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Title: Ecological Interrelationships Between Summer Resident Gray Whales (*Eschrichtius robustus*) and Their Prey, Mysid Shrimp (*Holmesimysis sculpta* and *Neomysis rayi*) along the Central Oregon Coast

Abstract approved: ___________________________________
Timothy J. Cowles

The ecological interaction between the largest coastal predator, the gray whale (*Eschrichtius robustus*) and the most abundant shallow water marcrozooplanktonic prey, mysids, were examined in a poorly-understood predator-prey relationship along the central Oregon coast. From 2002-2008, 83 seasonal gray whales were identified. These whales returned each year around the end of May and stayed until mid October preying on mysid swarms as determined from fecal material and feeding behaviors. The two mysid species preyed upon were *Holmesimysis sculpta* and *Neomysis rayi*. This research provided information on the spatial/temporal pattern of mysid distribution, patch composition, density and reproductive dynamics of the mysids and how they affect gray whale distribution, abundance, residency and body condition. A determination was also made how climate affected predator-prey interactions during a warm water climate regime in 2005. In 2005, gray whales spent little time in foraging and fewer days in residence than in other years and many were in poor body condition. Mysid swarms in 2005 were also sparse until August and a large percentage of females had empty brood pouches.

Ecological Interrelationships Between Summer Resident Gray Whales (*Eschrichtius robustus*) and Their Prey, Mysid Shrimp (*Holmesimysis sculpta* and *Neomysis rayi*) along the Central Oregon Coast

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Carrie Newell, Author

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INTRODUCTION

Gray whales (*Eschrichtius robustus*) and epibenthic aggregations of mysids (*Holmesimysis sculpta* and *Neomysis rayi*) are linked in a poorly understood predator-prey relationship off the northwest coast of North America. The goal of this research project was to investigate the temporal and spatial patterns of distribution of summer resident gray whales and examine the ecological interactions with their mysid prey along the central Oregon coast. These large predators must locate, track, and respond to changing prey patterns at different spatial and temporal scales (Russell & Hunt 1992). It is the distribution and density of prey that ultimately determines energetic gains and costs of foraging as well as foraging success and overall predator performance (Boyd 1996). Along the Oregon coast, the response of the ecosystem to variability in upwelling processes may influence the population dynamics of mysids, and those lower trophic level processes will likely influence the foraging and body condition of baleen whales in the region (Newell & Cowles 2006).

Ecological Interactions in the California Current System

The California Current System (CCS) is an eastern boundary current that extends along the west coast of North America from the Strait of Juan de Fuca to the tip of Baja California (Hickey 1998). The system is characterized by seasonal wind-driven upwelling that fuels a productive planktonic assemblage of phytoplankton and zooplankton. Baleen whales in these upwelling systems actively seek areas with high concentrations of prey (Murison & Gaskin 1989; Dunham & Duffus 2001). A good indicator of a productive food web is the presence of foraging baleen whales.

Cetaceans play an important role in the structuring of these productive ecosystems and additional research is needed to define the trophic linkages between cetaceans and their prey (Tynan et al. 2005). In the southern region of the CCS, Croll et al. (1998) found that offshore cetaceans responded to strong upwelling years by consuming certain species of euphausiids and concluded that the distribution of *Balaenoptera* was determined by the high densities of *Euphausia pacifica* and *Thysanoessa spinifera*. The northern sections of the CCS have been less studied than the southern sections, and the influence of upwelling dynamics on nearshore cetaceans in this region are relatively unknown (Tynan et al. 2005).

The research outlined in this thesis was motivated by the need to understand the predator-prey relationship between gray whales and mysids in the nearshore waters of the central Oregon coast. We hypothesize that a gray whale's foraging behavior, distribution and residency time off the Oregon coast is affected by the temporal and spatial distribution of the prey and prey population structure. The objectives of this research were to determine spatial/temporal patterns of mysid distribution, patch composition, density and reproductive dynamics of the mysids and how they affect gray whale distribution, abundance, residency and body condition.

Understanding the distribution patterns of the gray whale will improve our knowledge of how a higher level trophic predator responds to variability of prey abundance within an eastern boundary current system. Primary productivity affects mysid biomass and this ultimately affects the abundance and distribution of gray whales

(Newell & Cowles 2006). This exemplifies bottom up control of trophic interactions. In contrast, top down control is represented by the repeated and intense foraging on mysid swarms by gray whales where they dramatically alter mysid populations (Dunham & Duffus 2001). The gray whale/mysid coupling may include both top down and bottom up control. The research described in this thesis has been motivated by this fascinating ecological interaction.

Overview of the Mysids

There are over 1050 known species of mysids worldwide, with 90% of the species distributed in marine habitats and to a lesser extent freshwater habitats. Over 75% of the mysids are epibenthic, living on or just above the benthic-water interface (Heard et al. 2006). Mysids are commonly referred to as opossum shrimp with their shrimp-like appearance and the fact that adult females brood their young in a marsupium. They are placed in the order Crustacea and Superorder Peracarida. A unique and diagnostic characteristic of the largest family, Mysidae, is the presence of a prominent statocyst on the endopod of each uropod. Statocysts are seldom seen in any other crustacean group (Kathman et al.1986).

Mysids are often the most dominant mobile hyperbenthic faunas of mid-latitude continental shelves and therefore are important constituents of coastal food webs (Hopkins 1965; Heubach 1969). Unfortunately, they are frequently absent from coastal food web models. Their importance in these models is underestimated because mysids link pelagic and benthic food webs by feeding in both habitats and becoming prey to various types of predators in each habitat (Jumars 2006). Since part of the study area (Fig. 2.1: Sites 10,11,12) is also a proposed Marine Reserve, it is imperative that we acquire baseline data in this area on the most abundant macro-zooplankter, mysids, and their role in this coastal food web. Mysids provide the food base for a number of economically important fish in this proposed reserve locality.

Two species of nearshore hyperbenthic mysids, *Holmesimysis sculpta* (W. Tattersall 1933) and *Neomysis rayi* (Murdoch 1885) were collected along the central Oregon coast at the 10m isobath from 2002-2008. These mysids exhibited a clumped distribution termed patchiness. This clumped distribution is a general phenomenon of many oceanic zooplankters: mysids (Clutter 1969; Mauchline 1980; O'Brien 1988; Ritz 1997), euphausiids (Brinton 1962; Hamner et al. 1983; Hamner 1984; Nicol 1984; Daly & Macaulay 1991), and copepods (Alldredge et al. 1984; Ambler et al. 1991; Buskey & Peterson 1996; Yen & Bundock 1997). Patchiness is also seen in phytoplankters (Tiselius 1992), fish (Breder 1967, Pitcher et al. 1982), cephalopods (Hurley 1978; Sauer et al. 1992), and many other groups of species found in both terrestrial (Gueron et al. 1996) and freshwater (Caldwell 1989) habitats. The distribution of these species was patchy on a range of scales from fine to broad (Levin 1992). Since patchiness is seen on a broad range of scales and is a general phenomenon, it is of evolutionary and ecological importance to both predators and prey (Haury et al. 1978).

Mysid Sampling Problems

Patchiness causes difficulties in mysid population studies because mysids can occur in alternate parts of their environment at different times due to changing physical and chemical factors. When sampling mysids, large discrepancies can exist from one day to the next in the same locality. Often it is unclear as to whether changes are due to predation (Mauchline 1980) or immigration and emigration in conjunction with horizontal migration in an onshore-offshore direction (Jumars 2006) or if the sampling procedure simply missed the patch (Patterson 2004). To account for these discrepancies, one has to understand the horizontal and vertical range of each species and the species' habitat preference. An effective sampling regime introduced by Mauchline (1980) was to take small samples from relatively small volumes of water and sample through and beyond the local ranges of each of the species studied. This sampling methodology works well in coastal areas having a number of relatively discrete environments since many mysid species persist in certain areas and are therefore restricted only to that one habitat. The persistence of individuals staying in certain areas often is designated as site fidelity. A proximal cue to mysid persistence may be due to their affinity for certain substrates and depth specifications (Clutter 1969; Wittman 1977; O'Brien 1988).

Not only are mysids chronically undersampled in the field due to their extreme patchiness (Fulton 1982; Omori & Hamner 1982) but they also exhibit effective evasion and avoidance tendencies (Wiebe & Holland 1968). Another problem is that some hyperbenthic mysids bury themselves during daylight hours and totally disappear if crevices and vegetation are not available (Jumars 2006).These problems may misconstrue the relative importance of mysids in many coastal ecosystems. Therefore, mysids’ importance may not be fully recognized due to the underestimation of their abundance (Daly & Damkaer 1986).

An effective way to understand the spatial and temporal distribution of mysids and determine the density within hyperbenthic swarms has been SCUBA (Stelle 2002). Although this method allows direct observations of a swarm, it is plagued with numerous problems, including the risk to divers due to dangerous conditions in high surge areas, as well as poor visibility. To safely dive in these areas, you need optimal weather conditions.

School and Swarm Characteristics

Mysids are obligate swarmers that aggregate continuously throughout their life (O’Brien 1989). In common with fish schools (Pitcher 1986), mysid aggregations are characterized by having clearly defined margins, an abrupt change in density from inside to outside, concentrations inside the aggregation two to three orders greater than average abundance, no permanent leaders and members that don’t occupy fixed positions (Ritz 1994; Folt & Burns 1999). The aggregations can be called a school, swarm or shoal (Modlin 1990). Using a modification of terminology from Zelickman (1974), Wittman (1977), O’Brien (1988), and Modlin (1990), the terms school, swarm, and shoal will be defined based on the size of the aggregation and the orientation of its members. **Shoals** are large aggregations in horizontal extent, with individuals uniformly spaced, swimming parallel and in the same direction (polarized); **schools** are smaller polarized aggregations and **swarms** are smaller cohesive groupings composed of non-parallel swimming individuals.

Aggregations can also be classified as to their type of movement. They form either stationary or migratory aggregations on the basis of their social behavior. The stationary type is characterized by maintenance of the entire group of zooplankters at the same location. Many individuals within a stationary aggregation have a substrate or depth preference. The migratory type is characterized by active, horizontal migration (Ohtsuka et al. 1995). Individuals making up a stationary or migratory aggregation can be either obligate swarmers/schoolers like mysids that aggregate continuously throughout their life history or facultative swarmers/schoolers like euphausiids that aggregate only during certain seasons or stages of maturity (O'Brien 1989). Each aggregation also has a characteristic shape, density, size, species, stage and sex composition (Mauchline 1980).

Benefits and Costs of Swarming

It is assumed that cost-benefit functions have been the major factors driving the evolution of zooplankton swarming. The benefits of swarming behavior are generally assumed to be: protection from predators (Folt 1987; O'Brien & Ritz 1988; Ritz 1991; Parrish & Turchin 1997), feeding and foraging efficiency (Parrish & Turchin 1997; Ritz 1997), reproduction facilitation, (Clutter 1969; Mauchline 1980), and energy conservation (Buskey 1998; Ritz 2001). In contrast, the costs of swarming may include reduced foraging efficiency and increased risk of predation by large, engulfing predators (Ritz 1997).

Mysids as Part of the Food Wed

Mysids play an important role in the food chain of temperate inshore waters of the North American coast by being both predator and prey (Hopkins 1965). Acting as primary or secondary consumers, they are a link in the energy flow between primary and secondary production to higher trophic levels (Viherluoto et al. 2000). Mysids can be omnivorous, with diets ranging from detritus to large microalgae or carnivorous, eating protists and smaller zooplankters (Jumars 2006). Mysid feeding is often selective and many times they have the potential to influence zooplankton, phytoplankton, and meiofaunal communities (Roast et al. 1998). Mysids are important as convertors of organic detritus to animal tissue (Hopkins 1965).

Mysids also provide a food source for many potential predators due to their high densities, in excess of 10^5 individuals/m^3 (Moffat & Jones 1993) They are prey for many larger predators such as cephalopods and decapods (Jumars 2006), ostracods and isopods (Mauchline 1980) and various fish (Hostens & Mees 1999). Various species of *Neomysis* are eaten by chinook salmon, Pacific sanddab and petrale sole (Mauchline 1980). An ecologically important group of fish associated with kelp beds off the California coast prey to a considerable degree on swarms of mysids living in this habitat (Love & Ebeling 1978). Birds including penguins, eider ducks, kittiwakes, and various species of alcids (Mauchline 1980) and marine mammals (Dunham & Duffus 2002, Stelle 2002) also depend upon mysids as a prey base.

Overview of the Gray Whale

There are approximately 76 species of cetaceans in the Order Cetacea of which 12 species are baleen whales in the Suborder Mysicete (Carwardine 1995). All baleen whales depend upon patches of fish or zooplankton prey to sustain their massive bodies. One of the largest coastal predators along the central Oregon shoreline is the eastern Pacific gray whale at 13-14m and 35,000kg. The gray whale is the sole member in the family Eschrichtiidae and it is the only baleen whale that regularly suction feeds on infaunal benthic organisms especially gammaridean amphipods (*Ampelisca* sp.) (Nemoto 1959, Nerini 1984). Besides benthic suction, gray whales also exhibit surface skimming for pelagic crabs (*Pleuroncodes* sp.) and other crab larvae found in the upper water column (Oliver et al. 1984).

Gray whales must rely on dense concentrations of prey in order to obtain their daily caloric requirements and they typically forage only in areas of high prey abundance, normally found in high latitudes (Murison & Gaskin 1989; Dunham & Duffus 2001). Tynan et al. (2005) stated that baleen whales must encounter a critical threshold of prey density to make their foraging energetically efficient. To achieve this prey threshold, gray whales undergo one of the longest mammalian migrations recorded, from the breeding lagoons on the western coast of the Baja California Peninsula, Mexico to the northern seas of Alaska. In the Arctic, they harvest their entire year’s energy requirements in four to six months of feeding (Highsmith & Coyle 1992). In the Bering and Chucki Seas, they feed primarily on the 30mm benthic amphipod, *Ampelisca macrocephala,* which reach concentrations of 10,000 individuals per square meter (Feder 1981).

Recently, these feeding grounds have had lower productivity and may no longer contain sufficient biomass to meet gray whale feeding requirements (LeBoeuf et al. 2000). Two reasons may have attributed to this deficiency: an increase in gray whale numbers that have exceeded their carrying capacity or an overall decrease in amphipod biomass. Gray whales have increased by 3.2% per year and now an additional 500 whales are foraging in areas of the Bering and Chucki Seas. Carruthers (2000) states that whales have the capacity to alter the prey base by the large numbers of prey they consume and gray whales can depress amphipod numbers to a level where they can't recover. From the early to mid 90's, Highsmith and Coyle (1992) reported a 50% decrease in the amphipod biomass and suggested that this decrease may be attributed to increased water temperatures in the region. Amphipods exhibit temperature-dependent growth and maturation rates with warmer temperatures resulting in a smaller adult size, smaller brood size and a reduced life span. The starving of gray whales in 1999 and ultimately the die off of around one fourth of the Alaskan population was most likely caused by a decline in the biomass of their principal prey, amphipods, due to the combined effects of increased temperatures and increased predation from the growing population of the whales themselves (LeBoeuf et al. 2000).

Dunham and Duffus (2001) also noted a change in prey base off Vancouver Island. Previous to 1997, ampeliscid amphipods were the main prey item in Clayoquot Sound, British Columbia but after 1997, the whales switched to eating primarily mysids. These changes in the gray whales' prey in both Alaska and Clayoquot Sound may have been caused by bottom up control associated with decreased primary and secondary productivity or by top down control by overgrazing of a predator or a combination of both.

Seasonal Residents or Pacific Coast Feeding Aggregation (PCFA)

Over the last 20 years, about 250 gray whales out of a total population of 20,000 have abbreviated their northern migratory route and have taken up summer residency in various areas along the Northwest coast (Calambokidis 2002). These whales that feed through the summer and fall in the Pacific Northwest are a group that have been referred to as "seasonal residents" or the Pacific Coast Feeding Aggregation (PCFA) (Calambokidis 2009). Photographic identification of these individuals began in the 1970's off Vancouver Island (Darling 1984). Many individuals from this group consistently return to the same feeding areas (Calambokidis 2002) unless the prey base is absent (Newell & Cowles 2006).

