HABITAT, POPULATION STRUCTURE AND ENERGY VALUE OF BENTHIC AMPHIPODS, AND IMPLICATIONS FOR GRAY WHALE FORAGING IN CLAYOQUOT SOUND, BRITISH COLUMBIA

by

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A thesis submitted to the Department of Geography

in conformity with the requirements for the

degree of Master of Science

Queen's University
Kingston, Ontario, Canada
April, 2000

0-612-52885-5

ABSTRACT

The majority of Eastern Pacific gray whales (*Eschrichtius robustus*) migrate from southern breeding grounds to the Bering and Chukchi seas where they feed principally on benthic amphipods throughout the summer. However, increasing numbers are now summering in locales along the coast of Oregon, Washington and British Columbia. These secondary feeding grounds do not support high densities and extensive mats of benthic amphipods. The whales using these waters tend to be more opportunistic feeders and feed upon a combination of epibenthic, pelagic and infaunal prey.

Clayoquot Sound on the west coast of Vancouver Island is one area where gray whales are known to summer in relatively large numbers. Here, prey abundance, distribution and population structure are likely important drivers of gray whale foraging patterns. However, the details of prey numbers, distributions and nutritional value remain a hiatus to a better understanding of the feeding ecology of gray whales in the Sound and other mid-coastal regions. The overall objective of this thesis is to contribute to a better understanding of changing geographic patterning of gray whale populations through a detailed examination of amphipod abundance, population structure, and energy value in Clayoquot Sound. My approach is to examine the relationship between sedimentary environments (i.e., habitat) and amphipod population structures, and to construct a simple energy budget for gray whales in relation to available amphipod distribution, abundance, and caloric food value.

Ampelisca agassizi was the dominant benthic amphipod in Clayoquot Sound followed by *Ampelisca careyi*. Relative proportions of the two amphipod species shifted over the two-year sampling period and between two sampling bays. Both ampeliscids were found throughout the predominantly fine sand substrate of the feeding area. Thus, it would appear that habitat is not limiting amphipod numbers. Energy value of amphipods at the densities I documented is sufficiently low such that gray whales cannot meet their daily energy requirements by foraging exclusively on benthic amphipods in this region. I conclude that gray whales in Clayoquot Sound must forage on a variety of prey types rather than focussing on amphipods as this benthic-adapted predator typically does in arctic waters.

ACKNOWLEDGEMENTS

First, and most importantly, I thank my supervisor, Dennis Jelinski, for his patience, support and confidence.

This work would not have been possible without access to other labs for which I am very grateful. I thank Dr. Robert Gilbert and Dr. Scott Lamoureux for use of their labs for sediment analysis. I thank Dr. Brian Cumming for access to digital cameras used in morphometric analysis. I thank David Ball from the Queen's GIS Lab for compiling (and re-compiling) the FORTRAN program used for sediment analysis. Calorie determinations were carried out in Dr. Dave Lasenby's lab at Trent University. I appreciate all the help and enthusiasm I found at Trent. I thank Ed Hendrycks at the Canadian Museum of Nature for a crash course in amphipod physiology and access to collections.

I thank my examining committee - Dr. Brian Cumming, Dr. Robert Gilbert, Dr. Willem Vreeken, and Dr. Dennis Jelinski, whose questions and comments improved this thesis. I also thank Dr. Steve Lougheed, Dr. Gerry Barber and Jim Karagatzides for statistical help.

Fieldwork was carried out with the able assistance of Amanda Carr, Jim Karagatzides, Lindsey Mulkins and Andrea Smith. The UVic whale crew: JoAnna Bass, Christina Tombach, Sonya Meier, Chris Malcolm and Jason Dunham, all contributed to this thesis through either field support or discussions of gray whale ecology. I especially thank Jason Dunham and JoAnna Bass. I thank my undergraduate supervisors Drs. Dave Duffus and Phil Dearden for their support and frank discussions about research methodologies.

I thank my diving buddies: Dr. Bruce Cameron, Doug Biffard and Cam Wilson. I would not have been able to explore my study area without their capable assistance.

Heartfelt thanks go to Jim Karagatzides, Sonya Billiard, Janine Wiles, Clare Robinson, Åsa Chong, and Jennie Carruthers for their support and levity, especially in the final stages of this project. Thanks to Scott Barnes and David Mazzucchi for the best home cookin' a girl could ask for. And, finally, thank you to my family for their unconditional support and humour.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Approximately 70% of the Eastern Pacific gray whale (*Eschrichtius robustus*) population migrates from their winter breeding grounds in Mexican waters to the Bering and Chukchi seas to feed throughout the boreal summer (Highsmith and Coyle 1992). Gray whales accumulate energy stores during the summer months for use in prey-poor southern waters that support little or no foraging activity (Kvitek and Oliver 1986). Following the feeding season, southbound migrants typically weigh 16-30% more than when migrating northwards (Nerini 1984).

Gray whales are members of the order Cetacea and suborder Mysticeti (baleen whales). Gray whales are the only mysticeti that regularly consume benthic prey (Wursig 1989). Their baleen plates are thicker with coarser and less numerous bristles than other baleen whales, presumably to withstand contact with sediments (Nemoto 1970). Gray whales remove sediment and infauna by suction. Sediment and small particles, including small prey species are then expelled, and large particles are retained behind the baleen, which acts as a sieve. This feeding method leaves defaunated excavations in the seafloor averaging 2 m^2 (Kvitek and Oliver 1986). The highly specialised set of baleen permits extensive foraging on infaunal prey such that in the Bering and Chukchi seas benthic amphipods account for 90% of gray whale stomach contents (Rice and Wolman 1971). This is substantial as the daily energy requirements for a foraging gray whale average 3.8×10^5 kcal (Highsmith and Coyle 1992). Despite the seemingly specialised diet that is common to these arctic-feeding whales, it is also well known that gray whales are opportunistic feeders and have been reported feeding on epibenthic (Kim and Oliver 1989) and pelagic prey (Duffus 1996), as well as infauna.

As the eastern Pacific gray whale population has recovered from intense hunting in the 19th century, increasing numbers of whales remain throughout the summer in locales along the North American coast of Oregon, Washington and British Columbia, and forgo the journey to northern waters (Guerrero 1989, Avery and Hawkinson 1992, Weitkamp *et al.* 1993). It is well known that these regions do not typically support the same biomass of infaunal prey, especially amphipods (Oliver *et al.* 1984). Clayoquot Sound, on the west coast of Vancouver Island (Figure 1.1), is one region where a summering population of gray whales has existed over the last 25 years (e.g., Hatler and Darling 1974, Kvitek and Oliver 1986, Duffus 1996). Here gray whales feed on benthic amphipods (*Ampelisca* spp.), mysids (*Holmesimysis sculpta, Neomysis rayii, Acanthomysis* spp.), crab larvae (*Pachycheles* spp., *Petrolisthes* spp.), ghost shrimp (*Callianassa califoriensis)* and herring eggs (*Clupea harengus pallasi*) (Duffus 1996, Darling *et al.* 1998, Dunham 1999). Researchers, working in this area conjectured that gray whale feeding on benthic amphipods occurs when mysids are less abundant (Guerrero 1989, Kvitek and Oliver 1986, Dunham 1999).

It is clear that the foraging behaviour of whales, and hence, their local-scale geographic distribution in the Sound is markedly different from that which is observed in more northern waters. What might account for the differences in foraging strategy and behaviour of gray whales when one compares activities in their northern feeding grounds and secondary feeding areas such as Clayoquot Sound? MacArthur and Pianka (1966) argue that predators should have specialised diets when they are foraging in large prey

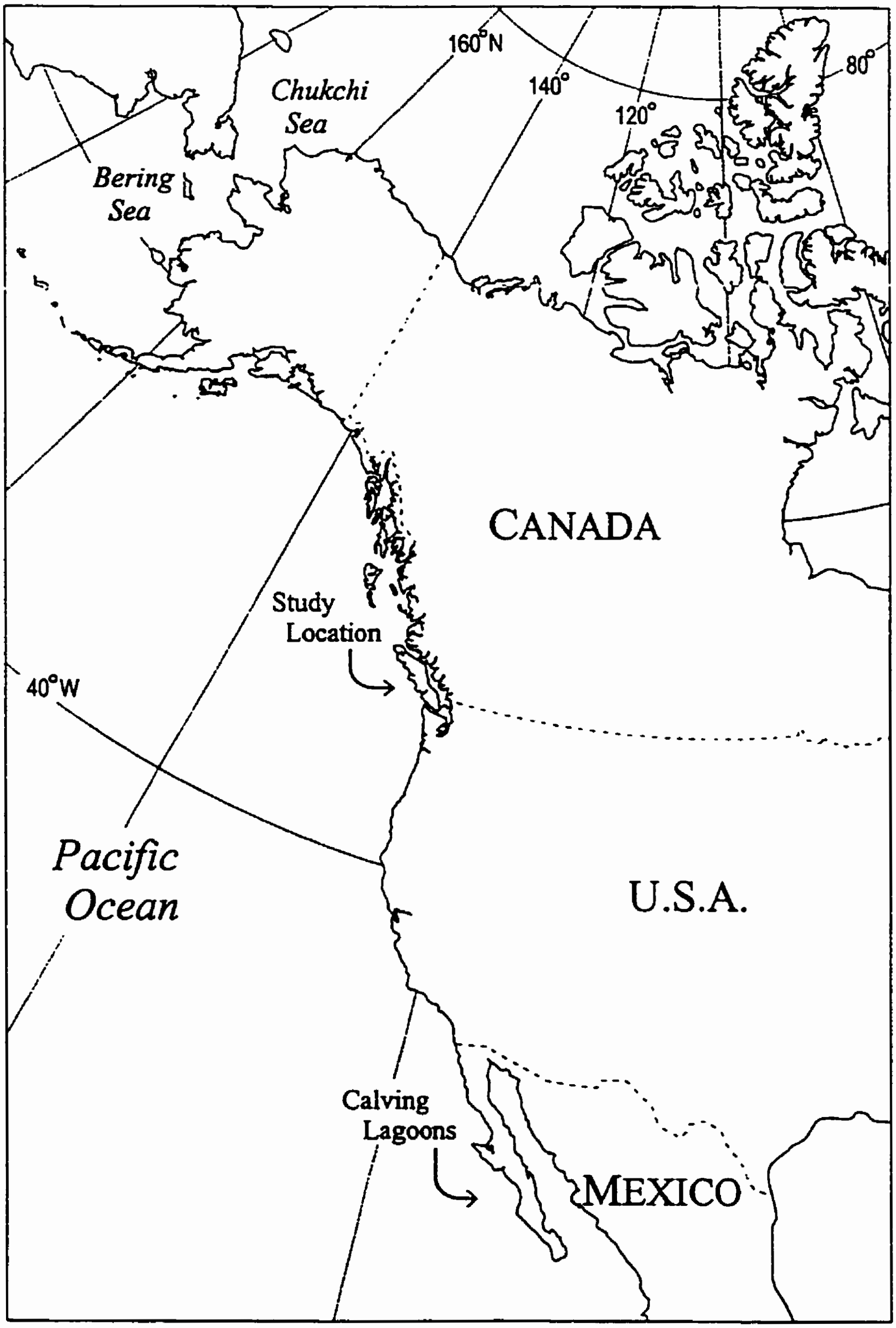

Figure 1.1 Location of study area relative to gray whale calving lagoons in Mexican waters and the primary feeding grounds in the Bering and Chukchi seas.

patches, and more generalised diets when faced with smaller patches of prey. It is well documented that the marine environment is characterised by a mosaic of patches created by biological and physical processes (Steele 1989, Thrush 1991). Moreover, it is known that the extent of benthic amphipod tube mats along the B.C. coast is typically an order of magnitude smaller than those found in the northern feeding grounds (Kim and Oliver 1989).

However, the distribution of foraging whales is often not a simple reflection of prey abundance or biomass. Whitehead and Carscadden (1985) found that whale foraging was correlated with the abundance of different capelin year-classes. Similarly, Wishner *et al.* (1995) showed that right whale foraging was associated with life stages, not abundance, of their copepod prey. Within Clayoquot Sound, Dunham (1999) found that there were significantly more benthic amphipods in the large cohort (i.e., of a size large enough to be retained by the baleen) taken from where gray whales were bottom feeding than from areas where whales were not feeding on benthic amphipods. Thus, it is clear that prey food value may also account for differences in foraging strategies.

Food value is determined by prey abundance but also by energy content, nutrient status and, capture and assimilation efficiency on the part of the predator (McClintock 1986, Hobbs 1989). Benthic amphipods found in northern waters are larger than those found in coastal British Columbia. Furthermore, polar invertebrates generally have higher energy content than temperate species (Norrbin and Båmstedt 1984). Conversely, planktonic crustaceans, which are common to Clayoquot Sound, generally have higher lipid content than benthic crustaceans (Griffiths 1977).

1.2 Research Objectives

It is hypothesised in this thesis that the differences in foraging strategies between the northern feeding grounds and Clayoquot Sound are a function of both prey abundance and distribution, and energy content of available prey. The overall objective of this thesis is to contribute to a better understanding of changing geographic patterns of foraging gray whales through a detailed examination of amphipod distribution, abundance, population structure, and caloric food value in the Clayoquot Sound region of coastal British Columbia. My approach is to examine the relationship between sedimentary environments (i.e., habitat) and amphipod population structures, and to construct a simple energy budget for gray whales in relation to available amphipod distribution and abundance. I posit that such a study will also contribute to a much-needed better understanding of the prey-switching ability shown by gray whales, which should in turn permit a greater understanding of how gray whales are able to expand their geographic distribution during the critical summer foraging season.

My specific goals are to: 1) characterise habitat (sediment) structure and identify correlations between sediment characteristics and amphipod distributions in two major bays of the Sound that, historically, were important bottom-feeding grounds for gray whales; 2) determine population structure of benthic amphipods in these bays; and 3) determine the caloric content of amphipods to provide a basis for comparison between prey types in this feeding area and those found in other areas, principally the gray whale's northern feeding grounds.

1.3 Thesis Outline

The remainder of the thesis is divided into four chapters. Chapter Two contains a description of the study area, the basic biology of amphipods, and field and laboratory methods. In Chapter Three, I present results of analysis of the sediment structure and report on the relationship between sediment characteristics and amphipod distributions. Following this, characteristics of amphipod population structure, caloric content and implications for gray whale feeding are presented in Chapter Four. In the final chapter, I summarise knowledge gained by this investigation and link it to previous, ongoing and prospective research.

CHAPTER 2: METHODS

2.1 Study Location

Clayoquot Sound is a biologically rich inshore region on the west coast of Vancouver Island, B.C. (Figure 2.1). Processes in upland and offshore regions influence water salinity and nutrient levels. Clayoquot Sound receives freshwater from the Kennedy Lake watershed and is influenced by the lower-salinity Juan de Fuca plume that contains Fraser River runoff (Mackas and Galbraith 1992). A north flowing coastal current dominates the west coast of Vancouver Island during summer (Pal and Halloway 1996). Winds from the northwest dominate in the summer, whereas during the winter southeast winds are more prevalent (Thomson *et al.* 1989). The mean depth within the Sound is 22 m and mean tidal range is 2.8 m (Fisheries and Oceans Canada 1998).

Cow and Ahous bays are two shallow bays in Clayoquot Sound where gray whales are known to feed on benthic amphipods (Kvitek and Oliver 1986, Duffus 1996). The physical structure and forces acting on benthic environments differ between the bays. Cow Bay has southern exposure to oceanic swell, whereas Ahous Bay faces west and is more sheltered from oceanic swell by reefs to the south and Blunden Island to the west. In both bays the substrate is predominantly sand. However, the bottom topography is more complex in Cow Bay and includes reefs and rock shelves in the bay and on the adjoining shelf (Figure 2.2). Both bays are gently sloping, approximately 0.5° to seaward.

My study region encompassed locations where gray whales were reported bottom foraging in previous years (e.g., Duffus 1996). The study area in Cow Bay is larger than

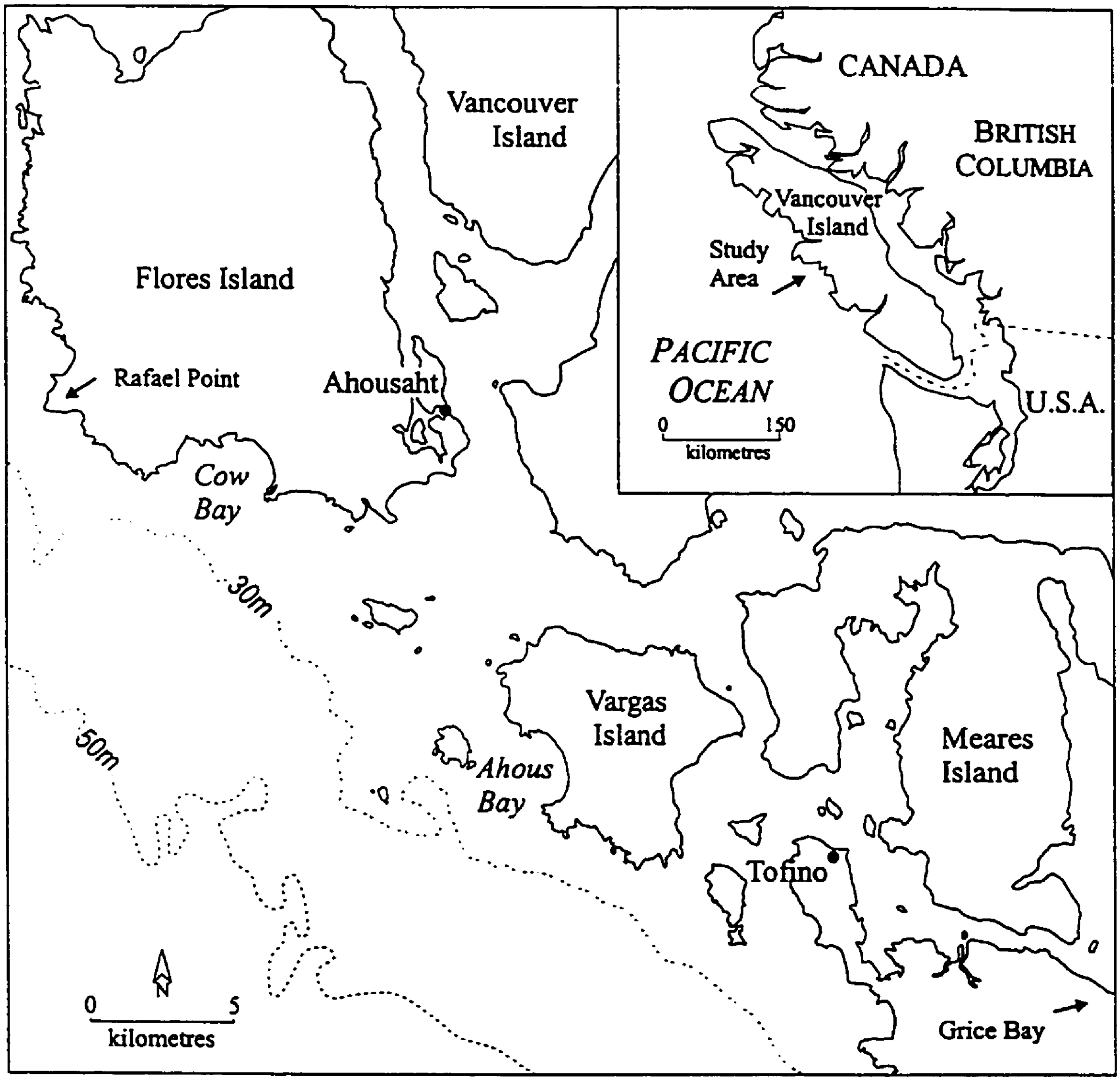

Figure 2.1 Regional map of Clayoquot Sound.

