Small – Scale Distributions and Dynamics of the Mysid Prey of Gray Whales (*Eschrictius robustus*) in Clayoquot Sound, British Columbia, Canada.

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ABSTRACT

Gray whales foraging in Clayoquot Sound, British Columbia, Canada exploit a variety of prey items. Hyperbenthic mysids are presently the main prey item of gray whales in Clayoquot Sound and have been under intense predation pressure by gray whales for several years. Little is known concerning their distributions and reproductive strategies on temporal and spatial scales finer than seasons and continents.

A comparison of the species and life stage composition of the mysid community within Clayoquot Sound based on data collected from net samples showed non random distribution of these parameters. Between – year comparisons showed differences in mysid reproduction and whale predation. These results are discussed within the context of whale distributions in the study area and physical oceanographic determinants.

Median mysid body length and the proportion of gravid females were greater in aggregations predated upon by gray whales however, while the difference in median mysid body length was statistically significant at the 0.05 level, the difference in gravid females was not ($p=0.068$). As gravid females tend to be longest, this statistically insignificant result likely has biological consequences pertaining to recovery of heavily utilized mysid populations.

The third part of this study centers on footage taken with an underwater video camera. Video footage enabled a qualitative assessment of mysid aggregations and allowed a true indication of mysid absence. Mysid habitat that had supported large populations of mysids in previous years was virtually empty during the 2000 season.

Baleen whales have the capability to depress prey populations below a useful density. The results of this study suggest that baleen whales may also be capable of inhibiting recovery of prey populations and render previously used feeding habitat temporarily unusable. Interactions with other factors, such as unusual algal blooms, pose a potential route by which a lower stable state could be achieved, thus rendering habitat unusable for prolonged periods of time.

Examiners:

TABLE OF CONTENTS

Appendices

LIST OF TABLES

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

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GENERAL INTRODUCTION

Gray whales (*Eschrictius robustus*) of the eastern Pacific Ocean are one of the better understood cetacean populations as a result of whaling interest in historical times and recent interests in population monitoring, conservation, coastal ecology and the growing popularity of marine mammal observation by tourists. The numbers of gray whales in the eastern Pacific have oscillated considerably since the 1850s because of short periods of intensive whaling effort that left the population so low that hunting was no longer cost-effective, followed by a cessation in whaling enabling some time for recovery. An historical estimate of the population is approximately 30,000 animals in the early 1850s reduced to 8,000 to 10,000 by the mid 1870s, at which time there was a reprieve in whaling effort, however the partially recovered numbers were further reduced to a handful of hundreds between 1920 and 1930 (Moore *et al.*, 2003).

Factors such as the development of the petrochemical industry and widespread public concern for the status of declining cetacean populations worldwide have facilitated a change in the interest in cetaceans from one focused solely on utilitarian and economic ends to one focused more on an understanding of the ecology and life history of cetaceans with conservation in mind (Duffus, 1988). Economic factors continue to represent a significant component of the interest in gray whales in the eastern Pacific- the last few decades have seen considerable growth in the whale - watching industry. This has raised concerns about the impacts of human behaviour in the presence of whales and has necessitated greater understanding of the specific habitat requirements of whales in order to ensure that the animals who live in areas where whale watching tours are conducted are not negatively impacted by their unwitting participation in a multimillion dollar industry (Duffus, 1988; Duffus & Dearden, 1990, 1992; Duffus & Wipond, 1992).

Recently there has been renewed interest in small - scale whaling by coastal indigenous peoples in western North America; the Makah Nation of Washington State exercised their treaty rights in 2000 by taking one of a possible five animals in that year. While no other First Nation has whaling rights specifically guaranteed in treaty there are numerous First Nations who are in the process of treaty negotiations and have expressed interest in small scale 'cultural' whaling. Successful management of such harvest requires an understanding of the ecology of eastern Pacific gray whales both as a whole population and on a finer scale at various locations along the western coast of North America.

Natural History of the Gray Whale

Gray whales undertake an annual migration between warm water breeding and calving lagoons in Baja California and high-productivity feeding grounds as far north as the Bering and Chukchi Seas (Rice & Wolman, 1971). These feeding grounds have historically been divided into primary, secondary and tertiary areas; the primary grounds comprise the southern Chukchi and northern Bering Seas, the secondary grounds the southeastern Bering Sea and the tertiary grounds being the area between southern Alaska and Baja California

(Kim & Oliver, 1989). The whales feed from May to October, head south to arrive in Baja in January, remain there until March and then return to the northern feeding areas (Pike, 1962; Rice & Wolman, 1971). Recently it has become apparent that the entire population does not complete the northward migration and that small groups of individual animals return to sections of the tertiary feeding grounds from year to year (Calambokidis & Quan, 1997); Clayoquot Sound, located along the coast of Vancouver Island, British Columbia, Canada, is one such location (Malcolm, 1997). It has been postulated that the increase in observations of gray whales feeding primarily in areas previously considered 'tertiary' may be in part due to a combination of the recovery of the population to near carrying capacity and that the primary and secondary feeding grounds have had lower productivity in recent years and do not contain enough food to meet current demand (Le Boeuf *et al.*, 2000). Moore *et al.* (2003) suggested that hydrographic changes in the region resulting from the Pacific Decadal Oscillation may be responsible for a lowering of available amphipod biomass in the Chirikov Basin in the northern Bering Sea. Such a reduction in productivity, coupled with heavier predation pressure by gray whales, could result in a discrepancy between demand and supply that Moore *et al.* feel would be met through an expansion of foraging range. Regardless of when or how it came about that some animals use the 'tertiary' feeding grounds almost exclusively, the importance of these areas to these whales is lost in the current classification.

Gray Whale Feeding Ecology

A wide variety of prey items are used by gray whales throughout their feeding range. Famed for being benthic foragers, these whales are known to have a significant effect on the community structure of the benthos in areas that support beds of tube-dwelling *Ampelisca* amphipods, the major prey item found in the primary and secondary foraging grounds (Oliver & Slattery, 1985; Oliver *et al.*, 1984; Nerini & Oliver, 1983). Gray whales are also known to prey upon ghost shrimp, a large benthic infaunal decapod of the genus *Calianassa* (Weitkamp *et al.*, 1992; Dunham & Duffus 2001, 2002).

Far from being exclusively bottom feeders, gray whales also exploit swarming hyperbenthic (occupying the water layer adjacent to the sea bottom- Mauchline, 1980) mysids (Dunham & Duffus, 2001, 2002; Stelle, 2001; Kim & Oliver, 1989), hyperbenthic cumaceans and shrimp (Kim & Oliver, 1989) and have been observed feeding throughout the water column, including at the surface, on porcelain crab larvae (Dunham & Duffus, 2001, 2002). This plasticity in diet is thought to have originated during periods in history when sea levels in the primary feeding grounds were very low. Amphipod beds became inaccessible to whales, thus necessitating the use of other prey items (Kim & Oliver, 1989). Swarming hyperbenthic mysids remain a significant component of the diet of gray whales in the primary and secondary feeding areas (Kim & Oliver, 1989) and are the primary prey item consumed by whales feeding in coastal waters off Vancouver Island (Dunham & Duffus, 2001, 2002; Stelle, 2001).

Gray Whales and Their Prey in Clayoquot Sound

Studies undertaken in Clayoquot Sound have shown that the different prey items occur in spatially discrete habitats and that, within a foraging season, gray whales exhibit 'prey switching' (Dunham & Duffus, 2002, 2001). In these studies, mysids were the primary prey item consumed until late August, when ampeliscid amphipods had grown to a size that would be retained by baleen and became the target of the whales' foraging efforts (Dunham & Duffus, 2001). Easily caught, prey items such as porcelain crab larvae, which aggregate at or just below the water's surface, and ghost shrimp, which occur in shallow tidal flats, are not always available, but when they are they represent an easily exploited food resource that gray whales will select over mysids or amphipods (Dunham & Duffus, 2001).

Within the last twelve years, the diet of gray whales in Clayoquot has shifted from being primarily ampeliscid amphipods to hyperbenthic mysids. In 1996, very little feeding on amphipods was observed and 1997 was the last year gray whales foraged upon amphipods consistently (Duffus, 1996; Dunham & Duffus, 2001). Gray whale predation upon the amphipod population may have depressed amphipod numbers below a level from which they may recover (Carruthers, 2000). Highsmith and Coyle (1992) suggested that this could occur in the Bering Sea because of the low fecundity and long generation times of ampeliscid amphipods and also suggested that there could be further impediment to recovery caused by colonization of the benthos by other species.

Mysids

The order Mysidacea is a cosmopolitan group of crustaceans. Mysids are found throughout the world and inhabit every aquatic realm- freshwater, marine, estuarine, pelagic, benthic and hyperbenthic from barely subtidal coastline to the abyssal plain (Mauchline, 1980). Their common name, 'opossum shrimp', is derived from the fact that females carry developing larvae in a pouch formed by their oostegites (Kathmann *et al.*, 1986). Males develop elongated fourth pleopods that are used in some species to facilitate transfer of sperm to the female, however in some species the sperm are released directly to the water and make their way to the eggs via water currents caused by the movement of the female's thoracic legs (Mauchline, 1980).

Mysid Reproduction and Development

During development the larvae pass through three visibly distinct phases- fertilized eggs, eyeless larvae and eyed larvae and are then released as free swimming individuals (Mauchline, 1980). Green (1970) reported that in *Acanthomysis sculpta,* the former name of *Holmesimysis sculpta,* time from fertilization to release of the juveniles from the brood pouch was five to six days. Both mating and the release of juveniles occurs at night, presumably this reduces predation risks. The age at which juveniles reach sexual maturity differs between species- it can be as little as six weeks or greater than two years. Slower growth is observed in colder water, yielding fewer generations of larger animals per season. As with many aquatic crustaceans, intersexuality, wherein a combination of gonadal tissues and/or secondary sexual characteristics of both genders are present in a single individual, has been observed in the Mysidacea (Yamashita *et al.*, 2001; Hough *et al.*, 1992). Maximum adult size ranges from barely a centimeter in some pelagic species to nearly 30 centimeters for one abyssal species (Kathmann *et al.*, 1986).

Given the diversity of the habitats and geographical locations in which mysids are found it is not surprising that the timing of reproductive events and fecundity vary both between and within species. Mauchline (1980) reported that the general pattern in temperate marine and estuarine waters is that reproduction may occur throughout the year, however there is an increase in reproductive activity during the summer months. This has been observed in more recent studies of mysid population dynamics (Zouhiri *et al.*, 1998; Turpen *et al.*, 1994; Fenton, 1992; San Vicente & Sorbe, 1993; Carleton & Hamner, 1989; Jones *et al.*, 1989; Johnston & Northcote, 1988; Corey, 1988; Woolridge, 1986; Allen, 1984). Multiple generations may be produced in one summer season (Mauchline, 1980). Fecundity is positively correlated with body size which, in turn, is attributed to ambient water temperature (Johnston & Northcote, 1988; Jones *et al.*, 1989; Astthorsson & Ralph, 1984; Tattersall, 1951). However, it is important to note that a number of these studies also report that the overwintering females are largest and produce the largest broods despite lower ambient water temperatures because they have a longer period of growth and thus achieve a greater length. The large size of the overwintering females may mitigate top – down pressures by giving the population a boost in between seasonal pulses of predation. Turpen *et al.* (1994) single out seasonally variable predation pressure by rockfish upon *Holmesimysis costata* as being the impetus behind the production of consistently large broods over the summer months.

Schools, Swarms and Shoals: The Importance of Not Being Seen

As with many fish and crustaceans, hyperbenthic mysids form densely packed groupings of dozens to thousands of individuals. A school of mysids contains polarized individuals (i.e. facing the same direction), a swarm contains individuals who are not facing the same direction and may be swimming in different directions, and a shoal is a very large group of mysids comprised of many schools and swarms (Clutter, 1969). Each individual school or swarm tends to be made up of individuals of similar body length (O'Brien, 1989). These dense aggregations are patchily distributed.

Aggregation has numerous benefits. There may be decreased risk of predation to the individual because a predator may become confused and be less likely to attack. Furthermore, an attack on a group that can respond to a variety of threat types is less likely to be successful (Ritz *et al.*, 1997; Ritz, 1994; O'Brien & Ritz, 1988). This strategy is ineffective in reducing risks of being eaten by large predators such as gray whales who are able to swallow large groups of individuals before any sense of danger is perceived (Ritz, 1994; Hamner 1988).

Mysids select the substrate over which they reside and are willing to incur significant energetic cost to maintain their position in an area sheltered from predators (Buskey, 1998). There are considerable energy savings to be garnered by aggregating in low flow areas such as in the lee of rocks, boulder piles and macroalgal clumps (Lawrie *et al.*, 1999). These structures may also provide places to hide from rockfish and other predators. Ritz (2000) proposes two advantages to mysids aggregating in larger cohesive groups compared to smaller disorganized groups. Currents are created by so many swimming legs allow individuals to maintain position at a lower metabolic rate and also maximize food capture. Group formation increases the likelihood of finding a mate (Ritz, 1994; Clutter, 1969). However when the resulting juveniles are newly released, social aggregation increases the chance of cannibalism (Ritz, 1994). The benefits of aggregation, as a defense mechanism against predation, outweigh intraspecific competition inherent in dense aggregations.

Diel vertical migration is well known in krill as a strategy to minimize predation risk when individuals are not aggregated during feeding. However Clutter (1969) noted that group cohesion in mysids was reduced at night but not entirely absent, and Carleton and Hamner (1989) did not observe any vertical migration whatsoever. In studying mysids and gray whales on the northern end of Vancouver Island, Stelle (2001) observed no vertical migration either, however sampling was limited to one night of diving. Stelle also makes two valid points concerning the mysids of coastal Vancouver Island: 1) movement of mysid legs likely triggers bioluminescence, thereby creating a nighttime predation risk to be mitigated through swarm preservation, and 2) there appears to be no resource concentration at the water's surface that would encourage mysids to spend time there at night when the risks of predation are reduced.

Mysid Sampling

The antipredator behaviour and patchy distribution of hyperbenthic mysids makes sampling difficult. Net sampling is problematic in that one can never be sure that an empty net is indicative of empty habitat as opposed to simply having missed the patch; the net can miss the patch by a small distance and not give any indication whatsoever of mysid presence. Flow meters cannot give accurate readings for biomass estimates because the horizontal component of the tow profile is small relative to the vertical components; furthermore it is not possible to know how much of the horizontal component was through the patch.

Over even substrates such as sand, a hyperbenthic sled could be used to sample mysids. However, the benthic habitat over which mysids aggregate in Clayoquot Sound is uneven, rocky, turbulent and encrusted with a variety of invertebrates and large algae. A sled is likely to become fouled, killing many organisms while failing to collect the target species.

SCUBA has been employed to sample mysids (Stelle, 2001). The logistics of safely conducting research dives along turbulent coastline in a remote location are daunting but not impossible to overcome. While SCUBA is an effective way to put human observers in a position where they may assess and sample mysid aggregations, it is severely limited by weather and lighting. Mysid habitat is shallow, rocky and turbulent and therefore requires optimal conditions for diving. When one adds omnipresent vessel traffic to the list of considerations, the number of days on which research dives may be conducted decreases rapidly. In other projects in the Clayoquot Sound research program, SCUBA has been used for amphipod sampling (Carruthers, 2000). However, the costs involved in employing the number of appropriately certified divers required to satisfy university regulations were prohibitively expensive for SCUBA to be a primary sampling tool in this study.

Selection by Consumers of Swarming Crustaceans

Mysids can form very large, dense aggregations which represent a great available biomass. Consequently, it is not surprising that they can comprise a considerable (30 to nearly 100%) portion of the diet of a variety of marine predators including *Mobula* rays (Notarbartolo-di-Sciaria, 1988), rockfish (*Sebastes spp.*) (Kathmann *et al.*, 1986), rockhopper penguins (*Eudyptes chrysocome*) (Tremblay & Cherel, 2000), black guillemots (*Cepphus grille*) (Cairns, 1987), oldsquaws (*Clangula hyemalis*) (Johnson, 1982) and Leach's storm petrels (*Oceanodrama leucorhoa*) (Steele & Montevecchi, 1994). It seems intuitive that gravid female mysids could be of particular interest to predators because the developing larvae represent an added nutritional value. Results of a study of krill-consuming seabirds in the Antarctic (Reid *et al.*, 1996) indicated that prey size and reproductive condition are important factors for prey selection, with gravid females being overly represented in stomachs compared to nets. However another paper by some of the same authors using data from the same area (Croxall *et al.*, 1997) suggests that when krill are very readily available it is differences in foraging range and feeding methods that are responsible for segregation in prey selection.

Stelle (2001) reported that gray whale foraging activity was significantly correlated with higher mean mysid body length. Because the distance between individuals in a school or swarm is determined by body length (Ritz, 1994), groups of smaller mysids will contain more individuals per unit volume, however a group of larger mysids will contain more biomass per unit volume. As female mysids tend to be slightly larger than males, the presence of a relatively high number of gravid females in a shoal will bring both the average body length and available biomass up rather than down. It is worth noting that the spacing of gray whale baleen dictates that animals below a certain size will not be retained. Dunham and Duffus (2001) found that gray whale selection of amphipod prey was based on high biomass and a high proportion of amphipods 6mm or longer.

While there is a good deal known about the non – mysid prey of gray whales, little is known about hyperbenthic mysids in general and even less is known about hyperbenthic mysids in Clayoquot Sound. Given that these animals have been the mainstay of the gray whale diet in Clayoquot Sound for several years and because this switch in diet is could be a result of whales having "fished out" the amphipod population, it is important to understand the spatiotemporal distribution, species diversity and reproductive dynamics of mysids and how all of these parameters respond to top – down pressure exerted by repeated and intense seasonal foraging by gray whales.

Through the location of mysids with an underwater video camera, I was able to confidently assess mysid presence and absence and able to categorize swarm characteristics such as density, patchiness and aggregation size. Collection of mysid samples yielded information concerning the proportions of each species and life stage present throughout the season. These data were used both to compare the mysid communities in differing parts of the study area and to correlate to whale foraging from transects in order to determine the nature of the predatory relationships between mysids and whales.

Chapter 2 analyzes the spatial distribution of gray whales and the species and life stages of mysids and includes a comparison between 1999 and 2000 observations. Relationships between the size and reproductive state of mysids and gray whale predation, and potential biological consequences, are discussed in Chapter 3. Chapter 4 explores the spatial distribution and characteristics of mysid aggregations determined via underwater video imaging and the relationships between these characteristics and gray whale predation. Chapter 5 contains a summation and discussion of major findings of this research and suggestions for future research.

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MULTIPLE SCALE SPATIAL AND TEMPORAL DISTRIBUTIONS OF GRAY WHALES AND CHARACTERISTICS OF A POST - DISTURBANCE MYSID COMMUNITY

INTRODUCTION

Eastern Pacific gray whales (*Eschrictius robustus*) are known to exploit a variety of prey types in their various feeding grounds along the northwestern coast of North America. These include benthic infaunal animals such as ampeliscid amphipods (Dunham & Duffus, 2001, 2002; Oliver *et al.*, 1984; Nerini & Oliver, 1983) and ghost shrimp (Dunham & Duffus, 2001, 2002; Weitkamp *et al.*, 1992), pelagic porcelain crab larvae (Dunham & Duffus 2001, 2002) and swarming hyperbenthic crustaceans such as cumaceans and shrimp (Kim and Oliver, 1989) and mysids (Dunham & Duffus, 2001, 2002; Stelle, 2001; Guerrero, 1989; Kim & Oliver, 1989). In the Bering and Chukchi Seas the major prey are Ampeliscid amphipods and hyperbenthic mysids are a significant component of the gray whale diet (Oliver *et al.*, 1984; Kim & Oliver, 1983). However, near the northern (Stelle, 2001) and central western coasts of Vancouver Island (Dunham & Duffus, 2001, 2002) hyperbenthic mysids are the major prey item. Twelve species have been recorded in the diet with *Holmesimysis sculpta* being the dominant species in both locations.

The order Mysidacea is a cosmopolitan group of crustaceans. Its members inhabit every aquatic realm- freshwater, marine, estuarine, pelagic, benthic and hyperbenthic from barely subtidal coastline to the abyssal plain (Mauchline, 1980). Their propensity for forming large dense aggregations (see Clutter, 1969) makes coastal hyperbenthic mysids a readily exploitable prey item. During certain seasons, mysids compose a considerable (30 to nearly 100%) portion of the diet of a variety of marine predators including *Mobula* rays (Notarbartolo-di-Sciaria, 1988), rockfish (*Sebastes spp.*) (Kathmann *et al.*, 1986), rockhopper penguins (*Eudyptes chrysocome*) (Tremblay & Cherel, 2000), black guillemots (*Cepphus grille*) (Cairns, 1987), oldsquaws (*Clangula hyemalis*) (Johnson, 1982) and Leach's storm petrels (*Oceanodrama leucorhoa*) (Steele & Montevecchi, 1994).

Mauchline (1980) reported that, in temperate marine and estuarine waters, mysids generally reproduce throughout the year, with an increase in reproductive activity during the summer. This observation has also been reported in more recent studies focused on mysid population dynamics (Zouhiri *et al.*, 1998; Turpen *et al.*, 1994; Fenton, 1992; San Vicente & Sorbe, 1992; Carleton & Hamner, 1989; Jones *et al.*, 1989; Johnston & Northcote, 1988; Corey, 1988; Woolridge, 1986; Allen, 1984). Stelle (2001) isolated three cohorts of *Holmesimysis sculpta* near northern Vancouver Island during the summers of 1999 and 2000. There is evidence that in some instances mysid aggregations are segregated based on body length (O'Brien, 1989) or lifestage (Stelle, pers. comm.), however the distribution of life stages on a scale more coarse than individual shoals is not yet known. Species composition of aggregations is known to be variable and can exhibit non-random spatial distribution between bays of a kilometer or two in breadth (Stelle, 2001).

Studies undertaken in Clayoquot Sound have shown that ampeliscid amphipods, ghost shrimp, porcelain crab larvae and hyperbenthic mysids occur in spatially discrete habitats and that gray whales exhibit 'prey switching' (Dunham & Duffus, 2001, 2002). Changes in the target prey groups are based on the availability, ease of capture and body size of the prey items (Dunham & Duffus, 2001). Within the last twelve years, the diet of gray whales in Clayoquot has shifted from being composed primarily of ampeliscid amphipods to being composed primarily of hyperbenthic mysids. In 1996, very little feeding upon amphipods was observed and 1997 was the last year gray whales foraged upon amhpipods with any consitency (Duffus, 1996; Dunham & Duffus, 2001). Highsmith and Coyle (1992) outlined the potential for this to occur in the Bering Sea because of the low fecundity and long generation times of ampeliscid amphipods and suggested that there could be further impediment to recovery caused by colonization of the benthos by other species.

Mysids had been under intense predation pressure by gray whales for several years before this study (Duffus, personal communication). The two year period of 1999 and 2000 contained remarkably little whale activity in Clayoquot Sound (Table 1), (this study; Duffus, unpublished data). Data for all years are not available, but 1999 and 2000 had the lowest whale abundance observed in eight years.

Top-down control by marine mammals in nearshore systems has been demonstrated for killer whales (*Orcinus orca*) preying upon sea otters (*Enhydra*

Table 1. Average number of whales per day observed in Clayoquot Sound, British Columbia, Canada between 1997 and 2001. Unpublished data from Duffus.

Year	Average number of whales per day
1997	54
1998	60
1999	40
2000	31
2001	54

lutris) and pinnipeds in Alaska, which resulted in a trophic cascade (Springer *et al.*, 2003). The effect of bottom-feeding by gray whales upon benthic communities in areas that support beds of tube-dwelling *Ampeleisca sp.* amphipods has been an initial colonization of feeding pits by scavengers, followed by a succession to the pre-predation ampeliscid-dominated state (Oliver *et al.*, 1984; Nerini & Oliver, 1983). Although other factors, such as sediment size (Grebmeier *et al.*, 1989) and current flow (Palmer 1988) are likely more important in determining benthic structure, both of these authors concluded that disturbance by predation plays a significant role in shaping these communities. Waterfowl in Lake Erie are known to depress zebra mussel biomass and are responsible for a change in mussel age structure (Petrie & Knapton, 1999). As the key prey item for gray whales in Clayoquot Sound, mysid populations come under intense foraging pressure. The top – down effects on mysid distribution, diversity and reproductive dynamics in this area are not yet known.

The effects of gray whale predation on mysid populations and communities could be a key component in the understanding of gray whale movements and coastal ecology. Obviously, mysid biomass is an important factor in driving whale distributions, however determining mysid biomass was not a goal of this research. Instead, I will determine and compare the spatial distributions of gray whales with those of mysid species and life stages within Clayoquot Sound during two feeding seasons, 1999 and 2000. These seasons follow several years of intense foraging by gray whales upon mysids in Clayoquot Sound and thus provide base line information concerning the nature of depleted mysid populations.

MATERIALS AND METHODS

Study Area

The core of my study area was the outer shore of Flores Island, Clayoquot Sound, British Columbia, Canada (Figure 1). During the 2000 season I was able to collect additional data from Nootka Sound and northwest of Estevan Point (Figure 1). Clayoquot Sound is a focus of ongoing research in to the distributions of gray whales in Clayoquot Sound in the contexts of prey distributions (Dunham & Duffus, 2001, 2002) and whale - watching activities (Bass, 2000; Duffus, 1996).

Collection of Whale Location Data

In order to quantify whale foraging in the study area I conducted weekly transects along a predetermined route that included habitat for pelagic, benthic and epibenthic prey items (Figure 2). Vessel speed during transects was approximately seven knots (13 km/h). Transects were aborted if visibility

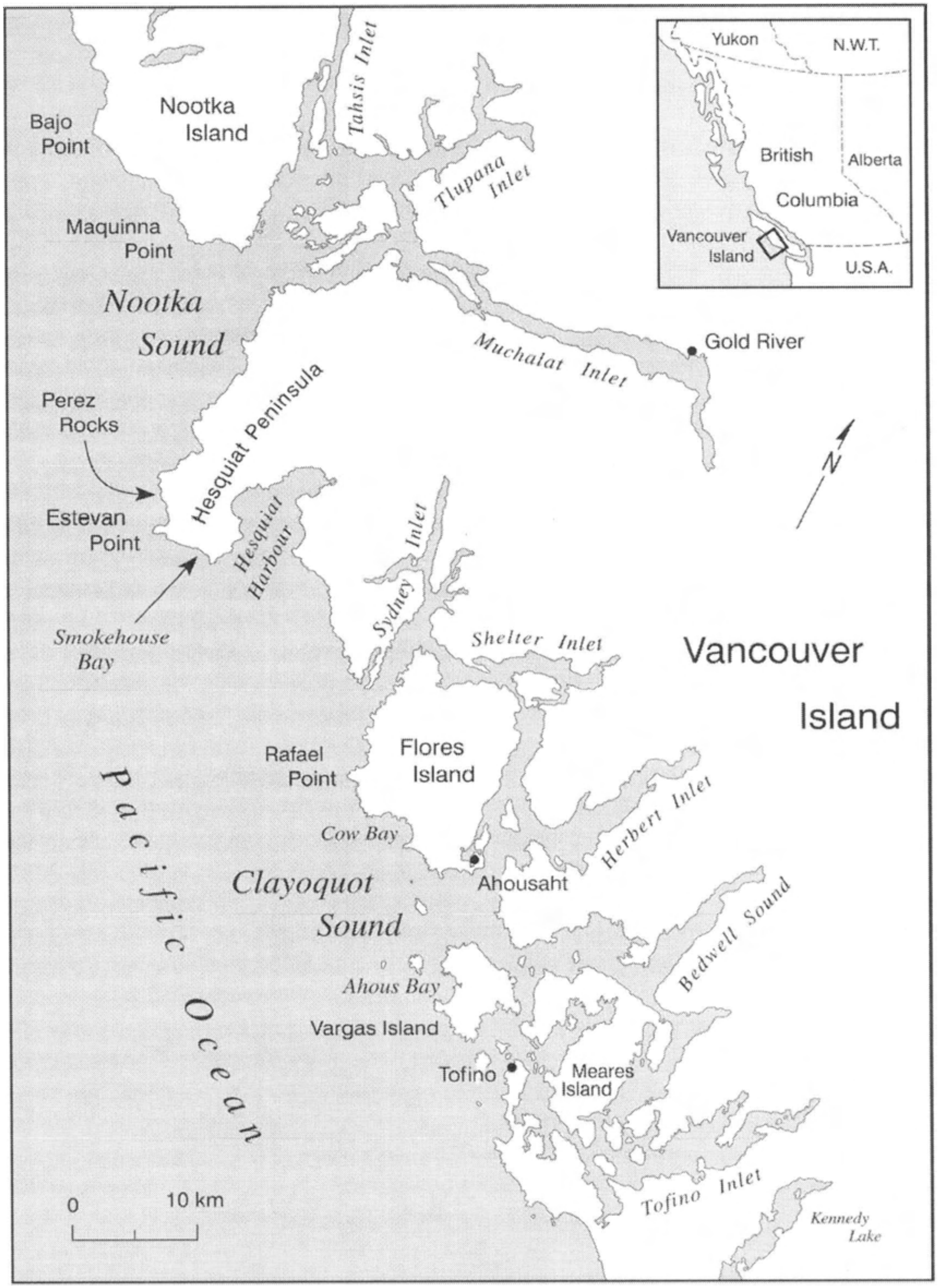

Figure 1. Map showing location of the study area, Clayoquot Sound, British Columbia, Canada.