There may be a number of reasons why this small population of gray whales have truncated their northward migration. The foremost reason is food. Over the years, a sufficiently dense and calorically efficient food source, mysids, was found along the coastal areas of the Pacific Northwest. Besides an ample food source, other advantages may include having a shorter round-trip migration with less energy expended from traveling, a longer foraging period and less heat energy lost in the warmer temperate waters versus the Arctic waters. In fin whales, the heat loss in the subtropics is 50% that of the Antarctic (Brodie 1975). Gray whales remaining off the Oregon coast may satisfy their lipid cache and pay less overhead for maintaining their body temperature since Oregon waters average 12.8°C in early summer whereas early summer in the Arctic only averages 2.1°C. On a purely caloric basis, Brodie (1975) found that fin whales needed 1825 kg/day of food in the Antarctic but only 800 kg/day in the warmer waters of temperate and subtropical oceans.

The following two chapters will describe how summer resident gray whales respond to changing climatic conditions, variability in mysid swarm parameters, and how both bottom up and top down control affect gray whales and their mysid prey.

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I collaborated with my advisor, Dr. Tim Cowles, to get this paper published.

UNUSUAL GRAY WHALE (*Eschrichtius robustus*) FEEDING IN THE SUMMER OF 2005 OFF THE CENTRAL OREGON COAST

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Abstract: The climate of the North Pacific underwent an unusual event in the summer of 2005 with a very late spring transition. This event had profound effects on both resident gray whales (*Eschrichtius robustus*) and their food source, mysids, off Depoe Bay, Oregon. Near bottom swarms of gray whales' major prey item, *Holmesimysis sculpta*, were sparse until August, a marked contrast to normal years when mysid swarms are abundant all summer. A large percentage of mysid females had empty brood pouches in 2005 while in 2003 and 2004 all observed females had full brood pouches. Gray whales spent little time foraging and spent fewer days in residence than in earlier years. The 2005 resident whales also showed signs of poor body condition, reflecting a nutritional deficit.

Introduction

The California Current System had unseasonably warm sea surface temperatures (SSTs) in early summer of 2005 (Kosro et al., submitted, Pierce et al. submitted), and the subsequent effects manifested themselves through all trophic levels (Thomas & Brickley, submitted, Brodeur et al., submitted). Ecosystem production and structure was affected by this climate abnormality. Upper trophic levels were especially responsive to these anomalous oceanographic conditions, with unprecedented reproductive failures of a planktivorous seabird, the Cassin's auklet, *Ptychoramphus aleuticus*, off northern California (Sydeman et al., submitted). Biomass of euphausiids was also reduced off central California compared to previous years (Sydeman et al., submitted). As will be described below, ecosystem responses observed off the central Oregon coast included substantial decreases in near-shore biomass of mysids (*Holmesimysis sculpta*) and reduced foraging, residency time, and poor body condition of resident gray whales (*Eschrichtius robustus)*. In this paper we examine the impact of anomalous atmospheric conditions and delayed upwelling in late spring/early summer on gray whale foraging behavior, most likely as a consequence of reduced availability of mysids to the whales.

Gray whales and other baleen whales rely on dense concentrations of prey in order to obtain their daily caloric requirements and they typically forage only in areas of above-average prey abundance (Murison & Gaskin 1989; Dunham & Duffus 2001**,** 2002). Gray whales migrate from breeding grounds in Baja California to high latitude feeding areas in the Bering and Chukchi Seas, and they harvest their entire year's energy requirement in four to six months of feeding (Highsmith & Coyle 1992). In the Arctic, they feed primarily on benthic amphipods which can reach concentrations of 10,000 individuals per square meter (Feder 1981). Over the last 20 years, about 250 gray whales have abbreviated this northern migratory route and have taken up summer residency in various areas along the Northwest coast (Calambokidis 2002).

Along the central Oregon coast, mysids are the primary prey of gray whales with porcelain crab larvae an occasional minor component of the diet. These items have been confirmed as prey by analysis of whale feces and observations of whale feeding behavior (Newell 2005).

Mysids form hyperbenthic swarms along the coast, attaining considerable biomass. These swarms may attain sufficient biomass in April or May for gray whales to consume the quantity of food per day (approximately 10^3 kg) which adults require (Nerini 1984). Swarms disappear from the shallow nearshore habitat in October or November, possibly due to predation pressure from the gray whales or due to population migration to deeper depths.

Methods

We have documented 19 different locations along the central Oregon coast between Lincoln City and Seal Rock where gray whales repeatedly forage. These locations have been surveyed since 2000 (Figure 1.1), and all possess recurring hyperbenthic swarms of mysids (*H. sculpta)* near the 10m isobath. Each mysid swarm location was characterized by the abundance of kelp, type of benthic substrate and water depth. Repeat sampling visits to swarm locations confirmed that mysid swarms recurred annually at most of these sites, based on plankton tows, underwater video observations, and in situ observations using SCUBA. This paper focuses on three distinct swarm locations between Government Point and North Point, a distance of 3.5 km (Figure 1.1), which were sampled repeatedly between April and November in

2003, 2004, and 2005. These feeding sites ranged from 4 m to 14 m in water depth, located approximately 0.4 km from shore and were over a basalt substrate. We characterized mysid swarms by collecting samples with a 0.5 m diameter, 70-*u*m mesh plankton net, and by using SCUBA surveys to obtain dimensions of swarms as well as spatial separation of individual mysids in the swarm. Underwater video observations and echosounder patterns (fish finder) complemented the net and SCUBA sampling in and around mysid swarms. Swarm thickness at each sampling location was estimated from echosounder traces and video observations. We confirmed the swarm dimensions estimated by the echosounder with monthly SCUBA observations, weather permitting. Since gray whales occasionally were observed skim feeding at the sea surface, we conducted additional net sampling to capture the crab larvae occupying the surface layer. These collections were done by towing the plankton net horizontally through the upper 2 m of water for a known distance.

Plankton samples from mysid swarms were preserved in 70% ethanol. Samples typically contained 20 to 500 mysids, which were identified and measured using a dissecting microscope which had 20X eyepieces and an ocular micrometer. Male mysids were identified by elongated fourth pleopods, while the presence of oostegites defined a female. If the specimen possessed neither, it was counted as a juvenile. The brood pouches of gravid females were dissected and the eggs or juveniles were counted.

We did not sample temperature or chlorophyll directly, but relied upon temperature information from moored sensors operated by the PISCO program (http://www.piscoweb.org) and from the long-term mooring 10nm west of Newport OR (see Kosro et al. this volume). Surface chlorophyll estimates were made available by Dr. A. Thomas (see Thomas & Brickly, this volume). Our interpretation of mysid and whale behavior is linked to physical conditions and surface chlorophyll conditions evaluated in the companion papers in this volume by Kosro et al., Pierce et al., Hickey et al., and Thomas & Brickly.

Resident Whales

Some gray whales leave the northern migration route from Baja California to Alaska and feed along the Oregon coast from May through October. We identify gray whales as residents if they: 1) return to one of the prey habitats around Depoe Bay or Newport in succeeding years, 2) spend a minimum of two days in a known feeding locality and 3) exhibit feeding behavior. Resident gray whales were observed daily during six summer field seasons (2000-2005) off central Oregon from observations made on fishing boats or Zodiacs when weather and sea conditions permitted.

Each gray whale was photographed to provide a photo library for subsequent identification of individual whales. The dorsal hump on a gray whale has characteristics unique to each individual, so both the right and left sides of each whale were photographed using a 300 mm lens. On each sighting, the whales' location (based on GPS) and behavior were noted and additional photographs were taken to determine body condition.

Two visible features of the whale body form permit us to assess body condition. Good body condition was assumed if the region from the blowholes to the upper back (distance of 2-3 m) was linear and the scapula was not a visible protuberance under the blubber layer (Figure 1.2a, 1.2b). In contrast, whales with poor body condition possessed a depression behind the blowholes or upper back and a pronounced protuberance of the scapula (Figure 1.2c, 1.2d, 1.2e). We note that such pronounced depression of the back profile is not seen during swimming movements of whales with good body condition.

Feeding Modes

Resident gray whales exhibit two distinct feeding behaviors off the Oregon coast. While feeding on benthic swarms of mysids, the whales roll onto their right side with the left tail fluke sticking above the water surface. This is the most common feeding behavior displayed by the resident gray whales in this area. We documented the presence of mysids during this whale behavior, using opportunistic and systematic plankton tows, SCUBA surveys, echogram traces, and underwater video. This “mysid feeding mode” was also confirmed through analysis of whale feces. During the second, much less common feeding mode, the whales swim at the surface with the mouth slightly agape. This “skim feeding mode” collected crab larvae, which was confirmed with plankton net tows.

Results

Using the criteria mentioned above, 33 gray whales have been identified as residents during the summer field season (May-October) from Lincoln City to Seal Rock, Oregon between 2000 and 2005 (Newell 2005). Of these 33 whales, 28 (85%) have returned during the last three years (2003-2005). Two calves from 2004 did not return and three other resident adult whales were last seen in the area in 2002. In 2005, only 15 gray whales were observed in the study area compared to 40 in 2004 and 29 in 2003.

Whales were observed for approximately six hours per day from 38-56 days per field season. Mysid feeding was the primary feeding mode observed, with over 80% of the feeding time spent in this feeding mode in 2003 and 2004. In contrast, less than 20% of the feeding time was spent in this feeding mode in 2005 (Table 1.1). A secondary feeding mode, skim feeding on porcelain crab larvae, accounted for less than 2% of the feeding time in all years.

In 2003 and 2004, most of the whales seen exhibited mysid feeding behavior (n=29-40) and an average of one month residency. Less than 20% of the resident gray whales passed through the area without feeding. In 2005, however, 80% of the resident whales passed through the area without displaying feeding behavior (Table 1.1). Only three resident whales were observed feeding on mysid swarms from late May through early August in 2005. Most of the returning resident gray whales swam slowly through previously productive areas two to three different times during the field season, but did not stop to feed. As will be described below, mysid biomass was extremely low from June to early August in the same areas where abundance was high in 2003 and 2004 (Figure 1.3). It wasn't until mid August that several whales began maintaining residence in the different feeding localities around Depoe Bay. By late August 2005, mysid swarm biomass approached levels of abundance seen in 2003 (Figure 1.3).

The body condition of resident whales varied considerably between 2003, 2004, and 2005. In 2003, 20% of the resident whales entered the area in poor condition, with both the scapula showing and depressions behind the blowhole (Figure 1.2c, 1.2d, 1.2e). In 2004, no whales were in poor condition (see Figure 1.2a, 1.2b). In striking contrast, 80% of the whales entering the study area in 2005 were judged to be in poor body condition (Table 1.1).

Prey availability for gray whales was unusually low in early summer 2005, as indicated by mysid swarm thickness along a line from Government Point to North Point (see Figure 1.1 inset). From June to August 2003 and in August 2005, mysid swarms were 2m thick, based on echogram traces. During 2004, mysid swarms were nearly 5m thick in this area. In contrast, in June 2005, mysids were found only at Government Point in a small swarm only 0.3m thick (Figure 1.3). The thickness of mysid swarms along this line in June 2005 was significantly less than found in either 2003 or 2004 (t-test, $p<0.001$). The swarm thickness in August 2005 had recovered to levels statistically indistinguishable from those in 2003.

Gray whales exhibited characteristic mysid feeding behavior throughout June, July and August in 2003 and 2004 along this survey line. In June and July 2005, however, no resident whales were seen foraging at North Point and only one whale was seen foraging at the Condos and Government Point in July of 2005.

Between 2000-2004, the only species of mysid found along this portion of the Oregon coast was *Holmesimysis sculpta.* Examination of preserved samples from 2000-2004 (June to September) has revealed that *H. sculpta* females carry 20-30 eggs or10-20 juveniles in the brood pouch (Table 1.1). Those same 2000-2004 samples showed that all females had brood pouches containing eggs or juveniles. In early May 2005, *H. sculpta* females had eggs and young in their brood pouches, but by August all collected females had empty brood pouches. This reproductive pattern was a significant departure from the patterns observed between 2000-2004.

Discussion

The California Current system in 2005 displayed several unusual conditions, including delayed upwelling and reduced surface chlorophyll concentration (Thomas and Brickley, this volume), elevated sea surface temperatures (Kosro et al., this volume, Pierce et al., this volume), depressed productivity through July (Brodeur et al.this volume) and complex ecosystem responses (Sydeman et al., submitted). Our results indicate that the predator/prey interaction between gray whales and mysids also responded to this large scale phenomenon.

Nearshore Oregon coastal waters, from 2m to 15m water depth, possess spatially distinct swarms of mysids. Our results show that mysids were less abundant in early summer 2005 than in previous summers, and that the late summer reproductive condition of the female probably reflected food limitation in early summer. As discussed by Schwing et al. (this volume) the delayed onset of upwelling, both in timing and intensity, is a critical factor in ecosystem productivity. Given that mysids are the dominant prey item for resident gray whales, fluctuations in mysid biomass directly affects gray whales residency.

Previous studies have documented the impact of temperature and food variability on mysid growth and physiology (e.g., Mauchline 1980, Turpen et al. 1994). Temperature can have a strong effect on mysid abundance. Decreased abundance of *H. costata* in 1990 appeared to be correlated with increased temperature (Turpen et al. 1994). Since mysids have about a two-month lag period from the time of initial brooding to growth of juveniles, recruitment into the population will represent a delay. This was seen in our data with females carrying juveniles in the marsupium in May, a reflection of ocean conditions two months earlier. Thomas & Brickley (submitted) showed a slight rise in chlorophyll levels in February and early March. This may have given the mysids enough food for reproduction. The lack of eggs or juveniles in early August reflects ocean conditions in June since mysids may brood their young for 65-73 days (Turpen et al. 1994). With less food available in early summer, mysids may have invested less energy towards reproduction than in normal years. This contrasts with observations of other years with earlier onset of upwelling where mysids had full brood pouches throughout the summer. Kosro et al. (submitted) documented late spring and early summer surface temperatures 3-5° C above normal in 2005 and Pierce et al (submitted) documented the warmest temperature ever recorded at NH-5 in July, 6.2^{o} above the average. The response by the mysids reflects some combination of lack of food and decreased reproductive effort due to increased temperature. The delayed onset of strong upwelling conditions until mid July (Kosro, submitted), resulted in a later than average increase of phytoplankton biomass. Environmental temperature affects many of the physiological processes of mysids (Mauchline 1980). For example, the freshwater *Mysis relicta* studied in Trout Lake, Minnesota, did not tolerate temperature increases as small as 1° C d-1 (Mauchline 1980). We conclude that the impact of reduced reproduction in *H. sculpta* was shown by the decreased thickness of swarms in June and July of 2005 compared to 2003 and 2004. In 2003 and 2004, all swarms noted in Figure 1.1 were present but in 2005 only two of the regularly sampled locations had swarms. Full recovery to typical physical, biological and chemical conditions was observed by early August (Hickey et al. this volume). We also observed a recovery in the number and thickness of mysid swarms. In August, mean mysid swarm thickness was at the same level as in 2003 (Figure 1.3) and nine swarms were present (Figure 1.1).

Gray whales demonstrated a local response to reduced prey availability by exhibiting a low proportion of mysid feeding behavior in early and mid summer of 2005 compared to 2003 or 2004. The small numbers of resident whales seen locally in 2005 (n=15) (Table 1.1) suggest that fewer whales were in the larger region of the coastal northeast Pacific than in 2003 (n=29) or 2004 (n=40). As noted in Table 1.1, the majority of residents in 2005 passed through the region without feeding. Furthermore, the relative large percentage of 2005 residents that exhibited poor body condition suggests that a nutritional deficit had developed while the whales migrated through a broad geographic region. A similar effect of food limitation was hypothesized by LeBoeuf et al. (2000) to explain the thinner than average blubber layers on whales off the Oregon/Washington coast that had experienced reduced food supplies in the Bering Sea during the 1997-1998 El Nino. A few other studies show a correlation between prey abundance and whale foraging. In Newfoundland and on George's Bank, humpback and fin whale numbers and residency times were significantly correlated with prey abundance (Whitehead 1981, Paine et al. 1986**).** In 1984, in the Bay of Fundy, the density and quality of prey patches affected the number of right whales and their length of stay and the whales departed when copepod biomass started to decrease (Murison & Gaskin 1989).