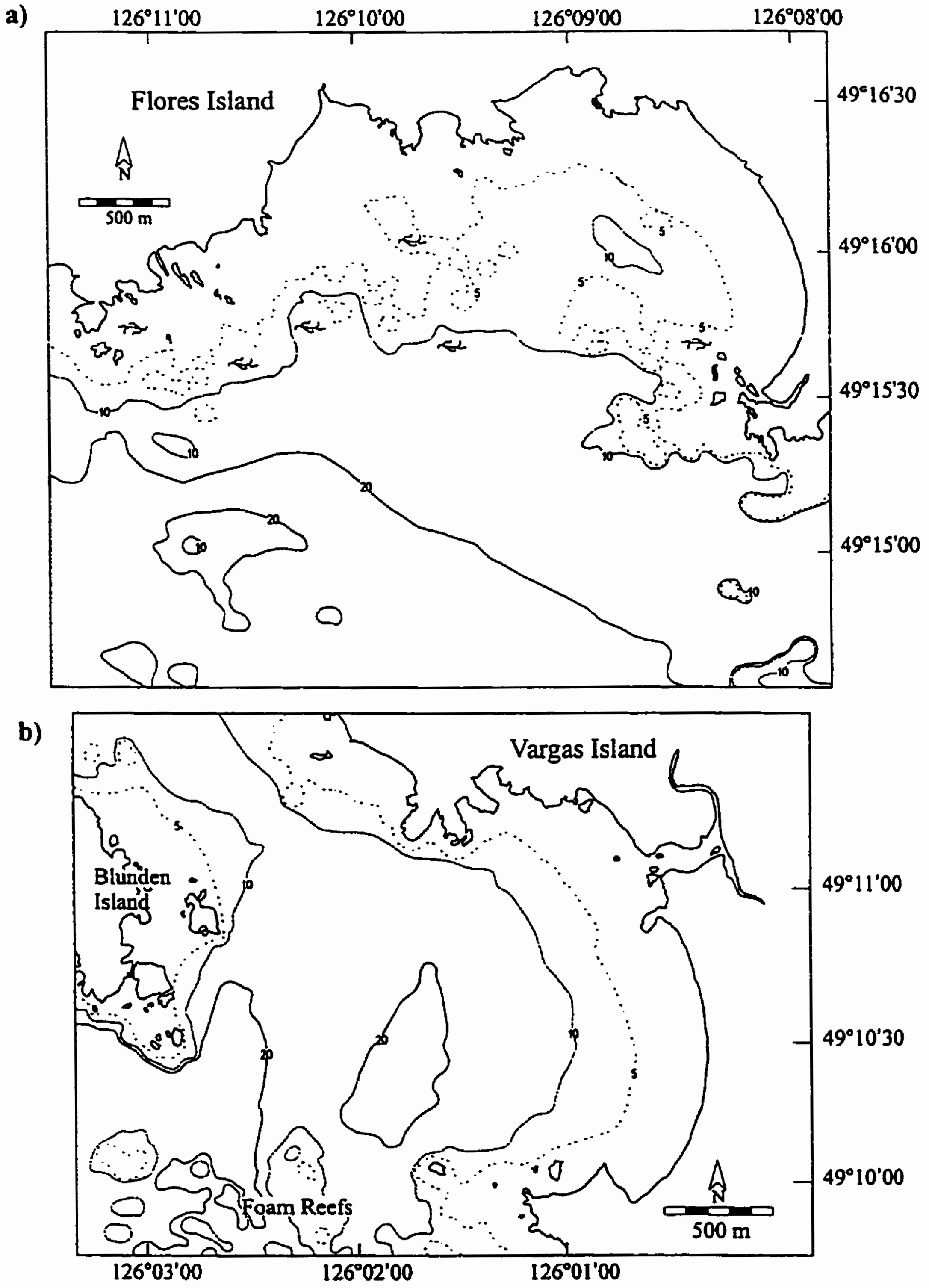

Figure 2.2 Bathymetry and physical features of Cow Bay (a) and Ahous Bay (b). Depth contours are in metres. Kelp beds (⇝) are present in Cow Bay and not in Ahous Bay.

in Ahous Bay, reflecting the former bay's size (4.5 km^2). In contrast, the smaller Ahous Bay sampling area reflects bay size (2 km^2) and generally shallower depths. The study sites are referred to as Cow and Ahous bays throughout the remainder of this thesis even though sediments and infauna were sampled somewhat beyond bay mouths and onto the adjoining shelf. This terminology is consistent with the literature (e.g., Hatler and Darling 1974, Guerrero 1989, Dunham 1999).

2.2 Study Species

Amphipods account for approximately 75% of the benthic biomass in Cow and Ahous bays (Dunham 1999). *Ampelisca agassizi* is the most abundant benthic amphipod in the bays followed by *Ampelisca careyi*. On a large geographic scale *A. agassizi* is much more widespread, as it is found in sublittoral sand habitats from equatorial waters as far north as Nova Scotia in the Atlantic and the Queen Charlotte Islands in the Pacific (Dickenson 1982). *A. agassizi* inhabits a wide range of depths, from shallow waters to those as deep as 266 m (Dickenson 1982). *A. careyi* has only been collected in the Pacific Ocean. Its range overlaps that of *A. agassizi* but it is also more northerly; *A. careyi* has been found from Baja California to southeastern Alaska, primarily at depths shallower than 100 m (Dickenson 1982).

Both *A. agassizi* and *A. careyi* are primarily sedentary animals and have limited dispersal ability. Unlike many benthic invertebrates, they do not have a pelagic dispersal stage. Instead, ampeliscids have direct development and are crawl-away brooders; juveniles emerge from the brood pouch looking much like adults and crawl away from the mother's tube. Ampeliscids build tubes from sediment and secreted mucous and remain in these tubes for much of their lives. They remain in their tubes while feeding on organic matter in suspension or from sediments surrounding the tube. Feeding behaviour and the type and quantity of food appear to be related to water flows (Wildish and Kristmanson 1997). Ampeliscids may disperse following mating but details and timing of mating and dispersal are not known for these species. In summary, ampeliscids are primarily sedentary benthic animals, dependent on sedimentation of organic material from overlying water for their energy supplies.

2.3 Field Sampling

In 1998, sediment and amphipod samples were obtained using an Ogeechee sand-pounder coring system (Gillespie *et al.* 1985) and SCUBA divers. Core samples were used to determine amphipod densities and size classes and sediment characteristics and to identify distribution patterns. SCUBA samples were used to assess small-scale variability (<10 m^2) in these feaures. In the 1999 field season amphipods were collected only using the coring system. These samples were primarily used for biomass and calorie determination but also to identify changes in species abundance, cohort structure, and distribution patterns between seasons.

2.3.1 1998 Field season

Cow and Ahous bays were systematically cored using sampling grids. A coarse-scale grid pattern was initially used to ensure complete coverage of the bays with sampling locations approximately 720 m apart. Following the initial sampling period, the sampling grid was made finer with the average distance between sample locations reduced to 360 m. The order of sampling was random within each sampling period. This sampling design minimised confounding questions of spatial distribution by sampling nearby stations sequentially. Twenty-seven locations were sampled in Cow Bay (Figure 2.3) and nineteen in Ahous Bay (Figure 2.4). Two short transects were included in the Cow Bay sampling scheme. The difference in the number of sampling locations reflects sampling area size. Sampling intensity was the same in both bays.

We navigated to each sampling location using an onboard differential global positioning system (DGPS: Trimble Pro XL Receiver). Sampling accuracy was more affected by boat drift and anchoring than by the DGPS. Accuracy of the DGPS is 1 m plus 2 mm for every kilometre from the nearest base station (Trimble Navigation Ltd. 1995). The nearest DGPS base station is Amphitrite Point, which is approximately 50 km south of the study area (Fisheries and Oceans Canada 1999); therefore, accuracy of the DGPS was approximately 1.1 m. In contrast, the anchor was set when the boat was within 20 m of the sampling location and sampling began after the boat settled at anchor. The position was recorded for each sample using the DGPS.

Three cores were obtained at each sample location using the sand-pounder (core diameter 0.05 m). A core was considered successful when at least the upper 0.10 m of core was retained. This is in accord with Guerrero's (1989) finding that amphipods tubes extend 0.05-10 m into the sand in Ahous Bay. Samples were discarded if they contained less than 0.10 m of core unless we were unable to collect three cores of sufficient depth in six attempts. In this case, the largest samples were retained. Sample location was recorded for each core to calculate boat drift distance between replicate cores. Cores

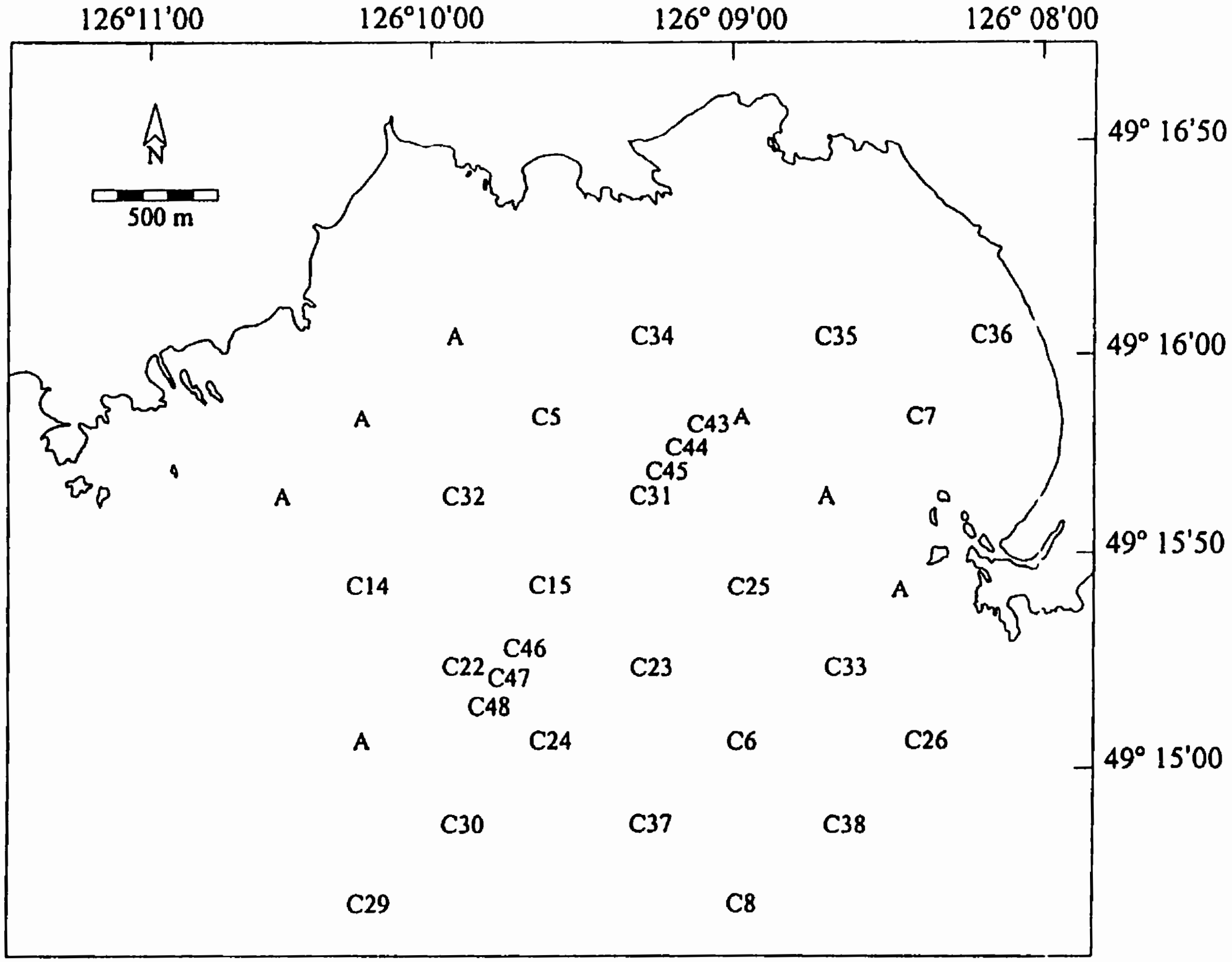

Figure 2.3 Sampling locations in Cow Bay visited in the 1998 field season. Cores are numbered sequentially and sites where sampling was attempted but not successful are identified by the letter A.

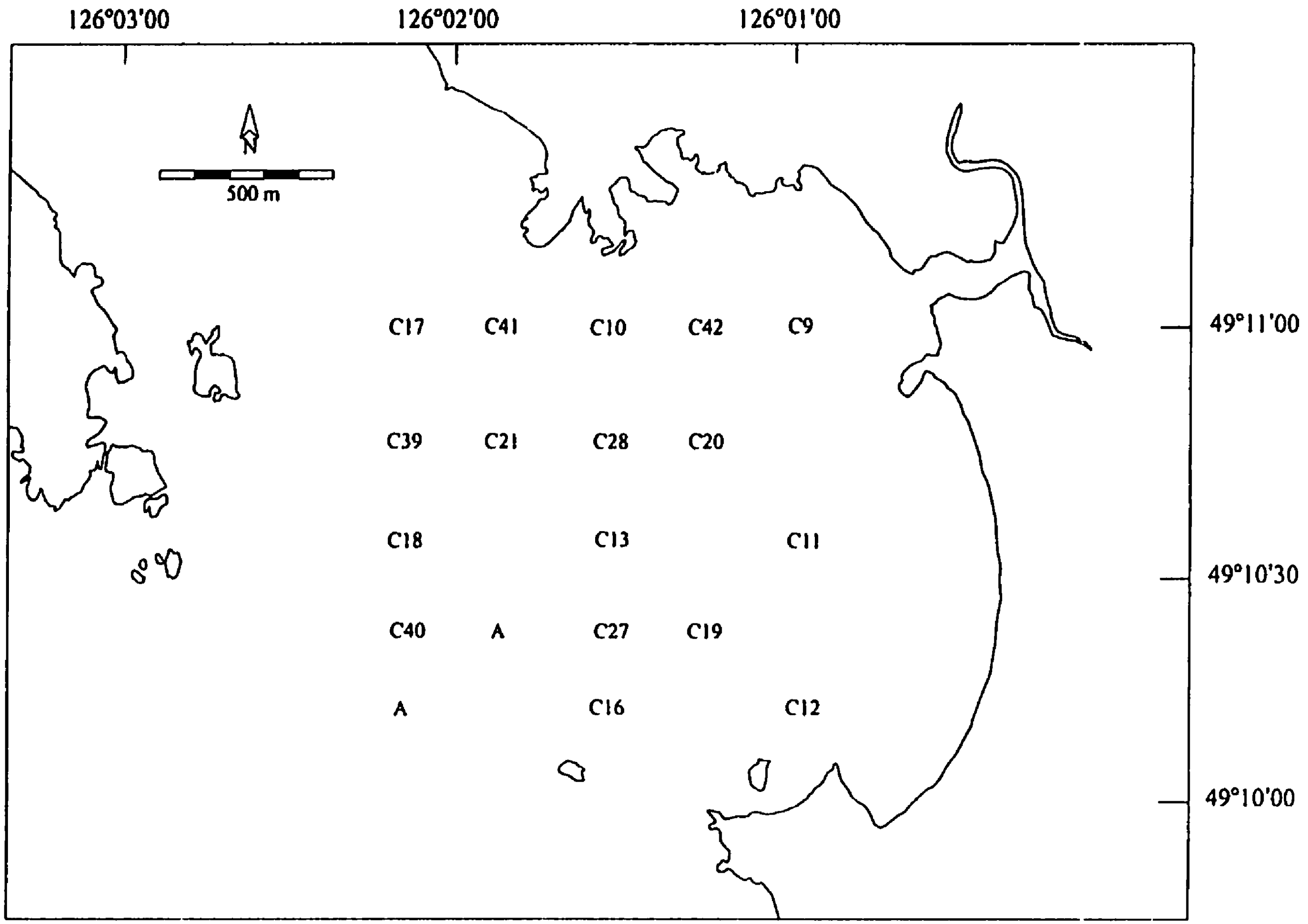

Figure 2.4 Sampling locations in Ahous Bay visited in the 1998 field season. Cores are numbered sequentially and sites where sampling was attempted but not successful are identified by the letter A.

were extruded into "ziplock" storage bags and placed in coolers for later processing. I was unable to obtain cores at 7 out of 28 sampling locations in Cow Bay (Figure 2.3) and 2 out of 19 locations in Ahous Bays (Figure 2.4) owing to rocky substrate. Samples were washed through a 0.5 mm mesh screen using seawater from the core. All amphipods were removed from the screen and fixed in a 4% buffered formalin and freshwater solution. Amphipods were transferred to vials containing 70% ethanol for storage. The presence of other animals in cores was noted, and these individuals were returned to the ocean.

All sediment and water from cores was retained. Water was retained because it contained fine sediment in suspension. Sediment and water were washed into bags and allowed to settle for 2-4 days. Supernatant water was decanted and samples were air-dried. Ethanol was added to damp sediments (approximately 20 ml of 95% ethanol per litre damp sediment) to facilitate drying and discourage mould growth.

SCUBA was used to take bottom samples to investigate small-scale spatial variability and to describe the bottom environment, e.g., presence and characteristics of benthic animals or sand ripples. Diving effort was concentrated in one bay due to the limited ability to cover large areas and dive samples were taken from Cow Bay in the past (D. Duffus pers. comm. 1998). Sixty-five samples were taken during eleven sampling dives in Cow Bay (Figure 2.5). No SCUBA sampling was done in Ahous Bay.

A transect was used to take samples at known distances from each other. Divers collected bottom samples using PVC pipe (diameter = 0 10 m, length = 0.15 m). The transect line was attached to the anchor and divers positioned the line by swimming perpendicular to any sand ripples or into the current. Sampling locations were marked

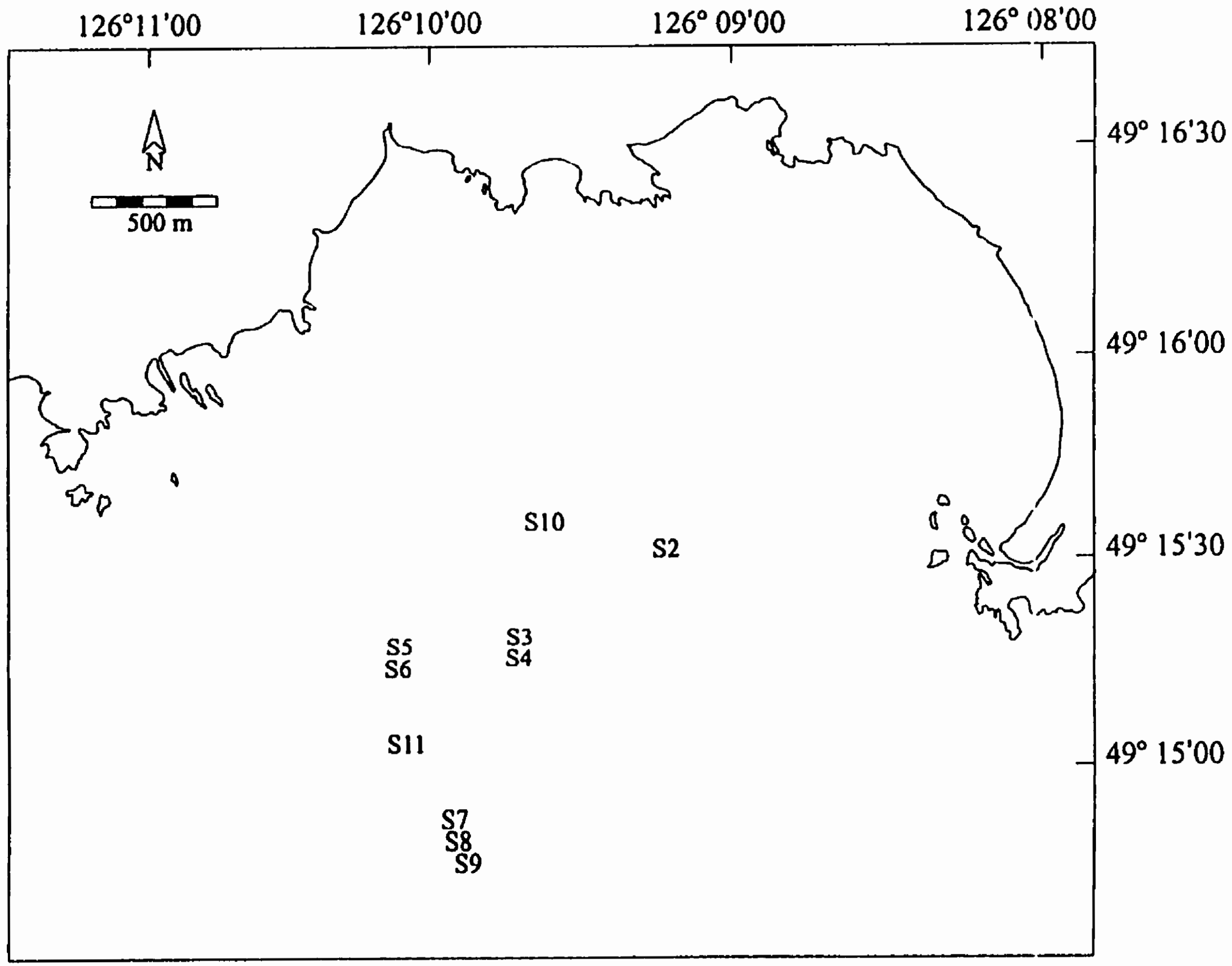

Figure 2.5 SCUBA sampling locations in Cow Bay. Sampling effort was concentrated within the area presumed to include the amphipod tube mat. SCUBA locations are numbered sequentially and were sampled between June 10 and August 24, 1998.

at 0.0, 0.5, 1 and 2 m intervals along the transect line. Sampling began at the end of the transect line furthest from the anchor. The sampling method minimised disturbance associated with the anchor. One transect was completed on nine dives and two transects were completed on two dives. When two transects were swum, the line was laid out opposite the anchor from the first sampling line. Ten samples were taken on each of these two dives. Samples were taken by pushing PVC pipes into the sediment until the tops were level with the sediment. Pipes were capped to create suction and samples were pulled from the sand and the bottoms were quickly capped. Amphipods from dive samples were preserved as described previously.

2.3.2 1999 Field season

The primary goal of the second field season was to collect amphipod samples for biomass and energy conversions. Sampling effort was directed at collecting a large number of amphipods instead of covering a wide area. Seven sites in Cow Bay and six sites in Ahous Bay were revisited in the 1999 field season to address the secondary goal: to assess changes in amphipod population structure and distribution between years. Although the stated accuracy of the DGPS used to navigate to these sampling locations is <1.5 m, resampling was not achieved to such precision due to the errors inherent in anchoring, and boat drift.

Thirty-five cores were taken from Cow and Ahous bays during two sampling periods in 1999: July 28-29 and September 1-3. Sampling order was designed to sample both bays but was restricted by weather conditions. The second sampling season was delayed in the hope that gray whales would bottom feed and permitting prey sampling from alongside feeding gray whales. Gray whales did not bottom feed on benthic amphipods during the 1999 field season.

All *A. agassizi* and *A. careyi* retained on a 0.5 mm screen were placed in vials containing seawater, which were then placed in an ice and rock salt slurry, and frozen (-10°C). Other organisms and sediments were returned to the ocean. Size and sexual maturity of amphipods were largely determined following procedures described in Section 2.4.2, and only protocol differences are described here. Fresh frozen amphipods were placed in 1 mm size classes based on straight-line measures of head and body lengths using a dissecting scope (10X) and a ruler mounted on the stage. All amphipods were manipulated to have the same curvature in body form. Field measurement protocol was repeated in the lab to enable a correction between the two methods.

