The Importance of the Mid-Trophic Layers in Ecosystem Structure, Process and Function: The Relationship between the Eastern Pacific Gray Whale (*Eschrichtius robustus*) and Mysids (order *Mysidacea*) in Clayoquot Sound

By

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B.Sc., University of Bath, 2009

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Geography

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University of Victoria

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Supervisory Committee

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ABSTRACT

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While the impact of top-down and bottom-up drivers of ecosystem functions has been given considerable argument, here the mid-trophic level is given focus. In marine systems the influence of mid-trophic level species operates in a 'wasp-waisted' structure, where they exert regulatory control by acting as a valve to energy flow between large seasonal pulses of primary production and upper level species. In this study I examine the impact of foraging eastern Pacific gray whales (*Eschrichtius robustus*) on mysid species at the 'wasp-waist' (Order *Mysidacea*), and vice versa, at feeding sites in Clayoquot Sound off the west coast of Vancouver Island. I appraise previously unknown aspects of the 'prey-scape', and further explore life-history traits that allow prey populations to persist in a given species array.

The set of problems that I examine are all based on the whales' top-down forcing in a localized area, and the prey response. I use several scales of observation as dictated by the nature of each question. I examine top down forcing and subsequent prey switching over a 25-year period, the variation in foraging intensity over a 15 year period, the differential prey species' response to persistent predatory pulses that creates dominance and diversity among the mysid species flock, and whales' within-season response to possible satiation. Each of these studies is linked by the common goal of illuminating the intimate relationship between predator and prey. Gray whale foraging has decimated amphipod prey resources in the study area past the point of recovery over the last 25 years, and the prey resource is no longer a viable energy source. This has led to the abandonment of benthic-feeding by gray whales in the area, and a switch to mysids as a primary prey source. It is in investigating these mysid species' ability to rebound following severe foraging pressure that I uncovered two principal life history strategies,

one held by the single dominant mysid species, and another used by 9 or 10 others consistently sampled. The capacity for renewal of mysid swarms is imperative if Clayoquot Sound is to persist as a productive foraging area for gray whales. The pattern of this relationship that I present, based on a 15 year span, was previously unknown. Intense foraging of mysids by gray whales during a summer affects the reserves for the following season, leading to a biennial fluctuation in the number of whales the area can sustain, although some of the heaviest foraging seasons require several years to show mysid recovery. I state 9 or 10 other species, as through the intense examination of mysids here, there may be a new species designated.

The data gathered by myself and colleagues over the past 25 years that whales have been studied in Clayoquot Sound, clearly shows that predation by baleen whales can affect the future quality of their foraging areas, as well as influencing the population, life-stage and diversity of prey species. My work furthers knowledge in life history characteristics of the mysid species present in the study area, particularly growth and reproduction, and ability to capitalize on a release of predation pressure over winter to recover. That, in turn creates a series of following questions about how different life history strategies make use of a variety of possible energy pathways to stabilize ecosystems at least at discrete spatial scales.

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Acknowledgements

Firstly my heart-felt thanks to the ‘Doc’ of the Whale Lab, Dave Duffus. This project would have failed before it started without you, although the words on the pages that follow are the least of the things I have achieved, under your guidance, in the past three years. Your support, encouragement and humour has been resolute, as has your belief in the city girl a long way from home. From greener than green, and fading into the forest, to plaid wearing lumber-jack in 4 field seasons! Words cannot encapsulate everything I have learnt, but one thing is particularly true ‘If something’s worth doing, its worth overdoing’!

I appreciate all the thoughtful comments from Dr. Mark Zacharias as my other committee member and his efforts, along with Ted Down as my eternal examiner, to help me draw out the best from the final draft of this thesis. The work on the possible new species of mysid had significant contributions from Melissa Frey at the Royal BC Museum and Kenneth Meland.

This work builds on all those ‘Whale Lab-ers’ that have gone before me, and goes some way in assimilating all our efforts. Particular support, friendship and advice has come from Laura-Joan Feyrer, Charlie Short, Lynn Kent, Kyle Muirhead, Tyler Lawson, and Christina Tombach-Wright. They, along with Jacqueline Clare and Kira Stevenson as current Whale Lab members, have given blood, sweat and (in some cases) vomit to help me in the field, as well as helping maintain perspective when the prospect of thousands of mysids (74,866 in fact) and thesis writing was too much!

My time on Flores Island was enriched by the people of Ahousaht and their culture. Hughie, Keith, and the rest of the Clarke family have also been key in making the ‘big red house’ a home away from home. All the SEACR interns and other student researchers that have joined us have also enhanced my time in the field, with the amount of work equaled to the amount of giggles! Particular mention to the ‘returnees’, Anna and Theresa who both caught the bug!

I must acknowledge all those outside of the lab that have been encouraging and helped me retain sanity during long winter months of lab work and writing (and occasionally joining me on mad mysid-catching weekends). All those that have become friends and have made me welcome, including, but not limited to: Krystal and the rest of the Bachen family, Ashley Stocks and the Joffre St. crew, Alisa and Tyler Preston, Dianne and Wayne Humphrey, Joelle Thurston, Pieter Mieras and Kathy Johnson, the Clare family, Harold Stevenson, Val Mucciarelli, Nate Duffus, Kim T, Mike Blazecka… thanks for all the adventures above and below the water line!

Finally, to those that loved me enough to set me free on this journey thousands of miles from home. Despite meeting some rough waters your friendship, encouragement and support has helped me see through the fog when I was lost and made the good times even better. My family, key friends, and a certain Silly Billy have been there in spirit to help guide me through my time 'at sea' and watch me mature into a marine scientist! It is the unwavering love and support of my parents that has given me the strength to go out and ask the questions for myself, come rain, shine, wind, hail, or snow – to try everything once and never halt on my path of learning - and for that I can never thank you enough.

CHAPTER 1
Foraging Ecology of Gray Whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia

Bottom-up and top-down trophodynamic forces, although often considered opposing influences, can work synergistically as system structuring agents. The more prevalent influence relies on the life history stage of the organisms, species redundancy and fungibility, area studied, relative mobility of predator and prey species, and the scale of the study (Levin 1992, Hunt & McKinnell 2006, Heath & Gallego 2007).

Productivity can fluctuate over time and space, and form patterns, which define the environment over coarse scales. For marine systems, resources change with seasonal blooms, upwellings, and stratification, and then are modified by current, tidal movement, topography, or terrestrial inputs. Conversely, the influence of apex predators can determine the community structure and stability of the interaction web from the top-down. Cetaceans impact the community in which they forage, due to their high metabolic requirements and subsequent prey consumption (Brodie 1975). Forming the upper trophic-levels, they have the power to define the abundance and diversity of prey species, preventing overgrazing or monopolization by mid-trophic levels (Hairston *et al.* 1960, Connell 1961, Paine 1966).

Predator pressure can drive prey numbers into decline. With a release of predation, prey populations can recover, forming a boom-bust pattern of co-dependent oscillations in predator-prey populations (*sensu* Lotka-Volterra models). Although not fully characterized, species in the mid-trophic levels also have the ability to influence the ecosystem to an extent similar to that of apex predators (Hutchinson 1959, 1961, Paine 1966, Connell 1978), or producers (Hairston *et al.* 1960, Hutchinson 1961). Work by Sapaikhina *et al.* (2003) suggests the amplitude of predator-prey oscillations could be affected by the heterogeneity of prey aggregations, ability of prey to disperse, and predator foraging success. Researchers characterize these systems as being under 'wasp-waisted' regulation. Briefly this means that higher trophic level predators are subject to bottom-up control by the abundance of mid-trophic level prey, whilst lower levels are subject to top-down control by the same mid-level species themselves acting as predators (Rice 1995, Bakun 2006, Hunt & McKinnell 2006).

In this study, I delineate the trophodynamic forces within marine systems influenced by the foraging ecology of the eastern Pacific gray whale (*Eschrichtius robustus)*. Population increases of these whales following commercial whaling have been implicated in large-scale system shifts including trophic cascades, regime shifts, food chain decoupling, and reductions in productivity. During their annual migration from breeding and calving grounds of the inshore waters of Baja California Sur to the principal summer foraging areas in the Bering and Chukchi Seas, gray whales pursue patchily distributed prey. A sub-group of the population, known as the Pacific coast feeding aggregation (PCFA, Moore *et al.* 2003), summer in tertiary foraging sites from California to Alaska (Kim & Oliver 1984). With intensified foraging pressure in primary Arctic feeding areas, numbers may now exceed the carrying capacity of the Arctic infaunal prey community (Highsmith & Coyle 1992, Moore *et al.* 2003), and so whales will become progressively more reliant on tertiary foraging areas, like that on Vancouver Island (Nerini 1984, Calambokidis *et al.* 2002).

Gray whales have the power to shape the system from the apex of the food chain downward (Estes & Palmisano 1974, Oliver & Kvitek 1984, Oliver & Slattery 1985, Estes *et al.* 2004), feeding on spatially discrete macro-zooplankton and benthic invertebrates. In Clayoquot Sound, on the west coast of Vancouver Island, food resources, and perhaps factors originating in the larger population, are the immediate determinants of the number and distribution of whales summering in the area (Duffus 1996). Prey switching behaviours allow whales to take advantage of the short-term energy availability to restore lipid reserves after over-winter losses (Dunham & Duffus 2001). Persistent pulse perturbation from gray whale foraging has overwhelmed sediment-dwelling amphipod reserves (Order *Ampeliscidea;* Kim & Oliver 1989, Carruthers 2000), with them now utilizing epibenthic mysid shrimp species (family *Mysidae*) as a principal prey item (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002, Stelle 2001), as well as opportunistically foraging on crab larvae (*Pachycheles* and *Petrolisthes* spp.) and ghost shrimp (*Callianassa californiensis,* Dunham & Duffus 2001, 2002).

Few studies that describe cetacean distribution examine the relationships with prey variables or ecological hypotheses (Wishner *et al.* 1995, Croll *et al.* 1998, 2005,

Torres 2008). Here I ask whether Clayoquot Sound is able to remain a productive foraging site for gray whales, with the pulse perturbation of their seasonal foraging having already decimated amphipod prey reserves, leading to a prey-switch to mysid species. In this study I examine the top-down forces of predation, and prey species' ability to recover when predation pressure is released, with much of the work here to assess mysids' ability to be resilient to annual removal.

Chapter Two describes the top-down influence gray whales have on the structure of local ecosystems. I compile data from more than 25 years of foraging studies to quantify the decline of ampeliscid amphipod stocks, and resulting rejection as a prey resource by gray whales, and document the prey switch to epi-benthic mysid species. Chapter Three further describes foraging intensity of gray whales within Clayoquot Sound on a range of temporal scales. Using 15 years of transect census data, I examine the peaks and patterns in predation, particularly in adjacent seasons. Whereas this chapter shows longer term foraging trends, the following chapter describes the temporal patterns of individuals to determine the 'satiation' point of gray whales. In Chapter Four seasonal satiation is defined as the point where energy reserves have been restored sufficiently over a single summer residency time of the whale. On arriving in the study area foraging whales behave in an edacious manner to recover from an extended fasting period overwinter. With reserves replenished, behaviour may be released from the tight requirement for foraging to dominate.

Chapters Five and Six give focus to mysid species as the mid-trophic prey. After describing the decline of amphipod reserves in Chapter Two, in Chapter Five, I consider the ability of mysid swarms to recover after severe predation pressure, and how this may be achieved on intra- and inter-annual time scales. There is limited knowledge of growth and reproduction for the mysid species in Clayoquot Sound, with a particular lack of data outside of the summer months. Here I address this gap, characterizing swarm presence and persistence by measuring reproduction and growth after predation pressure has been released. The influence of species-specific phenology on species dominance is considered to determine traits that enhance reproductive success, resources use, or both. Samples from over two winters are used to elucidate reproductive strategies of each species, particularly adult maturity sizes and proportion of gravid females, despite the fact that

overwinter brood production seems unlikely, given the overall nutrient dynamics of our coastal area. Finally, in Chapter Six I describe a possible new species of coastal mysid in the whales' prey base, found in addition to the 12 already known to be present in Clayoquot Sound. This discovery is the pleasant by-product of measuring and describing over 70,000 individual mysids.

In this study I look at the influence of mid and upper trophic levels in shaping the system, and consider that the major control in ecosystems may be neither solely bottom-up nor top-down but rather 'both up and down from the middle' (Hunt & McKinnell 2006). This knowledge may be generalized to other foraging sites, and utilized on a broader scale to inform management of threatened species and critical habitats.

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CHAPTER 2
The Demise of Amphipod Prey Reserves as a Result of Gray Whale (*Eschrichtius robustus*) Predation in Clayoquot Sound, British Columbia

Abstract

Following their migration from breeding grounds in Mexico to primary foraging areas in the Bering and Chukchi Seas, the eastern Pacific gray whale (*Eschrichtius robustus)* utilizes macro-zooplankton and benthic invertebrate prey to restore energy reserves. As populations recover from commercial whaling, they are thought to have exceeded the carrying capacity of prey stocks in these primary foraging areas, and so increasingly exploit alternatives.

Gray whales can influence prey species composition and system dynamics. Their foraging results in excavation pits where they have suctioned sediment to retrieve infaunal prey, primarily *Ampeliscid* amphipods. Persistent pulse perturbation has exhausted amphipod reserves, with declines mirroring those documented for the Bering Sea. Predation effects are compounded by amphipod life history characteristics, their slow growth rates and long generation times, all hindering recovery from disruption.

Here I examine the population decrease of benthic amphipods on a small study site, and propose that amphipod stocks are diminished past the point of recovery and are, as yet, unable to capitalize on more recent predatory release following prey-switching behaviours. Field data taken over twenty-five years of ecological study in Clayoquot Sound indicates a system driven into disequilibrium by gray whale predation, leading to a top-down push to hysteresis. This serves as a backdrop to further research on the effect of this loss of prey resources.

Introduction

Cetaceans are ecologically important, with their size affording them significance on an ocean-wide scale despite being less numerous than other aquatic organisms. Their metabolic requirements and high prey consumption influence system energy flux (Katona & Whitehead 1988). Predation represents an important structuring element of their prey community, and can be indicative of ecosystem health and productivity. For example, foraging by eastern Pacific gray whales (*Eschrichtius robustus)* in the south Chukchi Sea and Chirkov Basin of the north Bering Sea has been described as the equivalent to major geological forces acting on the benthic environment (Katona & Whitehead 1988). Gray whales forage for sediment-dwelling ampleliscid amphipods (Order *Ampeliscidea*) in these primary foraging areas by suctioning sediment to excavate invertebrates from the benthos (Oliver & Kvitek 1984).

Gray whale consumption of benthic organisms has been calculated to be 379-2496 kg per whale daily (Tomilin 1946) and in excess of 773000 metric tons by the total foraging whale population annually (Zimushko & Lenskaya 1970). Coyle and colleagues (2007) suggest that, with only using 3-6% of the estimated total whale population (16,000+, Laake *et al.* 2009), gray whale foraging would be able to remove 10-20% of annual ampeliscid production in the Chirikov Basin. Following the cessation on hunting, the whale population has rebounded to such an extent it is now believed to exceed the carrying capacity of the Arctic amphipod community (Highsmith & Coyle 1991). As a result they increasingly exploit secondary areas north of the Bering Strait and tertiary areas along their migration route (Moore *et al.* 2001, Perryman *et al*. 2002).

Life history characteristics of amphipods, their slow growth rates and long generation times, prevent rapid recovery from gray whale predation (Coyle *et al.* 2007). Amphipod growth is related to molt number, and is correlated to productivity (Kanneworff 1965) and water temperature (Highsmith & Coyle 1990) creating variability between seasons and years. Kanneworff (1965) states that body length increases approximately 10% with every molt, with an estimated 18 molts occurring before the egg carrying stage in females. Growth is continuous, rapid in spring, slowed by ovary and testes development in summer and autumn, and stagnant in winter for ovigerous females (Kanneworff 1965). Upon sexual maturity, males die directly after mating, and females

die after releasing their brood following a five-month gestation (Kanneworff 1965, Boudrais & Carey 1988, Leonardsson *et al.* 1988). Generally, brood size for cold-water species average from 15 to 60 (Kanneworff 1965, Sainte-Marie 1991). Juveniles do not disperse widely from their natal location, instead forming dense patches of high biomass. Whereas rates of increase in amphipod length are approximately linear, the rate of biomass accumulation is exponential (Morin *et al.* 1987, Highsmith & Coyle 1991). Productivity relative to biomass is greater in more established populations, due to contributions from the older age classes (Robertson 1979).

Ampeliscid amphipods are sedimentary tube dwellers, which rely primarily on phyto-detritus to maintain their population and productivity. Biomass in benthic communities also reflects the processes occurring in the overlying waters, with tight coupling demonstrated between amphipod production and carbon flux to the seafloor (Highsmith & Coyle 1991, Coyle *et al.* 2007). Quality of matter descending to the sea floor, and so resources for amphipods, depends on primary production, phytoplankton sinking rate, zooplankton grazing rate, mixed layer depth, overall water column depth, and proximity to land runoff sources (Parsons *et al.* 1977, Pace *et al.* 1984, Wassman 1984).

Pulse perturbation from gray whale predation can have a dramatic impact on the structure of the benthic community. Theoretically, it creates co-dependent population oscillations that, for single species predator-prey interactions, translate prey death to predator birth. This boom-bust cycling also predicts prey population recovery following release of predation pressure. Work by Coyle and colleagues (2007) did not, however, find this to be true of benthic communities in the Bering Sea. Whereas predictions imply ecological stability will be regained following severe pulse predation by recovery to the original state (Terborg *et al.* 2010), field data does not substantiate this. Whale foraging in the Arctic has induced such a decline in amphipod populations that they appear unable to recover. In accordance with conclusions made by Coyle *et al.* (2007) for primary foraging sites, I predict that instead of showing repopulation, the ampeliscid prey resource in Clayoquot Sound, a tertiary gray whale foraging site, will decline and the system may reach an alternative stable state. I will use field data collected over 25 years (1983-2008) in a small, spatially discrete study area to trace the decline in number,

particularly of large bodied individuals, and biomass of amphipods due to gray whale predation. Furthermore this data set includes a period of predator pressure release, following prey-switching behaviours from 1992 onwards, which should allow at least partial population recovery. Consistent foraging of amphipod resources was last observed in the late summer of 1997 (Dunham & Duffus 2001).

Methods

Study Area

I focus here on foraging areas in Clayoquot Sound, on the west coast of Vancouver Island. On the west coast of Vargas Island, Ahous Bay encompasses an area of approximately 8 km^2 of fine sand substrate. It is protected from oceanic swell by surrounding submerged reefs and Blunden Island (Figure 1). Designated a Marine Protected Area in July 1995, it is suggested that the benthic community here may have developed a resistance to disturbance after years of commercial crabbing in the bay (Dunham 1999). This site has been monitored constantly by Whale Research Lab teams since 1990. Its whale use has declined dramatically, while once creating the core area for recreational whale-watching, between 1988-1992, now is only occasionally visited by gray whales (D.A. Duffus 1996, Pers. Comm, Pers. Obs. 2009-2012).

On the south side of Flores Island, a second site in Cow Bay comprises approximately 10 km^2 of amphipod habitat, as well as patches of rocky substrate and kelp beds (Figure 1).

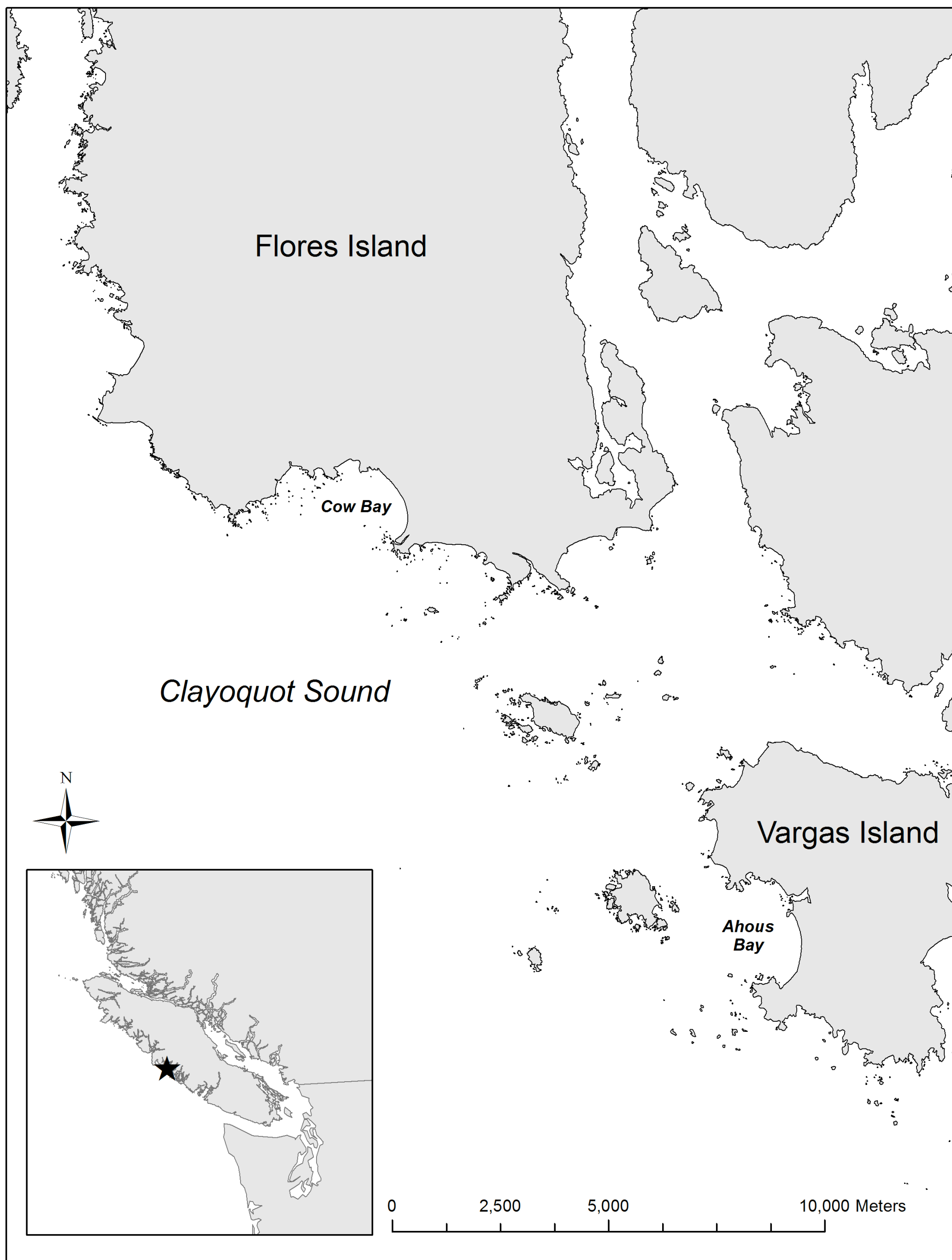

Figure 1: Map of study area indicating the two sample sites,Ahous Bay and Cow Bay

Data Collection

Gray whale feeding ecology studies in the Clayoquot Sound have included observations of spatial behaviours (Duffus 1996) and dive profiling (Malcolm & Duffus 2000), as well as determination of the prey types present and their abundance (Murison *et*

al. 1984, Oliver *et al.* 1984, Guerrero 1989, Duffus 1996, Bass 2000, Carruthers 2000, Dunham & Duffus 2001, 2002, Patterson 2004, Olsen 2006, Feyrer & Duffus 2011). Measurement of benthic prey in Clayoquot Sound began in 1983. Initial observations from scuba divers described the infaunal community and feeding pits, and side scan sonar was used to estimate biomass in Ahous Bay (Guerrero 1989). Similar work in 1993 by divers quantified reserves in Cow Bay and examined the small-scale variability in amphipod resources. Samples were taken using a 10 cm diameter diver-held corer, to a depth of 10-15 cm, with an area of 78.5 cm and volume ranging from 785 to 1178 cm^3, with site selection based on whale presence (Bass 2000). Use of a 0.06 m^2 core sampler (Ogeechee Sand Pounder, Gillespie *et al.* 1985) from 1995 onwards promoted a more comprehensive sampling regime. Dunham and Duffus (2001, 2002) sampled both Ahous and Cow Bays at randomly selected grid coordinates in 1996 and opportunistically at sites where gray whales had been foraging in Cow Bay in 1997. Samples were passed through a 1 mm mesh screen, with organisms removed and preserved, and the volume of sediment recorded. Amphipods were measured from eye to telson tip and blotted wet weight used to determine biomass per unit area (Dunham & Duffus 2001, 2002). Carruthers (2000) also used a core sampler to determine amphipod density, size class and sediment characteristics, augmented in 1998 by diver's samples to examine variability on a fine scale. Samples collected in 1999 were primarily used for biomass and caloric determination, species abundance, cohort structure, and distribution patterns (Carruthers 2000). Samples taken following this were collected with a 0.023 m^2 benthic grab (Wildco Petite Ponar Grab) using stratified random locations from Ahous and Cow Bay in 2005-6 and 2008 (Patterson 2006). Coincident to benthic sampling, whale use of the areas was noted.

