The Foraging Ecology of Gray Whales in Clayoquot Sound:
Interactions Between Predator and Prey Across a Continuum of Scales

By

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B.Sc., University of Victoria, 2006.

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in the Department of Geography

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ABSTRACT

Understanding the ecology of an organism is fundamental for defining conservation and management priorities for wildlife and natural ecosystems. The most basic ecological framework identifies the key components of an organism's habitat, and the scale for measuring the quality of those features. How these core needs are expressed and vary in the surrounding ecosystem changes over time and space. In marine systems, the physical environment has few strict boundaries, and variations regularly occur on a scale from days to decades. The dynamic and patchy nature of marine habitat makes defining the ecological roles of an animal difficult, even where baseline data exists. In this study I analyze long term field records on the ecological interactions between foraging gray whales (*Eschrichtius robustus*), and their mysid prey (Family *Mysidae*) in Clayoquot Sound, B.C. By looking at spatial and temporal shifts at both trophic levels, I measure foraging responses and requirements, and assess prey resource availability and resiliency in the marine environment at a series of scales. Appreciation for bottom-up and top-down trophic interactions provides the foundation for identifying natural variability in marine habitat, and a baseline for conservation measures that seek to use marine predators as a barometer of broader ecosystem health.

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Chapter One: The Ecology of a Spectacular Marine Predator, The Gray Whale (*Eschrichtius robustus*) in Clayoquot Sound, B.C.

Introduction

Large marine predators are a poorly defined ecological force. Assessments of the role of apex predators, such as whales and predatory fish are speculative or oversimplified, and many processes and patterns remain poorly understood (Bowen 1997, Estes 2006, Coyle *et al.* 2007). What is known is that the world's oceans have been subject to large-scale removals at several trophic levels in recent history through fisheries. While many marine predators continue to be commercially hunted, industrial whaling has largely ceased and some whale populations are thought to be recovering (Moore *et al.* 2001, Rugh *et al.* 2005, Alter *et al.* 2007). However, even establishing the historic or current abundance of a particular species is challenging in the marine environment. Estimates are typically based on molecular data, weak habitat models, and inconsistent records that vary considerably due to the cryptic nature of marine animals and continuous readjustments in our knowledge base (Springer *et al.* 2003, Rugh *et al.* 2005, Alter *et al.* 2007).

Discerning the ecological role of whales is limited by a lack of long-term data, and as a consequence, most of our knowledge is inferred from historical reflection (Katona & Whitehead 1988), correlation between systems, and generalized theories borrowed from the terrestrial environment (Estes 2006). With a lack of reliable or consistent data, broad scale assumptions of whale ecology provide little insight. Correlations and theory suggest that their distribution patterns are largely driven by food availability. The ecological nuances of cetacean habitat selection, across multiple scales, are highly variable and largely inadequate for effective conservation (Hunt & McKinnell 2006).

As whale populations recover from commercial whaling, the ocean ecosystems and prey resources that once influenced their distribution may be altered. In the period of the whales' absence, some species may find their preferred prey abundant, while others may have to contend with resource limitation, as prey in many areas have been similarly subject to large scale removals, trophic cascades, regime shifts, food chain decoupling, or reductions in productivity exacerbated by current trends in global climate (Highsmith & Coyle 1992, Steele 1998a, Bakun 2006, Estes 2006, Coyle *et al.* 2007, Grebmeier *et al.* 2007). Ultimately, determining the ecological role of whales in ocean ecosystems will require disentangling the fundamental interactions between the top-down effects of whales as predators, from the bottom-up effects of ocean primary productivity and variation in food availability at differing temporal and spatial scales (Levin 1992, Weins 1989, Steele 1989, Steele 1998b, Paine 1980).

The eastern Pacific gray whale (*Eschrichtius robustus*) is one of the few populations of baleen whale that is thought to have recovered to their pre-whaling population levels (Rugh 2005). During their annual migration from the breeding lagoons of Baja California Sur, to the foraging grounds of the Chirikov Basin and the northern parts of the Bering and Chukchi Seas, gray whales pursue patchily distributed prey. While most of the breeding population is thought to travel straight through, a number (low hundreds) of seasonal residents remain in the coastal waters from Oregon to Alaska, and forage on macro-zooplankton and benthic invertebrates over the summer foraging season. These seasonally resident animals have been recently named the Pacific Coastal Feeding Aggregation (PCFA).

Based on a gray whale's need to forage to restore energy reserves depleted over the course of the winter, their distribution has been closely aligned to the supply of prey in B.C. coastal waters (Dunham & Duffus 2001, Olsen 2006, Nelson *et al.* 2008). Gray whales found off the west coast of Vancouver Island in the boreal summer are opportunistic foragers that can switch prey and foraging tactics to take advantage of short term availability of energy (Dunham & Duffus 2001). Studying the interaction between prey resources and predation by gray whales in my study area presents a unique opportunity for lessons in the basics of whale ecology and identifying the primary drivers of energy flows through coastal marine ecosystems (Dunham & Duffus 2001, Hunt & McKinnell 2006, Nelson *et al.* 2008).

The ecological concepts at work in the interplay between top-down predation and bottom-up productivity have emerged from a body of theory which includes: the trophic energy transfer through food chains and webs (Watt 1947, MacArthur 1955); the role of predation in structuring ecological communities (Paine 1966, Menge & Sutherland 1976);

disturbance regulation of community structure, species diversity, and abundance (Hairston *et al*. 1960, Connell 1978); the relationship between a species' niche and its habitat (Grinnell 1916, Hutchinson 1957, MacArthur & Pianka 1966); and the influence of scale and pattern on the distribution of resources and processes (Levin 1992, Weins 1989).

This theoretical foundation has been the wellspring of a large body of ecological literature that has only recently been integrated into marine mammal research. While there is an increasing interest in habitat associations and models for use in management applications, only a few studies on cetaceans examine relationships with prey variables (Wishner *et al.* 1995, Croll *et al.* 1998, Croll *et al.* 2005, Torres 2008) or otherwise test specific ecological hypotheses to describe cetacean distributions. Redfern *et al.* (2006) review cetacean habitat and modeling research and conclude that future studies need to integrate theory from community ecology, move beyond preliminary habitat relationships, and include considerations for the abundance of prey species at multiple scales.

The subject of this study is how the interactions between top down predation and bottom up productivity influence the spatial and temporal patterns of gray whale foraging in Clayoquot Sound. Gray whale research conducted over the last two decades in the study area has developed some appreciation of the role of gray whales as a regulatory force in the local coastal ecosystem. Beginning with the spatial shift in foraging effort from benthic amphipods to epibenthic mysids (Family *Mysidae*) in 1992-93 (Duffus 1996, Dunham & Duffus 2001, 2002), whales have since foraged primarily for mysids. Individual whale foraging locations have spatial focus around the 10 m depth contour (Short 2005), while the hub of overall feeding activity moves northward in the study area over the course of the summer. Over the last 12 years, whale census surveys depict a dynamic but diminishing number of foraging summer resident gray whales in the study area (Feyrer, this thesis).

Acoustic measures of mysid swarm locations, density, and biomass were undertaken to link fluctuations in annual foraging effort to prey abundance and distribution between 2004 and 2008 (Nelson *et al.* 2008). In each season, prey quality oscillates from initial abundance, to depletion via predation, and subsequent reproductive replenishment. The overall density and biomass of mysid swarms in the study area fluctuates between years, but generally exhibits a declining trend. Spatially, there are relatively static "core" mysid swarms within, and even between seasons. This pattern reflects mysids' bottom referent behaviour, and the retention of progeny in the natal swarm (Stelle 2001, Patterson 2004, Short 2005, Nelson *et al.* 2008).

The timing and strength of bottom-up processes in any year could determine the abundance of prey resources. The initial spring pulse of productivity takes place prior to the onset of heavy foraging pressure, allowing swarms to grow in the whales' absence. Mysid swarming and avoidance response may have successfully evolved to reduce the strength of predation from hunt and peck predators, such as rockfish (McFarland & Kotchian 1982). However, it is counterproductive as a strategy against foraging gray whales, as they can engulf entire swarms. Increased prey density may be one cue for marine predators searching in a patchy environment, however, regardless of the initial abundance; foraging whales limit the resilience of prey populations to recover.

At the peak of the season, whales in the area consume large quantities of prey daily, significantly affecting the structure and abundance of mysid populations. Once mysid swarms have been reduced to levels no longer worth pursuing, whales leave the area for other foraging sites along the coast of Vancouver Island, and, possibly, farther afield. For mysids, the last summer pulse of reproduction, occurring after most whales abandon the area, largely determines the size of their over-wintering population. Between a long-term reduction in the density of amphipods (Carruthers 2000), and a decline in mysid abundance corresponding to lower whale numbers, foraging effort appears capable of altering prey community dynamics. The top-down structuring that I have studied in this marine community has long-term implications for local prey productivity, habitat quality, and our appreciation of the fine scale dynamics of whale ecology.

In Chapter Two, I begin by examining the variability in long-term temporal patterns of gray whale presence in the study area. These summer residents are part of a short food chain, phytoplankton–mysid-whale, which is subject to strong influence from top-down or bottom-up driving forces. Correlations between primary productivity and whale presence suggest relatively small changes in strength of bottom-up forcing. Here I examine the variability observed over 12 field seasons of whale census surveys in the study area (1997-2008). Using time series and correlation analysis, I evaluate the strength of the relationship between average annual primary productivity, from upwelling indices and sunshine variability to seasonal peaks in whale numbers and mysid biomass. I assess the relative importance of broad scale bottom up trophic energy transfers in determining the foraging ecology of this highly mobile marine predator.

Chapter Three details my study of the spatial ecology of individual whale foraging behaviour. I focus on the foraging dive patterns of individual gray whales during focal follow surveys along the southwest coast of Flores Island between 2006 and 2008. Gray whales exhibit distinct dive patterns when foraging on mysids, which is demonstrated by their fine scale movements in response to prey quality, measured by acoustic assessments of overall prey density. In this chapter, I test the strength of the linkages between individual foraging whales and their prey.

In Chapter Four, I refine my estimates of whale response to prey by conducting hydro acoustic surveys during continuous focal follow surveys from May to August, 2008, in Clayoquot Sound. I found that coincident prey density was, on average, higher than study area wide estimates, and that whales foraged at sites of higher prey density. Exploring the interaction between scales illuminates a distinct predatory strategy, and lends insight to how whales' relationship with their prey aggregates across scales.

In Chapter Five, I follow the argument that if prey populations are fluctuating then the structure of their community may also fluctuate. Here I assess some of the impact of foraging whales on the species structure of the mysid populations. I examine trends in species diversity between 1996-2008, in relation to predatory effort to illuminate the role of disturbance and some of the subtleties of the ecological impact of gray whales. The coastal mysid zooplankton complex consists of approximately 48 species with at least 10 identified in the study area. Interestingly, a diversity of apparently “redundant” mysid species are often found within the same swarm. Usually *Holmesmysis sculpta*, dominates the mysid species swarm (Stelle 2001, Dunham & Duffus 2002, Newell & Cowles 2006), but patterns of dominance have shifted over the last two years. What regulates and causes shifts in species diversity is hypothesized to be the interplay of life history attributes, such as fecundity, and regular intermediate disturbance. The impact of persistent and heavy predation by gray whales is strongly implicated, and I compare diversity indices to annual foraging pressure to find a pattern.

Finally in Chapter Six, as part of a larger question in my search for the driving force in species' structure of mysid communities, I count the brood size of several mysid species to search for one of several alternative explanations for the diversity and dominance issue. I compare the differences in embryo production between sympatric species of mysids to determine whether dominance may be a product of differential fecundity. As gray whale predation can rapidly reduce local mysid populations, the reproductive capacity of mysids is key to understanding the resiliency of prey populations. However, little is known about the life histories of the ten or more species of epibenthic mysids found in Clayoquot Sound. There are several potential routes by which a species can dominate, one of which is higher embryo production. I collected samples to address that question on five surveys between June and August of 2008.

My approach to the broad questions of baleen whale ecology in the coastal zone is based on a research framework that incorporates community ecology theory, behavioural ecology, and biogeography to determine the functional role of gray whales. Integrating different spatial and temporal scales provides an initial assessment of the interaction between top down-bottom up regulation in the coastal zone. Establishing a foundation for management of large cetaceans requires an ecological appreciation of their core needs, and how they change over time and space. More broadly, assessing the role of human impacts on whales in the coastal zone, such as those related to development or ecotourism must be based on the key components of an organism's habitat, at the appropriate scale for measuring the quality of those features.

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Chapter Two: Time and Space Partitioning by Gray Whales and Their Prey on the West Coast of Vancouver Island, Canada.

Abstract

During the summer months off Flores Island, on the west coast of Vancouver Island, B.C., gray whales (*Eschrichtius robustus*) cap a short food chain, phytoplankton–mysid-whale, where productivity is restricted by top-down and bottom-up driving forces. Here I examine variability observed during 12 field seasons (1997-2008) of whale census surveys. Foraging effort is significantly different between years. I connect whale foraging effort to variation in prey populations and proxies of primary productivity. I evaluate the strength of the relationship between annual primary productivity, based on the number of bright sunshine days and positive upwelling in spring, to whale numbers and mysid density. Over the 12 year period there is no significant relationship between the average number of whales in the study area and average spring upwelling value or number of spring upwelling days. Spring sunshine input was not significantly correlated to average whale foraging effort during the period 1997-2006. Average mysid density between the five-year period, 2004-2008, is significantly correlated to average number of whales in the study area. Year to year, the average physical spring conditions show little variation, in comparison to significant changes in prey and predator. These results strongly suggest that top-down forces prevail in this discrete summer foraging site.

Introduction

In the ocean, prey are found at varying scales of patchiness (Steele 1976, Levin 1992, Wishner *et al*. 1995, Fauchald *et al.* 2002). The physical and biological dynamics of the ocean, which operate at several different scales, significantly influence the degree and extent of that patchiness (Steele 1976, Pinel-Alloul 1995, Denman & Dower 2001). How local populations of upper trophic level species are regulated by energy flows through coastal marine ecosystems requires sorting the relative strength of primary drivers controlling ecosystem structure and dynamics, both resource limitation (bottom-up mechanisms) and predation (top-down mechanisms) (Hunt & McKinnell 2006).

In the spring, phytoplankton blooms are tightly coupled with herbivorous grazers that, in turn, fuel upper trophic levels from invertebrates to fish and large baleen whales. Typically, a pulse in algal production is triggered by oceanographic conditions, which stabilize the water column and increase available nutrients, and with the seasonal addition of bright sunlight, cause phytoplankton blooms. However, the diverse topography and terrestrial influences in the coastal zone complicate generalizations about the strength, direction and importance of broad scale events in localized areas (Longhurst 1998). For example, ecologically significant variation occurs in the timing of primary productivity and community diversity between sites within the same upwelling region off the Oregon coast (Menge *et al*. 1997). The cycle of spring upwelling varies annually in timing or strength, but historical reviews suggest that, cumulatively, physical upwelling conditions maintain annual averages (Schwing *et al.* 2006). Deviations in the normal timing of events may have immediate ecological consequences, but they are short term, and buffered within the annual cycle. Other variables, such as the Pacific Decadal Oscillation (PDO), may also influence productivity; however, altered sea surface temperatures would be captured in upwelling indices and should reflect this long-lived pattern. Although spring upwelling is often assumed to be the most important supply of limited nutrients for primary production, other sources of nitrates, for example, terrestrial subsidies or bacterial fixation of atmospheric nitrogen, are more influential in some areas (Gruber 2005, Ware & Thomson 2005, Tallis 2009).

Bottom up forcing clearly influences ocean ecosystems. However, consumption by top predators, like marine mammals, has a direct and significant impact on the community structure of prey species (Katona & Whitehead 1988, Bowen 1997). While studies of marine fish have shown that changes in predator populations can have strong effects on prey in oceanic food webs (Worm & Myers 2003), the top down view remains poorly understood in the case of marine mammals, in part due to the size and range of their habitats, and the lack of available baseline or historical data (Paine 2006). Despite the climate change paradigm shifting focus away from interspecific interactions as key factors in ecosystem structure (Ainley *et al*. 2007), studies by Estes (1998), Springer *et al.* (2003), and Coyle *et al.* (2007) have provided evidence that whales significantly alter food webs.

At broad scales, various oceanographic processes have been associated with the distribution patterns of top predators (Sims *et al.* 1998, Benson *et al*. 2002, Croll *et al.* 2005, Keiper *et al.* 2005, Balance *et al.* 2006, Newell & Cowles 2006). The movement patterns of whales are no exception, being largely driven by food availability during the foraging season (Murase *et al.* 2002, Hunt & McKinnell 2006). As many baleen whales spend half the year in warmer, less productive waters, they depend on locating dense aggregations of prey during the foraging season to rebuild energy reserves (Brodie 1975, Kenney 1986, Dunham & Duffus 2002). Foraging effort is focused at these sites until prey biomass is no longer sufficient, or a better prey resource becomes available (Charnov 1976, Piatt & Methven 1992, Kenney *et al.* 1995, Dunham & Duffus 2001, Kerr & Duffus 2005).

In the high latitude seas, gray whales (*Eschrichtius robustus*) typically feed on benthic prey, in addition to a variety of coastal plankton and invertebrates, in coastal areas from California to Alaska (Nerini 1984, Oliver & Slattery 1985, Kim & Oliver 1989, Dunham & Duffus 2001, 2002, Newell & Cowles 2006, Stelle *et al.* 2008). Gray whales foraging off the west coast of Vancouver Island, in Clayoquot Sound, B.C. (Fig. 1) are part of the Pacific Coast Foraging Aggregation (PCFA), and predominately feed on epibenthic mysids (*Crustacea: Mysidacea*) in this area (Moore *et al.* 2007). Mysids, also known as “opossum” shrimp, form dense swarms over rocky reefs, often in association with kelp forests (Roast *et al.* 1998). The ten or more species of mysids commonly found in the study area are euryphagous omnivores, seasonally exploiting various algae, phytoplankton, zooplankton, crustacea and detritus (Mauchline 1980, Mulkins *et al.*

2002). Estimates suggest that gray whales require between 250 and 1100 kg, or 7.6×10^5 kilocalories/ day (Rice and Wolman 1971, Nerini 1984, Highsmith & Coyle 1992, Greenwald 2005). Translating the caloric demand into mysids (assuming an average dry body weight of 0.8 mg, and a caloric content of 4.8 calories/mg dry weight), individual gray whales would need to consume between 1.9×10^7 and 7.5×10^7 mysids/day (Mulkins *et al.* 2002, Olsen 2006). The total number of mysids in the study site is unknown, but their available habitat is restricted by shallow areas ($<20\text{km}^2$) and limited by the extent of reef complexes.

In British Columbia coastal waters, increased phytoplankton productivity has been tied to the wane of winter low-pressure weather systems, and increased sunlight (Willette *et al.* 1999, Harris *et al.* 2009). Phytoplankton is the trophic foundation of many marine food webs, and the timing and intensity of the 'spring bloom' may provide additional resources necessary for mysid reproduction prior to the arrival of foraging gray whales (Vadeboncoeur 2005, Newell *et al.* 2006, Jumars 2007). They typically produce relatively small broods, roughly 50 fully developed young per generation, released into the natal swarm. Juvenile mysids take approximately 60 days to reach sexual maturity (Mauchline 1980, Wittmann 1984, Stelle 2001, Mulkins *et al.* 2002). The size of this first spring cohort creates the mysid prey base for the rest of the summer foraging season. Mysid density increases more so with the second generation, in time for the whales' arrival (Dunham & Duffus 2001, Stelle *et al*. 2008).

In a bottom-up driven system, the spring bloom determines the foraging opportunities for whales, through increased zooplankton production. While in a top-down structured system, gray whales appearing during the summer have lasting impacts on the size and number of mysid swarms, with productivity limited by predation, rather than broad oceanographic conditions. Here, I examine restraints in the relationship between gray whales and their prey by looking at differences in bottom-up and top down forces over a 12 year span. To characterize the magnitude of top down force, I define the peak and average foraging effort in each summer season (May 24 to September 8) for the years 1997-2008. I correlate this variable foraging effort to three primary drivers: spring sunlight, upwelling strength, and mysid density for each year data is available. I then compare the differences in annual foraging effort between each year, and test whether any year influences the next, and look for concomitant variation in bottom-up forces. My prediction is that, due to the size and predatory capacity of the predator, the number of whales in any given year determines the following years' prey base, and subsequently the whale foraging response. Bottom-up forces can only operate, whether weakly or strongly, on remnant overwintering mysids left from the previous foraging season.

Methods

Study Area

In this study I focus on the fine scale foraging patterns of gray whales along the southwest coast of Flores Island in Clayoquot Sound, (Fig. 1), (located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W) off the west coast of Vancouver Island, British Columbia. The study area is approximately 20 km^2. Bounded to the west by the 30m depth contour, the site is bordered to the north and south by unproductive foraging areas. Mysid habitat in this area is generally near shore (i.e. <1 km), on rock reefs in shallow water (i.e. < 15 m).

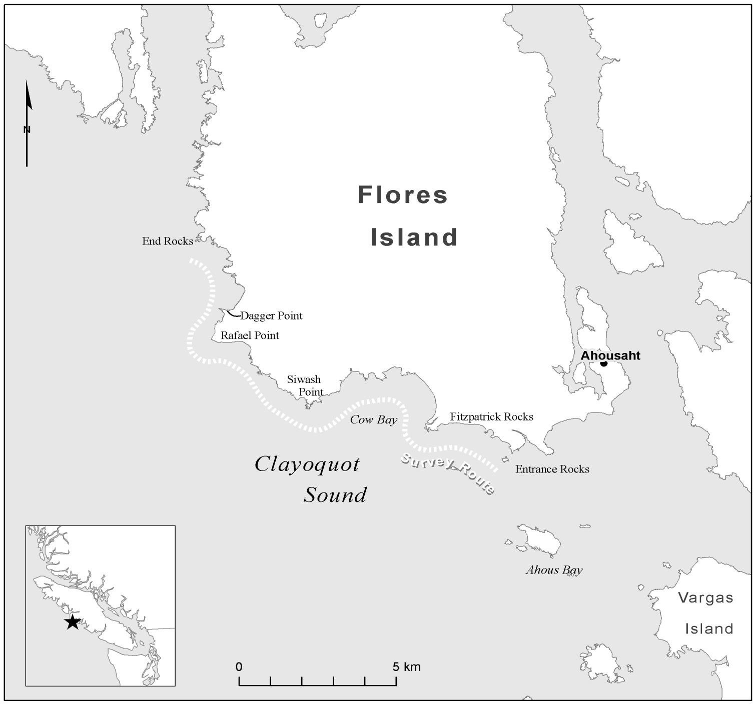

Figure 1: The study area showing survey area off Flores Island, Clayoquot Sound located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W.

Whale Surveys

In each summer between 1997 and 2008, gray whale foraging effort was measured by bi-weekly, boat-based, census surveys where a minimum of four observers scanned 360° for whale blows. Upon locating a blow, the vessel approached the whale to determine whether it was traveling or foraging, and recorded its last dive location using GPS. Vessel speed and unique markings were used to overcome double counts and to only record each individual once per survey. Between May 24, and September 8, 1997-2008, there were between 29 and 61 whale surveys conducted annually (Table 1). There is no significant relationship between the number of sample days and the number of whales recorded (Spearman's rho =0.08, N = 12, P = 0.8). Surveys were aborted if visibility became compromised by fog or a Beaufort sea state > 3. Differences in the timing and number of surveys in each season are due to poor weather conditions.

The average number of whales per survey is used as a measure of the level and timing of foraging effort. Average foraging effort is the cumulative number of whales observed divided by the number of surveys. I define the peak and mean foraging effort in each summer season (May 24 and Sept. 8) for the years 1997-2008. A Kruskal-Wallis test is used to assess whether foraging effort differed between years (1997-2008). The influence of average annual whale foraging effort on subsequent years is assessed for serial correlation using a runs test due to small sample of time series analysis.

Light Energy

Photosynthetic phytoplankton depend on light energy radiated over a range of wavelengths in the visible spectrum. In theory, photosynthesis increases with rising light intensity up to a plateau. As sunlight increases in the spring, so does plankton reproduction, making the amount of spring sunshine important to seasonal productivity. The term sunshine refers to the ability of the sun to cast an obvious shadow, and is more specific to visual radiation than to a general classification of radiance or energy radiated at all wavelengths (Ball *et al*. 2004). Sunlight, sunshine, or solar radiation is measured and reported on in a variety of ways, from hours of 'bright sunshine' to radiation in Watts/m^2. However, basic solar data is often unavailable at appropriate weather stations or for all time periods of interest (Thorton & Running 1999). In addition, because of variations in atmospheric turbidity and cloud thickness, the distinction between levels of sunshine is somewhat arbitrary, and largely dependent upon the type of data recorder in use, or on the quality of subjective estimates (WMO 2006).