Since baleen whales must harvest their entire year's energy requirement in four to six months, consistent availability of prey during this restricted feeding season is essential for deposition of the lipid and protein required for maintenance and reproduction (Murison & Gaskin 1989). Disruption of feeding habitat by large scale ecosystem change can have significant impact on upper trophic levels, as has been documented in 2005 for auklets (Sydeman et al., submitted) and for sea lions (Wiese et al., submitted).

A dramatic example of such a response by gray whales was examined by LeBoeuf et al. (2000). The 1997-1998 El Nino brought higher temperatures and reduced productivity in the Gulf of Alaska and the Bering Sea, one consequence was the mortality of nearly 300 gray whales in 1999, twice the number that died in 1998. It was hypothesized that higher than normal sea surface temperatures in the Bering and Chukchi Seas in 1997 may have caused a decrease in amphipod biomass. The decline in prey biomass may have weakened the physiological condition of gray whales, and likely contributed to the aberrant migration patterns and increased mortality observed in these whales in 1999. While no evidence of gray whale mortality was observed off Oregon in 2005, the number of resident whales in poor body condition suggests that feeding conditions across the coastal waters of the northeast Pacific were not favorable for weight gain.

Our results indicate the need to characterize the complex ecosystem linkages that exist in nearshore waters and to understand the response of those ecosystem components to environmental variability across a wide range of spatial scales. Warmer surface waters and delayed upwelling significantly perturbed the mysid – gray whale interaction in 2005, reinforcing the key role of climate variation on ecological processes in this region (Peterson & Schwing 2003). We suggest that the connection between lower and upper trophic level observations provide a unique perspective on the impacts of climate variability.

Acknowledgements. We acknowledge the illustrations of gray whales done by Ayesha Guzali, grants received from Mamie Markum Foundation and Holt Education Grants, and platform support to photograph and sample mysids from the boats of the Captains and Crew from Dockside Charters of Depoe Bay, Zodiac Tours of Depoe Bay, Zodiac Adventures of Depoe Bay, Whale Research Excursions of Depoe Bay, Tradewinds of Depoe Bay, Seagull Charters of Newport, and Discovery Tours of Newport.

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Table 1.1**.** Inter-annual comparison of whale behavior and mysid reproduction in 2003, 2004, and 2005 off the central Oregon coast. Reproductive data on mysids reported as mean (std deviation).

	2003	**2004**	**2005**
Resident Whales			
Observing Hours	276	342	228
Days Observing	46	57	38
Number of Resident Whales	29	40	15
Percent of Time of Whales in Residency	83%	88%	20%
Percent of Time in Mysid Feeding	81%	86%	19%
Percent of Whales in Poor Condition	21%	0%	80%
Mysids			
Mean Number of Eggs/Female in May (n=52)	27 (5.48)	19 (4.32)	22 (4.34)
Mean Number of Juveniles/Female in May (n=85)	12 (2.74)	15 (1.29)	19 (1.58)
Mean Number of Eggs/Female in August (n=67)	31 (4.32)	33 (1.59)	0
Mean Number of Juveniles/Female in August (n=75)	12 (1.3)	20 (2.16)	0

Figure Captions

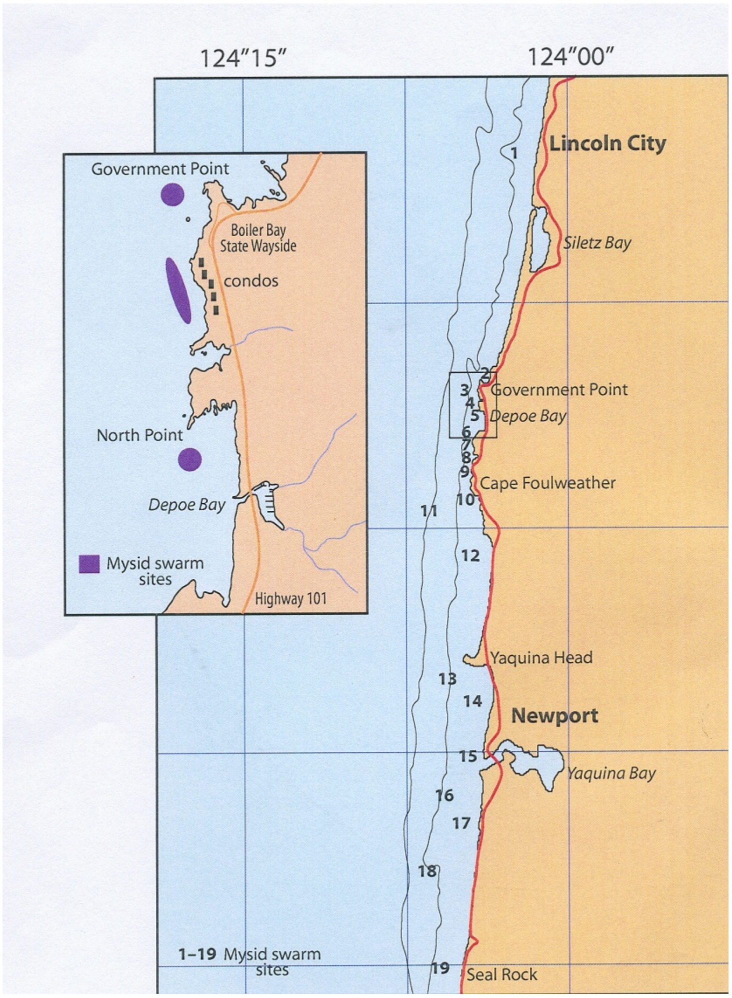


Figure 1.1 Study area with locations of mysid swarms noted numerically from Lincoln City to Seal Rock, Oregon. Inset shows mysid swarms at Government Point, the condos, and North Point (3.52 km), focus of the transects.

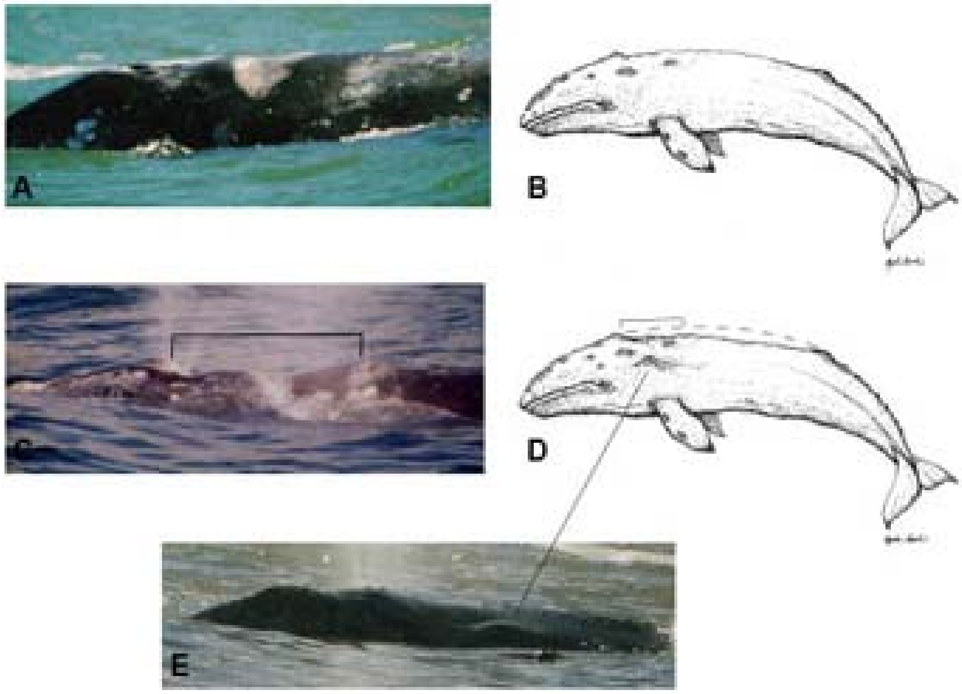


Figure 1.2 (**a**). Long time resident Whale # 22 in good condition in 2004 as seen by the fullness in the area behind the blowholes exhibiting a straight line. (**b**). The drawing illustrates a gray whale in good body condition by noting the robustness of the area behind the blowholes and no appearance of the scapula. (Drawing by Ayesha Guzali). (**c**). Long time resident Whale # 22 in poor condition in 2003 as defined by the depressions behind the blowholes. A similar photograph of whale #22 was taken in 2005 (not shown). (**d**). The drawing illustrates the full extent of poor body condition. The bracketed areas in Figure 2c and Figure 2d show the depressions behind the blowholes. (Drawing by Ayesha Guzali). (**e**). Resident Whale #16 in Poor Condition in 2005 as seen by the protuberance of the scapula by the back. Note in Figure 2d the scapula as seen from a whole body profile. The line between 2e and 2d points to the scapula protuberance.

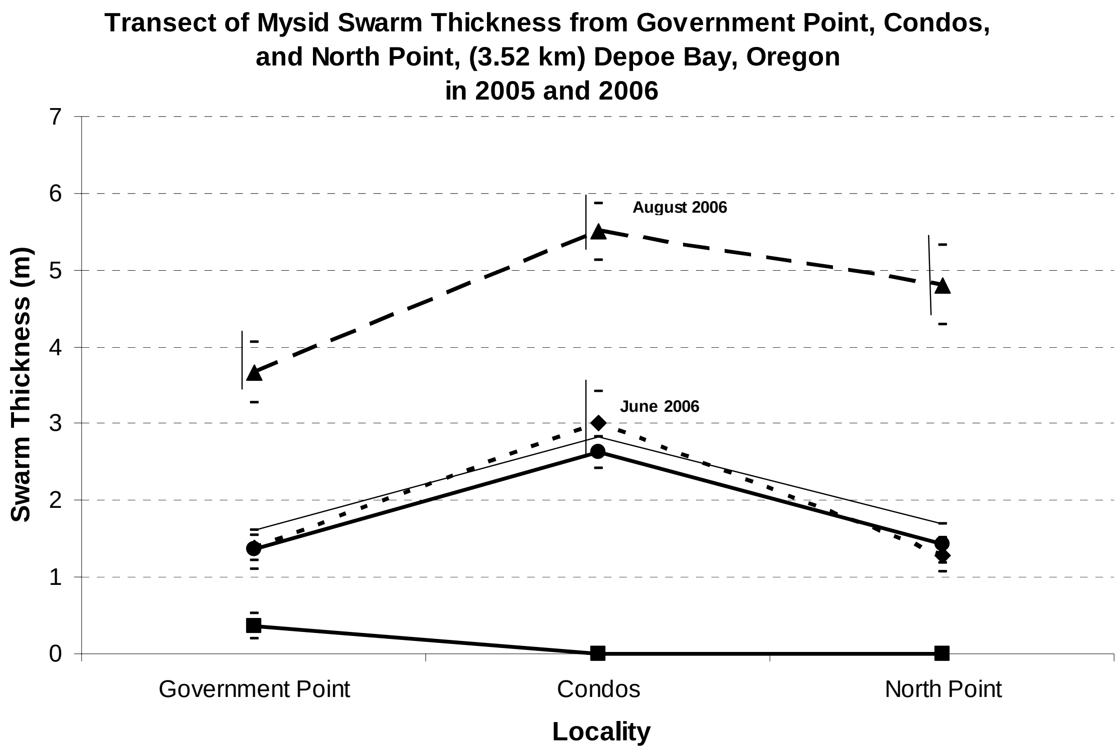


Figure 1.3 Mean mysid swarm thickness in 2003, 2004, and 2005 along a transect line from Government Point to North Point, Depoe Bay, Oregon. Error bars represent +/- 1 std dev.

INTRODUCTION TO MYSIDS AND SEASONAL RESIDENT GRAY WHALES

Presently, we have limited knowledge of the linkage between the largest coastal predator, gray whales, and the most abundant shallow water macro-zooplanktonic prey, mysids, along the central Oregon coast. To date, only a few published articles have addressed foraging behavior of seasonal resident gray whales off the Northwest coast and even fewer articles have focused on the specifics of the life history of Northwest coastal mysids. One of the few studies of temperate Pacific coast mysids was a population dynamics study of *H. costata* in the kelp beds of Monterey Bay, California (Turpen et al. 1994). Studies off Vancouver Island, British Columbia specifically Clayoquot Sound have described gray whale distributions, foraging and prey species (Darling 1984; Oliver et al. 1984; Darling et al. 1998; Dunham & Duffus 2001, 2002; Stelle 2002; Patterson 2004). Weikamp et al. (1992) determined that the seasonal residents in Puget Sound Washington were feeding on ghost shrimp (*Callianassa* sp.). Mallonee (1991) observed feeding behavior of gray whales off Crescent City, California but prey items were not determined. Sumich (1984) investigated various behaviors of seasonal whales in Oregon coastal waters and determined that gray whales were feeding during the summer months but was unclear as to what prey items they were consuming.

The research presented here has built upon the discovery that mysids are the primary prey items of summer resident gray whales off Newport and Depoe Bay, OR. Newell

(2009) has documented at least 72 seasonal residents and photographed another 11 whales that have been seen in central Oregon waters. This limited summer population of gray whales has provided a unique observational opportunity for investigating migratory patterns of summer residency, and summertime distributions in relationship to the patchy distribution of their mysid prey.

The earlier phases of this study permitted an examination of the trophic consequences of the unusual summer conditions during 2005. Three additional years of field data now permit us to examine in greater detail the patterns and variability of prey distribution in the context of high levels of predation.

Materials and Methods

Study Area

The work presented in this chapter was conducted within the study area along the central Oregon coast described in Newell & Cowles (2006). This region of the coast between Lincoln City and Seal Rock has an active population of seasonal resident gray whales and we have documented 19 different locations along this section of coastline where gray whales forage on mysids. These locations have been surveyed since 2000 and all possess recurring hyperbenthic swarms of mysids near the 10m isobath (Figure 2.1). Sites 3-12 have been sampled intensively from 2002 -2008 and are located in or near annual bullwhip kelp beds (*Nereocystis luetkeana*). (Mysid swarm assessment is described in a subsequent section).

The benthic substrate at these sites ranged from a basalt to sandy bottom. Many of the rocky sites had surge channels that were filled with large-grained silica sands and broken pieces of shells. The mysid swarms generally were located at or near the 10m isobath during the summer months although swarms occasionally were seen in waters as shallow as 4m or as deep as 20m.

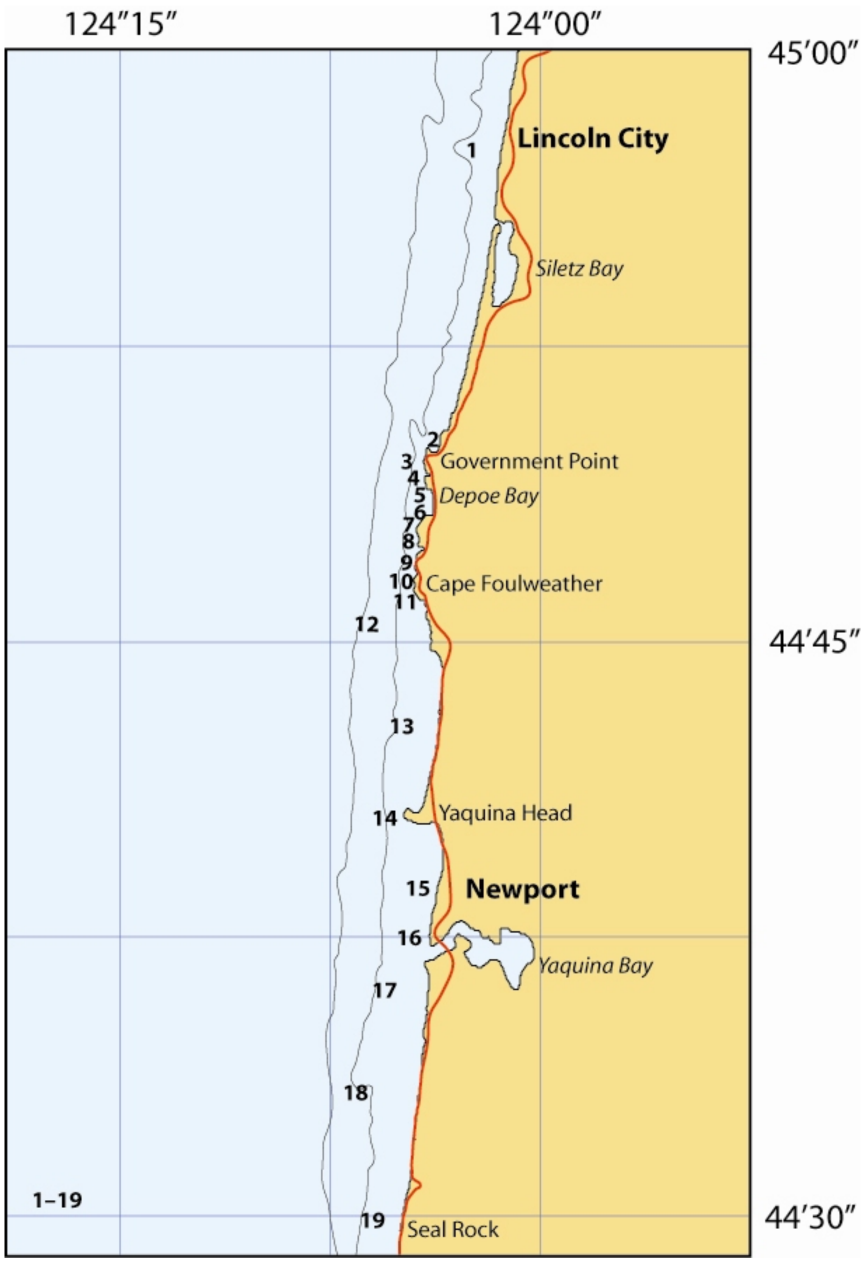


Figure 2.1: Map showing mysid swarm localities.

