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Variations in Gray Whale Feeding Behaviour in the Presence of Whale-Watching Vessels in Clayoquot Sound, 1993 - 1995

by

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

DOCTOR OF PHILOSOPHY

in the Department of Geography

We accept this dissertation as conforming
to the required standard

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ABSTRACT

The growing industry of whale-watching is allowing increasing numbers of people access to whales in their natural environment, and constitutes a non-consumptive use of the whales compared to whaling. At the same time, questions are often raised about the hidden effects of whale-watching on the whales. A population of gray whales (*Eschrichtius robustus*) which spends the summer feeding in Clayoquot Sound, on the West Coast of Vancouver Island, is regularly observed by whale-watchers from the nearby tourist centre of Tofino. Concern among whale-watching business operators and tourists about the possible effects of whale-watching on the feeding whales was heightened in the years preceding this study by an apparent northward movement of the whales, taking them farther from the Tofino, the point of departure for whale-watching tours. This study attempts to explain this apparent trend by finding out whether the whales' short-term behaviour is affected by the presence of whale-watching vessels, and by examining their short and long-term behaviour in the wider context of some of the features of their environment.

Whales were observed from a small research vessel for three feeding seasons, in five locations within the area known as Clayoquot Sound. The whales' ventilations were recorded continuously and their location and the number of whale-watching vessels present was recorded at regular intervals. The whales' benthic prey was sampled in all three seasons and their planktonic prey in 1995. A series of variables were calculated from the ventilation data and compared to the number of vessels.

The whales' dive behaviour was correlated much more strongly with feeding location than with vessel number. Even with these two factors taken into account, much of the variation in their behaviour remains unaccounted-for. Because of this, although the behavioural change in the presence of vessels is statistically significant, there is reason to doubt whether it is biologically significant. The effects of feeding location are probably a composite of the effects of depth, prey type and other factors which are difficult to measure. Of the two main components, prey type appears to have a greater effect than depth on gray whale behaviour.

Interaction exists between the effects of site and those of whale-watch vessels, meaning that the effects of vessels are different at different sites. The general pattern is that the effects of vessel presence are more pronounced in shallow sites than in deep, although there are some exceptions to this trend.

Gray whale prey shows considerable variation in location, density and composition from year to year. The long-term patterns of gray whale habitat use more closely resemble a prey-selection-driven pattern than a pattern of avoidance of whale-watch vessels.

The relatively small influence of vessel numbers on gray whale feeding behaviour suggests that the current guidelines in place for whale-watching vessels are effective in limiting disturbance of the whales. The variable nature of their prey supply suggests that gray whales use all the sites in Clayoquot Sound, and that the availability of a diverse selection of prey is necessary for their success in the tertiary feeding grounds.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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Chapter 1: INTRODUCTION

1.1 Background

The recent success of whale-watching is part of a larger trend which shows wildlife becoming increasingly important in the tourist industry (B.C. Min. of Tourism, 1991; Hoyt, 1992; Hoyt, 1995). The popularity of cetaceans in western countries is a recent phenomenon (Duffus, 1996). Among the more important results of public sympathy for these animals is the ban on whaling which exists in many countries (Aron, 1988) and the birth and dramatic growth of the new industry of whale-watching (Hoyt, 1992; 1995). In a study conducted in 1986-87, recreational whale-watchers showed a high level of education about and concern for whales (Duffus, 1988). One concern frequently voiced by the whale-watching public is that the commercial whale-watching vessels, and therefore they themselves as passengers, are disturbing or harrassing the whales in some way. Several studies support the claim that the whales are sensitive to boat noise (Finley & Davis, 1984, Dahlheim, 1987, Bursk, 1988, Myrberg, 1990) but much of the evidence is anecdotal and illustrates the uncertainty inherent in attempting to measure the reactions of whales to external stimuli. Corkeron (1994) studied the occurrence of different "behavioural units" in the presence and absence of whale-watching vessels in Queensland, Australia, and found that whale-watching did affect the whales' behaviour, but was unable to interpret the findings in terms of possible long-term effects on the whales.

With the growth of wildlife-based tourism, the management of wildlife is becoming more complicated (Duffus & Dearden, 1990). In comparison to the more traditional "consumptive" use of wildlife (for example, hunting and fishing) the requirements of the patrons are qualitative (an experience) rather than quantitative (a kill or catch). In addition, the effects of tourism on the wildlife are more subtle than simple population depletion, and therefore its management requires more than a population count. The wildlife may be affected in ways that are not immediately obvious, perhaps through damage to the surrounding habitat, and such effects may also diminish the attractiveness of the resource to tourists.

Given these concerns and the rapid growth of the whale-watching industry (Hoyt, 1995), with corresponding increases in the number of boats in proximity to the whales, it has become necessary to develop regulations or guidelines to manage boats which are involved with watching whales. Regulation covers the entire range from "Codes of conduct" and guidelines to firm legal restrictions. However, most rules are of a somewhat arbitrary nature. To be useful, regulations should be based on the biology and behaviour of the species they are designed to protect (Duffus & Dearden, 1992). Detailed studies of the effects of whale watching on all aspects of the marine environment and especially the whales (and other wildlife) that are the focus of attention are rare, but are of great value in formulating appropriate guidelines. Hoyt (1995) stresses the importance of careful research to monitor the effects of human activties on whales. A code of conduct based on scientific research is more likely to be followed by whale-watch operators, accepted by the public and supported by local authorities (Duffus & Dearden, 1992) than an arbitrary code. In addition, research that provides information concerning the results of human activities within the natural environment could form a useful part of a larger overall study in an area of interest such as Clayoquot Sound. Unfortunately, each whale-watching destination has different characteristics, and in most locations the type of detailed information necessary to formulate meaningful guidelines is not currently available (Duffus & Baird, 1995; Duffus & Dearden, 1992).

Clayoquot Sound, on the West Coast of British Columbia, Canada, is a tertiary feeding ground of the gray whale, *Eschrichtius robustus*, whose primary and secondary feeding grounds are the Arctic waters of the Bering and Chukchi Seas (Kim & Oliver, 1989). Gray whales breed in the lagoons of Baja California Sur, Mexico, and migrate 8000 kilometres each spring to reach their feeding grounds. During the migration, the whales remain close to the coast, and many of them stop at tertiary feeding grounds in British Columbia, Washington, Oregon and Northern California (Nerini & Oliver, 1983, Oliver *et al.* 1984, Guerrero, 1989), where some remain for the entire summer, taking advantage of local food sources. Vancouver Island and Puget Sound, however, are the only tertiary feeding grounds where infaunal feeding has been documented (Reeves & Mitchell, 1988). It has been suggested (Weitkamp *et al*, 1993) that these tertiary feeding grounds are increasing in importance as the gray whale's population recovers from whaling-era levels. Whales are regularly seen during the summer months off the West Coast of Vancouver Island (Darling, 1978; Hatler & Darling, 1974; Murison *et al*, 1984). There is evidence that gray whales which do not forage in the primary and secondary feeding grounds return year after year to the same place. It is not known whether the whales that frequent these tertiary feeding grounds represent a specific unit of the population, such as non-breeding whales, or whether they began to forage in areas south of the Bering Sea as a result of opportunistic feeding along the migration route or by following the example of other whales.

Clayoquot Sound is particularly interesting among tertiary feeding grounds due to its accessibility to whale-watchers. It provides a unique opportunity to study the foraging whales' reaction to human disturbance, particularly whale-watching. The majority of gray whale watching takes place in the breeding lagoons or along the migration routes, and Clayoquot Sound is one of the few areas where foraging whales can reliably be observed.

The whale-watching vessels which operate in Clayoquot Sound exemplify the problems associated with a burgeoning whale-watching industry in an area which has no official protection (Duffus & Dearden, 1992). The main attraction is the small population of gray whales which feed in the area during the summer, but the area is also known for its outstanding natural beauty and sport fishing. Primary locations at which gray whales feed, and are subject to whale-watching, include Cow Bay and Rafael Point, on Flores Island, and Ahous Bay, on Vargas Island (Guerrero, 1989, Garner, 1994, Duffus *et al.*, in press). Since 1984, when the first whale-watching vessel began operating from the village of Tofino, the whale-watching industry has increased in size every year. At the present time there are more than 20 vessels offering whale-watching trips. Many of the operators of commercial whale-watching vessels show concern for the whales. These operators attempt to self-regulate through peer pressure, but there are few official avenues for complaint or enforcement. In addition, such agreements are easily jeopardized by the refusal of one or two operators ("free riders" as described by Ostrom, 1990) to participate.

To put regulation on a sound footing requires a deeper understanding of gray whales' behavioural ecology than has previously been employed. Unfortunately, gray whale behaviour is difficult to measure or analyze and most previous research has been descriptive or anecdotal in nature (Darling, 1978, Gill & Hall, 1983, Oliver *et al*, 1983, Moore & Ljungblad, 1984, and Mallonee, 1991). Gray whales exhibit a narrower range of behaviour during the feeding season than that frequently observed on the migration or at the calving lagoons. The most readily quantifiable aspects of gray whale behaviour are the dive variables (dive duration and surface interval duration) and the whale's path of movement. The whales' foraging behaviour can be seen as a set of measureable variables which may be influenced by several variables in the foraging area, including vessel activity, depth, and prey diversity and distribution. The purpose of this research project is to undertake a quantitative analysis of gray whale behaviour, incorporating aspects of feeding ecology, so that these parameters can be used as tools with which to detect any changes which may occur in the whales' behaviour in the presence of vessels.

Three additional issues are addressed in the study. Chapter 4 addresses the distribution of the whales' prey items and its effect on the whales' use of space, and compares the different feeding locations and foraging tactics as they relate to the whales' energy gain and expenditure. Chapter 5 examines the changes in the whales' spatial distribution across different spatial and temporal scales. Ultimately it may be possible to gain information regarding the importance of vessel traffic, relative to other factors such as prey distribution, in affecting the whales' spatial behaviour. It can be argued that foraging and diving, aspects of behaviour which are closely linked to energetics, are the activities for which changes in the factors described above will have the greatest significance.

The study is divided into three sections, each of which analyzes foraging behaviour in a different context, corresponding to the issues described above. The first section (Chapter 3) compares the measureable behavioural parameters of the whales in the presence of various numbers of vessels. The second (Chapter 4) examines some other possible causes of variation in the whales' diving and foraging behaviour, particularly the whales' movements within the study area as compared to the different types and densities of prey available to them. The influence of prey type and density on the gray whale's movements is a key part of the overall picture of its behavioural ecology. This section also interprets dive parameters in light of the connection between oxygen consumption and energy expenditure, examines evidence of possible search behaviour, and discusses fine-scale decision-making by gray whales. The third part of the study (Chapter 5) is concerned with coarser spatial and time-scale shifts. Changes in foraging location are examined on a medium (within seasons) and coarse (between seasons) scale. The dynamics of long-term spatial shifts are discussed.

These three sections allow for the formation of a comprehensive picture of gray whale foraging ecology, and provide a background against which the effects of vessel numbers can be assessed. Ultimately it is hoped that the results obtained will contribute to the construction of meaningful guidelines for the whale-watching industry.

1.2 Research Design

The purpose of this study is to measure and compare the behaviour of foraging gray whales in the presence and absence of whale-watching vessels, in response to the need for more detailed studies of the effects of whale watching on marine mammals. Gray whales in the feeding grounds do not show diverse surface behaviours (Bogoslovskaya, 1986, Wursig *et al.*, 1986, Guerrero, 1989, Mallonee, 1991,) so it is not possible to document changes in relative rates of certain behavioural patterns - a commonly used indicator of disturbance (Corkeron 1994). Physiological measurements such as heart rate (Elsner, 1989) or the blood levels of certain hormones have been used as alternatives to behavioural indicators to identify stress in small marine mammals. These techniques require the use of invasive monitoring devices which must be fitted to the animal, and are not suitable for large animals such as the gray whale. Ventilation patterns, however, are quantifiable, accessible, and potentially responsive to changes in the whale's immediate environment, and therefore constitute the main focus of this study.

1.2.1 Vessel Numbers and Diving Behaviour

In deciding what characteristics of gray whale foraging behaviour to measure, it is important to consider the constraints placed on their behaviour by their life history. Because they have only a limited time in which to assimilate sufficient food stores for the breeding season and migrations, it is reasonable to expect gray whales to attempt to maximise their net energy gain. The energetics of diving animals involves a trade-off between time spent at the surface and time spent at the bottom or at feeding depth, so that the energy spent travelling between them is minimised. It is not possible to measure gray whale energy expenditure directly in the field. Sumich, 1994, sampled expired lung gas from "friendly" gray whale calves in Laguna San Ignacio, but this would be impractical with adult whales in the feeding grounds. Substitute parameters, such as breathing rates and dive depths, have been used to estimate the energy expenditure of some marine mammals (Dolphin, 1988).

An undisturbed whale's dive characteristics would be expected to show little variation over the short term once an "optimal" pattern had been established. A change in the whale's dive pattern - ventilation rate, dive time, surface interval or the relationship between surface and dive times - could be interpreted in terms of external influence. In addition, a change in the whale's turning behaviour could be similarly interpreted as a spatial influence.

The main focus of this study is to test the null hypothesis that gray whale surface behaviour is independent of vessel numbers. The principal measurements made in the study were dive variables (feeding dive time, surface interval time, dive cycle time, number of ventilations per surfacing and ventilation rate per hour), and location at the end of each feeding dive. The latter enables an estimate of "sinuosity" or path turning to be made, and also makes it possible to estimate the water depth in the location in which the whale was feeding. The number of vessels present, not including the research vessel, was noted at the end of each feeding dive.

1.2.2 Environmental Factors Affecting Fine-scale Spatio-temporal Variations in Gray Whale Behaviour

In addition to observing vessel activity and the whales' ventilation patterns, a prey sampling program was undertaken to aid in interpreting the ventilation data in terms of energetics. Over the three years of the study, gray whales were observed feeding in five different areas and under a diverse assortment of environmental conditions independent of vessel number. In order to place the whales' diving and turning behaviour in context, and to gain information concerning their search patterns and foraging "choices," measurements were taken to quantify factors other than vessel disturbance that were expected to affect the whales' behavioural patterns. Based on previous studies (Murison *et al.*, 1984, Wursig *et al.*, 1986, Dolphin, 1988, Guerrero, 1989) it was hypothesized that variations in foraging depth and prey density were likely, singly or in combination, to be correlated with changes in the whales' behaviour patterns. These were expected to be key factors affecting the whales' foraging strategy and can be seen as an important part of the overall picture of vessel effects and the whales' energy budgets.

The problems inherent in the study of cetacean energetics, which arise from the researchers' inability to observe their feeding behaviour directly and from the impossibility of making laboratory-type energy consumption measurements, can be mitigated somewhat by the use of substitute variables as indicators for energy gain and expenditure. Information about the sources of energy available to the whales can be obtained by sampling the prey in areas where they feed, provided that something of their feeding habits is known.

Gray whales in Clayoquot Sound were assumed to be feeding on benthic amphipods, and these were sampled in 1993 and 1994 in Cow Bay, the primary 1992/1993 feeding site, using diver-held cores. In 1993, the presence of feeding pits (author pers. obs., 1993) at the sampling sites confirmed that benthic feeding was occurring. However, in 1994, the whales did not feed in Cow Bay; instead, and unexpectedly, they fed farther west off Rafael Point, over a rocky (author pers. obs., July 6, 1994) substrate. It was eventually established, by occasional opportunistic sampling with a plankton net and by feces sampling with a dip net, that the whales were feeding primarily on swarming Porcellanid larvae (Crustacea; Anomura). In response to this prey switch, a plankton sampling program was introduced in 1995 in addition to continued benthic sampling with diver-held cores and also with a boat-deployed core sampler.

These Porcellanid larvae were seen to occur at a number of depths, from right at the surface (D. Duffus pers. comm. 1994) to 1 - 2 m off the seafloor (author pers. obs., July 6, 1994); such discrepancy can be expected to introduce considerable variability in the whales' feeding depth. In the case of gray whales feeding on amphipods, the dive depth is much less variable, since the prey only occurs on the sea floor. However, amphipods can still occur at a number of different water depths, and planktonic prey may occur at any depth or at the surface. In addition, within the local feeding site, patches of increased prey density may occur which would be more profitable for the whale than other locations. This heterogeneity in the food resource should be reflected in the whale's spatial patterns which are visible from the surface. There may be energetic tradeoffs between prey density and depth or ease of capture which are difficult to quantify. However, spatial behaviour can provide useful clues to the prey choices the whales are making, since by staying at one feeding site or moving to another, the whale is selecting a certain combination of features of the environment, which include (but are not limited to) water depth, prey type and prey density.

Based on previous studies (Guerrero, 1989, Garner, 1994) and on theoretical treatments of foraging behaviour (Kramer, 1988), certain predictions can be made regarding the whales' foraging behaviour under different conditions of prey availability and depth. It is important to understand these variations and to interpret gray whale foraging behaviour in the context of their patchy prey environment. Ventilation rates and possibly turning behaviour would be expected to vary between prey types (Guerrero, 1989). All five of the dive variables could be expected to vary with foraging depth, although it is difficult to predict in what way. Based on "pre-loading," Kramer (1988) predicts that both dive times and surface times should increase with dive depth, but that surface times should increase more quickly.

The selection of feeding sites by the whales may be the result of the interaction of many factors including depth, prey type, and prey density. Whales could be expected to select the prey type with the greatest density; however, Guerrero (1989) implies that exploiting free-swimming prey may require more energy than benthic feeding, which leads to the prediction that whales should select benthic over planktonic prey if benthic prey was available.

Within prey types, whales can be expected to feed at the site with the greatest density of prey animals and within that site, to concentrate their foraging activity in the "patches" of greatest prey density (Guerrero, 1989). Since it requires less energy to exploit prey in shallow water than in deep, whales are expected to preferentially feed in shallow water, moving to deeper water later

(Garner, 1994). On a fine (daily) temporal scale, this would mean starting their search behaviour in shallow water and moving to deeper water later. It is assumed (Garner, 1994) that low path sinuosity corresponds with search behaviour and high sinuosity (increased turning) with feeding itself. Foraging whales would be expected to leave areas of high prey concentration as they become depleted (Charnov, 1976), but predicting when this will occur is difficult without a comprehensive knowledge of the prey distribution in the surrounding area, and of other confounding factors such as the relative attractiveness of different species of prey.

1.2.3 Long-term Spatial and Temporal Shifts in Gray Whale Activity

At the beginning of this study, one of the serious concerns facing the stakeholders in the whale-watching community of Tofino was the apparent gradual northward trend in whale activity centers. The concern among whale-watch operators was that their whale-watching activities were driving the whales farther from Tofino, and that if this was the case, then their whale-watching industry was fundamentally unsustainable.

Another explanation for the whales' behaviour, however, could be that they are depleting their food supply in one of the feeding sites within the Clayoquot Sound area and moving on to other sites. In that case, the whales' northward movement could probably be considered coincidental; the growth of the whale-watching industry coincided with the exhaustion of the southernmost site in the area, and the whales' removal to more northern sites where the food supply was richer.

Changes in the whales' spatial patterns can be expected to occur from season to season. If prey is depleted under feeding pressure, the whales' feeding behaviour should focus on a different location each season, or even from one part of a season to the next. This change in focus can be measured using the harmonic mean measure of activity (Dixon & Chapman, 1980). Prey density in areas subject to intensive whale feeding can be expected (Oliver & Slattery, 1985) to show some depletion when compared to other feeding areas which have not been used recently by the whales. Areas of maximum whale activity are expected to be correlated with areas of maximum prey density. In this study, prey density was mapped to test the strength of this correlation.

If whales return to the same feeding grounds year after year, and depletion of individual sites is indeed occurring, then a longer-term study might be expected to reveal a pattern of rotation between feeding sites as they recover. During the course of this relatively short (three-year) study, an attempt was made to test whether such depletion and rotation was occurring, both by looking at the prey distribution from year to year and by comparing short, medium and long-term analysis of the whales' distribution patterns. It is hoped that the information from this study can be used in conjunction with earlier (Garner, 1994) and later (Dunham, 1999; Tombach, in preparation; Meier, in preparation) work to build a comprehensive picture of coarse-scale gray whale movements within Clayoquot Sound. The availability of a relatively small, accessible population (sensu Krebs, 1978) of gray whales provides an opportunity to gain insights into gray whales' spatial distribution and habitat use, some of which may be applicable to gray whales in the primary and secondary feeding grounds.

As discussed above, gray whales are expected to feed in the areas which provide them with the maximum energy return. Since there is evidence that it takes more than one season for an amphipod population to recover from extensive gray whale feeding (Oliver & Slattery, 1985), seasonal rotation of feeding locations is a probable long-term outcome of the whales' search patterns and foraging decisions. The fine-scale picture only tells a part of the story of gray whale foraging patterns. It is necessary to examine both whale and prey distribution patterns on a coarser (within and between entire feeding seasons) temporal scale in order to place the long-term movements of the whales in the wider context of their own spatial movements and the life histories of their prey.

The temporal aspect of prey distribution is closely tied to the ability of prey to recolonize areas in which gray whales have been feeding. Feeding pits are generally repopulated following whale predation (Nerini & Oliver, 1983, Weitkamp *et al.*, 1992, Oliver & Slattery, 1985), and whales should resume use of depleted areas once the populations have reached former levels. Measurement of whale activity and prey density over several years can be interpreted in the context of predator-prey dynamics and should enable a long-term temporal dimension to be added to the overall picture of the whale's behaviour and feeding energetics. Prior to starting this project, there appeared to be some tendency to show a shift in feeding location on approximately an annual scale (Garner, 1994), and the utilization of alternative forms of prey in each location may also form a pattern which will become apparent over the long term. Therefore both between-season and within-season scales are important. Optimal foraging theory does not specifically address medium- or long-term behaviour patterns, being more concerned with immediate decisions. However, an extrapolation of optimality theory's predictions regarding search behaviour and consideration of the documented effects gray whales have on their feeding substrate lead to the prediction that it would be energetically sound for whales to find one region which is most productive for any one feeding season, and exploit that exclusively.

Accordingly, it would be expected that all whales within the study area feed at the same prey site in any given season, that the feeding site selected by the majority of individuals will differ from that selected in the previous year or years, and that there is a recovery period after which whales return to a previously abandoned site. It is also reasonable to expect that if whales select benthic over planktonic prey on a daily time-scale, the same will be true on a seasonal scale, and also that they will show a gradual seasonal shift from shallow to deep water as the shallow sites become exhausted.

1.3 Summary

This study is designed to examine the diving behaviour of gray whales in relation to the presence of whale-watching vessels and in the wider context of their heterogeneous spatial environment. Relevant literature is reviewed in Chapter 2, with emphasis on gray whale feeding ecology, whale-vessel interactions and foraging theory. Chapter 3 describes the procedures followed and the data collected to answer several specific research questions, while Chapter 4 records the results obtained. Chapter 5 presents a primary analysis of the results, and discusses each variable with reference to the hypotheses outlined in Chapter 1. Chapter 6 summarizes the conclusions of the study and discusses the management implications of the findings, and suggestions for further research.

Chapters 3 through 5 represent three separate sections of the study:

Chapter 3: <u>Vessel Activity and Diving Behaviour</u>. Gray whale diving behaviour is sampled and compared to the number of vessels present. The measurement of dive variables addresses the stated purpose of the study; a quantitative analysis of gray whale behaviour in order to detect behavioural changes which may occur in the presence of vessels. The dive data is used to test the following pair of hypotheses:

Null Hypothesis: Gray whale ventilation behaviour is independent of vessel numbers

Alternative Hypothesis: Gray whale ventilation behaviour is affected by vessel numbers

Chapter 4: Influence of Prey Type, Prey Density and other Environmental Factors on Fine-scale Spatio-temporal Variations in Gray Whale Behaviour. Whale behaviour is compared to feeding site, and prey is surveyed at each feeding site to determine the type and density of the prey being utilized by the whales feeding at the various sites over the three years of the study. The whales' prey selection strategy and the influence of prey type and density on their spatial and temporal behaviour is analyzed.

The collection of prey data and other ecological information helps to provide context for the whales' spatial movements, in accordance with the study's purpose - a quantitative analysis of gray whale behaviour which incorporates aspects of their feeding ecology. It is important to assess the relative roles of feeding ecology and vessel activity in the interpretation of the dive behaviour measured in Chapter 3. The following set of hypotheses are addressed by the data reported in Chapter 4:

Null Hypothesis: Prey type and density and water depth do not influence gray whale behaviour

Alternative Hypotheses:

1. Variation in gray whale ventilation rate and turning behaviour is correlated with prey type

2. Feeding dive time and surface interval time increase with increasing depth, with surface interval time accounting for an increasing percentage of the whale's time
3. Whales select the prey type with the greatest density if more than one type is present
4. Whales select benthic over planktonic prey if both are present
5. Whales select the feeding site with the greatest density of prey
6. Within sites, whales select the patch with the greatest density of prey
7. Whales leave patches when they become depleted
8. Whales search in shallow areas first, moving to deeper water later on.

Chapter 5: Long-term Spatial and Temporal Shifts in Gray Whale Behaviour. Location data and prey data collected over the three years of the study - supplemented by reports from local vessel traffic - are analyzed for long-term patterns. Seasonal movements of foraging gray whales are described in an ecological context.

In order to fulfil the purpose of the study – the use of gray whale behaviour as a tool with which to detect biological changes in the presence of vessels – it is important to understand the scale at which the gray whales' behavioural processes are operating. The data presented in Chapter 5 examine the issue of scale, and address the following pairs of hypotheses:

1. Null Hypothesis: Gray whales' feeding activity is randomly distributed among possible feeding sites in Clayoquot Sound

Alternative Hypothesis: Whales focus on one location per season, and this location changes from one season to the next

2. Null Hypothesis: Gray whale spatial activity within seasons is independent of foraging depth

Alternative Hypothesis: Whales show a within-season shift from shallow water to deeper water

3. Null Hypothesis: The selection of a seasonal foraging site by gray whales is independent of the sites selected in previous seasons

Alternative Hypothesis: Rotation of feeding sites occurs between seasons, correlated with prey depletion

Alternative Hypothesis: Whales follow a directional trend in their feeding site selection between seasons

In Chapter 6, the conclusions of the study are summarized and recommendations are made regarding the whale watching industry and future research in the area of gray whale ecology and management.

Chapter 2: LITERATURE SURVEY

This chapter reviews existing information about the gray whale, with emphasis on its feeding behaviour and prey, its population and distribution, and its interactions with humans. Relevant aspects of the whale-watching industry are also discussed. The last part of the chapter covers foraging theory, on which this study is based, and issues concerning its application to marine mammal behaviour.

2.1 Gray Whale Distribution, Life History and Feeding Ecology

The gray whale, *Eschrichtius robustus*, is the only species in the family Eschrichtidae (Reeves & Mitchell, 1988), its distinctive skull structure and other characteristics setting it apart from other mysticete whales (Barnes & McLeod, 1984). Gray whales are also unique in being primarily benthic feeders. They have an important role in the recycling of nutrients from the ocean floor to the surface and the sorting of ocean floor sediments (Johnson & Nelson, 1984, Nelson *et al.*, 1987), due to their tendency to ascend for ventilation with bottom sediment still streaming from their mouths. Two populations of gray whales exist. The Californian (or Eastern Pacific) population ranges from Baja California to the Chukchi and Beaufort Seas, and the Korean (or Western Pacific) population migrates between the Korea Strait and the Sea of Okhotsk (Reeves & Mitchell, 1988). These stocks are thought to be geographically separate, although it is speculated that there may be some "migratory bleeding" from the eastern stock into the western, which may now number only one or two hundred individuals. There is evidence that there was once a third population of gray whales in the Atlantic, but this stock is now extinct, and information concerning its size and range is not available (Reeves & Mitchell 1988). The gray whales of Clayoquot Sound belong to the more numerous Eastern Pacific population.

Eastern Pacific Gray whales mate in the southernmost part of their range, the breeding lagoons of Baja California, Mexico. Their mating takes place in early winter, usually around December, and the females give birth 13 - 14 months later (Rice *et al.*, 1981). In the spring, the whales begin to move northward toward their summer feeding ground, the pregnant females leaving first, in mid-February, followed by other adult whales, and finally by females with newborn calves. Originally it was thought that all calves were born in the warm waters of the breeding lagoons, and needed to build blubber reserves before travelling to the colder northern waters, but there is now evidence that some are born as far north as Washington State (Jones & Swartz, 1984).

Little is known about how gray whales navigate during their migration. Some Odontocetes are thought to navigate by means of sonar (Lockyer & Brown, 1981) and by reference to earth's geomagnetic field (Klinowska, 1988). Mysticetes are not thought to use these methods of navigation. Pike (1962) suggested that gray whales may navigate visually, but Mass and Supin (1990) provide evidence that their visual acuity is relatively low, making visual navigation seem unlikely.

The whales arrive at the primary feeding grounds in the Bering and Chukchi Seas about two months later, and remain there until October (Rice *et al*, 1984). Gray whales gain, on average, 16 - 30% of their body weight in the five months they spend at the feeding grounds. This is equivalent to consuming 400 - 1200 kilograms of food per day (Nerini, 1984).

2.2 Biology of Common Prey Species

Unlike other baleen whales, gray whales are known to feed predominantly on benthic prey. They are not as well adapted for foraging on plankton, having shorter, coarser baleen than the other mysticetes (baleen whales), but instances of planktonic feeding have been frequently documented (Pike, 1962, Wellington & Anderson, 1977, Nerini, 1984; Duffus, 1996). Their diet has been known to include benthic polychaete worms, ghost shrimp (*Callianassa*), squid spawn, herring spawn, small bait fish, decapod larvae, mysids and euphausids (Nerini, 1984, Weitkamp *et al.*, 1992). The gray whale's ability to feed on planktonic prey in addition to benthos gives it a dietary flexibility unique among cetaceans. Kim and Oliver (1988) suggest that, since gray whales are mostly found in coastal environments, this characteristic flexibility may have arisen as a result of changing prey availability as sea levels fluctuated over the last 30,000 years. Their ability to feed opportunistically may be partly responsible for the gray whales' relatively fast recovery from whaling-era population levels (Nerini, 1984).

In order to be able to evaluate the gray whales' diving behaviour in the context of its foraging ecology, it is useful to understand the ecological circumstances in which the behaviour occurs (Duffus, 1996). These include the life histories of the various prey animals available to the whale, both in general and in the Clayoquot Sound area specifically. The primary food source of gray whales in the Bering and Chukchi Seas appears to be small tubicolous crustaceans (*Ampelisca* spp.) which are part of the order Amphipoda (Frost & Lowry, 1981). The Order Amphipoda is extremely widespread and diverse. Amphipods are well represented in freshwater and marine habitats and there are even a small number of terrestrial species. The Order contains forms as diverse as the skeleton shrimps (Suborder: Caprellidae) and the so-called "whale lice" (Family: Cyamidae). The infaunal tubicolous amphipods which dominate the benthic community of the whales' feeding grounds belong to the Family Ampeliscidae, Suborder Gammaridea; although the corophioid group also contains tubicolous forms, these appear to have developed separately from the ampeliscid tube-dwellers (Barnard & Karaman, 1991). The ampeliscids are the only tube-dwellers of the primarily benthic Gammarid Suborder. Adult ampeliscids construct tubes of material known as "silk" which is secreted by glands situated on their pereiopods (thoracic appendages). The tube-dwelling amphipods of the waters around Vancouver Island are primarily *Ampelisca agassizi*; their tubes are buried 10 - 15 cm deep in the sand bottom, with almost no part of the tube showing when undisturbed (Oliver *et al.*, 1983), so that a feeding whale would have to make an an excavation 15cm deep in the sediment to capture all of the crustaceans. It is possible to observe these "feeding pits" in areas where whales have been feeding (Nelson *et al.*, 1987, Oliver & Slattery, 1985, Weitkamp *et al.*, 1992). These benthic amphipods' partially-buried tubes form "mats" on the ocean floor. The mats are often extremely dense in some areas - up to 24,000 individuals per m^2 in the Eastern Bering Sea (Stoker, 1981). Ampeliscids are capable swimmers and crawlers, but spend most of their time in their burrows, since they feed upside down in the tube using their antennae, which have many long hairs or setae, as filters while creating a water current in the tube (Barnard & Karaman, 1991). This behaviour provides a relatively static prey on which the whales can "graze," rather than a mobile prey which must be pursued.

Gray whales feed by sucking or scooping the bottom sediments into their mouths, and then ejecting the water and sediment particles. The invertebrates which are taken in with the sediments are retained behind the whale's baleen and then swallowed. This method of feeding leaves large (average 1.6m. long) oval depressions in the seafloor which gradually degrade with time and are recolonized by amphipods (Nerini & Oliver, 1983, Nerini, 1984, Oliver & Slattery, 1985, Klaus, 1990).

The benthic amphipod community in the waters off the west coast of Vancouver Island has been described as ecologically analogous to the extremely productive benthic amphipod community in the Bering Sea, the whales' primary and secondary feeding grounds (Oliver *et al.*, 1983). Both are detritus-based trophic systems, dominated by relatively low-diversity assemblages of infaunal benthic filter-feeders. The Bering Sea floor is populated by assemblages consisting of "pioneer"-type species of the genus *Ampelisca* (Nerini 1984). Stoker (1981) describes the assemblages as temporally stable, but complex in the distribution and spatial arrangement of species, which seems contrary to Nerini's (1984) assessment that they are "nearly" monospecific. In his 5-year study in which 176 sampling stations were quantitatvely surveyed, Stoker (1981) found 472 species, including 76 amphipod species. He also found the distribution of individuals to be extremely patchy, causing him to classify some of his quantitative results as "marginally acceptable." For example, the density of organisms in the eastern Bering Sea ranges from 400 per m^2 to 24,000 per m^2. Mean benthic biomass is calculated as 482g/m^2, with amphipods accounting for 161g/m^2. Highsmith and Coyle (1990) calculated the mean number of amphipods in the Chirikov Basin (northern Bering Sea) as 4,606/m^2, again with a high standard deviation, and commented on the extremely high caloric content of the Chirikov amphipod community compared to examples from the English Channel and Chile. Guerrero (1989) reported a maximum infaunal biomass for Ahous Bay, Clayoquot Sound, of 160g/m^2 - considerably less than that found in the main feeding grounds. More recent sampling programs report somewhat lower values: 38g/m^2 (Cow Bay) and 21g/m^2 (Ahous Bay) in 1996, 97g/m^2 (Cow Bay) and 74g/m^2 (Ahous Bay) in 1997 (Dunham, 1999). Carruthers (2000) converts Dunham's wet weights to dry weights for comparison to her own data, which show much lower biomass - less than 75% of Dunham's values, for a combined number representing both Ahous Bay and Cow Bay.

