregaria*, as well as warm water-associated *E. eximia*, *E. gibboides*, *E. recurva*, and *N. simplex* (Fig. 7). *N. difficilis* (Fig. 7) was more abundant than *T. spinifera* in July 2014 and the most abundant of the 8 species in April 2016. In July 2014, *N. difficilis* was significantly more abundant inshore than offshore, with the bank not differing from either. In June 2015, both *N. difficilis* and *T. gregaria* were significantly more abundant offshore and on the bank than inshore. Of the warm water-associated species, only *E. gibboides* showed significant differences in abundance. In July 2014 *E. gibboides* was more abundant offshore than inshore, with the bank not different from either. Only larval *E. recurva* smaller than 10 mm were present during the entire study.

Pleuroncodes planipes, the pelagic red crab, first appeared as a single individual inshore in July 2014, but was much more abundant in June 2015 (Fig. 8A). In 2015, *P. planipes* was significantly more abundant inshore than on the bank or offshore. *P. planipes* was also present in April 2016 (Fig. 8B), but in much lower numbers than in 2015. There was no significant difference in abundances among inshore, on the bank, or offshore regions in 2016 ($p>0.05$).

4.4.3 Vertical prey distribution

The vertical distributions of target prey euphausiids (Fig. 9, 10), non-target euphausiid prey (Fig. 11) species, and *P. planipes* (Fig. 12) were determined from the MOCNESS tows. The secondary blue whale euphausiid prey species *E. pacifica* was numerically dominant in both years (Fig. 9B, D; 10B, D). During the summer 2014 sampling period, *T. spinifera* larvae were present above 150 m both day and night, but no adults large enough to be blue whale prey were collected (Fig. 9A, C). Below 150 m during the day, *E. pacifica* juveniles just smaller than the feeding range of >10 mm were present (Fig. 9B). These *E. pacifica* juveniles migrated to the

surface at night (Fig. 9D). A lesser concentration of larger *N. difficilis*, which is not a typical prey species of baleen whales in this region, was collected in 2014 below 250 m (Fig. 11A). In 2015, the largest individuals of the top 8 euphausiid species that were present all occupied a layer between 150-250 m during the day, with an aggregation of larger size class adult *T. spinifera* between 200-250 m (Fig. 10A). The large adult *T. spinifera* reflected in the average were collected during the 14 June 2015 tow, and the layer is apparent in the accompanying echogram as a thin red line within MOCNESS net 3 (Fig. 14B). Unlike the other species, *T. spinifera* larvae were vertically separated from the adults during the day, with the larvae generally concentrated above 100 m. In contrast, *E. pacifica* and *N. difficilis* larvae were present throughout the upper 300 m in 2015 (Fig. 10 B; 11 C). At night, the adult *T. spinifera* and *E. pacifica* vertically migrated toward the surface and spread out in the water column, occupying a shallower and wider depth stratum than during the day (Fig. 10 C, D).

P. planipes were not caught in the MOCNESS in 2014, but were present in large numbers in 2015 (Fig. 12). During the day, they occupied the upper 200 m of the water column, and were most abundant between 100 and 150 m (Fig. 12A). At night, they migrated toward the surface like the euphausiids, with their highest numbers in the upper 25 m (Fig. 12B).

Acoustic backscatter was measured concurrently with the MOCNESS tows in both July 2014 and June 2015. In July 2014, euphausiid-like backscattering (ELB) was present from the surface to approximately 200 m, with the highest intensity near the top and bottom of the depth range during the day (Fig. 13 A, B). Scattering penetrated to the same depth at night, but the highest intensity was concentrated in the upper 50 m (Fig. 13 C, D). Both 28 and 30 July show some thinning of the layer centered around 100 m, which is more pronounced on the latter day. 28 July appears as one continuous layer, while 30 July appears as 2 distinct layers, with an upper

layer between 0-50 m and a lower layer between 150-200 m. In June 2015, the daytime echograms both show two separate layers (Fig. 14 A, B). The upper layer spans 25-125 m and the lower layer 175-275 m. Some of the space between the layers in June 2015 was occupied by a layer of *P. planipes* (Fig. 14 C, D, Fig. 12 A). The most intense ELB was in the deeper layer, where larger adult euphausiids were collected by the MOCNESS (Fig. 14 A, B; 10 A, B). At night, the most intense backscattering was concentrated near the surface, penetrating to 100 m on 14 June (Fig. 14 E) and only 25 m on 15 June (Fig. 14 F). The shallow nighttime aggregations were composed of both euphausiids and *P. planipes* (Fig. 14 E, F; Fig. 12 B).

4.4.4 Effects of strobe light

Use of the strobe light had no significant effect on the abundances of adult and juvenile *T. spinifera*, *E. eximia*, *E. recurva*, *N. difficilis*, or *N. simplex* collected during the day or at night ($p>0.05$). While total *E. pacifica* abundance increased with the strobe lights on during one day tow ($p<0.05$), this was due to a higher catch of smaller juveniles (5-10 mm), thereby also reducing the median size collected. *T. gregaria* abundance increased with the strobe lights on during one night tow ($p<0.05$). *E. gibboides* abundance was significantly greater during one daytime tow ($p<0.05$), although the sample size for this tow was small and none were collected with the strobe lights off. During two of the night tows, *E. gibboides* abundance actually decreased with the strobe lights on ($p<0.05$).

The strobe lights did, however, significantly increase the abundance of *P. planipes* collected by the MOCNESS at night ($p<0.05$). The overall carapace length distribution of *P. planipes* was not significantly different between strobe on and off ($p>0.05$, Kolmogorov-Smirnov), but the largest *P. planipes* (carapace length 31-32 mm) were only collected with the strobe lights on. *P. planipes* was not adequately sampled to draw conclusions from the daytime

strobe light test, because they were vertically separated from the euphausiids during the day and the MOCNESS was only towed through the euphausiid layer.

4.4.5 P. planipes gut contents

Due to the high abundance and co-occurrence of sub-adult *P. planipes* with euphausiids, we chose to examine the gut contents of a subset of *P. planipes* to address what they were feeding on in situ. Boyd (1962) showed that *P. planipes* will suspension feed on phytoplankton in the euphotic layer, then consume zooplankton prey once they have reached suitable sizes. In all randomly selected sub-adults (N = 4), both phytoplankton and zooplankton prey items were found including: ostracods, euphausiids including metanauplii, calytopis, furcilia, juveniles, and some larger mandibles, and copepods (*Calanus pacificus, Clausocalanus* sp., *Corycaeus* sp., *Oithona* sp., *Heterohabdus* sp., and *Tortanus discaudatus,* another warm water indicator species). Some of these euphausiid parts were identifiable, and remains of both *T. spinifera* and *E. pacifica* were recognized.

4.5 Discussion

4.5.1 Euphausiid association with Nine Mile Bank

The distributions of the two primary prey species, *T. spinifera* and *E. pacifica*, overlapped inshore of and on the bank. *T. spinifera* is a more nearshore species compared to *E. pacifica*, with a much more restricted range (Brinton 1962). The distribution of the whales, however, more closely matched the distribution of *T. spinifera* than the more abundant *E. pacifica*. *E. pacifica* was equally abundant in all 3 regions in 2015, while *T. spinifera* was most abundant on the bank. The bank feature appears to function as an outer limit for both the whales

and high densities of *T. spinifera*, rather than a consistent site of aggregation. This co-variation is in agreement with dietary analysis from fecal samples that *T. spinifera* is the most preferred prey, followed by the more abundant, though generally smaller *E. pacifica* (Schoenherr 1991; Kieckhefer 1992; Croll *et al.* 1998; Fiedler *et al.* 1998; Croll *et al.* 2005; Nickels *et al.* in prep). Other species appear incidentally in the diet when consumed with these two, but are not targeted (Nickels *et al.* in prep).

In addition to species preferences, blue whales appear to have a size cutoff of prey at 10 mm (Croll *et al.* 1998; Nickels *et al.* in prep). There are several possible mechanisms leading to this observation, including escapment of smaller individuals through the baleen or the inability of smaller prey to survive digestion. Here we find both support and challenge for a third hypothesis: that the euphausiids are size segregated in the water column. In the vertically stratified samples, the adults of the primary prey *T. spinifera* were vertically separated from their larval phases during the daytime, when the blue whales feed (Croll *et al.* 1998; Fiedler *et al.* 1998; Calambokidis *et al.* 2007; Oleson *et al.* 2007). A whale targeting a monospecific *T. spinifera* patch would easily encounter and capture only mature adults. However, smaller *E. pacifica* and *N. difficilis* were present throughout the water column, making them more likely to be occasionally ingested along with larger individuals.

4.5.2 Whale association with Nine Mile Bank

We found that Nine Mile Bank (NMB) is an aggregation center, or "hot spot" for baleen whales. The density of blue, fin, and humpback whales around NMB was 30 whales 1000 km^{-2} (95% CI 17-52) in 2015. To put this number into perspective, the overall density of these whale species in the entire southern California Current system, as covered by the CalCOFI long-term sampling grid, averages 9.43 whales 1000 km^{-2} (Campbell *et al.* 2015). Another well-recognized

and well-studied blue whale aggregation center is Monterey Bay, CA, where Croll *et al.* (2005) found a blue whale density of 34 whales 1000 km^{-2}. The density of baleen whales at NMB is therefore much higher than the ambient average, and comparable to the most intense hotspots. We note that our density may be an underestimate, as our use of closing mode (in which observers go off effort and break the transect to obtain more certain species identifications) can lead to a negative bias in density estimates even for blue whales (Barlow 1997). We did spot some whales while off effort that were not re-sighted after resuming the trackline, supporting the conclusion that the true density may be even higher.

