AN ABSTRACT OF THE DISSERTATION OF

Andrew R. Szabo for the degree of Doctor of Philosophy in Wildlife Science presented on May 9, 2011.

Title: Aspects of the foraging Ecology of Humpback Whales (*Megaptera novaeangliae*) in Frederick Sound and Stephens Passage, Southeast Alaska.

Abstract approved:

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Bruce R. Mate

The North Pacific humpback whale (*Megaptera novaeangliae*) population has been increasing at an average annual rate of ~6% since the early 1990s. In northern Southeast Alaska alone, there are now more whales than estimated for the entire North Pacific several decades ago. An understanding of how this growing population is repopulating traditional foraging grounds will benefit from detailed investigations of their prey preferences and trends in whale abundance and distribution relative to those prey. This dissertation examines these issues from late May until early September 2008 in Frederick Sound and Stephens Passage, a Southeast Alaskan feeding area historically used by humpback whales. The foundation for the study is an analysis of the life histories and abundance patterns of euphausiids, the principal prey of humpbacks in the area, during late spring and summer. Four species, *Thysanoessa raschii*, *T. longipes*, *T. spinifera*, and *Euphausia*

pacifica, were identified in plankton net samples collected at random locations throughout the study site (n = 49) and in locations where a strong scattering layer was observed on a 120 kHz echosounder (n = 48). Both sample types varied in euphausiid species composition. Abundance patterns of immature euphausiids coupled with observations of females carrying spermatophores indicated differences between species in spawning schedules. *Thysanoessa* spp. began spawning in early April with the spring phytoplankton bloom and continued until late June, whereas *E. pacifica* began spawning in early June and continued until late August. This protracted recruitment of immature euphausiids was geographically widespread throughout the summer in contrast to adults, which, although present all summer, were found primarily in slope and shallow (< 100 m) areas.

To determine if humpback whales preferred one euphausiid species or life-stage over another, net sample and hydroacoustic data collected in the vicinity of whales were compared to similar data collected in random locations throughout the study site. This revealed that whales targeted dense aggregations of adult euphausiids, but did not discriminate between the various species, which was surprising because of presumed differences in the energy density linked to their different spawning schedules. Additionally, whales did not spend time in areas with concentrations of immature euphausiids, which were likely not large enough during the study period to be suitable prey.

With this preference for adult euphausiids, the abundance and distribution patterns of humpbacks were examined in relation to prey availability. Whale

abundance was lowest at the beginning of the study in late May at ca. 68 whales and peaked in late July at ca. 228 animals – approximately 12% of the region's estimated abundance for the study year. This study did not detect a concomitant increase in the availability of adult euphausiids, which is unsurprising since immature euphausiids would not recruit into the adult population until after the end of the study, and post-spawning mortality and predation pressure is presumably high during this time. Instead, whales clustered increasingly around comparatively fewer prey as the summer progressed. These observations, combined with a plateau in whale abundance after July, suggest that their abundance in the area was limited by euphausiid availability.

Estimates of whales using the study site during the summer have remained similar over several decades despite a dramatic increase in humpback numbers in Southeast Alaska and elsewhere in the North Pacific. The results from this study suggest that, although the study site remains important seasonally to some whales, it is not a significant source of prey responsible for regional population growth in general. More likely, it is part of a network of feeding areas that has influenced the population trend. Further insight into these and the other issues raised in this dissertation could come from several additional analyses. An extended sampling season that captures the recruitment of immature euphausiids into the adult population would reveal whether a given year's prey cohort represents an important resource to whales in that same year, which has potential implications for interpreting mid-late season whale abundance patterns. As well, a photo-identification study

would be useful in characterizing whale residency patterns and determining whether the abundance trends reflect a relatively small subset of the regional population using the area for most of the season or a continuous flow of a larger portion of the population. Finally, similar analyses as those outlined here but conducted in other areas within the region would provide additional insight into the network's capacity to support the recovering whale population.

ASPECTS OF THE FORAGING ECOLOGY OF HUMPBACK WHALES
(*Megaptera novaeangliae*) IN FREDERICK SOUND AND STEPHENS PASSAGE,
SOUTHEAST ALASKA

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APPROVED:

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Major Professor, representing Wildlife Science

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Head of the Department of Fisheries and Wildlife

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Andrew R. Szabo, Author

ACKNOWLEDGMENTS

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(*MEGAPTERA NOVAEANGLIAE*) IN FREDERICK SOUND AND STEPHENS
PASSAGE, SOUTHEAST ALASKA

CHAPTER 1: INTRODUCTION

Over the last several decades, there has been concern for the recovery of

humpback whales (*Megaptera novaeangliae*; NMFS 1991, FOC 2010), one of several

baleen whales (suborder Mysticeti) that were heavily exploited during the modern

whaling era and experienced a dramatic decline in worldwide abundance (Estes et al.

2006). In response to this concern, a number of large-scale and collaborative efforts

were mounted to examine humpback whale abundance, distribution and population

structure over large portions of their range (Calambokidis et al. 2008, Rosenbaum et

al. 2009, Straley et al. 2009). These provided new insights into many aspects of their

biology; however, one of the most striking findings to emerge is that some

populations, notably those in the North Pacific, are experiencing a dramatic

resurgence. As of 2005, approximately 18,000 humpbacks were estimated to reside

in the North Pacific (Calambokidis et al. 2008), which is well above the 1,200

animals estimated to remain after whaling ended in 1966 (Rice & Wolman 1982) and

potentially higher than their pre-exploitation abundance (~15,000; Rice 1978).

Furthermore, the population has been increasing at an average annual rate of ~6%

since the early 1990s (Calambokidis et al. 2008). An understanding of how this

growing population is repopulating traditional foraging grounds will benefit from

detailed investigations of their prey preferences and trends in whale abundance and distribution relative to those prey. This dissertation examines these issues in Frederick Sound and Stephens Passage, a Southeast (SE) Alaskan feeding area historically used by humpback whales.

Nearshore waters of SE Alaska and northern British Columbia together support the largest humpback whale feeding aggregation, estimated at ~6000 individuals, in the North Pacific (Calambokidis et al. 2008). Large humpback aggregations occur in several areas within SE Alaska, including Glacier Bay and Icy Strait (GB/IS), Sitka Sound (SS), and Frederick Sound and Stephens Passage (FS/SP) (Straley 1994, Dahlheim et al. 2009, Straley et al. 2009). Recent efforts to examine humpback whale abundance patterns have focused on GB/IS (Nielson & Gabriele 2008, Straley et al. 2009) and SS (Straley et al. 2009); however, FS/SP has received comparably less effort. Mark-recapture based humpback abundance estimates for FS/SP suggest that, as far back as 1986, 211-247 whales foraged in the area during mid-summer (Baker et al. 1992). More recently, Straley et al. (2009) estimated that >400 animals, nearly half of the northern SE Alaska total when the observations were made, visited FS/SP each year. These abundance estimates lend support to the general view that FS/SP is an important humpback feeding area within SE Alaska (Baker et al. 1992, Straley et al. 2009)

It has been suggested that whales arrive in FS/SP to exploit abundant mid-summer aggregations of euphausiids (Baker et al. 1992); however, this hypothesis has never been explicitly tested. Whale preferences for euphausiids have been inferred from

relatively limited sampling decades ago (*e.g..,* Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987) and no effort has been made to determine whether their arrival in the area and subsequent abundance patterns are correlated with the availability of prey. The goal of this dissertation is to formally examine the relationship between whales and euphausiids in FS/SP. As well, by considering the nature of this relationship in light of the findings of other studies regarding both seasonal and annual abundance trends, it will consider whether prey availability is limiting the number of animals that can forage in FS/SP, and more generally, how FS/SP fit into a regional perspective of SE Alaska as a principal humpback whale foraging ground.

BACKGROUND: HUMPBACK WHALES IN THE NORTH PACIFIC, WITH AN EMPHASIS ON SOUTHEAST ALASKA

Humpback whales in the North Pacific migrate to one of three principal wintering areas – Asia, Hawaii and Mexico – to mate and give birth (Nishiwaki 1966, Rice 1974, Calambokidis et al. 2008). Individuals generally travel to the same wintering area each year, and interchange between the three areas is low (Calambokidis et al. 2008). Whales begin to arrive in these areas in November and their abundance typically peaks in late February. Their numbers decline thereafter as animals depart for high-latitude feeding grounds (Norris & Reeves 1978). Females with newborn calves are the last of the migrants to leave the breeding grounds (Craig et al. 2003).

Each spring, North Pacific humpbacks assemble in several coastal feeding areas that form a near-continuous chain from the Russian Far East to northern California (Calambokidis et al. 2008). Individuals show strong maternally-directed fidelity to

these areas, and, as with the wintering areas, interchange between them is low. SE Alaska and northern British Columbia represent a discrete feeding area with an estimated abundance of approximately 6,000 whales, about one-third of the total North Pacific humpback population (Calambokidis et al. 2008). Within this general region there appears to be further structure to the population as sightings of the same individuals in both SE Alaska and N British Columbia are comparatively rare. At the time of this study (2008), there were an estimated 1875 whales in northern Southeast Alaska (J. Straley, University of Alaska Southeast, personal communication) - an area that includes FS/SP - and the population appears to be growing at an annual rate of ~6% (Calambokidis et al. 2008).

Animals feeding in SE Alaska winter primarily in Hawaii (Calambokidis et al. 2008). The shortest documented travel time between the two regions is 39 days (Gabriele et al. 1996), and a whale monitored by satellite made the trip in 30 days (B. Mate, personal communication). The majority of animals are assumed to migrate to Hawaii each year; however, whales are observed in SE Alaska in all months (Straley 1994). Whether this results from overlap of whales departing late in the foraging season for Hawaii with those returning early, or individuals remaining all year, is unclear. Because humpbacks fast while on the breeding grounds (Chittleborough 1965, Dawbin 1966, Brodie 1975), delaying or foregoing the migration could be strategies that allow individuals to increase their reproductive potential by acquiring additional resources on the feeding grounds.

In SE Alaska, humpback whales consume a variety of prey. In several areas (*e.g.*, GB/IS), foraging aggregations are associated with schooling forage fish, including Pacific herring (*Clupea pallasi*; Jurasz & Jurasz 1979, Krieger & Wing 1986), capelin (*Mallotus villosus*; Krieger & Wing 1986) and juvenile walleye pollock (*Theragra chalcogramma*; Krieger & Wing 1986). In FS/SP, whales feed primarily on euphausiids (Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987), and are generally associated with either *Thysanoessa raschii* (Krieger & Wing 1986, Dolphin 1987) or *Euphausia pacifica* (Jurasz & Jurasz 1979, Bryant *et al*. 1981, Krieger & Wing 1986). However, it is unclear whether these associations reflect preferences for one species over another or whether they simply correlate with patterns of seasonal availability of these prey. Although associations between whales and immature euphausiid have been observed (Krieger & Wing 1986), it is also unclear whether whales target them. Humpbacks typically forage alone or in loose, ephemeral groups (Weinrich 1991), although long-term stable associations are observed in SE Alaska and elsewhere among whales targeting piscivorous prey (Baker & Herman 1984, Weinrich 1991, Sharpe 2001).

The dissertation is comprised of three primary chapters that outline a series of independent studies addressing aspects of the foraging ecology of humpback whales in SE Alaska. Chapter 2 examines the euphausiid community in SE Alaska. There is a paucity of data on euphausiids in the region's inside waters despite widespread recognition that they are important to marine communities there and elsewhere (Falk-Petersen et al. 2000, Jahncke et al. 2005, Weitkamp & Sturdevant 2008). Chapter 2

outlines a standardized sampling protocol to: *i*) identify the euphausiids that are present in SE Alaska's inside waters; *ii*) describe their relative abundance patterns; and, *iii*) characterize their spawning schedules and recruitment patterns. The goal is to provide a more complete view of the euphausiid community in the region, and a foundation for the analyses of whale behavior, abundance and distribution in subsequent chapters. Chapter 3 builds on earlier studies that demonstrate an association between whales and euphausiids in FS/SP (Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987) by examining whether humpback whales target specific euphausiid species, life-stages, and/or patch characteristics. These have not been explicitly addressed to date and have considerable implications for interpreting the behavior of whales in the region. Chapter 4 considers whether the abundance and distribution patterns of humpback whales in FS/SP correlate with seasonal variability in prey availability, and compares these patterns to ones reported decades earlier to examine whether local whale abundance reflects regional trends in population growth. Finally, chapter 5 is a synthesis of the preceding chapters with a general summary of the research findings, and a discussion of: 1) the role of fish as prey for whales in the study area; and, 2) the role of FS/SP as a summer foraging area within SE Alaska.

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CHAPTER 2: OBSERVATIONS OF THE LIFE HISTORIES OF
EUPHAUSIIDS IN SOUTHEAST ALASKA

ABSTRACT

The life histories, abundance and distribution of euphausiids in Frederick Sound
and lower Stephens Passage, Southeast Alaska were examined over a three-month
period in late spring and summer, 2008. Net sampling at random sites and in areas
where a strong, sonar-detected scattering layer was observed yielded four species,
Thysanoessa raschii, *T. longipes*, *T. spinifera*, and *Euphausia pacifica*. Abundance
patterns of immature euphausiids combined with observations of adult females
carrying spermatophores suggested that the three *Thysanoessa* species spawned in
association with the spring phytoplankton bloom in early April, whereas *E. pacifica*
did so later in the spring. This difference in spawning chronology led to variability
across the summer in numerical dominance, with *T. raschii* dominating samples in
early summer and *E. pacifica* becoming increasingly prevalent later in the season.
The widespread distribution of immature euphausiids contrasted with the limited and
patchy distribution of adults, which were observed primarily in association with slope
habitat in the study site. This suggests that immature euphausiids had not yet
developed the ability of adults to maintain their position in the water column, and
were consequently far less aggregated.

INTRODUCTION

Inshore waters of Southeast (SE) Alaska are important foraging habitats for numerous marine mammal species (Dahlheim et al. 2009, Womble et al. 2009), including one of the largest feeding aggregations of humpback whales (*Megaptera novaeangliae*) in the Northern Hemisphere (Calambokidis et al. 2008). The region also supports a diverse array of marine fishes, including several that are commercially important (*e.g.*, *Oncorhynchus* spp; Johnson et al. 2005). Nevertheless, little is known about the biological patterns and processes that characterize the region's inshore waters. As noted recently: "we remain profoundly ignorant of the oceanography, marine biogeography and marine biology of SE Alaska" (Weingartner et al. 2009), a sentiment echoed by others (Dahlheim et al. 2009, Lindstrom 2009).

This paucity of information extends to the euphausiid community, which, to date, has received relatively little attention. Much of what is known about euphausiids in SE Alaska comes from research on the foraging behavior of baleen whales in the region (Jurasz & Jurasz, 1979, Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987). The picture that emerges from these studies is limited to an overview of the species that are present during mid to late summer (*i.e.*, *Thysanoessa raschii*, *T. longipes*, *T. spinifera* and *Euphausia pacifica*); however, the results are potentially biased because sampling was conducted in association with feeding whales. As well, these studies lack information about euphausiid life histories in the region. In coastal regions where euphausiids have been studied more extensively, they are important in the transfer of primary production to higher trophic levels (Falk-Petersen et al. 2000),

and are key prey for cetaceans (Bryant et al. 1981, Dolphin 1987), seabirds (Hunt et al. 1996, Jahncke et al. 2005), and many commercially valuable fish (Clausen 1983, Tanasichuk et al. 1991, Weitkamp et al. 2008). Therefore, a closer examination of the euphausiid community in SE Alaska is warranted.

The objective of this study was to examine life history attributes of euphausiids in SE Alaska. Immature euphausiids were sampled over a three-month period that captures the recruitment of juveniles and their subsequent development in the region. In addition, adult euphausiids were sampled and examined for reproductive structures. The data are used to infer the spawning schedules and relative abundances of euphausiid species in the region. The study was part of a larger research project examining the foraging ecology of humpback whales.

METHODS

All data were collected between 8 June and 31 August, 2008 in Frederick Sound and lower Stephens Passage, SE Alaska (56°-57° N, 133°-134° W; Figure 2.1). These bodies of water are part of a system of fjords and channels that comprise the inside waters of the region. Frederick Sound connects Stephens Passage to Chatham Strait, which is the primary channel through which offshore waters from the Gulf of Alaska enter the region. Sampling of euphausiids was conducted independent of the larger research project; however, it was constrained to some extent by the use of small inflatable vessels that were amenable to the larger focus of the research program. Consequently, it was not possible to sample at night or outside of the study

period, and net sampling was limited to single oblique tows. Because of these limitations, the sampling strategy was presumed to be insufficient to characterize adult euphausiid abundance given their well-documented escape reactions (Wiebe et al. 1982, Hovekamp 1989, Simard & Sourisseau 2009); therefore, adult specimens are only used as indicators of reproductive activity (*i.e.,* attached spermatophores).

Euphausiids were sampled from a 6.4 m rigid-hull inflatable boat (RhIB). Samples were collected during a series of daytime hydroacoustic surveys initiated at approximately 20-d intervals over the 12-week study. For each survey, the study region was partitioned into 18 strata, each 4.6 km-wide and oriented approximately perpendicular to the long axis of the Sound; a single transect was randomly placed within each stratum. Single oblique net tows were conducted at two randomly selected sites along the transects each day. Because these random tows might under-sample the presumably patchy distribution of the zooplankton community, two additional oblique tows were conducted daily in areas where the 120 kHz echosounder showed a strong scattering layer. It was not always possible to collect four samples daily, as both day length and transect length varied; therefore, sample sizes differed among surveys. The entire 18 strata could be surveyed in 6 d. Occasionally, inclement weather made it necessary to stop surveying a transect early or skip a day altogether. The data from these incomplete transects were discarded and the survey was resumed the next day at the beginning of the incomplete transect to accomplish a full survey. On no occasion did it take more than seven consecutive days to complete a single survey.

At each tow site, samples were collected using a black, 0.75 m diameter General Oceanics plankton net with a 3:1 length-to-opening ratio and 1 mm mesh size by first lowering the net vertically to 100 m (or within 5 m of the bottom where shallower) with the cod-end weighted to ensure that the open net back-flushed during its descent. Net depth was determined using marks painted onto the winch cable at 5 m intervals and verified later using data from a ReefNet Ultra Sensus dive logger (accuracy of ± 1 m) attached to the net. The net was retrieved to the surface at an approximate vertical and horizontal speed of 0.33 m/s and 2 m/s, respectively, by engaging the winch and simultaneously accelerating the vessel. A broad anticlockwise circular path was traversed to ensure that the winch cable, which was towed mid-ship on the port side of the vessel, did not foul the propeller. The contents from the tow were preserved at-sea in a buffered 4% formalin solution for later analysis.

Each sample was split using a Folsom plankton splitter to yield approximately 100 individuals of the most numerous taxa in the smallest subsample (these were typically copepods, which are not considered here). All euphausiids within successively larger sub-samples were counted and identified to species until at least 100 individuals had been examined. Each euphausiid's length - from the base of the eye stalk to the end of the telson - was recorded to the nearest 0.1 mm, and the number of terminal and postero-lateral spines, and presence or absence of a petasma and/or attached spermatophore were noted. Individuals with more than 2 postero-lateral spines were considered to be larvae and those with only 2 spines (and a single terminal spine) were considered to be juveniles (Brinton et al. 2000). Individuals

were considered to be adults if they had reproductive organs or were clearly larger than the juvenile cohort (typically > 16 mm).

Immature euphausiid density was calculated by dividing the count estimates from each sample by the volume of water sampled. To measure volume sampled, a General Oceanics flow-meter was attached to the net mouth for each net tow; however, the readings from the unit were unreliable. Instead, sample volume was estimated from the tow length multiplied by the net mouth area (~0.44 m^2), where tow length was estimated as the hypotenuse of the horizontal distance towed (from duration and speed) and maximum depth.

For density comparisons between species and within species between surveys, a series of Kruskal-Wallis nonparametric tests were used. The distribution of net samples was plotted in ESRI's ArcGIS (v9.3) with euphausiid density (all species combined) represented by scaled symbols; adult euphausiids were also plotted for comparison. The symbols were scaled to the maximum density for each survey (*i.e.,* 5 different maxima when all surveys are plotted together). The plots ignore widespread seasonal changes in density in favor of more effectively illustrating the within-survey spatial patterns of abundance.

RESULTS

A total of 49 random and 48 non-random samples collected during five different surveys in Frederick Sound and lower Stephens Passage were analyzed (Table 2.1). Four euphausiid species were observed: *Thysanoessa raschii*, *T. longipes*, *T.*

spinifera, and *Euphausia pacifica*. Immature *T. raschii* were present in > 80% of samples in all but the last survey (Figure 2.2). Although immature *T. longipes* were less prevalent in the first survey, a similar pattern to *T. raschii* was observed for *T. longipes* in later surveys. In contrast, the proportion of random samples containing immature *E. pacifica* was initially 0% but increased to approximately 75% in survey 4 (S4). Immature *T. spinifera* were relatively rare and only found in S3 and S4. Among samples in which a given species was present, the density was highest on average for immature *T. raschii* although relatively dense aggregations of *E. pacifica* were observed in S4 (Figure 2.3). When they were observed, both *T. spinifera* and *T. longipes* occurred in comparatively low densities (Figure 2.3).

To examine seasonal changes in the density of immature specimens within each species, the first survey where they were observed was excluded because density estimates prior to, and including, these early surveys were influenced by the low retention efficiency of the 1 mm mesh net for larval stages. The density of each species was lowest in the final survey (*E. pacifica*: $X^2 = 32.76$, $p < 0.001$, $n = 34$; *T. raschii*: $X^2 = 38.62$, $p < 0.001$, $n = 44$; *T. longipes*: $X^2 = 8.95$, $p < 0.062$, $n = 44$), although it is notable that, unlike the other species, *E. pacifica* reached a maximum in S4. There were too few samples to test for a seasonal peak in *T. spinifera*. In general, the proportion of samples where immature individuals from each species were present declined in later surveys (Figure 2.2).

The randomly located net samples were used to examine the size distribution of immature euphausiids. Only *T. raschii* and *T. longipes* were sufficiently abundant

across the five surveys to generate meaningful size distribution figures (Figure 2.4). The lower length limit observed for both species, which is likely a function of the net's 1 mm mesh size, was approximately 2.9 mm. *T. raschii* individuals of this size typically had 7 terminal spines, which is indicative of early furcilia stages. This agrees with estimates for the length of early furcilia of *T. raschii* from the Clyde Sea (Mauchline 1965). Juvenile *T. raschii*, which were identified by a reduction in terminal and postero-lateral spines to 1 and 2, respectively, were first observed in S2, suggesting that the earliest seasonal transition from larval to juvenile stage occurred sometime between 13 June and 27 June in the study area. Juvenile *T. longipes* were first observed in S1, suggesting an earlier transition from the larval stage than *T. raschii.* By the final survey, no larval *T. longipes* were found, whereas the remaining *T. raschii* larval stages were primarily (~78%) late stage furcilia. The size distribution of juveniles of both species shifted to larger lengths in successive surveys, as seen by the shift in the maximum immature length.

Because of the rarity of adult euphausiids in the random samples, random and non-random samples were combined to examine the proportion of females that were carrying spermatophores. Only *T. raschii* and *E. pacifica* were observed with attached spermatophores; however, there were notable differences between the two species in the timing and frequency of these observations. Overall, only 6% of female *T. raschii* (n = 17) had attached spermatophores and only during the first survey, although no adults of this species were observed again until the third survey. In contrast, 48% of all female *E. pacifica* ($n = 50$) were observed to be carrying

spermatophores, with 47% in S1 ($n = 15$), 67% in S2 ($n = 9$), 57% in S3 ($n = 7$), and 50% in S4 ($n = 14$). No females were observed carrying spermatophores in S5 ($n = 5$).

A single anecdotal sample collected on 21 April, 2008 in Petersburg Harbor at the confluence of Wrangell Narrows and the eastern arm of Frederick Sound, approximately 60 km east of the main study area (Figure 2.1), was analyzed to provide additional insight into the reproductive activity of several euphausiid species. At that time, a dense euphausiid surface aggregation observed within several meters of shore was sampled using a dip-net (~1 mm mesh). A random subsample of 100 individuals yielded only three species – all adults of both sexes - in the following proportion: *T. raschii,* 78% (60 females and 18 males); *T. spinifera*, 21% (13 females and 8 males); and *E. pacifica*, 1% (1 female)**.** Approximately 28% of female *T. raschii* and 31% of female *T. spinifera* were carrying spermatophores; however, the single female *E. pacifica* was not.

Immature euphausiids (all species combined) were widespread with no obvious spatial pattern in the study region (Figure 2.5). Only a few samples lacked immature euphausiids entirely. In contrast, adult euphausiids were largely absent from samples collected over the deep portions of the study site, and were limited primarily to samples from slope and shallow habitats.

DISCUSSION

All four euphausiid species identified in this study have been observed previously in SE Alaska (Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987, Paul et al. 1990). *T. raschii* was the most abundant euphausiid in the summer of 2008, occurring in the highest proportion of samples and in the highest densities within those samples. The numerical dominance of *T. raschii* has been reported previously in SE Alaska (Krieger & Wing 1986, Dolphin 1987, Paul et al. 1990) and in some regions of the Bering Sea (Hunt et al., 1996, Coyle et al. 2008), but differs from the northern Gulf of Alaska where *T. spinifera* and *T. inermis* dominate the shelf and *E. pacifica* the shelf break (Coyle & Pinchuk 2005).

High abundances of immature individuals and females carrying spermatophores provide an indication of when *T. raschii* reproduces in SE Alaska. Juvenile *T. raschii* first appeared in the second survey (S2). Combining development time estimates of 2-3 weeks from egg to calyptopis III (Paul et al. 1990) and 6 weeks from early furcilia to juvenile (Dehalt 1985) in SE Alaska provides an estimate of approximately 2 months for individuals to develop from egg to early juvenile, which is similar to the estimate for *T. raschii* in the Clyde Sea (Mauchline 1965). Using this estimate, the presence of juveniles in S2 (late June) suggests that *T. raschii* began spawning around mid to late April. This corresponds well with the anecdotal observation of 28 % of *T. raschii* females carrying spermatophores on 21 April in Petersburg Harbor. We observed *T. raschii* with spermatophores only in S1, which was in the second week of June. Females observed in mid-July were not carrying spermatophores. Therefore, it is likely that seasonal breeding ended sometime between the middle of June and the

middle of July, although late-stage furcilia present in samples collected towards the end of August suggest that breeding continued at least until the end of June.