Over the 25-year period, 194 samples were taken from both Ahous and Cow Bay. Gray whale use of Ahous Bay effectively ended in 1992, abandoning amphipods as a significant prey resource, with only short, sporadic feeding events noted from 1992 to 1997 (Duffus 1996, Dunham & Duffus 2001). They have not, however, deserted Clayoquot Sound as a foraging area, and continue to forage in Cow Bay. Nonetheless, foraging gray whales are now observed in more inshore waters, over rocky reefs and in kelp beds, characteristic of mysid shrimp habitat.

Results

In 1983-1984 Ahous Bay had a dense homogeneous tube mat extending from the surf zone sloping gradually to an offshore edge at 22 meters, where the substrate changes to coarse sand and gravel (Guerrero 1989). The greatest prey resource was found at 12 meters, correlated with the most benthic disturbance from gray whale foraging (Guerrero 1989). Benthic biomass in Cow Bay was at its highest in water 16-20 meters deep (Dunham & Duffus 2002). The dominant amphipod species in both Ahous and Cow Bay were *Ampelisca aggassizi* and *A. careyi* (Dunham & Duffus 2001, 2002).

Amphipod measurements were made in 11 summer seasons over a 25-year period (1983-2008). In this time, declines in mean biomass of amphipods were found to be 58.9% in Ahous Bay and 77% in Cow Bay (Patterson 2006). Sampling effort and amphipod number over the 11 summers sampled were compared (Table 1). Carruthers' (2000) quantification of caloric value found lipids increased as the summer progressed. However, on a larger temporal scale (1997-1999) the caloric value of large bodied amphipods per meter squared declined (Carruthers 2000, Patterson 2006)

Table 1: Quantitative estimations of biomass of amphipod prey in Clayoquot Sound, comparing Cow Bay and Ahous Bay. Biomass values represent calculated means. Values taken from Guerrero 1989, Dunham 1999, Bass 2000, Carruthers 2000, Patterson 2004, Vidal 2008

Year	**Ahous Bay**				**Cow Bay**			
	Number of samples	Number of amphipods	Biomass (g/m^2)	Size %≥6mm	Number of samples	Number of amphipods	Biomass (g/m^2)	Size %≥6mm
1983		250						
1993					8		164.56 (±31.25)	
1994					6		80.15 (±17.98)	
1995	17		152.48 (± 31.04)		8		175.99 (±64.95)	
1996	54	1369	21 (± 43)	11.7	45	1072	38 (±69)	6.3
1997	29	393	74 (±55)	19	14	804	97 (±80)	46.3
1998	17	981			86	1982		
1999	7	327			7	210	13	
2004	20	2319	13	10.7	20	4031	18	
2005	28	4828	28					
2008	22		27.31	17.7				

Discussion

The ability of an area to sustain foraging gray whales is not solely based on prey presence, but also its abundance, energy content, nutrient status, and capture and assimilation efficiency. Over the full time scale considered, the evidence suggests that amphipod reserves in Clayoquot Sound have declined to a point where they no longer represent a viable resource, with biomass and density declining over time. Observed patterns of exploitation of prey resources by gray whales is the a response to availability and profitability, with predictability of encounter also a possible factor (Dunham & Duffus 2001). Fluctuations in biomass values, with resurgences seen for example in 1995 and 1997 (Table 1), may be indicative of amphipod life histories. These peaks, however, represent a large number of small-bodied (<6mm) amphipods that are not thought to be a viable food source, as they would not be retained in the whales' baleen.

This overall declining trend of the amphipod population in Clayoquot Sound mirrors that reported for Arctic primary feeding areas, with prey quality not warranting the expenditure of retrieval (Highsmith & Coyle 1991, Coyle *et al*. 2007). This is also reflected in the whale use of Ahous and Cow Bay, with alternative prey switching behaviours first noted in 1992, and consistent benthic resource foraging last recorded in 1997, although this did not exceed two sequential days in late summer (Dunham & Duffus 2001). As catholic feeders, gray whales prey switch and utilize alternative foraging sites in the study area to restore energy reserves. In my study area they now preferentially exploit swarming epibenthic mysid shrimp species (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002, Stelle 2001) and episodically forage for crab larvae and ghost shrimp (Dunham & Duffus 2001, 2002).

Despite the reprieve from predation by prey switching and years of very low foraging intensity, amphipod reserves in Clayoquot Sound have not shown recovery. This may be due in part to the insular nature of amphipod communities. Recovery from predation may also be retarded due to the life history characteristics (absence of pelagic larvae, low dispersion, low fecundity), and the distance from non-perturbed populations, which could supply recruits (Dauvin 1987). The evidence suggests they have been forced past the point of rebound by persistent pulse perturbation. The relentless nature of annual

prey removal over an extended time period, in this case 25 years, results in prey population control more representative of that governed by press perturbation pressure.

Gray whale foraging is influential on community structure and productivity, with whales acting as both consumers and habitat architects (Oliver & Slattery 1985, Highsmith *et al.* 2006). The biogenic disturbance of the substrate and resuspension of sediment could shift organic matter between aerobic and anaerobic environments and release organic material, ammonium, and nitrate into the water column (Pilskaln *et al.* 1998). Excavations created by gray whale feeding also generate open habitat patches, which are then exploited by a diverse fauna of scavenger populations (Oliver & Slattery 1985). All of the above may have contributed to hysteresis and the establishment of an alternative stable state further hampering the recovery of amphipods, or preventing the return to the original state completely. With the demise of the infaunal amphipod stocks, other organisms may capitalize and utilize this uninhabited niche. This energy decoupling from amphipods to other invertebrate and benthic species will further impede population re-establishment. Accordingly, gray whales have shown almost total reliance on alternative prey species.

Conclusions

As the apex predator of a short interaction web of spatially discrete prey, the presence of gray whales can exert much control. Here I followed the decline of amphipod prey, and questioned its ability to recover after severe predation pressure. Long-term field data have not shown repopulation after predator release. Due to similarities in benthic composition, these findings may be applied to primary feeding areas in the Bering Sea, where in the future it may be obligatory for gray whales to capitalize on their ability to exploit a more extensive range of prey species. Although this work was conducted in a small, spatially discrete study area, the findings may be reflected on a larger scale, to foraging areas in higher latitudes, such as the Bering and Chukchi Seas in the Chirkov Basin. In these areas persistent annual gray whale foraging may drive ampeliscid populations to such low numbers that they too are unable to recover and their niche become occupied by other invertebrates, with projections showing possible out-competition by polychaetes (Grebmeier, J. Pers Comm).

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CHAPTER 3
Patterns in Foraging Intensity of Gray Whales (*Eschrichtius robustus*) in Clayoquot Sound

Abstract

The patterns of the distribution and behaviour of cetaceans are often studied outside of their ecological context, despite them often being shaped by variables such as prey location and availability. Here I examine the foraging behaviours of the eastern Pacific gray whale *(Eschrichtius robustus)* utilizing prey reserves of epi-benthic mysid species in the tertiary foraging site of Clayoquot Sound on the west coast Vancouver Island. I analyze how the presence of this apex predator can influence community structure from the top down, and in doing so affect the future persistence of the foraging area, where intense foraging presumably restricts the prey resource for the following season.

Data from 15 consecutive years were analyzed for patterns of foraging intensity. Five hundred and twenty-one twice-weekly surveys were conducted during summers from 1997 to 2011, recording the number of foraging gray whales. Heavy foraging diminishes prey reserves, and consequently the number of whales that can be sustained the following season. This relative predator release in turn allows prey re-establishment for the following season. Total whale foraging days per season showed an overall declining trend in years 1997-2009, with several consecutive years of decreased foraging intensity allowing a significant recovery of prey in 2010.

The patterns of presence and distribution of foraging gray whales are intimately linked to prey resources. The continuing ability of mysids, as the principal prey species, to recover from severe predation pressure will determine the future use of Clayoquot Sound as a foraging area in the future.

Introduction

Predation can structure ecological communities (Paine 1966, Menge & Sutherland 1976), yet few studies of cetaceans examine relationships with prey variables or consider ecological hypotheses to understand distribution and behaviour (Wishner *et al.* 1995, Croll *et al.* 1998, 2005, Torres 2008). Whales can significantly alter food webs, exacting an influence from the apex of the food chain downwards (Estes *et al.* 1998, Springer *et al.* 2003, Coyle *et al.* 2007). Their presence can exert ecological control, with the whales acting both as consumers and habitat architects with their foraging noted as critical to community structure (Oliver & Slattery 1985, Highsmith *et al.* 2006).

Here I examine patterns of foraging intensity of eastern Pacific gray whales (*Eschrichtius robustus)* in Clayoquot Sound, a foraging site on the west coast of Vancouver Island. In this area, gray whales cap a short food chain, feeding on spatially discrete epi-benthic mysid swarms (family *Mysidae*). In their quest to replenish blubber reserves following migration, gray whales can force prey populations into decline to attain their required caloric intake, estimated to be the equivalent of 1.6 x 10^8 mysids per day (Mulkins *et al.* 2002). Prey reserves may be able to recover from this persistent seasonal predation pressure following off-season predator release, although in some cases foraging has been so severe that populations have become overwhelmed and possibly locally extirpated (Coyle *et al.* 2007). I analyze 15 years of foraging intensity data in the study area, gathered from twice-weekly surveys throughout summer seasons. The number of foraging whales in any given year strongly influences prey resources, and so in turn the number of whales that can be sustained in subsequent seasons. This creates a release in predation pressure and allows re-establishment of prey populations and, consequently, whale numbers for the following summer.

Methods

Study Area

The study area is in Clayoquot Sound, on the west coast of Vancouver Island, British Columbia, between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W. The study site is approximately 20 km² along the coast of Flores Island, bounded to the west by the 30-meter depth contour, and bordered to the north and south by unproductive

foraging areas (Figure 1). From observations and sampling in the waters on the south-west coast of Flores Island, distinct gray whale prey locales have been classified according to distance from shore, substrate type and depth. Accordingly, a transect route along this shoreline was developed between 1994 and 1997 to census foraging sites. Approximately following the 10-meter isobath, the route encompasses habitat for amphipod, mysid and porcelain crab larvae prey and maximizes the possibility of encountering foraging whales (Figure 1, Dunham & Duffus 2001).

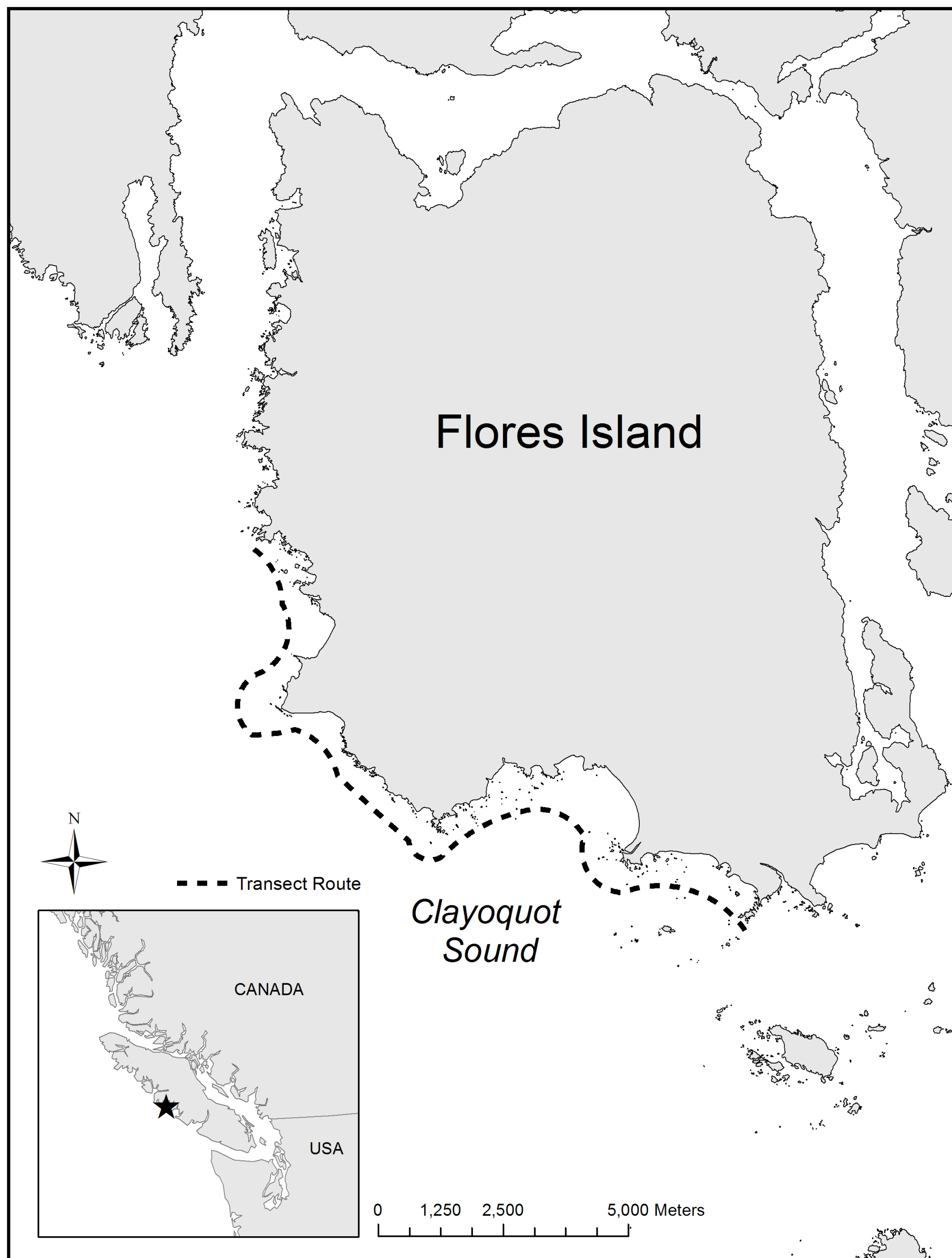

Figure 1: The study area, Clayoquot Sound. The survey route, indicated by the dotted line, follows the 10 m isobath, typically through rocky reef systems which are key mysid habitat

Whale Surveys

Between May 24th and September 8th for the years 1997-2011 gray whale foraging intensity in the study area was measured by twice-weekly, boat-based surveys. A minimum of four observers scanned 360° for whale blows. Vessel speed during the

survey was constant (15 to 20 km/h), following the transect route (Figure 1), and unique markings of the whale are used to avoid double counting. Surveys were aborted if visibility became compromised by fog or a Beaufort Sea state exceeding a level 3. Differences in the timing and number of surveys in each season are due to weather conditions. On locating a whale, the latitude and longitude were taken for the distinctive slick mark left by the fluke when diving. Diving behaviour and location are used to confirm whale is foraging, with non-foraging whale data discarded.

Data Analysis

The average number of foraging whales per survey for each year is used as a measure of foraging intensity. The maximum number of foraging whales on a single survey, and its timing (date of occurance), as well as total whale foraging days quantify the demand made on the prey stocks. Measures of skewness and kurtosis of the distribution of whale numbers are used to analyze the distribution and variability in foraging, and as a means to compare foraging patterns between years.

Skewness is a measure of symmetry in data around a center point, in this case the peak representing maximum number of whales. For data that is normally distributed this value is zero, with positive values indicating foraging intensity is greater in the earlier part of the season, and negative values representing a greater number of foraging whales in the latter part of the summer. Kurtosis is the degree to which data is peaked or flattened relative to a normal distribution around the mean. The greater the kurtosis value the more distinct the peak in the data.

A regression analysis is employed to determine the influence of the foraging intensity of whales present in the first four weeks of a season by the last four weeks of the previous season. In accordance with my hypotheses, I would expect a negative relationship, where a larger number of whales in the latter stages of a season would mean a reduced number of whales can be supported by prey reserves in early part of the following summer, and vice versa.

Results

Whale Surveys

For the seasons 1997-2011, the number of foraging whales in Clayoquot Sound oscillates, with every year of higher than average foraging activity followed by at least one year of a lower than average number of foraging whales and vice versa (Table 1). These mean values were subject of an ANOVA with post-hoc test to determine significance between years. The difference between years was found to be significant ($F(14, 506) = 26.241$, $p<0.001$) with the post hoc analysis finding homogeneity for years with low foraging intensity (1999, 2000, 2001, 2003, 2005, 2007, 2008, 2009) and those where the mean number of foraging whales is higher (1998, 2002, 2004, 2006, 2011), with 2010 set apart with a significantly higher mean number of whales per survey. The total and mean number of whale foraging days for each year was calculated, from 3512 records for the 15-year period. When considering the years where foraging intensity peaks prior to 2010 there is a general declining tendency. Overall the number of whales is trending almost to zero by 2009, followed by a significant recovery in foraging whale numbers in 2010 (Figure 2).

Table 1: Summary of survey effort, whale presence and foraging intensity for seasons 1997-2011, with surveys conducted twice-weekly between 24th May and 8th September inclusive.

Year	Number of surveys	First sighting	Last sighting	Range of whales/survey	Mean (S.D.)
1997	54	29-Jun	04-Sep	1-17	6.35 (3.39)
1998	60	06-Jun	26-Aug	1-25	10.05 (5.37)
1999	40	03-Jun	26-Aug	1-7	3.50 (1.80)
2000	31	02-Jun	08-Sep	1-10	3.63 (2.68)
2001	51	25-May	05-Sep	1-8	2.30 (1.60)
2002	40	24-May	07-Sep	1-29	10.53 (8.01)
2003	33	27-May	26-Aug	1-11	5.10 (2.78)
2004	28	24-May	07-Sep	1-33	11.50 (8.78)
2005	32	31-May	03-Sep	1-5	2.23 (1.21)
2006	28	25-May	08-Sep	1-22	7.80 (6.73)
2007	27	26-May	08-Sep	0-21	1.36 (3.15)
2008	41	01-Jun	02-Aug	0-12	3.12 (3.26)
2009	25	27-May	31-Aug	0-13	3.44 (3.61)
2010	30	26-May	09-Sep	1-28	16.06 (7.07)
2011	36	27-May	06-Sep	0-22	11.36 (6.23)
All years	521	24-May	08-Sep	0-33	6.74 (6.51)

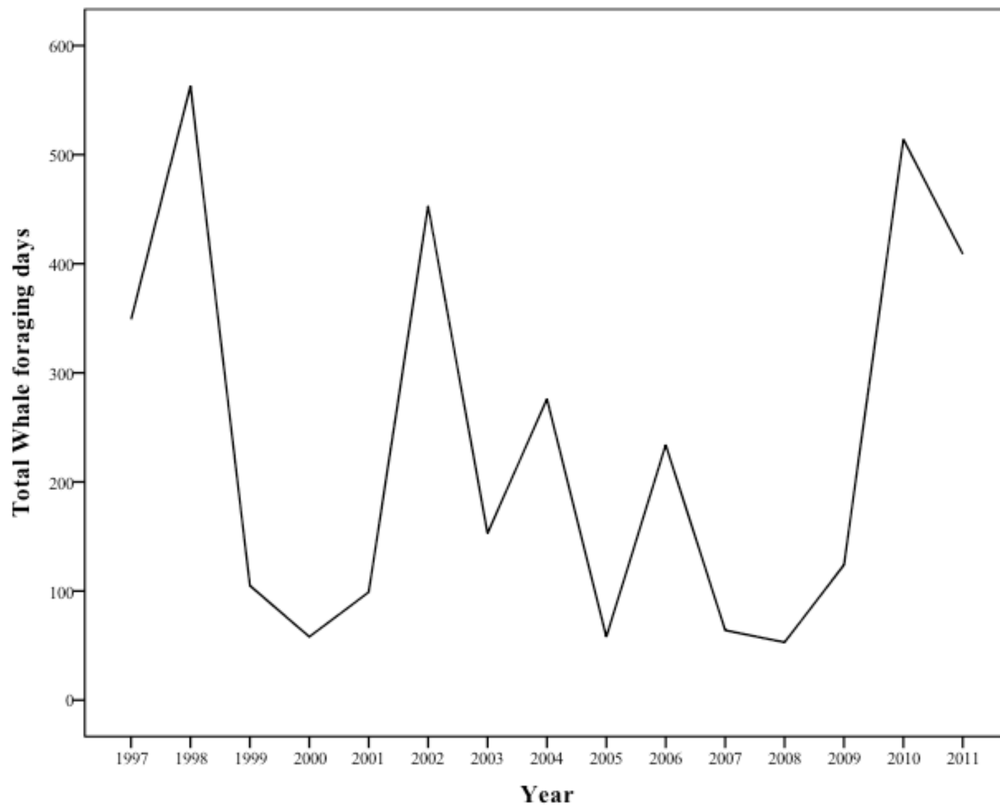

Figure 2: Total number of whale foraging days per season for 1997 to 2011. The cumulative total is 3512 for the 15-year period

Data Analysis

The distribution of the number of foraging whales in Clayoquot Sound over the summer showed significant positive skew in all years except 2010 and 2011, with the skew significant (exceeding 2 standard errors) in years 1997, 2000, 2001, 2002, 2008, and 2009 (Table 2). In general these years have lower than average numbers of foraging whales (Table 1), and the positive skew suggests foraging was at its most intense early in the season, despite the maximum number of whales on a single survey not recorded before mid July (Table 2). Results for 2002 are exceptional to this, with a high mean number of whales per survey, but with whale utility of Clayoquot Sound peaking in early July, represented in a significant value for skew (Table 1, 2). Both 2001 and 2007 also show significantly leptokurtic values, suggesting that foraging intensity peaks strongly around the mean value of foraging whales (Table 2). The particularly high value for 2007 suggests the survey data shows consistency in the number of whales seen per survey

throughout the summer. All other years show mesokurtic distributions, indicating an almost normal spread of values centered around the mean value of foraging whales per survey, with most, if not all, data points falling within 2 standard errors (Table 2).

In the regression analysis the number of whales in the last 4 weeks of the summer (August 12th-September 8th) was the variable determining the number of the whales observed foraging in the first 4 weeks of the following season (May 24th-June 20th). The relationship was positive ($R^2 = 0.464$, $p = 0.027$), with the regression equation:

$Y = 0.269 X + 2.287$, where Y is the number of whales in the early season, X is the number of whales in the late summer.

Table 2: Values of skew and kurtosis, with standard error, for each season for years 1997-2011. The date where the maximum number of whales on a single survey between May 24th and September 8th is also indicated

Year	Peak date	Skewness (Std. Error)	Kurtosis (Std. Error)
1997	19-Aug	0.718 (0.322)	0.469 (0.634)
1998	10-Aug	0.588 (0.319)	-0.342 (0.628)
1999	03-Jul/04-Aug	0.325 (0.427)	-0.885 (0.833)
2000	18-Jul	1.195 (0.564)	0.840 (1.091)
2001	25-Aug	1.538 (0.361)	2.812 (0.709)
2002	07-Jul	0.902 (0.361)	-0.100 (0.709)
2003	26-Jul	0.321 (0.427)	-0.901 (0.833)
2004	16-Jul	0.692 (0.472)	-0.198 (0.918)
2005	09-Jul	0.693 (0.456)	-0.549 (0.887)
2006	07-Jul	0.581 (0.427)	-1.129 (0.833)
2007	11-Aug	5.548 (0.347)	34.553 (0.681)
2008	02-Aug	1.283 (0.550)	2.055 (1.063)
2009	05-Aug	1.224 (0.393)	0.540 (1.063)
2010	26-Aug	-0.243 (0.414)	-0.635 (0.809)
2011	07-Aug	-0.346 (0.393)	-0.930 (0.768)

Discussion

The twice-weekly census data of Clayoquot Sound shows patterns in foraging intensity on different temporal scales. Inter-annual oscillations in the number of foraging whales occur where a year of high foraging intensity is followed by at least one year of lower level site use, relative to a mean number of foraging whales calculated for all 15

years (Table 1, Figure 2). Gray whale predation may drive mysid populations to such low numbers that it takes more than a year for them to recover to be a viable food source again, and attract whales. Using a one-way ANOVA test with post hoc analysis, homogeneity was found for years of low foraging intensity and high foraging intensity, defined by the mean number of whales foraging per year, with difference between these years found to be significant. Years with reduced whale foraging represent a period of predator release, and so prey are able to reproduce without significant population losses, allowing a greater number of foraging whales to be sustained the following season.