The high density of blue whales in Monterey Bay could be explained by a high density of prey euphausiids. Croll *et al*. (2005) found an acoustically inferred concentration of mostly *T. spinifera* and *E. pacifica* in Monterey Bay in summer of 3.9 individuals m^{-3} and 4,403 individuals m^{-3} within canyon-associated aggregations. Schoenherr (1991) measured a density of 60.7 individuals m^{-3} within surface swarms and 70.6 individuals m^{-3} within deep layers also around the Monterey Submarine Canyon. The highest densities in the Laurentian Channel baleen whale feeding ground were 4,500 individuals m^{-3} *Thysanoessa raschi* or 1,500 individuals m^{-3} *Meganyctiphanes norvegica* (Cotte and Simard 2005). In the present study at NMB, we found 9.7 individuals m^{-3} above 10 mm size class and 12.1 individuals m^{-3} total of primarily *E. pacifica* and *T. spinifera* within an inshore deep layer between 200 and 250 m depth in 2015. The predicted critical threshold for a whale to meet its energetic demands if it feeds continuously is approximately 100 individuals m^{-3} (Goldbogen *et al.* 2011; Hazen *et al.* 2015). While our estimate of the density of euphausiids in the deep inshore layer in summer 2015 is considerably below this, our count is likely an underestimate due to the ineffectiveness of the strobe light at mitigating avoidance during the day (Brinton 1967). Additionally, our density estimate is from

the entire volume of water filtered by a net instead of just over the volume of the euphausiid patch. Acoustically derived density estimates may be higher than net derived estimates because of the difference in water volume the euphausiids are presumed to be distributed within. The difference in volume can be seen in the day echogram from 15 June, 2015, where the thin euphausiid layer occupies only a small portion of the depth range sampled by net 3 (Fig. 14). An acoustic estimate can be confined to only the limits of a particular patch of euphausiids, while a net estimate must account for the volume of water filtered both within and outside of the patch sampled by the net. We did not attempt acoustic density estimates because we were not able to measure target strength *in situ*. Available target strength models for euphausiids are alsp designed predominantly for the much larger Antarctic species *Euphausia superba* (e.g., Hewitt and Demer 1993) and may not to accurately represent *T. spinifera* and *E. pacifica*. The relative index of euphausiid-like backscatter was better suited to address our main hypotheses. Our density estimate would likely be higher if it were derived from the acoustic backscatter over just the area of the patch itself, which is likely closer to how a whale would experience the prey density. Whales are more capable than nets of exploiting irregularly shaped euphausiid patches, executing more acrobatic maneuvers in lower density prey patches to maximize prey capture (Goldbogen *et al*. 2015).

4.5.3 Euphausiid patchiness

Patchiness and density can often be more informative than areal backscattering in describing the parameters of the prey field most relevant to a foraging predator (Benoit-Bird *et al.* 2013). The same number of individual euphausiids spread evenly throughout a volume of water would require a whale to expend more energy to consume than the same number of individuals tightly aggregated into patches in only some part of the volume. We expected that

euphausiid-like backscatter (ELB) would be more patchily distributed where the whales were present than where they were not. On the scale explored here, we did not find a consistent pattern of patchiness among regions. We did, however, find lower vertical patchiness in 2014 compared to the other years studied and an increasing horizontal patchiness with year. Despite similar total euphausiid abundance between the summers of 2014 and 2015, the latter year would have presented better feeding conditions for baleen whales due to the increased patchiness and therefore local density. Due to the timing of sampling, 2014 was assessed in more extreme climactic conditions than 2015. The development of the 2014 warm anomaly began early that year, and was pronounced before the summer sampling period (Zaba and Rudnick 2016). That anomaly had relaxed somewhat by June 2015, and the El Niño had not yet fully evolved (Jacox *et al.* 2016; Zaba and Rudnick 2016). 2016 ELB was also patchy, but the spring abundance was much lower and therefore would not have provided adequate food resources. Baleen whales would not be expected to arrive off of Southern California until prey abundance increases in the summer (Bissell 2013; Campbell *et al.* 2015).

T. spinifera has been documented to form dense surface swarms of mature adults (Brinton 1981; Smith and Adams 1988). Surface swarms of *Meganyctiphanes norvegica* in the North Atlantic may also form around bathymetric crests and attract euphausiid predators including humpback and fin whales (Stevick *et al.* 2008). Such swarms are thought to be particularly efficient food for lunge feeding whales (Schoenherr 1991; Fiedler *et al.* 1998). We were not able to sample a surface swarm either with quantitative nets or active acoustics during this study, but one was observed inshore of the bank during the whale visual survey on June 23, 2015. Sampling with a dip net revealed that it was composed of adult *T. spinifera*. While these surface aggregations may be of particular interest for a feeding whale, density of prey is a more

important factor in feeding efficiency than prey depth (Goldbogen *et al.* 2011). The deeper layers more routinely observed would still be attractive prey if they are composed of the correct prey species and sizes in sufficient density. Blue and humpback whales do track euphausiid ascent in the evening, but cease feeding when euphausiids are close to the surface, but at lower density, at night (Fiedler *et al.* 1998; Calambokidis *et al.* 2007; Goldbogen *et al.* 2011; Burrows *et al.* 2016).

4.5.4 P. planipes intrusion

In addition to the euphausiids, *P. planipes* sub-adults were enumerated from MOCNESS tows during 2015. The most abundant layers during both day and night tows revealed high abundances of *P. planipes* concentrated at shallower depths than adult *T. spinifera* during the day. Acoustic echograms also reflected these layers. We found an elevated population of *P. planipes* inshore of the bank in 2015. The NMB appears to be a suitable aggregating site for not only euphausiid prey, but other pelagic crustaceans such as *P. planipes,* likely caused by similar physical mechanisms described earlier. *P. planipe*s may also have aggregated behaviorally to feed on the euphausiids, as suggested by gut content analysis. Pelagic red crabs were found to aggregate similarly to euphausiids inshore of NMB and could have served as an alternate food source for visiting baleen whales. In southern California waters high numbers of pelagic red crab stranded along the coast and were observed within the water column and in the gut contents of many pelagic predators during 2014-2016 (McClatchie *et al.* 2016). The presence of this food item in many cases will serve as a less calorically valuable supplement to the diets of many seabirds, fish, and whales when sardine, and anchovy abundances are depressed during warm periods (Alverson 1963). In blue whale fecal samples collected inshore of the bank in 2015, we confirmed some feeding upon red crab through remains of an intact claw and several antennae.

While these animals are typically krill specific, in warm water years such as the warm water anomaly of 2014 and El Niño of 2015 when *T. spinifera* exhibits lower abundances in the Southern CA Bight, they may be cueing into decapod prey to supplement their diet. Humpback whales are known to feed upon another munid crab *Munida gregaria* in the Antarctic (Matthews 1937).

4.5.5 Implication for interannual variation

In 2014, NMB experienced the effects of the "warm blob" over the Northern Pacific and a potentially unrelated Southern California Warm Anomaly (Leising *et al*. 2015). Euphausiid abundance in 2014 was lower than in 2013 throughout the California Current (Leising *et al.* 2015). This warming was followed by El Niño conditions in 2015 and 2016 (McClatchie *et al.* 2016). We observed an influx of El Niño indicators including *P. planipes* and *Nyctiphanes simplex* during 2015, which were also reported during the 1997-98 El Niño in Monterey Bay (Marinovic *et al.* 2002). Based on historic evidence from the CalCOFI spring-time enumerations of euphausiids in the CCS, we would expect lower abundances of *T. spinifera* and *E. pacifica* during an El Niño (Brinton and Townsend 2003). During non-El Niño years, when abundances of baleen whale target euphausiid species are higher, we would expect NMB to be an even more suitable stop-over location for baleen whale feeding. Additionally, the persistence of available whale prey, despite these anomalous conditions, could mean that NMB and areas like it serve as food refuges along the blue whale migration route, such as Monterey Bay during the 1997-98 El Niño (Benson *et al.* 2002; Marinovic *et al.* 2002). The reliability of these areas would be important to foraging whales. The warm water anomalies could also mean that the present study represents a conservative estimate of the food resources available and baleen whale presence during normal conditions. The level of blue whale calling off of southern California during the

1998 El Niño was much lower during their typical peak in mid-September, indicating either lower presence or a change in behavior of increased foraging activity, but the level of calling returned to normal during the 1999 La Niña (Burtenshaw *et al.* 2004).

4.6 Conclusions

The distribution of blue, fin, and humpback whales around Nine Mile Bank (NMB) matched the distribution of primary prey species *Thysanoessa spinifera*. Both predators and prey were more abundant on or inshore of the bank than offshore. The bank serves as an offshore limit of increased prey abundance that may draw the whales to the area. The minor prey species *Euphausia pacifica* was more abundant and dispersed more evenly around the bank, but had less apparent influence on the distribution of whales. Euphausiids large enough to be whale prey were concentrated in a thin layer between 200 and 250 m, and *T. spinifera* adults and larvae were vertically segregated. The tighter link between the distributions of the whales and their preferred, but less abundant, prey highlights the importance of species-specific analysis of euphausiid distributions. The persistence of NMB as a hotspot through anomalously warm conditions in the California Current System may make it a food refuge for whales during periods of lower productivity.

