

MYSIDS OF QUEEN CHARLOTTE STRAIT: NOTES ON THEIR ECOLOGY,  
SWARM COMPOSITION AND DISTRIBUTION

by

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## Abstract

Kelp beds that were observed to be frequently visited by gray whales in a region of Queen Charlotte Strait were sampled for mysids during July to September, 1999. Net and photographic samples revealed 9 species in the area with *H. sculpta* and *A. columbiae* dominating. Swarms were principally juvenile and polyspecific in composition. Swarms displayed a high degree of coordination with specific orientations and distribution. Observed nearest neighbour distances ranged from 0.94 (0.041) to 2.82 (0.206) cm. Mean densities were large at about 600 individuals L<sup>-1</sup> and may reflect the usage of gray whales in these tertiary feeding grounds.

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## 1.0 INTRODUCTION

In the past few years, mysids have become important to scientists, fisheries personnel and even the public as species for research. They also represent a significant food source for commercially important fish and marine mammals. Mysids demonstrate intricate social behaviours that play a large part in determining their distribution and organization. These processes occur in marine environments where variability in currents, productivity, gradients of salinity and temperature and a number of other environmental conditions generate a very dynamic habitat.

The mysid marsupial pouch is one distinguishing feature of this group; for this reason, mysids are often referred to *as opossum shrimp*. However, although shrimp-like in appearance, mysids are actually crustaceans in the order Mysidacea. They are characterized by an aggregative existence, forming assemblages that can extend up to several hundred metres in length.

Despite their widespread occurrence, there are few data on the ecology and population structure of nearshore mysids along the coast of British Columbia. In particular, the marine environment of Queen Charlotte Strait is relatively unexplored. Investigations on the ecology of the Mysidacea in this area will serve not only to enhance our knowledge of their social structure and distribution, but may also provide useful information for studies of the feeding ecology of the locally abundant marine mammals.

## 1.1 HISTORICAL WORK

Work in the late 1800s and early 1900s from the freighter “Albatross” initiated further studies on Northeastern Pacific mysids by Holmes (1895, 1900) and Tattersall (1933). New species were described by Banner (1948, 1954) and later enhanced by the collections made by Holmquist (1973, 1982). About one third of the information on mysids in the Northeast Pacific is based on the knowledge gathered from species that have wide ranges, occurring in other waters (Kathman *et al.* 1986). However, these represent taxonomic studies that were concerned with identification rather than

descriptions of their composition or structure in assemblages. Therefore, it is necessary that further Northeastern Pacific mysid research be conducted to contribute to this limited information and offer relevant data to worldwide populations as well.

## 1.2 MYSID ECOLOGY

### 1.2 .1 Taxonomy

There are approximately 780 known species of mysids in the world. The Northeast Pacific supports about 58 species in habitats ranging from oceanic to neritic, littoral and freshwater (Kathman *et al.* 1986). The presence of a ventral marsupium or brood pouch classifies mysids in the Superorder Peracarida. As the largest Family, Mysidae encompasses the majority of the species found off the waters of British Columbia; members of this group possess the unique trait of a statocyst on the uropod.

### 1.2.2 Distribution

Mysids occur in both freshwater and marine environments, but are found principally in marine systems where they occur in association with various substrates including sand, gravel, rock, seaweed, caves and recesses. Some mysids burrow into the sand during the day and emerge again at night, while others live among algae and feed in the open water column at night. Substrate specificity has been studied by O'Brien (1988) who concluded that this quality is particularly evident in benthic species compared to those that are more planktonic in habit. In their study of Northwestern Pacific mysid species, Ohtsuka *et al.* (1995) found that substrate affinity was also species-specific. The Northeast Pacific mysids of interest in the present study are neritic in habitat and are usually either benthic or epibenthic.

### 1.2.3 Social organization and behaviour

Mysids assemble in groups of various shapes and sizes. Common forms include spheres, ellipses and extensive mats consisting of many individuals. A number of different terms based on size, motility and orientation of its members are used in describing such groups. According to Modlin (1990), a **swarm** is a small assemblage that is less than 1.0 m in length or diameter, composed of non-polarized or non-oriented individuals. A **school** has individuals that are migratory and uniformly orientated and is less than 2.0 m in length or diameter. A **shoal** is greater than 2.0 m in length or diameter, with individually spaced, polarized, swimming mysids. Other definitions have also been proposed but all involve some aspect of social interaction and geometric form (O'Brien, 1988). To simplify matters, I hereafter refer to any group of mysids as a swarms or aggregations (regardless of orientation or size) and will only consider motility in a qualitative sense in my analyses.

### 1.2.4 Hypotheses on the adaptive significance of swarming behaviour

There have been many hypotheses proposed to explain the adaptive benefit of swarming. Mauchline (1980) believed that protection and reproductive convenience were the two main motives for swarming behaviour. Having mature males and females present in the same area increases the chance of successful mating. Swarming for defense and feeding purposes were two proposals stressed by Ohtsuka et al (1995). For example, escape from visual predators was made possible by the camouflage attributed to the brown mysid ***Paracanthomysis hispida*** against beds of certain ***Sargassum*** sp. As well, areas of increased copepod and diatom concentrations such as in beach surf zones were observed to support mysids. O'Brien (1988, 1989) also suggested that mysid organization is biologically rather than physically induced and that any variability is due to adaptation by specific species. By species-specific variability O'Brien was referring largely to differences in substrate preference. For instance; ***Tenagomysis*** sp. was found to be associated with sand, whereas ***Doxomysis*** sp favoured rock and algae. O'Brien cites gregariousness, lack of a solitary life phase and monospecific clustering among the evidence for the innate nature of group formation.

The reasons underlying clustering are considered to be adaptive and to confer some sort of evolutionary advantage. In laboratory studies of *Neomysis mirabilis* Zelickman (1974) concluded that the spatial patterning of swarming individuals is a protective mechanism that has been “evolutionarily optimized”. This was suggested by the constancy of position maintained despite possibly threatening situations. Distributional packing within the swarm (*i.e.* involving specific distances maintained between individuals) was attributed to regulatory stimuli such as visual cues and vibrations in the water. Shadow casting and experiments involving decreasing illumination were also performed in this investigation. The reduced light intensities resulted in a response that was termed “locomotory chaos” where disorganization and erratic movement patterns were present. This further demonstrated the capacity for nervous control by mysids. This notion is also supported by Modlin (1990) who found that an increase in light intensity resulted in increased organization by mysids as a collective. Thus, (i) maintaining a favourable position in a favourable environment, (ii) reducing dispersal via currents and (iii) reducing risk of predation seem to be the most likely explanations for group organization in mysids. Zelickman (1974) suggested that factors such as current speed and direction, light intensity and other features of habitat, that are themselves variables, were insufficient in explaining the integrated swarms that are characteristic of mysid groups. Passive physical aggregation due to hydrological processes control large scale patterns and thus, serve as a framework for the smaller scale patterns that have been attributed to social behaviour (Levin, 1992).

#### 1.2.5 Population structure

Unlike the monospecific swarms observed by O’Brien (1988, 1989), Ohtsuka *et al.* (1995) investigated polyspecific swarms in temperate and subtropical waters. These swarms consisted of a single dominant species and up to 5 “guest” species. Dominant species accounted for between 50 to 100% of the individuals in the group. Thus, there appears to be two models of species composition in a typical swarm.

Swarm composition also seems to be variable in terms of the age classes present. For instance, Modlin (1990) found that a given swarm would often include both juveniles and

mature males and females. In these swarms, individuals have been found to segregate vertically according to size and/or maturity, with juveniles on top, followed by mature males and females, gravid females and the largest males at the bottom. However, Mauchline (1980) also found groups composed solely of juveniles as well as others that consisted of a mixture of juveniles and adults.

Mysid assemblages can thus be either monospecific or polyspecific with a dominant species, and either uniform or diverse in the range of developmental stages present. Consequently, there doesn't seem to be a standard "design" to mysid group composition. However, the unifying concept is that mysid organization has been found to incorporate consistent interindividual spacing, group behaviour and relative age structure uniformity. This has been found to be the case even within those clusters that include several life stages.

#### 1.2.6 Predatory response

Mysids also demonstrate integrated behaviour in response to potential predators. A study on *Mysidium columbiae* in mangroves by Modlin (1990) demonstrates the variable responses displayed. At the approach of a diver, the mysid swarms moved as a unit, maintaining a constant distance of about 0.5m if pursued. When retreating speeds weren't fast enough, an infolding in the assemblage at the end nearest the threat was observed, presumably to maintain distance from the potential predator. A physical disturbance often caused the fragmentation of the shoal into smaller swarms that consisted of a specific life stage. When further threatened, this coordinated splitting was often followed by "flash expansion", a technique that visually distracts the predator as individuals collectively perform skitters (Modlin 1990, O'Brien 1989). To the predator, the effect is that of witnessing an explosion of mysids. In addition, there was decreased nearest neighbour distance (hereafter NND or compaction and decreased polarization with greater threat. This range of responses has been documented in other studies (O'Brien and Ritz, 1988; Ritz *et al*, 1997) and demonstrates a level of coordination that is similar to those found in fish schools (Pitcher and Parrish, 1993).

## 1.3 MYSIDS AS RESEARCH SPECIMENS

### 1.3.1 Problems associated with sampling

Oviparous females and juveniles were found at each sampling period in a study by O'Brien (1988) as well as one by Carleton and Hamner (1989). Subsequent investigations have included samples taken from months throughout the year. This implies that mysids breed continuously and are readily available for population studies. However, the coordinated response of mysids to potential threats is a source of many problems when sampling. In particular, their rapid escape responses (Clutter, 1969; O'Brien and Ritz, 1988; Kim and Oliver, 1988) make it difficult to sample them effectively with nets. As well, the visual acuity and vibrotactile perceptivity (Modlin, 1990 and Zelickman, 1974) of mysids are impediments to accurate surveys of abundance and assemblage composition. Attributes such as sex ratios, frequency, size classes, density and species distribution are affected by undersampling or errors in sampling due to these mysid escape responses. In addition, swim speeds have been reported to be anywhere from 1 to 20 cm/sec (Mauchline 1980), a reminder that mysids are not the passive animals often associated with the term zooplankton.

### 1.3.2 The use of photographic techniques in mysid sampling

Given their behavioural repertoire it is therefore important that more than one technique be applied when investigating mysid swarm dynamics. Photographic techniques can give a better estimate of density (or at least enhance net-based estimates) than can net sampling alone. Even benthic traps that are designed to make use of mysid escape responses fail to give reliable counts because of the different assemblage types that can be present. Some assemblages are small, discrete spheres while others are massive shoals, making comparisons inaccurate when only portions of larger groups are counted (Carleton and Hamner, 1989).

## 1.4 THE IMPACT OF MYSIDS ON THE ECOLOGY OF GRAY WHALES

Gray whales (*Eschrichtius robustus*) have been recently removed from an endangered species listing and are recovering successfully from the effect of early 20<sup>th</sup> Century commercial whaling with an estimated eastern North Pacific population of 26,000 (Hobbs and Rugh, 1999). The annual migration of the gray whale consists of movement from winter breeding and calving grounds off Baja, California to summer feeding grounds in the Bering and Chuckchi Seas (Rugh, 1984) where they feed on a number of infaunal and benthic prey (Kim and Oliver, 1988). However, summer residency among part of the population exists along several locations outside of the typical Arctic feeding grounds.