Table 2.1 Locations of mysid swarms, kelp species present or absent in area and the type of bottom; basalt, sandy or surge channels. Surge channels made of basalt with a bottom substrate of sand.

Mysid Locations	*Nereocystis luetkeana*	*Laminaria* sp.	No Kelp	Basalt	Sandy	Surge Channels
1 Nelscott Reef	X			X		
2 Boiler Bay		X		X	X	X
3 Government Point	X			X		X
4 Worldmark Condos	X			X		X
5 North Point	X			X		
6 Depoe Bay	X			X		
7 South Point	X			X		X
8 Little Whale Cove	X			X		X
9 Outside of Whale Cove	X			X		X
10 Rocky Creek	X			X		X
11 Cape Foulweather	X	X		X	X	
12 Gull Rock	X	X		X	X	
13 Whaleback				X		X
14 Yaquina Head	X			X		
15 Nye Beach			X		X	
16 North of N. Jetty				X		
17 South Reef			X	X	X	
18 Airport Reef			X	X	X	
19 Seal Rock	X			X	X	

Mysid Sampling

Samples were taken at least semimonthly, conditions permitting, from April through October from 2002-2008. Preliminary samples were collected in 2000 and 2001. Mysids were collected in daylight at depths ranging from 4-20m by deploying a weighted 0.5 m diameter, 70-*u*m mesh net vertically to the bottom. The net remained in contact with the bottom for 60 seconds and then was rapidly retrieved to minimize avoidance behaviors. Samples were preserved in 70% ethanol. Each individual was identified to species, sex, and measured using a dissecting scope with 20X eyepieces and an ocular micrometer. Length was measured to the nearest tenth of a millimeter from the anterior margin of the rostrum to the apex of the telson. Male mysids were identified by elongated fourth pleopods, while the presence of oostegites or a brood pouch defined a female. If the specimen possessed neither, it was counted as a juvenile. Brood size was determined by counting eggs or larvae only from intact brood pouches (marsupiums). Eggs and larvae were counted and larvae classified as eyeless or eyed.

The population structure was defined by looking at the composition of the swarms (homotypic or heterotypic), sex ratio, stage of maturity, and size class of each individual in the swarm. Homotypic swarms consisted of one species while heterotypic swarms consisted of more than one species in the swarm. The internal arrangement of the mysids in each swarm was determined by using nearest neighbor distances (NND) of individuals determined from video footage or SCUBA observations. Video footage was analyzed using a 25” monitor and for each video segment, the mysid NND were digitized into 1mm bins (<1mm, 1-2, 2-3, 3-4, 4-5, 5-6, >6mm). In addition, a subjective estimate of density was made based on the number of individuals in each video frame. An alternative, in situ estimation of swarm density was obtained using a specially designed cube (Figure 2.4) in conjunction with SCUBA observations.

Mysid swarm locations were mapped using north-south and east-west transects with vessels of opportunity. North-south transects were from North Point to Government Point and from South Point to Whale Cove while east-west transects were from the Depoe Bay channel opening to the bell buoy (Figure 2.2). We lacked sufficient resources for more extensive mapping of the region. We determined mysid swarm distribution and swarm dimensions using various sampling methods. We documented mysid swarm presence or absence in these localities with a fish finder (Furuno 200 KHz), which detected mysids as a band above the bottom on the echogram trace (Figure 2.3). We used an underwater camera, net sampling, and SCUBA to confirm that mysids were the most abundant organisms in the fish finder echograms. Along the transect lines, GPS coordinates, depth, thicknesses of the echogram traces, whale sightings and whale behaviors were documented.

Density, defined as the number of mysids per unit volume, was estimated in two ways. The first method relied on echogram traces. Density was determined by estimating the thickness of the mysid layer from the echogram trace and obtaining nearest neighbor distances (NND) from video recordings and SCUBA. The second method used a specially designed cube for in situ capture of mysids within a swarm. A 0.3 m^3 acrylic cube was designed to be deployed while within a mysid swarm (Figure 2.4). A diver would open opposite sides of the cube and wait for a wave surge. When the wave surge swept mysids into the cube, the sides would be shut, trapping the mysids inside. The cube was then lifted aboard the surface vessel where the mysids were removed and counted.

Subsamples of collected mysids were brought into the lab. Samples were weighed and gut content analysis of a small number of mysids (n=21) were conducted to determine prey preferences. A small subsample (n=12) of living mysids were put into cold water aquaria to observe their life span and brooding period. The dozen mysids ranged in size from 7mm and 8mm juveniles to11mm and 12mm adults. The seven adults were females brooding young. They were put into 10-11 C^o water and fed a diet of *Artemia.*

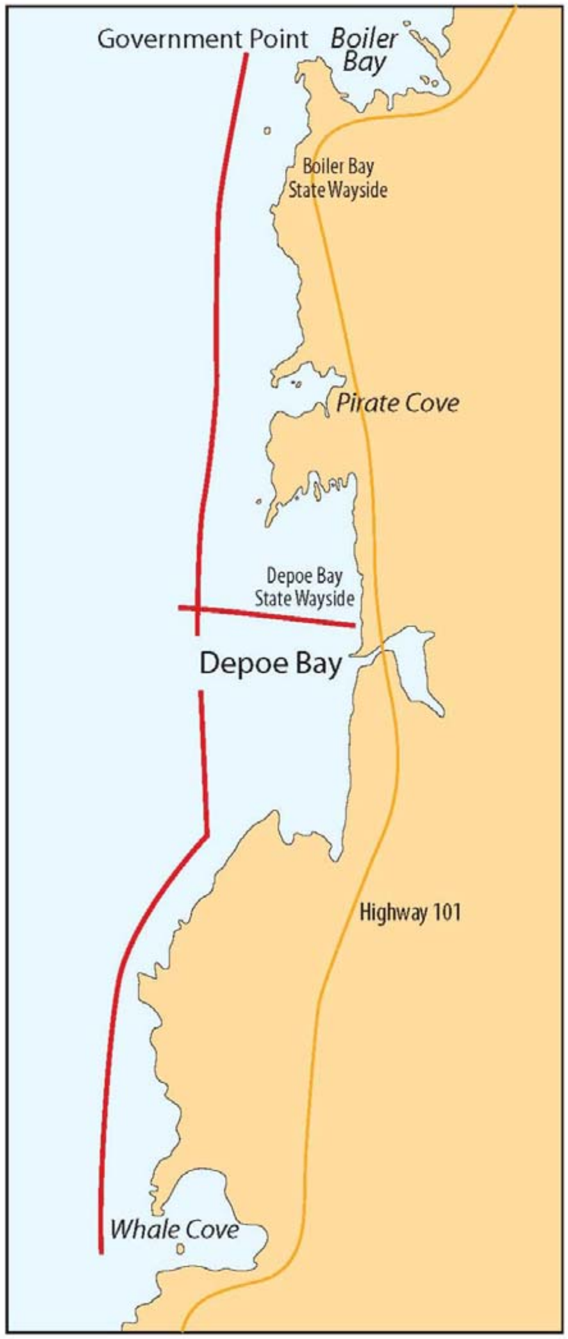


Figure 2.2 Map showing north-south and east-west transect routes.

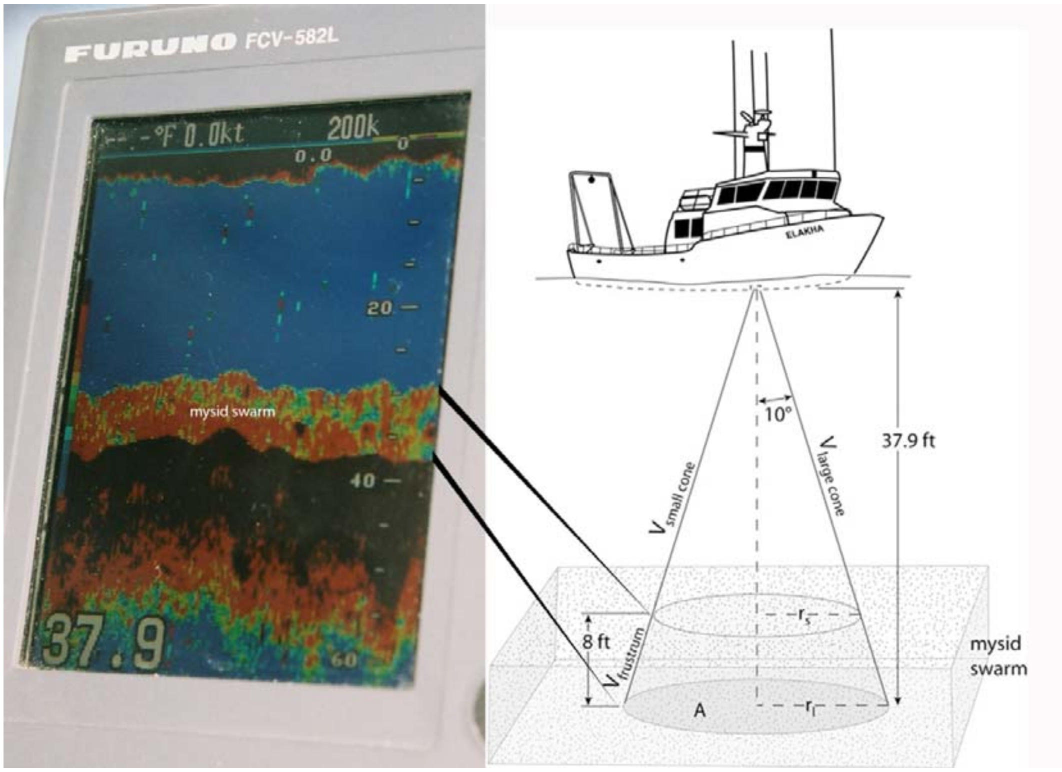


Figure 2.3 The left photograph shows an echogram trace of mysids (red band above black substrate). This swarm was eight feet thick (2.4m) at a depth of 37.9 feet (11.5m). The diagram at the right shows the area of sweep from the fish finder. The area of "sweep" was 13.01 m^2 at 11.5 m. The shadowed lower portion of the cone ($V_{frustrum}$) represents the same 2.4 m (8 feet) of mysids as shown on the echogram trace.

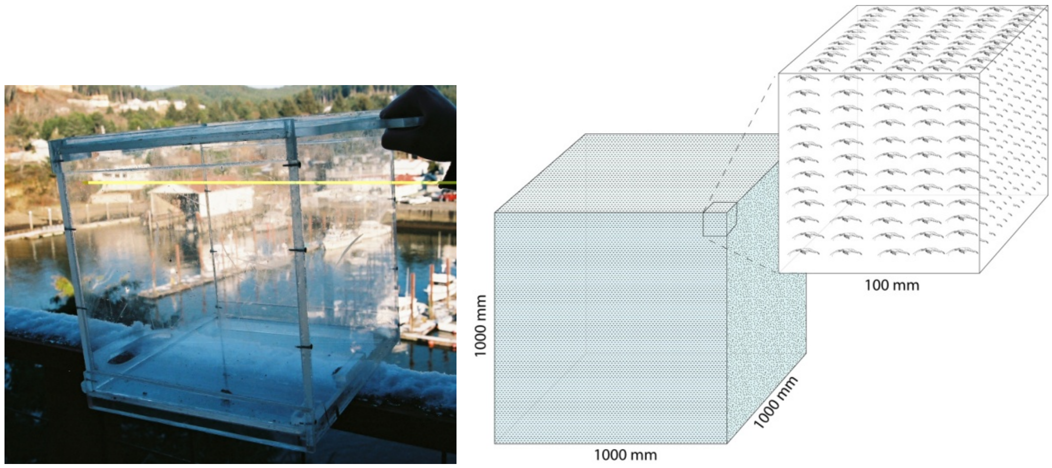
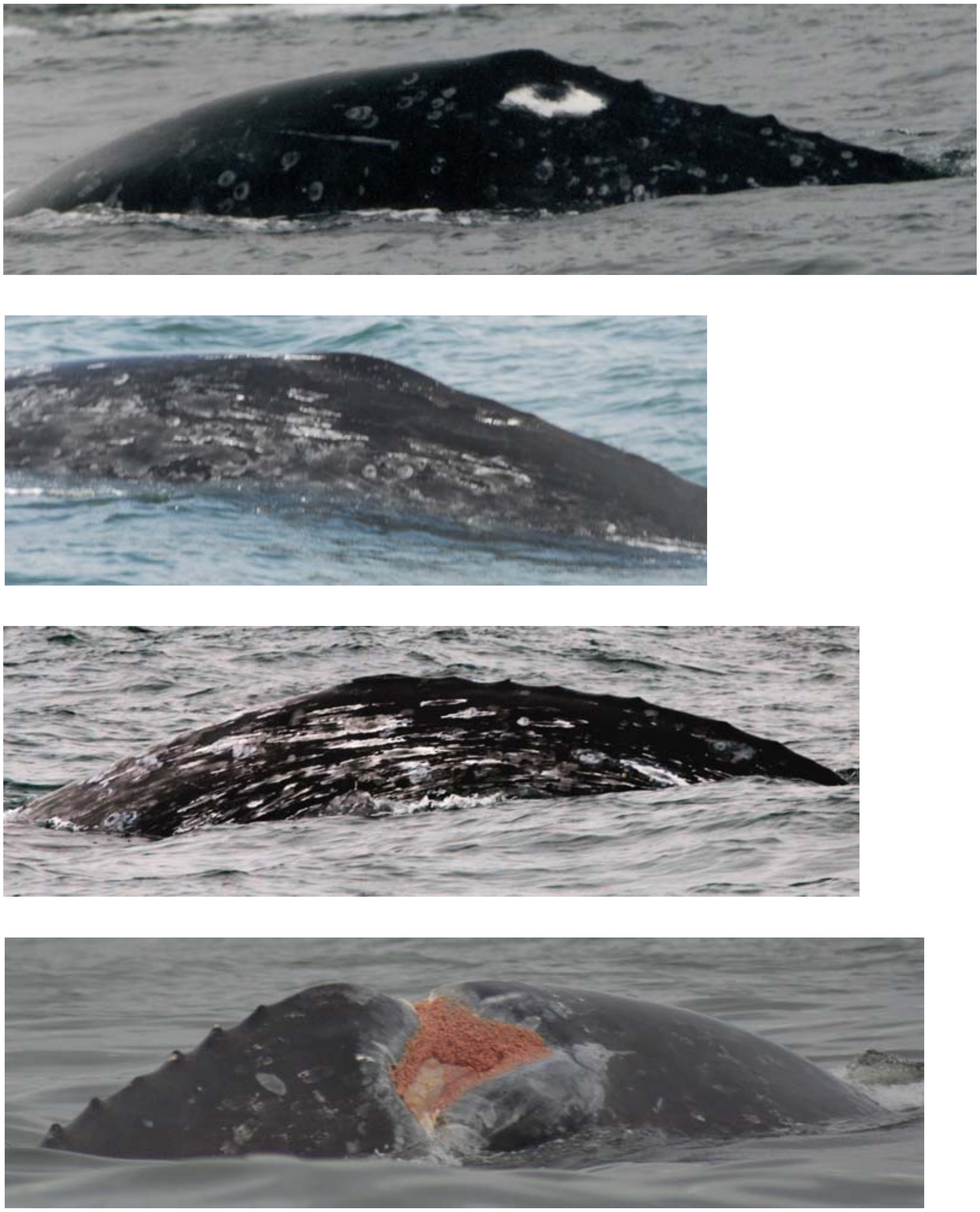


Figure 2.4 On the left, acrylic cube with opposing doors and on the right optimal packing density.