4.7 Acknowledgements

We would like to thank the many people who made this study possible. We thank the science parties of SKrillEx I, II, and III, CCE-LTER P1408, and the crews of the R/V *New Horizon*, R/V *Robert Gordon Sproul*, R/V *Sikuliaq*, and R/V *Melville*. The whale visual surveys were made possible by boat operators Brett Pickering and Josh Jones as well as the volunteer

observers, with guidance and assistance from John Hildebrand and Jay Barlow. Visual surveys were conducted under NMFS Permit 17312 issued to the Scripps Institution of Oceanography. Tony Koslow, Jian Liu, Pete Davison, and Alex DeRobertis provided help and guidance with the active acoustics. Tais Castellano, Han Zou, Shelbi Richardson, Doris Stumps, and Jui-Yuan Chang provided additional laboratory assistance. Annie Townsend taught us euphausiid species identification. We thank the Pelagic Invertebrate Collection of Scripps Institution of Oceanography for use of samples, lab space, and equipment. Dave Jensen provided valuable visualization and statistical code. Mike Landry and Jon Shurin provided additional comments throughout the process. This work was supported by the U.S. National Science Foundation via the California Current Ecosystem LTER site (OCE-10-26607 and OCE-16-37632), UC Ship Funds, and the Scripps Institution of Oceanography Graduate Department.

Chapter 4 is being prepared for journal submission as: Nickels, Catherine F.; Sala, Linsey M.; Ohman, Mark D. "The euphausiid prey field for baleen whales around a steep bathymetric feature in the southern California Current System." It is presented as part of this dissertation with the acknowledgement of the study coauthors Linsey M. Sala and Mark. D. Ohman. The dissertation author was the primary investigator and is the primary author of this material.

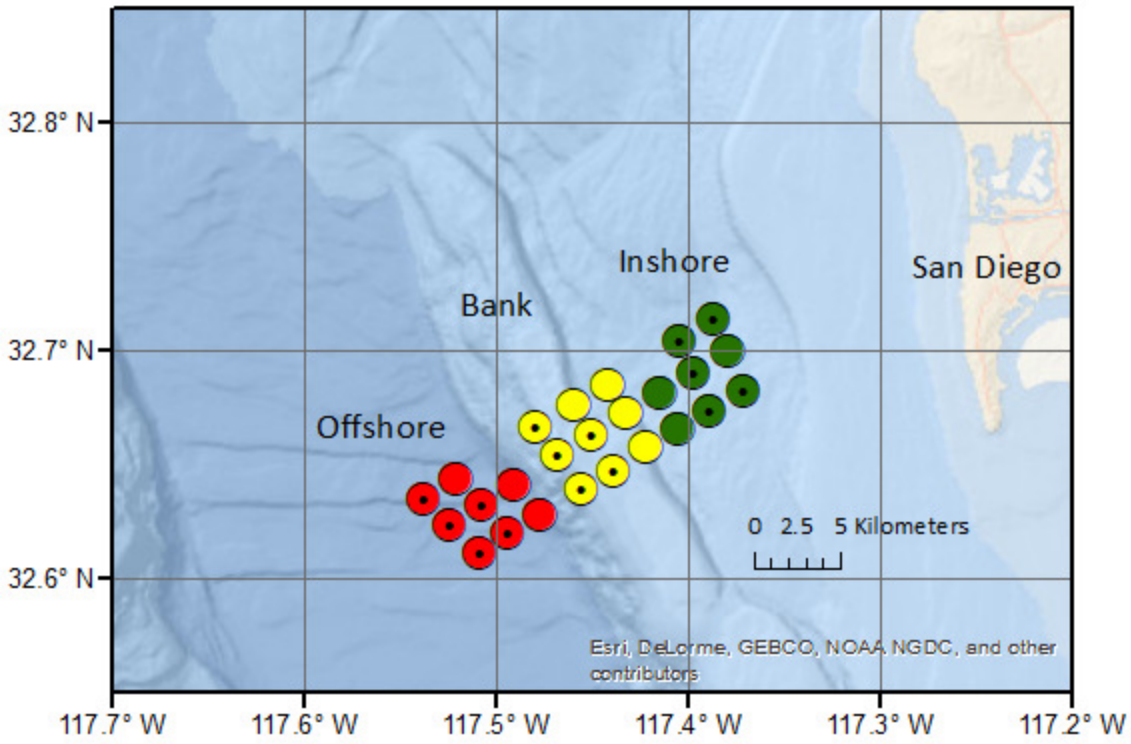


Figure 4.1: Nine Mile Bank (NMB) study area near San Diego, CA. The study area was subdivided into 3 regions: inshore, the bank itself, and offshore. Open circles represent bongo tow locations sampled in 1 year of the study; circles with a dot inside bongo tow locations sampled in 2 or 3 years.

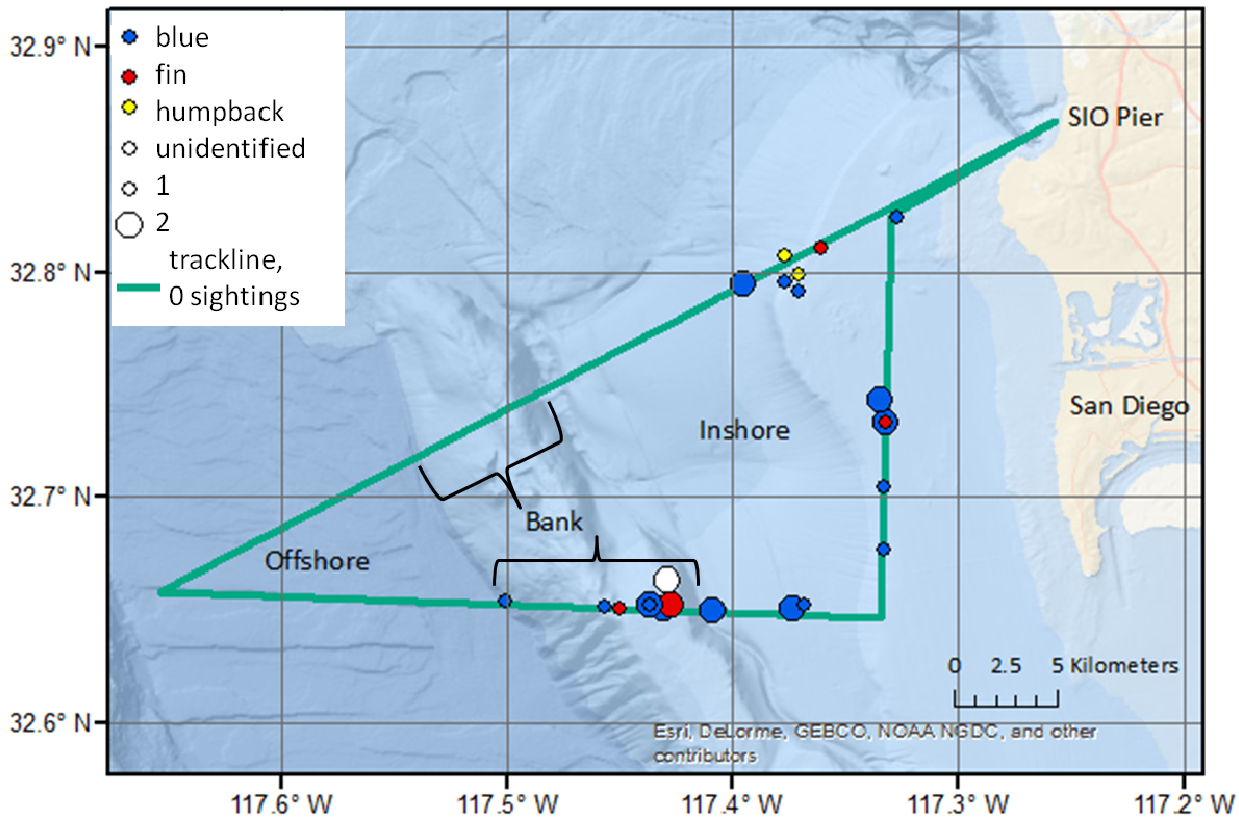


Figure 4.2: Tracklines and sightings from the 2015 whale visual survey.