Benthic faunal distribution in the Bering was correlated more strongly with sediment size than with other variables, although factors such as currents, primary productivity, natural predation and fisheries also appeared to have some effect on their distribution (Stoker, 1981). Carruthers (2000) reported that the floor of Ahous and Cow Bays were dominated by fine-grained sand, and found no relationship between sediment size and amphipod numbers.

Despite the resemblance between the benthic community in the Bering Sea and those of Clayoquot Sound, the gray whales summering at Clayoquot Sound appear to utilize a far more diverse selection of prey species than those in the Bering Sea. Dunham (1999) found thirteen species of prey being utilized by gray whales in Clayoquot Sound, including, in addition to ampeliscid amphipods, four species of porcelain crab larvae (Crustacea; Anomura; Porcellanidae); six species of mysids (Crustacea; Mysidacea) and one species of ghost shrimp (Crustacea; Anomura; Callianassidae). This prey diversity adds complexity to the task of interpreting the whales' ventilation patterns, since prey type must be taken into account as well as prey density.

The four species of porcellanids found in Dunham's (1999) study belong to two genera - *Pachycheles* and *Petrolisthes* - which are commonly found in the coastal waters around Vancouver Island (Morris *et al.*, 1980). Knudsen (1964) studied adult porcelain crabs at six coastal sites around Puget Sound, Washington. Both genera were represented in Knudsen's study, and both were found in the highest numbers in areas of strong current. *Pachycheles* was found at only one of the six locations. The study indicated that two or three broods of eggs may occur in each breeding season. Adult porcelain crabs live in the intertidal zone, generally underneath rocks or in cavities - and are predominantly filter feeders. The eggs are carried by the female until they hatch. The first larval stage, the prezoea, is short-lived and its rounded shape, with few body projections, is intererpreted by Gonor and Gonor (1973) as an adaptation for negotiating the surf zone. The larva then passes through two zoeal stages, each lasting 10 - 15 days. The zoea larvae are fast swimmers and voracious predators, and possess a characteristic long rostral spine. The advantage of this body form is unclear, since it appears to reduce the larva's ability to manoeuvre, but it may assist with flotation. During the next stage, the megalopa, the larva's feeding style changes from predation to filter feeding, which is the adult feeding method, and its behaviour from swimming to crawling (Gonor & Gonor, 1973), thus removing it - in general - from availability as a planktonic food source for gray whales.

Murison *et al.* (1984), Guerrero (1989) and Dunham (1999) document instances of gray whales feeding on mysids, which are free-swimming crustaceans which tend to live around kelp (*Macrocystis* or *Nereocystis* spp.) plants. Dunham (1999) found large numbers of mysids, mainly *Holmesimysis stricta,* near feeding gray whales in Clayoquot Sound. Murison *et al.* (1984) report collecting large numbers of mysids belonging to two genera, *Holmesimysis* and *Acanthomysis,* near feeding gray whales off the west coast of Vancouver Island. The largest numbers were obtained during epibenthic daytime tows in areas of kelp. Nighttime tows, midwater and surface tows, and tows made outside the kelp beds yielded few or no mysids. There is some evidence that gray whales feed mainly during the day, and rest at night. Guerrero (1989) watched one whale overnight and observed a change in behaviour and ventilation pattern compared to the pattern observed during the day. The whale stayed near the surface and took shallow breaths, remaining almost motionless. Guerrero interpreted this as "resting" behaviour. However, it is not known whether this whale's behaviour was typical of other gray whales in the feeding grounds.

Ghost shrimp are benthic anomuran crustaceans of the genus *Callianassa.* They are burrowing animals often found in the sandy or muddy bottoms of estuaries on the West Coast of the United States and Canada. Weitkamp *et al.* (1992) studied an area in Puget Sound where gray whales were feeding on ghost shrimp, and concluded that they represented an extremely energy-rich food source for the whales (20.5 + 2.1 joules per microgram dry weight, 0.214g dry weight being equal to 1g wet weight). They calculated the biomass of the standing stock of ghost shrimp in Puget sound as 1,058 g/m^2 and 1,917 g/m^2 wet weight (1990 and 1991 respectively) - considerably greater than the 482 g/m^2 biomass from Stoker's (1981) study of benthic Amphipods in the primary feeding grounds in the Bering Sea. Hudnall (1985) describes one juvenile gray whale feeding on ghost shrimp in the Clayoquot Sound area during the summer of 1984. No whales returned to the feeding site in subsequent years, until the time of this study, when gray whales returned to feed there (Author pers. obs. 1995), although other feeding sites in the Sound remained in regular use by gray whales. Dunham (1999) reported that the benthic community of Grice Bay contained 14 - 25% ghost shrimp and 73 - 84% *Cryptomya,* a bivalve, which may also be a source of nutrition for gray whales.

Clayoquot Sound, as a tertiary feeding ground, represents an extension of the main feeding grounds off Alaska. In addition to increasing use of these tertiary feeding grounds (Weitkamp *et al.*, 1992), gray whales appear to be extending their range in the primary and secondary feeding grounds (Miller *et al.*, 1985). It is hypothesized that they may be searching for additional food resources because their population is increasing, although the figures may also be an artifact of increased observation effort in recent years. An apparent decline in the population of northern Bering Sea amphipods between 1986 and 1988 (Highsmith & Coyle, 1992) supports the hypothesis that the gray whale population may be reaching the carrying capacity of the amphipods in their primary feeding grounds.

2.3 Whale-Human Interactions

At the time of the current study, gray whales had been protected for more than 50 years, and their population was considered to be approaching historic levels. Scammon (1874) estimated that pre-whaling-era gray whale population levels had been around 30,000, and "not more than 40,000." Ohsumi (1976) calculated that the gray whale population dropped to around 4,000 in 1875 as a result of whaling, and increased to 11,000 by the early 1960s after they were protected from whaling in 1937 by the "International Agreement for the Regulation of Whaling." The population was estimated from Unimak Pass, Alaska as 11,000 in 1977 (Reilly 1984), and 17,000 in 1979 (Rugh, 1984). A 13-year shore census in California led to a population estimate of 15,647 in 1980 and the conclusion that numbers were rising at the rate of about 2.5% per annum (Reilly *et al.*, 1983).

Gray whales were protected from whaling in 1937, and since 1955 humans have begun to utilize gray whales commercially for a new purpose - recreational whale-watching. Naturalists have expressed concern from the outset about the impacts of the whale-watching industry on the gray whale population (Reeves & Mitchell, 1988). The gray whale's removal from the U.S. list of endangered and threatened wildlife was proposed in 1993 (NMFS 1993) and became final in June of 1994 (Federal Register, 1994). Buckland *et al.*, 1993, give a recent population estimate as 21,000 whales, based on 1987 and 1988 counts. The U.S. National Marine Fisheries Service is conducting a program of research to monitor the status of the gray whale following its removal from the list; priorities include estimation of numbers and calf production, and determination of the degree to which anthropogenic factors (for example, chemical contaminants and marine noise) may compromise the viability of the gray whale (NMFS, 1992). Some disagreement exists as to whether the whales are at carrying capacity; arguments in support include recent decline in pregnancy rate and apparent overexploitation of the benthos in the Bering and Chukchi Seas (Reilly, 1992, Highsmith and Coyle, 1992).

Although the Eastern Pacific (California) population of gray whales has recovered, at least to a large degree, from the effects of whaling, they are now subject to hazards of a different sort. They are shallow-water whales rarely found outside the continental shelf (Reeves & Mitchell, 1988), and this near-shore distribution pattern brings them into contact with fishing vessels, shipping lanes, whale-watching centers and oil and gas fields (Moore & Clarke, 1990).

The effects of such hazards on the gray whale population are more difficult to observe than the effects of whaling. In a review of research documenting gray whales' responses to human activities, Moore and Clarke (1990) list increased underwater noise, pollution, and the possibility of collisions or entanglement among the potential adverse effects of human activities. Gray whales responded negatively to continuous noise sources louder than 120 db, and intermittent sources louder than 170 db (Malme *et al.*, 1988); with course changes being used as an indication of the whales' reaction. They also showed a weak negative response to recreational vessels closer than 550 m (Richardson *et al.*, 1989). Reactions vary with other factors; for example, presence of calves and background noise levels. Dahlheim, 1987, studied gray whales' behavioural responses to artificially produced sounds in the calving lagoons, and recorded an increased tendency for the whales to change direction at the onset of the artificial noise. The direction of movement varied with the type of sound played; artificially produced outboard motor sounds evoked a positive response (where the whales swam towards the sound source) in several cases. The whales also responded by increasing or decreasing their own "calling" frequency. Their "calling" frequency increased if sounds were played which were similar to those which occur in the lagoons as ambient noise. Novel sounds were correlated with a decrease or (in the case of killer whale sounds) a complete cessation in "calling." Underwater noise is a problem for whales in part because of its potential to mask the whales' vocalizations, although gray whales seem to have the ability to be somewhat flexible in their vocal behaviour and thus apparently minimize the adverse effects (Dahlheim, 1987).

The purpose of the current study is to compare the behaviour of gray whales in the presence and absence of vessels. While it is possible to conduct a controlled experiment like the one conducted by Dahlheim (1987) to test whales' response to a stationary source of noise, studying their response to vessels is more difficult, and few such studies exist. Finley and Davis (1984) studied the directional responses of belugas and narwhals to ice-breaking vessels in the Canadian Arctic. They interpreted the cetaceans' reactions as negative, but the evidence is not conclusive. Bursk (1988) found no difference in respiration rates or swimming speed overall between gray whales off San Diego escorted by boats and those not, but found much greater course variability in the former. Bursk also described "snorkeling," in which the whales decrease forward motion and breathe "inconspicuously," presumably an above-surface interpretation of the purpose of their behaviour. He describes a significant correlation between course changes and number of boats (but no data is given to support the conclusion) and suggests noise pollution as the culprit. Very few studies document the effects of whale watching on gray whale behaviour. Uncertainties in researchers' abilities to estimate gray whale hearing capabilities and difficulty in measuring local sound transmission properties often make such studies inconclusive (Malme *et al.*, 1989).

There is disagreement as to whether vessel traffic can cause gray whales to abandon an area (as feared by the whale-watching community of Clayoquot Sound). Guerrero Negro Lagoon, Mexico, and San Diego Bay, California, are both areas apparently abandoned by gray whales due to shipping traffic (Moore & Clarke, 1990), although Guerrero Negro was reoccupied once the ship traffic lessened. On the other hand, San Ignacio, another calving lagoon, has not been abandoned despite considerable whale-watching traffic, and there is some evidence that the whales become habituated to the vessels as the season progresses (Jones & Swartz, 1984).

The lack of a consensus among scientists about the effects of vessel traffic on gray whale movements makes it difficult to design and enforce protective measures for the whales. The National Marine Fisheries Service in the U.S. plans to monitor whale watchers and recreational boaters to ensure that they comply with the Marine Mammal Protection Act of 1972, and "will encourage the governments of Mexico and Canada to use similar standards for whale watching within their waters." (NMFS, 1993). The U.S. Marine Mammal Protection Act prohibits "harassment" as a "take." Guidelines are established for whale watchers and regulations may be (1993) implemented. In Mexico, the Federal Penal Code prescribes up to six years in prison for harassing or killing marine mammals (Dedina & Young, 1995). In Canada, marine mammals fall under the jurisdiction of the Department of Fisheries and Oceans, and are covered by the 1993 regulations pursuant to the Fisheries Act of 1868. The Fisheries Act contains language protecting marine mammals from "disturbance", but no specific behavioural guidelines are included (Government of Canada, 1993).

Problems with commercial traffic are more likely when whales and vessel traffic are confined to narrow channels. The effects are difficult to generalize, since cetacean behaviour around boats varies with species, age, sex, and the type of vessel activity (Blane, 1997). Actual collisions or entanglements between vessels and gray whales in the study area are few; Baird *et al.* (1990) estimated the gray whale mortality in Canadian waters incidental to fishing operations to be 2.02 whales annually. A more difficult concern to address (Duffus & Dearden, 1992) is the issue of the potential for harassment of gray whales by the increasing number of whale-watching vessels in the study area. Duffus (1988) suggests that controlled experiments are necessary in order to gain information about the whales' ability to tolerate sustained interaction with whale-watching vessels. The current study attempts to address in part the question of the whales' tolerance to whale-watching by determining whether or not a change in their behaviour occurs in the presence of whale-watching vessels.

The growth of whale-watching worldwide makes the disturbance issue a significant international concern. Since its beginnings in California in 1955, whale-watching has grown to a 500 million-U.S.-dollar industry and spread to 30 countries (Hoyt, 1995). In his survey of whale-watching worldwide, Hoyt found no evidence that whales were reacting adversely to boats. However, he stresses that, since there is no information yet about potential long-term effects, caution should be used, and he recommends a strategy for the whale-watching industry to follow. It includes the careful construction of precautionary rules before problems develop, continued monitoring of whale behaviour and baseline studies so that long-term effects may be identified, and the inclusion of a scientific and informational component on whale-watching trips, in order to raise public awareness. Duffus and Baird (1995) and Duffus (1996) point out that in the current situation, where there is insufficient information concerning the effects of whale-watching on whales, it is easier to manage the industry conservatively and then relax restrictions as information becomes available than to allow unrestricted access to the whales and then restrict whale-watching activities at a later time.

The current study was initiated mainly to respond to the problem described in Duffus and Baird (1995) - that there is frequently insufficient information to guide cetacean conservation and management decisions. There are other reasons for careful monitoring of the whale-watching industry. Whale-watching and other wildlife and nature-oriented forms of recreation are becoming increasingly popular and marketable (B.C. Ministry of Tourism, 1991). Several communities have found their economy revitalized by whale-watching (Hoyt, 1995). However, as they grow and become more popular, the nature of the "product," a recreational experience, changes. Duffus and Dearden (1990) propose a model to describe the growth of a non-consumptive wildlife-based tourist industry. As the sequence progresses and the number of tourists increases, the tourists attracted to the site tend to be less experienced and less knowledgeable than earlier patrons, with little specific interest in the site and greater dependence on facilities external to the attraction itself. The quality of the experience also decreases as the site's popularity increases. Stress on both the community and the wildlife resource may result.

2.4 Theoretical Approaches to Foraging Behaviour

It is hoped that the current study will provide useful data which contribute to sound guidelines or regulations based on the biology of the whales in question (Duffus & Dearden, 1992). However, marine environments are particularly hard to regulate, primarily because marine wildlife often crosses international boundaries, because of the large number of agencies which may be responsible for the various uses of a marine area, and because water is a fluid medium that is difficult to enclose within regulatory boundaries (Parks Canada, 1994). Duffus and Dearden (1992) use Clayoquot Sound and the Robson Bight (Michael Bigg) Ecological Reserve as case studies to illustrate some of these problems. They stress the importance of specific research and rigorous study to make certain that regulations and boundaries are set in such a way as to offer genuine protection to the wildlife and/or ecosystem under consideration. The research needs to be particularly exhaustive because relatively little is known about marine wildlife, marine ecosystems and their interaction with terrestrial ecosystems.

In order for a research project such as the current study to satisfy the conditions set out in Duffus and Dearden (1992) to be a useful tool for management, it should focus on a specific issue and have a strong theoretical basis. When studying natural systems, it is not always possible to isolate one issue to study or measure, since the effect that can be observed is often the result of the interaction of many factors, some of which cannot themselves be observed (Perry & Pianka, 1997). Because of this, and because of the difficulty of observing marine mammals in a controlled setting, much existing behavioural research on marine mammals, especially large cetaceans, is qualitative in nature, and involves interpretation of observed behaviours, with little or no theoretical component. In other cases marine mammal research uses a theoretical framework developed in a different area of research. In such cases where a theory is used in the research design to make testable predictions, greatly increased understanding may be gained from the results of the study. One such theory, Optimal Foraging Theory (Pyke *et al.*, 1977), was first developed through studies of terrestrial animals such as birds, but has since been applied to animals with a wide variety of life histories, including marine mammals (Houston and Carbone, 1992; Kramer, 1988; Dolphin, 1988).

Optimality theory looks at animal behaviour in the way an engineer or economist would (Stephens & Krebs, 1986). It involves the study of the usefulness of behavioural (or other) attributes in order to make a quantitative assessment of adaptations. Predictions made based on "design" and "efficiency" can be tested with carefully designed experiments or observation routines. Optimality theory can be used to generate a null hypothesis, to discriminate between alternative hypotheses (Parker & Maynard Smith, 1990), or as a thinking tool to provide a theoretical framework within which to design an experiment (Stephens & Krebs, 1986). This last describes the way it is used in this study.

There are relatively few models available which are applicable to behavioural ecology. The Ideal Free Distribution model (Fretwell & Lucas, 1970) involves the key assumption that a predator's fitness is increased by moving to areas in which there are few conspecifics (Farnsworth & Beecham, 1997). This seems an unsuitable choice to explain gray whale foraging behaviour, since gray whales sometimes form temporary feeding associations in which the whales feed together for a period from several minutes to several hours, surfacing close together and breathing synchronously (author pers. obs. 1993, 1994). Wursig *et al.* (1986) recorded several instances of what he termed "socialization," a term applied whenever a whale was within a body length of another whale and oriented towards it, in the primary feeding grounds of the Bering Sea. These observations indicate that the Ideal Free Distribution is probably not useful in explaining gray whale foraging behaviour and habitat selection.

In developing a focused study of whale foraging behaviour it is possible to use these assumptions as a framework to direct the emphasis of the research (*sensu* Stephens & Krebs, 1986). This makes it possible to determine what aspects of behaviour should be studied (Kramer, 1988, Garner, 1994). For example, the foraging "decisions" of animals whose prey is distributed in patches can be predicted assuming a diminishing rate of energy gain with time spent in patch (gain function) although sometimes the rate is initially constant (Krebs, 1978; MacArthur & Pianka, 1966; Charnov, 1976). Travel time between patches is the other main variable, since the forager must "decide" how long to stay in one patch. If whale foraging behaviour can be interpreted in terms of the "patch" model, travel time between patches and the researcher's ability to identify search behaviour on the part of the whale become important. Consequently, the whale's spatial movements are very important, both in helping to determine the foraging and as an indicator of search behaviour (Garner, 1994). Ventilation rates are also important, because they can be used as an indicator of energy costs to the whale (Sumich, 1983). However, patch type (that is, prey type) preference is difficult to predict other than as a function of the relative abundances of different prey types; there is no way to separate the effects of discrepancies between the energy required to dig and consume benthic prey and that required to pursue and consume planktonic prey (Piatt & Methven, 1992, Dunham, 1999).

It is possible, but difficult, to quantify the energy budget of whales (Dolphin, 1988; Houston & Carbone, 1992). The difficulty of measuring energy gain and expenditure in absolute terms constitutes an experimental design issue for the current study. Whales' energy use can be coarsely estimated from their breathing rates and dive depths (Sumich, 1983; Wursig *et al.*, 1986); their energy gain by sampling the prey in areas where the whales are feeding (Weitkamp *et al.*, 1992). Taking energy costs into account, Sumich (1983) predicted fairly closely the speed at which a migrating whale should swim. While Sumich's research was focussed on one aspect of optimality theory - that involving the determination of cost - other studies have sought to apply the theory to marine mammal foraging as a whole. In a study by Dolphin (1988), prey patches at different depths were assigned a profitability rank which incorporated time and energy costs and prey density. In 89% of dives, humpback whales restricted their feeding to patches for which prey profitability was maximised, ignoring other available prey patches and foraging in a manner which appeared to agree with predictions based on optimal foraging theory. In the case of gray whales feeding on amphipods, one aspect of the energy cost - the dive depth - is much less variable, since the whales are always feeding on the bottom.

Pierce and Ollason (1987) criticize optimal foraging theory on the grounds that fitness is difficult to define. Stearns and Schmid-Hempel (1987) define fitness as "that parameter best representing differential reproductive success," but state that there is no unified measure of "fitness." It is possible to avoid the circular definition of rewards and activities in terms of each other by carefully defining local or short-term fitness measures within the wider concept of fitness as a predictor of gene frequencies (Stearns & Schmid-Hempel, 1987). Haccou and Van der Steen (1992) distinguish between the "defining features" of a concept (for example, "fitness") and the "accompanying features" of the concept. If the defining features are under test, then the reasoning becomes circular - it is the accompanying features that should be tested. Perry and Pianka (1997) suggest that the goal should be to identify an optimal foraging strategy (leading to foraging success) rather than an optimal foraging behaviour (leading to fitness). In the case of gray whales, we are interested in their behaviour in the presence and absence of vessels, in the context of their spatio-temporal foraging choices, which are assumed to be the result of an optimal foraging strategy. Garner (1994) suggests that their foraging strategy may be disrupted by the presence of vessels in much the same way as other animals' strategies are disrupted by the presence of predators and the accompanying need for vigilance.

It is reasonable to assume that adult whales are maximising their long-term net rate of energy gain while in the feeding grounds, since they are restricted to a short temporal window in which to gain all the food they need for the winter season and the fall and spring migrations. Weitkamp *et al.*, (1992) calculated that, for a particularly rich food source, whales could satisfy their requirements by feeding only 2 - 4 hours per day. However, the food source they consider - ghost shrimp (*Callianassa*) - is only utilized by a small fraction of the population of gray whales. The whales in this study, in Clayoquot Sound, usually feed on animals similar to those which sustain the main population of gray whales in the Bering Sea, and which have a much lower biomass per square meter than those described in Weitkamp's (*et al.*) study (Dunham, 1999).

For aquatic animals which also breathe air, the spatial, temporal and energetic constraints placed on them by the need to ventilate regularly are confounding factors in their foraging behaviour. Kramer (1988) extended the concept of "foraging" to breathing; capturing a spatially constrained resource whose acquisition shows diminishing returns over time. Diving animals - or, more properly, "surfacing animals" - forage for oxygen in much the same way as they and other animals forage for food. Dives to a greater depth (analogous to an increased travel time between patches) should lead to increased time being spent at the surface gaining oxygen. The logical extension of this analogy, Kramer argues, is that not only should the surface time increase with depth of dive, but that it should increase at a proportionally greater rate. Kramer's model may be an oversimplification when applied to animals such as large marine mammals which build up energy stores in one location and fast in another location. A further complication is the aerobic dive limit or ADL (Kooyman *et al.*, 1980). Some marine mammals are able to function anaerobically underwater, and would exhibit two different respiration patterns depending on whether they were diving aerobically or anaerobically. However, it seems unlikely that gray whales, being shallow-water animals, utilize the ability to dive anaerobically.

An empirical test of Kramer's theory was carried out in 1989 on minke whales (Lynas, 1989). Surface interval was found to increase with feeding dive duration, which, since dive duration is affected by depth, implies that there would be some support for Kramer's model in deeper-diving minke whales. The limiting factor in controlling ventilation patterns was found to be prey handling time, which is consistent with the shallow location of the prey and the lack of other limiting factors. For a gray whale engaged in benthic feeding, it is more likely that depth will be a limiting factor, since handling time remains fairly constant at shallow depths but in most cases food is not available there.

For planktonic feeding, prey density can be expected to play a primary role (Darling *et al.*, 1998), and the whale's spatial search behaviour may be the key to recognizing foraging decisions. The method by which gray whales locate their prey is not clear. In part because of the impracticability of keeping them in captivity, little is known about the sensory abilities of gray whales. Mass and Supin (1990) estimate the gray whale's visual acuity as 10-11 minutes in the frontal and 12-13 minutes in the temporal part of its field of vision (by comparison, human 20/20 vision is equivalent to an angle of resolution of about 1 minute). This estimate was achieved by examination of the structure of gray whale eyes, and is considered by the authors an "optimistic" assessment of visual acuity. That gray whales "spyhopped" when played recordings of killer whale sounds is interpreted by Mobley and Helweg (1990) as evidence that they use vision for predator avoidance, although since cetacean vision is usually thought to be better in water than in air, this conclusion is arguable.

A study in which sounds were played to passing whales while their behaviour was monitored from shore (Dahlheim & Ljungblad, 1990) placed their hearing ability in the 800 - 1500 Hz range. This is towards the low end of the human hearing range (20 - 20,000 Hz). Although amphipod "tube mats" are detectable by side-scan sonar (Johnson & Nelson, 1984), there is no evidence that gray whales use echolocation to find their prey. Unlike those of Balaenopterid whales, the baleen plates on each side of the gray whale's mouth do not meet in the front of the whale's mouth; the resulting gap may allow them to sample continuously from the water column as they swim (Reeves & Mitchell, 1988). Based on these sources of information about gray whales' ability to sense their environment, it seems most likely that they "find" planktonic prey by continuously sampling for it as they swim, although it is not known to what extent they are able to remember and relocate productive plankton-feeding locations once they find them.

The mechanisms by which gray whales locate and select their prey are not well understood; however, they do appear to make prey choices and switch prey in response to factors which cannot always be observed (Dunham, 1999). If the whales' ventilation and spatial use patterns are to be interpreted, it is important that the current study involve some prey sampling in order to take into account the effects of prey choice and prey availability on the whales' behaviour.

2.5 Application of Foraging Theory to Gray Whale Behaviour

Gray whales are, in some ways, easier targets for optimal foraging theory than other whales, because their major prey is benthic, and therefore relatively stationary and measureable. However, the variety of prey utilized by gray whales can lead to difficulty, since the various prey types are seldom randomly distributed within the foraging area. The rigor of marine mammal research design is limited mostly by practical concerns: the difficulty of actually observing the subjects, of making accurate or representative measurements, of assessing the representativeness of the measurements, and of designing programs of study which involve control treatments.

Similar difficulties are present to some degree in most of the natural sciences, and are partly overcome by the use of an easily-measured variable to represent an inaccessible one, and by careful approximation, and regression to determine trends. Further studies are always called for, and in this way the approximations can be narrowed down and the relevance of the surrogate variables more closely assessed.

Since spatial use patterns are part of optimal feeding (Krebs, 1978), they can be good sources of information regarding foraging behaviour. The spatial foraging behaviour of the whale can be measured and compared to the expected pattern in light of the spatial distribution of prey in the study area. Garner (1994), citing Pyke *et al* (1977), hypothesizes that an increase in turning (path sinuosity) can be interpreted as indicating a shift from searching behaviour to foraging behaviour in gray whales. He states that it should be possible to compare their turning behaviour with the distribution of their prey, as mapped by SCUBA sampling or by other methods. If correlation can be found then it may also be possible to identify any effects of vessel traffic on whale feeding behaviour (Garner, 1994).

Since it is not within the scope of this study to measure the whale's path of movement underwater, a series of surface position fixes corresponding to the beginning of each feeding dive will be taken for each focal whale. In addition to providing a "sinuosity ratio" value which can be compared with vessel activity to test the main hypothesis that whale behaviour is unaffected by vessel traffic, these data will also serve as a record of the whales' spatial feeding activity on a larger scale, and may be used for comparisons within and between seasons. A prey sampling program in combination with the location data will enable the density and biomass of the food source in one foraging location to be compared with that of other foraging locations (Dunham 1999). Relative whale activity at different locations can be analyzed to test predictions based on Optimal Foraging Theory. Ventilation data in the presence and absence of whale-watching vessels will be collected to further test the main hypothesis, and will also be compared to the prey location data to determine the extent to which prey type or density affects the whales' ventilation patterns.

It is hoped that by collecting data on these key aspects of the complex series of relationships and environmental factors which combine to influence gray whale behaviour, it will be possible to exctract useful information and make a relevant contribution to future management decisions.

Chapter 3: Vessel Numbers and Diving Behaviour

This section of the study addresses the null Hypothesis that Gray whale ventilation and turning behaviour is independent of vessel numbers. Gray whale ventilation and position data was collected in the presence of various numbers of vessels. The location at which the data was collected was also taken into account.

3.1 Vessel Numbers and Diving Behaviour: Data Collection

Whale behaviour data were collected through direct observation of feeding whales from a 5-meter rigid hull inflatable vessel during the primary feeding period. Observations were made in July and August for the first two years of the study, and for a three-month period from mid-June through mid-September in 1995. On each day during the study period, unless prevented by weather conditions, a search was conducted starting in the Southeast corner of Flores Island (see Figure 1) at Fitzpatrick Bay and proceeding towards Siwash Point until a whale was located. Exceptions to this search protocol occurred approximately once a week - on these occasions Ahous Bay was checked first, and the vessel proceeded to Fitzpatrick Bay if no whales were encountered in Ahous Bay. This procedure was followed to ensure that Ahous Bay was being regularly checked, and reduced reliance on radio reports from other boaters.

Bottom-feeding gray whales typically spend from three to eight minutes on a deep dive, then take several breaths (ventilations) in succession, remaining near the surface, before commencing another deep dive. These surface intervals between dives typically last one to two minutes (see Figure 2).

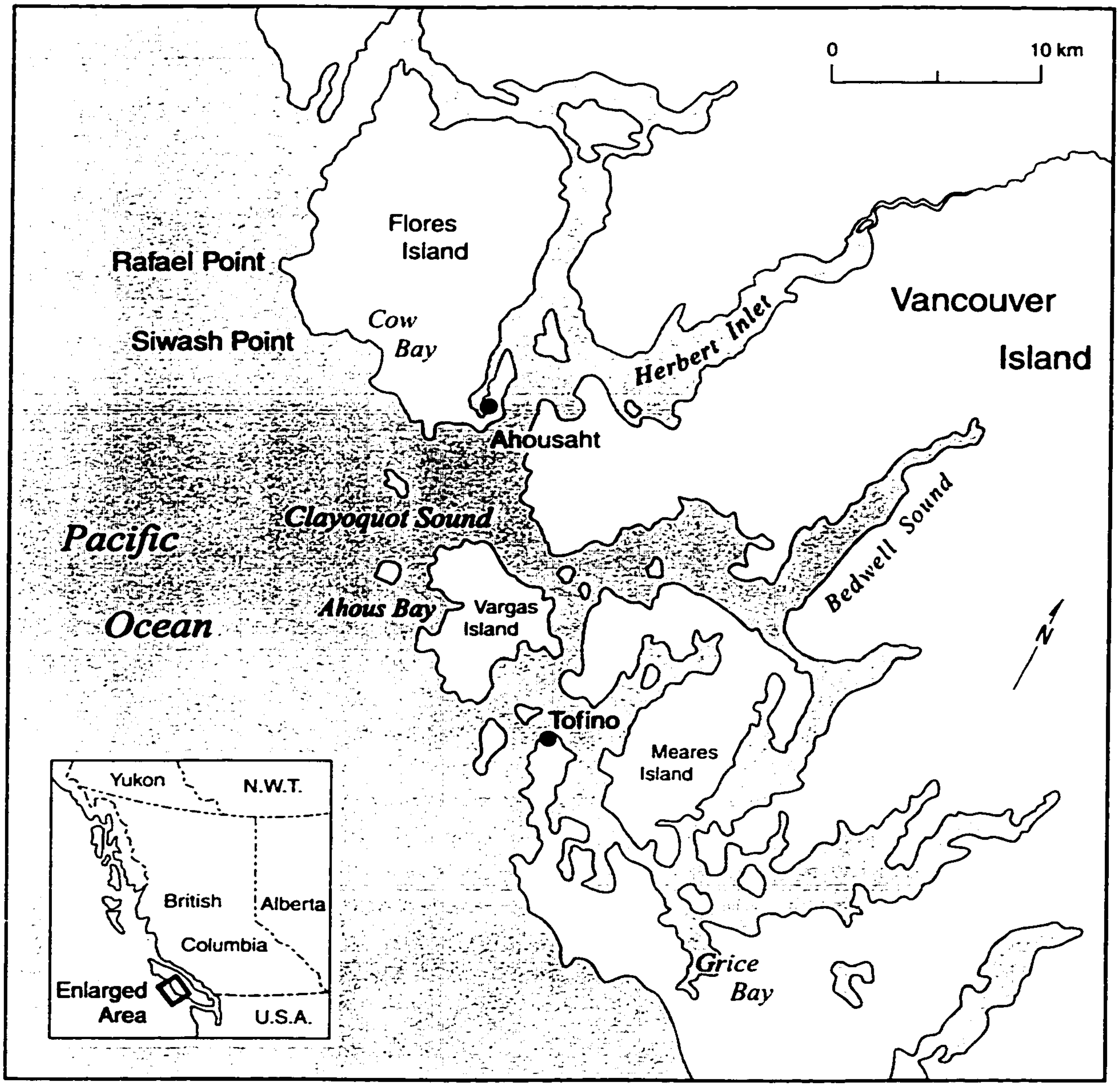


Figure 1: Location Map of Clayoquot Sound, Showing the 5 Major Gray Whale Foraging Areas

Latitude and longitude were measured for each dive cycle with a Global Positioning System (GPS) receiver. The position of the whale was obtained using a feature called "projection," in which the GPS unit calculates the position of an object if given its distance and bearing relative to the vessel. A digital flux compass was used to measure the bearing, and the distance of the whale from the vessel was determined by estimation. It was assumed that the accuracy of the estimations decreased as the range increased, so for each position the range was recorded to serve as an approximate measure of accuracy.