Bakun (2006) described prey population renewal after extreme predator-induced decline in marine systems as a 'predator-pit topography'. His model allows prey population recovery, labeled a 'breakout' period, following periods of prey 'refuge' and predator forced 'carnage'. The boom-bust cycle can be seen in the total annual number of whale foraging days, with 2010 showing the most recent and extreme example of intensified foraging by gray whales consequent to a prey recovery after several years of low whale numbers (Figure 2).

Intra-seasonally, all years, except 2010 and 2011, show at least a slight positive skew in the number of whales foraging in the study site over the summer. This suggests whale utilization of Clayoquot Sound is typically greater earlier in the season relative to the date when the maximum number of whales per survey is recorded (Table 2). This skew is significant in 1997, 2000, 2001, 2002, 2007, 2008 and 2009. This may be a function of prey availability, where by late summer predation has diminished mysid swarms, in an already low-prey situation. Conversely, 2010 and 2011 both had abundant prey reserves and so the demise of prey over the summer may not be as pronounced allowing continued foraging late in the season, shown by the slight negative skews (Table 2). Kurtosis values suggest the data for number of foraging whales are evenly distributed around the annual mean value for each summer of the 15 years examined for all years except 2001 and 2007, where the number of whales is significantly peaked around the mean. This suggests that foraging intensity was consistently low with low variance in these years (Table 1, 2).

The results from the regression analysis (R^2=0.464, p = 0.027) were not as expected. I anticipated that a greater number of foraging whales in the latter 4 weeks of a

season would result in reduced site use by gray whales in initial 4 weeks of the following season, and vice versa, creating a negative regression. The outcome, however, may be influenced by intra-seasonal prey availability as well as the inter-annual predation pattern. In late May, early in the season, mysid populations are still in a stage of growth and swarm stabilization following spring productivity blooms, and so it might not be until later into June that swarms become a viable food source for gray whales. Similarly, several months of foraging pressure may have considerably reduced mysid swarms by late summer, which consequently no longer represent a worthwhile food source. This is further supported by the temporal patterns of foraging intensity over the summer for each year, where gray whale utilization of Clayoquot Sound peaks from early July to late August (Table 2).

Patterns of foraging over the 15-year period, although intrinsically linked to prey availability, may also be influenced by broad scale oceanographic regimes. The most intense peaks in foraging intensity (1998, 2002, 2010) are coincident to El Niño events, however a more in-depth analysis by Hare and Mantua (2001) found marine systems of the north Pacific to strongly filter climate variability showing a non-linear response to environmental forcing.

Conclusions

I examined 15 years (1997-2011) of census data of summer foraging gray whales in Clayoquot Sound for patterns of foraging intensity. During this time the preferential prey was epi-benthic mysid species. Oscillations in the number of whales utilizing foraging sites were found on an annual scale, and attributed to predator driven prey depression followed by recovery afforded by predator release. Peaks of whale foraging within a season also appear to be prey driven, both in terms of timing and the number of whales sustained.

This long term data set shows the ability of mysid prey to continue to recover despite persistent predation from gray whales. The life history characteristics of these mysids species allows them to capitalize on periods of reduced predation to re-establish population size, allowing Clayoquot Sound to remain a productive tertiary foraging area for gray whales.

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CHAPTER 4
Changes in Time budgeting as Gray Whales (*Eschrichtius robustus*) Approach Satiation

Abstract

The migration of the eastern Pacific gray whale (*Eschrichtius robustus)* from Mexican breeding grounds to Arctic foraging areas, as well as extended fasting during the southbound journey, and time spent in resource-poor calving lagoons, reduces body weight up to 30%. Although smaller in size, tertiary foraging areas off the west coast of Vancouver Island represent prey resources analogous to those in the Bering and Chukchi Seas, but with half the usual migratory travel time.

When the gray whales arrive in foraging areas they are edacious. Their need to restore lipid reserves dominates behaviours. In this study, which follows on from an investigation to classify foraging bouts by individuals on a fine time scale, I use observations of focal individuals from June to September 2011 in Clayoquot Sound to establish whether there is a seasonal level satiation point. Here satiation is defined as the juncture where blubber reserves have been restored sufficiently for foraging to not dominate behaviours, represented in this case by a reduction of time afforded to feeding activities when analyzing whales' behavioural time budgets. The seasonal average time allocation to foraging was 78%, increasing in early summer and remaining high through to the end of the season. Changes in feeding behaviours are seemingly also dependent on prey resources, with other variables including, but not limited to, subjectivity in dive classification, individual variance in whales, and social interactions, playing a yet undefined role.

Introduction

The annual migration of eastern Pacific gray whales (*Eschrichtius robustus)* covers over 10,000 km from the breeding and calving lagoon in Baja California Sur, Mexico, to primary feeding areas in the Bering and Chukchi Seas (Rugh *et al.* 2001). Although the energy costs of this migration are high, reducing body weight up to 30%, it is assumed that there is a net energy saving by vacating the cold, high-latitude foraging grounds when suitable prey are unavailable, or have become diminished (Rice & Wolman 1971, Sumich 1983).

Driven by the need to recover from the over-winter exertions and fasting, gray whales are edacious on arriving in productive foraging sites in early summer. It is their blubber, a highly vascularized lipid-rich hypodermic adipose layer (Palmer & Weddell 1964), which allows them to withstand this extended period of low energy intake (Austin *et al.* 2000). Although blubber represents a portable cache of food (Brodie 1975), its metabolism could affect the buoyancy, gait, and thermoregulatory capacity of the whale (Rosen *et al.* 2007). It is therefore essential that prey are available during the summer for blubber reserves to be restored (Rice & Wolman 1971, Murison & Gaskin 1989, Highsmith & Coyle 1992).

Typically gray whales are solitary, foraging alone or in ephemeral groups, except in the case of cow-calf pairs. They forage on high-density, spatially discrete prey aggregations to meet the metabolic demands associated with their size (Brodie *et al.* 1978*,* Kenney *et al.* 1986), and demonstrate prey-switching to take advantage of short-term energy availability (Dunham & Duffus 2001). Typically, organisms feed either until food-resources are depleted to an energetically inefficient threshold, or until they achieve satiation. On a fine time scale, food intake by gray whales in a single foraging-bout, defined as a series of foraging dive sequences initiated and terminated by non-foraging dives, is regulated by a complex set of physiological feedback mechanisms. Satiation is presumably evoked by brain signals received from the gastro-intestinal system, including that of stomach distention, triggered by the physical and chemical properties of the ingested food (Eisen *et al.* 2001, Ritter 2004). Feeding behaviours on a more coarse scale may adjust for changes in body mass or composition, or seasonal or ontogenetic changes in overall energy requirements (Steffens & Strubbe 1987, Rosen & Renouf 1998), with

satiety being regulated by longer term signals regarding body condition and nutrient balance (Rosen & Trites 2004). In this case satiation on a seasonal level for gray whales would be defined as the restoration of energy reserves by summer foraging.

Here I examine foraging behaviour of gray whales feeding in Clayoquot Sound, a tertiary foraging site on the west coast of Vancouver Island, to identify this longer-term satiation level. In this site, whales utilize epi-benthic mysid shrimp species (family *Mysidae*) as a principal prey resource (Kim & Oliver 1989, Duffus 1996, Dunham & Duffus 2001, 2002). Work by Feyrer and Duffus (2006) in this area showed a hierarchical decision process by foraging whales in their foraging bouts, with focal follows showing a systematic sequence of mysid patch exploitation. In this study foraging effort is quantified by use of behavioural time budget analysis, comparing the time that whales are engaged in foraging, rather than non-foraging behaviours throughout their summer residency in the study area. In this way I hope to define a satiation point on a seasonal time-scale, represented by the point where foraging behaviours no longer dominate. I hypothesize, that in the early season, the proportion of time spent foraging will be high, increasing as mysid prey resources become established following their first annual reproductive brood, which occurs in the spring plankton bloom. A maximum will be reached as whales approach satiation, and then subsequent time spent foraging should decline. Once lipid reserves are replenished, feeding should no longer monopolize behaviour, confirmed by a proportional reduction in foraging time.

Methods

Study Area

Clayoquot Sound, on the west coast of Vancouver Island, British Columbia, is located between 49°14'36"N, 126° 6'10 "W and 49°18'51"N, 126°14'30"W, and is a productive foraging ground with half the travel time in comparison to Arctic sites. The study area is approximately 20 km² along the coast of Flores Island. It is bounded to the west by the 30-meter depth contour, and bordered to the north and south by unproductive foraging areas. Foraging is predominantly within 1 km from shore, typically in rocky reefs at a depth of around 10 m, which are known to be key mysid habitat (Figure 1, Feyrer 2010, Laskin *et al.* 2010).

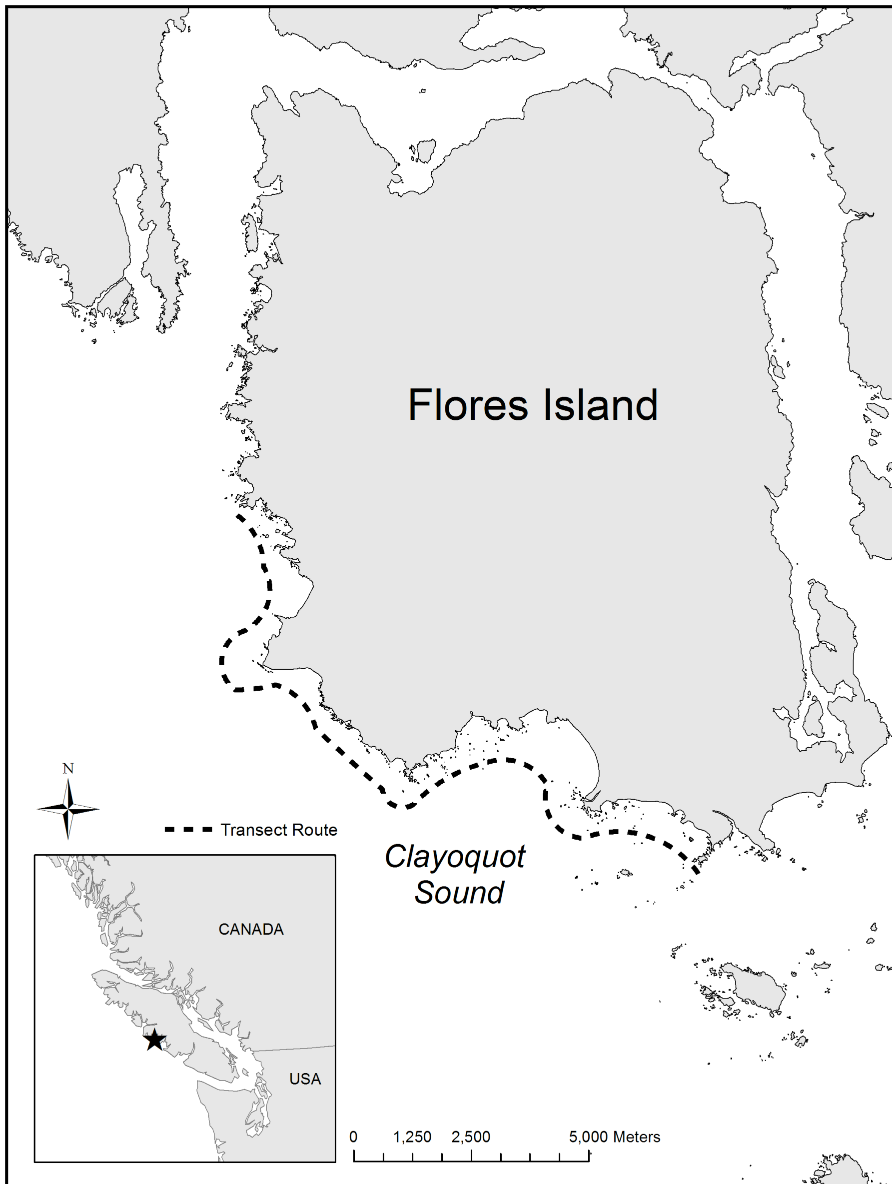

Figure 1: The study area, Clayoquot Sound. The study area survey route, indicated by the dotted line, follows the 10 m isobath. It passes through core foraging sites in Clayoquot Sound, and was designed to maximize the encounter rate of whales.

Whale Observations

Focal individuals were chosen for observation by an irregular selection method (Altmann 1974). I selected the first whale encountered within foraging habitat of the study area. In the case of several whales foraging in the same location, the individual seemingly more solitary from the group and/or with the most distinctive natural markings

was observed. These unique markings were used throughout each survey to track the focal individual and document their dive sequences.

Ventilation times were recorded (hh.mm.ss) along with behaviour, classed as either foraging or non-foraging. Gray whales ventilate with several brief submersions before diving to depth, both when travelling and foraging. The dive length and distance travelled was used to distinguish between dive function (Malcolm & Duffus 2000, Feyrer 2010). Dive geometry and length has been studied at this site using a time-depth recorder, and that information is used here to classify dive function (Malcolm & Duffus 2000). Inter-ventilation dives were characterized as no longer than 30 seconds, which are thought to not allow feeding or prey searching. Foraging and non-foraging dives were classified based on a threshold of distance between surfacing events based on the average size of prey swarms (Feyrer 2010). Foraging dives usually center on a prey patch, and so diving and surfacing is repetitively focused in approximately the same area. This contrasts with travelling dives, which are typically longer, and covering more space, with the defining distance here being dives that exceed 60 meters (Feyrer 2010).

Surveys were terminated after five hours of continuous observation of an individual, if the individual disappeared, if observations were obscured, or another whale was mistakenly recorded in the data stream. If visibility was compromised by weather conditions or the Beaufort Sea State exceeded level 3 observations were aborted. Weather permitting, all observations began in early morning.

To make time budgeting comparisons, data from foraging and non-foraging dives were separated, and the inter-ventilations of less than 30 seconds removed. Dive times for dives classified as foraging or non-foraging were then pooled, and expressed as a function of the total dive time for each survey.

Results

Observation time of 11 individuals on 24 occasions between June 9th and September 2nd, 2011 totaled 102.3 hours. The focal observation on July 27th was of a cow-calf pair with ventilations from both individuals recorded, but only the adult data was used for analysis. The average survey length was 267 min (range 70 to 450 min) (Table 1).

Table 1: Date and length (in hours) of each focal observation through the 2011 season. Each individual whale is assigned a letter, with 3 whales observed on more than one occasion.

Date	Whale	Observation time (hours)	Running total (hours)
09-Jun	A	5.00	5.00
12-Jun	B	3.17	8.17
16-Jun	C	7.50	15.67
21-Jun	D	5.00	20.67
24-Jun	A	5.25	25.92
25-Jun	A	5.00	30.92
28-Jun	A	5.00	35.92
02-Jul	A	5.00	40.92
11-Jul	E	5.00	45.92
13-Jul	F	3.08	49.00
18-Jul	E	5.17	54.17
21-Jul	A	5.00	59.17
24-Jul	G	3.17	62.33
27-Jul	H	4.50	66.83
06-Aug	I	4.00	70.83
09-Aug	D,J	1.17, 4.00	76.001
11-Aug	A	5.00	81.00
13-Aug	F	5.00	86.00
15-Aug	F	4.50	90.50
21-Aug	K	5.00	95.50
30-Aug	A,D	0.30, 3.00	98.801
02-Sep	A	3.50	102.301

In total, whales spent an average of 78% of their time foraging, and 22% on non-foraging activities (travelling, searching). To eliminate some of the individual variability among the sample whales, the proportion of time spent foraging was aggregated by week (Figure 2). Although there are differences in time allocation to foraging between weeks, effort given to feeding activities is consistently high throughout the summer, with the variation found to be non-significant ($F = 2.090$, d.f. = 12, $p = 0.126$).

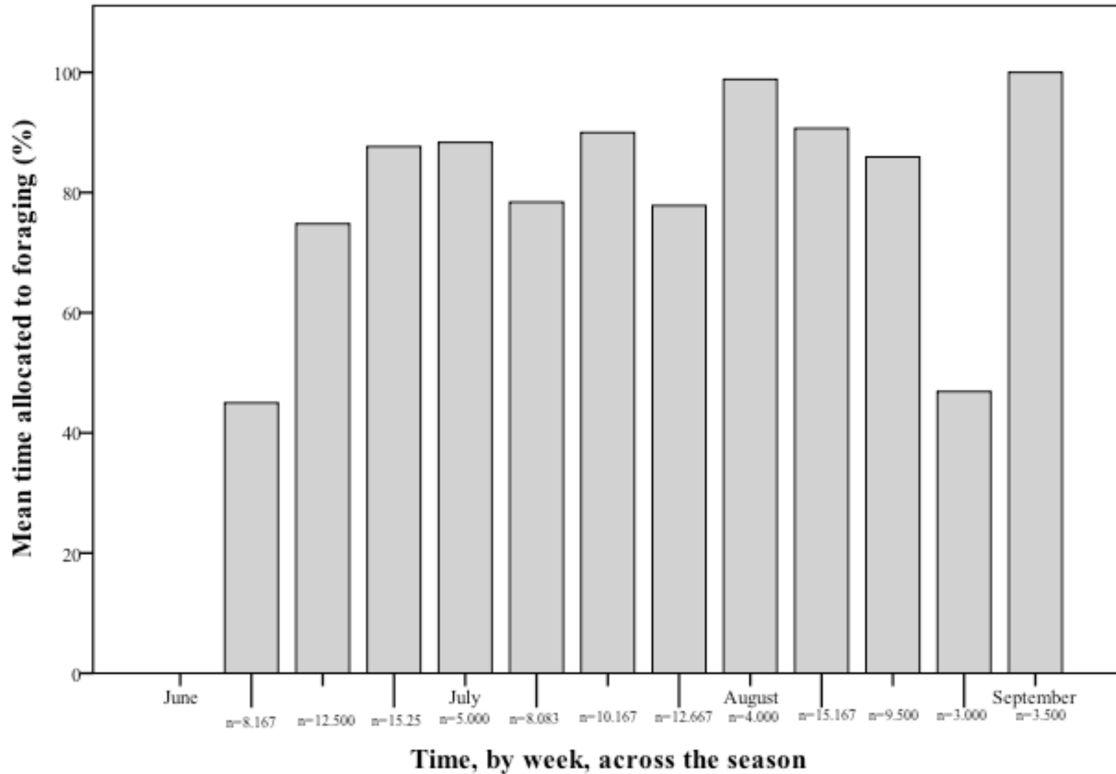

Figure 2: Time allocation to foraging behaviours by individuals surveyed from June to September 2011 aggregating data by week, with n indicating the number of hours of observation pooled for each week

The relationship between foraging effort, based on the percentage of time allocated to feeding, over time was analyzed, but was not found to be significant (r_s = 0.387, p = 0. 075). Although it is not possible in this study to compare foraging effort with quantitative values of prey availability and quality, the proportion of gravid female mysids was used as proxy of changes in energetic value of prey resource over time. Semi-monthly samples taken from twelve sights in the study area were pooled and the proportion of gravid females, of all species, calculated. This was then correlated to proportion of time spent foraging using values from the third week of June, the first and third weeks of July and August, and the first week in September, but was not found to be significant (r_s = 0.200, p = 0. 704).

Discussion

Gray whales are in a negative energy balance after leaving summer feeding grounds, relying predominantly on stored energy (Rice & Wolman 1971). The summer of foraging serves to both restore blubber that is metabolized during migration and

wintering, and to reacquire lipid reserves in preparation for another winter. I hypothesized that foraging would dominate behavioural time budgets for whales summering in Clayoquot Sound. I suggest that this would be particularly true for the early season to replenish lipid reserves. Accordingly, time allocation in favour of feeding is consistently high throughout the summer (Figure 2), representing the strong need to restore energy stores on the part of the whales observed. The ability to distinguish a definitive satiation point may be obscured by factors including variations in prey resource, and differences in feeding strategies of the individuals observed.

Variations in prey availability and quality may be reflected in foraging behaviours. In accordance to foraging optimality models (*e.g*. Norberg 1977) the increase in time allocation to feeding behaviours by gray whales in the early summer is coincident with growth and swarm stabilization of mysid prey species. Time budgets and length of foraging bout may also be influenced by size and aggregation of prey patches, where whale behaviour is linked to ease of capture due to swarm density and size increases. Temporal variation in effort expended in prey capture and assimilation are not considered here, but may be influential to foraging behaviours. As a means to compare resource value over time, the proportion of gravid females in samples taken coincident to observations serve as one proxy of prey quality, although a correlation between the percentage of gravid mysids and time spent foraging on a semi-monthly basis was not found to be significant. Although it is not possible in this study to compare foraging effort with quantification of mysid resource in terms of swarm size and density this type of data may be found to correlate more strongly with foraging effort, as might a comparison of mysid caloric value over time.

Variation between individual whales is difficult to control for. Several individuals were followed on multiple occasions to distinguish patterns in time budgets and foraging behaviours without these intrinsic factors, and any future work should focus surveys to fewer individuals on a greater number of occasions throughout the season. Pooling data by week may also dilute any individual difference, while still displaying trends in foraging effort.

Although gray whales are typically observed to be alone, there were cases, in particular the cow-calf pair (Whale-H), when proximity to other foraging whales may

influence diving sequences, where dives seem to be more synchronous with other whales that are nearby. Individuals observed in Clayoquot Sound are typically cow-calf pairs, pre-breeding juveniles, and some post or non-breeding adults that are distinct from the breeding nucleus found feeding in primary and secondary areas (Duffus 1996). Patterns in foraging and satiation may also be influenced by these life history and ontogenetic factors.

Furthermore, the idea of satiation may operate differently in whales, rapid digestion and very high storage capacity of lipids might mean that whales can and will forage constantly as long as prey is available. Whales may be observed to continue to capitalize on prey reserves despite blubber reserves being restored, with the possibility of individuals adapting different foraging strategies after satiation has been achieved. Little is known about digestive physiology of large whales. A sated baleen whale may not be what we find in terrestrial predators.

Finally, subjectivity in dive classification must be considered, where whale behaviour is inferred from events at the surface. However, foraging behaviour is easily distinguishable from non-foraging, with clear metrics used to help inform classification (>30 sec in length, <60m travelled), with these divisions supported statistically by past work using a Time-Depth Recording (TDR) tag (Malcolm & Duffus 2000). A more diverse ethogram of behaviour classification may influence results with, for example, a clearer distinction made between feeding, foraging/searching, travelling and resting behaviours. This inclusion of more subtle variations in time budgeting may help the results from data analysis be more true to in-field observations, where season variation in gray whale foraging has been noted anecdotally prior to this study. Variation of water depth or time of observation does not seem to affect overall trends.

Conclusions

Foraging behaviours are underpinned by the need to restore lipid reserves after expenditure during winter migration and breeding. Satiation, on a seasonal level, indicates restoration of these stores, but also may be an initiator for the southbound migration. Timing of whales abandoning foraging sites may be prey determined, or when migratory individuals are sufficiently satiated. Conversely, the fact that the data indicates

foraging still dominates time budgeting into the late season suggests that other environmental variables might also play a role, for example photoperiod (see Rugh *et al.* 2001).

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CHAPTER 5
Overwintering Reproductive Strategies of Mysid Species in Clayoquot Sound

Abstract

Despite mysids (Order *Mysidacea*) being common zooplankton in coastal marine aquatic systems, little is known about their ecology and distribution. Of the 48 species recorded in the north Pacific, 12 are known from Clayoquot Sound off the west coast of Vancouver Island. Here multi-species swarms constitute the primary prey of summering eastern Pacific gray whales (*Eschrichtius robustus*), whose seasonal predation may be the mechanism that drives this species diversity. Of those dozen species, 4 are present in samples consistently, *Holmesimysis sculpta, Neomysis rayi, Acanthomysis columbiae, Columbiaemysis ignota*.

Through sampling over a 24-month period (May 2010-April 2012), I characterize growth and reproductive strategies of mysids and establish the mechanisms by which species dominance might be achieved. Prior work identified 3 broods for the species in Clayoquot Sound with reproduction peaking in warmer and more productive months. I reaffirm that, but also extend sampling into winter months to examine mysid reproductive strategy when predation pressure is released.

Gravid females of *H. sculpta* were found in all samples except those in September and October 2011. Dominance over its sister-species may result from a more consistent, year-round reproduction strategy with a fourth brood identified in the overwinter period. Although winter is thought to be in a resource-limited scenario, *H. sculpta* is able to derive enough energy to sustain reproduction throughout.

Introduction

Mysids (Order *Mysidacea*) are shrimp-like invertebrates that occupy epi-, meso- and bathypelagic oceanic realms; the pelagic, hyperbenthic and benthic intertidal and subtidal coastal areas; and estuaries (Kathman *et al.* 1986). Despite this, little is known about their distribution and ecology. Our knowledge of morphology, life history characteristics, diet, and motility is not comprehensive. Of the 48 species identified in the north Pacific, a dozen are found in the same habitats in Clayoquot Sound, off the west coast of Vancouver Island. As the principal prey of gray whales (*Eschrichtius robustus*) in this area, it is likely the disturbance from this predator that confers this level of species diversity (Feyrer & Duffus 2011).