Historical records of daily weather data reported at the Tofino Airport (49° 4.8'N, 125° 46.2'W), the closest weather station, do not include sunshine hours for the entire period of this study. However, common meteorological measurements of daily maximum and minimum temperatures, and precipitation can be used to predict solar radiation (R_s) (Ball *et al.* 2004).

Since sunshine duration is closely related to the amount of solar radiation received at the earth's surface (Gopinathan 1988, Iqbal 1983, Soler 1990), incoming solar radiation was calculated using the Bristow–Campbell model, as described by Thornton and Running (1999). I employ an estimate of average daily solar radiation, derived from daily temperature differentials between the spring months of February 1 to May 31, 1997-2006, to compare differences in the relative magnitude of radiance received between years using a Kruskal-Wallis test.

Upwelling Days

The National Oceanic and Atmospheric Administration's (NOAA) Pacific Fisheries Environmental Laboratory (PFEL) generates monthly indices of the intensity of large-scale, wind-induced coastal upwelling at 15 locations along the west coast of North America. Using measures of wind friction and Coriolis effect, indices estimate offshore Ekman transport of surface waters away from the coast, a process that allows nutrients such as nitrate and phosphate to become available to phytoplankton (Levington 2009). The magnitude of the offshore component is an index of the amount of water upwelled from the base of the Ekman layer. The units are presented as meters per second per 100 meters of coastline (PFEL 2008). Daily upwelling data are extracted for the study period from 48°N 125°W. The range of positive upwelling index values is identified for Spring (February to May) in each year, 1997 to 2008. The difference in upwelling days between February and May is compared between years using a Kruskal-Wallis test.

Mysid Surveys

Mysid density was measured by weekly surveys along a standard route, from May to September (Fig. 1), 2004 - 2008. Abundance was estimated using an echosounder with two transducers operating at 110 kHz and 220 kHz calibrated with multiple standard target spheres (Vagle *et al*. 1996). Transducers were mounted on a plate 0.3 m apart and submerged 0.5 m below the surface of the water, emitting pings at a pulse length of 200 µs every 0.5 seconds. Mysids, represented at target strength of -98 decibels (dB) (Olsen 2006), form carpet-like patches above the substrate that vary in length and thickness (Hahn & Itzkowitz 1986). Mysid patches were monitored by an onboard computer and verified opportunistically with a bongo-style (2 x 30 cm diameter) plankton net.

With no established method for interpreting high-resolution backscatter data for mysids (Jumars 2007, Axenrot *et al.* 2009), I applied the distorted wave-borne approximation (DWBA) model for fluid-like zooplankton (Stanton *et al*. 1998). The DWBA model assumes a weakly scattering organism, and is valid for all angles of orientation closely approximating a range of zooplankton species (Stanton & Chu 2000). The body shape of mysids suggests this model is applicable (Kringel *et al*. 2003, Sutor *et al*. 2005). Akin to Sutor *et al.* (2005), here I employ Foote *et al.*'s (1990) measurements for euphausiids.

The acoustic processing method was developed in collaboration with Dr. Svein Vagle at the Institute of Ocean Science, Sidney, B.C. Canada who built the echosounder and associated software. Matlab® scripts read raw sounder files, calibrate the data, detect the bottom, distinguish mysid patches based on the model of target strength for mysids, and calculate time, location, average depth, length, height, patch volume and mysid density for each patch. Mysid density from the prey survey occurring within a week of each whale census survey was averaged for the study area. Average density of all surveys is compared between years using a Kruskal-Wallis test, due to an uneven number of surveys.

Top Down or Bottom Up?

Average whale foraging effort (1997-2008) was correlated to spring sunshine input (1997-2006), average index value and total number of positive upwelling days

(1997-2008), and average mysid density (2004-2008) for each year data was available. Average mysid density was tested for correlation with spring upwelling variables (2004-2008).

Results

Variability in Whale Foraging

The daily mean number of foraging whales for all years (1997-2008) is 5.4. Average foraging effort is highest in 2002 (12.2) and lowest in 2007 (0.96) (Fig. 2). Foraging effort is significantly different between years (Kruskal-Wallis χ^2 = 196.7, df = 11, P = 0.000). There is no evidence for positive serial autocorrelation between the average number of whales in each year, based on a runs test (Z = 1.49, Runs = 9, P = 0.13).

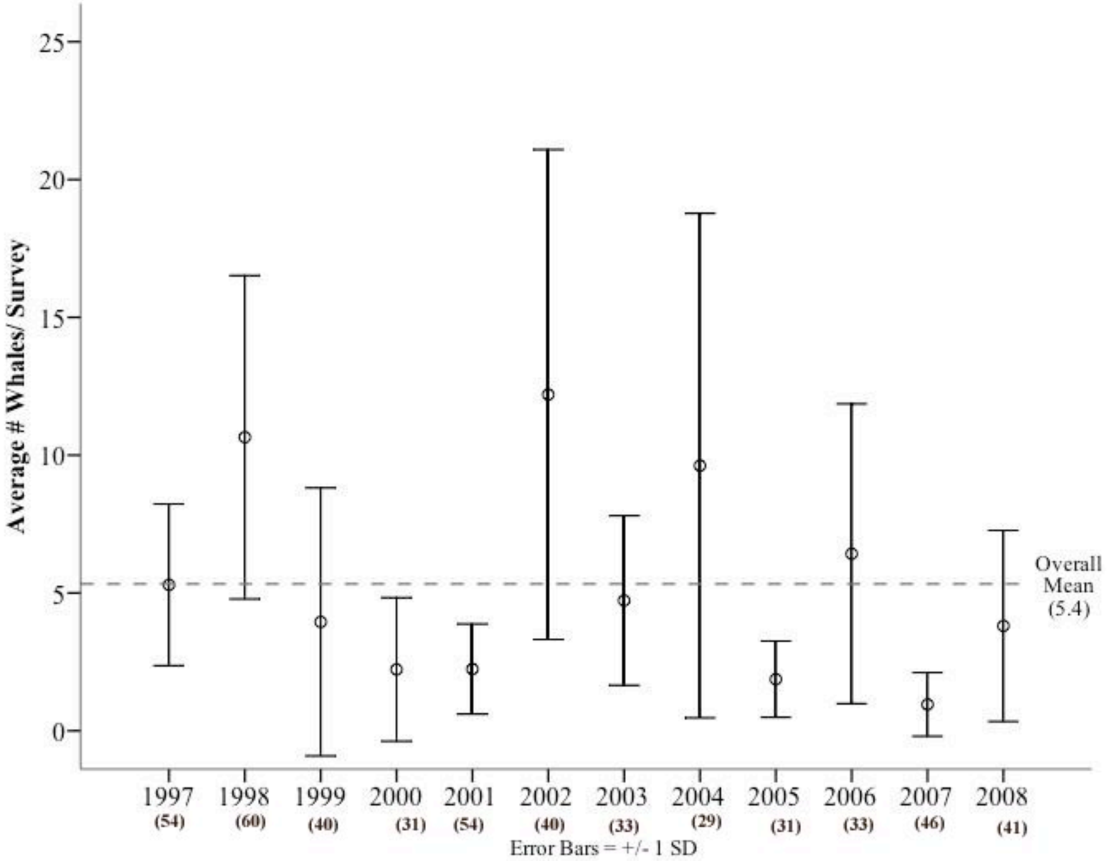

Figure 2. Box plot of Difference in Whale Foraging Effort, 1997 – 2008. Dashed line is mean foraging effort for all years (5.4). Number of surveys is indicated under each year.

Upwelling Productivity

Between 1997 and 2008, the spring upwelling index reached its peak in 2004 (226), while 2002 had the largest number of positive upwelling days (67) (Table 1). The minimum number of upwelling days, in any year, was 39 (1997). There is a significant difference between years in positive upwelling days (Kruskal-Wallis $\chi^2 = 28.9$, df = 11, P = 0.002), but not average upwelling value (Kruskal-Wallis $\chi^2 = 11.0$, df = 11, P = 0.44)

Table. 1. Difference in Upwelling Index, Feb – May, 1997-2008

Year	N + Days	Max Value	Mean + Value
1997	39	149	32
1998	62	86	22
1999	44	125	43
2000	45	86	26
2001	56	102	32
2002	67	173	31
2003	47	91	22
2004	59	226	27
2005	52	113	24
2006	58	146	38
2007	52	158	37
2008	59	104	32
All Years	53	226	30

Sunshine Inputs

Between 1997 and 2006, spring solar radiance values ranged from a low of 31 to a high of 525 W/m^2. Mean spring radiance for all years is 246 W/m^2 (Table 2). There is no significant difference in the relative magnitude of spring radiance between years (Kruskal-Wallis $\chi^2 = 2.1$, df = 9, P = 0.9).

Table 2. Difference in Solar Radiance (W/m^2), Feb – May, 1997-2008

Year	Range	Minimum	Maximum	Mean	SD
1997	477.4	31.3	508.7	243.2	118.9
1998	448.3	53.1	501.4	252.3	117.5
1999	465.0	48.9	513.9	249.7	121.3
2000	459.3	51.1	510.4	242.9	117.9
2001	455.3	54.1	509.5	247.8	117.5
2002	457.4	40.5	497.9	247.2	131.7
2003	443.9	53.7	497.6	240.5	113.7
2004	426.8	62.0	488.9	259.3	117.4
2005	481.8	43.2	525.0	243.2	105.4
2006	425.5	77.9	503.5	246.9	116.5
Grand Mean	454	51.6	506.0	246.6	116.7

Mysid variability

Average mysid density varies significantly between years (Kruskal-Wallis χ^2 = 27.5, df = 4, P = 0.000). Annual average density in the study area is lowest in 2007 (1,170 / m^3), and highest in 2004 (9,150/ m^3) (Table 3). Maximum density was found in 2004 (29,960 / m^3), and minimum in 2008 (79/ m^3).

Table 3. Difference in Mysid Density (/m^3), 2004-2008

Year	Survey N	Minimum	Maximum	Mean
2004	12	2,267	29,960	9,150
2005	6	3,428	8,720	6,130
2006	15	583	18,660	7,410
2007	15	102	3,320	1,170
2008	16	79	18,270	3,680
All Years	64	79	29,961	5,508

Relationship between primary drivers and whale response

Average whale foraging effort is compared to primary drivers measured between 1997 and 2008 (Table 4, Fig. 3). Only spring upwelling was available during the entire period where whale foraging effort has been monitored. There is no significant relationship between the mean number of whales in the study area and average spring upwelling value (Spearman's rho = -0.15, N = 12, P = 0.65) or number of spring upwelling days (Spearman's rho = 0.52, N = 12, P = 0.08). Spring sunshine input was not significantly correlated to average whale foraging effort during the period 1997-2006 (Spearman's rho = 0.49, N = 10, P = 0.1). Average mysid density between the five-year period, 2004-2008, is significantly correlated to average number of whales in the study area (Spearman's rho = 0.9, N = 5, P = 0.037) (Fig. 4).

Average mysid density is only compared to spring upwelling, as it is the only variable available during the entire period where mysid density was measured. There is no significant relationship between average annual mysid density and mean spring upwelling value (Spearman's rho = -0.2, N = 5, P = 0.7) or number of spring upwelling days (Spearman's rho = 0.47, N = 5, P = 0.4).

Table 4. Difference in Whale Foraging Variability and Primary Drivers, 1997-2008

Year	Mean Whales	Mean + Upwelling	N + Upwelling	Mean Mysid Density (/m^3)	Mean Sun (W/m^2)
1997	5.30	32	39	-	243
1998	10.65	22	62	-	252
1999	3.95	43	44	-	250
2000	2.23	26	45	-	243
2001	2.24	32	56	-	248
2002	12.20	31	67	-	247
2003	4.73	22	47	-	241
2004	9.62	27	59	8,835	259
2005	1.87	24	52	6,128	243
2006	6.42	38	58	7,408	247
2007	0.96	37	52	1,167	-
2008	3.8	32	59	3,635	-
Mean	5.4	30	53	5,434	247

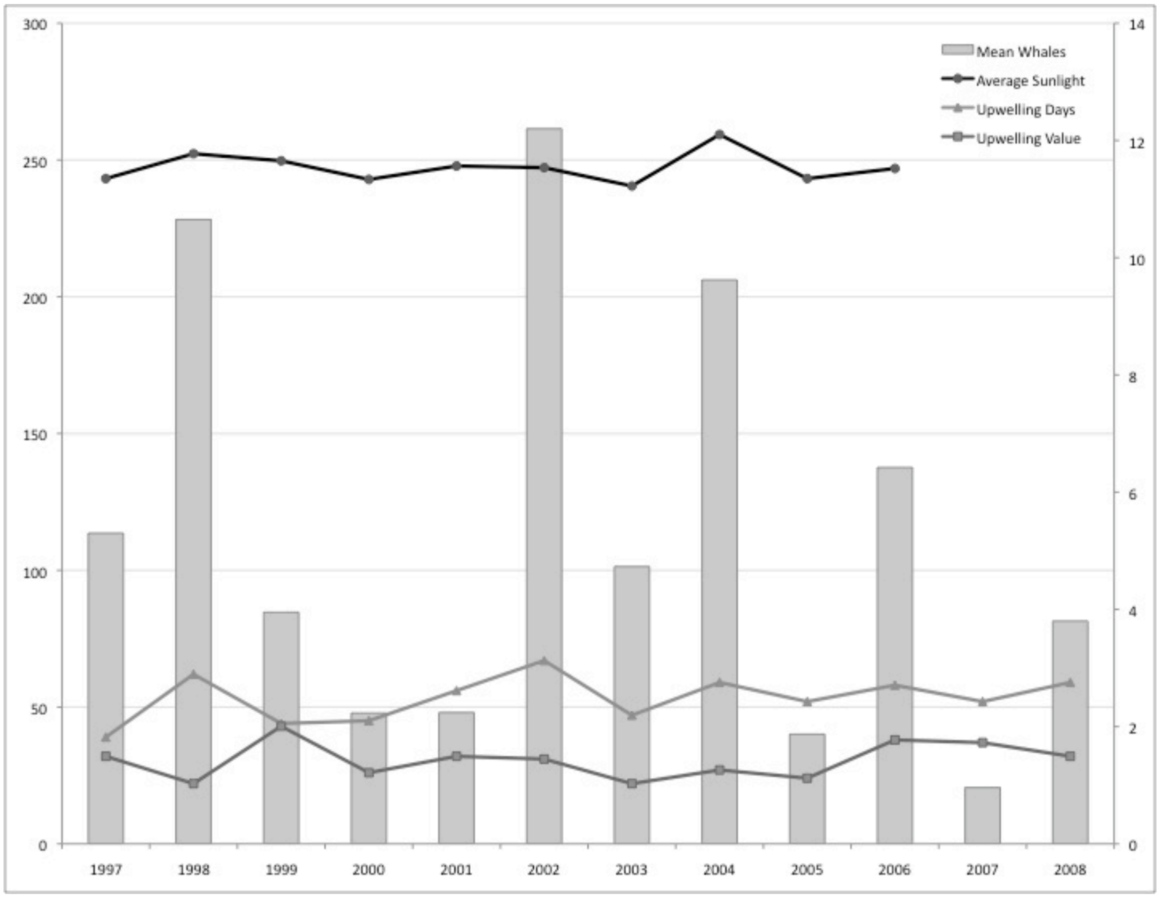

Figure 3. Difference between bottom up drivers (average spring sunlight, average number of upwelling days and index value) on left axis, and average whale foraging effort in each year, 1997-2008, right axis.

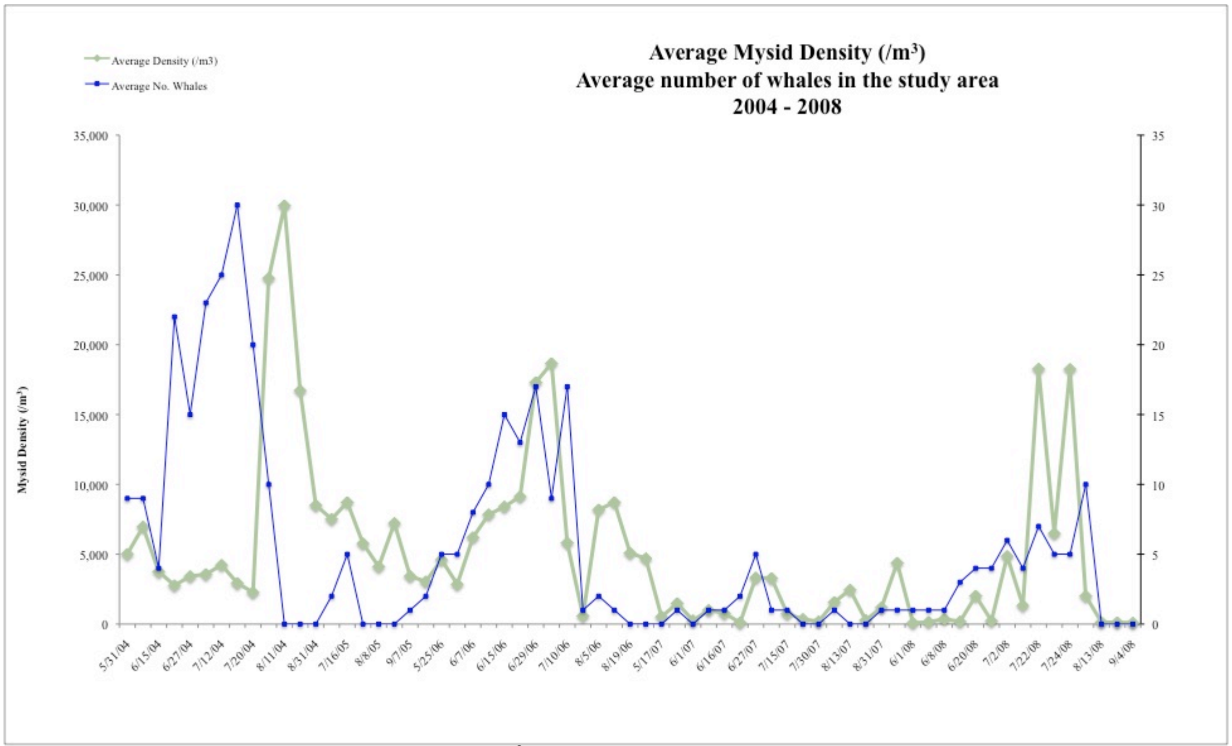

Figure 4. Average mysid density (per m^3), left axis, summarized from biweekly overall hydro acoustic surveys of the study area, and average number of whales, right axis, recorded from weekly whale census, 2004 - 2008.

Discussion

In the twelve-year period, between 1997 and 2008, the connection between lower and upper trophic levels does not reflect significant differences in climate variability or regional oceanographic patterns. While foraging gray whales are closely tied to the density of mysid swarms, the link to regional scale oceanographic productivity drivers is weak.

Although annual foraging effort is significantly different between years, the relationship between high and low years is not statistically significant as measured by serial autocorrelation. While consistent monitoring of foraging effort may represent a significant achievement in marine mammal studies, when it comes to testing for serial autocorrelation, the sample size is small. That said, every year of higher than average foraging activity is followed by a lower than average foraging year.

I correlate average foraging effort to three primary drivers: spring sunlight, upwelling strength, and mysid density in each year. There was no significant difference between average solar radiance, upwelling strength or number of upwelling days in the spring of each year. Although I do not assess the differences in the timing of upwelling onset or increased sunshine between years, if such differences do occur, they are averaged out over the course of the spring season. Mysid density is significantly different in each of the five years it was available, and density appears to be declining over time.

If spring productivity measures are generally equivalent in each year, but mysids and whales oscillate dynamically, it suggests that top-down pressure by foraging whales is a determining force in this localized system. The other forces that influence this relationship are discussed in turn.

Sustained sunlight is required for phytoplankton production, however, the number and variability in other parameters involved in photosynthesis has limited the predictive capacity of simplistic models of primary production in coastal areas (Cote & Platt 1983). Here, there is no significant relationship between average spring sunlight and whale foraging effort between years. Although there is a within-season pattern increase in sunshine, the timing and duration of stable weather systems that bring sunny conditions varies between years. While sunlight does not vary significantly when averaged over the spring season year to year, data on the frequency of sustained sunshine duration events is not available. I have, however, a re-construction from modeled data. Other short-term environmental phenomena, such as storms, increased tidal mixing, or turbidity, further compound productivity of coastal plankton, and can dramatically alter plankton communities' composition and necessary conditions for growth (Cote & Platt 1983, Cloern 1996).

Next to sunlight, nitrogen is the main limitation for primary productivity in the ocean (Gruber 2005). I have no direct measure of nitrogen compounds, so I am using a generalized proxy measure, upwelling strength, which may have limitations. However, there is no significant relationship between whale foraging effort and spring upwelling days or average upwelling index value, over the twelve-year period. There are likely other factors besides upwelling that provide nutrients to the inshore coastal zone. As Ekman transport diminishes with increasing latitude, and the width of the continental margin increases, more of the primary production can reside and cycle through the food webs of the North Pacific coast (Ware & Thomson 2005). Although spring upwelling is relatively weak in this region, chl-a concentrations remain high, suggesting that other sources, likely terragenous, contribute nutrients to fuel primary production in the spring (Ware & Thomson 2005). Mulkins *et al.* (2002) found that over the course of the summer in Clayoquot Sound, marine derived organic carbon (DOC) increased in the diet of mysids, suggesting that mysids shift their diet opportunistically as riparian inputs are reduced during the summer. In addition, the temporal shift in traceable DOC represents food metabolized by mysids late spring (i.e. two to twelve weeks prior to sampling), signifying that terrestrial food sources were more prevalent earlier in the season. This corresponds well with the insignificant relationship between mysids and upwelling, and my interpretation that spring upwelling is of limited importance in providing nutrients that determine production of mysids.

Whale foraging is strongly correlated to average mysid density in each year (Spearman's rho = 0.900, N = 5, P = 0.037). While attempts were made to couple the trophic relationship between primary productivity and whales, prey remains the strongest link to annual variability in whale numbers and vice versa. There may be a number of reasons for fluctuations in annual mysid density, considering the number of variables contributing to the dynamics of primary production. However, in this data, spring pre-conditions for mysid production only exhibit minor timing differences.

Mysid density exhibited a decreasing trend similar to whale foraging effort over the latter part of the twelve-year period when it was measured. This pattern supports my hypothesis that whale numbers constrain the breeding stock of mysids available in the following spring. When predatory pressure is high, mysid population renewal, and subsequently whales, decline the next year. Reduced foraging pressure allows mysids to partly recover. It is of note that whale numbers in recent years have not approached earlier peaks, and mysid density in the study area is less than half of what it was five years ago. Whether this trend continues, for mysids or whales, is part of a longer story.

Fine scale measurements, spanning time periods necessary to resolve the ultimate ramifications specific to predation pressure imposed by a long lived marine mammal, are unusual at best. What is known about gray whales is that they have evolved over periods of considerable climatic variability, where despite substantial differences in ocean nutrient cycling and ice edge location, a historically larger population survived large scale environmental changes (Alter *et al.* 2007). The results here suggest that gray whales may either buffer energetic losses over longer time periods with high productivity, or they rely on a series of alternative resources, beyond the spatial or temporal scope of this study.

Conclusion

The limited variability in spring upwelling and sunshine in the study area, did not correlate to whale foraging observations over the twelve year period 1997 -2008. Whale foraging effort was highly dependent on mysid density for the five-year period 2004-2008. The results of this study suggest that regional, bottom up, trophic energy transfers are not as significant as fine scale measures of prey density in determining the local foraging opportunities for gray whales. In restricted areas, gray whales may engineer prey conditions, ultimately to the point of prey limitation. While prey limitation seems unlikely for baleen whales, at fine scales it may move whales in and out of areas for periods of time. Thus habitat analysis, designation of critical habitat, and management actions, such as protected areas, may be largely irrelevant for this species.

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Chapter Three: Eat While the Eating is Good. Opportunity Drives Foraging Efficiency in Focal Studies of Gray Whales (*Eschrichtius robustus*), Feeding on Mysids (*Mysidae*) off Flores Island, Clayoquot Sound.

Abstract

Movements of baleen whales in ocean space are largely unrestrained. Thus, an individual whale's spatial behaviour in a foraging ground should closely reflect their response to prey quality. As part of this interactive process, large mobile predators influence the underlying prey structure, as avoidance behaviour and mortality act to decrease the density of discrete planktonic prey. Here, I focus on the fine scale foraging patterns of individual gray whales (*Eschrichtius robustus*) along the southwest coast of Flores Island in Clayoquot Sound, British Columbia, Canada. Gray whales have distinct search and exploit patterns when foraging on mysid shrimp (Family *Mysidae*) and increases in this pattern of behaviour should correspond to prey density in the overall study area. To test the strength of this relationship, I conducted hydro acoustic surveys for mysids along a standardized transect and compared the variations in prey density to foraging behaviour classified from focal surveys of individual gray whales between 2006 and 2008. Foraging is positively correlated to average overall mysid density in all years and foraging dominates whale behaviour at prey densities > 4,400 mysids per cubic metre.