Gray whale residency and feeding

We determined the residency times of specific whales through repeated observations of individual gray whales that had characteristic markings (documented in a photo-ID library). Gray whale behaviors during this residency period were also documented.

The number of observing days through each year is shown in Table 2.3. Individual recognition of a gray whale relies on unique characteristics of the dorsal hump (Figure 2.5). Each side of the dorsal hump had characteristics unique to that individual, so both the right and left sides of each whale were photographed along with fluke shots using a Canon EOS equipped with a 300 mm lens. Additional photographs were taken of the area behind the blowholes to aid in the determination of body condition (see Newell & Cowles 2006). Every seasonal resident gray whale was photographed to provide a photo library for subsequent identification of individual whales. We also recorded GPS position and foraging behavior for every whale sighting. Whale abundances were tallied daily at each locality. Mysid samples were collected near the foraging whales along with opportunistic whale fecal samples.



a.

b.

c.

d.

Figure 2.5 Unique pattern of the left dorsal humps of whales nicknamed a.Eagle Eye, b.Comet, and c.Stretch. d.Unique pattern showing a wound on the right dorsal hump of Scarback.

The same terminology is used in this chapter for percent time in residency and percent time in foraging modes as was used in Newell and Cowles (2006).

Material contained in whale fecal matter was collected by towing a 70-*u*m mesh plankton net through the egested fecal material. These samples were preserved in 95% ethanol and analyzed for identifiable parts of prey organisms.

Rockfish Predators

The behavior of black rockfish (*Sebastes melanops*) were observed and documented while SCUBA diving near mysid swarms. A few hours after each of the three dives, *S. melanops* were caught on fishing gear by local fishing charters at the dive localities. The specific location and depth where the black rockfish were caught was documented. The black rockfish were weighed and measured at a cleaning station. The stomach contents were removed and analyzed in the lab for prey composition.

Results

Data Analysis Description of Mysids

From 2000-2008, two species of mysids were identified, *Holmesimysis sculpta* (Figure 2.6) and *Neomysis rayi* (Figure 2.7). Adult *H. sculpta* had a mean length of 12.7 mm (+/- 0.4 n=1055) and adult *N. rayi* had a mean length of 22.4 mm (+/- 2.0 n=147). *H. sculpta* males were slightly smaller (0.5-1.0mm) than females.

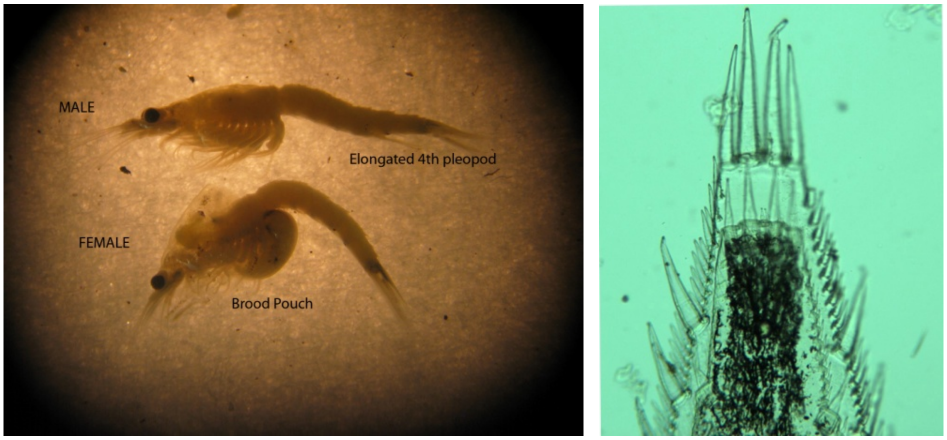


Figure 2.6 Male and female *Holmesimysis sculpta* with their characteristic telson on the right.

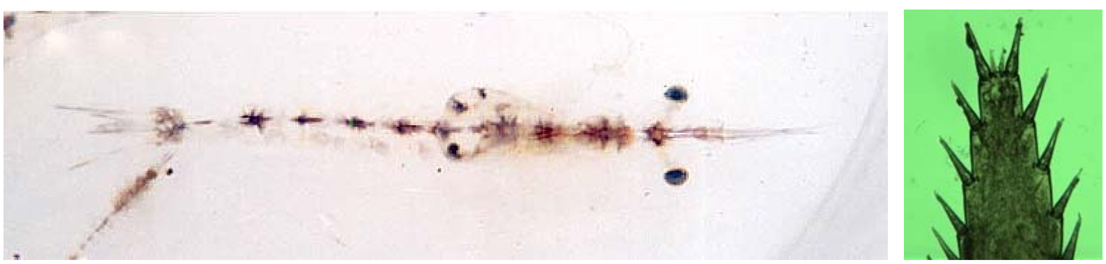
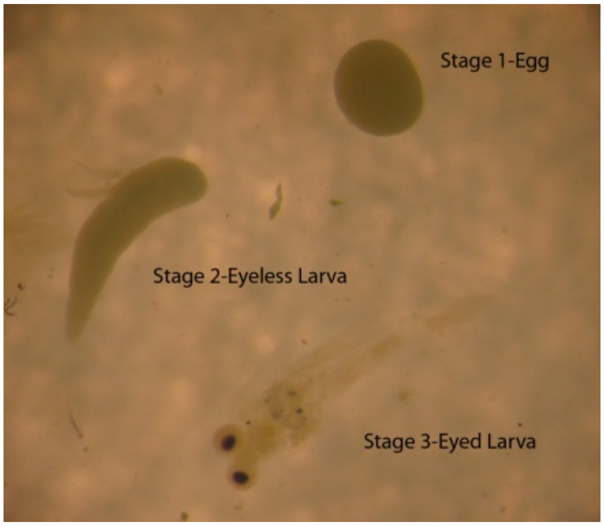
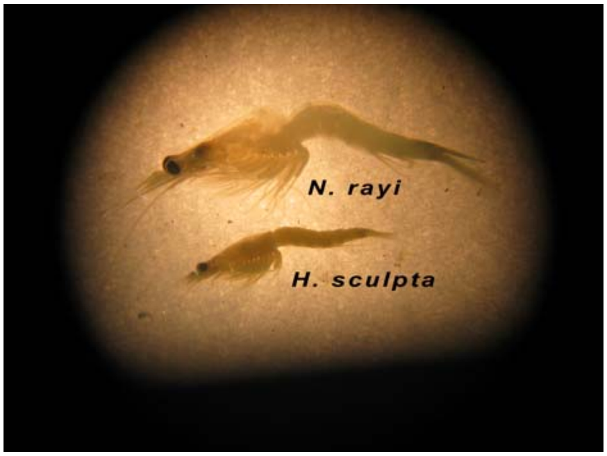


Figure 2.7 Female *Neomysis rayii* showing brood pouch and characteristic telson on the right.



a.



b.

Figure 2.8 a.The three stages of mysid larval development within a female's marsupium. b. Comparison in size between *H. sculpta* (12.7mm) and *N. rayi* (22.4mm).

a.  b.  c. 

Figure 2.9. Females carrying larvae in their three stages of development: a. Eggs b. Eyeless Larvae and c. Eyed Larvae

The females carried their eggs and larvae in a marsupium (Figures 2.6, 2.7, 2.9). Within the marsupium, the young underwent three stages of development: Stage 1-eggs, Stage 2-eyeless larvae and Stage 3-eyed larvae (Fig. 2.8a).

Brooding *H. sculpta* were 10-13.8 mm in length with a mean length of 12.7 mm (+/- 0.3) whereas brooding *N. rayi* were 20-23.2 mm in length with a mean length of 22.4 mm (+/- 0.8) Female *H. sculpta* carried a mean of 32 eggs-stage 1, a mean of 26 eyeless larvae-stage 2 and a mean of 20 eyed larvae-stage 3. Female *N. rayi* carried a mean of 40 eggs-stage 1, a mean of 36 eyeless larvae-stage 2 and a mean of 22 eyed larvae-stage 3. In both species the average egg diameter was 0.5mm, eyeless larvae were 1.5mm and eyed larvae were released at 2mm (Figure 2.9c).

Within a swarm, the various females had all stages of egg and larval development within their brood pouches. These young were collected in all sampling months, April-October, and occasionally into November. Recently released juveniles, 2-3 mm in length, were also present between April-October. Representative samples of the number of young/female are shown in Figures 2.10 a-e. Brooding females from 2006 had the largest clutches of eggs (Figure 2.10e) with brooding females from 2004 having the next most abundant number of eggs and larvae (Figures 2.10 c,d). Females from early summer in 2005 had no young or larvae in their marsupia and females from 2003 had the second lowest number of eggs and larvae in their marsupia (Figure 2.10 a). Juveniles comprised

90% of the total population sampled in spring whereas adults comprised at least 60% of the population sampled during late summer and early fall (Figures 2.11a,b). Sampling was limited from December – March due to adverse ocean conditions. The half dozen transects conducted from Government Point to Whale Cove did reveal that there were no mysids found near the 10 m isobath from mid December to mid March. Ten very small swarms of *H. sculpta* and *N. rayii* were found and collected at the 20 m isobath in December 2006 and January 2007.

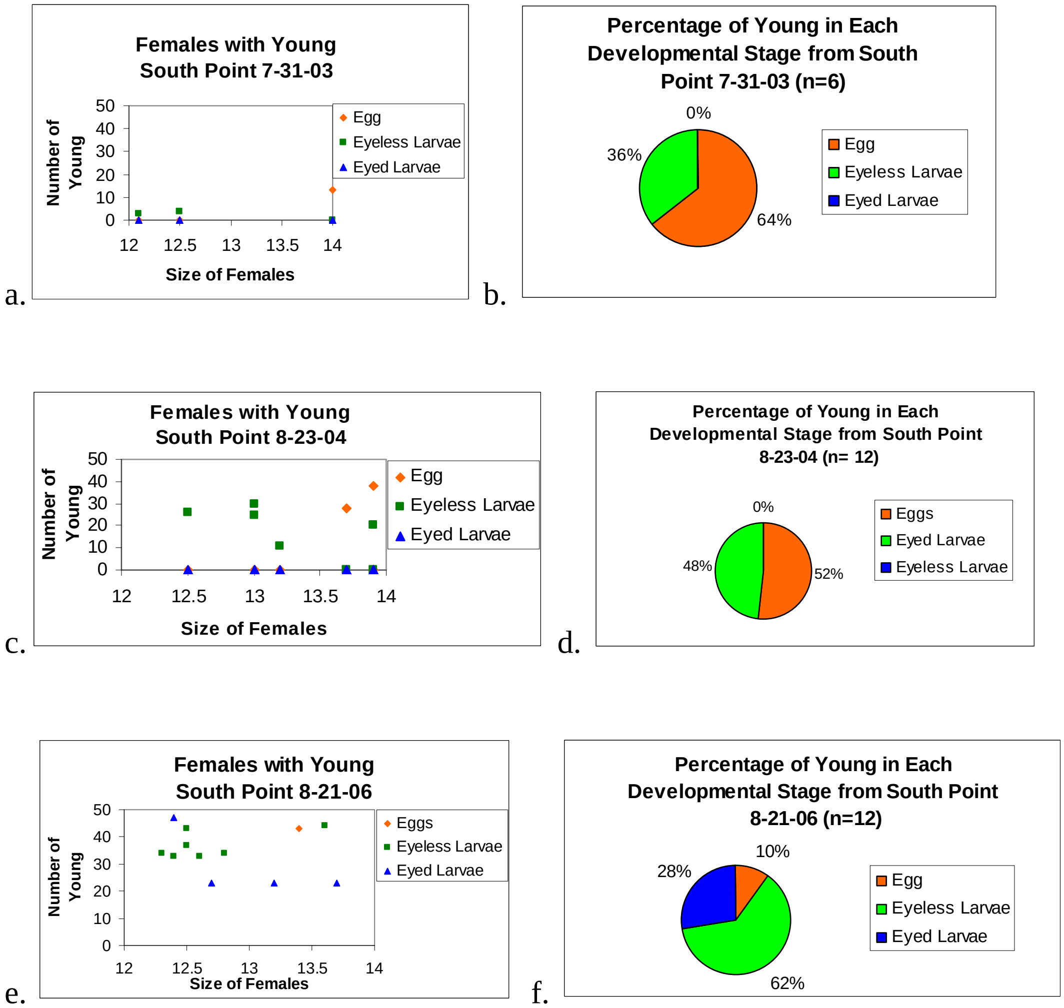
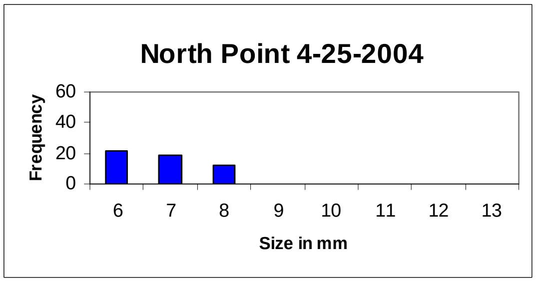


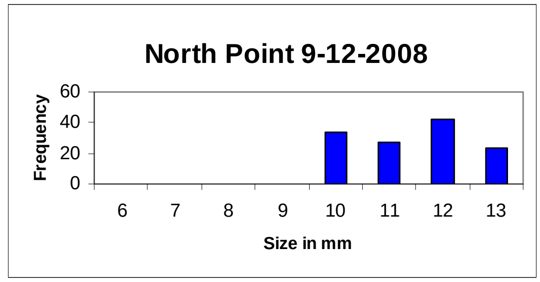
Figure 2.10 a-f. Inter-annual comparison of brooding females from South Point and the percentage of young in each of the three stages of development from *H. sculpta*.

Swarm characteristics

The majority of the sampled swarms were homotypic, with 85% of the swarms consisting of only *H. sculpta* and 7% with only *N. rayi*. The remaining 8% of the swarms were heterotypic with 6% consisting of both *H. sculpta* and *N. rayi* and the other 2% consisting of a few amphipods interspersed with *H. sculpta*. All swarms showed variation in age class and species composition (Figures 2.11-2.15). Some samples consisted only of juveniles with size classes ranging from 5mm to 8mm (Figure 2.13 b), others had juveniles and adults combined (Figure 2.13 a), and some samples consisted only of adults (Figures 2.11 b, 2.14a). Some samples contained mysids from almost all size classes ranging from recently released juveniles (3mm) to adults (Figures 2.12 a). A few samples had a heterotypic composition with both *H. sculpta* and *N. rayi* present as seen in South Cove on 10-1-06 (Figure 2.14 a.) Collections from this same locality almost a year later, 8-21-07, showed only *H. sculpta* and primarily adults. Samples from Little Whale Cove in 2002 showed a heterotypic composition throughout the summer (Figure 2.15 a, b, c). When adult mysids were found in samples, both sexes were always present with the M:F ratio varying between 1:10 to 9:10.

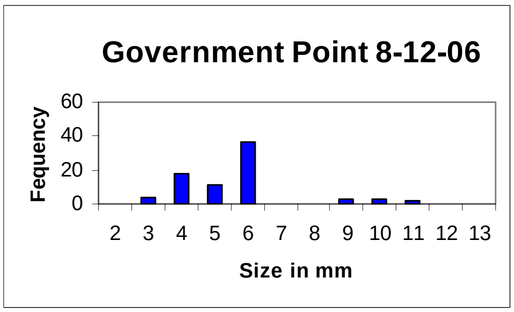


a.