Thirty-four out of 119 amphipods larger than 6 mm in length were examined for the presence and developmental stage of secondary sexual characteristics. Specimens were placed on individual pieces of aluminium foil and dried overnight in a conventional oven at 60 °C. Dried specimens were wrapped in aluminium foil, placed in whirl bags and frozen for transport back to Queen's University for analysis.

2.4 Lab Methods

2.4.1 Sediment analysis

Sediment samples were dried, homogenised and subsampled for different types of analyses (Figure 2.6). Samples were dried overnight at 80 °C in a convection oven and volume was measured using a graduated cylinder (±10 ml). Each sample was

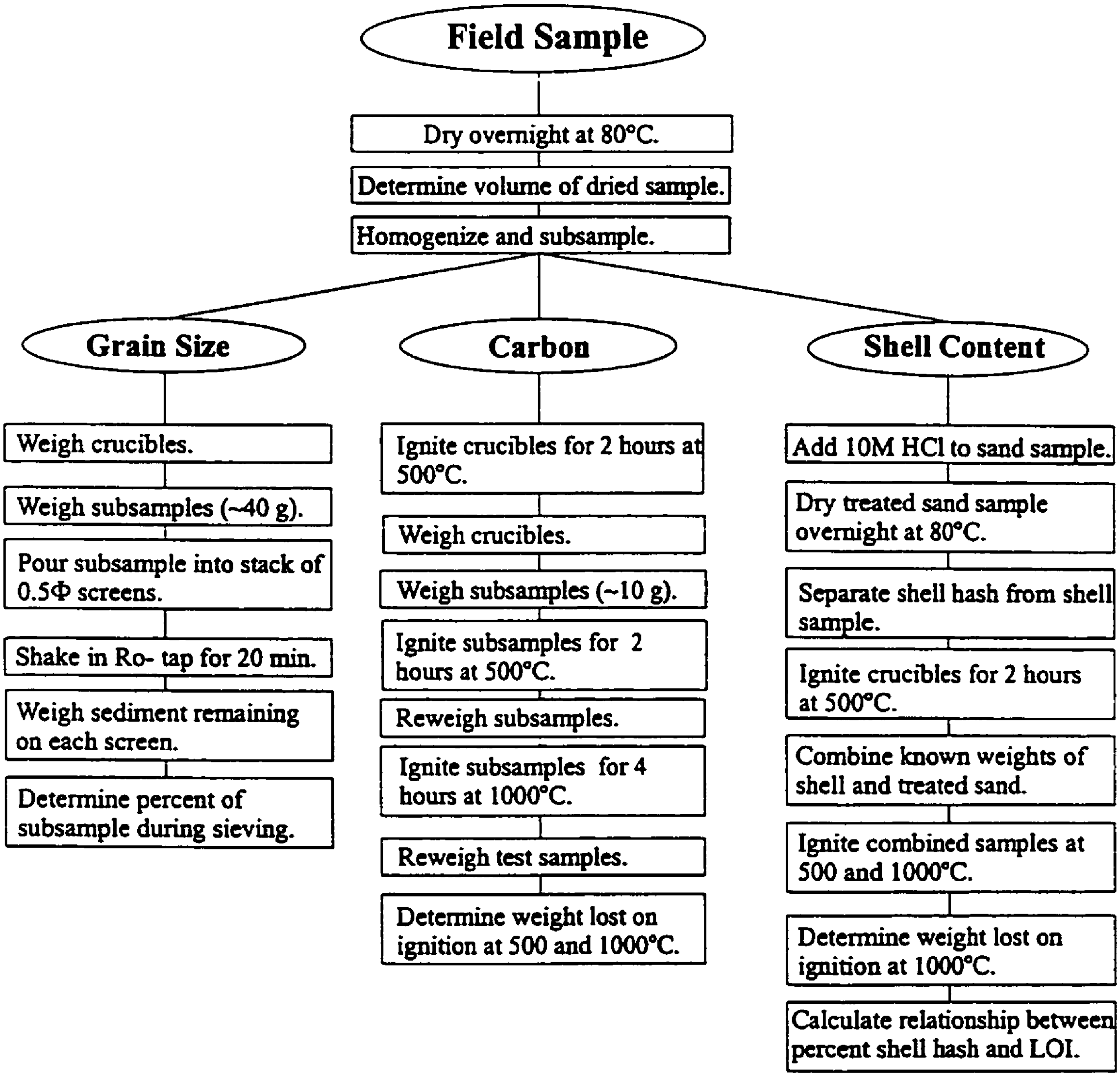

Figure 2.6 Flow diagram of methods used in sediment analysis.

homogenised by passing it through a Jones sample splitter (Krumbein and Pettijohn 1938) three times. The splitter was then used to make subsamples for grain size determination (~40 g), and organic and inorganic carbon determination (5-20 g).

Grain size was determined by dry sieving. Subsamples were weighed and then placed in the top pan of a series on Tyler sieves in a Ro-Tap for 20 minutes (Irani and Callis 1963). Sediment grain size composition was determined using one half phi intervals (Table 2.1). The sediment fraction retained on each sieve was weighed cumulatively; the 1.0 phi fraction was weighed, tared and then the 1.5 phi fraction was added to the same pan and weighed (etc.). Sieving error was the difference between the initial weight and the cumulative weight of each sieve fraction. If sieving error was larger than 2% of the initial weight, then that subsample was discarded and a second subsample was split and analysed.

Table 2.1 Sediment classes used in determination of grain size composition.

Sediment grade Particle diameter (mm)	Phi	Grade limits Sieve openings (mm)
	-0.5	>1.41
Very coarse sand (1 - 2)	0	1-1.41
	0.5	0.71-1
Coarse sand (0.5 - 1)	1	0.5-0.71
	1.5	0.35-0.5
Medium sand(0.25 – 0.5)	2	0.25-0.35
	2.5	0.177-0.25
Fine (0.125 – 0.25)	3	0.125-0.177
	3.5	0.88-0.125
Very fine (0.062-0.125)	4	0.062-0.88
Silt and clay (< 0.062)	>4	<0.062

Organic and inorganic carbon in each sample was determined using loss on ignition techniques (LOI). LOI techniques are based on Dean (1974) with the conservative assumption that it took one hour for the muffle furnace to heat to 500°C and two hours to heat to 1000°C. Empty crucibles were ignited at 500°C for 2 h in a muffle furnace to remove organic carbon. Empty crucibles were then weighed, subsamples added and crucibles were reweighed to determine initial subsample weight. Subsamples were ignited in a muffle furnace at 500°C for 2 h to remove organic carbon. Subsamples were cooled to room temperature in a desiccator, reweighed and the difference between initial and new weights assumed to represent organic carbon lost on ignition. After reweighing, subsamples were again placed in the muffle furnace, and ignited to 1000°C for 4 h. Subsamples were placed in a desiccator to cool to room temperature, were reweighed and LOI at 1000°C was measured as an indicator of inorganic carbon content. Organic and inorganic carbon content was compared for fifteen paired subsamples to permit investigation of variance due to subsampling and measurement error (Model II ANOVA) (Yezerinac *et al.* 1992).

The relationship between inorganic carbon lost on ignition and percent shell fragments was investigated by measuring LOI after ignition at 1000°C of samples containing known weights of sand and shell fragments. Inorganic carbon was removed from a sediment sample by adding 3N HCl until there was no visible reaction (Bühl-Mortensen and Høisieter 1993). Sediment was then dried in a convection oven at 80°C overnight. Shell fragments were separated from a sample containing large amounts of shell. Shell fragments retained on coarse sand mesh screens were removed from the screen and approximately on half was pulverised using a mortar and pestle to approximate smaller shell fragments. Known weights of intact and pulverised shell fragments were then mixed with sediment that had been treated with HCl and placed in ignited (500°C) and pre-weighed crucibles. Mixed samples were combusted at 500 and 1000°C. LOI was weighed and the relationship between percent shell fragments and weight lost on combustion at 1000°C was regressed.

2.4.2 Amphipod population structure and distribution

To investigate population structure and distribution patterns, amphipods sampled in the 1998 field season were counted, body size was estimated, and sexual characteristics identified. Amphipods were removed from storage vials and counted under a dissecting microscope. If broken specimens were encountered, only heads were counted. Head capsule length was measured on all *A. agassizi* (Figure 2.7) and *A. careyi* (Figure 2.8). Also, the presence and developmental stage of secondary sexual characteristics were noted for a subsample of large ampeliscids (>6 mm).

Head capsule length was used as the primary measure of amphipod size. Head capsule length is not subject to the measurement difficulties associated with other measures of body size. It is chitinous and therefore, does not change in preservatives and can be used to estimate weight of preserved samples (Edwards and Cowell 1992). Body length is much more variable as amphipods are preserved in varying degrees of contraction, thereby eliminating the ability to make accurate straight-line measures of body size. Head capsule length was used to predict body length (Delong *et al.* 1993, Wilhelm and Lasenby 1994) and dry weight (Highsmith and Coyle 1991, Edwards and Cowell 1992). Methods of dry weight determination are detailed in Section 2.4.3.

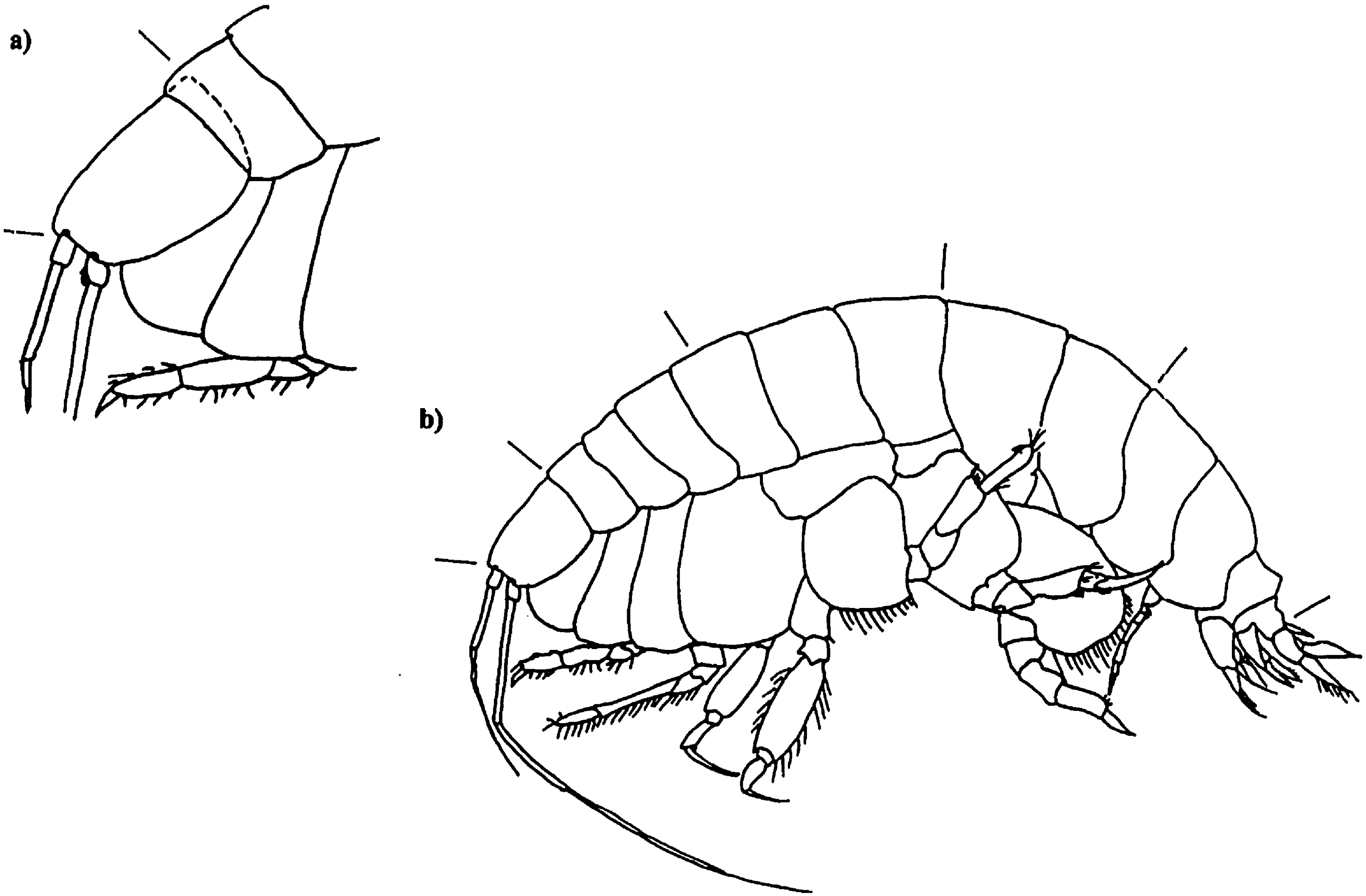

Figure 2.7 Head (a) and body (b) length measures on *Ampelisca agassizi*. The presence of brush setae on the second antennae indicate that the head drawing is of a mature male amphipod.

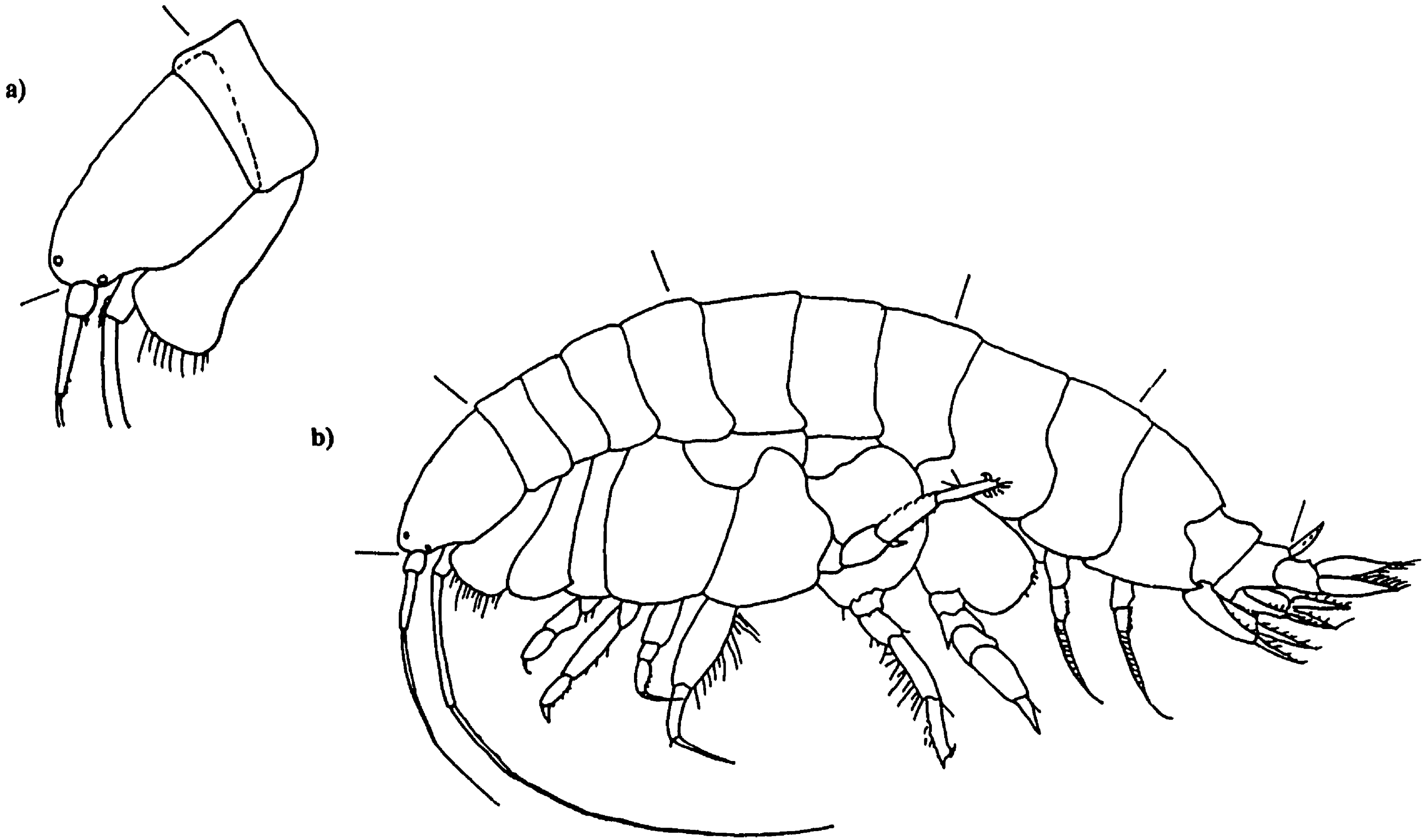

Figure 2.8 Head (a) and body (b) length measures on *Ampelisca careyi*. The presence of brush setae on the second antennae indicate that the head drawing is of a mature male amphipod.

Digital images of 30 *A. agassizi* and 18 *A. careyi* were used to confirm the relationship between head and body length in these species (e.g., Dauvin 1988, Chappelle 1995). A digital camera mounted on a dissecting microscope was used to take photographs of amphipods and of a micrometer on the microscope stage. Images were imported into AutoCAD Map 3. Body length was measured as the dorsal body length from rostrum to telson. A series of 5 arcs was used to incorporate amphipod curvature in the measures (Figures 2.7 and 2.8). Head capsule length was measured between defined "landmarks" on digital images and preserved specimens using an ocular micrometer and dissecting scope with transmitted light (Figures 2.7 and 2.8). Body and head capsules lengths of digital images were converted into millimetres using imported images of the micrometer.

Body length was regressed against head capsule length for both digital and ocular micrometer measures. A regression model with dummy variables was used to determine if the relationship between head and body length was different for the two species. Once the relationship between head length and body length was confirmed, head capsule length was measured on remaining amphipods using the ocular micrometer.

A subset (n = 225) of ampeliscids with body lengths over 6 mm was examined for the presence and developmental stage of sexual characteristics. Females were identified by the presence of oostegites (brood plates). The developmental stage of oostegites ranged from oostegite buds (short, hairless protrusions) to fully developed brood plates where the oostegites are long (overlapping over the midline of the animal) and setous (Skadsheim 1984). Embryos were only found in females with long setous oostegites. The number of females with setous oostegites and minimum length at maturity was recorded for both species (Highsmith and Coyle 1991). Males were identified by the presence of brush setae on the peduncle of the second antennae (Dickenson 1982).

No biomass measures were made on amphipods collected in the 1998 field season because weight and lipid stores decrease in formalin and ethanol causing inaccurate measurements (Mills *et al.* 1982, Frithsen *et al.* 1986, Ellis 1987). Further, these changes are not constant and vary with the type of preservative, the organism preserved, and storage time (Mills *et al.* 1982). For these reasons, dried and frozen amphipods collected in the 1999 field season were used to calibrate the relationship between length and dry weight. This relationship was then used to back calibrate dry weights of preserved amphipods from the 1998 field season (*sensu* Lehtonen and Andersin 1998). Details on sampling, preservation methods and weight determination are included in Section 2.4.3.

2.4.3 Biomass and caloric content of ampeliscids

Biomass and energy content were measured on dried and frozen amphipods collected in the 1999 field season. Biomass measures used in this study are dry weight (DW) and ash free dry weight (AFDW). Dry weight measures do not have the error associated with wet weight measures (due to adherent and varying water content) (Wetzel 1983) and AFDW is recommended as a basis for comparisons of caloric content between species (Cummins and Wuycheck 1971).

Specimens were thawed and dried in a convection oven at 60°C for 2 h, placed in a desiccator to cool, and weighed (± 0.1 mg) (a container of desiccant was placed in the weighing chamber) (Cummins and Wuycheck 1971). Individual specimens were grouped by species, 1 mm size classes, sampling period and source bay to approach a minimum dry weight of 1 mg. Consequently, more DW and AFDW measures were made on larger size classes. Amphipods were placed in pre-ashed crucibles and ashed at 500°C for 2 h and weighed to determine AFDW. Mean weights (± 1sd) were used in subsequent analyses. An estimate of carbonate content was obtained by combusting ashed amphipods at 1000°C.

A Phillipson microbomb calorimeter (Phillipson 1964) was used to determine the caloric content of benthic amphipods equal to or larger than 7 mm. Bomb calorimetry is based on measuring the temperature change from energy released by combustion. Amphipod caloric content was calculated by comparing the temperature change from amphipod combustion to the temperature change from a sample of known caloric content. Benzoic acid (6.318 cal/mg) was used to calibrate the bomb and chart recorder. Standard methods were used in calorie determination and are only briefly outlined here. For a complete listing of microbomb materials and experimental protocol, the reader is directed to Fraschetti *et al.* (1994).

Five benzoic acid pellets, spanning the approximate weight range of sample pellets (average = 6.9 mg ±1.7), were combusted to calibrate the bomb and chart recorder (Fraschetti *et al.* 1994). The temperature change recorded by firing samples of known caloric content were used to calculate the number of calories liberated per line on the chart recorder. Calories/line were averaged for five runs and the coefficient of variation (CV) was calculated. The calibration was considered successful if the CV was less than 10% of average (Fraschetti *et al.* 1994). Average caloric value per line was then used to calculate caloric content of amphipod samples.