The spawning period for *T. raschii* varies considerably among different locations. In the Gulf of St. Lawrence, individuals typically spawn in April and May (Berkes 1976), but in Balsfjorden, northern Norway they spawn for 2-3 weeks in May only (Falk-Petersen & Hopkins 1981). In the Barents Sea, spawning occurs in late July and early August (Timofeyev 1994). In the Bering Sea, a high proportion of female *T. raschii* in the stomachs of short-tailed shearwaters (*Puffinus tenuirostris*) in August had spermatophores indicating that the birds were foraging on surface swarms of breeding individuals (Hunt et al. 1996). It appears that in SE Alaska, *T. raschii* breeding occurs earlier than in the Bering Sea, and may last 2.5-3 months. Variability in the spawning period between these geographic regions correlates with regional differences in the timing, duration and magnitude of the spring phytoplankton bloom. High concentrations of euphausiid eggs have been observed previously in association with the spring phytoplankton bloom in Auke Bay, Alaska (Paul et al. 1990). *T. raschii* uses the bloom as the major source of energy for forming reproductive products (Mauchline & Fischer 1969, Paul et al. 1990, Dalpadado & Skjoldal 1991). Secchi disk data from Auke Bay in 2008 suggested that the bloom started around the beginning of April (B. Wing, Auke Bay Laboratory, personal communication). Typically, the bloom in Auke Bay begins as many as 7-10 days earlier than in other areas in the region (B. Wing, Auke Bay Laboratory, personal communication); therefore, it is possible that the phytoplankton bloom in Frederick Sound and lower

Stephens Passage occurred in the first weeks of April. This is consistent with the mid-April estimate for the onset of *T. raschii* spawning.

Although less abundant, immature *T. longipes* were nearly as widespread as *T. raschii* and showed a similar seasonal pattern of occurrence in the region. *T. longipes* is distributed widely in the subarctic Pacific Ocean and its marginal seas (Brinton et al. 2000), and is generally considered to be epi- or meso-pelagic (Brinton et al. 2000, Iguchi & Ikeda 2004). In the Japan Sea, it is found from near the surface to a depth of 1000 m, with the majority of specimens found at 150-500 m during the day (Iguchi & Ikeda 2004). Generally, the species has been reported to depths of 250 m or more (Brinton et al. 2000). Therefore, it is possible that SE Alaska net samples collected during daytime from depths greater than 100 m would have yielded higher densities; however, previous sampling to 200 m in the region resulted in similarly low numbers of *T. longipes* (Bryant et al. 1981). Because adult female *T. longipes* were not observed until mid-August (S5) and were not carrying spermatophores, little can be inferred about their breeding activity in the region other than the species had likely stopped breeding earlier. In addition, the earlier appearance of juvenile and subsequent disappearance of larval *T. longipes* relative to *T. raschii* suggests that *T. longipes* may spawn earlier than *T. raschii*, although different development times could account for this as well. Observations in the northern North Pacific and the Japan Sea indicate that spawning in *T. longipes* is confined to spring (Nemoto 1957, Iguchi & Ikeda 2004).

The seasonal pattern of immature *E. pacifica* abundance was different than that of *T. raschii* and *T. longipes*. Both the proportion of samples with immature *E. pacifica* and the density of individuals within those samples were initially low but increased to a maximum in early August (S4). In addition, a relatively high proportion of females carried spermatophores during all but the last survey at the end of August. This suggests that the breeding season for *E. pacifica* in SE Alaska is later and more prolonged than that of *T. raschii* and *T. longipes*. *E. pacifica* is a numerically dominant euphausiid throughout much of its range, including the California Current system (Ressler et al. 2005, Gómez-Gutiérrez et al. 2005), coastal British Columbia (Tanasichuk 1998), and the northern Gulf of Alaska (Coyle & Pinchuk 2005, Pinchuk et al. 2008). The median time for *E. pacifica* to develop to the first furcilia stage in the lab is 21 days at 10.5 °C (Feinberg et al. 2006) and 22 days at 8 °C (Ross 1981). At that rate of development, the early-stage furcilia larvae first observed in this study during the second survey (27 June) were likely spawned sometime in early June, which is consistent with the observation that nearly half of the females were carrying spermatophores in survey 1. If these larvae marked the beginning of the primary spawning period, coupled with females carrying spermatophores during - but not after – survey 4, then spawning is likely to have occurred over a 2.5 month period, from mid-June through August. Timing of spawning in *E. pacifica* varies widely across the species range, and in some areas may even occur year-round (Gómez-Gutiérrez et al. 2006, and references therein). In Dabob Bay, Washington, (lat. 48°N) spawning takes place from March through mid-May (Bollens et al. 1992), whereas slightly to

the north in the Strait of Georgia, BC, (lat. 49°-51°N), peak spawning occurs from May to June (Heath 1977). The estimated June-August spawning period in SE Alaska (lat. 57°-58°N) fits with the trend of later spawning in the north. In general, however, the delayed breeding activity in SE Alaska calls into question the link between *E. pacifica* spawning and the spring phytoplankton bloom, as has been reported to occur elsewhere (Smiles & Pearcy 1971, Brinton 1976). In that regard, others have suggested that protozoan and/or metazoan microplankton might provide significant nourishment for pre-spawning adults, allowing them to uncouple their breeding activity to some extent from peaks in primary production (Bollens et al. 1992).

T. spinifera was the least abundant euphausiid in the study region. *T. spinifera* is numerically co-dominant with *E. pacifica* in the California Current system (Ressler et al. 2005, Gómez-Gutiérrez et al. 2005), coastal British Columbia (Tanasichuk 1998), and the northern Gulf of Alaska (Coyle & Pinchuk 2005, Pinchuk et al. 2008). Immature and adult *T. spinifera* were infrequently observed so it was not possible to identify the breeding pattern for this species in the study area. The observation of breeding *T. spinifera* females in Petersburg Harbor on 21 April, but at no other time from early June onwards suggests that, as with the other *Thysanoessa* spp, *T. spinifera* spawned primarily in spring in association with higher phytoplankton concentrations.

Regardless of the timing of breeding and larval recruitment in the region, all four euphausiid species had lower abundances during the final survey in late August.

Several studies have suggested that euphausiids experience a high rate of larval/juvenile mortality. Laboratory-reared *E. pacifica* suffered high mortality in the early larval stages (Feinberg et al. 2006), and survival to juvenile stage for this species has been estimated at 2.4 % at 8°C (Ross 1981). These laboratory-based estimates do not include the loss due to predation that occurs in the field. Prior field studies on various zooplankton populations in SE Alaska reported substantial declines in abundance from spring to autumn (Park et al. 2004, Sturdevant et al. 2007). Additionally, other factors could contribute to the observed decline in abundance, such as an increased ability to avoid nets as larvae develop, advection from the study site, or vertical migration of a larger fraction of the community below the depths sampled in this study. To this last point, the hydroacoustically-determined depth of the scattering layer became deeper in the last survey (Figure A.1), which could account for the lower net tow densities; however, it is not known to what extent immature euphausiids contributed to the acoustic scattering layer.

The different spawning periods for the four species observed here might explain earlier reports that are in conflict regarding euphausiid species dominance in the region. In the previous studies, no distinction was made between different life-stages when estimating abundance and it is likely that immature euphausiids contributed more to the net tow samples than adults. Therefore, it is not surprising that studies where sampling occurred from spring to mid-summer (Dehalt 1985, Dolphin 1987, Paul et al. 1990) concluded that *T. raschii* was the dominant species, whereas those that sampled in late summer (Bryant et al. 1981) found primarily *E. pacifica*. It is

clear from the present study that the timing of sampling can greatly influence the relative proportion of species within those samples and that numerical dominance is potentially a spatially and temporally varying feature of the community.

Finally, there appeared to be differences in the spatial distribution of immature and adult euphausiids. Immature euphausiids were nearly ubiquitous throughout the study area, occurring in all but five random net tows. The eggs and early larval stages of euphausiids behave as relatively passive drifters and can be widely dispersed by the currents of the inshore waters of SE Alaska. However, as they develop through the furcilia stages and become juveniles their swimming ability increases dramatically and they may begin diel vertical migrations, which allows them to avoid daytime predators in the surface waters (*e.g.,* Iwasa 1982, Gliwicz 1986). Presumably, this increased swimming ability also allows them to aggregate in areas of higher productivity. In contrast, adults were less widespread than immature euphausiids. Although this patchiness might be an artifact of the difficulty with which adult euphausiids are sampled, their tendency to be found over the slope habitats within the study area is consistent with reports of their distribution in other regions (Mackas et al. 1997). If so, the differences in the distribution of adult and immature euphausiids suggest that immature euphausiids had not yet fully developed the ability of adults to maintain their position in the water column.

This study suggests the four euphausiid species in SE Alaska differ in their relative abundance and breeding chronology. Differences in reproductive timing between *E. pacifica* and the *Thysanoessa* species led to a protracted period of larval

recruitment and availability to predators that depend on these early life-stages. This, coupled with variability in species- and age- specific patterns of energy metabolism and lipid storage (Falk-Petersen et al. 2000), may result in more complex trophic interactions and energy pathways than simpler systems dominated by a single species or several species having similar reproductive timing.

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Table 2.1. Survey dates (2008) and number of associated random and non-random net samples used in the analyses of euphausiid distribution and abundance in Frederick Sound/Stephens Passage.

Survey	Date	Random (N)	Non-random (N)	Combined
1	8 June - 13 June	5	10	15
2	27 June - 3 July	10	9	19
3	15 July - 22 July	10	10	20
4	5 August - 10 August	14	10	24
5	27 August - 31 August	10	9	19
Total		49	48	97
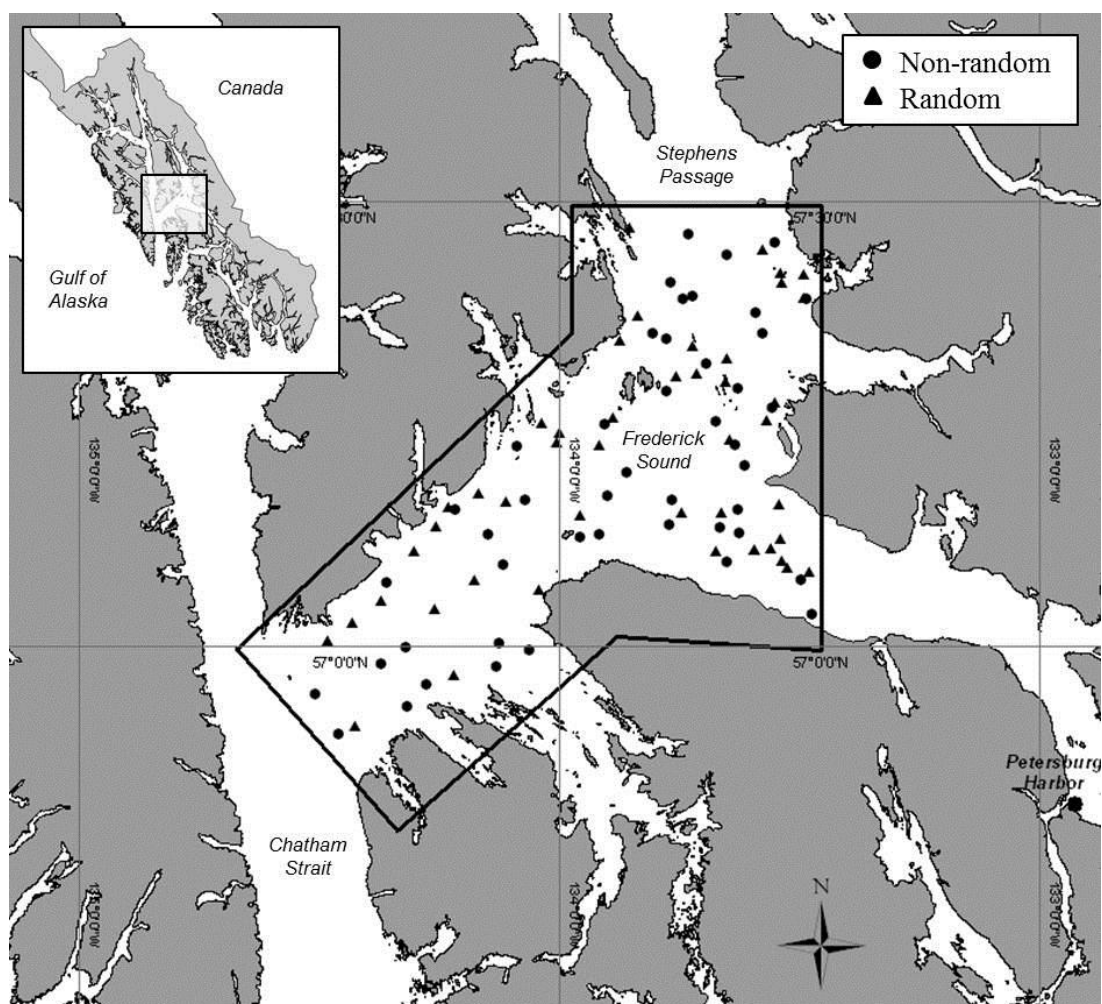
Figure 2.1. Study area in Frederick Sound and lower Stephens Passage with location of random and non-random net tow sites. The site of a single sample collected on 21 April 2008 in Petersburg Harbor is shown in the bottom right corner. The inset shows the location of the study area in Southeast Alaska.
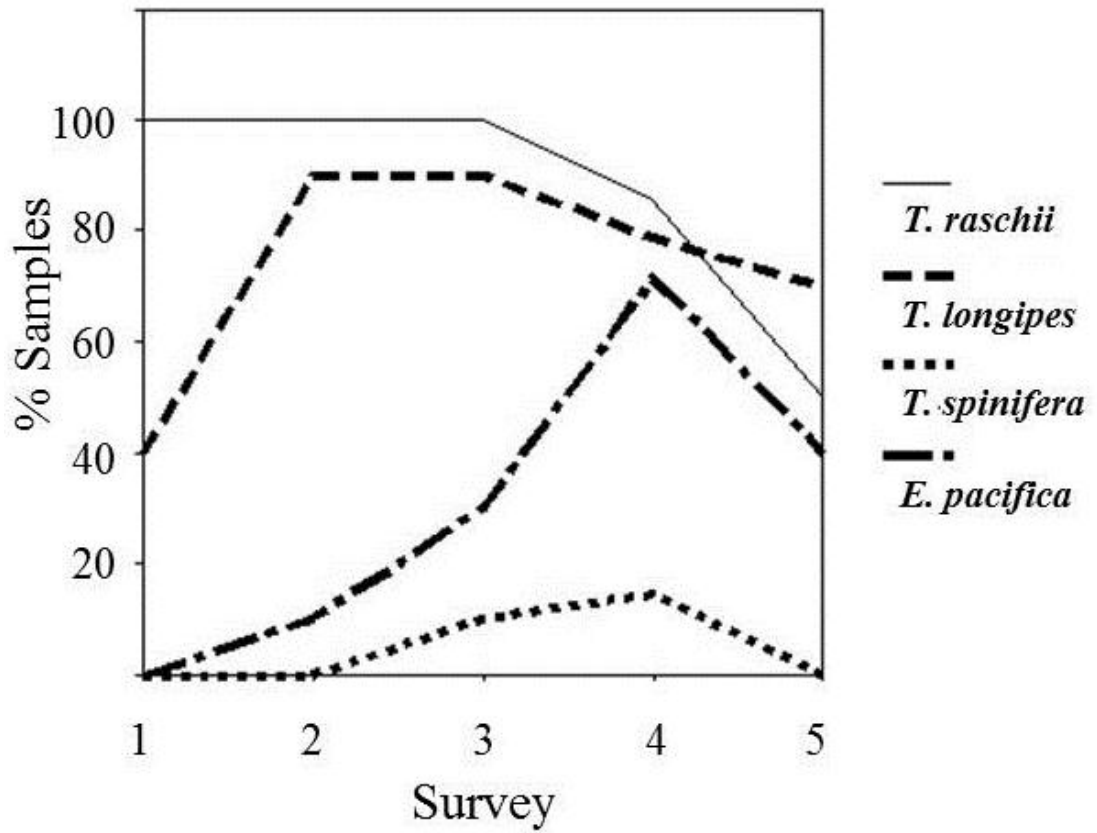
Figure 2.2. Proportion of random samples collected in Frederick Sound/Stephens passage, Southeast Alaska containing immature euphausiids from each of four species across the field season.
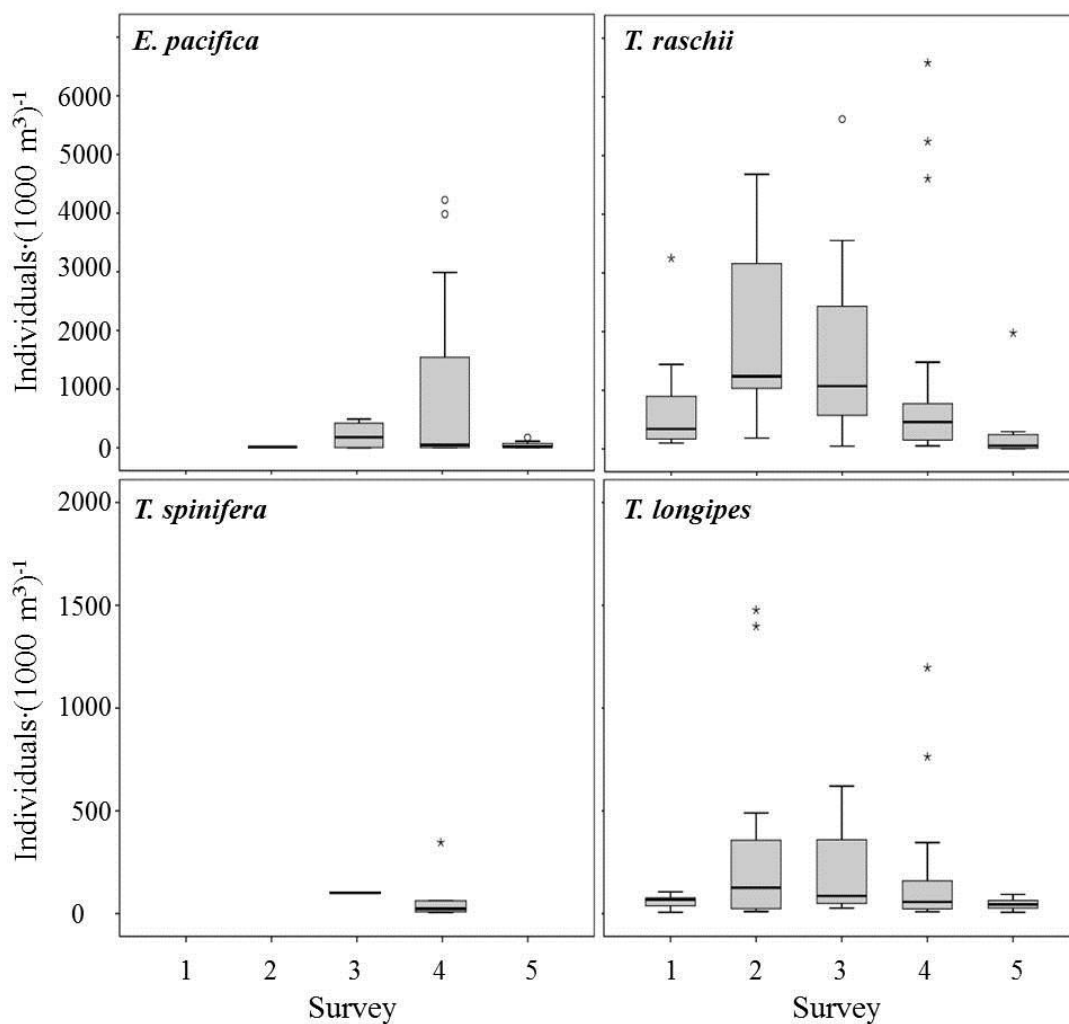
Figure 2.3. Density of immature euphausiids from randomly-located samples where individuals were present. Boxes represent interquartile range with median indicated by the line. Circles represent outliers (cases with values between 1.5 and 3.0 box lengths from the box edge) and asterisks represent extreme cases (those with values greater than 3.0 box lengths from the box edge). A single extreme case is not shown for *T. raschii* in survey 2 (84,145 individuals per 1000m^3). Note the difference in scale between the upper and lower plots.
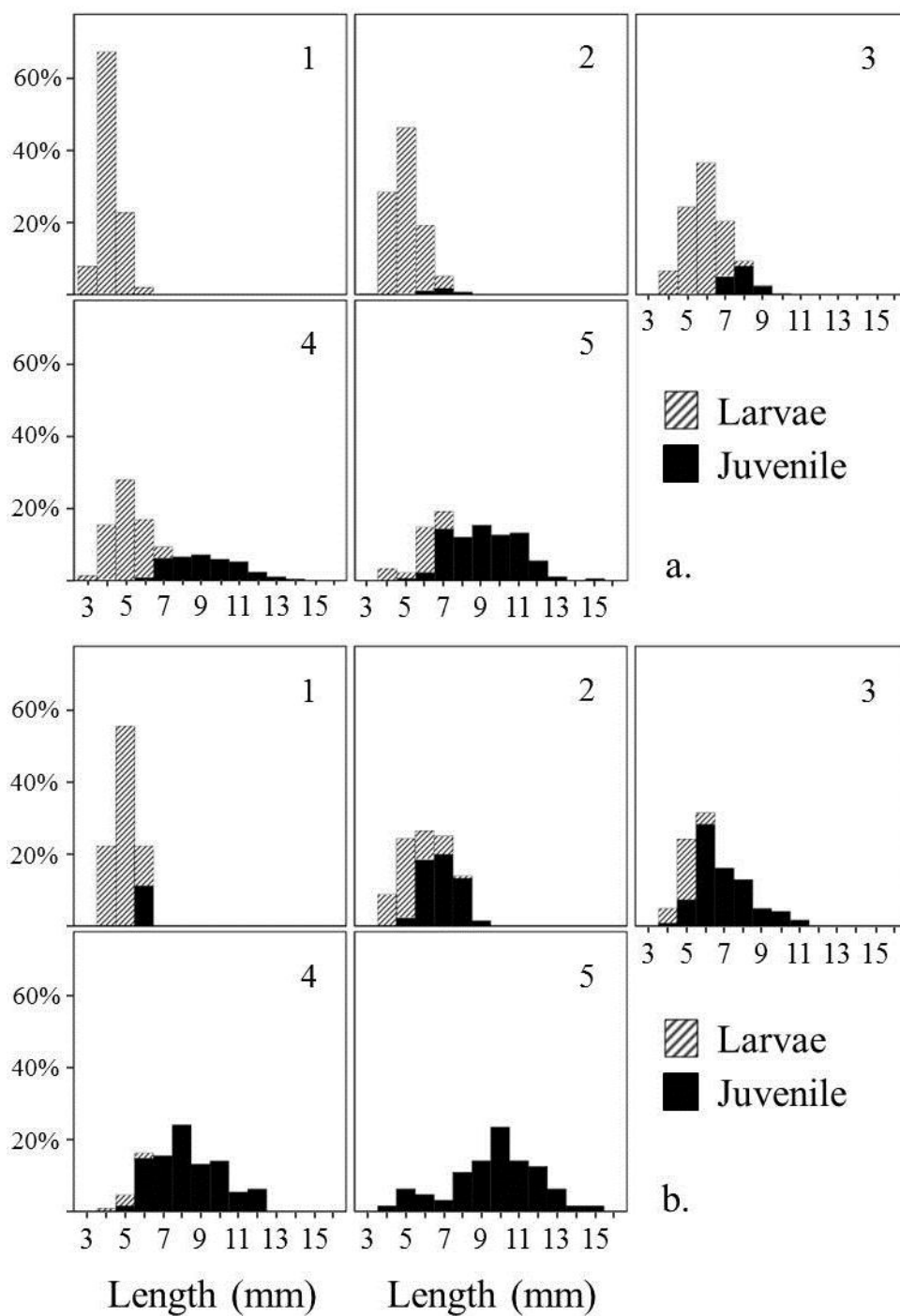
Figure 2.4. Length distribution of immature (*a*) *Thysanoessa raschii* (n = 4580) and (*b*) *T. longipes* (n = 471) from random net samples collected during the five surveys in Frederick Sound/Stephens Passage, Southeast Alaska.
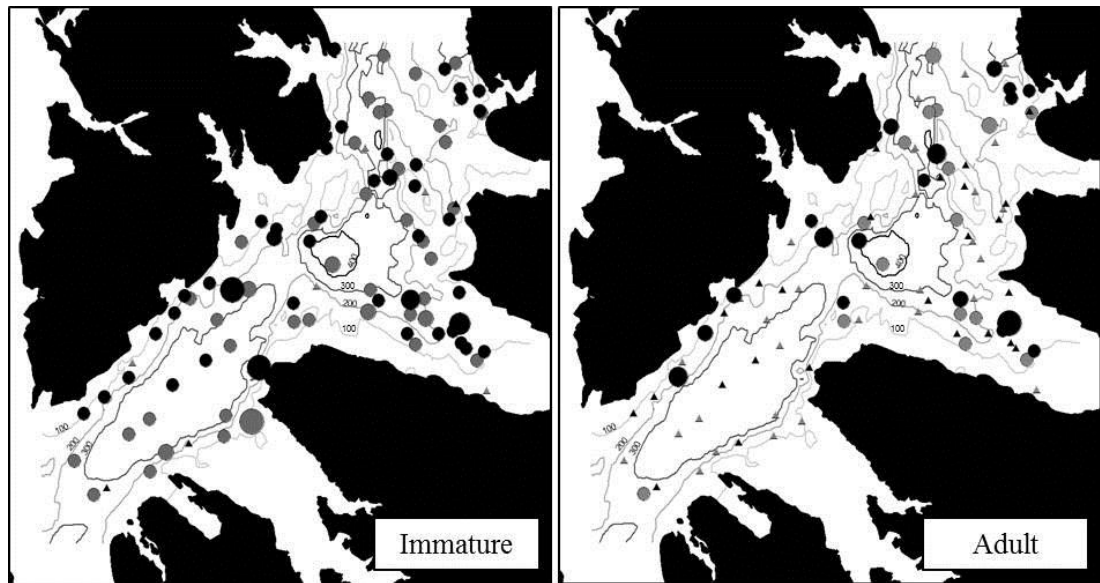
Figure 2.5. Distribution of immature and adult euphausiids from random (gray) and non-random (black) net samples from all surveys in Frederick Sound/Stephens Passage, Southeast Alaska. The scale represents percentage, in 20% increments, of the maximum densities observed during the study. Samples where no individuals were found are represented by triangles. Contours were generated from the sonar-detected bottom data during the hydroacoustic surveys and represent 100 m depth intervals.

CHAPTER 3: ARE HUMPBACK WHALES SELECTIVE FORAGERS WITH RESPECT TO EUPHAUSIIDS IN SOUTHEAST ALASKA?