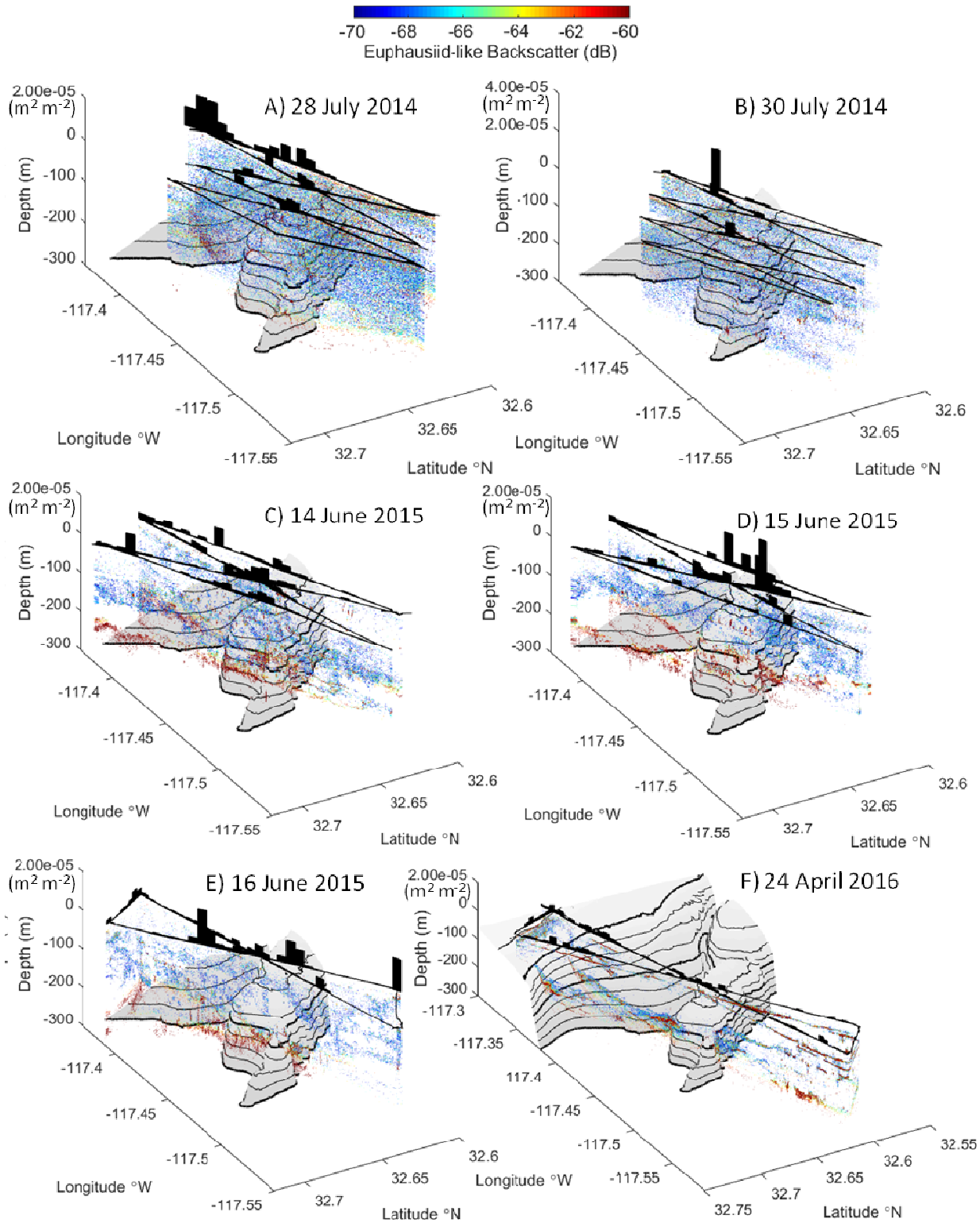


Figure 4.3: Echograms of euphausiid-like backscattering (dB) from (A,B,C) July 2014, (D,E) June 2015, and (F) April 2016. Bars above the black lines indicate the area backscattering coefficient (sa, m2 m-2) summed from 0-300 m over 500 m distance bins. Gray shading indicates Nine Mile Bank (contour interval 25 m).

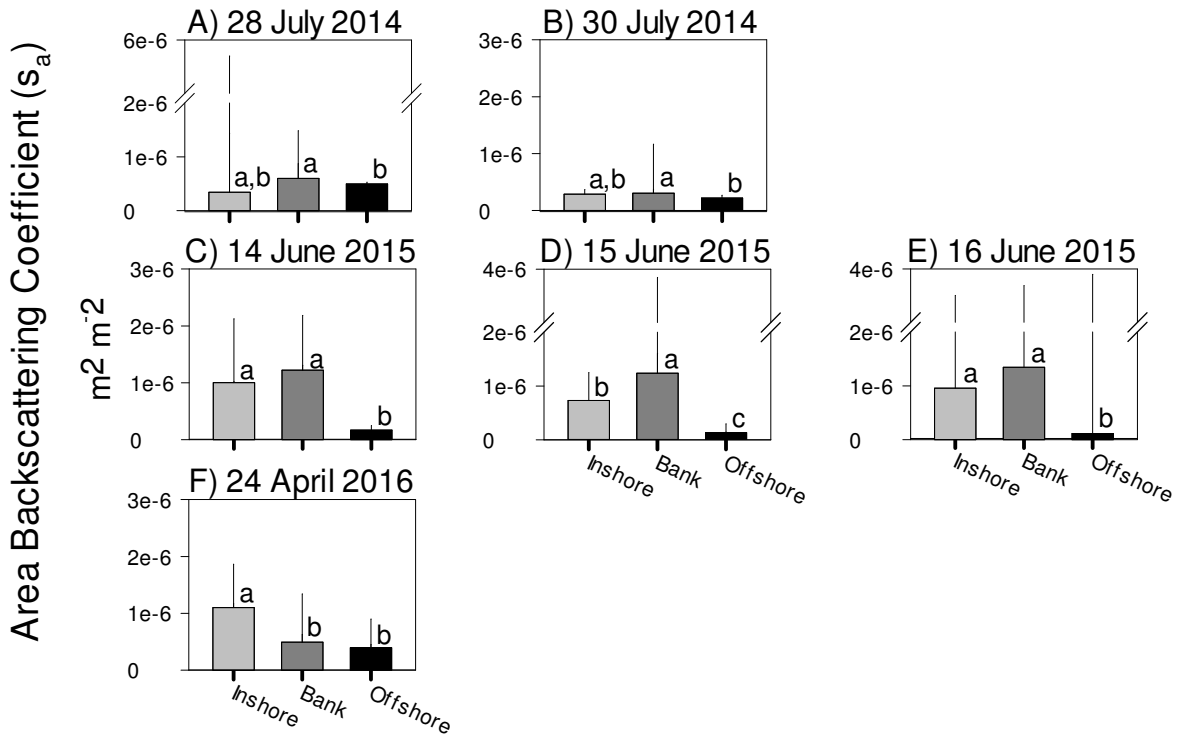


Figure 4.4: Mean (±95%) area backscattering coefficients (sa, m^2 m^{-2}) for euphausiid-like backscatter in three regions of Nine Mile Bank: inshore, on the Bank, and offshore. Statistically significant groupings denoted with a, b, c ($p<0.05$).

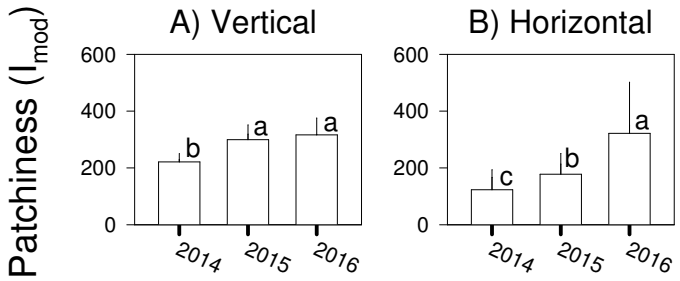


Figure 4.5: Mean (±95%) patchiness (Imod) in (A) the vertical and (B) the horizontal dimension from acoustic surveys. Statistically significant groupings denoted with a, b, c ($p<0.05$).