Darling (1977) recorded the first observations of these residents off Vancouver Island, an aspect of gray whale ecology that has made research by the Coastal Ecosystem Research Foundation (CERF) possible. Since 1994, CERF has been investigating the gray whales in the area of Queen Charlotte Strait from Allison Harbour to Rivers Inlet along the Central Coast of British Columbia. This represents a portion of their tertiary foraging grounds that extend from Alaska to Baja, California (Kim and Oliver, 1988). This research has included the essential role of mysids in the feeding ecology of gray whales (currently under examination in a PhD study by Lei Lani Stelle of UCLA). Along the coast of British Columbia, mysids constitute the majority of the prey consumed by gray whales (Kim and Oliver, 1988). Thus, an understanding of the ecology of the principal prey of gray whales will be advantageous for determining carrying capacities as well as usage of specific feeding sites.

## 1.5 PRESENT INVESTIGATION

As previously mentioned, mysid ecology has not been extensively studied along the BC coast. This includes the remote locale of Queen Charlotte Strait. The purpose of this study is to obtain baseline data of mysid group structure and dynamics consisting of sex ratios, size classes, substrate affinity, species composition and abundance. This dataset will serve to provide a framework for future studies on the mysids in Queen Charlotte Strait and the Northeast Pacific.

Investigations by previous researchers have revealed that gray whales can be useful locators of the mysid swarms they prey upon. Gray whales have been observed by members of CERF to target certain kelp beds and not others. Subsequent dives in these areas have indicated a high mysid presence. Therefore, an analysis of nearshore mysid collections instead of oceanic collections was undertaken. Hand samples (collected using a plankton net) were combined with underwater video samples to assess the species composition, sex ratio, size variation and abundance of each swarm encountered. Representative neritic mysids in Queen Charlotte Strait exist in aggregations that have distinctive features of size, species presence and density or NND. Seasonal fluctuation in abundance or species associations, however, cannot be determined as this study was confined to the months of July to September, 1999. Thus, this investigation is limited in that the temporal effects of changes in food availability, predator numbers or climatic variability cannot be properly examined.

## 2.0 MATERIALS AND METHODS

### 2.1 STUDY AREA

Swarms of mysids were observed directly underwater in various kelp beds in Queen Charlotte Strait during the months of July to September, 1999. Dive sites were chosen based on recordings of gray whale foraging by CERF and incorporated a portion of those employed by the other researchers. Kelp beds were further targeted based on the absence of mysids outside these areas in the epibenthic tows of Murison *et al.* (1984). The study area includes kelp beds in Silvester Bay, Burnett Bay, North Bay and South Bay in Queen Charlotte Strait (Figure 1). In North Bay, these sampling sites were Zero Rock, Pisspot, No. 4 Reef and Skull Cove. South Bay sites comprised of the Emilies and Elizabeth Rock; Burnett Bay sites included Bumaby Rock, Y Beds and Mall Rock. Finally, there were two sites in Silvester Bay, not near any topographic reference points.

### 2.2 SAMPLING

There were two components involved in the sampling of mysid swarms in this investigation. Net samples were used to supplement video data that were gathered for density estimates. As previously mentioned, avoidance behaviour by mysids is an issue for any quantitative analysis. Therefore, net samples were used primarily to verify the composition of swarms both in terms of species and life history stages present.

#### 2.2.1 Equipment

Samples of mysids were obtained using a plankton net of 0.2 mm mesh size, 19 cm in diameter supported by a clear plexiglass rim to reduce the instigation of escape responses to an approaching net. The plankton net incorporated a cod end where several containers could be exchanged for new samples. Video data was recorded with an I.A.S. Seemate Underwater Video camera system. The apparatus consisted of the camera and lens unit within a metal net ring. This was attached by way of a 25m cable to a television and VCR unit on the surface that recorded the information. The video camera was originally

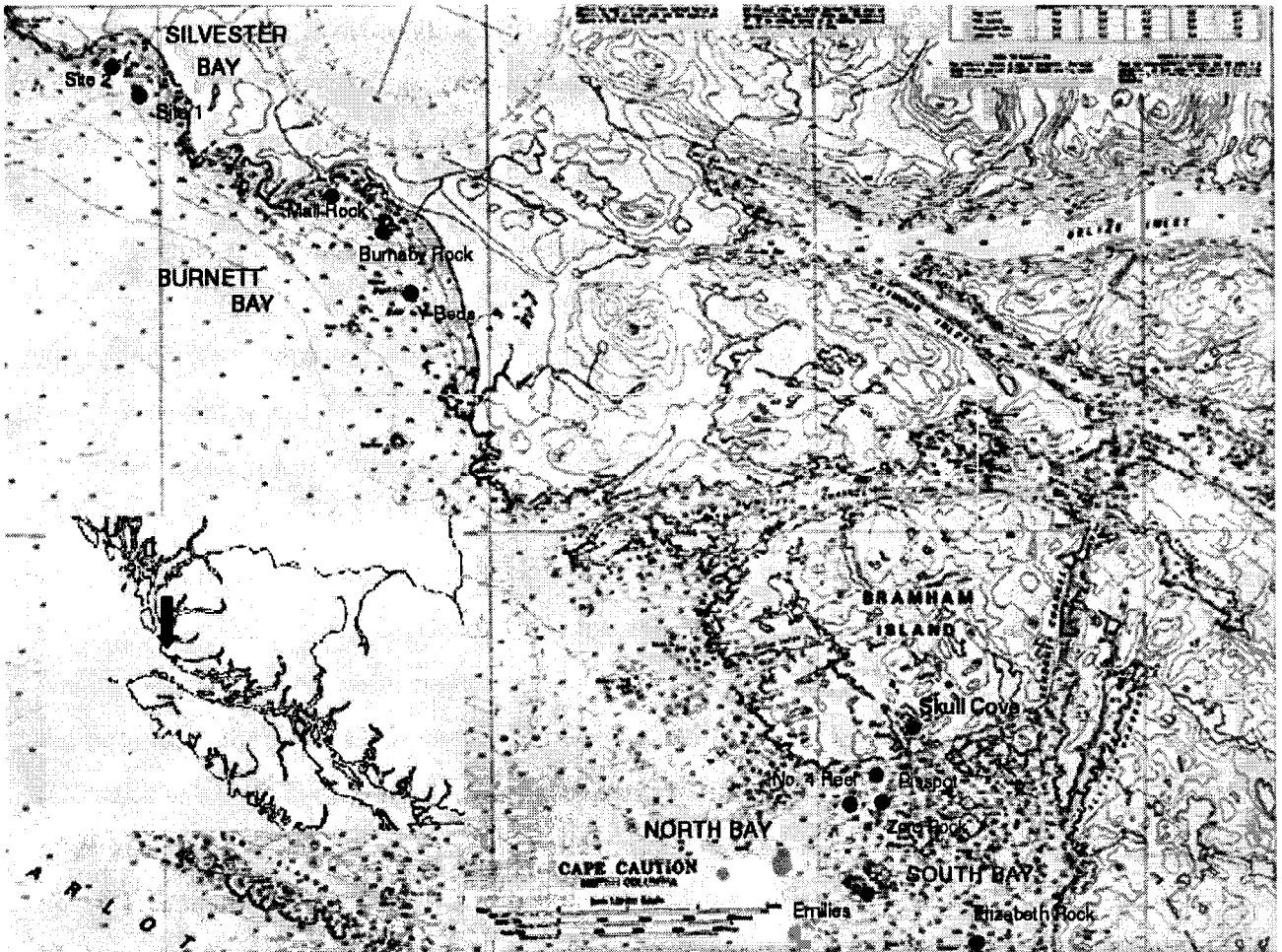


Figure 1. The study area in Queen Charlotte Strait depicting locations of dive sites in kelp beds and Skull Cove. Arrow denotes location off the coast of British Columbia.

meant for stationary recording but was converted to a moving camera system, connected to the boat on the surface. This was due to difficulties in obtaining available swarms near base camp and to later difficulties in finding a stable surface for the television and VCR once swarms were found. The consequence of this modification was the inability of the operator to view the footage during shooting underwater.

### 2.2.2 Sampling technique and data collection

Specimens were captured randomly at different stages of the tide and were generally found between 6 and 15 m of water. Divers swam until a swarm was observed which provided a sampling opportunity. Video was taken using different angles and backgrounds but a lateral view of the mysids was always sought for the camera. Some footage employed a black plastic background for better contrast but, unfortunately, this usually prompted escape responses from the mysids. Observations were made using a writing slate recording information on (1) bottom topography; (2) depth recorded from the bottom of the swarm; (3) swarm dimensions using diver body length approximations (Ohtsuka *et al*, 1995); (4) presence of a current; (5) presence of gravid females; and (6) other additional behavioural data. The collecting diver performed several swoops with the net and funnelled the specimens into the cod end where a new container was present. Multiple swarms were sampled during each dive where possible using the detachable containers on the plankton net. In preparation for subsequent swarms, the net was shaken out to prevent previous individuals from being present. Upon completion of the dive, samples were transferred to storage bottles and preserved using a solution of 5% buffered formalin in seawater.

## 2.3 DATA ANALYSIS

### 2.3.1 Microscope work

Preserved specimens were examined to determine species, sex and length for each swarm which was represented by one sample. Identification followed that of Kathman *et al* (1986) and Kozloff (1996). Diagnostic structures included the telson (Figure 2) and

rostrum (Figure 3) as well as the presence of abdominal folds and processes in the genus *Holmesimysis*. Sex was determined by the presence of a ventral marsupium in females and penes in males (Figure 4). Those individuals without these structures were classified as juveniles. Length measurements were made using the Scion Image@ image analysis software package tools and established by the length from the rostrum to the end of the last abdominal segment.

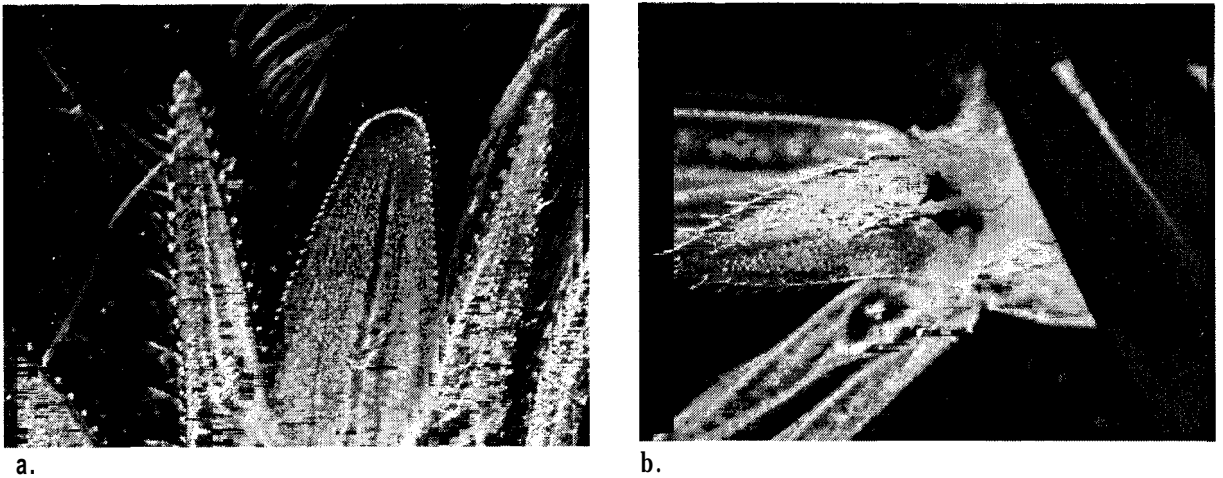


Figure 2. Telson structures of a. *Acanthomysis columbiae* showing several small spines around a rounded apex and of b. *Neomysis mercedis* showing larger spines with greater distance separating them *than* is found in *A. columbiae*.