Mysids swarm in multi-species aggregations, with distinct groups formed as a function of age, size, or swimming speed (Clutter 1969, Stelle 2001, Dunham & Duffus 2002). As with many of the coastal marine mysid species, there is limited knowledge of growth and reproduction for the species in Clayoquot Sound, with a particular lack of knowledge about the animals outside the summer months.

Mysid growth is by a succession of molts, regulated by a multi-hormone system also responsible for reproduction and embryogenesis (Verslycke *et al.* 2003). Time to maturity can be species specific, varying from less than one year to greater than 2 years of age, and also differing within a single species both between and within populations at different times of the year (Kathman *et al.* 1986). Growth rate slows following maturation, with resources allocated between somatic growth and gonad production (Clutter & Theilacker 1971).

Most mysid species are able to produce several generations during a lifetime (Kathman *et al.* 1986), with brood production rate ranging from more than 3 per year to less than 1 every 2 years (Mauchline 1980, Stelle 2001). Copulation typically occurs at night, immediately following the female molting (Clutter & Theilacker 1971, Mauchline 1971, Kathman *et al.* 1986). Embryo development is within a marsupium pouch, giving mysids the common name ‘opposum shrimp’. Mysids are epimorphic lacking larval stages, with juvenile release following complete development of body appendages (Kathman *et al.* 1986).

In temperate waters, mysid species are thought to be iteroparous, breeding year round with peak reproduction in warmer and more productive months with broods in late spring/early summer and late summer/early fall (Mauchline 1980, Wittman 1984, Azeitero *et al.* 1999). In colder waters, however, resources may be limited during winter, which in turn may suppress growth, fecundity, and developmental rates. A number of studies have shown temperature to influence both growth rate and size at maturity. Lower water temperatures decrease growth factors, increase intermolt period and carapace length at sexual maturity (*e.g*. Mauchline 1976, Astersson & Ralph 1984, Winkler & Greve 2002, Fockedey *et al.* 2005). The number of eggs held in the marsupium (1-350), and duration of development (4 days to 1 year) varies among and between species, and is also correlated with factors such as size, season, and temperature (Mauchline 1980).

Here I examine whether mysid species in my study area are able to overcome a presumable food limited situation for growth and reproduction overwinter, and take advantage of this period of major predator release for population recovery. Of the species known in Clayoquot Sound, *Holmesimysis sculpa* is dominant, and its competitive advantage may be achieved through the interplay of life history attributes enhancing fecundity or foraging efficiency of the species (Hairston *et al.* 1960, Menge & Sutherland 1976). *H. sculpta* has been dominant in all years since 1996, except in 2007, where *Neomysis rayi* became dominant (Dunham & Duffus 2002, Mulkins *et al.* 2002, Patterson 2004, Feyrer & Duffus 2011). I speculate this dominance results from traits enhancing reproductive capacity in frequency, timing or both. Reproducing either more often or earlier than the other species, or overwinter, creates a distinct advantage.

Through frequent sampling in my study area over a 24-month period I examine growth and reproduction patterns of the mysid species group. The size spectra found in samples shows the progression of broods over time during the 2 years, and serves to identify reproductive pulses. Bi-modality in length-frequency data of individuals in the sample, with a large proportion of both small and larger bodied mysids, is used to establish timing of reproductive peaks.

Methods

Study Area

Clayoquot Sound, on the west coast of Vancouver Island, British Columbia, is located between 49°14'36"N, 126° 6'10"W and 49°18'51"N, 126°14'30"W (Figure 1). The study area is approximately 20 km² along the coast of Flores Island and is also a productive gray whale foraging grounds. It is bounded to the west by the 30-meter depth contour, and bordered to the north and south by unproductive foraging areas. Key mysid habitat has been identified to be rocky reefs at a depth of around 10 m and within a kilometer from shore (Feyrer 2010, Laskin *et al.* 2010).

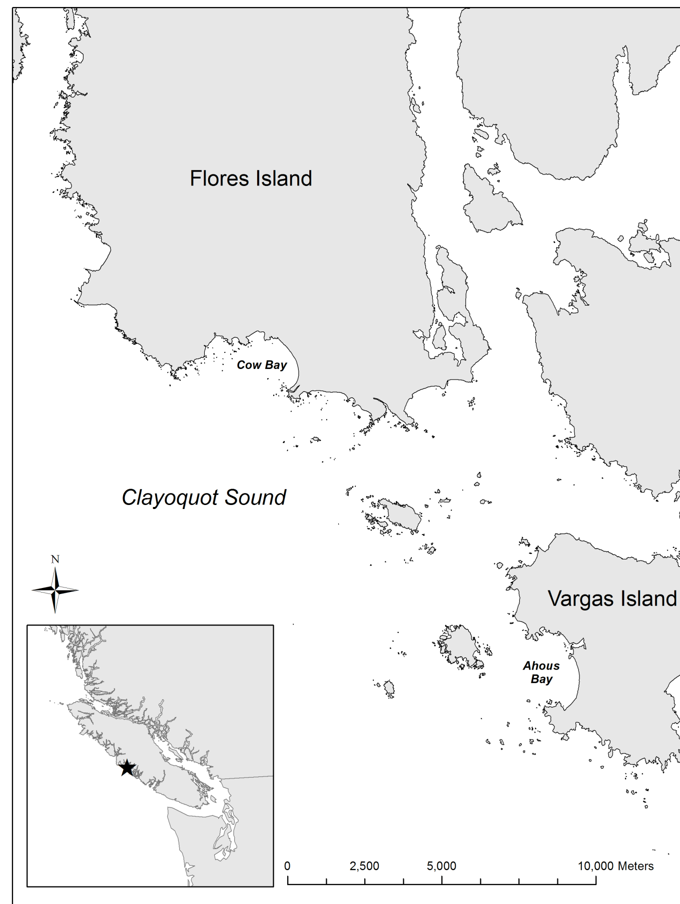

Figure 1: The study area, Clayoquot Sound. Mysid habitat is the rocky reefs within 1 kilometer from the south/south-west coast of Flores Island in rocky reef and kelp bed areas.

Mysid Sampling

Samples were collected by towing a 'bongo' plankton net with two 30 cm openings and a 500 µm mesh. The mesh size is believed to be fine enough to successfully

sample all size classes of mysids. A series of 12 random locations, centered around the 10 m isobath in known mysid habitat were sampled (Figure 2). Sampling occurred, weather permitting, once a month during the winter and every other week in the summer. To collect samples, the net was deployed, allowed to sink to the bottom, dragged for several seconds, and then pulled straight to the surface. This was repeated three times at each of the sampling stations, and the mysids collected for each deployment were pooled. The mysids were preserved in 70% ethanol. Each mysid in the sample was enumerated, body length (rostrum to telson tip) measured, gender determined, and species identified according to Kathman *et al.* (1986) using a 40x dissecting microscope. For analysis the samples were pooled by sampling date across the study area. This highlights temporal changes in mysid populations in Clayoquot Sound with sampling effort focused within the strata of key mysid habitat, and then results generalized over this area.

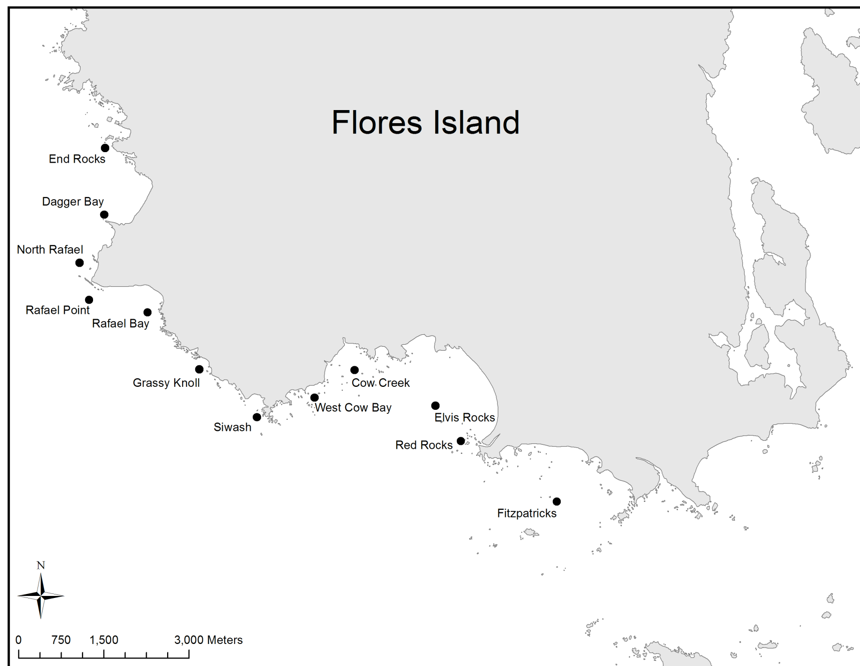

Figure 2: Locations of the 12 sampling stations in Clayoquot Sound. Weather permitting; each site was sampled monthly during the winter and twice monthly during the summer.

Results

Of the 12 species known from Clayoquot Sound, 10 were observed in my samples (Table 1). Species diversity is at its greatest in spring and early summer, and declines

towards late summer and overwinter. Despite the diversity, only four species are present in samples with regularity, and *H. sculpta* is clearly dominant (Table 1).

The presence and proportion of gravid females in all of the samples was recorded (Table 1). Comparison of percentage of gravid females per species per season was also made for the four most common species (Figure 3). The average length, size range and coefficient of variation for all samples was determined for gravid females for the 4 most prominent species (*H. sculpta, N. rayi, A. columbiae,* and *C. ignota*) (Table 2). Furthermore, a comparison of average body length for gravid females by season was made for *H. sculpta* to further clarify the mechanism by which it retains dominance (Table 3).

Patterns of growth for each species over the 2-year period were examined by comparing mean length for each sample (Figures 4-13). To more clearly visualize growth over time, frequency of individuals was plotted against length in size classes of millimeter increments. For this analysis the 4 common species in samples were highlighted, and the remaining 6 species aggregated (see Appendix). In addition to showing the numerical supremacy of *H. sculpta,* this time series also indicates the timing of brood release, with the samples showing bi-modality in body lengths of individuals.

Table 1: Presence and absence of gravid females by species for each sample, where n indicates total number of mysid individuals in the sample with all 12 sites pooled. HS = *Holmesimysis sculpta,* NR= *Neomysis rayi,* AC = *Acanthomysis columbiae,* CI = *Columbiaemysis ignota,* DD = *Discanthomysis dybowskii,* ED = *Excanthomysis davisi,* EG = *Eucopia grimaldii,* AB = *Acanthomysis borealis,* NM = *Neomysis mercedis,* AG = *Archaeomysis grebnitzkii.* A number represents the number of gravid females present per species in the sample, 0 represents no gravids of that species present in the sample, NC denoted that the species is not present at all in the sample.

Sample	n	HS	NR	AC	CI	DD	ED	EG	AB	NM	AG
May 2010	388	72	1	2	0	0	1	2	0	NC	NC
June 2010 (a)	611	47	2	0	5	0	1	NC	0	0	NC
June 2010 (b)	2466	161	0	0	27	5	8	0	NC	0	NC
July 2010 (a)	948	246	1	0	0	NC	3	0	NC	0	NC
July 2010 (b)	219	12	0	1	4	2	0	0	NC	NC	NC
August 2010 (a)	164	12	NC	0	0	0	1	0	NC	NC	NC
August 2010 (b)	195	22	0	0	NC	0	NC	NC	NC	NC	NC
September 2010	80	5	NC	0	0	NC	NC	NC	NC	NC	NC
November 2010	1033	53	2	0	0	0	0	0	1	NC	NC
January 2011	2378	74	0	0	0	1	0	2	NC	NC	0
February 2011	748	36	0	0	0	NC	NC	NC	NC	NC	NC
March 2011	2107	185	NC	0	3	NC	0	NC	NC	NC	NC
May 2011 (a)	8233	95	2	5	7	2	NC	1	0	NC	1
May 2011 (b)	3066	43	0	3	2	NC	0	0	0	NC	NC
June 2011 (a)	2618	38	3	1	11	0	0	1	NC	NC	0
June 2011 (b)	16144	174	2	5	0	0	7	0	0	0	NC
July 2011 (a)	6082	366	3	3	5	NC	NC	0	NC	0	NC
July 2011 (b)	3322	893	0	0	12	NC	NC	0	NC	NC	NC
August 2011 (a)	3692	389	0	0	3	NC	NC	0	NC	NC	NC
August 2011 (b)	2225	505	0	NC	3	NC	NC	0	NC	NC	NC
September 2011	130	0	6	2	0	NC	NC	0	NC	NC	NC
October 2011	93	0	0	0	0	NC	0	0	NC	NC	NC
November 2011	349	19	0	0	0	NC	1	0	NC	NC	NC
December 2011	1986	184	4	3	0	0	1	NC	NC	NC	NC
February 2012	2416	125	0	1	3	NC	3	0	NC	NC	NC
March 2012	5465	56	0	0	7	NC	0	0	NC	NC	NC
April 2012	7461	22	0	8	0	NC	0	0	NC	NC	NC

Figure 3: Seasonal comparison of the percentage of gravid females per species for *H.sculpta, N.rayi, A. columbiae* and *C.ignota*. Spring: March, April, May; Summer: June, July, August; Autumn: September, October, November; Winter: December, January, February

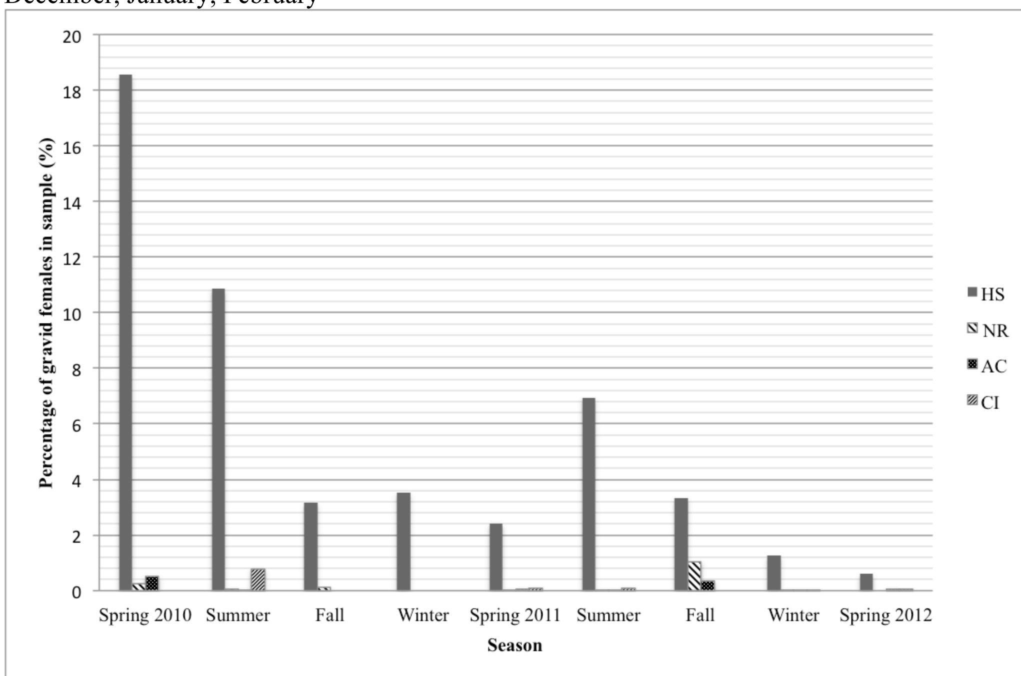

Table 2: Summary of length data for gravid females for all samples over the 24 months for the 4 most common species

Species	n	Range (mm)	Mean length (mm) (SD)	CV
H. sculpta	3834	4-21	14.96 (2.05)	28.13
N. rayi	23	12-34	24.17 (7.89)	247.51
A. columbiae	28	5-28	18.86 (5.59)	166.02
C. ignota	93	5-25	16.47 (5.57)	188.56

Table 3: One way ANOVA post hoc analysis comparing mean length of gravid females for *H. scupta* by season. Spring: March, April, May; Summer: June, July, August; Autumn: September, October, November; Winter: December, January, February. ($F (8, 3825) = 348.341$, $p<0.001$). Mean sample size 78.65

Season	n	1	2	3	4	5	6	7
Winter 2010	110	11.8						
Summer 2010	500		12.74					
Autumn 2010	58		13.07	13.07				
Winter 2011	309			13.53	13.53			
Spring 2012	78				14.09	14.09		
Spring 2011	323					14.37	14.37	
Spring 2010	72					14.79	14.79	
Autumn 2011	19						15.11	
Summer 2011	2365							15.93
Significance		1.000	0.925	0.646	0.377	0.110	0.073	1.000

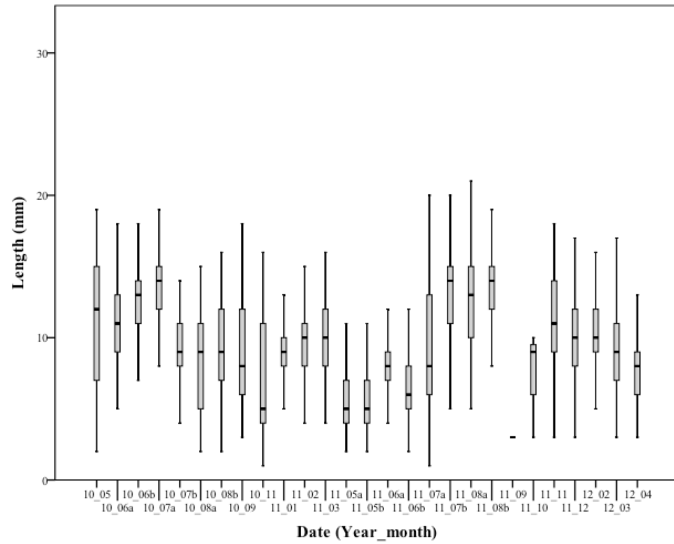

Figure 4: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Holmesimysis sculpta*

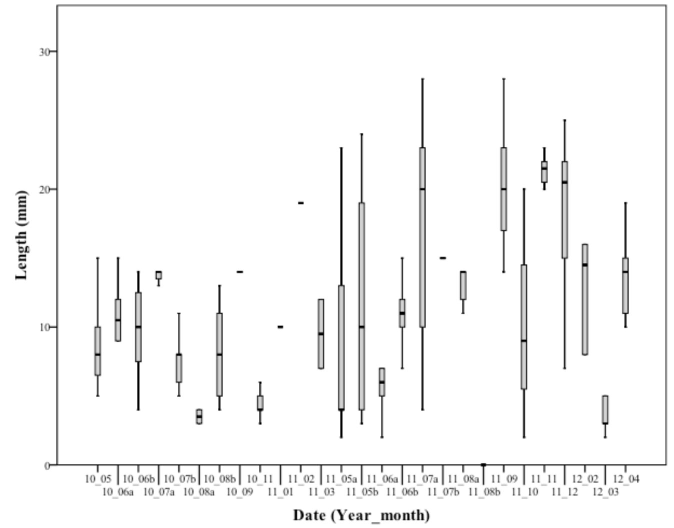

Figure 6: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Acanthomysis columbiae*

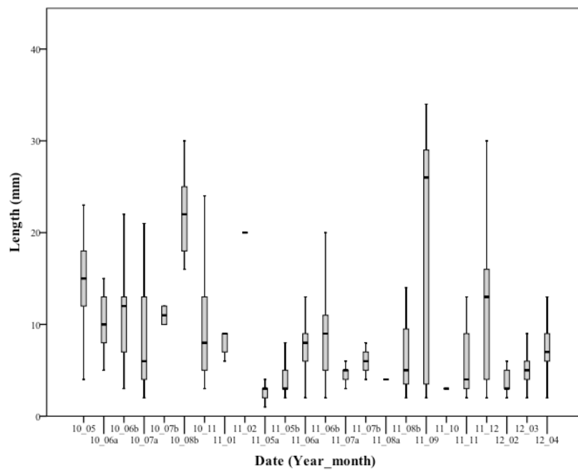

Figure 5: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Neomysis rayi*

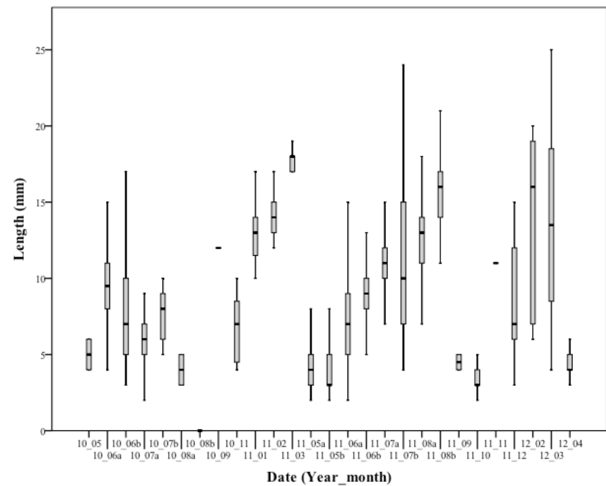

Figure 7: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Columbiaemysis ignota*

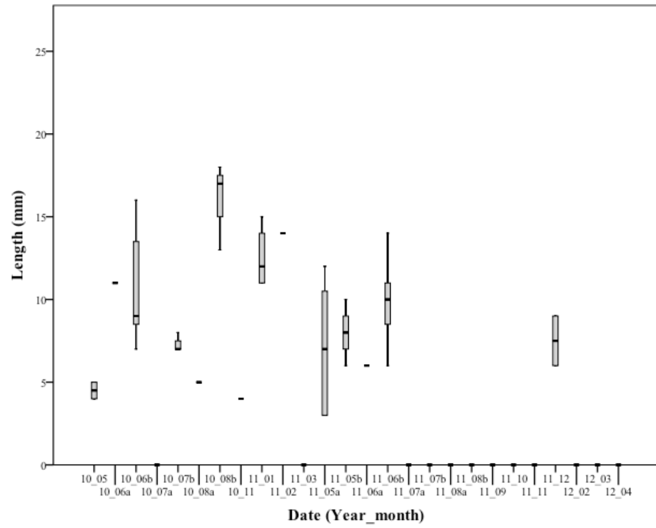

Figure 8: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Discanthomysis dybowskii*

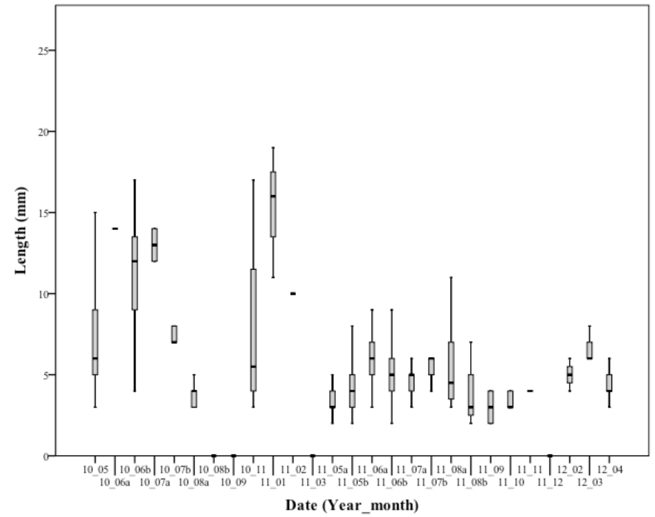

Figure 10: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Eucopia grimaldii*

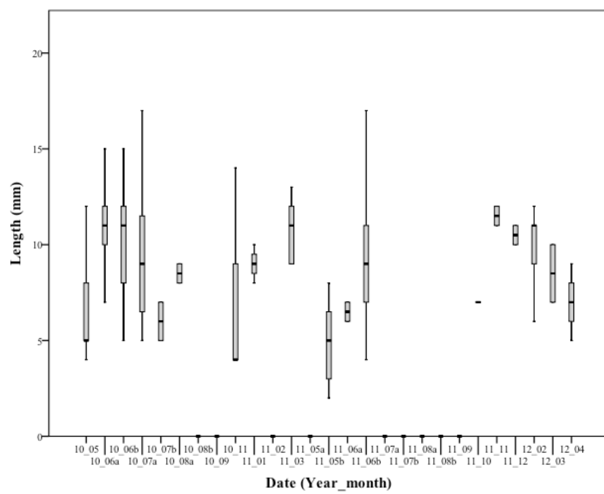

Figure 9: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Excanthomysis davisi*