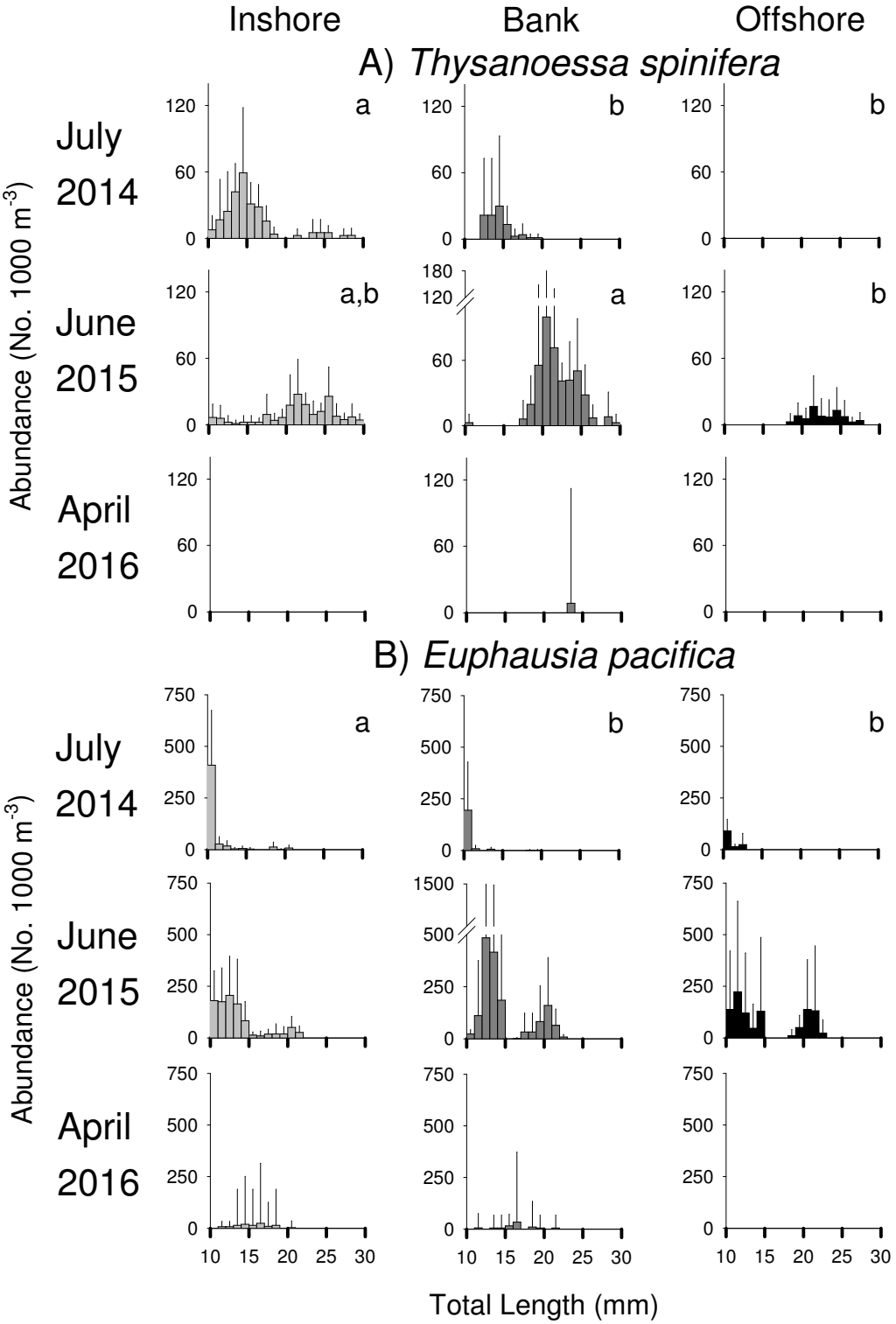


Figure 4.6: Mean (±95%) euphausiid abundance by length class from bongo net transects for target prey species (A) *Thysanoessa spinifera* and (B) *Euphausia pacifica*. Statistically significant groupings denoted with a, b; ($p<0.05$).

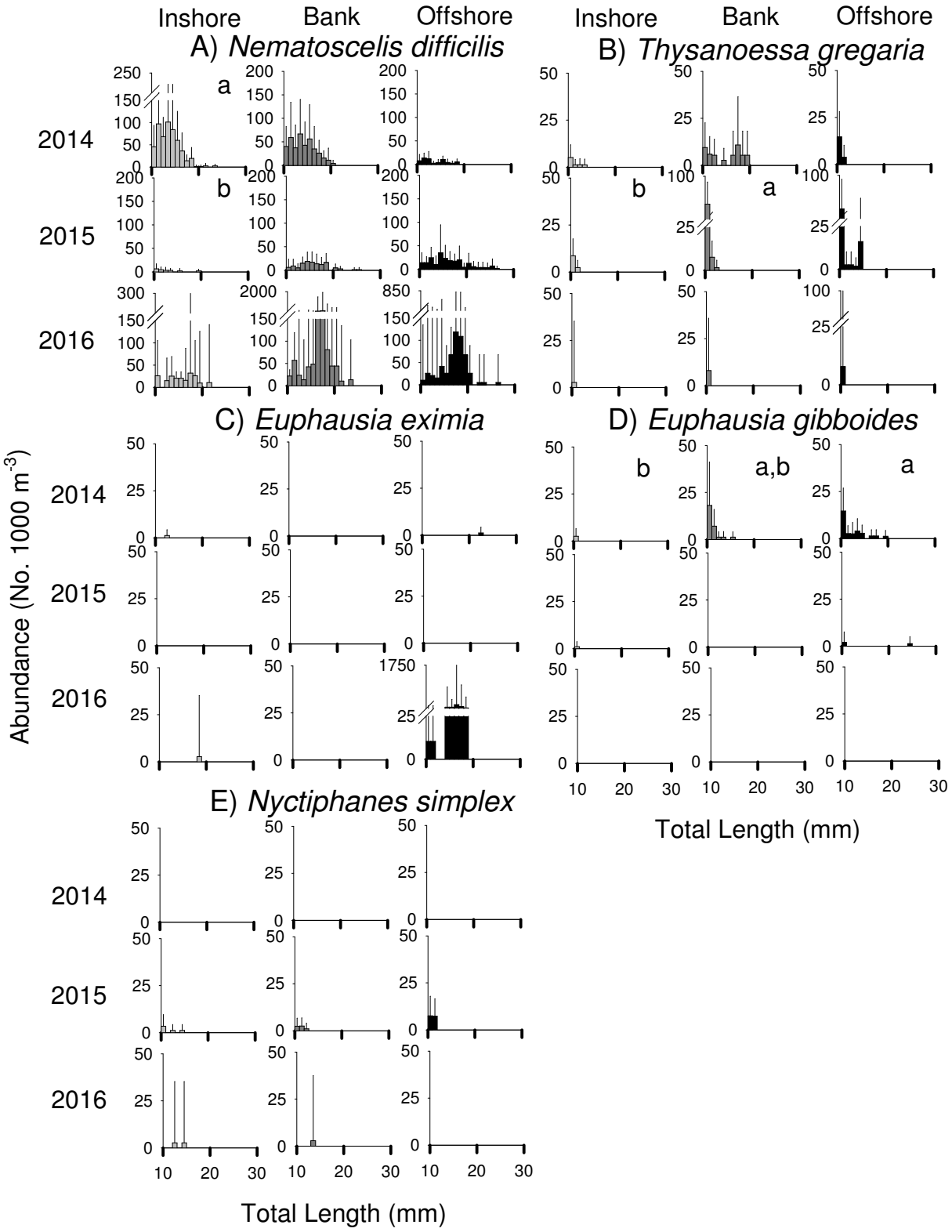


Figure 4.7: Mean (±95%) euphausiid abundance by length class from bongo net transects for incidental prey species (A) *Nematoscelis difficilis*, (B) *Thysanoessa gregaria*, (C) *Euphausia eximia*, (D) *Euphausia gibboides*, and (E) *Nyctiphanes simplex*. Statistically significant groupings denoted with a, b ($p<0.05$).

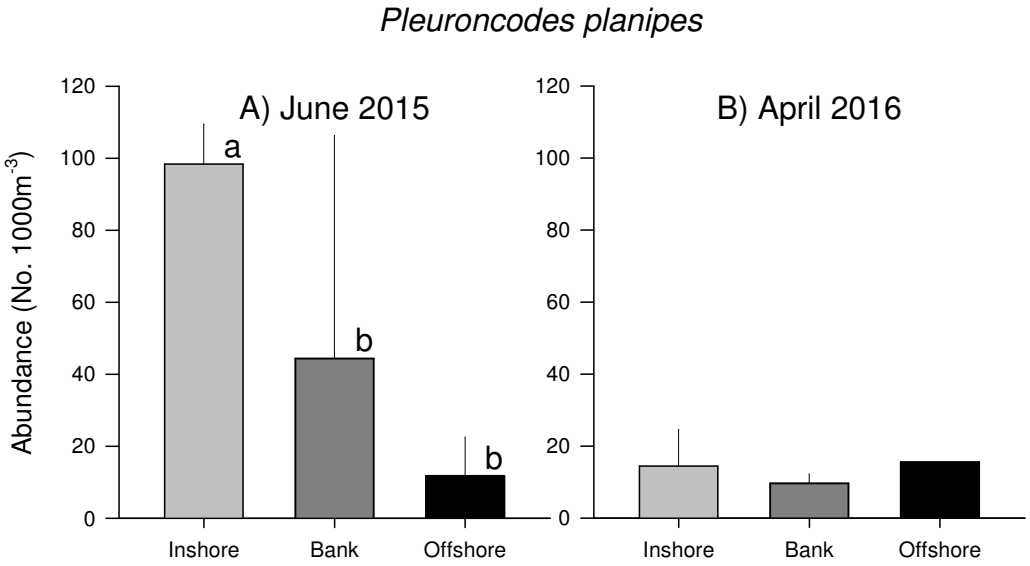


Figure 4.8: Mean (±95%) abundance of *Pleuroncodes planipes* abundance from (A) 2015 and (B) 2016 bongo net transects. Statistically significant groupings denoted with a, b; $P<0.05$.