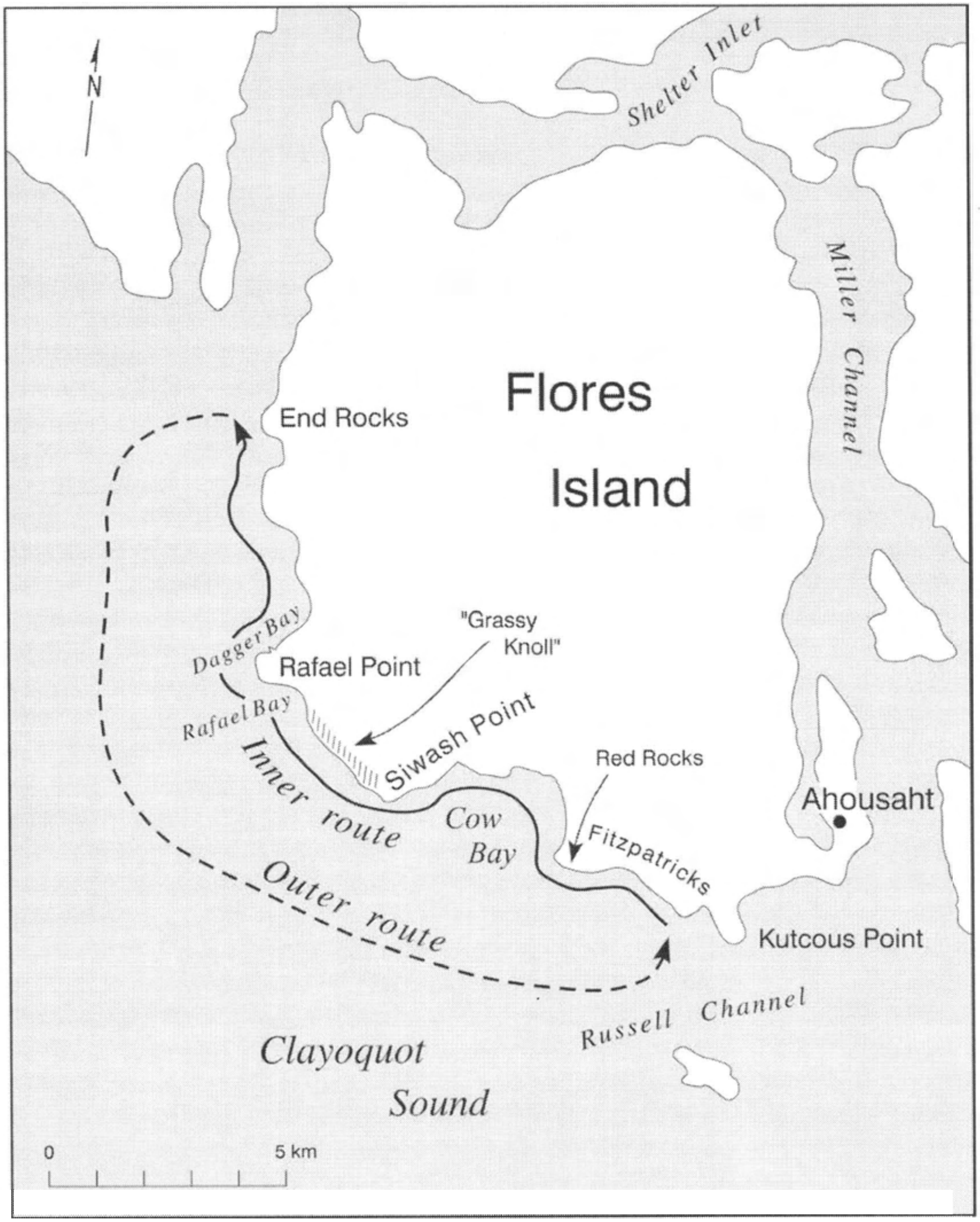

Figure 2. Map showing transect route along the coast of Flores Island.

became compromised by wave height or fog. Whales encountered outside the transect area and during other research activities were also recorded. Whales were determined to be foraging upon mysids by two factors- habitat and whale behaviour. The study area contains discrete habitat patches particular to prey type, the location of these patches are well known (Dunham & Duffus 2001, 2002). Gray whales do not leave a mud-plume when foraging for mysids. Also, the dive times of gray whales foraging upon benthic amphipods are considerably longer than those foraging upon hyperbenthic mysids (Guerrero, 1989).

Three whale variables were constructed. The first was simply the number of foraging whales in the immediate area at the time a mysid tow was conducted. The number of foraging whales encountered within the pre- and proceeding five and ten days, corrected for search effort by dividing the number of days on which full surveys of the study area were conducted, were also calculated for each mysid tow. Five and ten days were used as the time periods because they best suited the temporal scale at which the whale data were collected. Although the goal of weekly transects was generally met, sometimes this was not possible due to weather conditions.

Collection of Mysid Samples

To collect mysids I used a bongo net with two 30 cm openings and 500 µm mesh. Whenever I observed gray whales feeding in mysid habitat I deployed the net at the location of the animal after it had made its final dive of its surfacing run. At times when no foraging whales were encountered I conducted five net tows in randomly selected locations within known mysid habitat (Dunham & Duffus, 2002). In order to be counted as a valid tow, the net had to drag along the bottom for several seconds, otherwise the tow was not included in analyses. As the profile of these tows contains large vertical components and the horizontal component is at varying speeds over uneven benthos, the accuracy of measurements obtained with a flow meter while towing for mysids is unreliable (Dunham, personal communication) and so no such device was employed. In order to mitigate the potential problem of patchy distribution of species and life stages *within* mysid aggregations, multiple tows taken at the same location on the same day were combined.

Enumeration of Mysid Samples

Mysid samples were fixed in a 7% buffered formalin solution and subsequently transferred to 70% ethanol for preservation and analyses. Some samples contained large numbers of mysids. During these instances I examined the whole sample and removed individuals belonging to the rarer taxa in the sample for individual enumeration and then split the remaining homogeneous portion of the sample using a Folsom splitter. Numbers of mysids in enumerated samples ranged from 50 to 500.

Individual mysids were identified and measured using a Bausch and Lomb dissection microscope with 20x eyepieces and an ocular micrometer. Each individual was identified to species according to Kathmann *et al.*, 1986. Elongated fourth pleopods were employed as the indicator of a male and the presence of oostegites as the indicator of a female; if neither were present the animal was counted as a juvenile. When I observed gravid females I noted whether they were carrying eggs, eyed or eyeless larvae and also noted spent females. I used the distance between the anterior tip of the rostrum and the posterior end of the telson to measure total body length in millimeters; as body length was non-normally distributed, median was used as a measure of central tendency. To compensate for the inability to correct for the volume of water sampled, proportions, rather than absolute numbers, of individual mysids of particular species or life stages were calculated. Two indices of species heterogeneity were used. One was simply the number of species observed in a sample. Simpson's index (*D*) was also calculated because it is best employed in communities with a dominant species (Magurran, 1988).

$$D = \sum_{i \to j} p_i^2 = \sum_{i \to j} (n_i/N)^2$$

where *D* represents the probability of any two randomly selected individuals belonging to the same species, p_i represents the proportion of individuals in the *i*th species, *j* represents the total number of species in the study area, n_i represents the number of individuals in the sample belonging to the *i*th species and N represents the total number of individuals in the sample. A large value of *D* indicates a community dominated heavily by one species, a small value of *D* indicates a community whose members are more evenly spread among species.

Statistical Analyses

For the purposes of spatial analyses I divided the study area in to three, six and fourteen areas representing three levels of spatial scale (Figures 3 through 5). Distinctions between areas were made based on patches of habitat, such as rock reefs and kelp beds, and on oceanographic criteria such as divergence and convergence zones (Kopach, 2004). As an example, the coastline of Cow Bay is made up of a number of kelp beds attached to rock reefs. Between these discrete patches of mysid habitat, and throughout the middle of the bay, there are expanses of sand that contain patches of ampeliscid amphipods. The terms "fine", "medium" and "coarse" applied to the three spatial scales are relative within this study only. These areas were used as groups to determine random or non - random distribution of whales and mysid parameters; all tows taken within the same area on the same day were aggregated. Because many variables were non - normally distributed (Table 2), had non-homogenous variances (Table 3) and because sample sizes were small and uneven (Tables 4 through 6), Kruskal-Wallis tests with pairwise Mann-Whitney post-hoc tests, treating areas as groups, were employed as a non - parametric alternative to ANOVA (Sokal & Rohlf, 1973). All statistical analyses were conducted with SPSS 11.0 for Windows. Mapping was done using ArcView 3.1 GIS software.

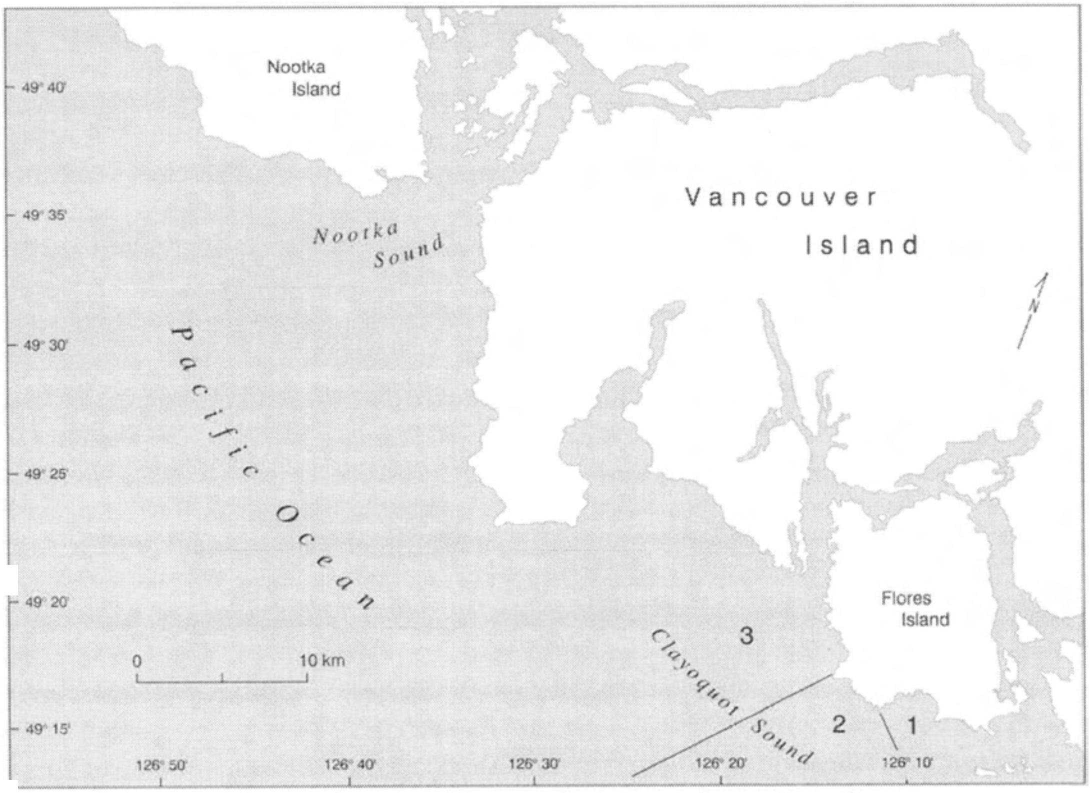

Figure 3. Map of the study area showing divisions of coarse scale areas.

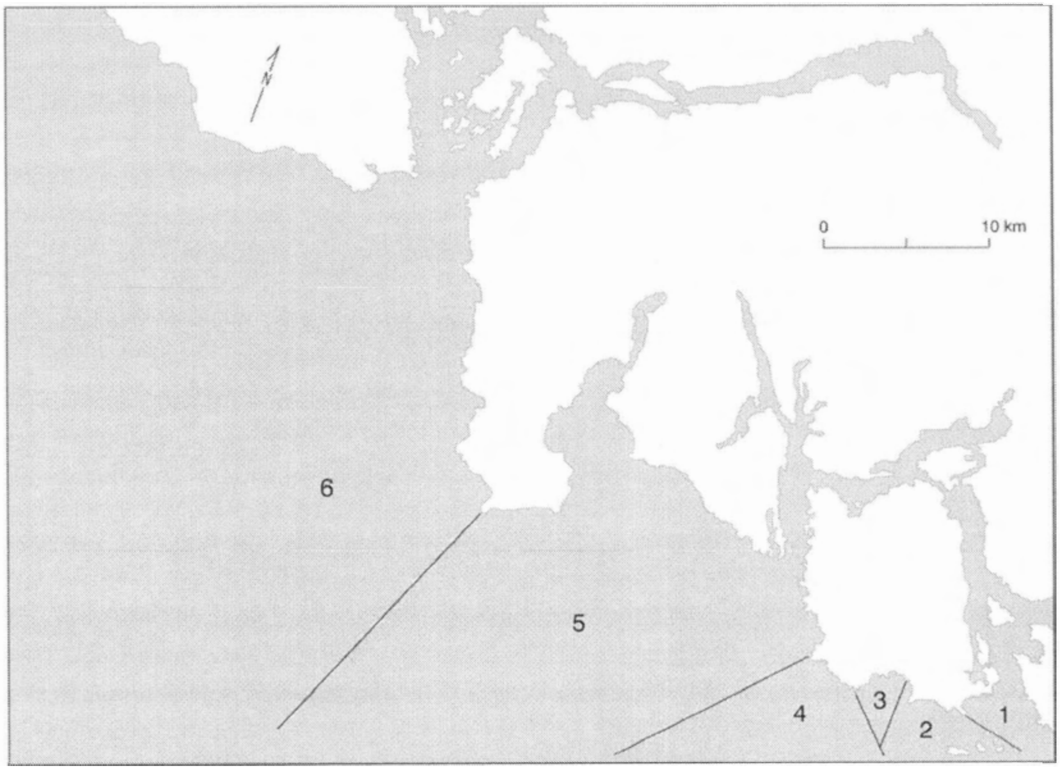

Figure 4. Map of the study area showing divisions of medium scale areas.

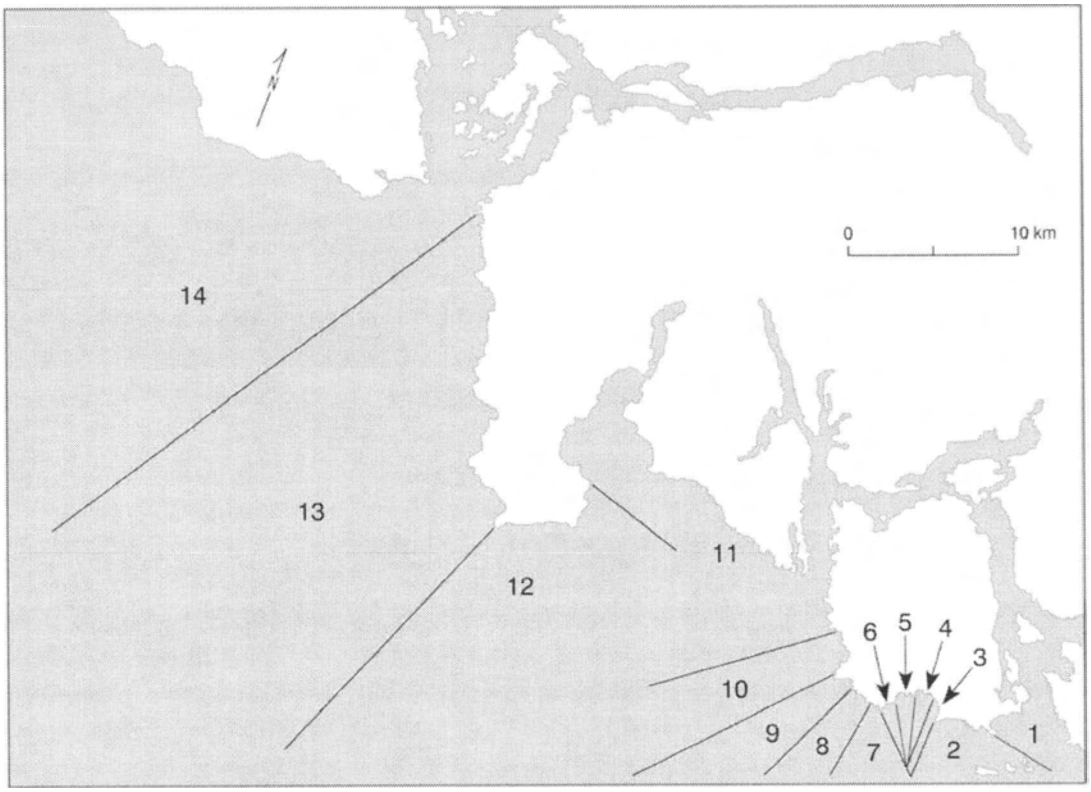

Figure 5. Map of the study area showing divisions of fine scale areas.

Table 2. Results of one-sample Kolmogorov-Smirnov tests to determine normality of mysid characteristic and whale foraging variables. D = most extreme difference.

		Fine Scale	Medium Scale	Coarse Scale
Median body length	D	0.134	0.141	0.166
	p	0.611	0.610	0.446
% Gravid	D	0.206	0.197	0.190
	p	0.120	0.195	0.262
% Juvenile	D	0.212	0.211	0.233
	p	0.102	0.140	0.096
% Male	D	0.115	0.120	0.139
	p	0.776	0.781	0.654
% Female	D	0.117	0.148	0.158
	p	0.754	0.525	0.491
% Gravid / % Female	D	0.112	0.143	0.155
	p	0.843	0.617	0.562
Female : Male	D	0.213	0.223	0.236
	p	0.120	0.113	0.100
Number of species observed	D	0.207	0.231	0.248
	p	0.130	0.091	0.072
% *Holmesimysis sculpta*	D	0.292	0.279	0.261
	p	0.009	0.022	0.050
% *Neomysis rayi*	D	0.295	0.298	0.313
	p	0.008	0.012	0.010
% *Columbiaemysis ignota*	D	0.402	0.438	0.456
	p	0.000	0.000	0.000
% *Disacanthomysis dybowskii*	D	0.523	0.521	0.519
	p	0.000	0.000	0.000
% *Acanthomysis columbiae*	D	0.427	0.423	0.419
	p	0.000	0.000	0.000
% *Alienacanthomysis macropsis*	D	0.462	0.457	0.455
	p	0.000	0.000	0.000
% *Exacanthomysis davisi*	D	0.539	0.539	0.539
	p	0.000	0.000	0.000
% *Acanthomysis borealis*	D	0.502	0.504	0.501
	p	0.000	0.000	0.000
% *Neomysis mercedis*	D	0.539	0.539	0.539
	p	0.000	0.000	0.000
Simpson's Index	D	0.169	0.166	0.154
	p	0.103	0.136	0.218
Whales present	D	0.238	0.239	0.241
	p	0.000	0.000	0.000
Whales +/- 5 days	D	0.162	0.162	0.164
	p	0.000	0.000	0.000
Whales +/- 10 days	D	0.184	0.184	0.186
	p	0.000	0.000	0.000

Table 3. Results of Levene's test for homogeneity of variance for mysid characteristic and whale foraging variables. F = Levene's F.

		Fine Scale	Medium Scale	Coarse Scale
Median body length	F	2.325	3.135	4.319
	p	0.051	0.033	0.025
% Gravid	F	3.148	0.785	0.986
	p	0.013	0.546	0.387
% Juvenile	F	3.472	7.360	4.436
	p	0.008	0.000	0.022
% Male	F	2.028	0.606	0.479
	p	0.083	0.662	0.625
% Female	F	3.279	2.503	2.310
	p	0.010	0.068	0.140
% Gravid / % Female	F	2.125	0.307	0.322
	p	0.077	0.870	0.728
Female : Male	F	4.355	3.419	5.651
	p	0.003	0.024	0.010
Number of species observed	F	1.656	1.989	0.020
	p	0.161	0.128	0.980
% *Holmesimysis sculpta*	F	2.454	3.276	4.281
	p	0.041	0.028	0.026
% *Neomysis rayi*	F	8.323	15.947	22.275
	p	0.000	0.000	0.000
% *Columbiaemysis ignota*	F	13.279	45.335	14.394
	p	0.000	0.000	0.000
% *Disacanthomysis dybowskii*	F	1.833	1.785	2.120
	p	0.119	0.165	0.142
% *Acanthomysis columbiae*	F	6.114	4.997	2.148
	p	0.000	0.004	0.139
% *Alienacanthomysis macropsis*	F	1.797	1.734	2.2025
	p	0.126	0.175	0.154
% *Exacanthomysis davisi*	F	6.417	15.517	6.568
	p	0.000	0.000	0.005
% *Acanthomysis borealis*	F	7.999	6.780	8.122
	p	0.000	0.001	0.002
% *Neomysis mercedis*	F	6.417	15.517	6.568
	p	0.000	0.000	0.005
Simpson's Index	F	1.687	2.664	1.840
	p	0.108	0.045	0.171
Whales present	F	5.789	27.600	35.917
	p	0.000	0.000	0.000
Whales + / - 5 days	F	3.289	3.697	3.057
	p	0.000	0.000	0.049
Whales + / - 10 days	F	9.925	45.376	41.482
	p	0.000	0.000	0.000

Table 4. Number of tows with n > 50 mysids in each area aggregated at coarse spatial scale.

Variable group	Area 1	Area 2	Area 3	Total
Mysid species	15	7	10	32
Mysid life stage- %	15	8	10	33
Mysid life stage- ratio	13	7	10	31
Mysid body length	15	7	10	32

Table 5. Number of tows with n > 50 mysids in each area aggregated at medium spatial scale. There were no successful mysid tows with n > 50 mysids in area 1.

Variable group	Area 2	Area 3	Area 4	Area 5	Area 6
Mysid species	4	11	7	4	6
Mysid life stage- %	4	11	8	4	6
Mysid life stage- ratio	4	9	7	4	6
Mysid body length	4	11	7	4	6

Table 6. Number of tows with n > 50 mysids in each area aggregated at fine spatial scale. There were no successful mysid tows with n > 50 mysids in areas 1, 4, 11 or 14.

Variable group	A2	A3	A5	A6	A7	A8	A9	A10	A12	A13
Mysid species	3	1	7	4	1	3	3	4	3	3
Mysid life stage- %	3	1	7	4	1	3	4	4	3	3
Mysid life stage- ratio	3	1	5	4	1	3	3	4	3	3
Mysid body length	3	1	7	4	1	3	3	4	3	3

For between - year comparisons, Mann - Whitney U tests were conducted. Because the 2000 data included May and June and the 1999 season did not, early data from the 2000 season were not included in these tests.

RESULTS

Collection of Mysid Samples

A total of 859 tows were conducted, 93 of which actually yielded mysids. Tows containing mysids and taken on the same day within the same area were aggregated. Only aggregated tows with at least 50 sufficiently complete mysids were included in analyses (Tables 4 through 6). Tables 7 and 8 show the dates and locations of tows conducted during the study.

Spatial Distribution of Mysid Species

Nine species of mysids were collected during this study: *Holmesimysis sculpta, Neomysis rayi, Columbiaemaysis ignota, Acanthomysis columbiae, Alienacanthomysis macropsis, Acanthomysis borealis, Disacanthomysis dybowskii, Exacanthomysis davisi, Neomysis mercedis* (Figures 6 through 8). Three of these species, *Alienacanthomysis macropsis, Acanthomysis borealis* and *Neomysis mercedis* were not collected in Clayoquot Sound in previous studies (Dunham & Duffus, 2001) but were collected in another study conducted along the mainland British Columbia coast northeast of Vancouver Island (Stelle, 2001). *H. sculpta* was numerically dominant and was collected in 42 of 52 tows that contained mysids. The other ten tows contained *N. rayi* and *C. ignota*. If only the samples with greater than 50 mysids are considered, *H. sculpta* was present in 31 out of 32 samples, the other one was comprised solely of *N. rayi*.