ABSTRACT

Several euphausiid species co-occur in the inshore waters of Southeast Alaska. Differences in their life histories result in different patterns and timing of juvenile recruitment and, presumably, energy density that predators could potentially exploit by targeting one species or life-stage over another. Euphausiids are the primary prey of humpback whales (*Megaptera novaeangliae*) in the region. Whether whales target some species or life-stages over others has not been explored. In this study, euphausiids were sampled in association with whales in Frederick Sound and Stephens Passage, Southeast Alaska both hydroacoustically and using plankton nets. Those samples were compared to random samples collected throughout the study site to determine whether whales targeted species or life-stages in disproportion to their availability in the area. The results suggested that whales selected high density adult euphausiid 'micropatches', but did not discriminate between species. It is possible that euphausiid species do not segregate sufficiently to allow the whales to be selective. Whales did, however, discriminate between life-stages and ignored immature euphausiids, which, presumably, were not large enough to be suitable prey. The results indicate that whales are both selective and opportunistic foragers with respect to euphausiids in the region.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) have shown a remarkable population recovery in the North Pacific from an estimated 1,200 individuals at the end of the whaling era (Johnson & Wolman 1984) to a present abundance of more than 18,000 individuals (Calambokidis et al. 2008). As a result, conservation concern for this humpback whale population is gradually giving way to concerns regarding the impacts that population growth has on North Pacific marine communities (*e.g.*, Witteveen et al. 2006). Central to the issue is the foraging ecology of these animals. Humpbacks are considered generalist predators that feed on a variety of macro-zooplankton and schooling forage fish (Nemoto 1970, Perry et al. 1999, Clapham & Link 2006). Optimal foraging theory predicts that whales will select prey types that maximize the energetic returns of foraging (Schoener 1971, Pyke et al. 1977). Where several potential prey species co-occur, there is suggestive evidence that whales preferentially target some species over others (Witteveen et al. 2008); however, it is unclear to what extent this occurs. To address how humpback whales fit into contemporary food webs, a clearer understanding of their foraging patterns is required.

Southeast (SE) Alaska supports one of the largest summer feeding aggregations of humpback whales in the northern hemisphere (Calambokidis et al. 2008, Straley et al. 2009). Despite a documented preference for euphausiids in the region (Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987) and the co-occurrence of several species with different life histories and abundance patterns (see Chapter 2), no study has

determined whether whales preferentially forage on one euphausiid species or life-stage over another. Studies that have identified euphausiid species in association with humpbacks in the region have supported different conclusions; some have described humpbacks in association primarily with *Thysanoessa raschii* (Krieger & Wing 1986, Dolphin 1987), while others have indicated that humpbacks associate primarily with *Euphausia pacifica* (Jurasz & Jurasz 1979, Bryant et al. 1981). These results may be indicative of whales shifting their preference from one species to another in response to, for example, inter- or intra- annual variability in the availability of those species, or to seasonal variation in aggregation behavior or energy density per unit volume of seawater. There is also anecdotal evidence that humpbacks target juvenile euphausiids (Krieger & Wing 1986), which start to appear regionally in June (Chapter 2). However, published studies rarely mention the life-stage of euphausiids associated with foraging whales, and whale preferences for specific life-stages have not been addressed.

Here, I explore whether humpback whales target specific euphausiid species or life-stages as prey over others. I also examined whether whales targeted high-density euphausiid patches ("micropatches"), similar to those described in association with humpback whales by Dolphin (1987), or simply fed in euphausiid patches as they were encountered. Plankton net samples and hydroacoustic data collected in the vicinity of whales were compared to samples and hydroacoustic data collected in random locations throughout the region in an effort to distinguish features used by whales disproportionately to their occurrence in the study area. Where humpbacks

were associated with prey features in direct proportion to their occurrence, I further considered whether these reflected prey that were consumed as they were encountered (*i.e.,* opportunistically) or reflected features that were ignored by the animals and therefore represented random or coincidental associations. Sampling was conducted over 3.5 months to capture a period of high whale abundance (Chapter 4) and the initial recruitment of juvenile euphausiids in the study area (Chapter 2). The start of sampling coincided approximately with the end of the spawning period for *Thysanoessa* spp. and the beginning of spawning for *E. pacifica*.

METHODS

General Prey Sampling

All data were collected between 22 May and 9 September 2008 in Frederick Sound and lower Stephens Passage, SE Alaska, USA (57° 40.5' N, 133° 50.5' W; Figure 3.1). A split-beam 120 kHz (Simrad EK 60) echosounder was used to characterize the patch structure and vertical distribution of the prey field. The transducer was mounted to the end of a 6.6 cm diameter aluminum pole that extended downward from the port-side and mid-ship of a 6.4 m rigid-hull inflatable boat so the face of the transducer was 0.5 m below the surface. The unit used a 256 µs pulse and a power of 0.5 W, and was calibrated using a 38.1 mm diameter tungsten carbide sphere following Foote & MacLennan (1984).

Hydroacoustic surveys were conducted approximately every 20 d. For each survey, the study region was partitioned into 18 strata, each 4.6 km-wide and oriented

approximately perpendicular to the long axis of Frederick Sound, and a single transect was randomly placed within each stratum (Figure 3.1). Transects were surveyed during daylight at a vessel speed of 8 - 10 km h^{-1}. During good weather, two single-oblique net tows were conducted each day at randomly selected sites along the transects. Net samples were collected by lowering a 0.75 m diameter General Oceanics plankton net with a 3:1 length-to-opening ratio and 1-mm mesh size to 100 m (or within 5 m of the bottom where shallower), and hauling the net to the surface at an approximate vertical and horizontal speed of 0.33 m s^{-1} and 2 m s^{-1}, respectively. A broad anticlockwise circular path was traversed to ensure that the winch cable, which was towed mid-ship on the port side of the vessel, did not foul the propeller. The maximum depth was limited by the sampling winch. Both the upper limit of the scattering layer and the peak acoustic backscatter depth were generally shallower than 100 m (Figure A.1), and previous research in the study area had shown that whales rarely dive greater than this depth (Dolphin 1988). Because there are difficulties inherent in daytime sampling of adult euphausiids with plankton nets (Wiebe et al. 1982, Hovekamp 1989)**,** the data were used primarily to examine the presence/absence of adult euphausiids and to compare the relative proportion of the different species. Plankton samples were preserved at sea in a buffered 4% formalin solution in seawater for later analysis. An entire survey of the study site was completed within seven consecutive days during each of six 20 d blocks.

Sampling Prey Associated with Whales

During each hydroacoustic survey, whale sightings were recorded to identify general foraging areas within the study region. Once a survey was complete, the vessel traveled to one of those areas on the next suitable day and a search for a whale was conducted. The specific area to be searched was selected based upon its proximity to the survey vessel and the local weather conditions; however, on each subsequent day a different area was selected to ensure that whales were sampled broadly across the study site. Once a whale was sighted, a 1.85 x 1.85 km survey region was identified with the animal at its center. The region was partitioned into five equal 0.37 km-wide strata and a single transect was randomly placed within each (Figure 3.1). The long axes of the strata were oriented 138° / 318° to match the orientation of the strata from the general prey surveys. Starting in a random corner of the whale region, the transects were surveyed following the hydroacoustic protocol outlined earlier. Once complete, a net tow was conducted at a random location along one of the five transects following the described tow protocol. The vessel then traveled outside the survey region and searched for another whale. This process was repeated until dusk or weather conditions were no longer suitable for data collection. The prey fields in association with whales were sampled in this manner after each general prey survey within each 20-d block. Because it is generally not possible to identify whale behavior from surface observations alone, all individuals were treated as though they were foraging. Although this likely means traveling and resting whales were included in the subsequent analysis, whales likely forage most of the

time on their foraging grounds because they need to meet their annual energetic requirements in an abbreviated foraging season. In the only study that has attempted to quantify this in the region, mother-offspring pairs were considered to be foraging during ~80% of daylight observations (Szabo 2004).

Net Tow Data Analysis

Each net sample was split using a Folsom plankton splitter to yield approximately 100 individuals from the most numerous taxa in the smallest subsample. Starting with the smallest sub-sample, all euphausiids were counted and identified to species following Brinton et al. (2000) within successively larger sub-samples until at least 100 individuals were examined. Additionally, each euphausiid's length from the base of the eye stalk to the end of the telson was recorded to the nearest 0.1 mm. Finally, age and sex class were noted. Individuals with more than 2 postero-lateral spines were considered larval euphausiids and those with only 2 postero-lateral spines (and a single terminal spine) were considered juveniles (Brinton et al. 2000). Individuals were considered adults if they had reproductive structures or were clearly larger (typically > 16 mm in length) than the immature cohort.

The density of each taxon was calculated by dividing the count estimates from each sample by the volume of water sampled. The sampled volume was estimated for each tow by estimating the horizontal distance traversed during the tow using the tow duration and vessel speed, and then subsequently determining the oblique tow length - the hypotenuse of the triangle formed by the horizontal distance and the initial net

depth. Finally, the tow length was multiplied by the net mouth area. ANOVA was used to test for differences between random and whale samples with respect to the density of immature euphausiids. Survey number was included as a factor in the analysis. A residual plot indicated the data were not normally distributed so they were log-transformed.

Hydroacoustic Data Analysis

   Hydroacoustic data were processed into sample sets that could be compared between the general surveys and the whale surveys. The 18 transects from each prey survey were partitioned into 1.85-km transect segments to match the shorter transects sampled for the whale surveys. Three replicate sample sets were generated from each survey by randomly sampling transect segments ($n = 15$) without replacement from the resultant pool of 255. For comparison, a single set of transects was generated from each whale observation period that followed each survey by randomly sampling one of the five transects associated with each whale. As a result, four sets of 1.85-km transects were generated for each 20-d block: three replicate random sets and one whale set.

   All hydroacoustic data were processed using Sonardata Echoview (v4.3). The upper 1.5 m of data (*i.e.*, data < 2 m below the surface when transducer depth was accounted for) were excluded, which eliminated approximately 90 % of the surface noise. When necessary, additional surface noise was manually removed after examining the echograms. Data within 2 m of the sounder-detected bottom were also

excluded. Finally, additional noise in the water column (*e.g.*, periodic electrical interference from an unknown source on the survey vessel) was removed by excluding portions of transects where such noise was evident. The data were integrated to obtain Nautical Area Scattering Coefficients (m^2 / nmi^2; NASC) in 100 m horizontal by 10 m vertical bins to a depth of 150 m using volume backscatter (S_v) thresholds of -75 dB and -25 dB – chosen to remove backscatter resulting from targets too small/sparse or too large to be prey - and a time-varied threshold (TVT) of -125 S_v re 1 m. TVT was arrived at by examining the acoustic signal in clear water and fitting the associated time-varied gain curve following the approach outlined in the analysis software. The maximum depth for integration was chosen due to limitations of the sampling gear; however, Dolphin (1988) observed that whales in the region rarely ($< 3\%$ of observations) dove below 120 m. Theory (Mori 1998) and observations (Goldbogen et al. 2008) suggest that whales target the shallowest available prey, and both the upper limit of the scattering layer and the peak acoustic backscatter were generally shallower than 100 m (Figure A.1). The sampled depth range is considered appropriate for this study.

Echoview's single target (ST) detection algorithm was used to detect acoustic targets considered too big to be prey for the whales. For ST detection, the target strength (TS) threshold was set at -55 dB and only echoes where the normalized detected pulse length at 6 dB below the peak value was between 0.70 and 1.60 were considered to come from single targets. The ST data were exported in complimentary

100 m x 10 m bins so that the acoustic backscatter from these targets could be excluded from the general NASC estimates.

A single water-column integrated estimate of NASC was produced for each 1.85-km transect segment. Because electrical noise was occasionally present at depths > 100 m, NASC was integrated to 100 m only so that comparisons could be made between all samples. In addition, small-scale regions of high relative backscatter (hereafter referred to as 'patches') were identified using Echoview's school detection feature. This is based on the SHAPES detection algorithm and is typically used to identify fish schools that occur in discrete aggregations (Coetzee 2000); however, it is used more generally here to provide a consistent approach to detect notably dense regions of acoustic targets that may or may not occur as discrete schools. The upper and lower volume backscatter thresholds for patch identification were set at -25 dB and -60 dB, respectively, and individual patches had to exceed 5 m in length and 1 m in height. Echoview identified three large ($>10^3$ m in length) patches that appeared to represent bottom-associated fish schools; these were removed from this analysis and are discussed in Chapter 5. The remaining patches (n = 16,298) were subjected to a two-step cluster analysis (SPSS 16.0) using Akaike's Information Criterion (AIC) and the standardized variables S_v, patch area (PA, the cross-sectional area of the patch's bounding rectangle in the echogram), and S_v "skewness" (a measure of the acoustic data symmetry from the patch). The analysis identified two distinct patch types (clusters) and these were examined individually in the subsequent analyses. The density of each patch type was estimated for each transect segment as the number of

patches of type *i* divided by the number of 100 m horizontal increments in the transect segment; although typically 1.85 km, some segments were shorter if, for example, they terminated at shore or portions with electrical noise were excluded. Average PA was determined for each patch type as well. Although this is an overestimate of the true average cross-sectional area, it is consistent and allows for comparisons among samples.

ANOVA was used to test for differences between the whale and random samples for each measure. Survey number and the two-factor interaction term were included in the final models. Several measures were log-transformed after examining the associated residual plots. Bonferroni corrections were applied to balance the family-wise confidence levels from multiple comparisons of all combinations of the four sample sets (Ramsey & Schafer 2002). Where variances were unequal, a Tamhane correction was used instead (SPSS v10). The whale dataset was considered to differ from the random datasets if the corrected p-value was < 0.05 for all three of the individual whale-random dataset comparisons.

Regression Analysis

To determine the association between NASC and euphausiid abundance, a vertically-integrated NASC estimate was produced for each net tow by identifying the tow region in the echogram from the associated hydroacoustic data. These data regions were frequently 'noisy' because the circling tow vessel often passed over its own wake. Therefore, a data region of similar size and acoustic signature

immediately preceding (or, rarely, following) the sample region was used to estimate NASC for the net tows. As before, the contribution to NASC from single targets was excluded. In addition, one of the two patch types (type 2 patches), which potentially represent schooling fish (see Discussion), were excluded as well. The final NASC estimate was regressed on euphausiid density with survey number as a blocking variable to account for changes in the target strength of specimens across the field season.

RESULTS

Net Tow Data

Net samples from the first survey block and part of the second were not included in the analysis due to mechanical problems with the sampling gear. A total of 44 random and 41 whale-associated net samples were used in this analysis. Adult euphausiids were found in a greater proportion of whale samples than random samples in all but the second survey (Figure 3.2a). A Mann-Whitney test using the proportion estimates from each individual survey as data points indicated that the difference was significant ($Z = -2.440$, $p = 0.015$). Four euphausiid species were observed as adults: *Euphausia pacifica*, *Thysanoessa raschii*, *T. longipes*, and *T. spinifera*. Of these, *E. pacifica* was the most common species of adult euphausiid in both sample sets (Figure 3.2b). With the exception of *T. spinifera*, each species was found in a greater proportion of whale samples than random samples; however, the relative proportions of the four species of adult euphausiids were similar between the

two sample sets (Figure 3.2b). Immature euphausiids were present in all samples from both random and whale net tows, with the exception of 1 whale sample and 2 random samples in survey 5. There was a significant interaction between survey number and sample type when the effect of these factors on the log-transformed abundance of immature euphausiids was considered (F = 2.959, p = 0.026). This resulted from a general decrease in immature euphausiid abundance in the later surveys (F = 12.436, p < 0.001 for the main effect of survey number), coupled with their relatively low abundance in the whale samples from survey 3 (Figure 3.3). The main effect of sample type on immature euphausiid abundance was not significant (F = 1.978, p = 0.164).

Hydroacoustic Data

A total of 353 transect segments from the whale and random sample datasets from six surveys was analyzed. Unless otherwise noted, 'whale sample' refers to the collection of randomly selected transects from each of the individual whale surveys.

The results from the regression analysis indicate that NASC was positively correlated with adult euphausiid abundance (F=18.931, p < 0.001, r^2=0.390); however, there was no correlation between NASC and immature euphausiid abundance (p > 0.05). Log-transformed NASC was significantly higher among whale samples than any of the replicate random samples (F = 18.068, p < 0.001, Figure 3.4).

A total of 16,298 patches were identified from all hydroacoustic transects combined. Type 1 patches (n = 13,431) were relatively small regions (mean = 233.5

m^2, SD = 725.64) characterized by low S_v (mean = -54.7 dB, SD = 1.66) relative to type 2 patches. Type 1 patches were often nested within the dominant scattering layer and their edges were not well-defined. In contrast, type 2 patches (n = 2,867) were smaller (20.3 m^2, SD = 670.2), typically discrete regions with well-defined edges that were characterized by high Sv (mean = -48.8 dB, SD = 2.73). ANOVA tests from the cluster analysis indicated that the differences between the two groups in S_v and size were significant at the 0.05 level.

Whales were associated with a significantly higher abundance of type 1 patches than occurred randomly throughout the habitat (log-transformed density of patches, F = 8.182, p < 0.001, Figure 3.5a). Patch areas were also significantly larger among whale samples (F = 16.958, p < 0.001, Figure 3.5c). The results from an ANOVA suggested that whale and random samples differed with respect to the abundance of type 2 patches (F = 2.791, p = 0.041, Figure 3.5b); however, a Tamhane post-hoc test failed to detect a difference based on individual pair-wise comparisons (p > 0.05). In addition, there was no difference in the size of type 2 patches between the whale and random samples (F = 0.732, p = 0.535, Figure 3.5d).

DISCUSSION

Adult euphausiids were found in a higher proportion of whale samples than in samples collected randomly throughout the study site. This is consistent with earlier reports that humpback whales were associated with euphausiids in the region (Jurasz & Jurasz 1979, Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987), and

supports the hypothesis that whales target these prey rather than exploit them opportunistically. Whales were observed in association with all four species that occur in Southeast Alaska: *E. pacifica*, *T. raschii*, *T. longipes*, and *T. spinifera* (Chapter 2). Of these, *E. pacifica* was the most common species among the whale samples; however, the relative proportion of each species was similar between both whale and random samples, suggesting that whales forage opportunistically rather than preferentially with respect to species. Estimating the energy content of adult euphausiids was beyond the scope of this study, but broad correlations between energy density and reproductive state - pre-spawning euphausiids typically have higher energy densities than post-spawning individuals (Falk-Petersen et al. 2000) - suggest that whales should ignore *Thysanoessa* spp., which, at the time of the study had recently spawned (Chapter 2), in favor of pre- or actively spawning *E. pacifica*. However, species-specific variation, such as lower lipid reserves for *E. pacifica* (Ju et al. 2009), may negate the benefits of targeting this species over others. As well, if several species co-occur within patches, it may not be possible for whales to select one species over another. Further work to examine the fine-scale abundance and distribution patterns of adult euphausiids and their proximate compositions in relation to their spawning schedules would help resolve this issue.

In contrast to adult euphausiids, there is no evidence that humpbacks target immature euphausiids as prey in the study area. Although whales might opportunistically exploit immature euphausiids when they encounter them, the apparent relatively low importance in driving whale behavior is underscored by the

whales' inability to find them any better than random sampling. More likely, whales may ignore immature euphausiids, which have average lengths ranging from ~4 mm in early June to ~10 mm by the end of August (Chapter 2). No data exist on the lower size limit of prey that can be exploited by humpbacks, but it is plausible that organisms of this size are too small to be retained efficiently by the whales' baleen. Additionally, estimates of biovolume for immature euphausiids calculated from the relationship between length, *l*, and biovolume, *V*, for *Thysanoessa* spp. (Mauchline 1967) range from ~0.4 % - 8.5% that of an average 21-mm adult euphausiid (Figure A.2). Consequently, whales would need to feed on immature euphausiid aggregations that were 12 – 250 times denser than adult aggregations to obtain the equivalent prey biovolume. The widespread distribution of immature euphausiids relative to adults (Chapter 2) suggests that immature individuals were unable to maintain their position in the water column, and therefore, may not aggregate in sufficient densities for the whales to exploit efficiently.

The approach of comparing whale samples to random samples was used with the hydroacoustic data to determine whether whales are opportunistic or selective foragers with respect to specific features of prey aggregations. Assuming a positive relationship between NASC and adult euphausiid abundance, which is supported by the regression analysis, the hydroacoustic data suggest that whales target regions of significantly higher adult euphausiid abundance at a scale of 10^3 m (*i.e.*, the length of the transect segments) than is typical for the study area. Freidlander et al. (2006) found support for the same measure (surface-to-100 m integrated volume backscatter)

as a useful index for examining humpback whale-euphausiid interactions in Antarctica. In general, high prey abundance at these and larger scales permits individual whales to feed longer before prey become depleted; however, this alone may not be sufficient if those prey are not present in sufficient local densities (Piatt & Methven 1992). Humpback whales feed by engulfing parcels of prey-laden water in discrete lunges (Gaskin 1982). Humpbacks can engulf ~57 m^3 of water in a single lunge (Lambertsen 2000) and the number of lunges a whale can make is limited by the high metabolic cost associated with lunge feeding (Acevedo-Gutierrez et al. 2002, Goldbogen et al. 2008) and the physics of acceleration and deceleration. As a consequence, the absolute quantity of prey a whale can consume depends on the local density of those prey so whales should specifically target sites of high prey-density within general areas of high prey abundance in order to maximize their rate of energy acquisition. This appears to be the case for whales in the study area, which targeted sites with more abundant and larger patches categorized as 'type 1' than were observed in random samples. Type 1 patches were regions with high acoustic backscatter that were typically nested within, and continuous with, broad scattering layers. This is consistent with dense euphausiid regions within heterogeneous scattering layers. Assuming that only adult euphausiids contributed to the acoustic backscatter, these patches were estimated to contain ~91.4 kcal m^{-3} (Table A.1). By targeting type 1 patches, adult humpback whales can meet their daily energetic requirements (approximately 442.1×10^3 kcal d^{-1}; Witteveen et al. 2006, and references therein) at an average rate of 4 lunge h^{-1} (Table A.1). This lunge rate is

lower than observed for humpback whales feeding on euphausiids off the central coast of California (Goldbogen et al. 2008).

Unlike type 1 patches, there is no evidence that whales targeted type 2 patches, which were found to be of similar size and in similar densities among both whale and random samples. Type 2 patches were generally small, discrete regions with comparatively high acoustic backscatter and edges that were well-defined over a range of backscatter thresholds. They were typically found above, rather than nested within, the scattering layer. These features are suggestive of small schooling fish aggregations. Pacific herring (*Clupea pallisi*) and juvenile walleye pollock (*Theragra chalcogramma*) are two abundant forage fish species that occur in the study area. Herring spawn in spring throughout SE Alaska (Womble et al. 2005) and are found in scattered schools from late May through September (Carlson 1980) from 15 m – 85 m (Sigler & Csepp 2007). Csepp et al. (2011) noted that in summer herring were typically found in bays within the study site and schools were small and difficult to catch by midwater trawl. Juvenile pollock, which are the most abundant small schooling fish in the region during the summer (Csepp et al. 2011), are found over a similar range of depths as herring, although they tend to occur in schools that are more spread out than the small, dynamic herring schools (Sigler & Csepp 2007). Without incorporating multiple hydroacoustic frequencies and collecting associated trawl samples, it is not possible to unequivocally separate acoustic backscatter from schooling fish and dense euphausiid aggregations; however, the observation that these patches are not targeted by the whales is consistent with the general view that forage

fish do not constitute a substantial portion of the diet of whales in Frederick Sound
and Stephens Passage (Krieger & Wing 1986). The relative rarity (typically, < 1
patch km^{-1}) and small size (~20 m^2) of these type 2 aggregations may make them less
suitable as prey for whales in the area. In this regard, Piatt & Methven (1992)
demonstrated that humpback whales in the North Atlantic ignored capelin (*Mallotus
villosus*) schools when they fell below 5 patches km^{-1}. In another study, the average
size of fish schools exploited by humpback whales were ~140 m in length (Hazen et
al. 2009), which is approximately 7 times larger than the average type 2 patch
observed here. Furthermore, Gende & Sigler (2006) attributed the unpredictability of
herring in Frederick Sound as the reason why Steller sea lions (*Eumetopias jubatus*)
do not exploit them during the summer. Therefore, small size, relative rarity, and
unpredictability likely contribute to these patches being ignored by the whales in the
region, especially when presented with an alternative in the form of comparatively
abundant euphausiids.

Optimal foraging theory suggests that natural selection should have optimized the
whales' foraging behavior in ways that maximize their rate of energy acquisition
(Schoener 1971, Pyke et al. 1977). For whales that fast for several months during
migration and on the breeding grounds (Dawbin 1966, Lockyer & Brown 1981,
Baraff et al. 1991) and therefore must meet their annual energetic requirements
during only part of the year, selection for foraging efficiency would be particularly
intense. The results from this study indicate that humpback whales enhance their
foraging efficiency by targeting locally dense aggregations of adult, but not

immature, euphausiids during the summer in Frederick Sound and Stephens Passage. However, the whales do not appear to select one euphausiid species over another. Instead, they appeared to have fed opportunistically on whichever euphausiid species were present in high-density patches of adults. That earlier studies differ regarding the euphausiid species most commonly associated with foraging humpback whales in the region likely reflects inter- or intra-annual variability in relative euphausiid species availability. In this regard, Chapter 2 revealed a seasonal pattern of change in relative abundance that is consistent with the relative timing of these earlier studies: observations in early summer tended to identify *T. raschii* as the predominant prey for humpback whales (Dolphin 1987), whereas those made in late summer indicated *E. pacifica* was the principal prey for the whales (Bryant et al. 1981).

As humpback whale populations recover from overexploitation, their role in marine ecosystems is likely to increase as well. Before the nature of these effects can be understood, additional data are needed to provide accurate estimates of humpback whale energy requirements and energy consumption rates, their regional abundance and distribution patterns, and their foraging behavior at other times of the year. Additionally, the role that nocturnal foraging plays for humpback whales towards meeting their daily energetic requirements remains uncertain; given that euphausiids typically migrate to the surface at night (Bollens et al. 1992) and may therefore be easier to exploit, this could be substantial and warrants investigation. However, this study improves our understanding of their role in the study area by revealing where the trophic linkages are strongest and where they are weak or non-existent.