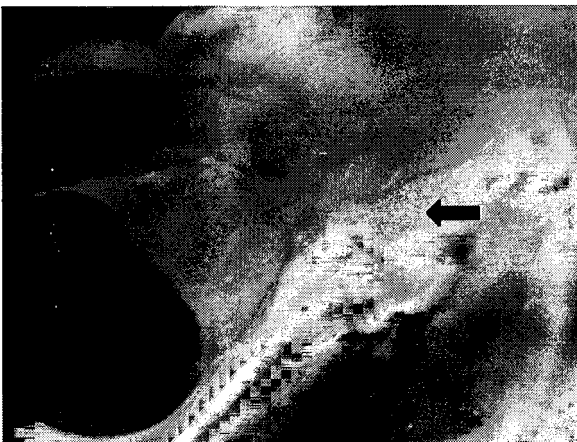
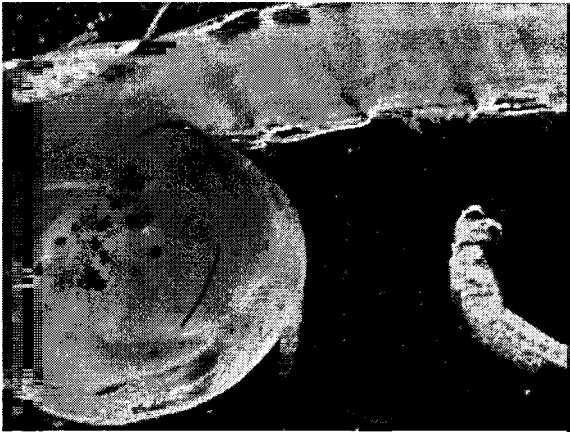
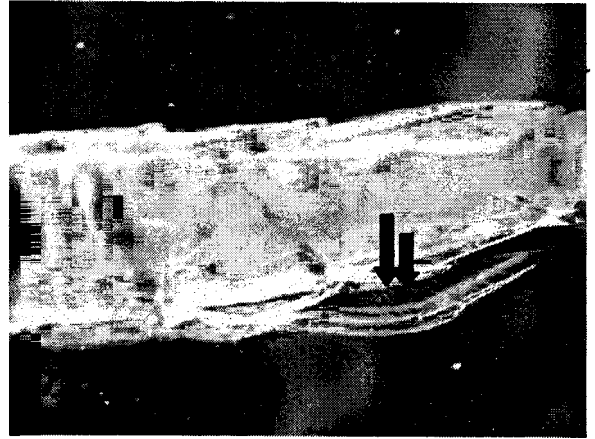


Figure 3. Supraorbital spine (*arrow*) on *the* rostrum of *Acanthomysis columbiae*.



a.



b.

Figure 4. Reproductive structures showing a. the marsupium of a gravid female and b. the male penes (arrow).

### 2.3.2 The use of nearest neighbour distance

Another way of looking at the concentration of mysids in a swarm is through the analysis of nearest neighbour distance (NND), the distance between two neighbouring individuals. NND is used to express the degree of aggregation of mysids assuming that this is a constant distance between all individuals in a swarm. The use of this characteristic as a swarm descriptor minimizes the effects of assemblage variability **i n** terms of the various shapes that a swarm can achieve. NND is also useful when dealing with the reality of high net avoidance (Ohtsuka et **al**, 1995) and thus, inaccurate abundance estimates. I used two different formulations for NND, each assuming a different packing geometry. The hexagonal close packing model assumes each individual to be at the centre of a sphere that when combined, occupies 74% of the total volume (Mackie and Mills, 1983). The density of N individuals is then calculated as:

$$N/\text{volume} = 1.41/\text{NND}^3 \quad ,$$

In a slightly different configuration, isahedronically packed individuals cluster symmetrically along all three axes and also have equal centre to centre dimensions

(Hamner and Carleton, 1979). Here, density can be calculated as follows:

$$N/\text{volume} = 1/0.589 \times \text{NND}_3$$

### 2.3.3 Video analysis for nearest neighbour distance

For each swarm, representative frames of video footage were used for NND determination. Frames were chosen for clarity of the image and the availability of adequately visible specimens. Consequently, several swarms were excluded from the analysis due to poor video resolution, excessive water debris or lack of insufficient contrast. The lengths of individual mysids were measured on screen using Scion Image@ and compared with preserved sample lengths for calibration purposes. For each frame, the xy-coordinates of approximately 30 individuals in the same plane were recorded. The choice of mysids in the same z-coordinate from the camera lens was made visually by choosing animals of similar size and focus. A measurement of the total area occupied by the chosen individuals was also recorded. Coordinate data was inserted into MatLab where matrices were constructed to calculate the distance of each individual mysid to its nearest neighbour.

### 2.3.4 Statistical analyses and data considerations

In order to determine a mean nearest neighbour distance (NND) for each swarm, measurements from multiple video frames were averaged and these values compared using a Student's t-test. The NND values in the first and last frames were compared. As these frames were sequential, if no difference was found between the estimates of the first and last frames, it was assumed that the resultant mean was a reasonable estimation of the NND for that swarm. This mean was calculated from all the frames within this sequence, resulting in 19 NND estimates.

As a supplemental test of non-random organization of mysid swarms, expected NND for both randomly and hexagonally arranged scenarios based on equations provided by Clark and Evans (1979) were compared to observed NND from video analysis. For swarms to display randomness,

$$\text{NND} = 0.5 r^{-1}$$

Alternatively, those displaying hexagonal packing displayed the following relationship,

$$\text{N-ND} = 1.076 r^{-1}$$

The density,  $\rho$ , values were obtained from the two-dimensional density of individuals chosen for xy-coordinate determination within a measured area on the video screen. A further Mann Whitney Rank Sum test was performed for the three-dimensional densities derived from the NND based on these two modes of packing.

To provide an additional perspective on mysid distribution, NND were also converted to absolute distances based on the body lengths of preserved specimens. Pearson's correlations and regression analysis, where applicable, were conducted to examine the relationship between NND, length and density.

### 3.0 RESULTS

#### 3.1 MYSID SPECIES SAMPLED

The 35 swarms consisted of nine species, all within the family Mysidae: *Acanthomysis columbiae*, *Holmesmysis sculpta*, *H. nudensis*, *H. nuda*, *Alienacanthomysis macropsis*, *Xenacanthomysis pseudomacropsis*, *Neomysis rayi*, *N. mercedis* and *Mysidella americana*. All swarms were coastal species that occurred in shallow water. The two dominant species, expressed in terms of occurrence in Figure 5 were *A. columbiae* and *H. sculpta* that were both found in 30% of the swarms sampled. *A. columbiae* was sampled in all four bottom types and was found on rock substrate 67% of the time (Figure 6). Similarly, *H. sculpta* was found on rock substrate the majority of the time it was sampled (61%); however, *H. sculpta* was only found on three substrates. These two distributions closely resemble the relative availability of the substrates available to the mysids (Figure 8) although this represents only the bottom topography that was sampled and may not be truly representative of the entire study area. Nonetheless, this suggests that mysid swarms represented by the two most common species in this area do not show a preference to substrate type.

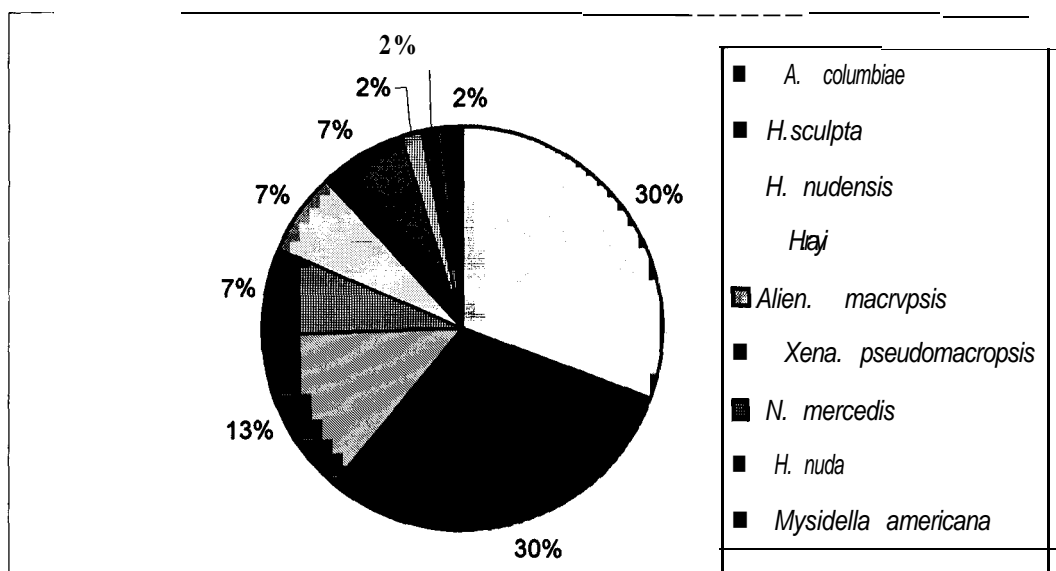


Figure 5. Percent composition of species over all samples expressed in terms of occurrence. (For example, *H. sculpta* occurred 18 out of 59 times.)

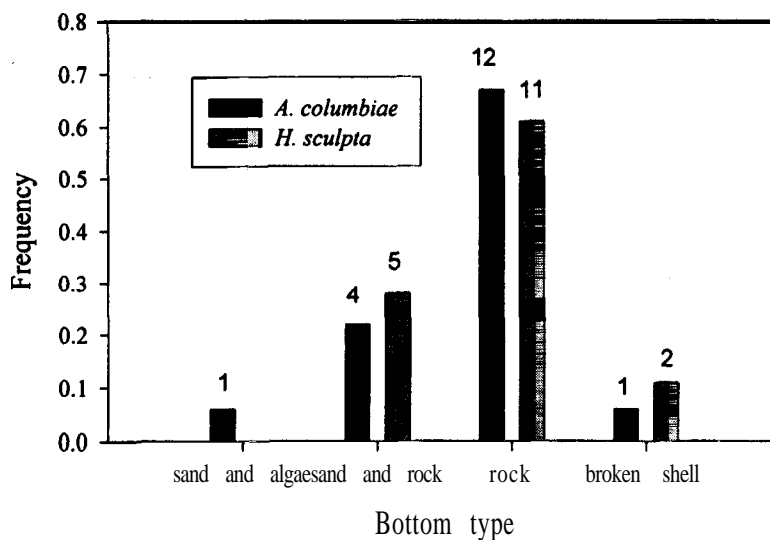


Figure 6. Distribution of *A. columbiae* and *H. sculpta* over bottom types. Frequencies are scored out of the 18 occurrences for each species with actual numbers over the bars.