Introduction

Ecological theory proposes that an animal's life history is the result of the pressure to maximize the fitness of their physical and behavioural adaptations, within environmental constraints. Natural selection defines and refines the optimum allocation of time and energy for foraging, growth, and reproduction of each species (Estes 1979). Optimal foraging models suggest that the fitness of an animal is a function of foraging income and energetic expenditures (Charnov 1976). Many facets of optimal foraging theory are difficult to use when studying wild populations, such as whales, as the net foraging cost, a product of dive efficiency and foraging success, is largely inaccessible.

The first law of optimization is that foraging animals should minimize energetic costs and maximize caloric returns. This is reflected in the overall life history of baleen whales in terms of energy storage and thermoregulatory capacity. Another aspect of optimality, search efficiency, provides measurable predictions for whale behaviour (Norberg 1977, Piatt & Methven 1992). Optimal choice in food-searching behaviour assumes that maximum foraging efficiency requires higher expenditure, but is repaid by increasing return. Norberg's (1977) model of food-searching argues that increased movement, a proxy for higher energy expenditure, is necessary to increase efficiency. Generally, he argues that the most expensive, and thus efficient, foraging method should be employed by a predator at the highest prey densities. When prey density decreases, a predator should switch to less costly behaviours. As whales have to find prey in a patchy environment under seasonal time constraints, I expect an efficient predatory response to increases in prey quality.

Due to the challenges of conducting experiments on large ocean predators, studies of whale foraging have been limited to observations of their surface behaviour or location, and indirect measures of prey abundance, such as chlorophyll or ocean temperature (Hooker *et al.* 2002, Bluhm *et al.* 2007, Kenney *et al*. 1995, Tynan *et al.* 2005). However, recent studies using acoustic techniques provide estimates of the location and abundance of zooplankton prey (Benoit-Bird & Au 2002, Croll *et al.* 2005, Trevorrow *et al.* 2005, Lavery *et al.* 2007, Axenrot *et al.* 2009, Pendleton *et al.* 2009). When whales have been directly compared to the co-distribution of their prey, foraging whales appear to be the best measure of the quality and distribution of underlying prey

(Kenney *et al.* 1986, Murison & Gaskin 1989, Piatt & Methven 1992, Dunham & Duffus 2001, Croll *et al*. 2005). However valuable the knowledge of a whale's surface location is, quantitative measurements of their prey are required to determine baseline patterns of exchange between them (Duffus 1996).

Ideal predator-prey systems are self-regulating, as predators respond in a non-linear fashion to threshold levels of prey density (Fauchald 2009). Threshold foraging has previously been demonstrated in baleen whales at regional scales (Piatt & Methven 1992, Croll *et al.* 2005), but individual foraging behaviour has yet to be correlated to prey density (Hamner *et al*. 1988*)*. Gray whale (*Eschrichtius robustus*) dive behaviour while foraging on epibenthic mysids (Family *Mysidae*) has been the subject of a number of studies (Malcolm & Duffus 2000, Dunham & Duffus 2001, 2002, Stelle *et al*. 2008); however, measuring prey density while tracking individual whales has not been done (but see Sims & Quayle 1998).

The recovery of the eastern Pacific gray whale from decimation by industrial whaling is a conservation success (Saterson *et al.* 2004, Moore *et al.* 2001). As the gray whale population expanded, they have proven to be flexible predators, switching prey and foraging tactics in response to prey availability (Dunham & Duffus 2001, Moore 2003, Coyle *et al.* 2007). Over the last 10 years, there have been both spatial, and temporal shifts in their distribution in the higher latitudes. Foraging effort is moving north, and residency extends through the winter in southeast Alaska and the Beaufort Sea (Moore *et al.* 2007, Moore *et al.* 2006). This movement is in conjunction with a sharp decrease in prey density at their former feeding grounds (Highsmith & Coyle 1992, Coyle *et al.* 2007), coinciding with broadly altered ecosystems, the cause of which, is arguable (Grebmeier *et al.* 2006, Coyle *et al.* 2007, Moore & Huntington 2008).

Gray whale population stability depends on their response to variations in prey quality at multiple scales across their foraging range. Future conservation of this species depends on mitigating human activities that impact individual animal's use of high quality foraging habitat in local areas. Management requires an appreciation of fine scale patterns in foraging behaviour and the underlying response of their prey.

To understand the mechanics of gray whale foraging on mysids in Clayoquot Sound, British Columbia, I classify fine scale dive patterns of individual gray whales during focal follow surveys and correlate foraging behaviour to overall prey quality. Akin to Norberg (1977), I predict that whales will increase foraging dive times and decrease distance between dives, under conditions with higher mysid concentrations. I approach the problem through measurement of time budgets for 25 individual whales using 30 focal follow studies conducted between 2006 -2008. These surveys are compared to generalized hydroacoustic measurements of prey quality across the study area.

Methods

Study Area

In this study, I focus on the fine scale foraging patterns of gray whales along the southwest coast of Flores Island in Clayoquot Sound, (Fig. 1), (49°16'N, 126°15'W) on the west coast of Vancouver Island, British Columbia. The study area is approximately 20 km^2. Bounded to the west by the 30m depth contour, the site is bordered to the north and south by unproductive foraging areas. Mysid habitat in this area is generally near shore (i.e. <1 km), on rock reefs in shallow water (i.e. < 15 m).

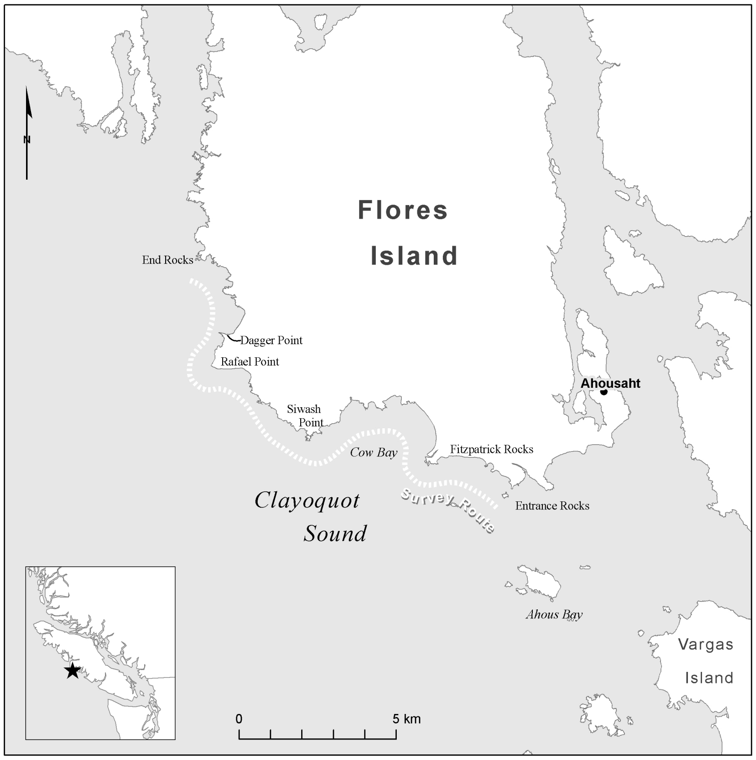


Figure 1: The study area showing survey area off Flores Island, Clayoquot Sound located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W.

Data Collection

Focal Follows

During individual focal animal observations (*sensu* Altman 1974), I recorded the location (latitude and longitude) and time (hh.mm.ss) of each whale's ventilation (or blow). During a dive cycle (Fig. 2), whales typically respire several times at surfacing, with a brief submergence between blows. These events are not classified as “dives” because there is a low potential for feeding or searching. The number of inter-ventilations and the distance traveled between are significant for analyzing response to prey quality and location, and are included in this analysis (Malcom & Duffus 2000, Stelle *et al.* 2008).

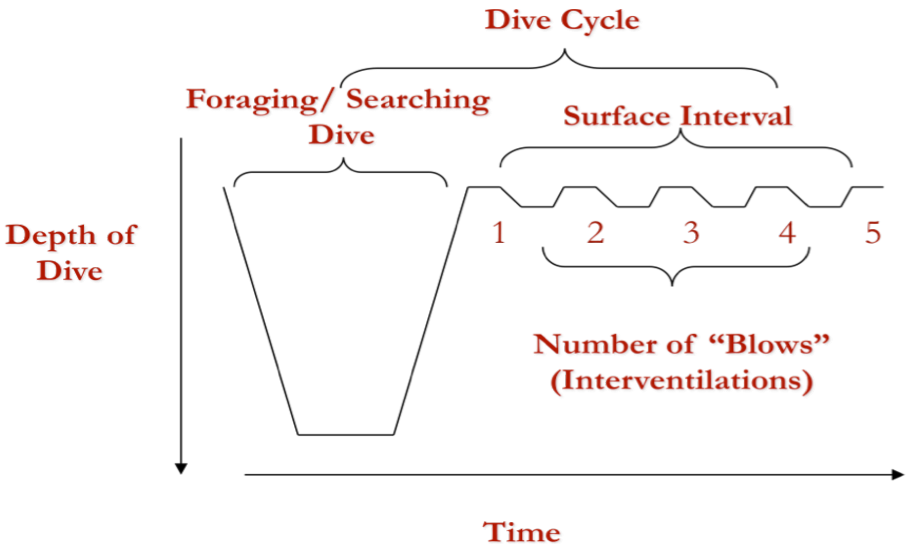


Figure 2. The typical Gray whale dive cycle.

Using irregular selection (Altman 1974), the focal animal was the first whale sighted within 100 metres of the boat, ten minutes after beginning a survey. Whales were monitored for 5 -10 minutes to ensure they were foraging and undisturbed before beginning the observations. I kept track of individual whales using their natural markings (Calambokidis *et al.* 2002).

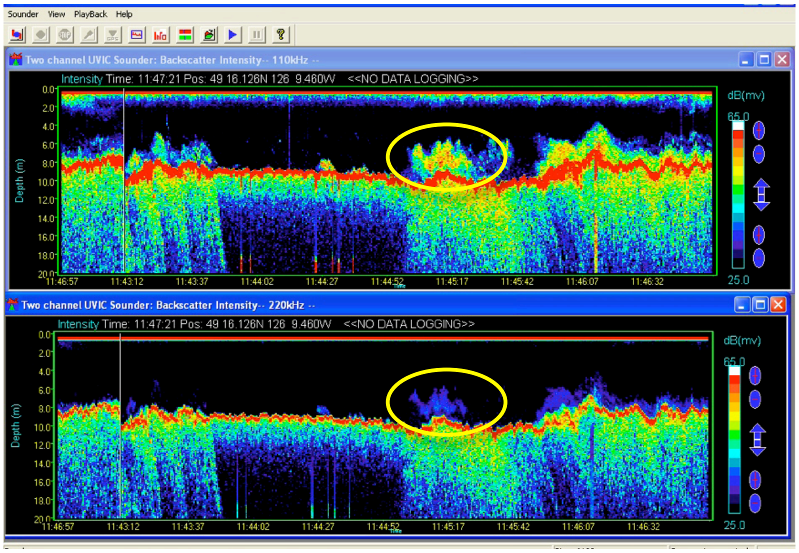
The time, location, and water depth of each ventilation was recorded by placing the boat over a whale’s dive “footprint”, the distinct slick marking the water surface after a whale submerges, and recording the GPS coordinate. Vessel speed was in neutral drift when in close proximity to a whale. If the animal entered shallow reef complexes (< 3m deep), dive locations were determined using a range and bearing measurement from the closest available location. Observations were terminated when the survey was interrupted by another vessel entering the bay, the whale disappeared, or another whale was accidentally recorded in the data stream. Surveys were aborted if visibility became compromised by fog or a Beaufort sea state > 3. Focal surveys used in this study took place over 5 days between July 10 and July 16 in 2006; on 6 days between August 3 and September 3 in 2007; and on 12 days between May 24 and September 1, in 2008.

Whale Census Surveys

Study area wide gray whale foraging effort has been measured bi –weekly since 1997 using a standardized boat-based census. A minimum of four observers scan 360° for whale ventilations. Upon locating a blow, the vessel approaches the whale, and records its last dive location using a GPS. While vessel speed is intended to overcome double counts, unique markings are also noted or photographed in order to only record each individual once per survey. Between May 24, and September 8, 2006-2008, there were between 33 and 41 dedicated whale surveys conducted annually. Differences in the timing and number of surveys in each season are due to weather conditions.

Prey Surveys

Prey variability was measured by weekly acoustic surveys along a standard survey route, from May to September (Fig. 1). Prey abundance was estimated using an echosounder with two transducers operating at 110 kHz and 220 kHz calibrated with multiple standard target spheres (Vagle *et al*. 1996). Transducers were mounted on a plate 0.3 m apart and submerged 0.5 m below the surface of the water, emitting pings at a pulse length of 200 μs every 0.5 seconds. The return echoes' strength and location were recorded directly onto a computer. Mysids, represented at target strength of -98 decibels (dB) (Olsen 2006), form carpet-like patches above the substrate that vary in length and thickness (Hahn & Itzkowitz 1986) (Fig. 3). Mysid patches were visually monitored using a computer onboard the vessel and were verified opportunistically with a bongo-style (2 x 30 cm diameter) plankton net.



Intensity Time: 11:47:21 Pos: 49 16.126N 126 9.460W <<NO DATA LOGGING>>

Intensity Time: 11:47:21 Pos: 49 16.126N 126 9.460W <<NO DATA LOGGING>>

Figure 3. Visual display of mysid swarm detected at 110kHz (above), and 220 kHz (below).

Data Analysis

Focal Follows

During the summer season in the study area, whales are focused on feeding, thus when they are not actively feeding they may be engaged in a number of other behaviours, likely dominated by searching. Although animal behaviour is a continuous process, in this analysis I create mutually exclusive categories to determine the dominant activity. Dive cycle patterns documented by similar studies of mysid feeding gray whales have classified dives using a time-depth recorder and focal studies. Time and distance between dives are integrated to create dive time budget (Sumich 1983, Mallonée 1991, Malcolm & Duffus 2000, Stelle *et al.* 2008). Using the natural breaks in the data, I distinguish three dive types, (1) ***ventilations*** (dives < 30 seconds), (2) ***foraging*** (dives > 30 seconds and < 60 m apart from a subsequent dive) and (3) ***non-foraging*** (dives > 30 seconds and > 60 m from a subsequent dive). Using the original dive sequence, the dive types are divided into either a *foraging* bout or a *non-foraging* sequence. A foraging bout is classified as a sequential string of foraging dives, with their associated ventilations, terminated by a non-foraging dive (Fig. 4).

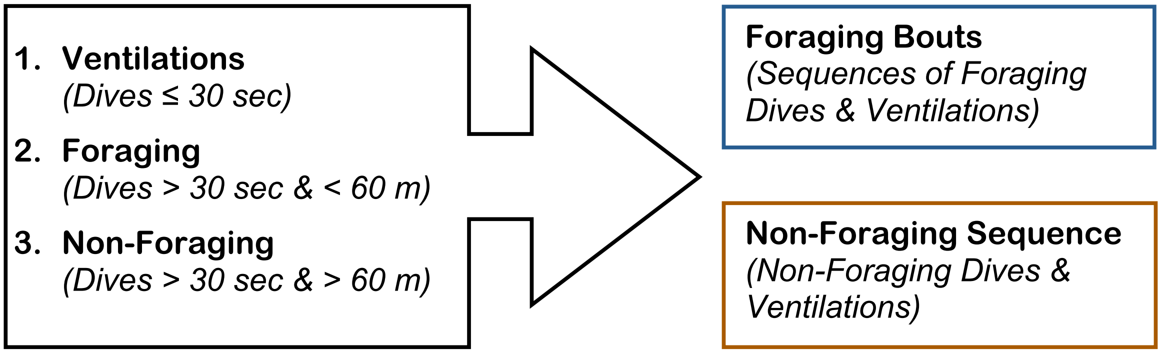


Figure 4. Classification scheme for identifying foraging behaviour from focal follow data.

Whale Census

The number of whales per survey is not a measure of abundance, rather it is an indication of the level and timing of foraging effort. Foraging effort in each year is the average number of whales per survey in each season. This effort is ranked against an average number of whales foraging in any year (1997-2008) as either high (above average) or low (below average).

Prey Conditions

Although there are models for acoustic measurement of zooplankton, such as euphausiids (Family *Euphausiidae*), there are few acoustic measurements of mysids (Axenrot *et al.* 2009). With no established method for interpreting high-resolution backscatter data for mysids, I selected the distorted wave-borne approximation (DWBA) model for fluid-like zooplankton (Stanton *et al*. 1998). The DWBA model assumes a weakly scattering organism, and is valid for all angles of orientation closely approximating a range of zooplankton species (Stanton & Chu 2000). The body shape of mysids suggests this model is applicable (Kringel *et al*. 2003, Sutor *et al*. 2005). Akin to Sutor *et al.* (2005), here I employ Foote *et al.*'s (1990) measurements for euphausiids.

The acoustic processing method was developed in collaboration with Dr. Svein Vagle at the Institute of Ocean Science, Sidney, B.C. Canada who built the echosounder and associated software. Matlab® scripts were developed to read raw sounder files, calibrate the data, detect the bottom, distinguish mysid patches based on the estimated model of target strength in dB for mysids, and calculate patch attributes. The output includes the time, location (latitude and longitude), average depth (m), length (m), height (m), patch volume (m^3) and density of mysids /m^3.

Mysid density from the prey survey occurring within a week of each focal whale survey was averaged for the study area. Average density in each year was compared using a Kruskal-Wallis test, due to an uneven number of surveys.

Whale Response to Overall Prey Conditions

The average density of mysids in the study area, measured within a week of each focal survey, is compared to the proportion of time that focal whales spent foraging. The relationship is measured by correlation and a visual assessment of resulting scatter plots. Regression is applied to test the strength and character of the relationship between foraging behaviour and density.

Results

Focal Follows

In 2008, I recorded 14 focal follows on 13 days. In 2007, 6 follows were recorded on 6 days, and in 2006, 10 follows were done on 5 days. Whales were observed for an average of 83 min (range of 23 to 303 min) in 2008, 64 min (range of 19 to 126 min) in 2007, and of 60 min (range of 9 to 107 min) in 2006, a combined total of over 388 hours of observation. Whale identities were confirmed for 9 individuals during 14 surveys in 2008, for 3 whales during 6 surveys in 2007 and for 7 whales during 10 surveys in 2006. Six whales were followed more than once.

Dive times are classified by an iterative cluster analysis to distinguish breaks. As the majority of dives are inter-ventilations, the first dive length cluster centres on 23 seconds. The class break sets a 30 second threshold for an inter-ventilation dive. Dives longer than 30 seconds are classified as foraging or searching based on a distance threshold of 60m between surfacing events. The distance threshold for foraging behaviour was chosen because: 1) Over 75% of the dive lengths observed were 59.5 meters (+/-100m); 2) the average length of a mysid swarm is 57m, and; 3) the speed of actively foraging whales is estimated at 1.8 km/hr (Calambokidis *et al.* 2002). As dives over 60m apart averaged a travel speed of 5.4 km/ hr, this behavior is classified as "searching" (Mate & Urban 2003).

The average time spent foraging in each year varied significantly (Kruskal-Wallis $\chi^2 = 9.83$, df = 2, P = 0.007). The average time spent foraging between July and August (the only months sampled in more than one year) also appears different (Table 1). Direct comparisons between dominant behaviour and underlying prey variability can be seen in Figures 5 and 6, and are discussed further in the following sections.

Table 1. Average Time Spent Foraging in Each Year

	Annual Average % Foraging	May	June	July	Aug
2006	64	-	-	64	-
2007	25	-	-	-	25
2008	52	71	34	64	5

Seasonal Whale Census Variability

The daily mean number of foraging whales for all years (1997-2008) is 5.6. Average foraging effort is higher in 2006 (6.42) than either 2007 (0.96) or 2008 (3.8).

Seasonal Prey Variability

Average mysid density varies significantly between seasons (Kruskal-Wallis $\chi^2 = 16.40$, df = 2, P = 0.000). Average mysid density in the study area is lowest in 2007 (1,170 / m^3), and highest in 2006 (18,660/ m^3) (Fig. 4). Average densities during 2006 range from 580 -18,660 mysids / m^3 and prey density in the study area peaks on July 7. In 2007, average densities range between 100 – 3,300 mysids/ m^3 and average density peaks on June 27. Average prey densities in 2008 range from 80 – 18,267 mysids / m^3 and density reaches the maximum on July 22.

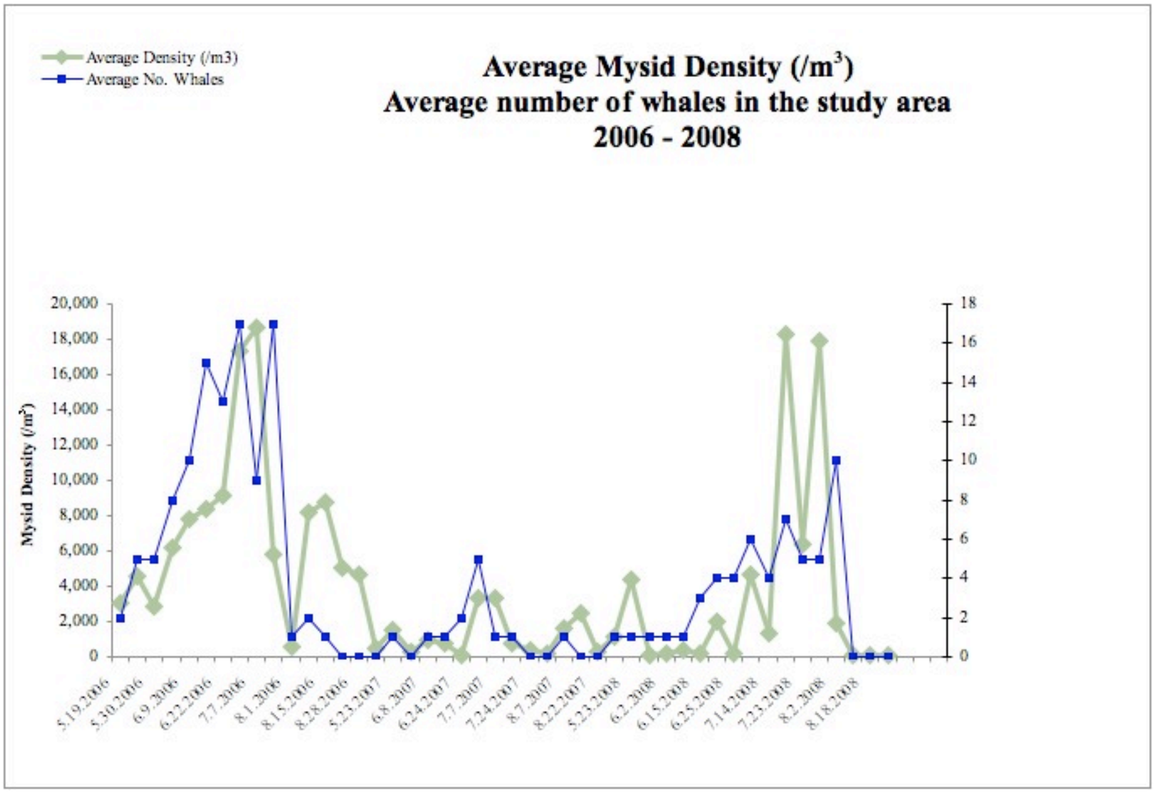


Figure 5. Average mysid density (per m^3) summarized from biweekly overall hydro acoustic surveys of the study area, and average number of whales, recorded from weekly whale census, 2006 - 2008.

Prey Abundance and Foraging Variability

Whale foraging is compared to average overall mysid density in the study area in each year (Fig. 6 & Fig. 7). Foraging is positively correlated to average mysid density in all years (Spearman's rho = 0.575, N = 30, P = 0.001). Foraging bouts dominate whale behaviour in July 2006 surveys when overall prey density is high (Fig 7a), while foraging time decreases in August 2007 when overall prey densities were low (Fig. 7b). In 2008, focal surveys extend from May to August, and time spent foraging fluctuates coincident with measures of average density (Fig. 7c). In all years when average prey density is greater than 4,400 mysids/ m^3, foraging behaviour dominates.