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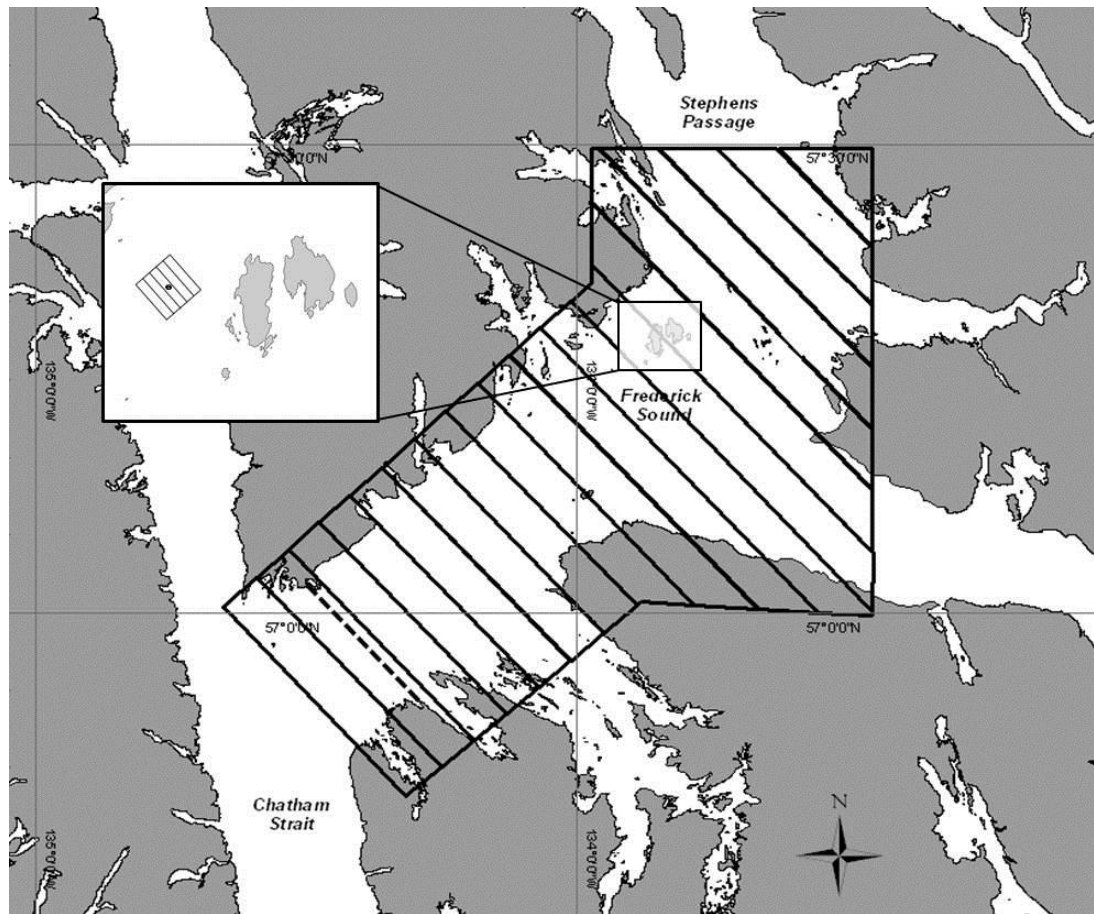
Figure 3.1. The study site in Frederick Sound and lower Stephens Passage, Southeast Alaska, partitioned into 4.6 km-wide strata. A single, random transect is shown by the dashed line in stratum 2. The expanded view shows a 1.85 km x 1.85 km whale grid orientated to match the strata. The initial location of a whale is shown at its center.
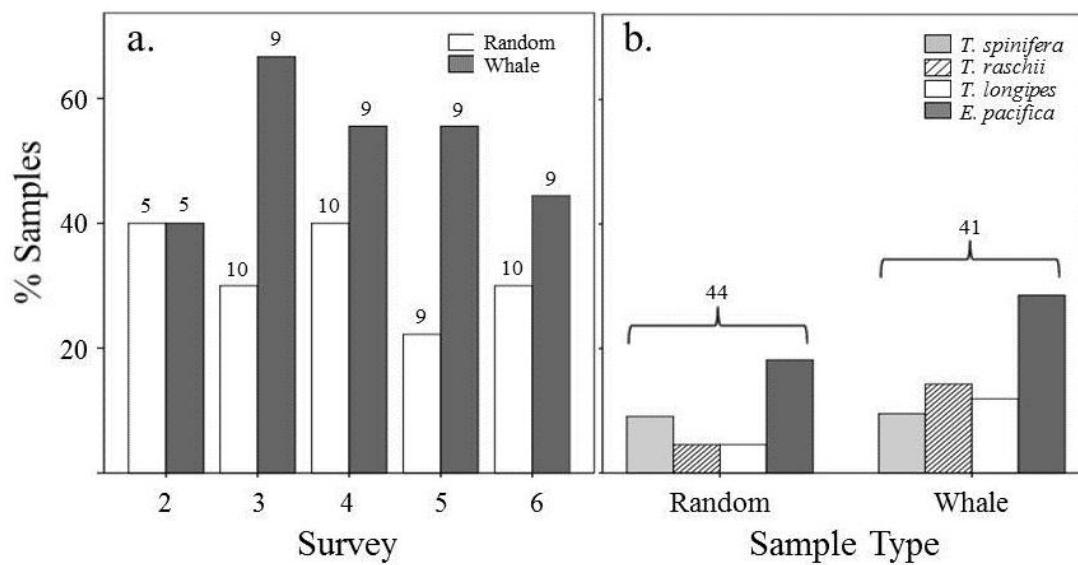
Figure 3.2. Proportion of random and whale net samples with adult euphausiids (all species combined) from each survey (a), and proportion of random and whale net samples with adult euphausiids from all surveys combined (b). Sample sizes are shown.
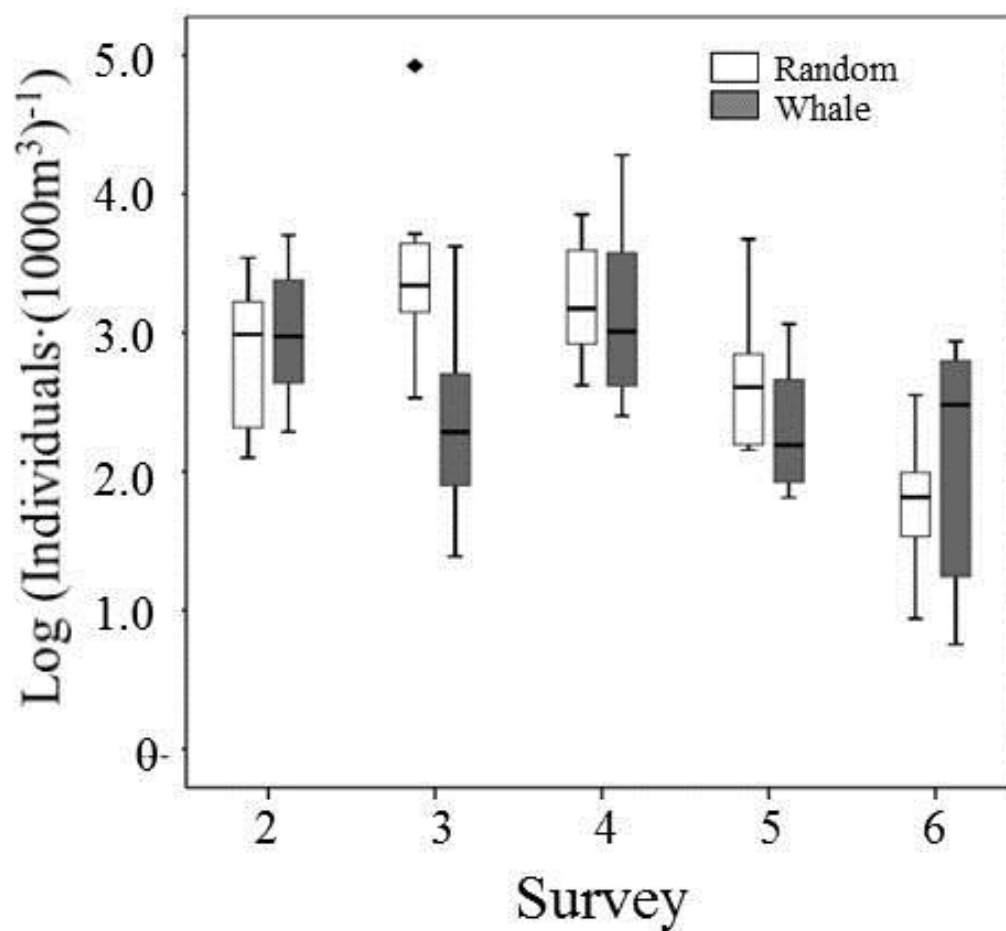
Figure 3.3. Density of immature euphausiids from random and whale net samples collected during five of the six surveys in Frederick Sound/Stephens Passage, Southeast Alaska. Boxes represent interquartile range with median indicated by the line. Circle represents a single outlier (case with value between 1.5 and 3.0 box lengths from the box edge).
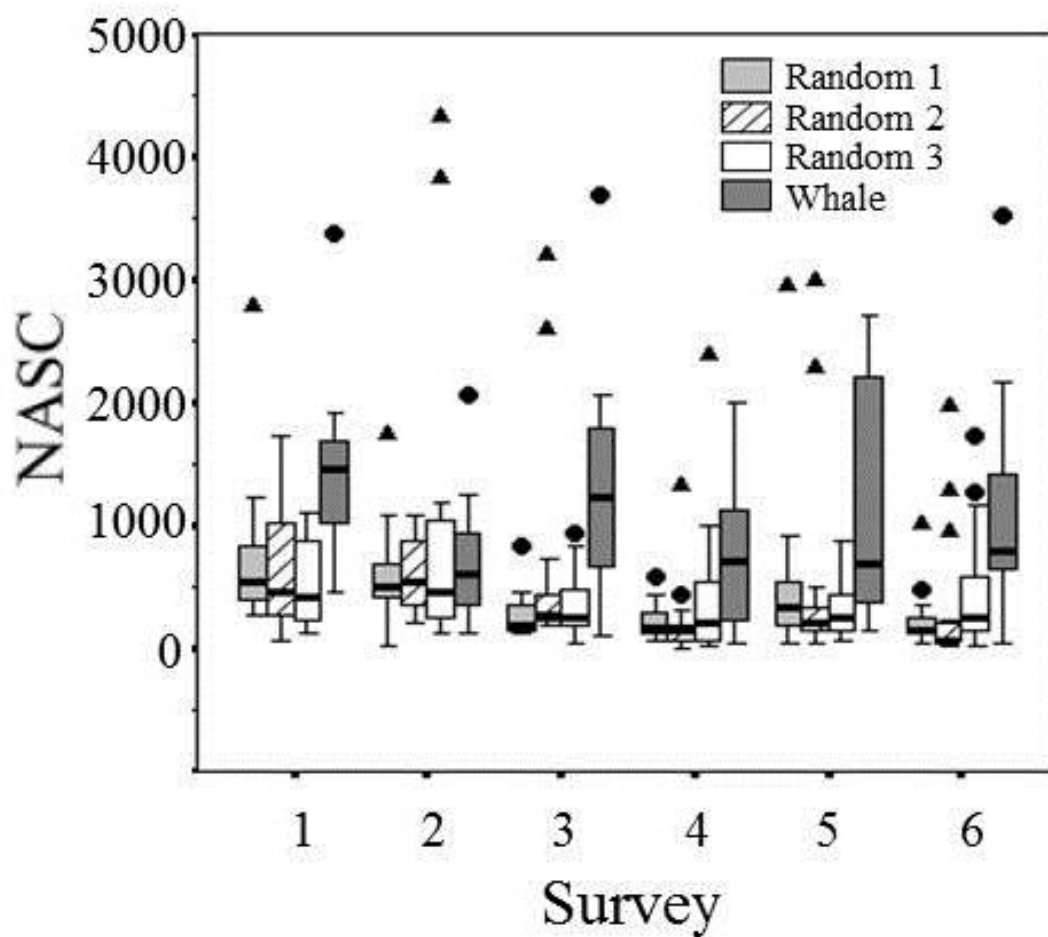
Figure 3.4. Integrated water-column NASC from random and whale-associated hydroacoustic sample sets. Boxes represent interquartile range with median indicated by the line. Circles represent outliers (cases with values between 1.5 and 3.0 box lengths from the box edge) and triangles represent extreme cases (those with values greater than 3.0 box lengths from the box edge). ANOVA analysis was performed on log-transformed NASC; however, raw data are shown here.
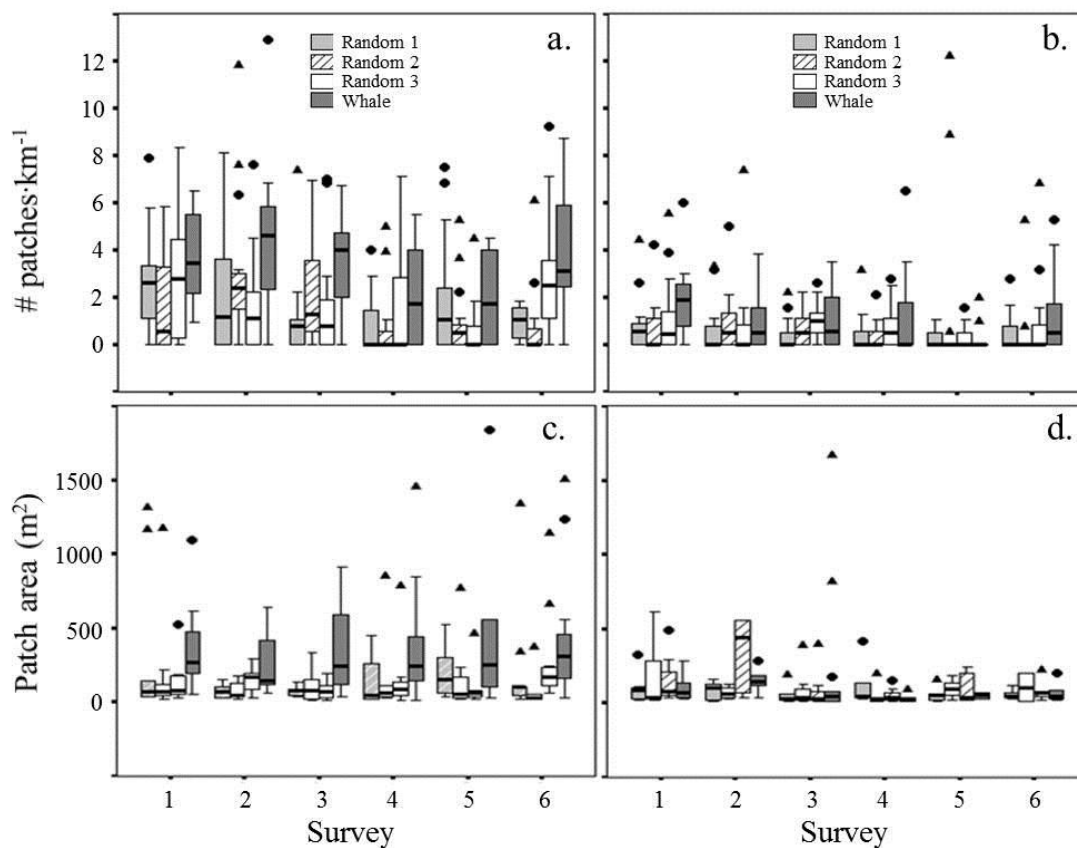
Figure 3.5. Abundance and area of type 1 (*a* and *c*, respectively) and type 2 (*b* and *d*, respectively) patches from random and whale-associated hydroacoustic sample sets. Boxes represent interquartile range with median indicated by the line. Circles represent outliers (cases with values between 1.5 and 3.0 box lengths from the box edge) and triangles represent extreme cases (those with values greater than 3.0 box lengths from the box edge). ANOVA analyses were performed on log-transformed density; however, raw data are shown here.

CHAPTER 4: HUMPBACK WHALE ABUNDANCE AND DISTRIBUTION
PATTERNS RELATIVE TO HYDROACOUSTICALLY-DETERMINED PREY
AVAILABILITY IN FREDERICK SOUND AND STEPHENS PASSAGE,
SOUTHEAST ALASKA

ABSTRACT

The abundance and distribution patterns of humpback whales (*Megaptera noavaengliae*) in Frederick Sound and Stephens Passage, Southeast Alaska were examined in relation to the availability of euphausiids, their principal prey in the area. Whale abundance increased significantly across the summer; however, this was not associated with an increase in prey, as indicated by hydroacoustic surveys, suggesting the whales were responding to changing conditions elsewhere in the region. As the summer progressed, whale abundance reached a plateau and individuals clustered around comparatively few prey, suggesting that prey availability may have limited the numbers of whales in the study area. Numbers during the period of peak abundance were similar to estimates made decades earlier for the study area, despite a region-wide annual rate of population increase of approximately 6%, suggesting that the capacity of Frederick Sound and Stephens Passage to support a growing population may be limited.

INTRODUCTION

Together, Southeast (SE) Alaska and northern British Columbia are a principal foraging ground for humpback whales (*Megaptera novaeangliae*) in the North Pacific, where an estimated ~6,000 whales make it the largest humpback whale

feeding aggregation (~30%) in the Northern Hemisphere (Calambokidis et al. 2008). Within the region, large aggregations of humpback whales are found in several areas, including Glacier Bay and the neighboring waters of Icy Strait (GB/IS), Sitka Sound (SS), and Frederick Sound and Stephens Passage (FS/SP) (Straley 1994, Dahlheim et al. 2009, Straley et al. 2009). Although humpback whales are assumed to move between these areas in response to seasonal variability in their prey (Baker et al. 1992, Straley 1994), this has not been directly investigated. To date, efforts to assess associations between patterns in whale distribution and abundance to regional patterns of prey availability have relied on sequentially sampling prey in different areas over relatively limited timeframes (*e.g.*, Krieger & Wing 1986). Although these provide a snapshot of whale foraging patterns, they cannot identify how whales respond to seasonal variability in prey. What is required to answer this question is a study with a sampling duration that can capture potential variability in either whale or prey abundance.

The objective of this study is to determine if whale abundance and distribution patterns in FS/SP vary across the summer and are correlated with changes in hydroacoustically-determined features of their prey. Less effort has been dedicated to examining general abundance and distribution patterns of humpback whales and their prey in FS/SP relative to other areas in SE Alaska (*i.e.*, GB/IS and SS; Nielson & Gabriele 2008, Straley et al. 2009) despite recognition that it is particularly important to humpback whales summering in SE Alaska (Baker et al. 1992, Straley et al. 2009). The goal is to examine the degree to which local-scale whale abundance and

distribution patterns reflect prey availability and to consider the findings in the context of regional-scale whale distribution patterns.

METHODS

From 22 May to 31 August 2008, visual surveys for humpback whales and hydroacoustic surveys for their prey were conducted in Frederick Sound and lower Stephens Passage (56°-57°N, 133°-134°W), which are part of the channels and fjords making up the inshore waters of SE Alaska. The study area was partitioned into 18 survey strata, each 4.6 km-wide. A single, randomly-located transect was placed within each stratum parallel to its long axis (see Figure 3.1). The set of transects was surveyed during daylight from a 6.4 m rigid-hull inflatable boat (RhIB) at $8-10$ km/h approximately every 20 days (Table 4.1).

Whale Surveys and Analyses

During each survey, a dedicated observer scanned continuously for whales from the bow of the vessel while another recorded estimated range and bearing to the whale using a sighting compass and the vessel's GPS chart-plotter to place the whale relative to visible charted points of reference. Throughout the study, observers reinforced their ability to estimate distances to whales, small vessels, and other points on the water by practicing and confirming their estimates with a radar or chart-plotter on a support vessel. The recorder also noted the time of sighting, the vessel's position, and survey conditions (*i.e.*, sea state and weather conditions). To minimize observer fatigue, the two individuals rotated between observing and recording every

30 – 60 min, and were replaced with a second pair of observers mid-way through each day.

Whale abundance was estimated for the study area using the line-transect data and Conventional Distance Sampling (CDS) following Buckland et al. (2001). The data were truncated by removing the greatest 10% of estimates of whale-to-vessel distance. Data were also grouped into distance intervals with cut points at 1.4, 2.8, 4.6, 6.5, 9.3, and 12.8 km after observing evidence for "heaping" (*i.e.*, the errors that result when observation angles or distances are rounded to convenient values) in the histogram of distance estimates (Buckland et al. 2001). Only data from surveys where visibility was estimated to be > 10 km (ca. 90 % of all survey time combined) were used in the analysis. Akaike's Information Criterion (AIC) was used to judge fit among multiple models with additional adjustment terms (*i.e.*, sequential selection; Buckland et al. 2001). The final detection model incorporated a half-normal key function with cosine expansion. Abundance was estimated for each individual survey.

Whale distribution plots were generated in ArcGIS 9.3 (ESRI). The location of each whale was determined using the vessel's position at the time of sighting and the estimated bearing and distance to the animal. To minimize plotting repeat sightings of the same individuals from neighboring transects, whales were only included in the distribution plots if they were observed within the stratum being surveyed. Whale distribution was analyzed for each individual survey in ArcGIS using a Multi-Distance Spatial Cluster (MDSC) analysis based on Ripley's K-function (Perry et al.

2006). This analysis identifies how the clustering or dispersion of points (*i.e.*, whales) varies over a range of spatial scales. A polygon that approximated the shape of the study area was used to define the analysis surface. Confidence envelopes were generated from maximum and minimum K estimates from 99 permutations of the true whale distributions. The null hypothesis was that K estimates from the observed distribution fell within the confidence envelope, indicating a random distribution of locations. Conversely, K estimates that were below the envelope indicated significant over-dispersion (*i.e.,* evenness) of locations and those above the envelope indicated significant clustering at the associated spatial scales.

Hydroacoustic Surveys and Analysis.

During the whale surveys, a 120 kHz split-beam echosounder (Simrad EK60) was continuously operated to characterize the structure and distribution of the acoustic scattering layer. Details of the hydroacoustic surveys and subsequent data processing are provided in Chapter 3. Briefly, the hydroacoustic data were imported into EchoView's Sonar Data (v4.3) and data within 2 m of the surface and 2 m of the sounder-detected bottom were removed. Obvious noisy portions of the transects due to electrical interference or poor survey conditions were also removed. The data were then integrated in 100 m horizontal by 10 m vertical bins (to 150 m) to estimate Nautical Area Backscatter Coefficients (NASC), a linearized measure of acoustic volume backscatter. Maximum and minimum volume backscatter (*Sv*) thresholds of -25 dB and -75 dB and a time-varied threshold (TVT) of -125 dB were applied prior to

integration. These thresholds were chosen to remove backscatter resulting from targets presumed to be too small/sparse or too large to be prey, and TVT was arrived at by examining the acoustic signal in clear water and fitting the associated time-varied gain curve. EchoView's single target detection algorithm was used to identify targets from individual fish and their contributions to NASC were subsequently removed. In addition, EchoView's school identification algorithm was used to identify acoustic regions characterized by comparatively high volume backscatter (hereafter referred to as 'patches'). The upper and lower Sv thresholds for patch identification were set at -25 dB and -60 dB, respectively, and only patches that exceeded 5 m in length and 1 m in height were considered. The lower Sv threshold (-60 dB) was selected through trial-and-error to capture the majority of visually-identified acoustic patches. A two-step cluster analysis (SPSS v16.0) using AIC clustering criteria and the standardized variables Sv, patch area (*i.e.*, the cross-sectional area of a patch's bounding rectangle in the echogram), and Sv "skewness" (a measure of the acoustic data symmetry from the patch), was used to classify patches into two types. Patches from the first cluster (type 1 patches) were typically regions of high volume backscatter (mean = -54.7 dB, SD = 1.66) nested within lower average backscatter scattering layers. The size and shape of these patches were variable (mean = 233.5 m^2, SD = 725.64) and their boundaries were determined by the specific lower detection threshold (-60 dB). These patches were assumed to represent high density euphausiid regions (Chapter 3). Patches from the second cluster (type 2 patches) were typically small (20.3 m^2, SD = 670.2) features with high

absolute volume backscatter (mean = -48.8 dB, SD = 2.73) and distinct boundaries, and therefore easily distinguished from the background scattering layer. Previous analysis suggested that whales did not target type 2 patches, assumed to represent small forage fish schools (Chapter 3), so they are not considered here.

The integrated bin and patch hydroacoustic data were imported into ArcGIS. The raw sounder-detected bottom data from all surveys combined were kriged to generate an approximate bathymetry surface for the study area (Figure A.3). The area was then partitioned into three bathymetric zones: i) a shallow zone with bottom depths < 100 m; ii) an intermediate zone with bottom depths from 100 m to 300 m; and, iii) a deep zone with bottom depths > 300 m. The three zones were chosen to approximate shallow, slope and basin habitats of the study area. The region was further partitioned into sub-areas that were associated with prominent geographical features of the study area (*e.g*., headlands). Overlap of the bathymetric zones and sub-regions resulted in a total of 38 individual cells (Figure 4.1). A single, vertically-integrated NASC estimate from the surface to a depth of 100 m was produced for each cell, similar to that used as an index of euphausiid abundance during humpback whale studies by Friedlaender et al. (2006) and in Chapter 3. The vertical cross-sectional area for each individual patch was estimated by the area of the patch-bounding rectangle within the echogram. The total cross-sectional area for all type 1 patches within each cell was then divided by the length of the transects in that cell to obtain the average combined vertical cross-sectional area of patches $\cdot$ km^{-1} (CVCA). The surface area (km^2) of each cell was obtained directly from ArcGIS.

Analysis of Whales and Their Prey

Whale density was estimated for each cell by dividing the number of whales within the cell by the cell's surface area. A second measure, the proportional whale-to-area ratio (PWA), was calculated as $(N_{ij} / N_j) / (A_i / A_{Total})$, where: N_{ij} = number of whales in cell i from survey j; N_j = number of total whales from survey j; A_i = surface area of cell i; and A_{Total} = surface area of all cells combined. PWA reflects whether a cell is occupied by fewer or more animals than predicted for a random distribution. An estimate of 1 indicates that the number of animals in a cell is proportional to that cell's area (*i.e.,* as predicted if whales are randomly distributed throughout the region), whereas PWA > 1 indicates that whale density is higher than the regional average (*i.e.,* disproportionate use) and PWA < 1 indicates that whale density is lower than the regional average (*i.e.,* avoidance). Individual cells were also ranked by their NASC and CVCA estimates relative to the maximum estimate for each survey (*i.e.,* cells received a new rank for each survey). Cells were ranked from 1 to 5 corresponding to successively larger 20% increments, so that cells with rank = 5 were within 80 – 100% of the survey maximum with respect to either measure. For each survey, every cell received a ranking for each criterion, which were treated individually in the analyses. The ranks were compared to the PWA estimates to determine whether whale use or avoidance of cells correlated with the cells survey-wide relative value in terms of NASC or CVCA.

RESULTS

Whale Abundance and Distribution

From the CDS analysis, whale abundance in the study area increased from 68 in survey 1 (S1) to a maximum of 228 in S4 and remained high thereafter despite a marginal decline in the final two surveys (S5 and S6; Table 4.1). Non-overlapping confidence intervals from the CDS analysis indicate that the increase in abundance from S2 to S4 was significant.

No estimate in the MDSC analysis fell below the lower 95% confidence intervals, so the results were expressed as the difference between the observed Ripley's K estimates and the estimated upper 95% confidence intervals at each spatial scale (Figure 4.2). Therefore, positive values indicate significant spatial clustering based on the MDSC analysis at the associated distances, and negative values indicate a random distribution. Significant clustering was evident in all six surveys; however two general patterns were evident: *i*) clustering was increasingly significant at small scales (< 10 km) as the field season progressed, and *ii*) clustering was evident at large scales (> 20 km) in the first four surveys, but not in S5 and S6. These patterns are reflected in the whale distribution plots (Figure 4.3): whales formed increasingly dense local aggregations in later surveys, but these aggregations were distributed widely (*i.e.*, randomly) throughout the study area.