A summary of individual properties gathered from preserved sample data for each species is listed in Table I. *H. sculpta* occurred predominantly in juvenile (72%) multispecies swarms (67%) with *A. columbiae*, *H. nudensis*, *H. nuda* and *Xenacanthomysis pseudomacropsis* in order of association. *H. sculpta*'s length class varied from a juvenile length of 0.34 cm to a mature length of 1.10 cm. *A. columbiae* showed a similar length distribution of 0.30 to 1.2 cm but was more common in multispecies swarms than *H. sculpta*. *Xenacanthomysis pseudomacropsis* displayed the largest body length with a range of 0.89 to 1.11 cm and thus, was only ever present as mature individuals (Kathman *et al*, 1986). *Alienacanthomysis macropsis*, *Xenacanthomysis pseudomacropsis*, *N. mercedis*, *Mysidella americana* and *H. nuda* were never found as a single-species swarm. This may indeed reflect their low degree of occurrence in nature or may be a result of the sampling technique targeting certain kelp beds that were fed upon by gray whales.

Table 1. Species-specific characters derived from preserved samples. Standard errors appear in brackets after mean lengths are reported. The species composition of all 35 swarms is depicted in figures of Appendix B. Typical developmental stages are reported as a percent of their occurrences. Those without values indicate low sample size (<50 individuals) or single occurrences.

Species	Occurrences (in 35 swarms)	Length (cm)	Single-species swarms	Multipecies Swarms	Association in multispecies swarms	Life stage in swarm
<i>H.sculpta</i>	18	0.34 (0.020) - 1.10 (0.029)	33%	<b>39%</b> 17% 6% 6%	<i>A. columbiae</i> <i>H.nudensis</i> <i>H.nuda</i> <i>Xena. pseudomacropsis</i>	juvenile (72%)
<i>A. columbiae</i>	18	0.30 (0.009) - 1.20 (0.096)	17%	44% 17% 17% 6%	<i>H. sculpta</i> <i>Xena. pseudomacropsis</i> <i>Alien. macropsis</i> <i>N. rayi</i>	juvenile (78%)
<i>H. nudensis</i>	8	<b>0.21 (0.011) - 0.69 (0.084)</b>	<b>25%</b>	12.50% 25% 50% 12.50%	<i>Alien. macropsis</i> <i>A. columbiae</i> <i>H.sculpta</i> <i>H.nuda</i>	juvenile (75%)
<i>N. rayi</i>	<b>4</b>	0.25 (0.005) - 1.08 (0.019)	<b>50%</b>	25% 25%	<i>A. columbiae</i> <i>N. mercedis</i>	juvenile (50%)
<i>Alien. macropsis</i>	<b>4</b>	0.28 (0.018) - 0.81 (0.470)	0%	75% 25% 25%	<i>A. columbiae</i> <i>Mysidella americana</i> <i>H. nudensis</i>	juvenile
<i>Xena. pseudomacropsis</i>	4	0.89 (0.017) - 1.11 (0.069)	0%	100% 25%	<i>A. columbiae</i> <i>H.sculpta</i>	adult (100%)
<i>N. mercedis</i>	<b>1</b>	0.85 (0.036)	0%	100%	<i>N. rayi</i>	mixed juvladult
<i>Mysidella americana</i>	<b>1</b>	0.23 (0.002)	0%	100%	<i>Alien. macropsis</i>	juvenile
<i>H.nuda</i>	<b>1</b>	0.38 (0.013)	0%	100% 100% I	<i>H.sculpta</i> <i>H. nudensis</i>	juvenile

### 3.2 GENERAL SWARM ATTRIBUTES

A total of 35 swarms were investigated from various regions in Queen Charlotte Strait for a 5-week period from July 29 to September 1, 1999. Overall, the swarms were found in 7.3 - 13.3 m of water with relatively invariable temperatures of 9 to 10 C. Using the formula for density based on hexagonal close packing (Mackie and Mills, 1983), swarm densities were estimated to be from 60 - 1700 individuals L<sup>-1</sup> (Table II). A Mann Whitney Rank Sum tests comparing observed NND and expected NND (random) and NND (hexagonal) revealed no significant difference between observed NND and expected NND for a hexagonally-organized distribution ( $p=0.935$ ) but a difference between observed NND and expected NND in a random distribution ( $p<0.001$ ). Although this suggested that individuals were not randomly organized, it was not possible to determine whether swarms were hexagonally close packed or isahedronically packed. There was no significant difference between the hexagonal and ishedronic approximations (Mann Whitney Rank Sum,  $p=0.425$ ) but hexagonal close packing revealed a more conservative density estimate (Appendix A). Direct visual observations and video recordings revealed that mysid swarms occurred within 0.3 to 1.0 m of the bottom during all sampling events.

Table II. A statistical summary of the 35 sampled swarms. Sex ratio calculated from the numbers of mature individuals. Coefficient of variation = standard deviation density/ mean density.

Depth (m)	Swarm Density (individ/L)					Swarm composition			
	Max.	Min.	Mean	Median	Coefficient of variation	Monospecific	Polyspecific	Sex ratio (MF)	Life stage
7.3 - 13.3	1699	63	569	636	66.3%	40%	51% two species 9% three species	0.04 - 6.0	5% adult 26% mixed 69% juvenile

There were four basic substrates available to the mysids. Of these, almost 60% was rock substrate, with sand and rock, sand and algae and broken shell accounting for the rest (Figure 7). Swarms had a common shape of a three dimensional rectangle with the lengths and widths greater than its height and had individuals that were oriented into the current when undisturbed. These swarms occupied volumes of anywhere from 300 L to as much as over 800000 L. Monospecific swarms were observed 40% of the time

(Appendix B) with the majority being polyspecific (Table I). Within these multispecies swarms there was a dominant species that accounted for over 50% of the sampled individuals (Appendix B).

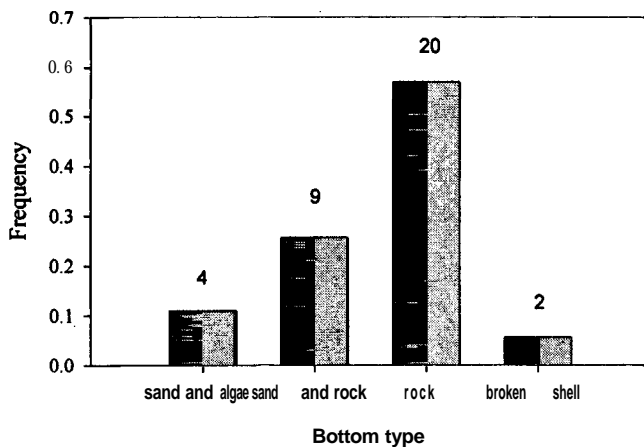


Figure 7. Frequency of swarms found on sand and algae, sand and rock, rock and broken shell bottoms. Actual numbers of swarms for each type are indicated.

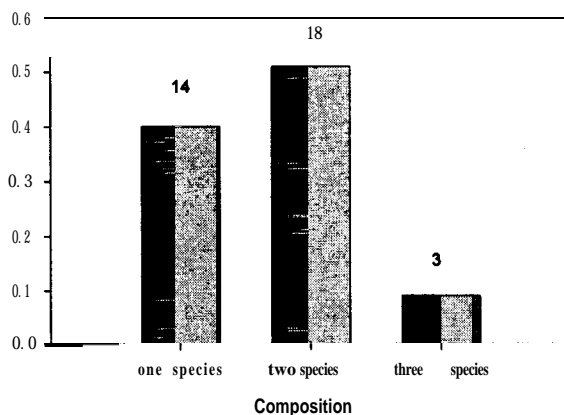


Figure 8. Frequency distribution of number of species in each swarm. Actual numbers for each form of arrangement are included.

Swarms were juvenile in composition 70% of the time with a sex ratio (M/F) of 0.04 to 5.0 in those containing adults (Table II). The preserved samples revealed few gravid females in 23% of the swarms with no swarms showing only gravid females.

Of the 35 swarms, video footage was available for density estimates in 19. Figure 9 demonstrates that there was considerable variation in swarm density. Although the majority of the swarms had densities below 800 individuals/L there were two swarms with densities in excess of 1200 individuals/L. This large range of observed densities is revealed in the 68.3% variation from the mean density of 569 individuals/L. This mean appears to be a representative statistic of the swarms as it is closely matched by the median (Table II).

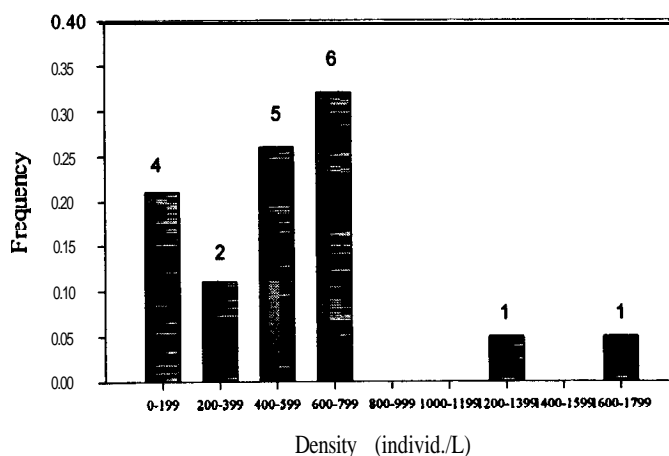


Figure 9. Frequency distribution of density over 19 swarms with actual number in each density class indicated.

### 3.3 SPATIAL DISTRIBUTION

As previously stated for the density estimates, nearest neighbour distances were available for 19 of the 35 swarms. Student's t-tests revealed that there were no differences between the NND calculations derived from successive frames for each swarm. The

resultant mean NND distances varied from 0.94 cm (S.E. 0.041) to 2.82 cm (S.E. 0.206) with the majority falling within the NND class of 1.20 to 1.49 cm (Figure 10). When these distances are examined in terms of the mysid body lengths (BL) resolved from preserved specimens, the range is 0.82 BL (S.E. 0.035) to 4.99 BL (S.E. 0.281) with a greater variation present (Figure 11).

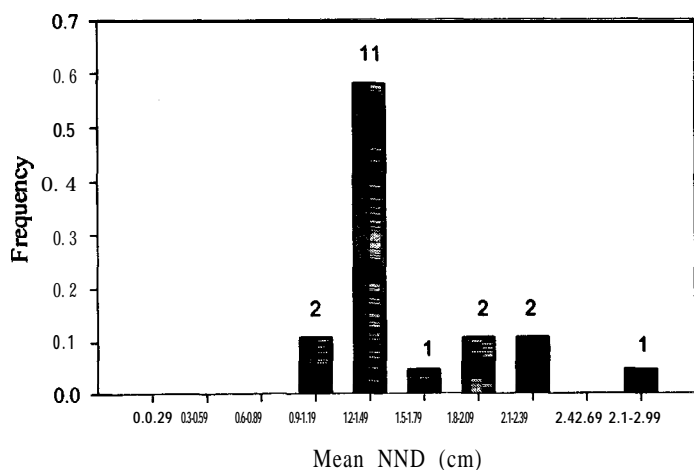


Figure 10. Distribution of mean NND (cm) over 19 swarms.