Although Cummins and Wuycheck (1971) recommend applying corrections for endothermic reaction if carbonate content is greater than 25% dry weight, Crisp (1984) did not recommend correcting for endothermic reactions because other sources of error offset any heat loss. As well, comparable studies of marine benthic amphipods did not correct for inorganic carbon (Klein *et al.* 1975, Boates and Smith 1979, Highsmith and Coyle 1992); thus, corrections were not applied in this study. A fuse wire correction was calculated; temperature change was recorded for three runs when the combustion chamber was pressurised but did not contain samples, and any temperature change attributed to the fuse wire was subtracted from subsequent calculations (Fraschetti *et al.* 1994).

Amphipods used in calorie determinations were thawed and redried at 60° for 2 h to remove any moisture accumulated while frozen. Amphipods were pressed into pellets and then redried at 60°C for 2 h. Attempts were made to have three replicate calorie determinations for each species, size class, bay and sampling period category. However, this was not always possible due to incomplete combustion, pellet loss and breakage. Sixty percent of calorie determinations were successful. Averaged calories/mg were compared between different species, sampling periods and bay using separate Student's *t*-tests.

2.5 Statistical Analyses

Sediment and amphipod distribution patterns were analysed separately before comparisons were made between the two sets of data. Entropy analysis (Johnson and Semple 1983) was used to identify sediment subenvironments within the bays. Sediment samples were grouped so that 75% of the observed variation between sediment distributions was explained (Forrest and Clarke 1989). Sediment grain size fractions that contributed most to the classification were identified by comparing averaged sediment grain size distributions for each entropy group with the average for all sediment samples (Forrest and Clarke 1989). This classification method was used on sediment grain size distributions averaged for each site using both half and full phi sediment grain size divisions. The relationship between amphipods and entropy sediment groups was then investigated using both ANOVA, with tests for interaction effects, and the non-parametric equivalent – the Kruskal-Wallis test. Amphipod abundance patterns were further investigated by testing for correlation between amphipod groups using Spearman's Rho.

CHAPTER 3: SEDIMENT CHARACTERISTICS AND AMPHIPOD DISTRIBUTIONS

3.1 Introduction

Analysis of organic distribution patterns is often used as an initial step in understanding the role of ecological processes governing biotic distributions because these patterns are the sum of a species' interactions with their abiotic and biotic environment. However, one major limitation in investigating distribution patterns is that analysis of distribution patterns cannot be used to identify causal structuring mechanisms without running risk in drawing incorrect inferences. This may occur in part because distribution patterns change through time and space, and reflect many intersecting physical and biological structuring processes. Further, these patterns may be closely tied to historical processes as well as contemporary ones.

Accordingly, distribution patterns of benthic marine animals are tied to a range of oceanographic and ecological processes on the sea floor, in the water column, and over time (Snelgrove and Butman 1994). Ecological investigations of species distributions on soft substrates often focus on identifying community composition and describing sediments and other physical variables that are subject to spatial variation (e.g., Sanders 1958, Palacin *et al.* 1991, Feder *et al.* 1994). Sediment variation in particular influences community composition and strongly covaries with other processes acting on the sea floor, such as near-bed water flows, larval supply and food supply (Snelgrove and Butman 1994).

Benthic tube-dwelling amphipods, primarily of the genus *Ampelisca*, are present in large numbers in Cow and Ahous bays. Although abundance and, to a degree, distribution, of these animals have been noted (Kvitek and Oliver 1986, Duffus 1996, Dunham 1999), amphipod distribution patterns in relation to habitat structure have not been studied in detail. Cow Bay and Ahous Bay offer tremendous opportunity to expand our understanding of amphipod/sediment relationships, particularly insofar as these relationships influence gray whale foraging activity and patterns. The bays differ in physical processes acting on sedimentary environments, and the relationship between amphipods and sediments has been key to arguments on the implications of gray whale foraging on amphipod benthic communities (Nerini and Oliver 1983, Johnson and Nelson 1984).

Historically, gray whales are known to bottom feed extensively on ampeliscids in Cow and Ahous bays (Duffus 1996, Darling *et al.* 1998, Dunham 1999). Gray whales feed on benthic amphipods by suctioning up sections of sediment and infauna. Sediment and small debris are then expelled back through the baleen and prey is retained on the baleen filter. This feeding method creates defaunated "pits" on the seafloor (Oliver and Slattery 1985). This in turn alters sediment characteristics (Oliver *et al.* 1984, Nelson *et al.* 1987) and benthic community composition (Oliver and Slattery 1985, Coyle and Highsmith 1994). Other researchers have argued that gray whale foraging structures bottom communities by altering sediment composition (Johnson and Nelson 1984). However, our understanding of the long-term impacts of gray whale foraging on prey communities is limited by our knowledge of amphipod habitats and ecology in these particular bays.

Cow Bay and Ahous Bay are also appropriate field "laboratories" for this investigation because forces acting on sedimentary environments likely differ between the two bays. Cow Bay faces south and is exposed to oceanic swell. In contrast, Ahous

Bay faces west and is sheltered by reefs to the south and Blunden Island to the west, protecting it from prevalent southeast winter winds (Thomson *et al.* 1989). Both bays have predominantly sand substrates. *Ampelisca agassizi* and *Ampelisca careyi* are the two most common amphipods in Cow and Ahous bays.

Studies elsewhere suggest that distribution patterns of these ampeliscids and other benthic amphipods may be strongly correlated to sediment characteristics. In the Atlantic, Schaffner and Boesch (1982) found that *A. agassizi*'s distribution was associated with fine sand grain sizes and negatively associated with the presence of congeners. As well, Oliver *et al.* (1984) noted spatial segregation between these ampeliscids in Pachena Bay, which is approximately 50 km south of Clayoquot Sound (where gray whales are also known to feed on benthic amphipods). They found that *A. careyi* was found in higher densities outside of an *A. agassizi* tube mat.

In this portion of the study, I describe sediment characteristics in relation to amphipod distribution patterns, with the aim of increasing our knowledge of amphipod ecology in relation to habitat occupancy and gray whale foraging behaviour. My specific objectives are to 1) describe the sediments of Cow Bay and Ahous Bay; 2) identify regions or subenvironments within the bays using entropy analysis; and 3) determine the relationship between sediment characteristics and ampeliscid distributions. An investigation of the distribution patterns of sediment characteristics and benthic amphipods may yield important insights into amphipod ecology in Cow and Ahous bays, which, in turn, are essential to understanding gray whale feeding patterns in Clayoquot Sound.

3.2 Literature Review

3.2.1 Association between sediment and benthic animals

Much work in benthic ecology has focussed on the relationship between benthos and sediment of soft substrates (see reviews by Gray 1974, Probert 1984, Snelgrove and Butman 1994). Quantitative study of sediment and infauna associations began when Petersen (1913) identified recurring benthic communities associated with particular sediment types (Burd *et al.* 1990, Snelgrove and Butman 1994). Benthos distribution patterns have subsequently been investigated at different levels of biological organisation including communities (e.g., Schnaffer and Boesch 1982, Long and Lewis 1987), functional groups, (e.g., Rhoads and Young 1970, Mancinelli *et al.* 1998), and species (e.g., Fenchel *et al.* 1975).

Investigations into the composition and biogeography of benthic communities often begin with a matrix of species abundance and physical variables. The measurement unit (community) is defined by species abundance data, and corresponding physical variables are subsequently identified (e.g., Petersen 1913, McRae *et al.* 1998). Implicit in this approach is the assumption that species (and assemblage) geographic distribution patterns are stable or at least predictable with respect to measured physical variables within the time and space scale of the study (Burd *et al.* 1990). Thorson's (1957) influential "parallel communities" concept illustrates one extreme example. Parallel communities are defined by dominant species, from the same genus or family, and are associated with particular sediment types. Thorson (1957) held that such benthic communities are associated with particular sediment types and these patterns are evident at a global scale.

Sanders' (1958) observations of spatial differentiation between suspension and deposit feeders led to an increase in studies focused on feeding group distribution patterns (Snelgrove and Butman 1994). This "functional-group" approach to understanding species distributions represents further differentiation in the levels of biological organisation and is based on the relationship between ecological (feeding) and physical (water flow) processes. Water flow can both impede and enable feeding by transporting particles into or out of the area from which the animal eats (Miller *et al.* 1984). As such, deposit feeders were thought to be associated with muds and slower water, which would allow organic matter (most abundant in the silt and clay fraction) to settle out of suspension. Conversely, suspension feeders were thought to be associated with larger sediment grain sizes and faster water, which would enable the delivery of more food to flow past.

The feeding group approach presented a compelling rationale for examining observed distributions in relation to a physical process (water flow) that affects both benthic feeding and sediment characteristics. Rhoads and Young (1970) further developed the feeding group approach, known as the "trophic group amensalism hypothesis", and described an ecological process that they argued established and maintained distribution patterns. Rhoads and Young (1970) attributed distribution patterns to the behaviours of deposit feeders – they asserted that the action of deposit feeders negatively affected suspension feeders by destabilising and resuspending sediments, and by preying on suspension feeders' larvae. Although biological interactions, such as competition and predation, are believed to be important in structuring distribution patterns of benthos (see review by Wilson 1991), the trophic group amensalism hypothesis, and the feeding group approach in general, were undermined by results from a third approach in benthic ecology: detailed autecological studies of soft substrate species.

Detailed studies of soft substrate species showed that the relationship between benthos and their environment is more complex than previously thought. For example, Mills (1967) and Kanneworff (1969) showed that benthic ampeliscid feeding methods are flow dependent. Ampeliscids feed on suspended material until water flow is too slow to bring sufficient amounts of food, whereby they then become deposit feeders under low flow conditions. Substratum choice experiments with larvae and adults identified other ecological mechanisms for observed distribution patterns (Snelgrove and Butman 1994).

The relationship between sediment characteristics and benthos distribution patterns has been investigated from a range of scales of biological organisation. The progression to increasingly specific ecological studies was not strictly sequential; early experiments of larval sediment choice (e.g., Wilson 1932) preceded the use of some ordination and community identification techniques (see review by Burd *et al.* 1990). Overall, the trend in benthic ecology is towards more detailed and experiment-oriented approaches to identify causal mechanisms. Nonetheless, there are repeated calls to increase the experimental rigour of this field (e.g., Dayton and Oliver 1980, Underwood 1990, Snelgrove and Butman 1994).

A parallel progression is not apparent in sediment analytical and descriptive methods used in benthic ecology. In the 1970s, Johnson (1974) advocated microscopic analysis of sediment structure in benthic ecology. An early call to describe sediments "holistically", based on the shape of the distribution profile (Gray 1974), was also largely ignored. Sediment grain size and total organic carbon are bulk measures frequently used to describe sediments (Snelgrove and Butman 1994). In benthic surveys, sediments are usually described by some measure of central tendency or dispersion of grain size distributions, or specific fractions of the sediment grain size distribution profile (e.g., Biernbaum 1979, Weston 1988, McRae *et al.* 1998).

3.2.2 Sediment characteristics

Sediment grain size is the most commonly used descriptor of marine sediments. It is used to identify sedimentary regions, and to infer depositional processes based on the close relationship between grain size and water's ability to erode, transport and deposit material (Buchanan 1984). Other sediment measures also reflect processes affecting the benthos. For example, inorganic carbon is largely derived from the remains of shelled animals on the sea floor (Olausson 1980, Kristensen and Andersin 1987), but the supply and distribution of inorganic carbon is related to near-bed water flows. Similarly, the supply of organic carbon is derived from production in the water column, however the amount of organic carbon retained in sediments is a function of bottom sediment characteristics and water flows (Tyson 1995). Thus, sediment characteristics are important not only in describing structure in soft substrates, but also form the basis for further understanding of processes that structure the sea floor.

3.2.2.1 Organic carbon

Sedimented organic carbon is an important food source for benthos since these animals often live below the photic zone and, consequently, are largely dependent on productivity in the water column (Wassman 1984, Cocito *et al.* 1990). Both suspension and deposit feeders consume sedimented organic material; by definition, deposit feeders feed on detritus and much of the organic matter used by suspension feeders is resuspended material that is laterally transported near the seabed (Snelgrove and Butman 1994).

Although sedimented organic material is derived from production in the water column, the location of sediments with high organic carbon content is not directly associated with highly productive waters (Tyson 1995). Since organic matter is often clay or silt sized, it settles slowly and resuspension is limited more by cohesion to adjacent particles than by minimum water flows (Johnson 1974). Further, the specific gravity of organic sediments is typically close to that of water; therfore, settling velocity is low. Consequently, organic carbon content is often high in muddy sediments due to similar settling rates and cohesion with like-sized sediments. In contrast, sandy substrates typically have low levels of organic carbon because fine particles are resuspended by near-bed water flows (Hartwig 1976).

A number of correlative surveys have found an association between benthos distributions and organic carbon content despite error associated with measuring organic carbon content (Ishikawa 1989). Organic carbon content is measured as total organic carbon (TOC), which includes both refractory and labile organic carbon.

3.2.2.2 Inorganic carbon

The amount of shell fragments in marine sediments is one physical variable that correlates with some benthic animal distributions. Biernbaum (1979) argued that large shell fragments would interfere with tube building by some animals such as ampeliscids.

Indeed, *A. agassizi* distributions are negatively correlated with shell fragments (Schnaffer and Boesch 1982). However, other benthic amphipods are found in association with shell fragments including *Ericthonius fasciatus* (Collie 1985) and *Unciola inermis* (Schaffner and Boesch 1982). These amphipods may benefit from increased suspension feeding opportunities in faster near-bed currents (Collie 1985) or for protection from predation (Schaffner and Boesch 1982).

Inorganic carbon in marine sediments is predominantly composed of shells and echinoderm tests (Kristensen and Andersen 1987), and thus is produced by biological processes on the sea floor. However, shell fragments distribution patterns are shaped by near-bed water flows. Shell fragments quickly abrade, so the presence of large amounts of shell fragments may be indicative of a nearby shell source. Like most coarse sediment particles, large shell fragments are often indicative of high-energy environments (Collie 1985).

3.2.2.3 Sediment grain size

Grain size influences characteristics of bottom sediments, such as porosity and redox potential (Buchanan 1984) and strongly covaries with water flows. Erosion and entrainment, transportation, and deposition of sediment particles are based on the relationship between water speed and sediment grain size. Sediment particles are moved when lift and drag forces exceed the submerged weight of the sediment particle, which is determined by its density and size (Wheatcroft and Butman 1997). The relationship between sediment grain size and water processes is seemingly intuitively simple, but becomes complex in natural environments where there are many interacting processes.

There are three processes that shape sediment grain size: source and supply, transportation and deposition (Buchanan 1984). Grain-size distributions are dependent on source sediments. Source sediments are further altered during transport and differentially deposited based on the relationship between grain size and water speed. There is some debate on the relative importance of these different processes. Larson *et al.* (1997) stated that source sediment is the most important factor shaping sediment grain size distributions; this accounts for different grain size distributions between geographic regions with similar energy environments. By contrast, McLaren (1981) argued that most grain size distributions are skewed as a function of changes to sediments during transport, i.e. fine particles are winnowed out of source sediments during transport. However, Folk and Ward (1957) argued that skewed sediment distribution profiles were the result of mixing different sediment sources. Despite the varied arguments regarding the complexities of sediment erosion, transport and deposition, there is a clear relationship between particle size and movement. But the specific processes responsible for a given sediment grain size distribution are location specific (Solohub and Klovan 1970).

3.2.3.1 Sediment grain size description and analysis

Sediment samples are not comprised of a single sediment size; instead grain size distributions contain a range of particle sizes. Descriptions of sediment grain size are summary measures and some information is lost in this summation. There is much debate about grain size measurement and analytical methods and their collective impacts on the ability to identify regions or processes (e.g., Ehrlich 1983).

Sand-sized sediment samples are often dry sieved. This produces a distribution profile of proportional weight of the sample that remains on a particular mesh size. The degree of detail shown in the distribution profile is determined by measurement choices (gradations of sieve sizes) made by the researcher. This choice may affect the conclusions of the study.

There are two types of analyses used to describe sediment distributions: those that assume a normal (or log-normal) grain size distribution profile and those that do not. Both the graphic plot (Folk and Ward 1957) and the method of moments (Friedman 1967) assume unimodality and normal grain size distributions. They are derived differently but produce analogous measures of central tendency, dispersion and shape (McManus 1988). However, graphic and moment measures are problematic because many sediment samples do not contain a normal distribution of grain sizes. Although graphic plot and moment methods are able to handle a degree of non-normality (Swan *et al.* 1978) information contained in multiple modes is lost.

Other descriptive methods such as log-hyperbolic modelling (Sutherland and Lee 1994), factor analysis (Soluhub and Klovan 1970), and entropy analysis (Forrest and Clarke 1989) were developed to addresses the perceived shortcomings of graphic and moment measures. These methods address the normality and unimodality issue in a number of ways. In log-hyperbolic modelling, grain size distributions are fitted to a log hyperbolic distribution profile instead of a normal profile (Sutherland and Lee 1994). In entropy analysis sediment samples are described and grouped based on the degree of difference between adjacent sediment classes. Entropy analysis is employed in this study.

3.2.3.2 Entropy analysis

Entropy analysis is well suited for classifying sediment grain size samples because classification is based on the shape of the distribution profile, and there are no assumptions made on the data structure (Forrest and Clarke 1989). Entropy analysis is derived from information theory and, as such, samples are grouped - based on the degree of difference or information in a sample. High entropy values indicate low contrast between classes; when percentages are approximately equal between classes, knowledge of one class does not increase our ability to predict the others. Thus, there is high uncertainty or entropy. Low entropy values characterise samples with considerable differences between classes (Forrest and Clarke 1989).

In multivariate entropy analysis, samples are initially expressed as proportions of the grand total and then the inequality statistic can be calculated for the matrix as

$$I(Y) = \sum_{j=1}^{J} Y_j \sum_{i=1}^{N} Y_i \log_2 NY_i$$

where: Y_j = relative weight [of sand grains] in phi interval (column) j; J = number of intervals; N equals the number of rows (sediment samples); and Y_i = relative weight value [of sand grains] in phi interval (column) j that are in sample row i. $I(Y)$ is the inequality statistic for the distribution of phi intervals across all samples based on the relative weight of sand grains in each phi interval. Between group inequality is then calculated from

$$I_B(Y) = \sum_{j=1}^{J} Y_j \sum_{r=1}^{R} Y_{jr} \log_2 \frac{Y_{jr}}{N_r / N}$$

where r = number of groupings and $I_B(Y)$ = between group inequality.

Following the calculation of the overall inequality statistic, each sediment sample is assigned to an entropy group based on the number of groups specified in the program.

Group membership is iteratively reordered to maximise between class and minimise within class entropy. The classification is not hierarchical; group membership in a particular class is not based on group membership in a prior iteration of the program. Like many other classification systems, the decision on the optimal number of groups is subjective; however, the number of entropy groups can be guided by plotting a percent explained curve for the problem (Johnson and Semple 1983). Entropy groups can be compared by calculating means for grain size class and comparing those percentages to global means. This highlights which aspects of the sediment distribution characterise the entropy groups.

3.3 Present study

In sedimentology, using grain size analysis to identify depositional environments has been roundly criticised (e.g., Erlich 1983). Critics state that observed grain size distributions are produced by a complex interaction of processes that cannot be identified by the relationship between summary measures of a distribution profile. However, much of the criticism of both sediment grain size analysis, and the study of sediment and benthos associations stems from a perceived lack of concordance between the level of analysis and scope of predictions or conclusions. In benthic ecology, the general criticism is that a correlation between sediment measures and benthic organism's distributions does not imply a causal relationship, since sediment characteristics covary with other processes on the sea floor (Johnson 1974, Jumars and Nowell 1984). Further concerns are that sampled sediment does not correspond with the ambit of the organisms, and that sediment and benthos distribution patterns should be analysed separately prior to any study of association. However, critics of both grain size analysis and infauna studies agree that surveys of either sediment structure or sediment and infauna associations are still important initial approximations and form the basis of more directed, locally-specific studies.

I have addressed these criticisms. Depth of sediment samples corresponds with the vertical location of study species within the sediment. Sediment and benthos distributions were analysed separately, and the sediment classification method used (entropy analysis) is not based on *a priori* assumptions of data structure. Finally, the purpose of this section of the research is to provide a description of sediment and amphipod distributions in Cow and Ahous bays thereby enabling more detailed study of sedimentology and amphipod ecology within the bays.

3.4 Results

3.4.1 Sediment

3.4.1.1 Organic carbon

Total organic carbon was measured as a first approximation of food availability in the sediments. Mean organic carbon content was less than one percent of sediment dry weight in both bays, however, standard deviations associated with these means approach the measurement capabilities of the instrument (Table 3.1). Repeatability of organic carbon determinations was investigated using fifteen pairs of subsamples. The organic carbon content of subsamples were strongly correlated ($r^2 = 0.70$) and the null hypothesis that subsamples were from the same sample was accepted (Model II ANOVA: $F = 30.7231$, $df = 1$, $P < 0.0001$, $n = 15$). When mean organic carbon content was multiplied by the 30% not accounted for in the regression of subsample pairs, it was shown that half of the standard deviation may be due to subsampling or measurement error, hereafter referred to as subsampling error. Due to low values, high variability and subsampling error, organic carbon content was not further analysed.

Table 3.1 Mean percent organic carbon of sediment sample dry weight. Stated precision of Mettler PE360 balance is 0.001g.