Table 7. Number of tows containing mysids / total number of tows conducted for each fine scale area during each week of the 1999 season. NS denotes no sampling.

mon dd-dd	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Jul 15 21	0 / 15	0 / 11	0 / 5	0 / 15	0 / 10	0 / 12	1 / 17	0 / 16	0 / 10	NS	NS	NS	NS
Jul 22 - 28	2 / 17	2 / 12	1 / 5	1 / 15	2 / 13	2 / 12	1 / 17	0 / 15	0 / 10	0 / 4	0 / 7	0 / 6	NS
Jul 29 Aug 4	2 / 11	0 / 10	0 / 5	2 / 18	0 / 10	0 / 11	0 / 15	0 / 15	3 / 12	NS	NS	NS	NS
Aug 5 - 11	0 / 16	1 / 10	1 / 5	0 / 16	2 / 11	0 / 10	0 / 15	2 / 17	0 / 10	0 / 5	0 / 12	2 / 14	NS
Aug 12 - 18	0 / 15	0 / 10	0 / 5	4 / 17	0 / 10	0 / 10	0 / 16	0 / 16	0 / 10	0 / 5	2 / 15	0 / 15	NS
Aug 19 - 25	0 / 15	0 / 10	0 / 5	0 / 15	0 / 10	0 / 11	0 / 15	2 / 22	0 / 10	NS	NS	NS	NS
Aug 26 Sep 1	0 / 16	0 / 10	0 / 5	0 / 15	0 / 10	0 / 10	0 / 15	0 / 15	2 / 11	0 / 5	2 / 10	3 / 10	NS
Sep 2 - 8	0 / 15	0 / 10	0 / 5	0 / 15	0 / 12	0 / 10	0 / 15	0 / 15	0 / 10	NS	NS	NS	NS
Total 1999	4 / 120	3 / 83	2 / 40	7 / 126	4 / 86	2 / 86	2 / 125	4 / 131	5 / 83	0 / 19	4 / 44	5 / 45	NS

Table 8. Number of tows containing mysids / total number of tows conducted for each fine scale area during each week of the 2000 season. NS denotes no sampling.

mon dd-dd	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
May 23 - 29	0 / 16	0 / 10	0 / 5	0 / 15	0 / 10	0 / 11	0 / 15	0 / 15	0 / 11	NS	NS	NS	NS
May 30 Jun 5	0 / 17	0 / 11	0 / 5	0 / 15	0 / 11	0 / 10	0 / 16	0 / 15	0 / 10	NS	NS	NS	NS
Jun 6 - 12	1 / 16	0 / 10	1 /6	0 / 15	2 / 11	2 / 13	1 / 17	0 / 15	2 / 11	NS	NS	NS	NS
Jun 13 - 19	0 / 15	0 / 10	1 / 7	2 / 16	2 / 10	0 / 11	0 / 15	0 / 15	2 / 11	NS	NS	NS	NS
Jun 20 - 26	0 / 15	3 / 14	1 / 5	0 / 15	0 / 10	0 / 12	2 / 18	0 / 15	0 / 10	NS	NS	NS	NS
Jun 27 Jul 4	0 / 3	0 / 3	0 / 5	0 / 3	5 / 5	0 / 5	8 / 8	3 / 3	0 / 5	NS	NS	NS	NS
Jul 5 - 11	2 / 2	0 / 5	0 / 1	3 / 3	0 / 5	0 / 5	2 / 2	2 / 2	0 / 1	NS	NS	NS	NS
Jul 12 - 18	4 / 4	2 / 3	0 / 2	0 / 1	0 / 3	0 / 0	2 / 2	0 / 3	0 / 5	NS	NS	NS	NS
Jul 19 - 25	0 / 1	0 / 1	0 / 1	0 / 0	0 / 1	0 / 1	0 / 1	3 / 4	3 / 3	2 / 6	2 / 6	2 / 7	1 / 7
Jul 26 Aug 1	0 / 1	0 / 0	0 / 2	0 / 1	0 / 2	0 / 0	0 / 2	0 / 0	0 / 1	0 / 5	2 / 12	3 / 12	2 / 11
Aug 2 - 8	0 / 0	0 / 2	0 / 1	2 / 5	2 / 2	0 / 2	0 / 1	2 / 2	0 / 0	NS	NS	NS	NS
Aug 9 - 15	0 / 2	0 / 1	0 / 1	0 / 1	0 / 3	0 / 0	0 / 2	0 / 1	0 / 1	0 / 5	2 / 15	3 / 15	NS
Aug 16 - 22	0 / 1	0 / 1	0 / 0	0 / 1	0 / 2	0 / 2	0 / 0	2 / 5	0 / 5	NS	NS	NS	NS
Aug 23 - 29	0 / 2	0 / 2	0 / 2	0 / 2	0 / 0	0 / 2	0 / 0	0 / 2	0 / 2	NS	NS	NS	NS
Aug 30 Sep 5	0 / 0	0 / 0	0 / 1	0 / 0	0 / 1	0 / 0	0 / 5	0 / 0	0 / 1	0 / 5	2 / 2	3 / 3	NS
Sep 6 - 12	0 / 2	0 / 1	0 / 1	0 / 0	0 / 1	0 / 1	0 / 5	0 / 1	0 / 1	NS	NS	NS	NS

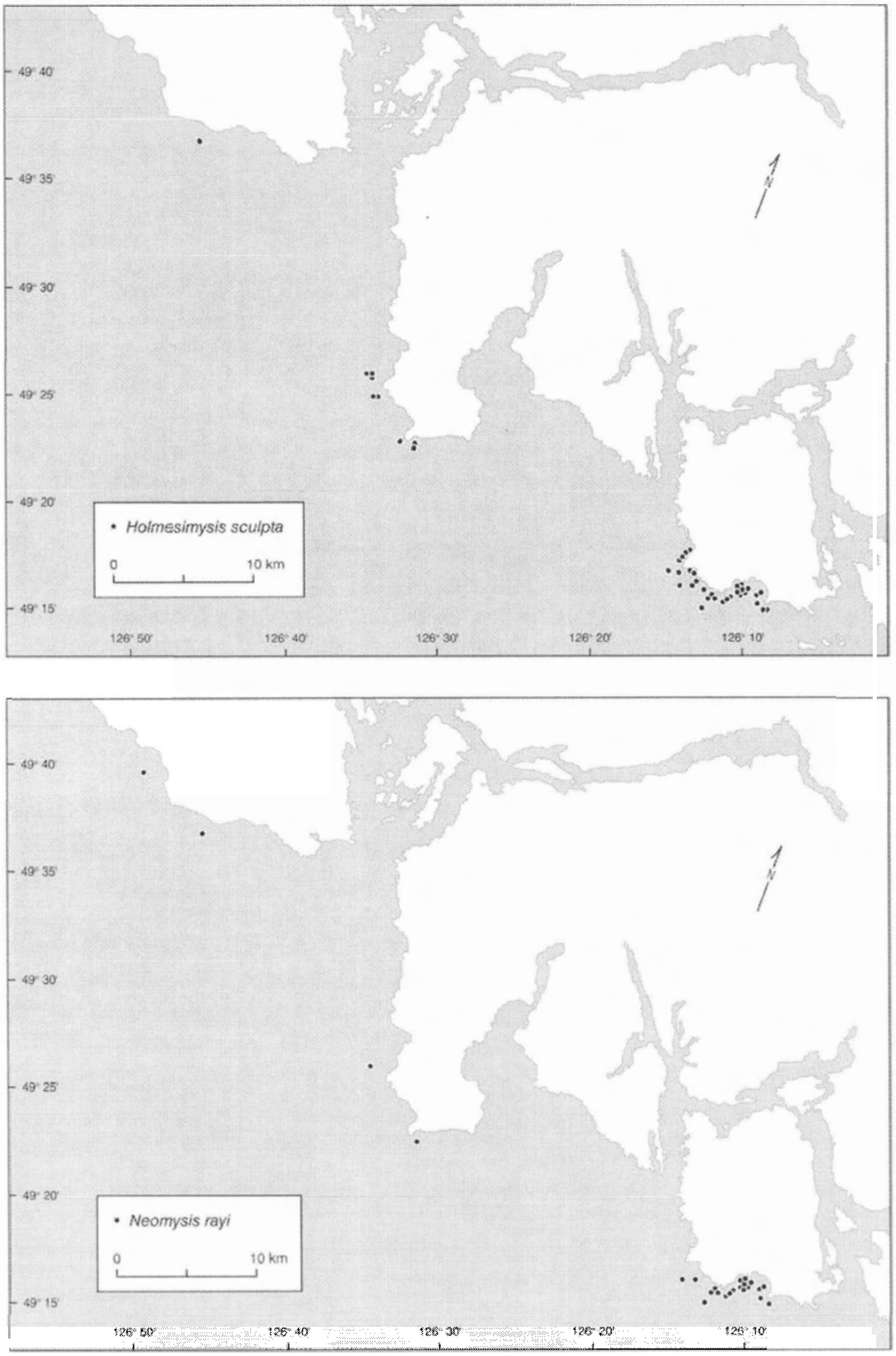

Figure 6. Maps showing locations of samples containing *Holmesimysis sculpta* (n = 42) and *Neomysis rayi* (n = 33).

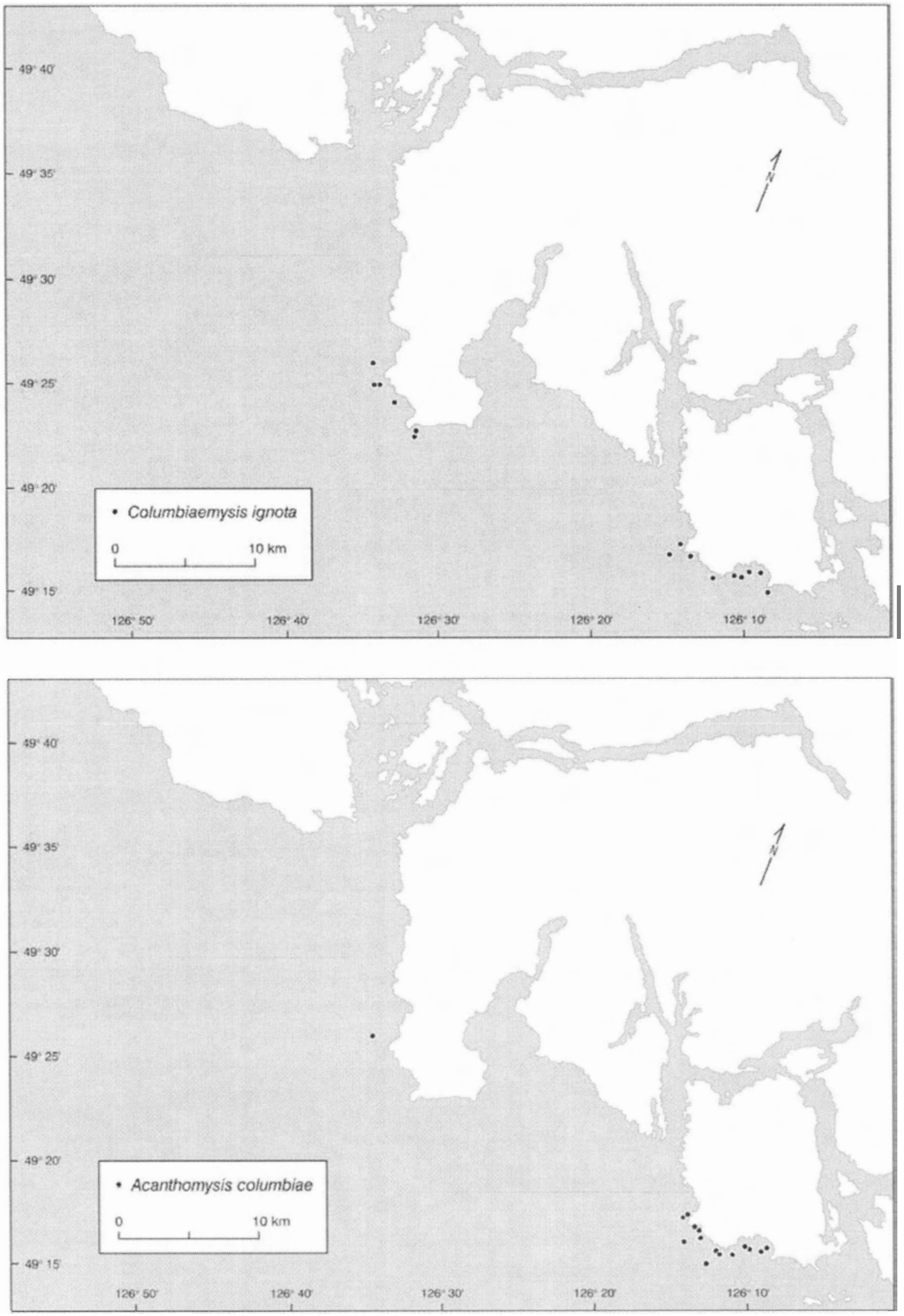

Figure 7. Maps showing locations of samples containing *Columbiaemysis ignota* (n = 15) and *Acanthomysis columbiae* (n = 15).

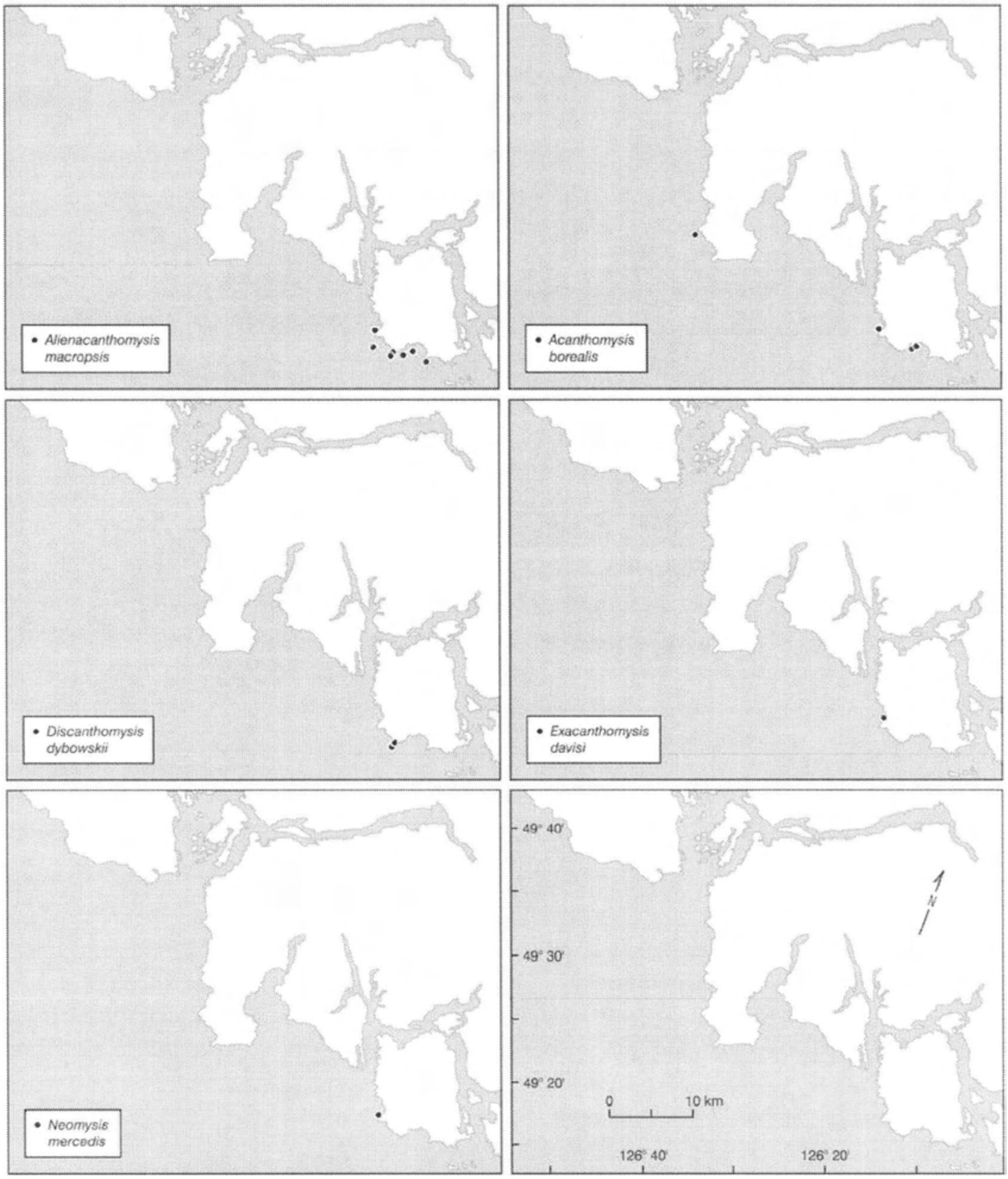

Figure 8. Maps showing locations of samples containing *Alienacanthomysis macropsis* (n = 7), *Acanthomysis borealis* (n = 4), *Disacanthomysis dybowskii* (n = 2), *Exacanthomysis davisi* (n = 1) and *Neomysis mercedis* (n = 1).

Kruskal - Wallis tests were conducted to test the effect of location on the relative abundances of mysid species (Table 9). Pairwise Mann - Whitney U tests were employed post - hoc to determine the existence of any areas that stood out in terms of community structure. These results are attached as Appendix 1. Summary maps of significant results are presented in Figures 9 through 12.

Table 9. Results of the Kruskal - Wallis tests between areas for the mysid species variables.

Variable		Fine scale	Medium Scale	Coarse scale
% *Holmesimsys*	χ^2	17.606	10.858	0.319
sculpta	p	0.040	0.028	0.852
% *Neomysis rayi*	χ^2	12.995	8.646	1.273
	p	0.163	0.071	0.529
% *Columbiaemysis*	χ^2	14.705	7.875	5.60
ignota	p	0.099	0.096	0.061
% *Disaanthomysis*	χ^2	15.945	1.536	1.037
dybowskii	p	0.068	0.820	0.596
% *Alienacanthomysis*	χ^2	13.619	5.307	4.128
macropsis	p	0.137	0.257	0.127
% *Acanthomysis*	χ^2	11.036	5.675	4.714
columbiae	p	0.273	0.225	0.095
% *Exacanthomysis*	χ^2	7.000	6.250	2.375
davisi	p	0.637	0.181	0.305
% *Neomysis*	χ^2	7.000	6.250	2.375
mercedis	p	0.637	0.181	0.305
% *Acanthomysis*	χ^2	8.409	3.805	2.105
borealis	p	0.494	0.433	0.349
Number of species	χ^2	11.826	7.599	2.737
observed	p	0.223	0.107	0.255
Simpson's Index	χ^2	11.347	11.610	3.031
	p	0.253	0.021	0.220

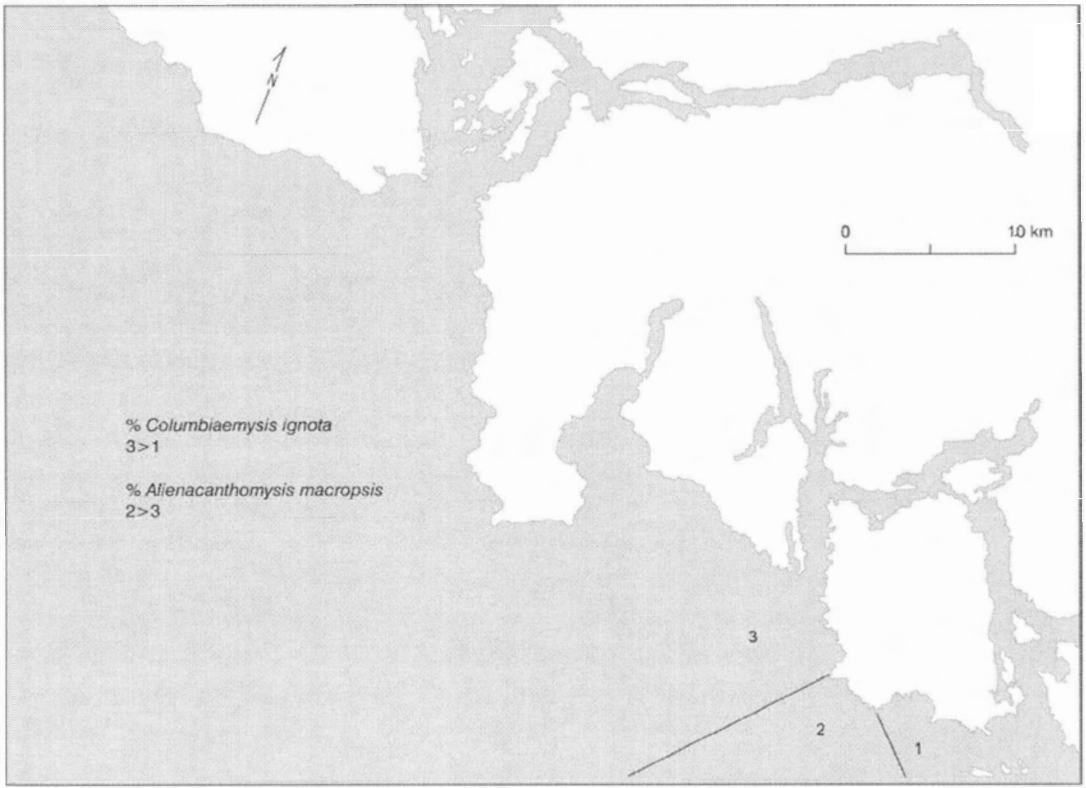

Figure 9. Summary of significant differences between coarse scale areas for all mysid species variables.

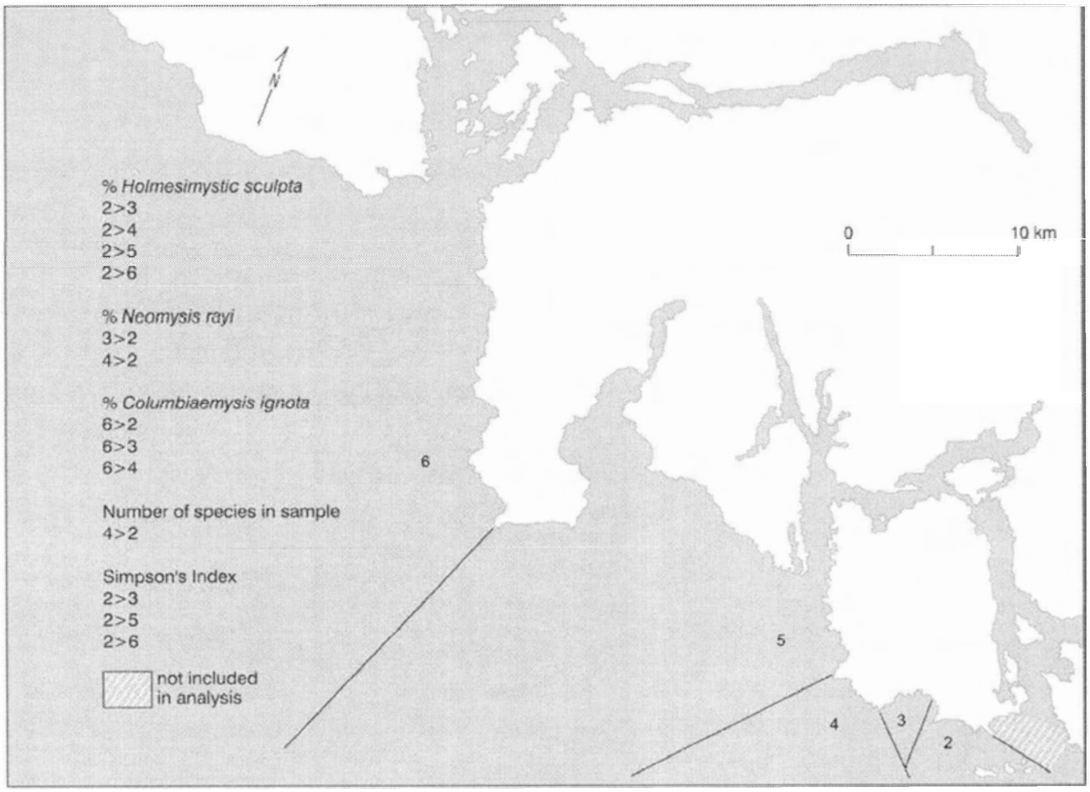

Figure 10. Summary of significant differences between medium scale areas for all mysid species variables.

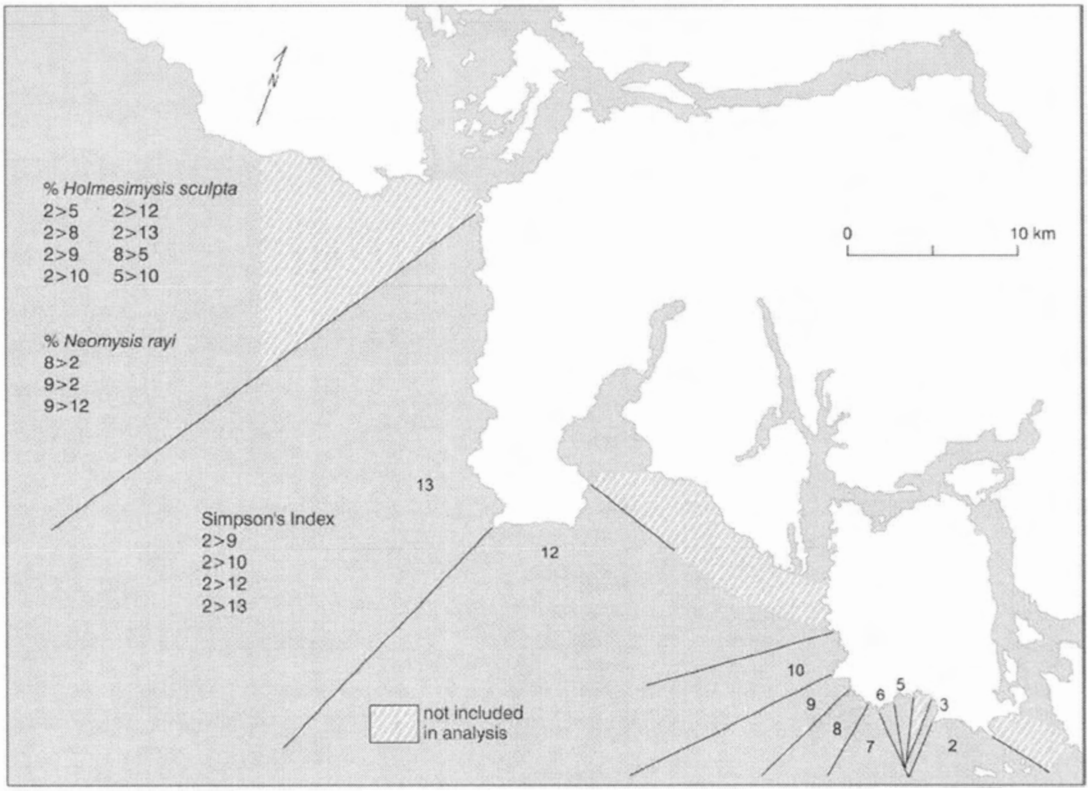

Figure 11. Summary of significant differences between fine scale areas for % *Holmesimysis sculpta*, %*Neomysis rayi* and Simpson's Index.

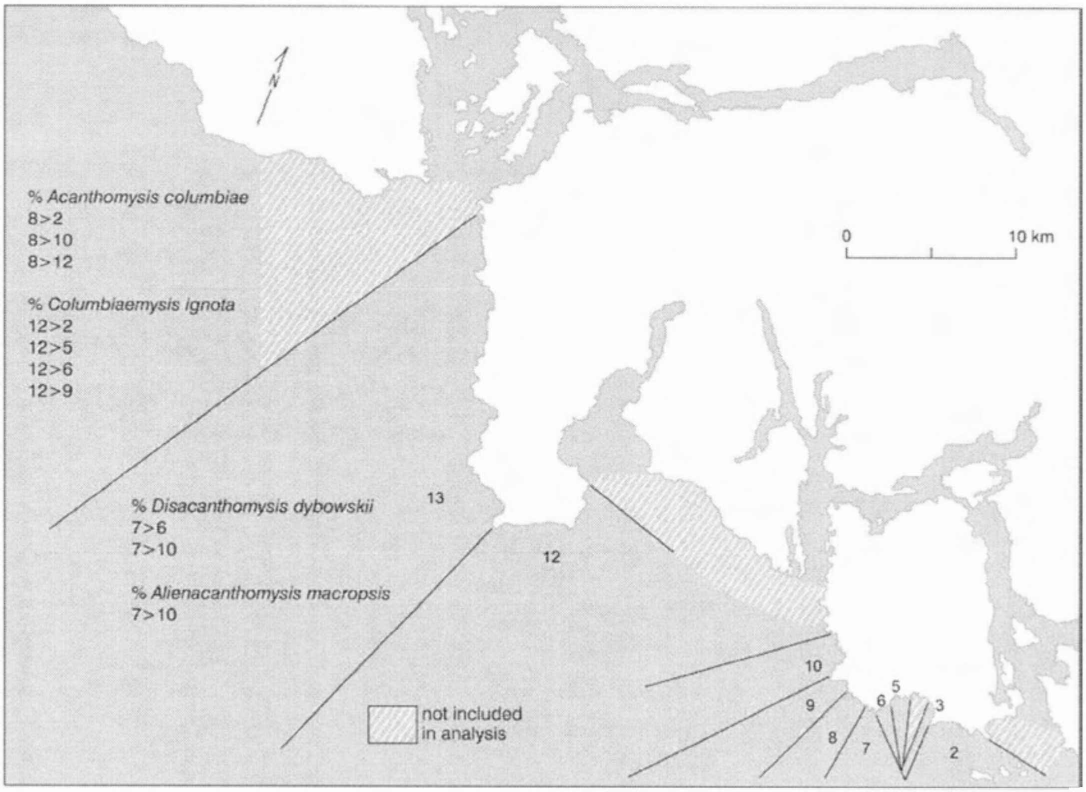

Figure 12. Summary of significant differences between fine scale areas for % *Acanthomysis columbiae*, % *Columbiaemysis ignota*, % *Disacanthomysis dybowskii* and % *Alienacanthomysis macropsis*.