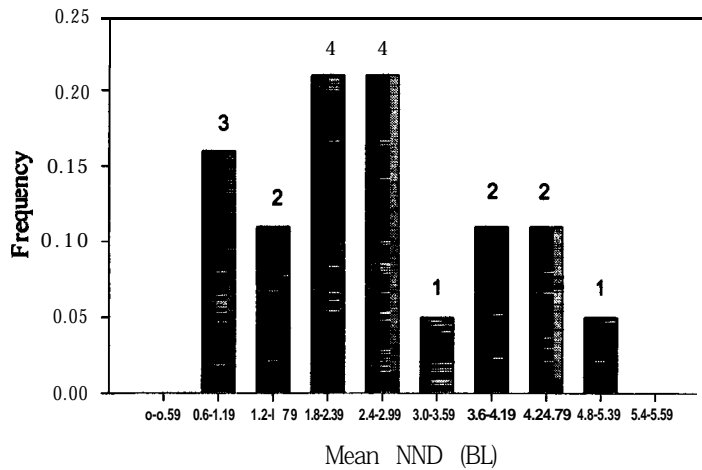


Figure 11. Distribution of mean NND (BL) over 19 swarms.

Mysid body length was not significantly correlated with either swarm density (Pearson's,  $p=0.443$ ) or NND (Pearson's,  $p=0.572$ ). However, when NND's were converted to body lengths, there was a significant relationship found (Pearson's,  $p<0.001$ ). Figure 12 demonstrates the linear regression of this relationship. This implies that NND (BL) decreases proportionately with increasing average mysid length ( $r^2=0.75$ , S.E 0.156).

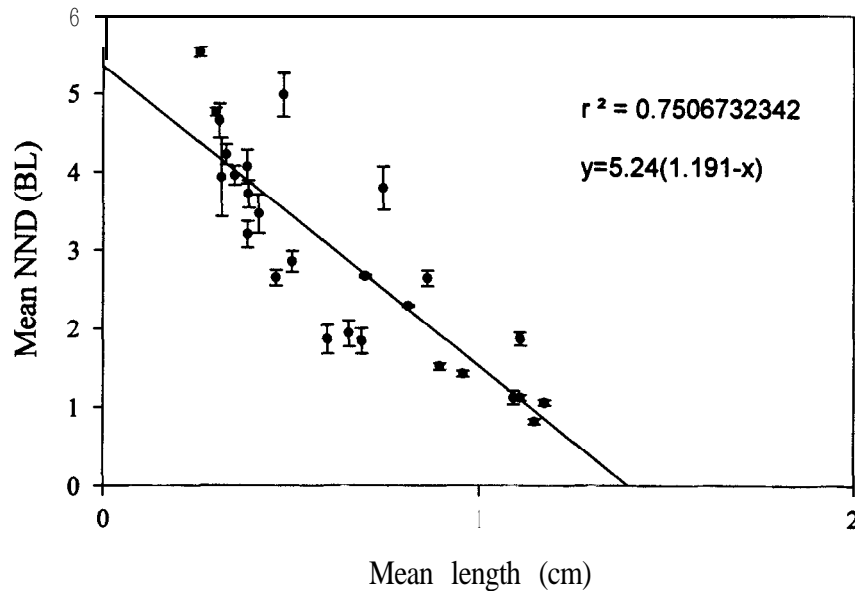


Figure 12. Linear regression of mean length (cm) and mean NND (BL).

### 3.4 BEHAVIOURAL AND ADDITIONAL OBSERVATIONS

Mysids formed aggregations during all sampling events with some errant, larger individuals straying independently in some instances. Direct visual observations while sampling along with observations from the video data demonstrated that mysids maintained position against the various currents that were present. In general, individuals were observed to orient into the current but were randomly located when there was an absence of current such as in Skull Cove. On the two occasions where no swarms were detected, the currents were extremely strong and divers themselves had trouble manoeuvring. Mysids were also displaced in surge conditions but were found to remain in a distinct region. Position maintenance was further enhanced by the location of several swarms on the lee side of boulders or within crevasses formed by larger rocks.

Mysids were observed to segregate into smaller aggregations consisting of one developmental stage alongside another. It was difficult to distinguish whether these individuals belonged in the same swarm or were separate members of another. An interesting behaviour involved observations of the outermost individuals of a swarm moving into the interior of the swarm after a length of time spent at this boundary. The fact that no collisions were evident during these movements reinforces the high degree of order entailed in swarm structure and the sensory capabilities of mysids in detecting at least their immediate surroundings.

The presence of black rockfish (*Sebastes melanops*) in close vicinity to the swarms did not appear to disturb the swarming behaviour of the mysids in the Y Beds of Burnett Bay. Only when the fish moved through the swarm did individuals break swarm integrity. However, even then, the individuals quickly realigned to reform the swarm after the disturbance had passed. This manner of maintaining position was also true of diver proximity where mysids seemed undisturbed until actively approached. Larger individuals seemed to react faster to divers which was also evidenced by the difficulty of net sampling these adult stages that swam with greater speeds compared to more juvenile ones. In particular, the mysids did not react well to the black background that was used on a limited number of occasions. No predation on the mysids was ever witnessed, although mysids were found to have been ingested by a penicillate jellyfish (*Polyorchis penicillatus*) specimen that was inadvertently sampled.

Predation was assumed to have taken place during foraging by a gray whale for 40 minutes at No. 4 Reef in North Bay on August 11, 1999. Repeated dives by the whale in the same spot suggested feeding behaviour as did movement back and forth within the kelp bed. Data was collected before and after the incident but no obvious differences in either mysid abundance or swarm composition could be discerned between the samples.

## 4.0 DISCUSSION

Due to the lack of relevant information in the literature, the findings in this study in terms of species-specific ecology cannot be entirely compared to previous investigations. Nonetheless, a general comparison to mysid data from other studies is still of value for understanding these neritic Northeastern Pacific species.

### 4.1 SPECIES COMPOSITION, SEX RATIOS AND STRATIFICATION

This study revealed that mysid swarms were monospecific about 40% of the time. This is neither supported nor disproven by previous findings of O'Brien (1988) who found fully monospecific swarms from Tasmania and Ohtsuka *et al.* (1995) who found polyspecific coastal swarms in the Northwest Pacific. However, Ohtsuka *et al.* (1995) also made note of up to five "guest species" with a dominant species accounting for 50 to 100% of the individuals, which is consistent with the observations of this study. These findings suggest that the extent of species domination is variable within different swarms. Whether this pattern is true of swarm composition throughout the year cannot be determined as the present study sampled for only a short period of time. One might reasonably expect the same species to be present throughout the year as encountered by Carleton and Hamner (1989) with the same dominance regime. **Thus, *A. columbiae*** and ***H. sculpta*** would continue to be most abundant at other times during the year as well. This is based on the assumption that these species are reproductively active year round such as was true for those species studied by O'Brien (1988) and Azeiteiro *et al.* (1999).

The observation of monospecificity prompts the question of whether mysids actively seek out members of the same species. If so, it would suggest that mysids possess recognition capabilities beyond being able to discern shapes and movements. Clutter (1969) suggests that the presence of young assembled in the marsupium facilitate swarming once they are released. However, the ability of adults to stray from the group, as documented in this study, indicates that mature individuals are able to migrate to other swarms in the vicinity, much like the join, leave and stay decisions exhibited by schooling fish (Pitcher,

1998). Due to the relatively low number of swarms studied, coupled with a low number of mature individuals recovered in this study, it cannot be entirely determined whether species composition is effected by the life history stage of the individual.

The abnormally high incidence of males in samples containing adults may also be an artifact of low sample size (Appendix B). There was a wide range in the sex ratio of the preserved samples (MF : 0.4-5.0). Sex ratios are said to vary among samples and seasons with females being favoured (Grabe and Hatch, 1981; O'Brien, 1988; Ohtsuka *et al*, 1995). Grabe and Hatch (1981) suggest that males suffer high mortality after mating while females live on longer and usually only die after spawning. The inability to resolve the sex of immature mysids also has a considerable effect on sex ratio estimates.

There is also the possibility of uneven hand net sampling due to vertical segregation of the mysids. Recall that Modlin (1990) reported vertical segregation by size with juveniles, immatures, mature males and females and gravid females forming distinct layers from the top to the bottom of the swarm. Due to the relatively primitive net sampling methodology used in this study and the fact that video footage by chance only filmed uniform swarms of one age class, it was impossible to detect vertical stratification of individuals in this study. However, if this were a common property of all mysid swarms, taking what was believed to be a random, representative sample of the swarm might have in fact been an event of sampling a discrete layer within a swarm,

Nonetheless, the observation of swarms consisting of a single developmental stage nearly 75% of the time (Table II) suggests a high degree of age segregation. These results agree with the findings of O'Brien (1988) and Clutter (1969) who observed that some shoals were made up of smaller cohesive groups of individuals from a common life stage. A two to threefold swim-speed difference between juveniles and adults (Clutter, 1969) may also contribute to the incompatibility of the two stages in the same swarm. Results indicate that juvenile swarms were prevalent in the latter portion of the sampling period. As there was a 2-week period prior to this latter half where sampling was not possible, it

may be supposed that there was a corresponding increase in the presence of gravid females at this time.

#### 4.2 SWARM DENSITIES

The density estimates derived from NND (cm) in this study were not only quite variable, but also quite high when compared with values found in other studies of mysids (Table III). However, the fact that density estimates from successive video frames revealed similar NND (cm) provides some measure of accuracy to these values. Data collected in the same region and encompassing the same time frame revealed estimates of 10 to 600 individuals/L (Stelle, pers. comm.). This upper limit represents the mean for the density estimates of the present study which in the majority, fall below 800 individuals/L (Table II). It is possible that that this region of Queen Charlotte Strait sampled through the various kelp beds is one of relatively high mysid residency, a region that supports more mysids than previously investigated regions. This may have profound effects on higher trophic levels as will be discussed later on in the context of gray whale foraging.

Table III. Density estimates as reported in the literature.

Mysid species	Density (individ./L)	Location	Reference
<i>Anisomysis sp.</i>	25	Western Japan; S. Korea	Ohtsuka, 1995
<i>Nipponomysis sp</i>	65	Western Japan; S. Korea	Ohtsuka, 1995
<i>Siriella sp</i>	33	Western Japan; S. Korea	Ohtsuka, 1995
<i>T. tasmaniae</i>	3.9*	Tasmania	Fenton, 1992
<i>A. mixta australis</i>	1.29'	Tasmania	Fenton, 1992
<i>A. rufa</i>	0.74'	Tasmania	Fenton, 1992
<i>Mysis mixta</i>	0.03	New Hampshire coastal waters	Grabe and Hatch, 1982
<i>Mysidium columbiae</i>	24.2	Belize	Modlin, 1990
<i>Mesopodopsis slabberi</i>	20	Sundays Estuary, S. Africa	Wooldridge and Erasmus, 1979
over all species found	569	Queen Charlotte Strait, BC	this study
* denotes maximum estimates, all others are assumed to be means			

There remains the issue of reliability of using videographic data for calculations from a dynamic system. Mysids, by necessity, are constantly in motion. They are subject to the

effect of variable currents, predation pressure and movements of conspecifics to other environmental stimuli. Thus, video snapshots of their organization at an instant in time may not always be representative of the order which they are known to exhibit. For instance, there were observations of displacement from more peripheral regions at the edge of the swarm to central ones. This observation has been substantiated by research by Zelickman (1974). This would have reduced the NND determination for that individual or that of a neighbour. Thus, calculating NND would be subject to errors if continual motion to different positions is a common feature of swarm dynamics. Nonetheless, the advantage of video over still photography is that many estimates can be calculated from sequential frames and then averaged.