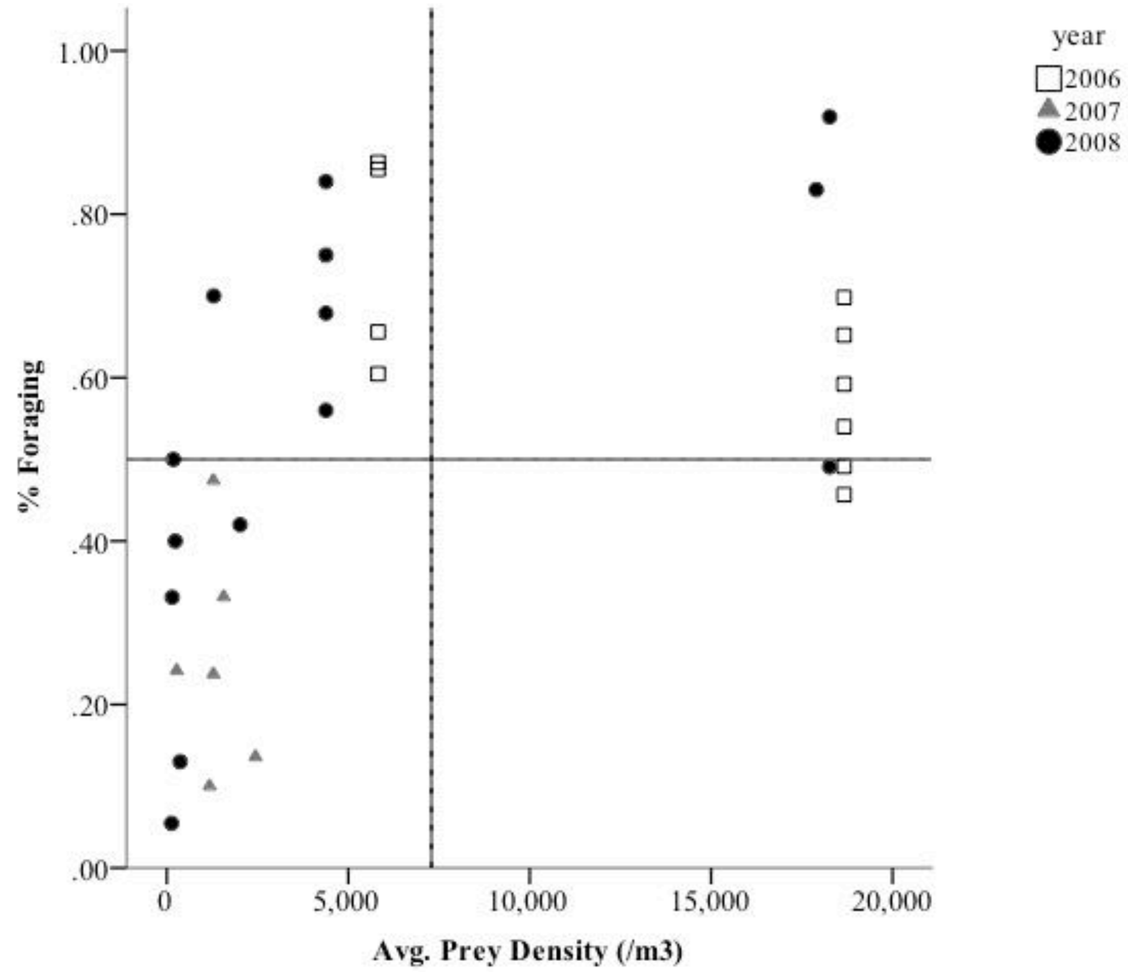
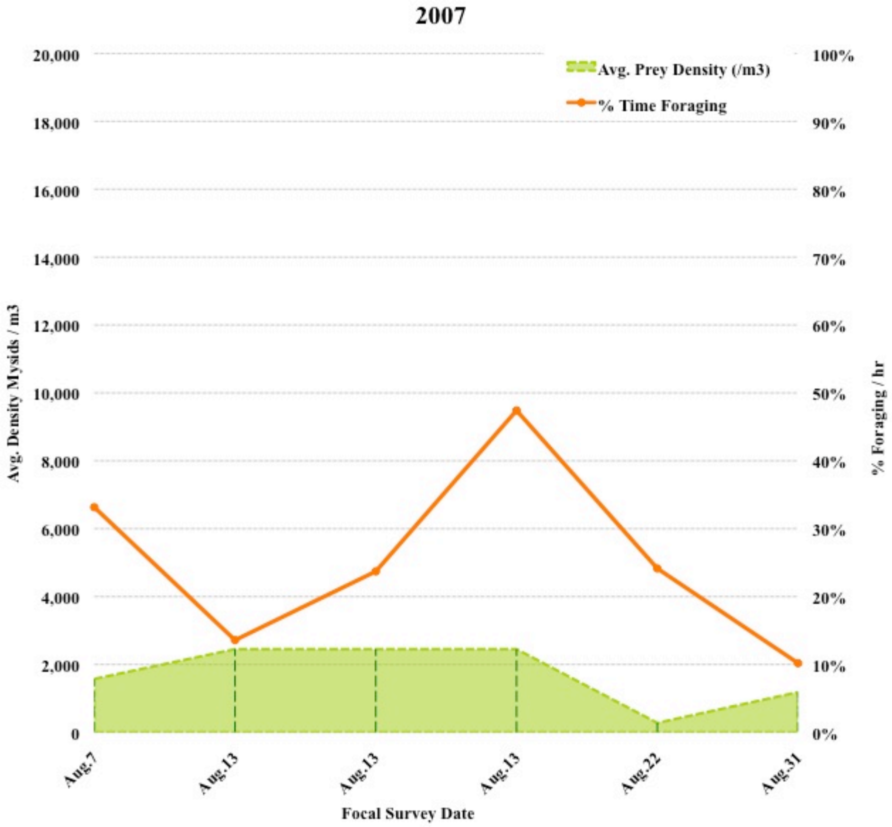


Figure 6. Relationship between average mysid density in the study area and time spent foraging during each focal follow, 2006 - 2008.

a).


2006
Average Density (/m3)
% Time Foraging
Avg. Density Mysids / m3
% Foraging / hr
20,000
18,000
16,000
14,000
12,000
10,000
8,000
6,000
4,000
2,000
0
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Jul.11
Jul.11
Jul.11
Jul.11
Jul.11
Jul.13
Jul.14
Jul.14
Jul.14
Jul.14
Focal Survey Date

b).


2007
Avg. Prey Density (/m3)
% Time Foraging
Avg. Density Mysids / m3
% Foraging / hr
20,000
18,000
16,000
14,000
12,000
10,000
8,000
6,000
4,000
2,000
0
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Aug.7
Aug.13
Aug.13
Aug.13
Aug.22
Aug.31
Focal Survey Date

c).

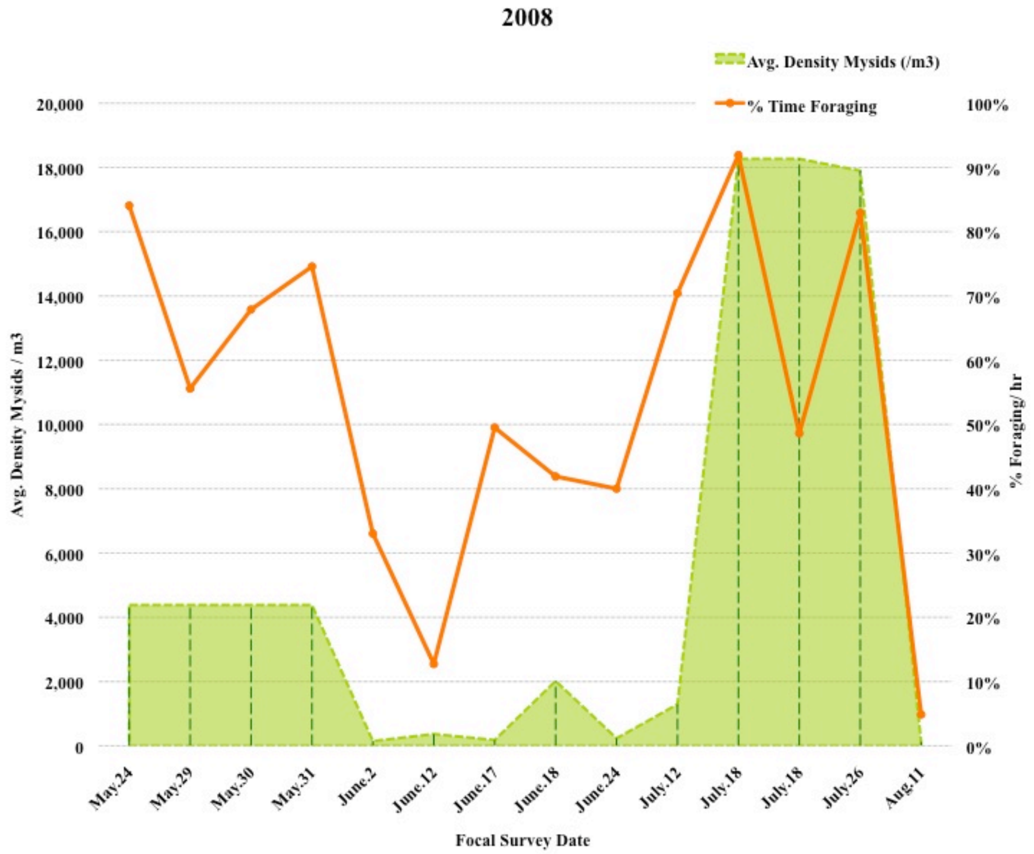


Figure 7. Whale foraging effort and overall prey density (mysids/ m^3) for surveys in 2006 (a), 2007 (b), and 2008 (c). The focal survey period on the x axis is different in each year.

The form of the scatter plot (Fig. 6) indicates a different pattern between foraging and prey density in each year. As the prey surveys were coarsely matched to the focal surveys in 2006 and 2007, they are removed from further analysis. The positive correlation and the extended survey period in 2008 provide a reasonable case for a regression. A linear and logarithmic regression test the relationship between overall prey density and time spent foraging (Table 2, Fig. 8). The logarithmic model has the highest explanatory power (r^2 = .49, df =12, P = 0.005). The linear model is not significant (P = 0.14).

Table 2. Model summary and parameter estimates for the relationship between foraging behaviour and average prey density for 2008 surveys

	Model Summary					Parameter Estimates	
Equation	r^2	F	df1	df2	Sig.	Constant	b1
Linear	.18	2.55	1	12	.14	.47	1.496E-5
Logarithmic	.49	11.73	1	12	.005	-.16	.096

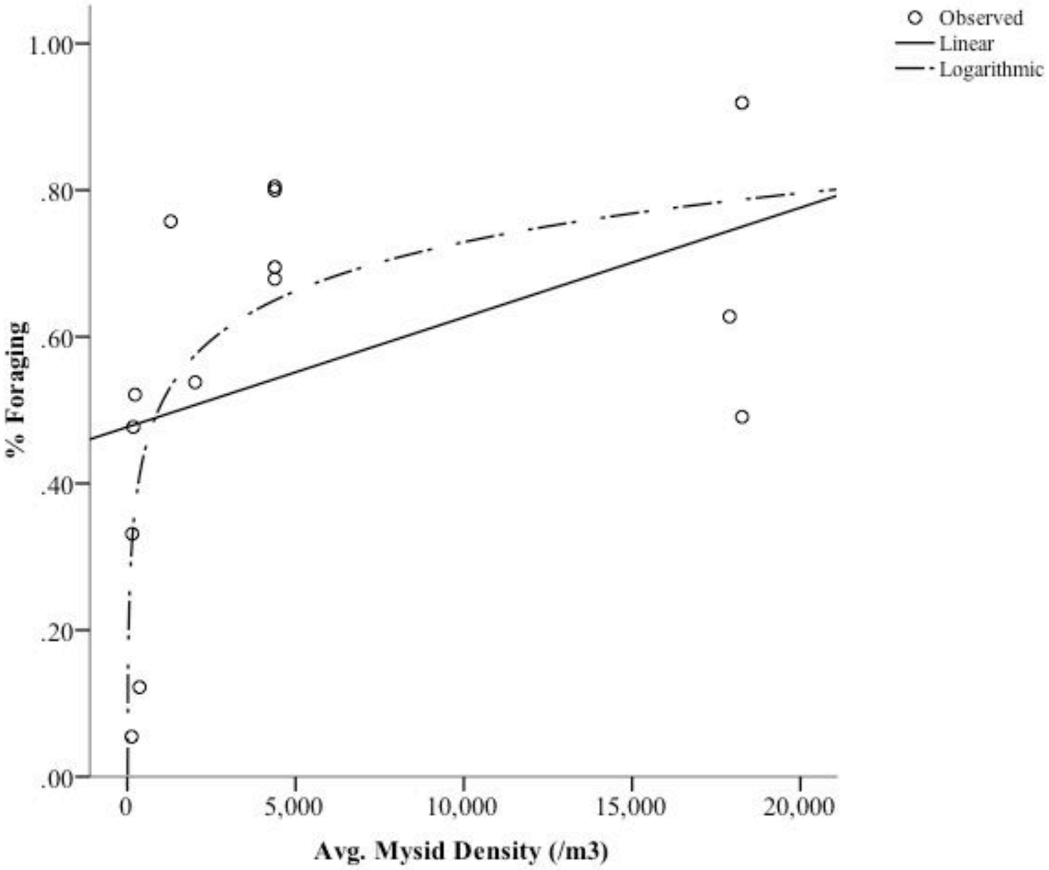


Figure 8. Linear and logistic regression models for relationship between overall prey density and time spent foraging, 2008.

The form of the scatter plot, and the explanatory power of the logistic regression, is similar to a classic type II functional response (Holling 1959).

Discussion

My hypothesis is that whale foraging should be more efficient when overall prey density rises, as yield per unit effort is higher. Although efficiency cannot be directly measured without precise knowledge of the energetic costs and benefits, I use the proportion of time spent foraging as a proxy for efficiency. By classifying the ventilation and spatial movement patterns of dives, I compare the efficiency of focal animals to overall acoustic measures of prey density to test the hypothesis. Foraging effort between 2006 -2008 corresponds to increases in overall average density of mysids. This relationship held in year to year comparisons as well as within-season during 2008. Thus my hypothesis is supported.

Focal surveys in my shorter field periods occurred at different points in the pattern of seasonal productivity, at the peak in 2006, and at the low end in 2007. This contrasts with 2008, where surveys extended over the entire season. In addition, outside of the time frame when the focal surveys occurred, 2006 was a highly productive year, whereas 2007 was unproductive for both prey and whales (Fig 5, Table 1). Having focal surveys from time periods with strong differences in prey availability highlights the distinct foraging strategies under high and low prey scenarios. This may be somewhat confounded by the seasonal requirements of migrating whales. Migrating whales should be edacious when they first arrive, and may feed harder on sparse prey to replenish diminished blubber reserves. However, in the latter part of the season when energy stores should be replenish, whales may reach satiation more easily and corresponding, prey levels are diminished.

The close relationship between predator and prey varies across spatial and temporal scales. As a result, responses may occur at an even finer spatial and temporal variation in prey availability. As mysids form discrete swarms (Clutter 1969), average density estimates for the study area are unlikely to capture the whale's appreciation of the entire 'preyscape'. In 2006, only two prey surveys were conducted within a week of the period when focal surveys took place. In addition, more than one focal survey took place on a single day, resulting in a range of foraging efficiencies being matched to a single estimate of prey density. The measurement of the prey is temporally coarse when compared to the foraging response.

The geometry of the foraging relationship to prey density in 2008 mimics a classic type II functional response. The interplay between the functional predator and the numerical prey does not fit the assumptions of the Holling's (1959) theory. Specifically, in the case of whales foraging on mysids, the probability of capture upon detection is high, rather than low and the consideration for handling time does not apply well to baleen whale predation.

In this study, I assume that the behaviour of individual whales outlines their assessments of prey swarms. The regression results suggest that these foraging decisions are influenced by additional factors outside of this analysis. Intrinsic features of individual animals are impossible to control for, and while I do not include surveys of cow-calf pairs, other measures of proficiency, preference, age class or any other idiosyncratic aspects of behaviour, could distort the strength of the prey driven signal.

In the surveys considered here, no interaction with other whales influenced my assessment of the behaviour of the focal animal. However, there were other animals foraging in close spatial (the same bay) or temporal (the same area, but different day) proximity that, through unseen elements of behaviour, or localized prey depletion, may have reduced the signal strength in my results. Now that the relationship between prey density and foraging behaviour has been documented for individual animals, testing the influence of competition may be possible in future studies.

As plankton prey patch dynamics can fluctuate faster than can be measured, characterizing the relationship between prey patchiness, and their marine predators is limited in studies of marine systems (Piatt & Metheven 1992, Bowen 1997, Croll *et al.* 2005, Jumars 2007). Using quantitative acoustic measures of the location, density and biomass of swarms is a considerable advance in understanding the requirements of foraging baleen whales (Croll *et al*. 2005). Although continuous acoustic assessments are more accurate than net or point sampling methods for measuring density, they cannot provide specific details of species composition or age class. Here, nets are used simply to verify the presence of mysids, as it is not feasible to analyze and build a model for each swarm composition. Thus, prey density estimates are built on a single, typically dominant prey species of a single age class (Stelle 2001, Newell & Cowles 2006). Mysid densities as high as 600,000/m^3 (Stelle 2001) have been documented, however, they are typically composed of small-bodied juvenile mysids (Clutter 1969). As animals with a body length < 6 mm are not large enough to be filtered by gray whale baleen (Stelle 2001), early in the season, swarms of juveniles may artificially inflate average density estimates without providing a worthwhile foraging opportunity.

Conclusion

To understand the mechanics of gray whale foraging on mysids in Clayoquot Sound, British Columbia, I classify fine scale dive patterns of individual whales during focal follow surveys, and correlate foraging behaviour to prey quality. When variation in prey biomass estimates across the study area is compared to behaviour, baseline prey conditions necessary to sustain whale foraging emerge. Whales respond to variations in mysid density at a fine scale, and high prey density corresponds to increased foraging.

The quality and quantity of prey is reflected in the spatial and temporal patterns of gray whale foraging. Gray whales display the ability to respond to shifting prey quality, suggesting a behavioural plasticity indicative of how they buffer against longer-term changes in availability, and how they may respond to broader changes in ecosystem productivity (Dunham & Duffus 2001, Moore & Huntington 2008, Nelson *et al*. 2008).

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Chapter Four: 'Preyspective' and 'Oppreytunity'. Prey Driven Foraging Response in Focal Studies of Gray Whales (*Eschrichtius robustus*) Feeding on Mysids (*Mysidae*) off Flores Island, Clayoquot Sound.

Abstract

Understanding the foraging patterns and constraints of marine predators requires tracking individuals at a fine scale. Thus far studies have been unable to make a strong link between the predator and prey, likely because of differences between the scales of measurement, and other broad-scale processes that diffuse interactions. Here, I focus on the fine scale foraging patterns of individual gray whales (*Eschrichtius robustus*) feeding on mysid shrimp (Family *Mysidae*), during focal follow surveys from May to August, 2008, in Clayoquot Sound. In a similar study, using additional data from 2006 - 2007, I hypothesized that patterns in gray whales' fine scale foraging behaviour corresponds to measures of overall prey density. Here, I refine my understanding of whale response to prey by conducting acoustic prey surveys alongside foraging whales. Prey density coincident to focal animals, never fell below 2,300 mysids per cubic metre, and was, on average, higher than overall estimates for the study area. The relationship between foraging behaviour and spatially coincident prey density is less distinct. Focusing on only one scale of measurement confounds the behavioural connection to overall prey density; however, a perspective that includes the interaction between scales, illuminates a distinct predatory strategy and lends insight to how whales' relationship with their prey aggregates across scales.

Introduction

Across a continuum of scales, ocean resources are typically aggregated in patches, which, over large regions are predictable due to their association with upwelling zones, frontal formations, or bathymetric structure (Haury *et al.* 1978, Pinel-Alloul 1995, Bonadonna *et al.* 2001, Fauchald 2009). Many ecological processes, from population dynamics to trophic interactions, are determined by fine scale prey variability, which have less predictable spatial and temporal patterns (Pinel-Alloul 1995, Croll *et al.* 1998, Zouhiri *et al*. 1998). As plankton patches often fluctuate faster than they are measured, characterizing the relationship between prey quality and marine predators in studies of marine systems is often limited by research design, sampling methods and interpretation of results (Piatt & Methven 1992, Bowen 1997, Sims & Quayle 1998, Croll *et al.* 2005, Torres *et al.* 2008, Pendleton *et al.* 2009).

To understand the strategies of gray whales *(Eschrichtius robustus*) foraging on mysids in Clayoquot Sound, British Columbia, I previously classified the dive behaviour of individual animals during focal follow surveys as either foraging or searching, and then correlated foraging behaviour to overall prey density. I found that between 2006 - 2008, whales spent more time foraging when average mysid density across the entire study area was high. However, I recognized that alongside the fine scale surveys of whale behaviour, the coarser spatial and temporal scale in the measurement of overall prey density could be influencing my interpretation.

To clarify the relationship between prey density and foraging strategy, in addition to overall surveys, I conducted continuous hydro acoustic surveys coincident to ten focal follow survey paths in 2008. I predict that coincident prey density will be higher than overall prey density. I also predict that an individual whale's foraging behaviour should correspond to overall and coincident measures of increased mysid density. By comparing the predatory response to variations in prey density at two scales I refine the grain and extent of my analysis of the relationship between marine predator and prey.

Methods

Data Collection

The 10 continuous focal surveys used in this study took place on 9 days between May 30th and August 11th, 2008, using methods described earlier in this thesis. Prey variability coincident with individual focal surveys and the overall study area was measured by weekly acoustic surveys (May to September) of the study area (Fig. 1, Chapter 2), using methods previously described.

Data Analysis

I selected foraging dives based on criteria presented earlier in this thesis. Acoustic output was processed as per methods developed by Olsen (2006) described in the previous chapter. In coincident prey surveys, data files were processed using the same model for mysid detection as overall prey surveys. The only analytical difference was that mysid density estimates were integrated along the path of the survey as a continuous series of latitude and longitude points, with a single density variable.

In the coincident prey surveys, density values were mapped and point values interpolated to create a density surface to capture all dive locations in the subsequent overlay. The interpolation process employed the ordinary kriging surface estimator available in ArcMap to create a field perspective of average prey density. Kriging is an advanced geostatistical procedure that predicts the values at unsampled locations by incorporating the spatial structure of the data, estimated by a semivariogram, in a simplified statistical model of non-independent random variables (McBratney & Webster 1986, O'Sullivan & Unwin 2003). The general formula is given as a weighted sum of the data:

(EQ. 1)

$$\hat{Z}(s_0) = \sum_{i=1}^{N} \lambda_i Z(s_i)$$

where:

$Z(s_i)$ = the measured value at the $_i{}^{th}$ location.
λ_i = an unknown weight for the measured value at the $_i{}^{th}$ location.
s_0 = the prediction location.
N = the number of measured values.

Resulting prey density surfaces for each focal survey are overlaid with the focal tracks, and the average prey density coincident to individual dive locations is extracted in GIS (*e.g.* Fig. 1). The density values underlying each dive in the focal survey are merged with behaviour attributes, and averaged for each behaviour class and the survey as a whole. Average mysid density from each overall prey survey of the study area, occurring within a week of a focal survey is selected for comparison of differences between spatial and temporal scales.

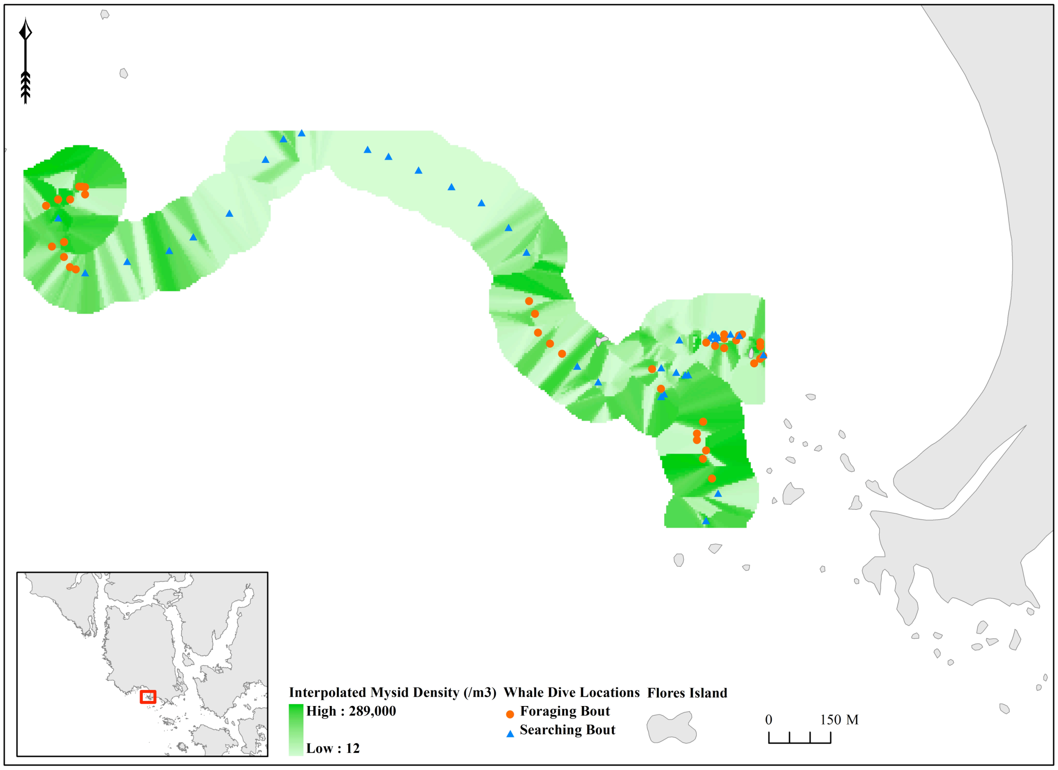

Figure 1. June 24, 2008. Map of coincident prey density surface generated by kriging interpolator (dark areas are higher densities), overlaid with focal follow dive locations. Orange circles are foraging bouts, and blue triangles are searching bouts. Interpolation surface was clipped to within 100m of the survey track.