Whale Relationships to Prey

A significant positive relationship was found between whale density and both log-transformed NASC (F = 15.442, p < 0.001) and log-transformed CVCA (F = 32.267,

$p < 0.001$); however, interactions between the factor SURVEY and each index were significant in both analyses ($F = 2.281$, $p = 0.048$ for NASC; $F = 3.684$, $p = 0.003$ for CVCA), indicating that the relationships differed across the season as evidenced by the increasing slope of the NASC (Figure 4.4) and CVCA (Figure 4.5) regression lines. Furthermore, whales were significantly over-represented (*i.e.,* PWA > 1) in cells with a rank of 5 for both NASC and CVCA (Figure 4.3, Table 4.2), and were significantly underrepresented (*i.e.,* PWA < 1) in cells ranked ≤ 2 and ≤ 3 with respect to NASC and CVCA, respectively (from individual *t*-tests for each rank corrected for multiple comparisons; Table 4.2). Finally, neither prey index (NASC or CVCA) increased across the study period. There was no significant difference in NASC across the study period among cells ranked 5 for that measure ($F = 0.924$, $p = 0.475$) and there was a significant decline in CVCA as the study period progressed ($F = 3.316$, $p = 0.013$; Figure 4.6).

DISCUSSION

Humpback whale abundance in Frederick Sound and lower Stephens Passage (FS/SP) during the study period was lowest in late May and peaked at ca. 228 animals by late July. An approximately threefold increase occurred between mid-June and mid-July with little subsequent change in August. It is unlikely that this increase in early summer reflects the arrival of whales from their winter breeding grounds. Humpback whales that summer in SE Alaska winter primarily in the Hawaiian archipelago (Calambokidis et al. 2008), where their abundance peaks in late February

and begins to decline thereafter; few whales are observed in the wintering area after April until the subsequent breeding season (Baker & Herman 1981). A single whale monitored by satellite migrated from Hawaii to SE Alaska in 30 days (Mate, unpublished data). Additionally, two humpback whales monitored for the first portion of their northbound migration would have made the trip in as few as 35 days and 29 days had they maintained their observed average rate of travel after the tags stopped transmitting (Mate et al. 1998). Using photo-identification records, Gabriele et al. (1996) documented the migration of a humpback whale between the two regions in 39 days, although this is a conservative estimate based on the last time the individual was observed in Hawaii and the first time it was subsequently observed in Alaska. At these rates, the last animals to leave Hawaii in late April would have arrived in Alaska towards the end of May and the majority would have arrived sooner.

The early-summer arrival of humpback whales to the study area likely reflects whales traveling to FS/SP from other parts of SE Alaska, which is consistent with previous movement reports (Baker et al. 1992, Straley et al. 1995) and satellite-tracking data showing extensive intra-seasonal travel within the region (Mate et al. 2007). It has been suggested that whales traveling from Glacier Bay and neighboring Icy Strait (GB/IS), an important late-spring/early-summer feeding area for humpback whales in SE Alaska (Jurasz and Palmer 1981, Baker et al. 1983, Baker et al. 1992), leads to the mid-summer increase in FS/SP (Baker et al. 1992, Straley et al. 1995). In 2008, whale abundance in GB/IS increased dramatically in June and remained stable

through late August (Nielson & Gabriele 2008), a pattern similar to - rather than opposite - the one observed in the FS/SP study area. Further, the total number of individually identified humpback whales in GB/IS in 2008 (n = 157; Nielson & Gabriele 2008) was similar to the number of whales that were estimated to have entered the study area between mid-June and mid-July (n = 150). Because the majority of the GB/IS whales remained there, it is unlikely that individuals moving between the two feeding areas were responsible for the influx of humpback whales in FS/SP. Although GB/IS and FS/SP are cited as having the highest abundances of humpback whales in northern SE Alaska (Baker et al. 1985, Krieger & Wing 1986, Baker et al. 1992, Straley et al. 1994), combined mid-summer numbers – using n = 124 for GB/IS during the period from early July-early August (Nielson & Gabriele 2008) and n = 228 for FS/SP in late July – is only ~19% of the estimated 1,875 humpback whales summering in northern SE Alaska in 2008 (Straley, unpublished data). Clearly, the majority of whales foraging in SE Alaska during the period of peak abundance in FS/SP did so elsewhere in the region. Movement of a relatively small proportion of these animals could account for the increase in abundance in the study area during early summer.

Regardless of where in SE Alaska the humpback whales emigrated from, the nearly threefold increase in abundance in FS/SP from late spring to mid-summer is substantial. Baker et al. (1985) speculated that the movement of humpback whales in SE Alaska reflects complex foraging strategies to exploit seasonal changes in prey availability. Adult euphausiids are the primary prey for humpback whales in FS/SP

(Krieger & Wing 1986, Dolphin 1987, Bryant et al. 1981, Baker et al. 1992, Chapter 3). In this study, whale density was examined in relation to two prey indices: NASC and CVCA. NASC was positively correlated with adult euphausiid abundance (Chapter 3), whereas CVCA was a measure of the availability of type 1 patches, which were assumed to represent high-density euphausiid aggregations (Chapter 3). Whale density was significantly positively associated with both indices. Whales were also significantly over-represented in areas ranked in the top 20% with respect to the survey-wide maximums of both NASC and CVCA, and avoided areas ranked in the lower 40% and 60% of NASC and CVCA estimates, respectively. The results of these analyses underscore the relevance of NASC and CVCA in influencing whale foraging patterns and support previous assertions that adult euphausiids are important to humpback whales foraging in the study area. Additionally, they show that whales disproportionately forage in areas with the highest prey densities within the study area, and were able to track spatially-varying prey aggregations over relatively short temporal scales ($\sim 10^1$ d). How whales track these aggregations remains unclear; however, they may detect dense prey aggregations directly, through chemical, visual and/or tactile cues, or indirectly, by responding to oceanographic features that are often associated with prey aggregations, such as tidal currents (*e.g.*, Cotté & Simard 2005) or thermal fronts (*e.g.*, Doniol-Valcroze et al. 2007). Additionally, humpback whales may detect audible cues made by foraging conspecifics, such as feeding calls (Sharpe 2001) or patterned ventilations. Such "eavesdropping" is widespread among

predators that track patchy prey (Giraldeau & Beauchamp 1999), and remains an intriguing area for future research on cetacean foraging behavior.

In light of the relationship between whale distribution and the prey indices, it is tempting to infer that whale abundance patterns mirrored prey availability in the study area. However, NASC remained stable and CVCA declined significantly across the summer within the local foraging sites targeted by the whales. CVCA is probably a better indicator of prey availability to the whales as it is the high-density, type 1 prey patches that are targeted rather than the larger-scale 'average' conditions represented by NASC (Chapter 3). This is consistent with what is known about the life history of euphausiids in the region. Spawning ended in June for the three *Thysanoessa* species and in early August for *Euphausia pacifica* in the study area, with recruitment of immature euphausiids into the adult population not occuring until after the end of the study (Chapter 2). With no new recruitment, the combined effect of post-spawning mortality and predation likely causes a reduction in abundance of adult euphausiids. This was reflected in the distribution of whales as well. Despite occupying more of the study area in later surveys, whales formed increasingly dense local aggregations, and within those aggregations they associated with comparatively fewer prey. These observations are consistent with the prediction from Ideal Free Distribution (IFD; Fretwell & Lucas 1972) that foragers will form increasingly dense aggregations as resource availability declines.

If prey conditions were unchanging or declining, what prompted the dramatic influx of animals into the study site in early summer? In this case, additional factors,

such as an increase in average energy density of prey or availability of alternate prey (*e.g.*, immature euphausiids or schooling forage fish), are unlikely to be responsible. Seasonal patterns in euphausiid energy density have not been examined in the region; however, euphausiids are typically at an annual low in lipid reserves and energy density after spawning (Falk-Petersen et al. 2000). Whales responding to seasonal changes in euphausiid energy density should arrive prior to spawning in early spring (Chapter 2) or later in the fall when adult euphausiids begin to store lipids as an overwintering strategy (Falk-Petersen et al. 2000). Immature euphausiids, which first appeared in late spring (Chapter 2), were not targeted by the whales (Chapter 3). Immature euphausiids, which were ca. 5-6 mm in length and only 0.4% the biovolume of a typical adult euphausiid when the influx of whales began (Chapter 3), were probably too small to be suitable prey. Finally, humpback whales have rarely been observed feeding on fish in the study area (Krieger & Wing 1986, Baker et al. 1992). Herring (*Clupea pallasi*) spawn in FS/SP in spring and decline in abundance from May onwards (Sigler et al. 2009). In summer, herring tend to form small, dynamic schools (Sigler & Csepp 2007) that are less predictable than at other times of the year (Sigler et al. 2009). Cooperative bubble-net foraging, which is indicative of herring-feeding, is relatively infrequent in the study area (Sharpe 2001) and was not observed during 2008 despite the dedicated whale surveys employed in this study. Moreover, hydroacoustic features consistent with herring aggregations were not targeted by whales during the study (Chapter 3). Juvenile walleye pollock (*Theragra chalcogramma*) are considerably more abundant than herring during the summer in

FS/SP but form schools that are less dense than those of herring (Sigler & Csepp 2007), which presumably makes them less profitable prey for the whales. Whales in association with apparent juvenile pollock aggregations in FS/SP were in relatively large and predictable schools (Krieger & Wing 1986, Chapter 5), as is the case for whales feeding on herring schools in late fall and early winter in Sitka Sound (Straley 1994). However, such patches appear to be rare in the study area (Krieger & Wing 1986, Chapter 5). Although opportunistic foraging on smaller fish schools probably occurs, the availability of schooling forage fish is unlikely to drive the abundance and distribution patterns of humpback whales in FS/SP.

Alternatively, the seasonal increase in whale abundance in FS/SP may have reflected a decline in prey conditions elsewhere in SE Alaska. Although whales in the study area feed primarily on adult euphausiids, elsewhere in the region they target schooling forage fish, including Pacific herring, juvenile walleye pollock, capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes hexapterus*) (Krieger & Wing 1986, Baker et al. 1992). Herring spawn in spring (Womble et al. 2005, Csepp et al. 2011), and whales exploit these spawning aggregations (Straley 1994, personal observation). Once spawning ends and the local availability and energy density of the fish decline, whales likely shift to other prey species, such as euphausiids, and/or foraging areas. As well, there is growing recognition that SE Alaska humpback whales regularly forage throughout the feeding season in the Gulf of Alaska waters adjacent to the Alexander Archipelago (J. Straley, University of Alaska Southeast, personal communication). Some individuals may take advantage of springtime

spawning euphausiid aggregations in these offshore waters before moving to the inshore waters to forage, which could explain the similar abundance pattern for humpback whales in GB/IS as well (Nielson & Gabriele 2008). A future study that identifies the early season distribution, abundance and foraging patterns of whales in the region would be useful in resolving this issue.

The numbers of humpback whales that forage seasonally in FS/SP underscore the area's importance to this population; however, there appears to have been relatively little change over the past few decades in the number of animals using the area despite an annual ocean basin-wide humpback whale population growth of ~ 6% per year (Calambokidis et al. 2008). Mark-recapture estimates for mid-summer FS/SP humpback abundance in 1986 (n = 211-247; Baker et al. 1992) are similar to the mid-summer estimate from this study. Further, there is no evidence that the numbers of humpback whales visiting FS/SP annually increased from 1996 to 2000 (n = 484 and 346, respectively; Straley et al. 2009). It is possible that prey availability limits the number of whales that can forage in the area, which is consistent with observations of increasingly dense local whale aggregations in association with comparatively fewer prey, and stable (or possibly declining) whale abundance after the early summer influx. This is also consistent with reports that, as the population grows, humpback whales are increasingly observed in parts of SE Alaska where they were previously rare (*e.g.*, Sumner and Clarence Strait; Dahlheim et al. 2009). Although the number of animals foraging in the FS/SP appears to have remained relatively stable, it is not clear from the available data how many animals visit the area each year. A dedicated

photo-identification study in the area would be useful towards assessing the turn-over

rates and residency patterns of individual whales, and establishing whether older

whales utilize "traditional" areas with the region (*e.g.,* FS/SP) while younger whales

disperse into previously underutilized areas.

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Table 4.1. Estimated numbers of humpback whales occupying the study area in Frederick Sound/Stephens Passage, Southeast Alaska, during summer 2008, based on Conventional Distance Sampling analysis (CDS; Buckland et al. 2001) and including upper and lower 95% confidence intervals. The total number of individual whale sightings recorded during each survey (Raw) and the number of sightings once whales observed outside the stratum being surveyed were removed (Corrected) are included.

| Survey | Start | End | Individual sightings | | CDS | |
			Raw	Corrected	Estimate	95% C.I.
1	22-May	27-May	105	49	68	46 - 101
2	8-Jun	13-Jun	120	52	78	52 - 118
3	27-Jun	3-Jul	217	65	132	85 - 204
4	15-Jul	22-Jul	396	162	228	163 - 319
5	6-Aug	10-Aug	390	155	215	153 - 301
6	27-Aug	31-Aug	314	136	190	123 - 294

Table 4.2. Results from individual t – tests comparing mean PWA (proportion of total humpback whales observed in a cell relative to the cell's proportional area) to a test value of 1 (PWA = 1 indicates the number of whales in a cell is proportional to the cell's area) for each rank with respect to NASC and combined vertical cross-sectional patch area per transect kilometer (CVCA) in Frederick Sound/Stephens Passage, Southeast Alaska. Results are Bonferroni-corrected for multiple comparisons. Ranks reflect 20th percentiles of survey–wide maximum NASC (rank 5 = 80% - 100% of maximum). Results in bold are significant at $p \leq 0.05$.

	NASC			CVCA		
Rank	PWA	t	*p*	PWA	t	*p*
1	0.5321	-2.807	**0.008**	0.393	-4.969	**0.001**
2	0.4733	-4.484	**0.001**	0.5325	-2.813	**0.007**
3	0.8337	-0.772	0.445	0.543	-3.019	**0.004**
4	1.105	0.079	0.937	1.101	0.498	0.622
5	1.684	2.522	**0.015**	1.894	3.225	**0.002**
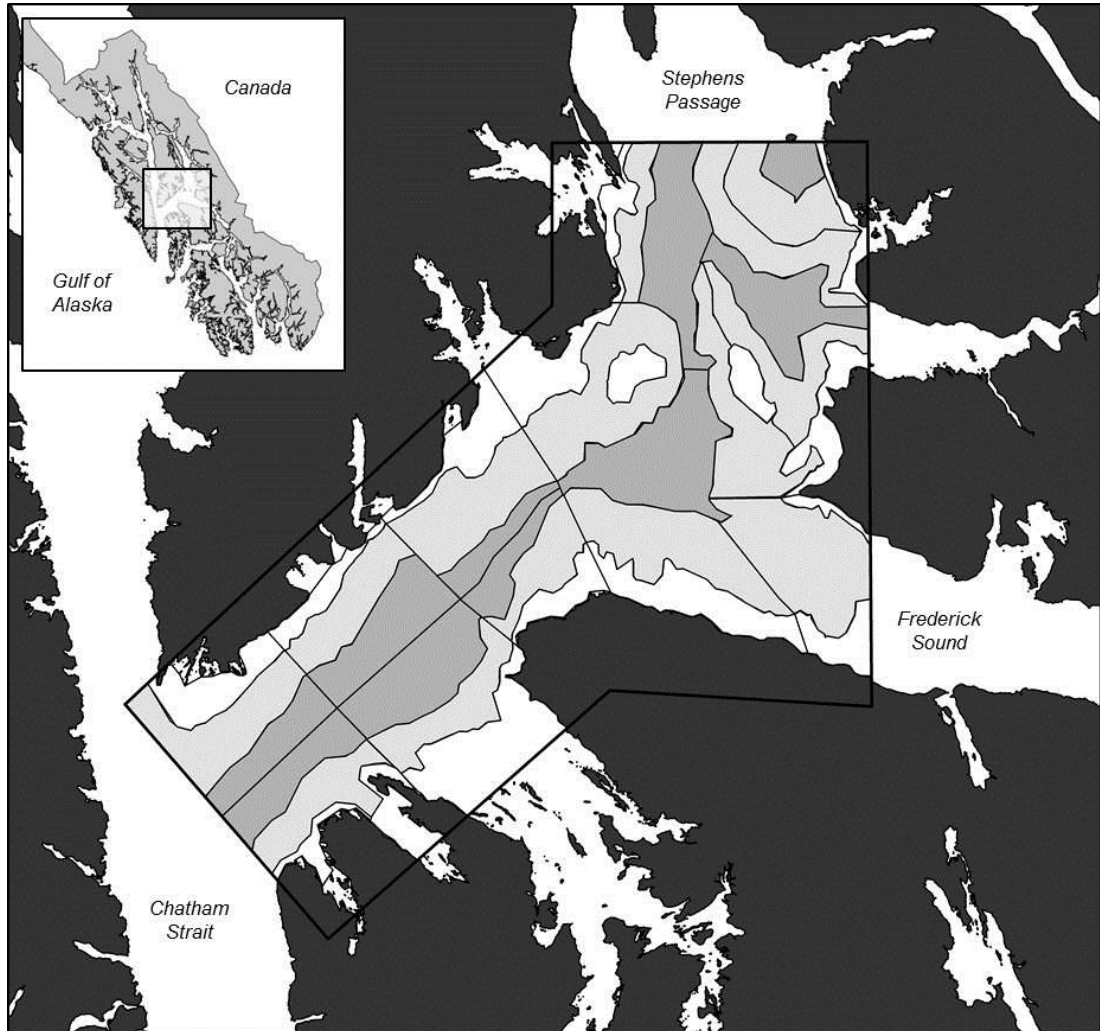
Figure 4.1. The study area in Frederick Sound and Stephens Passage, Southeast Alaska partitioned into humpback whale and prey hydroacoustic analysis cells. Individual cells result from the overlap of geographic sub-areas and the bathymetric zones (white < 100 m, light gray = 100 m – 300 m, dark gray > 300 m).
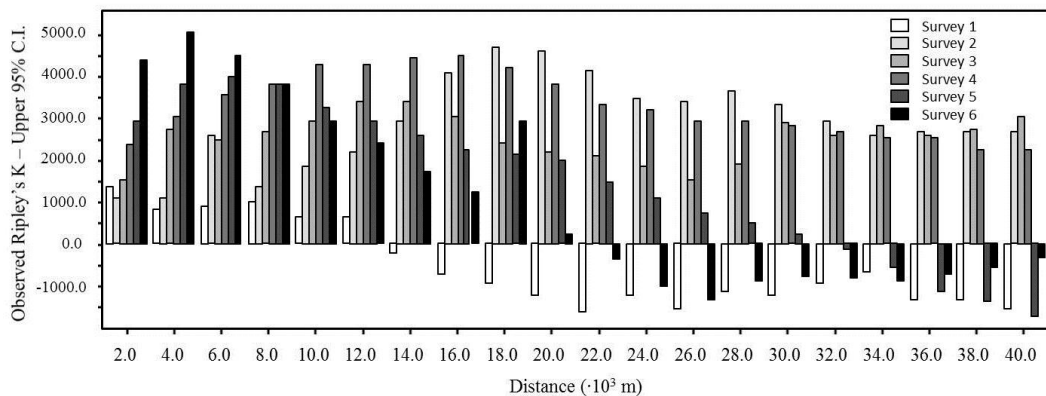
Figure 4.2. Results from a Multi-Distance Cluster Analysis (MDSC) that examined the distribution of humpback whales in Frederick Sound/Stephens Passage, Southeast Alaska. Y-axis shows the difference between the estimate of Ripley's K and the upper 95% confidence interval from 99 permutations of the humpback whale distribution data collected in Frederick Sound/Stephens Passage during summer 2008. Differences > 0 indicate significant clustering of whale locations at the associated distances; differences < 0 indicate no deviation from a random distribution of locations.

Figure 4.3. Distribution of humpback whales in the study area in Frederick
Sound/Stephens Passage, Southeast Alaska during surveys 1 through 6 in summer
2008 overlaid on the humpback whale and prey hydroacoustic analysis cells. Cells
ranked 5 with respect to the average combined vertical cross-sectional area of patches
per transect kilometer (*i.e.,* they are within 80 – 100 % of the survey-wide maximum
value for that measure) are shown in gray.
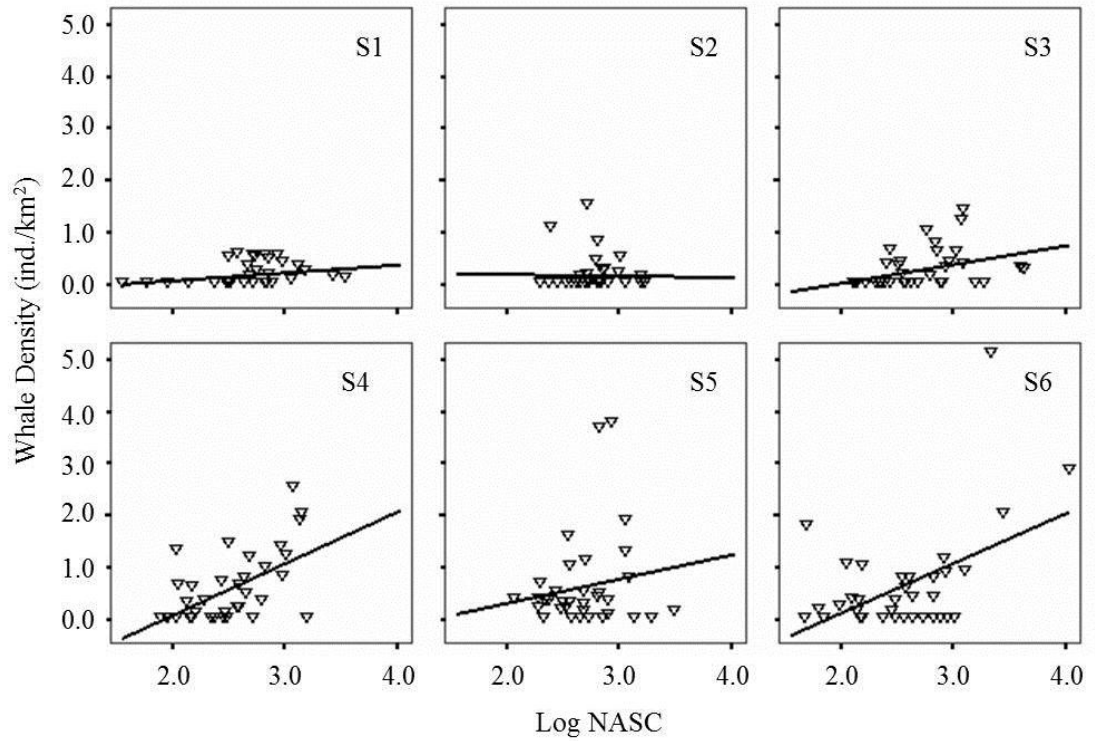
Figure 4.4. Density of humpback whales versus log-transformed NASC within humpback whale and prey hydroacoustic analysis cells for surveys 1 through 6 in Frederick Sound/Stephens Passage, Southeast Alaska during summer 2008.
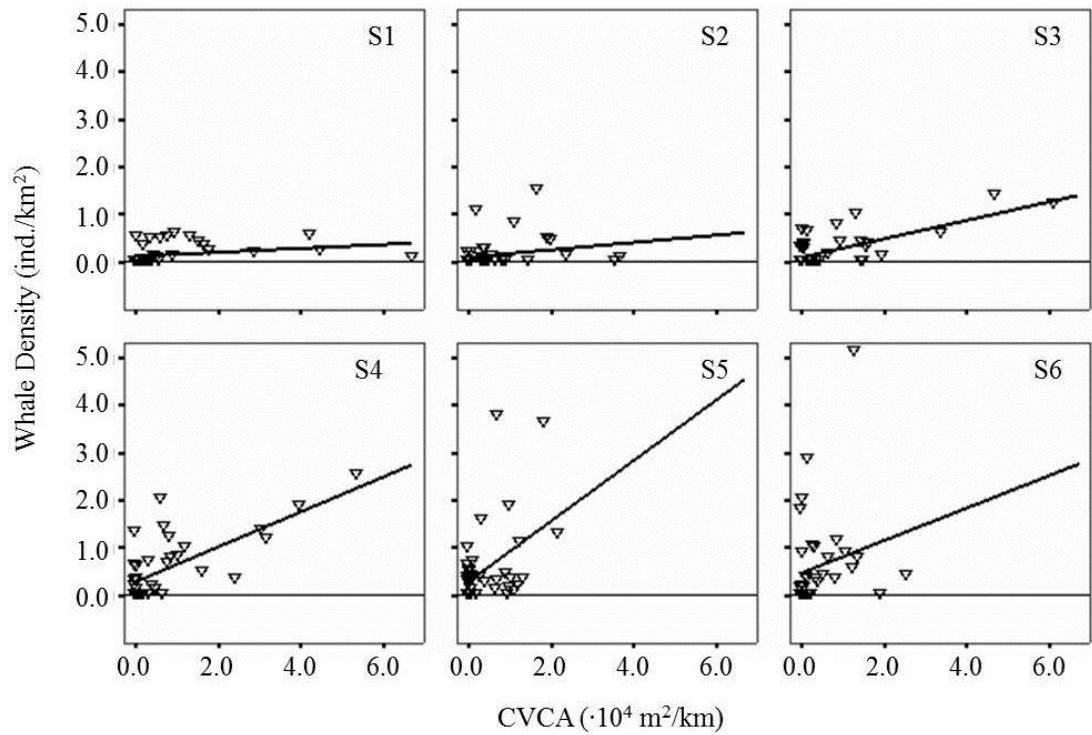
Figure 4.5. Density of humpback whales versus average combined cross-sectional area of patches per transect kilometer (CVCA) within humpback whale and prey hydroacoustic analysis cells for surveys 1 through 6 in Frederick Sound/Stephens Passage, Southeast Alaska during summer 2008. Analysis was performed on log-transformed CVCA.
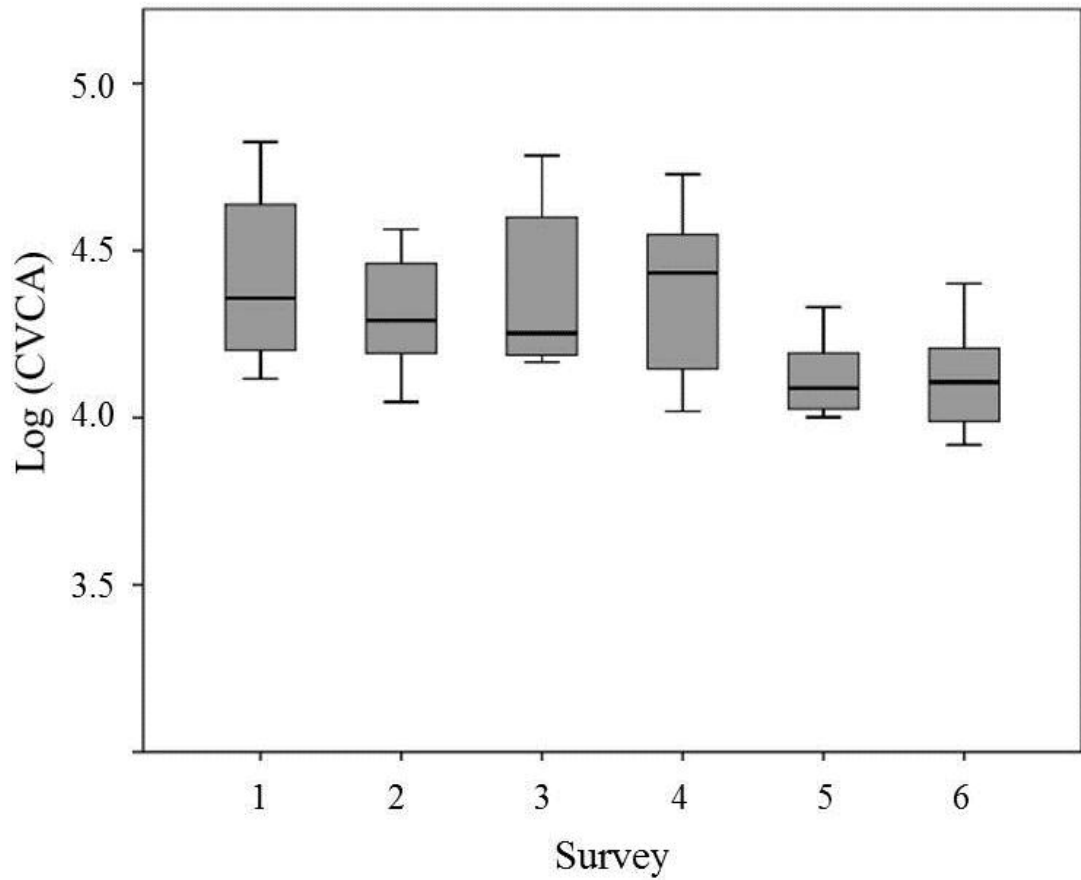
Figure 4.6. Log-transformed average combined vertical cross-sectional area of patches per transect kilometer (CVCA) in cells ranked 5 with respect to that measure (*i.e.*, they are within 80 – 100 % of the survey-wide maximum value of CVCA) across the season. Boxes represent interquartile range with median indicated by the line.