The whales were observed and monitored using the technique of recording all occurrences of one behavioural event, in this case the surface ventilation, or "blow" (Altmann, 1974). For each ventilation that occurred the time was recorded in hours, minutes and seconds. Other behaviours, such as breaches and spyhops, were occasionally recorded if their recording did not interfere with the ventilation monitoring. Visual identification marks were used to keep track of individual whales, and photo-identification was used where possible to document the visual cues.

The number of whale-watching vessels present in the immediate area, close enough to be watching the focal whale, was determined from VHF radio communications with whale-watch vessels, and from observation of the people on board the vessels, and was recorded each time the focal whale surfaced from a feeding dive. The dive variables could then be compared under conditions of vessel presence and absence, to test the null hypothesis that gray whale ventilation behaviour is unaffected by vessel presence or number.

The monitoring was maintained until the research vessel lost contact with the whale or weather conditions prevented continued observation. It was found to be possible to monitor up to three whales at a time if conditions were conducive (calm water; easily distinguishable whales; experienced crew).

3.2 Vessel Numbers and Diving Behaviour: Data Analysis

Sinuosity Ratio, a measure of turning, was obtained by calculating the total distance moved by the whale over five dive cycles, using the program *Homerange* (Dixon & Chapman, 1980) to calculate the distance moved between sequential whale positions. The total distance was then divided by the distance between the whale's starting point (position at the first dive cycle) and ending point (position at the fifth dive cycle). The index thus obtained compares the whale's actual path between the starting and ending points of the time interval with a straight-line path; the more turning exhibited by the whale, the higher the index number. The Sinuosity indices can then be compared between whales in the presence and whales in the absence of whale-watching vessels, to test the null hypothesis that their turning behaviour is unaffected by vessel presence or number.

The interval of five dive cycles - corresponding in most cases to approximately half an hour - was chosen because it allows the whale time to react to a possible disturbance, but is not long enough that short-term changes in turning behaviour would be masked. Overlapping intervals were analyzed (cycles 1 through 5, cycles 2 through 6, cycles 3 through 7 and so on), rather than sequential intervals, allowing the index to act as a kind of "moving average" which has the effect of smoothing the data.

The data collected were in the form of ventilation times, and these times were used to calculate five dive variables for each dive cycle. The first, dive cycle duration, is the time for one entire "dive cycle" to occur, from the beginning of a feeding dive to the beginning of the next feeding dive.

The feeding dive duration is the length of time from when the whale leaves the surface at the beginning of each feeding dive to when it resurfaces at the end of the dive, and the feeding dive percentage is the percentage of each complete dive cycle taken up by the feeding dive itself. The number of ventilations per cycle is a straightforward count of the number of ventilations, or "blows," between one feeding dive and the next, and the ventilation rate is the number of ventilations per hour, calculated from the number of ventilations in a given dive cycle, treating the duration of that dive cycle as a fraction of one hour.

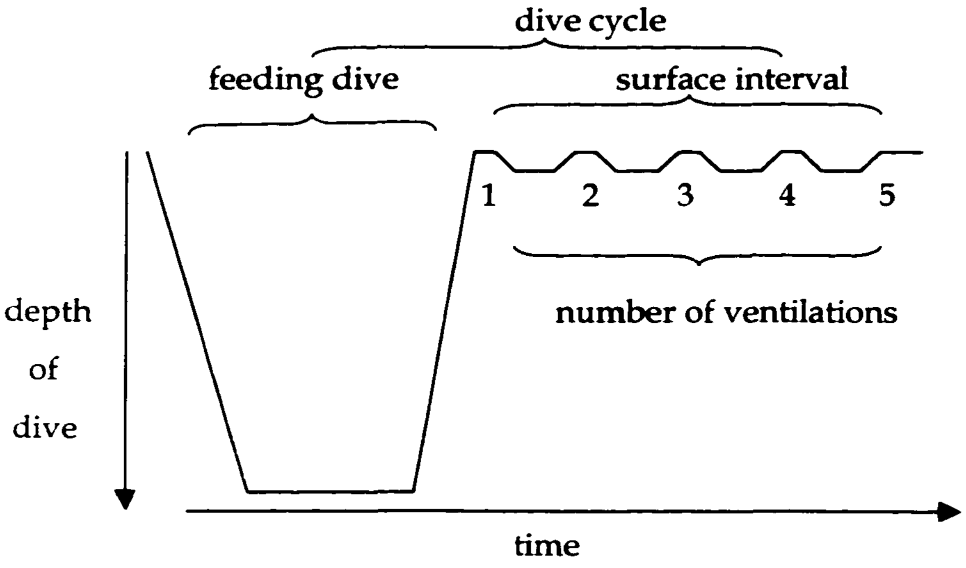


Figure 2: Typical Dive pattern of a Feeding Gray Whale

The variables calculated from the ventilation data were analyzed by vessel number classes using three different strategies: nine vessel number classes (no vessels, one vessel, two vessels etc. up to eight vessels); three vessel number classes (no vessels, 1 - 4 vessels, 5 - 8 vessels), and two vessel number classes (no vessels/vessels).

Standard descriptive statistics (mean, standard deviation and 95% confidence intervals) were calculated for each dive variable using the statistical package SPSS. In the case of vessel presence/absence, since only two vessel activity classes were used, the means were compared by means of a t-test. The Levene test was used to detect inequality of variances between the samples being compared in order to select the correct t-test for each statistic. With more than two vessel activity classes, Analysis of Variance (ANOVA) was used to test for significant differences between the dive variables, using number of vessels as a *post hoc* treatment. If significant differences were found, the individual classes were then compared with each other using Tukey's HSD multiple-range test *post hoc* to pinpoint the significant differences.

Two-way ANOVA were used to compare the effects of vessels with the effects of site for each dive variable.

3.3 Vessel Numbers and Diving Behaviour: Results

The whales were observed on a total of 39 days in 1993, and 1493 dive cycles were recorded, representing 99 hours of observation. In 1994, whales were located on 31 days, but ventilation data were only collected on 17 days. 1124 dive cycles were recorded in 44 hours of observation. On the remaining 14 days, the whales were present in large numbers in a restricted area, which made it impossible to continuously track one whale, and only position (latitude and longitude) data were recorded. In 1995, data were collected on 53 days and represent 129 hours of observation. The total number of dive cycles recorded was 1573 (this number does not include the data recorded at Grice Bay. Because of the shallow water the whales there did not dive in a cyclic pattern like the one shown in Figure 2 - see Chapter 4 for further explanation of Grice Bay ventilation patterns). The whales were observed for a total of 272 hours in the course of the study. See Appendix 1 for further breakdown of the research effort.

3.3.1 Dive Parameters and Vessel Numbers

No significant changes in sinuosity ratio were observed in the presence of different numbers of vessels. Significant differences between different vessel activity conditions were found in three dive variables (see Section 3.3.1.2), but two-way Analysis of Variance showed interaction between the site and vessel treatments in two of these.

3.3.1.1 Variation of Dive Variables with Vessel Presence/Absence

When the vessel numbers were grouped into two classes, present and absent ("absent" meaning that only the research vessel was present), significant differences between the two classes were found for three of the five ventilation parameters. Feeding dive percentage was included instead of surface interval duration, since surface interval duration is redundant if feeding dive duration and dive cycle duration are both included. Table 1 summarizes the descriptive statistics for the five ventilation variables.

Ventilation rate increased significantly (Independent t test, $t = -3.87$, $P = 0.00$) in the presence of vessels, as did dive cycle duration ($t = -4.14$, $P = 0.00$) and feeding dive duration ($t = -6.66$, $P = 0.00$) (Table 2). The feeding dive percentage and the mean number of ventilations per dive cycle were unaffected by the presence of vessels. The increase or decrease in the mean value of each dive

	Duration of Dive Cycle (sec)	Duration of Feeding Dive (sec)	Ventilation Rate	Number of Ventilations per Dive Cycle	Feeding Dive Percentage
No Vessels	271.4 (132.92) [643]	193.8 (109.68) [512]	64.2 (29.02) [561]	5.2 (2.45) [637]	79.5 (16.03) [902]
Vessels	297.6 (125.32) [1267]	234.7 (110.55) [876]	70.8 (42.64) [1239]	5.3 (2.32) [1387]	79.0 (17.37) [1761]
1 - 4 Vessels	297.0 (127.01) [1215]	233.8 (111.57) [845]	71.0 (43.18) [1196]	5.3 (2.35) [1314]	79.1 (17.38) [1699]
5 - 8 Vessels	311.8 (75.51) [52]	259.4 (74.68) [31]	66.9 (22.92) [43]	5.5 (1.84) [72]	78.7 (9.71) [60]

Table 1: Descriptive statistics for gray whale ventilation data in Clayoquot Sound, 1993 – 1995.

Numbers reported show mean, (standard deviation) and [number of observations]

	Duration of Dive Cycle (sec)	Duration of Feeding Dive	Ventilation Rate	Number of Ventilations per Dive Cycle	Feeding Dive Percentage
No Vessels: Vessels	***+9.63%*** ***(t = -4.14, P =0.00)***	***+21.07%*** ***(t = 6.66, P =0.00)***	***+10.40%*** ***(t = -3.87, P =0.00)***	+2.28% (t = -1.04, P =0.28)	-0.61% (t = -1.30, P =0.19)
No Vessels: 1 - 4 Vessels	***+9.41%*** ***(F =9.24, P =0.00)***	***+20.61%*** ***(F =23.01, P =0.00)***	***+10.62%*** ***(F =5.90, P =0.00)***	+2.03% (F =0.98, P =0.38)	-0.48% (F =1.74, P =0.18)
1 - 4 Vessels: 5 - 8 Vessels	+5.00%	+10.94%	-5.79%	+5.05%	-0.53%

Table 2: Percentage difference between means for gray whale ventilation patterns in the presence of different numbers of vessels, 1993 - 1995; significant changes shown in bold type

parameter for each vessel number class, expressed as a percentage of the mean of the preceding class, is shown in Table 2.

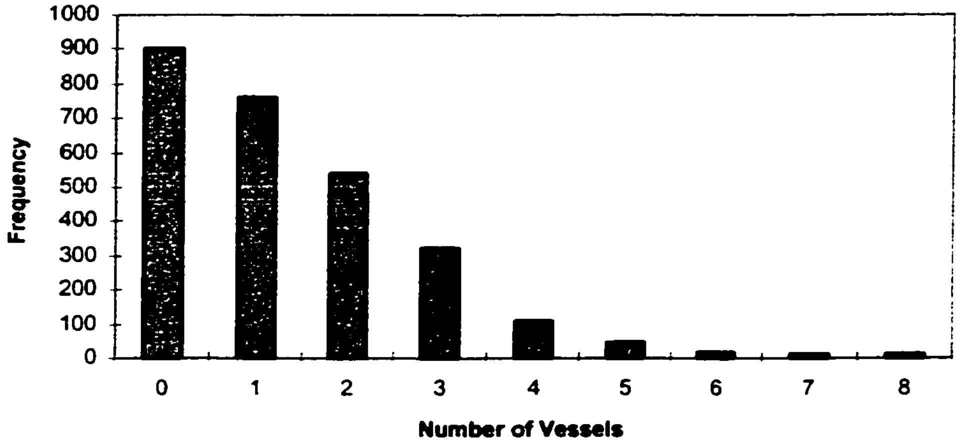
3.3.1.2 Variation of Dive Parameters with Number of Vessels (grouped)

Table 1 summarizes the descriptive statistics for the five dive parameters when the numbers of vessels were grouped into three classes (Class 1; no vessels, Class 2; 1 - 4 vessels and Class 3; 5 - 8 vessels). Significant differences between the classes were detected using ANOVA (Table 2). Significant differences between individual groups were identified using Tukey's HSD test. The variables dive cycle duration (F ratio = 9.24, $P = 0.00$) and feeding dive duration (F ratio = 23.01, $P = 0.00$) both increased significantly with increasing vessel number, although for dive cycle duration the increase between groups 2 (1 - 4 vessels) and 3 (5 - 8 vessels) was not found to be significant. Ventilation rate increased significantly between groups 1 and 2 (Tukey's HSD, $P > 0.05$), but group 3 was not significantly different either from group 2 or group 1. The mean number of ventilations per dive cycle was found to be independent of number of vessels. Feeding dive percentage was unaffected by vessel number. Table 2 shows the increase or decrease in the mean value of each dive parameter for each vessel number class, expressed as a percentage of the mean of the preceding class.

3.3.1.3 Variation of Dive Variables with Number of Vessels

When the data were analyzed by individual vessel number classes (from no vessels to 8 vessels), some of the frequencies were extremely small (see Figure 3). Because of the resulting reduction in statistical power, no tests were run for individual vessel number classes, since any vessel number effects would have been masked or weakened to the point that the analysis would not be useful in interpreting the whales' behaviour.

Figure 3: Frequency of Observations of Different Numbers Whale-Watch Vessels, Clayoquot Sound 1993 - 1995



3.3.2 The Effect of Feeding Site on Dive Parameters

Dive variables were significantly different between feeding sites when compared using one-way analysis of variance. The changes in the whales' behaviour in response to feeding site also influences their behaviour in the presence of vessels, and is an important part of the overall context in which their behaviour is studied.

Two-way ANOVA were used to compare the interaction between the two factors (feeding site and number of vessels) which are correlated to variation in dive behaviour. As above, the numbers of vessels were expressed in terms of vessel presence or absence (see Table 3) and in terms of three levels of activity (no vessels, 1 - 4 vessels, 5 - 8 vessels; see Table 4). Tables 3 and 4 show the F-ratios and probability levels for the variation of dive behaviour with two main factors (site and vessel presence or number). An F-ratio is also reported for each

	Duration of Dive Cycle	Duration of Feeding Dive	Ventilations per Hour	Ventilations per Dive Cycle
Explained Variation	107.35 (0.00)	103.876 (0.00)	41.04 (0.00)	39.819 (0.00)
Site	213.81 (0.00)	302.420 (0.00)	47.372 (0.00)	76.694 (0.00)
Vessel Presence/Absence	5.567 (0.018)	16.903 (0.00)	9.69 (0.002)	0.442 (0.506)
Site x Vessel Presence	4.546 (0.004)	1.580 (0.00)	20.712 (0.00)	5.956 (0.00)

Table 3: F-ratios (and significance levels) for 2-way ANOVA comparing correlations between whale behaviour, site and vessel presence/absence, 1993 - 1995

dive variable for the interaction between these two factors ("site x vessel presence") and for the main factors and the interaction combined ("explained variation"). In contributing to the overall variation, feeding site accounts for the majority of the explained variation in both cases. The significance of the effect of feeding site is discussed in more detail in Chapter 4.

	Duration of Dive Cycle	Duration of Feeding Dive	Ventilations per Hour	Ventilations per Dive Cycle
Explained Variation	68.914 (0.00)	73.097 (0.00)	28.747 (0.00)	25.703 (0.00)
Site	18.907 (0.00)	119.787 (0.00)	23.032 (0.0)	18.324 (0.00)
Vessel Number Group	3.734 (0.024)	8.746 (0.00)	4.836 (0.008)	0.278 (0.757)
Site x Vessel Presence	3.224 (0.004)	1.361 (0.236)	12.471 (0.00)	3.625 (0.001)

Table 4: F-ratios for 2-way ANOVA comparing correlations between whale behaviour, site and vessel number, 1993 - 1995

3.3.3 Interaction Between Vessel Factors and Site Factors

For all four of the dive variables analyzed, interactions were found between the effects of vessel presence/absence and and those of feeding site (Table 3). In the second case, with three classes of vessel activity, interaction effects were found in three (dive cycle duration, ventilation rate and number of ventilations) of the four variables analyzed (Table 4). This means that the effect of one factor is modified by the effect of the other.

If interaction exists between two independent variables, further statistical analysis using ANOVA is not useful. However, some information can be obtained by comparing the whales' behaviour in the presence and absence of vessels at each of the sites individually. Table 5 shows the dive data grouped by

Site		Duration of Dive Cycle (sec)	Duration of Feeding Dive (sec)	Ventilations per Hour	Number of Ventilations per Surface Interval	Dive Time Percentage
Ahous Bay						
Vessels present	mean:	**263.47**	**216.93**	**53.86**	4.05	85.27
Vessels absent	mean:	**225.50**	**193.86**	**58.54**	4.16	84.94
	difference:	**37.97**	**23.07**	**-4.68**	-0.11	0.33
	t-value:	**-3.55(0.00)**	**-2.64 (0.01)**	**2.32 (0.02)**	0.67 (0.50)	0.32 (0.75)
Cow Bay						
Vessels present	mean:	381.25	325.24	56.92	**5.19**	83.71
Vessels absent	mean:	387.71	309.87	57.61	**4.57**	83.30
	difference:	-6.46	15.37	-0.69	**0.62**	0.41
	t-value:	0.71(0.48)	-1.53 (0.13)	0.31(0.76)	**-3.56 (0.00)**	0.87 (0.39)
Rafael Point						
Vessels present	mean:	313.27	211.33	78.36	6.31	**68.78**
Vessels absent	mean:	320.78	202.85	80.47	5.97	**71.95**
	difference:	-7.51	8.48	-2.11	0.34	**-3.17**
	t-value:	0.61 (0.54)	-0.69 (0.49)	0.56 (0.58)	1.100 (0.27)	**-2.90 (0.00)**
Siwash Point						
Vessels present	mean:	**215.49**	**160.72**	**91.53**	**5.52**	**79.47**
Vessels absent	mean:	**188.90**	**122.44**	**62.82**	**6.09**	**74.25**
	difference:	**26.59**	**38.28**	**28.71**	**-0.57**	**5.22**
	t-value:	**-2.60 (0.01)**	**-3.92 (0.00)**	**6.54 (0.00)**	**2.58 (0.01)**	**2.54 (0.01)**

Table 5: t-values and Differences Between Means of Vessel Presence-absence Classes for the Four Gray Whale Foraging Sites in Clayoquot Sound: Pooled Data for 1993 through 1995

site. Ahous Bay and Siwash Point show significant changes (P = 0.05) in dive cycle duration, feeding dive duration and ventilation rate. Siwash Point and Cow Bay also show significant changes in number of ventilations per cycle. Dive time percentage varied significantly with vessel presence at Rafael Point and Siwash Point.

This study found Gray Whale foraging behaviour in Clayoquot Sound to be variable. This contradicts previous information (Murison *et al.*, 1984; Wursig *et al.*, 1986) that it is predictable and shows a consistent pattern. Foraging behaviour in Clayoquot Sound varies with foraging location, and to a much lesser extent with vessel activity, but the majority of the variation cannot be accounted for in terms of the factors considered in this study.

3.4 Vessel Numbers and Diving Behaviour: Discussion of Results

All the variables except number of ventilations per surface interval show some variation related to number of vessels. For all except feeding dive duration, changes in whale behaviour which occur under different conditions of vessel abundance are also dependent on the feeding site at which they occur. This means that the "vessel effects" described below are really combined effects of vessels and site, and should not be interpreted as the effects of vessels only.

No significant changes in sinuosity ratio were observed with different numbers of vessels. The sinuosity ratio data were extremely variable, lowering the explanatory power of the statistical tests even with relatively large sample sizes. The apparent randomness of the data may be due in part to the very narrow spatial distributions exhibited by feeding gray whales, and the lack of accuracy of the GPS technology. However, it is also likely that the turning behaviour of gray whales is genuinely random - or at least, is not correlated with vessel number.

3.4.1 Dive Parameters and Vessel Numbers

Gray whale feeding behaviour is much more variable than expected based on previous studies, and only a very small portion of the variation can be accounted for in terms of vessel number. In the following sections, the vessel number classes are grouped into two and three composite classes to increase the explanatory power of the data.

3.4.1.1 Variation of Dive Variables with Vessel Presence/Absence

The presence of whale-watching vessels was associated with significant changes in the dive variables. The number of ventilations per dive cycle was not significantly affected by the presence of vessels. Dive cycle duration and feeding dive duration were significantly greater in the presence of whale-watching vessels than in their absence. The percentage of the dive cycle duration spent at the surface did not change with vessel presence (one-way ANOVA, $P=0.05$) which means that the overall time spent at the surface is not affected by the presence of whale-watching vessels. The whales' hourly ventilation rate was found to increase significantly (by an average of 7 breaths per hour or 10.4 percent) with the presence of whale-watching vessels.

The increased dive time and ventilation rate are typical of the patterns predicted by Kramer (1988) with increasing depth. In a situation where the changes are independent of depth, as they may be here, they could be a result of increased travel time for other reasons. For example, the whale might be spending time locating vessels during its ascent, or ascending diagonally rather than vertically from its selected food patch to surface farther from the group of whale-watching vessels (Malcolm, 1999). In the case of increased depth (or travel time to the surface), the surface interval is also expected to increase, to compensate for the increased energy used on the longer dive, and in making this prediction Kramer is assuming that increased surface interval corresponds with increased ventilations. In the presence of vessels, the gray whales' ventilation rate indeed shows an increase as the dive duration increases. A decrease in percent time spent at the surface could have been interpreted as a predator-avoidance strategy (Kramer, 1988) but the whales' dive characteristics in the presence of vessels do not conform to this interpretation. It is interesting that, while the whales' surface time as a percentage of dive cycle time is unchanged in the presence of vessels, their ventilation rate (per hour) is slightly - but significantly - increased. This implies that the whales are compensating for increased energy use in the presence of vessels without increasing their time at the surface.

3.4.1.2 Variation of Dive Parameters with Number of Vessels (grouped)

In most cases, the directional relationships between dive variables and vessel presence/absence are maintained (although with some loss of ability to make statistically significant distinctions) as the "vessel presence" category is partitioned into two subclasses, 1 - 4 vessels and 5 - 8 vessels. In the only departure from the pattern, Ventilation rates increase between "no vessels" and "1 - 4 vessels," following the pattern seen in the vessel presence/absence data. The mean for "5 - 8 vessels" is intermediate in value between the means of "no vessels" and "1 - 4 vessels," and is statistically indistinguishable from either, so the pattern is not maintained across all three vessel number classes.

The increase of feeding dive duration with vessel presence was maintained after the division into three classes, but the 11% increase (just over 25 seconds) between class 2 (1 - 4 vessels) and class 3 (5 - 8 vessels) is not statistically significant. Dive cycle duration also increased with vessel number, again with no statistical difference between classes 2 and 3. In addition, the mean dive duration for class 3 was not statistically distinguishable from that of class 1, despite the fact that the means of classes 1 and 3 differed considerably in value. Since a difference between the means does exist, and is greater than the difference between those of classes 1 and 2, the lack of statistical separation may be due to the small sample size (52) of class 3. Number of ventilations per dive cycle did not vary with vessel number ($P < 0.05$).

It was hoped that partitioning the data into three vessel activity classes instead of two would enable trends or "cut-off points" which might be present within the data to be more clearly observed. However, little information is actually gained from the re-grouping, since the sample size of class three (five to eight vessels) is too small in most cases to allow it to be separated statistically from class 2.

3.4.1.3 Variation of Dive Variables with Number of Vessels

The partitioning of the data into nine separate vessel activity classes resulted in a loss of statistical power sufficient to make the results difficult to interpret. The lack of clear trends or statistically significant patterns, even with such a large data set, again point to the large overall variability of the data and the small between-class variation in whale behaviour correlated with vessel numbers.

3.4.2 The Effect of Feeding Site on Dive Parameters

The null hypothesis that gray whale behavioural parameters are unaffected by vessels could be rejected based on the data. The data show that some aspects of gray whale diving behaviour change significantly in the presence of whale-watch vessels, but the level of significance is small. It is difficult to determine the effect of these changes on the whales' foraging success, either in the long or the short term. Feeding site correlates much more strongly with ventilation behaviour than vessel abundance does (Tables 3 and 4). This disparity calls into question the validity of equating statistical significance with "biological significance." A further complication is introduced by the interaction between the influence of vessel numbers and that of feeding site.

3.4.3 Interaction between Vessel Factors and Site Factors

Significant interactions were found between the effects of vessels and feeding site in three of the four dive parameters tested - ventilation rate, number of ventilations per cycle, and dive cycle duration. There are management implications here because the whales may be more sensitive to the effects of vessels in some sites than they are in others. Unfortunately, running a separate ANOVA for each feeding site reduces the sample sizes to the point where the effects at each site cannot be evaluated with confidence.

For those variables which show interactions, the changes in whale behaviour which occur under different conditions of vessel activity cannot be interpreted directly, since it is impossible to separate out the effects of vessels from the effects of site. This makes it difficult to make definitive statements about the relationship between vessel presence and whale behaviour, especially since feeding site accounts for a much larger portion of the variation than does vessel presence, and since most of the variation obtained is unaccounted for by either treatment. It can be inferred from the existence of an interaction that whale behaviour changes more with vessel activity at some sites than at others, although it is impossible to tell from the ANOVA in which direction the behaviour changes and at which sites.

However, if the data for each site are partitioned into two classes (vessel presence and absence), a t-test can be run separately for each site to determine whether the whales' behaviour changes significantly with the presence of vessels at that particular site. The results of the t-tests are shown in Table 5.

Paired t-tests (vessels vs. no vessels) show significant vessel-related differences in dive cycle duration, feeding dive duration and ventilation rate at Ahous Bay and Siwash Point, more often than at the deeper sites, Cow Bay and Rafael Point. Only two parameters registered a significant effect for a deep site - the number of ventilations per surface interval were significantly different in the presence of vessels at Cow Bay as well as at Siwash Point, and the dive time percentage was significantly different in the presence of vessels at Rafael Point and Siwash Point.

With the exception of ventilations per cycle in Cow Bay, and dive time percentage at Rafael Point, these findings support the suggestion - inferred from the two-way ANOVA - that the relationship between vessel presence/absence and gray whale behaviour varies between sites. They also highlight the complexity of the relationship, and draw attention to the difficulty of separating out the effects of site from those of vessel activity. The effects of site are themselves a complex combination of the effects of depth, prey type, and perhaps other factors such as currents and runoff from shore. Significant differences between dive variables in the presence and absence of vessels occur mainly in the shallower sites; Ahous Bay and Siwash Point (Table 5), indicating that depth accounts for the largest component of the interaction effect.

As shown in Table 5, dive cycle durations and feeding dive durations increased significantly with vessel presence both in Ahous Bay and at Siwash Point. Dive time percentage also increased at Siwash Point, indicating that the whales spend proportionally less time at the surface when vessels are present. This could reflect additional time spent assessing the position of vessels during feeding dives (Malcolm, 1999). Ventilation rate decreased with vessel presence in Ahous Bay but increased at Siwash Point.

Two-way ANOVA shows the effect of vessels on dive duration to be independent of location at a probability value of 0.05. Dive duration was the only parameter for which there was no interaction between vessel number and site.

Chapter 4: Fine-Scale Patterns of Whale Activity and Environmental Factors

In order to understand the gray whales' fine-scale behaviour in the presence and absence of whale-watching vessels, it is also important to understand some of the other factors which might be influencing their behaviour patterns. Since the whales' primary activity while in the study area is foraging, prey distribution was thought to be the most important factor to examine. The null hypothesis addressed by this section of the study is that prey type and density and water depth do not influence gray whale behaviour. Based on previous research and on verbal reports from whale-watching vessel operators, the following alternative hypotheses were generated:

1. Variation in gray whale ventilation rate and turning behaviour is correlated with prey type
2. Feeding dive time and surface interval time increase with increasing depth, with surface interval time accounting for an increasing percentage of the whale's time
3. Whales select the prey type with the greatest density if more than one type is present
4. Whales select benthic over planktonic prey if both are present
5. Whales select the feeding site with the greatest density of prey
6. Within sites, whales select the patch with the greatest density of prey
7. Whales leave patches when they become depleted
8. Whales search in shallow areas first, moving to deeper water later on.

4.1 Fine-Scale Patterns: Data Collection

Ventilation data and GPS positions were collected at five different foraging sites within the study area (Figure 1). In 1993, most of the data were collected in Cow Bay, and in 1994 from Rafael Point. In 1995 Cow Bay and Grice Bay were the main sites at which data were collected.

4.1.1 Behavioural Variation between Feeding Sites

For each dive cycle recorded as described above, the GPS location was used to place it at one of the five foraging sites shown in Figure 1 - Ahous Bay, Cow Bay, Grice Bay, Rafael Point and Siwash Point - so that dive behaviour could be compared between sites. If the whale appeared to be foraging between two sites, the sequence of data was allocated to the site at which the majority of the day's activity took place. This was a rare occurrence, since the site locations were not arbitrary, but represented naturally discrete foraging areas for the whales.

4.1.2 Prey Distribution

Benthic Prey was sampled in Cow Bay for each of the three years of the study, and in Ahous Bay in 1995. Plankton sampling took place in 1995 only. Benthic and planktonic prey data were used to directly address alternative hypotheses 1, 3, 4, 5, 6 and 7 above.

4.1.2.1 Benthic Prey

In total, five sites were sampled in Cow Bay in 1993, four in 1994, and in 1995, 19 sites in Ahous Bay and eight in Cow Bay were sampled. The invertebrates were extracted from the sediment, by hand in 1993 and 1994, and with a 1mm screen in 1995, and preserved in 70% ethanol after fixing for 5 - 10 minutes in 5% formaldehyde.

The placement of benthic sampling sites in Cow Bay (see Figure 4) was determined according to the whales' use of the area, currently and in previous years for which data exist, in order that the spatial distribution of whale activity could be compared with the availability and relative quality (represented by density or biomass) of prey. In 1993, Cow Bay was the only site sampled, and sites were selected randomly.

1993 was the only year when feeding pits were visible to divers; one replicate at each sampling location was taken inside the pits and two outside. In 1994, Cow Bay sample sites were selected based on the whales' use of the bay in 1992 (data from Garner, 1994) using the harmonic mean measure of activity. Sites were chosen from areas of high, low and medium whale activity. In 1995, sampling sites in both Ahous and Cow Bays were determined using a grid which was designed to allow stratified systematic sampling over the entire area of the bay in each case. The Ahous Bay sampling sites are shown in Figure 5.

Bad weather conditions prevented the Cow Bay grid from being completed, and it was abandoned as a sampling tool. Three replicates were taken at each site in 1993, and five in 1994 and 1995. No feeding pits were visible in 1994 or 1995.