Bay	Number of Samples	Mean Weight Organic Carbon (g)	Mean Percent Organic Carbon
Cow	85	0.035 (±0.025)	0.72(±0.17)
Ahous	53	0.038 (±0.021)	0.85(±0.29)
Both	138	0.036 (±0.023)	0.77(±0.24)

3.4.1.2 Inorganic carbon

Inorganic carbon content was low in most samples and in both bays. Percent inorganic carbon as measured by LOI was directly related to the amount of shell fragments in the sample, although 9.2% (the intercept) of inorganic carbon measured by LOI could not be attributed to shell fragments (Figure 3.1). The regression slope (0.34) is lower than the molecular mass of calcium carbonate (44 g mol^{-1}) suggesting that other matter is lost on combustion (i.e., organic carbon contained within a matrix of inorganic carbon).

When this equation was used to calculate shell weights, only one site (C16) had large amounts of shell fragments. In all other samples, LOI (1000°C) fell below the intercept of the regression equation and, therefore, inorganic carbon lost on ignition could not be attributed to shell fragments. Again, site C16 differed markedly from all other sampled sites; shell fragments accounted for thirty-four percent of sediment dry weight from this site. There was less variance associated with inorganic carbon subsamples

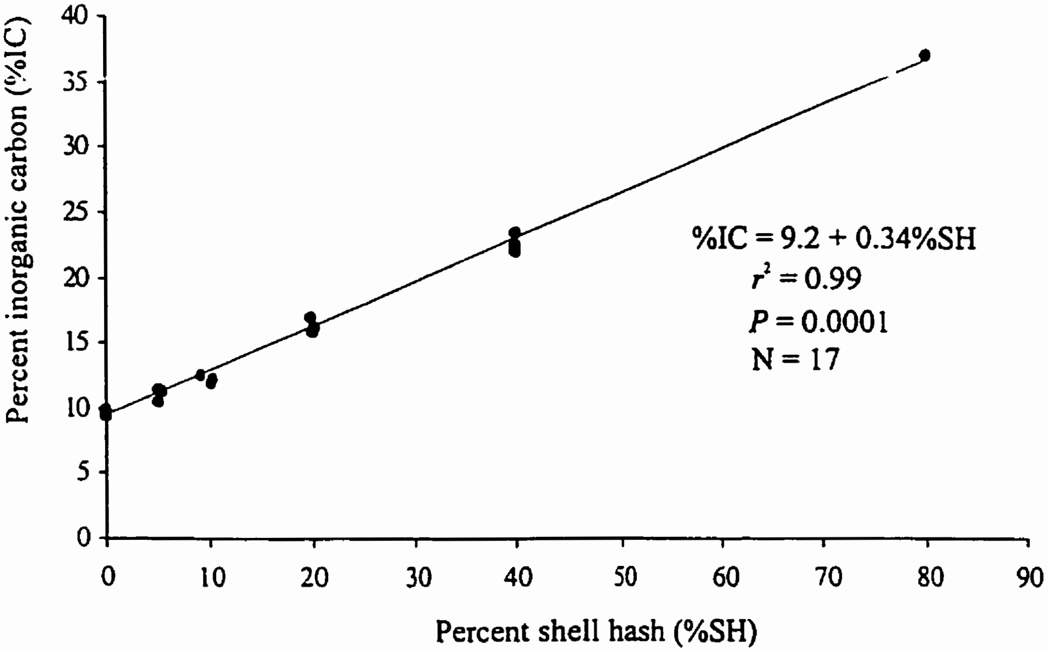

Figure 3.1 Percent inorganic carbon lost on ignition (1000°C) in relation to percent shell fragments of sediment dry weight.

($r^2 = 0.99$, n= 15, $P = 0.0001$) than with organic carbon subsamples. Since the same subsamples were used for both organic and inorganic subsampling error determinations, the higher correlation coefficient suggests that inorganic carbon measures were more reliable in this study.

3.4.1.3 Sediment grain size

Sediment samples from both Ahous and Cow bays were predominantly composed of fine sand (0.125 to 0.25 mm) (Figure 3.2). Very-fine sand was the next most abundant grain size fraction. Three samples from each Cow and Ahous bays had higher amounts of medium sand sizes. The Ahous Bay samples with larger sediment particles were the three replicate samples from site C16, as mentioned above. Similarly, all three samples with higher percentages of medium sand from Cow Bay were also from a single sampling site (C36).

Entropy analysis was performed on all sampling sites for both half phi and full phi intervals (11 and 6 sediment classes, respectively). Five entropy groups were needed to explain 79% of total variation at half phi intervals whereas only three groups were needed to account for 77% of total variation when there were six full-phi classes. The first entropy group in both sets of analyses accounted for much of the variation from all sediment samples (57 and 51% respectively). This group contained one sampling location from each Cow and Ahous bays that had higher percentages of coarse grains (C36 and C16). Relative proportions of fine-grained sediments distinguish the remainder of the groups (Figure 3.3). Some spatial aggregation was exhibited in the location of samples from each entropy group in Cow (Figure 3.4) and Ahous bays (Figure 3.5).

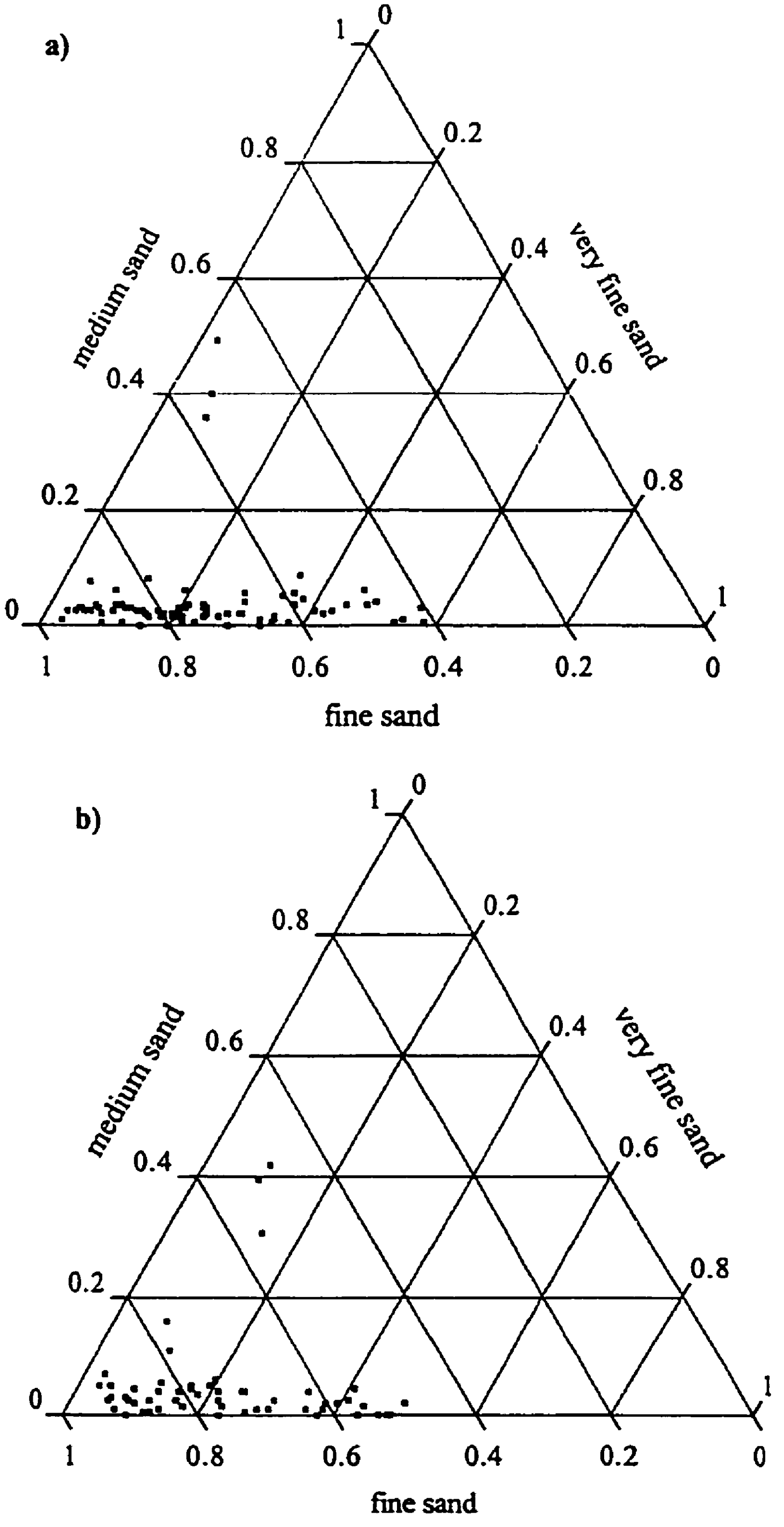

Figure 3.2 Ternary plots of sediment grain size in Cow (a) and Ahous (b) bays. Points represent individual sediment cores. Sediment classes were chosen to maximise dispersion along the axes.

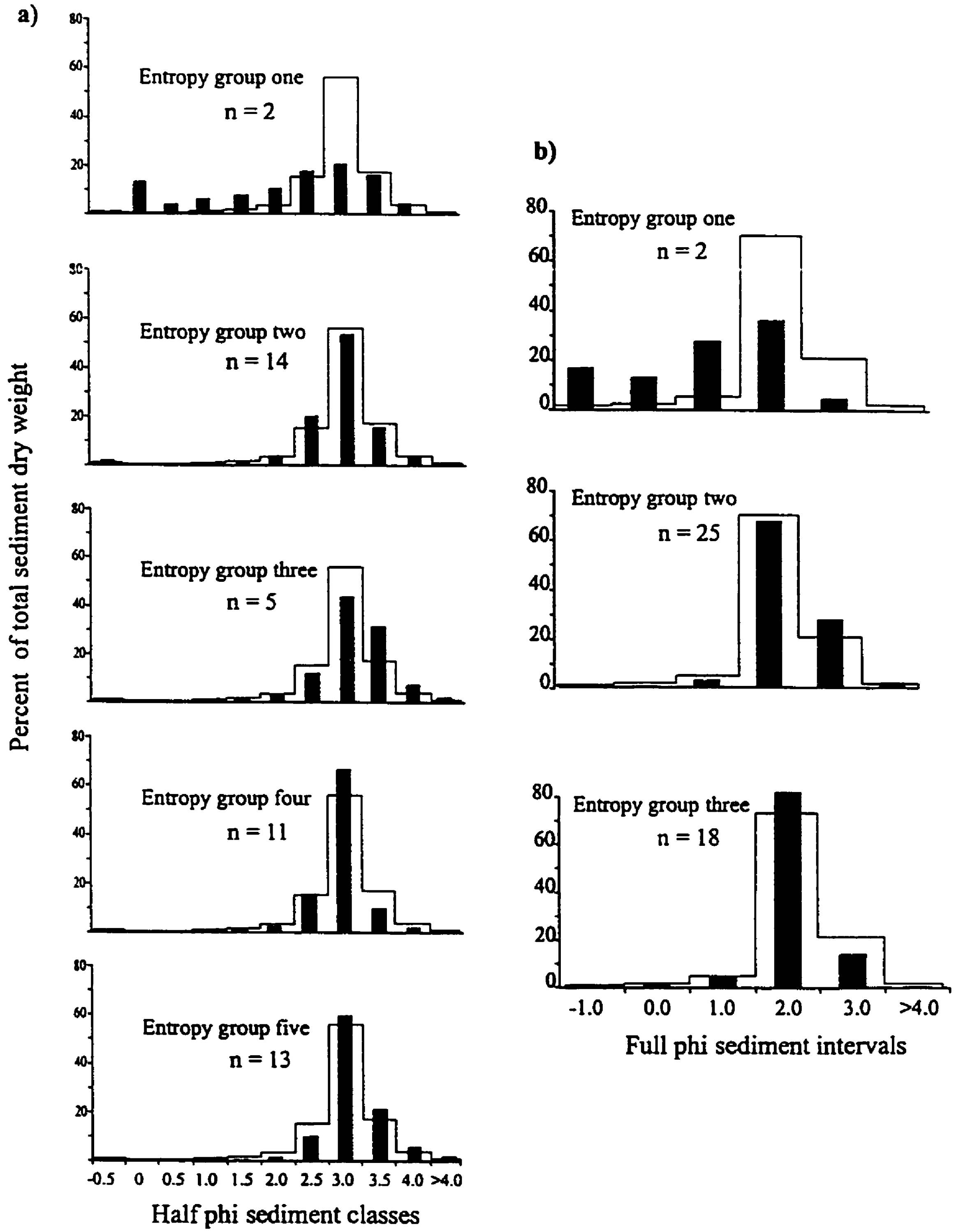

Figure 3.3 Sediment grain size distribution profiles for entropy groups using half (a) and full (b) phi sediment classes. Mean sediment distribution profile is shown in outline. Grain size ranges from very coarse sand to silt and clay-sized particles.

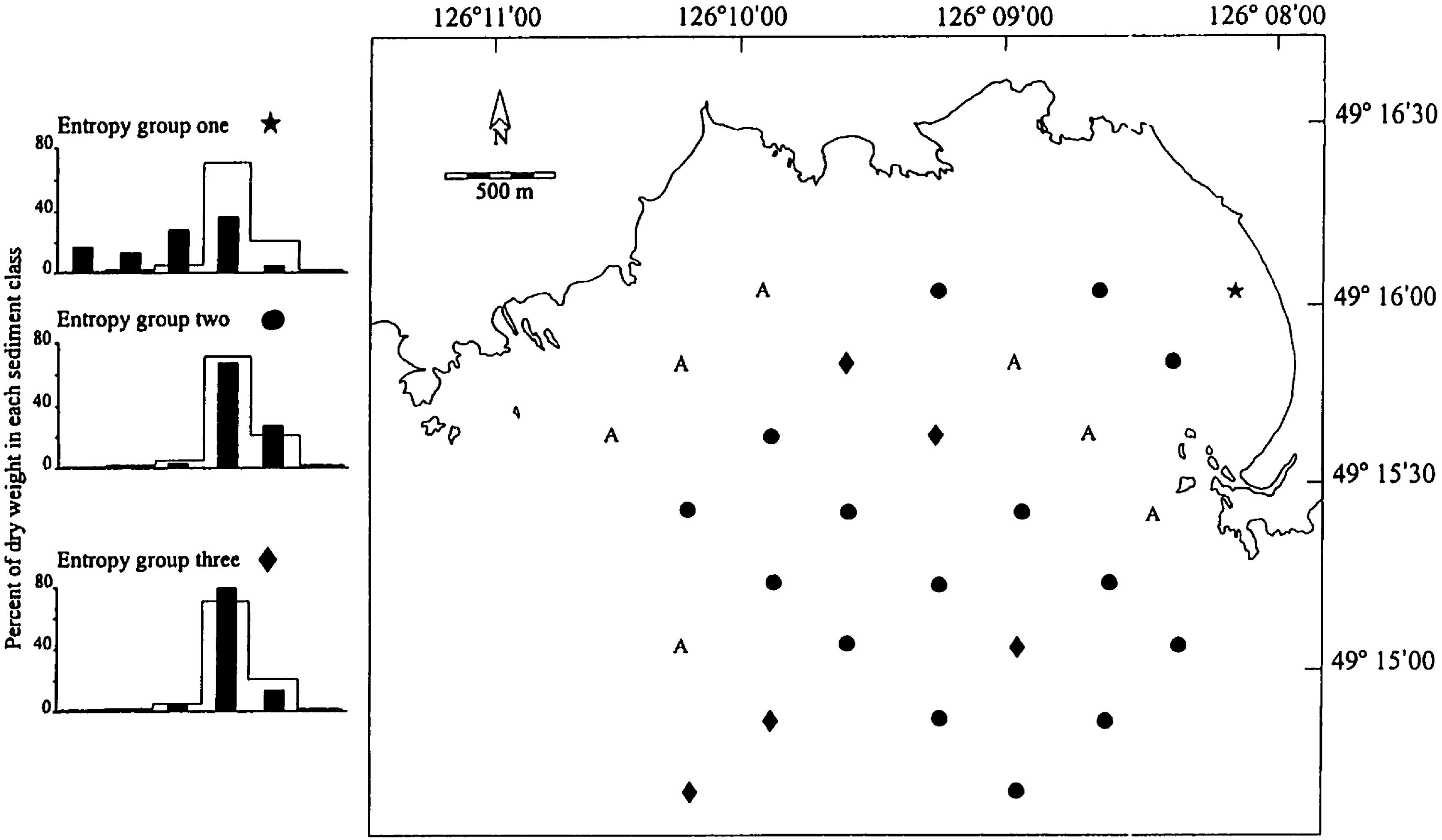

Figure 3.4 Location of entropy groups based on full phi sediment classes within Cow Bay. Mean sediment grain size distribution profiles for each entropy group are shown on the left with mean sediment distribution profile for all samples is shown outline. Sites where sampling was attempted but not successful are identified by the letter A.

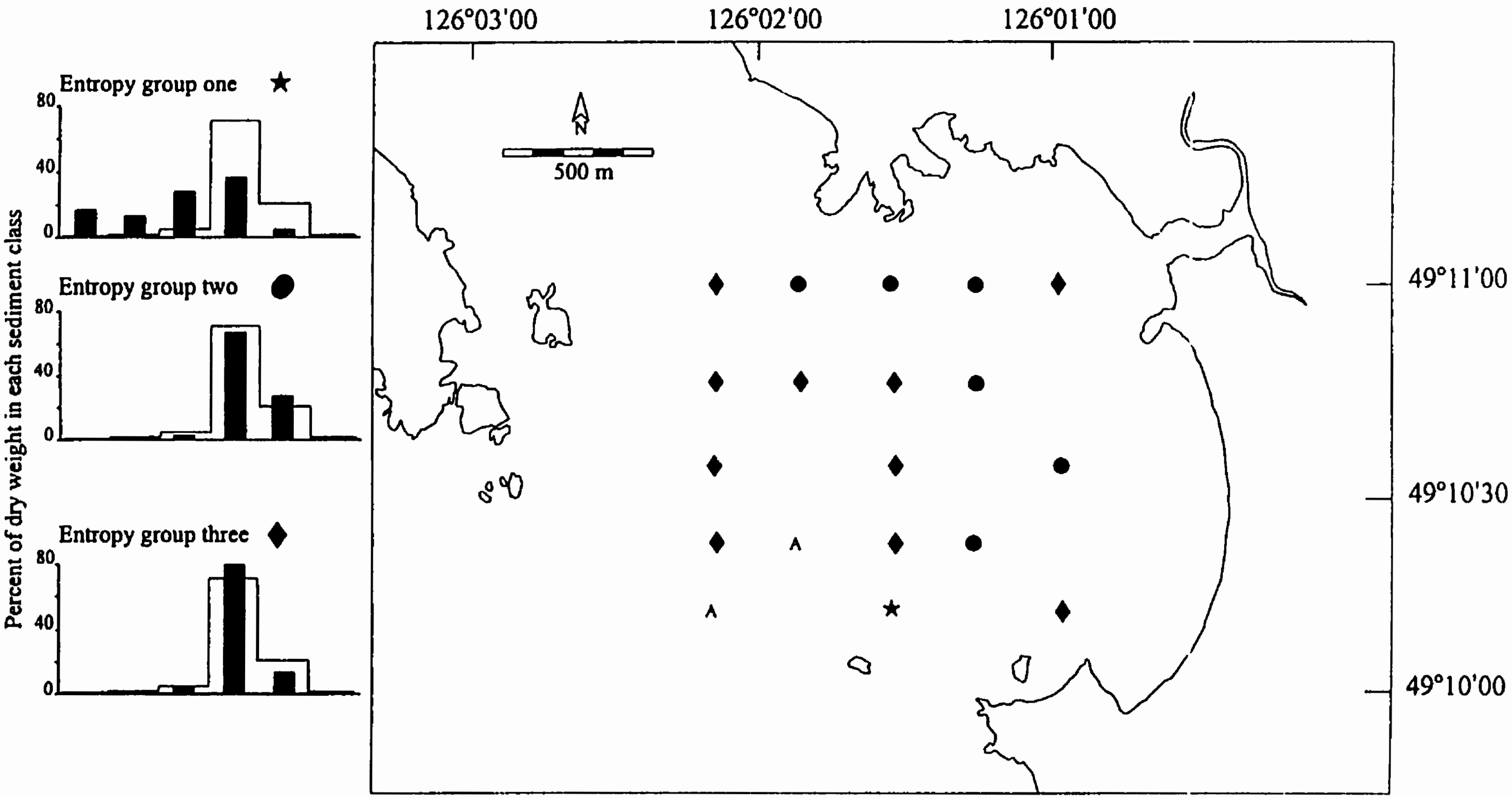

Figure 3.5 Location of entropy groups based on full phi sediment classes within Ahous Bay. Mean sediment grain size distribution profiles for each entropy group are shown on the left with mean sediment distribution profile for all samples is shown outline. Sites where sampling was attempted but not successful are identified by the letter A.

3.4.2 Amphipods

A. agassizi was the most common amphipod in core samples from Cow and Ahous bays (Table 3.2). In 1998 abundance ratios between *A. agassizi* and *A. careyi* were an order of magnitude higher in Cow Bay than in Ahous Bay. Interestingly, this relationship did not hold the following year. Other amphipod species, mainly lysianassid amphipods, were as abundant as *A. careyi* in 1998. Only ampeliscids were collected in 1999. Variable core volumes did not compromise abundance measures or further investigations of amphipod distribution patterns; there was no correlation between sediment volume and number of amphipods in a core (Figure 3.6).

Table 3.2 Total number of amphipods collected from Cow and Ahous bays core samples. Ratios between *A. careyi* and *A. agassizi* are shown.