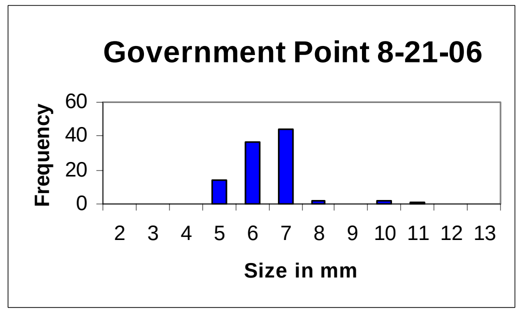


b.

Figure 2.11. a. Juveniles in an early spring sample. b. Adults in an early fall sample.

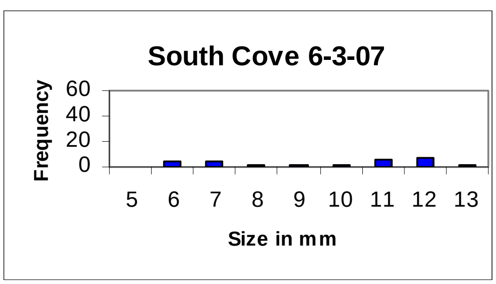


a.

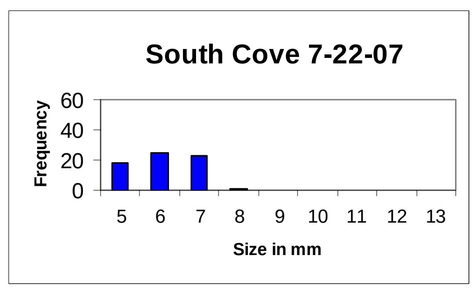


b.

Figure 2.12 Government Point samples showing juvenile and adult *H. sculpta* on 8-12-06 (a) and 8-21-06 (b) with a possible size increase at this swarm location in a 9-day period under the assumption of no immigration or emigration.



a.



b.

Figure 2.13 South Cove samples showing juveniles and adults (a) of *H. sculpta* in all size classes on 6-3-07 and only juveniles (b) in the 7-22-07 sample.

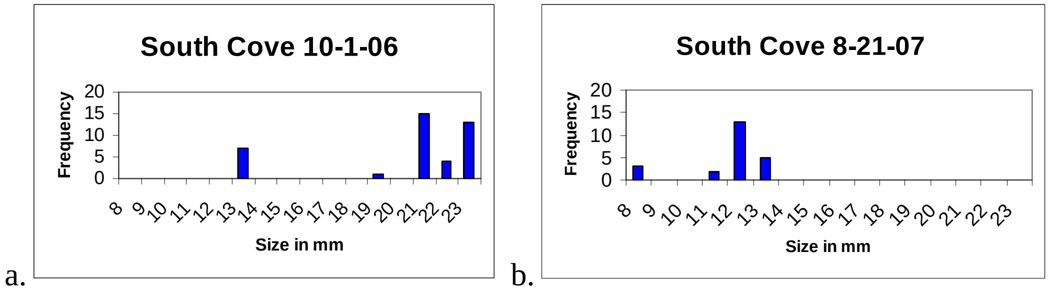


Figure 2.14 a. South Cove sample in October of 2006 had a heterotypic swarm of both mysid species, the larger *N. rayi* (19-23mm) and the smaller *H. sculpta* (13mm) but in August 2007 only *H. sculpta* was present mostly as adults.

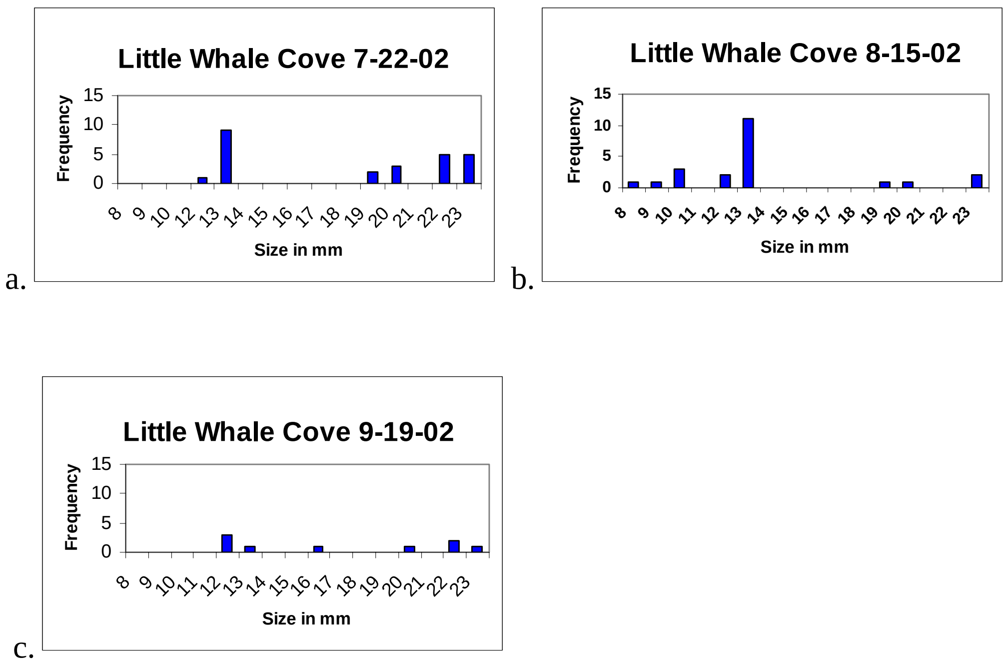


Figure 2.15 a. Samples from Little Whale Cove on 7-22-02 showing adults of both the larger *N. rayi* and the smaller *H. sculpta*. b. On 8-15-02, a few juveniles are present from both species. c. On 9-19-02, only a few adults of both species were collected along with a few juvenile (17mm) *N. rayi*.

During the sampling period from 2000-2008, we found swarms in water depths ranging from 4 to 20 m, approximately 0.2 km-0.6 km from shore. Visual observations with SCUBA showed that at all depths the swarms' benthic edge began abruptly 2-3 cm above the bottom. Mysids within a school swam in a polarized direction in strong current and a random direction in weak currents. The swarms of each species tended to be substrate specific, with *H. sculpta* found over a basalt bottom usually associated with *N. leutkeana*. *N. rayi* was most often found over a coarse-grained sandy bottom although in some samples it was also found over a basalt substrate and in *N. leutkeana*. Both species showed a preference for crevices or any low spot in the bottom topography.

In situ observations with SCUBA and analysis of video footage showed that individuals in swarms of adult *H. sculpta* were separated horizontally by 1-2 body lengths (BL) while individuals within juvenile swarms were less dense and separated by 2-3 BL. Individuals of adult *N. rayi* swarms were separated horizontally by 2-3 body lengths.

Density determinations were done by in situ collections with an acrylic cube and by estimating the maximum packing density. The mean number of mysids collected using the 0.028 m^3 cube was 139 (+/- 37.4, n=7) giving a density of around 4900 mysids per m^3. This number undoubtedly represents an underestimate since many of the mysids escaped the collection process due to their avoidance behaviors. Maximum packing density was calculated using 2 BL separations horizontally and 2 body width separations vertically. Maximum packing density, assuming a length of adult *H. sculpta* of 10mm and a width of 3.3mm, gives a density of approximately 330,000 /m^3. Using the density numbers from each method, it was calculated that within the spatial domain captured by the echogram trace in Figure 2.3, there would be from 153,000 mysids (using the cube estimate) to 10.3 million mysids (using maximum packing density), over 6 orders of magnitude difference between each method. The actual number of mysids is probably somewhere between the low and high numbers.

Swarm dimensions at all sites showed considerable variability from 2003-2008. The dimensions of a swarm were measured at specific points in time during each month with both a fish finder and kick cycles with SCUBA (Table 2.2). An up and down motion for a specified number of meters was one kick cycle. Kick cycles were counted from one end of the swarm to the other end.

We observed inter-annual variability from 2003 to 2008 in the size of the mysid swarm found at North Point-Site 5 (Figure 2.15). We estimated the number of mysids present in the swarm at North Point during a good year, 2006, an average year, 2008 and a poor year, 2003 (Figure 2.15). To calculate the number of mysids in this swarm from 2003, 2006, and 2008, we used the density estimates from both methods, assumed a depth of mysids 1m thick and took the square footage from the North Point swarm for those specific years. The mysid swarm thicknesses and square footage were an average of a number of individual estimates from mid July based on echograms from the fish finder and SCUBA. In 2003, a poor year, the low and high values ranged from 235,200 mysids to15.8 million mysids. In 2006, a good year, the number of mysids ranged from 784 million to 52.8 billion and an average year, 2008, the number of mysids ranged from 4.1 million mysids to 277.2 million. Other swarms showed similar ranges of variability and mysid numbers.

The life span and brooding experiments in the laboratory were unsuccessful. Of the 12 mysids introduced into the tank, only the largest one survived. The smaller mysids were cannibalized by the larger mysids until ultimately only the largest female, 13.1mm, was left. This female lived five months but none of the stage 3 larvae were ever released from the marsupium. The eggs and larvae from all the brooding females disappeared from the marsupium a week after introduction into the tank. Analysis of the gut samples revealed bits of diatom frustules in the digestive tract.

It was observed on a dozen different dives that from one to 12 black rockfish (*S. melanops*) took up positions around the periphery of *N. leutkeana* and preyed on mysids. To confirm these SCUBA observations, a total of twenty *S. melanops* ranging from 20 cm to 41 cm and 2.2 kg to 8.8 kg were caught at the 10m isobath near *N. leutkeana* on three different occasions. On the first trip, eight *S. melanops* were caught, on the second trip, seven *S. melanops* were caught and on the last trip, five *S. melanops* were caught. Analysis of the contents from the 20 stomachs showed that *S. melanops* selectively choose adult mysids ranging from 10.1mm-13.2mm in length (mean 11.6mm +/-1.02), both males and females. Stomach contents contained between 32-88 (mean 58 +/-17.6) adult *H. sculpta*. Female mysids with brood pouches containing all developmental stages made up 50% of the gut contents.

Table 2.2. Inter-annual Variability at North Point-Site 5 in mid July from 2003-2008.

Year	**Width of Swarm East to West in m**	**Length of Swarm North to South in m**	**Average thickness of swarm in m**
2003	6	8	1.5
2004	20	30	4.7
2005	0	0	0
2006	800	200	3
2007	30	40	2.5
2008	28	30	2

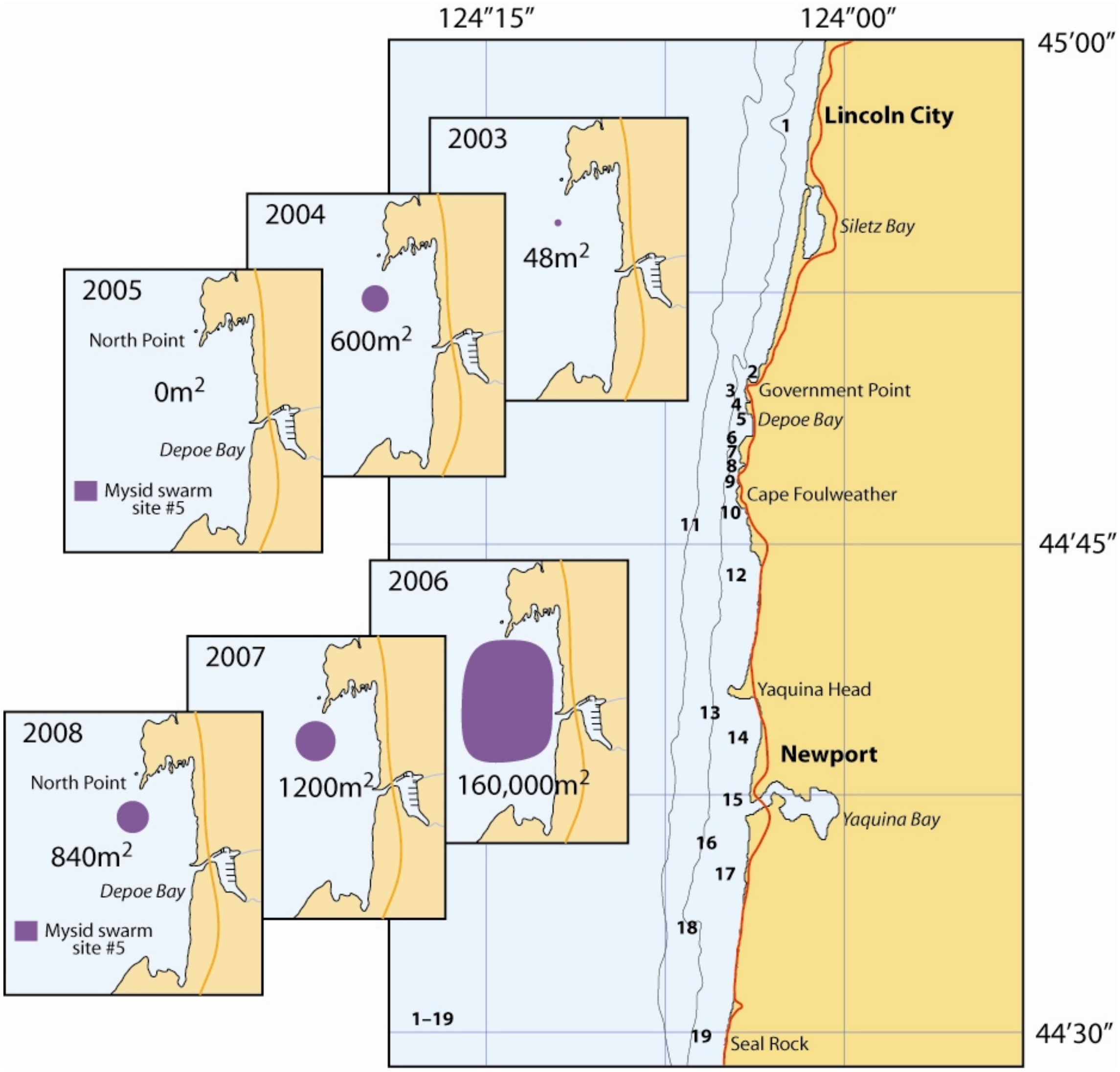


Figure 2.15. Inter-annual variability at North Point-Site 5 from 2003-2008.

Gray whales: Residency and Foraging

From 2000-2008, 83 individual gray whales were categorized as summer residents. A whale was classified as a summer resident if it returned in succeeding years, stayed in one locality for at least 48 hours and exhibited feeding behavior (Newell & Cowles 2006). Summer gray whales usually arrived by the end of May and remained in residence from 2 days to 4 months, depending on the individual whale. Mid November was usually the latest a summer resident was seen. Gray whale residency was determined by the amount of time a photo-identified whale spent in certain localities. A gray whale spending less than two days in the area, was not considered in residency. Maximum residency times ranged from 102 days for Eagle Eye (Figure.2.5 a, 2.16) in 2004 to114 days for Comet (Figure.2.5 b, 2.16) in 2007 while minimum residency times were two days for all years. The longest residency period for individual whales in other years was 35 days in 2003, 33 days in 2005, 52 days in 2006, and 60 days in 2008, (Figure 2.16 a-f). Each year a different identified whale had the longest residency period even though many of the same residents returned each year.

Gray whale abundance was determined by the number of individuals identified and by the frequency of sightings seen daily or monthly (Figure 2.17). “Sightings” differed from the “number of individuals” because whales that were too far away could not be individually identified. Undoubtedly some of the sightings were repeat whales. The greatest number of seasonal whales in terms of both sightings and identified individuals almost always occurred in August and September (Figure 2.17). During the time period of this study, the greatest number of individually identified whales seen in one month was 20 in September of 2006. The greatest number of individuals identified in a single season was 49 in 2004 (Table 2.3).