CHAPTER 5: A GENERAL OVERVIEW OF THE FORAGING ECOLOGY OF HUMPBACK WHALES IN FREDERICK SOUND AND STEPHENS PASSAGE, SOUTHEAST ALASKA

Aspects of the foraging ecology of humpback whales in Frederick Sound and lower Stephens Passage (FS/SP), Southeast Alaska were examined during 2008, yielding several notable findings. First, the study provided a more detailed understanding of euphausiids in the study area than previously available. While earlier studies offered glimpses of the euphausiid community composition, especially around foraging humpback whales (*e.g.*, Krieger & Wing 1986), they lacked the temporal resolution and sampling strategy necessary to assess life histories and relative abundance patterns. Chapter 2 addressed these issues explicitly, and, in doing so, identified the numerically dominant taxa and revealed how their breeding chronologies differed. It also established a baseline for the study area from which interannual and interdecadal variability can be examined, and set the stage for analyzing the role that euphausiids play in the foraging ecology of humpback whales in the study area. In Chapter 3, whales were shown to target high-density 'micropatches' of adult euphausiid, but not to discriminate between euphausiid species in the area. Whales did, however, discriminate between life-stages and apparently did not target immature euphausiids. In light of the small size and low estimated biovolume of immature euphausiids, it is unlikely they are suitable prey for the whales. Finally, Chapter 4 revealed that whale abundance increased significantly in FS/SP early in the summer; however, this did not coincide with a concomitant

increase in the availability of their principal prey, adult euphausiids. Instead, whales appeared to cluster increasingly around patches of fewer prey as the summer progressed. This last point raises an important issue regarding the role of FS/SP as a key foraging area for the whales during the summer months. Before considering this further, the importance of alternative prey, namely schooling forage fish, needs to be examined.

FORAGE FISH AS PREY FOR WHALES IN FREDERICK SOUND AND STEPHENS PASSAGE

A potential shortcoming of this research was the inability to directly sample small schooling forage fishes despite the fact that two potential prey species, juvenile walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*), are known to occur in FS/SP (Csepp et al. 2011). Both species are important prey for humpback whales elsewhere in SE Alaska (*i.e.*, Glacier Bay and Icy Strait; Krieger & Wing 1986); however, previous surveys have yielded few observations of associations between humpback whales and forage fish in FS/SP (Krieger & Wing 1986, Baker et al. 1992). Acknowledging these earlier surveys, Sharpe (2001) inferred that exploitable fish aggregations were relatively rare in FS/SP and argued that this results in demonstrable differences (*e.g.*, transient affiliations, large and unstable pods) in cooperative bubble-net foraging there when compared to other areas where fish are more abundant. Cooperative bubble-net foraging – a tactic used by humpback whales to exploit herring aggregations (Jurasz & Jurasz 1979, D'Vincent et al. 1985, Sharpe 2001) - was not observed during this study despite extensive

whale surveys (Chapter 4). There were no differences in the size or abundance of hydroacoustic features observed in the study area that were consistent with fish aggregations (*i.e.*, type 2 patches) between whale samples and random samples, suggesting they were not targeted by the whales (Chapter 3). Collectively, these observations suggest that schooling forage fish are not important prey for humpback whales in FS/SP during the summer.

If schooling forage fish are prey for humpback whales elsewhere, why do they not target them in FS/SP – an area where herring, and especially juvenile walleye pollock, are abundant (Csepp et al. 2011)? The answer may lie in differences in the size, abundance and/or predictability of fish schools between these areas. In studies where these parameters of forage fish schools are reported, whales associate with fish schools that are typically large (on average ~1100 m^2 and up to 4 km long, Hazen et al. 2009) and/or abundant (> 5 schools $\cdot$ km^{-1}, Piatt & Methven 1992). This is consistent with echo-tracings from Glacier Bay and Icy Strait (GB/IS) that show schools in association with humpback whales to be similarly large and, judging from the frequency with which they were encountered, widespread (Krieger & Wing 1986). Further, whales can be reliably observed exploiting large herring aggregations in other areas of SE Alaska in mid-summer (*e.g.*, Chatham Strait; Sharpe 2001, personal observation), suggesting that fish predictably aggregate in those areas each year. In contrast, the presumed fish schools observed in this study were typically small (< 25 m^2) and in low abundance (< 1 school $\cdot$ km^{-1}) in FS/SP (Chapter 3), which is consistent with previous descriptions of small, dynamic herring schools in the study

area (Sigler & Csepp 2007). These small and ephemeral schools may be opportunistically exploited by the whales, but there is no evidence that whales target them during the summer.

Whales should exploit large and/or abundant schools if they encounter them in FS/SP. We observed this on three survey days (14 August, 30 August, and 2 September), when large (> 1 km long and > 20m high), bottom-associated hydroacoustic features with notably strong echo returns were observed in the vicinity of the Five Finger Island group in FS/SP (Figure 5.1). Krieger & Wing (1986) observed a similar hydroacoustic feature on 7 September 1984 in the same area and attributed it to 0+ age walleye pollock. Juvenile pollock are the most abundant small schooling fish in FS/SP and are found concentrated around large islands in the study site during the summer (Csepp et al. 2011). Seventeen whales were observed within 1 nautical mile of the prey aggregation during the 30 August whale abundance/hydroacoustic survey (Figure 5.2). Similarly, 8 and 14 whales were recorded within 1 nautical mile of the prey aggregations during the 14 August and 2 September focal whale surveys (as outlined in Chapter 3), respectively. Krieger & Wing (1986) also reported a large group of whales (n = 8 individuals) associated with the pollock aggregation they observed during their study. These observations suggest that whales in FS/SP exploit fish schools if they are sufficiently large. Additionally, these aggregations, which were observed decades apart in the same location and at the same time of year, may be reliable prey for the whales during mid- to late-summer in FS/SP, raising an intriguing question as to whether whales anticipate them each year.

Such fish schools appear to be relatively rare, as they were only observed in one location during the final weeks of the study with a small number of whales. Thus, these fish likely contribute little to the population-level patterns of whale abundance and behavior in FS/SP.

FREDERICK SOUND AND STEPHENS PASSAGE AS A LOCAL FORAGING SITE WITHIN SOUTHEAST ALASKA

FS/SP is an important northern SE Alaska foraging area, where, at a peak in late July, ~12% of the region's estimated whale population occurred (Chapter 4). However, the arrival of whales in the area did not coincide with an increase in either the availability or suitability of their primary prey during that period (Chapter 4). In Chapter 4, I suggested that whales responded to changing (*i.e.*, increasingly poor) foraging conditions elsewhere in the region rather than an improvement in the conditions within FS/SP, which led to the mid-summer influx of whales into the study area. Conditions elsewhere in the region may include over-wintering and/or spring spawning aggregations of forage fish, especially herring, which also occur throughout SE Alaska (Womble et al. 2005). Humpback whales are observed exploiting these aggregations as early as March each year (personal observation). Additionally, humpback whales could target pre-spawning euphausiid aggregations that occur offshore in the Gulf of Alaska, an area where humpback whales from the SE Alaska are known to forage (J. Straley, University of Alaska Southeast, personal communication). The spring phytoplankton bloom, and by inference, euphausiid spawning, occurs later (*i.e.,* mid-May) in the northern Gulf of Alaska than in the

inshore waters (Parsons et al. 1966). By early summer, when spawning herring and euphausiids are no longer available, animals that were exploiting them likely move elsewhere, such as FS/SP, to target other prey. In this way, FS/SP in summer may best be viewed as increasing in relative, rather than absolute, suitability among the available foraging areas within the region.

Whales in FS/SP cluster increasingly around fewer resources later in the summer (Chapter 4), which is consistent with a decline in euphausiid availability and may indicate that whales can substantially reduce the local availability of euphausiids - an observation that should come as no surprise given the energy requirements necessary to sustain a population of this size. This suggests that whales experience an increase in competition for limited food. It is notable that the number of humpback whales in FS/SP during the mid-summer peak in whale abundance does not differ substantially from the 1984 estimate (Baker et al. 1992), despite a 6% annual population growth rate for the region (Calambokidis et al. 2008). This, coupled with the apparent seasonal prey limitation may indicate that prey availability limits the number of animals that can forage in the area at one time. Not surprisingly, humpback whales are becoming increasingly widespread in SE Alaska in recent years (Dahlheim et al. 2009), which is to be expected if traditional foraging 'hot-spots', such as FS/SP, are limited in their capacity to support a growing population.

Humpback whales are highly mobile foragers; photo-identification (Straley 1994) and satellite-tagging (Mate et al. 2007) data demonstrate that they are capable of traveling widely throughout the region in relatively short intervals of days to weeks.

Within SE Alaska, FS/SP and other key foraging areas (*e.g*, GB/IS and SS) exist as part of a network of foraging 'patches', and some or all of these may be visited by the same individual whales, perhaps even multiple times within a single season. Therefore, prey limitations in one area would only limit the growth of the whale population if prey were also limited elsewhere in the region. Whether or not this is the case is unclear. Additionally, humpback whales occur in the region throughout the year, and it is possible that mid-summer – a time when whale abundance in the region is high - represents a period when the energy available to them is comparatively low since euphausiid energy density is typically lowest during summer (Falk-Petersen et al. 2000), as is zooplankton biomass (Park et al. 2004, Sturdevant et al. 2007). Spring resource pulses from spawning forage fish and euphausiids, overwintering and energy-rich herring and euphausiid aggregations, and potentially late-fall juvenile euphausiid aggregations (anecdotal observations exist that large numbers of humpback whales target these north of the study area in November and December when, presumably, they are of sufficient size and occur in sufficiently dense patches; J. Moran, Auke Bay Laboratories, personal communication) may ultimately be more important to the animals in terms of meeting their annual energetic requirements than summer prey aggregations.

Additional studies could resolve several issues raised in this dissertation. An extended sampling season that captures the recruitment of immature euphausiids into the adult population would reveal whether a given year's cohort represents an important resource to humpback whales in that same year. This has potential

implications for interpreting summer whale abundance patterns, and could reveal if whales arrive in the area in anticipation of this recruitment event. Additionally, a dedicated photo-identification study that extends over a substantial portion of the foraging season would be useful in characterizing whale residency patterns. This would establish whether whale abundance trends reflect a relatively small subset of the regional population using the area for most of the season, or a larger proportion of the population entering and leaving the area more readily across the foraging season. Comparing the identity of those whales to the identification catalogues compiled over the last several decades could help establish whether the same animals have been returning to this traditional foraging area or whether it is being used to a similar extent by new - and, for example, younger - animals. Finally, similar studies as those outlined in this dissertation but conducted elsewhere in SE Alaska would provide additional insight into the seasonal importance of other prey types and foraging areas, and provide a more comprehensive view of the foraging ecology of humpback whales within the region.

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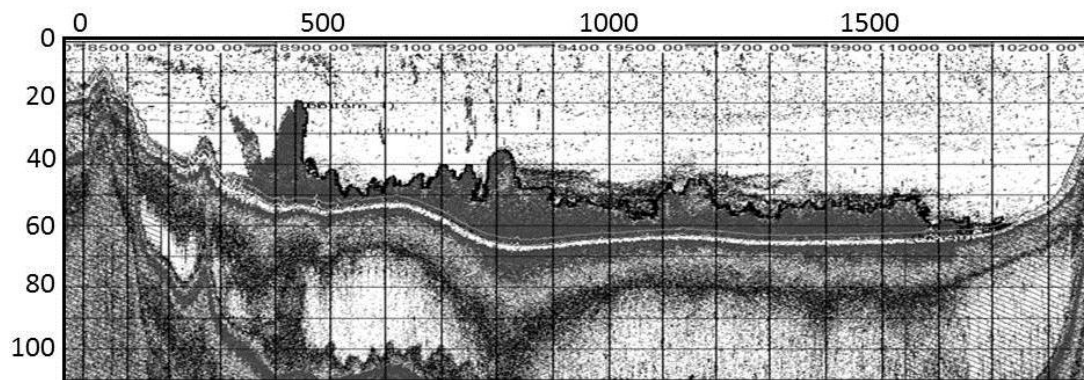
Figure 5.1. Echogram from 14 August 2008 hydroacoustic survey showing bottom-associated feature presumed to represent juvenile walleye pollock. Grid represents depth and distance in meters.
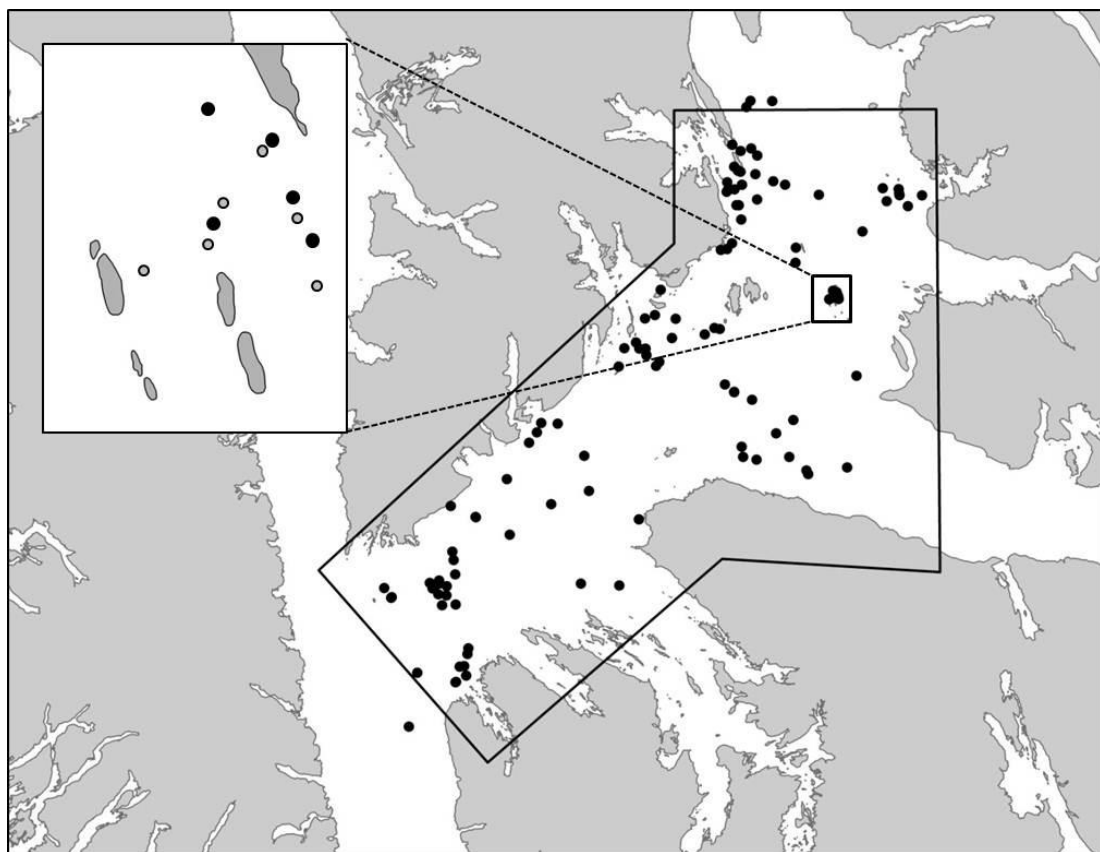
Figure 5.2. Distribution of humpback whales from survey 6 of the Frederick Sound/Stephens Passage study area (Chapter 4) highlighting the whales associated with the presumed pollock aggregation in the vicinity of the Five Finger Islands (inset). Grey circles represent whale pairs and black circles represent single whales in inset.

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APPENDICES

Table A.1. Estimated krill and caloric density for type 1 patches, and associated lunge rate necessary for an average adult humpback whale to meet its daily energy requirements.

| | NASC[1] | Depth[2] | Density[3] | Caloric density[4] | Lunge rate[5] |
	m^3 n mile^{-2}	m	g m^{-3}	kcal m^{-3}	lunge h^{-1}
Type 1 patch	373	2.33	87.05	91.40	4

[1] Obtained directly from hydroacoustic data

[2] Average depth of integration layer from hydroacoustic data

[3] $(((NASC \cdot \sigma^{-1}) \cdot M^{-1}) \cdot 1852^{-2}) \cdot z^{-1}$ where

$\sigma = 4 * \pi * 10^{(TS/10)}$ (MacLennan & Simmonds 1992),

$TS = -127.45 + 34.85 \log(l)$ (Green et al. 1991),

$l = 21$ mm   (average adult krill length, Figure A.2),

$M = 2.31 * 10^{-2} * l2.6976$ (krill weight, Laidre et al. 2010), and

z = integration layer depth

[4] Based on caloric density of 1.05 kcal g^{-1} (Childress & Nygard 1974)

[5] Based on a $3.04 \cdot 10^4$ kg whale (Trites & Pauly 1998) with a 57 m^3 buccal volume (Lambertsen 2000) and a digestion efficiency of 90% (Nordoy et al. 1993) that requires approximately $4.42 \cdot 10^5$ kcal d^{-1} (Witteveen et al. 2006).

Table A.2. Counts and average lengths of *Thysanoessa raschii* from non-random ('targeted'), random, and whale-associated net tows in 2008 in Frederick Sound/Stephens Passage, Southeast Alaska.

Survey	Sample	Date	Latitude	Longitude	Larvae #	Larvae Len.	Juvenile #	Juvenile Len.	Adult #	Adult Len.
2	Non-Ran	8-Jun-08	56.54.692	134.25.460	368	3.7	0		0	
2	Non-Ran	8-Jun-08	57.55.246	134.19.157	204	4.1	0		0	
2	Non-Ran	9-Jun-08	57.08.124	134.15.317	41	4.3	0		0	
2	Non-Ran	10-Jun-08	57.09.447	134.13.806	12	4.1	0		1	22.4
2	Non-Ran	11-Jun-08	57.6.515	133.40.372	148	4.2	0		0	
2	Non-Ran	11-Jun-08	57.05.846	133.32.266	90	4.4	0		0	
2	Non-Ran	11-Jun-08	57.6.698	133.33.532	336	4.3	0		1	22.9
2	Non-Ran	12-Jun-08	57.20.295	133.43.322	20	4.3	0		0	
2	Non-Ran	13-Jun-09	57.25.241	133.32.473	54	4.3	0		0	
2	Random	11-Jun-08	57.09.921	133.45.931	136	4.1	0		0	
2	Random	11-Jun-08	57.9.241	133.37.79	680	4.4	0		0	
2	Random	12-Jun-08	57.13.633	133.37.986	126	4.1	0		0	
2	Random	12-Jun-08	57.19.151	133.41.698	21	4.1	0		0	
2	Random	13-Jun-08	57.23.405	133.29.200	88	4.3	0		1	18.6
2	Whale	15-Jun-08	57.22.072	133.48.085	144	4.1	0		0	
2	Whale	15-Jun-08	57.16.918	134.02.646	54	3.9	0		0	
2	Whale	17-Jun-08	57.12.272	133.38.753	1440	4.1	0		0	
2	Whale	17-Jun-08	57.15.899	133.36.833	228	3.9	0		0	
2	Whale	22-Jun-08	57.9.853	134.01.629	113	4.9	0		0	
3	Non-Ran	27-Jun-08	56.58.149	134.13.134	2624	5.5	0		0	
3	Non-Ran	29-Jun-08	57.03.918	134.02.569	1136	5.1	64	8.3	0	
3	Non-Ran	30-Jun-08	57.14.515	133.59.976	100	4.7	0		0	
3	Non-Ran	30-Jun-08	57.09.067	133.44.654	36	4.8	0		0	
3	Non-Ran	1-Jul-08	57.14.013	133.38.702	55	4.8	0		0	
3	Non-Ran	1-Jul-08	57.18.257	133.45.384	376	4.8	0		0	
3	Non-Ran	2-Jul-08	57.18.479	133.42.876	760	5.0	8	7.1	0	
3	Non-Ran	2-Jul-08	57.19.487	133.39.064	140	5.2	4	7.4	0	
3	Non-Ran	3-Jul-08	57.23.562	133.29.414	116	5.1	0	7.4	0	
3	Random	27-Jun-08	56.57.421	134.16.556	464	4.8	16	8.1	0	
3	Random	29-Jun-08	56.59.783	134.03.692	6464	5.0	0		0	
3	Random	29-Jun-08	57.09.963	134.04.185	244	5.1	0		0	
3	Random	30-Jun-08	57.13.555	134.05.302	122	4.5	0		0	
3	Random	30-Jun-08	57.14.998	133.54.388	84	5.4	20	7.1	0	
3	Random	1-Jul-08	57.08.032	133.39.918	288	5.2	8	6.0	0	
3	Random	1-Jul-08	57.15.254	133.40.428	124	5.1	56	6.9	0	
3	Random	2-Jul-08	57.20.792	133.46.613	656	4.8	0		0	
3	Random	2-Jul-08	57.16.133	133.33.422	88	5.1	8	7.6	0	
3	Random	3-Jul-08	57.26.385	133.39.146	36	4.6	0		0	
3	Whale	4-Jul-08	57.22.537	133.47.245	94	4.7	4	8.4	1	17.4
3	Whale	4-Jul-08	57.23.367	133.51.469	114	4.5	10	7.5	8	20.4

3	Whale	8-Jul-08	57.19.332	133.51.260	22	4.9	0		0	
3	Whale	9-Jul-08	57.21.982	133.37.128	4	5.9	1	6.3	0	
3	Whale	10-Jul-08	57.14.178	133.39.744	44	5.5	0		0	
3	Whale	10-Jul-08	57.11.457	133.35.280	156	5.4	20	7.7	0	
3	Whale	11-Jul-08	57.17.370	133.33.450	7	6.4	6	7.5	0	
3	Whale	12-Jul-08	57.01.561	134.26.156	268	5.1	0		0	
3	Whale	12-Jul-08	57.04.707	134.23.439	72	5.1	4	6.9	1	18.7
4	Non-Ran	15-Jul-08	57.01.677	134.25.865	114	5.2	8	7.3	0	
4	Non-Ran	16-Jul-08	57.2.615	134.15.583	130	5.3	16	7.7	0	
4	Non-Ran	17-Jul-08	57.8.891	133.57.482	256	5.8	32	7.5	0	
4	Non-Ran	20-Jul-08	57.13.608	133.55.069	28	5.9	28	8.1	1	21.3
4	Non-Ran	20-Jul-08	57.6.544	133.35.69	82	5.8	40	7.3	0	
4	Non-Ran	20-Jul-08	57.16.685	133.52.663	7	5.6	0		0	
4	Non-Ran	21-Jul-08	57.09.693	133.32.553	308	6.0	12	7.9	0	
4	Non-Ran	21-Jul-08	57.15.309	133.34.033	77	6.4	9	8.6	0	
4	Non-Ran	22-Jul-08	57.28.262	133.51.252	376	5.8	4	7.3	4	21.6
4	Non-Ran	22-Jul-08	57.26.766	133.34.690	180	5.7	24	7.6	1	21.3
4	Random	15-Jul-08	56.54.127	134.27.492	48	5.2	8	8.2	0	
4	Random	15-Jul-08	57.04.337	134.21.612	192	5.5	16	7.3	0	
4	Random	16-Jul-08	57.09.252	134.13.027	144	5.1	4	7.8	0	
4	Random	17-Jul-08	57.07.605	133.55.089	176	5.7	26	7.7	0	
4	Random	20-Jul-08	57.08.239	133.46.205	248	5.8	24	7.5	0	
4	Random	20-Jul-08	57.07.697	133.37.549	180	6.3	268	8.1	1	20.2
4	Random	21-Jul-08	57.12.280	133.36.810	11	5.9	8	7.0	0	
4	Random	21-Jul-08	57.17.422	133.37.641	162	6.1	28	7.8	0	
4	Random	22-Jul-08	57.27.785	133.43.956	272	5.9	52	7.5	0	
4	Random	22-Jul-09	57.23.643	133.43.421	38	5.8	9	8.1	0	
4	Whale	23-Jul-08	57.19.863	133.51.231	24	5.3	3	7.9	0	
4	Whale	23-Jul-08	57.22.566	133.50.655	43	5.9	1	8.8	2	19.8
4	Whale	23-Jul-08	57.25.569	133.48.887	34	5.9	24	7.6	0	
4	Whale	23-Jul-08	57.26.900	133.51.753	21	5.5	8	8.0	2	19.4
4	Whale	24-Jul-08	57.15.698	133.57.613	116	5.7	58	8.4	0	
4	Whale	24-Jul-08	57.8.11	133.50.373	164	5.5	80	7.7	0	
4	Whale	24-Jul-08	57.10.594	133.46.966	108	6.1	56	8.0	0	
4	Whale	24-Jul-08	57.9.697	133.41.094	48	5.8	240	7.9	0	
4	Whale	25-Jul-08	57.17.237	133.34.288	70	6.2	60	8.3	0	
4	Whale	25-Jul-08	57.20.681	133.33.121	160	5.9	1072	8.4	0	
5	Non-Ran	6-Aug-08	57.04.499	134.10.616	50	4.4	9	7.8	0	
5	Non-Ran	6-Aug-08	57.09.882	134.06.580	368	5.3	160	7.6	0	
5	Non-Ran	7-Aug-08	57.13.874	134.00.286	74	5.3	22	9.2	0	
5	Non-Ran	8-Aug-08	57.09.115	133.39.795	16	5.7	624	10.9	1	20.5
5	Non-Ran	8-Aug-08	57.05.136	133.28.834	15	5.3	48	8.8	0	
5	Non-Ran	8-Aug-08	57.07.327	133.32.447	16	5.7	440	9.7	3	18.0
5	Non-Ran	9-Aug-08	57.22.364	133.50.195	9	5.5	17	8.9	2	21.4
5	Non-Ran	9-Aug-08	57.16.541	133.33.056	0		0		0	
5	Non-Ran	10-Aug-08	57.24.536	133.32.215	10	5.9	0		0	