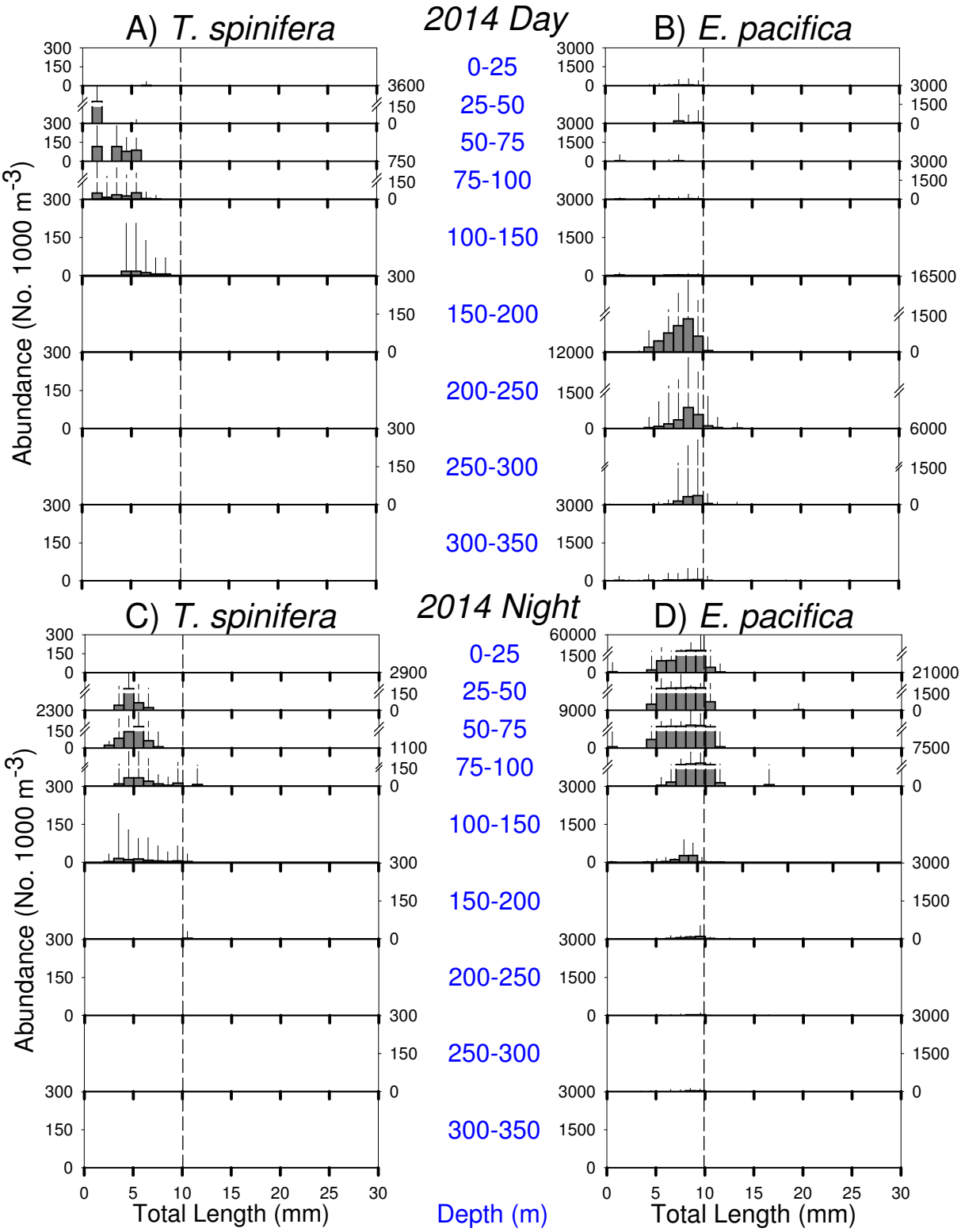


Figure 4.9: Vertical distribution of euphausiids by length class from MOCNESS tows for target prey species (A,C) *T. spinifera* and (B,D) *E. pacifica* from July 2014 along the offshore slope of the bank. (A,B) Daytime tows and (C,D) nighttime tows. Dashed vertical line indicates 10 mm lower size limit of blue whale feeding.

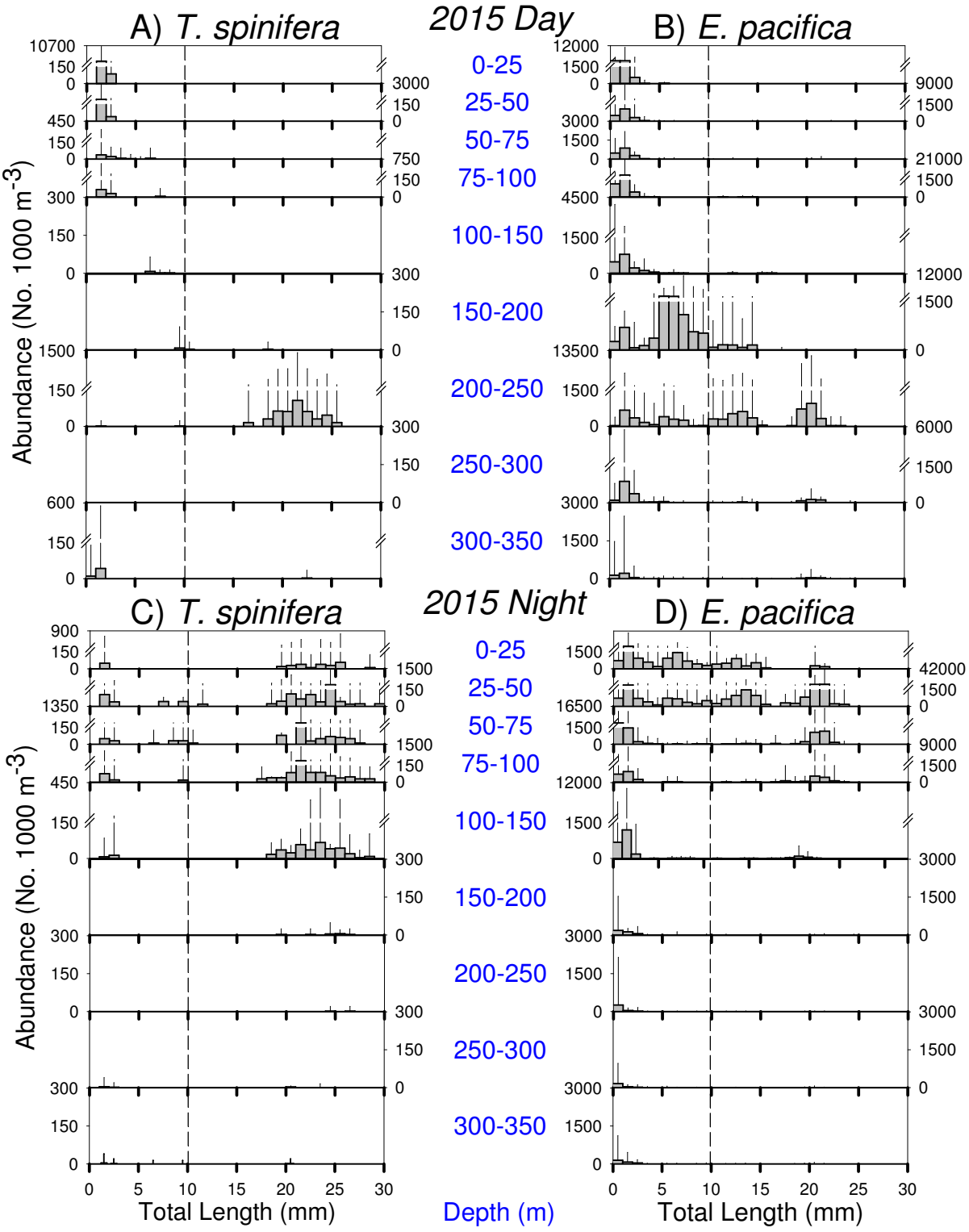
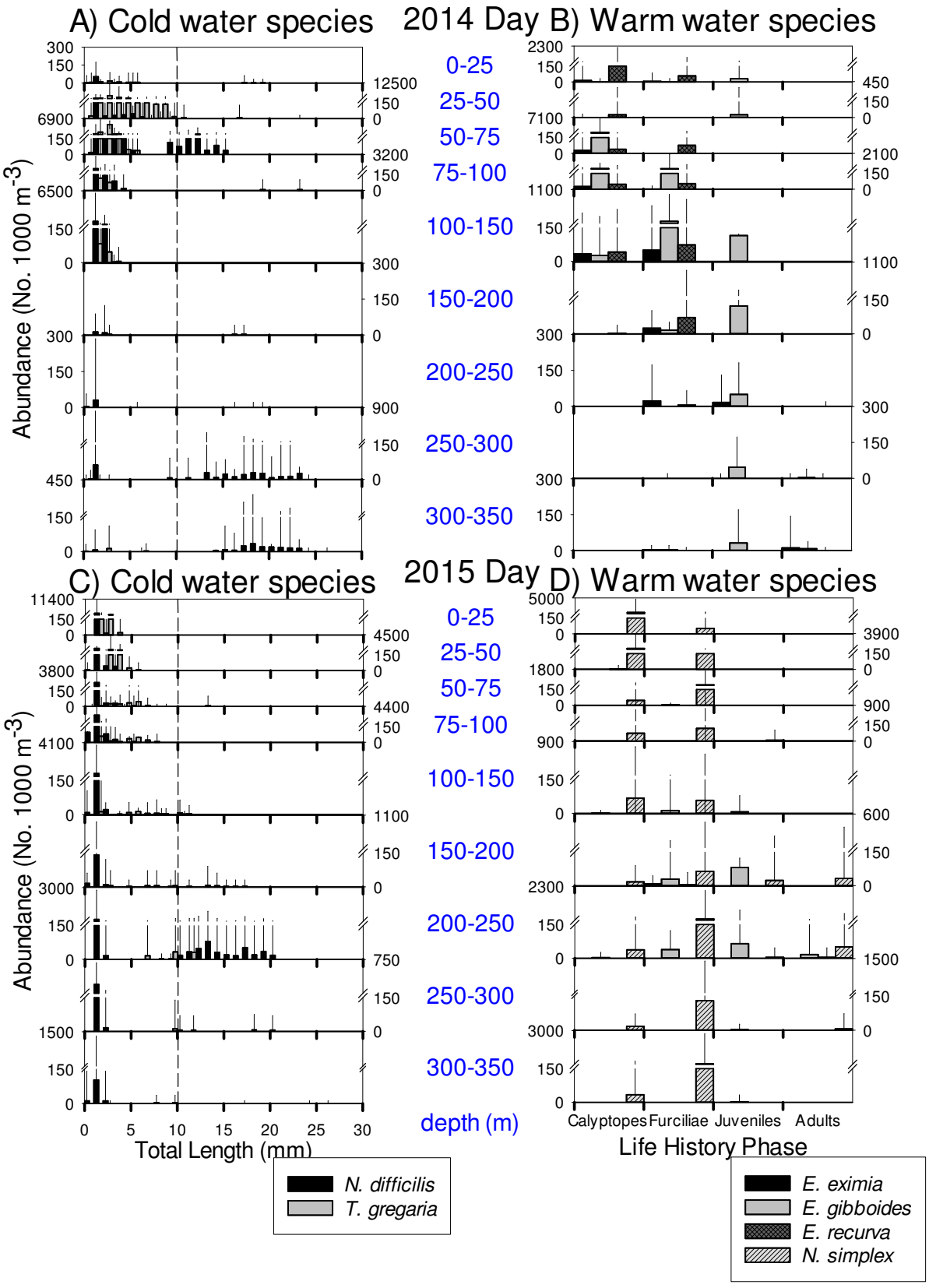


Figure 4.10: Vertical distribution of euphausiids by length class from MOCNESS tows for target prey species (A,C) *T. spinifera* and (B,D) *E. pacifica* from June 2015 along inshore of the bank. (A,B) Daytime tows and (C,D) nighttime tows. Dashed vertical line indicates 10 mm lower size limit of blue whale feeding.