Bay	Year	Total	*A. agassizi* (Aa)	*A. careyi* (Ac)	Other Species	Ratio Ac:Aa
Ahous	1998	891	883	8	20	1:110
	1999	327	310	17	--	1:18
Cow	1998	1982	1809	173	25	1:10
	1999	210	182	28	--	1:6.5

Relative abundance of each amphipod group was investigated using Spearman's rank correlation coefficient. In 1998, abundance of *A. careyi* and *A. agassizi* at each site were positively correlated ($r_s = 0.586$, $P = 0.01$). Ranked abundance of other amphipods was not correlated with either ampeliscid species. In contrast, ampeliscid abundance was not correlated in samples collected in 1999 ($r_s = 0.05$, $P = 0.784$).

Small-scale variability in amphipod abundance was investigated using SCUBA transects within Cow Bay. Variance in amphipod abundance within one SCUBA transect ($n = 5$) was compared with the variance between SCUBA transects ($n = 10$). There was no difference in variance levels between transects and the larger SCUBA sampling

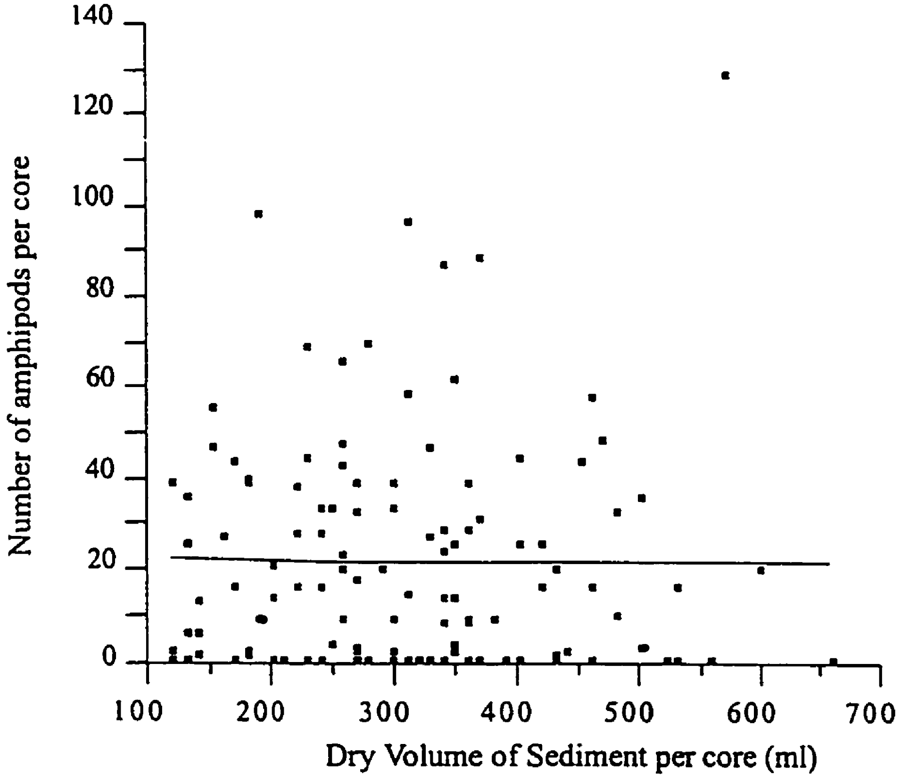

Figure 3.6 Scatterplot of the relationship between amphipod abundance and volume of dry sediment from a core. Line indicates mean number of amphipods per core.

set (F_s = 4.72, P= 0.05). This suggests that there was high variability in amphipod abundance within a 4 m area.

3.4.3 Association between amphipod and sediment groups

The relationship between sediment entropy groups and amphipod abundance was investigated using univariate ANOVA and non-parametric equivalents. Parametric tests were used even though some heteroscedasticity was found, as ANOVA is well known to be robust to violations of the assumptions (Zar 1974). However, the possibility of committing a Type I error is increased using ANOVA when the number of samples is not equal, as is the case here. Relationships identified with ANOVAs were thus confirmed using Kruskal-Wallis test, a non-parametric analog to ANOVA.

The relationship between amphipod abundance and sentiment entropy groups was investigated for both full and half phi sediment classes. In both analyses the dependent variable (mean number of animals per amphipod group) had unequal error variance (Levene's test: F = 21.657, $df1$ = 8, $df2$= 126). Amphipods were not related to sediment structure when eleven sediment fractions were used (one half phi intervals). There was no significant difference (α = 0.05) in the number of amphipods per entropy group (F = 2.350, df= 4, P= 0.58) and no interaction effect (F = 1.866, df = 8, P = 0.072). However, the average number of animals in each amphipod group was significantly different; *A. agassizi* was the most abundant amphipod and significantly different from abundances of the other amphipod groups (Scheffe's post hoc test: F = 19.141, df = 2, P = 0.001). Abundances of *A. careyi* and 'other amphipods' were not different.

Complementary analyses were run using full phi intervals and these analyses showed significant differences at the sediment (*F*= 5.672, *df* = 2, *P* = 0.004) and amphipod level (*F*= 6.812, *df* = 2, *P*= 0.002). As well, there was a significant interaction effect (*F*= 4.337, *df* = 4, *P*= 0.003), indicating that the same amphipod group was not dominant throughout all of the entropy groups (Figure 3.7). Similar results were obtained using post hoc tests following this ANOVA. There were no significant differences between the sediment groups, but *A. agassizi* abundance was still significantly different from that of the other amphipod groups (Scheffe's post hoc test: *F* = 19.141, *df* = 2, *P* < 0.0001).

As stated earlier, although ANOVAs are robust to unequal error variance, unequal sample sizes increased the likelihood of Type I errors in these analyses (Zar 1974). The relationship between full phi entropy groups and amphipod groups was investigated using a non-parametric 2-way ANOVA (an extension of the Kruskal–Wallis test). There was a significant difference in the number of amphipods between entropy groups (*df* = 2, *P*< 0.001) but the difference between amphipod groups was significant only at the *P* = 0.1 (*df* = 2, *P* = 0.065). There was no significant interaction effect between entropy and amphipod groups.

3.5 Discussion

Fine-grained sand dominated sediment samples from Cow and Ahous bays. Organic carbon content and dominant infauna in these bays are similar to those reported in the literature for fine sand substrates. Organic carbon content is normally highly correlated with silt and clay sized particles; these make up a very small portion of sediment samples

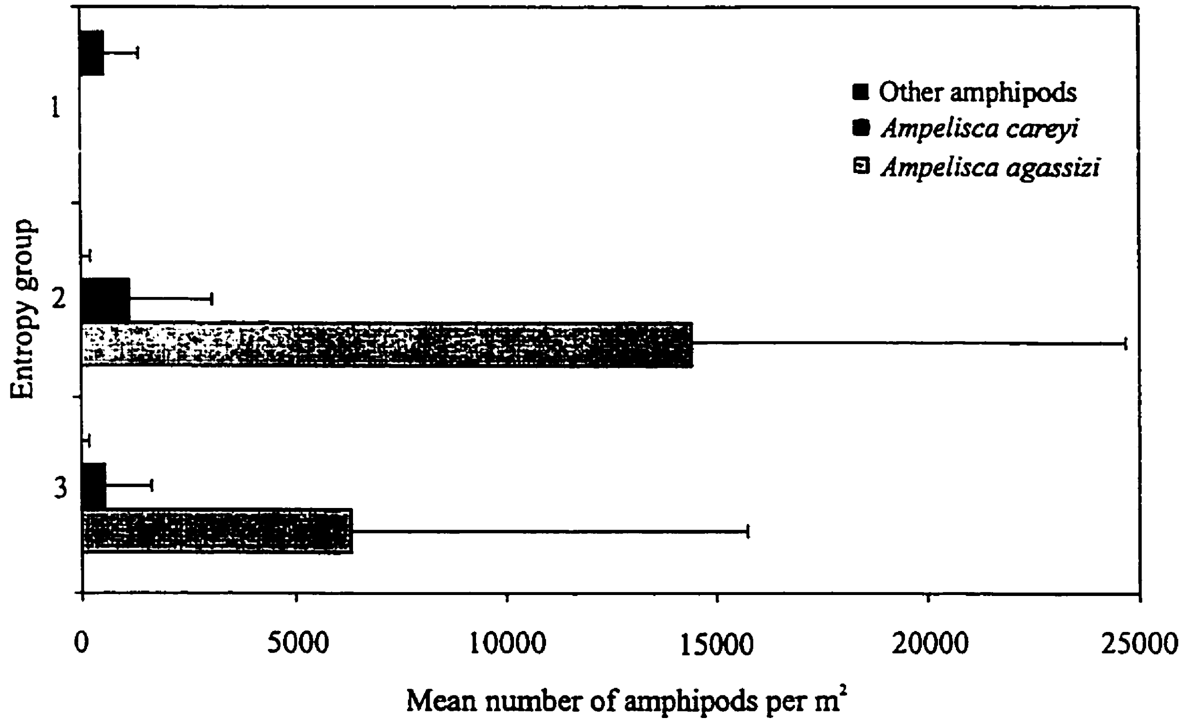

Figure 3.7 Mean densities of amphipods in each sediment entropy group calculated on full phi sediment size class intervals. Error bars indicate +1 sd.

(1.13 ± 1.2% dry weight). Further, measured values fell within the published range for sand-dominated sediment. Tyson (1995) stated that organic carbon contents ranging from 0.3 to 1.0% dry weight are high for fine- to medium-grained sand.

In Cow and Ahous bays *A. agassizi* and *A. careyi* are associated with fine-grained sand with relatively high organic carbon for that sediment type. Schaffner and Boesch (1982) similarly found that *A. agassizi* dominated fine sand environments. Sanders (1958) noted that ampeliscids in general dominated fine sand substrates. However, other ampeliscids are the dominant infauna in both coarser (e.g., *A. abdita;* Mills 1967) and finer (e.g., *A. araucana;* Carrasco and Arcos 1984) sediments. Thus, it appears as if there is no global pattern of association between this genus and a particular sediment type (*sensu* Thorson 1957). Neither ampeliscid was found at the sites with coarser sediment grain sizes. In contrast, the grouping 'other species', was primarily found at site C16, which had the highest proportion of shell fragments.

My finding of little variation in grain size distributions may explain differences in results between half and full phi sediment intervals and correlations with amphipod groups. In both sets of analyses the first entropy group accounted for much of the variation in sediment grain size; further information (from half phi intervals) may have obscured this relationship. There are no *a priori* reasons for choosing full phi over half phi sediment divisions because this scale is arbitrary (Krumbein and Pettijohn 1938) and is based on measurement concerns instead of sedimentological or ecological factors. Since both scales are equally arbitrary, the difference must be in the statistical properties of using six versus eleven sediment classes. I contend that the conflicting results of ANOVAs of half and full phi entropy groups is a function of the degree of information (noise) in the association. There was a significant interaction effect in the ANOVA using full phi intervals but this relationship was not evident in the non-parametric test. This is a result of the different number of samples within each entropy group. There were only two sediment samples in the entropy group that was not numerically dominated by *A. agassizi*, since the sample size of this entropy group was so low the difference in abundance was not significant using non-parametric tests. Thus, I deduce from these data that sediment samples were not evenly distributed between the entropy groups and that the number of amphipods differed between the entropy groups. Similar results can be seen in the less mathematically complex methods such as the ternary diagram and abundance profiles of amphipod species in each of the sediment groups (Figures 3.2 and 3.7).

Some of the results and limitations of this study are similar to those identified in other benthic surveys (Snelgrove and Butman 1994). General patterns between amphipods and bulk sediment characteristics were identified but the ecological processes that establish, maintain and alter these patterns remain unknown. However, like other surveys of benthic distribution patterns, these results suggest possibly fruitful avenues for future study of the processes that establish the patterns. Intriguing relationships were highlighted such as the shift, between sampling seasons, in abundance and rank correlations between *A. agassizi* and *A. careyi*. In 1998, ampeliscid abundance was positively correlated between the two species. However, ampeliscid abundance was not correlated in 1999 samples.

In summary, in this portion of the study I describe sediment structure within the bays. Sediment grain size is largely homogeneous and is predominantly fine sands. Shell fragments were concentrated at a single site and organic carbon comprised a small percentage of sediment dry weight. Other researchers (e.g., Johnson and Nelson 1984, Oliver *et al.* 1985) have based much conjecture on the impacts of gray whale on sediment grain size. These data provide a beginning for evaluating such scenarios.

CHAPTER 4: AMPELISCID POPULATION STRUCTURE, BIOMASS AND CALORIC CONTENT RELATIVE TO GRAY WHALE ENERGY REQUIREMENTS

4.1 Introduction

The feeding ecology of gray whales foraging in Clayoquot Sound is markedly different from that which gray whales exhibit in their primary feeding grounds in the Bering and Chukchi seas. In the primary feeding grounds gray whales feed almost exclusively on benthic amphipods (Highsmith and Coyle 1992). Within Clayoquot Sound there is considerable variation in the diet of gray whales both within a feeding season and between years, and frequent prey-switching occurs between pelagic, epibenthic, and benthic prey (Duffus 1996, Darling *et al.* 1998). These contrasting and highly differentiated feeding behaviours are hypothesised to result principally from spatial and demographic variance in their prey populations. Since gray whales get much of their annual energy requirements during the feeding season, an average of 1.8×10^8 kcal per whale (Highsmith and Coyle 1992), high energetic demands must be responsive to changes in prey populations insofar as they affect gray whale feeding efficiency and energy return. My objectives here are to 1) describe population structure, biomass, and caloric content of benthic amphipods from Cow Bay and Ahous Bay, and 2) compare my results to other findings in relation to gray whale energy requirements.

4.2 Literature Review

4.2.1 Gray whale foraging patterns

The majority of eastern Pacific gray whales annually undertake one of the longest mammal migrations, from breeding lagoons in Baja California, to the Bering and

Chukchi seas, where they primarily feed on benthic amphipods. Gray whale stomach contents collected from specimens in the northern feeding grounds showed that they contained up to 90% benthic amphipods (Nerini 1984). Conversely, analysis of stomachs of gray whales hunted during their northern migration or in southern waters were empty (Rice and Wolman 1971). After spending the winter in southern breeding grounds, northbound migrants typically weigh 16-30 % less than their southbound counterparts following five months feeding in arctic and northern temperate waters (Nerini 1984). The extent of weight loss is a function of the time spent in southern waters (Rice and Wolman 1971).

As the Eastern Pacific gray whale population has rebounded following heavy hunting in the 19th century, increased sightings of gray whales summering and feeding in the waters of northern California, Oregon, Washington and British Columbia have been documented (e.g., Avery and Hawkinson 1992, Weitkamp *et al.* 1992, Murrison et al. 1984, Sumich 1983). Of these regions, perhaps the best known is Clayoquot Sound, on the west coast of Vancouver Island where gray whales have been found feeding during the summers of the last 25 years or so (e.g., Hatler and Darling 1974, Darling 1984, Oliver *et al.* 1984, Duffus 1996). Although bottom feeding on benthic amphipods has been documented in this region, it is known that gray whales feed on a range of primarily invertebrate prey, and amphipods do not appear to be the primary prey (Guerrero 1989, Kim and Oliver 1989, Dunham 1999). Gray whales in Clayoquot Sound have been observed feeding on mysids (*Holmesimysis sculpta, Neomysis rayii, Acanthomysis* spp.), crab larvae (*Pachycheles* spp., *Petrolisthes* spp.), ghost shrimp (*Callianassa califoriensis)* and herring eggs (*Clupea harengus pallasi*) (Duffus 1996, Darling *et al.* 1998, Dunham

1999). This is in sharp contrast with the foraging behaviour of whales feeding in arctic waters.

There is considerable variation in gray whale feeding patterns within Clayoquot Sound. Prey type, foraging location and duration of feeding events differ within seasons and between years (Duffus 1996, Darling *et al.* 1998). For example, 8-12 gray whales fed on benthic amphipods in Cow Bay through most of July and August in 1993 (pers. obs. 1993, Duffus 1996), whereas the following year whales were not observed bottom feeding until November (Darling *et al.* 1998). In 1994 some 20 whales were feeding on planktonic crab larvae off nearby Rafael Point (Duffus 1996). In the following year, several gray whales were found to be feeding on ghost shrimp in Grice Bay throughout the summer (Darling *et al.* 1998). In addition to this variation in feeding both spatially and on varying prey species between years, within in a single feeding season gray whales have been known to feed on mysids, crab larvae, benthic amphipods and ghost shrimp (Dunham 1999). Darling *et al.* (1998) summarised feeding observations for a number of seasons and concluded that the only pattern that could be discerned was that gray whales tend to feed on benthic amphipods later in the season. It remains, however, that gray whales are highly unlikely to forage at random, and there are indeed patterns that have yet to be fully described or understood.

4.2.2 Amphipod growth and reproductive rates

Amphipod growth and reproductive rates are tied to aspects of their environment, including water temperature and salinity, food availability and quality, and ecological processes such as competition with other benthic amphipods (Sainte-Marie 1991). These relationships are evident at a range of scales varying from differences in growth rates between neighbouring populations to global-scale patterns in size and reproductive timing.

In general, amphipod species found at depth, at high latitudes or in cold environments, live longer and have slower growth rates than amphipods living in warmer waters (Bellan-Santini and Dauvin 1989). For example, *A. macrocephala* lives 5-6 years in the Bering Strait (Highsmith and Coyle 1991) compared to only 2-3 years in warmer Danish waters (Kanneworff 1969). Water temperatures annually vary from −1.5 to +2.5°C in the Bering Sea compared to +5 to 12°C in the Øresund (Highsmith and Coyle 1991). Differing growth rates between generations of temperate amphipods have also been attributed to water temperature. For example, spring generations in *Ampelisca vadorum* and *A. abdita* have a 4-month life span, whereas overwintering generations live for 8 months (Mills 1967). Mills (1967) argued that slow winter growth rates were a function of temperature, not food availability, since there was evidence of food throughout the winter. Clearly variations in growth and reproductive rates of amphipod prey affect the amount of energy garnered by predators, such as bottom feeding gray whales, since catchability and caloric content differ between amphipod life stages.

A number of researchers argue that sexual maturation rates are also driven by water temperature which accounts for differing reproductive rates between generations of temperate ampeliscids (Mills 1967, Skadsheim 1984, Highsmith and Coyle 1990). Within a population, overwintering generations typically reach sexual maturity at larger sizes than summer generations. Mills (1967) suggested that both somatic growth and gonad development is limited by minimum water temperatures but that body tissue growth can occur at slightly lower temperatures than gonad development. Highsmith and Coyle (1990) modified this idea and posited that sexual maturity is related to molt number, which is dependent on temperature. These explanations would account for interspecific differences in body length at sexual maturity between years or seasons.

Monoporeria affinis (also referred to as *Pontoporeria affinis*: Conlan 1994), is a detritus-feeding benthic amphipod that experiences exponential growth following the spring plankton bloom (Lehtonen and Andersin 1998). Lehtonen and Andersin (1998) identified food availability as the dominant environmental factor driving differential seasonal growth rates. In this case, seasonal growth was not driven by water temperature, since high growth rates occurred during colder months of the year.

Other processes are important to growth rates of a co-occurring species, *Pontoporeria femorata*. *P. femorata* is also a deposit feeder but has more even growth rates throughout the year (Uttito and Sarvala 1991). Uttito and Sarvala (1991) suggest that the differences in growth rates may be due to competition and, consequently, different food type. Possible explanations for differential food use between these species can be inferred from behavioural data. *P. femorata* is less active and inhabits deeper burrows than *M. affinis* (Elmgren *et al.* 1990). This behaviour may decrease epibenthic predation (Elmgren *et al.* 1990) but it also inhibits this species' ability to garner resources that settle out of the water column. Consequently, growth rates are not as tightly linked to the timing of large sediment fluxes in this species.

Amphipod growth rates also have a strong genetic component with evidence of population substructuring (i.e., ecotypes). Using a reciprocal transplant experiment, Clancy (1997) showed that within bay differences in growth rates reflect both environmental conditions and source population. Growth rates in juveniles of the marine amphipod *Jassa marmorata* were a function of both available resources (transplant location) and limited by genotypic (source population) differences between these two local populations. Fine-scale genetic differentiation has also been documented in amphipod populations from adjacent bays (e.g., Wilson *et al.* 1997).

Last, fine-scale differentiation in growth rates may also occur as a result of food quality. Delong *et al.* (1993) found that riverine amphipod growth rates differed with food type. Amphipods grew quickest when fed algae and dead animal material instead of dissolved organic matter (Delong *et al.* 1993). Thus, co-occurring species that are utilizing varying food sources may have different growth rates.

In summary, amphipod growth and reproductive rates vary at a range of biological, temporal and geographic scales. General trends, i.e. number of broods produced and maximum life span, occur over latitudinal gradients or other large scales. Within a small geographic area, such as Clayoquot Sound, there may be small-scale temporal or spatial variation in growth and maturation rates of amphipods, but these may have major implications for gray whale feeding if the prey reach the critical size at which they are retained by the baleen.

4.2.3 Relationship between gray whale foraging and amphipod population

Foraging whales are capable of focussing on specific age classes of prey populations. For example, right whales (*Eublaena glacialis*) feed where there are higher proportions of older (i.e. energetically rich) life stages in their primary prey (Wishner *et al.* 1995). The extent of such behaviour is important to understand for gray whales feeding in Clayoquot

Sound given that there is ample evidence of prey switching. Accordingly, gray whales may feed upon amphipods only when they meet a certain minimum density and of a critical size needed to be retained by the baleen, which is thought to be around 6 mm (Rice and Wolman 1971). In the absence of sufficient densities in the larger size classes, gray whales may switch to alternate pelagic or epibenthic prey. Support for such conjecture comes from Dunham (1999) who found that gray whales were bottom feeding on benthic amphipods in 1997 when approximately 60% of the prey population was greater than 6 mm in length. By concentrating foraging activities on particular life stages of amphipods, whales both conserve energy expended, and energy return is maximized with variable prey and foraging techniques. Clearly, then, knowledge of prey population structure is important to understand behaviour and energetics of whales that seem to target specific life stages (Wishner *et al.* 1995).