Prey was sampled with a 10-cm. diameter diver-held core, 20cm in length, to a depth of 10 - 15 cm (volume 785 – 1,178 cm^3 and area 78.5 cm^2). Due to the time- and energy-consuming nature of sample collection using SCUBA, and the limited availability of qualified personnel, it was not possible to sample extensively in 1993 and 1994. In 1995, I acquired a boat-deployed 2" diameter core sampler (Wildco "Ogeechee Sand Pounder," with drive hammer) which enabled more extensive sampling of Ahous Bay. However, calm water was necessary for the core sampler to function successfully, and in Cow Bay, which is

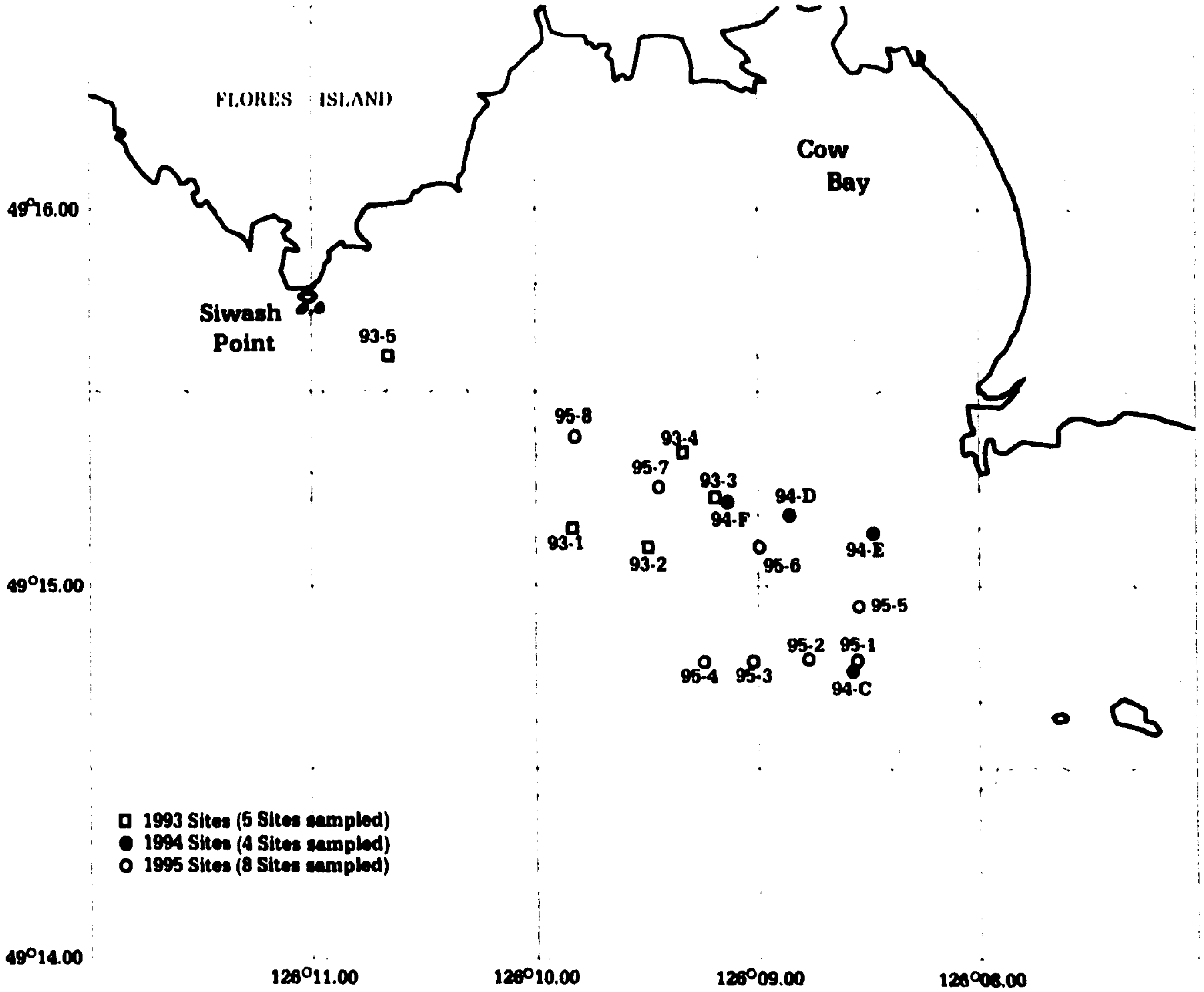


Figure 4: Benthic Sampling Sites in Cow Bay, Clayoquot Sound During the Summer Seasons of 1993 - 1995

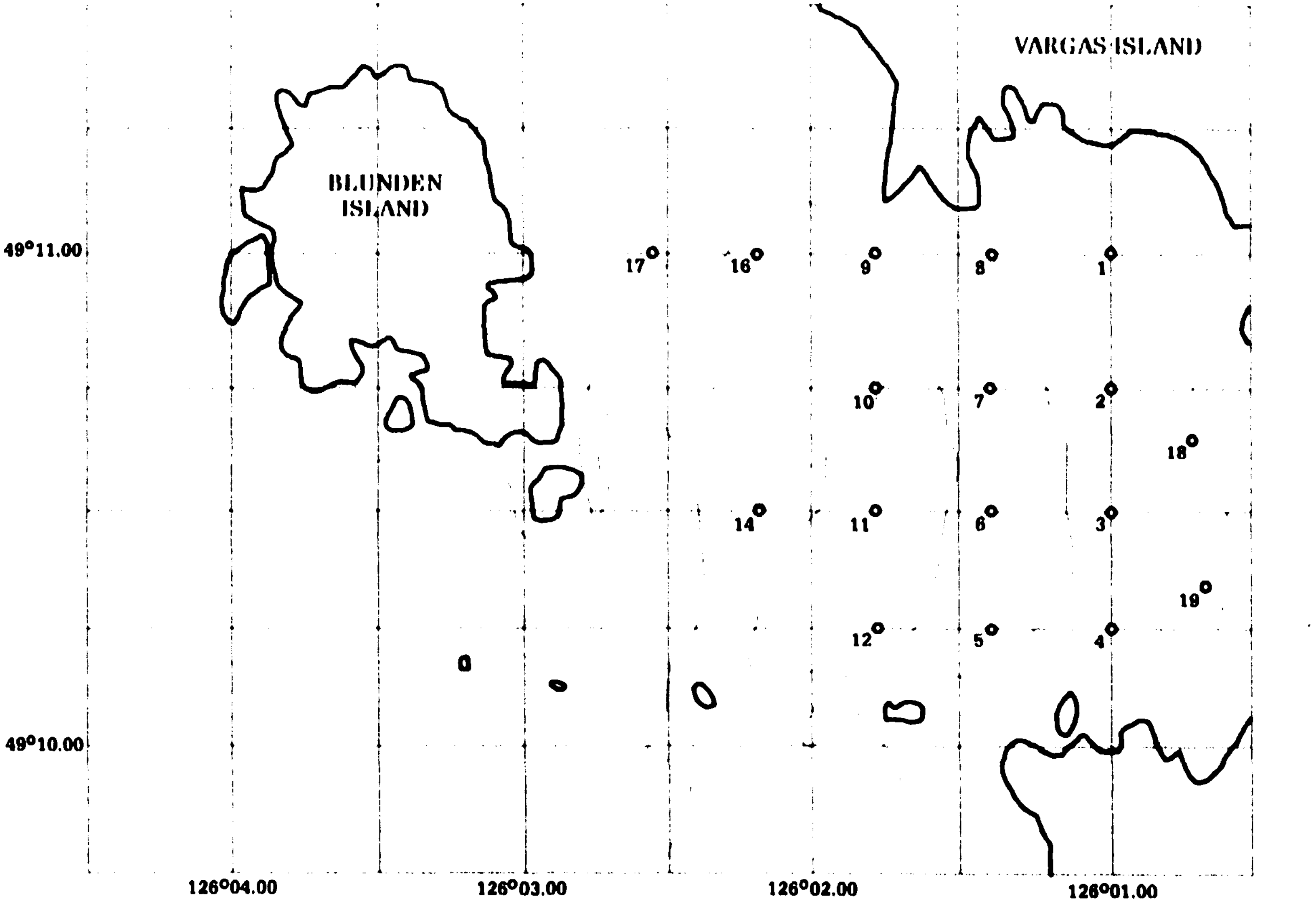


Figure 5: Benthic Sampling Stations in Ahous Bay, Clayoquot Sound, During July 1995

less sheltered than Ahous Bay, the ground swell prevented its use for most of the summer. 19 sites were measured in Ahous Bay and four in Cow Bay. Four replicates were taken at each site. Four of the Ahous Bay samples were duplicated by sampling with the diver-held corers, and the same four were also re-sampled later in the season with the boat-deployed corer.

4.1.2.2 Planktonic Prey

Plankton tows were carried out at least once a month throughout the 1995 season in Cow Bay and at Rafael Point. Other areas, with the exception of Grice Bay, were sampled occasionally, when feeding whales were present, using an 8" diameter plankton net with 1mm mesh or smaller. A labeled 2-dram glass vial was attached to the bottom of the net by means of a threaded attachment, and when the net was recovered the vial was detached and capped, the location and depth noted, and a new vial was put in place. The net was lowered a number of times at each location, to enable the approximate depth of large concentrations of plankton to be ascertained. Most tows took place in water that was 20 - 25m deep. The first tow at each location was dropped to the bottom, using a 1.4Kg. lead weight, and quickly raised. If porcellanid larvae were obtained, the net was dropped again, this time to half the total depth. Samples were taken at approximately 6m intervals using a marked line until the depth of the main plankton patch was identified.

Rafael Point was sampled twice during each of the months of June, July and August and once in September, although the July samples represent only one site each due to difficulties with equipment. The locations of the sampling transects at Siwash Point and Rafael Point are shown in Figure 6. Cow Bay was sampled five times; twice in June and once in each of the other three months. In the presence of feeding whales, Ahous Bay was sampled once and Siwash Point

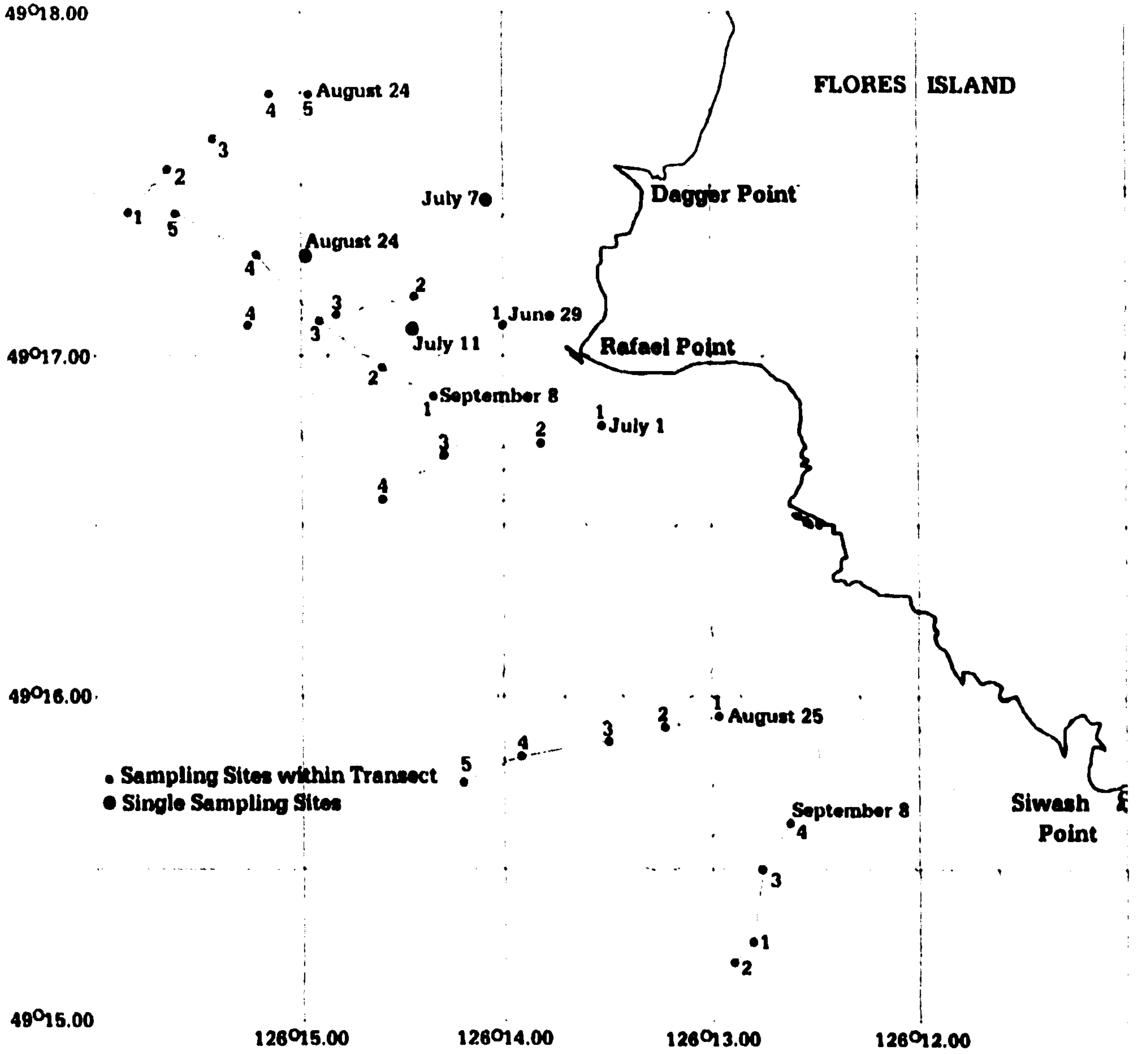


Figure 6: Location of Plankton Tows near Rafael Point,Clayoquot Sound, from June to September, 1995

twice. Plankton tows were also made opportunistically near actively feeding gray whales.

Attempts were made to sample the porcelain crab larvae using diver-held containers (Kim & Oliver, 1988) but these were unsuccessful, in part due to the evasive ability of the larvae. Guerrero (1989) used underwater photography to quantify mysid density, but due to their transparency and small body size it is doubtful that this technique would have been effective with porcelain crab larvae.

4.2 Fine-Scale Patterns: Data Analysis

In order to examine other factors affecting dive behaviour, the ventilation data (Chapter 3) were analyzed in terms of foraging location. Whale location data were compared to prey location, type and density to address the effect of prey characteristics on gray whale foraging choices.

4.2.1 Behavioural Variation between Feeding Sites

The dive data were partitioned by site, and the class sizes were equalized by means of random re-sampling from the larger populations until each reached a new maximum class size equal to the smallest of the four class sizes (Ahous Bay, Cow Bay, Rafael Point and Siwash Point). Grice Bay was analyzed separately due to its unusual dive characteristics. The mean, standard deviation and 95% confidence intervals were calculated using SPSS for each dive variable at each site. Analysis of Variance (ANOVA) was used to test for significant differences between the dive parameters when recorded at each site, using Tukey's HSD multiple-range test *post hoc* to pinpoint the significant differences.

4.2.2 Prey Distribution

Prey number and biomass data were mapped to indicate areas of high and low prey density in the study site. The whale sighting data were mapped and analyzed using the first inverse moment measure of activity (harmonic mean; Dixon & Chapman, 1980) to ascertain areas of maximum use.

4.2.2.1 Benthic Prey

Invertebrates collected in the benthic samples were counted, identified, and weighed to give a wet-weight biomass value for each point sampled. Large, mobile individuals (those weighing more than 2g.) of any species were removed before counting and weighing. This was necessary on only two occasions in the entire study. The most commonly found taxa were identified to genus, and if possible to species. For less common taxa, identification was made at least to the level of family.

Mean biomass, number of individuals, number of amphipods, percent amphipods and mean individual mass was calculated for each sampling location. Absolute numbers were converted to numbers per square meter so that SCUBA core samples could be compared to boat-deployed core samples.

4.2.2.2 Planktonic Prey

Invertebrates collected with the plankton net were counted, identified, and weighed to give a wet-weight biomass value for each point sampled. The most commonly found taxa were identified to genus. Identification of porcellanids to species would have required making a permanent mount of each individual, and since the individuals were extremely numerous, this was not attempted. Larval stage, however, was noted wherever possible. For less common taxa, identification was made at least to the level of family.

4.2.3 Fine-scale Patterns: Evidence of Possible Search Behaviour

The position fixes obtained at each dive cycle for bottom-feeding whales were mapped using the program *Homerange* (Dixon & Chapman, 1980), and the plots analyzed for sequences in which the whales showed a relatively straight path (indicative of searching) followed by increased turning and movement within a restricted area (indicative of feeding). These were then compared to water depth to test Garner's (1994) prediction that whales begin searching for prey in shallow areas before moving to deeper water.

4.3 Fine-scale Patterns: Results

Ventilation data were obtained at five feeding sites: Ahous Bay, Cow Bay, Grice Bay, Rafael Point and Siwash Point (see Figure 1). Data were collected at Cow Bay in 1993 and 1995 over a total of 150 hours, representing 1,380 dive cycles. Ahous Bay data, also collected in 1993 and 1995, represent 33.5 hours of observation, and 476 dive cycles. Data for Rafael Point were collected in 1993 and 1994, representing a total of 47.15 hours and 548 dive cycles. At Siwash Point, data were collected in 1994 and 1995, totalling 24.01 hours and 455 dive cycles. In 1995, 17.5 hours were spent collecting data in Grice Bay. No dive cycles are reported because the ventilation of whales at this site was regular rather than cyclic (see page 105).

Dive variables were significantly different between feeding sites when compared using one-way analysis of variance (Table 6). Examination of the differences in dive behaviour between the five feeding sites provided evidence to

	Duration of Dive Cycle (sec)	Duration of Feeding Dive (sec)	Ventilation Rate	Number of Ventilations per Surface Interval	Dive Time Percentage
Ahous Bay	253.22 (104.98)	209.16 (82.91)	55.55 (20.62)	4.09 (1.76)	85.15 (10.56)
Cow Bay	383.18 (91.44)	320.46 (86.71)	57.12 (19.95)	5.01 (1.72)	83.59 (7.27)
Rafael Point	315.65 (125.47)	208.91 (103.32)	78.99 (30.01)	6.21 (2.89)	68.78 (13.44)
Siwash Point	203.2531 (113.17)	139.98 (91.54)	82.11 (56.46)	5.71 (2.33)	77.11 (21.88)
F-Ratio (P)	**242.0881 (0.00)**	**231.50 (0.00)**	**72.23 (0.00)**	**86.26 (0.00)**	**165.58 (0.00)**

Table 6: Descriptive statistics (Means, with standard deviations in parentheses) for gray whale dive variables at 4 feeding sites in Clayoquot Sound, 1993 - 1995. F-Ratios are shown for one-way ANOVA (dive variables x site), with 0.05% probability values in parentheses.

support Alternative Hypothesis 1, that variations in the whales' ventilation patterns are correlated with prey type. In accordance with Alternative Hypothesis 2, feeding dive time increases with depth, as predicted by Kramer (1988). The second part of Kramer's prediction, that surface time as a percentage of dive cycle time increases with depth, does not appear to be borne out by the data presented here. It should be noted that "depth" is discussed only in terms of a general comparison between foraging sites, and was not one of the factors measured during data collection.

The results show little evidence to support Alternative Hypotheses 3 through 8.

4.3.1 Behavioural Variation between Feeding Sites

Table 6 and Figures 7 through 11 show the mean, and the standard deviation of the five dive variables, partitioned by feeding site. Considerable variation between sites is apparent. In general, the sites at which benthic feeding occurs - Ahous Bay and Cow Bay - were characterized by less variation and lower standard deviations than the other sites.

One-way Analyses of variance show significant differences between the different feeding sites for the dive variables. Siwash Point had the shortest mean dive cycle time (Figure 7) of the four sites, with Ahous Bay the next shortest, Rafael Point third and Cow Bay the longest. Mean dive cycle times at the four feeding sites were significantly different from one another. Mean feeding dive duration (Figure 8) for Siwash Point was significantly lower than for all other sites; the Cow Bay data showed the longest mean feeding dive duration,

Figure 7: Duration of Gray Whale Dive Cycle at Four Sites in Clayoquot Sound, 1993 - 1995

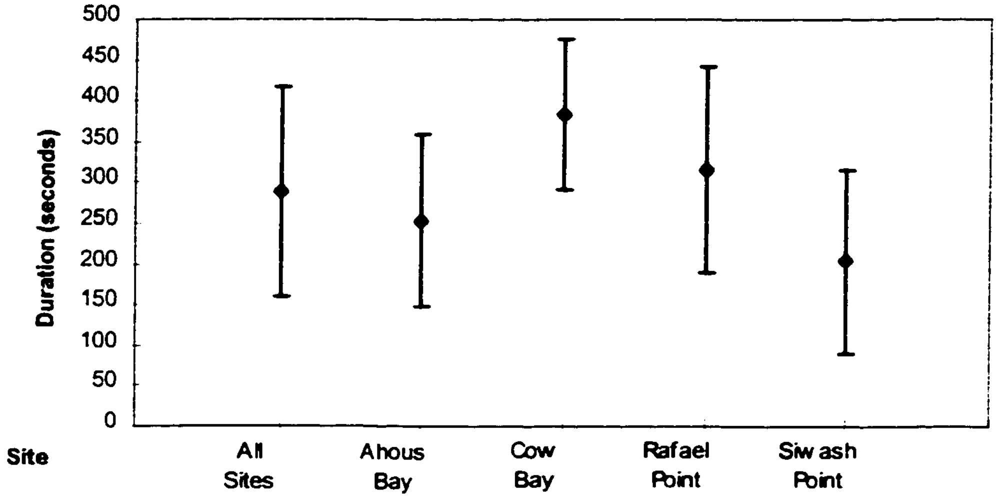
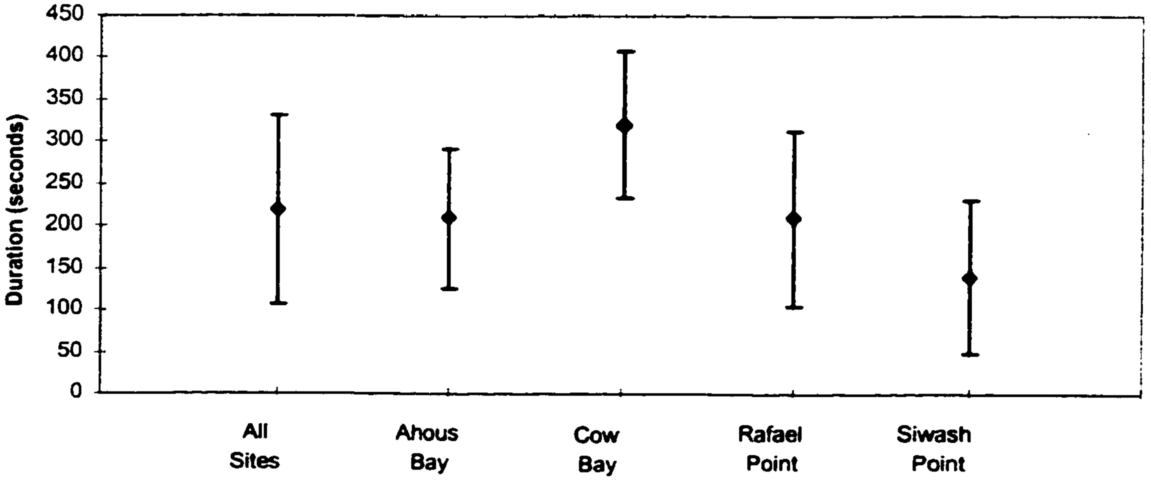


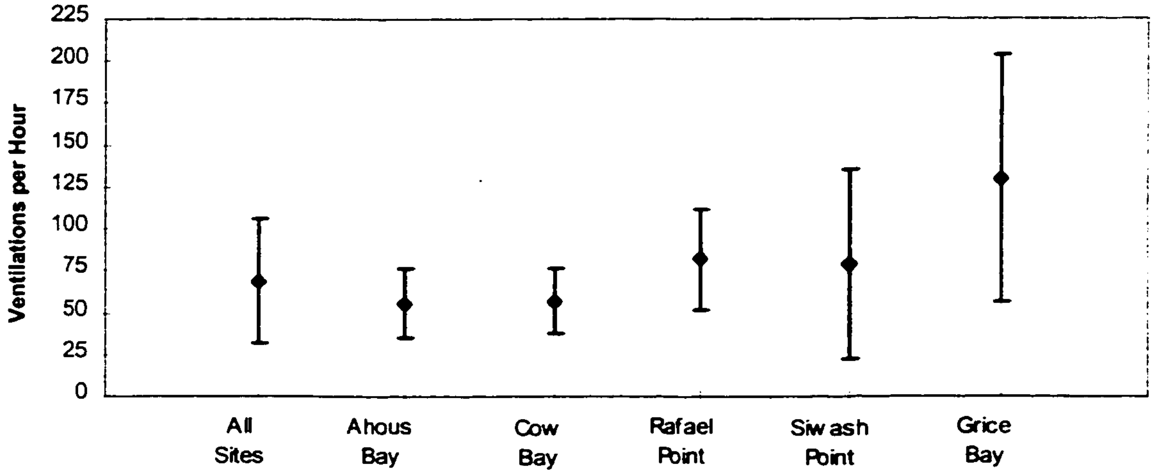
Figure 8: Duration of Gray Whale Feeding Dive at Four Sites in Clayoquot Sound, 1993 - 1995



significantly different from that of the other three sites. Ahous Bay and Rafael Point formed a subgroup of intermediate dive duration, and were not significantly different from each other.

For ventilation rate, two statistically distinct subgroups were formed, one consisting of Ahous Bay and Cow Bay with the lower mean ventilation rates, the other consisting of Rafael Point and Siwash Point, showing high mean ventilation rates. The data for Grice Bay were not included in the ANOVA, but

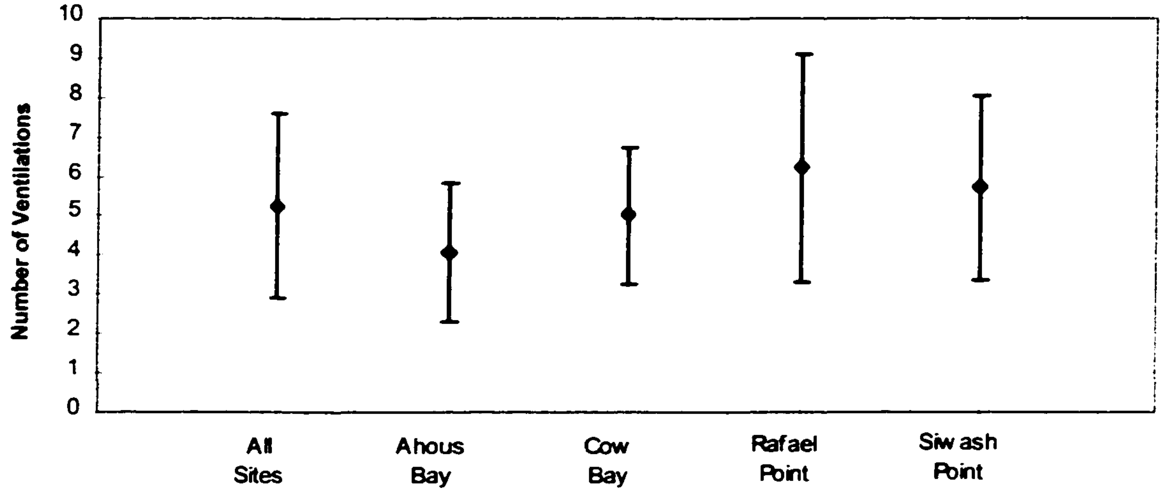
Figure 9: Gray Whale Ventilation Rates at Five Sites in Clayoquot Sound, 1993 - 1995



showed the highest ventilation rate, noticeably higher than all other groups (see Figure 9).

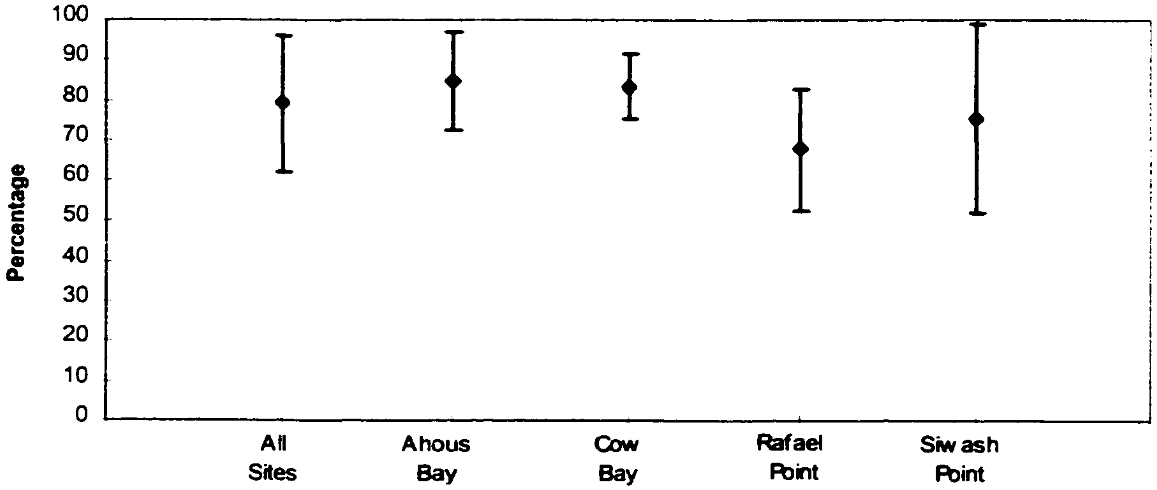
Ahous Bay whales showed lower mean numbers of ventilations (Figure 10) per dive cycle than whales at any other site, with Cow Bay the next lowest. Of the other two sites, Rafael Point had a higher Number of Ventilations than Siwash Point. All groups were significantly different from each other.

Figure 10: Gray Whale Ventiiations per Dive Cycle at Four Sites in Clayoquot Sound, 1993 - 1995



Whales feeding at Rafael Point showed the smallest dive time percentage (Figure 11) of any site, and those in Ahous Bay the largest. Mean surface interval durations at Siwash Point and Cow Bay were of intermediate value. The benthic-feeding sites (Ahous Bay and Cow Bay) showed low variation in the percentage of the dive cycle accounted for by the feeding dive, while the plankton-feeding sites, Rafael Point and Siwash Point, showed greater variation.

Figure 11: Gray Whale Dive Time Percentage at Four Sites in Clayoquot Sound, 1993 - 1995



4.3.2 Prey Distribution

The benthic and planktonic surveys carried out in this study reveal a complex spatio-temporal distribution of potential gray whale prey, with variation at all levels - within sites, between sites, and between years.

4.3.2.1 Benthic Prey

In Ahous Bay, samples were taken only in the final year of the study, so no comparison is possible between years. In July of 1995, sediment samples were successfully obtained at 21 of the 23 sites at which sampling attempts were made,

Site	Average Biomass/ m^2	Average Total Numbers/ m^2	Average Numbers Amphipods/ m^2
Ahous Bay 1	9.03	1654.63	1504.21
Ahous Bay 2	114.32	15794.23	15643.81
Ahous Bay 3	162.45	11833.14	11632.58
Ahous Bay 4	243.68	34596.89	33844.78
Ahous Bay 5	228.64	11833.28	10980.75
Ahous Bay 6	160.95	24067.4	22713.61
Ahous Bay 7	209.69	27858.02	27075.83
Ahous Bay 8	189.53	32039.73	30836.36
Ahous Bay 9	139.89	14139.6	12635.39
Ahous Bay 10	12.03	2858	601.69
Ahous Bay 11	57.16	1052.95	150.42
Ahous Bay 12	169.98	3459.69	1654.63
Ahous Bay 13	90.25	2858	2858
Ahous Bay 14	252.71	2557.16	1504.21
Ahous Bay 15	42.12	1203.37	300.84
Ahous Bay 16	22.56	3459.69	2557.16
Ahous Bay 17	134.38	3409.55	601.69

Table 7: Mean Numbers and Biomass of Benthic Invertebrates Sampled at a Gray Whale Feeding Site, Ahous Bay, Clayoquot Sound, 1995

although at Site 17 (in the northwest corner of the bay) only 2 replicates were obtained. Among the 17 sites sampled, the average biomass varied from 9g/m to 311g/m^2, and the number of individuals from 1,052.95 to 3,4596.89 per m^2 (Table 7). In all but five of the sampling locations, greater than half the individuals were amphipods, and at 13 locations amphipods accounted for 90% or more of the total number of organisms. The distribution of total numbers, biomass and amphipod numbers within Ahous Bay is shown in Figures 12, 13 and 14. Four sites in Ahous Bay were re-sampled in August 1995, both with SCUBA and with the boat-deployed core sampler. Table 8 shows the results of the re-sampling.

Site/Date	Sampling Device	Average Biomass/m^2	Average Total Numbers/m^2	Average Individual Mass (g)	Average Numbers Amphipods/m^2	Percentage Amphipods
Ahous Bay 1						
July	Corer	9.03	1654.63	0.005	1504.21	90.91
August	Corer	269.25	4211.80	0.064	1203.37	28.57
August	SCUBA	47.55	1688.96	0.028	1065.34	63.08
Ahous Bay 6						
July	Corer	218.11	24067.40	0.009	22713.61	94.38
August	Corer	269.25	19554.76	0.014	17298.44	88.46
August	SCUBA	173.83	11406.98	0.015	10627.46	93.17
Ahous Bay 7						
July	Corer	209.69	27858.02	0.008	27075.83	97.18
August	Corer	200.06	19404.34	0.010	17599.29	90.70
August	SCUBA	227.88	25152.51	0.009	24113.15	95.87
Ahous Bay 11						
July	Corer	57.16	1052.95	0.054	150.42	14.29
August	Corer	20.06	2206.18	0.009	200.56	9.09
August	SCUBA	33.00	1377.15	0.024	51.97	3.77

Table 8: Mean Numbers and Biomass of Benthic Invertebrates Re-sampled by Two Different Methods at a Gray Whale Feeding Site (Ahous Bay, Clayoquot Sound) during the Summer of 1995

There does not appear to be a trend in total numbers, biomass or amphipod numbers, either between July and August or between diver-held and boat-deployed core samplers.