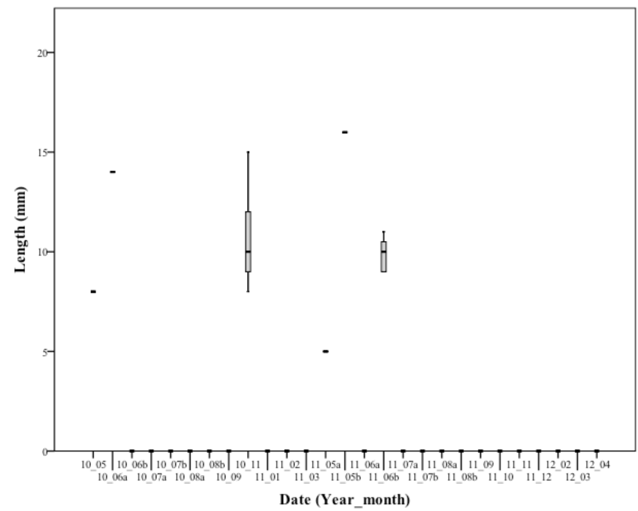

Figure 11: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Acanthomysis borealis*

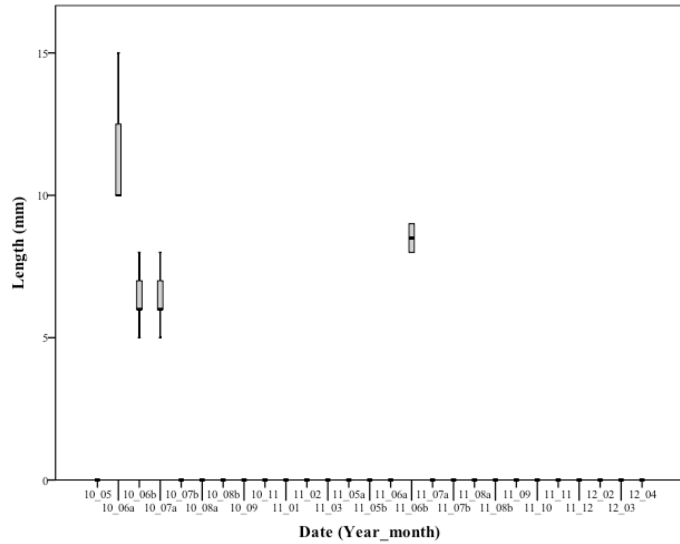

Figure 12: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Neomysis mercedis,*

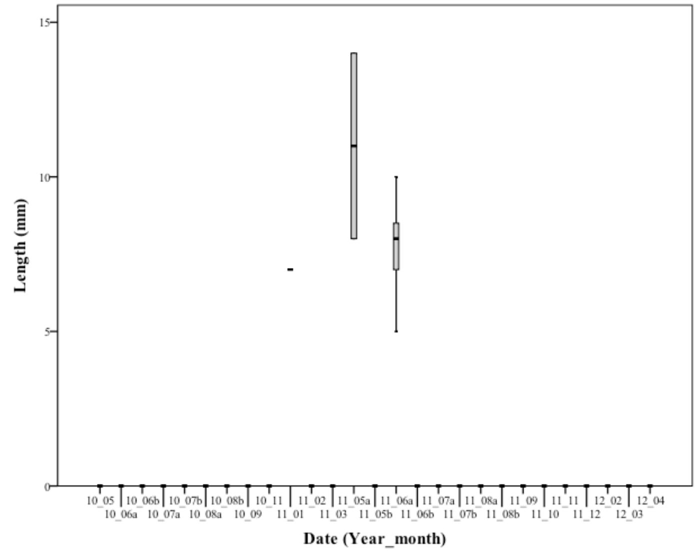

Figure 13: Boxplot showing mean and standard deviation of body length of individuals in each sample over time for *Archaeomysis grebnitzkii.*

Discussion

This is the first examination of species-specific growth and reproductive strategies of mysid species in Clayoquot Sound. It also demonstrates how swarms recover, and species dominance is maintained in the face of strong predation. Episodic perturbation from gray whale foraging, acting from the top down plays a fundamental role in maintaining the mysid species heterogeneity (Feyrer & Duffus 2011). This, and variety in environmental conditions that organisms experience through time, space, or both, prevents monopolization of resources by one species, and so diversity is maintained (Paine 1966, Connell 1978, Brawn *et al.* 2001).

Reproduction for all species peaks in the summer, suggesting temperature and nutrient availability are factors. However, *Holmesimysis sculpta* shows more iteroparous life history characteristics, with gravid females collected in all samples except September and October 2011 (Table 1). Examples of gravid females are lacking for all species, except *H. sculpta*, throughout the 2-year study period and particularly outside spring and summer, with reproduction seemingly limited to these warmer and more productive months. Autumn also represents a period where water temperatures are still elevated following several months of warming (Figure 3).

Mysids in Clayoquot Sound were previously thought to have 3 distinct broods, in late spring, mid-summer and late summer, to capitalize on increased productivity. Changes in the proportions of juvenile and adult mysids show the reproductive peaks, and growth of the cohorts over time. The cohorts are visualized by bi-modality in length-frequency data with an upsurge in small juveniles coinciding with increased larger bodied mysids (see for example Appendix figures i, vi, vii, viii and ix for broods in 2010). Although *H. sculpta* shows less seasonality, with a low level of consistent reproduction effort throughout the year, a possible fourth brood was identified in the fall, with bimodality shown in November samples (see Appendix figures ix and xxiii). With brood size more strongly correlated to body length than species (Feyrer 2011), it is likely that it is this aspect of increased reproductive capacity (Figure 3) that allows continued dominance over a number of years, only failing after repeated high levels of disturbance. *H. sculpta* dominated the species cohort throughout sampling in my 2-year study period, only relinquishing it in May 2011 and March 2012 to *N. rayi*. This may, however, be

more reflective of population recovery of other species following the spring bloom, rather than a decline in *H. sculpta* numbers.

The range of body lengths for gravid females is given (Table 2), and the changes in body length of gravid females for *H. sculpta* were traced over time, distinguishing significant seasonal differences (Table 3). Although previous studies suggest that body length of gravids may be greatest during the winter, due to the colder water temperatures (Mauchline 1976, Fockedey *et al*. 2005), an extended breeding window with winter reproduction may lead to the contradiction of these hypotheses as shown by the results of this study. A one-way ANOVA and post-hoc tests showed all spring samples to be homogeneous, as are summer and autumn 2010, autumn 2010 and winter 2011, and winter 2011 and spring 2012. Winter 2010 was distinct in having the lowest mean body length and summer 2011 set part with the highest mean body length (Table 3). Although season allocation in this case is arbitrary, mean length of gravid females was found to significantly differ between seasons, particularly summer and winter ($F(8, 3825)=348.341$, $p<0.001$). Although fecundity is presumed to be higher during the summer months, differences in brood size determined by changing body length were not examined as part of this study, but may be a relevant extension to future work.

A number of studies have shown an influence of water temperature for both growth rate and size at maturity. A decrease in water temperature, for example during winter, may decrease growth, and increase intermolt period, time to reach maturity, and carapace length at maturity (*e.g*. Mauchline 1976, Astersson & Ralph 1984, Winkler & Greve 2002, Fockedey *et al.* 2005). Length-frequency data of samples show decreased growth rate by approximately a half to quarter, when comparing winter to summer. This is most evident when looking at the shift in length-frequency peaks in early to mid-summer compared to the November to February period, where very little change is seen (see Appendix). Reproduction, and subsequent growth, of species populations is clearly visualized when comparing frequency at each length class over time (see Appendix). Consider an example for *H.sculpa*: Bi-modality in May 2010 (Appendix figure i) suggests sampling occurred soon after a reproductive brood. As well as peaks for larger bodied, presumably sexually mature adults, and very small bodied, newly-released juveniles there is a peak at 7 mm. This peak has shifted to 10 mm by the first sample

taken in June (Appendix figure ii), two weeks later is at 12 mm (Appendix figure iii), and 15 mm after a further 2 weeks, for the first sample of July (Appendix figure iv). Natural mortality as well as predator removal may explain the lack of further progression of this peak. Comparing growth rates between summer and winter I now consider the length/frequency data from November 2010. There are peaks of *H. sculpta* at 4-5 mm, which result from a possible reproduction brood (Appendix figure ix), which are then seen to have shifted to 9 mm by January 2011 (Appendix figure x), and then 10 mm in February and 10-11 mm in March (Appendix figures xi and xii respectively). This would suggest a growth rate of approximately 1 mm per month compared to the up to 4 mm per month at the peak of summer. Similar growth is seen in the other species, but growth still hampered in May and early June with growth rate increasing after this, for example see length/frequency distributions for *C. ignota* for both 2010 and 2011 (Appendix figures i-iv and xiii-xvi respectively).

Calculation of the coefficient of variation for each sample by species in length-frequency of individuals showed consistency in values throughout, with the greatest variation shown in those samples following periods with a brood; May and early June for the early summer brood, July to early August for the mid-summer and September and October for late summer broods. Patterns of growth following brood production are particularly evident for *N. rayi* (for example see Appendix figures iv-v and viii-xvi, Figure 5) and *C. ignota* (Appendix figures iii-v and xiv-xv, Figure 7), where mean length increases in subsequent samples following reproduction peaks. For both of these species the influence of the May brood appears the greatest (for example see Appendix figures i-ii). The mean length of *H. sculpta,* however, appears to be more consistent, regardless of season, which may be attributed to its steady rate of reproduction throughout the year (Table 2, Figure 4) and possible greater tolerance to colder waters. Variables described by Turpen *et al.* (1994) such as changes in kelp biomass, day length, and competition for food and space may mean that energy allocation between growth and reproduction may differ over time. Predator evasion may also be a seasonal draw on resources, and may be more influential in this study site as seasonal gray whale foraging is intense.

Net sampling for mysids can be problematic. Avoidance behaviours may influence samples. Gravid females represent a greater resource energetically for

predators, but their size may allow them to escape more efficiently through greater swimming strength (Patterson 2004), and so may be underrepresented in samples. This dichotomy of survival strategy may also apply to larger bodied species such as *N. rayi*.

Despite the presumption that nutrients would be limited over winter, there must be sufficient for *H. sculpta* to sustain reproduction at a lower level throughout. *H. sculpta* may be able to gain sufficient energy from detritus or perhaps re-suspended diatomaceous ooze, enjoying a window where resources are available with competitors and predators relatively scarce.

Conclusions

Despite their global aquatic presence, mysids are poorly sampled in the field and underrepresented in studies of interaction webs. This study addresses the shortage of knowledge of growth and reproduction for the mysid species in Clayoquot Sound, particularly outside of the summer months. My findings show that *H. sculpta* retains dominance in multi-species aggregations through reproductive strategies, with production later, into winter months, and more frequently than other species exploiting a period of time when their primary predator is absent. *H. sculpta* demonstrates less seasonality in both growth and reproduction, where sister species are seemingly more reliant on the increase of productivity and/or water temperature in spring for these processes.

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APPENDIX

Frequency histograms of mysid body length for each sampling period, 27 samples (i-xxvii) over a 24 month period (May 2010-April 2012). The four most common species are depicted individually, with the remaining species present in each sample (up to a maximum of 6) represented by the category 'Other'.

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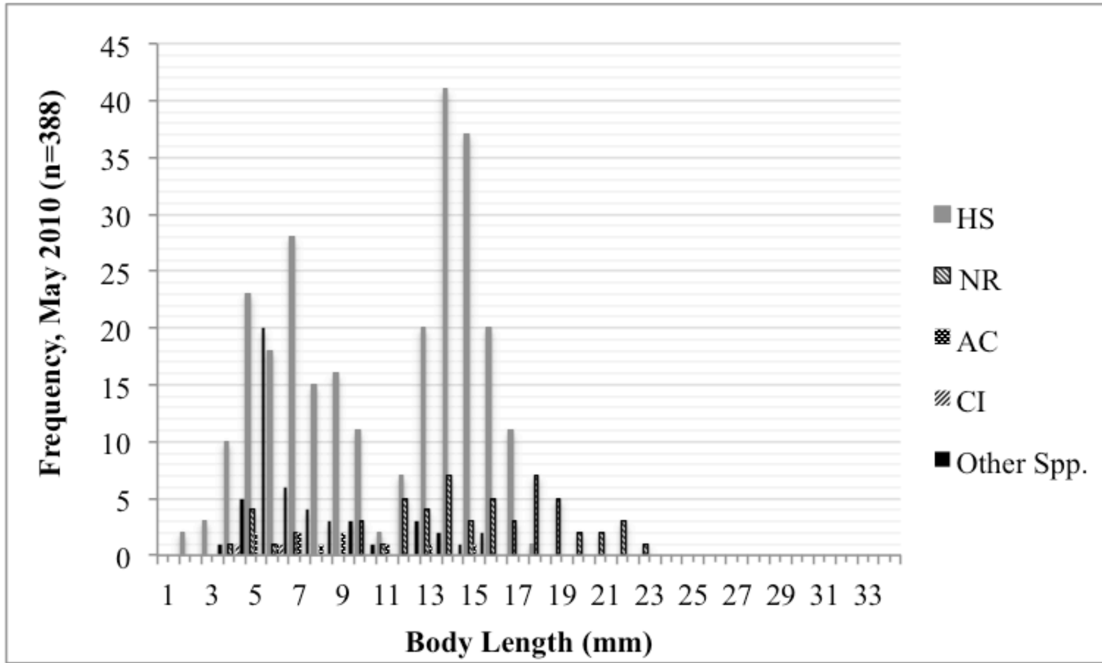

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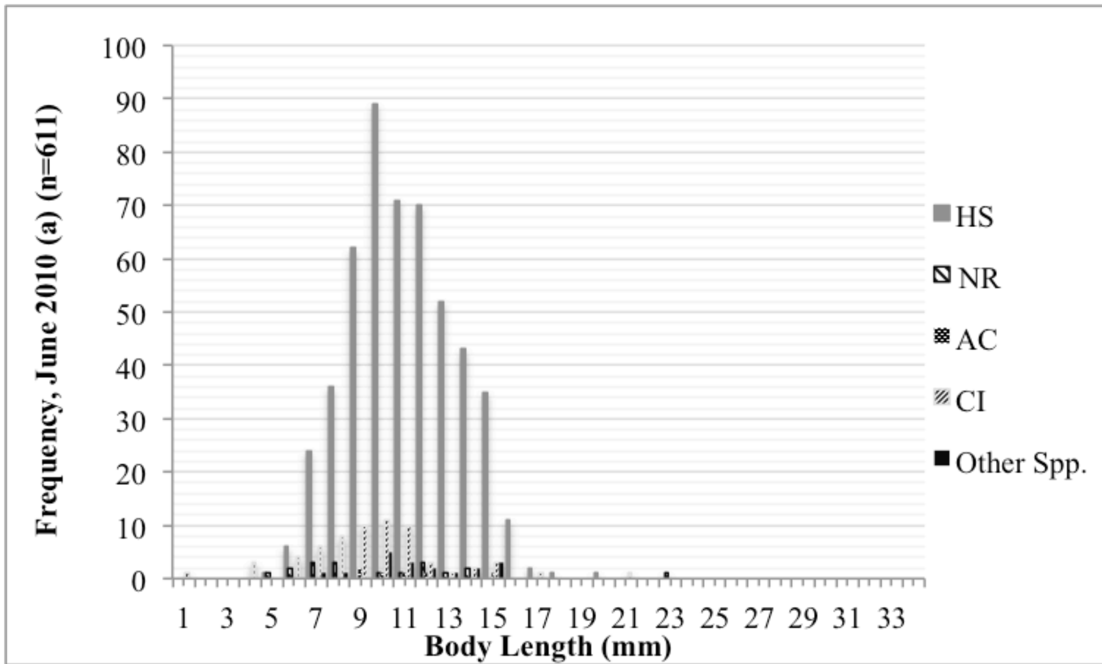

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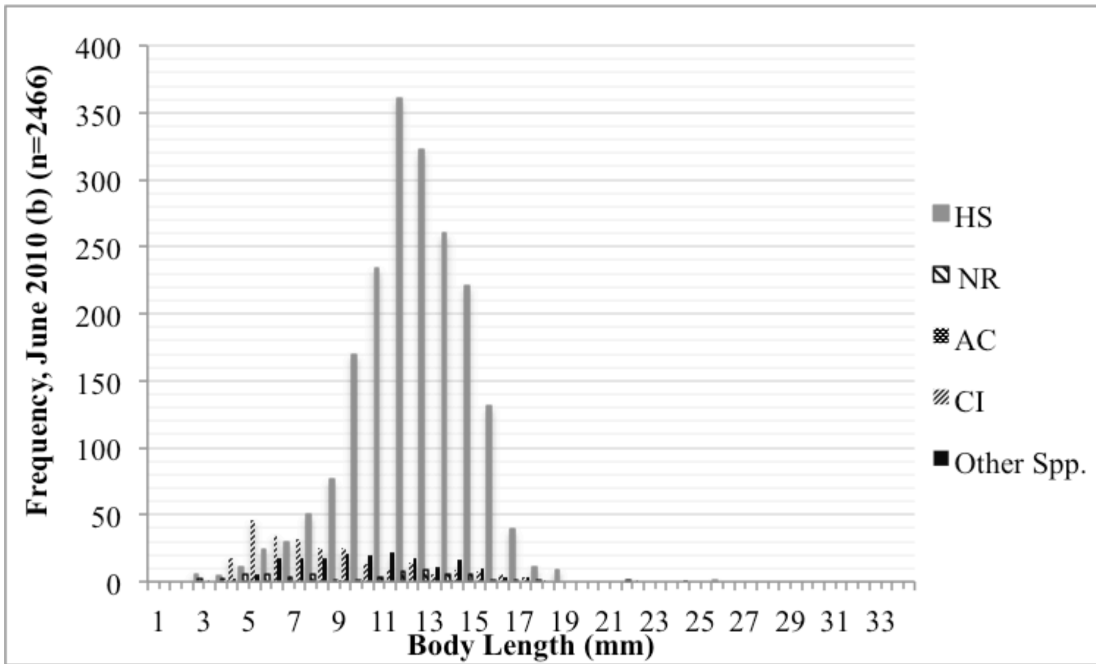

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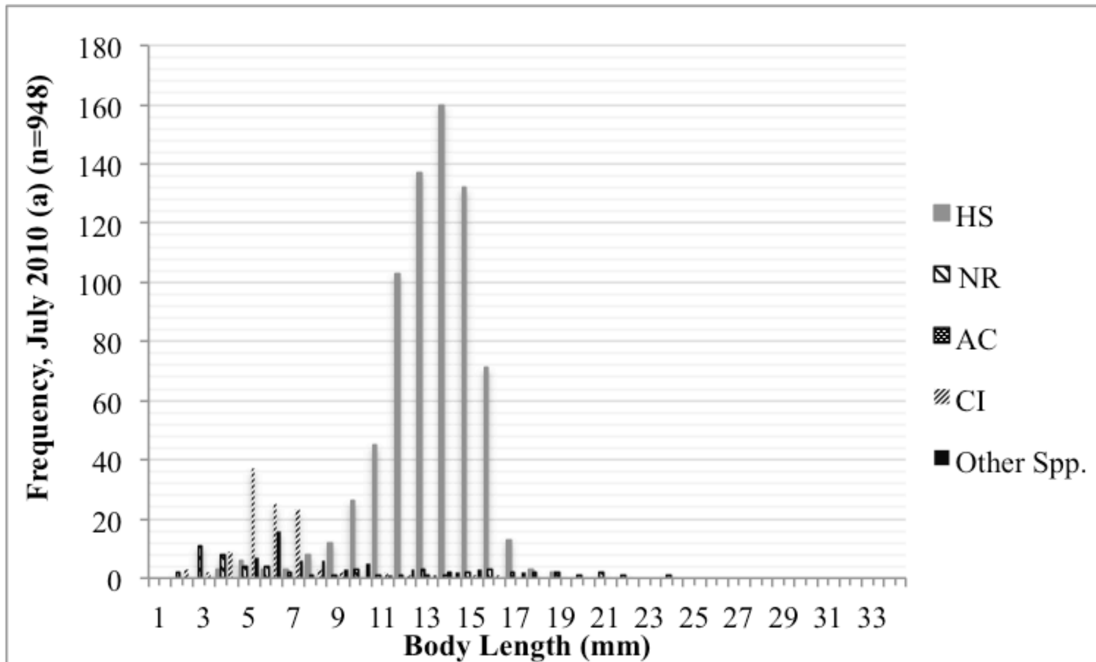

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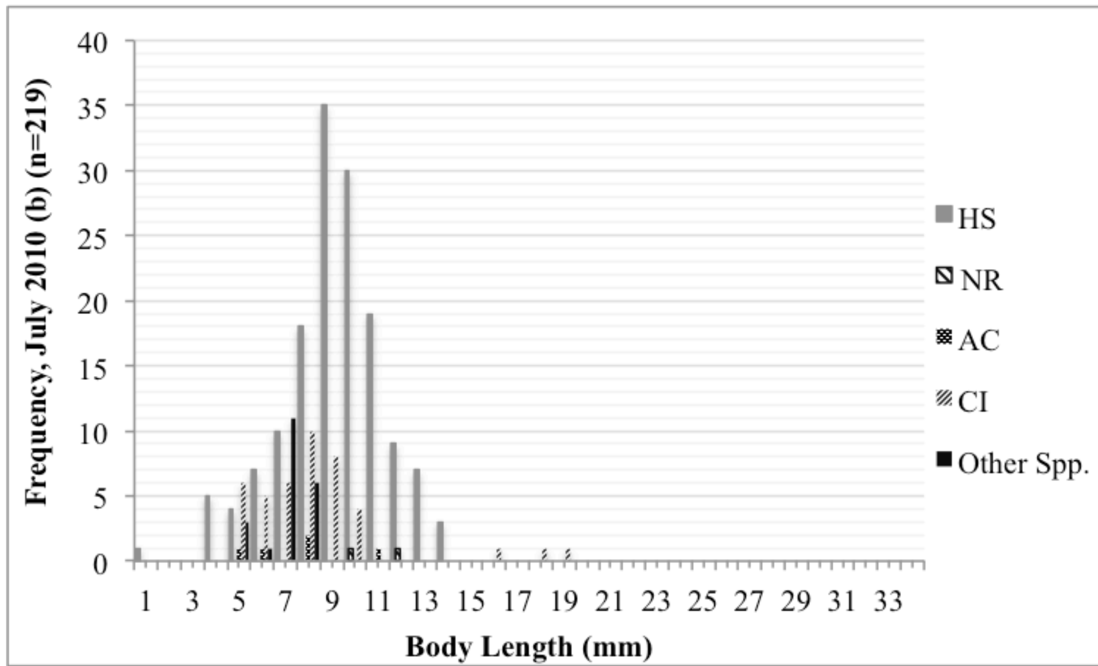

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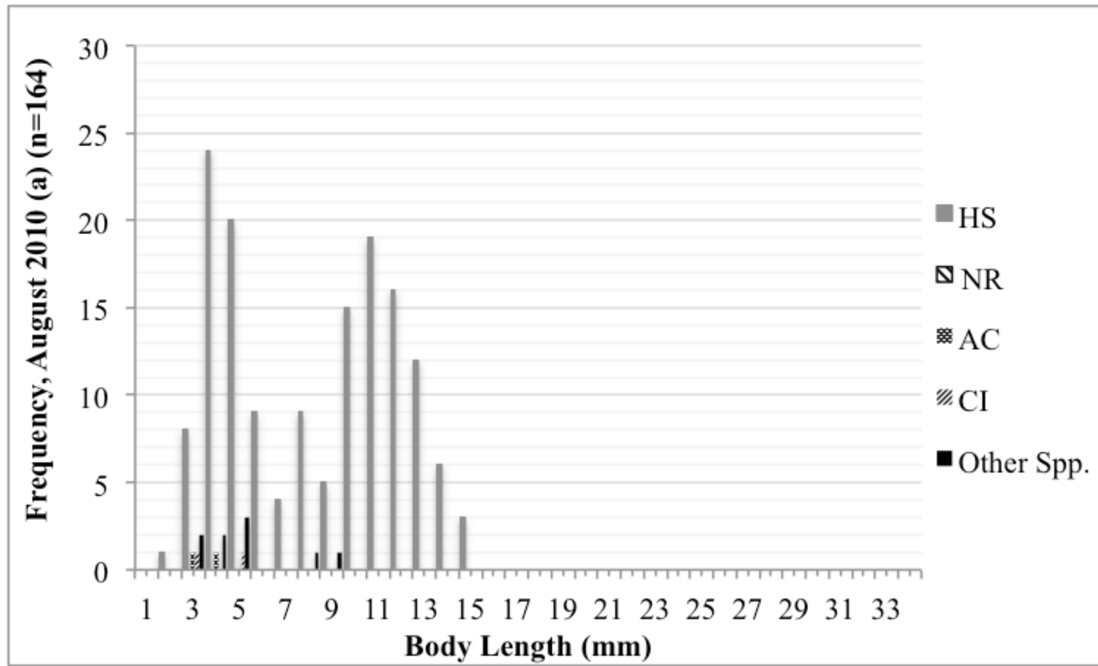