Capture efficiency is a measure of energy expended while foraging on a particular prey type and, in the case of migratory gray whales, it includes the cost of migration and time spent not foraging. Both prey capture efficiency and energy content are shaped by prey population structure including size and reproductive state. Size is important insofar as the whale's ability to retain prey on the baleen. Reproductive state is important because sexually mature individuals typically have higher energy content. Thus, relative proportions of a prey population that are either in large size classes or are sexually mature would affect energy return for foraging gray whales. These aspects of gray whale foraging behaviour have hitherto been little explored. Variation in the life-history of amphipods may be important in explaining differences in foraging behaviour among gray whales inhabiting northern waters compared to temperate waters of British Columbia.

However, small-variation in sexual maturity and size may also be important to the energy budget of gray whales within Clayoquot Sound, and may differ within the Sound between species, location (e.g., bays), and time.

Energy content of prey is largely a function of stored lipids (Griffiths 1977). High arctic and pelagic species generally have higher lipid stores than temperate and benthic species, respectively (Norrbin and Båmstedt 1984). Griffiths (1977) reported a bimodal distribution in the caloric content of crustaceans corresponding to whether they were benthic or pelagic animals. Since stored lipids are used to offset periods of low food availability, Norrbin and Båmstedt (1984) argued that species living in variable environments generally have higher lipid stores. Benthic ampeliscids in Clayoquot Sound likely have lower caloric content than planktonic prey within the Sound and northern benthic prey.

Although the common amphipod prey in Clayoquot Sound are taxonomically closely related to the dominant amphipod in northern feeding grounds, caloric content of these species differs due to growth and reproductive patterns. *A. macrocephala* is the most common prey species in the northern feeding grounds (Rice and Wolman 1971) and comprises 80% of the benthic biomass (Highsmith and Coyle 1990). *A. macrocephala* is a slow growing, long-lived species that reaches maximum lengths of 30 mm. By contrast, *A. agassizi* is the most common benthic amphipod in Clayoquot Sound (Dunham 1999) and grows to 8-11 mm in length (Dickenson 1982).

Further variation in caloric content occurs at the species level. Caloric content varies with reproductive status, life history stage, season, sex and nutritional history (Griffiths 1977). For example, Highsmith and Coyle (1990) reported an increase in caloric content over the summer sampling season. However, Klein *et al.* (1975) also cautioned that neither biomass nor production is constant throughout the year in ampeliscids and that this is important to note for those interested in ampeliscids as a food source for other organisms.

Individual prey size affects capture efficiency as well as energy return. Gray whales feed by suctioning up sections of benthos and sediment, engulfing prey in the water column, or by skimming swarming invertebrates at the sea surface (Nerini 1984). Most prey found in gray whale stomach content analyses are larger than 5 mm in length, reflecting the sieve size of the baleen (Rice and Wolman 1971). Grebmeier and Harrison (1992) presented further evidence that small sized amphipods are not retained by foraging gray whales. They found that the proportion of small (2-5 mm) amphipods in gray whale oral waste streams was much higher than their relative abundance in the benthos (71 and 34%, respectively).

4.3 Research Objectives

The objectives of this portion of my research are to describe population structure in benthic ampeliscid populations in Cow Bay and Ahous Bay and to determine biomass and caloric content of this benthic prey. Assessment of these population parameters is considered to be paramount in understanding the nature or drivers of prey-switching by gray whales. Estimates of biomass and caloric content enable comparisons with other prey types with respect to gray whale energetics. Measures of amphipod population structure used in this study are length frequency distributions, number of cohorts, minimum size at maturity, and percent of the population that is sexually mature or brooding.

4.4 Results

4.4.1 Biomass and morphometric measures.

Head length was used to predict less easily obtained measures: body length and dry weight. Head length is linearly related to body length in both *A. agassizi* ($r^2 = 0.81$, $P < 0.0001$) and *A. careyi* ($r^2 = 0.93$, $P < 0.0001$). Using regression models and dummy variables it was shown that body length size classes were predictable from two distinct regression equations for the two species (Figure 4.1).

Straight-line measures of body length are sufficient when the desired outcome is 1 mm-size classes. Amphipod body length was measured as a straight-line from tip to telson using a ruler mounted on the microscope stage. Straight-line measures were in very strong agreement with 1 mm body length size classes calculated from measurements made from digital images ($r^2 = 0.93$, $n = 17$). However, straight-line body length measurements were at least 1 mm smaller that those measured on the digital images, consequently a correction factor was applied to all amphipods measured in the field.

An exponential relationship was established between dry weight and body length using *A. agassizi* collected in 1999. Small sample sizes precluded determining dry weights for *A. careyi.* A single regression equation was used to estimate dry weight of ampeliscids collected in 1998 ($r^2 = 0.88$), since analysis of sampling periods only increased explanatory power of minimally: *A. agassizi* collected in July ($r^2 = 0.89$) vs. September ($r^2 = 0.90$) (Figure 4.2).

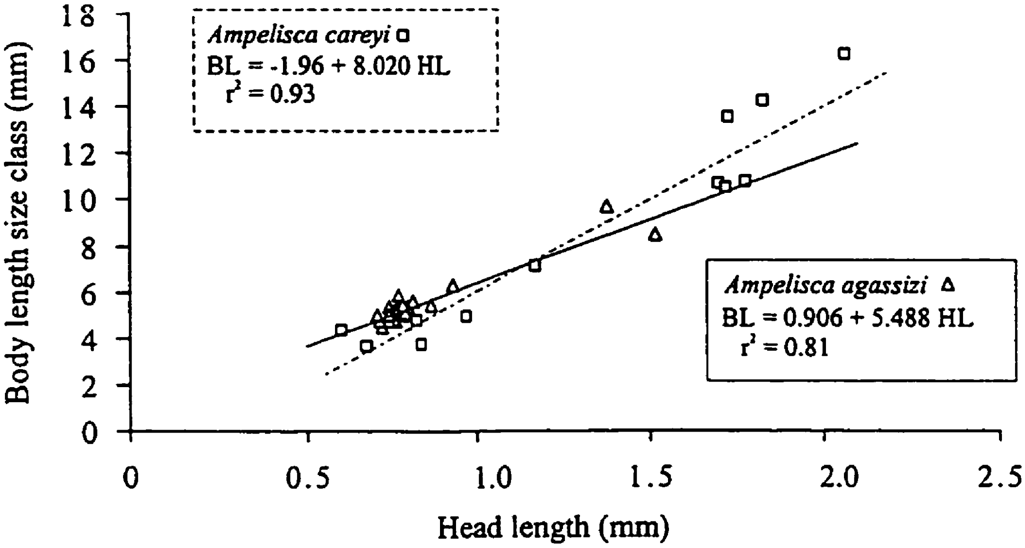

Figure 4.1 Linear regression of head length (HL) and body length (BL) for *Ampelisca agassizi* (△) and *Ampelisca careyi* (□). Body length was measured along the dorsal surface from digital images and head length was measured using an ocular micrometer.

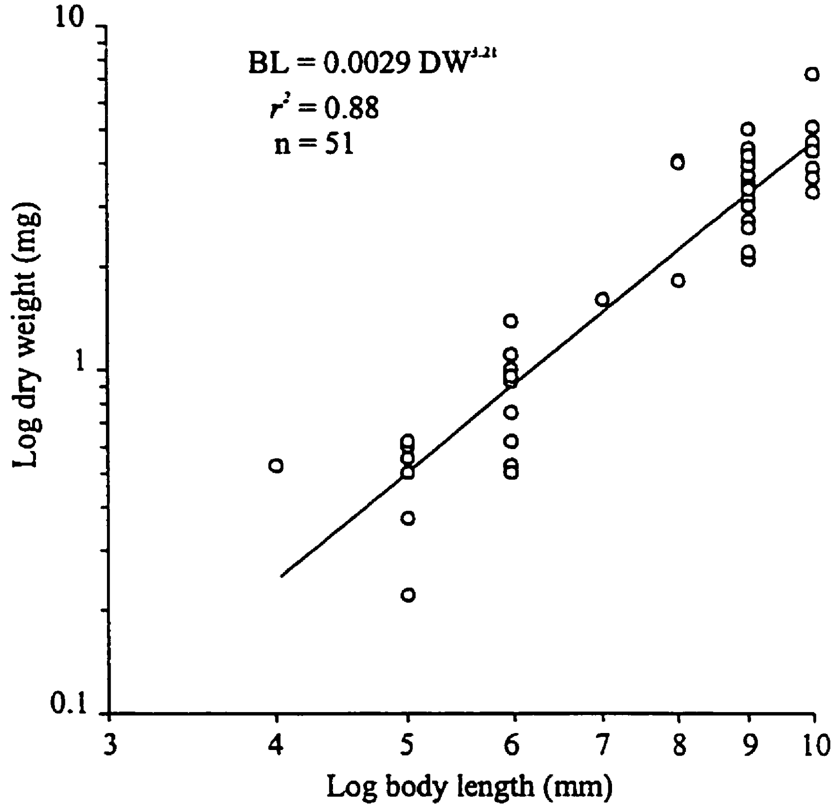

Figure 4.2 Relationship between log transformed body length size class (BL) and dry weight (DW). Minimum body lengths reflect sampling bias not minimum sizes of juveniles.

Organic carbon content of amphipods was measured to calculate ash free dry weight (AFDW). There was no significant relationship between amphipod body length and percent organic content (Figure 4.3). Further, organic carbon content was not different between amphipods sampled in July (43 ± 3%) and those sampled in September (37 ± 13%). An average of 40% organic carbon was used for all ampeliscids.

4.4.2 Population structure

There was little increase in average body length or dry weight over the 1998 sampling season but sampling date may account for some variation in either measure of amphipod size ($r^2 = 0.30$, for both relationships). More detailed scrutiny of residuals shows that these regression lines were largely influenced by a single data point. When the outlier, a 13 mm long amphipod, was removed, the regression coefficient dropped markedly ($r^2 = 0.009$ for body length, and $r^2 = 0.012$ for dry weight). Thus, there was no clear relationship between sampling date and amphipod size.

There are however, differences between species. *A. careyi* were larger than *A. agassizi* in 1998: average lengths were 9 mm (±3.4) versus 6 mm (±1.2), respectively. Bear in mind that 6 mm is close to the critical size needed to be retained by baleen. Accordingly, most *A. agassizi* collected in 1998 were smaller than minimum gray whale retention sizes: 84% of *A. agassizi* had body lengths of 6 mm or less. Only 34% of *A. careyi* were 6 mm or less in body length. Since only 7% of all amphipods collected in 1998 were *A. careyi*, the majority of benthic ampeliscids collected in July and August 1998 were smaller than gray whale baleen sieve size. There were proportionately more

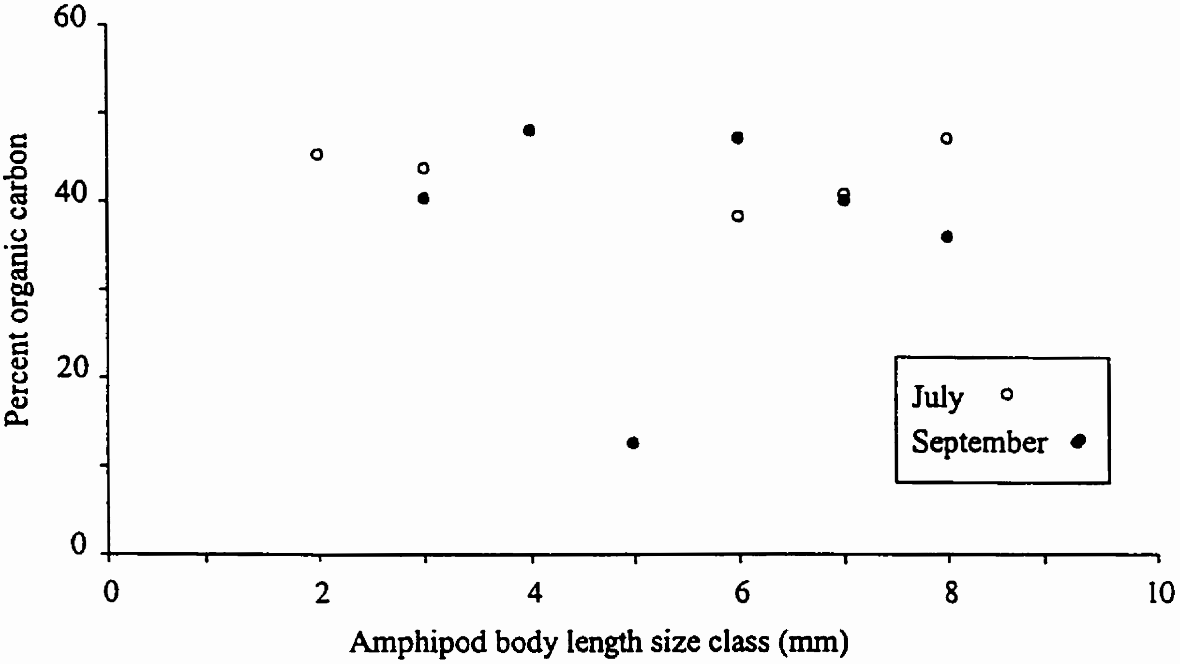

Figure 4.3 Percent organic carbon of amphipod dry weight for amphipods collected in July (○) and September (●) 1999 in relation to body length size classes.

large-sized *A. agassizi* collected in 1999 (35%). Sixty percent of *A. careyi* collected in 1999 were larger than minimum sizes of gray whale prey retention.

Interestingly, length frequency distributions of amphipods indicate that population structure differed between years in Cow Bay and Ahous Bay (Figure 4.4). *A. careyi* has a bimodal length frequency distribution, which is most evident in Cow Bay samples where *A. careyi* was more common. Length frequency distributions of *A. careyi* from Ahous bay are based on limited numbers (*n* = 8 in 1998 and *n* = 13 in 1999). Because of these small sample sizes, the frequency distribution should be treated with caution; nonetheless, there is some evidence of spatial variation in size distributions with geography. *A. agassizi* length frequency distributions from samples collected in 1998 are similar in Cow and Ahous bays. There is a single peak in the distribution profile centred on the 6 mm body length size class. The range of body lengths is smaller in 1999 but *A. agassizi* distribution profiles are bimodal in both bays.

Sexual characteristics were examined to determine the age and reproductive status of ampeliscid populations. Most amphipods with identifiable secondary sexual characteristics were immature females. Approximately 70% of the amphipods (from 1998 core samples) examined for sex determination had identifiable sexual characteristics (n=225): 11 males and 144 females. The minimum size of sexually mature male amphipods was 12 mm in *A. agassizi* and 13 mm in *A. careyi.* The minimum size of sexual characteristics (oostegites) could be identified in females was 8 mm in *A. agassizi*

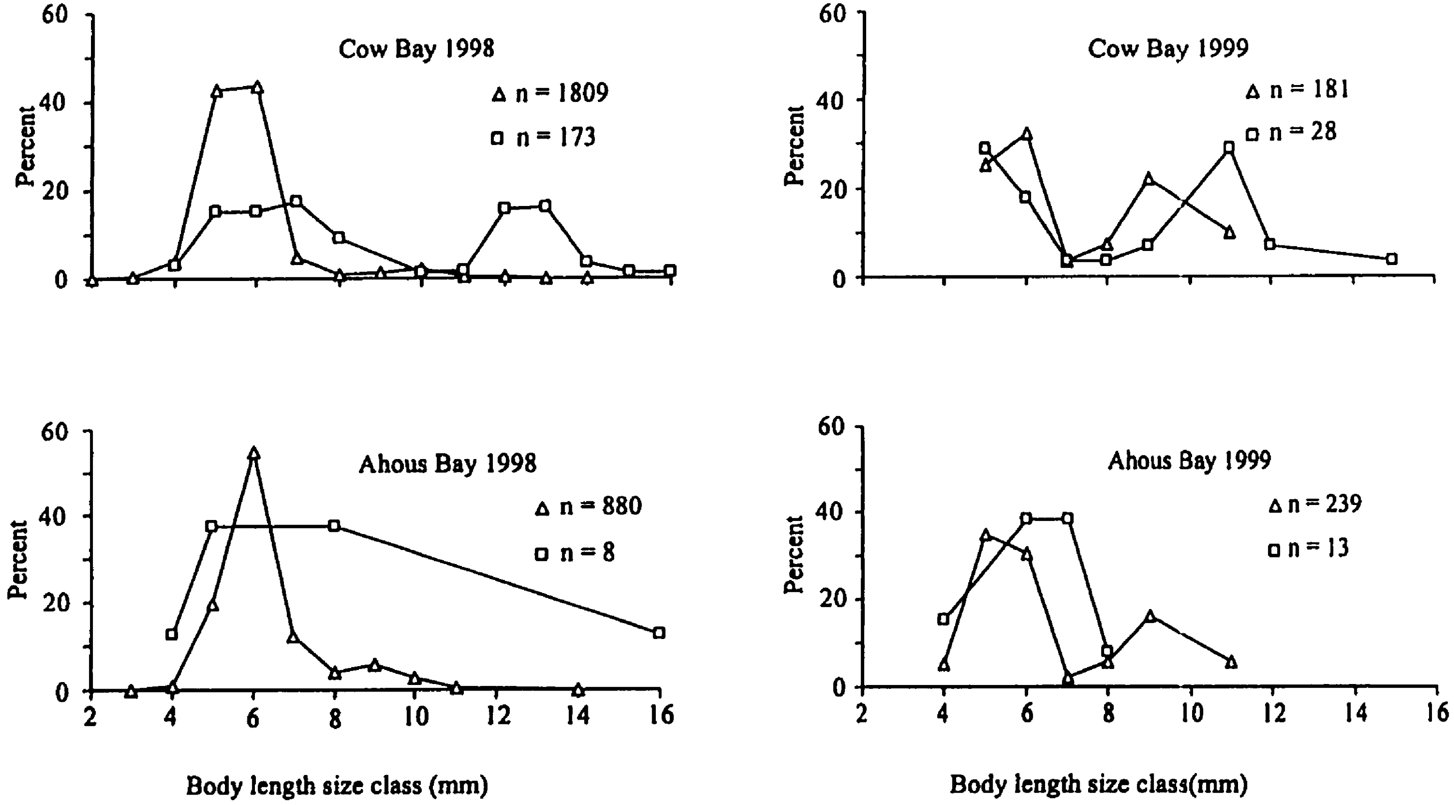

Figure 4.4 Length frequency distributions of ampeliscids collected from Cow and Ahous bays in both sampling seasons. The bimodal distribution of *A. agassizi* (△) and *A. careyi* (□) from Cow Bay in 1999 represents two cohorts.

and 11 mm in *A. careyi*. Despite this, not all amphipods larger than these minimum sizes could be sexed: 68% of *A. agassizi* and 62% *A. careyi* larger than 8 and 11 mm, respectively, had secondary sexual characteristics. Very few females were sexually mature, only six had setous oostigites (1 *A. agassizi* and 5 *A. careyi).* Minimum length at sexual maturity was 11 mm in *A. agassizi* and 12 mm in *A. careyi.* Four sexually mature *A. careyi* had eggs in the brood pouch. The only sexually mature *A. agassizi* was not carrying eggs. All sexually mature amphipods were collected from Cow Bay. One mature *A. careyi* was collected on August 4; all other mature ampeliscids were collected between August 18 and 20, 1998. Based on these small sample sizes it appears that growth and maturation rates differ between the bays.

No amphipods could be sexed from samples collected in July 1999. Twenty-three amphipods from September 1999 samples were examined for secondary sexual characteristics. Three immature females were found in September 1999 samples (1 *A. agassizi* and 2 *A. careyi*).

4.3.3 Caloric content

Caloric content was determined for large (>7 mm (see below for discussion on departure from findings of Dunham 1999 on critical size) amphipods since these would be retained by feeding gray whales. However, caloric content did not seem to increase with increasing body length and mean caloric content for all ampeliscids was 4.9 cal/mg AFDW (Figure 4.5). There was no significant difference in caloric content of *A. agassizi* taken from Cow Bay and those taken from Ahous Bay in September (*t* = 1.246, *df* = 18,

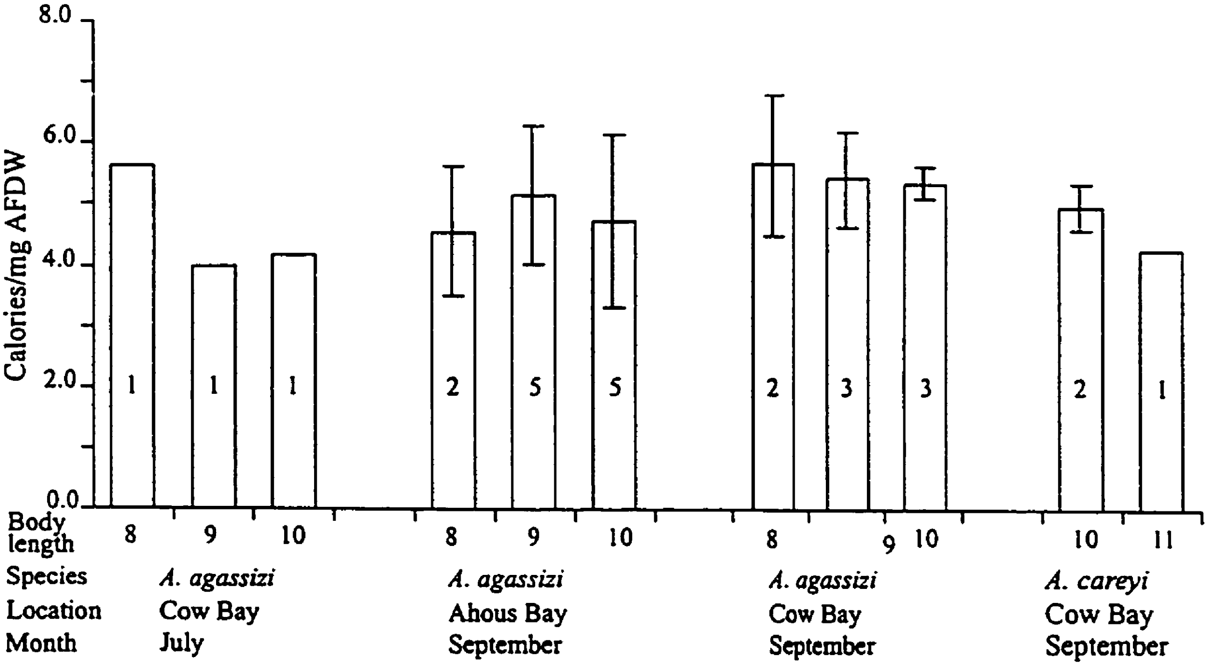

Figure 4.5 Caloric content of ampeliscids from Cow and Ahous bays and two sampling periods. Numbers inside bars represent the number of runs used to determine mean caloric value. Error bars represent ± 1 sd.