Resolution of similar-sized individuals, a key component in determining the xy-plane of the 2-dimensional screen image, was also largely a factor of judgement. Differences in focus of smaller mysids were less apparent than for larger ones and so may have resulted in incorrect incorporation of individuals from a further distance. Juveniles dominated mysid swarms in this study, especially in the latter half of the sampling period. This may have increased the chance of error in density estimates.

#### 4.3 SPATIAL DISTRIBUTION

The precise nature by which mysids organize are reminiscent of other swarming groups such as fish schools and bird flocks. All three animal assemblages demonstrate a high degree of organization and behaviour integration in their structures. One interesting related behaviour is the lack of leaders in the group. Individuals take turns at the periphery of the swarm through either a conscious decision to equate group effort or as a competitive expulsion of neighbours vying for the favourable positions.

Distribution of mysids by maintaining a specified distance between neighbours has been proposed to be an evolutionarily-optimized strategy to minimize predation. Zelickman (1974) has noted swarm compaction when individuals are threatened as well as the effect of light intensity on NND. It is also an important regulator for swarm formation and

maintenance (Roast *et al*, 1998). The indiscriminate nature of the samples from Skull Cove reflect this deterioration of swarm integrity when NND is not upheld.

Individuals tended to be about 1.20 to 1.49 cm apart from their nearest neighbour in this study (Figure 10). This is an underestimate when compared to those of previous investigations (Table IV). Once again, this may reflect miscalculations of actual distance separating individuals and the variability in NND when resolved to distance in terms of body lengths (Figure 11). This finding of variable NND (BL) is contrary to the assertion of Carleton and Hamner (1989) who detected little variation between species. However, this reflects the size variability for each species when juveniles and adults are considered (Table II). Clutter (1969) also encountered species dissimilarity of NND and noticed variation among size groups.

Table IV. Various NND (cm) for different epibenthic species found in the literature determined through photographic techniques assuming isahedronic packing.

Species	NND (cm)	Source
<i>Anisomysis sp.</i>	3.4	Ohtsuka, 1995
<i>Nipponomysis sp</i>	2.5	Ohtsuka, 1995
<i>Siriella sp</i>	3.1	Ohtsuka, 1995
<i>Anisomysis pelewensis</i>	1.9	Carleton and Hamner, 1989
<i>Prionomysis stenolepis</i>	4.9	Carleton and Hamner, 1989
<i>Anisomysis lamellicauda</i>	3.8	Carleton and Hamner, 1989
<i>Anisomysis australis</i>	3.8	Carleton and Hamner, 1989
this study	0.94 - 2.82	

The importance of NND is further emphasized by its use in determining density. This was supported by the lack of relationship between length and density, suggesting that spacing has a greater impact on organization than individual length. Actual NND (cm) for each swarm had no association with the size of the individuals. This makes sense as there is a variety of lengths demonstrated within a given swarm but only a limited range of NND (cm). However, when NND is expressed in units of body length and compared to length, a significant correlation does exist. This implies that mysids respond to relative

length in terms of bodylengths rather than absolute distance between neighbours. This further demonstrates the visual capabilities of mysids as well as the importance of visual cues as mysids are able to resolve images and not just movements (Clutter, 1969).

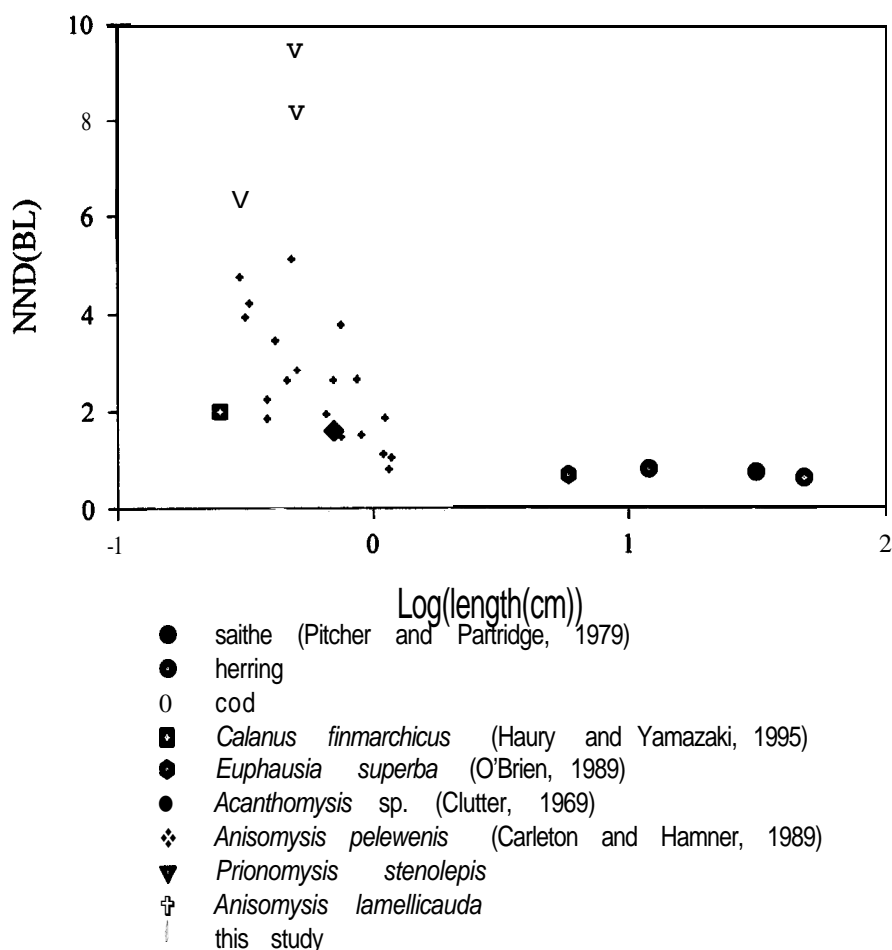


Figure 14. The relationship of NND(BL) and length(cm) found in the present study and compared to different taxa. Lengths were log transformed to include larger body sizes. Data from the same study are represented by similar symbols.

The regression in Figure 12 suggests that with increasing size of individuals, mysids tend to be more closely packed. In the perspective of greater sensory capabilities that is associated with increasing age and size, this relationship may be reasonable. Mysids may thus be able to take advantage of greater compaction to be able to respond better as a unit to predators. Waves of movement transferred between neighbours would be more quickly detected if inter-individual distances were smaller. Figure 14 suggests that this linear relation is not a consistent phenomenon across other taxa such as copepods, euphausiids and fish. However, it appears that mysids may in fact occur on just a portion of an exponential relation between NND (BL) and length. With greater body size represented by *Euphausia superba* and various schooling fish species, NND appears to level off, suggesting a threshold level of compaction. Nonetheless, with the limited data that is available for these other species, it is difficult to say whether this trend would be sustained with more information on aggregating species.

#### 4.4 BOTTOM DISTRIBUTION

Mysid swarms did not appear to be associated with the four available bottom types in this study. Still, this does not mean that there is no association of mysids to the bottom. These results only imply that no specific substrate types are targeted. Hyperbenthic species are known to fall into two categories: non substrate-associated and substrate-associated (O'Brien and *Ritz*, 1988); *thus*, it would seem that *A. columbiae* and *H. sculpta* fall into the former class given that their distribution closely corresponded to the bottom types present over all samples. However, it is possible that this may not have been true for the other reported species. Sample sizes were too small in these species for any relationships to be significant and there still remains the question of whether the various kelp beds were sampled effectively. Kelp beds were visited without any established strategy but instead, was subject to constraints of accommodating several research activities.

The high occurrence of rock bottom type is of no surprise as kelp beds were targeted; this substrate is required for attachment by the kelp holdfasts (Murison *et al*, 1984).

Nonetheless, the observation that swarms were present at about 0.3 to 1.0 m off the bottom during the day is consistent with other accounts of benthic species (Clutter, 1969; Kim and Oliver, 1988; Ohtsuka *et al.*, 1995) and may imply some form of bottom association if not substrate-specific.

#### 4.5 POSITION MAINTENANCE AND RESPONSE TO PREDATORS

The most visually striking behaviour of the mysids under investigation was the coordinated orientation and stationary nature of group members in the presence of current. This appears to be a characteristic of mysid communities (Clutter, 1969; Omori and Hamner, 1982; Zelickman, 1974) and invokes images of coordinated fish schools. Roast *et al.* (1998) suggested that maintenance of position is dependent on the maximum velocity that could be sustained. This implies that mysids will always keep station in favourable environments unless prevented by physical processes. This ability to withstand a range of velocities is determined by size as juveniles are more disposed to be displaced at lower measures than adults are (Clutter, 1969). Mysids avoided both areas of high as well as low velocities in investigations by Dadswell (1974) and Lawrie *et al.* (1999). Presumably, absence in the latter condition is due to decreased food transport with the absence of current.

The lack of organization displayed by specimens in the calm waters of Skull Cove also suggest that a degree of current is required for swarm formation to occur. O'Brien (1988) and Roast *et al.* (1998) both emphasized water patterns as a stronger stimulus than other factors such as salinity and temperatures for mysid distribution. The conceivable absence of predators in these sheltered waters may also have been a factor in the disorder.

Since many large visual predators cannot discern between an individual and a swarm, (Clutter, 1969) being in a swarm should reduce the frequency of detection as well as the incidence of predation per individual. O'Brien and Ritz (1988) suggested a threshold distance of 3 to 4 m whereby avoidance behaviour to an approaching predator is displayed. Laboratory experiments performed with model predators also revealed

habituation to stationary fish. This is consistent with the observations of this study where fish, although often within this proposed limit, failed to evoke any responses from the mysids as fish were motionless. O'Brien and Ritz (1988) also observed greater swarm cohesion with increasing approach speed although, this could not be detected in the present investigation.

#### 4.6 MYSIDS AND GRAY WHALE FORAGING

Both *A. columbiae* and *H. sculpta* have been found to be fed upon by gray whales in past investigations (Murison *et al*, 1984; Kathman *et al*, 1986; Stelle and Megill, 1999). Both species are known to occur in shallow coastal waters (Kozloff, 1996) with *H. sculpta* noted for its association near algae (Murison *et al*, 1984). With the present data, it can be said that *A. columbiae* is also a common resident of kelp communities in addition to the sandy bottoms it inhabits (Kozloff, 1996). However, the presence of the seven other species (although to a lesser extent), and the fact that 60% of the observed swarms were polyspecific, suggests that they are also available to gray whales as prey items.

Mysids have been stated to be the most important food resource along the migration route of gray whales (Kim and Oliver, 1988). The lack of other swarming species such as euphausiids and cumaceans in the observed samples of the present study supports this assertion of a less diverse prey community in these tertiary feeding grounds. Both euphausiids and cumaceans are also preyed upon by gray whales (Kim and Oliver, 1988). Additionally, infaunal species such as amphipods, which are preferred prey in the primary feeding grounds of the Chukchi and Bering Seas, have smaller geographic ranges in this region and so would be easily exploited by gray whale feeding (Kim and Oliver, 1988). In contrast, the predominant mysid species in the Bering Sea was *Xenacanthomysis pseudomacropsis* at low densities of 0.02 to 0.35 individuals/L (Kim and Oliver, 1988). Thus, mysids represent a substantial and dependable resource for gray whales only in these tertiary feeding grounds.