Spatial Distribution of Mysid Life Stages

All life stages were observed in all areas throughout both the 1999 and 2000 seasons with the exception of fine scale area 8, an area west of Siwash Point locally known as "the grassy knoll". No gravid females were collected in this area during this study.

To compare the population structure of mysids in different areas, Kruskal - Wallis tests were conducted to test the effect of location on relative abundance of mysid life stages (Table 10). Pairwise Mann - Whitney U tests were employed post - hoc to determine the existence and identity of any single areas that stood out in terms of population structure. These results are attached as Appendix 2. Summary maps of significant results are presented in Figures 13 and 14.

Table 10. Results of the Kruskal-Wallis tests between areas for the mysid life stage variables.

Variable		Fine scale	Medium Scale	Coarse scale
% Gravid female	χ^2	8.395	2.066	1.209
	p	0.495	0.724	0.546
% Juvenile	χ^2	10.562	7.951	0.208
	p	0.307	0.093	0.901
% Male	χ^2	16.727	11.737	4.206
	p	0.053	0.019	0.122
% Female	χ^2	5.502	1.639	0.158
	p	0.789	0.802	0.924
% Gravid female /	χ^2	8.702	2.507	1.815
% Female	p	0.465	0.643	0.404
Female : Male	χ^2	10.952	4.356	1.906
	p	0.279	0.360	0.386

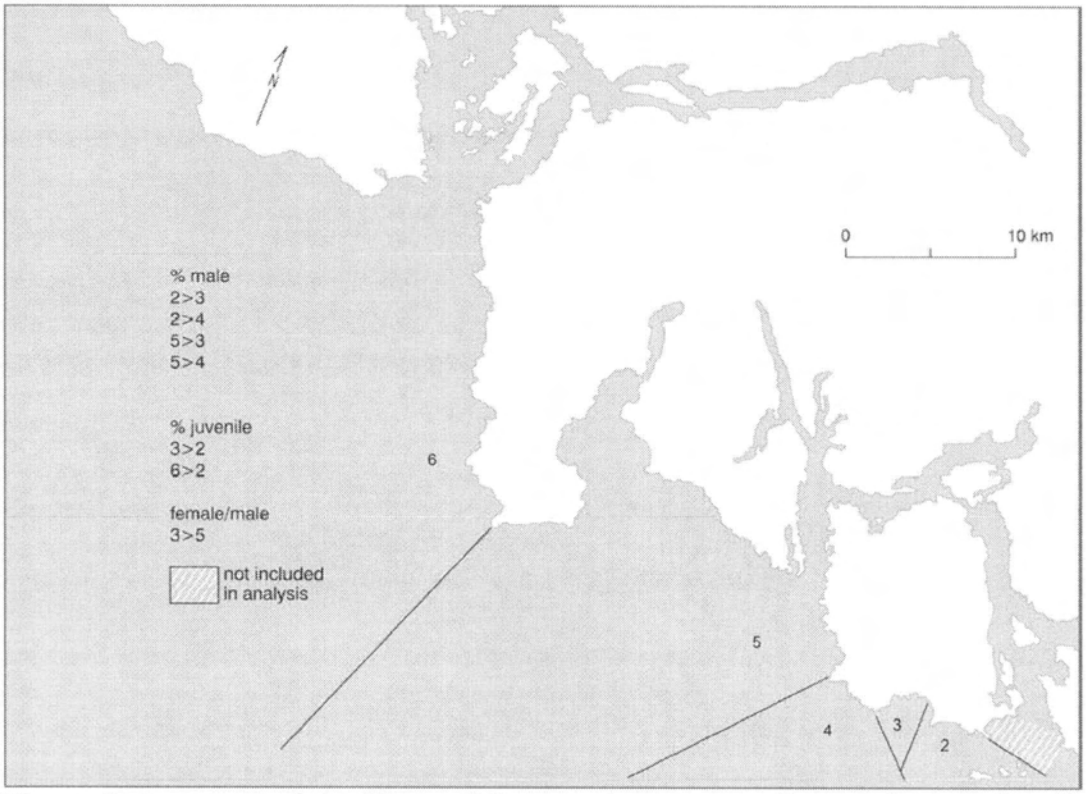

Figure 13. Summary of significant differences between medium scale areas for all mysid life stage variables.

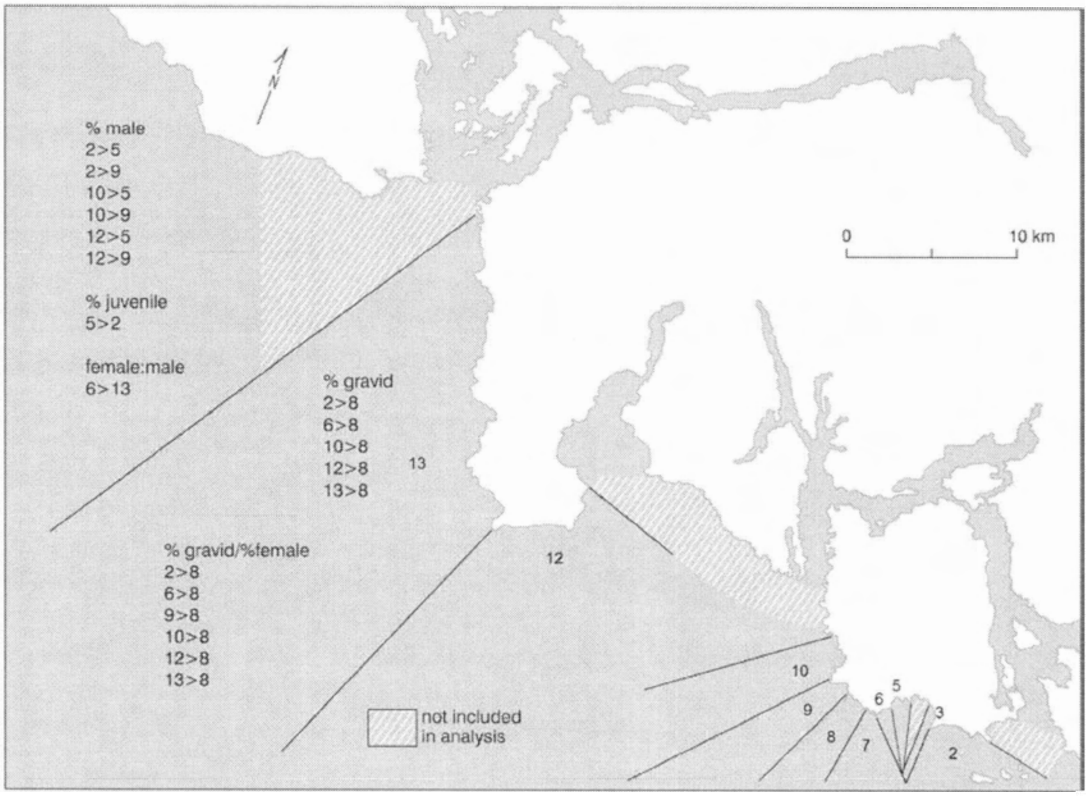

Figure 14. Summary of significant differences between fine scale areas for all mysid life stage variables.

Spatial Distribution of Mysid Body Length

To compare the body length of mysids in different areas, Kruskal - Wallis tests were conducted to assess the distribution of mysid body length across all areas. No significant differences were detected at fine, medium or coarse scale ($\chi^2 = 11.328$, $p = 0.254$; $\chi^2 = 3.216$, $p = 0.522$; $\chi^2 = 0.101$, $p = 0.951$). Pairwise Mann - Whitney U tests were employed post - hoc to determine the existence and identity of any single areas that stood out in terms of mysid body length (Tables 11 through 13). Summary maps of significant results are presented in Figure 15.

Table 11. Results matrix of pairwise Mann -Whitney U tests using coarse scale areas for the mysid variable 'Median mysid body length (mm)'.

Area		1	2
2	U	39.000	NA
	p	0.799	
3	U	45.500	25.000
	p	0.846	0.727

Table 12. Results matrix of pairwise Mann -Whitney U tests using medium scale areas for the mysid variable 'Median mysid body length (mm)'.

Area		2	3	4	5
3	U	10.000	NA		
	p	0.155			
4	U	9.000	31.000	NA	
	p	0.344	0.696		
5	U	6.500	13.000	11.000	NA
	p	0.663	0.320	0.570	
6	U	3.000	19.000	14.000	3.000
	p	0.146	0.887	1.000	0.139

Table 13. Results matrix of pairwise Mann -Whitney U tests using fine scale areas for the mysid variable 'Median mysid body length (mm)'.

Area	**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3 U	1.000	NA							
p	0.655								
5 U	5.000	2.000	NA						
p	0.209	0.502							
6 U	2.000	1.000	13.500	NA					
p	0.157	0.480	0.924						
7 U	1.000	0.000	1.000	1.000	NA				
p	0.655	0.317	0.272	0.480					
8 U	0.000	0.000	7.000	2.000	0.000	NA			
p	0.050	0.180	0.424	0.157	0.180				
9 U	4.000	1.000	5.000	2.000	1.000	0.500	NA		
p	1.000	0.655	0.209	0.157	0.655	0.077			
10 U	5.000	1.000	9.000	4.000	1.000	0.000	4.000	NA	
p	0.724	0.717	0.340	0.248	0.480	0.034	0.480		
12 U	2.000	0.000	10.500	4.500	0.000	1.000	2.000	0.500	NA
p	0.275	0.180	1.000	0.593	0.180	0.127	0.275	0.050	
13 U	3.000	1.000	7.000	3.000	0.000	0.000	3.000	4.000	1.000
p	0.507	0.637	0.422	0.285	0.157	0.046	0.507	0.483	0.405

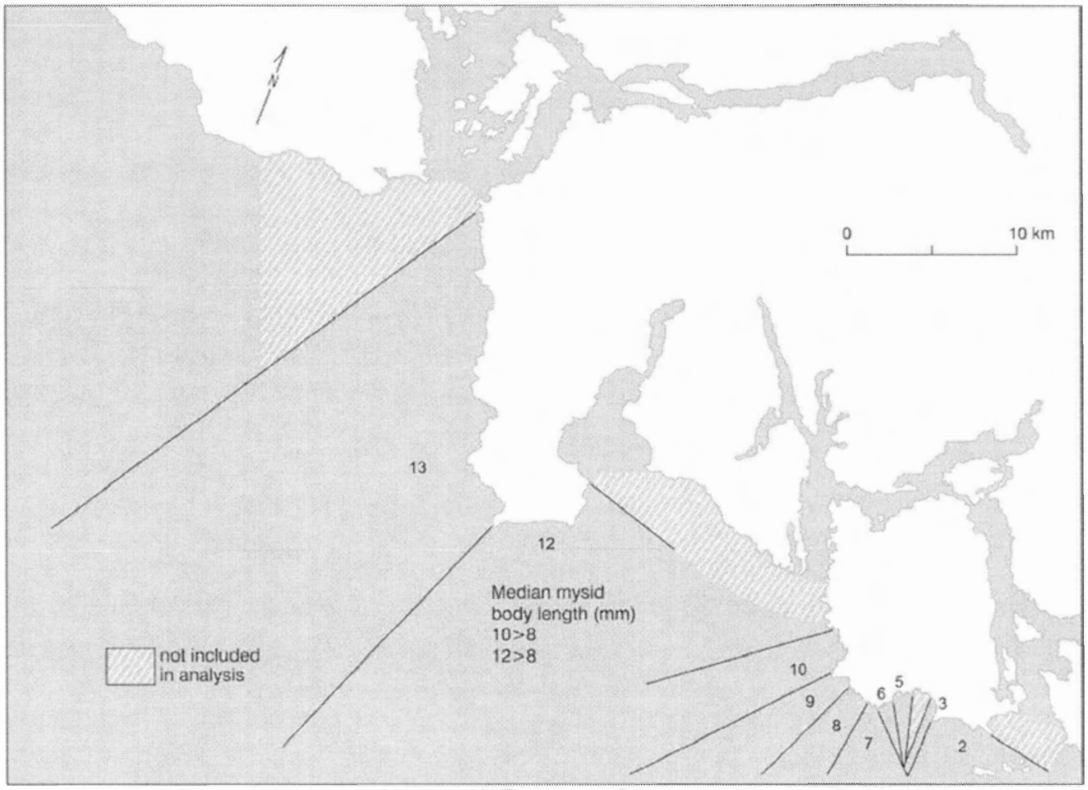

Figure 15. Summary of significant differences between fine scale areas for median mysid body length (mm).

Whale Transects

The dates of transects conducted during the 1999 and 2000 seasons are shown in Table 14. Whale data was collected for June 1999 but not utilized in these analyses because no mysid sampling was conducted during this time.

Table 14. Dates of whale transects during the 1999 and 2000 seasons.

Month	1999 dates	2000 dates
June	NA	2, 4, 8, 17, 23, 30
July	11, 15, 19, 22, 28, 30	7, 15, 18, 24
August	2, 4, 7, 12, 16, 22, 26	2, 16, 20, 27
September	2, 8	4

Trips to Nootka Sound were made on three occasions during the 2000 season- July 20, July 29 and August 12/13. Trips to Estevan Point were made during both the 1999 and 2000 season. Trips during 1999 were on July 22 and August 8, 13 and 31; 2000 trips were on July 20 and 29, August 1 and 12 and on September 2.

Spatial Distribution of Gray Whales

A total of 30 transects were made during the two seasons (Table 11).On three occasions during 2000, trips were made to Nootka Sound, north and west of Clayoquot Sound. During these trips, numerous (30 to 40) animals were observed foraging upon mysids between Perez Rocks and Bajo Reef (Figure 1). Approximately three quarters of these animals were immediately recognizable as individuals who had been sighted in Clayoquot Sound in previous seasons.

To compare the presence of gray whales in different areas, Kruskal - Wallis tests were conducted to assess the randomness of the distribution of single variables across all areas. The sample sizes for each of these areas are shown in Tables 15 through 17. All variables were non - randomly distributed over all scales except the Whales + / - 5 days variable at fine scale (Table 18).

Table 15. Sample sizes for the whale foraging variables in each of the three coarse scale areas.

Area	Whales present	Whales +/- 5 days	Whales +/- 10 days
1	180	88	84
2	176	87	42
3	180	87	55
Total	352	305	322

Table 16. Sample sizes for the whale foraging variables in each of the six medium scale areas.

Area	Whales present	Whales +/- 5 days	Whales +/- 10 days
1	0	0	0
2	80	76	80
3	100	100	100
4	88	87	87
5	41	38	41
6	43	4	14
Total	352	305	322

Pairwise Mann - Whitney U tests were employed post - hoc to determine the existence and identity of any single areas that stood out in terms of whale foraging (Appendix 3). Summary maps of significant results are presented in Figures 16 through 20.

Table 17. Sample sizes for the whale foraging variables in each of the fourteen fine scale areas.

Area	Whales present	Whales +/- 5 days	Whales +/- 10 days
1	0	0	0
2	48	44	48
3	11	11	11
4	21	21	21
5	50	50	50
6	50	50	50
7	8	8	8
8	37	36	36
9	43	43	43
10	37	37	37
11	4	1	4
12	25	1	11
13	11	3	3
14	7	0	0
Total	352	305	322

Table 18. Results of the Kruskal-Wallis tests between all areas for the whale foraging variables.

Variable		Fine scale	Medium Scale	Coarse scale
Whales present	χ^2	77.6614	99.347	111.755
	p	0.000	0.000	0.000
Whales +/- 5 days	χ^2	0.502	12.815	20.253
	p	0.778	0.012	0.042
Whales +/- 10 days	χ^2	23.918	30.342	57.708
	p	0.000	0.000	0.000

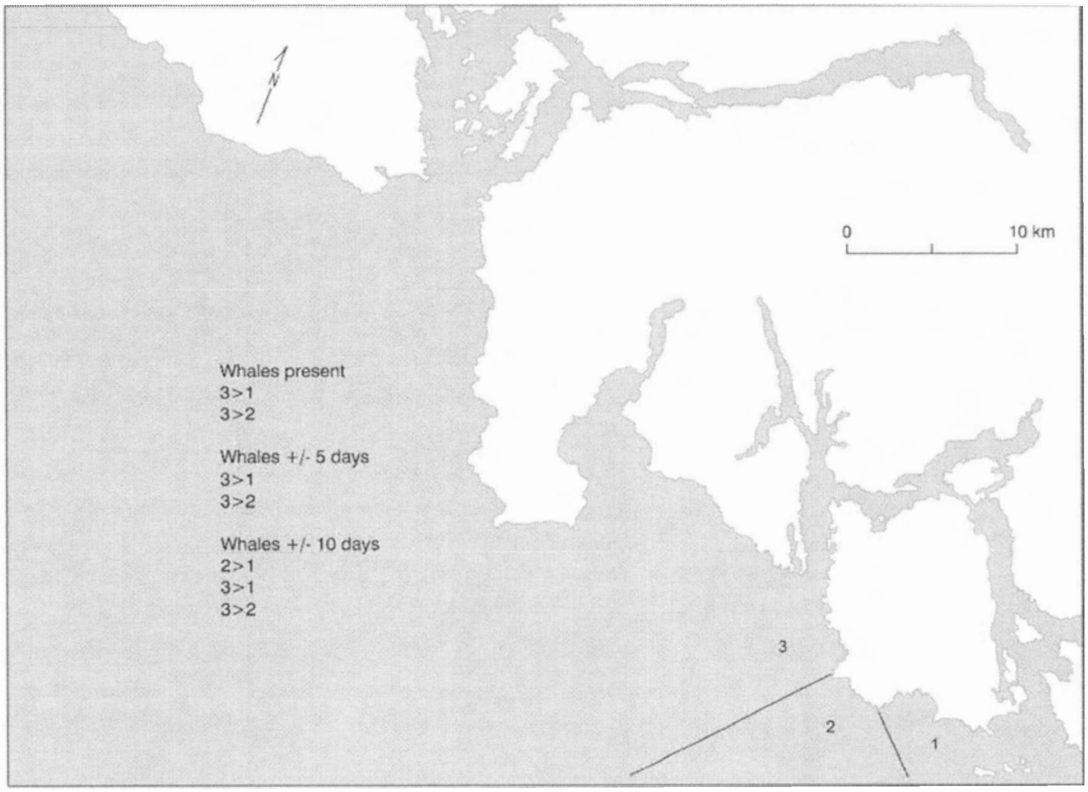

Figure 16. Summary of significant differences between coarse scale areas for all whale foraging variables.

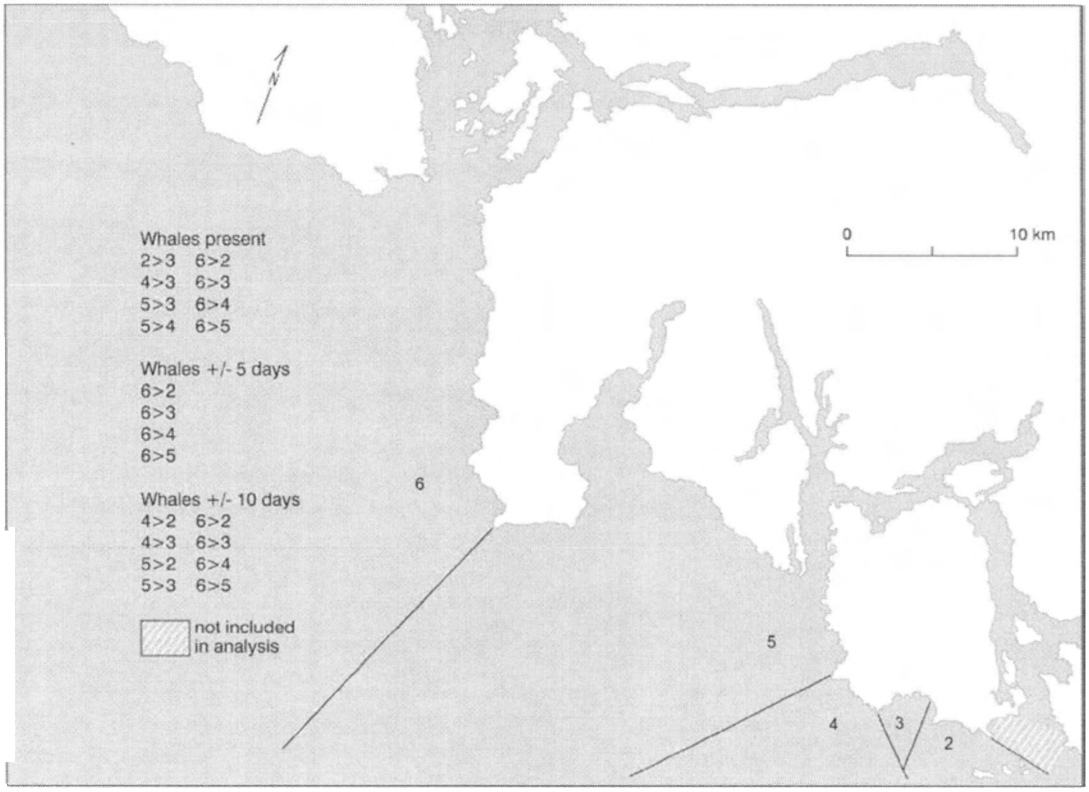

Figure 17. Summary of significant differences between medium scale areas for all whale foraging variables.

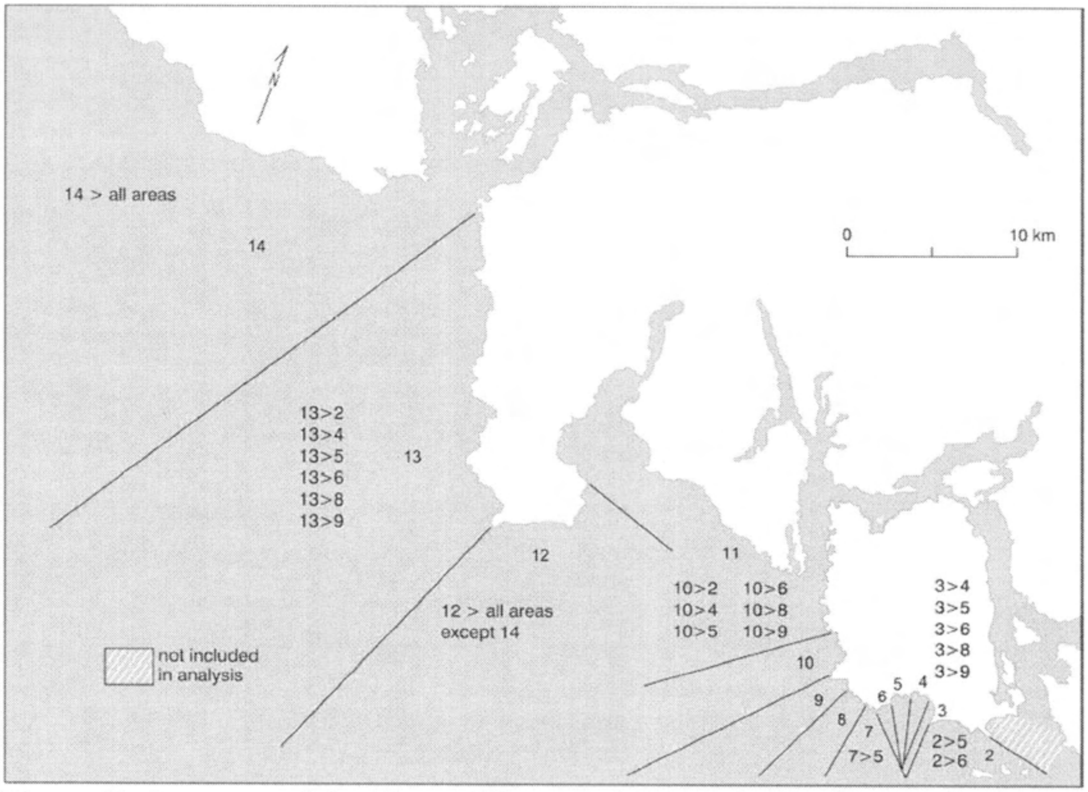

Figure 18. Summary of significant differences between fine scale areas for the whale foraging variable 'whales present'.

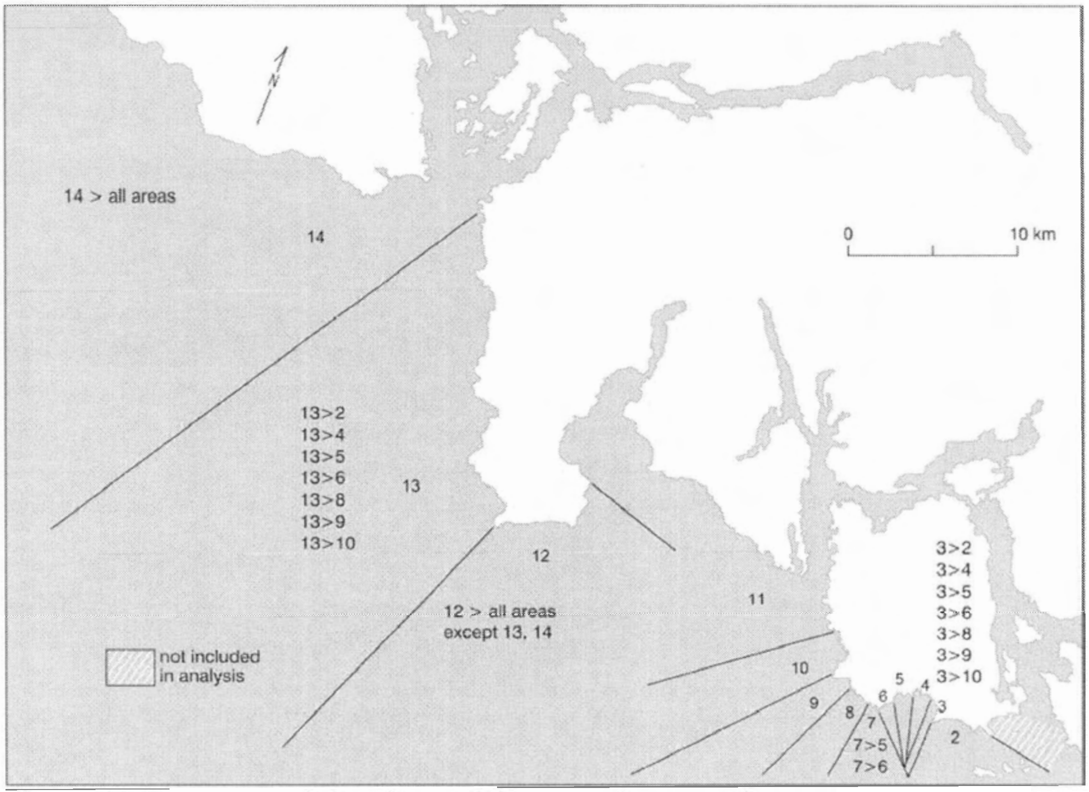

Figure 19. Summary of significant differences between fine scale areas for the whale foraging variable 'whales + / - 5 days'.