Table 9 shows the mean numbers and biomass at each of the benthic sampling stations in Cow Bay in 1993, 1994 and 1995. Figures 15 (total

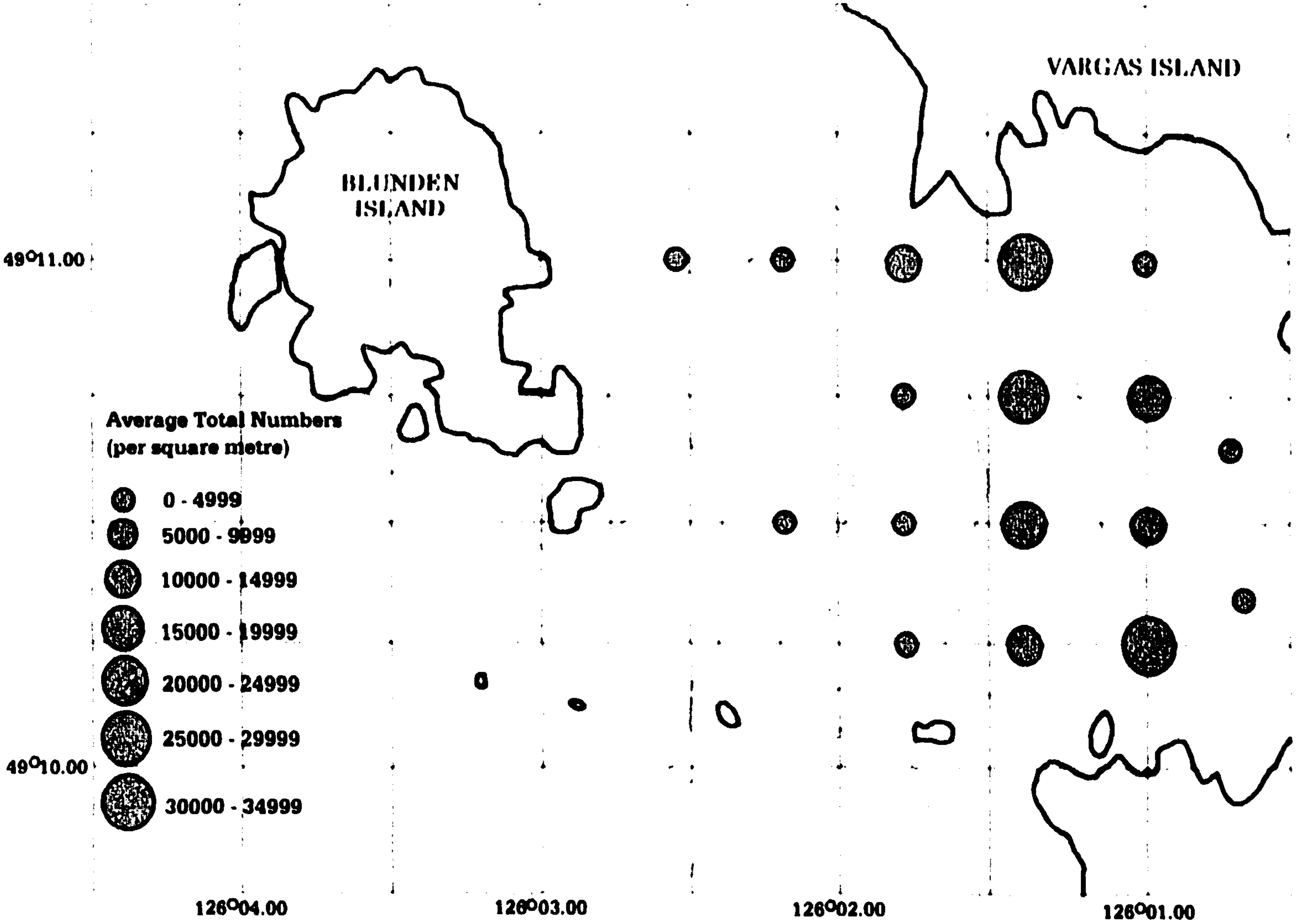


Figure 12: Total Number of Benthic Organisms per Square Metre Sampled at 17 Sites in Ahous Bay, Clayoquot Sound, During July 1995

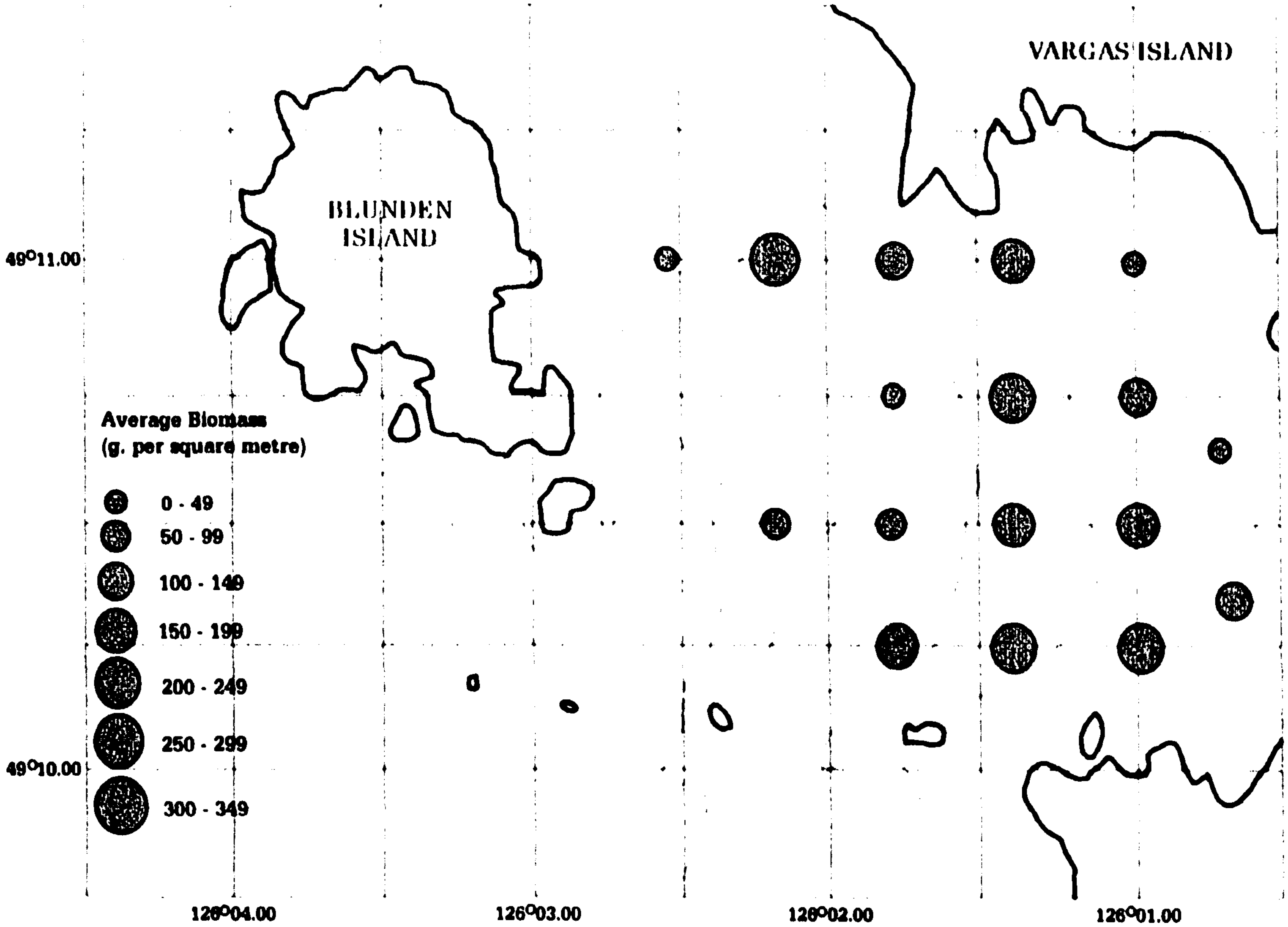


Figure 13: Total Biomass of Benthic Organisms per Square Metre Sampled at 17 Sites in Ahous Bay, Clayoquot Sound, During July 1995

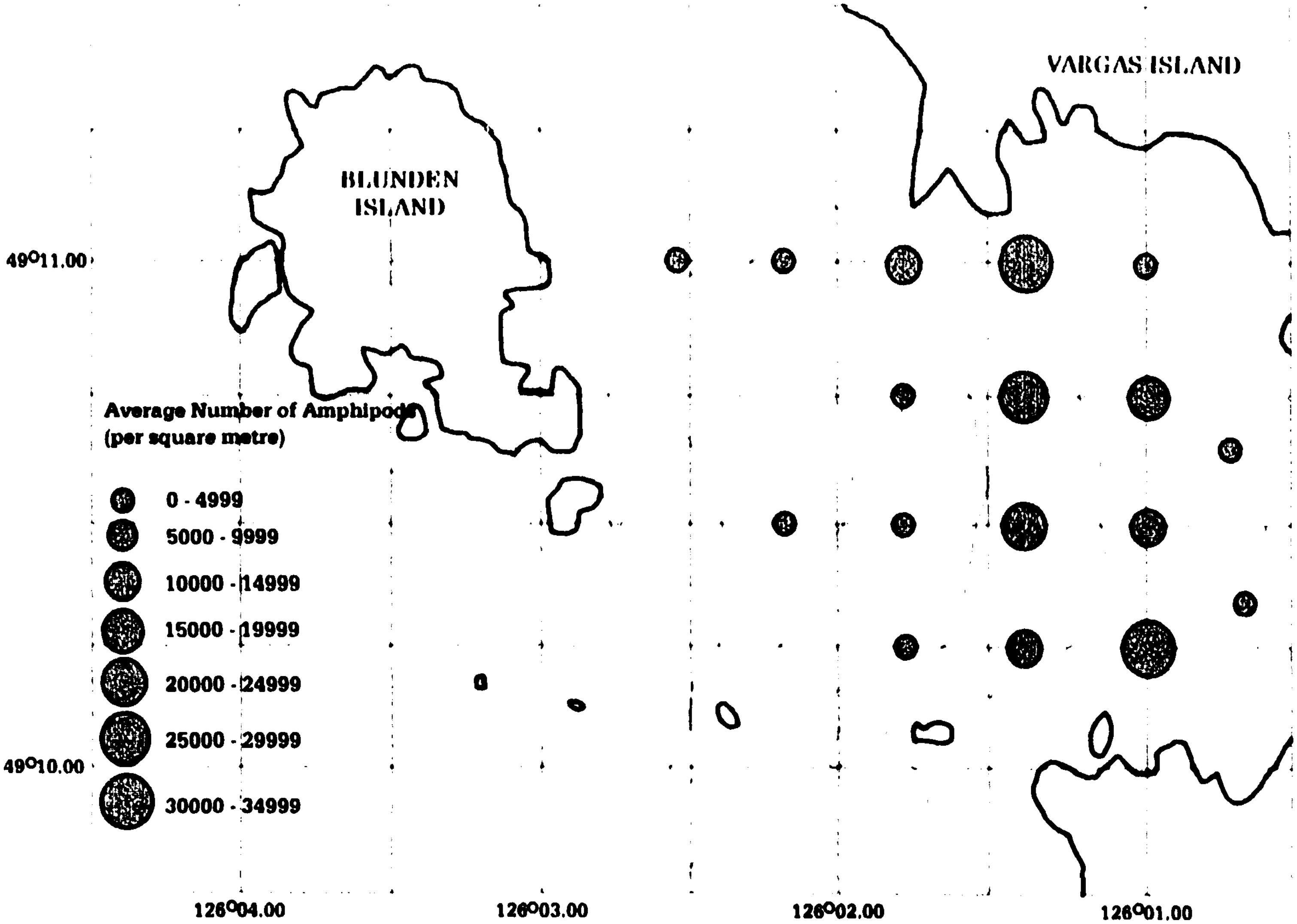


Figure 14: Numbers of Benthic Amphipods per Square Metre Sampled at 17 Sites in Ahous Bay, Clayoquot Sound, During July 1995

numbers), 16 (biomass) and 17 (amphipod numbers) show the data spatially. Site C in 1994 was sampled twice in the season (C and C(2) in Table 9). Due to space constraints, only the first sampling is included in figures 15 through 17. Biomass in Cow Bay was lower in 1994 than in either 1993 or 1995, averaging 164.56g/m^2 in 1993, 71.56 in 1994 and 126.68 in 1995. The number of individuals, however, shows a different pattern over the three years, being considerably

1993		Average Biomass/m^2	Average Total Numbers/m^2	Average Numbers Amphipods/m^2
Cow Bay 3	Outside Pit	144.8608	6041.28	5586.56
	Inside Pit	80.5504	1039.36	1039.36
Cow Bay 4	Outside Pit	135.1168	9354.24	8704.64
	Inside Pit	84.448	4677.12	4287.36
Cow Bay 5	Outside Pit	298.3613	10458.56	10003.84
	Inside Pit	15.5904	1688.96	1688.96
Cow Bay 6	Outside Pit	79.9008	6366.08	5911.36
	Inside Pit	25.984	2078.72	1848.8
Cow Bay 7	No Pits	0	0	0
1994				
Cow Bay	Site A	98.7392	22476.16	22164.352
Cow Bay	Site C	55.6058	22684.032	30972.928
Cow Bay	Site C (2)	133.8176	31102.848	22424.192
Cow Bay	Site D	61.8419	9458.176	9354.24
Cow Bay	Site E	39.4957	6184.192	6158.208
Cow Bay	Site F	102.1171	14914.816	14732.928
1995				
Cow Bay 1	Boat Corer	150.4123	3369.44	3369.44
Cow Bay 2	Boat Corer	192.5392	12184.12	12184.12
Cow Bay 3	Boat Corer	130.5656	9626.96	9626.96
Cow Bay 4	Boat Corer	186.5224	13086.65	13086.65
Cow Bay 5	SCUBA Corer	64.96	4200.75	4049.17
Cow Bay 6	SCUBA Corer	49.3696	5684	5521.6
Cow Bay 7	SCUBA Corer	176.6912	7535.36	7431.42
Cow Bay 8	SCUBA Corer	62.3616	3475.36	3312.96

Table 9: Mean Numbers and Biomass of Benthic Invertebrates Sampled at a Gray Whale Feeding Site, Cow Bay, Clayoquot Sound; 1993 - 1995

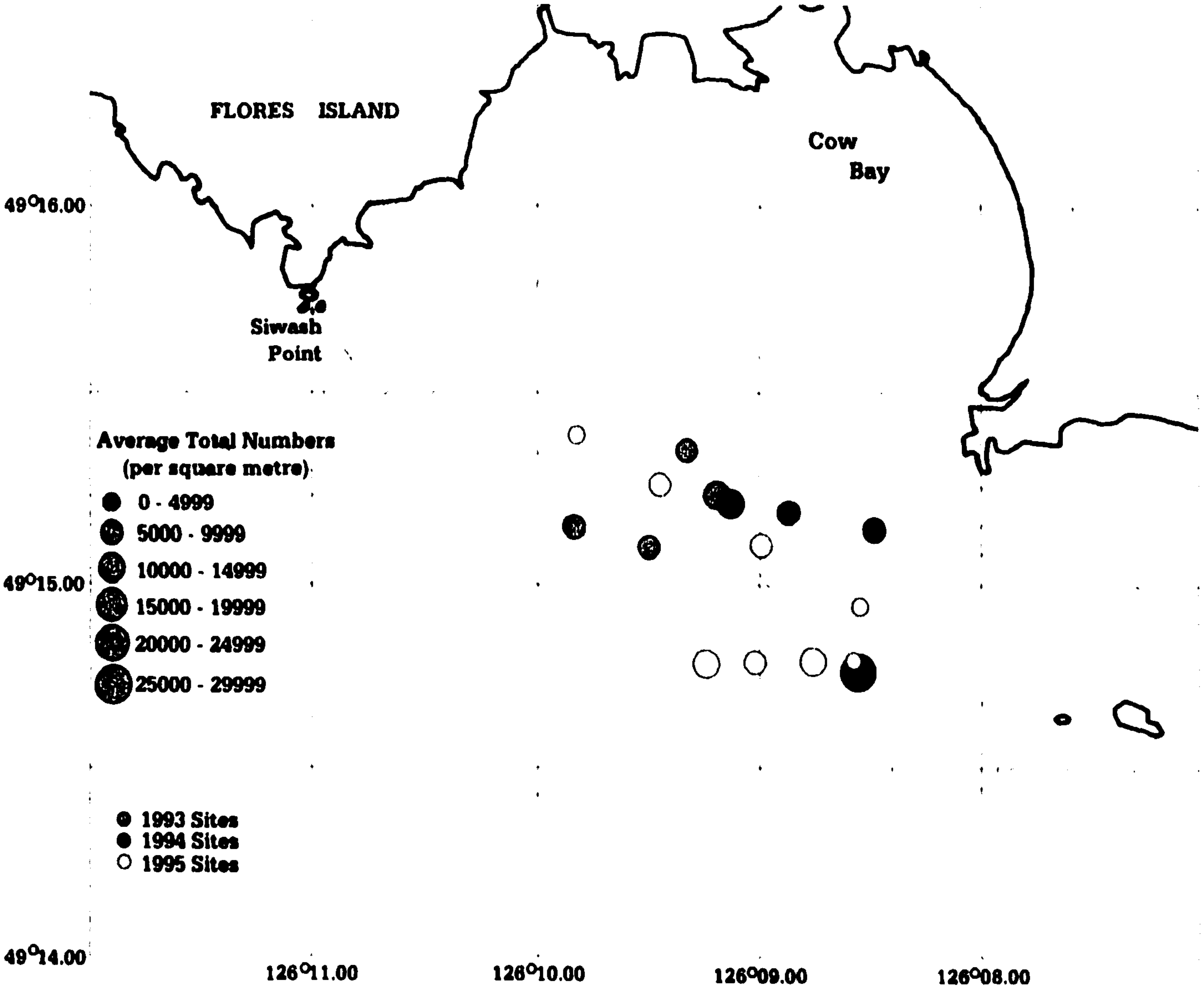


Figure 15: Total Numbers of Benthic Organisms per Square Meter Sampled in Cow Bay, Clayoquot Sound During the Summer Seasons of 1993 - 1995

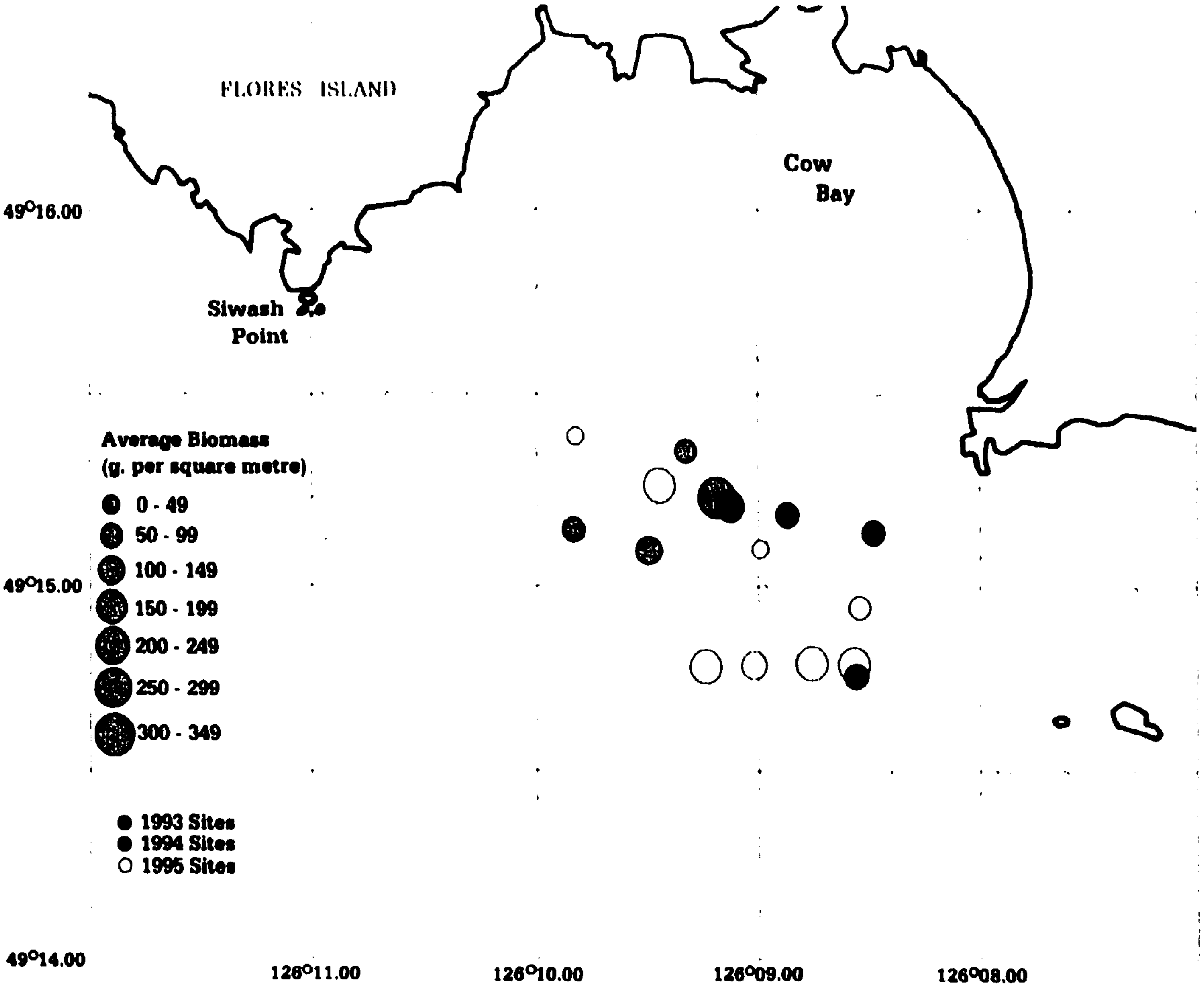


Figure 16: Total Biomass of Benthic Organisms per Square Metre Sampled in Cow Bay, Clayoquot Sound During the Summer Seasons of 1993 - 1995

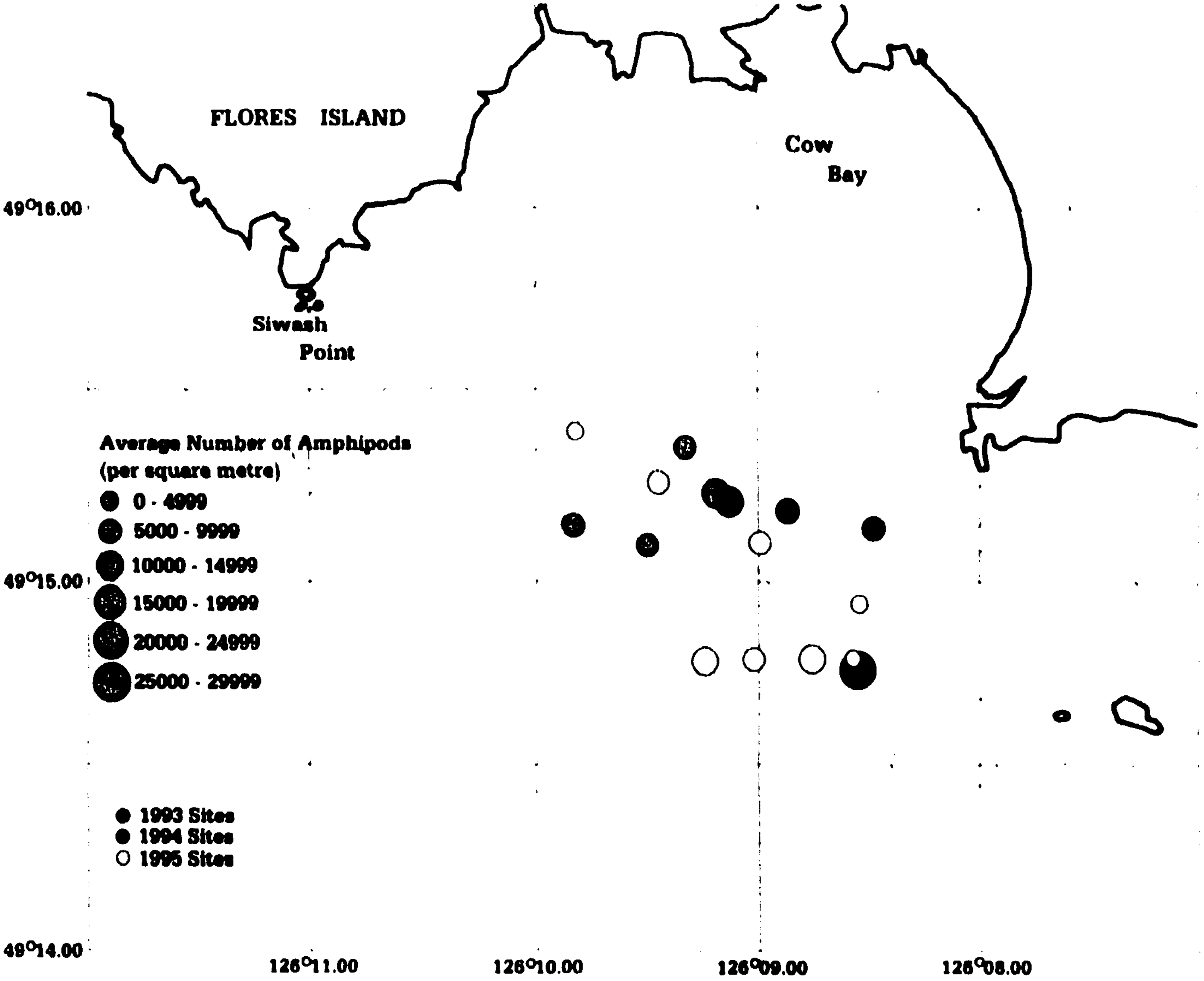


Figure 17: Numbers of Benthic Amphipods per Square Metre Sampled in Cow Bay, Clayoquot Sound, During the Summer Seasons of 1993 - 1995

higher in 1994 (15143.48 individuals per m^2) than in the other two years (1993: 8055.04 and 1995: 5489.12 individuals per m^2). The mean weight of individuals was correspondingly lower in 1994 than in the other two years.

In 1993, when feeding pits were visible to divers, some replicates at each sampling location were taken inside the pits and some outside. In all cases the number of individuals found inside the feeding pits was less than half that found outside. Although pits were numerous, no pits were seen which appeared "fresh" according to the definition of Oliver and Slattery (1985). Since whales were actively feeding in the area within days before most of the samples were taken, it can be assumed that at least some of the pits were fresh, but that the water movement conditions in Cow Bay do not permit the steep sides and exposed tubes to remain visible for long after the pits are made.

4.3.2.2 Planktonic Prey

Table 10 shows the 1995 plankton data by site and date. Where a number of tows were taken on a transect; the data are summarized in the table and the number of sites on the transect is noted in each case.

Figure 18 (page 85) shows the total numbers of porcelain crab larvae obtained in each plankton tow, arranged in ascending order. Samples with more than 800 larvae were considered to represent a dense patch.

Date	Number of Sites Sampled	Mean Number of Individuals	Range (Number)	Mean Biomass	Range (Biomass)
RAFAEL POINT					
21-Jun-95	3	63.20	1 - 270	0.14	<0.01 - 0.69
29-Jun-95	4	1241.50	0 - 5247	2.80	0 - 11.05
01-Jul-95	4	240.33	16 - 1156	0.66	0.02 - 2.77
07-Jul-95	1	2236.00	20 - 6068	4.74	<0.01 - 11.36
11-Jul-95	1	47.00	-	0.21	0.01 - 0.81
24-Aug-95	5	82.86	0 - 173	0.27	0.20 - 0.36
24-Aug-95	1	640.00	429 - 851	7.59	0.69 - 14.28
08-Sep-95	5	15.00	3 - 29	0.07	0.01 - 0.22
COW BAY					
27-Jun-95	6	40.17	9 - 148	0.10	0.01 - 0.31
01-Jul-95	4	17.50	8 - 28	0.07	0.01 - 0.13
17-Jul-95	4	252.67	1 - 579	0.93	0.01 - 2.33
09-Aug-95	4	0.50	0 - 1	<0.010	-
04-Sep-95	4	10.40	0 - 20	0.02	0 - 0.05
SIWASH POINT					
25-Aug-95	5	251.36	5 - 528	0.64	0.01 - 1.33
04-Sep-95	4	13.25	7 - 17	0.01	0.01 - 0.02
AHOUS BAY					
07-Jul-95	3	12.00	0 - 42	0.13	0 - 0.32
HESQUIAHT					
25-Jul-95	1	0.00	-	0	-

Table 10: Mean Numbers and Biomass of Planktonic Invertebrates Sampled at the Gray Whale Feeding Sites Rafael Point, Siwash Point, Cow Bay, Ahous Bay and Hesquiaht during the Summer of 1995

Figure 18: Total Numbers of Organisms Obtained in Each Plankton Tow During the Summer of 1995 in Clayoquot Sound, Arranged in Ascending Order

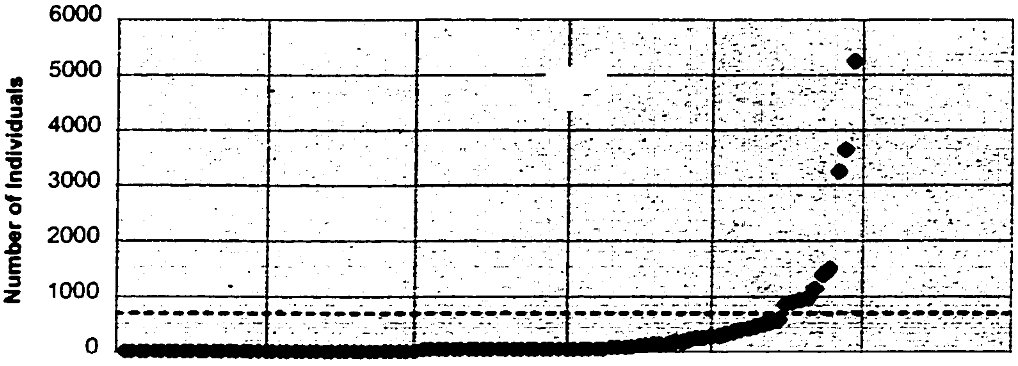


Table 11 and Figures 19 and 20 show the locations and dates on which dense porcellanid patches were encountered. Where multiple tows at the same site yielded more than 800 porcelain crab larvae, only the tow with the largest number of larvae is represented on the map. The numbers of larvae and the depths at which these dense patches of porcellanids occurred are summarized in Table 11. In general, the dense patches were found just off the bottom, and in every case they occurred in the lower half of the water column. Other than this, there is no immediately discernible pattern to their location in space and time.

4.3.3 Evidence of Possible Search Behaviour

Figures 21, 22, 23 and 24 are daily whale activity plots which appear to show "search behaviour" as described by Garner (1994). On July 11, 1993 (Figure 21), the whale starts out at the Eastern end of Cow Bay, between the 10 and 20 meter contours, swims West into deeper water, and then back around to the North and East, finishing the pattern in water of intermediate depth in the centre of Cow Bay. On August 14, 1993 (Figure 22), the whale is first recorded swimming in a South-easterly direction, parallel to the 20m contour but outside

Date	Location	Depth (m)	Total Numbers	Total Number of Porcellanids	% Porcellanids	Total Number of Zoea 2 Larvae	% Identifiable Porcellanids as Zoea II Larvae	Number of *Pachycheles* sp.	% Zoea II Identified as *Pachycheles* sp.
June 29, 1995	Rafael Point 2	10	2	1	50.00	1	100.00	1	100.00
		25	5247	5227	99.62	5227	100.00	5227	100.00
June 29, 1995	Rafael Point 3	10	931	927	99.57	927	100.00	927	100.00
		25	3640	3577	98.27	3577	100.00	3577	100.00
July 1, 1995	Rafael Point 3	13	1156	1138	98.44	not possible to identify species or larval stage			
July 7, 1995	Rafael Point	3	20	20	100.00	11	61.11	11	100.00
		7	891	889	99.78	887	n/avail	885	99.77
		10	3236	3235	99.97	1121	34.75	1104	98.48
		13	6068	6068	100.00	1040	45.38	1032	99.23
		13	965	955	98.96	184	19.31	183	99.46
August 24, 1995	Rafael Point	15	429	427	99.53	282	67.30	280	99.29
	(feeding whale)	23	851	850	99.88	406	49.75	395	97.29
August 25, 1995	Siwash Point 5	5	200	198	99.00	96	48.98	89	92.71
		10	313	304	97.12	190	65.07	182	
		20	968	952	98.35	139	59.91	128	92.09
		30	244	234	95.90	166	73.13	152	91.57

Table 11: Locations, dates, and contents of dense porcellanid patches encountered during plankton sampling in Clayoquot Sound, B.C., July and August 1995

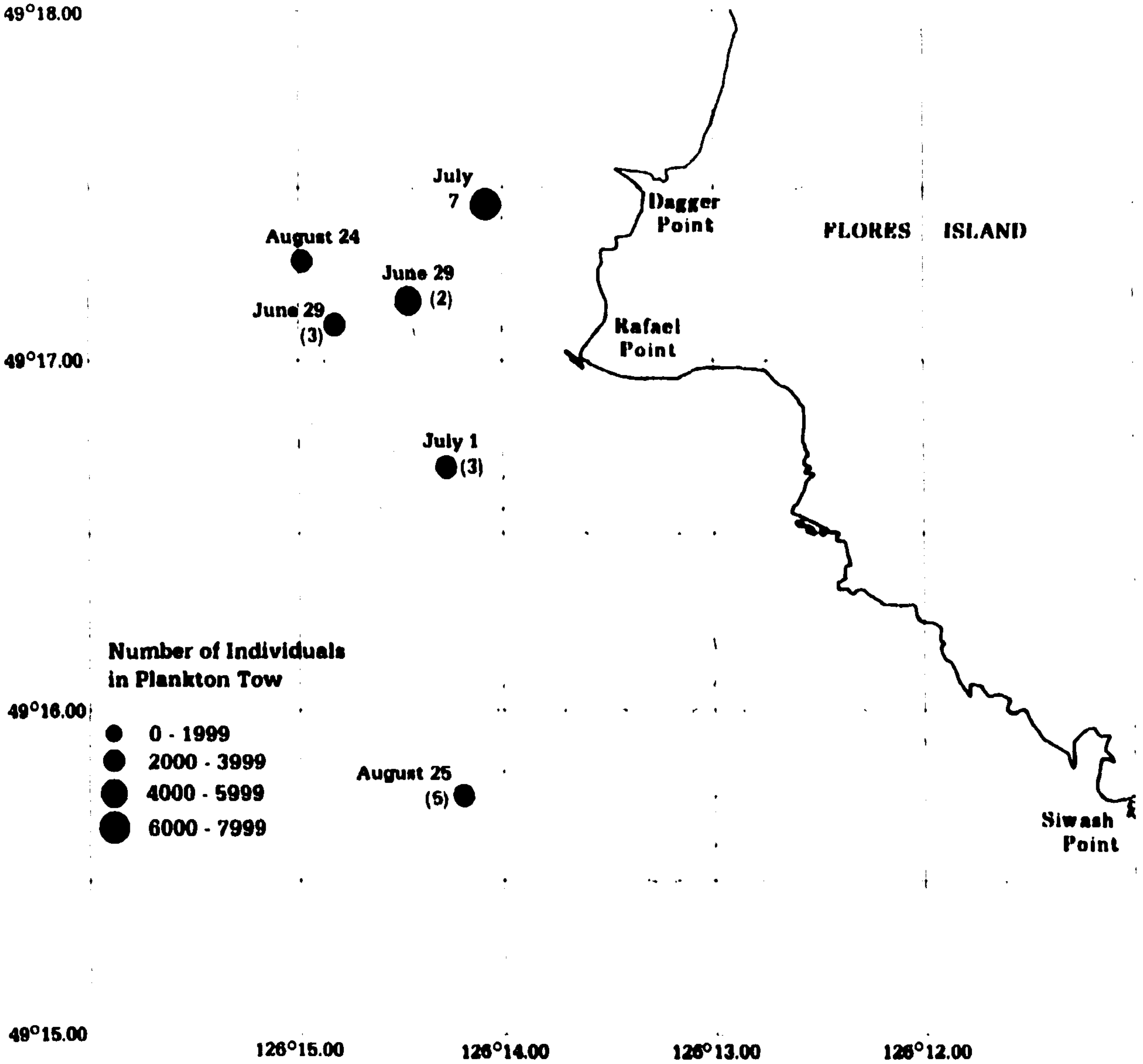


Figure 19: Locations, Dates and Numbers of Individuals in Large Plankton Samples Collected at Rafael Point, Clayoquot Sound, During the Summer of 1995