Prey Density and Foraging Variability

Average density in coincident surveys is compared to the corresponding overall prey survey (of the study area, occurring within a week of the focal survey). The relationship between foraging behaviour and average density from overall and coincident prey surveys is compared using a non-parametric correlation. I compare the difference in average density of mysids coincident to where whales were classed as foraging or non-foraging using a Mann-Whitney U test.

Results

Focal Follows

In 2008, I completed 10 individual focal follows accompanied by hydroacoustic surveys on 9 days. Whales were observed for an average of 83 minutes (range of 23 to

303 mins) in 2008, totaling 17 hours of focal observations of over 1000 dives. Whale identities were confirmed for 9 individual whales in 10 surveys.

Variations in Prey Conditions

Prey was measured biweekly across the study area, from May through August. Average mysid density did not vary significantly between overall surveys of the study area in 2008 (Kruskal-Wallis $\chi^2 = 438.8$, df = 16, P = 0.000). Average density in the study area during the period of the focal surveys was 6,100 mysids/m^3 in 2008, and ranged from between 130 – 18,000 mysids/m^3 , reaching peak density on July 18 (Fig. 2).

Focal surveys with coincident prey measures extend from May through August. Average mysid density did not vary significantly between each coincident survey (Kruskal-Wallis $\chi^2 = 180.8$, df = 9, P = 0.000). Average density from coincident prey surveys was 11,000 mysids/m^3, and ranged from between 2,300 – 32,000 mysids/m^3. Peak density was recorded on June 17 (Fig. 2).

There is no significant correlation between average mysid density measured during coincident prey surveys, and corresponding overall prey surveys (Spearman's rho = -0.35, N = 10, P = 0.33). Coincident prey density is higher than overall mysid density when overall density is below 4,400 mysids/m^3 (Fig. 2).

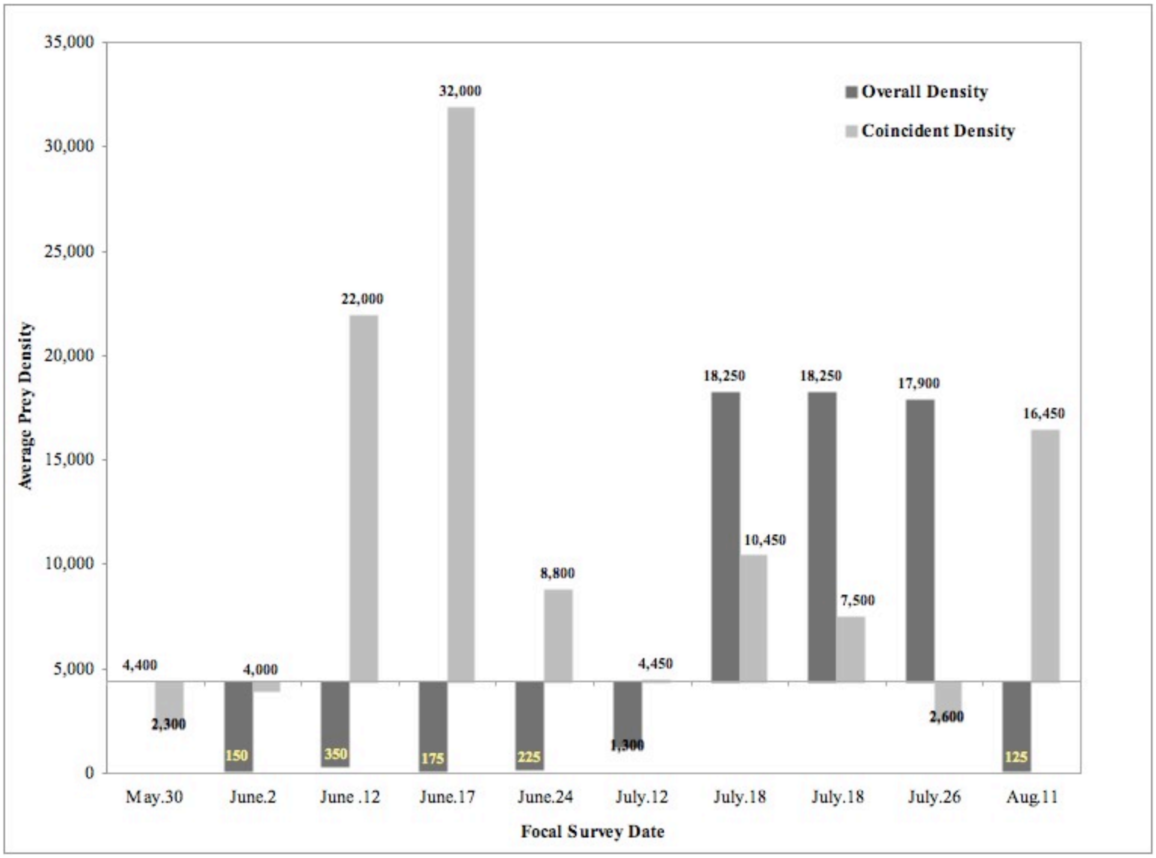

Figure 2. Average Mysid Density (per m^3) from overall surveys, and coincident prey surveys, 2008. X-axis is set at 4,400 (per m^3) threshold for comparison. Density above the line includes values up to this threshold and bars extending below are the negative difference from 4,400. Actual densities are noted on the graph.

Prey Abundance and Foraging Variability

Whale dive behaviour is compared to overall and coincident prey surveys (Fig. 3). There is a significant positive relationship between foraging and average mysid density from overall surveys (Spearman's rho = 0.73, N = 10, P = 0.017). Foraging dominates whale behaviour when overall mysid density is above 4,400 mysids/m^3 (Fig. 3). The relationship between foraging behaviour and average mysid density in coincident prey surveys is not significant (Spearman's rho = -0.38, N = 10, P = 0.28). Foraging increases when coincident prey density is low, relative to overall prey density. Notably, while overall average prey density was depressed well below the foraging threshold in six out of ten surveys, coincident prey density never fell below 2,300 mysids/ m^3.

Figure 3. Percent time spent foraging (orange line) on right axis, coincident (light green bars) and overall (blue bars) average prey density (mysids/ m^3) on left axis, 2008.

In coincident prey surveys, there is a significant difference in average density of mysids, between dives that were classed foraging or non-foraging (Mann-Whitney U =108,400, Z = -3.43, N = 997, P = 0.001). In the early part of the season, foraging dives occur in areas of higher density; as overall density peaks in mid July, non-foraging dives occur at higher densities, with the exception of one survey on July 18 (Fig. 4).

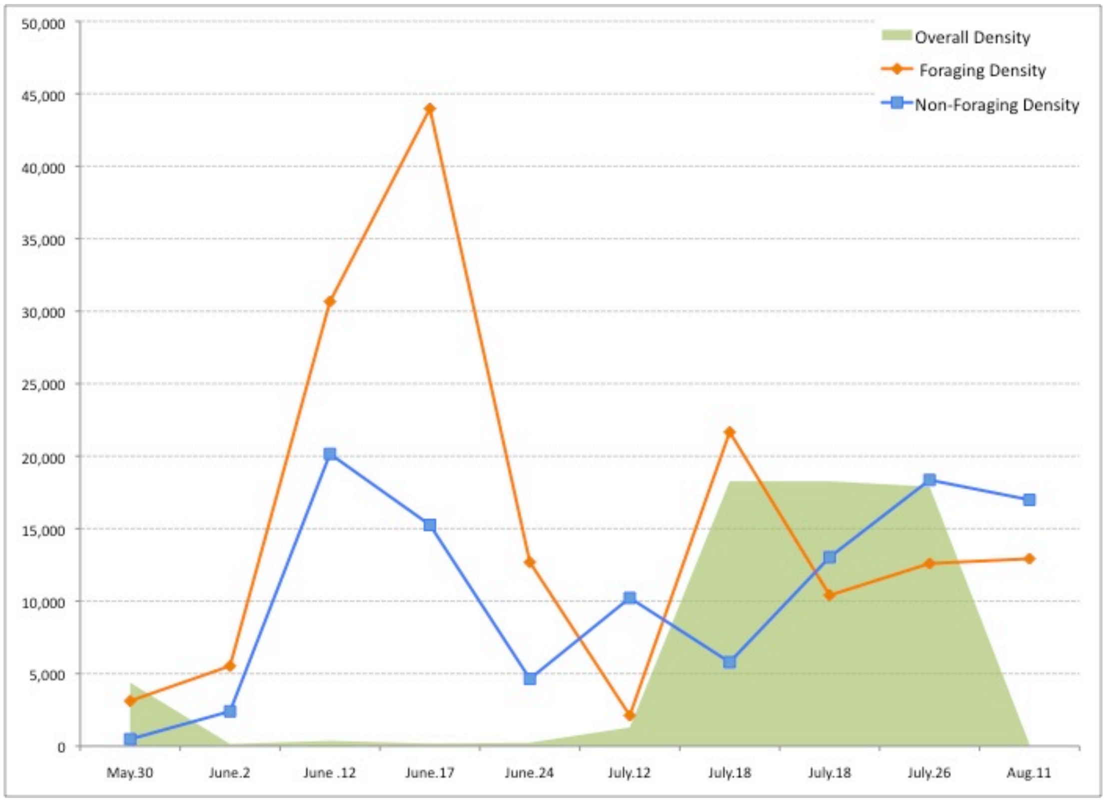

Figure 4. Coincident prey density while focal animal was foraging (orange diamond line), or non-foraging (blue square line) and overall prey density (mysids/m^3) (light green area).

Discussion

Here I refine my estimates of whale response to prey density and distribution by undertaking continuous acoustic prey surveys immediately along focal follows of foraging gray whales. I predicted that coincident prey density will be higher than overall prey density and that an individual whale's foraging behaviour should correspond to overall and coincident measures of increased mysid density. In comparing variations between prey measurement scales, in agreement with my hypothesis, I found density coincident to whales higher on average than overall estimates. Looking at the behaviour of 10 individual whales between May- August, 2008, I found that foraging did correspond to overall concentrations of mysid prey in the study area confirming my predictions. While the relationship between foraging and coincident density measures was not significant, prey density measured next to a foraging animal whale never falls below 2,300 mysids/ m^3.

Although there was no significant relationship between overall and coincident prey density, when overall density is low (< 4,400 mysids/m^3), coincident density is high (>= 4,400 mysids/m^3) (Fig 2). This suggests that whales are able to locate high quality prey patches well above the overall local average when necessary (Fig. 3). The interactions of these multi-scale relationships suggest that the predatory strategy of gray whales is highly efficient and closely tied to the distribution and abundance of their prey.

The Season of the (S)witch

Focal surveys occurred at different points in the pattern of overall seasonal production, from initial bloom in May, to a peak in July, to the low ebb in August. Having focal surveys from time periods with strong differences in prey availability has the effect of highlighting the distinct foraging strategies under high and low prey quality scenarios. While animals may be proficient at locating higher than average densities when overall conditions are low, these patches may be composed of smaller juvenile mysids, and sparsely distributed across the region (Turpin *et al.* 1994, Dunham & Duffus 2001, 2002). As a result, whales may spend more time engaged in non-foraging behaviours, such as searching, rather than foraging, as they try and locate the highest quality prey.

As mysid body size and swarm density increases, whales can focus on foraging. Despite coincident prey densities being lower than overall values during the seasonal peak in productivity, coincident density still averaged 6,200 mysids/m^3 during July surveys. As prey density is maximized across the region, other factors may influence foraging behaviour. Whales may not have to feed on the densest patches, as all the patches in the study area are of reasonable quality. This effect may be compounded by the seasonal requirements of migrating whales. In the latter part of the season, when whales' energy stores should be maximized, they may reach satiation more easily and, correspondingly, do not require the highest densities of prey.

Scale Jumpers

The distribution of marine resources has been characterized as hierarchical patches aggregating along a continuum of scales (Haury *et al.* 1978, Pinel-Alloul 1995).

As mysids form discrete swarms (Clutter 1969), overall density estimates for the study area only represent one aspect of the whales' appreciation of the entire preyscape. Although this measure of prey variability corresponds well to their general behaviour budget, whales feed in response to even finer spatial and temporal variation in prey availability. As a result, the estimate of the minimum prey density to sustain foraging behaviour is coarse, as prey densities in the vicinity of foraging whales were on average much higher than overall measures.

When the density values were compared directly to dives, foraging dives occurred coincident to higher densities during the first half of the season. This suggests that when overall prey productivity is low, whales respond to finer scale variations in prey density. As productivity increases, however, the spatial distinction between areas of high and low density may blur, and non-foraging behaviour may appear in areas of higher density. This may reflect a form of foraging behaviour, not captured by the dichotomized behavioural classification, or may simply paint a picture of greater underlying productivity blurring the spatial scale of response. As patches of mysids grow and aggregate, overall measures of prey quality may be a better match to the scale of whale foraging decisions.

In addition, foraging whales disturb mysid swarms through the process of suction filter feeding, causing swarms to temporarily disperse, and lose density (Hahn & Itzkowitz 1986, Buskey 1998). Although this method for measuring prey density represents the finest spatial and temporal estimate of predation pressure I am aware of, the prey estimation will always lag the behavioural response. As a result, the focal animal has already influenced the existing mysid density, potentially reducing or disturbing mysid swarms, and affecting the coincident estimates in relation to behaviour classes.

In this study, I assume that the behaviour of individual whales outlines their immediate assessment of prey swarms. The strength of the correlation analysis suggests that foraging decisions are also influenced by additional outside factors. With a limited sample of animals, it is possible that the patterns described here could be more related to intrinsic features of the individual (Mann 1999). Such behavioural variation is impossible to control for. Now that the relationship between coincident prey density and foraging behaviour has been documented for individual animals, it may be possible to test and detect the influence of other factors in future studies.

Conclusion

This study identifies how the close relationship between predator and prey varies across time and space scales. To understand the foraging strategies of gray whales feeding on mysids in Clayoquot Sound, British Columbia, I correlate prey density at two scales, with classified foraging behaviour of individual whales during continuous focal follow surveys. When variation in overall prey density across the study area is compared to prey density in the vicinity of foraging whales, prey availability changes with the scale of measurement. Whales respond to variations in mysid density at both an overall and a fine scale, however, the prey density measured coincident to foraging whales was blurred by seasonal variations in productivity. The minimum mysid density found coincident to a foraging whale was 2,300 mysids/m^3. This estimate is likely dependent on within-season timing, overall conditions of prey availability, and other potential influences such as individual preference, competition, and broader scale prey availability, such as pull factors from other foraging sites.

Patterns in spatial and temporal variability of prey correspond to the fine spatial and temporal responses of foraging gray whales. Gray whale foraging behaviour reflects timing in the life history of both whale and mysids, and a response to shifting prey quality at multiple scales (Dunham & Duffus 2001, Moore & Huntington 2008, Nelson *et al*. 2008).

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Chapter Five: Predatory Disturbance Controls on Prey Species Diversity: Gray Whale (*Eschrichtius robustus*) Foraging and a Multi-species Mysid (Family *Mysidae*) Prey Community

Abstract

Community ecology provides a number of explanations as to why competitive exclusion does not appear to regulate the seemingly redundant number of coexisting plankton species. A useful explanation comes from Connell's (1978) Intermediate Disturbance Hypothesis, which proposes that high species diversity is more likely after moderate levels of disturbance that leave space for the invasion of less competitive species. Here I focus on the shifts in species diversity in a mysid (Family *Mysidae*) zooplankton community, the primary prey base of seasonally resident gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia. I hypothesize that foraging whales create an intermediate level disturbance that alters mysid community structure and species dominance patterns. I assess the community structure of mysids (species dominance, diversity, richness, evenness, abundance) across the Flores Island study area in 1996, 1997, 1999, 2000, 2001, 2002, 2007 and 2008 field seasons (May - September). Diversity between mysid species composition is significantly different in each year and diversity has increased between 1996 and 2008. *Holmesimysis sculpta* has typically been the dominant mysid species over the last ten year period. In 2007, *Neomysis rayi* became significantly more abundant, while whale foraging activity in the previous year was high. 1997 and 2002, the years with highest whale foraging effort have the lowest species diversity. I discuss how predatory disturbance affects competitive exclusion and dominance of *H. sculpta*, and the implications of proficient foraging by marine predators, including the potential for current prey resources to be exhausted.

Introduction

The wide variety of planktonic life has intrigued community ecologists, often stemming from Hutchinson's (1961) foundation paper on the 'paradox of the plankton' (Richerson *et al.* 1970, Herbert & Crease 1980, Huisman & Weissing 1999, Scheffer *et al.* 2003). Why competitive exclusion, the force that propels the dominance of one over a diversity of similar species, does not apply strongly in many marine systems has been the subject of ongoing debate. While the question may be an artifact of our crude application of terrestrial theory to aquatic systems, alternative hypotheses continue to develop. Explanations for species redundancy range from symbiosis, to the near invisible aspects of niche partitioning (Hutchinson 1961, 1957), and from resource limitations on competitive efficiency (Richerson *et al.*1970)*,* to intermediate disturbance regimes (Connell 1978).

Although none of these hypotheses are mutually exclusive, the assumption is that species complexity is built on a tendency towards at least a temporary equilibrium in community structure. Ocean systems are typically considered homogenous habitats over small spaces and short time periods. The lack of boundaries and constant mixing at different scales leads to difficulties in identifying and monitoring shifts in equilibrium as they occur (Steele 1989). Examining the dynamics of species diversity has, as a result, often been relegated to laboratory studies (Scheffer *et al.* 2003, Romanuk *et al.* 2009).

Competitive exclusion is typically thought to regulate species diversity, chiefly through the interplay of life history attributes, such as fecundity or foraging efficiency (Hairston *et al.* 1960, Menge & Sutherland 1976). Fox (2007) compared the relationship of species diversity and composition to the strength of top-down and bottom-up effects. He found temporal variability in the strength of predation so dynamic as to preclude equilibrium predictions based solely on trophic diversity. The implication of his hypothesis for temporally variable marine systems, where resource limited pulses of productivity have been widely regarded as the regulating force (Steele 1998), is that disturbance by predation also regulates community structure (Hunt & McKinnell 2006). The strength and frequency of disturbance drives Connell's (1978) Intermediate Disturbance Hypothesis (IDH), which proposes that elevated species diversity is a product of moderate levels of disturbance that allow for the subsequent invasion of less competitive species. While there are issues in defining what is exactly meant by disturbance (i.e. components and units), it is likely that there are multiple scales of disturbance-diversity patterns varying in resiliency (Svensson *et al.* 2009).

Here I examine shifts in species diversity of mysids (Family *Mysidae*) off the west coast of Vancouver Island, B.C. (Fig. 1). Mysids are free-swimming, shrimp-like crustaceans ranging from 2-30 mm in length, depending on species and age class. The study area holds large dense swarms of mysids where they typically aggregate in swarms of varying extent, just above the bottom in association with rocky reefs and kelp stands (primarily *Nereocystis luetkeanai* and *Macrocystis integrifolia*) near shore (Green 1970, Kim & Oliver 1989, Turpen *et al.* 1994).

In the north Pacific, there are 48 species of coastal mysid zooplankton, with at least 10 found in our study area. Although a diversity of mysid species is typically found within the same swarm, *Holmesimysis sculpta* has been the numerically dominant species (Dunham & Duffus 2002, Mulkins *et al.* 2002, Patterson 2004). Other studies further north (Stelle 2001, Maud 2008), and south of our study area (Newell & Cowles 2006) have also found *H. sculpta* to be dominant at their research sites. This suggests that *H. sculpta* holds a competitive advantage over other mysid species in the coastal zone of the Northwest Pacific.

Over the last two decades, mysids have been increasingly targeted as a seasonal prey item by gray whales (*Eschrichtius robustus*) in the Pacific Coast Foraging Aggregation (PCFA) (Dunham & Duffus 2001, 2002, Buckland & Breiwick 2002, Rugh *et al.* 2005, Swartz *et al.* 2006, Moore 2007*)* (Fig. 1). Baleen whales must consume large quantities of prey to maintain blubber layers for migration and thermoregulation (Moore & Huntington 2008). Estimates suggest that gray whales require between 250 and 1100 kg, or 7.6 x 10^5 kilocalories/ day (Rice and Wolman 1971, Nerini 1984, Highsmith & Coyle 1992, Greenwald 2005). Translating the caloric demand into mysids [assuming an average dry body weight of 0.834 mg, and a caloric content of 4.8 calories/mg dry weight] gray whales would need to consume between 1.88 x 10^7 and 7.5 x 10^7 mysids/day (Mulkins *et al.* 2002, Olsen 2006). Gray whales foraging in a restricted area, as in this study (< 20km^2), can reduce the overall abundance of mysids in both the short and long term. In each foraging season, beginning in April until early October, mysid swarm density fluctuates from early growth, to initial abundance, to depletion through predation, and reproductive replenishment.

Here I test the hypothesis that through foraging, whales alter the species structure of the prey assemblage. I test the hypothesis that gray whale foraging affects the mysid community by reducing dominance and increasing species diversity. I investigate the impact of predatory disturbance over seven years by comparing the seasonal abundance of foraging whales to mysid species diversity.

Methods

Study Area

I focus my investigation on the sample species richness (SR_s) or the α diversity of mysids (Gray 2000) off the west coast of Vancouver Island, British Columbia, between May 15 and September 8, 1996 to 2008. The study area is a 20 km^2 foraging site off the southwest coast of Flores Island, Clayoquot Sound, between 49°14'36.71"N, 126° 6'10.16"W and 49°18'51.93"N, 126°14'30.37"W. It is bounded by deep inlets, essentially nonproductive whale foraging areas to the north and south, and by the 30 metre depth contour. The study area is monitored by a standardized survey, beginning at Entrance rocks and terminating just north of Dagger Point, at End Rocks (Fig. 1).

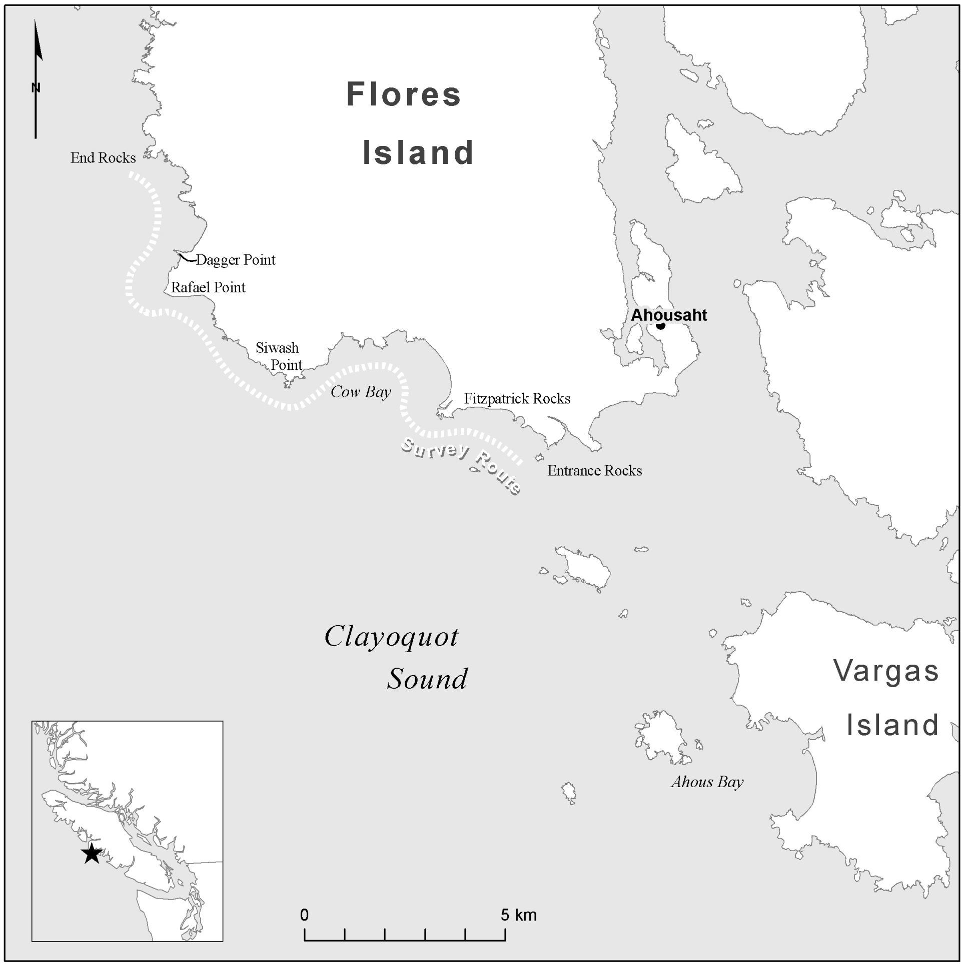

Figure 1. Prey survey area off the west coast of Vancouver Island, B.C., Canada located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W.