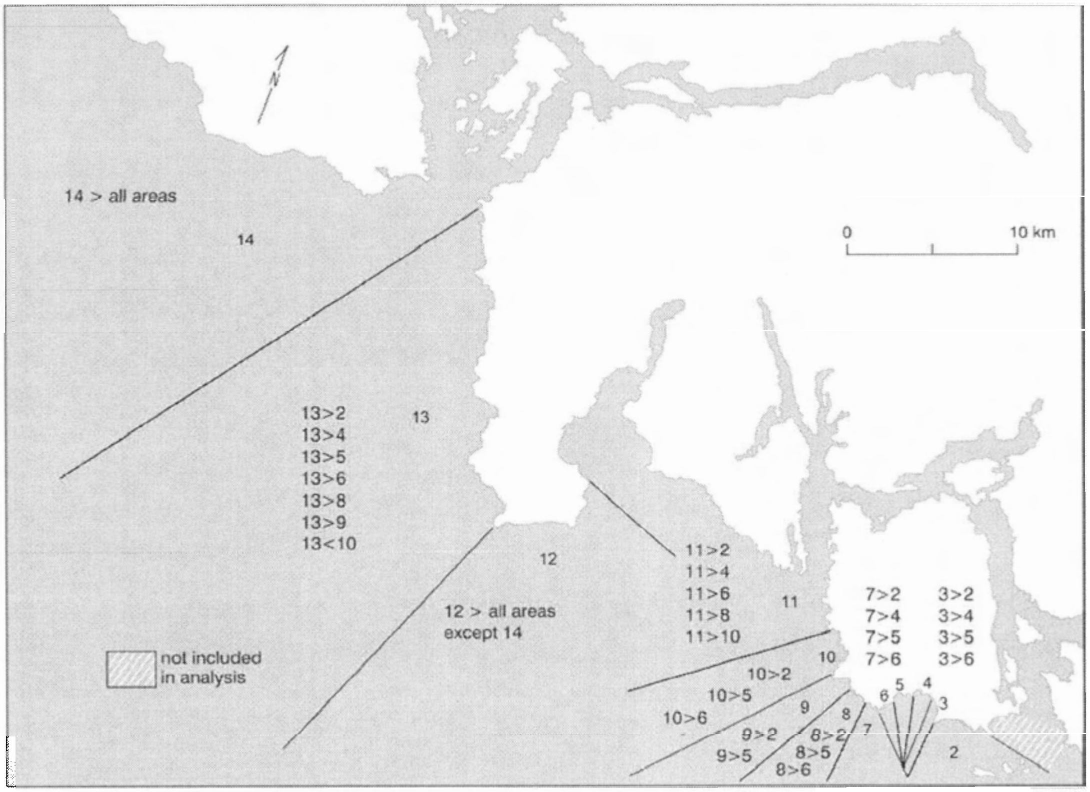

Figure 20. Summary of significant differences between fine scale areas for the whale foraging variable 'whales + / - 10 days'.

Between - Year Comparisons

Mysid community structure was consistent between years (Table 19). The percentage of female mysids (Table 20) and the number of foraging gray whales present and within ten days before and after the tow (Table 21), however, differed between the 1999 and 2000 seasons. Percentage of female mysids was higher in 1999 than in 2000 and the opposite was true for the whale foraging variables. Mysid body length was not significantly different between years (Mann - Whitney U = 35.000, p = 0262).

Table 19. Between - year comparisons (1999 vs. 2000) for mysid species variables. $n_{1999} = 6$, $n_{2000} = 18$.

Variable	Mann-Whitney U	p
% *Holmesimysis sculpta*	40.500	0.491
% *Neomysis rayi*	36.000	0.262
% *Columbiaemysis ignota*	49.000	0.967
% *Disacanthomysis dybowskii*	40.500	0.189
% *Alienacanthomysis macropsis*	45.000	0.366
% *Acanthomysis columbiae*	48.000	0.942
% *Exacanthomysis davisi*	49.000	0.942
% *Neomysis mercedis*	44.000	0.269
% *Acanthomysis borealis*	38.000	0.286
Number of species in sample	49.000	0.942
Simpson's Index	46.500	0.817

Table 20. Between - year comparisons (1999 vs. 2000) for mysid life stage variables. $n_{1999} = 11$, $n_{2000} = 9$ except ratio variables $n_{2000} = 7$.

Variable	Mann-Whitney U	p
% Gravid female	32.500	0.196
% Juvenile	30.500	0.149
% Male	41.500	0.543
% Female	23.500	0.048
% Gravid female / % Female	32.500	0.587
Female : Male	22.500	0.291

Table 21. Between - year comparisons (1999 vs. 2000) for whale foraging variables.

Variable	n_{1999}	n_{2000}	Mann-Whitney U	p
Whales present	71	115	2797.000	0.000
Whales + / - 5 days	64	83	2561.000	0.684
Whales + / - 10 days	64	96	2534.000	0.047

DISCUSSION

A number of mysid population and whale foraging parameters were non - randomly spatially distributed within Clayoquot Sound and were significantly different between the two years of study. Potential sources of this variability include oceanographic currents and the effects of predation pressure by whales and other predators upon mysids.

Spatial Distribution of Mysid Species

As observed in other studies of mysids on the coast of Vancouver Island (Stelle, 2001; Dunham & Duffus, 2002), *Holmesimysis sculpta* was the most frequently encountered species in Clayoquot Sound in the summers of 1999 and 2000. Found throughout the study area, it is generally the numerically dominant species. On a coarse and medium spatial scale, the percentage of *H. sculpta* in a sample was not significantly different among areas, however the fine scale spatial analysis of the percentage of *H. sculpta* showed that this dominance was significantly higher in area 2, Red Rocks and the western end of the Fitzpatricks, a rocky area outside the eastern entrance to Cow Bay. The distribution of *H. sculpta* was very closely tied to the distribution of high values of Simpson's Index, a measure of dominance, further reinforcing *H. sculpta* as the dominant species in the region.

Neomysis rayi was the next most frequently encountered species and was also collected throughout the study area. At medium scale, percentages of *N. rayi* were significantly higher in areas 3 and 4, Cow Bay and Siwash Point to Rafael Point, than in area 2, Eastern Cow Bay to the western Fitzpatricks. The higher percentage of *N. rayi* between Siwash and Rafael points compared to Red Rocks and the Fitzpatricks was also evident at fine scale, in addition the percentage of *N.rayi* was significantly higher between Siwash and Rafael points than in area 12, between Estevan Point and the western entrance of Hesquiat Harbour. As the regions with lower percentages of *N. rayi* include the areas with high proportions of *H. sculpta* and *Columbiaemysis ignota* (see below), these results do not necessarily indicate the existence of a center of *N. rayi* abundance. This region is quite turbulent (Kopach, 2004), stronger currents may be more easily tolerated by *N. rayi* because they are a large - bodied species. Guerrero (1989) noted that *Neomysis* was very capable of avoiding nets. It is therefore possible that this genus is underrepresented numerically in this study. If true, this may indicate that *Holmesimysis sculpta* is not as dominant as appears. As for the spatial distribution of *Neomysis* within this study, the accuracy of results depends upon the assumption that avoidance behaviour is constant across locations.

Another species found throughout the region was *Columbiaemysis ignota*. On a coarse scale, it appeared that the percentage of *C. ignota* was higher in area 3, west of Rafael Point, than in area 1, east of Siwash Point. At first glance the medium and fine scale results appear to be in conflict; the fine medium scale area 6, west of Estevan Point yielded higher percentages of *C. ignota* than areas 2, 3 and 4, representing the entire study area east of Rafael Point, however the area just east of Estevan Point, area 12, was significantly higher than three other areas at fine scale, areas 2, 5 and 9. It is most likely that the aggregation of area 12 with area 10, which contained many rare species (see below), diluted the high percentages of *C. ignota* in the resulting medium scale area 5. It should also be noted that all of the tows in area 12 were taken barely east of Estevan Point and that these tows were not significantly different from those taken on the western side of Estevan Point. The differences in percentage of *C. ignota* at the fine and medium scale are likely either artifacts of the designation of the area codes or artificially inflated as a result of insufficient sampling and are best ignored. If any conclusion is to be made concerning the distribution of this species it should be restricted to a higher prevalence in the extreme western portions of the study area relative to the eastern end of the study area.

Acanthomysis columbiae was also found throughout the study area, however its distribution was not significantly different among any areas at any of the three spatial scales. Stelle (2003) reported this species as a major component of the mysid community northeast of Vancouver Island, in Clayoquot Sound it is a regularly encountered species.

Five other species of mysids were collected only occasionally. They were, in descending order of frequency; *Alienacanthomysis macropsis* (8 locations), *Acanthomysis borealis* (5 locations), *Disacanthomysis dybowskii* (2 locations), *Exacanthomysis davisi* (2 locations) and *Neomysis mercedis* (1 animal only). Although a few significant differences between areas were detected, such as *Alienacanthomysis macropsis* and *Disacanthomysis dybowskii* in fine scale area 7, the Grassy Knoll west of Siwash Point, these should be interpreted with caution or simply ignored- given the small number of encounters with these species it is possible that these few significances arose out of of small percentages compared with zero values meeting with an artifically agreeable critical value of U.

Perhaps the most interesting information concerning the rare species was that every species collected, except *Disacanthomysis dybowskii*, was encountered south of Dagger Point. The area just east of this, Rafael Point to Siwash Point, had a significantly higher number of species per sample than area 2, which was dominated by *H. sculpta,* and also yielded the samples containing *D. dybowskii.* Both of these areas correspond to a convergence zone described by Kopach (2004). Therefore it is likely that any animals from areas transited by both currents would be carried in to this convergence zone.

Spatial Distribution of Mysid Life Stages

Gravid females did not occur in significantly higher proportions in any areas at either the coarse or medium scale. At fine scale, several areas, 2- Red Rocks, 6- West Cow Bay, 10- Dagger Bay, 12- Smokehouse Bay, and 13- Perez Rocks, had a significantly higher proportion of gravid females than area 8- the grassy knoll, where no gravid females were collected at any point during the study. Clutter (1969) reported that higher proportions of gravid females occurred in "small" populations of coastal mysids, however the term "small" was not defined either qualitatively or quantitatively. Given that the mysid populations west of Estevan Point were considerably higher, indicated by video data collected during this study, it would be expected that gravid females would be more common east of Estevan Point, however this was not observed. Area 8 is in the middle of the aforementioned convergence zone, an area with high current velocities. It is possible that gravid females, being large, are more capable of avoiding being swept in to this zone. It is also possible that gravid females have some interest in avoiding high-turbulence areas, either for their own benefit or for the benefit of newly released juveniles.

Non-gravid females were homogeneously distributed throughout the study area at all three scales. The ratio of gravid to non-gravid females was homogeneously distributed at the coarse and medium scale, at fine scale this ratio was significantly lower in area 8 than in areas 2, 6, 10, 12, and 13. Given that no gravid females were collected in area 8, these results do not provide any additional insight in to mysid reproductive activity relative to location.

Generally, males made up a greater component of the population in the westernmost regions of the study area. On the medium scale, areas 2 and 5, Red Rocks and Rafael Point to Estevan Point, had a significantly higher percentage of male mysids than did areas 3 and 4, Cow Bay and Siwash Point to Rafael Point. When these areas are broken down in to the fine scale, the source of these differences becomes more focused- areas 2, 10 and 12, Red Rocks, Dagger Bay, and Smokehouse Bay, all had a significantly higher male percentage than areas 5 and 9, the mouth of Cow Creek and Dagger Bay. It is arguable that males, being of smaller body size than adult females, are more likely to be dispersed by currents, however both of the high and low male regions occur in areas of both relatively high and low currents, which suggests that something other than currents may be influencing the distribution of male mysids.

Female to male ratios were not significantly higher in any one area at coarse scale, however at medium scale, this ratio was significantly greater in Cow Bay than between Rafael and Estevan points. Finer scale analysis showed that mysids inhabiting the reefs and kelp beds near the mouth of Cow Creek had a higher female to male ratio than mysids at Perez Rocks. Given that these ratios are based on percentages of males and females, no insight in to the relative potential productivity of juveniles in these areas can be made, rather this just illustrates that the relative numbers of males and females were not randomly distributed throughout the study area. Clutter (1969) found significant increases in fertilization rates among small populations of mysids but made no mention of whether or not the sex ratios vary between small and large mysid populations. Clearly an increase in female population is likely to result in increased reproduction, however the altering of sex ratios requires an external regulation mechanism rather than modification of individual behaviour, though it is possible to influence both of these via hormonal cues.

On a coarse spatial scale, the proportion of juvenile mysids was not significantly greater in any one area than another. At medium scale, area 2, Red Rocks, had a significantly lower proportion of juveniles than did area 3, Cow Bay, and area 6, Perez Rocks. Kopach (2004) reported that the currents in Cow Bay were quite slow in comparison with other parts of the coast of Flores Island, which could make this region amenable to juveniles as they are not capable of fighting the same strength currents as are adults. The relatively calm waters of Cow Bay may represent a favourable area for the release of juveniles. If this is the case then questions concerning the dispersal of mysids arise, such as whether this is done via swimming or currents, at what age this movement occurs and what distances mysids travel from their place of birth. It is also possible that higher proportions of juveniles in Cow Bay could represent an increase in mysid productivity in response to many years of intensive predation by gray whales.

Spatial Distribution of Mysid Body Length

Generally, the median body length of mysids collected was homogeneous throughout the study area, there were no significant differences between coarse and medium scale areas. On the fine scale, mysids in area 8, the grassy knoll, were significantly smaller than those in areas 10 and 12, Dagger Bay and Smokehouse Bay. No gravid females were collected in area 8, therefore it is not surprising that the median mysid body length in this area should be comparatively small.

Whale Foraging Variables

Predation by whales was greater in western regions of the study area, particularly west of Estevan Point. The fine scale spatial data showed that whale predation was lowest in Cow Bay, save for the easternmost region (Appendix 3 Tables 7 through 9, Figures 18 through 20). The medium and coarse spatial scale data corroborate this and, in addition, show that the area between Siwash and Dagger Points was also a low-use area for gray whales in the summers of 1999 and 2000 (Appendix 3 Tables 4 through 6, Figure 22). These regions correspond to areas of low mysid presence (see Chapter 4) and were areas of intensive gray whale predation upon mysids during several seasons previous to 1999 (Dunham & Duffus, 2001, 2002). This does not represent the first time that the distribution of gray whales in Clayoquot Sound has changed following years of intense predation pressure in a specific region. After several years of regular sightings of whales preying upon ampeliscid amphipods in Ahous Bay during the late 1980s and early 1990s, the number of whales encountered dropped markedly in this area but increased along the coast of Flores Island (Duffus, 1997).

Between - Year Comparisons

The species composition of mysids and median mysid body length did not differ significantly in the two years of the study. The median mysid body length was insignificantly higher in 1999 than in 2000, this difference is explained by the higher percentage of females in 1999 as females tend to be larger than males.

Significantly more whale foraging activity occurred in Clayoquot Sound in the summer of 2000 than in the summer of 1999. It is interesting that the number of whales present and within ten days before and after the mysid tow were significantly higher in 2000 than in 1999, but not the number of whales present within five days before and after the tow. Whether this indicates some temporal patterns in whale foraging requires further investigation.

It is likely that the proportions of female mysids increased in 1999 in response to the effects of several years of intensive predation by gray whales and that in the following summer, these mysids were preyed upon more intensively. Higher proportion of female mysids in small populations is consistent with observations by Clutter (1969). Mysids continued to be scarce in Clayoquot Sound through the 2001 season but recently conducted research in the area indicates that mysid populations in the region seemed to have recovered by 2002.

Conclusions

Holmesimysis sculpta was numerically dominant in all areas, however the degree of this dominance was not spatially uniform and was particularly high in the Fitzpatricks. *Neomysis rayi* and *Columbiaemysis ignota* were encountered regularly and were more numerous near Rafael Bay and Estevan Point respectively. *Acanthomysis columbiae* was also encountered regularly, but no more or less in any one area. The other five species of mysids, *Alienacanthomysis macropsis*, *Acanthomysis borealis*, *Disacanthomysis dybowskii*, *Exacanthomysis davisi* and *Neomysis mercedis*, were encountered infrequently but notably all within a convergence zone, suggesting the possibility that this is an area where mysids may arrive if taken up by strong currents. The lower diversity areas correspond with high predation in previous years, whether or not these two are merely coincidental or causally linked is beyond the scope of this study.

No gravid female mysids were found in one particular part of the convergence zone between Siwash and Rafael Points. This may account for the lower median body length of animals found in this area. Male mysids were proportionally higher in the westernmost regions in the study area, while juveniles were more prevalent in Cow Bay and Perez Rocks. Slower currents may explain this prevalence in Cow Bay, no current information was available for the Perez Rocks area. The regions of higher male proportions had lower predation in previous years than those with lower male proportions. It is possible that this is an artifact of slightly higher proportions of females and juveniles, which is a predictable response to heavy predation (Clutter, 1969). Although females and juveniles were not statistically significantly higher in these areas, the combined effect of small differences in two variables that must be rectified in a single third variable may account for the statistically significant differences in the proportion of male mysids observed here.

Generally speaking, gray whale foraging was non - randomly distributed throughout Clayoquot Sound during the summers of 1999 and 2000. The three measures of whale foraging showed higher foraging activity west of Estevan Point and in Nootka Sound than in eastern Clayoquot Sound. Whale utilization of Clayoquot Sound was slightly higher in 2000 than in 1999, however whale sightings in both of these seasons were very low in comparison to previous and subsequent years. Surveys in the area conducted during the mid - nineties, 2002 and 2003 reported many gray whales preying upon mysids. During 1999 and 2000, mysids were not found in the vast majority of net tows and video tows in mysid habitat that readily yielded full nets in previous and subsequent seasons.

Between the two years covered by this study, there were small but significant differences in whale foraging activity with the 2000 season being slightly higher than 1999. Conversely, proportions of female mysids were higher in 1999 than in 2000, suggesting that the increased level in foraging activity in 2000 was a response to a partial recovery in mysid populations. Mysid and whale foraging in the area were low again in 2001 and may be a result of the predation observed in 2000. This, and the fact that the whale and mysid presence were both very low in comparison to other years, underline the need for quantitative biomass data in order to determine the fluctuations of mysids within and between seasons and how this relates to whale distributions.

Taken on their own, these results do not make any concrete conclusions about what dictates the spatial distribution of different species, sexes and life stages of mysids. They do, however, suggest that these distributions are not random at a variety of spatial scales and that the potential for selection of habitat based on both body size and reproductive goals exists. They also provide baseline information concerning the reproductive dynamics of a population of mysids during a period of recovery following several years of intense predation pressure. Similarly, these data will be useful in future comparisons of the species diversity and abundance to determine if these are showing the effects of top - down pressure. More research is needed in order to confirm the prevalence and dearth of juveniles, males, and gravid females in certain areas and to determine of the causes of these variabilities as they may give answers to questions concerning mysid habitat utilization, reproductive dynamics and dispersal.

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RELATIONSHIPS BETWEEN MYSID CHARACTERISTICS AND PREDATION BY GRAY WHALES

INTRODUCTION

It is well established that gray whales (*Eschrictius robustus*) in the eastern Pacific feed extensively along their migration route on a variety of prey including benthic amphipods (Ampeliscidae) (Dunham & Duffus, 2001, 2002; Carruthers, 2000), mysids (Mysidae) (Dunham & Duffus, 2001, 2002; Stelle, 2001), porcelain crab larvae (Porcellanidae) (Dunham & Duffus 2001, 2002) and ghost shrimp (Dunham & Duffus 2001, 2002; Weitkamp *et al.*, 1992). In Clayoquot Sound, British Columbia, Canada, swarming hyperbenthic mysids are the primary prey item of gray whales, however the whales are known to switch back and forth between all of the above prey items occurring in spatially discrete habitats (Dunham & Duffus 2001, 2002). Mysids were found in *Macrocystis pyrifera* and *Nereocystis lutkeana* kelp forests and above rock reefs and boulder piles, whereas amphipods dwelled in the fine sediment of sandy bays and porcelain crab larvae were found throughout the water column. This 'prey switching' prompts the question "What makes gray whale prey *good* prey?"

Two studies of gray whale prey dynamics have discussed body length as a significant factor in prey quality. Dunham and Duffus (2001) reported selection for amphipod patches with a high proportion of individuals 6mm or greater in length and Stelle (2001) reported a positive correlation between gray whale utilization and mysid body length.

Foraging baleen whales are known to seek high prey biomass (Reid *et al.*, 2000; Kann & Wishner, 1995; Murison & Gaskin, 1989; Piatt *et al.*, 1989) as well as particular prey species assemblages (Kann & Wishner, 1995). Penguins foraging upon Antarctic krill *Euphausia superba* target gravid females during times when prey are not readily available (Croxall *et al.*, 1997; Reid *et al.*, 1996). Gravid female mysids carry larvae throughout their development and thus represent additional food value for a prolonged period of time compared to krill or other crustaceans that release larvae in to the water. A study on lipid content of the freshwater mysid (*Mysis relicta*) showed a seasonal variation in lipid content of both male and female mature mysids, however eggs and larvae were removed from gravid females in order to prevent obfuscation of seasonal trends (Adare & Lasenby, 1994). In studying midwater crustaceans in the Southern Ocean, Clarke and Holmes (1986) reported very high lipid content for gravid females of the Caridean shrimps of the genus *Pasiphea.*

Through the comparison of mysids collected randomly to those collected in the presence of foraging whales, this study seeks to determine what, if any, associations exist between the degree of gray whale utilization of mysid prey and the size and reproductive condition of mysids in Clayoquot Sound. This information is key in the identification of critical food resources and habitat of gray whales in the region.

As part of an ongoing program studying the distribution and ecology of gray whales and their prey in Clayoquot Sound, I was able to make use of knowledge gained during previous years, including established whale transects and the locations of patches of mysid habitat. In addition to data collected in this core region, three trips were made to Nootka Sound (40 km north of Clayoquot) in the 2000 season for the purposes of whale census and yielded the opportunity for some mysid sampling.

MATERIALS AND METHODS

Study Area

The study was conducted in the months of May through September of 1999 and 2000 along the outer shore of Flores Island in Clayoquot Sound, located in British Columbia, Canada (Figure 1). During the 2000 season I was able to collect additional data from Nootka Sound, from an area west of Estevan Point and, on one occasion, from Barkley Sound. This area is a focus of ongoing research in to the distributions of gray whales in Clayoquot Sound in the contexts of prey distributions (Dunham & Duffus, 2001, 2002) and whale - watching activities (Bass, 2000; Duffus, 1996).

Collection of Whale Location Data

In order to quantify whale presence in the study area I conducted weekly transects in a discrete summer foraging area (Figure 2). Vessel speed during transects was approximately seven knots (13 km/h). Transects were aborted if visibility became compromised by wave height or fog. The whales' location and activity (traveling or foraging) were recorded. Whales encountered outside the transect area and during other research activities were also recorded.

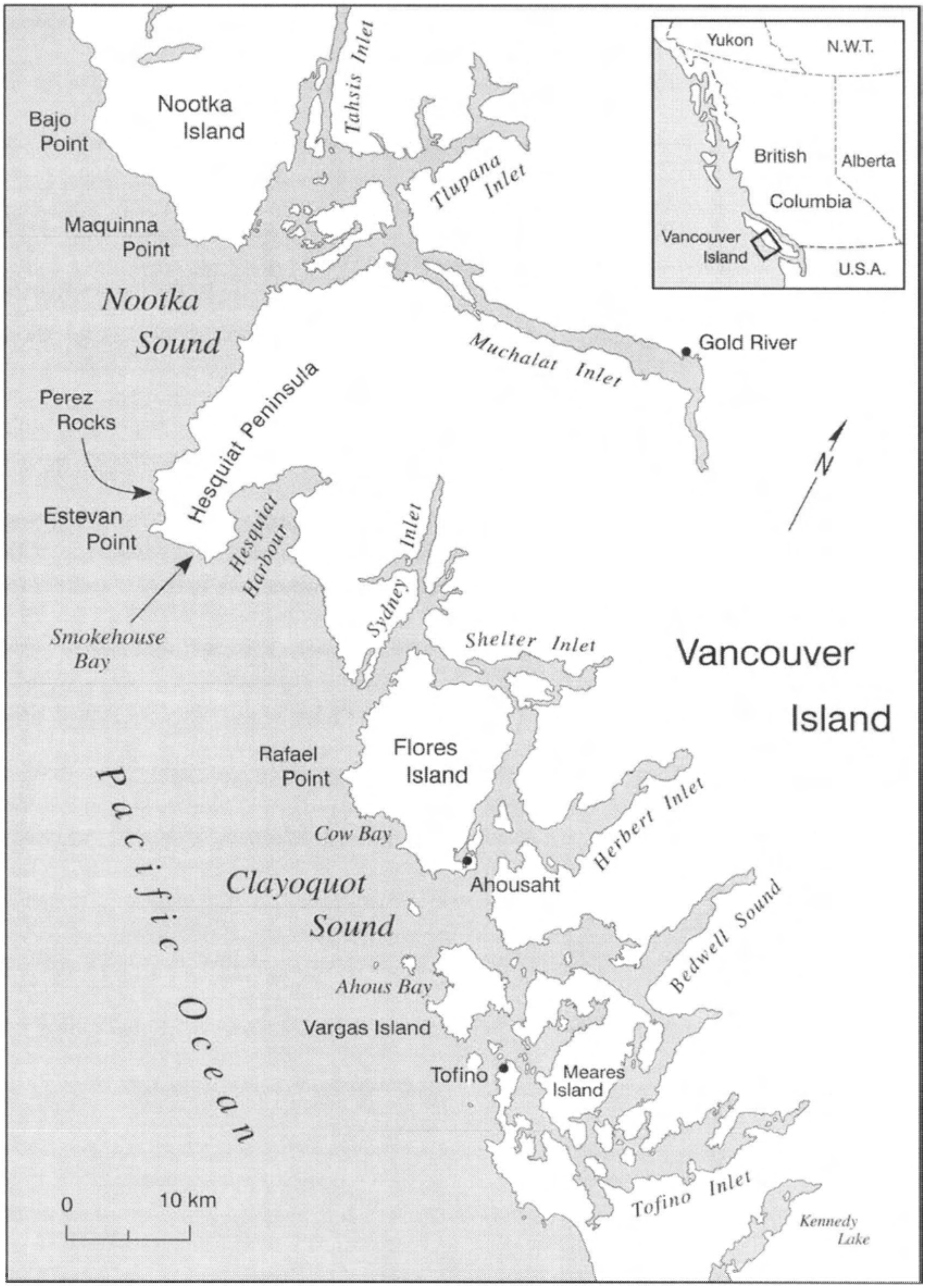

Figure 1. Map showing location of the study area, Clayoquot Sound, British Columbia, Canada.

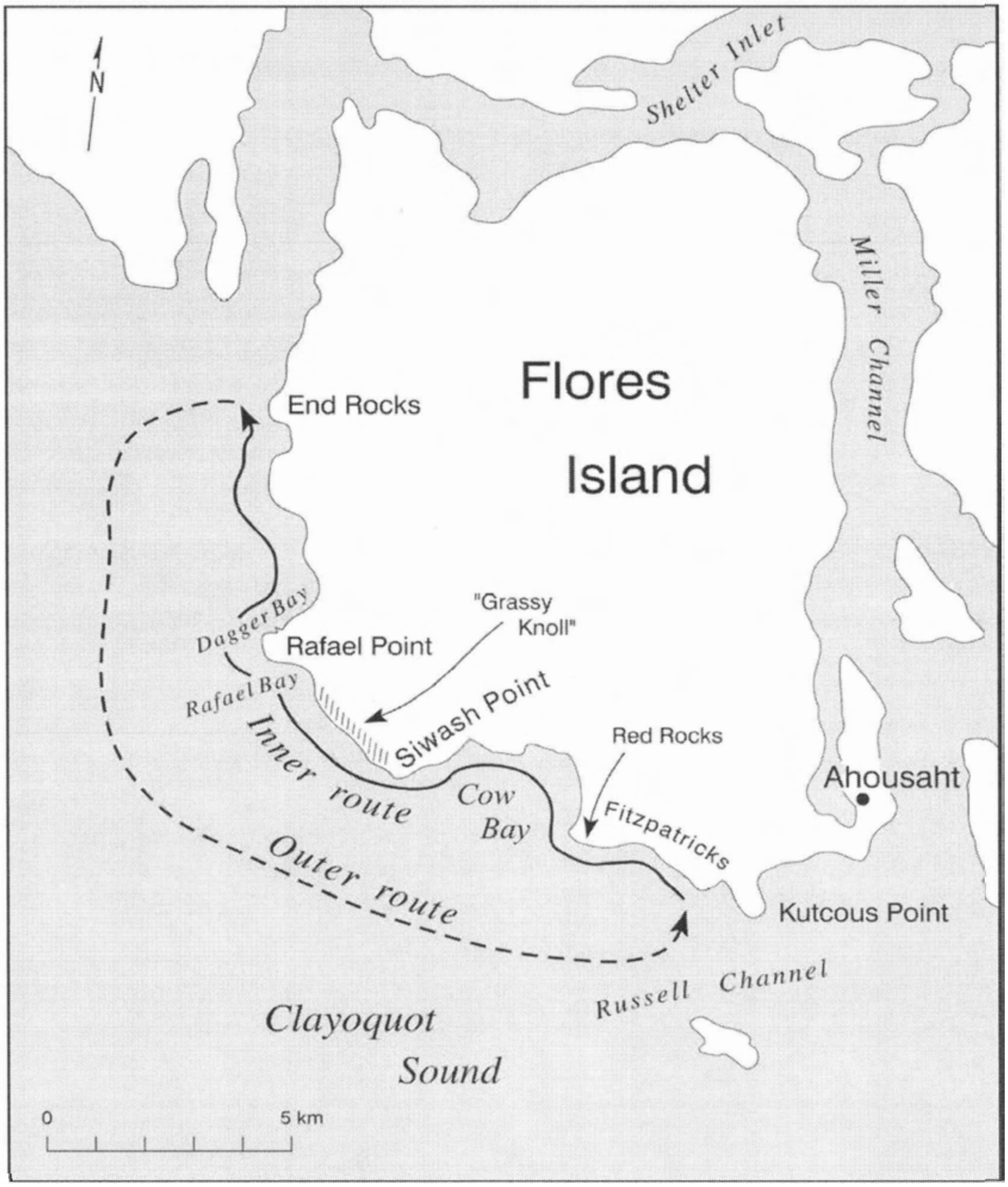

Figure 2. Map showing transect route along the coast of Flores Island.