5	Non-Ran	10-Aug-08	57.25.081	133.29.553	133	5.2	13	10.4	0	
5	Random	5-Aug-08	56.55.921	134.19.023	24	4.9	10	8.1	0	
5	Random	5-Aug-08	56.59.975	134.19.120	24	4.8	6	6.6	0	
5	Random	6-Aug-08	56.58.635	134.07.922	36	4.5	3	8.6	0	
5	Random	6-Aug-08	57.05.609	134.06.983	29	5.0	14	8.9	0	
5	Random	7-Aug-08	57.10.204	133.54.005	0		0		0	
5	Random	7-Aug-08	57.11.818	133.51.542	28	5.2	28	6.9	0	
5	Random	8-Aug-08	57.02.173	133.28.392	0		0		0	
5	Random	9-Aug-08	57.21.135	133.48.247	17	5.5	19	9.0	0	
5	Random	9-Aug-08	57.23.464	133.44.574	19	4.9	5	8.6	0	
5	Random	10-Aug-08	57.22.482	133.35.509	39	5.3	4	7.4	0	
5	Random	10-Aug-08	57.22.523	133.33.596	36	5.2	4	8.8	0	
5	Random	10-Aug-08	57.22.529	133.33.595	18	5.3	5	7.6	0	
5	Random	10-Aug-08	57.27.209	133.33.111	7	5.9	5	10.8	0	
5	Random	10-Aug-08	57.27.207	133.33.099	9	5.4	10	10.4	0	
5	Whale	11-Aug-08	57.19.437	133.33.004	4	7.3	226	9.4	0	
5	Whale	11-Aug-08	57.21.879	133.29.902	12	5.8	8	9.2	0	
5	Whale	11-Aug-08	57.16.323	133.33.779	13	5.4	6	7.5	0	
5	Whale	14-Aug-08	57.18.111	133.40.065	11	5.3	2	8.3	0	
5	Whale	14-Aug-08	57.15.129	133.47.760	6	5.9	25	9.8	0	
5	Whale	15-Aug-08	57.20.496	133.50.888	0		0		0	
5	Whale	15-Aug-08	57.20.811	133.44.334	2	5.6	15	10.8	0	
5	Whale	15-Aug-08	57.25.872	133.41.845	6	4.7	7	9.3	0	
5	Whale	15-Aug-08	57.14.357	133.35.177	22	5.7	118	9.6	2	20.6
6	Non-Ran	27-Aug-08	57.0.402	134.28.99	1	4.5	1	6.6	0	
6	Non-Ran	27-Aug-08	57.03.167	134.22.203	48	6.2	100	8.4	1	17.9
6	Non-Ran	28-Aug-08	57.06.534	134.18.141	0		0		0	
6	Non-Ran	28-Aug-08	57.10.391	134.10.027	6	5.6	31	9.8	0	
6	Non-Ran	29-Aug-08	57.15.159	134.02.225	10	5.7	14	9.7	0	
6	Non-Ran	29-Aug-08	57.15.526	133.53.295	2	4.1	12	10.9	0	
6	Non-Ran	30-Aug-08	57.5.413	133.31.513	0		0		0	
6	Non-Ran	30-Aug-08	57.20.720	133.52.460	0		1	10.2	0	
6	Non-Ran	31-Aug-08	57.17.865	133.39.234	0		0		0	
6	Random	27-Aug-08	56.56.759	134.30.416	0		4	7.8	0	
6	Random	27-Aug-08	56.58.808	134.22.177	6	5.2	12	9.8	0	
6	Random	28-Aug-08	57.00.255	134.07.587	0		2	10.7	0	
6	Random	28-Aug-08	57.07.620	134.08.948	0		0		0	
6	Random	29-Aug-08	57.07.458	133.57.382	0		0		0	
6	Random	29-Aug-08	57.5.719	133.39.103	0		0		0	
6	Random	30-Aug-08	57.04.505	133.29.900	0		0		0	
6	Random	30-Aug-08	57.17.217	133.46.545	0		18	8.3	0	
6	Random	31-Aug-08	57.24.538	133.46.163	0		0		0	
6	Random	31-Aug-08	57.21.174	133.34.592	0		1		0	
6	Whale	1-Sep-08	57.17.753	133.31.511	1	4.0	0		0	
6	Whale	2-Sep-08	57.18.318	133.39.791	1	5.2	0		0	
6	Whale	2-Sep-08	57.19.845	133.33.578	0		0		0	

6	Whale	2-Sep-08	57.20.726	133.52.358	16	6.1	76	9.5	0	
6	Whale	4-Sep-08	57.28.478	133.44.571	9	4.9	37	10.6	0	
6	Whale	7-Sep-08	57.19.328	133.52.059	0		7	11.7	9	22.0
6	Whale	8-Sep-08	57.24.288	133.45.240	3	4.3	8	10.9	0	
6	Whale	8-Sep-08	57.21.309	133.50.197	2	5.3	5	9.2	0	
6	Whale	10-Sep-08	57.21.103	133.38.544	0		1	13.4	1	16.0

Table A.3. Counts and average lengths of *Thysanoessa spinifera* from non-random ('targeted'), random, and whale-associated net tows in 2008 in Frederick Sound/Stephens Passage, Southeast Alaska.

Survey	Sample	Date	Latitude	Longitude	Larvae #	Larvae Len.	Juvenile #	Juvenile Len.	Adult #	Adult Len.
2	Non-Ran	8-Jun-08	56.54.692	134.25.460	0		0		0	
2	Non-Ran	8-Jun-08	57.55.246	134.19.157	0		0		0	
2	Non-Ran	9-Jun-08	57.08.124	134.15.317	0		0		0	
2	Non-Ran	10-Jun-08	57.09.447	134.13.806	0		0		0	
2	Non-Ran	11-Jun-08	57.6.515	133.40.372	0		0		0	
2	Non-Ran	11-Jun-08	57.05.846	133.32.266	0		0		0	
2	Non-Ran	11-Jun-08	57.6.698	133.33.532	0		0		2	23.0
2	Non-Ran	12-Jun-08	57.20.295	133.43.322	0		0		0	
2	Non-Ran	13-Jun-09	57.25.241	133.32.473	0		0		0	
2	Random	11-Jun-08	57.09.921	133.45.931	0		0		0	
2	Random	11-Jun-08	57.9.241	133.37.79	0		0		0	
2	Random	12-Jun-08	57.13.633	133.37.986	0		0		0	
2	Random	12-Jun-08	57.19.151	133.41.698	0		0		0	
2	Random	13-Jun-08	57.23.405	133.29.200	0		0		0	
2	Whale	15-Jun-08	57.22.072	133.48.085	0		0		0	
2	Whale	15-Jun-08	57.16.918	134.02.646	0		0		0	
2	Whale	17-Jun-08	57.12.272	133.38.753	0		0		0	
2	Whale	17-Jun-08	57.15.899	133.36.833	0		0		0	
2	Whale	22-Jun-08	57.9.853	134.01.629	0		0		0	
3	Non-Ran	27-Jun-08	56.58.149	134.13.134	0		0		0	
3	Non-Ran	29-Jun-08	57.03.918	134.02.569	0		0		0	
3	Non-Ran	30-Jun-08	57.14.515	133.59.976	0		0		0	
3	Non-Ran	30-Jun-08	57.09.067	133.44.654	0		0		0	
3	Non-Ran	1-Jul-08	57.14.013	133.38.702	0		0		0	
3	Non-Ran	1-Jul-08	57.18.257	133.45.384	0		0		2	22.8
3	Non-Ran	2-Jul-08	57.18.479	133.42.876	0		0		0	
3	Non-Ran	2-Jul-08	57.19.487	133.39.064	0		0		0	
3	Non-Ran	3-Jul-08	57.23.562	133.29.414	0		0		0	
3	Random	27-Jun-08	56.57.421	134.16.556	0		0		0	
3	Random	29-Jun-08	56.59.783	134.03.692	0		0		0	
3	Random	29-Jun-08	57.09.963	134.04.185	0		0		0	
3	Random	30-Jun-08	57.13.555	134.05.302	0		0		0	
3	Random	30-Jun-08	57.14.998	133.54.388	0		0		0	
3	Random	1-Jul-08	57.08.032	133.39.918	0		0		0	
3	Random	1-Jul-08	57.15.254	133.40.428	0		0		0	
3	Random	2-Jul-08	57.20.792	133.46.613	0		0		0	
3	Random	2-Jul-08	57.16.133	133.33.422	0		0		0	
3	Random	3-Jul-08	57.26.385	133.39.146	0		0		0	
3	Whale	4-Jul-08	57.22.537	133.47.245	0		0		0	
3	Whale	4-Jul-08	57.23.367	133.51.469	0		0		1	20.8

3	Whale	8-Jul-08	57.19.332	133.51.260	0	0		0	
3	Whale	9-Jul-08	57.21.982	133.37.128	0	0		0	
3	Whale	10-Jul-08	57.14.178	133.39.744	0	0		0	
3	Whale	10-Jul-08	57.11.457	133.35.280	0	0		2	20.6
3	Whale	11-Jul-08	57.17.370	133.33.450	0	0		0	
3	Whale	12-Jul-08	57.01.561	134.26.156	0	0		0	
3	Whale	12-Jul-08	57.04.707	134.23.439	0	0		0	
4	Non-Ran	15-Jul-08	57.01.677	134.25.865	0	0		0	
4	Non-Ran	16-Jul-08	57.2.615	134.15.583	0	0		0	
4	Non-Ran	17-Jul-08	57.8.891	133.57.482	0	0		0	
4	Non-Ran	20-Jul-08	57.13.608	133.55.069	0	0		0	
4	Non-Ran	20-Jul-08	57.6.544	133.35.69	0	0		0	
4	Non-Ran	20-Jul-08	57.16.685	133.52.663	0	0		0	
4	Non-Ran	21-Jul-08	57.09.693	133.32.553	0	0		0	
4	Non-Ran	21-Jul-08	57.15.309	133.34.033	0	0		0	
4	Non-Ran	22-Jul-08	57.28.262	133.51.252	0	0		0	
4	Non-Ran	22-Jul-08	57.26.766	133.34.690	0	0		0	
4	Random	15-Jul-08	56.54.127	134.27.492	0	0		0	
4	Random	15-Jul-08	57.04.337	134.21.612	0	0		0	
4	Random	16-Jul-08	57.09.252	134.13.027	0	0		0	
4	Random	17-Jul-08	57.07.605	133.55.089	0	0		0	
4	Random	20-Jul-08	57.08.239	133.46.205	0	0		0	
4	Random	20-Jul-08	57.07.697	133.37.549	0	8	10.1	0	
4	Random	21-Jul-08	57.12.280	133.36.810	0	0		0	
4	Random	21-Jul-08	57.17.422	133.37.641	0	0		0	
4	Random	22-Jul-08	57.27.785	133.43.956	0	0		2	23.6
4	Random	22-Jul-09	57.23.643	133.43.421	0	0		0	
4	Whale	23-Jul-08	57.19.863	133.51.231	0	0		0	
4	Whale	23-Jul-08	57.22.566	133.50.655	0	1	10.8	0	
4	Whale	23-Jul-08	57.25.569	133.48.887	0	0		0	
4	Whale	23-Jul-08	57.26.900	133.51.753	0	0		0	
4	Whale	24-Jul-08	57.15.698	133.57.613	0	4	8.6	0	
4	Whale	24-Jul-08	57.8.11	133.50.373	0	0		0	
4	Whale	24-Jul-08	57.10.594	133.46.966	0	0		0	
4	Whale	24-Jul-08	57.9.697	133.41.094	0	16	10.5	1	25.1
4	Whale	25-Jul-08	57.17.237	133.34.288	0	0		0	
4	Whale	25-Jul-08	57.20.681	133.33.121	0	0		1	23.5
5	Non-Ran	6-Aug-08	57.04.499	134.10.616	0	0		0	
5	Non-Ran	6-Aug-08	57.09.882	134.06.580	0	0		0	
5	Non-Ran	7-Aug-08	57.13.874	134.00.286	0	4	12.5	0	
5	Non-Ran	8-Aug-08	57.09.115	133.39.795	0	48	12.4	3	23.3
5	Non-Ran	8-Aug-08	57.05.136	133.28.834	0	0		0	
5	Non-Ran	8-Aug-08	57.07.327	133.32.447	0	2	12.3	1	21.4
5	Non-Ran	9-Aug-08	57.22.364	133.50.195	0	0		0	
5	Non-Ran	9-Aug-08	57.16.541	133.33.056	0	0		0	
5	Non-Ran	10-Aug-08	57.24.536	133.32.215	0	0		1	20.3

5	Non-Ran	10-Aug-08	57.25.081	133.29.553	0	0		0	
5	Random	5-Aug-08	56.55.921	134.19.023	0	0		0	
5	Random	5-Aug-08	56.59.975	134.19.120	0	2	6.6	0	
5	Random	6-Aug-08	56.58.635	134.07.922	0	2	12.5	0	
5	Random	6-Aug-08	57.05.609	134.06.983	0	0		0	
5	Random	7-Aug-08	57.10.204	133.54.005	0	0		0	
5	Random	7-Aug-08	57.11.818	133.51.542	0	0		1	20.8
5	Random	8-Aug-08	57.02.173	133.28.392	0	0		0	
5	Random	9-Aug-08	57.21.135	133.48.247	0	0		0	
5	Random	9-Aug-08	57.23.464	133.44.574	0	0		1	22.4
5	Random	10-Aug-08	57.22.482	133.35.509	0	0		1	23.7
5	Random	10-Aug-08	57.22.523	133.33.596	0	0		0	
5	Random	10-Aug-08	57.22.529	133.33.595	0	0		0	
5	Random	10-Aug-08	57.27.209	133.33.111	0	0		0	
5	Random	10-Aug-08	57.27.207	133.33.099	0	0		0	
5	Whale	11-Aug-08	57.19.437	133.33.004	0	0		0	
5	Whale	11-Aug-08	57.21.879	133.29.902	0	0		0	
5	Whale	11-Aug-08	57.16.323	133.33.779	0	0		0	
5	Whale	14-Aug-08	57.18.111	133.40.065	0	0		0	
5	Whale	14-Aug-08	57.15.129	133.47.760	0	0		0	
5	Whale	15-Aug-08	57.20.496	133.50.888	0	0		0	
5	Whale	15-Aug-08	57.20.811	133.44.334	0	0		0	
5	Whale	15-Aug-08	57.25.872	133.41.845	0	0		0	
5	Whale	15-Aug-08	57.14.357	133.35.177	0	8	13.3	0	
6	Non-Ran	27-Aug-08	57.0.402	134.28.99	0	0		0	
6	Non-Ran	27-Aug-08	57.03.167	134.22.203	0	0	13.8	0	
6	Non-Ran	28-Aug-08	57.06.534	134.18.141	0	0		1	16.8
6	Non-Ran	28-Aug-08	57.10.391	134.10.027	0	0		0	
6	Non-Ran	29-Aug-08	57.15.159	134.02.225	0	0		0	
6	Non-Ran	29-Aug-08	57.15.526	133.53.295	0	0		0	
6	Non-Ran	30-Aug-08	57.5.413	133.31.513	0	0		0	
6	Non-Ran	30-Aug-08	57.20.720	133.52.460	0	0		0	
6	Non-Ran	31-Aug-08	57.17.865	133.39.234	0	0		0	
6	Random	27-Aug-08	56.56.759	134.30.416	0	0		0	
6	Random	27-Aug-08	56.58.808	134.22.177	0	0		0	
6	Random	28-Aug-08	57.00.255	134.07.587	0	0		0	
6	Random	28-Aug-08	57.07.620	134.08.948	0	0		0	
6	Random	29-Aug-08	57.07.458	133.57.382	0	0		1	18.1
6	Random	29-Aug-08	57.5.719	133.39.103	0	0		0	
6	Random	30-Aug-08	57.04.505	133.29.900	0	0		0	
6	Random	30-Aug-08	57.17.217	133.46.545	0	0		0	
6	Random	31-Aug-08	57.24.538	133.46.163	0	0		0	
6	Random	31-Aug-08	57.21.174	133.34.592	0	0		0	
6	Whale	1-Sep-08	57.17.753	133.31.511	0	0		0	
6	Whale	2-Sep-08	57.18.318	133.39.791	0	0		0	
6	Whale	2-Sep-08	57.19.845	133.33.578	0	0		0	

6	Whale	2-Sep-08	57.20.726	133.52.358	0	4	12.5	0
6	Whale	4-Sep-08	57.28.478	133.44.571	0	0		0
6	Whale	7-Sep-08	57.19.328	133.52.059	0	0		0
6	Whale	8-Sep-08	57.24.288	133.45.240	0	0		0
6	Whale	8-Sep-08	57.21.309	133.50.197	0	0		0
6	Whale	10-Sep-08	57.21.103	133.38.544	0	0		0

Table A.4. Counts and average lengths of *Thysanoessa longipes* from non-random
('targeted'), random, and whale-associated net tows in 2008 in Frederick
Sound/Stephens Passage, Southeast Alaska.

					Larvae		Juvenile		Adult	
Survey	Sample	Date	Latitude	Longitude	#	Len.	#	Len.	#	Len.
2	Non-Ran	8-Jun-08	56.54.692	134.25.460	0		0		0	
2	Non-Ran	8-Jun-08	57.55.246	134.19.157	0		0		0	
2	Non-Ran	9-Jun-08	57.08.124	134.15.317	2	6.3	0		0	
2	Non-Ran	10-Jun-08	57.09.447	134.13.806	0		0		0	
2	Non-Ran	11-Jun-08	57.6.515	133.40.372	0		0		0	
2	Non-Ran	11-Jun-08	57.05.846	133.32.266	16	4.8	0		0	
2	Non-Ran	11-Jun-08	57.6.698	133.33.532	16	5.4	0		0	
2	Non-Ran	12-Jun-08	57.20.295	133.43.322	0		0		0	
2	Non-Ran	13-Jun-09	57.25.241	133.32.473	0		0		0	
2	Random	11-Jun-08	57.09.921	133.45.931	10	5.1	0		0	
2	Random	11-Jun-08	57.9.241	133.37.79	16	4.2	0		0	
2	Random	12-Jun-08	57.13.633	133.37.986	0		0		0	
2	Random	12-Jun-08	57.19.151	133.41.698	0		0		0	
2	Random	13-Jun-08	57.23.405	133.29.200	0		0		0	
2	Whale	15-Jun-08	57.22.072	133.48.085	8	5.4	0		0	
2	Whale	15-Jun-08	57.16.918	134.02.646	0		0		0	
2	Whale	17-Jun-08	57.12.272	133.38.753	0		0		0	
2	Whale	17-Jun-08	57.15.899	133.36.833	8	4.9	0		1	16.2
2	Whale	22-Jun-08	57.9.853	134.01.629	22	5.9	2	10.7	0	
3	Non-Ran	27-Jun-08	56.58.149	134.13.134	320	5.8	0		0	
3	Non-Ran	29-Jun-08	57.03.918	134.02.569	16	5.4	0		0	
3	Non-Ran	30-Jun-08	57.14.515	133.59.976	4	5.0	0	6.0	0	
3	Non-Ran	30-Jun-08	57.09.067	133.44.654	1	5.4	3	6.5	0	
3	Non-Ran	1-Jul-08	57.14.013	133.38.702	3	5.1	0		0	
3	Non-Ran	1-Jul-08	57.18.257	133.45.384	0		0		0	
3	Non-Ran	2-Jul-08	57.18.479	133.42.876	0		0		0	
3	Non-Ran	2-Jul-08	57.19.487	133.39.064	0		0	6.3	0	
3	Non-Ran	3-Jul-08	57.23.562	133.29.414	0		0	7.5	0	
3	Random	27-Jun-08	56.57.421	134.16.556	64	4.7	16	6.6	0	
3	Random	29-Jun-08	56.59.783	134.03.692	0		0		0	
3	Random	29-Jun-08	57.09.963	134.04.185	16	4.9	92	6.7	0	
3	Random	30-Jun-08	57.13.555	134.05.302	0		2	6.2	0	
3	Random	30-Jun-08	57.14.998	133.54.388	32	6.3	92	7.1	0	
3	Random	1-Jul-08	57.08.032	133.39.918	36	4.9	16	6.8	0	
3	Random	1-Jul-08	57.15.254	133.40.428	18	5.0	14	6.9	0	
3	Random	2-Jul-08	57.20.792	133.46.613	8	5.4	8	7.0	0	
3	Random	2-Jul-08	57.16.133	133.33.422	0		2	6.2	0	
3	Random	3-Jul-08	57.26.385	133.39.146	2	4.9	0		0	
3	Whale	4-Jul-08	57.22.537	133.47.245	0		4	7.4	0	
3	Whale	4-Jul-08	57.23.367	133.51.469	0		8	7.4	0	

3	Whale	8-Jul-08	57.19.332	133.51.260	0		0		0	
3	Whale	9-Jul-08	57.21.982	133.37.128	0		0		6	18.3
3	Whale	10-Jul-08	57.14.178	133.39.744	0		2	7.0	1	18.1
3	Whale	10-Jul-08	57.11.457	133.35.280	4	5.6	8	7.5	0	
3	Whale	11-Jul-08	57.17.370	133.33.450	0		6	9.5	4	19.7
3	Whale	12-Jul-08	57.01.561	134.26.156	48	6.3	0		0	
3	Whale	12-Jul-08	57.04.707	134.23.439	8	5.3	2	6.6	0	
4	Non-Ran	15-Jul-08	57.01.677	134.25.865	0		0		0	
4	Non-Ran	16-Jul-08	57.2.615	134.15.583	16	5.0	24	7.2	0	
4	Non-Ran	17-Jul-08	57.8.891	133.57.482	0		4	5.9	0	
4	Non-Ran	20-Jul-08	57.13.608	133.55.069	0		50	6.4	0	
4	Non-Ran	20-Jul-08	57.6.544	133.35.69	12	4.8	4	7.1	0	
4	Non-Ran	20-Jul-08	57.16.685	133.52.663	0		4	5.9	0	
4	Non-Ran	21-Jul-08	57.09.693	133.32.553	0		0		0	
4	Non-Ran	21-Jul-08	57.15.309	133.34.033	0		4	7.8	0	
4	Non-Ran	22-Jul-08	57.28.262	133.51.252	0		0		0	
4	Non-Ran	22-Jul-08	57.26.766	133.34.690	36	5.0	16	6.9	0	
4	Random	15-Jul-08	56.54.127	134.27.492	8	5.0	16	8.8	0	
4	Random	15-Jul-08	57.04.337	134.21.612	8	4.6	16	7.5	0	
4	Random	16-Jul-08	57.09.252	134.13.027	0		4	6.4	0	
4	Random	17-Jul-08	57.07.605	133.55.089	0		0		0	
4	Random	20-Jul-08	57.08.239	133.46.205	0		4	7.3	0	
4	Random	20-Jul-08	57.07.697	133.37.549	28	4.9	8	6.2	0	
4	Random	21-Jul-08	57.12.280	133.36.810	3	4.9	4	8.2	0	
4	Random	21-Jul-08	57.17.422	133.37.641	4	5.8	0		0	
4	Random	22-Jul-08	57.27.785	133.43.956	0		12	5.5	0	
4	Random	22-Jul-09	57.23.643	133.43.421	0		5	8.2	1	20.8
4	Whale	23-Jul-08	57.19.863	133.51.231	0		1	6.2	0	
4	Whale	23-Jul-08	57.22.566	133.50.655	2	6.1	1	5.8	0	
4	Whale	23-Jul-08	57.25.569	133.48.887	1	5.4	3	7.8	0	
4	Whale	23-Jul-08	57.26.900	133.51.753	4	4.6	0		0	
4	Whale	24-Jul-08	57.15.698	133.57.613	14	4.9	60	6.7	0	
4	Whale	24-Jul-08	57.8.11	133.50.373	0		36	8.2	0	
4	Whale	24-Jul-08	57.10.594	133.46.966	0	5.2	48	7.8	0	
4	Whale	24-Jul-08	57.9.697	133.41.094	48	4.5	88	7.2	0	
4	Whale	25-Jul-08	57.17.237	133.34.288	0		8	7.6	0	
4	Whale	25-Jul-08	57.20.681	133.33.121	0		16	6.7	0	
5	Non-Ran	6-Aug-08	57.04.499	134.10.616	0		2	8.1	0	
5	Non-Ran	6-Aug-08	57.09.882	134.06.580	32	4.8	64	7.6	0	
5	Non-Ran	7-Aug-08	57.13.874	134.00.286	0		4	9.0	0	
5	Non-Ran	8-Aug-08	57.09.115	133.39.795	0		48	10.0	0	
5	Non-Ran	8-Aug-08	57.05.136	133.28.834	0		13	6.7	0	
5	Non-Ran	8-Aug-08	57.07.327	133.32.447	0		192	9.7	0	
5	Non-Ran	9-Aug-08	57.22.364	133.50.195	0		1	10.9	0	
5	Non-Ran	9-Aug-08	57.16.541	133.33.056	0		0		0	
5	Non-Ran	10-Aug-08	57.24.536	133.32.215	0		6	8.5	0	