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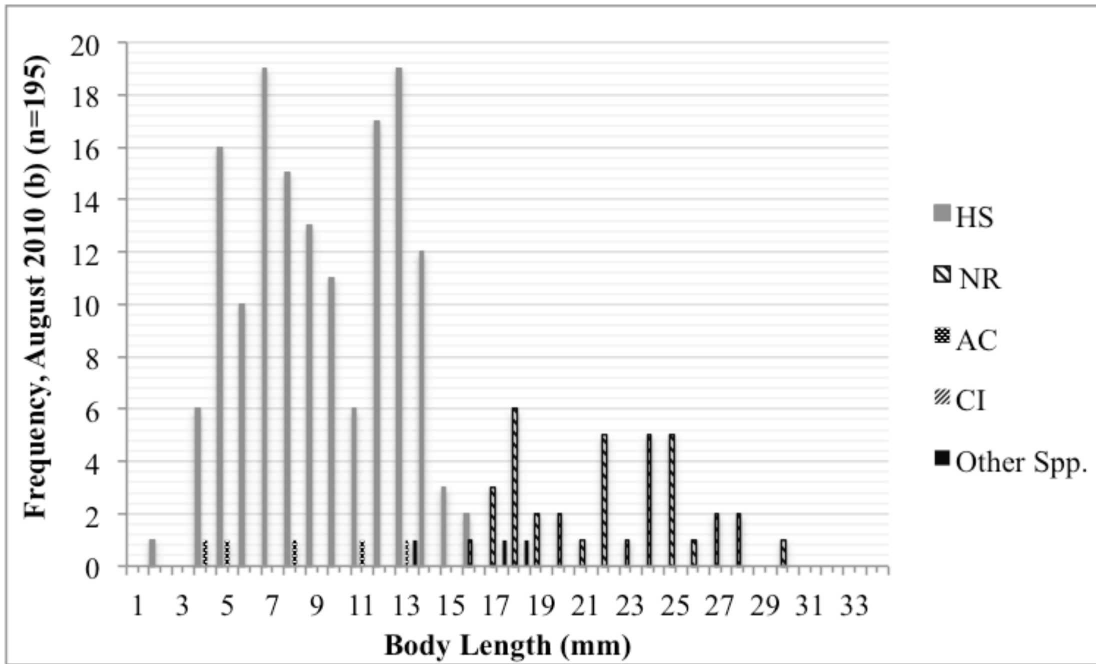

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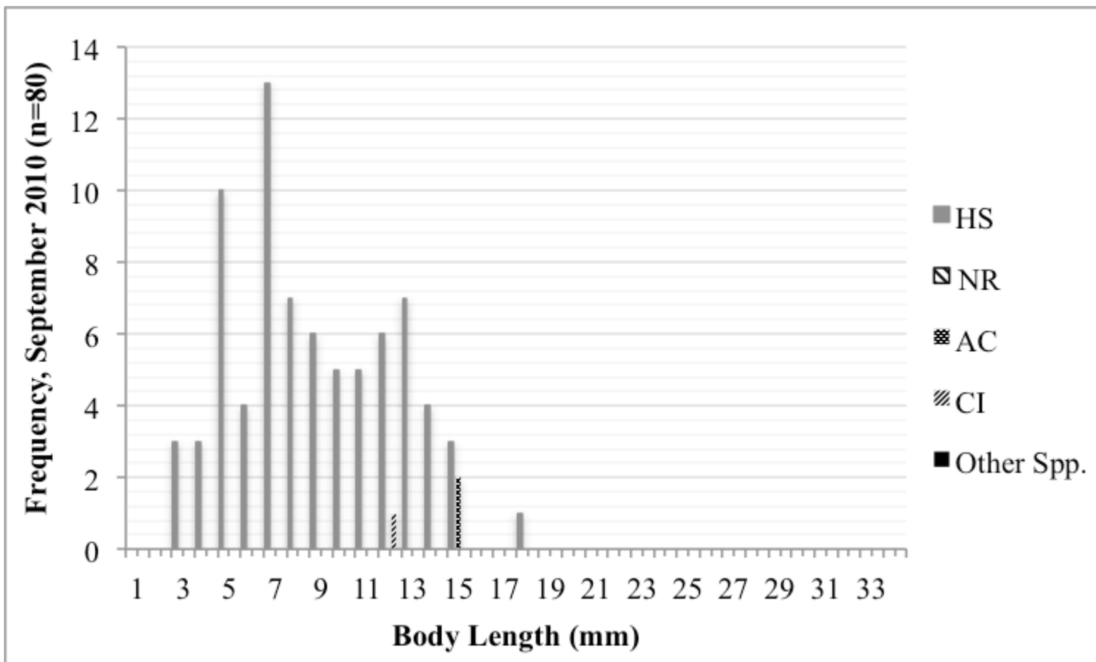

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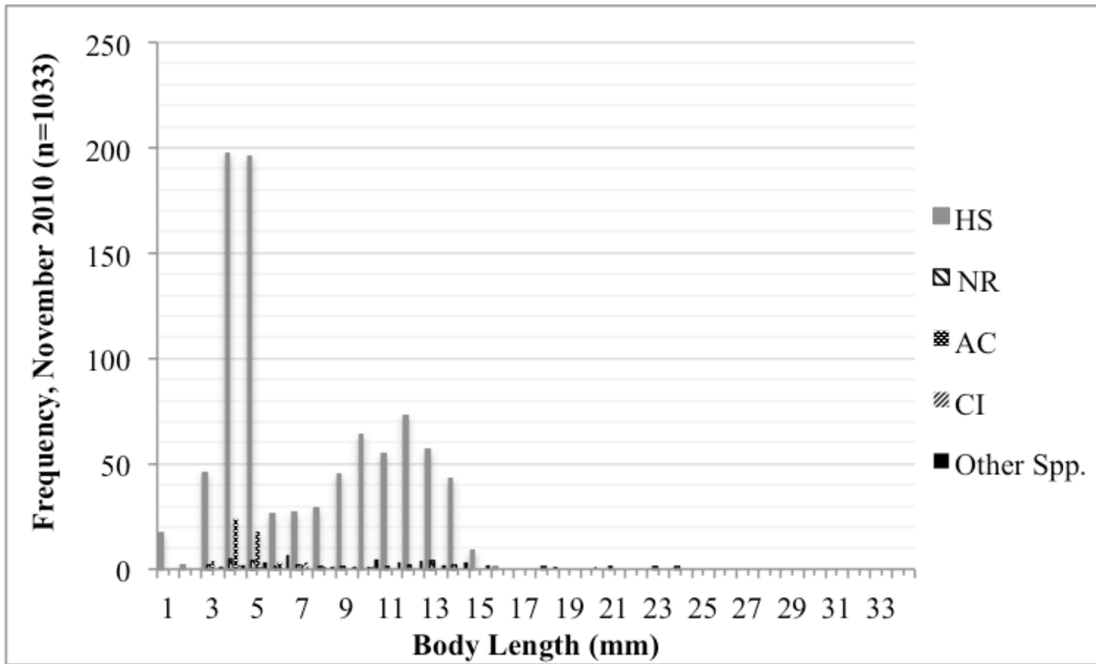

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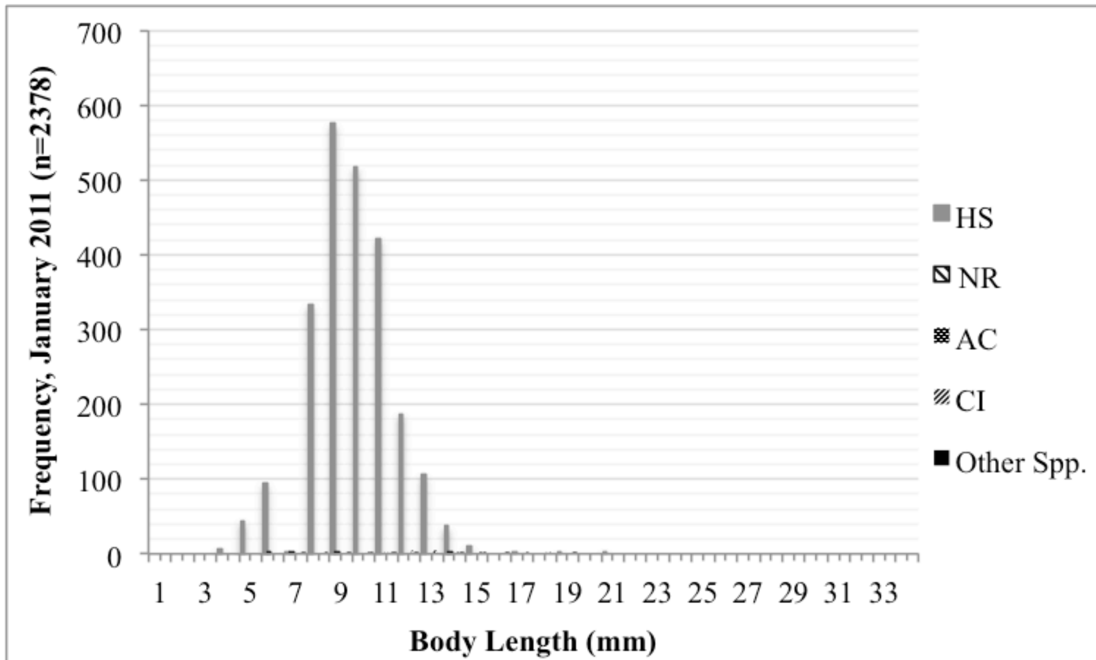

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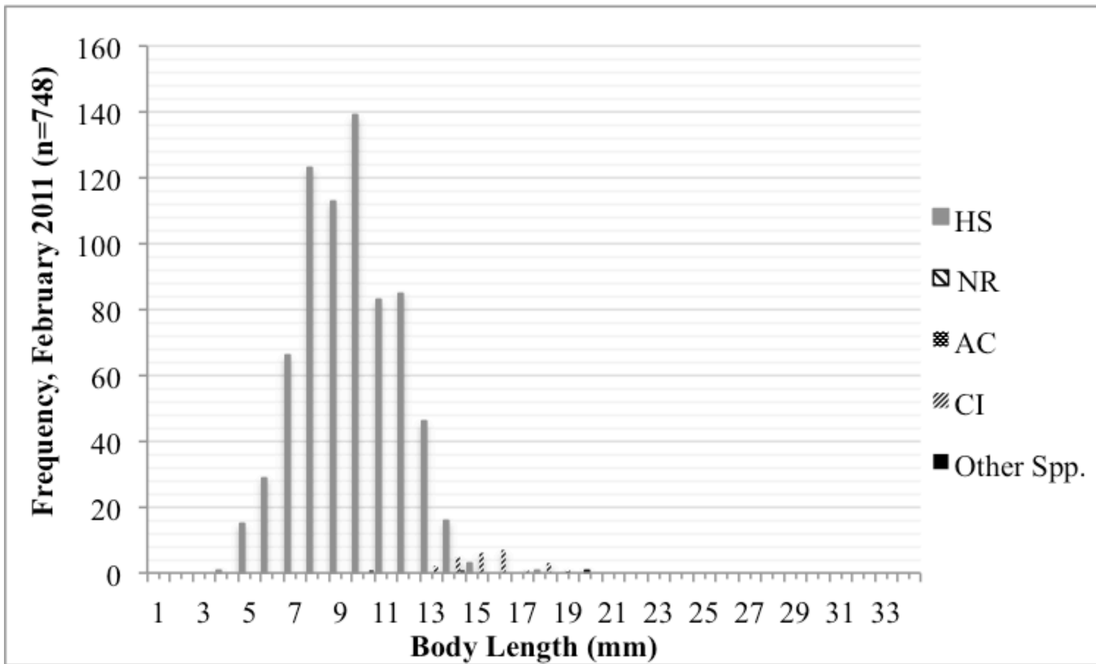

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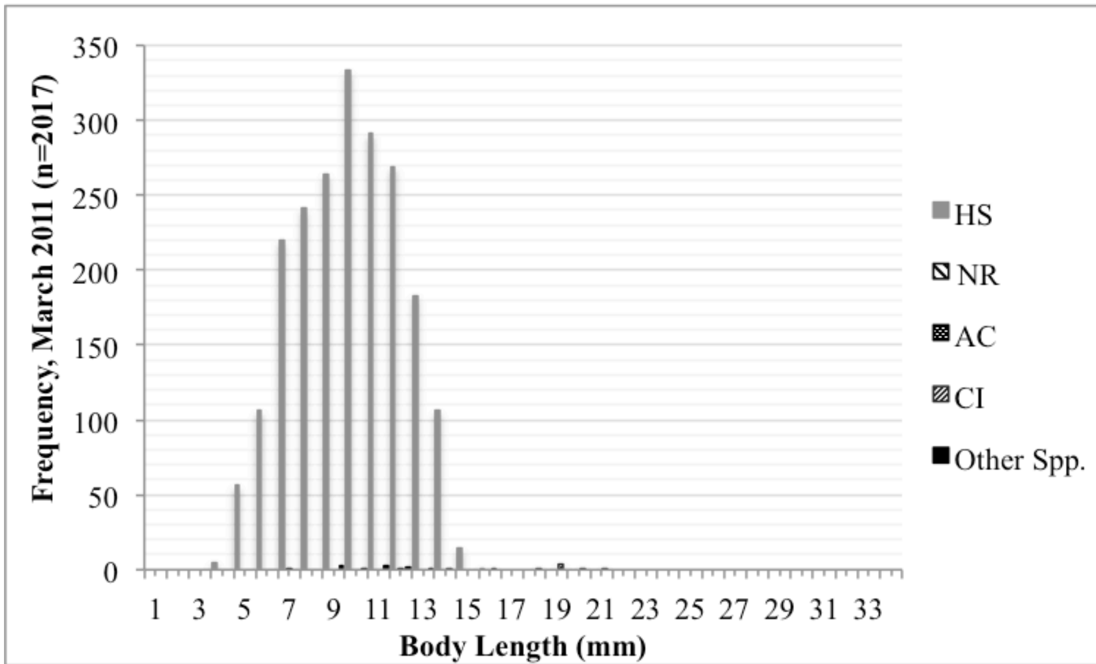

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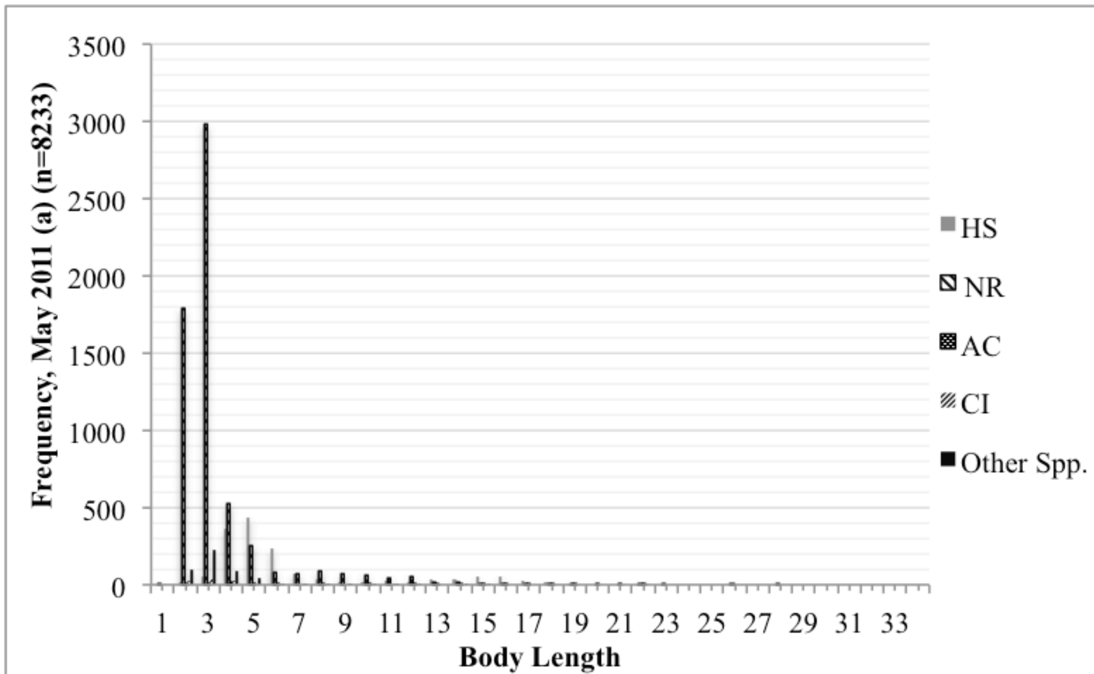

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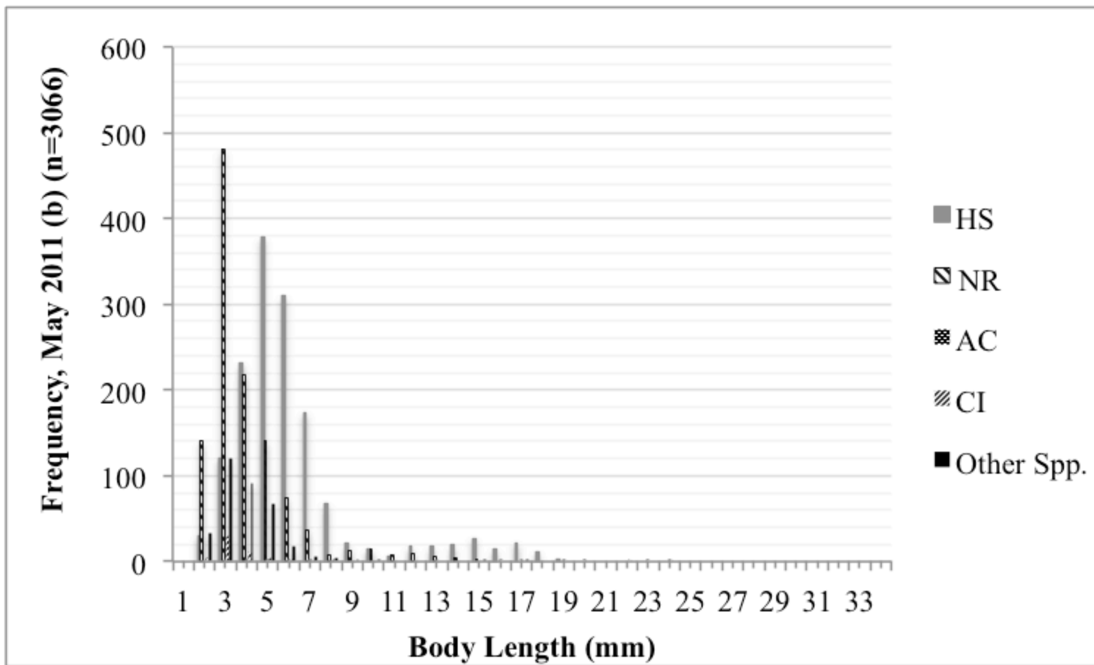

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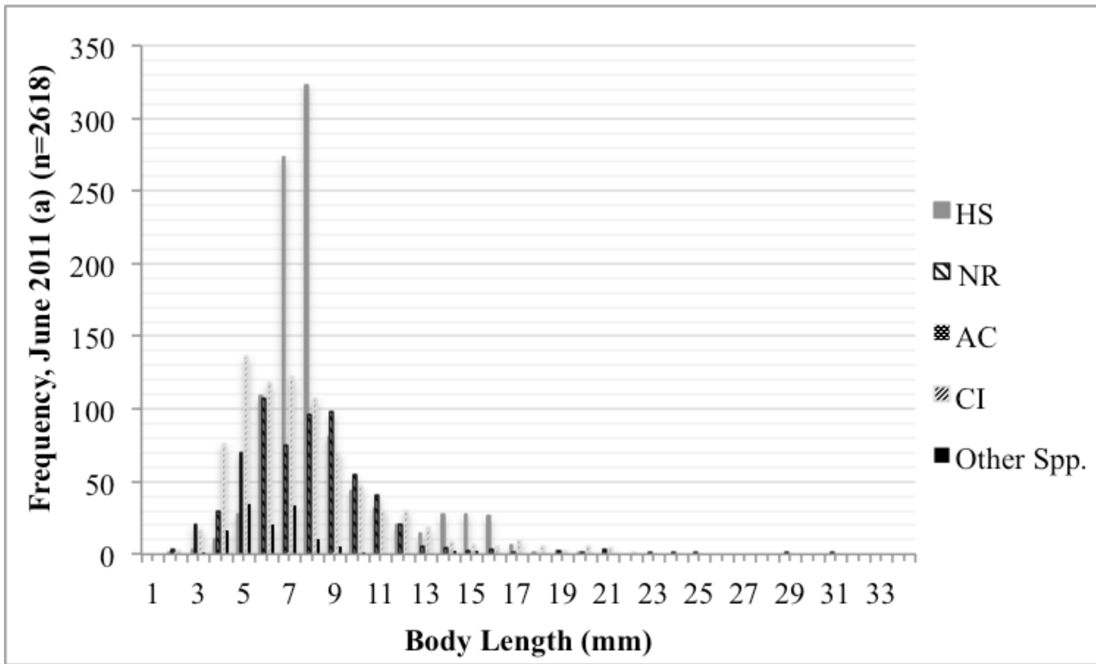

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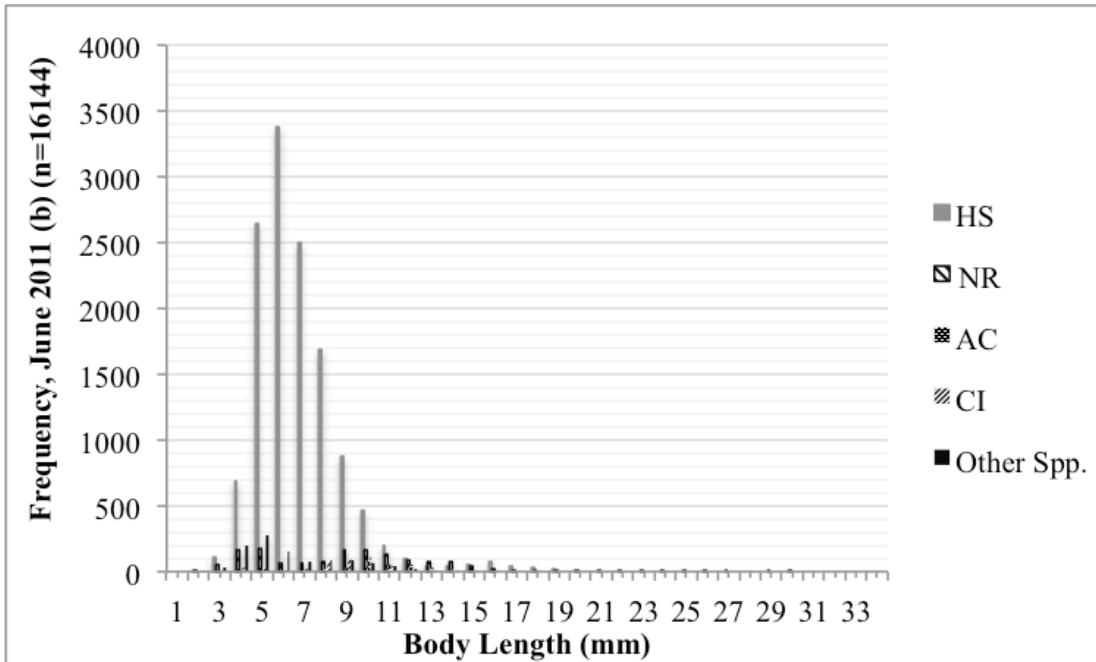