Whales were determined to be foraging upon mysids by two factors- habitat and whale behaviour. The study area contains discrete habitat patches particular to prey type, the location of these patches are well known (Dunham & Duffus 2001, 2002). Gray whales do not leave a mud-plume when foraging for mysids. Also, the dive times of gray whales foraging upon benthic amphipods are considerably longer than those foraging upon hyperbenthic mysids (Guerrero, 1989).

Three whale variables were constructed. The first was simply the number of foraging whales in the immediate area at the time a mysid tow was conducted. The number of foraging whales encountered within the pre- and proceeding five and ten days, corrected for search effort by dividing the number of days on which full surveys were conducted, were also calculated for each mysid tow. Five and ten days were used as the time periods because they best suited the temporal scale at which the whale data were collected. Although the goal of weekly transects was generally met, sometimes this was not possible due to weather conditions.

Collection of Mysid Samples

To collect mysids I used a bongo net with two 30 cm openings and 500 μm mesh. Whenever I observed gray whales feeding in mysid habitat I deployed the net at the location of the animal after it had made its final dive of an identifiable surfacing run. At times when no foraging whales were encountered I conducted five net tows in randomly selected locations within known mysid habitat. In order to be counted as a valid tow, the net had to drag along the bottom for several seconds, otherwise the tow was not included in analyses. As the profile of these tows contains large vertical components and the horizontal component is at varying speeds over uneven benthos, the accuracy of measurements obtained with a flow meter while towing for mysids is unreliable (Dunham, personal communication) and so no such device was employed. Potential bias against the collection of gravid females because of increased escape ability (Stelle, personal communication) and its effects on this study are detailed in the Discussion.

Enumeration of Mysid Samples

Mysid samples were fixed in a 7% buffered formalin solution and subsequently transferred to 70% ethanol for preservation and analyses. Some samples were too large for each individual mysid to be examined. When this was the case I examined the whole sample and removed individuals belonging to the rarer taxa for individual enumeration and then split the remaining homogenous portion of the sample using a Folsom splitter.

I examined individual mysids using a Bausch and Lomb dissection microscope with 20x eyepieces and an ocular micrometer. Each individual was identified to species according to Kathmann *et al.* (1986). I used elongated fourth pleopods as the indicator of a male and the presence of oostegites as the indicator of a female; if neither were present I counted the animal as a juvenile. When I observed gravid females I noted whether they were carrying eggs, eyed or eyeless larvae and also noted spent females. I used the distance between the anterior tip of the rostrum and the posterior end of the telson to measure total body length in millimeters.

Statistical Analyses

Correlation analysis was used to determine relationships between whale foraging and mysid characteristics such as median body length and percent of individuals of a given life stage. The same mysid characteristics were compared between predated and non - predated swarms. As the whale foraging variables were non - normally distributed (Table 1), nonparametric statistics were employed.

Table 1. Results of one-sample Kolmogorov-Smirnov tests to determine normality of mysid characteristic and whale foraging variables. D = most extreme difference.

Variable		
Median body length	D	0.134
	p	0.611
% Gravid	D	0.206
	p	0.120
% Juvenile	D	0.212
	p	0.102
% Male	D	0.115
	p	0.776
% Female	D	0.117
	p	0.754
% Gravid / % Female	D	0.112
	p	0.843
Female : Male	D	0.213
	p	0.120
Whales present	D	0.238
	p	0.000
Whales + / - 5 days	D	0.162
	p	0.000
Whales + / - 10 days	D	0.184
	p	0.000

Kendall's τ -b, used for ranked data wherein ties are common (Sokal & Rohlf, 1973), was used for correlation analysis. In lieu of two sample t - tests, Mann - Whitney U tests were employed to compare parameters of predated and non - predated mysid aggregations (Sokal & Rohlf, 1973). All statistical analyses were performed using SPSS 11.0 for Windows.

RESULTS

Mysid Sampling

A total of 41 mysid samples, 26 collected at foraging locations and 15 not, were used for analyses. These were collected between July 19 and September 1 1999, between May 25 and September 2, 2000, on June 20 2001 and June 13 2002.

Whale Transects

A total of 30 transects were conducted in 1999 and 2000 (Table 2). Whale data was collected for June 1999 but not utilized in these analyses because no mysid sampling was conducted during this month.

Table 2. Dates of whale transects during the 1999 and 2000 seasons.

Month	1999 dates	2000 dates
June	NA	2, 4, 8, 17, 23, 30
July	11, 15, 19, 22, 28, 30	7, 15, 18, 24
August	2, 4, 7, 12, 16, 22, 26	2, 16, 20, 27
September	2, 8	4

Three trips to Nootka Sound were made during the 2000 season- July 20, July 29 and August 12/13. Trips to Estevan Point were made during both the

1999 and 2000 season. The 1999 trips were made on July 22 and August 8, 13 and 31; the 2000 trips were made on July 20 and 29, August 1 and 12 and on September 2. The goal of longer range trips was to ascertain the presence of whales in adjacent regions when there were no whales in the core study area.

Whale foraging data for mysid samples collected during June 2001 and 2002 were obtained from whale sighting records and transects performed between 10 June and 28 June 2001 and between 4 June and 21 June 2002.

Correlations Between Whale and Mysid Variables

No significant correlations (Kendall's τ -b) were found between whale foraging in the study area and mysid body length or reproductive condition (Table 3).

Table 3. Matrix of correlation coefficients for relationships between whale foraging and mysid body length (mm) and mysid life stage variables.

		Body length	**% gravid**	**% female**	**% gravid / % female**	**% juvenile**	**% male**
Whales	τ	0.046	0.127	-0.031	0.163	-0.025	0.217
present	p	0.740	0.349	0.816	0.247	0.855	0.103
	n	31	32	32	29	32	32
Whales	τ	-0.036	-0.098	-0.125	-0.069	0.178	-0.174
+/- 5	p	0.801	0.483	0.361	0.638	0.196	0.204
days	n	27	28	28	25	28	28
Whales	τ	-0.003	0.075	-0.078	0.075	0.171	-0.245
+/- 10	p	0.983	0.590	0.565	0.606	0.211	0.071
days	n	27	28	28	25	28	28

Characteristics of Predated vs. Non-Predated Mysid Aggregations

When mysids collected from a whale foraging dive location were compared with those collected where whales were not foraging, statistically significant differences in median mysid body length in millimeters and the proportion of juveniles present were detected (Table 4). Mysids collected from dive locations had a higher median body length and a lower proportion of juveniles.

Table 4. Results of Mann - Whitney U tests treating predated and non - predated swarms as groups 1 and 2.

	Body length	**% gravid**	**% female**	**% gravid / % female**	**% juvenile**	**% male**
n_1	25	26	26	26	26	26
n_2	14	15	15	15	15	15
U	102.000	128.000	133.000	123.000	114.500	134.500
p	0.032	0.068	0.093	0.172	0.029	0.101

DISCUSSION

Correlations Between Whale and Mysid Variables

In contrast to a similar study conducted northeast of Vancouver Island (Stelle, 2001), no significant correlations between the presence of foraging whales and mysid body length were found in this study, nor were any significant correlations between the presence of foraging whales and the reproductive state of mysids. A notable difference between this study and Stelle's study is the fact that, because years of heavy predation before this study, mysid populations in Clayoquot Sound were extremely low (see Dunham & Duffus, 2001). Consequently, mysids may have been harder to catch and therefore were sampled in numbers insufficient to disclose existing relationships by correlation analysis, or that under these conditions, whales change their foraging strategy because of a lack of choice in foraging.

Characteristics of Predated vs. Non-Predated Mysid Aggregations

Mysid groups targeted by foraging gray whales contained larger individuals and fewer juveniles than did non – targeted groups. Juveniles of *Holmesimysis sculpta,* the dominant species in this area, ranged from three to eight millimeters. Dunham and Duffus (2001) found that gray whale selection of amphipod prey was based on high biomass and a high proportion of amphipods greater than or equal to six millimeters and suggest that the latter criterion is perhaps a minimum size of amphipod that would be retained in baleen. Thus it is no surprise that whales targeted aggregations containing fewer juveniles.

Another potential avenue for selection against juvenile mysids as prey is that, as a group, they represent less biomass per unit volume than do larger mysids. Stelle (2001) pointed out that, because the distances between individuals in an aggregation are based on body length (Ritz, 1994), a given volume of mysids will yield a higher number of individuals if the body length is smaller but a higher biomass if a lower number of larger individuals are present. This accounts for the greater median mysid body length observed in predated swarms in this study.

The higher proportion of gravid females in mysids in foraging locations approached statistical significance ($p = 0.068$). As gravid females are generally the longest mysids within the population (Clutter, 1969) it is possible that this result is merely an artifact of selection based on body length, however it is possible that gravid females are under – represented in net samples as a result of increased avoidance (Stelle, pers. comm.); gray whales are capable of employing suction to overcome such behaviour, whereas bongo nets are not suitably equipped.

This leads to questions concerning how gray whales select prey- is this done on a visual or trial – and – error basis? Regardless of whether the distinction is made via the eye or the mouth, gray whales target mysids of greater body length. If visual distinction of longer mysids can be made, it is plausible that a distinction could be made for the increased girth of a gravid female. Similarly, if the added biomass of a group of longer mysids is detectable in the mouth, it is plausible that the added biomass of the same number of gravid females is detectable. It is not my intention to suggest either that Stelle's conclusions were in error (gravid females were not reported upon) or that a statistically insignificant, or less significant, factor might be a tail wagging the significant dog. Rather, I wish to suggest that it is not unreasonable to suspect that body length may not be the sole driving factor in gray whale mysid selection for the following three reasons: 1) Gravid females may be under-represented in net samples, therefore an existing significant difference between predated and non – predated mysid aggregations may be discounted because of an artificially inflated p - value. 2) If gravid females are indeed targeted, a significant result for greater body length could be overcalculated because gravid females are the longest animals. 3) Gravid females carry a biomass bonus over non – gravid females or males of the same length, therefore targeting gravid females represents more energetically efficient foraging.

In any event, the greater body length of gravid females dictates that the result of a preference for either fatter or longer mysids will be a preference for gravid female mysids. In large mysid populations, some degree of predation is not likely a detriment to perpetuation. Considering that small populations of mysids tend to contain a higher proportion of gravid females (Clutter, 1969; this study- see Chapters 2 and 4), that gravid females tend to be the longest in a population, that fecundity is a function of body length (Turpen *et al.*, 1994) and that gray whales target mysids of greater body length (Stelle, 2001; this study), predation of already reduced mysid populations has the potential to both hasten depopulation and be very detrimental to reproduction and hence population recovery. Further predation pressure or bottom-up limitations during mysid population recovery could slow or perhaps even preclude recovery. If a new, low stable state is achieved by the mysid population it could be at a level at which efficient foraging by gray whales is not possible, thus rendering previously heavily utilized habitat useless. Further understanding of these processes is necessary in order to accurately assess the habitat requirements of whales and to contextualize changes in whale distribution within areas where human activities, such as fishing, aquaculture, whale watching and coastal development, are taking place at increasing rates.

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MYSID PRESENCE AND AGGREGATION DYNAMICS DETERMINED THROUGH THE USE OF AN UNDERWATER VIDEO CAMERA

INTRODUCTION

Hyperbenthic mysids are known to be an important prey item to foraging gray whales in Clayoquot Sound, BC (Dunham & Duffus, 2001, 2002; Stelle, 2001; Kim & Oliver, 1989). Foraging baleen whales are known to seek high prey biomass abundance (Reid *et al.*, 2000; Kann & Wishner, 1995; Murison & Gaskin, 1989; Piatt *et al.*, 1989). However Piatt *et al.* (1989), citing Brodie 1997 and Kenney *et al.* 1986, suggest that prey biomass density, meaning the amount of biomass per unit volume of water, rather than numerical abundance, is a factor that should be investigated in the predatory habits of baleen whales. Stelle (2001) reported that gray whale predation upon mysids was significantly correlated with a higher mean mysid body length. She reasoned that despite the fact that aggregations of smaller mysids would contain a higher density in terms of the number of individuals, the same volume of water containing an aggregation of larger mysids would represent more biomass.

Clutter (1969) categorized aggregations of mysids based on body orientation of individuals. A swarm contains individuals who are not facing the same direction and may be swimming in different directions, a school contains polarized individuals and a shoal is a very large group comprised of many schools and swarms. Distances between neighbouring individuals in these aggregations are dependent upon body length (Clutter, 1969; Ritz, 1994). The range of these distances tends to be limited in comparison to many other swarming crustaceans (Clutter, 1969).

Patchiness of aggregations creates a number of challenges to the quantitative sampling of mysids. Dunham and Duffus (2001) employed a flow meter in order to quantify water volume, however they pointed out two factors which render it difficult to ascertain precisely how much of the towed volume actually contained mysids. Firstly, the profile of the net tows has an unacceptably high and variable vertical to horizontal ratio; secondly there is no way to know how much of the horizontal component of the tow was made through a group of mysids and how much was made through empty water. Another drawback of net sampling is that it gives no insight in to the nature of the aggregations sampled or how they are distributed in space.

Underwater video imaging has many advantages as a sampling tool. It is relatively inexpensive, nonintrusive and yields reliable data concerning parameters such as the size of the organisms being observed (Pfister & Goulet, 1999; Tiselius, 1998) and community structure (Zettler, 2001). One study of krill aggregations targeted by humpback whales (Dolphin, 1987) yielded insight into the within - patch variability in krill density which drastically improved on previous estimates of whales' caloric intake. A video camera can also provide information about the behaviour of predators and their prey which may or may not, depending on the species and habitat involved, be practically collected by divers (Acevedo - Gutiérrez, 2002; Vostokov *et al.*, 2001; Ponganis *et al.*, 2000).

A major advantage of using video imaging over nets is that the absence of patchily distributed organisms may be determined with confidence and so the distribution of organisms that occur in patches can be accurately described. Net sampling of hyperbenthic mysids undertaken in Clayoquot Sound during the summer of 1999 met with some success, though at the time it was unclear whether the mysids were there but repeatedly missed or simply not there. This chapter reports an attempt to resolve the aforementioned sampling issues with the use of underwater video. Firstly, I aimed to get a clearer picture of the presence and spatiotemporal distribution of mysids in areas of known mysid habitat, one region having experienced several years of intensive predation of gray whales upon the mysid community and another not. Secondly, I wished to determine how the smaller scale dynamics of mysid aggregations, such as density and size, relate to predation and foraging effort by gray whales.

MATERIALS AND METHODS

Study Area

My study area was the outer shore of Flores Island in Clayoquot Sound, located in British Columbia, Canada. I was able to collect some additional data from Nootka Sound and from areas near Estevan Point, Vancouver Island (Figure 1). Flores Island is a focus of ongoing research in to the distributions of gray whales in Clayoquot Sound in the contexts of prey distributions (Dunham & Duffus, 2001, 2002) and whale - watching activities (Bass, 2000; Duffus, 1996).

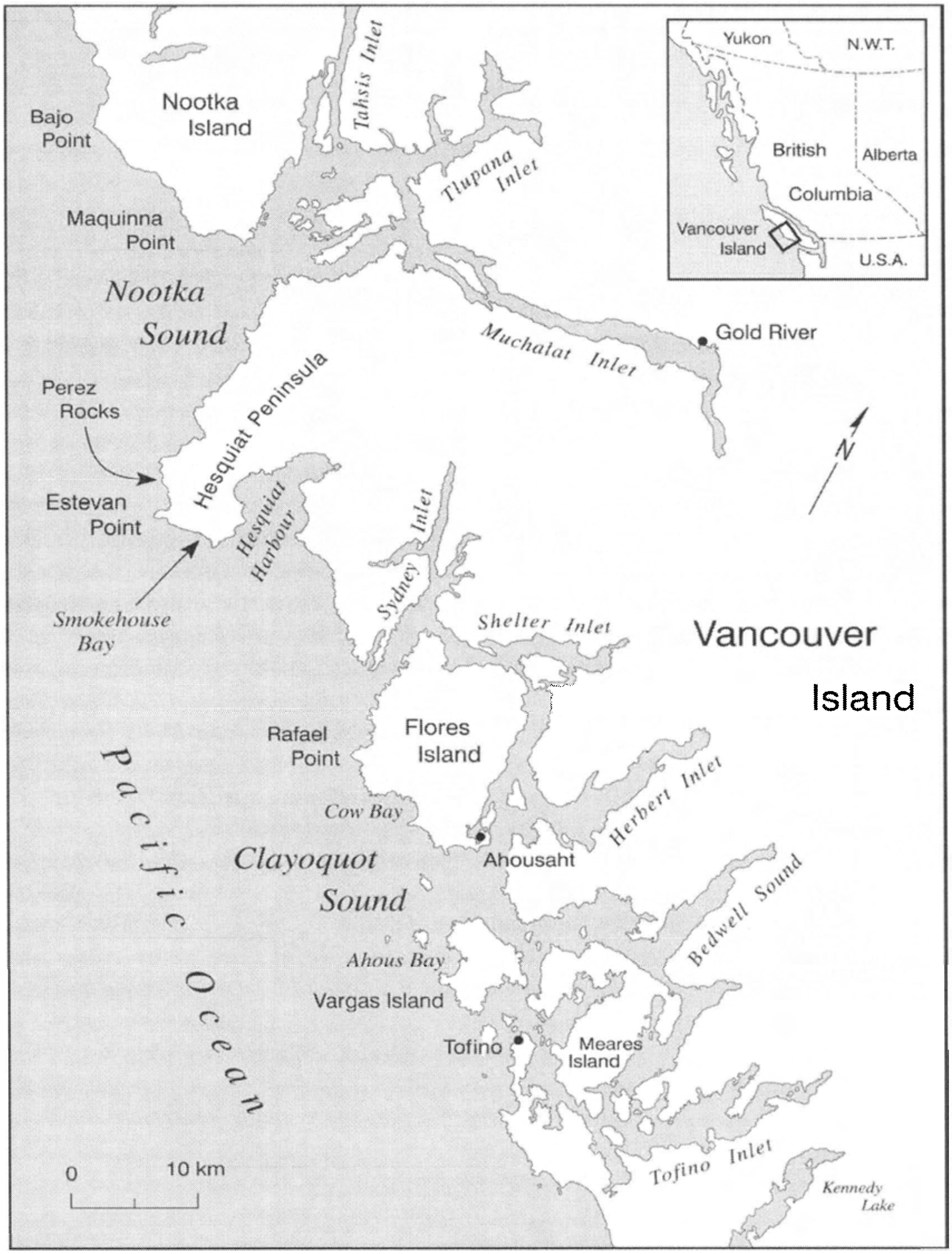

Figure 1. Map showing location of the study area, Clayoquot Sound, British Columbia, Canada.

Deployment of the Underwater Video Camera

To record video data of mysid aggregations I used a low light (2 lux) colour camera in a waterproof housing with a 40 watt light held in an adjacent housing and a scale positioned within the camera's field of view. This array was was connected to a portable VCR/TV monitor, which displayed video in real-time. One individual manipulated the camera array as guided by a second who operated the VCR.

The camera was deployed at randomly selected stations within known mysid habitat on a weekly basis from June through mid-September 2000. When mysids were not encountered I searched throughout the kelp bed or boulder field for no less than fifteen minutes before qualifying this as an absence of mysids. Positions were recorded using GPS.

Interpretation of Video Footage

Video footage of mysid swarms was analyzed on a 27" monitor. For each video segment, the following information was recorded:

- density of the swarm, based on the number of body lengths of individuals and categorized as < 1, 1 - 3, 3 - 5, 5 - 7, > 7 body lengths
- extensiveness of the swarm, based on the degree to which the aggregation appeared to extend when viewed at an oblique angle as opposed to head on. This was a subjective assessment of percent cover, which could not be calculated because it requires knowledge of both camera angle and sea slope.

- patchiness of the swarm, based on the degree to which the aggregation appeared to be a small, isolated cloud of mysids
- classification of the type of aggregation (Clutter, 1969)
- avoidance behaviour (O'Brien and Ritz, 1988)
- the number of other predators, predominantly rockfish (*Sebastes spp.*)
- visibility, rated 1 (very poor) to 5 (excellent) based on colour distortion, obscuring of the scale and reflection of light created by particulate matter

As some of these variables are subjective, all of the material was scanned before interpretation to establish the range of observed qualities. During interpretation I had no knowledge of the location from which the footage was taken, nor did I have any knowledge of the presence or absence of foraging whales in the area with the exception of one segment during which a gray whale appeared in the field of view. This process was repeated and the two sets of records were later compared so as to ensure consistency of interpretation.

Collection of Whale Location Data

In order to quantify whale distribution in the study area I conducted weekly transects in a discrete summer foraging area (Figure 2). Vessel speed during transects was approximately seven knots (13 km/h). Transects were aborted if visibility became compromised by wave height or fog. The whales' location and activity (traveling or foraging) were recorded. Whales encountered outside the transect area and during other research activities were also recorded.

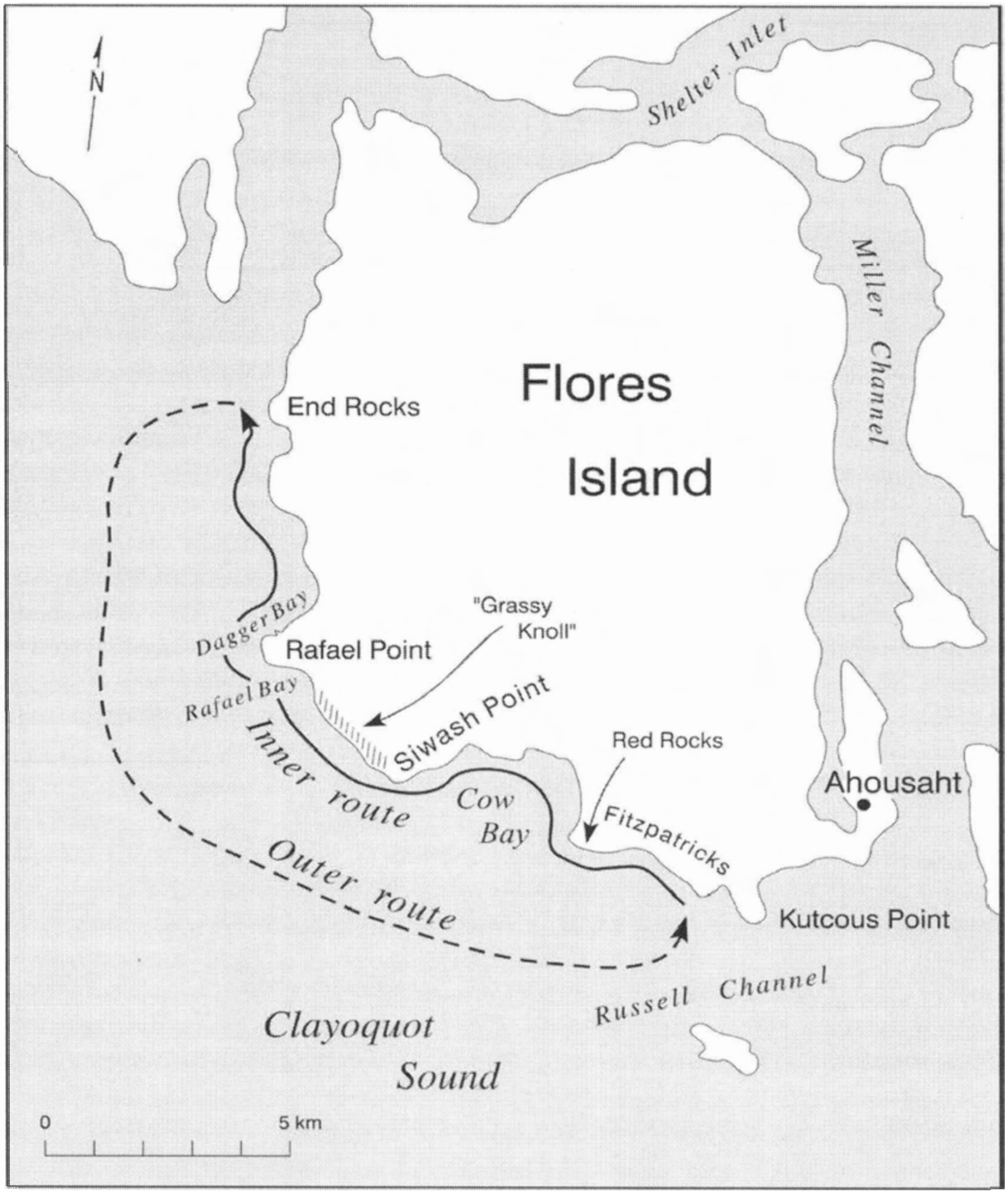

Figure 2. Map showing transect route along the coast of Flores Island.

Whales were determined to be foraging upon mysids by two factors- habitat and whale behaviour. The study area contains discrete habitat patches particular to prey type, the location of these patches are well known (Dunham & Duffus 2001, 2002). Gray whales do not leave a mud-plume when foraging for mysids. Also, the dive times of gray whales foraging upon benthic amphipods are considerably longer than those foraging upon hyperbenthic mysids (Guerrero, 1989).

Three whale variables were constructed. The first was simply the number of foraging whales in the immediate area at the time a video tow was conducted. The number of foraging whales encountered within the pre - and proceeding five and ten days of the video tow, corrected for search effort by dividing the number of days on which full surveys were conducted, were the second and third variables. Five and ten days were used as the time periods because they best suited the temporal scale at which the whale data were collected. Although the goal of weekly transects was generally met, sometimes this was not possible due to weather conditions.

Statistical Analyses

Estevan Point was used as the boundary delineating two areas for spatial analyses. The mysids in the region southeast of Estevan Point were heavily utilized by gray whales in the mid 1990s but not 1999 and 2000, whereas the mysids northwest of Estevan Point were intensively foraged by gray whales during the 2000 season (Duffus, unpublished data). A previous change in the focus of gray whale distributions within Clayoquot Sound is likely a result of changes in prey availability brought about by top -down forces (Dunham & Duffus, 2002; Duffus, 1996), this was considered during analysis of these data.