Data Collection

Whale Surveys

Gray whale foraging effort was measured by bi-weekly, boat-based census surveys in an open seven meter vessel along a pre-defined route within 1 km of the southwest coast of Flores Island (Fig. 1). Surveys were aborted if visibility became compromised by fog or a Beaufort sea state > 3. Vessel speed during whale surveys averaged approximately 6 knots (11 km/h). A minimum of four observers scanned 360° for whale ventilations. Upon locating a blow, the vessel approached the whale and determined whether it was traveling or foraging, and recorded its last dive location using a GPS. While vessel speed is intended to overcome double counts, unique markings were also noted or photographed in order to only record each individual once per survey. Between May 24, and September 8, 1997-2008, there were 29 to 60 dedicated whale surveys conducted annually. Standardized whale surveys were not conducted in 1996, and differences in the timing and number of surveys per season are due to weather conditions.

Whale Foraging Analysis

The number of whales per survey is not a measure of abundance, rather it is an indication of the level and timing of foraging effort. Foraging effort in each year is represented as the average number of whales per survey within each season. A Kruskal-Wallis test is used to assess whether foraging effort differed between years (1997-2008).

Mysid Sampling

Mysids were collected between May and September in 1996, 1997, 1999, 2000, 2001, 2002, 2007 and 2008. I, and earlier colleagues, used a random selection of sites within mysid habitat strata (Dunham & Duffus 2002, Nelson *et al.* 2008), and in the vicinity of foraging whales in those same strata. Survey effort varied slightly between years, due to weather, and overall variation in mysid abundance within and between years (making sampling more intensive in low abundance years in order to obtain a substantial sample).

Mysids were captured by deploying a bongo style net with two 30 cm openings and 500 μm mesh, which was allowed to sink to the bottom, dragged for several seconds and pulled straight to the surface at each site. The procedure was repeated up to three times before moving to another sampling location. The data used in this study was collected during 64 surveys, consisting of over 365 hours of sampling effort, between 1996 and 2008.

Mysid Sample Processing

Mysid samples were preserved in 70% ethanol for identification. Prior to 2007 the homogeneous portion of the sample was split using a Folsom splitter. After 2007, all mysids in a sample were enumerated. Samples contained anywhere between 20

– 2500 animals. Individual mysids were identified to species, sexed and measured, according to Kathmann *et al*. (1986) using a 40x dissecting microscope. Over the course of sampling 225 replicate net tows contained mysids, of which 101,370 animals were identified to species. Sampling was aggregated by date across the area.

Species Diversity Analysis

All of the individuals collected in each prey survey are pooled to calculate the proportion of each species by survey and by year. The overlap between species in each year is used to designate the most common species, while the least frequent species are those below the first quartile in terms of overall abundance (Gaston 1994, Magurran 2004). The most common species are used to identify patterns in species dominance.

Diversity statistics are calculated for the pooled results of each year. The most basic is simply the number of species observed in a sample. Margalef's diversity index is used as an additional estimate of the number of species, or species richness (D_{Mg}) as it takes into account sample size (Magurran 2004):

$$\mathbf{D_{Mg} = (S-1)/\ln(N)} \qquad \textbf{(Eq. 1)}$$

where S represents the number of species in the sample and N represents the number of individuals. Larger values of D_{Mg} indicate greater species richness compared to the number of individuals in the community (Magurran 2004). Simpson diversity (D) is calculated because it provides a good estimate of diversity that is relatively independent of different sample sizes and emphasizes the dominance component of species diversity (Lande *et al.* 2000, Magurran 2004):

$$\mathbf{D = \Sigma\left(\frac{n_i[n_i-1]}{N[N-1]} \right)} \qquad \textbf{(Eq. 2)}$$

where n_i = the number of individuals in the sample belonging to the $_i^{th}$ species, and N = the total number of individuals in the sample. As *D* increases, diversity decreases. However, Simpson diversity is typically expressed as its complement ***1 – D***, so that an increasing value indicates a more diverse community (Magurran 2004). Simpson diversity stresses species dominance over richness. It is not specifically a measure of evenness, or the relative individual contribution of each species to overall abundance.

The Simpson's evenness index more directly estimates this variability in species abundance, distinguishing between communities that have an equal number of individuals of each species as "even," and those with a different or "uneven" number of individuals of each species. Ranging from 0 – 1, Simpson's evenness is calculated by dividing the reciprocal form of Simpson diversity (D, Eq. 2), by *S* the number of species in a sample (Krebs 1999, Magurran 2004):

$$\mathbf{E_{1/D} = \frac{(1/D)}{\boldsymbol{S}}} \qquad \textbf{(Eq. 3)}$$

Diversity indices from mysid samples taken in 2002 are calculated, but not included in correlations with whale foraging as sampling occurred on only a single day. Species richness and diversity indices are compared to the number of samples and number of individuals in each year to assess the influence of sampling effort.

Multivariate CLUSTER analysis in PRIMER 6.1.1 (Plymouth Routines in Multivariate Ecological Research software; Clarke & Warwick 1994) was used to compare the 64 samples of abundance data for the most common mysid species. In CLUSTER analysis, the pooled samples for each year are transformed to the fourth-root, and the Bray-Curtis similarity coefficient is computed between each sample to create the resemblance matrix to implement hierarchical agglomerative clustering of the samples. Samples with a small Bray-Curtis similarity coefficient are clustered to indicate the most similar composition.

Foraging Disturbance and Mysid Diversity

In each year that prey sampling occurred, Simpson diversity is compared to the level of foraging given by the average number of whales per survey. As comparisons based on species richness are vulnerable to sample size bias (Magurran 2004), other measures of mysid diversity are not directly compared to foraging. Mysid diversity data from 1996 is used as a pre-disturbance baseline for changes in mysid species diversity in subsequent years. Whale foraging is also ranked as high or low, as measured against the mean of all years, and compared to species diversity in that season.

Analysis of similarity (ANOSIM) in PRIMER (Clark & Warwick 1994), takes the resemblance matrix values to test for differences between samples in each year. All samples (except for 2002) are grouped based on average foraging pressure in that year (above or below average) and ANOSIM tests for significant differences in species compositions between high and low foraging classes.

Results

Whale Foraging Effort

The daily mean number of foraging whales for all years is 5.4. Average foraging effort is significantly different between all years (Kruskal-Wallis χ^2 = 196.7, df = 11, P = 0.000) (Table 1). There is a consistent pattern where each high year (above average) is followed by *at least* one low year (below average) pattern over the twelve-year period, exacerbated by a descending sequence from 2002 onward where high years and low years approximately half themselves in each subsequent year.

Table 1. Daily average number of foraging whales and foraging effort rank for each season. Years where mysid surveys occurred are highlighted in gray.

Year	Mean number of whales	Rank
1997	5.3	Low
1998	10.65	High
1999	3.95	Low
2000	2.23	Low
2001	2.24	Low
2002	12.2	High
2003	4.73	Low
2004	9.62	High
2005	1.87	Low
2006	6.42	High
2007	0.96	Low
2008	3.80	Low
All Years	5.42	

Mysid Species Diversity

The proportion of each species found in each sample becomes progressively more variable between 1996 and 2008 (Fig. 2). The proportion of *H. sculpta* found in each sample decreases through time, while the abundance and occurrence of *Neomysis rayi, Acanthomysis borealis, Acanthomysis columbiae, Columbiaemaysis ignota, Exacanthomysis davisi, Disacanthomysis dybowskii, Alienacanthomysis macropsis,* and *E.unguiculata* increases. *H. sculpta,* and *N. rayi* were observed in all years, and *C. ignota,* and *A. columbiae* were found in all but one year. *N. mercedis* was only found once and was the rarest species according to Gaston's (1994) first quartile definition (Table 3).

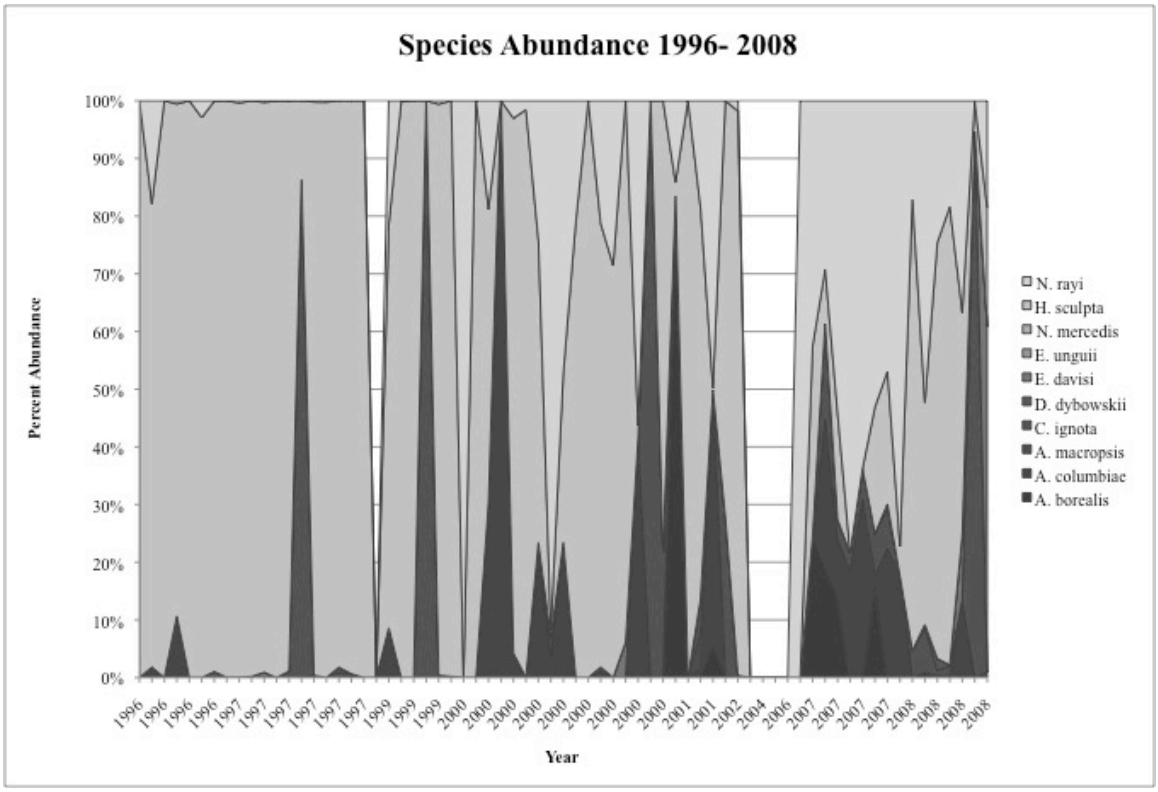

Figure 2. Proportional abundance of all Mysid species collected during each survey, 1996 - 2008

When year is applied as a treatment to the proportion of each species, the abundance of *H. sculpta, N. rayi, A. borealis, A. columbiae,* and *E. davisi* are significantly different between all years, and *C. ignota* is nearly significant (p = 0.055). Kruskal-Wallis test statistics (Table 2) detect significant difference between species identified in all years (*H. sculpta, N. rayi*) as well as the difference for species found in only a few years (*A. borealis, E. davisi*). *N. mercedis* and *E.unguiculata* are not included as they were found in only a single year.

Table 2. Results of Kruskal-Wallis (KS) tests for numerical abundance values of all mysid species between years.

	H. sculpta	*N. rayi*	*A. borealis*	*A. columbiae*	*E. davisi*	*C. ignota*	*A. macropsis*	*D. dybowskii*
KS χ^2	27.787	29.863	21.450	14.761	15.150	13.803	7.779	5.935
df	7	7	7	7	7	7	7	7
Asymp. Sig.	**.000**	**.000**	**.003**	**.039**	**.034**	.055	.352	.547

Table 3. Average species composition in each year, with dominant species highlighted in bold.

Year	**% H. sculpta**	**% N. rayi**	**% C. ignota**	**% A. columbiae**	**% A. borealis**	**% E. davisi**	**% A. macropsis**	**% D. dybowskii**	**% E. unguiculata**	**% N. mercedis**
1996	**95.0**	3.1	0.0	1.8	0.0	0.0	0.0	0.1	0.00	0.000
1997	**92.2**	0.1	7.3	0.1	0.0	0.2	0.0	0.1	0.00	0.000
1999	**78.0**	3.8	16.7	1.3	0.0	0.0	0.1	0.1	0.00	0.000
2000	**54.5**	24.3	7.5	12.4	0.0	0.4	0.9	0.0	0.00	0.001
2001	**48.7**	16.5	6.7	9.1	17.9	0.0	1.2	0.0	0.00	0.000
2002	**97.8**	1.8	0.4	0.0	0.0	0.0	0.0	0.0	0.00	0.000
2007	12.3	**60.7**	4.7	14.0	8.2	0.0	0.0	0.03	0.1	0.000
2008	**47.4**	24.0	15.7	2.1	0.1	10.3	0.03	0.3	0.00	0.000
All Years	65.76	16.76	7.40	5.09	3.28	1.34	0.28	0.08	0.01	0.0001

The relative abundance of *H. sculpta* varies from over 90% percent in 1996-97, decreasing through 1999-2001 (78- 48%), increasing in 2002 (97%, based on one sample), losing dominance in 2007 (12%) and increasing again to become dominant in 2008 (47%) (Fig. 3). *N. rayi* maintains its representation, averaging about 15% in all the samples, except in 2007 when it became the numerically dominant species at approximately 60% (Table 3, Fig. 3). *C. ignota* and *A. columbiae* maintained low (<20%) but fluctuating patterns, increasing alongside *N. rayi* when *H. sculpta's* dominance declined. *C. ignota* and *A. columbiae* alternated in abundance relative to each other. *C.*

ignota surpassed *N. rayi* in 1997 and 1999.

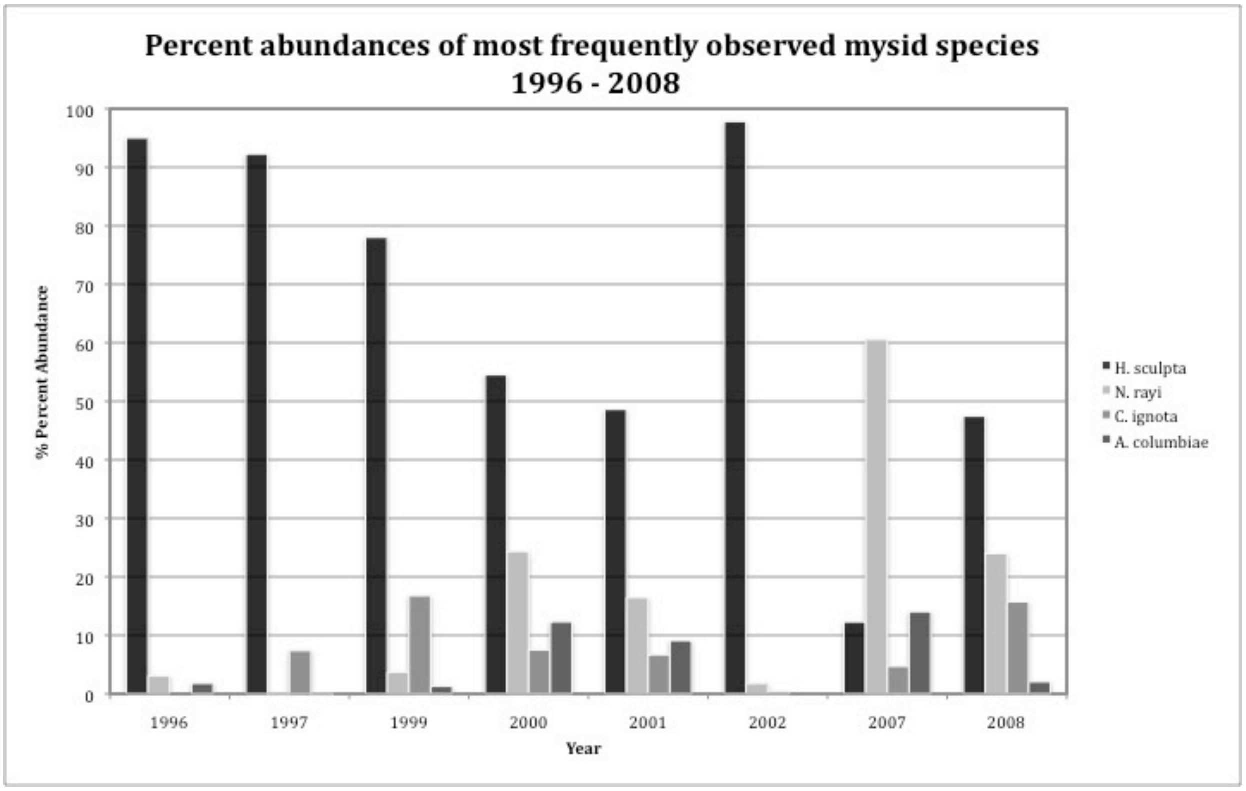

Figure 3. Change in mysid species dominance over time. Based on numerical abundance of most frequently observed species between 1996 and 2008.

The results of the CLUSTER analysis shows five clusters with similar mysid species composition with at least a 60% overlap in species composition (Fig. 4). The years with highest similarity in composition are 2001 and 2007 with an overlap of 85.1%. 2000 and 2008 also have a very similar species composition, with a similarity of 82.5%. The years 1997 and 2002 are clustered separately from any other year with an overlap of 62.1% and 48.5% respectively.

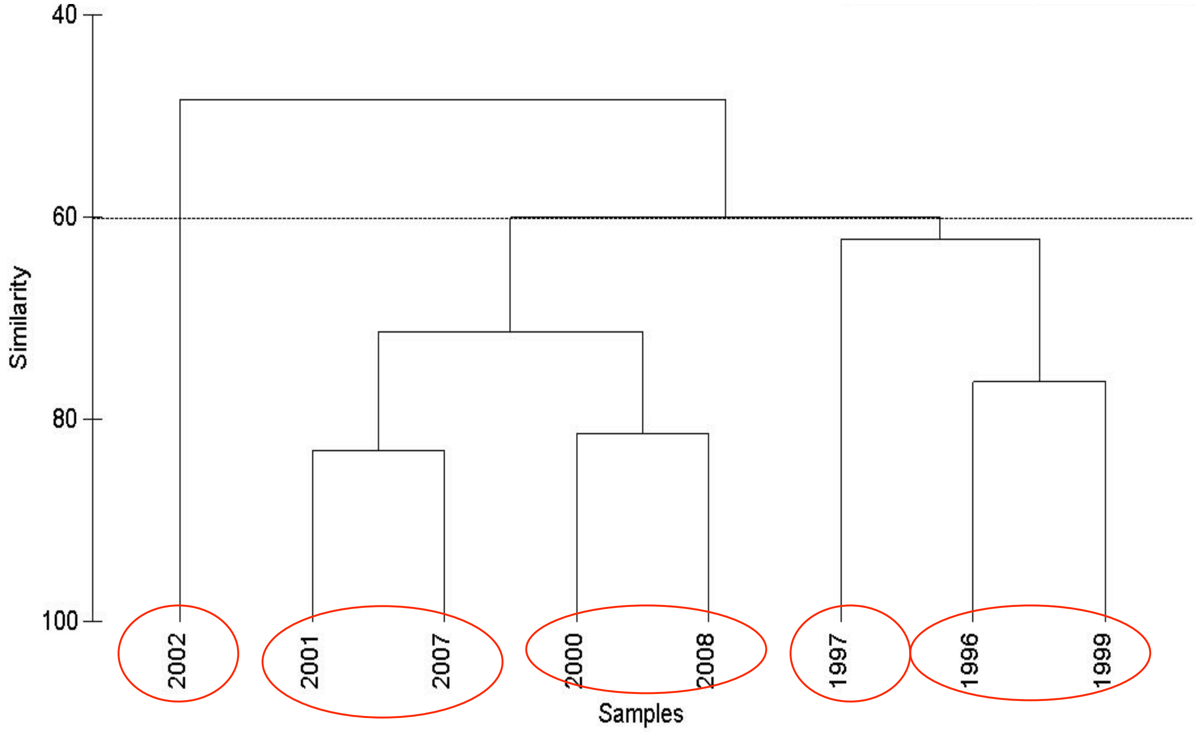

Figure 4. A dendrogram of a CLUSTER analysis based on mysid species composition. Final clusters are highlighted by red ovals. The horizontal dotted line represents 60% overlap in species composition.

Diversity between mysid species composition is significantly different in each year (ANOSIM global R = 0.21, p < 0.001). The pairwise results (Table 4) indicate that the strongest differences between years occurs in years paired with 2007, namely 1996, 1997, 1999, and 2002. Larger differences also occur between 1996 and 2008, and 1997 and 2001.

Table 4. Pairwise Similarity ANOSIM Test Results. Results from ANOSIM are a resemblance matrix of R values. The larger the value, the greater the separation between mysid species composition in those years.

	1996	1997	1999	2000	2001	2002	2007	2008
1996								
1997	0.34							
1999	0.03	0.19						
2000	-0.06	0.19	-0.03					
2001	0.33	0.55	-0.04	0.02				
2002	0.17	-0.12	-0.42	-0.31	-0.52			
2007	0.75	0.79	0.59	0.05	0.33	0.66		
2008	0.60	0.41	0.19	0.01	0.18	-0.09	0.36	

The sampling effort and values of several community parameters (richness, diversity, evenness) are compared between years (Table 5). The number of species found is not significantly correlated to the number of individual mysids collected (Spearman's *rho* = 0.39, n = 8, p = 0.35). However, the number of species is correlated to the number of sample days in a season (Spearman's *rho* = 0.79, n = 8, p < 0.02). When 2002, which only had one sample day, is removed from the correlation, the significant relationship disappeared (Spearman's *rho* = 0.69, n = 8, p = 0.09). Neither the number of mysids, nor the number of sample days is related to Margalef's index of species richness (Spearman's *rho* = 0.05, n = 8, p = 0.91; Spearman's *rho* = -0.22, n = 8, p = 0.64).

Table 5. Sample effort, diversity measures and dominant species, 1996-2008.

Year	Number of Sample Days	Number of Replicates	N (mysids)	Number of Species	Margalef's Richness Index	Simpson Diversity (1-D)	Simpson Evenness (1/D)/ S
1996	7	27	4,416	4	0.36	0.03	0.26
1997	12	39	63,921	6	0.45	0.12	0.19
1999	15	9	3,381	9	0.62	0.20	0.21
2000	15	37	8,506	9	0.55	0.45	0.31
2001	5	9	2,248	6	0.65	0.74	0.63
2002	1	3	735	3	0.30	0.04	0.35
2007	9	44	3,248	7	0.74	0.67	0.44
2008	7	57	14,915	8	0.73	0.57	0.29

Foraging Disturbance and Diversity

The correlation between Simpson diversity and daily foraging pressure in each year is significant and negative (Spearman's *rho* = -0.81, n = 6, p < 0.05). Years with high whale foraging (1997, 2002) have low species diversity, due to the dominance of *H. sculpta* (Fig. 5). Diversity increases in low foraging years, as the dominance of *H. sculpta* decreases, until 2007 when *N. rayi* became the dominant species, subsequent to a biennial sequence of high foraging years (2002, 2004, 2006).