$P = 0.229$). However, when the data were considered on a temporal basis, there was a significant ($P = 0.1$) difference between mean caloric content of *A. agassizi* from different sampling periods ($t = 1.1812$, $df = 9$, $P = 0.52$). Amphipods collected in September from Cow Bay had higher caloric content than those sampled in July (Figure 4.5). Variances were not significantly different for both *t*-tests (Levene's test for equality of variances) (Sokal and Rohlf 1981).

4.5 Discussion

4.5.1 Morphometric and biomass measures of benthic amphipods

A strong relationship was established between head and body lengths. Dorsal body length from rostrum to telson can be predicted from head capsule measures. When the desired level of precision is 1 mm size classes, straight-line body length measures are sufficient. However, straight-line body length measurements were at least 1 mm smaller than those measured on the digital images. Consequently, a correction factor was applied to amphipods collected in 1999. This finding highlights the need to use comparable methods between studies. Dunham (1999) used straight-line measures of body length; therefore and importantly, the 6 mm size class discussed in Dunham's analysis is comparable to a 7 mm size class in this thesis.

There was no discernible relationship between ash content and body length or sampling season in this study. This differs from the results of Highsmith and Coyle (1991) who found that ash content decreased with increasing size and that there was a relationship between percent ash content and sampling season. Highsmith and Coyle (1991) used high percentages of ash to indicate recent molting. In contrast, my results compare favourably to those of Boates and Smith (1979) who also found that percent ash did not relate to body length.

Neither Boates and Smith (1979) nor Highsmith and Coyle (1991) specified whether they removed salt water from specimens, and salt water was not removed from specimens prior to drying in this study. High inorganic content in marine animals is contains inorganic salts, including seawater salts, silica, calcium phosphate and carbonate (Crisp 1984). Therefore, differences in percent ash weight may in part be a function of measurement protocol instead of differences between species. The other notable difference in these studies is that Highsmith and Coyle (1991) were measuring arctic amphipods, which may require higher lipid stores at the end of the summer as compared to temperate species.

Although inorganic carbon values were high, no conversion factors were applied to calorie determinations for the endothermic reaction. Crisp (1984) does not recommend correcting for endothermic reactions, since other sources of error likely offset any heat lost to endothermy. As well, comparable studies of marine benthic amphipods did not correct for inorganic carbon content (Klein *et al.* 1975, Boates and Smith 1979, Highsmith and Coyle 1992), so for the purpose of comparison, such conversion was not undertaken here. A fuse wire correction was done but there was no noticeable temperature change associated with the fuse wire.

The caloric content of benthic amphipods from Cow and Ahous bays (4.9 cal/mg AFDW and 2.9 cal/mg DW) is less than values reported for *A. macrocephala* from the Bering and Chukchi seas. The caloric content of *A. macrocephala* averages 4 cal/mg DW, although caloric value increased over the five-month sampling season (Highsmith and Coyle 1992). The difference in caloric content is due to factors other than latitudinal or temperature geographic gradients. Dauvin and Joncourt (1989) reported values of 5.1 cal/mg DW for ampeliscids collected from the English Channel, and Brawn *et al.* (1968) reported intermediate values (3.7 cal/mg DW) for amphipods from Nova Scotian waters. However, for the purposes of this study it is important to note that ampeliscid caloric value is lower in Clayoquot Sound than in the northern feeding areas on a per individual item basis.

4.4.2 Amphipod population structure and implications for gray whale feeding

Amphipod populations were sampled early in their reproductive cycle. Samples were primarily composed of juvenile amphipods that could not be sexed and most sexed specimens were immature females. This has implications for estimation of the caloric value of the amphipods as prey, since sexually mature females, especially egg carrying individuals, typically have the highest caloric content within a population (Griffiths 1977, Mauchline 1980). Very few male amphipods were found. However, one must note that most of the sexed individuals were immature females and adult males can only be identified after the last molt (Mills 1967); males were not clearly identifiable at the time of sampling. Moreover, mature males are both rare and undersampled in benthic surveys because of their increased time in the water column where they face higher predation (Mills 1967). Banard (1960) commented that "sexually mature males are exceedingly rare generally in the proportion of 1 to 50 or 1 to 100" in Californian sublittoral ampeliscids (in Mills 1967). Given the age of the sample population and the difficulties in identifying males, it is not surprising that proportions are even lower in this study (1:170).

Other researchers reported 1-2 year life cycles for ampeliscids in temperate waters (e.g., Mills 1967, Klein *et al.* 1975, Collie 1985). Length frequency distributions show that Clayoquot Sound ampeliscids probably have a 1-2 year life cycle. Peaks in length frequency histograms are interpreted as separate cohorts within amphipod populations (e.g., Highsmith and Coyle 1991). Although cohort analysis typically spans a longer time period than that sampled here, the bimodal distribution profiles of benthic ampeliscids from Cow Bay and Ahous Bay indicate two generations (Figure 4.4). The large peak is centred one the 6 mm length class, suggesting that the majority of amphipods sampled in 1998 were young of the year. The lack of concordance between *A. agassizi* and *A. careyi* suggests that different ecological processes are affecting growth and reproductive rates in these ampeliscids.

These results suggest that gray whale foraging may closely be linked with amphipod population structure in Clayoquot Sound. Gray whales primarily fed on pelagic prey during the summers of 1998 and 1999 (Meier pers. comm 1999, Tombach pers. comm. 1999). There were no confirmed sightings of gray whales bottom feeding in Cow and Ahous bays until mid September in both years. In 1999, two whales occasionally bottom fed in Cow and Ahous bays in late September and were steadily feeding by mid-October. By November 4, six were feeding in Ahous Bay and two in Cow Bay (J.D. Darling pers. comm. 1999). A similar feeding pattern was observed in 1998 (J.D. Darling pers. comm. 1999). Bottom feeding began later than usual in these years. By October and November, the large cohort of immature amphipod would have grown to minimum gray whale retention size, and probably reached sexual maturity by the time bottom feeding began.

4.5.3 Gray whale energy requirements

My results permit the construction of a simple energy budget for gray whales foraging on amphipods in Clayoquot Sound. Estimates of gray whale energy requirements are based on respiration data and whale size. Wahrenbrock *et al.* (1974) measured lung volume and oxygen consumption on two captive juvenile gray whales. The equation developed from these data and Kleiber's (1975) conversion (4.8 kcal required for each litre of oxygen consumed), were used to calculate daily energy requirements. Averaging various energy calculations and adjusting them for a 20 t gray whale yields a daily energy requirement of 3.8×10^5 kcal (Table 4.1) (Highsmith and Coyle 1992).

Table 4.1 Estimates of gray whale daily energy requirements. Modified from Highsmith and Coyle (1992).

Source	Comments	Daily energy requirement[1] (kcal d^{-1})
Rice and Wolman (1971)	Based on estimated lung volume and fat oxidation.	3.7×10^5
Sumich (1983)	Based on estimated rates of lipid depletion in migrating whales.	3.7×10^5
Thomson and Martin (1986)[2]	Estimated capture and digestive efficiency.	2.6×10^5
Highsmith and Coyle (1992)	Based on tidal lung volume and energy released for oxygen consumed.	5.2×10^5
Mean		3.8×10^5

1) Daily energy requirements are calculated for a 19.6 t individual.
2) From Highsmith and Coyle (1992).

Since few migratory gray whales feed throughout the year, the daily energy requirement must be adjusted to account for days spent fasting. Highsmith and Coyle (1992) doubled the averaged daily requirement based on the assumption that gray whales only feed for 6 months of every year (7.6×10^5 kcal d^{-1}). In this study I make a more conservative assumption that gray whales feed for 8 months of the year, which is based on reports of feeding on the northern migration (Braham 1984) and timing of migrations. Gray whales begin arriving on the breeding grounds in late December and the majority has left by mid-March (Jones and Swartz 1984). Further, gray whales have been reported feeding in Clayoquot Sound from April through to October (Darling *et al.* 1998). Accordingly, the more conservative estimate of 5.7×10^5 kcal/day is used in the remainder of this thesis. This value was calculated by multiplying daily requirements by 1.5 assuming that whales feed for 8 of the 12 months of the year.

Important to the argument that follows is that gray whales summering in Clayoquot Sound do not have the energy losses associated with migrating to northern waters. Sumich (1983) estimated energy used on the southern migration from breathing rates and average weight loss between north and southbound migrants to be 0.10 kcal kg^{-1} km^{-1}. Given the distances involved, forgoing the balance of the journey to the northern feeding grounds represents a substantial energy savings. Gray whale migrations typically span 50° of latitude and 8000-9000 km in each direction (Rice and Wolman 1971). Clayoquot Sound is roughly located in the middle of the migration route and migrating whales travel approximately 4000 km to reach this feeding area. This results in a saving of 1.6×10^7 kcal, or in other words, the energy required for 28 days.

4.4.4 Caloric value of benthic amphipods in compared to other prey types

Measured caloric values of benthic ampeliscids were lower than those reported for other gray whale prey types, though most of these estimates come from other geographic regions (Table 4.2). Calculated values from this study are an order of magnitude less than those reported for the Chirikov Basin, in the northern Bering Sea, and lower than those for other amphipod prey. However, caloric content measured in this study is not directly comparable to all values listed in Table 4.2.

Table 4.2 Comparison of biomass and caloric estimates of gray whale prey.

Location	Prey type	AFDW (g m^{-2})	Calories (kcal m^{-2})	Study
Puget Sound WA [1]	Ghost shrimp	219	1172	Weitkamp et al. 1992
Clayoquot Sound, B.C.[2]	Mysids	210	1066	Guerrero 1989
Clayoquot Sound, B.C.[2]	Mysids	3.5	18	Dunham 1999
Chirikov Basin, AK	Benthic amphipods	52.7	230	Highsmith and Coyle 1992
Pachena Bay, B.C. [3]	Benthic amphipods	(31.6)	(154)	Oliver et al. 1984
Cow and Ahous bays, B.C. (whales feeding)[3]	Benthic amphipods	15 (26.5)	75 (125)	Dunham 1999
Cow and Ahous bays, B.C.	Benthic amphipods	9.7	28	This Study

(1) Biomass values were reported for fresh frozen shrimp, they were converted to AFDW using Riccardi and Bourget's (1998) values for Decapoda.

(2) Estimates of mysid biomass were reported in formalin wet weight, converted using Riccardi and Bourget's (1998) values for Mysidacea and average caloric content values for mysids compiled from Mauchline (1980).

(3) Dunham (1999) and Oliver *et al.* (1984) reported biomass in formalin preserved wet weight. These values were converted to AFDW using Riccardi and Bourget's (1998) conversion values for amphipods and multiplied by caloric values calculated in this study. Values in parentheses indicate caloric content of all amphipod biomass – values are not adjusted for amphipod size. Oliver *et al.* (1984) did not discuss benthic amphipod size.

Caloric content measured in this study can be compared to values calculated for the Chirikov Basin, which are an order of magnitude higher. Although Highsmith and Coyle (1994) did not specify the size class used in calorie determinations, the majority of ampeliscids on the northern feeding grounds are larger than 6 mm. Dunham (1999) attributed higher biomass values per square metre near feeding gray whales to a larger portion of amphipods greater than 6 mm (7 mm in this study; see Section 4.5.1). These proportions were used to calculate amphipod biomass and caloric content available for foraging gray whales. However, the caloric content of benthic amphipods fed on by gray whales is still far below those reported from the northern feeding grounds. Biomass estimates for Pachena Bay are included for comparison but could not be adjusted for prey size, since amphipod size was not reported (Oliver *et al.* 1984); actual caloric value of these ampeliscids may well be lower than presented here.

The considerable difference in biomass estimates of Clayoquot Sound mysid prey may reflect differences between years or sampling locations, but is more likely a function of different sampling protocol. Dunham (1999) sampled mysids using a plankton net, whereas Guerrero (1989) estimated densities from underwater photographs of mysid swarms. Both values are included, since it is not known which is actually a better approximation of the correct mysid caloric value within Clayoquot Sound.

Importantly, infaunal populations are not subject to the same sampling difficulties as pelagic or epibenthic species. Aside from Guerrero's (1989) estimate of mysid densities as discussed earlier, caloric value of littoral ghost shrimp from Puget Sound mud flats are markedly higher than other prey values. Weitkamp *et al.* (1993) noted that ghost shrimp studied provided 2-15 times higher standing stocks than any other reported prey. Foraging on littoral ghost shrimp is limited by factors other than energy value. Gray whales foraging on littoral ghost shrimp are limited to high tide periods and whales incur risks of being stranded. Weitkamp *et al.* (1993) suggested that ghost shrimp might be highly vulnerable to gray whale foraging since they have long lives (>4 years) and a limited depth range or habitat, and thus populations can be relatively easily decimated.

Gray whales do feed on ghost shrimp within Clayoquot Sound but this feeding method appears to be restricted to young whales, and feeding on this resource is episodic, being separated by extended periods of non-use (Darling *et al.* 1998). Although ghost shrimp have by far the highest energy value, gray whale foraging on this prey type likely reflects processes other than caloric content, such stranding risk and long-term density and biomass levels. The extent of possible impacts of foraging events on the prey population is suggested by the long time periods between gray whale foraging events in Grice Bay, the ghost shrimp habitat within Clayoquot Sound.

Feeding effort required to maintain daily energy requirements for benthic amphipods can be estimated from caloric densities, feeding pit size and number of foraging pits created per dive. The following estimates are based on mean feeding pit size of 2 m^2 (Kvitek and Oliver 1986, Nelson *et al.* 1987), six pits per feeding dive (Oliver *et al.* 1984) and feeding rates of 20 dives per hour (Oliver *et al.* 1984). In the northern feeding grounds daily energy requirement (5.7×10^5 kcal d^{-1}) could then in theory be met by steady feeding for approximately ten hours. This estimate is not unreasonable as six hours of continuous feeding have been documented (Oliver *et al.* 1984). In contrast, amphipod (caloric) densities are not sufficient to provide daily energy requirements in Clayoquot Sound. Using caloric values based on amphipod biomass near feeding gray whales (Dunham 1999) a gray whale would have to feed on benthic amphipods for some 32 hours to fulfil daily energy requirements, which clearly is impossible. Energy return is considerably lower when calculated from 1998 and 1999 biomass estimates. Thus, gray whales may require the variety of more dense and caloric rich prey resources within the Sound.

Darling *et al.* (1998) suggested the prey assemblage instead of a single key species is important to whale distribution and feeding behaviour within the Sound, though this conjecture was not based on estimates of energetic return. My results show that the biomass, size, and caloric content of benthic amphipods are insufficient to meet gray whale's daily energy requirements. Gray whales remaining in Clayoquot Sound throughout the feeding season must include other energy-rich prey types in addition to or instead of benthic amphipods.

CHAPTER 5: GENERAL DISCUSSION

5.1 Summary

Ampelisca agassizi is the dominant benthic amphipod in fine sand substrates of Cow and Ahous bays, followed in abundance by *A. careyi*. Distribution patterns and relative abundance of these two species shifted over the course of the two years studied (1998-1999). During the first sampling season there appeared to be strong spatial segregation between the two species corresponding to the two bays sampled. However, this relationship did not hold for the following year; spatial segregation was lessened and abundances of the two species were not correlated in 1999. Relative abundance of *A. careyi* and *A. agassizi* has important implications for gray whale foraging. The average size of *A. careyi* was larger than the minimum prey size that gray whales can retain on their baleen filter, whereas the average size of *A. agassizi* was not.

Amphipod populations were sampled early in their reproductive cycle and were predominantly comprised of sexually immature, small individuals. However, the findings of this research also show that the energetic demands of gray whales feeding within Clayoquot are such that they could not be solely supported by amphipods based on the composition, density, size and caloric content of the two dominant ampeliscids. This condition necessitates feeding on other more energy-rich prey types.

The caloric content of benthic ampeliscids averaged 4.9 cal/mg AFDW. This is lower than that reported for ampeliscids in the primary feeding grounds of the Bering and Chukchi seas but within the range reported for other benthic amphipods found in temperate waters. However, densities of large sized amphipods was such that the energy return associated with amphipod tube mats in Cow and Ahous bays was lower than calculated values for other prey within the Sound. This finding supports the suggestion of other researchers that gray whale bottom feeding on benthic amphipods occurs when other prey types are not available (e.g., Guerrero 1989, Kim and Oliver 1989, Dunham 1999) or, I believe, later in the fall when amphipods reach a larger size.

Benthic prey distributions and population structure are also important for the ability of a species to recover from gray whale feeding disturbance and predation. Thus, knowledge gained in this study is applicable to future studies of the impacts and, hence, long-term foraging patterns of gray whales within the Sound. Gray whale bottom foraging represents a landscape level disturbance event in amphipod tube mats. The importance of disturbances, such as gray whale bottom feeding, in structuring bottom communities is a product of the extent, frequency and duration of disturbance relative to ability of the prey species to recolonise (e.g., mobility and reproductive potential and timing) (Zajac and Whitlatch 1991). Researchers agree that gray whale bottom foraging shapes benthic communities; however, there are different scenarios based on the relative importance on different aspects of amphipod biology, such as habitat selection and the timing and rates of reproductive events.

Two contrasting views have been proposed to explain the impacts of gray whale foraging on benthic amphipod populations in the primary feeding grounds. Johnson and Nelson (1984) stated that gray whale bottom feeding modifies sediments in a way that benefits the long-term persistence of their primary prey. Whereas, Coyle and Highsmith (1994) argued that gray whale foraging negatively affects future gray whale feeding because the timing of disturbance events is such that smaller, less energetically important species are better able to recolonise the disturbed area. Both hypotheses have been applied to feeding grounds in more southern waters (e.g. Oliver *et al.* 1985, Weitkamp *et al.* 1993, Darling *et al.* 1998) though I believe neither is appropriate for Clayoquot Sound.

In this study, both species of ampeliscids were associated with fine-grained sand in Cow and Ahous bays. In the Bering and Chukchi seas, and specifically on the Beringan Platform, ampeliscid tube mats only dominate the areas with relict fine sand (Nelson *et al.* 1987). Ampeliscids are not abundant in regions overlaid with silt and clay sized particles from the Yukon River drainage. Nelson *et al.* (1987) argued that gray whales maintain a sand habitat by injecting sediments into the water column and the silts and clays are carried from the Beringan Platform by a constant northward current - maintaining silt-free habitat.

Coyle and Highsmith (1994) argued that the timing of gray whale feeding patterns relative to amphipod growth rates was such that gray whale predation favoured an increase in smaller, less energetically important benthic amphipods. Further, Coyle and Highsmith (1994) hypothesised that space was a limiting resource for benthic amphipods in the Bering and Chukchi seas based on knowledge of amphipod reproductive patterns and oxygen consumption in these areas. My research shows that the abundance ratio between ampeliscids shifted over the two seasons. But to evaluate the possible role of gray whale foraging on species composition in Cow and Ahous bays an analysis, parallel to this one, of amphipod population structure while whales are bottom feeding is needed.

5.2 Future Study

The results of this work suggest many avenues for future research in Clayoquot Sound. Understanding the linkages between the physical environment, prey and foraging whales could be greatly increased by focussed study of the following three areas. First, our ability to evaluate the differences between the bays and food supply depends on an understanding of water flows and sedimentation rates within the bays. A detailed study of differences in sedimentation rates within and between Cow and Ahous bays could identify causal mechanisms for differences in amphipod growth and maturation rates between the bays identified in this study (e.g., Lehtonen and Andersin 1998). Further, an understanding of the oceanographic and sedimentological patterns in the bays is required to evaluate Johnson and Nelson's (1984) hypothesis.

Second, the shift in relative abundance between these two species identified during the course of this study is also particularly intriguing and bears on gray whale feeding. The ecological relationship between these species would be further clarified by detailed analysis of annual growth rates and of resource use. A study of gut contents in these species would be helpful in identifying causal mechanisms for shifts in relative abundance.

Last, and perhaps the most important finding of this study in terms of gray whale feeding ecology is that whales are not able to meet their daily energy requirements from feeding exclusively on benthic amphipods. How then do whales meet their annual energy requirements by foraging in Clayoquot Sound? This question could be answered by documenting the foraging patterns of individual whales throughout the foraging season including analysis of prey density and energy content for species other than benthic amphipods.

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