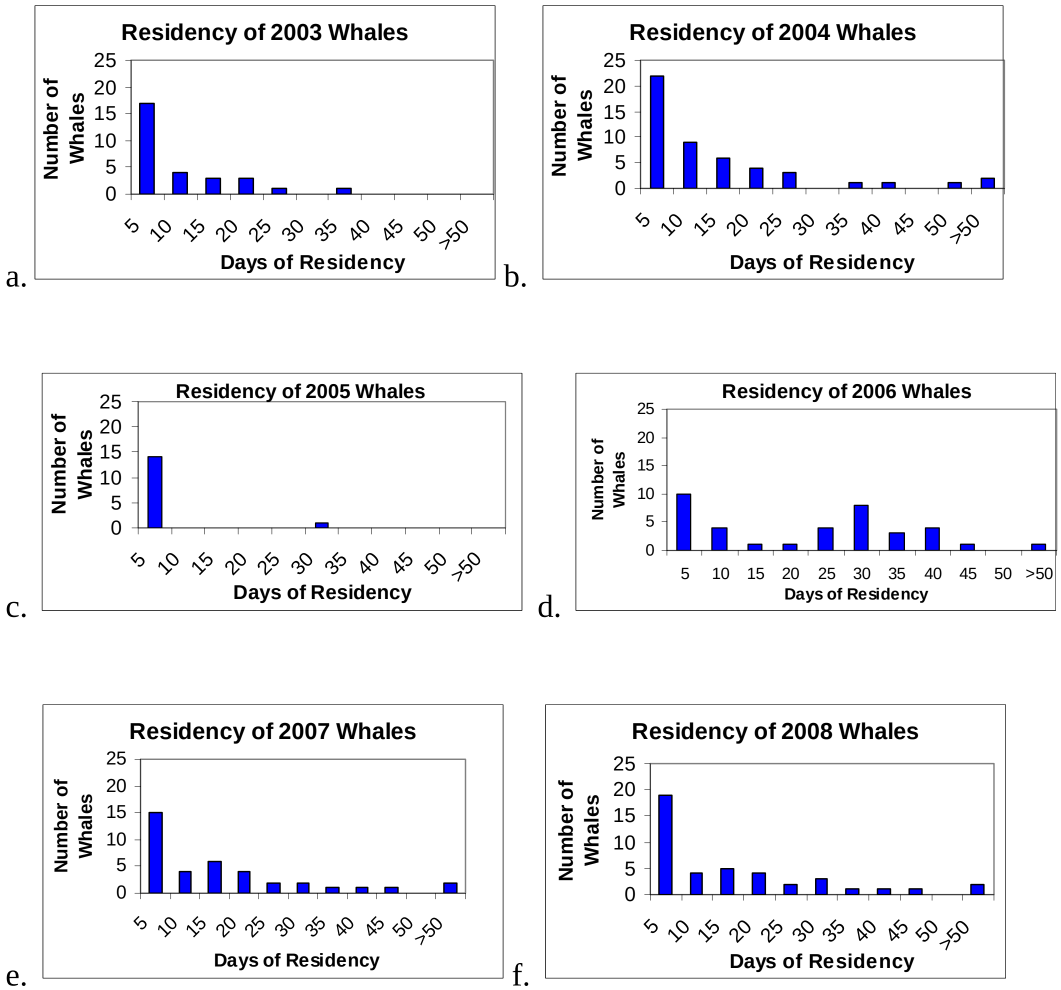


Figure 2.16 Variability in residence times between different whales in different years.

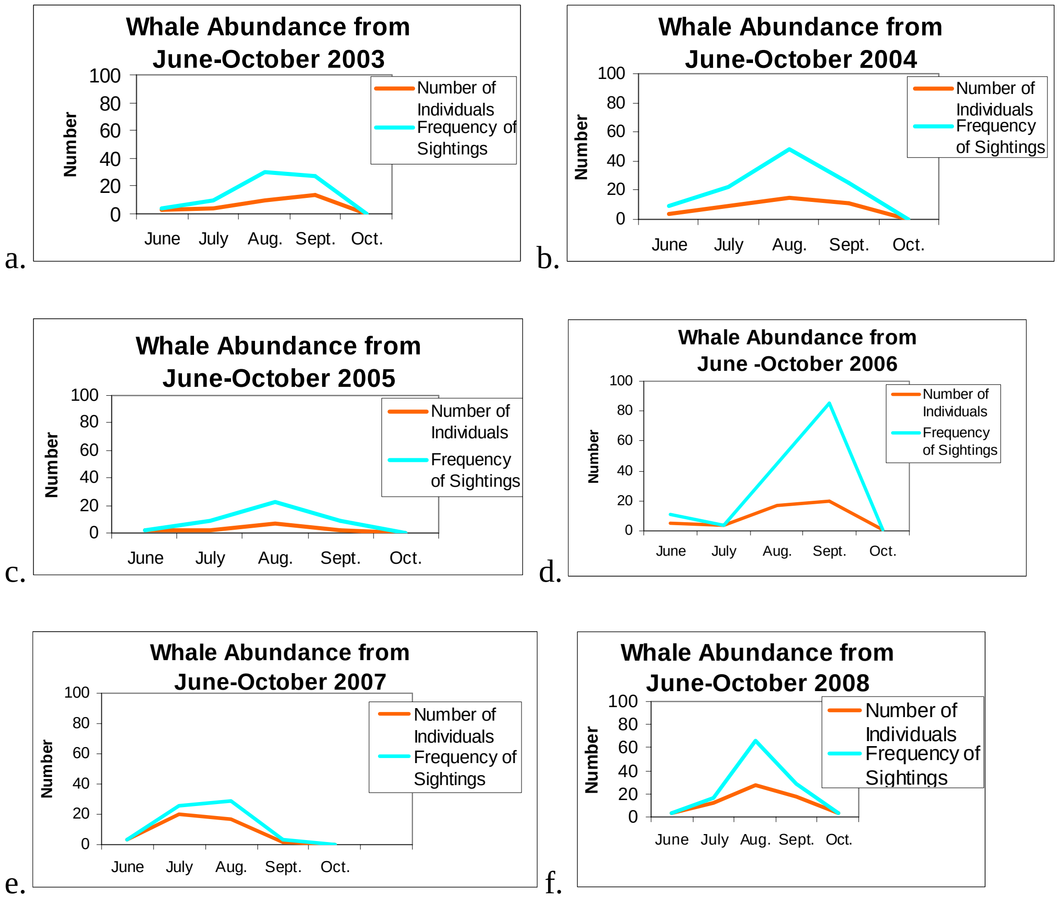


Figure 2.17. Variability between years in terms of frequency of sightings and number of individuals.

Resident gray whales along the Oregon coast exhibited two distinct feeding behaviors. While benthic feeding, usually on swarms of mysids, the whales rolled on their right side with the left tail fluke sticking above the water surface (Figure 2.18a). This was the most common feeding behavior displayed by the resident gray whales in this area. We documented the presence of mysids during this whale behavior, using opportunistic and systematic plankton tows, SCUBA surveys, echogram traces, and underwater video. To definitely confirm that this feeding mode was engulfing mysids, we collected gray whale fecal material which contained identifiable mysid parts. Analysis of 25 separate samples of gray whale fecal material produced identifiable mysid telsons and statocysts. The telsons came through the fecal material relatively unaltered and therefore the specific species of mysid preyed upon could be identified (Figure 2.18b).

During the second, much less common feeding mode, the whales swam at the surface with the mouth slightly agape (Figure 2.19a). This “skim feeding mode” usually collected porcelain crab larvae (Figure 2.19b). To confirm the prey item, we conducted additional net samplings. These collections were done by towing a 70-*u*m mesh net through the upper 2 m of water for a specified distance. The collected crab larvae were preserved in 70% ethanol and analyzed at a later date.

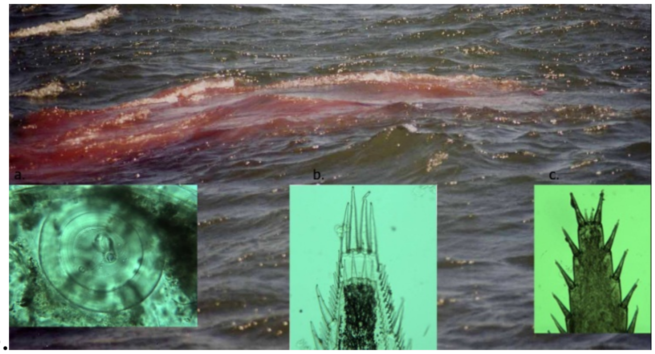
a.  b. 

Figure 2.18 a. Characteristic mysid feeding behavior with the left fluke raised.
b. Whale fecal material showing a statocyst and identifiable telsons.

a.  b. 

Figure 2.19 a. Gray whale skim feeding for porcelain crab larvae (photo by Richard Newton). b. Porcelain crab larvae on a finger.

The gray whales identified as seasonal residents refer to those whales returning in succeeding years. Seasonal residents approaching the study site either remained in residency or traveled through the area to another locality outside of the area being studied. To be counted in the "percentage of time in residency," whales had to remain in the study area for at least two days and exhibit feeding behavior (Table 2.3). When in residency, their primary activity was feeding on mysids with skim feeding occurring opportunistically (Figure 2.18, 2.19). In Table 2.3 and Figure 2.20, the "percentage of time in other" refers to traveling to another mysid swarm locality within the study area, resting, or courting. To distinguish between "traveling through the area" with "traveling to another mysid swarm locality," we documented the depth at which they traveled. Those whales "traveling through the area" typically would be at depths of 19 m or more while those whales "traveling to another mysid swarm locality" would usually travel along the 10m isobath.

Every whale that remained in residency had photographs taken of cervical and thoracic areas so body condition could be ascertained. Body condition of the gray whales were determined by observing and photographing two visible features of the whale, the cervical area behind the blow hole and the appearance or lack of the scapula in the thoracic region. Whales in poor body condition had a pronounced depression behind the blow holes and/or the sunken appearance of the skin around the scapula (Figure 2.21) (Newell & Cowles 2006). The percent of whales in poor condition ranged from 80% in 2005 to 0% in 2004 and 2006. In

2008, only 2% and in 2007 only 5% of the whales were in poor condition. The year with the second highest percentage of whales in poor condition was 2003 with 21% (Table 2.3). As discussed in Chapter 1 (Newell & Cowles 2006), poor body condition in 2005 likely was a consequence of limited prey availability throughout the range of the gray whale population. Conversely, the good body condition exhibited by resident gray whales in other years of the study suggest that prey availability has been sufficient.

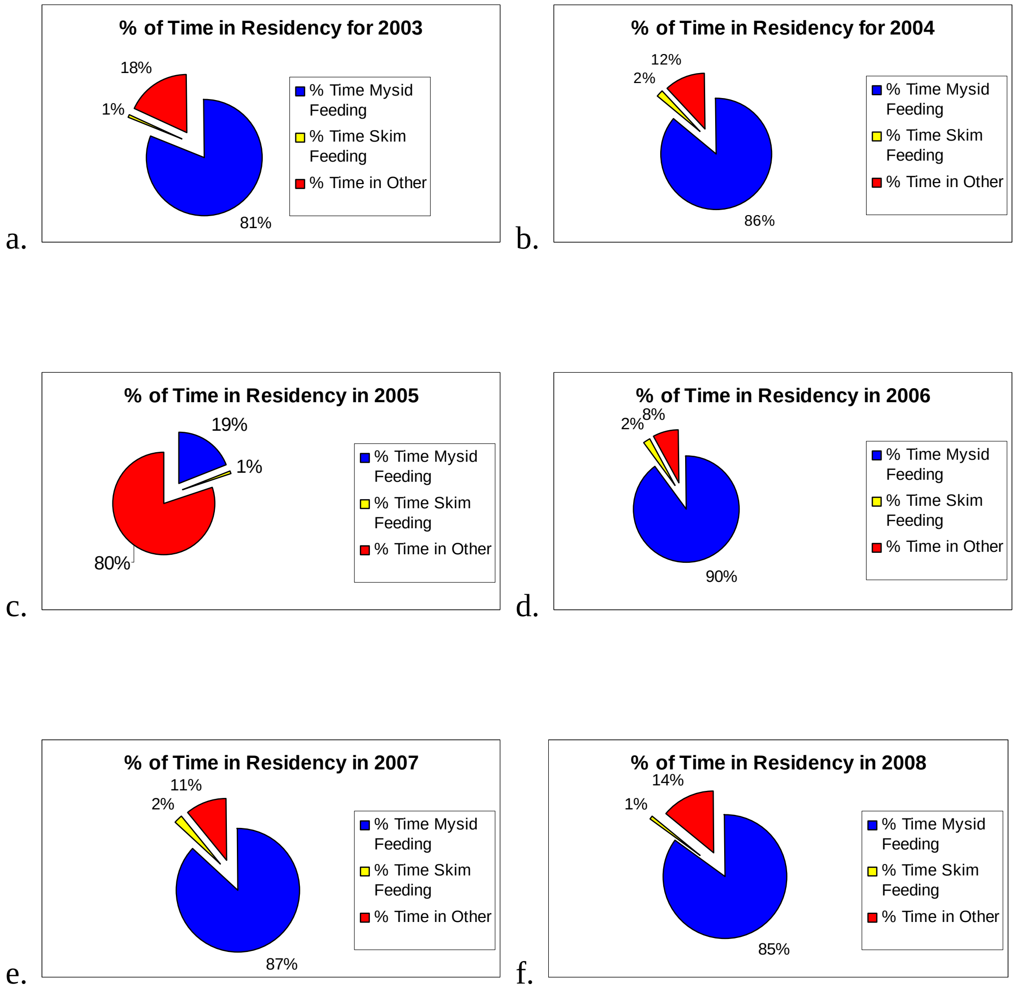


Figure 2.20 Determination of how seasonal resident gray whales spent their time while in residency: percent of time mysid feeding, skim feeding or other from 2003-2008.

Figure 2.21. This whale seen in 2007 was classified as “poor body condition” because of the depressions behind the blowholes and the appearance of the scapula through the skin (see white arrows). This was one of the few whales seen in 2007 in poor condition.

Table 2.3. Inter-annual Comparison of Whale Behavior and Mysid Reproduction from 2003-2008 off the Central Oregon Coast.

Years	2003	2004	2005	2006	2007	2008
Hours Observing	276	342	228	462	483	522
Days Observing	46	57	38	77	85	98
Summer Resident Whales						
Number Identified	29	49	15	37	38	42
% of Time in Residency(>2days)	83%	88%	20%	90%	90%	89%
% of Time Traveling Through	17%	12%	80%	10%	10%	11%
% of Time Mysid Feeding	81%	86%	19%	90%	87%	85%
% of Time Skim Feeding	1%	2%	1%	2%	2%	1%
% of Time in Other	18%	12%	80%	8%	11%	14%
% of Whales in Poor Condition	21%	0%	80%	0%	5%	2%
Mysids						
Mean Number of Eggs/Female in May (St Dev.)	27 (5.48)	19 (4.32)	22 (4.34)	28 (3.32)	23 (2.12)	24 (3.42)
Mean Number of Juveniles/Female in May (St Dev.)	12 (2.74)	15 (1.29)	19 (1.58)	23 (2.20)	19 (2.46)	21 (1.21)
Mean Number of Eggs/Female in August (St Dev.)	31 (4.32)	33 (1.59)	0	32 (2.12)	34 (4.21)	30 (2.12)
Mean Number of Juveniles/Female in August (St Dev)	12 (1.30)	20 (2.16)	0	26 (2.22)	25 (3.42)	22 (1.56)

Discussion

Homotypic swarms of thousands to billions of individuals of *H. sculpta* were common in the nearshore, temperate waters of central Oregon. Heterotypic swarms of *H. sculpta* and *N. rayi* were less frequently encountered and contained fewer individuals. All swarms were found in specific localities along the central Oregon coast. This site specificity is probably attributed to various physical conditions of that site which may include substrate type, light, depth, and the presence and/or abundance of kelp. Proximate causes that may enhance persistence of mysids in certain areas include specific light intensities or sources of food (Modlin1990).

Light seems to be the primary extrinsic factor in the formation of most swarms (Buskey & Peterson 1996). Studies by Modlin (1990) and Buskey & Peterson (1996) showed how mysids were concentrated in light shafts around mangrove roots. Swarms of *Mysidium columbiae* were absent in areas where light intensity was < 60% of the surface value. The degree of light sensitivity appeared to be size-dependent with the smallest juveniles showing the greatest phototaxis and the largest individuals being least sensitive (Modlin1990). Some species of mysids also have a specific site fidelity. O'Brien (1988) found that the mysid, *Tenagomysis*, was attracted to sandy substrates.