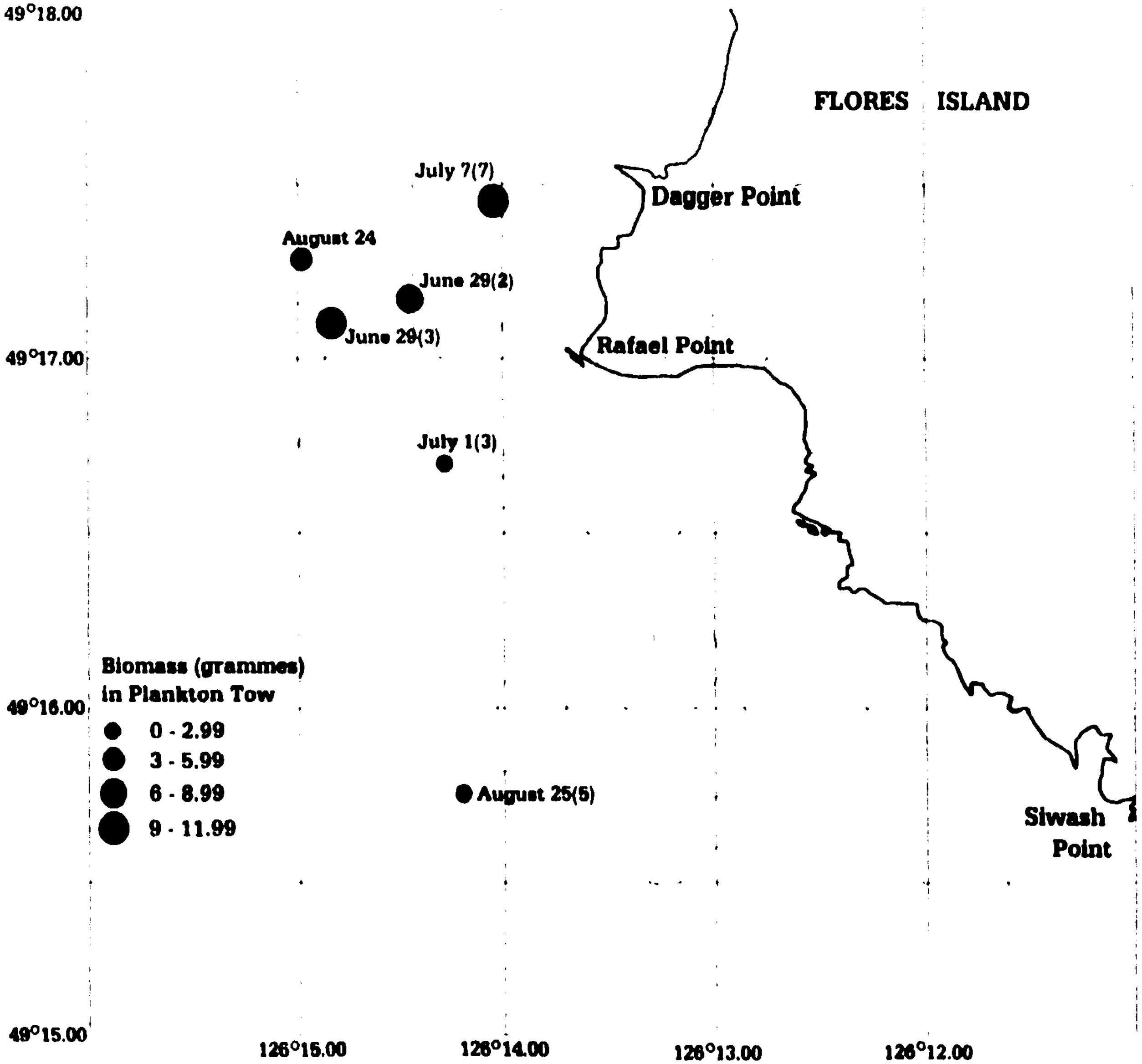


Figure 20: Location, Dates and Biomass of Large Plankton Samples Collected at Rafael Point, Clayoquot Sound During the Summer of 1995

Figure 21: Single Whale Activity Plot for July 11, 1993 in Cow Bay, Clayoquot Sound

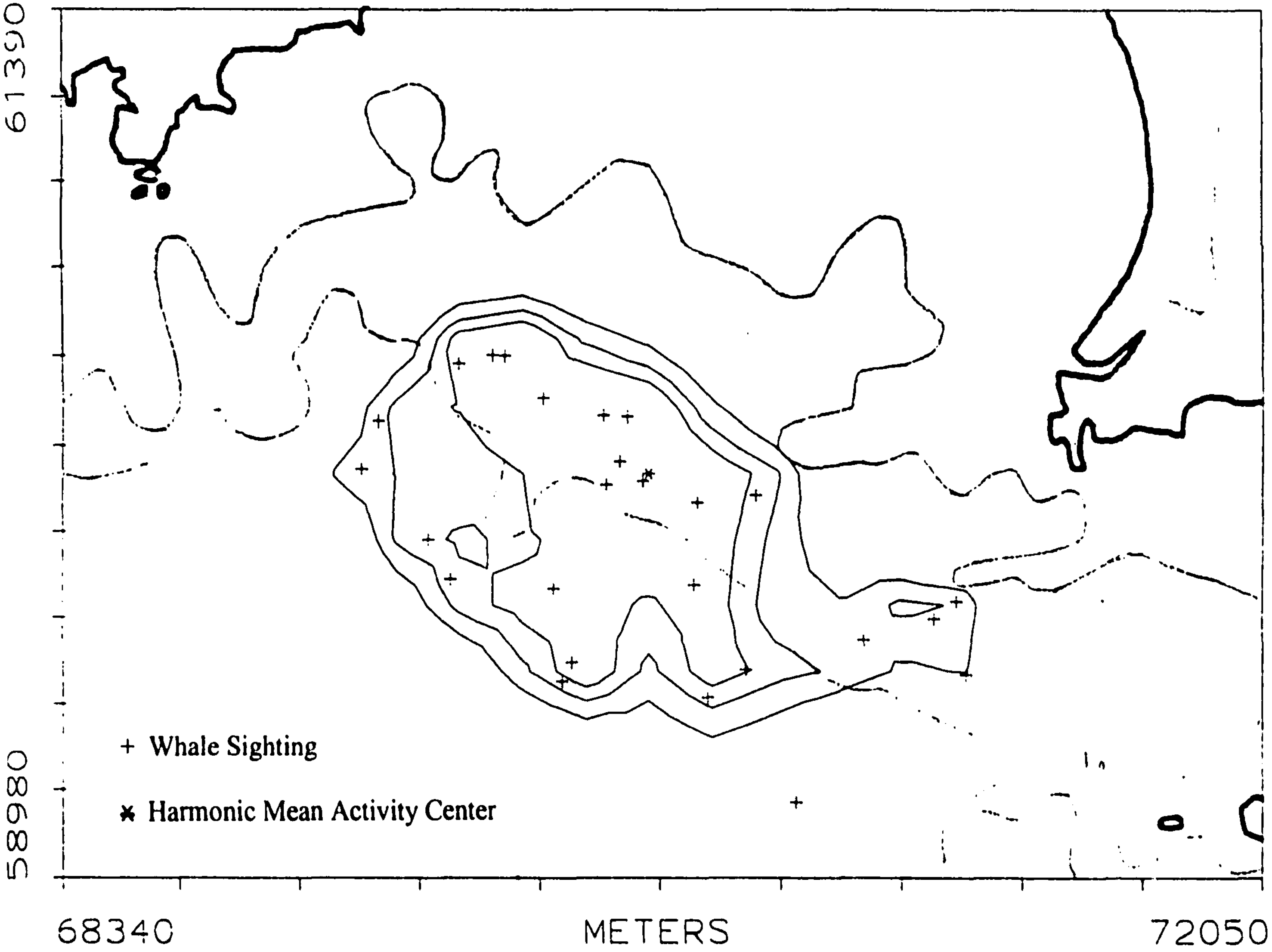
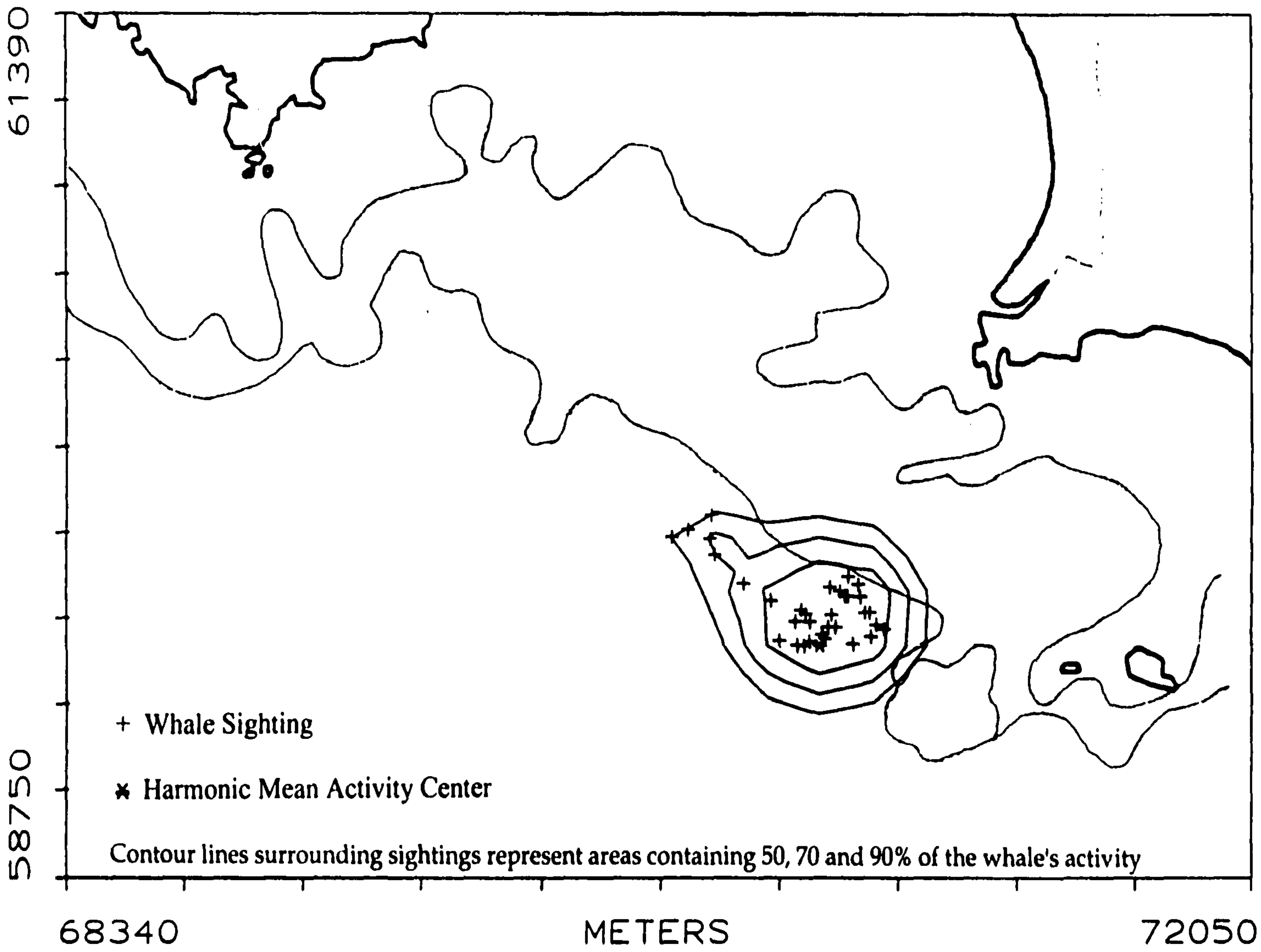


Figure 22: Single Whale Activity Plot for August 14, 1993 in Cow Bay, Clayoquot Sound



Contour lines surrounding sightings represent areas containing 50, 70 and 90% of the whale's activity

Figure 23: Single Whale Activity Plot for August 7, 1995 at Siwash Point, Clayoquot Sound

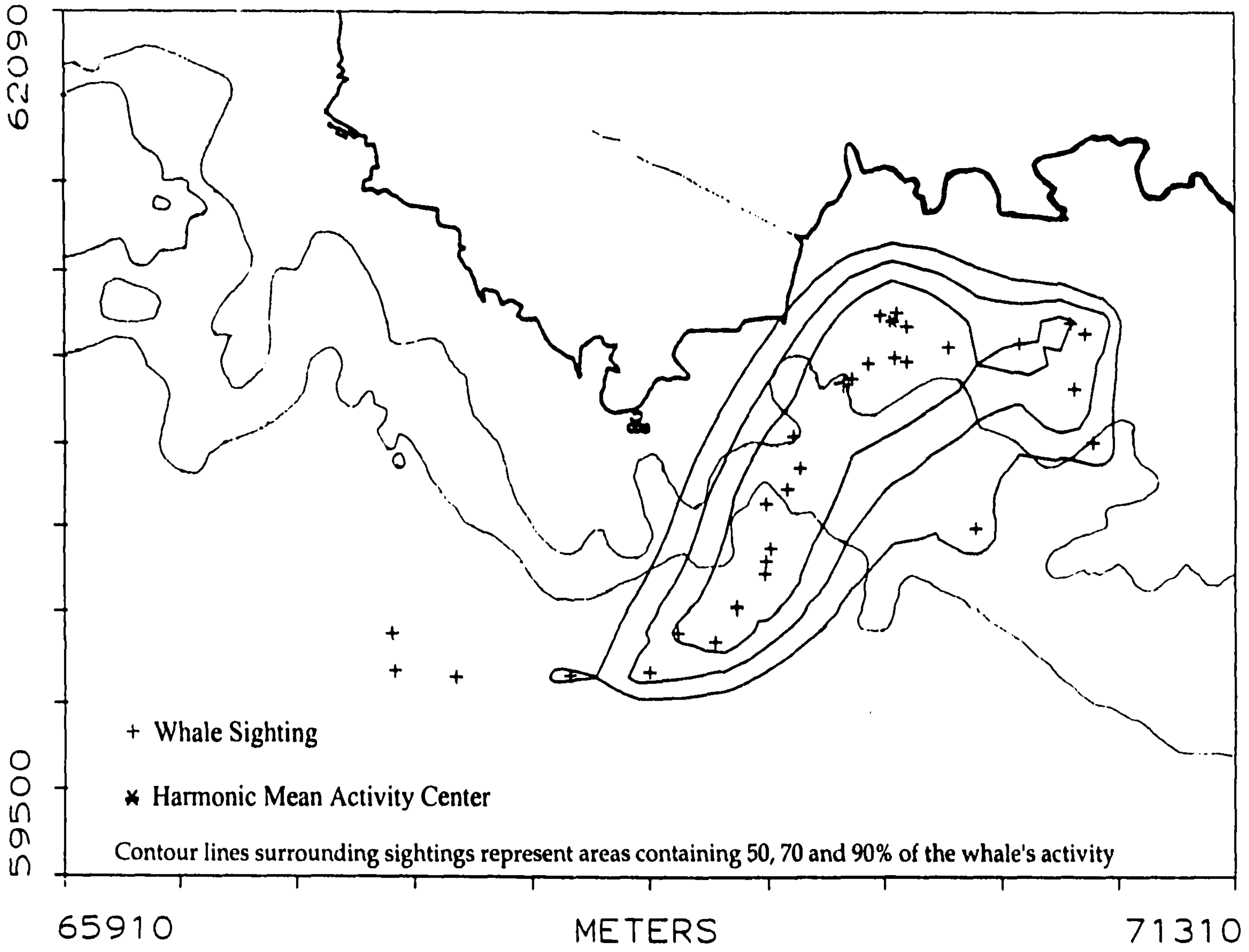
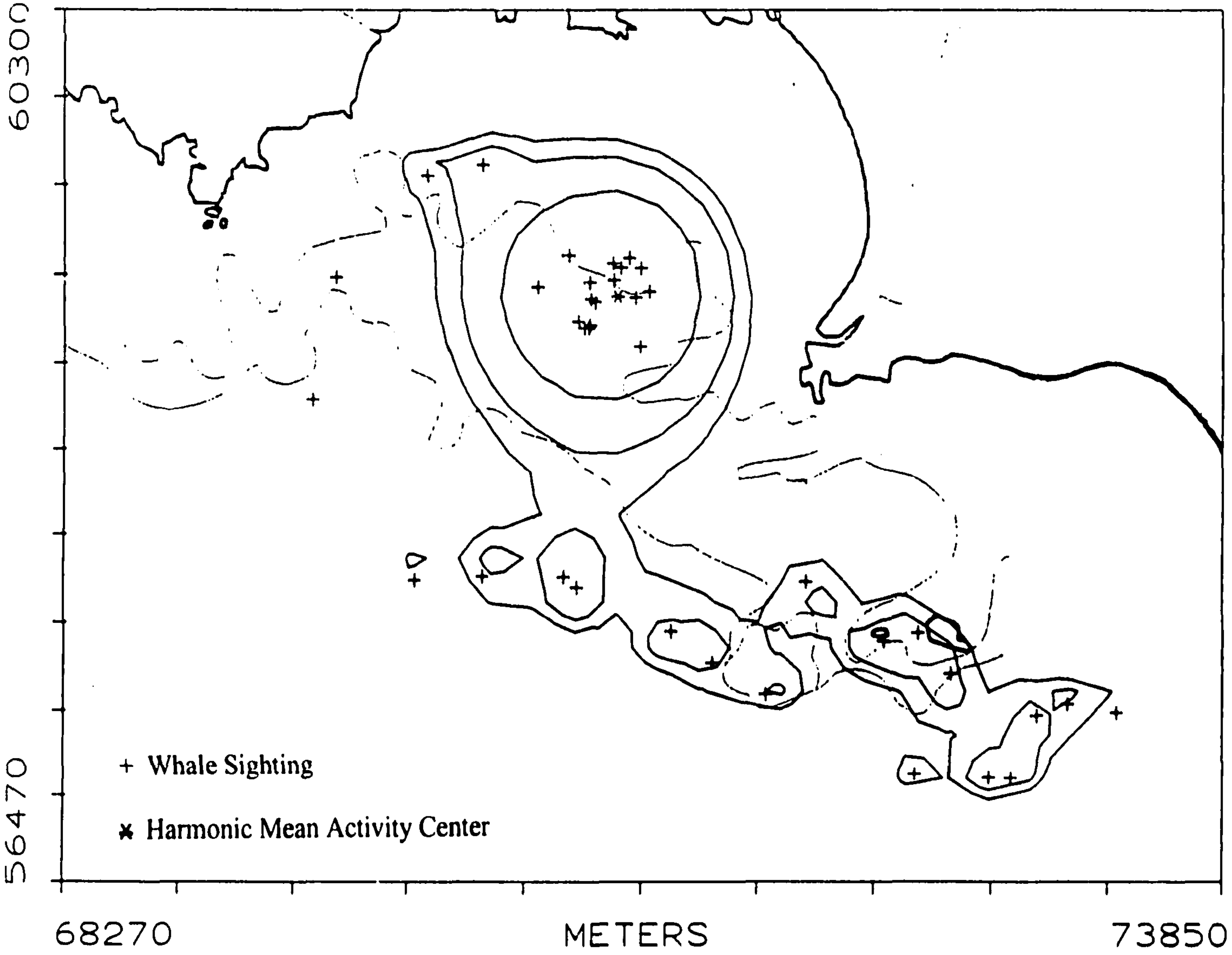


Figure 24: Single Whale Activity Plot for August 12, 1995 in Cow Bay, Clayoquot Sound



it. The latter part of the plot shows the whale moving in a spatially constrained pattern typical of feeding activity. The entire day's recorded activity takes place in water deeper than 20m., with no apparent shallow-to-deep search strategy. On August 7, 1995 (Figure 23), the whale starts out in deep water on the Western side of Siwash Point. It moves East and then North, and appears to slow down once it reaches the shallower water of Western Cow Bay. This is the opposite of the shallow-to-deep search progression predicted in Chapter 1.

On only one of the four highlighted occasions did the whale appear to search in a way that agrees with Garner's prediction, starting in shallow water and moving to deep. On August 12, 1995 (Figure 24), the whale starts out in the middle of Cow Bay, in water of intermediate depth, and moves to shallow water below the 10m contour. Following this, the whale swims out to deeper water to the South and East. This sequence appears to follow the predicted fine-scale search pattern, but since it is the only example which does, it should not be considered to support the prediction.

4.3.4 Fine-scale Patterns: Summary of Results

Behavioural variation with foraging site is mainly a result of the combined effects of prey type and water depth. Comparisons between sites with similar depths but different prey types, and between sites of different depth at which the same prey type is available, enable some separation of the effects of these two factors. Whales feeding on planktonic prey show significantly higher ventilation rates than whales feeding on benthic prey. In accordance with Kramer's (1988) prediction, whales foraging in deep water show longer feeding dive durations than whales feeding in shallow water on the same prey. In most cases the effect of prey type appears to be somewhat stronger than that of depth.

There are evidently many sources of variation that are not accounted for by this study. The effects of water temperature and ocean currents on foraging behaviour are unknown. Individual differences between whales are likely to account for part of the unexplained variation. The data show consistent differences between the dive patterns of individual whales feeding at the same site. However, individual whales tracked between different locations showed variations in foraging behaviour in keeping with the aforementioned effects of prey type and depth. When the means were compared, between-site variation for individual whales was greater than the variation between whales at a particular feeding site.

Most of the explained variation in gray whale behaviour is correlated with prey type. The considerable variability of prey distribution and abundance over space and time provides a complex backdrop to the foraging behaviour and food choices of gray whales, and is fundamental to the interpretation of gray whale foraging and diving behaviour.

4.4 Fine-scale Patterns: Discussion of Results

Considerable and significant variations in dive behaviour occurred between the different feeding sites. These variations are likely to be due to a complex combination of prey type, prey distribution, depth, and other factors. The harmonic mean (whale activity) data are inconclusive concerning the whales' foraging decisions with regard to finding and exploiting the densest patches of benthic prey. Possible instances of fine-scale search behaviour do not support the prediction (Garner, 1994) that gray whales search in shallow areas first and move to deeper areas later.

Contrary to Guerrero's (1989) prediction, the whales do not always appear to select benthic prey over planktonic prey when both are available. One explanation for this is that the difficulty of feeding on planktonic prey is offset in some cases by its density, although this is difficult to confirm without being able to measure exactly how much of each type of prey the whales are able to ingest per unit time.

4.4.1 Behavioural Variation between Feeding Sites

The major source of explainable variation in the ventilation data was related to site. This is likely to be due to the different prey types that are available at these sites. When feeding on benthos, gray whales typically show very structured, repetitive patterns (Guerrero, 1989, Mallonee, 1991), staying underwater for several minutes and then spending 1 - 2 minutes on the surface before diving again. Mysid feeding is characterised by short, variable dive times. This study includes ventilation data from whales feeding on swarming porcelain crab larvae. The characteristic pattern for whales feeding on porcelain crab larvae appears to include a very short dive duration (around half of that generally observed in benthic-feeding whales) and a large number of breaths (frequently 10 or more) during each surface interval.

Since ventilation rates and the amount of time spent at the surface are used as indicators of energy expenditure while foraging, the characteristic ventilation patterns described above, it is possible to make a partial comparison between the energetic costs of different types of prey. Gray whales are unique among cetaceans in that they utilize both benthic and planktonic prey, enabling a comparison to be made between dive patterns for the different types of prey. Since oxygen is needed for cellular respiration, rates of oxygen consumption (and hence ventilation rates) can be used as an analog of energy expenditure

(Sumich, 1983). It could be expected that planktonic prey, which is mobile and attempts to evade capture (author pers. obs., July 6, 1994) would require expenditure of more energy than would benthic prey, which are non-motile by comparison. This is borne out by the data, which show the mean ventilation rate for Rafael Point and Siwash Point, the two rocky-bottom sites where benthic feeding would be impossible, to be significantly higher than for Cow Bay and Ahous Bay, the two sites where evidence of bottom-feeding was observed.

Dunstone and O'Connor (1979:b) used principal component analysis to separate out the trade-off between prey density and ease of locating prey for mink foraging in a controlled setting. They found that a relatively large percentage of the variation in diving behaviour was explained by factors relating to prey density, while a smaller percentage was linked to the ease with which the prey could be located. These priorities do not seem to be reflected in the behaviour of the gray whales in the current study. It is difficult to assess the importance of ease-of-capture relative to density when two or more very different types of prey are involved, but this study indicates that prey type is of great importance in determining behavioural parameters.

4.4.1.1 Dive Parameters

For the four primary dive variables, one-way ANOVA identified significant differences among the feeding-site classes. The Tukey-HSD multiple range test was used to compare pairs of classes to indicate which were significantly different from each other.

4.4.1.1.1 Sinuosity Ratio

The Sinuosity Ratios do not show much differentiation between sites, except to separate the Rafael 1994 site from the other feeding sites. It is probable that turning behaviour is not greatly influenced by feeding site. In addition, the data-gathering method, although useful for showing distribution within the feeding sites and within the study area as a whole, was not sufficiently accurate to plot whale travel paths, making it still harder to detect changes if any existed. The increased path sinuosity seen off Rafael Point in 1994 is likely to be a prey effect, since the whales were known to be feeding on porcelain crab larvae, an unusual prey type, requiring a somewhat different feeding strategy on the whales' part than the more static prey (amphipods).

4.4.1.1.2 Feeding Dive Duration

The variation of feeding dive duration with feeding site appears to be influenced by prey type, Rafael Point and Siwash Point - both rocky-bottom sites where the whales were feeding on planktonic prey - having the shortest feeding dive times (see Figure 8). The two feeding sites with the longest mean feeding dive times are the two amphipod-feeding sites, Cow Bay and Ahous Bay. This difference may be due to the different foraging styles necessary for each prey type, or to differing energetic costs of each prey type, or to a combination of factors. If the plankton-feeding whales are spending less time at depth than the benthos-feeding whales, there are two probable explanations. The first is that they are feeding higher in the water column, and thus travel time to and from the surface is minimized. The second is that they are depleting their blood oxygen levels faster because they are using more energy. It is also possible that the dense swarms of planktonic prey are disturbed by the whales' feeding activity, and that the whales cannot forage in a patch for longer than a few minutes without some dispersal of the patch occurring. Whale foraging is more successful when prey patches are dense than when they are dispersed (Piatt & Methven, 1992). For the benthic-feeding whales in Cow Bay and Ahous Bay, it can be assumed that the whales gain efficiency by maximising their bottom time (within limits; Kramer, 1988) since benthic prey is static, and longer bottom times reduce the amount of time the whales spend travelling to and from the surface.

Mean dive durations in the two benthos-feeding sites are also characterized by relatively smaller standard deviations than in the plankton-feeding sites. This corresponds with other observations (Wursig *et al*, 1986, Guerrero, 1989, Mallonee, 1991, Garner, 1994) that the dive patterns of bottom-feeding gray whales are very structured and regular. By contrast, the plankton-feeding sites, particularly Rafael Point, show higher standard deviations and more variable dive times. Since plankton are mobile and unpredictable, feeding on plankton requires a somewhat flexible foraging tactic which could easily account for this variation.

Within each of the two main prey types, the differences in feeding dive duration can be interpreted as an effect of depth. The majority of the foraging activity in Cow Bay takes place in deeper water than the foraging activity in Ahous Bay, and the mean dive duration is correspondingly longer. Similarly, the foraging activity at Rafael Point, which yielded a longer mean feeding dive duration than at Siwash Point, takes place in deeper water than the Siwash Point activity. This agrees with Kramer's (1988) prediction that feeding dive duration should increase with depth. In the cases of Ahous Bay and Rafael Point, the influences of depth and prey type effectively cancel each other out, causing their means to be statistically indistinguishable.

4.4.1.1.3 Surface Interval Duration

Feeding whales at Rafael Point showed the longest surface interval duration, with those at Siwash Point the next longest, and those in Ahous Bay the shortest. Mean surface interval durations at Cow Bay were of intermediate value.

As for dive cycle duration, the feeding site data for surface interval duration appear to partition themselves primarily according to prey type. The two plankton-feeding sites show longer surface intervals than the two benthic-feeding sites. This finding supports the expectation that whales feeding on plankton use more energy than whales feeding on benthos (Guerrero, 1989), since increased energy use should be correlated with increased time on the surface for ventilation (Kramer, 1998).

Within the prey-type subgroups, the deeper sites show longer surface interval times than the shallower sites. Between Rafael Point and Siwash Point, surface interval time increases as a percentage of overall dive cycle duration, as predicted by Kramer (1988). Surface interval time at Siwash Point represented 22.89% of the total Dive Cycle Duration, while at Rafael Point it increased to 31.22%. This increase reflects the "diminishing returns" gained by staying increasingly long at the surface for the purpose of blood-oxygen loading. For the benthic-feeding sites, however, the percentage of the dive cycle accounted for by the surface interval does not increase with depth. In Ahous Bay, the shallower of the two sites, surface interval accounts for 14.85% of the dive cycle time, but in Cow Bay, which is deeper, only 16.40%. The means for the two bottom-feeding sites are statistically indistinguishable, but superficially the data contrasts with the findings of Wursig *et al.* (1986) for gray whales bottom-feeding at depths of up to 250ft near St. Lawrence Island in the Bering Sea, which showed increased surface interval time, but not increased feeding dive time, with increasing depth.

4.4.1.1.4 Dive Cycle Duration

The main influence on dive cycle duration appears to be feeding depth. In the case of Cow Bay, the evidence suggests that the whales were feeding on amphipods on the ocean bottom, 20 - 30m deep. At Rafael Point, they were likely to have been feeding on porcelain crab larvae, which were swarming near the bottom (20m or deeper) both in 1994, when observed by divers, and in 1995 when sampled by multiple-depth net tows. Most of the foraging activity at Ahous Bay and Siwash Point - the two sites showing shorter Dive Cycle Durations - takes place at shallower depths of 20 - 30m. Siwash Point had the shortest mean dive cycle duration, with Ahous Bay the next shortest, Rafael Point third and Cow Bay the longest (see Figure 7). All the Feeding Site groups were significantly different from one another.

Of the two deeper-water groups, Cow Bay shows a longer dive cycle time than Rafael Point, and of the two shallow groups, Ahous Bay shows a longer dive cycle time than Siwash Point. These differences are likely to be a result of the effects of prey type on feeding dive duration. The dive cycle duration pattern shows a strong similarity to the Dive Duration results, suggesting that the feeding dive component of the dive cycle is the principal source of the variation in dive cycle duration. This is to be expected since it is also the larger component (mean 80.64%) of the cycle.

4.4.1.1.5 Number of Ventilations

The number of ventilations per dive cycle appear to be strongly influenced by site, with each of the four sites having a statistically distinct mean (see Figure 10). Ahous Bay and Cow Bay show the lowest number of ventilations, again with relatively low standard deviations which reflect the highly stereotyped patterns typical of benthic feeding. Rafael Point and Siwash Point showed higher numbers of ventilations per cycle, which indicates higher energy expenditure, especially in the case of Siwash Point, where the mean dive cycle duration was significantly shorter than for any of the other groups. The high variability in the data collected at Rafael Point and Siwash Point may be due in part to the opportunity to feed on two different types of planktonic prey - mysids and porcellanids - which generally occur at different water depths and are likely to require different foraging techniques on the part of the whale.

Ahous Bay shows fewer ventilations per cycle than Cow Bay, and Siwash Point fewer than Rafael Point. These data are consistent with the prediction (Kramer, 1988) that deep-diving whales should minimize travel time by "pre-loading" oxygen with large numbers of ventilations, thus enabling them to stay down longer on a dive than the shallow-diving whales.

4.4.1.1.6 Ventilation Rate

The ventilation rate probably gives the most information regarding energy expenditure, since the number of ventilations - used as a surrogate variable for the use of energy - is expressed as an hourly average for each dive cycle. This enables direct comparisons to be made between different feeding patterns, irrespective of the relative duration of surface interval or feeding dive, and can even include non-cyclic patterns like those of the Grice Bay whales (see Figure 9).

The "ventilation rate" data segregates the sites cleanly into prey-type subgroups, with the whales showing consistently lower ventilation rates when feeding on benthos than on plankton. This is interesting because it strongly supports Guerrero's (1989) suggestion that plankton-feeding is energetically costly, and yet the whales do not, as she predicts, select benthic prey over planktonic when both are present. Whales have been observed switching prey within a season (Dunham, 1999) and even within a single day (Author pers. obs. 1997). The prey type selected by gray whales on any given day is probably the result of a trade-off between the quality of the available benthic versus planktonic prey. It could be assumed that, because of the extra costs involved, the quality of planktonic prey must be higher than that of the benthic prey by a certain specific amount in order for it to be selected as prey. However, because of the multiple factors which contribute to prey "quality," and because the density and distribution of planktonic prey is problematic to measure, it would be extremely difficult to quantify this amount (Duffus, 1996). Conversely, the ephemeral nature of plankton swarms, especially those which are the larval form of a species which is not planktonic as an adult, may be a factor in the whales' prey choice, encouraging a strategy in which the whales feed on the temporary food source while it is there, and switch to the more stable benthic prey later (Dunham, 1999). This explanation implies that whales are capable of distinguishing between ephemeral and stable prey types - a degree of strategic sophistication gray whales were not previously thought to possess.

The mean ventilation rates of Cow Bay and Ahous Bay have the low standard deviations typical of the very regular patterns observed in benthic-feeding whales. The Rafael Point and Siwash Point data are more variable, the mean ventilation rate at Siwash Point having a standard deviation more than twice that of Cow Bay or Ahous Bay. The extreme low end of the distribution -

small numbers of ventilations per hour - can be interpreted as being the result of those occasions where the whales were feeding on mysids in shallow water. The high end of the distribution is harder to explain; it is not clear why some whales feeding at Siwash Point should have ventilation rates so much higher than those at Rafael Point. One explanation for these results, if ventilation rate is interpreted as being directly correlated to energy use (Dolphin 1988, Kramer 1988, Sumich, 1994) is that, of the three prey types, the least energy expenditure is required to feed on amphipods; porcellanid feeding requires somewhat more energy, and mysid-feeding requires the greatest expenditure of energy. The actual foraging energetics are complicated by the fact that the energy return may be different on the various types of prey, and that some of the energy expended (for instance, when the prey is found at or near the bottom) may not be used directly for feeding but for travel to and from the surface.