The link between mysid occurrence in kelp beds and gray whale targeting of kelp beds is an interesting topic for future consideration and is the subject of ongoing research by Stelle and company. The observation that some kelp beds are bypassed despite mysids being present (Megill, CERF, pers. comm.) suggests that gray whales are not the opportunistic feeders (Nerini, 1984) once thought. Instead, they appear to be capable of discerning the energy availability of a kelp bed.

The tendency for mysids to disperse with decreasing light intensity (Clutter, 1969; Modlin, 1990) may have an effect on the decision of gray whales to feed in kelp beds at night or during days of heavy cloud cover. In this case, capture efficiency would be less than during the day when swarms are more compact. Incorporated in this examination would be the impact of patchiness of the mysid swarms. Swarm size may not be a critical feature for gray whale consideration. For instance, feeding activity of gray whales during the extent of this study was not found to correspond to mysid abundance (Stelle, UCLA, pers. comm.). Instead, distance between patches of food concentration may be important. This would require measurements of inter-swarm distance to disclose information on distribution of swarms over a region. Patterns of mysid swarm clustering can be modeled using techniques used for describing fish schools (Mackinson *et al.*, 1998). Here, the ratio of mean NND to mean inter-school distance is used to identify clustering intensities. A 'cluster coefficient' (CC), close to 1 reveals diffuse swarms not clustering intensely while a CC closer to zero demonstrates tight clustering. The extent of exploitation of a patch, once found, is also largely unknown. An incident of direct whale predation on a mysid swarm in this investigation revealed little impact of predation on swarm abundance, at least visually. Despite this qualitative assessment and singularity in circumstance, this implies that mysid density is large enough to support isolated gray whale predation. This further supports the contention that Queen Charlotte Strait is an important feeding ground for gray whales, enough so that residency is sustainable.

## 5.0 IMPLICATIONS OF THIS STUDY

This study has revealed that the mysid swarms in Queen Charlotte Strait are characterized by unusually high densities of mysids (relative to other studies of mysids). Furthermore, although limited in scope and time, this work has shown that studies of this sort can provide valuable information on the ecology of coastal mysid communities. However, given the scarcity of information on mysid ecology along the coast of BC, further data will be needed. Much can be gained from understanding mysid distribution and behaviour as they exhibit complex associations and a high degree of organization that can be related to other aggregating organisms. Finally, since they also represent a significant resource for gray whales in this area, the distribution of mysids (i.e. over km's to 10's of km) may in large part determine foraging areas for these animals. In light of this, a larger scale survey of the co-occurrence of dense mysid swarms and gray whale feeding areas might prove valuable.

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Appendix A. Mean densities of 19 swarms based on isahedronic and hexagonal close packing models.

Swarm	Mean Density (individuals·L <sup>-1</sup> )	
	isahedronic packing	hexagonal close packing
3	271.65	225.60
4	879.69	730.57
6	673.73	<b>559.52</b>
10	648.01	538.17
12	587.47	<b>487.89</b>
19	191.41	158.96
20	75.39	62.61
21	577.48	479.59
22	1239.26	1029.20
23	836.35	694.58
24	948.49	787.71
25	125.00	95.98
27	141.36	117.40
28	457.00	379.00
30	930.00	770.00
32	903.08	750.00
33	922.71	766.30
34	581.44	482.88
351	2045.53	1698.80

Appendix B. Species composition from individuals in preserved samples. For each figure, percent composition of each occurring species is provided along with the actual numbers, given by N.

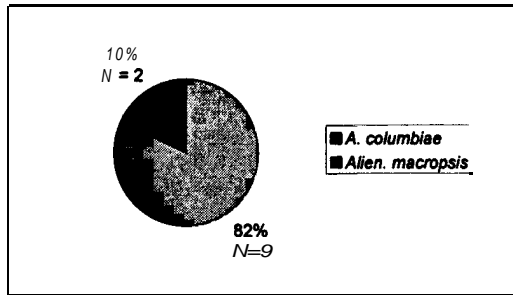


Figure 15. Swarm 1 species composition.

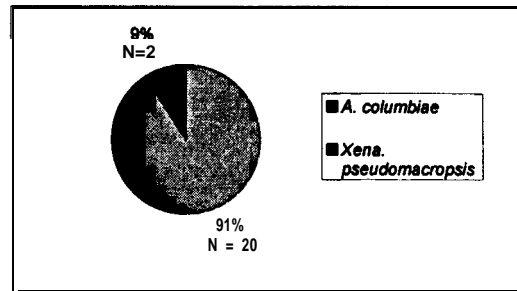


Figure 16. Swarm 2 species composition

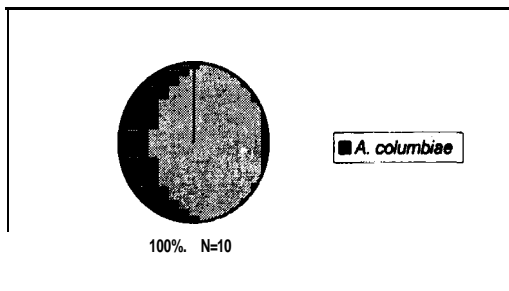


Figure 17. Swarm 3 species composition.

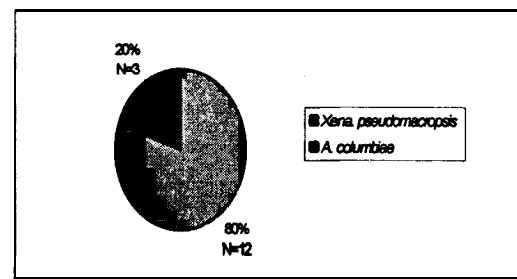


Figure 18. Swarm 4 species composition.

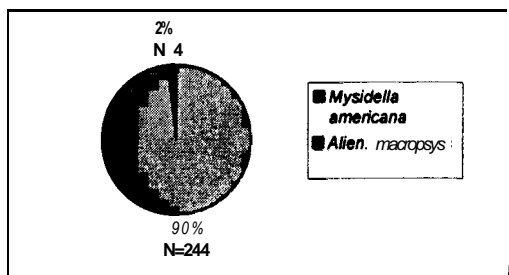


Figure 19. Swarm 5 species composition.

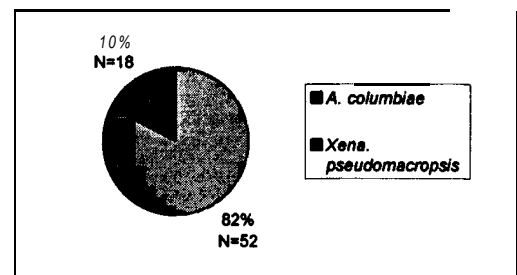


Figure 20. Swarm 6 species composition.

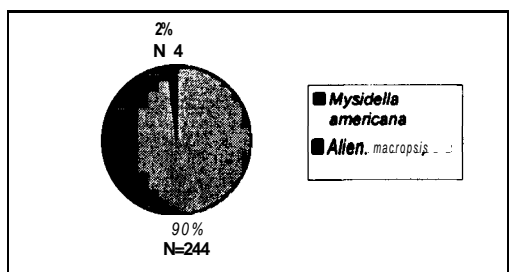


Figure 21. Swarm 7 species composition.

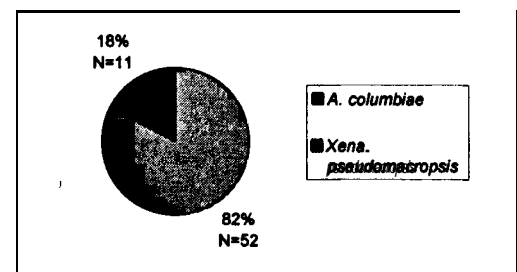


Figure 22. Swarm 8 species composition.

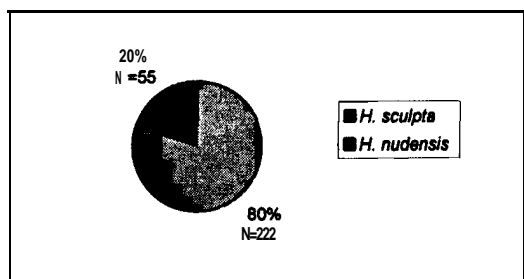


Figure 23. Swarm 9 species composition.

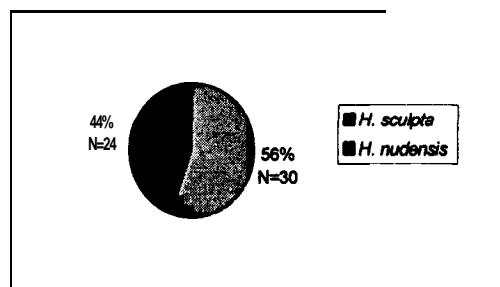


Figure 24 . Swarm 10 species composition

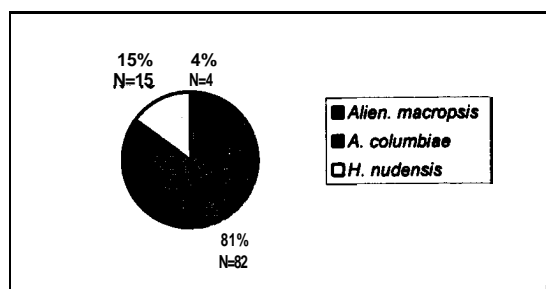


Figure 25. Swarm 11 species composition.

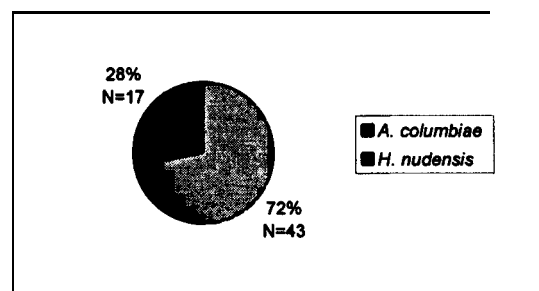


Figure 26. Swarm 12 species composition.

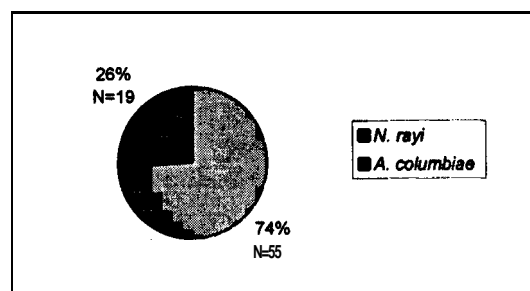


Figure 27. Swarm 13 species composition.

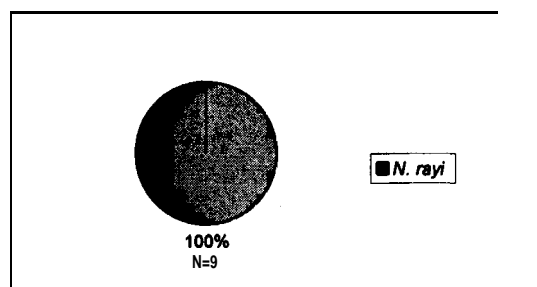


Figure 28. Swarm 14 species composition.