Correlation analyses were used to determine relationships between whale and rockfish presence and mysid aggregation characteristics. As variables were non - normally distributed (Table 1), nonparametric statistics were employed. Kendall's τ -b, used for ranked data wherein ties are common (Sokal & Rohlf, 1973), was used for correlation analysis. In lieu of two sample t - tests, Mann - Whitney U tests were used (Sokal & Rohlf, 1973) to compare parameters of mysid aggregations based on two criteria; location either southeast and northwest of Estevan Point and whether or not the aggregation was being predated upon by a whale. All statistical analyses were performed using SPSS 11.0 for Windows.

Table 1. Results of one-sample Kolmogorov-Smirnov tests to determine normality of mysid characteristic and whale foraging variables. D = most extreme difference.

Variable		
Mysid density	D	0.191
	p	0.029
Mysid extensiveness	D	0.304
	p	0.000
Mysid patchiness	D	0.279
	p	0.001
Rockfish	D	0.304
	p	0.000
Whales present	D	0.159
	p	0.036
Whales + / - 5 days	D	0.151
	p	0.180
Whales + / - 10 days	D	0.192
	p	0.040

RESULTS

The video unit was deployed 183 times and a total of 58 segments of video footage containing mysids were analyzed (Table 2, following page). The spatial categories represent areas of known mysid habitat based on previous studies of prey (Dunham & Duffus, 2001, 2002) and current profiles (Kopach, 2004). The presence of the camera appeared to be non -intrusive; avoidance behaviour was observed in 55% of segments, however in all cases this was a mild type of avoidance in which the mysid aggregation parted briefly and then reformed around the camera.

Video Footage In and Out of Gray Whale Foraging Locations

Neither rockfish presence nor any of the mysid variables were significantly different for footage taken from foraging locations compared to footage taken from non - foraging locations (Table 3).

Table 3. Results of Mann - Whitney U tests for mysid and rockfish variables for video footage taken from Gray whale foraging locations (Group 1) and non - foraging locations (Group 2).

	Density	Extensiveness	Patchiness	Rockfish
n_1	43	40	36	33
n_2	15	12	15	14
MWU	262.500	180.500	205.500	230.000
p	0.283	0.187	0.173	0.980

Table 2. Mysid presence established by underwater video camera in each segment of the study area during each week of the 2000 season and 2 dates in 2001 and 2002. Y denotes mysid presence, N denotes absence, NS denotes no sampling.

mon dd-dd	2	3	4	5	6	7	8	9	10	11	12	13	14
Jun 27 Jul 4	N	N	Y	N	Y	NS	NS	NS	NS	NS	NS	NS	NS
Jul 5 - 11	Y	Y	N	Y	Y	Y	Y	Y	N	NS	NS	NS	NS
Jul 12 - 18	Y	Y	N	N	Y	N	Y	N	Y	NS	NS	NS	NS
Jul 19 - 25	N	N	N	N	N	N	N	Y	Y	NS	NS	NS	NS
Jul 26 Aug 1	N	N	N	N	N	N	N	N	N	NS	NS	NS	NS
Aug 2 - 8	N	N	N	Y	Y	N	N	Y	N	NS	NS	NS	NS
Aug 9 - 15	N	N	N	N	N	N	N	N	N	NS	NS	NS	NS
Aug 16 - 22	N	N	N	N	N	N	N	NS	NS	NS	NS	NS	NS
Aug 23 - 29	N	N	N	N	N	N	N	N	N	NS	NS	NS	NS
Aug 30 Sep 5	N	N	N	N	N	N	N	N	N	NS	Y	Y	NS
Sep 6 - 12	N	N	N	N	N	N	N	N	N	NS	NS	NS	NS
June 20, 2001	N	N	N	Y	N	N	Y	Y	NS	NS	NS	NS	NS
June 13, 2002	Y	N	N	Y	Y	N	NS	NS	NS	NS	NS	NS	NS

Video Footage From Southeast and Northwest of Estevan Point

Table 4 shows the results of Mann-Whitney U tests utilizing location, either southeast or northwest of Estevan Point, as the grouping variable. Mysid density did not differ significantly between the two areas, however mysid extensiveness and rockfish presence were significantly higher northwest of Estevan Point, while mysid patchiness was significantly greater southeast of Estevan Point.

Table 4. Results of Mann - Whitney U tests for mysid and rockfish variables for video footage taken from southeast of Estevan Point (Group 1) and northwest of Estevan Point (Group 2).

	Density	**Extensiveness**	**Patchiness**	**Rockfish**
n_1	47	42	40	39
n_2	11	10	11	8
MWU	243.000	88.500	29.000	47.000
p	0.757	0.000	0.002	0.000

Correlations of Predator and Prey Variables

The results of correlation analyses of whale, rockfish and mysid variables are shown in Table 5. Mysid density was weakly positively correlated with the number of whales present within ten days before and after the date of collection of the footage. Mysid extensiveness was weakly positively correlated with the number of whales present within both five and ten days before and after the date of footage collection and moderately positively correlated with the presence of rockfish. Mysid patchiness was weakly negatively correlated with the number of whales present at the time of footage collection. Rockfish presence was weakly positively correlated with the number of whales present at the time of footage collection and within ten days before and after footage collection.

Table 5. Correlation matrix of whale, mysid and rockfish variables.

		Whales Present	**Whales +/- 5 days**	**Whales +/- 10 days**	**Rockfish**
Mysid	τ	-0.082	0.188	0.255	0.175
Density	**p**	0.432	0.066	0.013	0.131
	n	58	53	53	47
Mysid	τ	-0.101	0.233	0.368	0.487
Extensiveness	**p**	0.370	0.039	0.001	0.000
	n	52	47	47	42
Mysid	τ	-0.272	0.029	0.072	-0.161
Patchiness	**p**	0.018	0.799	0.524	0.179
	n	51	46	46	47
Rockfish	τ	0.261	0.184	0.348	NA
Presence	**p**	0.035	0.126	0.004	
	n	47	44	44	

DISCUSSION

Mysids were not located frequently during the 2000 season- only a quarter (21 out of 84) of the weekly samples conducted in each area revealed mysids. On a number of occasions, mysids were seen on camera but I was not able to catch them with the plankton net. The degree to which underwater camera improved the probability of locating mysids cannot be quantified as the net was not deployed at the same frequency during the 2000 season when the camera was in use. However, because the camera enabled me to make a thorough visual inspection of mysid habitat and because mysids were never caught at times when they were not located using the underwater video camera, I am confident that mysid absence was not falsely gauged in the video camera data.

Video Footage In and Out of Gray Whale Foraging Locations

Unlike mysid body length and life stage, discussed in Chapter 3, no significant differences in density, extensiveness or patchiness were detected between video footage taken in and out of foraging locations. Though it is possible that this is truly the case, it is also possible that the camera can not reasonably assess these differences. It was much more difficult to accurately place the camera at a foraging location than it was the plankton net and the process takes more time. It is therefore questionable that the video camera was collecting truly representative data in all foraging locations.

Video Footage From Southeast and Northwest of Estevan Point

Mysid extensiveness and rockfish presence were significantly higher northwest of Estevan Point, while mysid patchiness was significantly higher southeast of Estevan Point, suggesting that mysid aggregations located southeast of Estevan Point were both smaller and patchier. This is consistent with Clutter's description of a smaller population of mysids (1969). From a purely descriptive point of view, the discrepancy between footage of a small, patchy aggregation and a large, extensive aggregation of mysids is remarkable. A small swarm is essentially a group of a few dozen loosely aggregated individuals, whereas a large, extensive swarm is a layer of mysids a third of a meter thick that entirely obscures the sea floor from horizon to horizon with the camera panning at several angles. These large aggregations may be several hundred meters in both length and width (Stelle, personal communication). Not surprisingly, whale distributions, on all three temporal scales, were significantly higher northwest of Estevan Point (see Chapter 2). Nearly every animal encountered northwest of Estevan Point was immediately identified as a known individual from previous photoidentification in Clayoquot Sound.

The 1999 and 2000 seasons followed several years of intensive gray whale predation upon mysids in Clayoquot Sound and contained few whale sightings compared to previous years (Duffus, unpublished data). During the 2002 and 2003 seasons, mysids and gray whales preying upon mysids were again abundant. It is most likely that gray whales are capable of depressing mysid populations significantly, though it is also likely that the threshold at which mysid foraging becomes energetically unfeasible is not so low so as to preclude mysid reproduction and population recovery. It is possible that predation upon the amphipod population within the last decade and a half has depressed amphipod numbers below a level from which they may recover, accounting for the lack of bottom - feeding whales observed in Clayoquot Sound in recent years (Duffus, 1996; Dunham & Duffus, 2001). Highsmith and Coyle (1992) outlined the potential for this to occur in the Bering Sea because of the low fecundity and long generation times of ampeliscid amphipods and suggested that there could be further impediment to recovery caused by the subsequent changes to the ecology of the benthos. More information concerning the effects of whale and rockfish predation upon mysids and the effects of bottom - up forces upon mysids is needed to fully understand these cycles so that it is possible to determine the habitat requirements of gray whales.

Correlations of Predator and Prey Variables

Density of mysids was not significantly correlated with the number of whales present at the time when footage was collected or within five days before and after the footage collected, nor was density correlated with rockfish presence. A positive weak relationship was detected between mysid density and the number of whales present in the area within ten days before and after the footage was taken. Stelle's results (2001) showed a negative relationship between mysid density and gray whale foraging, however her measurements were based on the number of individuals per volume of water whereas these are based on the number of body lengths of individual animals in the footage, which was not known. That being the case, this measurement of density does not account for the actual body length of the mysids in the aggregations and therefore no inference concerning the actual biomass represented can be made.

Mysid extensiveness was weakly positively correlated with the number of rockfish present and the number of whales present both five and ten days before and after video footage collection, but not the number of whales present at the time the footage was taken. It is fairly intuitive that predators are going to be spatially linked with their prey, however it has been suggested that the manner in which this occurs in marine systems is variable and dependent upon the species being studied (Benoit-Bird & Au, 2003). While correlations with the whale variables are weak, it should be mentioned that the segments that scored the highest values of mysid extensiveness were not included in the five and ten day analyses because they were collected in areas in the extreme western regions of the study area where the frequency of whale data collection was insufficient to make such calculations. Coupled with the lack of significance for the correlation between the number of whales present at the time and the extensiveness of mysids, this suggests that whales forage in the presence of, but do not spend very long periods of time in the presence of, small mysid aggregations.

Mysid patchiness was weakly negatively correlated with whale foraging at the time data was collected, but no significant correlations were observed with the five and ten day whale variables. It would be reasonable to expect that these negative correlations would strengthen over time as a more patchy mysid aggregation would seem less likely to keep a whale in the area over a prolonged period of time. More sampling is required to further explore this relationship.

Rockfish presence was significantly but weakly correlated with mysid extensiveness. Again, it is no surprise that a more extensive patch will attract more predators, but it is surprising that no other significant relationships were observed between rockfish presence and mysid variables. The rockfish foraging behaviour observed in this study consisted of slow, steady swimming with an open mouth to catch whatever mysids are encountered. No darting movements were observed and no avoidance behaviour was observed in the mysid swarms being preyed upon; this is consistent with the idea that slow moving objects within mysid swarms trigger mild to no avoidance behaviour (Ritz *et al.*, 1997).

Therefore, this type of foraging strategy would seem to be most successful in swarms of a certain size and degree of spatial cohesion- patchy swarms with large inter-individual distances hold less promise in terms of foraging success, although it is possible that other tactics are employed by foraging rockfish under these conditions.

Rockfish presence was also significantly positively correlated with gray whale foraging at the time of data collection and within ten days before and after data collection, but not whale foraging in the five day period. Given the difference in body size between whales and rockfish, it is reasonable to expect that their ranges of movement and temporal foraging scales differ. Marine predators are known to have discernible spatial and temporal foraging patterns on multiple scales (Benoit-Bird & Au, 2003; Fauchald & Erikstad, 2002; Boyd, 1996) and so it is possible that rockfish and gray whales overlap on some scales but not others. Given the potential for whales to reduce mysid populations to low levels and that predation by gray whales likely results in a high proportion of gravid females being removed from the population, further investigation of the foraging habits of rockfish would yield important information concerning the nature and magnitude of impact of rockfish predation upon recovering mysid populations.

Overall, underwater video was useful in determining mysid presence and absence and holds promise as a quantitative tool if a reliable scale device, such as a pair of lasers at known width and angles, is employed. The utility of qualitative data is questionable, though it does represent an improvement over net sampling alone. In addition, the ease of deploying this gear, in comparison to the expense and risks of SCUBA diving in a remote location, make underwater video an attractive method for gaining visual insight in to the distribution and behaviour of epibenthic invertebrates.

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GENERAL CONCLUSIONS

Generally speaking, gray whale foraging and mysid characteristics were non - randomly distributed throughout Clayoquot Sound during the summers of 1999 and 2000. The three measures of whale foraging showed higher foraging activity west of Estevan Point and in Nootka Sound than in eastern Clayoquot Sound. Whale utilization of mysids in Clayoquot Sound was slightly higher in 2000 than in 1999, however whale sightings in both of these seasons were very low in comparison to previous and subsequent years. Surveys in the area conducted during the mid - nineties, 2002 and 2003 reported many gray whales preying upon mysids. During 1999 and 2000, mysids were not found in the vast majority of net tows and video tows in mysid habitat that readily yielded full nets in previous and subsequent seasons. The slight increase in the presence of foraging whales in 2000 may have inhibited the recovery of mysids, resulting another low mysid and whale season in 2001 (Duffus, unpublished data).

The diversity of mysid species was lowest along the eastern portion of the south coast of Flores Island and was highest south of Dagger Point and between Rafael and Siwash Points. This area is known to be very turbulent and a convergence zone (Kopach, 2004) and it is likely that the high diversity of mysid species in this area is a result of oceanographic forces- any animals taken up by strong currents are transported to this area.

Life stages of mysids also exhibited non -random spatial distribution. Males made up a higher proportion of individuals in swarms in the western regions of the study area and represented the lowest proportion in swarms located within Cow Bay. No gravid females were found along a stretch of mysid habitat in the middle of the aforementioned convergence zone. Female to male ratios were higher in Cow Bay than in Perez Rocks. Cow Bay, known to have relatively slow currents, also contained more juveniles than Red Rocks.

Mysid aggregation characteristics were also non – randomly distributed. When groups of mysids were encountered, they were more extensive and less patchy west of Estevan Point than those located east of Estevan Point.

As a whole, the distributions of these characteristics are consistent with the notion that currents and whale predation are both determining factors in mysid distribution and dynamics. The current flow patterns in Clayoquot Sound indicate areas of consistently high and low flow, which may result in non – random distribution of mysid species and life stages. This leads to questions concerning the reproductive strategies of adults and subsequent dispersal of juvenile mysids.

Whales can exert top-down pressure that depresses prey populations to a point where successful and efficient foraging by whales is not possible, thus essentially "fishing out" an area. Because the food chain leading from primary productivity to gray whales is very short, it is very unlikely that predation can result in a trophic cascade. A more likely scenario is that gray whales shape the mysid community in terms of sheer numbers and life stages. The resulting bottom-up effects upon gray whale spatial distribution afford mysid communities respite from predation pressure, during which time it is possible that the low population levels trigger changes in sex ratios and reproductive rates, thus increasing mysid productivity.

Foraging gray whales appeared to target larger aggregations of mysids with greater median body length. Considering that small populations of mysids tend to contain a higher proportion of gravid females and gravid females tend to be the longest in a population (Clutter, 1969), that fecundity is a function of body length (Turpen *et al.*, 1994) and that gray whales target mysids of greater body length (Stelle, 2001; this study- see Chapter 4), predation of already reduced mysid populations has the potential to be detrimental to reproduction and recovery. Should this happen repeatedly, or in conjunction with bottom – up limitations such as low primary productivity or unusual algal blooms, it is possible that habitat previously valuable to gray whales may become effectively empty for years or perhaps decades. Further understanding of these processes is necessary in order to accurately assess the whales' habitat requirements and to understand changes in whale distributions within areas where human activities, such as fishing, aquaculture, whale watching and coastal development, are taking place at increasing rates.

The greatest weakness of this study was that it took place in years of low mysids abundance and it was not possible to collect large numbers of samples containing large numbers of mysids. The lack of samples collected precluded any within – season analysis or description of changes within the ecological and reproductive structure of the mysid community in Clayoquot Sound. This did, however, provide valuable baseline data concerning the characteristics of a recovering population which will be useful for future comparison in low - mysid years. Some questions that arise out of the non -random spatial distribution of gravid females, males and juveniles are what is the home range of a mysid and how far do they disperse as juveniles? How isolated are these animals in terms of reproduction and genetic diversity?

Another hurdle encountered was the quantification of the size of mysid aggregations and the biomass contained within. Originally, the intent was to collect these kinds of data with the video camera, however the precious little footage of mysid aggregations did not yield enough footage of mysids between the lens of the camera and the scale and so quantitative analysis was not possible. As mentioned in Chapter 4, a laser scale device would rectify this, or acoustic methods could be employed.

There are also a few locations within the study area that were not sampled because they were in waters apparently easily navigable by foraging gray whales but not by research vessels. It would be ideal to sample some of these areas by SCUBA, however in most of these locations this can be done safely on only the calmest of days.

Much has been said here concerning the top - down effects of foraging gray whales, but what are the effects of other predators, especially during mysid recovery periods? Conversely, what are the bottom - up forces in this system?

Without the benefit of algal blooms in the winter, how are mysids sustained? The answer to these questions are key to the understanding of the movement of gray whales, and other coastal predators, on a variety of spatial and temporal scales and provide the context necessary to differentiate balanced cycles of abundance from habitat loss.

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APPENDIX 1 - Tabular Results of Pairwise Mann - Whitney U Tests for Mysid Species Variables

Table 1-1. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Holmesimysis sculpta*'.

Area		1	2
2	U	40.000	NA
	p	0.866	
3	U	42.000	20.000
	p	0.643	0.355

Table 1-2. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Neomysis rayi*'.

Area		1	2
2	U	40.000	NA
	p	0.169	
3	U	32.500	23.000
	p	0.226	0.561

Table 1-3. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Columbiaemysis ignota*'.

Area		1	2
2	U	41.000	NA
	p	0.894	
3	U	25.000	15.000
	p	0.037	0.090

Table 1-4. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Disacanthomysis dybowskii*'.

Area		1	2
2	U	40.000	NA
	p	0.751	
3	U	44.000	24.000
	p	0.414	0.285

Table 1-5. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Alienacanthomysis macropsis*'.

Area		1	2
2	U	32.000	NA
	p	0.276	
3	U	40.000	16.000
	p	0.236	0.047

Table 1-6. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Acanthomysis columbiae*'.

Area		1	2
2	U	22.000	NA
	p	0.060	
3	U	47.000	14.000
	p	0.919	0.079

Table 1-7. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Exacanthomysis davisi*'.

Area		1	2
2	U	42.000	NA
	p	1.000	
3	U	42.000	24.500
	p	0.221	0.350

Table 1-8. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Neomysis mercedis*'.

Area		1	2
2	U	42.000	NA
	p	1.000	
3	U	42.000	24.500
	p	0.221	

Table 1-9. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% *Acanthomysis borealis*'.

Area		1	2
2	U	31.500	NA
	p	0.162	
3	U	45.000	21.000
	p	0.761	0.171

Table 1-10. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable 'Number of species observed'.

Area		1	2
2	U	23.500	NA
	p	0.089	
3	U	41.000	20.500
	p	0.560	0.363

Table 1-11. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable 'Simpson's Index'.

Area		1	2
2	U	29.000	NA
	p	0.272	
3	U	38.000	13.000
	p	0.440	

Table 1-12. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Holmesimysis sculpta*'.

Area		**2**	**3**	**4**	**5**
3	U	2.500	NA		
	p	0.012			
4	U	0.000	24.000	NA	
	p	0.008	0.283		
5	U	0.000	11.000	10.000	NA
	p	0.018	0.203	0.450	
6	U	0.000	15.000	10.000	3.000
	p	0.018	0.480	0.450	0.149

Table 1-13. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Neomysis rayi*'.

Area		**2**	**3**	**4**	**5**
3	U	5.000	NA		
	p	0.030			
4	U	0.000	22.000	NA	
	p	0.008	0.204		
5	U	3.500	13.000	14.000	NA
	p	0.166	0.320	1.000	
6	U	5.000	9.000	9.000	5.000
	p	0.321	0.116	0.344	0.375

Table 1-14. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Columbiaemysis ignota*'.

Area		**2**	**3**	**4**	**5**
3	**U**	16.000	NA		
	p	0.353			
4	**U**	12.000	33.000	NA	
	p	0.450	0.769		
5	**U**	4.000	16.000	10.000	NA
	p	0.131	0.479	0.336	
6	**U**	2.000	8.000	5.000	4.000
	p	0.047	0.048	0.049	0.237

Table 1-15. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Disacanthomysis dybowskii*'.

Area		**2**	**3**	**4**	**5**
3	**U**	18.000	NA		
	p	0.527			
4	**U**	12.000	34.000	NA	
	p	0.450	0.862		
5	**U**	8.000	18.000	12.000	NA
	p	1.000	0.527	0.450	
6	**U**	8.000	18.000	12.000	8.00
	p	1.000	0.527	0.450	1.000

Table 1-16. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Alienacanthomysis macropsis*'.

Area		2	3	4	5
3	U	16.000	NA		
	p	0.353			
4	U	8.000	28.000	NA	
	p	0.149	0.397		
5	U	8.000	16.000	8.000	NA
	p	1.000	0.353	0.149	
6	U	8.000	16.000	8.000	8.000
	p	1.000	0.353	0.149	1.000

Table 1-17. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Acanthomysis columbiae*'.

Area		2	3	4	5
3	U	20.000	NA		
	p	1.000			
4	U	5.000	19.000	NA	
	p	0.074	0.080		
5	U	7.500	20.000	5.000	NA
	p	0.850	1.000	0.074	
6	U	7.500	181.000	9.000	7.500
	p	0.850	0.694	0.322	0.850

Table 1-18. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Exacanthomysis davisi*'.

Area		2	3	4	5
3	U	20.000	NA		
	p	1.000			
4	U	14.000	35.000	NA	
	p	1.000	1.000		
5	U	6.000	15.000	10.500	NA
	p	0.317	0.114	0.186	
6	U	8.000	20.000	14.000	6.000
	p	1.000	1.000	1.000	0.317

Table 1-19. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Neomysis mercedis*'.

Area		2	3	4	5
3	U	20.000	NA		
	p	1.000			
4	U	14.000	35.000	NA	
	p	1.000	1.000		
5	U	6.000	15.000	10.500	NA
	p	0.317	0.114	0.186	
6	U	8.000	20.000	14.000	6.000
	p	1.000	1.000	1.000	0.317

Table 1-20. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% *Acanthomysis borealis*'.

Area		2	3	4	5
3	U	14.000	NA		
	p	0.238			
4	U	14.000	24.500	NA	
	p	1.000	0.123		
5	U	6.000	17.500	10.500	NA
	p	0.317	0.658	0.186	
6	U	6.000	17.500	10.500	7.500
	p	0.317	0.658	0.186	0.850

Table 1-21. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable 'Number of species observed'.

Area		2	3	4	5
3	U	7.5000	NA		
	p	0.056			
4	U	2.500	21.000	NA	
	p	0.024	0.137		
5	U	2.000	16.500	12.500	NA
	p	0.074	0.602	0.770	
6	U	2.500	20.000	8.000	7.000
	p	0.820	1.000	0.214	0.762

Table 1-22. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable 'Simpson's Index'.

Area		**2**	**3**	**4**	**5**
3	U	2.500	NA		
	p	0.012			
4	U	4.000	15.000	NA	
	p	0.056	0.051		
5	U	0.000	19.000	7.000	NA
	p	0.018	0.888	0.186	
6	U	0.000	17.000	6.000	5.000
	p	0.018	0.671	0.131	0.386

Table 1-23. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Holmesimysis sculpta*'.

Area	**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3 U	1.000	NA							
p	0.564								
5 U	0.000	0.000	NA						
p	0.016	0.127							
6 U	2.000	0.500	2.000	NA					
p	0.142	0.277	0.023						
7 U	0.000	0.000	0.000	2.000	NA				
p	0.157	0.317	0.127	1.000					
8 U	0.000	0.000	1.000	6.000	1.000	NA			
p	0.046	0.180	0.030	1.000	0.655				
9 U	0.000	0.000	7.000	4.000	1.000	2.000	NA		
p	0.046	0.180	0.425	0.480	0.655	0.275			
10 U	0.000	0.000	3.000	7.000	1.000	3.000	6.000	NA	
p	0.032	0.157	0.038	0.773	0.480	0.289	1.000		
12 U	0.000	0.000	2.000	4.000	1.000	3.000	4.000	3.000	NA
p	0.046	0.180	0.053	0.480	0.655	0.513	0.827	0.289	
13 U	0.000	0.000	3.000	4.000	1.000	3.000	4.000	6.000	4.000
p	0.046	0.180	0.087	0.480	0.655	0.513	0.827	1.000	0.827

Table 1-24. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Neomysis rayi*'.

Area		**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3	**U**	1.000	NA							
	p	0.564								
5	**U**	2.000	0.500	NA						
	p	0.050	0.188							
6	**U**	2.000	0.500	8.500	NA					
	p	0.142	0.277	0.298						
7	**U**	0.000	0.000	1.000	2.000	NA				
	p	0.157	0.317	0.275	1.000					
8	**U**	0.000	0.000	3.000	6.000	0.000	NA			
	p	0.046	0.180	.087	1.000	0.180				
9	**U**	0.000	0.000	4.000	6.000	1.000	1.000	NA		
	p	0.046	0.180	0.138	1.000	0.655	0.127			
10	**U**	3.000	0.500	7.500	5.500	2.000	6.000	6.000	NA	
	p	0.271	0.277	0.218	0.468	1.000	1.000	1.000		
12	**U**	4.000	1.000	2.000	3.000	0.000	2.000	0.000	3.000	NA
	p	0.796	0.564	0.050	0.271	0.157	0.268	0.046	0.271	
13	**U**	4.000	1.000	3.000	3.000	1.000	3.000	3.000	3.000	4.000
	p	0.796	0.564	0.084	0.271	0.637	0.507	0.507	0.271	0.796

Table 1-25. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Columbiaemysis ignota*'.

Area		2	3	5	6	7	8	9	10	12
3	U	1.500	NA							
	p	0.564								
5	U	7.500	2.500	NA						
	p	0.329	0.568							
6	U	6.000	2.000	10.000	NA					
	p	1.000	1.000	0.262						
7	U	1.500	0.500	2.500	2.000	NA				
	p	1.000	1.000	0.568	1.000					
8	U	3.000	1.000	10.000	4.000	1.000	NA			
	p	0.317	0.564	0.888	0.248	0.564				
9	U	4.500	1.500	7.500	6.000	1.500	3.000	NA		
	p	1.000	1.000	0.329	1.000	1.000	0.317			
10	U	3.000	1.000	13.000	4.000	1.000	6.000	3.000	NA	
	p	0.186	0.429	0.827	0.131	0.429	1.000	0.186		
12	U	0.000	0.000	2.000	0.000	0.000	1.000	0.000	1.000	NA
	p	0.037	0.180	0.039	0.019	0.180	0.121	0.037	0.074	
13	U	1.500	0.500	6.500	2.000	0.500	4.000	1.500	3.000	2.000
	p	0.121	0.346	0.304	0.078	0.346	0.817	0.121	0.271	0.275

Table 1-26. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Disacanthomysis dybowskii*'.