Grice Bay has the highest ventilation rate of all, by a considerable margin. At first, these data appear to suggest that energy expenditure is greater for ghost shrimp than for other types of whale prey, but this is unlikely since the activities performed by the whales in the course of bottom-feeding in Grice Bay are very similar to those associated with bottom-feeding in Cow Bay. In Grice Bay, by contrast, the bottom, and therefore the prey, is located very close to the surface, thus minimising the travel time between the two. Whales feeding in Grice Bay would be expected to have similar - or possibly somewhat lower - energy expenditure than those feeding in Ahous Bay and Cow Bay.

The Grice Bay data, then, may represent a completely different breathing strategy by the whales - one that occurs in the presence of an unlimited air supply. When there is no spatial separation between feeding and breathing, the whales do not have to partition their time between the two activities, and the whales can breathe more often and take shallower breaths than they would when feeding at depth. Guerrero (1989) found differences in breathing rates between whales feeding on different types of prey, but found the highest blow rate in a resting whale. It is unlikely that resting is a more energy-expensive activity than feeding; however, the resting whale remained at the surface, and therefore experienced an unlimited supply of air. Kramer (1988) describes oxygen "loading" before diving animals make a deep feeding dive. Whales which do not have to make such dives do not need to achieve optimum "loading" and can breathe less efficiently. Therefore, when interpreting blow rates in terms of energy expenditure, it is important to address the issue of the quality of the blows as well as the blow rate itself.

4.4.1.2 Fine-scale Patterns: Characteristics of Individual Feeding Sites

Here the data from the four subtidal sites are discussed individually. Each site is characterized by a different combination of environmental factors and examination of the whales' behaviour at each site may enhance understanding of the whales' behavioural responses to these environmental factors.

4.4.1.2.1 Ahous Bay

The dive pattern of whales feeding in Ahous Bay is characterised by low ventilation rates, short surface intervals and intermediate-length dive and dive cycle durations. Of the four sub-tidal sites, Ahous Bay whales showed the lowest number of ventilations per dive cycle and the shortest surface intervals. Their low ventilation rates - statistically similar to those of whales feeding in Cow Bay - are characteristic of benthic-feeding whales, amphipods being a static prey which does not require great energy expenditure. While benthic-feeding whales are expected to show fairly long dives to minimize travel time to the surface, the Ahous Bay whales' intermediate dive cycle values are likely to result from a trade-off between this long-dive pattern and the effects of foraging in shallow water (relative to Cow Bay and Rafael Point), which reduces the necessity for long dives.

4.4.1.2.2 Cow Bay

Whales feeding in Cow Bay had the longest dive times and dive cycle times of any feeding site, with means which were statistically different from those of all the other sites. Their low ventilation rates were statistically similar to those found in Ahous Bay, and are characteristic of benthic-feeding whales. Their mean dive times, however, are significantly longer than those shown by whales feeding in Ahous Bay. This is likely to be an effect of feeding depth; in Cow Bay most of the feeding activity was distributed around the 20 - meter depth contour (see Chapter 5, Figures 28 and 29), while in Ahous Bay the feeding activity took place near the 10 - meter contour (Figure 30).

4.4.1.2.3 Rafael Point

Rafael Point shows a distinctive pattern with a very high mean number of ventilations per dive cycle and a correspondingly high surface interval duration. No benthic feeding is possible at Rafael Point, since the sea floor is rocky; therefore it can be inferred that the whales are feeding on plankton. The high number of ventilations and relatively high overall ventilation rate reflect the relatively high energy cost of this prey type. Diver observations and plankton tows indicate that the prey was usually located on or near the bottom. In spite of this, dive durations are short - about equivalent to those observed in Ahous Bay, a much shallower location - possibly because when pursuing plankton, the whales' oxygen reserves become exhausted relatively quickly.

4.4.1.2.4 Siwash Point

Like those of Rafael Point, the Siwash Point data are characterised by shorter dive times, higher ventilation rates and greater variability than the benthic-feeding sites. The shortest mean dive duration of the four feeding sites was observed at Siwash Point. Much of the feeding activity at Siwash Point took place close to the shore in shallow water, which may account for the extremely short dive times. In addition, two types of planktonic prey are available at Siwash Point - mysids and porcellanids. The mean ventilation rate is statistically indistinguishable from that of Rafael Point, but its standard deviation is considerably higher. The high variability of the ventilation rates of the Siwash Point whales could be in part a result of the different feeding styles used to exploit these two prey types.

4.4.2 Prey Distribution

Gray whale prey was sampled in Cow Bay, the primary gray whale foraging site, in all years of the study. In 1995 prey was also sampled in Ahous Bay, Rafael Point and Siwash Point, enabling some comparison to be made between the various foraging sites occupied by gray whales during the course of the study. Such comparisons are useful in evaluating the foraging behaviour of gray whales on a fine (daily) scale but, due to the nature of the sampling program, are most relevant when compared with gray whale activity on a coarse (within and between season) scale.

Alternative hypothesis 3 states that whales feed on the prey type with the greatest density. A major confounding factor is the difficulty of getting accurate estimates of the density - or even the presence - of planktonic crab larvae in space and time. The only times that dense populations of crab larvae were able to be located for sampling was when feeding whales were present. Because the larvae are mobile, it is difficult to know how reliable our estimates of plankton density are, and this makes a comparison with the density of benthic organisms less meaningful. Additionally, the distribution of the porcellanid larvae was extremely patchy, and they were apparently concentrated in small, very concentrated swarms. Even within several hundred meters of feeding whales, it was impossible to locate these swarms by stratified transect sampling, only by sampling in close proximity to the whales themselves. It was therefore impossible to determine whether the whales were feeding on all occasions when a swarm was present or if some swarms were present but ignored.

In the two most productive plankton tows, the porcellanid biomass was a little more than 11 grammes. The cross-sectional area of the water column sampled by a 23cm tow is 415.6cm^2. If expressed per square meter for comparison with benthic samples, a plankton tow with a biomass of 11 grammes is equivalent to 264 grammes per square metre. In Cow Bay, the mean biomass for the sites sampled was 164.56 grammes per square metre in 1993, 80.15 in 1994 and 123.62 in 1995. If plankton were regularly present at this density, it is entirely possible that they would be more profitable for the whales than benthos despite the fact that they have to be chased. No tows were taken in 1994, the year whales did appear to be selecting porcellanids over amphipods. A more thorough sampling program than was within the scope of this study would probably increase our understanding of plankton dynamics (including mysids as well as porcellanids) as a factor in gray whale prey choices. It cannot be stated that gray whales are selecting the prey type with the greatest density because of the difficulty in comparing the density of a two-dimensional static prey item with that of a three-dimensional, mobile one.

Alternative hypothesis 4 - that gray whales select benthic over planktonic prey if benthic prey is available - seems to be refuted by the 1994 data, which indicate that the whales fed on planktonic prey at Rafael Point for most of the summer, while samples taken in Cow Bay indicate the presence of benthic prey. However, there are several confounding factors, some of which are discussed above. The most important is that the amphipods found in Cow Bay in 1994 were of a much smaller size than those sampled in 1993 and 1995. It is probable that these were, on average, too small for the whales to utilize and therefore do not constitute "available" benthic prey.

Alternative hypothesis 5 involves the selection by feeding whales of the site with the greatest density of prey. Within each site, whales are expected to show the greatest amount of feeding activity at the location or locations with the greatest density of prey. Due to the mobile nature of planktonic prey, a comparison between sites with the same prey type is only practical for benthos sites. In 1995, the only year in which both benthic prey sites were sampled, higher biomass values and prey densities were found in Ahous Bay. Although Cow Bay was not sampled extensively, some samples were taken at locations at which whales were recorded feeding. The prey densities in these areas were not as rich (in terms of biomass) as some areas in Ahous Bay, yet the whales fed in these locations in Cow Bay rather than in Ahous Bay. It is possible that the "quality" of benthic prey depends not on direct numbers or biomass, but on some other specific characteristic of the local amphipod population which is difficult to identify. Mean individual amphipod mass may be a factor, but several locations in Ahous Bay show higher values for mean individual mass than do the locations in Cow Bay used by the whales.

Insufficient data was collected to address alternative hypothesis 6, but there is some evidence (discussed more fully in Chapter 5) that the whales do not distinguish "patches" of benthic prey within a feeding site. The hypothesis (alternative hypothesis 7) that whales leave patches when they become depleted is not borne out by the data in this study. The daily harmonic-mean activity plots for Cow Bay, the area most utilized by benthic-feeding whales during the three years of this study, show the whales returning repeatedly to areas in which they have been observed feeding on previous days. Neither do they appear to utilize shallow areas first and move to deeper ones later (alternative hypothesis 8). Indeed, little identifiable search behaviour was recorded; it remains unclear exactly how the whales determine where to feed on any given occasion. It is possible that there is a trade-off between depth and prey quality, so that it is beneficial to the whales to feed at certain nutrient-rich sites first even though they are in deeper water. A more detailed prey study of a benthic site during a season in which it is being utilized by whales may provide insight concerning such a trade-off. Conversely, depth may simply not be an influential factor in gray whale prey selection, or may not become an influential factor until the depth reaches a certain threshold.

4.4.2.1 Benthic Prey

The data from the benthic samples taken from Cow Bay are similar to those from the Ahous Bay samples. Amphipods dominated the benthic infauna in both feeding areas, making up 78.78% of the Cow Bay samples and 74.8% of the Ahous Bay samples in 1995. At 13 of the 17 sites successfully sampled in Ahous Bay, amphipods accounted for 90% or more of the total number of organisms. In 1995, the only year when both sites were sampled, the stations sampled in Cow Bay showed a mean biomass of 175.99 (± 64.95) g/m^2, while Ahous Bay's mean biomass was 152.48 g/m^2 (± 31.04). Kvitek and Oliver (1986) found the mean infaunal biomass in Ahous Bay to be 160g/m^2 ± 36, also a close match to the values obtained in this study.

Unfortunately, no samples are available for Ahous Bay during the years between this study and Kvitek and Oliver's, a gap of ten years or more. The data from the three consecutive years in which Cow Bay was sampled indicate that there may be variation in population structure from year to year. Although Cow Bay was not sampled as extensively during the three years of the study as Ahous Bay was in 1995, the samples taken each year were randomly positioned (with some stratification) and covered, in general, the same part of the Bay, enabling a valuable comparison to be made.

The increase in amphipod numbers between 1993 and 1994 in Cow Bay, without a corresponding increase in biomass, and subsequent decrease again in 1995 are suggestive of a two-year cycle in which large numbers of young amphipods alternate with smaller numbers of larger, mature animals. Further evidence for this pattern was found in 1996 and 1997 (Dunham, 1999). However, Carruthers (2000) reports data for 1998 and 1999 which appear to show a continuing decline in amphipod numbers. A parallel decline has also been observed in the gray whales' primary and secondary feeding grounds (Mate, pers. comm. 1999).

The gray whales appear to prefer to feed in Cow Bay when the benthic infauna is dominated by larger amphipods. This could be expected, since smaller amphipods would be less likely to be retained by the whales' baleen. A sample of amphipods (many still alive) from a gray whale plume, taken from a whale feeding in Ahous Bay in August 1995, consisted of amphipods whose mean individual weight was 0.005g. This figure is considerably lower than the average individual weight for the main set of Ahous Bay benthic samples, 0.01g, and is also lower than the average from the later samples taken in Ahous Bay in the same month, 0.013g. Although not a statistically significant sample, this evidence supports the suggestion that smaller amphipods escape through the gray whales' baleen, while the larger ones are retained. The mean individual mass of the escapees was, in fact, larger than the mean individual mass of 0.0044g from the pooled Cow Bay samples in 1994 - a year in which the whales did not feed in Cow Bay. If, as it appears from the latter comparison, most of the amphipods present in Cow Bay in 1994 were small enough to fall through a gray whale's baleen, this goes a long way towards explaining the whales' absence from Cow Bay that year. In 1993 and 1995 – years in which the whales were observed feeding in Cow Bay – the mean individual amphipod mass was considerably larger than in 1994 (0.021g and 0.012g respectively).

The high standard deviations (shown in Table 12) of the benthic prey number and biomass data support previous observations (Stoker, 1981) that the prey distribution is patchy and highly variable. In 1995, both sites showed a standard deviation which is greater than the mean for the number of organisms per square meter; for biomass, the standard deviation is similar to the mean at both sites. The 1993 and 1994 data for Cow Bay also show high standard deviations for numbers of organisms and biomass.

Site	Year	Average Number of Individuals per square metre	Average Biomass (g) per square metre
Cow Bay	1993	8055.04 ± 1167.09	164.56 ± 31.25
Cow Bay	1994	17803.37 ± 4072.57	80.15 ± 17.98
Cow Bay	1995	11,145.81	
Ahous Bay	1995	15832.29 ± 3947.16	152.48 ± 31.04

Table 12: Average Density and Biomass of Benthic Organisms Sampled in Cow Bay, 1993 - 1995, and Ahous Bay, 1995

The benthic data from Cow Bay and Ahous Bay show considerably lower mean density and biomass than that found in the Bering Sea. Stoker (1981) reported average total density to be 28,923/m^2, compared with 11,145.81/m^2

(Cow Bay 1995) and 15,832.29/m^2 (Ahous Bay 1995). Biomass in the Bering Sea was reported (Stoker, 1981) as being 482 g/m^2 - as expected, considerably greater than this study's findings of 123.62 g/m^2 (Cow Bay 1995) and 152.48 g/m^2 (Ahous Bay 1995). However, Oliver and Kvitek (1984), in a study of Pachena Bay, another tertiary feeding site on the west coast of Vancouver Island, found the infaunal density to be 118,583/m^2 - greater than either of the two Clayoquot Sound sites or the Bering Sea. The biomass found in Pachena Bay, however, was 197 g/m^2, similar to the Clayoquot Sound figures and considerably less than that found in the Bering Sea study.

The four Ahous Bay sites that were re-sampled in August of 1995, approximately one month later than the original samples were taken, did not show any clear trend across all sites (Table 8). However, the two amphipod-rich locations (stations 6 and 7) showed a trend towards increasing individual mass, but a decrease in the overall number of amphipods. Biomass in these two samples remained similar from July to August, as did the percentage of amphipods. The sample sizes are not sufficient to be statistically valid, but if the trend were supported by further sampling, the implication would be that amphipod growth continues throughout the season. It could therefore be expected that, all other things being equal, the benthic sites would represent a better food supply to feeding gray whales later in the season. The data collected by Dunham (1999) support this prediction.

4.4.2.2 Planktonic Prey

1995 was the only year of the study in which plankton was sampled. The main goal of the sampling program was to obtain an estimate of the magnitude and distribution of the population of porcellanid larvae in the Rafael Point area. A secondary goal was to check for the presence of porcellanid larvae in other known gray whale feeding areas. Unfortunately, due to the mobility and extreme patchiness of the porcellanids, the data obtained were not as informative as was hoped. Extremely high densities of porcelain crab larvae (up to 6068 in one tow) were found within patches, but in the majority of cases where dense patches were located, the samples were not part of a systematic sampling transect but were isolated samples taken under feeding whales. Dense patches were consistently missed by systematic transect sampling even when the transect passed close to feeding whales.

As expected, porcelain crab larvae dominated the plankton at Rafael Point, especially in the larger samples. At all the sites, including Cow Bay, in any sample with a total number of organisms of 30 or greater, at least 50% of the organisms were porcelain crab larvae. The porcelain crab larvae themselves were typically dominated by larvae at the second zoeal stage, except for a few isolated instances in which first zoeae outnumber second zoeae. These instances occur in all sites, and are mostly distributed towards the end of the season (July 7, July 17, August 25, September 4, and September 8). The age of the zoeae could be an important factor in the whales' seasonal foraging choices if the second zoeae represent a more profitable source of food. The appearance of younger larvae in the later part of the season is in accordance with Knudsen's (1964) suggestion that two or more broods may occur within a breeding season. Dunham (1999) also recorded a hatching episode for *Pachycheles* sp. in Clayoquot Sound in the first part of August, 1997, but found no evidence that gray whales were preferentially targeting porcellanid patches based on the proportions of the different larval stages they contained.

Since foraging location (which is strongly correlated with prey type and density) has a much greater effect on the whales' dive behaviour than does vessel number, it is likely that their spatial behaviour is also influenced mainly by prey availiability, rather than by vessel activity. Information regarding prey type, distribution and density is useful in interpreting the whales' movements, although such interpretation is not straightforward because of the changes in prey quality and the difficulty of comparing quality across prey types. Because benthic prey resources remain fairly constant within seasons (sampling results imply a small increase in size later in the season, but no statistically significant trends were revealed; see Table 9), the fine-scale movements of gray whales are most likely to be driven by variations in the availiability of planktonic prey. Considerable difficulties exist in evaluating gray whales' fine-scale spatial movements because the data contain a large amount of random variation. The spatial behaviour of whales foraging on plankton is particularly variable; however, whales foraging on benthos tend to have tightly constrained behaviour patterns, both spatially and temporally, and can potentially be evaluated for changes in an expected pattern; these whales' behaviour may be more easily tested for correlations with vessel abundance.

4.4.3 Evidence of Possible Search Behaviour

Search behaviour is one aspect of spatial foraging behaviour which can be expected to conform to a pattern based on foraging efficiency, and can therefore be evaluated for its degree of conformity. Since it is not known in detail how whales determine what prey is present, it is difficult to say with much certainty that what is being observed is actually search behaviour. In the majority of observations of whales feeding in Cow Bay or Ahous Bay, the whales' path sinuosity was typical of the tightly-grouped, within-patch pattern described by Garner (1994) for an actively feeding whale. However, on two occasions in 1993 and two in 1995, (Figures 21 through 24) the whales exhibited a relatively straight approach path and then switched to increased turning within a restricted area - a switch from low to high sinuosity that could indicate a successful search for prey. On only one of these occasions did the whale appear to search in a way that agrees with Garner's prediction, starting in shallow water and moving to deep. Four observations does not constitute a sufficiently large sample to really answer the question of whether depth influences search behaviour on a fine scale; however, the observations made during this study do not appear to support Garner's hypothesis that it does. The patterns of long-term spatial utilization by the whales (see section 5 - C 1) suggest that the whales perceive each entire feeding site (Cow Bay, Ahous Bay, Rafael Point and - or possibly including - Siwash Point) as one patch, and do not distinguish areas of different depth within those sites.

4.4.4 Summary: Fine-scale Decision-making by Foraging Gray Whales

Most of the whales' foraging activity seems to take place within a fairly narrow depth range at each site; this could be related to prey distribution or to foraging energetics. In Ahous Bay, the greatest infaunal biomass was found at intermediate depths, between the 10-meter and 20-meter depth contour (Figure 13). In Cow Bay, high infaunal biomass occurred at similar depths, but also in deeper water (Figure 16). The whales in Cow Bay seemed to forage in fairly deep areas compared to where amphipods were found, apparently selecting amphipods of higher quality in spite of the deeper water (Figures 29 and 30), and certainly did not thoroughly exploit prey in shallow areas before moving to deeper ones. Despite Garner's (1994) suggestion that it should be possible to accurately map prey patches, the practical reality was that patch boundaries were impossible to see while using SCUBA, the visibility being poor and the ocean bottom appearing mostly homogeneous. As a result, detailed mapping of the patches, which seem likely to take the form of fine-scale areas of relatively high amphipod concentration among areas of lower concentration, was not within the scope of this survey. This made it difficult to compare whale activity with the location of actual food patches. When whale activity values were plotted against various prey characteristics (biomass, density, amphipod content, mean individual mass) no trends were apparent. Unfortunately in this project the site with the best whale activity database is Cow Bay, while the site with the best prey distribution database is Ahous Bay. A study in which high quality data is obtained for both whale activity and prey distribution at the same feeding site could provide further information about gray whales' foraging choices.

This problem was compounded at Rafael Point, where the prey patches were mobile. The whales' spatial distribution was much wider at Rafael Point than in either Cow Bay or Ahous Bay. Whales rarely fed in, or even close to, the same location twice. It was therefore possible that, on days when plankton tows were taken, the whales were feeding in a new location not represented in the database of whale locations (it was not practical to combine the prey-sampling activity with the whale-location and blow data recording). An attempt to assign a harmonic-mean activity value to each prey sampling site for the purpose of comparing whale activity with prey density was unsuccessful. In more than one instance, the "*Homerange*" program was unable to assign an activity value because the point was outside the main Rafael Point feeding range recognized by the program (a range based on recorded locations of feeding whales). In at least one of these cases, the sample was taken in the footprint of an actively feeding whale, but the daily feeding locations were so variable that there were no whale position data which showed whales feeding in that location on a day when their locations were being recorded. This illustrates the practical difficulties of mapping porcellanids, and the unsuitability of the harmonic mean activity measure for describing the movements of whales relative to mobile prey.

In 1995 (the only year in which plankton was sampled) very few mysids were found in the plankton samples, and it was initially concluded that they were not important prey animals for the whales during the study period. However, Dunham (1999) refined the sampling technique and was able to find mysids at Rafael Point, Siwash Point and in some areas of Cow Bay. In Cow Bay they were generally associated with reefs or shallow water and aquatic plants and probably did not constitute part of the food supply for those whales recorded feeding at that site in 1993 and 1995. At Rafael Point and Siwash Point they were found close to shore, but were also several hundred meters from shore, and may have formed a significant part of the whales' prey during 1994 and 1995. Since, like porcellanids, they are mobile and tend to swarm near the ocean bottom, it is likely that gray whales feeding on mysids in fairly deep water would not behave differently from gray whales feeding on porcellanids. One difference between mysids and porcellanids as prey, however, is that mysids are found in both shallow and deep water, while porcellanids seem to be mainly distributed far from shore in deeper water (Figures 19 and 20). The distribution of foraging whales at Rafael and Siwash Point (Chapter 5, Figure 31) shows the whales feeding much of the time in shallow water over rocky reefs; mysids were probably their prey when foraging in this location.

The role of mysids in the prey selection of foraging gray whales is uncertain. Since they occur often in shallow water, and are larger than porcelain crab larvae, they should represent a more attractive prey than porcellanids if present in sufficient numbers. Dunham (1999) presented some evidence that this is in fact what occurs.

Chapter 5: Long-term Spatial Patterns of Whale Activity in Clayoquot Sound

The question which initiated this research involved the longer-term movements of gray whales within - and outside - Clayoquot Sound. Residents of Tofino were concerned that a long-term trend was occurring which took the whales farther North each year. The purpose of the fine-scale observations described in Chapters 3 and 4 was to attempt to quantify gray whale behaviour so that it could be measured under different conditions. In Chapter 5 the information obtained in Chapters 3 and 4 is examined on a coarser scale (within and between seasons) that more closely fits the scale of the initial question. Three sets of hypotheses were constructed to describe the whales' long-term spatial movements.

1. Null Hypothesis: Gray whales' feeding activity is randomly distributed among possible feeding sites in Clayoquot Sound

Alternative Hypothesis: Whales focus on one location per season, and this location changes from one season to the next

2. Null Hypothesis: Gray whale spatial activity within seasons is independent of foraging depth

Alternative Hypothesis: Whales show a within-season shift from shallow water to deeper water

3. Null Hypothesis: The selection of a seasonal foraging site by gray whales is independent of the sites selected in previous seasons

Alternative Hypothesis 1: Rotation of feeding sites occurs between seasons, correlated with prey depletion

Alternative Hypothesis 2: Whales follow a directional trend in their feeding site selection between seasons

5.1 Long-term Spatial Patterns of Whale Activity: Data Collection

In addition to direct observation of the whales, a log was kept which recorded all whale sightings, each day, within the Clayoquot Sound area. This information was obtained from whale-watching operators, who follow a different route than the research vessel en route to the whales and also have greater range and speed for searching, from tourist vessels headed to the Maquinna Hot Springs, at the northern end of Clayoquot Sound, and from local sailors, fishing boat operators and water taxi operators.

5.2 Long-term Spatial Patterns of Whale Activity - Data Analysis

The position fixes obtained at each dive cycle for bottom-feeding whales were mapped using the program *Homerange* (Dixon & Chapman, 1980) to find the Harmonic Mean activity centre for each separate whale on each day of monitoring. Figures 25, 26 and 27 each show typical whale activity during one day's monitoring. The crosses represent separate sightings of the whale at the end of each dive cycle, while the asterisk represents the activity center for that day's behavioural sample. Activity centers are calculated using the first inverse moment (harmonic mean) measure of activity (Dixon & Chapman, 1980). The contour lines show approximate water depth. Daily Harmonic Mean activity centres were combined on one map and compared to water depth to test for evidence of a shallow-to-deep progression within each season. This data addresses the first pair of hypotheses outlined on the previous page.

Gray whale observation records from this study and from other sources were summarized in the form of a matrix showing the number of whales at each of the different feeding sites at different times in each season. These matrices were used to address the second and third sets of hypotheses on page 118-119.

Figure 25: Single Whale Activity Plot for August 3, 1993 in Cow Bay, Clayoquot Sound

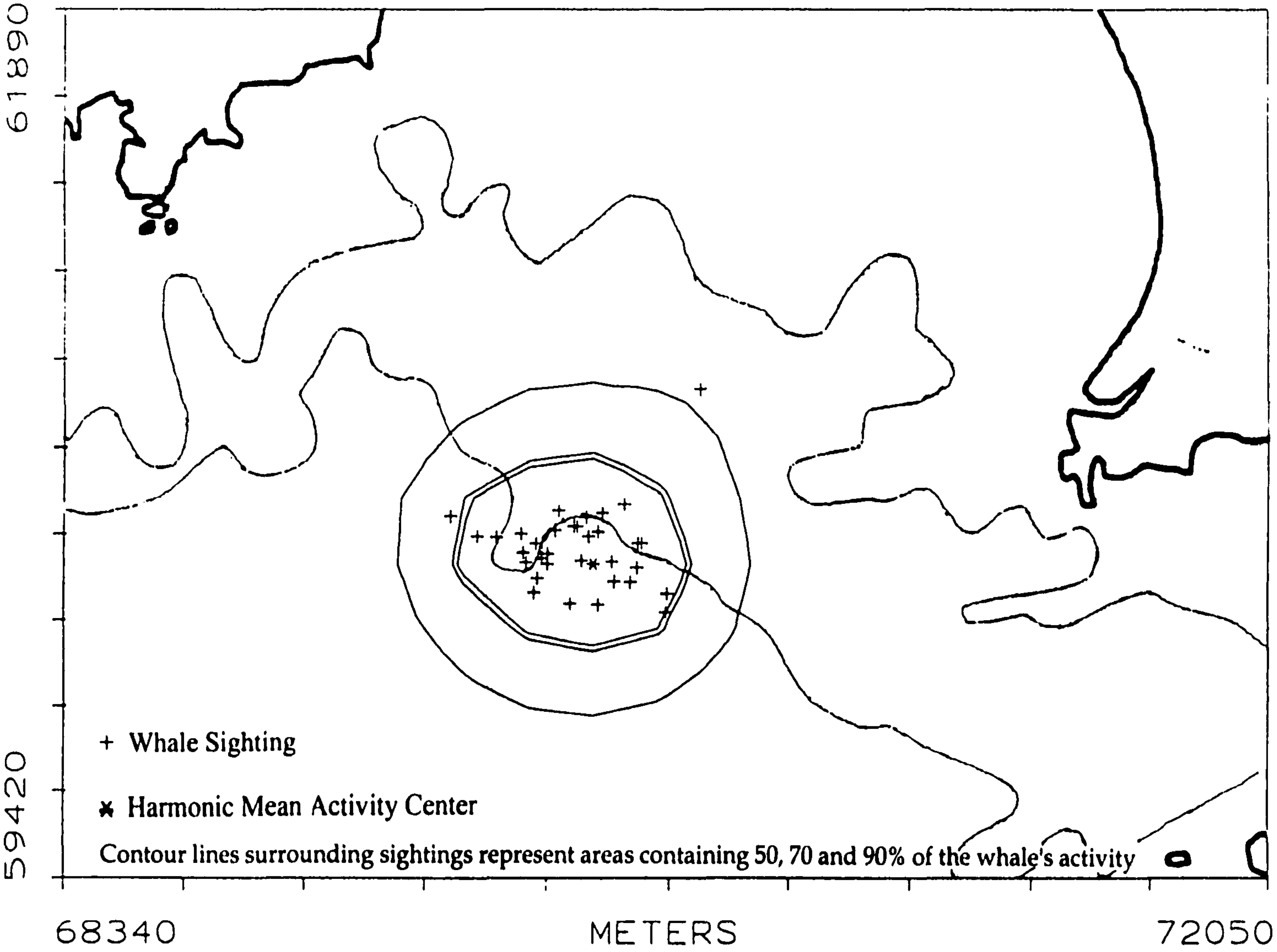
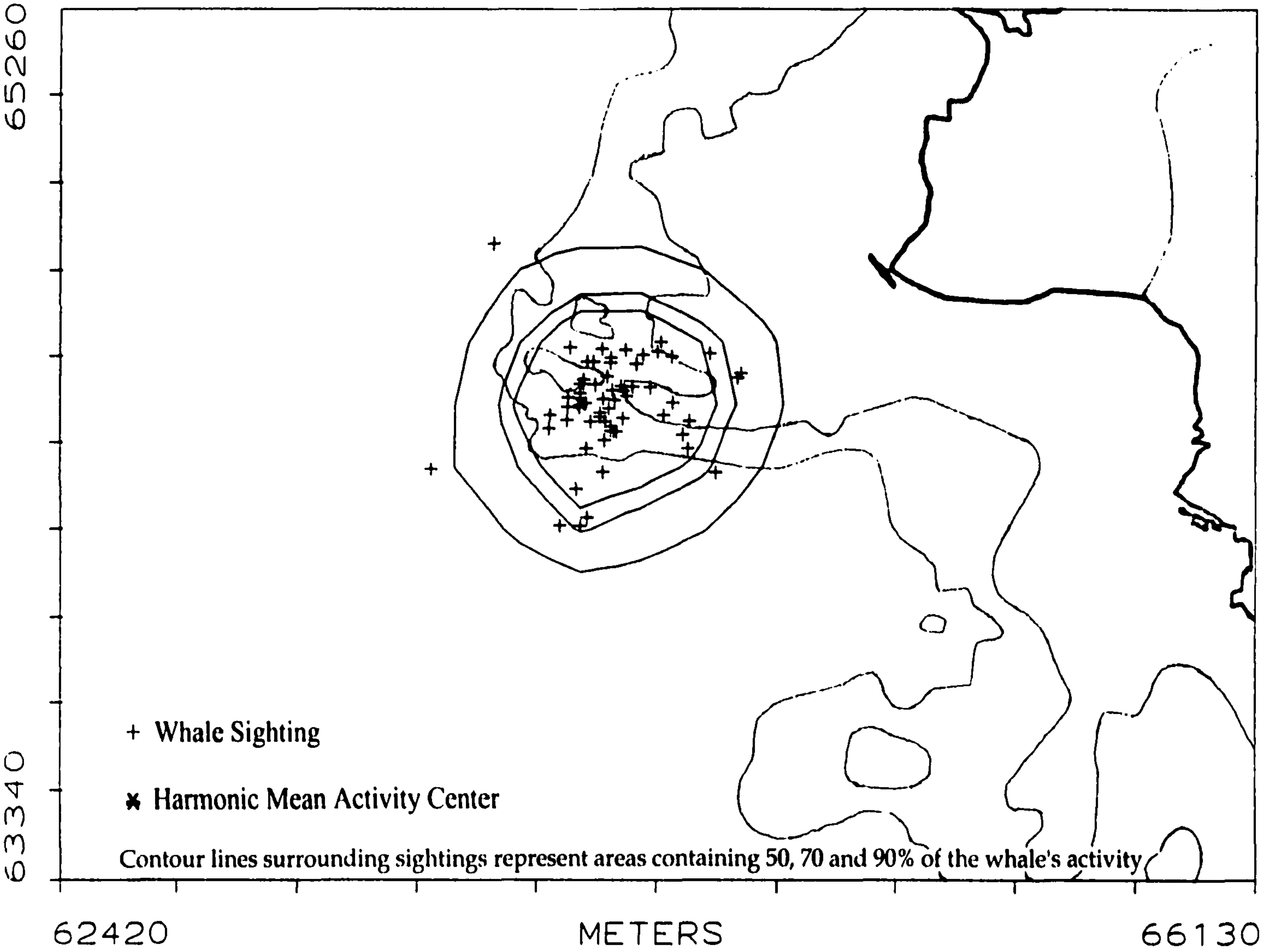


Figure 26: Single Whale Activity Plot for August 6, 1994 at Rafael Point, Clayoquot Sound



Contour lines surrounding sightings represent areas containing 50, 70 and 90% of the whale's activity

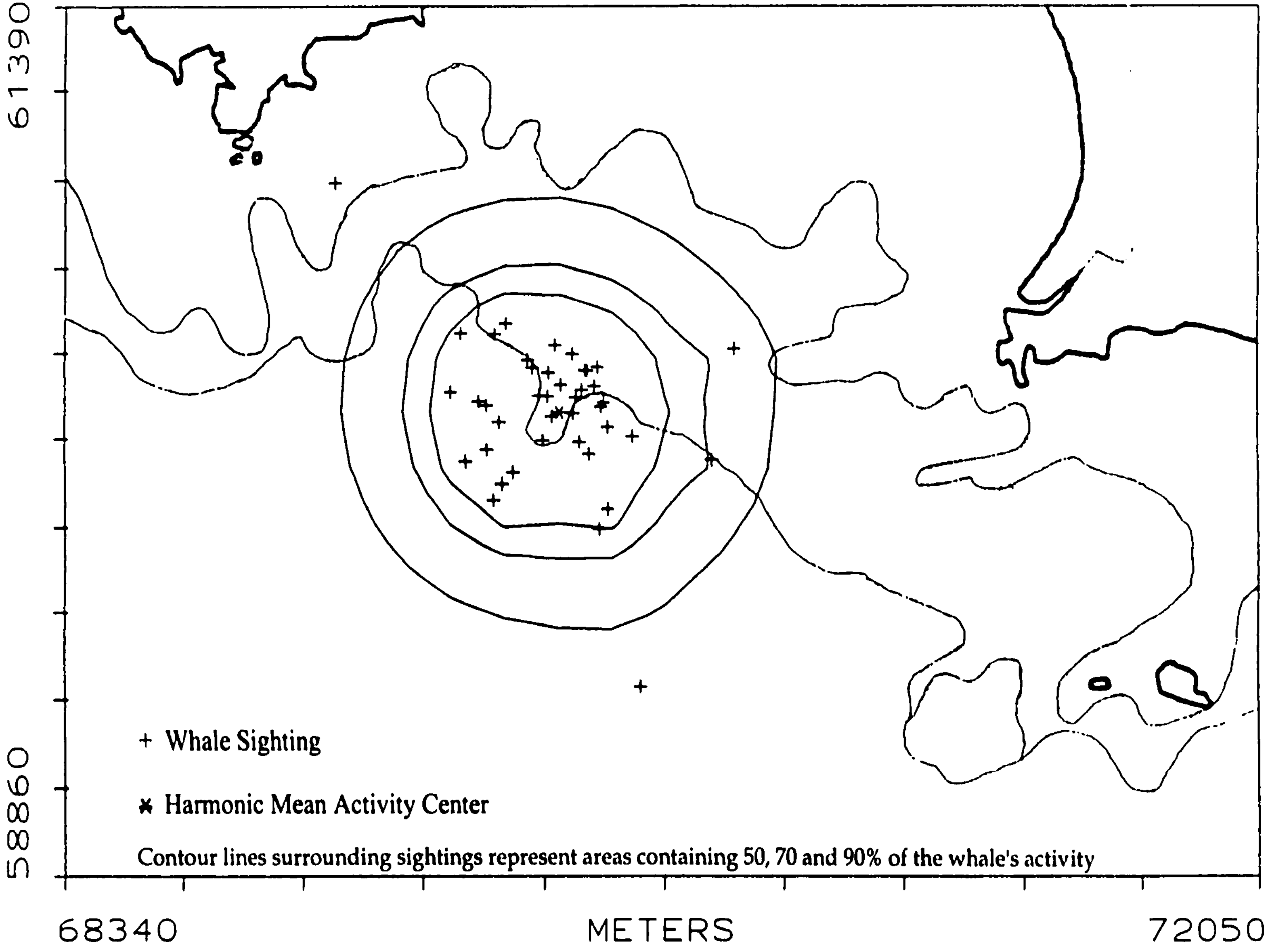


Figure 27: Single Whale Activity Plot for August 31, 1995 in Cow Bay, Clayoquot Sound

5.3 Long-term Spatial Patterns of Whale Activity - Results

Figures 28 (Ahous Bay, 1993 and 1995), 29 (Cow Bay, 1993), 30 (Cow Bay, 1995) and 31 (Rafael Point, 1994) summarize the major concentrations of the whales' spatial activity during the three years of the study. Each point represents the center of activity (see Figures 25, 26 and 27) for one whale during one day's data recording. The distribution of foraging activity centers in both Ahous and Cow Bay was similar in 1993 and 1995, although whale activity in 1995 averages shallower than 1993, and Ahous Bay activity shallower than Cow Bay.