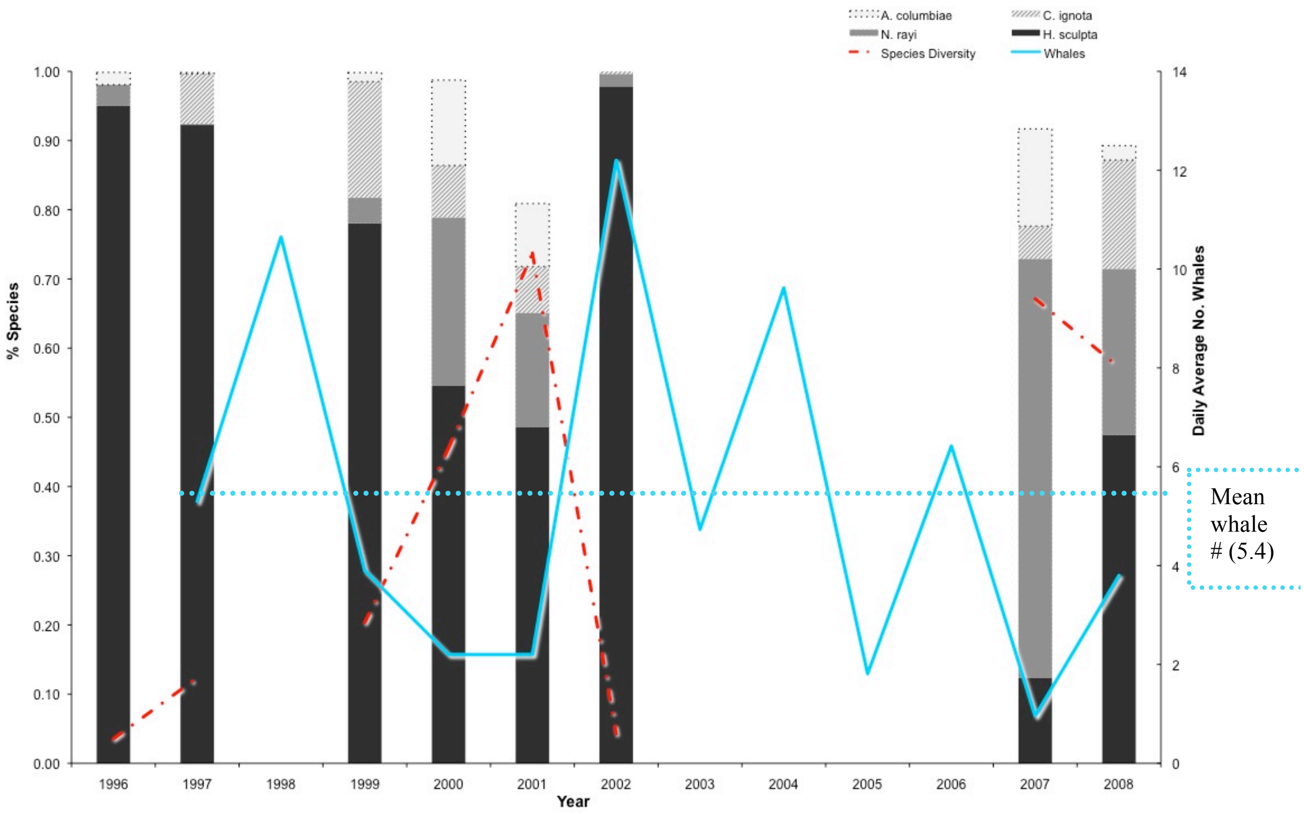

Figure 5. Mysid species diversity and whale foraging effort, 1996-2008. The relationship between the abundance of the four most frequently occurring species (bars) on left axis, Simpson diversity (red dashed line) on left axis, and average number of whales (blue solid line) on right axis. The average number of whales in all years (5.4) is indicated by blue dotted line.

Diversity statistics from each year are also compared to the 1996 baseline (Fig. 6). While relative differences in index values fluctuate between years, since 1996 there has been an overall pattern of increasing diversity. The case of species evenness is less clear, as it decreases in 1997 and 1999, before values increase in following years. Species richness also increases in each of the subsequent years, except 2002, where limited sampling reduces the confidence in this comparison.

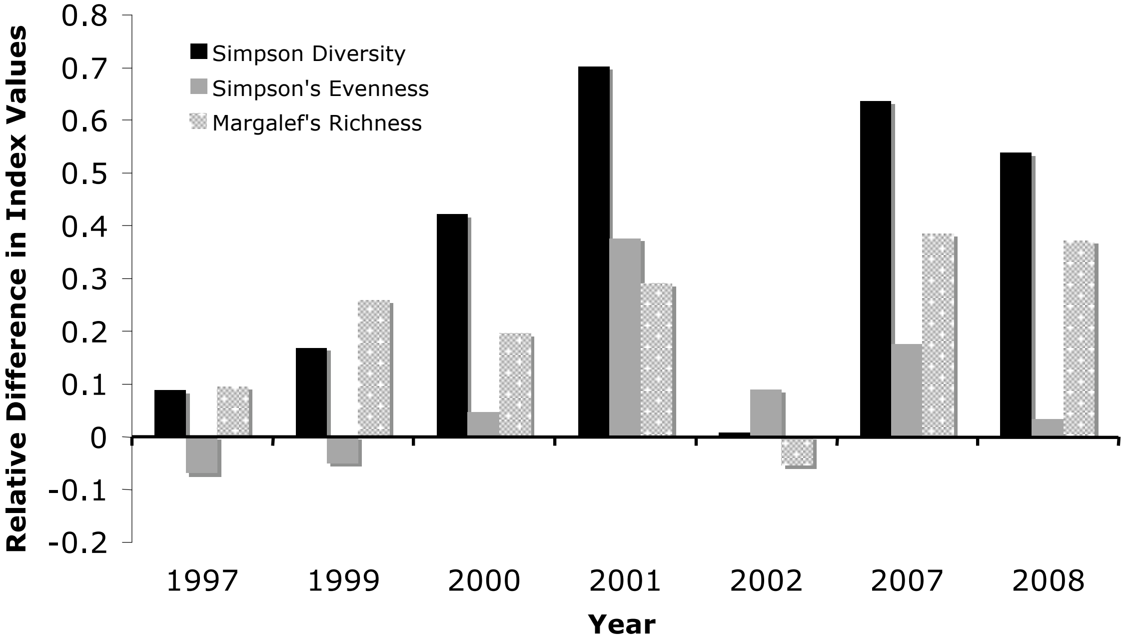

Figure 6. Comparison of change between the 1996 baseline species diversity measures, and those found in subsequent years.

Discussion

I hypothesized that gray whale predation increases mysid species diversity. The results here indicate that increased whale foraging activity is followed by subsequent years of increased diversity. Over the period of this study, I found that species diversity increased. Peaks in whale foraging occur during years where *H. sculpta* dominates and diversity is low. In those years, it is likely that their abundance presents a strong cue to gray whales searching for prey. Increased diversity follows higher than average whale foraging years, suggesting that *H. sculpta* takes time to recover from the impact of higher foraging pressure. High diversity is associated with small mysid populations and sparse swarms, which attracts fewer whales, and relieves the prey from predation. Although the dynamics of other frequently found species contribute to diversity and species richness, the impact of foraging on their overall abundance is difficult to assess as they appear at low numbers across samples taken in both high and low whale years.

Whether the 1996 mysid community is representative of a baseline or a state of equilibrium is arguable. The trend among the most frequently occurring species emphasizes an increase in diversity over the 12 years between 1996 and 2008, culminating in 2007 with the switch in species dominance, an event that was reversed in 2008. As the abundance of *H. sculpta* decreases, the corresponding increases in diversity suggest that mortality events may be frequency dependent, whereby the most abundant species becomes the target of predation (Huston 1979, Connell 1978). The shifting proportions of these species illuminate long-term patterns, and the homeostatic capacity of a marine community.

Clustering based solely on the species' proportions pooled by-year, class low whale years together (1996 and 1999, 2007 and 2001, 2000 and 2008) and isolate high whale years (1997, 2002). The pattern of gray whale foraging effort over the last decade off Flores Island has also varied considerably across space and over time (Nelson *et al.* 2008, 2009). In the last 20 years, gray whales have changed from primarily feeding on benthic and other ephemeral prey to focusing their foraging effort on mysids, a switch that coincides with the trend of increasing Simpson diversity of mysids from 1996 onwards (Duffus 1996, Dunham & Duffus 2001, 2002). A temporary release of predation pressure in low whale years results in higher diversity while the abundance of local mysid populations recover. When predation intensifies, it is in concert with a significant increase in dominance and abundance of *H. sculpta.* The variability and declining trend in whale numbers, and associated mysid community dynamics over the last 12 years, suggest that continuous heavy foraging on limited local prey resources by gray whales may have a number of potential ecological consequences (Coyle *et al.* 2007).

Ten of the approximately 48 species of coastal mysids were identified in polyspecific swarms found in the nearshore habitat of this study (Kathman 1986, Dunham & Duffus 2002, Patterson 2004). The numerical dominance of one species, *H. sculpta* in seven out of eight years of sampling, and corresponding dominance patterns found in other sites in British Columbia (Stelle 2001, Newell & Cowles 2006) suggests this medium-sized mysid has a competitive advantage. A number of authors (Guerrero 1989, Stelle 2001, Dunham & Duffus 2002,) report that concentrated patches of individuals of similar size or age class exist within larger mysid shoals, possibly pointing to a form of resource partitioning (Schoener 1974). This nearly hidden niche dimension could indicate competitive exclusion (Hutchinson 1957), although the competitive equilibrium of the mysid community has yet to be determined. Similarities in mysid anti-predatory swarming responses and habitat overlap between species, however, indicate it is more likely an aspect of reproductive capacity, as generation time and brood size varies considerably between species (Mauchline 1980).

If summer reproductive events fail due to predation, mysid swarms can still persist, as in temperate waters they are generally able to produce offspring year-round (Mauchline 1980). Females that over-winter grow larger, and produce bigger broods as reproduction peaks during the warmer months of the spring and summer (Mauchline 1980, Johnston & Northcote 1989, Jones *et al.* 1989, Mees *et al.* 1994). While *H. sculpta* did recover dominant status in 2008, marine systems are subject to constantly changing conditions occurring at a number of spatial and temporal scales (Wiens 1989, Steele 1989, 1998, Levin 1992). As a result it is difficult to ascertain, even from data collected over a twelve-year period, whether this shift in 2007 was a unique event, or part of a larger trend in mysid community dynamics. Regular shifts in mysid diversity may occur naturally due to resource availability. The effect of other predators and other processes may intervene and compound or diminish the disturbance impacts of an apex predator. However, Crawley (2004) found that the difference in timing of disturbance significantly impacted the biomass, frequency, and relative abundance of coexisting species, as some species succeeded while others were driven close to local extinction by disturbance occurring at the "wrong" time of year. In addition Short's (2005) genetic study on the dispersive capacity of mysids found little evidence of recruitment from nearby populations, suggesting that small or isolated swarms of *H. sculpta* may not readily reestablish dominance after a disturbance. Thus the timing of reproductive events, while not a part of this study, could either help to rebuild or extirpate locally depleted mysid populations.

The variations in mysid community structure found in this study correspond to the theoretical predictions resulting from an intermediate type of disturbance. Predatory disturbance has been found to have profound effects on species diversity of aquatic and terrestrial assemblages, and Connell's (1978) intermediate disturbance hypothesis predicts a maximum diversity at intermediate levels of disturbance. Numerous studies have examined predatory disturbance in aquatic communities (*e.g.* Paine 1966, Menge &

Sutherland 1976), while some have found predation to have profound effects on species diversity, other results have often been confounded by loose definitions of disturbance and masked by variance inherent in natural assemblages (Svensson *et al.* 2009). As gray whale foraging on mysid populations has been continuous over the last decade, the impact of disturbance is likely cumulative, making distinguishing absolute thresholds for what constitutes an intermediate level difficult.

As Huston (1979) suggests, an "intermediate frequency" can be anywhere along a range of frequencies depending on the rate of competitive displacement. He proposes intermediate disturbance be defined as the frequency of disturbance at which the greatest numbers of species can recover from the reduction, as far from a competitive equilibrium as possible. Detecting and quantifying the extent and frequency of disturbance of manipulative experiments is inherently easier than field based studies (Romanuk *et. al.* 2009). Linholm *et al.* (2009), in their study of zooplankton diversity patterns resulting from annual floods in the Okavango Delta, argued that the form of temporally intermittent disturbance, akin to predation events on mysids, was intermediate. Similarly, Svensson *et al.* (2009) classified infrequent, but large area disturbances as intermediate in their experiments with a marine hard substrate community on the west coast of Sweden. In this study, lower numbers of whales do appear to correspond with decreased mysid abundance, and increased diversity, indicating that when foraging pressure is temporarily released, it permits the greatest number of species to coexist. Here I assert that on average gray whale foraging represents a typical intermediate disturbance for prey populations, as the concentrated target area and discontinuous frequency of predation should allow recovery from high mortality events.

Gray whales are opportunistic predators, in terms of prey type, foraging tactics, and geographic range, acting rapidly to take advantage of short-term availability of energy as prey biomass varies (Dunham & Duffus 2001, Moore *et al.* 2003). Gray whales require high concentrations of energy over short time periods in order to gain the necessary 16-30% of their body weight for migration (Nerini 1984, Greenwald 2005). It may be no coincidence that alongside the expanding population of gray whales, amphipod prey biomass in the Chirikov Basin area of the Bering Sea declined nearly 50% over a 17-year period between 1986 and 2003 (Coyle *et al.* 2007). While the ultimate cause for the decrease in prey productivity has been the subject of some debate (*c.f.* Moore *et al.* 2003, Grebmeier *et al.* 2006), the impact of gray whale predation over a constrained area implicates the power of top down control in altering marine invertebrate communities (Kim & Oliver 1985, Highsmith & Coyle 1992, Coyle *et al.* 2007).

Conclusion

Revisiting Hutchinson's (1959) original question, "why so many species?" reflects on the equilibrium paradigm in community ecology, where ecosystem stability persists through reinforcing mechanisms such as resource partitioning and predictable successional stages (Lindeman 1942, Watt 1947, Schoener 1974). Connell's (1978) work on disturbance and diversity, alternatively suggests that unpredictable external forces will disrupt any temporary equilibrium state, ultimately confounding the forecasted competitive elimination of inferior species. This debate has provoked numerous studies that seek to characterize the mechanisms of stable communities and define the components of disturbance (Huston 1979, Herbert & Crease 1980, Gaedeke & Sommer 1986, Huisman & Weissing 1999, Gray 2000, Crawley 2004, Fox 2007, Lindholm *et al.* 2009, Svensson *et al.* 2009). Although often difficult to isolate in the field, many studies, including this one, support the idea that regular intermediate level disturbances act to reinforce and maintain species diversity (Gaedeke & Sommer 1986, Scheffer *et al.* 2003, Svensson *et al.* 2009).

In this study, I argue that seasonal gray whale predation is an intermediate level disturbance to mysid prey populations and community structure. I test the hypothesis that gray whale foraging alters the mysid community by decreasing dominance and increasing species diversity of mysids. This relationship is confirmed by correlating Simpson diversity, measured from species taken over seven years of sampling in Clayoquot Sound, B.C., to the seasonal abundance of foraging whales. The analysis suggests that over the last two decades, foraging pressure has reduced the dominance of one species *H. sculpta,* resulting in a significant increase in the local mysid species diversity over the period 1996 - 2008. This response corresponds with Connell's (1978) intermediate disturbance hypothesis, and results of other studies (Svenson *et al.* 2009, Lindholm *et al.* 2009), which suggest that disturbance regimes that infrequently affect large areas, should display higher species richness. Although there are inherent limitations to conclusions drawn from field experiments, this long-term study presents evidence of a shift in the community dynamics of mysid zooplankton, an important trophic link in aquatic food webs of the coastal zone (Mauchline 1980, Kathman 1986, Albertsson 2004, Gorokhova & Lehtiniemi 2007).

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Chapter Six: Differences in Embryo Production Between Sympatric Species of Mysids (Family *Mysidae*) in the Shallow Coastal Waters Off Vancouver Island, B.C.

Abstract

Gray whales (*Eschrischtius robustus*) foraging in Clayoquot Sound, B.C. feed predominantly on epibenthic mysids (*Mysidae*). As gray whale predation diminishes local mysid populations, their reproductive capacity is key to their resiliency. However, little is known about the life history of the ten or more species of mysids found in Clayoquot Sound. Usually one species, *Holmesmysis sculpta*, dominates multi-species swarms, but patterns of dominance have shifted in relationship to the varying levels of foraging pressure by summering gray whales. There are several potential routes by which *H. sculpta* out-competes other species, one of which is higher embryo production. Samples were collected on five surveys between June and September of 2008. Mysids were identified to species, gravid females were removed, and embryos counted for each individual in the sample. I counted the number of embryos per brood of the three most commonly found species, *H. sculpta, Neomysis rayi* and *Exacanthomysis davisi*. Embryo numbers were found to vary significantly between the species, however, length is a stronger factor in embryo production. Here I report previously unknown life history attributes of coastal mysid species, with important consequences for community structure and local marine food webs.

Introduction

In marine ecosystems, plankton are the trophic foundation that supports higher animal life (Durbin *et al.* 2003, Choi *et al.* 2004). Zooplankton from the Euphausiacea and Mysidacea play key roles in marine food webs and are important prey for a variety of marine animals, including sea birds, predatory fish and whales. Mysids or "opossum shrimp," are a cosmopolitan order, encompassing 780 species, 48 in the northeast Pacific Ocean, and 23 along the coast of British Columbia (Kathman *et al.* 1986). Mysids aggregate in order to avoid predators and mate, forming swarms that are patchily distributed (O'Brien & Ritz 1988). In the shallow coastal waters of Clayoquot Sound, polyspecific swarms are found just above rocky reef structures, where mysids can take advantage of the hydrodynamic aspects of rugose substrates in the strong tidal bores (Clutter 1969). The swarming behaviour of mysids imparts protection against small hunt and peck type predators, but creates an easy foraging target for coastal gray whales (*Eschrichtius robustus*) (O'Brien & Ritz 1988).

Gray whales typically feed on benthic prey in the Arctic seas, in addition to a variety of coastal plankton and invertebrates, in coastal areas from California to Alaska (Oliver & Slattery 1985, Kim & Oliver 1989, Dunham & Duffus 2001, 2002, Newell & Cowles 2006, Stelle *et al.* 2008). In the last decade, gray whales foraging in Clayoquot Sound have focused primarily on hyper-benthic mysids (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002). Any number of gray whales appearing during the summer has strong impacts on the size and abundance of mysid swarms. However, the timing and extent of mysid's early spring and summer reproductive events may determine the annual level of gray whale foraging in Clayoquot Sound. The timing and extent of whale predation on mysids influences their population in the following year. Mysids' reproductive capacity is known to vary considerably both between species and age/size classes (Johnston & Northcote 1989, Jones *et al.* 1989, Fenton 1994, Mees *et al.* 1994). The length of incubation and number of embryos per brood has significant implications for population dynamics and predator-prey interactions.

The patterns of reproduction in mysids varies between and within species at different latitudes. Although the generation time for one common species *Holmesmysis sculpta* is known to be approximately six weeks, the generation interval for the remaining species considered here have not been documented. Mauchline (1980) recognizes that the life history of any one species of mysid may be typified as either: (1) species requiring more than two years to achieve sexual maturity, producing one generation; (2) species that reach sexual maturity at two years, producing one generation; (3) a species that produces one generation per year; (4) a species that produces two generations per year; (5) a species that produces three generations per year; or (6) a species that produces more than three generations per year.

At sexual maturity, mysids produce relatively small numbers of juveniles from embryos that are brooded in a pouch developed on the female's abdomen, formed by an overlapping of the lamellae or oostegites on the thoracic legs. The young pass through three stages: fertilized eggs, eyeless young and eyed young, until they are fully developed and ready for release, having a larval mortality of approximately 10% over the entire period of marsupial development (Mauchline 1980, Wittmann 1984). Green (1970), who studied a breeding aggregation of *Holmesmysis sculpta* at Botanical Beach, B.C., found that the time between fertilization of the eggs and release of the young, took five to six days. Incubation periods for other species of mysids range from four to over 300 days (Mauchline 1980). Juveniles moult almost immediately and begin life within the natal swarm, generating increasingly large shoals composed of several cohorts.

The time to sexual maturity ranges from approximately six weeks to over two years, dependent on the size of the female, water temperature, seasonality and species (Green 1970, Mauchline 1980, Wittmann 1984, Johnston & Northcote 1989, Adare & Lasenby 1994, Turpen *et al.* 1994, Johnston *et al.* 1997, Garnacho *et al.* 2001, Fockedy *et al.* 2006). In the temperate waters of British Columbia, mysid species are thought to be iteroparous, breeding year round with peak reproduction taking place during the warmer months of the year (Mauchline 1980, Wittmann 1984).

Many life history attributes are common among mysids, though few researchers have focused specifically on the marine species found in the Pacific Northwest (Banner 1948, Green 1970, Kathman 1986, Stelle 2001, Patterson 2004). Over the past twelve years *H. sculpta* is typically the dominant species in several sites in the Pacific Northwest. However, twelve other mysids have been identified locally including: *Neomysis rayi, Columbiaemaysis ignota, Acanthomysis columbiae, Alienacanthomysis* *macropsis, Acanthomysis borealis, Disacanthomysis dybowskii, Exacanthomysis davisi, Eucopia unguiculata, Neomysis kadiakensis, Proneomysis wailesi, Holmesimysis nuda* and *Neomysis mercedis* (Stelle 2001, Dunham & Duffus 2002, Patterson 2004, Maud 2008).

Here I focus on six mysid species commonly found in Clayoquot Sound (Fig. 1). I compare the average brood size of *H. sculpta, N. rayi, E. davisi, C. ignota,* and *A. columbiae,* to assess whether reproductive capacity, in terms of average number of embryos, varies by species or body length. A difference in reproductive output between species could contribute, alone or in consequence, to *H. sculpta's* dominance. If mysids survive the gray whale summer foraging season, they have the opportunity to grow over winter and produce larger broods in the spring and summer. These differences have implications for trends in species diversity as well as overall abundance in the face of whale predation.

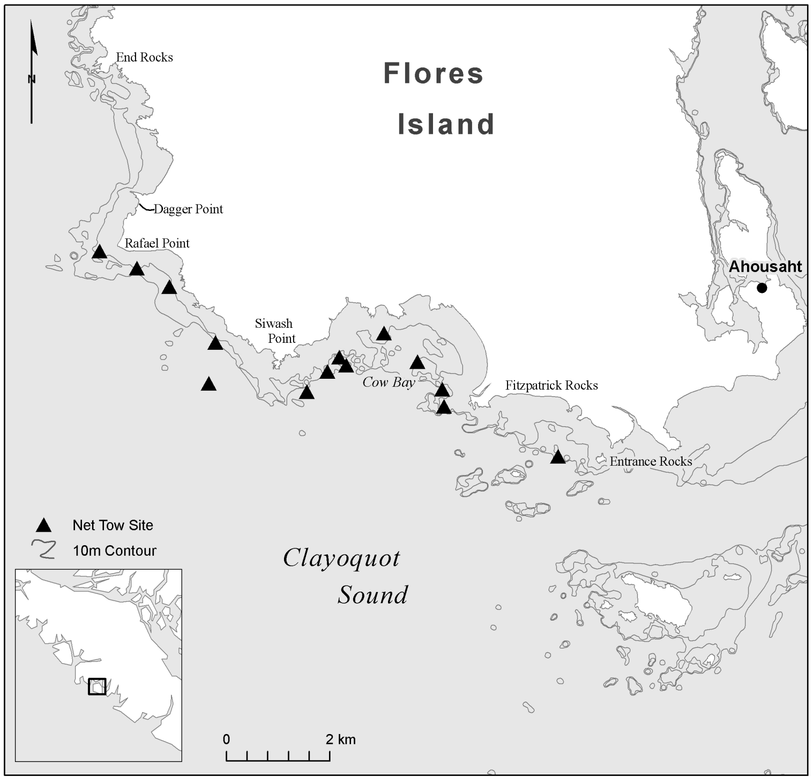

Figure 1. The study area and sampling stations off the coast of Flores Island, B.C. located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W.

Methods

Mysid Sampling

Mysids were collected between June and August, 2008, either from stations selected randomly within areas of known mysid habitat (Dunham & Duffus 2002, Nelson *et al.* 2008), or from sites in the vicinity of foraging whales. Sampling occurred approximately every two weeks, weather permitting. Mysids were captured with a bongo style net with two 30 cm openings and 500 μm mesh, which was allowed to sink to the bottom, dragged for at least 15 seconds and then pulled straight to the surface at each site. If the net contained few or no mysids, the procedure was repeated up to three times before moving to another sampling location. In order to mitigate the shifting distribution of species and life stages within mysid aggregations, multiple tows taken at the same site on the same day were combined on board the vessel. There was no significant relationship between number of replicates where mysids were found and the total number of mysids collected in a survey (Pearson's r = 0.39, N = 7, P = 0.38).

The data used in this study were collected from 14 stations in the area (Fig. 1), during 5 surveys, consisting of over 30 hours of sampling effort. For the purpose of this analysis, stations were pooled by survey date across the entire area.

Mysids were preserved in 70 % ethanol for identification and all mysids in a sample were enumerated. Samples contained anywhere between 20 – 2500 animals. Individuals were identified to species, sexed and measured, according to Kathmann *et al*. (1986) using a 40x dissecting microscope. Gravid females, identified by the presence of the brood pouch, were separated from the larger sample. Each brood pouch was emptied and the number of embryos, regardless of developmental stage, were counted and recorded. Over the course of sampling 32 net tows actually contained mysids, of which 7,861 were identified to species, and 444 were identified as gravid.

The number of embryos per brood is normally distributed (Z = 1.2, n = 444, P = 0.1), however, mysid body length is bimodal and not normal (Z = 3.8, n= 444, P = 0.000). As a result Spearman's rho is used to measure the correlation between brood size and length. Due to inadequate sample sizes for *A. Columbiae*, only the differences between *N. rayi*, *H. sculpta*, *E. davisi, and* C. *ignota* are compared. A non-parametric Kruskal-Wallis test is used to assess differences in brood size as there are an uneven number of individuals from each species in the sample.