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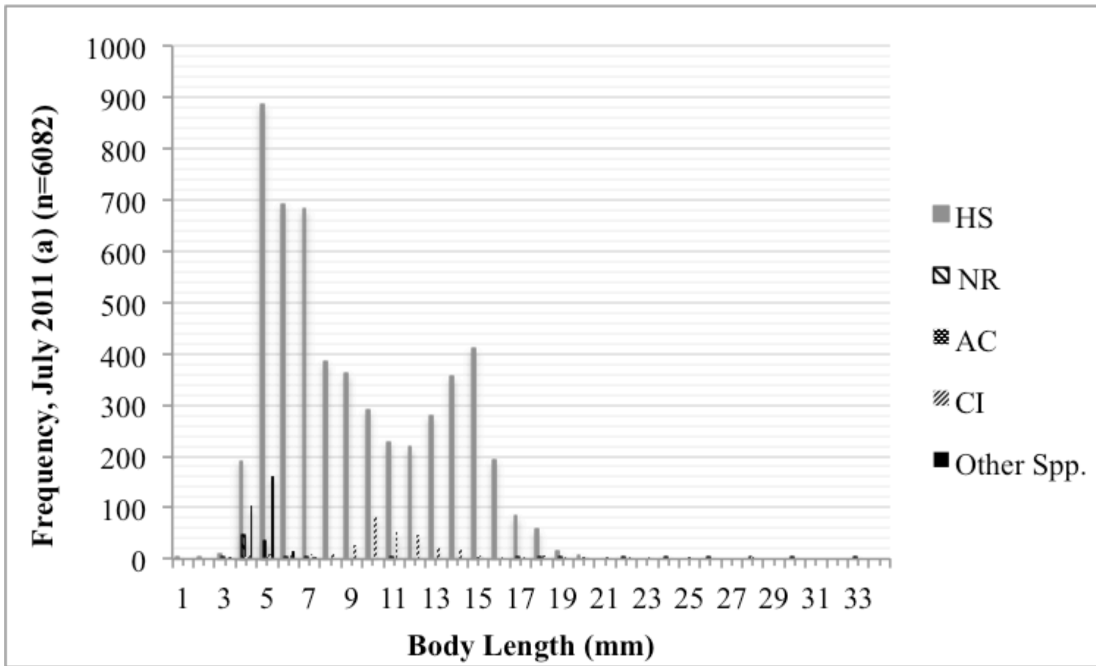

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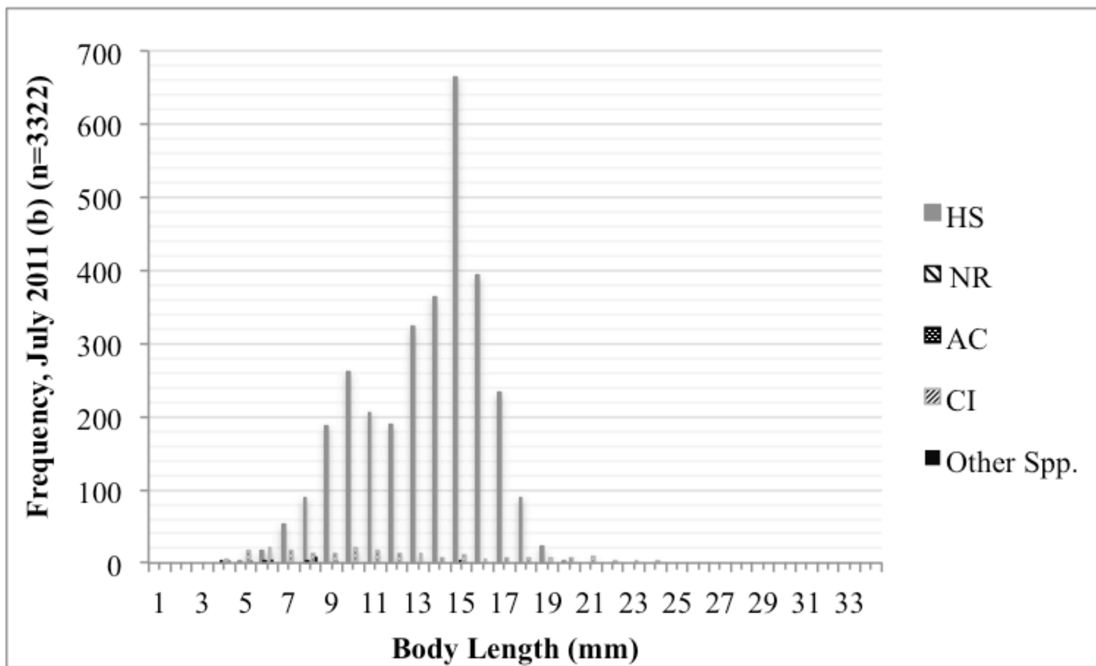

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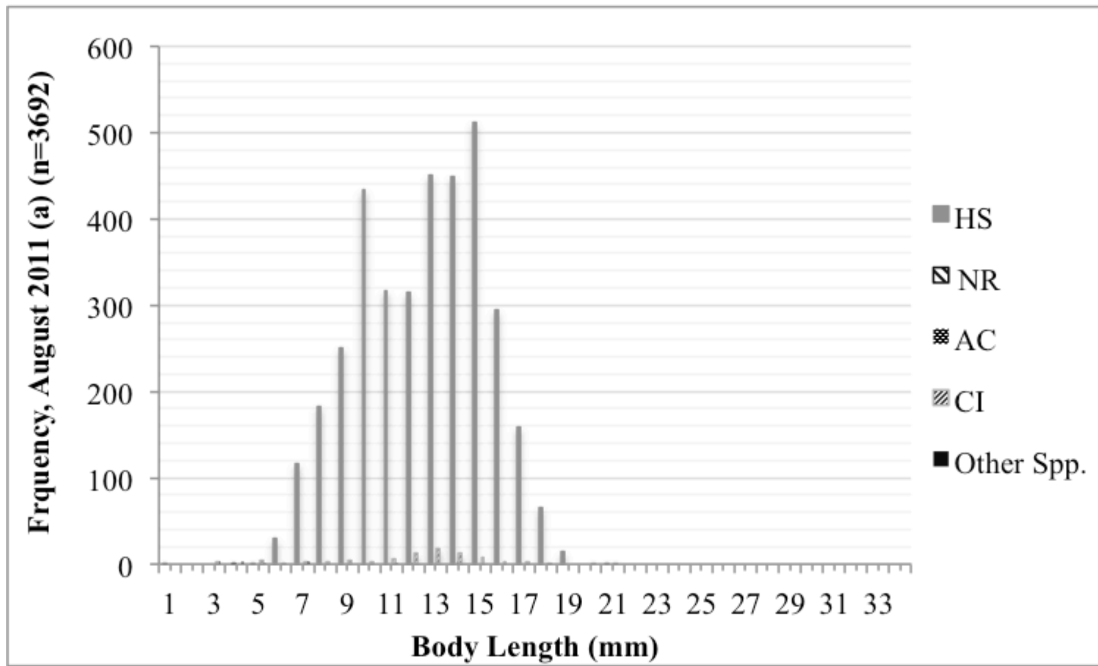

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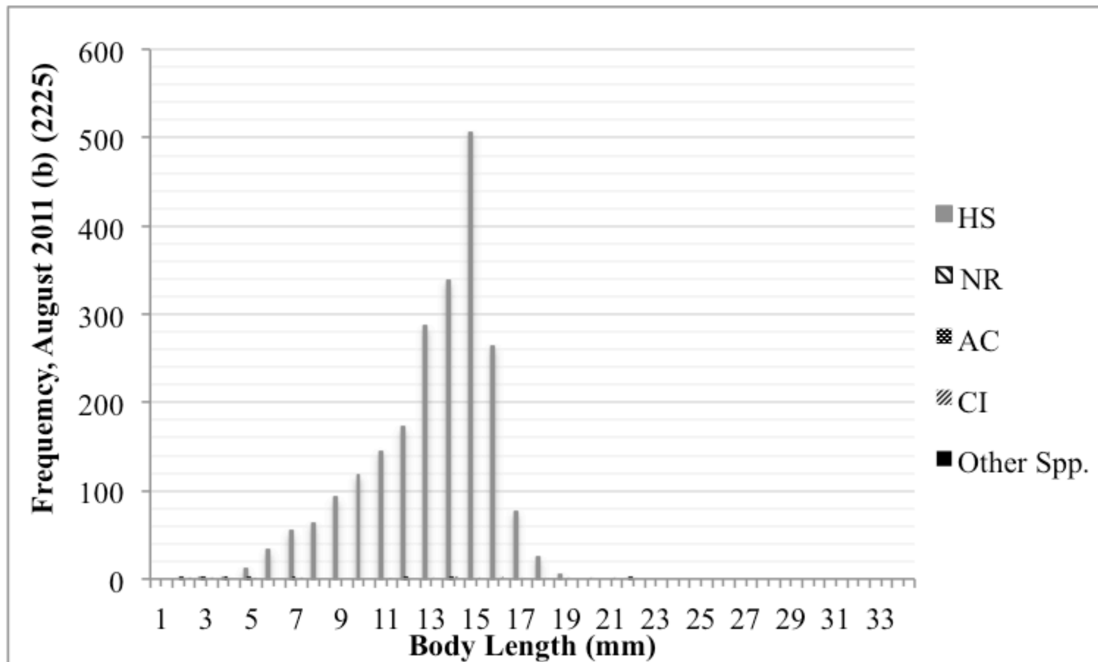

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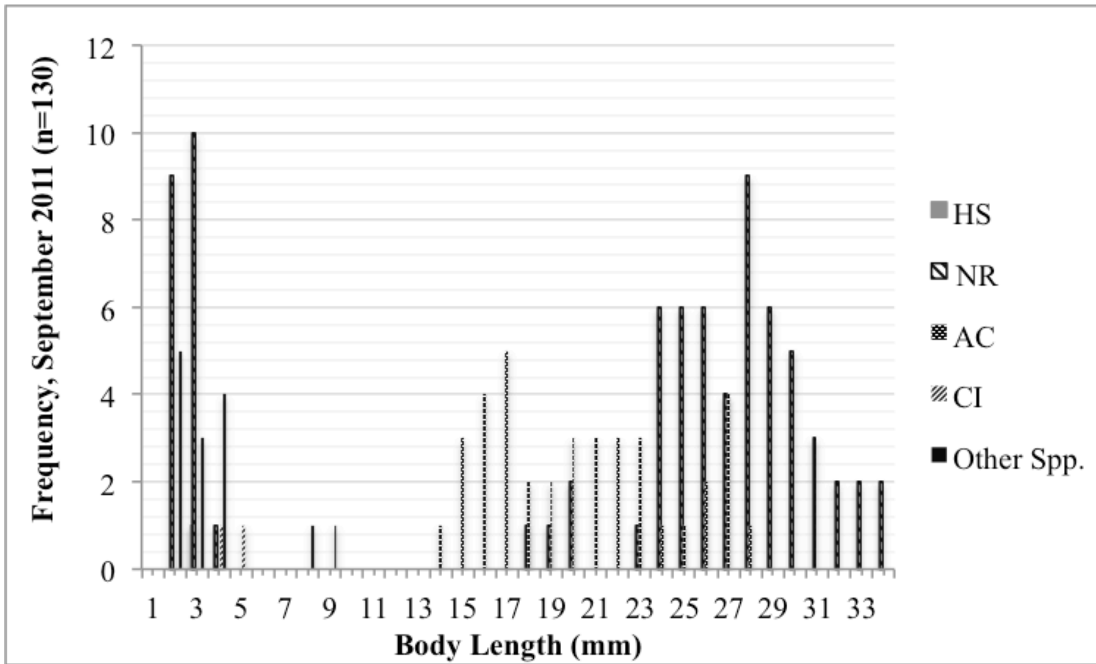

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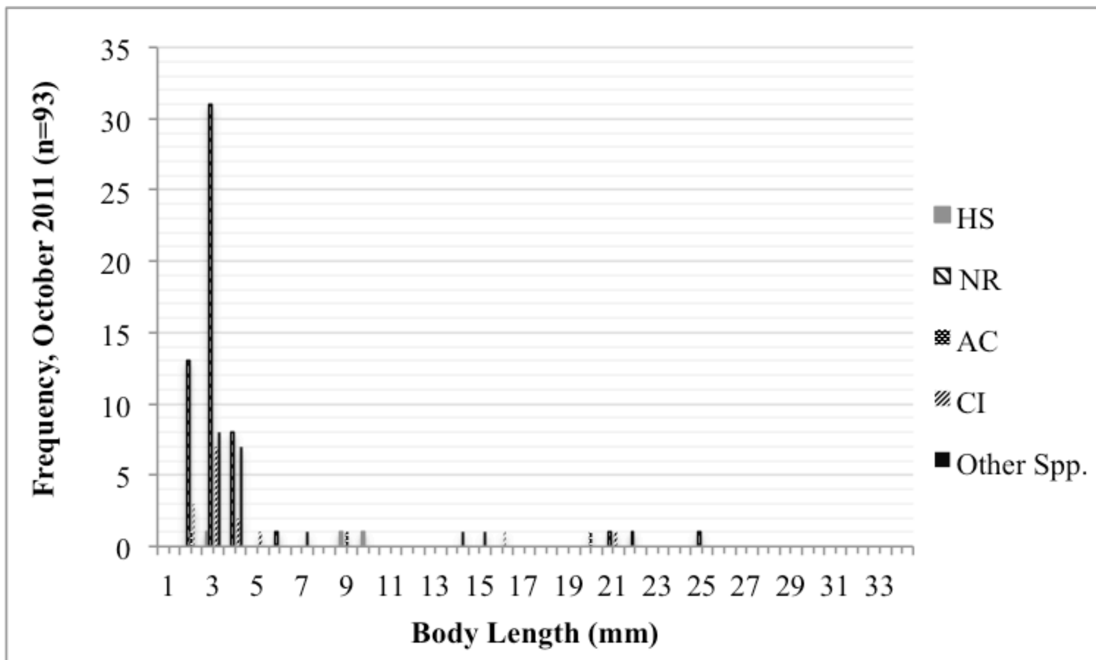

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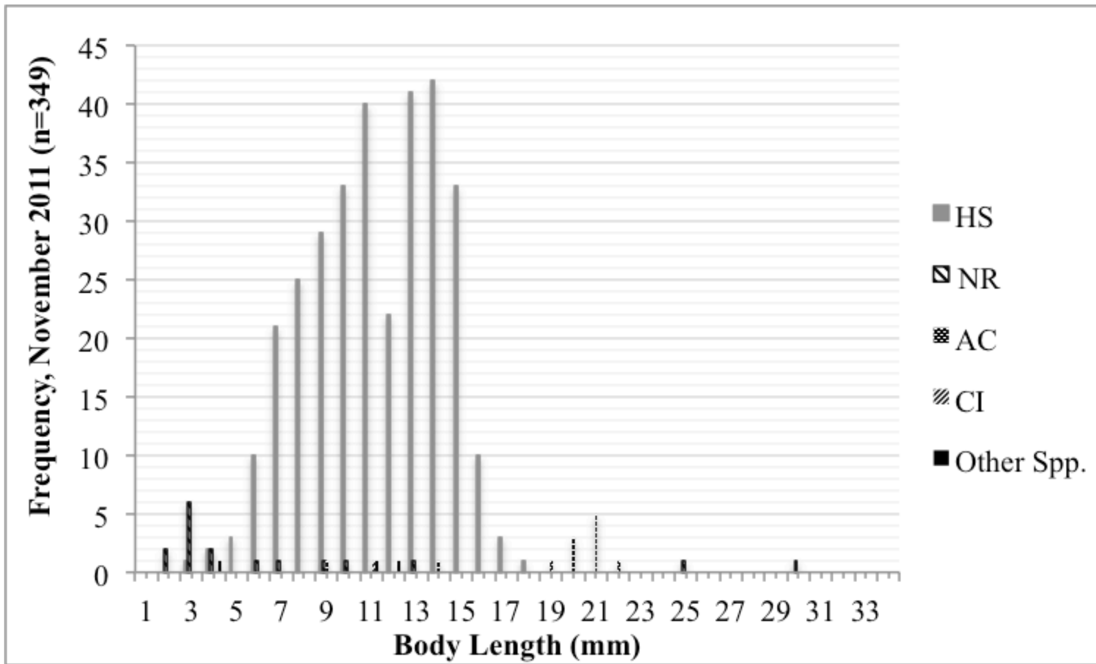

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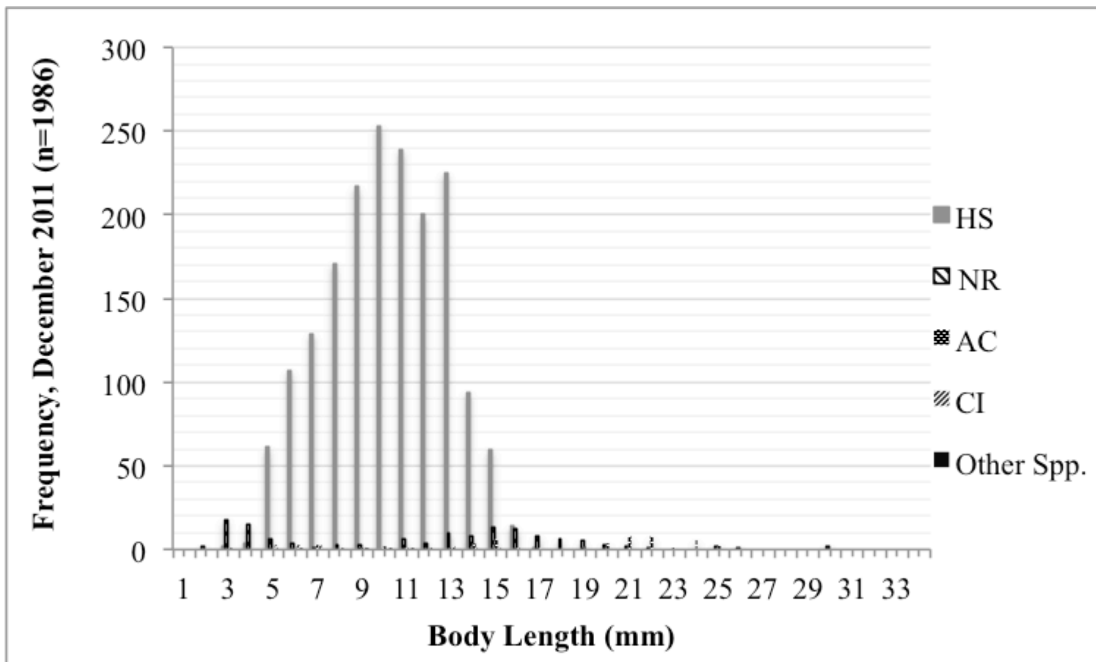

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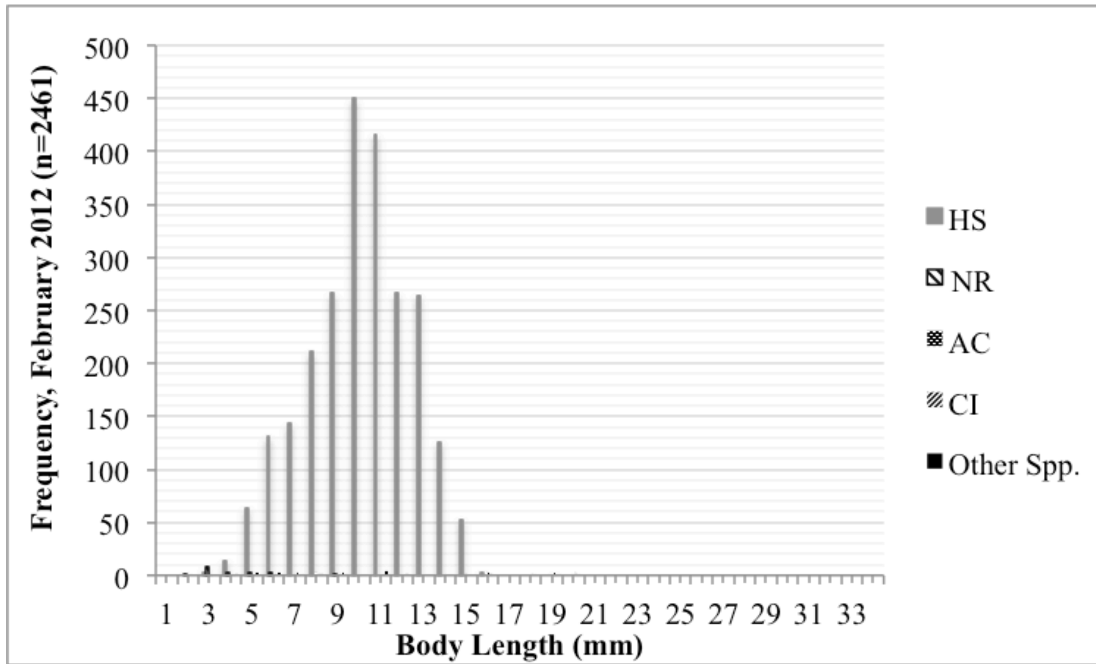

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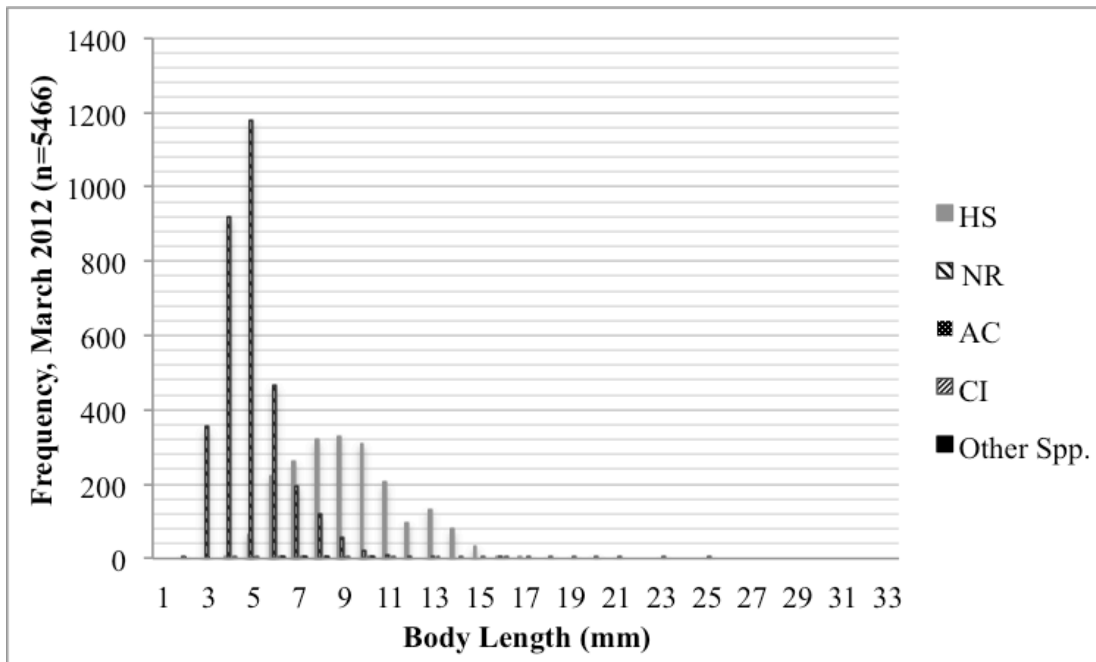

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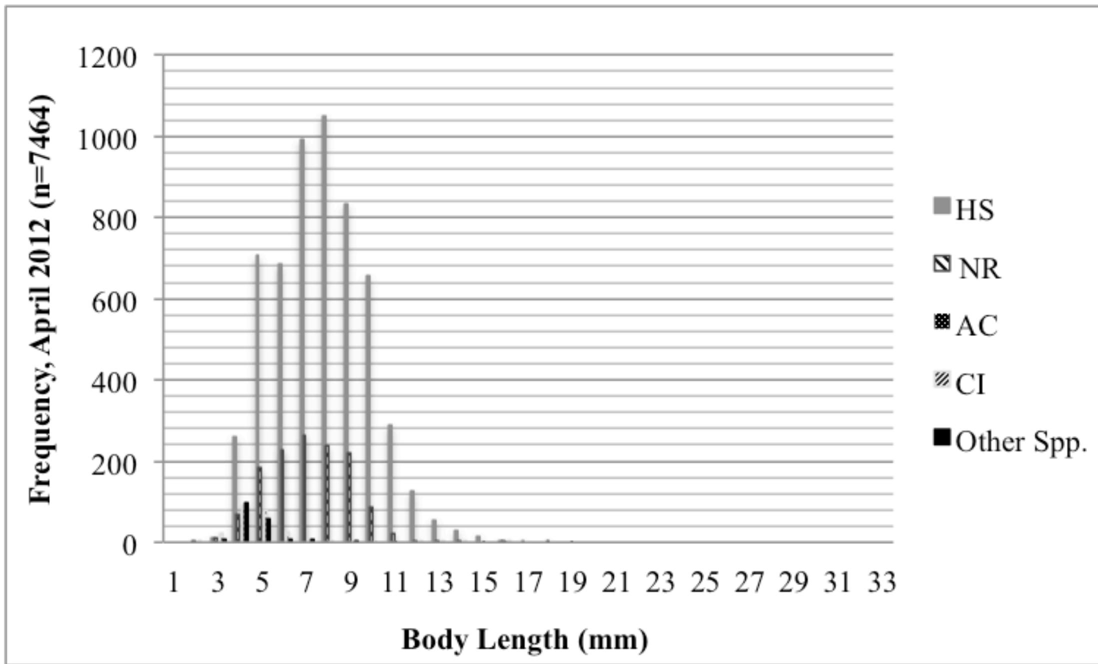

CHAPTER 6
Description of a Possible New Mysid Species found in Clayoquot Sound, British Columbia

Abstract

Multi-species swarms of mysid shrimp (Order *Mysidacea*) are the primary diet of gray whales summering in Clayoquot Sound, off the west coast of Vancouver Island. There are 12 species known to the area, with the disturbance from seasonal whale foraging promoting this level of species diversity. During a 24-month period (May 2010-April 2012) field samples were taken fortnightly during the summer and monthly during the winter, weather permitting. In this research, specimens of a species not recognized in the known group were found, with these specimens subsequently not recognized in any of the mysid keys.