The shape of an aggregation can vary according to the species, function, and locality. Mysid swarms have been described as adopting shapes ranging from long ribbons, to columns and compact ovals and spheres (Omori & Hamner 1982). We commonly encountered spherical and ribbon-shaped swarms with *H. sculpta* and *N. rayi*. The ribbon shape was commonly seen when *H. sculpta* was found in the lowest depression of the surge channels in uneven topography. The spherical shape was seen over a flatter bottom. Many aggregations adopt an elongated or cigar shape when traveling and a more spherical or globular shape when stationary (O'Brien 1988). The spherical shape may be an effective way to reduce predation pressure under certain conditions (Clutter 1969; Nicol 1984), but it also provides a large target for an engulfing forager such as the gray whale.

The size of aggregations can vary from dense fist-sized balls to immense shoals covering many hectares and extending 20 km or more in the longest direction (Nicol 1984). We observed extreme variability in the size of the swarms over the nine years of this study. This variability is dramatically exemplified at North Point. In mid July of 2003, the swarm was only 6m by 8m whereas in July of 2006, it was a shoal extending 800 m East to West and 200 m N-S.

Mysids that are substrate specific appear to have swarm shapes dictated by the local topography. The mysid, *Tenagomysis* sp., is associated with sandy substrates between rocky depressions and the shape of its swarm is ribbon-like with the boundaries of the swarm defined by the boundaries of the depressions (O'Brien 1988). *H. sculpta* was commonly found in the surge channels between basalt outcrops producing a ribbon-like swarm. Occasionally some *N. rayi* also formed ribbon-shaped swarms in this locality. This substrate specificity probably reduced predation pressure since a large predator like the gray whale may be unable to effectively consume mysids in these smaller channels.

The density of an aggregation (individuals per unit volume) is a direct result of the individual spacing of the zooplankters. Estimates of NND's under different conditions can be one way to estimate swarm density. Clutter (1969) working with the mysid, *Acanthomysis*, the former name of *Holmesimysis,* found that swarms actively maintained a nearest neighbor distance of 1.1 to 2 cm or 1-4 times the body length. Swarms of *M. columbiae* had NND of <0.5 cm to 2.0 cm during daylight hours (Modlin 1990). The densest swarms of adult *H. sculpta* off Depoe Bay had NND of 1-2 times the body length. Juvenile swarms of *H. sculpta* and *N. rayi* had NND of 3-4 times the body length. In studies of the NND of fish (Pitcher et al. 1982), euphausiids (Daly & Macaulay 1991), and mysids (O'Brien 1988), it was observed that individuals preferred positions alongside their nearest neighbor or directly in front of or behind but avoided positions directly above or below their neighbors. We observed similar behavior by both species off Depoe Bay.

Densities can vary enormously within aggregations on a daily or seasonal basis. Densities in mysid swarms approach 10^5 individuals/ m^3 with a NND of 2.0 cm, depending on the body size of the average individual in the swarm (Mauchline 1980). The density of krill in a study by Greene et al. (1988) was 1000 individuals/m^3 while Hamner et al (1983) found krill densities of 30,000-600,000 individuals/m^3. Using the density estimate methods described earlier, along with NND, we estimated that a large swarm can have over 300 million individual mysids in it and a large shoal could possibly contain over 50 billion individual mysids. The NND within the mysid swarms of this study varied from 2.7 cm for the dense swarms of juvenile *H. sculpta* to 2.4 cm for denser adult swarms of *H. sculpta*. In contrast, swarms of *N. rayi* had NND of 6.6 cm. In 87% of the swarms observed with SCUBA or by video footage, adult swarms had a smaller NND than juveniles and in the other 13%, juvenile swarms were denser. O'Brien (1989) observed that adult swarms of the mysid, *Paramesopodopsis rufa*, had a smaller NND and were denser than juvenile swarms. In the same study, O'Brien (1989) noted that NND decreased as the size of the school/swarm increased. Modlin (1990) showed that NND of mysids varied dielly with denser swarms seen at the surface during the day and less dense or dispersed swarms at night. The limited number of night dives done in this study showed no difference between diurnal and nocturnal swarm densities. O'Brien (1989) noted that swarms of substrate specialized mysids had smaller NNDs than non-substratum associated species. He also determined that the structure of the swarm became more compact with a predator nearby.

Swarm density may be related to both antipredation and foraging. Ritz (1997), observed that mysid swarms were less compact when feeding but became more compact after feeding. These studies indicate that mysids may be maximizing inter-individual spacing to enhance foraging and then minimizing space to decrease predation. Therefore, there may be an ecological trade-off between foraging success and protection from predators (Ritz 1994).

The ultimate cause for many crustacean aggregations that consist of both sexes is reproductive enhancement (O'Brien 1988). Off Depoe Bay and Newport, male and female *H. sculpta* and *N. rayi* were always present in the same swarm. With both sexes in the same swarm, contact between sexes is maximized which is a necessity since females are receptive to impregnation for only two to three minutes after they molt (Clutter 1969; O'Brien 1988). No observations have yet been made documenting mysid swarms containing only a single sex (Clutter 1969; Ohtsuka et al. 1995). Sex ratios in mysid populations are known to vary among samples and seasons, usually in favor of the females. Females can make up from 20% to 90% of the total swarm (Mauchline 1980). The sex ratio of *Lycomysis bispina* in a study by Ohtsuka et al. (1995) was on the average 89% female. In this study, adult females averaged 43% on average of the total swarm from late spring to early fall. Fewer females were found in late spring samples with percentages ranging from 11-30% whereas late summer and early fall percentages ranged from 60-90% female. In most samples, 85% of the females were gravid and collected throughout the sampling season, April-October. It is unknown as to whether these mysids species are reproductively active throughout the year although recently released juveniles have been found in all months except February and March. Many mysid species are fertile all year (O'Brien 1988).

Ohtsuka et al. (1995) observed that stage composition fluctuated seasonally with juveniles comprising 2% in some months and 73% in other months. On the other hand, mature adults only made up 3% during one season and up to 60% another season. A similar situation was seen in this study. Stage composition varied throughout the study period with juveniles comprising approximately 80% of the samples in April and May as compared to August and September when adults dominated the composition of the swarms with around 85%. We observed considerable variability in our samples with some composed only of juveniles or adults and others composed of various size classes or even different species.

Modin (1990) found that *Mysidium columbiae* segregated by life stage, forming vertically stratified swarms with the smallest juveniles at the top and mature males and gravid females at the bottom. Visual observations from SCUBA showed that a pronounced zonation was seen in the heterotypic swarms of *H. sculpta* and *N. rayi*. The vertical gradient of size and maturity increased with depth with the larger adult *N. rayi* found directly above the bottom, then adult *H. sculpta* and juvenile *H. sculpta* at the top. It is possible that some of the variability in samples may reflect a bias in size classes that were captured with the net. For example, if juveniles are towards the top of the swarm, then they may be the only ones captured plus they are the slower swimmers. However, in situ observations with video and SCUBA confirmed that some swarms were composed entirely of juveniles or adults or a combination.

There are both ultimate and proximate causes for size and sex sorting within aggregations. Hamner et al.(1983) states one of the ultimate cause of size and sex aggregation is minimizing competition or cannibalism. Alternatively, differences in swimming speeds or behavioral differences between developmental stages are often invoked as proximate causes for size sorting within aggregations (Mauchline 1980;

Nicol 1984). The swimming speeds of juveniles and adults of a species differ considerably with the result that a mixed-size, stationary aggregation becomes a size-sorted aggregation after swimming some distance, resulting in similar age or body size (Clutter 1969). The occurrence of mixed age groups within a swarm may indicate that the swarm is not migratory and live a more lethargic life style (Mauchline 1980). The aggregations off Depoe Bay may be both stationary and migratory groups since some swarms consisted only of juveniles, some only of adults and some a mixture of various sizes, both adults and juveniles. Immigration, emigration or selective foraging by gray whales may also have caused these differences. Stelle (2002) reported that gray whale foraging was significantly correlated with mean mysid body length with adults being preferentially selected. Dunham and Duffus (2001) determined that foraging gray whales selected amphipods larger than 6 mm as the primary prey, perhaps in relation to the spacing between the plates of the gray whale baleen.

Within a single swarm, we found that individual gravid females possessed any one of three developmental stages of the larvae (stage1, stage 2, and stage3) within their marsupium. Having all larval stages seen in one swarm is a good indication that the brooding period is probably quite short. Individual females released mysids of the same stage, stage 3, synchronously. In a single swarm, various females carried young in one of the three stages of larval development so different females would be releasing juveniles at different times. For example, in Figure 2.10 f, 28% of the females in that swarm had eyed larvae and these would be synchronously released. This synchronous release leads to size-selected aggregations of those larvae to minimize predation (Johnson and Ritz 2001). The remaining 62% of the eyeless larvae and 10% of the eggs would be released at a later date. The staggered release may be an evolutionary adaptation to prevent complete annihilation by predators or their release may be at a time when environmental conditions are more conducive to survival.

Our results indicate that significant predation pressure on mysids along the Oregon coast comes from gray whales, along with additional predation from rockfish. Usually predation risk on mysids decreases as swarm size increases (Ritz 1997). In a larger swarm, when an attack is mounted in one area then a means of defense is to reduce the density of the school at that point of attack (Ritz 1994). This tactic is ineffective with large predators since baleen whales threaten the whole school. The best defense against baleen whales is probably to avoid detection altogether by burying themselves in the substrate or perhaps by living in an area that is difficult for predators to hear or see you. The high surge, shallow water habitat of mysids probably makes capture by baleen whales more difficult.

“Mass” predators, such as baleen whales, seem to benefit positively from prey aggregation and they have evolved capture techniques that encourage even tighter groupings before the prey is engulfed. Humpback whales have perfected the technique of bubble net feeding where they concentrate euphausiids by using a bubble net (Hamner 1984). Along the Oregon coast two specific gray whales have evolved a modified bubble net feeding mode. Approximately 20 seconds after they take a deep dive, they release bubbles underwater from their blow holes and then encircle the bubble net presumably sucking up the mysids trapped in the bubbles.

Since 2000, over 83 individual whales have been photo-identified along the central Oregon coast. Whale numbers at any one time varied from one to 20. Mysids were their primary prey item with porcelain crab larvae only occasional minor components of the diet. These prey items have been confirmed by analysis of whale feces and observations of whale feeding behavior. In all years except 2005, the whales spent 81-90% of their time feeding on mysids. The whale's main feeding behavior when foraging on mysids was to roll on their right side with a partial tail fluke sticking above the surface when water depths were 14m or less. Skim feeding behavior only occurred 1-2% of the time when crab larvae became abundant for a few days in late May or early June. When the crab larvae became available, grays abandoned mysid feeding and exploited the crab larvae by skimming the surface of the water. Dunham & Duffus (2001) reported that gray whales preferentially chose the crab larvae over mysids and amphipods since they were a readily available and easily exploited prey item.

Mysids are important as a food resource for gray whales because of their lipid content. The lipids are an important energy source not only for the mysids but also for the predators that consume them. The lipid value of various genera of the suborder Mysida is 1-6% of their body weight (Mauchline 1980). In comparison, *Euphausia pacifica* has a lipid value of 0.4-7% (Mauchline and Fisher 1969). In a study by

Childress and Nygaard (1974), female *Mesopddopsis slabberi* and *Neomysis integer* stored significantly greater quantities of lipids than males. The sex ratio of mysids in a swarm affected lipid content, with swarms comprised of more females having an overall higher lipid content in that swarm. In *Neomysis integer*, gravid females had the highest lipid content at 1.7%, non gravid females 1.6% and males 0.9% (Mauchline 1980). Both predators, the gray whales (Stelle 2002) and the black rockfish preyed on swarms that were predominantly adults. A high ratio of gravid females were found in rockfish gut contents. There also appears to be a correlation between lipid content and environmental temperature with lower environmental temperatures producing mysids with a higher lipid content (Mauchline 1980).

Ontogenetic and seasonal changes of mysid diet has been documented and can affect the lipid content of the mysid. Kost and Knight (1975) found that diatoms were most important in the diet of young (2mm) and juvenile *Neomysis mercedis*. Diatoms became less important for adult *N. mercedis* at a 15mm body length, while detritus became more important. In this study, gut content analyses of juvenile *H. sculpta* showed pieces of diatom frustules in the digestive tract. In California, *Acanthomysis sculpta* (now known as *Holmesimysis sculpta*) fed on *Macrocystis pyrifera* and crustaceans (Hobson & Chess 1976). It is possible that seasonal increases in the size of bullwhip kelp beds, *Nereocystis luetkeana*, provide a food source and additional shelter from predators during late summer.

Whale numbers and frequency of sightings was low during the early part of the summer. Some seasonal residents appeared around Memorial Day possibly when the swarms became dense enough to exploit efficiently or when the porcelain crab larvae hatched. Many of these early summer residents left the area but some returned later in the summer. There was considerable variability in the duration of residency during this study. The residency inconsistencies where early summer whales leave the area may be due to swarms not being able to sustain prolonged predation pressure during early summer. Also, the samples analyzed from April and May consisted primarily of juveniles and these may not be selected for due to their size, lipid content or density.

Predation pressure on the mysids increased throughout the summer with the greatest number of seasonal residents seen in August and September. In September of 2004, 20 individual gray whales remained in residency most of the month at Sites 5 and 6. An incredible amount of mysid biomass was removed during this time period. Considering a gray whale eats a ton/day, which is 908 kg/day and that the weight of a mysid is approximately 0.1mg, then a single whale is feeding on 9 billion individual mysids/day. When the 20 whales were in the area and stayed an average of 27 days, then over 4.8 trillion mysids were consumed during that time period. Sampling these two sites after the whales left in September showed an absence of mysids. The whales may have “fished out” the area, an excellent example of top down control. Dunham and Duffus (2002) also observed this top down control at certain sites off Vancouver Island where areas were “fished out” by intense gray whale foraging. In most years, swarms disappeared in late October or early November, possibly due to predation pressure from the gray whales or most likely, movement offshore.

Many mysid species are horizontal migrators (Jumars 2006). Seasonal onshore-offshore migrations have been inferred from widely varying seasonal changes in abundance across habitats on fine scales (Bamber & Henderson 1994). Mysids horizontally navigate using polarized light with movements of their stalked eyes and information from the statocysts. Polarized light is probably the directional cue for migrating (Jumars 2006). This polarization or e-vector orientation is a useful indicator of solar azimuth throughout continental shelf depths. The highest information content occurs near dawn and dusk because of the high inclination of the e-vector with respect to the horizontal (Waterman 2005). A majority of the onshore-offshore migrators show winter maxima offshore and summer maxima inshore (Mauchline 1980). This study showed the inshore summer maxima and limited sampling performed during the winter months showed small pockets of mysids in water depths of 20 m or more offshore.

Both the black rockfish and gray whales appeared to choose swarms of adult mysids as foraging targets. Analysis of gut contents showed that rockfish may selectively choose swarms of adults with brooding females possibly because the brooding females contained an enhanced, lipid content and therefore a better caloric value. With gray whales, the larger individuals may be trapped in the baleen more efficiently. Since gray whales are primarily benthic feeders, they have coarser hairs, fewer plates and a greater spacing between the plates than pelagic feeding baleen whales. Since the spacings between each plate varied from 7mm-13mm, only prey this size or larger would be effectively trapped. This observation is supported by the fact that gray whales spent little time in areas where swarms were dominated by juvenile mysids less than 7 mm in length.

Mysid distribution at fine and coarse scales is probably a result of both bottom up control due to available food resources (Newell & Cowles 2006) and top down control due to the predation pressure from gray whales (Dunham & Duffus 2001). Whales exerting top down pressure, may shape the mysid communities. Mysid densities and sizes also control where gray whales feed and how long they remain in that specific locality.

Conclusion

The evaluation of this six-year time series has provided us with information on the spatial and temporal linkages between the largest coastal predator, the gray whale and the most abundant macro-zooplankter, mysids along the central Oregon coast.
The location of the mysid swarms determined the spatial and temporal distribution of the gray whale predators. The abundance and residency times of gray whales was related to mysid population parameters (ie. swarms made up of adults vs juveniles) and their density. Gaining an understanding to aspects of the population structure and localities of the swarms will undoubtedly expand our understanding of cetacean

distribution patterns in the nearshore waters of the CCC along the central Oregon coast.

The unique interplay of both predator and prey exemplifies both bottom up and top down control. This research has provided us with a better understanding of the interplay of these opposing controlling forces in this gray whale/mysid coupling. This knowledge may be of predictive importance when evaluating the future effects of climate change in this coastal ecosystem.

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