Results

Out of 444 mysids examined, *N. rayi* had the largest average brood size of 56.9 (SD=17.4), with one individual having 140 embryos. *E. davisi* had the minimum brood size of seven embryos, and the smallest average brood size of 27 (SD =13.4) (Fig. 2). The maximum brood for *H. sculpta* contained 68 embryos, nearly half of *N. rayi*'s maximum (Table 1).

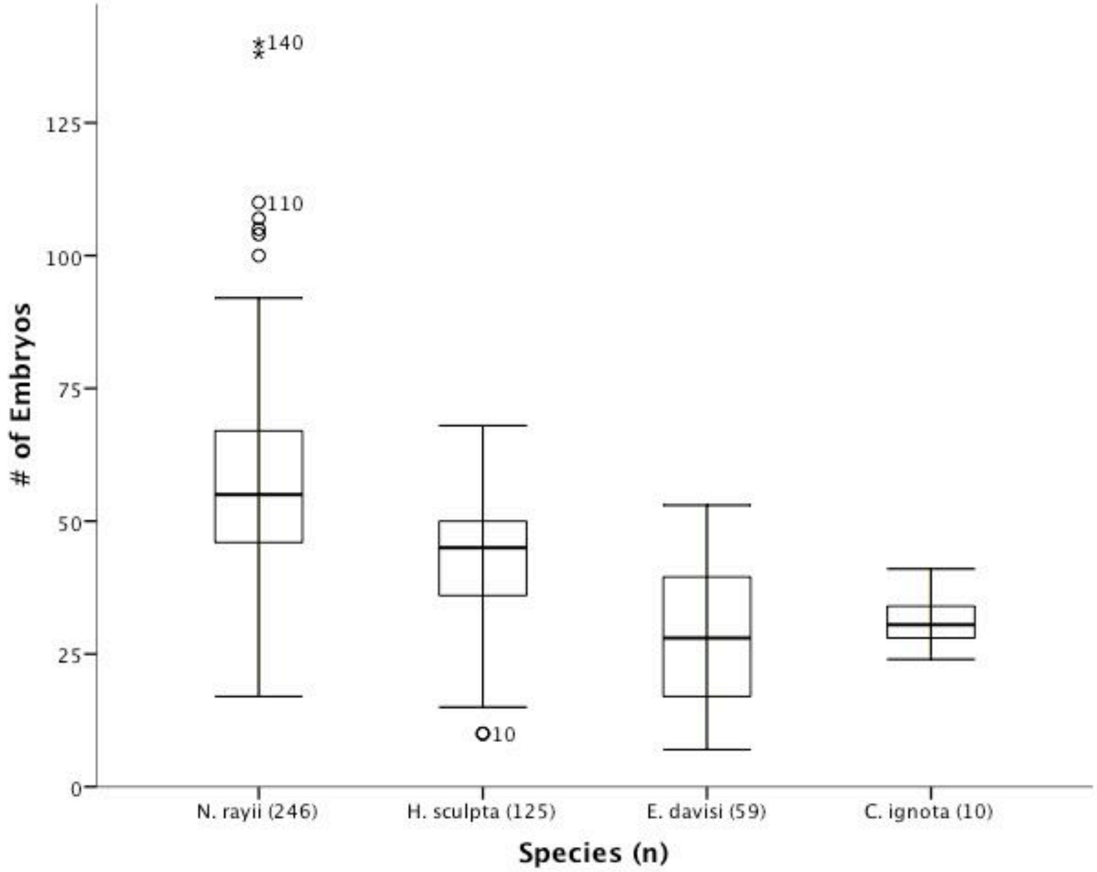

Figure 2. Boxplot of the average number of embryos, interquartile range and outlier brood sizes found in four species of mysids. Cases are labeled by brood size.

When the number of embryos between gravid *N. rayi*, *H. sculpta, E. davisi* and *C. ignota* is compared, there is a significant difference (χ^2 = 157.3, n = 440, df = 3, P =

0.000). The relationship between reproductive output and species loses significance when controlling for the effect of body length (r = 0.05, df = 427, P = 0.38).

The maximum length for any gravid female is 35mm (*N. rayi*) and the minimum length is six mm (*E. davisi*). *N. rayi* has the highest mean length of 23mm (SD=4.6) while *E. davisi* has the smallest mean length 9.5mm (SD=1.3) (Fig. 3).

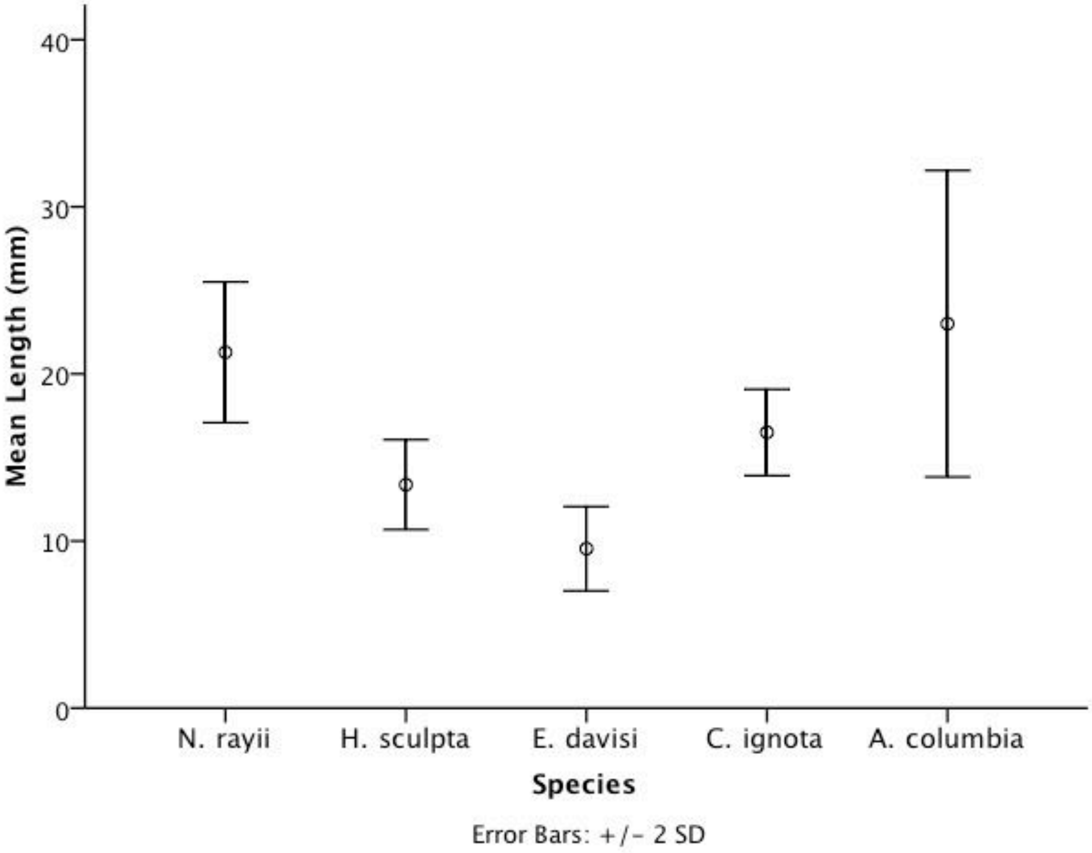

Figure 3. Average length of gravid mysids by species.

There is a significant positive relationship between gravid female length and number of embryos per brood (Spearman's rho = 0.59, df = 444, P = 0.000) (Fig. 4). The relationship between length and reproductive output remains significant while controlling for the effect of species using a partial correlation (Partial Corr = 0.35, df = 427, P = 0.000) and when species are considered individually: *N. rayi* (Spearman's rho = 0.25, n = 246, P = 0.000), *H. sculpta* (Spearman's rho = 0.29, n = 125, P = 0.001), and *E. davisi* (Spearman's rho = 0.46, n = 59, P = 0.000).

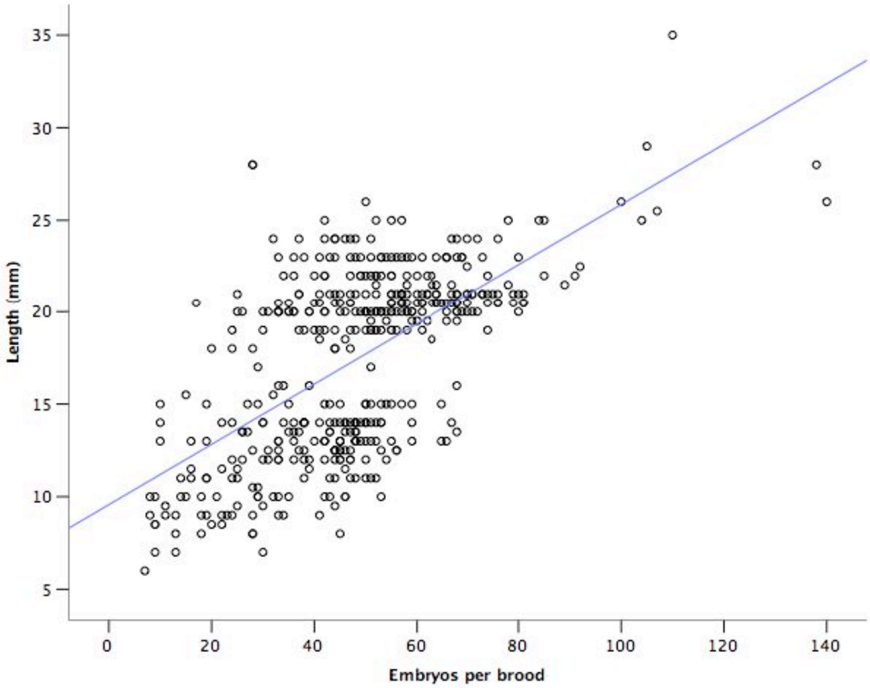

Figure 4. The relationship between body length and brood size for all species

Discussion

In this study I asked whether brood size varied between sympatric species of mysids. I also tested the overall relationship between body length and brood size. Although six species of gravid females were identified, only three were found in adequate numbers to statistically compare embryo production. The brood size of *H. sculpta, N. rayi,* and *E. Davisi* is significantly different. However, this difference disappears when considering the relationship between embryo production and body length, as there was a significant positive relationship between body length and brood size across species.

Similar to Jones *et al.* (1989) and Stelle (2001), here, gravid mysids have a wide range of body lengths and number of embryos per brood, reflecting considerable variation in reproductive output between and within species. Average *E. davisi* body length is substantially smaller than previously documented, as small as 6 mm, corresponding to significantly smaller brood sizes than either *H. sculpta* or *N. rayi.. C. ignota* is longer on average (16.5 mm) than *H. sculpta* (13.3 mm)*,* while average brood size is smaller. This difference may be an artifact of the smaller sample of gravid *C. ignota* (n= 10). The longest gravid *H. sculpta* is 19 mm and the largest brood contains 68 embryos. This exceeds Green's (1970) previously published record of *H. sculpta* at Botanical Beach, B.C. with length ranging from 10-14 mm and brood size from 5-46, and the largest gravid *H. sculpta* reported by Stelle (2001) at 16mm. Although *H. sculpta's* brood size is greater than previously reported, it was smaller on average than *N. rayi's* brood size. As *N. rayi* is a larger bodied animal, this corresponds to the established relationship between body size and reproductive output (Mauchline 1980). It is worth noting that due to the fragile nature of the specimens and the marsupium, damage and loss of embryos can occur during storage and transport. Green (1970), comments on how eggs can be easily lost from the brood pouch in preserved specimens, as over time, samples inevitably break down. Although care was taken to process and count individuals in a timely manner, the average number of embryos for the species in this analysis may be underestimated.

A range of strategies have been adopted by mysids in order to maintain population size. Here I focused on comparing summer brood sizes, rather than other elements of reproduction occurring year round. *H. sculpta* has typically been the most abundant animal found in the local mysid species complex (Dunham & Duffus 2002, Newell & Cowles 2006). Dominance does not appear to be maintained through larger brood sizes, as length is a stronger factor in embryo production. *N. rayi* has often been sub-dominant in Clayoquot Sound, until 2007, when it was found to outnumber *H. sculpta*, and shift the familiar diversity patterns (Feyrer, Chapter 5). Although *N. rayi* can produce more offspring per brood than *H. sculpta,* other aspects of *N. rayi's* life history, such as time from fertilization to sexual maturity, is unknown. Larger species, such as *N. rayi*, may require more time to reach sexual maturity. Thus, there are a number of other routes by which *H. sculpta* may be able to out reproduce a larger bodied species. Despite these differences, other aspects of reproductive capacity, such as, broods produced per female, cohorts per year or season, age of sexual maturity, or developmental mortality, may explain *H. sculpta's* competitive advantage.

In accord with the range found generally for coastal mysids, the positive relationship between body size and reproductive output is consistent across the mysid species found in Clayoquot Sound, B.C. (Mauchline 1980, Turpen *et al.* 1994, Hanamura 1999, Okumura 2003, Hanamura *et al.* 2008). In a number of species, larger body and brood size has previously been associated with increases in temperature, food availability and age (Mauchline 1980, Fockedy *et al.* 2006).

Regardless of species, however, increasing body size increases brood size. This suggests that peak reproductive capacity may depend on overwinter survival and growth extending into another summer season. Alternatively, increasing the number of smaller cohorts could improve summer recruitment. Considering the impact of summer predation by gray whales, whether the strategy is to produce a single large or several small broods, the timing of reproduction may do more to maintain mysid populations than anything else. As a dense patch of gravid females of any species is a desirable target, heavy predatory disturbance prior to the peak of *H. sculpta's* summer productivity would reduce overall reproductive output and future populations. While the exact nature of *H. sculpta's* specific advantage is unknown, whale foraging reduces the summer reproductive output of all prey species.

Reproduction that occurs in the absence of their primary predator, either prior to the summer foraging season or after the whales leave for the winter may contribute significantly to the recovery of any one species in the mysid community. Crawley (2004) found that the difference in timing of disturbance could have large effects on the biomass, frequency, and relative abundance of coexisting species, as some species succeeded while others were driven close to local extinction by disturbance occurring at the "wrong" time of year. Thus the timing of reproductive events, while not considered as part of this study, could either help to rebuild or extirpate locally depleted mysid populations.

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Epilogue: The Tail of the Tale

The objective of this thesis is to assess the relative influence of bottom up and top down processes that determine the habitat quality for a baleen whale. I approach this question by examining three aspects of the ecological relationship between predator and prey, at different spatial and temporal scales. I begin by testing the relationship between indicators of broad scale ocean productivity, and longer-term patterns in mysid (*Mysidae)* populations reflected by gray whale (*Eschrichtius robustus*) abundance. Moving to a fine scale, I examine the behaviour of individual whales to determine the threshold level of prey required, in either the overall study site, or in the immediate area surrounding the whale, to maintain foraging. Finally, I evaluate the prey response to predation, by connecting shifts in prey species diversity to disturbance by foraging gray whales, and estimate the variation in reproductive capacity of the most common mysid species.

There are some underlying assumptions made throughout the thesis that could not be verified: 1) whales' primary prey, mysids, are linked directly to phytoplankton production; 2) primary production, based on upwelling indices and solar radiance in the study area, indicate phytoplankton, which is an important component of mysid production; and 3) that the spatial distribution and foraging effort of gray whales in this part of their range is dictated by fluctuations in prey.

In Chapter Two, I examine the variability during twelve field seasons (1997-2008) of whale census surveys, prey populations and proxies of annual primary productivity. I evaluate the strength of the relationship between bottom-up productivity, to average whale numbers and mysid density. Year to year variations in spring upwelling and sunshine in the study area were small, and did not correlate to whale foraging observations, or mysid density. Whale foraging effort was, however, highly dependent on mysid density for the five-year period 2004-2008. This suggests that bottom up transfers of broad scale ocean productivity are not as significant as local prey density in determining the abundance of gray whales. In fact, in restricted areas, gray whales may determine prey conditions, ultimately to the point of prey limitation. Persistent differences in productivity (i.e. Nelson *et al.* 2008), at discrete geographical locations may have an effect on community assemblages, including mammalian predators like cetaceans (Menge *et al.* 1997, Croll *et al.*

1998, Benson *et al.* 2002). Whales move in and out of feeding areas, as prey populations fluctuate. Thus, habitat analysis, designation of critical habitat, and management actions, such as protected areas, may require long term ecological data to be effective for this species.

In Chapter Three I look for evidence that the relationship between prey quality and foraging would hold across temporal scales. Between 2006 -2008, I compare prey quality within-season directly to the time budgets of individual whales, and found animals spent more time foraging when overall prey density conditions were high. This relationship corresponds with one aspect of optimality, search efficiency (*sensu* Norberg 1977), and presents an experimental method for determining the baseline patterns of exchange between predator and prey (Duffus 1996). While whales may, in fact, be the best measure of the quality and distribution of underlying prey, these baseline measures are necessary for including additional ecological complexities, and testing the influence of human activities (Kenney *et al.* 1986, Murison & Gaskin 1989, Piatt & Methven 1992, Dunham & Duffus 2001, Croll *et al*. 2005). With the potential of large scale climatic or regime changes occurring in the North Pacific, the stability of the gray whale population depends on their ability to respond to temporal variations across localized areas of high quality foraging habitat (Grebimeir *et al.* 2006).

In Chapter Four I further develop the connection between overall prey quality and whale behaviour, by refining the spatial and temporal assessment of prey density coincident to foraging whales across the 2008 season. I found that coincident prey density was, on average, higher than study area wide estimates, and that whales foraged at sites of higher density. While foraging dives occur coincident to higher prey densities during the first half of the season, this pattern switches as overall prey productivity peaks. This suggests that when overall prey productivity is low, whales respond to finer scale variations in prey density. It may be that whales increase their satiation over the course of a foraging season. As prey productivity increases, however, the spatial distinction between areas of high and low density also blur, and searching dives may appear in areas of high density. This may reflect transitional behaviour not captured by the dichotomized behavioural classification, or simply paint a picture of greater underlying productivity blurring the spatial scale of response. As patches of mysids grow and aggregate, overall measures of prey quality may be a better match to the scale of whale foraging decisions. Regardless of behavioural state, coincident prey density never fell below 2,300 mysids/ m^3, presenting an improved estimate of the prey density threshold targeted by foraging whales. A perspective that includes the behavioural interaction between scales, illuminates a distinct predatory strategy, and lends insight to how whales' relationship with their prey aggregates across time and space.

While our understanding of predator prey relationships is often focused on how the prey drive the predator, future conservation of apex species may require an understanding of how foraging animals influence their prey (Fauchald 2009). In Chapter Five I propose that the temporally intermittent nature of gray whale foraging represents an intermediate level disturbance to the species composition of the mysid community (Connell 1978). I assess the community structure and species dominance of mysids across the study area in eight years between 1996 and 2008. *Holmesimysis sculpta* has typically been the dominant mysid species over the last ten year period; however, in 2007, *Neomysis rayi* was significantly more abundant when whale foraging activity in the previous year was high. This study presents evidence that over the last two decades, foraging pressure has reduced the dominance of one species *H. sculpta,* resulting in a significant increase in the local mysid species diversity over the period 1996 - 2008. A shift in the community dynamics of mysid zooplankton, an important trophic link in aquatic food webs of the coastal zone, could have ecological implications for gray whales and other predators (Mauchline 1980, Gorokhova & Lehtiniemi 2007).

A range of strategies have been adopted by mysids in order to maintain population size and dominance in a mixed community. In Chapter Six I compare summer brood sizes, of commonly occurring mysid species. *H. sculpta* has typically been the most abundant animal found in the local mysid species complex (Dunham & Duffus 2002, Newell & Cowles 2006); however, I found that length is a stronger factor in embryo production. Larger species, such as *N. rayi*, may require more time to reach sexual maturity, which suggests that *H. sculpta's* competitive advantage over larger bodied species, may be explained through other aspects of reproductive capacity. Considering the impact of summer predation by gray whales, whether the strategy is to produce a single large or several small broods, the timing of reproduction may do more to maintain mysid populations than anything else. While the exact nature of *H. sculpta's* specific advantage is unknown, whale foraging reduces the summer reproductive output of all prey species.

The interaction between marine mammals and human activities has increased interest in the ecological relationships underlying their distributions. Although acoustic noise from seismic testing, oil and gas exploration, ship collisions, entanglement in fishing gear and habitat alteration, are known threats to gray whales, they regularly occur within the coastal zone (Rugh *et al*. 1999, Baird *et al*. 2002, COSEWIC 2004). Despite these threats, gray whales are considered a conservation success, largely because of their recovery following the cessation of commercial whaling, and were removed from endangered status by American authorities in 1994 (Rugh *et al.* 1999). In Canada gray whales are still listed as a species of 'special concern' under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Rugh *et al*. 1999, Baird *et al*. 2002). Despite the optimism of gray whale conservation, between 1999 and 2000, shortly after delisting occurred in the United States, there was a dramatic increase in the number of mortality events recorded. The cause of death for most animals appeared to be starvation, leading to speculation ranging from whales reaching their population carrying capacity (Moore *et al*. 2001), to broader scale ecosystem changes in their northern feeding grounds (Grebemier *et al*. 2006). Due to the extensive foraging range and opportunistic nature of the animals, testing hypotheses such as these are difficult. Genetic backcasts for the species, have suggested that historic populations in the North Pacific may have been as much as triple their current size (Alter *et al*. 2007). The account of the gray whale 'recovery' illustrates how cetaceans everywhere are returning to ecosystems that have been widely altered and are continuing to transform in the face of ocean regime shifts (Springer et al. 2003, Grebemier *et al*. 2006, Estes 2006, Jackson 2006). A weak appreciation of the interactions between longer periodic cycles in ocean food webs may also compound an uncertain future for ocean ecosystems. What is clear is that optimism should be restrained in forecasting the recovery of endangered species that play a substantial role in ecosystem structure, such as large predators like marine mammals. In addition, conservation and management policies cannot be abandoned in the face of apparent recovery, as ongoing work is required to mitigate the impact of anthropogenic disturbances on gray whales.

Understanding the ecology of an organism is a basic condition for defining effective conservation and management priorities for wildlife and natural ecosystems. Policies that employ an ecological framework should identify the key components of an organism's habitat, and the scale for measuring the quality of those features. Ecological data in the marine environment, however, is often in short supply. Long-term field studies of baleen whales are challenging, in part due to the ability of cetaceans to move with few limitations through ocean space. In addition, the surrounding ecosystem, and an animal's core needs, can vary, sometimes, rapidly over time and space. Thus if improving conservation policies for coastal ecosystems requires integrating long-term ecological data into the management process, then it also requires the political will necessary to support ongoing scientific research, and reassessments of the design of Marine Protected Areas, and species-at-risk recovery plans.

In this thesis I advocate that using fine scale, site-specific, long-term field data can answer the challenge presented by the dynamic nature of marine habitat. By looking at spatial and temporal shifts at both trophic levels, across a series of scales, I identify patterns of natural variability and long-term trends in marine habitat. The long-term trends occurring in one geographic site can indicate the response at larger scales. Such measures are necessary for models that seek to use marine predators as a barometer of broader ecosystem health (Redfern *et al.* 2006, Moore & Huntington 2008). This method may be most useful for a coastal species, where logistics of a long-term field study are more feasible. With additional support, this method may yet be applied to other wide-ranging species in marine environments.

Over the course of this project I explored and integrated some new techniques, including an adapted hydro acoustic method for measuring mysid zooplankton (Olsen 2006). Although the method was not specifically an aspect of this study, it was a novel application of acoustic technology to measure mysids in shallow waters. Analysis of the survey results required verification based on field experience, extensive ground truthing, and familiarity with the biology and behaviour of mysids. Having adapted these methods from previous studies (Olsen 2006), I estimate that these are conservative measures of the density of mysids in this region. This study is also unique in demonstrating an application of acoustic technology to quantify mysids in the presence of foraging gray whales.

It should be acknowledged that as with all field experiments, there are limitations to any absolute conclusions. The challenges faced in this study were largely overcome; however, conclusions should be considered in light of the sample size, inherent noise in ecological data, and confounding linkages to whale habitat outside the immediate study area. Technical issues in data collection were minimal; in most cases data loss was due to inclement weather. Analysis error was reduced through redundancy, backups of survey information, and single handedly processing all data to reduce operator error. While Mae West was famous for saying, "Too much of a good thing can be wonderful", here a major consideration was the assembly and organization of almost too much data, required in documenting a long-term study of baleen whale ecology. That said, a more detailed investigation at other sites or in future years, may uncover complexities that further describe the dynamic lives of gray whales.

In focusing on the interactive process of predator-prey relationships, I found that gray whales are both dependent on and influential in engineering the underlying prey communities in Clayoquot Sound. I present evidence of threshold foraging requirements for gray whales and investigate the synecological implications of predation for mysids. Linking environmental conditions to local processes, the behavioural response and requirements of gray whales to environmental variation, and implications of predation for prey communities provides an ecological appreciation of the key components of habitat and scale, for a marine predator. These experiments reinforce what Lewontin (1991) most eloquently and simply put; “Organisms do not experience environments. They create them.”

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