Figure 4.11: Vertical distribution of euphausiids by length class from MOCNESS tows for incidental or non-prey species associated with the (A,C) cold water assemblage (*N. difficilis*, *T. gregaria*) and (B,D) warm water assemblage (*E. eximia*, *E. gibboides, E. recurva, N. simplex*) from daytime tows. (A,B) from July 2014 along the offshore slope of the bank and (C,D) June 2015 along inshore of the bank. Dashed vertical line indicates 10 mm lower size limit of blue whale feeding.


A) Cold water species
2014 Day
B) Warm water species
C) Cold water species
2015 Day
D) Warm water species
Abundance (No. 1000 m-3)
0-25
25-50
50-75
75-100
100-150
150-200
200-250
250-300
300-350
depth (m)
Total Length (mm)
Life History Phase
Calyptopes
Furciliae
Juveniles
Adults
N. difficilis
T. gregaria
E. eximia
E. gibboides
E. recurva
N. simplex

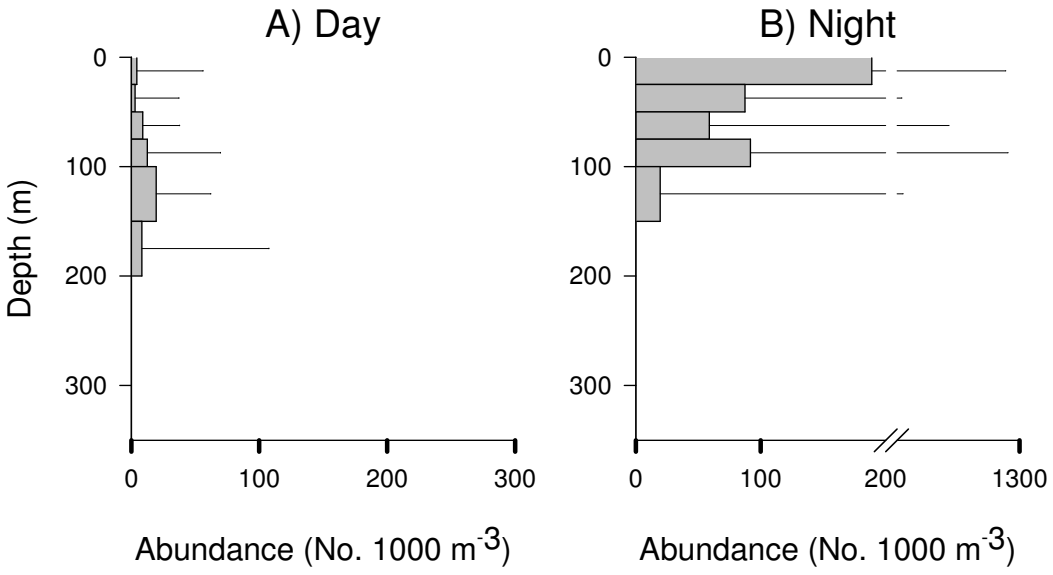


Figure 4.12: Mean abundance of *Pleuroncodes planipes* from June 2015 MOCNESS tows inshore of the bank. (A) Daytime and (B) nighttime tows.

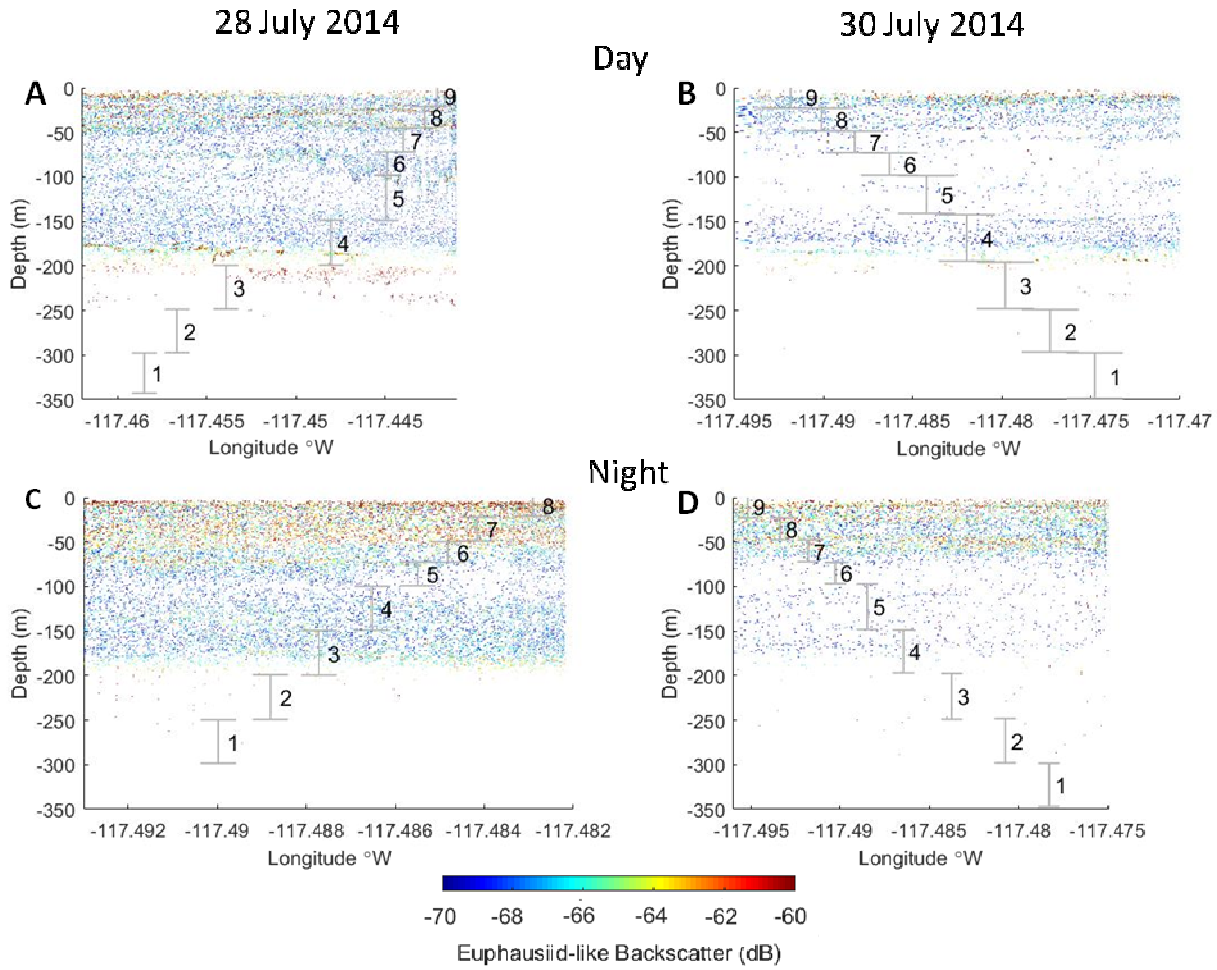


Figure 4.13: Echograms of euphausiid-like backscattering concurrent with MOCNESS sampling from July 2014 along the offshore slope of the bank. Gray bars mark the vertical extent of each net through the echogram. (A, B) Daytime and (C,D) nighttime tows.