External morphological features, in particular, appendages, antennal scale, telson, and uropods were used to try and identify the specimen, but results were inconclusive. Abdomen, antennae and uropod shape and structure resemble *Holmesimysis nuda,* whereas the telson showed similarities to *Disacanthomysis dybowskii.* Through more in-depth examination, characters, especially telson characteristics suggest the specimens to belong to the genus *Pacifacanthomysis*. Further examination of mandible processes will help confirm new species status, with molecular information to determine phylogeny.

Introduction

Mysids (Order *Mysidacea*) are shrimp-like crustaceans, and are the primary prey of summering eastern Pacific gray whales (*Eschrichtius robustus)* in Clayoquot Sound, off the west coast of Vancouver Island. Seasonal foraging pressure from these whales confers species diversity via an intermediate disturbance regime (Feyrer & Duffus 2011). This disruption creates open niche space that is available for less competitive species to invade and utilize. In my study area there are a dozen species now seen regularly, which has increased significantly from the 4 initially noted in 1996. An inter-annual analysis found species diversity to be greatest following a summer of increased foraging pressure (Feyrer & Duffus 2011).

Ninety percent of mysid species are marine, and 65% of these live in shallow coastal waters, like Clayoquot Sound. The first record of a species from the Order *Mysidacea* was published in 1776 by Müller. The species number currently exceeds 1,000 and spans 160 genera, and 4 families (Meland 2002, Heard *et al.* 2006), with no indication that the species list is nearing completion (Mauchline 1977).

Defining morphological features of *Mysidacea* include: a shield-like smooth carapace enveloping the thoracic region, fused dorsally with the head and not more than four of the most anterior of the eight thoracic somites; paired stalked eyes with moveable pedunculate; antennule with a three-segmented peduncle and two many-segmented branched flagella; exopod of the antenna in the form of a flattened scale and flangelliform endopods; thoracic limbs with natatory adapted exopods; ventrally flexed and elongated abdomen; and a fan-like tail composed of the last pair of unsegemented appendages, paired uropods and telson (Tattersall & Tattersall 1951). At the base of the uropods are prominent statocysts, balance sensory receptors, which are not present in any other crustacean. They have additional diagnostic value as statocyst statoliths can display high morphological diversification between families, tribes and genera (Schlacher *et al.* 1992).

The marsupial brood pouch of gravid females gives the Order the common name 'oppossum shrimp', first used by Thompson in 1828. It is this character, along with the incisor process *lacina mobilis* on the mandible, which distinguishes *Mysidacea* from sister Orders *Amphipoda, Isopoda, Cumacea,* and *Tanaidacea* (Heard *et al.* 2006, Martin & Davis 2011). The pouch chamber is formed by large, thin-walled concave plates of 2,

3, or 7 pairs of lamellae, attached to the thoracic limbs, which are secured by interlocking of the short, strong setae fringes (Tattersall & Tattersall 1951). Young are released as free-swimming progeny resembling miniature adults, except they are lacking one or more secondary sexual characteristics (Kathman *et al.* 1986). Growth is through a series of hormone-controlled molts, with the time to maturity varying from less than a year to greater than two years, and generations produced at the rate of more than three per year, to less than one every two years (Mauchline 1980).

Species identification is through differences in external morphology, in particular using the structure of appendages such as thoracic legs, antennal scale, telson, and uropods. Holmquist (1956) also demonstrated that biometric relationships between these characters to be unique to species. The telson apex may be cleft or entire, with distinctive teeth and/or spinal projections lining the margins. Eye form can also be distinguishing, differing in the degree of development. The eyes may be characteristic in shape, or a modified-compound eye, described as accessory (Mauchline 1980).

Many species display sexual dimorphism in form, with it often more difficult to determine maturity or development of secondary sexual characteristics in females compared to males. Pleopods are fully formed with a 2-segmented sympod in both genders, but the fourth pair in sexually mature males shows elongation. The fourth pleopod pair typically has outgrowths from the endopods of various forms in males, whereas they remain simple, unjointed and uniramous in females (Tattersall & Tattersall 1951, Mauchline 1980, Kathman *et al.* 1986, Meland & Willassen 2007). This specialization can be of taxonomic value, with pleopod adaptation a principal character for genera identification within some tribes (Mauchline 1980). Males may also have modified or enlarged antennular peduncles armed with setae compared to females (Mauchline 1980). In general, females attain a larger body size, which may, in conjunction with differences in longevity and prey selection, affect population sex ratios. In all morphological features mentioned there might also be ontogenetic variation in characters additional to natural variability.

Mysids form multi-species aggregations through social attraction and are maintained by visual and tactile cues (Ritz 1994). Distance between individuals was found to be a function of body length (Stelle 2001), with swimming speed presumed to be

a sorting mechanism, separating the shoal by age groups and forming swarms of individuals similar in body size rather than by species (Clutter 1969). Within swarms, mysid gustatory behaviours have been shown to aid kin species recognition, particularly by gravid females, where chemical composition is also an implied mechanism in the gregarious behaviours in swarm maintenance (Sato & Murano 1994). A swarm can cryptically blend with its surroundings through mysids' ability to change colour through the expansion or contraction of chromatophores distributed in neural, visceral, and caudal groups across the body and appendages (Mauchline 1980). This system, laid down in embryo and operated under hormone control, involves dark brown/red pigments complimented by a yellow/white, or sometimes blue/blue-green, reflecting substance which is adaptive to light and changing environmental conditions (Keeble & Gamble 1904, Mauchline 1980). Typically, littoral species are black, with deeper species often golden or red-brown (Tattersall & Tattersall 1951).

In samples taken to characterize life history of the mysid species in Clayoquot Sound, I located first one, and subsequently more specimens that do not fit a recognized form. Features of morphology and pigmentation contrast with those species already identified to the area, and do not fit a description of any species found in the literature.

Methods

Study Area

Clayoquot Sound, on the west coast of Vancouver Island, British Columbia, is located between 49°14'36"N, 126° 6'10"W and 49°18'51"N, 126°14'30"W. The study area is approximately 20 km² along the coast of Flores Island and is a productive gray whale foraging ground. It is bounded to the west by the 30-meter depth contour, and bordered to the north and south by unproductive foraging areas. In this area key mysid habitat is rocky reefs at a depth of around 10 m and within a kilometer from shore (Feyrer 2010, Laskin *et al.* 2010). A series of 12 random locations within mysid habitat along the south/south-west coast of Flores Island were sampled twice-weekly during the summer and once a month over-winter, weather permitting (Figure 1).

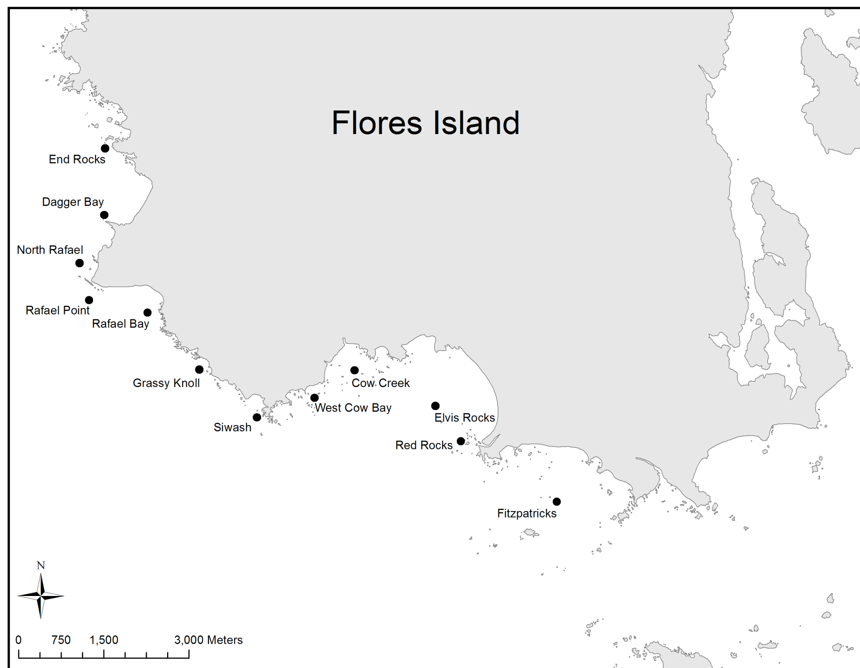

Figure 1: Locations of the 12 sampling stations in Clayoquot Sound. Weather permitting; each site was sampled monthly during the winter and twice monthly during the summer.

Mysid Sampling

The samples were obtained by towing a 'bongo' plankton net with two 30 cm openings and a 500 µm mesh. Sampling occurred, weather permitting, once a month during the winter and every other week in the summer. To collect samples, the net was deployed, allowed to sink to the bottom, dragged for several seconds, and then pulled straight to the surface. This was repeated three times at each of the sampling stations, and the mysids collected for each deployment were pooled. The mysids were preserved in 70% ethanol for later analysis. Any examples of the possible new species found either during the initial sorting or later analyses were stored in ethanol exceeding 90% in order to preserve as much genetic material as possible. Each mysid in the samples was enumerated, carapace length (rostrum to telson tip) measured, gender determined, and species identified according to Kathman *et al.* (1986) using a 40x dissecting microscope.

Results

Mysids belonging to this possible new species were first sampled in May 2010, in the area between Cow Bay and Rafael Point, locally called the Grassy Knoll (Figure 1).

Subsequent samples were collected that summer and through the over-winter period throughout the study area (Table 1).

Table 1: Occurrence of specimens collected by time and location. Details of length, gender, maturity and gravidity are also given.

Date (DD/MM/YY)	Location (from Figure 1)	Location (lat, long)	Length (mm)	Gender	Comments
20/05/10	Grassy Knoll	49.26830, -126.20455	9 8 5	Male Male Unknown	 Juvenile
20/06/10	Rafael Point	49.27060, -126.15676	10	Female	
20/07/10	Rafael Point	49.27060, -126.15676	10	Female	
23/03/11	Rafael Point	49.27531, -126.21660	14	Female	Gravid
23/07/11	End Rocks	49.31261, -126.24159	16	Female	Gravid
19/11/11	West Cow Bay	49.26471, -126.17271	9	Unknown	Juvenile
06/12/11	Grassy Knoll	49.26690, -126.20168	8	Unknown	Juvenile
11/02/12	End Rocks	49.31159, -126.24211	9 10	Female Female	

Specimen Description

Through consultation of several taxonomic keys including those by Banner (1948), Tattersall (1951), Holmquist (1956), and Kathman *et al.* (1986) the specimens were found to resemble *Holmesimysis nuda* in shape and structure of abdomen, antennae and uropods. As with *H. nuda*, abdomen segments are smooth, with no folds, and there are spines lining the inner margin of the endopod adjacent to the statocyst. However, the telson is similar to *Disacanthomysis dybowskii,* but a much shorter and rounded variety (Figure 2).

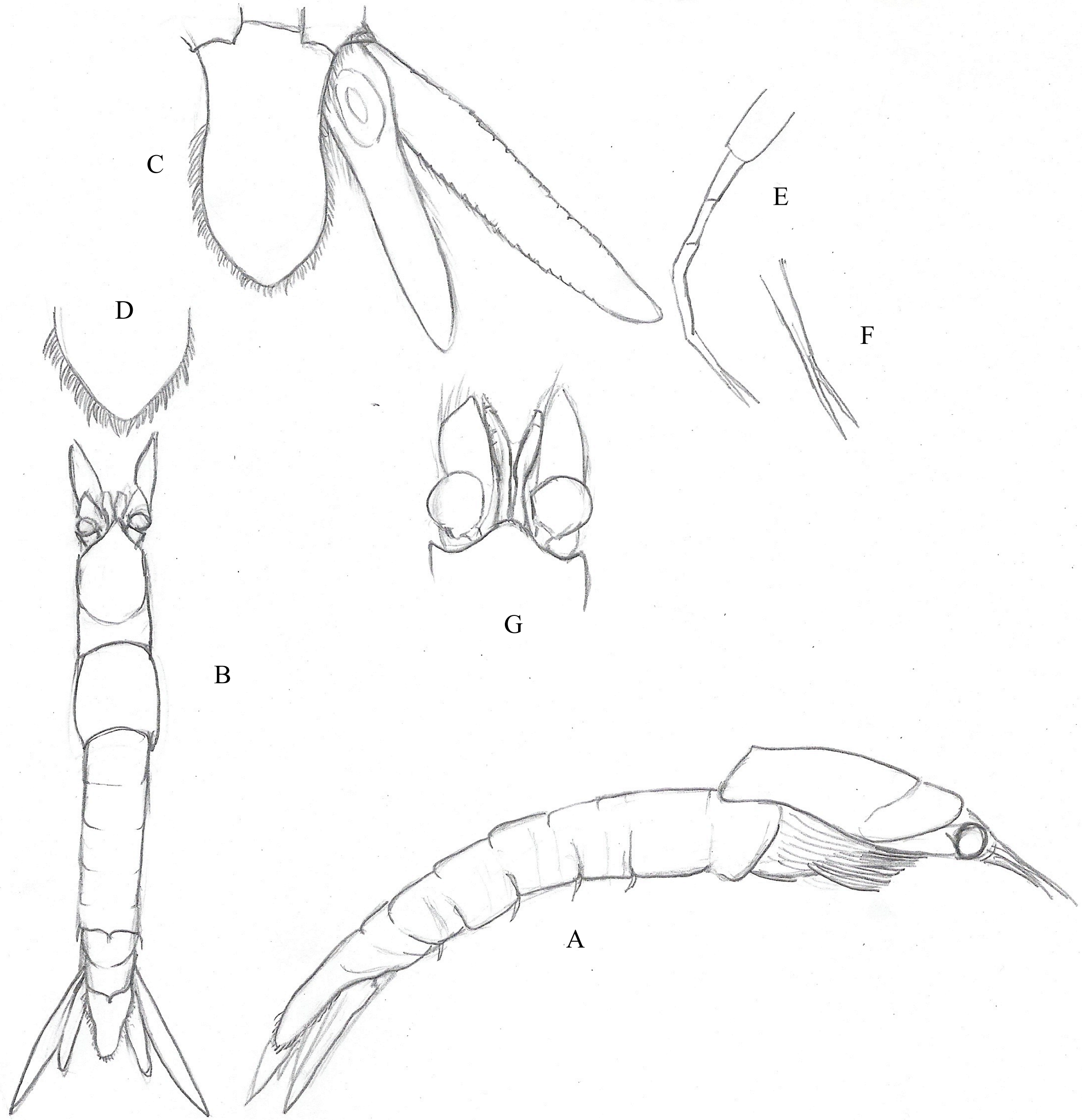

Figure 2: Unknown mysid species. A: Juvenile in side view, no secondary sexually characteristics visible; B: Juvenile specimen; C: telson and uropods; D: telson showing apex detail; E: male 4th pleopod; F: distal detail of 4th pleood; G: anterior end, dorsal view.

From the locations sampled (Figure 1, Table 1) and pigmentation patterns of many of the specimens, dark brown/black in colour, it was initially believed to be a tidal to sub-tidal, coastal species from the genus *Acanthomysis* (M. Galbraith Pers. Comm.). Some generic characteristics of *Acanthomysis* are a thrice-segmented carpopropodus, unequal terminal setae of the 4th ploepod, and no spines on the proximal laterals of telson,

which, with more detailed examination, were found to be lacking in the specimens. Although the telson does represent that of *Disacanthomysis*, the shape and structure of the uropods differ. The rounded rather than acute antero-lateral uropods, as well as the number of spines on these uropods, and presence of pereiopods setae exclude this genus (K. Meland Pers. Comm.). Due to observed characteristics, particularly the uniqueness of the telson, the specimens may be a new species of *Pacifacanthomysis*.

Further notes on the external morphological characters include: antennal scale reaches a third past the antennular peduncle; antero-lateral corners rounded; labrum (lip-like mouth part) has long acute process; endopods of pereipods, primarily 'walking legs' also used in food gathering in mysids, have a 5-segmented carpopropodus; female oostegites formed by thoracopods 7 and 8; 4th male pleopod has a 2-segmented expopod, where the last segment has 2 long setae; and uropod endopod bears 6-9 spiniform setae near statocyst region (Figure 2, K. Meland Pers. Comm).

Discussion and Conclusions

There is no comprehensive worldwide taxonomic key published for the *Mysidacea* and, as Mauchline noted in 1980, with the rate of new species description, many keys quickly become out of date. There have also been several reclassifications of the Order *Mysidacea*, with many species renamed since first discovery. This is particularly true for the genus *Acanthomysis* that, due to its immensely diverse nature, has been divided into several smaller genera, with only one species true to the original genus (Kathman *et al.* 1986). This may account for some of the confusion in genus assignment for the specimens found in Clayoquot Sound. However, examinations of external morphology lead to the tentative appointment of the genus *Pacifacanthomysis.* Work on further specimens, particularly sexually mature individuals, with detailed comparisons of female oostegites, male pleopods, and mouthpart morphology will be required before a more conclusive species designation can be made. Genetic work may also help formalize the species lineage, with it being a result of hybridization also a possibility.

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CHAPTER 7
Up and Down from the Middle

In this study I examine a part of the trophodynamic forces acting on marine systems, and the influence of some of the constituents in an interaction web. While the influence of top-down and bottom-up drivers has been given to considerable argument, here the mid-trophic prey level is given focus. By defining the 'prey-scape' of a spatially discrete study area, the mutual influence of predator and prey can be determined.

The recovery of whale species following the ban on commercial whaling opens up a renewed frontier for the examination of the influence of top-level predators in marine systems, thought to have been once dominated by large, slow maturing animals and rapidly reproducing producers (Jackson 2006). Population numbers of the eastern Pacific gray whale (*Eschrichtius robustus)* have shown significant recovery and are now thought to be reaching the carrying capacity of their primary feeding grounds in the Bering and Chukchi Seas. The increased foraging pressure has had significant top-down affects on these feeding areas (Highsmith & Coyle 1992) forcing them to exploit secondary areas north of the Bering Strait and tertiary areas along their migration route (Moore *et al.* 2001, Perryman *et al*. 2002).

Protected bays along the coast of Vancouver Island supported the most extensive community of benthic amphipods south of the Bering Sea (Oliver *et al.*1984, Kim & Oliver 1989), and were roughly analogous to the high latitude seas (Oliver *et al.* 1984, Oliver & Slattery 1985). In Chapter Two I describe the influence that gray whales have had on the benthic prey population in Clayoquot Sound off the west coast of Vancouver Island, and demonstrate their ability to decimate prey stocks. I use data covering 25 years of foraging studies to show the decline of ampeliscid amphipod stocks over time in this area. As in the Arctic foraging areas, this prey source now represents an inefficient resource for gray whales as a result of their own consumption. The seasonal regime of whale foraging generated a schedule of persistent pulse perturbation, apparently driving ampeliscid populations to such low numbers they are yet to show recovery, despite almost complete release from whale foraging. The relentless nature of the perturbation may better be thought of as a press rather than pulse in its ability to control prey population, given the slow rate of reproduction of benthic amphipods. Currently, other

organisms may now be capitalizing on the open niche left by amphipods, further preventing population recovery.

Patterns in foraging intensity of gray whales in Clayoquot Sound, by season, over time are examined further in Chapter Three. I use census data collected over the 15 years (1997-2011) following the prey switch from amphipods to mysids. I distinguish long-term trends, where the number of whales utilizing Clayoquot Sound oscillates biennially. Every year of higher than average foraging is followed by at least one year of below average numbers, and vice versa. There is also an overall declining trend in the oscillations, with predation diminishing prey reserves from 1997-2009. However, several years of predation release preceding 2010 allowed a prey ‘break-out’ recovery of mysids, and so an increase the number of whales sustained in the area, in this year. I also examine the correlation of foraging intensity between seasons. I use a regression to compare the number of foraging whales recorded in the last 4 weeks of a season and the first 4 weeks of the subsequent season (May 24th-September 8th), with a positive relationship determined, contrary to what I predicted. This presages the importance of the winter prey reproduction study in following chapters.

On a finer time scale Chapter 4 defines the seasonal satiation point of gray whales. Through the use of behavioural budgets, I determined the time allocated to foraging activities throughout a summer season. Gray whales are edacious upon arriving in the study area, underpinned by the need to restore blubber reserves after the expenditure of wintering, migration, and breeding. This is vital, with blubber not only an energy store, but also influential for buoyancy, gait, thermoregulation, and foraging ability. I presume that feeding should no longer dominate behaviours once blubber reserves are replenished. However, I found foraging to dominate behaviours consistently throughout the summer, with variability possibly resulting from variance in individual foraging strategies and energetic needs. Foraging was also seen to follow prey availability, with time allocation to foraging increasing through the early season as the mysid swarms grow and stabilize following their first brood in late May as waters become warmer and more productive. High mortality rates of prey are expected while gray whales forage before achieving satiation and with prey exceeding the ‘threshold of interest’ (Bakun & Cury 1999). This experiment was developed in response to the

observation that differential seasonal foraging may be implicit in fall reproductive behaviour of the mysid prey.

If Clayoquot Sound is to remain a productive foraging area for gray whales the continued ability for mysid swarms to recover following predation is imperative. In Chapter Five I focus on defining the life history characteristics, specifically growth and reproduction, of the 12 mysid species present in the study area. To understand how renewal of populations work, I sampled over winter, following the departure of whales from the area. In addition to the recognized summer broods, the dominant species of mysids in Clayoquot Sound, *Holmesimysis sculpta,* was also found to have a further reproductive peak in mid autumn, and winter broods. Its dominance over the other species may be maintained by showing less seasonal tendencies in reproduction perhaps linked to some ability to exploit a wider range of resources.

Gray whales directly influence the size and life-stage of mysids in the population, via disturbance from seasonal foraging, which in turn drives species diversity found in mysids in the study area. Prior to this work, 12 species had been described in the area, 10 of which were sampled regularly. In Chapter Six, however, I hope to add further to this species list, and therein I explain my initial work to designate a possible new species found in collections taken during the 2 years of sampling. Here I briefly describe external morphological features that may be used to identify its lineage. Further work is still needed, however, to confirm new species.

Although marine systems are typically considered to be driven by resource availability, this study demonstrates the power of the predator. I show how spatially discrete prey populations can become locally depleted following severe and repeated predation. However, in their strong interaction roles as predator and prey, gray whale presence and distribution are intimately linked to mysid populations. Indeed, the patterns of foraging intensity of whales in the study area are very closely tied to prey abundance, both in timing and number of whales sustained (Olsen 2006, Feyrer 2010). From their apex predator role, whales affect the future quality of their own foraging areas, however mysids have so far shown themselves able to capitalize on periods of reduced predation to re-establish swarms. If however, like amphipods, mysid prey stocks were driven to such low population numbers that they were not able to recover, gray whales may be

again forced to relocate, prey switch, or both to find sufficient prey resources to restore their blubber reserves. This may create system instability, possibly leading to a hysteresis event, similar to that documented in Chapter Two following exhaustion of amphipod reserves. In addition to the loss of mysids in food chains, the potential resultant loss of gray whale use of the area may also influence the broader ecological structure of Clayoquot Sound.

In this study I examined whale foraging over a range of temporal scales, complimenting this with an analysis of growth and reproduction strategies of mysids, primarily to determine their ability to recover following predation, and allowing Clayoquot Sound to remain a productive foraging area. The interaction of gray whales and mysid species in Clayoquot Sound provides a further understanding of whale ecology, as well as identifying the drivers and valves of energy flow in the system (Dunham & Duffus 2001, Hunt & McKinnell 2006, Nelson *et al.* 2008). The data presented here points to the importance of considering all trophic inputs to understand the ecology of a system, neither solely bottom-up nor top-down but rather 'both up and down from the middle' (Hunt & McKinnell 2006). Findings from my study area may be generalized to some other foraging sites, with many of the results found in Clayoquot Sound already mirrored in much larger primary foraging areas in the Bering and Chukchi Seas. It also may inform us about behaviours in other tertiary foraging areas, as gray whale are increasingly forced to use these areas with declining prey stocks in high latitude sites. Top-down structuring, as shown here, has long-term implications for prey productivity and habitat quality, with gray whales acting as the regulatory force.

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