5	Non-Ran	10-Aug-08	57.25.081	133.29.553	4	5.8	7	8.0	2	18.7
5	Random	5-Aug-08	56.55.921	134.19.023	0		8	8.1	0	
5	Random	5-Aug-08	56.59.975	134.19.120	0		5	7.7	0	
5	Random	6-Aug-08	56.58.635	134.07.922	0		8	9.6	0	
5	Random	6-Aug-08	57.05.609	134.06.983	2	4.8	7	8.0	0	
5	Random	7-Aug-08	57.10.204	133.54.005	0		0		0	
5	Random	7-Aug-08	57.11.818	133.51.542	0		60	8.1	0	
5	Random	8-Aug-08	57.02.173	133.28.392	0		0		0	
5	Random	9-Aug-08	57.21.135	133.48.247	0		2	6.4	0	
5	Random	9-Aug-08	57.23.464	133.44.574	0		6	7.2	0	
5	Random	10-Aug-08	57.22.482	133.35.509	0		4	7.3	1	20.8
5	Random	10-Aug-08	57.22.523	133.33.596	0		0		0	
5	Random	10-Aug-08	57.22.529	133.33.595	3	5.3	5	7.0	0	
5	Random	10-Aug-08	57.27.209	133.33.111	0		5	8.5	0	
5	Random	10-Aug-08	57.27.207	133.33.099	0		4	10.0	0	
5	Whale	11-Aug-08	57.19.437	133.33.004	4	5.3	6	7.8	0	
5	Whale	11-Aug-08	57.21.879	133.29.902	4	6.6	0		0	
5	Whale	11-Aug-08	57.16.323	133.33.779	0		2	11.2	0	
5	Whale	14-Aug-08	57.18.111	133.40.065	0		0		0	
5	Whale	14-Aug-08	57.15.129	133.47.760	0		19	10.3	0	
5	Whale	15-Aug-08	57.20.496	133.50.888	0		0		0	
5	Whale	15-Aug-08	57.20.811	133.44.334	0		0		0	
5	Whale	15-Aug-08	57.25.872	133.41.845	0		1	7.5	0	
5	Whale	15-Aug-08	57.14.357	133.35.177	0		39	8.7	0	
6	Non-Ran	27-Aug-08	57.0.402	134.28.99	0		1	6.0	0	
6	Non-Ran	27-Aug-08	57.03.167	134.22.203	0		6	7.9	0	
6	Non-Ran	28-Aug-08	57.06.534	134.18.141	0		5	11.5	1	16.5
6	Non-Ran	28-Aug-08	57.10.391	134.10.027	0		6	9.7	0	
6	Non-Ran	29-Aug-08	57.15.159	134.02.225	0		2	10.2	0	
6	Non-Ran	29-Aug-08	57.15.526	133.53.295	0		2	10.0	0	
6	Non-Ran	30-Aug-08	57.5.413	133.31.513	0		4	11.1	0	
6	Non-Ran	30-Aug-08	57.20.720	133.52.460	0		0		0	
6	Non-Ran	31-Aug-08	57.17.865	133.39.234	0		7	10.4	0	
6	Random	27-Aug-08	56.56.759	134.30.416	0		3	8.5	0	
6	Random	27-Aug-08	56.58.808	134.22.177	0		0		0	
6	Random	28-Aug-08	57.00.255	134.07.587	0		3	11.9	0	
6	Random	28-Aug-08	57.07.620	134.08.948	0		3	9.1	0	
6	Random	29-Aug-08	57.07.458	133.57.382	0		3	8.3	0	
6	Random	29-Aug-08	57.5.719	133.39.103	0		6	11.1	1	24.0
6	Random	30-Aug-08	57.04.505	133.29.900	0		17	8.7	0	
6	Random	30-Aug-08	57.17.217	133.46.545	0		6	10.2	0	
6	Random	31-Aug-08	57.24.538	133.46.163	0		0		0	
6	Random	31-Aug-08	57.21.174	133.34.592	0		0		0	
6	Whale	1-Sep-08	57.17.753	133.31.511	0		0		0	
6	Whale	2-Sep-08	57.18.318	133.39.791	0		0		0	
6	Whale	2-Sep-08	57.19.845	133.33.578	0		0		0	

6	Whale	2-Sep-08	57.20.726	133.52.358	4	4.8	58	7.9	0	
6	Whale	4-Sep-08	57.28.478	133.44.571	0		0		0	
6	Whale	7-Sep-08	57.19.328	133.52.059	0		7	11.4	0	
6	Whale	8-Sep-08	57.24.288	133.45.240	0		29	10.9	1	15.5
6	Whale	8-Sep-08	57.21.309	133.50.197	0		8	10.6	0	
6	Whale	10-Sep-08	57.21.103	133.38.544	0		1	5.9	0	

Table A.5. Counts and average lengths of *Euphausia pacifica* from non-random ('targeted'), random, and whale-associated net tows in 2008 in Frederick Sound/Stephens Passage, Southeast Alaska.

Survey	Sample	Date	Latitude	Longitude	Larvae #	Larvae Len.	Juvenile #	Juvenile Len.	Adult #	Adult Len.
2	Non-Ran	8-Jun-08	56.54.692	134.25.460	0		8	11.7	1	17.1
2	Non-Ran	8-Jun-08	57.55.246	134.19.157	0		0		0	
2	Non-Ran	9-Jun-08	57.08.124	134.15.317	0		0		0	
2	Non-Ran	10-Jun-08	57.09.447	134.13.806	0		0		3	18.2
2	Non-Ran	11-Jun-08	57.6.515	133.40.372	0		0		0	
2	Non-Ran	11-Jun-08	57.05.846	133.32.266	0		0		0	
2	Non-Ran	11-Jun-08	57.6.698	133.33.532	0		0		4	21.6
2	Non-Ran	12-Jun-08	57.20.295	133.43.322	0		0		5	20.2
2	Non-Ran	13-Jun-09	57.25.241	133.32.473	0		0		4	19.6
2	Non-Ran				0		1	14.0	5	12.8
2	Random	11-Jun-08	57.09.921	133.45.931	0		0		0	
2	Random	11-Jun-08	57.9.241	133.37.79	0		0		0	
2	Random	12-Jun-08	57.13.633	133.37.986	0		0		0	
2	Random	12-Jun-08	57.19.151	133.41.698	0		0		2	19.8
2	Random	13-Jun-08	57.23.405	133.29.200	0		0		0	
2	Whale	15-Jun-08	57.22.072	133.48.085	0		0		0	
2	Whale	15-Jun-08	57.16.918	134.02.646	0		0		0	
2	Whale	17-Jun-08	57.12.272	133.38.753	0		0		4	19.8
2	Whale	17-Jun-08	57.15.899	133.36.833	0		0		0	
2	Whale	22-Jun-08	57.9.853	134.01.629	0		0		0	
3	Non-Ran	27-Jun-08	56.58.149	134.13.134	0		0		0	
3	Non-Ran	29-Jun-08	57.03.918	134.02.569	0		0		0	
3	Non-Ran	30-Jun-08	57.14.515	133.59.976	0		0		0	
3	Non-Ran	30-Jun-08	57.09.067	133.44.654	0		0		0	
3	Non-Ran	1-Jul-08	57.14.013	133.38.702	0		0		0	
3	Non-Ran	1-Jul-08	57.18.257	133.45.384	0		0		0	
3	Non-Ran	2-Jul-08	57.18.479	133.42.876	0		0		0	
3	Non-Ran	2-Jul-08	57.19.487	133.39.064	0		0		0	
3	Non-Ran	3-Jul-08	57.23.562	133.29.414	0		0		0	
3	Random	27-Jun-08	56.57.421	134.16.556	0		0		0	
3	Random	29-Jun-08	56.59.783	134.03.692	0		0		0	
3	Random	29-Jun-08	57.09.963	134.04.185	0		0		0	
3	Random	30-Jun-08	57.13.555	134.05.302	0		0		0	

3	Random	30-Jun-08	57.14.998	133.54.388	0		0		1	18.9
3	Random	1-Jul-08	57.08.032	133.39.918	0		0		1	20.6
3	Random	1-Jul-08	57.15.254	133.40.428	0		4	7.4	1	19.8
3	Random	2-Jul-08	57.20.792	133.46.613	0		0		0	22.1
3	Random	2-Jul-08	57.16.133	133.33.422	0		0		0	
3	Random	3-Jul-08	57.26.385	133.39.146	0		0		0	
3	Whale	4-Jul-08	57.22.537	133.47.245	0		0		0	
3	Whale	4-Jul-08	57.23.367	133.51.469	0		0		0	
3	Whale	8-Jul-08	57.19.332	133.51.260	0		0		0	
3	Whale	9-Jul-08	57.21.982	133.37.128	0		0		0	
3	Whale	10-Jul-08	57.14.178	133.39.744	0		0		0	
3	Whale	10-Jul-08	57.11.457	133.35.280	0		2	12.7	5	13.6
3	Whale	11-Jul-08	57.17.370	133.33.450	0		0		4	21.2
3	Whale	12-Jul-08	57.01.561	134.26.156	0		0		0	
3	Whale	12-Jul-08	57.04.707	134.23.439	0		0		2	21.5
4	Non-Ran	15-Jul-08	57.01.677	134.25.865	0		0		0	
4	Non-Ran	16-Jul-08	57.2.615	134.15.583	0		0		0	
4	Non-Ran	17-Jul-08	57.8.891	133.57.482	0		0		1	22.1
4	Non-Ran	20-Jul-08	57.13.608	133.55.069	0		0	8.8	3	19.7
4	Non-Ran	20-Jul-08	57.6.544	133.35.69	0		0		0	
4	Non-Ran	20-Jul-08	57.16.685	133.52.663	0		0		0	
4	Non-Ran	21-Jul-08	57.09.693	133.32.553	0		0		0	
4	Non-Ran	21-Jul-08	57.15.309	133.34.033	0		2	11.0	0	
4	Non-Ran	22-Jul-08	57.28.262	133.51.252	4	5.8	0		4	19.6
4	Non-Ran	22-Jul-08	57.26.766	133.34.690	0		0		1	20.6
4	Random	15-Jul-08	56.54.127	134.27.492	0		0		1	21.0
4	Random	15-Jul-08	57.04.337	134.21.612	0		8	8.0	0	
4	Random	16-Jul-08	57.09.252	134.13.027	0		0		0	
4	Random	17-Jul-08	57.07.605	133.55.089	0		0		0	
4	Random	20-Jul-08	57.08.239	133.46.205	0		28	8.4	0	
4	Random	20-Jul-08	57.07.697	133.37.549	0		40	8.5	0	
4	Random	21-Jul-08	57.12.280	133.36.810	0		0		0	
4	Random	21-Jul-08	57.17.422	133.37.641	0		0		0	
4	Random	22-Jul-08	57.27.785	133.43.956	0		0		2	20.0
4	Random	22-Jul-09	57.23.643	133.43.421	0		0		0	
4	Whale	23-Jul-08	57.19.863	133.51.231	0		0		1	19.2
4	Whale	23-Jul-08	57.22.566	133.50.655	0		0		0	
4	Whale	23-Jul-08	57.25.569	133.48.887	0		5	8.6	0	
4	Whale	23-Jul-08	57.26.900	133.51.753	0		0		0	

4	Whale	24-Jul-08	57.15.698	133.57.613	0		8	8.7	0	
4	Whale	24-Jul-08	57.8.11	133.50.373	0		64	7.4	0	
4	Whale	24-Jul-08	57.10.594	133.46.966	0		12	8.3	0	
4	Whale	24-Jul-08	57.9.697	133.41.094	0		208	7.8	0	
4	Whale	25-Jul-08	57.17.237	133.34.288	0		4	7.9	1	19.0
4	Whale	25-Jul-08	57.20.681	133.33.121	0		144	8.6	0	
5	Non-Ran	6-Aug-08	57.04.499	134.10.616	0		2	9.1	0	
5	Non-Ran	6-Aug-08	57.09.882	134.06.580	0		320	8.6	0	
5	Non-Ran	7-Aug-08	57.13.874	134.00.286	4	6.3	6	9.8	3	20.5
5	Non-Ran	8-Aug-08	57.09.115	133.39.795	0		416	9.7	2	21.7
5	Non-Ran	8-Aug-08	57.05.136	133.28.834	0		8	8.0	1	21.9
5	Non-Ran	8-Aug-08	57.07.327	133.32.447	0		368	9.2	6	20.8
5	Non-Ran	9-Aug-08	57.22.364	133.50.195	0		1	9.8	1	24.0
5	Non-Ran	9-Aug-08	57.16.541	133.33.056	0		0		0	
5	Non-Ran	10-Aug-08	57.24.536	133.32.215	0		2	9.2	0	
5	Non-Ran	10-Aug-08	57.25.081	133.29.553	0		5	10.6	5	19.8
5	Random	5-Aug-08	56.55.921	134.19.023	0		16	7.0	0	
5	Random	5-Aug-08	56.59.975	134.19.120	0		0		0	
5	Random	6-Aug-08	56.58.635	134.07.922	0		0		0	
5	Random	6-Aug-08	57.05.609	134.06.983	0		6	10.7	0	
5	Random	7-Aug-08	57.10.204	133.54.005	0		0		0	
5	Random	7-Aug-08	57.11.818	133.51.542	0		232	8.6	0	
5	Random	8-Aug-08	57.02.173	133.28.392	0		0		0	
5	Random	9-Aug-08	57.21.135	133.48.247	0		2	9.3	1	23.2
5	Random	9-Aug-08	57.23.464	133.44.574	0		3	9.3	1	19.5
5	Random	10-Aug-08	57.22.482	133.35.509	0		3	10.9	1	20.8
5	Random	10-Aug-08	57.22.523	133.33.596	0		3	11.1	2	20.2
5	Random	10-Aug-08	57.22.529	133.33.595	0		5	10.5	3	18.8
5	Random	10-Aug-08	57.27.209	133.33.111	0		4	11.6	0	
5	Random	10-Aug-08	57.27.207	133.33.099	1	6.2	4	9.7	0	
5	Whale	11-Aug-08	57.19.437	133.33.004	0		8	8.7	1	20.5
5	Whale	11-Aug-08	57.21.879	133.29.902	0		0		1	21.1
5	Whale	11-Aug-08	57.16.323	133.33.779	2	6.3	8	7.1	0	
5	Whale	14-Aug-08	57.18.111	133.40.065	0		0		0	
5	Whale	14-Aug-08	57.15.129	133.47.760	0		2	9.4	1	20.0
5	Whale	15-Aug-08	57.20.496	133.50.888	0		0		0	
5	Whale	15-Aug-08	57.20.811	133.44.334	0		2	11.7	0	
5	Whale	15-Aug-08	57.25.872	133.41.845	0		1	10.2	1	21.3
5	Whale	15-Aug-08	57.14.357	133.35.177	0		28	10.4	0	

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6	Non-Ran	27-Aug-08	57.0.402	134.28.99	0		0		0	
6	Non-Ran	27-Aug-08	57.03.167	134.22.203	4	5.0	10	10.6	3	19.2
6	Non-Ran	28-Aug-08	57.06.534	134.18.141	0		0		1	19.7
6	Non-Ran	28-Aug-08	57.10.391	134.10.027	0		3	9.7	0	
6	Non-Ran	29-Aug-08	57.15.159	134.02.225	0		0		1	21.0
6	Non-Ran	29-Aug-08	57.15.526	133.53.295	1	5.6	7	9.0	0	
6	Non-Ran	30-Aug-08	57.5.413	133.31.513	0		0		0	
6	Non-Ran	30-Aug-08	57.20.720	133.52.460	10	3.8	0		0	
6	Non-Ran	31-Aug-08	57.17.865	133.39.234	0		0		0	
6	Random	27-Aug-08	56.56.759	134.30.416	0		0		0	
6	Random	27-Aug-08	56.58.808	134.22.177	4	4.8	0		0	
6	Random	28-Aug-08	57.00.255	134.07.587	4	4.7	0		0	
6	Random	28-Aug-08	57.07.620	134.08.948	0		0		0	
6	Random	29-Aug-08	57.07.458	133.57.382	0		0		0	
6	Random	29-Aug-08	57.5.719	133.39.103	0		0		0	
6	Random	30-Aug-08	57.04.505	133.29.900	0		0		1	20.3
6	Random	30-Aug-08	57.17.217	133.46.545	4	4.0	2	11.4	0	
6	Random	31-Aug-08	57.24.538	133.46.163	2	3.1	0		0	
6	Random	31-Aug-08	57.21.174	133.34.592	0		0		0	
6	Whale	1-Sep-08	57.17.753	133.31.511	0		0		0	
6	Whale	2-Sep-08	57.18.318	133.39.791	1	3.4	0		0	
6	Whale	2-Sep-08	57.19.845	133.33.578	0		3	11.5	0	
6	Whale	2-Sep-08	57.20.726	133.52.358	10	3.7	12	9.6	0	
6	Whale	4-Sep-08	57.28.478	133.44.571	6	3.9	6	10.5	0	
6	Whale	7-Sep-08	57.19.328	133.52.059	14	3.8	4	12.1	1	19.7
6	Whale	8-Sep-08	57.24.288	133.45.240	1	3.4	3	9.3	0	
6	Whale	8-Sep-08	57.21.309	133.50.197	1	2.7	1	11.0	1	15.0
6	Whale	10-Sep-08	57.21.103	133.38.544	0		4	12.4	2	20.8
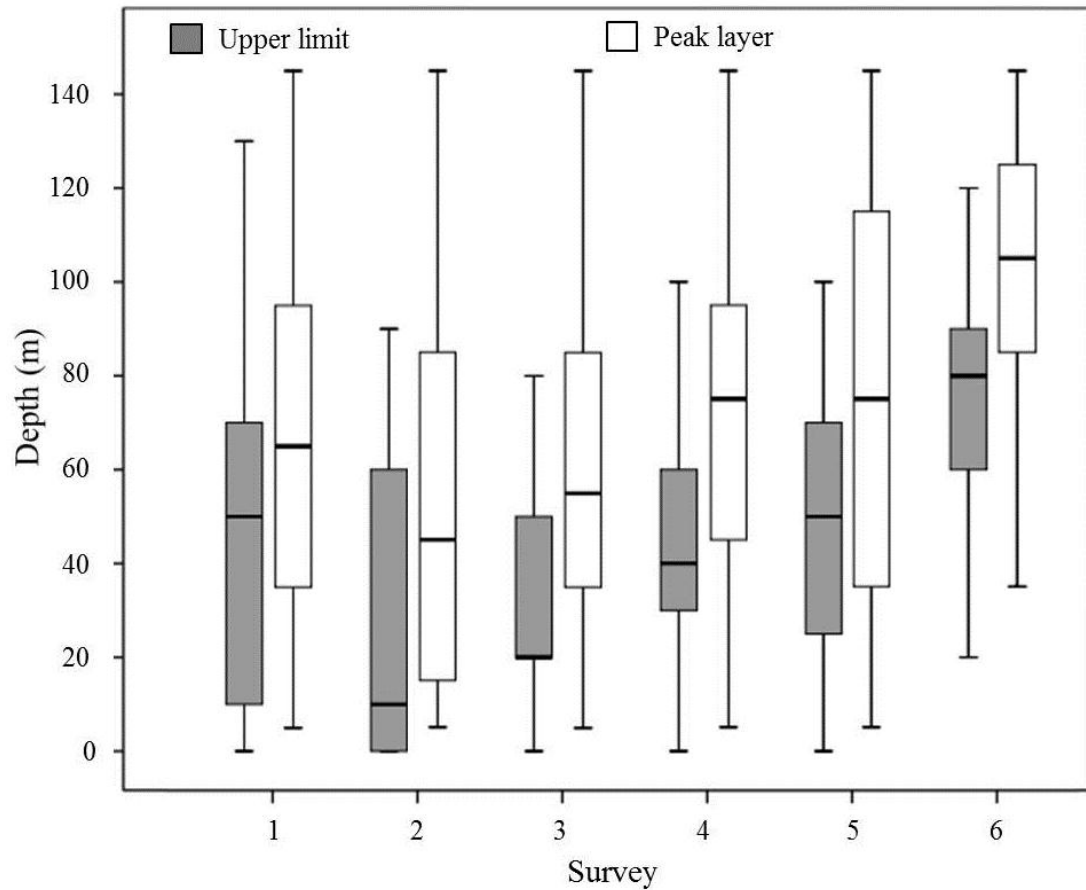
Figure A.1. Depth of the upper limit of the acoustic scattering layer and peak acoustic backscatter from each hydroacoustic survey in Frederick Sound/Stephens Passage, Southeast Alaska in 2008. Boxes represent interquartile range with median indicated by the line.
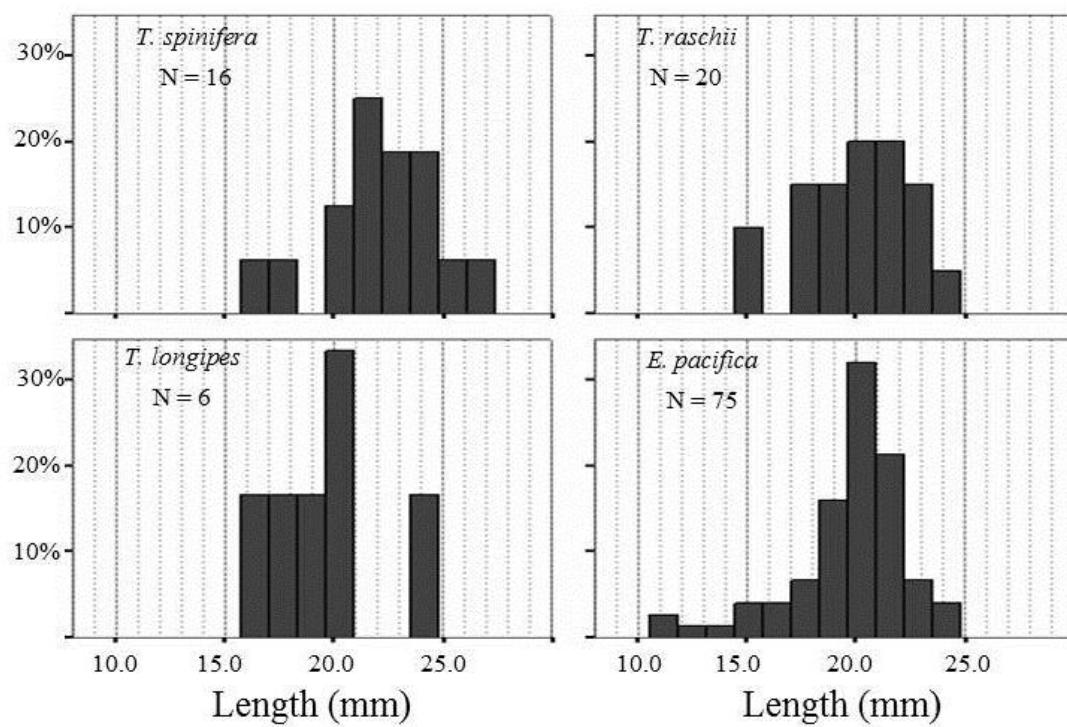
Figure A.2. Length distribution of adult euphausiids from all net samples collected in Frederick Sound/Stephens Passage, Southeast Alaska in 2008.
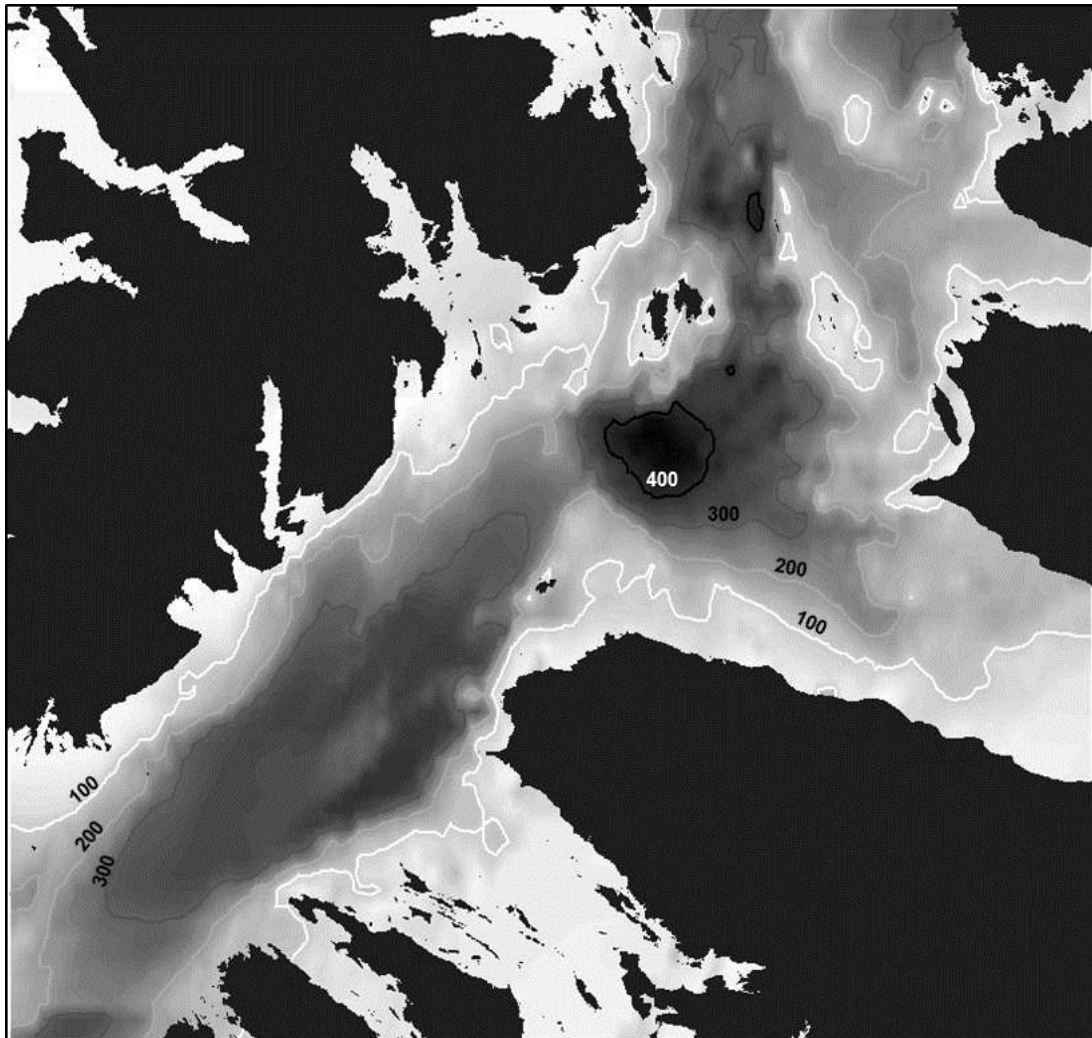
Figure A.3. Bathymetry of Frederick Sound and Stephens Passage, Southeast Alaska generated from kriging the echosounder-detected bottom data from the hydroacoustic surveys conducted during the study in 2008. 100m depth contours are labeled.

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