Area		**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3	**U**	1.500	NA							
	p	1.000								
5	**U**	9.000	3.000	NA						
	p	0.513	0.705							
6	**U**	6.000	2.000	12.000	NA					
	p	1.000	1.000	0.450						
7	**U**	0.000	0.000	1.000	0.000	NA				
	p	0.083	0.317	0.153	0.046					
8	**U**	4.500	1.500	9.000	6.000	0.000	NA			
	p	1.000	1.000	0.513	1.000	0.083				
9	**U**	4.500	1.500	9.000	6.000	0.000	4.500	NA		
	p	1.000	1.000	0.513	1.000	0.083	1.000			
10	**U**	6.000	2.000	12.000	8.000	0.000	6.000	6.000	NA	
	p	1.000	1.000	0.450	1.000	0.046	1.000	1.000		
12	**U**	4.500	1.500	9.000	6.000	0.000	4.500	4.500	6.000	NA
	p	1.000	1.000	0.513	1.000	0.083	1.000	1.000	1.000	
13	**U**	4.500	1.500	9.000	6.000	0.000	4.500	4.500	6.000	4.500
	p	1.000	1.000	0.513	1.000	0.083	1.000	1.000	1.000	1.000

Table 1-27. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Alienacanthomysis macropsis*'.

Area		2	3	5	6	7	8	9	10	12
3	U	1.500	NA							
	p	1.000								
5	U	9.000	3.000	NA						
	p	0.513	0.705							
6	U	4.500	1.500	13.000	NA					
	p	0.386	0.617	0.779						
7	U	0.000	0.000	1.000	0.000	NA				
	p	0.083	0.317	0.153	0.114					
8	U	1.500	0.500	6.000	3.500	1.000	NA			
	p	0.121	0.346	0.207	0.329	0.655				
9	U	4.500	1.500	9.000	4.500	0.000	1.500	NA		
	p	1.000	1.000	0.513	0.386	0.083	0.121			
10	U	6.000	2.000	12.000	6.000	0.000	2.000	6.000	NA	
	p	1.000	1.000	0.450	0.317	0.046	0.078	1.000		
12	U	4.500	1.500	9.000	4.500	0.000	1.500	4.500	6.000	NA
	p	1.000	1.000	0.513	0.386	0.083	0.121	1.000	1.000	
13	U	4.500	1.500	9.000	4.500	0.000	1.500	4.500	6.000	4.500
	p	1.000	1.000	0.513	0.386	0.083	0.121	1.000	1.000	1.000

Table 1-28. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Acanthomysis columbiae*'.

Area	2	3	5	6	7	8	9	10	12
3 U	1.000	NA							
p	1.000								
5 U	9.000	3.000	NA						
p	0.626	0.705							
6 U	6.000	1.500	13.000	NA					
p	1.000	0.617	0.779						
7 U	1.000	0.500	3.000	1.500	NA				
p	0.564	1.000	0.705	0.617					
8 U	0.000	0.000	3.000	2.000	0.000	NA			
p	0.046	0.180	0.054	0.142	0.180				
9 U	2.000	0.500	5.000	3.500	0.500	4.000	NA		
p	0.246	0.346	0.123	0.329	0.346	0.827			
10 U	6.000	1.500	13.000	7.500	1.500	0.000	2.500	NA	
p	1.000	0.617	0.779	0.850	0.617	0.028	0.172		
12 U	3.000	1.500	9.000	4.500	1.500	0.000	1.500	4.500	NA
p	0.317	1.000	0.513	0.386	1.000	0.037	0.121	0.386	
13 U	4.000	1.000	8.000	5.000	1.000	3.000	3.000	5.000	3.000
p	0.796	0.564	0.416	0.659	0.654	0.507	0.487	0.659	0.317

Table 1-29. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Exacanthomysis davisi*'.

Area		2	3	5	6	7	8	9	10	12
3	U	1.500	NA							
	p	1.000								
5	U	10.500	3.500	NA						
	p	1.000	1.000							
6	U	6.000	2.000	14.000	NA					
	p	1.000	1.000	1.000						
7	U	1.500	0.500	3.500	2.000	NA				
	p	1.000	1.000	1.000	1.000					
8	U	4.500	1.500	10.500	6.000	1.500	NA			
	p	1.000	1.000	1.000	1.000	1.000				
9	U	4.500	1.500	10.500	6.000	1.500	4.500	NA		
	p	1.000	1.000	1.000	1.000	1.000	1.000			
10	U	4.500	1.500	10.500	6.000	1.500	4.500	4.500	NA	
	p	0.386	0.617	0.186	0.317	0.617	0.386	0.386		
12	U	4.500	1.500	10.500	6.000	1.500	4.500	4.500	4.500	NA
	p	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.386	
13	U	4.500	1.500	10.500	6.000	1.500	4.500	4.500	4.500	4.500
	p	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.386	1.000

Table 1-30. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Neomysis mercedis*'.

Area		2	3	5	6	7	8	9	10	12
3	**U**	1.500	NA							
	p	1.000								
5	**U**	10.500	3.500	NA						
	p	1.000	1.000							
6	**U**	6.000	2.000	14.000	NA					
	p	1.000	1.000	1.000						
7	**U**	1.500	0.500	3.500	2.000	NA				
	p	1.000	1.000	1.000	1.000					
8	**U**	4.500	1.500	10.500	6.000	1.500	NA			
	p	1.000	1.000	1.000	1.000	1.000				
9	**U**	4.500	1.500	10.500	6.000	1.500	4.500	NA		
	p	1.000	1.000	1.000	1.000	1.000	1.000			
10	**U**	4.500	1.500	10.500	6.000	1.500	4.500	4.500	NA	
	p	0.386	0.617	0.186	0.317	0.617	0.386	0.386		
12	**U**	4.500	1.500	10.500	6.000	1.500	4.500	4.500	4.500	NA
	p	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.386	
13	**U**	4.500	1.500	10.500	6.000	1.500	4.500	4.500	4.500	4.500
	p	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.386	1.000

Table 1-31. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% *Acanthomysis borealis*'.

Area	**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3 U	1.500	NA							
p	1.000								
5 U	6.000	2.000	NA						
p	0.207	0.453							
6 U	6.000	2.000	8.000	NA					
p	1.000	1.000	0.149						
7 U	1.500	0.500	2.000	2.000	NA				
p	1.000	1.000	0.453	1.000					
8 U	4.500	1.500	6.000	6.000	1.500	NA			
p	1.000	1.000	0.207	1.000	1.000				
9 U	4.500	1.500	6.000	6.000	1.500	4.500	NA		
p	1.000	1.000	0.207	1.000	1.000	1.000			
10 U	4.500	1.500	10.000	6.000	1.500	4.500	4.500	NA	
p	0.386	0.617	0.381	0.317	0.617	0.386	0.386		
12 U	4.500	1.500	6.000	6.000	1.500	4.500	4.500	4.500	NA
p	1.000	1.000	0.207	1.000	1.000	1.000	1.000	0.386	
13 U	4.500	1.000	8.000	4.000	1.500	3.000	3.000	3.000	4.500
p	1.000	0.564	0.521	0.248	1.000	0.317	0.317	0.317	1.000

Table 1-32. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable 'Number of species observed'.

Area		2	3	5	6	7	8	9	10	12
3	U	1.000	NA							
	p	0.564								
5	U	5.000	0.500	NA						
	p	0.175	0.160							
6	U	4.000	0.500	10.000	NA					
	p	0.445	0.264	0.407						
7	U	0.000	0.000	0.500	0.000	NA				
	p	0.157	0.317	0.160	0.147					
8	U	0.500	0.000	3.500	1.000	1.500	NA			
	p	0.072	0.180	0.088	0.067	1.000				
9	U	2.000	0.000	9.500	4.500	0.000	1.000	NA		
	p	0.239	0.157	0.797	0.554	0.157	0.105			
10	U	2.000	0.000	11.500	5.000	1.500	4.000	0.500	NA	
	p	0.150	0.147	0.625	0.372	0.709	0.467	0.711		
12	U	2.500	0.000	7.000	6.000	0.000	0.500	3.000	4.000	NA
	p	0.361	0.157	0.388	1.000	0.157	0.072	0.456	0.435	
13	U	2.000	0.000	9.500	4.500	0.000	1.000	4.500	5.000	3.000
	p	0.289	0.157	0.797	0.554	0.157	0.105	1.000	0.711	0.456

Table 1-33. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable 'Simpson's Index'.

Area		2	3	5	6	7	8	9	10	12
3	U	1.000	NA							
	p	0.564								
5	U	2.000	0.500	NA						
	p	0.050	0.188							
6	U	2.000	0.500	13.500	NA					
	p	0.142	0.277	0.925						
7	U	0.000	0.000	1.000	2.000	NA				
	p	0.157	0.317	0.275	1.000					
8	U	3.000	1.000	3.000	4.000	1.000	NA			
	p	0.507	0.655	0.087	0.480	0.655				
9	U	0.000	0.000	5.000	6.000	1.000	2.000	NA		
	p	0.046	0.180	0.210	1.000	0.655	0.275			
10	U	0.000	0.000	13.000	7.000	1.000	2.000	4.000	NA	
	p	0.032	0.157	0.850	0.773	0.480	0.157	0.480		
12	U	0.000	0.000	8.000	2.000	1.000	2.000	3.000	3.000	NA
	p	0.046	0.180	0.569	0.157	0.655	0.275	0.513	0.289	
13	U	0.000	0.000	8.000	6.000	1.000	3.000	4.000	4.000	3.000
	p	0.046	0.180	0.569	1.000	0.655	0.513	0.827	0.480	0.513

APPENDIX 2 – Tabular Results of Pairwise Mann – Whitney U Tests for Mysid Life Stage Variables

Table 2-1. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% Gravid'.

Area		1	2
2	U	40.000	NA
	p	0.532	
3	U	40.000	22.000
	p	0.532	0.290

Table 2-2. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% Juvenile'.

Area		1	2
2	U	45.000	NA
	p	0.817	
3	U	42.000	30.500
	p	0.643	0.875

Table 2-3. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% Male'.

Area		1	2
2	U	40.000	NA
	p	0.531	
3	U	26.000	15.000
	p	0.090	0.074

Table 2-4. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '% Female'.

Area		1	2
2	U	41.500	NA
	p	0.616	
3	U	48.000	31.000
	p	1.000	0.916

Table 2-5. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable '& Gravid / % Female'.

Area		1	2
2	U	26.500	NA
	p	0.275	
3	U	42.000	17.000
	p	0.869	0.201

Table 2-6. Results matrix of pairwise Mann -Whitney U tests between coarse scale areas for the mysid variable 'Female : Male'.

Area		1	2
2	U	43.000	NA
	p	0.934	
3	U	28.000	22.000
	p	0.186	0.294

Table 2-7. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% Gravid'.

Area		2	3	4	5
3	U	16.000	NA		
	p	0.571			
4	U	10.000	36.000	NA	
	p	0.300	0.717		
5	U	6.000	14.000	10.000	NA
	p	0.564	0.396	0.300	
6	U	5.000	18.000	12.000	5.000
	p	0.386	0.777	0.489	0.386

Table 2-8. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% Juvenile'.

Area		2	3	4	5
3	U	2.500	NA		
	p	0.013			
4	U	8.000	31.000	NA	
	p	0.171	0.424		
5	U	2.500	8.000	12.500	NA
	p	0.110	0.090	0.551	
6	U	1.000	15.000	14.000	4.000
	p	0.043	0.480	0.734	0.248

Table 2-9. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% Male'.

Area		2	3	4	5
3	U	3.000	NA		
	p	0.016			
4	U	3.000	38.000	NA	
	p	0.027	0.859		
5	U	7.000	2.000	4.000	NA
	p	0.773	0.011	0.042	
6	U	4.000	10.000	11.000	4.000
	p	0.248	0.157	0.396	0.248

Table 2-10. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% Female'.

Area		2	3	4	5
3	U	13.000	NA		
	p	0.322			
4	U	14.000	32.500	NA	
	p	0.734	0.505		
5	U	2.000	17.000	15.000	NA
	p	0.083	0.671	0.865	
6	U	5.000	19.000	16.000	7.000
	p	0.386	0.888	1.000	0.773

Table 2-11. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable '% Gravid / % Female'.

Area		2	3	4	5
3	U	17.000	NA		
	p	0.877			
4	U	11.000	20.500	NA	
	p	0.567	0.241		
5	U	6.000	12.000	7.000	NA
	p	0.564	0.355	0.182	
6	U	7.000	16.000	10.000	6.000
	p	0.773	0.758	0.446	0.564

Table 2-12. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the mysid variable 'Female : Male'.

Area		**2**	**3**	**4**	**5**
3	**U**	12.000	NA		
	p	0.355			
4	**U**	13.000	31.000	NA	
	p	0.610	0.630		
5	**U**	6.000	5.000	10.000	NA
	p	0.564	0.045	0.308	
6	**U**	7.000	10.000	12.000	3.000
	p	0.773	0.217	0.497	0.149

Table 2-13. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% Gravid'.

Area	2	3	5	6	7	8	9	10	12
3 U	1.000	NA							
p	0.655								
5 U	8.000	2.000	NA						
p	0.564	0.502							
6 U	5.000	1.000	13.000	NA					
p	0.724	0.480	0.849						
7 U	1.000	0.000	2.000	1.000	NA				
p	0.655	0.317	0.502	0.480					
8 U	0.000	0.000	4.500	0.000	0.000	NA			
p	0.037	0.083	0.123	0.028	0.083				
9 U	5.000	2.000	9.500	6.000	2.000	1.500	NA		
p	0.724	1.000	0.384	0.564	1.000	0.079			
10 U	5.000	1.000	10.000	5.000	1.000	0.000	7.000	NA	
p	0.724	0.480	0.446	0.386	0.480	0.028	0.773		
12 U	4.000	1.000	9.000	3.000	1.000	0.000	6.000	5.000	NA
p	0.827	0.655	0.729	0.289	0.655	0.037	1.000	0.724	
13 U	2.000	0.000	9.000	6.000	1.000	0.000	5.000	2.000	3.000
p	0.275	0.180	0.729	1.000	0.655	0.037	0.724	0.157	0.513

Table 2-14. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% Juvenile'.

Area		2	3	5	6	7	8	9	10	12
3	U	0.000	NA							
	p	0.180								
5	U	1.500	0.000	NA						
	p	0.039	0.124							
6	U	1.000	0.000	11.000	NA					
	p	0.077	0.157	0.570						
7	U	0.000	0.000	2.000	1.000	NA				
	p	0.180	0.317	0.510	0.480					
8	U	1.000	0.000	8.000	5.000	1.000	NA			
	p	0.127	0.180	0.568	0.724	0.655				
9	U	6.000	1.000	8.000	5.000	2.000	4.000	NA		
	p	1.000	0.429	0.255	0.384	1.000	0.476			
10	U	2.500	0.000	6.000	2.000	2.000	2.000	7.500	NA	
	p	0.212	0.157	0.130	0.083	1.000	0.157	0.884		
12	U	1.000	0.000	6.000	3.000	1.000	3.000	5.000	3.000	NA
	p	0.127	0.180	0.304	0.289	0.655	0.513	0.721	0.289	
13	U	3.000	0.000	5.000	3.000	1.000	3.000	5.000	6.000	3.000
	p	0.513	0.180	0.209	0.289	0.655	0.513	0.721	1.000	0.513

Table 2-15. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% Male'.

Area	2	3	5	6	7	8	9	10	12
3 U	0.000	NA							
p	0.180								
5 U	0.000	1.000	NA						
p	0.016	0.272							
6 U	1.000	1.000	9.000	NA					
p	0.077	0.480	0.344						
7 U	0.000	0.000	0.000	1.000	NA				
p	0.180	0.317	0.124	0.480					
8 U	1.000	1.000	8.000	5.000	1.000	NA			
p	0.127	0.655	0.568	0.724	0.655				
9 U	0.000	0.000	12.000	5.000	0.000	6.000	NA		
p	0.034	0.157	0.705	0.386	0.157	1.000			
10 U	5.000	0.000	0.000	2.000	2.000	2.000	0.000	NA	
p	0.724	0.157	0.008	0.083	1.000	0.157	0.021		
12 U	2.000	1.000	1.000	2.000	1.000	2.000	0.000	4.000	NA
p	0.275	0.655	0.030	0.157	0.655	0.275	0.034	0.480	
13 U	3.000	1.000	4.000	4.000	1.000	4.000	3.000	5.000	4.000
p	0.513	0.655	0.137	0.480	0.655	0.827	0.289	0.724	0.827

Table 2-16. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% Female'.

Area		**2**	**3**	**5**	**6**	**7**	**8**	**9**	**10**	**12**
3	**U**	0.000	NA							
	p	0.180								
5	**U**	8.000	2.000	NA						
	p	0.568	0.510							
6	**U**	3.000	0.000	14.000	NA					
	p	0.289	0.157	1.000						
7	**U**	1.000	0.000	3.000	1.000	NA				
	p	0.655	0.317	0.826	0.480					
8	**U**	2.000	0.000	10.000	5.000	1.000	NA			
	p	0.275	0.180	0.909	0.724	0.655				
9	**U**	1.000	2.000	8.000	4.000	1.000	3.000	NA		
	p	0.480	1.000	0.252	0.248	0.480	0.289			
10	**U**	2.000	0.000	11.000	6.000	1.000	3.000	5.000	NA	
	p	0.157	0.157	0.570	0.564	0.480	0.289	0.386		
12	**U**	2.000	0.000	9.000	5.000	1.000	3.000	3.000	5.000	NA
	p	0.275	0.180	0.732	0.724	0.655	0.513	0.289	0.724	
13	**U**	4.000	0.000	10.000	4.000	1.000	2.000	4.000	6.000	3.000
	p	0.827	0.180	0.909	0.480	0.655	0.275	0.480	1.000	0.513

Table 2-17. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable '% Gravid / % Female'.

Area	2	3	5	6	7	8	9	10	12
3 U	1.000	NA							
p	0.655								
5 U	7.000	2.000	NA						
p	0.881	0.770							
6 U	6.000	1.000	9.000	NA					
p	1.00	0.480	0.806						
7 U	1.000	0.000	2.000	2.000	NA				
p	0.655	0.317	0.770	1.000					
8 U	0.000	0.000	1.500	0.000	0.000	NA			
p	0.037	0.083	0.057	0.028	0.083				
9 U	3.000	1.000	6.000	6.000	1.000	0.000	NA		
p	0.513	0.655	0.655	1.000	0.655	0.037			
10 U	5.000	1.000	7.000	5.000	1.000	0.000	6.000	NA	
p	0.724	0.480	0.462	0.386	0.480	0.028	1.000		
12 U	4.000	1.000	7.000	6.000	1.000	0.000	4.000	5.000	NA
p	0.827	0.655	0.881	1.000	0.655	0.037	0.827	0.724	
13 U	4.000	1.000	5.000	4.000	1.000	0.000	3.000	3.000	4.000
p	0.827	0.655	0.456	0.480	0.655	0.037	0.513	0.289	0.827

Table 2-18. Results matrix of pairwise Mann -Whitney U tests between fine scale areas for the mysid variable 'Female : Male'.

Area	2	3	5	6	7	8	9	10	12
3 U	0.000	NA							
p	0.180								
5 U	3.000	2.000	NA						
p	0.180	0.770							
6 U	2.000	0.000	4.000	NA					
p	0.157	0.157	0.142						
7 U	0.000	0.000	1.000	0.000	NA				
p	0.180	0.317	0.380	0.157					
8 U	4.000	0.000	2.000	4.000	0.000	NA			
p	0.827	0.180	0.101	0.480	0.180				
9 U	3.000	1.000	6.000	4.000	1.000	3.000	NA		
p	0.513	0.655	0.655	0.480	0.655	0.513			
10 U	6.000	0.000	3.000	4.000	0.000	6.000	4.000	NA	
p	1.000	0.157	0.086	0.248	0.157	1.000	0.480		
12 U	3.000	0.000	3.000	6.000	0.000	3.000	3.000	4.000	NA
p	0.513	0.180	0.180	1.000	0.180	0.513	0.513	0.480	
13 U	3.000	0.000	3.000	0.000	0.000	4.000	3.000	6.000	0.000
p	0.513	0.180	0.180	0.034	0.180	0.827	0.513	1.000	0.050

APPENDIX 3 - Tabular Results of Pairwise Mann - Whitney U Tests for Whale foraging variables

Table 3-1. Results matrix of pairwise Mann-Whitney U tests between coarse scale areas for the whale foraging variable 'Whales present'.

Area		1	2
2	U	7431.000	NA
	p	0.371	
3	U	2863.000	1605.000
	p	0.000	0.000

Table 3-2. Results matrix of pairwise Mann-Whitney U tests between coarse scale areas for the whale foraging variable 'Whales + / - 5 days'.

Area		1	2
2	U	7233.500	NA
	p	0.304	
3	U	3845.000	1964.500
	p	0.000	0.000

Table 3-3. Results matrix of pairwise Mann-Whitney U tests between coarse scale areas for the whale foraging variable 'Whales + / - 10 days'.

Area		1	2
2	U	5702.000	NA
	p	0.000	
3	U	3107.000	2403.000
	p	0.000	0.002

Table 3-4. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the whale foraging variable 'Whales present'.

Area		2	3	4	5
3	U	3078.500	NA		
	p	0.004			
4	U	3290.500	3681.500	NA	
	p	0.439	0.032		
5	U	3290.500	977.000	1174.500	NA
	p	0.439	0.000	0.001	
6	U	422.500	306.000	430.500	293.000
	p	0.000	0.000	0.000	0.000

Table 3-5. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the whale foraging variable 'Whales +/- 5 days'.

Area		2	3	4	5
3	U	3349.500	NA		
	p	0.053			
4	U	3383.00	3656.500	NA	
	p	0.754	0.055		
5	U	1607.500	1645.000	1597.000	NA
	p	0.857	0.057	0.338	
6	U	278.500	314.000	367.500	150.000
	p	0.000	0.000	0.000	0.000

Table 3-6. Results matrix of pairwise Mann -Whitney U tests between medium scale areas for the whale foraging variable 'Whales +/- 10 days'.

Area		**2**	**3**	**4**	**5**
3	**U**	3423.500	NA		
	p	0.089			
4	**U**	2719.000	2983.000	NA	
	p	0.014	0.000		
5	**U**	1192.000	1325.000	5090.500	NA
	p	0.013	0.001	0.165	
6	**U**	272.000	318.000	349.000	145.500
	p	0.000	0.000	0.000	0.000

Table 3-7. Results matrix of fine scale pairwise MWU tests for the whale foraging variable 'Whales present'.

Area		2	3	4	5	6	7	8	9	10	11	12	13
3	U	191.000	NA										
	p	0.137											
4	U	390.500	45.000	NA									
	p	0.108	0.003										
5	U	889.5	101.000	500.500	NA								
	p	0.014	0.000	0.721									
6	U	948.500	115.500	523.500	1195.000	NA							
	p	0.047	0.001	0.983	0.660								
7	U	184.000	39.500	47.000	109.500	126.00	NA						
	p	0.842	0.694	0.051	0.021	0.063							
8	U	828.000	112.500	345.000	781.500	809.000	116.000	NA					
	p	0.565	0.019	0.438	0.163	0.264	0.309						
9	U	937.000	120.000	402.500	909.500	946.000	121.000	785.500	NA				
	p	0.418	0.009	0.446	0.155	0.271	0.161	0.917					
10	U	651.500	183.000	171.500	396.000	450.000	96.500	447.500	484.000	NA			
	p	0.027	0.608	0.000	0.000	0.000	0.116	0.008	0.002				
11	U	95.000	16.500	27.000	62.000	69.000	13.500	61.500	66.500	43.000	NA		
	p	0.971	0.442	0.223	0.149	0.248	0.647	0.553	0.427	0.161			
12	U	114.500	36.000	15.000	36.000	48.500	9.000	74.500	78.500	124.000	3.500	NA	
	p	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003		
13	U	137.000	49.000	45.000	102.000	103.500	21.000	98.500	127.500	130.500	10.500	69.000	NA
	p	0.009	0.442	0.003	0.000	0.000	0.052	0.006	0.014	0.066	0.121	0.017	
14	U	19.500	4.000	2.500	6.500	9.500	3.000	10.000	8.500	23.500	1.000	36.000	8.000
	p	0.000	0.001	0.000	0.000	0.000	0.002	0.000	0.000	0.001	0.007	0.017	0.004

Table 3-8. Results matrix of fine scale pairwise MWU tests for the whale foraging variable 'Whales + / - 5 days'.

Area		2	3	4	5	6	7	8	9	10	11	12	13
3	U	163.000	NA										
	p	0.045											
4	U	476.000	73.500	NA									
	p	0.708	0.086										
5	U	1058.000	125.500	403.500	NA								
	p	0.293	0.004	0.214									
6	U	1124.500	147.000	464.000	1194.000	NA							
	p	0.577	0.013	0.424	0.684								
7	U	118.000	36.000	51.500	107.500	114.500	NA						
	p	0.075	0.503	0.105	0.029	0.045							
8	U	815.000	103.000	357.000	738.000	794.500	111.000	NA					
	p	0.663	0.016	0.726	0.148	0.346	0.312						
9	U	1019.000	113.000	417.500	910.500	991.500	115.000	746.500	NA				
	p	0.916	0.008	0.623	0.195	0.512	0.136	0.784					
10	U	827.000	120.000	384.500	741.000	805.000	100.500	595.000	701.000	NA			
	p	0.580	0.038	0.947	0.103	0.290	0.151	0.429	0.357				
11	U	53.500	21.000	26.500	47.500	51.000	12.500	41.000	45.000	49.500	NA		
	p	0.135	0.893	0.237	0.070	0.092	0.547	0.159	0.114	0.273			
12	U	39.000	11.000	18.000	38.500	39.000	13.000	53.000	51.000	35.500	4.000	NA	
	p	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005		
13	U	117.000	33.000	54.000	115.500	117.000	21.000	99.000	117.000	94.500	12.000	69.000	NA
	p	0.003	0.068	0.013	0.002	0.002	0.052	0.012	0.010	0.006	0.180	0.165	
14	U	4.000	1.000	1.500	2.500	1.500	4.000	6.000	3.500	3.000	1.000	29.000	8.000
	p	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.007	0.036	0.004

Table 3-9. Results matrix of fine scale pairwise MWU tests for the whale foraging variable 'Whales + / - 10 days'.

Area		2	3	4	5	6	7	8	9	10	11	12	13
3	U	109.000	NA										
	p	0.002	NA										
4	U	447.000	65.500	NA									
	p	0.446	0.045										
5	U	1115.000	90.500	392.000	NA								
	p	0.531	0.000	0.083									
6	U	1191.000	137.000	480.000	1132.000	NA							
	p	0.947	0.008	0.561	0.399								
7	U	93.000	29.000	42.000	86.000	97.000	NA						
	p	0.017	0.212	0.038	0.008	0.017							
8	U	556.000	190.000	283.500	553.500	586.000	137.000	NA					
	p	0.005	0.840	0.115	0.002	0.005	0.830						
9	U	778.000	161.000	419.500	803.500	857.000	150.000	710.000	NA				
	p	0.041	0.103	0.645	0.033	0.088	0.566	0.526					
10	U	610.000	187.000	310.000	614.000	654.000	97.000	493.000	738.000	NA			
	p	0.012	0.681	0.196	0.006	0.017	0.121	0.054	0.576				
11	U	27.000	11.000	14.000	26.000	31.000	14.000	67.000	68.000	27.000	NA		
	p	0.015	0.147	0.036	0.011	0.019	0.730	0.820	0.490	0.034			
12	U	39.000	11.000	18.000	39.000	40.500	7.000	33.000	39.000	32.000	4.000	NA	
	p	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004		
13	U	117.000	33.000	54.000	117.000	121.500	21.000	99.000	117.000	96.000	12.000	37.000	NA
	p	0.003	0.068	0.013	0.002	0.003	0.052	0.012	0.010	0.007	0.179	0.004	
14	U	0.000	0.000	0.000	0.000	0.000	4.000	17.000	12.000	0.000	1.500	29.000	8.000
	p	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.008	0.031	0.004