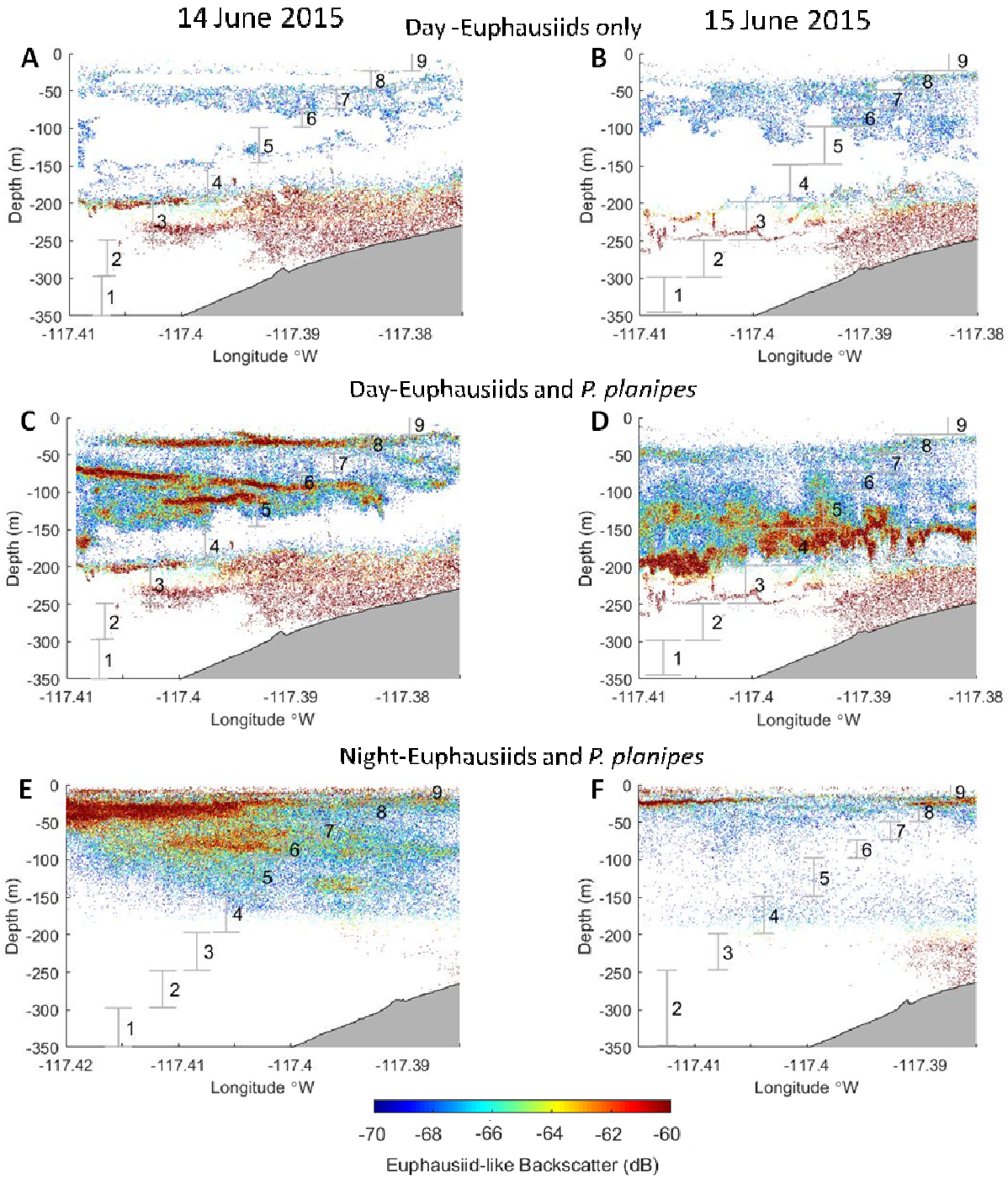


Figure 4.14: Echograms of euphausiid-like backscattering concurrent with MOCNESS sampling from June 2015 inshore of the bank. Gray bars mark the vertical extent of each net through the echogram. (A,B) Daytime tows with *P. planipes* backscattering removed, (C,D) daytime tows with *P. planipes* backscattering included, and (E,F) nighttime tows with *P. planipes* backscattering included. Gray shading indicates bathymetry.

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CHAPTER 5 Summary of the Dissertation

5.1 Introduction

The motivation for the research in this dissertation was to understand how large blue whales can gain enough energy to survive solely from eating small crustacean euphausiids. The first part of the problem was to determine the composition of the diet of blue whales. Building on that foundation, I then investigated the co-location of blue whales and their specific prey to begin to address how blue whales can find the specific prey that meets their needs in the vast ocean. In this concluding chapter, I summarize the key findings and connections among chapters.

5.2 Blue whale diet specificity

The data presented in chapter 2 demonstrate that blue whale diets are extremely limited in both size and species of prey. Euphausiids consumed by blue whales were almost exclusively larger than 10 mm in total body length, which means that only adult and some species of juvenile euphausiids are relevant as prey. *Thysanoessa spinifera* was consistently and overwhelmingly the dominant euphausiid consumed. Blue whale diets have been assessed previously through the analysis of fecal samples in the Channel Islands (Fiedler *et al.* 1998) and Monterrey Bay (Schoenherr 1991; Croll *et al.* 2005). At these locations, blue whales fed preferentially on *Thysanoessa spinifera*. Chapter 2 brings together analysis of fecal samples from a longer timespan (1998-2015) and greater spatial range (Cordell Bank to San Diego, California) to establish the persistence of *T. spinifera* as the dominant component of eastern North Pacific blue whale diets.

The consistency of blue whale preference for *T. spinifera*, even when other species such as *Euphausia pacifica* were dominant in the water where the whales were feeding, suggests that

the distribution of the whales would be influenced by the distribution of *T. spinifera*. The finding highlights the importance of investigating the spatial patterns between predator and prey at the same size and species specificity as they occur. A bulk measure of euphausiid abundance may be numerically dominated by younger, smaller life history phases that are not of energetic value for a whale to pursue. Likewise, an area may have high overall euphausiid productivity, but if it is dominated by a species other than *T. spinifera*, it may not be an attractive feeding location for blue whales.

Chapter 2 establishes that the mandible morphology of the eight dominant California Current System (CCS) euphausiid species vary distinctly by species. The descriptions of euphausiid mandible structures and mandible length to body length regressions will be useful in future studies of the diet composition of whales and other euphausiid predators through stomach or fecal sample analyses. Mandible identification could also be used for euphausiid samples that are too damaged to display crucial external taxonomic characteristics.

5.3 Scales of blue whale-euphausiid co-location

The analysis of chapter 3 builds on the definition of blue whale diet from chapter 2 by comparing the distribution of blue whales with primary prey euphausiids *T. spinifera* and secondary prey euphausiids *E. pacifica*. Spatial pattern at large scales can be thought of as the sum of the interactions between patterns at smaller scales (Levin 1992). Interactions between species, however, are not always clear-cut at all levels of organization. I hypothesized that blue whale distributions would be tightly coupled to the distributions of *T. spinifera* at all spatial scales analyzed, while there would be a weaker relationship between the distributions of blue whales and *E. pacifica*. As expected, *E. pacifica* is widely distributed (Brinton 1962; Brinton *et*

al. 2000) and did not explain the distribution of blue whales at any scale. More surprising was that blue whale and *T. spinifera* distributions were only related at the two largest scales investigated: the North Pacific Basin and the California Current System. At the smaller scales of the region covered by the CalCOFI program and the local scale near blue whale aggregation centers, blue whale and *T. spinifera* distributions were not connected. A scale even smaller than the local scale must be invoked to explain the spatial association observed at larger scales.

Chapter 3 also tested the hypothesis that a reduction in the availability of euphausiid prey off Southern California was the cause of an expansion of blue whale habitat northward off British Columbia beginning in 1997 (Barlow and Forney 2007; Calambokidis *et al.* 2009). Blue whales do demonstrate food-related migrations between high-latitude winter breeding grounds and low-latitude summer feeding grounds (Burtenshaw *et al.* 2004; McDonald *et al.* 2006; Bailey *et al.* 2009; Campbell *et al.* 2015). In the case of the northward expansion, a reduction in available prey off Southern California did not take place and therefore could not have been the cause. Other factors will need to be invoked to explain the habitat expansion.

5.4 Association of predators and prey with steep bathymetric features

Chapter 4 follows from the conclusions of chapter 3 by investigating the distributions of whales and euphausiids within the local scale around a single bathymetric feature: Nine Mile Bank (NMB) near San Diego, California. The whale surveys in chapter 4 include humpback and fin whales in addition to blue whales. Humpback and fin whales are also euphausiid predators, but are not as limited as blue whales and do consume other prey (Watkins and Schevill 1979; Kieckhefer 1992; Tershy *et al.* 1993; Fossette *et al.* 2017). The blue whale preferred prey *Thysanoessa spinifera* were found on or inshore of the bank, which served more as an offshore limit of whale feeding habitat rather than a point of increased abundance relative to both sides.

Other researchers have also found that abrupt bathymetric features serve as aggregation sites for feeding whales (Schoenherr 1991; Fiedler *et al.* 1998; Cotte and Simard 2005; Croll *et al.* 2005; Friedlaender *et al.* 2006; Lesage *et al.* 2017). The larvae of *T. spinifera* were vertically separated from adults and juveniles large enough to be whale prey, which were concentrated in a thin layer between 200 and 250 m depth. Multiple sampling techniques must be employed synoptically to determine the fine spatial distribution of preferred prey around these features.

5.5 Summary

Blue whale diets are restricted to euphausiids longer than 10 mm total body length, mainly *Thysanoessa spinifera* and to a lesser extent *Euphausia pacifica*. The spatial co-location of blue whales is apparent at ocean basin and current scales, but not at smaller regional and local scales. The larger scale patterns are created at an even smaller scale closer to the ambit of a feeding whale. Whales are able to co-locate with their preferred prey both vertically in the water column and around bathymetric features that aggregate the prey. Future research should combine a detailed analysis of the prey field, as done here, with concurrent tagging of whales to make more direct inferences about the interaction of whale feeding behavior with prey characteristics. Dietary analysis should also expand beyond the northeastern Pacific population, so that common characteristics of preferred prey worldwide can be discovered and interpreted.

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