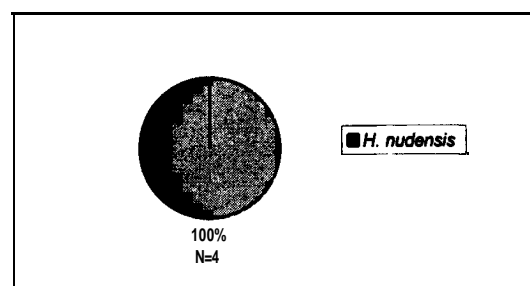


Figure 29. Swarm 15 species composition.

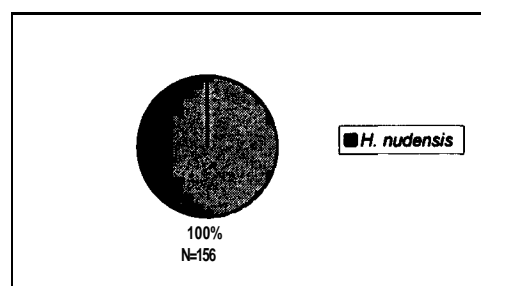


Figure 30. Swarm 16 species composition

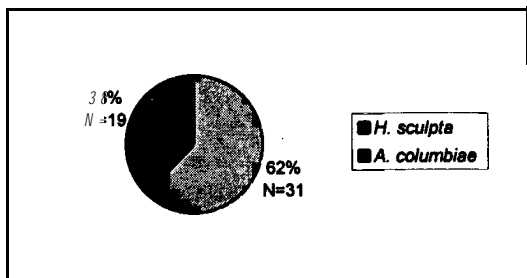


Figure 31. Swarm 17 species composition.

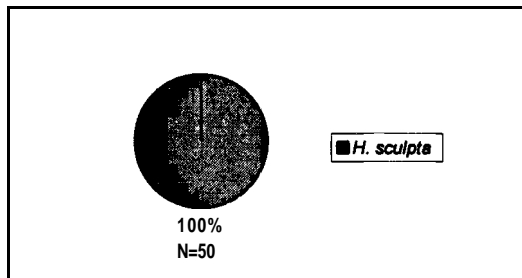


Figure 32. Swarm 18 species composition.

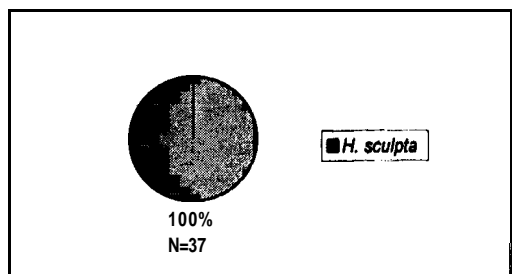


Figure 33. Swarm 19 species composition.

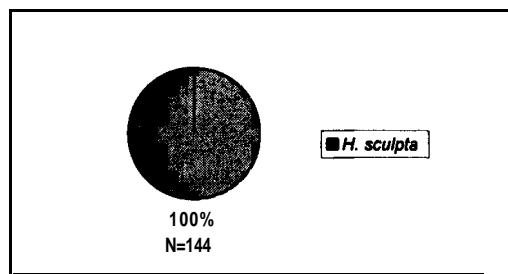


Figure 34. Swarm 20 species composition.

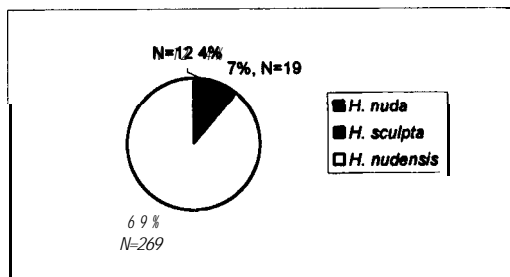


Figure 35. Swarm 21 species composition.

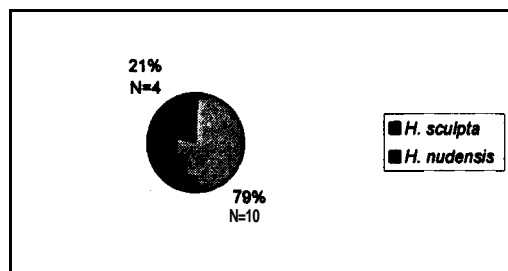


Figure 36. Swarm 22 species composition.

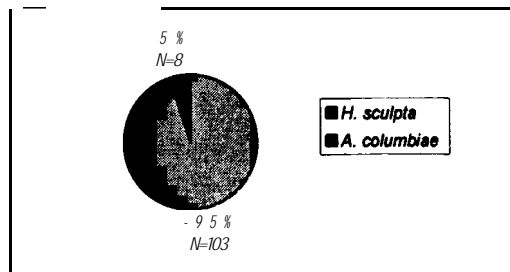


Figure 37. Swarm 23 species composition.

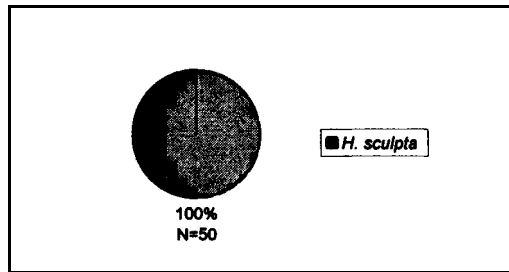


Figure 38. Swarm 24 species composition.

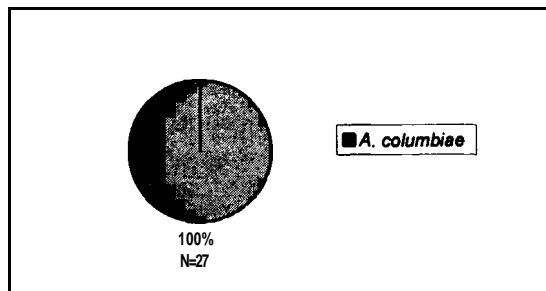


Figure 39. Swarm 25 species composition.

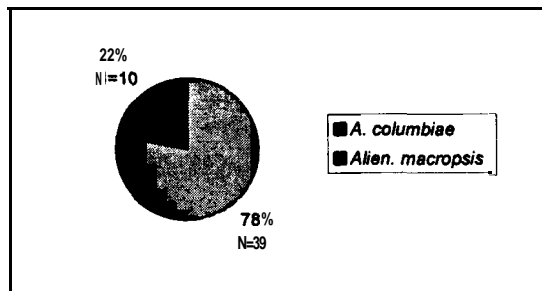


Figure 40. Swarm 26 species composition.

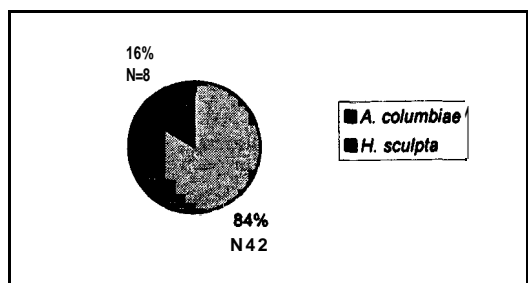


Figure 41. Swarm 27 species composition.

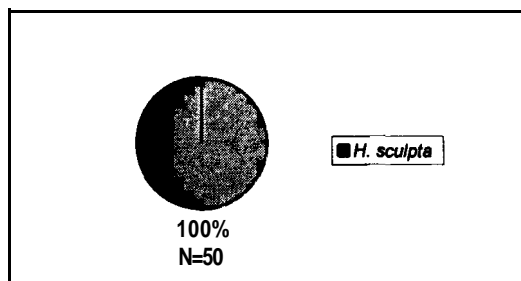


Figure 42. Swarm 28 species composition.

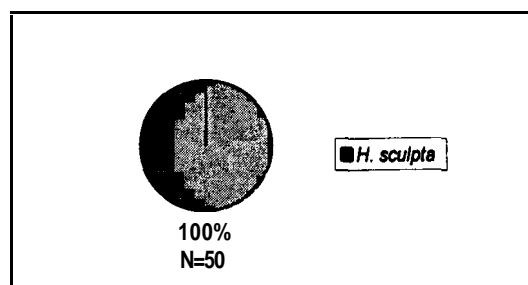


Figure 43. Swarm 29 species composition.

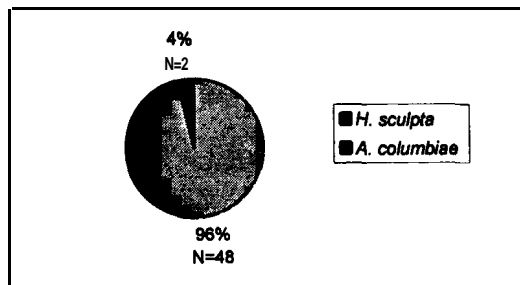


Figure 44. Swarm 30 species composition.

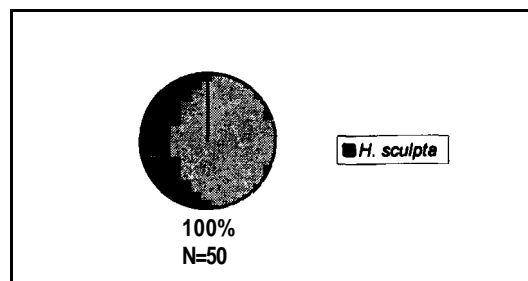


Figure 45. Swarm 31 species composition.

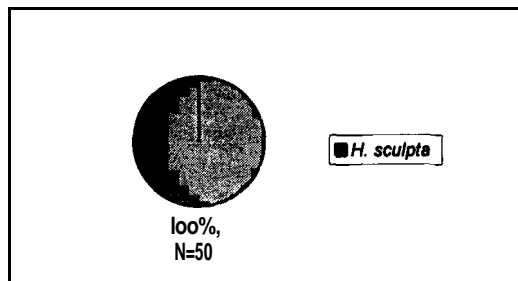


Figure 46. Swarm 32 species composition.

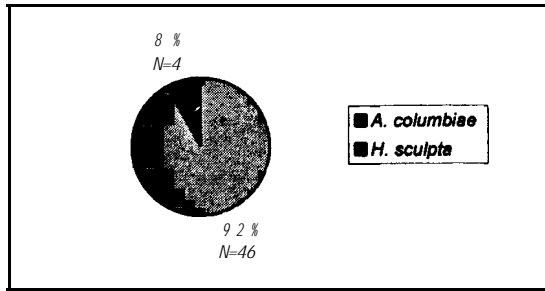


Figure 47. Swarm 33 species composition.

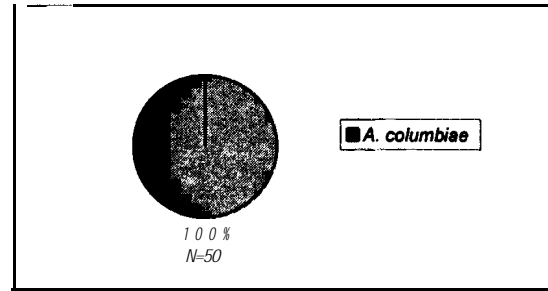


Figure 48. Swarm 34 species composition.

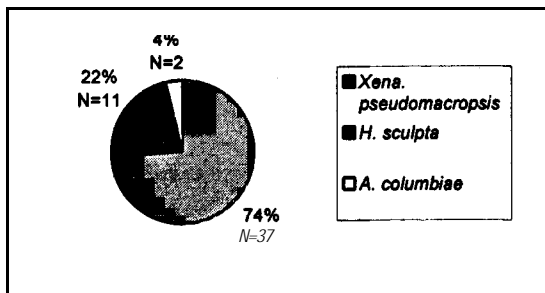


Figure 49. Swarm 35 species composition.