Figures 32, 33 and 34 show the changes in the whales' use of the study area over the 3 seasons of the study, based not only on observation but on reports from whale-watching vessels and other local boaters. Squares for which no information is available are shown in white. These matrices should be considered to show a more comprehensive picture of whale activity than the location data shown in figures 28, 29, 30 and 31, since whales may have been present in more remote areas than those in which data were gathered, and these whales would not have been recorded in the main body of the data.

The general patterns demonstrated by the distribution of the GPS location data are reflected in the more inclusive (but less precise) data in figures 32 - 34. In 1993 by far the greatest amount of whale activity occurred in Cow Bay, rather than in any of the other feeding locations within the area. In 1993, while most whale-watch vessels remained in Cow Bay once they had sighted a whale, one vessel in particular made regular trips to Rafael Point and for most of the season reported only one juvenile whale feeding close to the rocks. During 1994, regular checks were made in Cow Bay and Ahous Bay, but the majority of whale activity

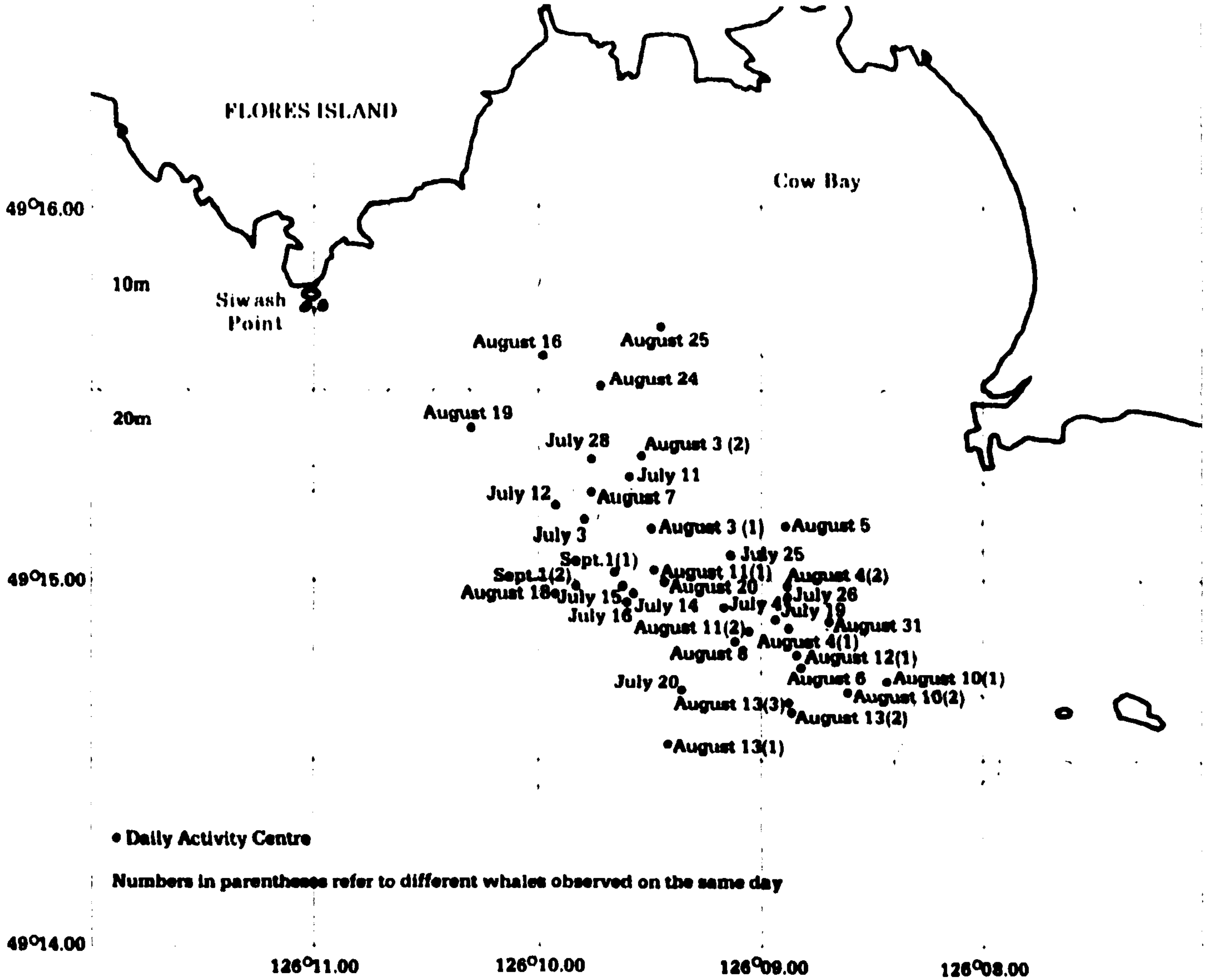


Figure 28: Whale Activity Centres (Harmonic Mean Measure of Activity) for Each Day of Monitoring During the Summer of 1993 in Cow Bay, Clayoquot Sound

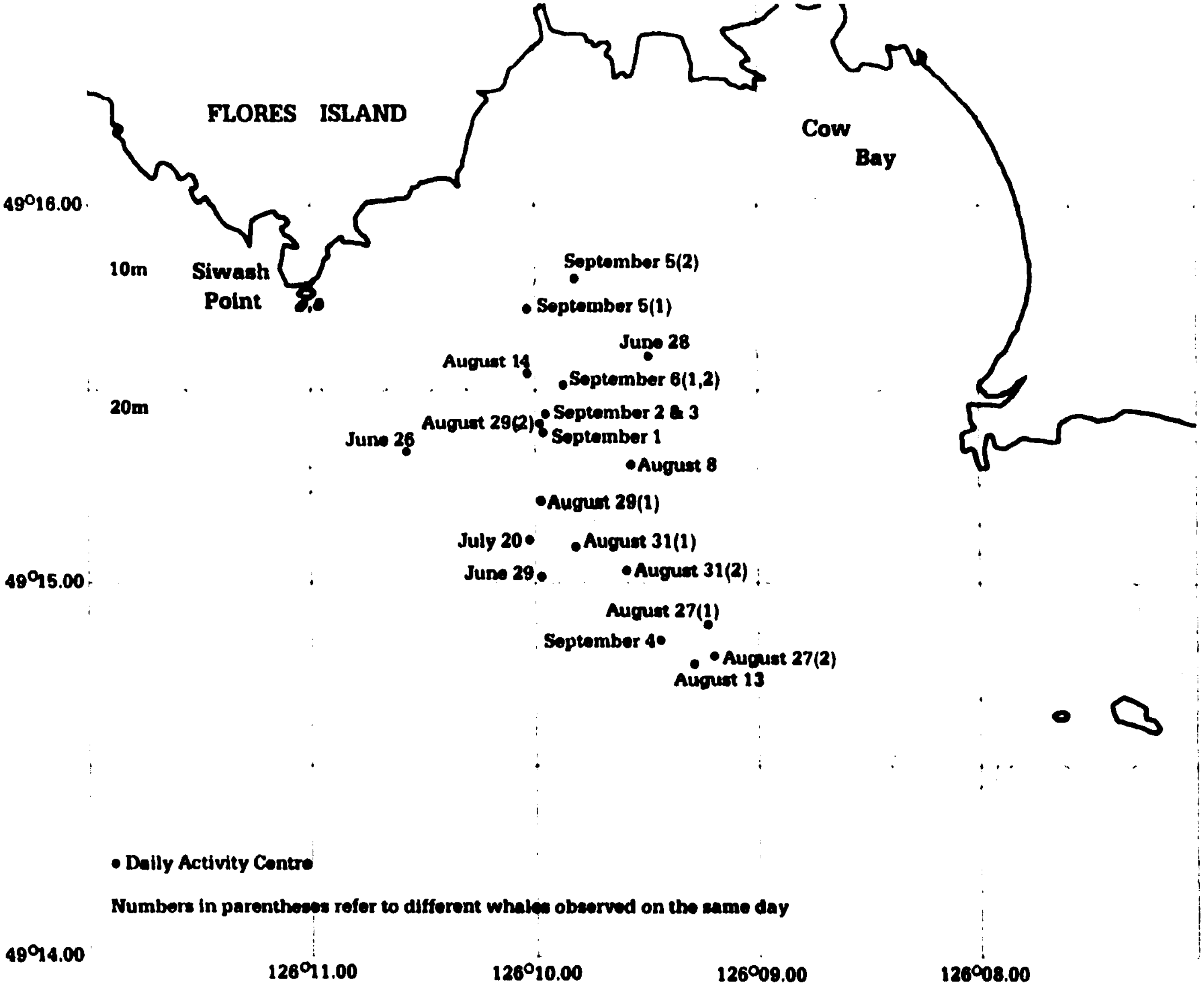
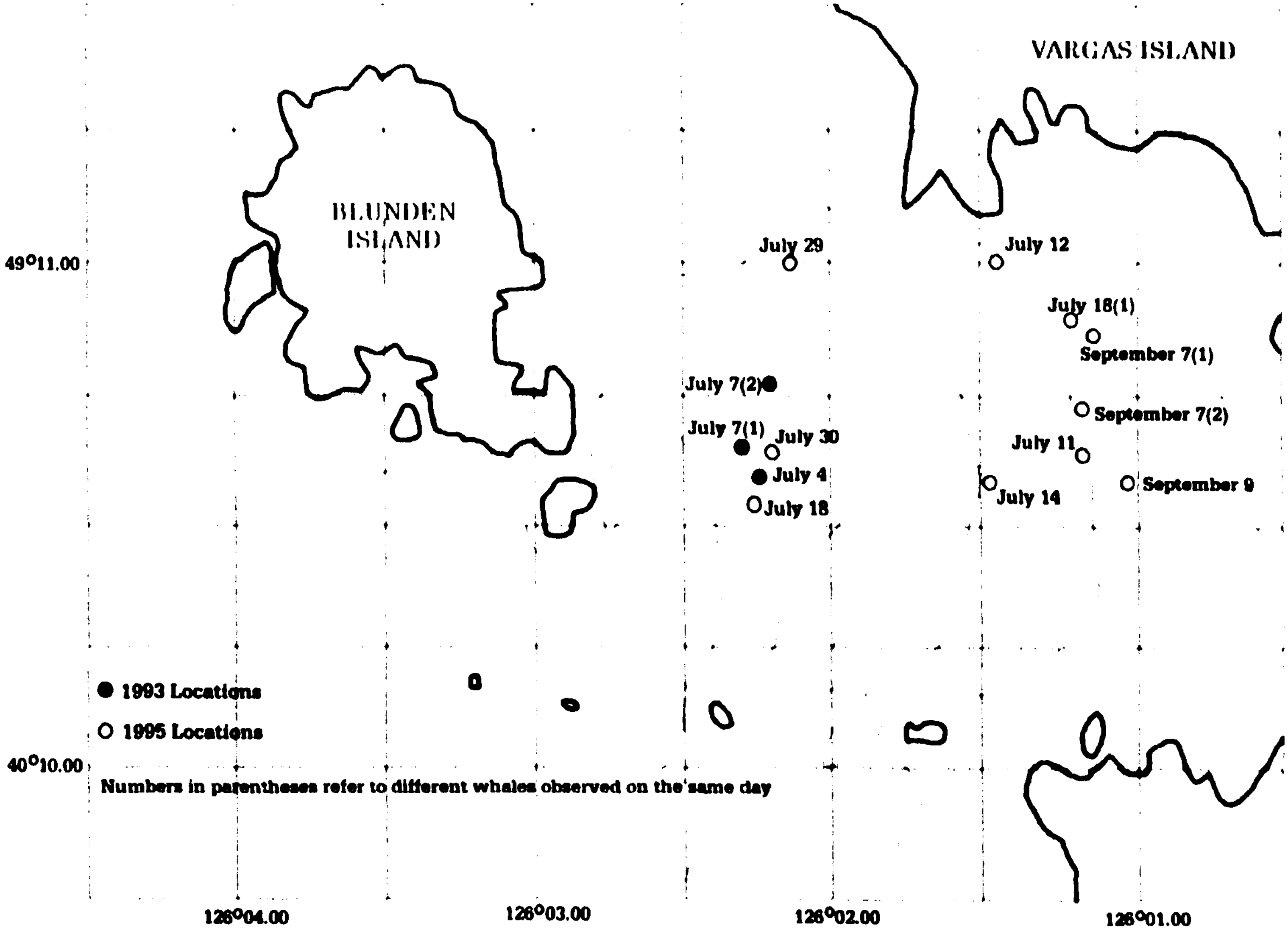


Figure 29: Whale Activity Centres (Harmonic Mean Measure of Activity) for Each Day of Monitoring During the Summer of 1995 in Cow Bay, Clayoquot Sound



Numbers in parentheses refer to different whales observed on the same day

Figure 30: Whale Activity Centres (Harmonic Mean Measure of Activity) for Each Day of Monitoring During the Summer of 1993 and the Summer of 1995 in Ahous Bay, Clayoquot Sound

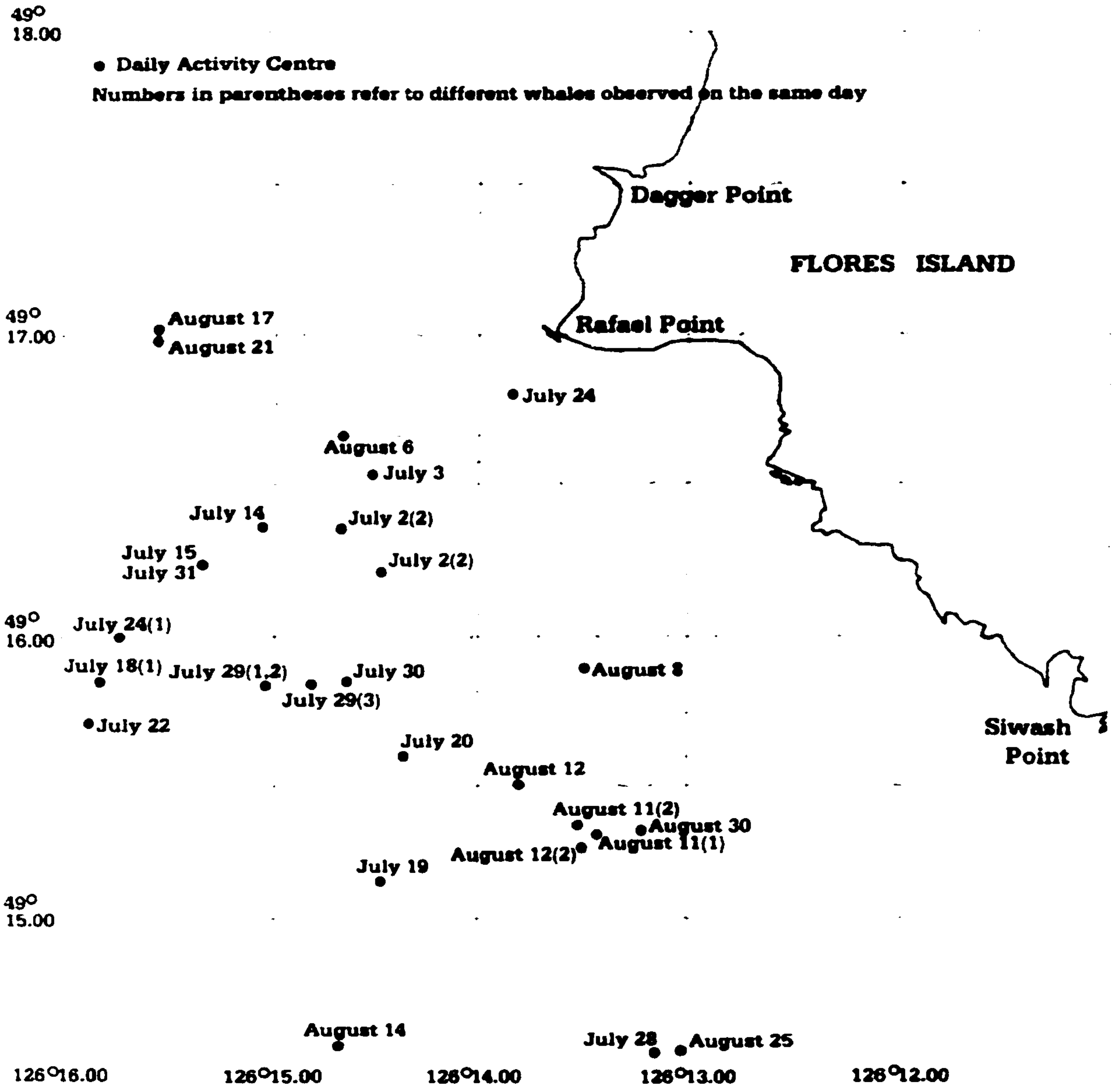


Figure 31: Whale Activity Centres (Harmonic Mean Measure of Activity) for Each Day of Monitoring During the Summer of 1994 off Southwest Flores Island, Clayoquot Sound

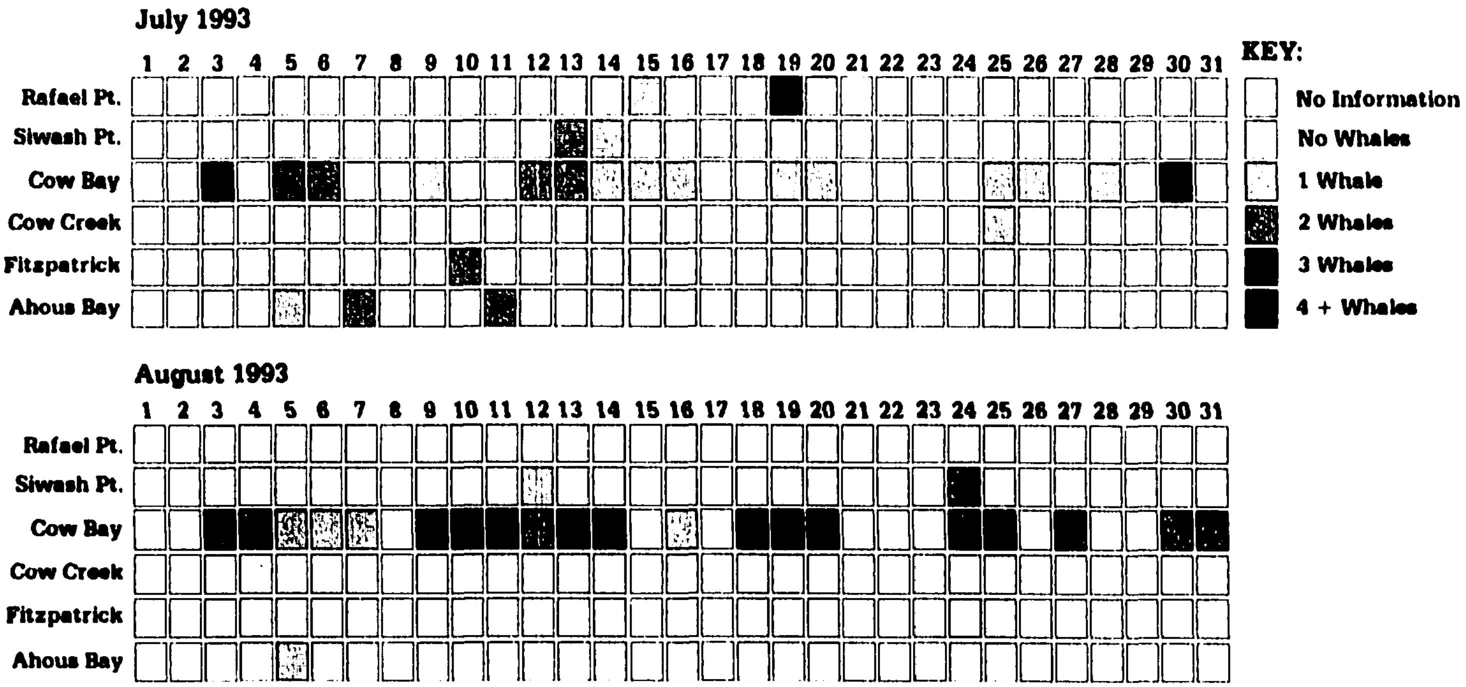


Figure 32: Spatial Use of Clayoquot Sound by Gray Whales During July and August 1993

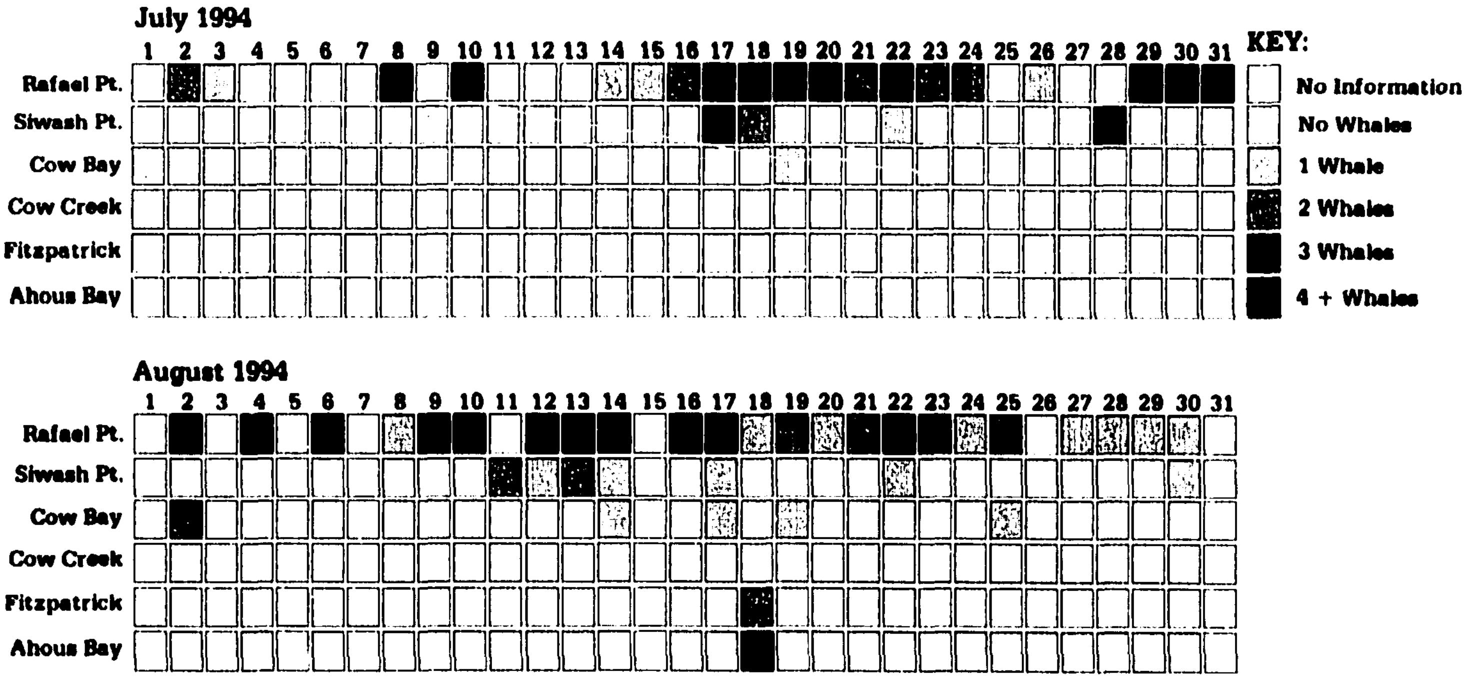


Figure 33: Spatial Use of Clayoquot Sound by Gray Whales During July and August, 1994

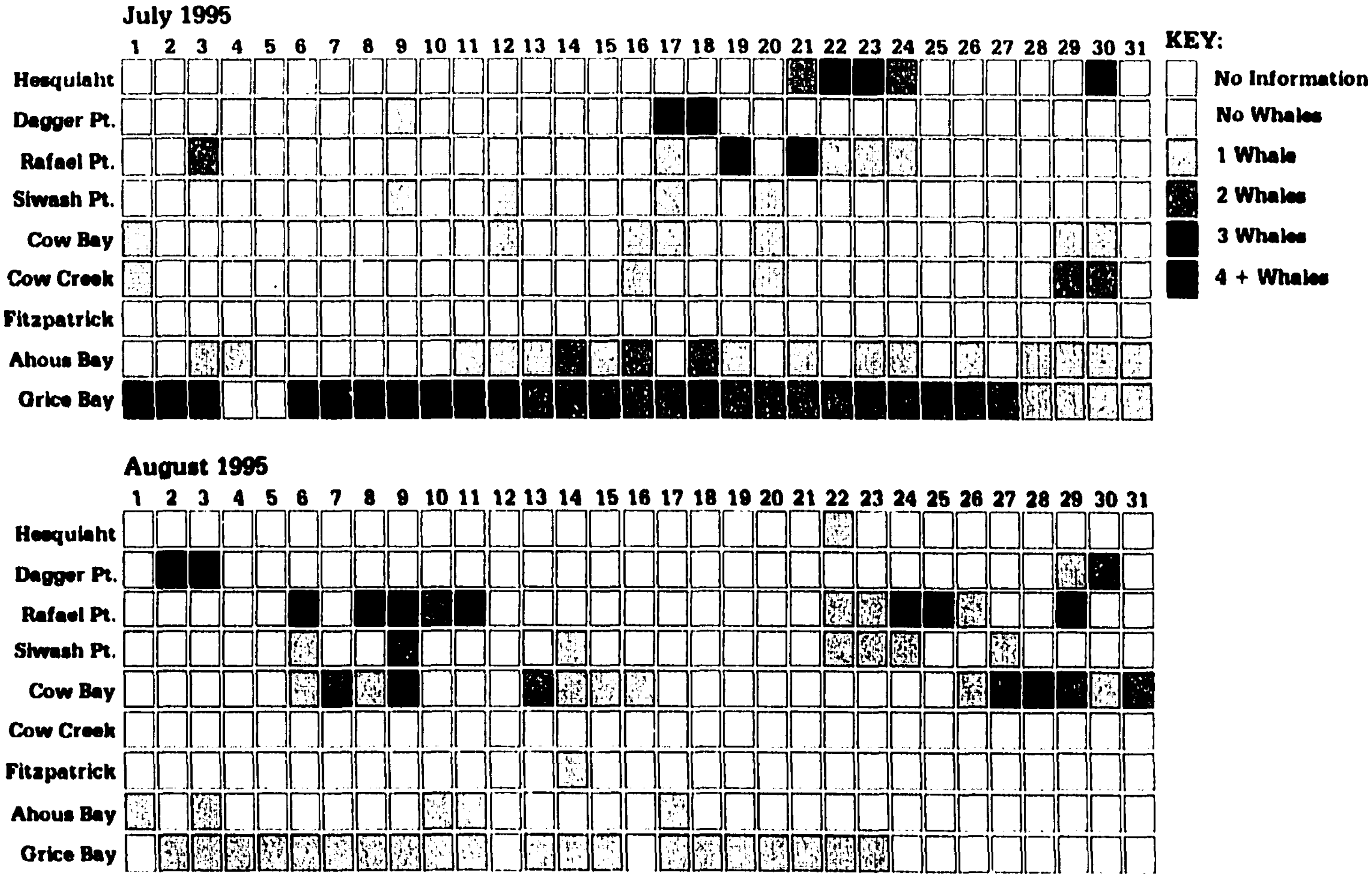


Figure 34: Spatial Use of Clayoquot Sound by Gray Whales During July and August, 1995

was concentrated around Rafael Point. In 1995, although a large amount of the whale-watching activity was centered around the highly accessible Grice Bay, several vessels made regular checks on other sites in the Clayoquot Sound area.

5.4 Long-term Spatial Patterns of Whale Activity: Discussion of Results

Possibly one of the most interesting findings of this study was the lack of coarse scale site fidelity among gray whales. Based on information from local boaters and some prior research data, the whales were expected to feed at the same sites each season, or at least to feed at the same site for the duration of one season. Instead, the whales changed their feeding site and prey type frequently, both within and between seasons, with more than one site in the study area being utilized concurrently.

5.4.1 Factors Influencing Seasonal Site Selection

Since the whales did not, as predicted, focus on one location per season, there is no evidence that null hypothesis 1 should be rejected. However, there is some evidence that the apparent "randomness" of their movements is instead the result of their response to a combination of environmental factors which is much more complex than was originally assumed.

The data collected in this study seem to suggest that coarse-scale changes in feeding location occur mainly in response to changes in prey dynamics. The whales fed on planktonic prey at Rafael Point for most of the summer, despite the availability of benthic prey in Cow Bay. However, the amphipods found in Cow Bay in 1994 were of a much smaller size than those sampled in 1993 and 1995. It is likely that these smaller amphipods were not a suitable prey for gray whales, since a sample of expelled amphipods from a gray whale's baleen during feeding yielded larger organisms, on average, than those found in Cow Bay in 1994. Several other factors, which have been discussed in Chapter 4, affect the changing relative profitability of planktonic and benthic prey. The difficulty of getting accurate estimates of the density - or even the presence - of planktonic crab larvae in space and time has a detrimental effect on any attempts to compare their relative attractiveness to whales.

Since this study was completed, individual whales have been observed switching from feeding on mysids to feeding on amphipods (and back again) on the same day (Author pers obs., August 1997). This occurred on several occasions and certainly seems to be in conflict with the hypothesis (alternative hypothesis 2) that whales select one site (therefore, one type of prey) and feed on it consistently throughout a season.

5.4.2 The Effect of Depth on Within-season Spatial Activity

The whales do not appear to utilize shallow areas first and move to deeper ones later in the season (the coarse-scale corollary to alternative hypothesis 8 discussed in Chapter 4). The summary plots (Figures 28, 29, 30 and 31) of daily harmonic-mean activity centers in Cow Bay, the area most utilized by benthic-feeding whales during the three years of this study, show the whales returning repeatedly to areas in which they have been observed feeding on previous days. The plots show the whales moving from deep to shallow and back again several times in the course of each feeding season. These patterns support the view that each feeding site is treated as a single prey "patch" by the whales. They can also be interpreted to mean that depth is not a major factor in foraging site selection for gray whales, or that the detrimental aspects of increased foraging depth are easily overridden by prey quality. The absence of gray whales from Ahous Bay -

a shallower benthic feeding site than Cow Bay - in 1995, a year when benthic prey was plentiful in Ahous Bay, is further evidence that depth is not always a factor in gray whale prey selection.

5.4.3 The Dynamics of Long-term Spatial Shifts

When the three years covered by the current study are combined with Garner's (1994) data from the previous two years, the whales' spatial movements do not appear to be affected by depth, only by prey type. Some evidence exists for a form of feeding site rotation, but it is more complex than that predicted by alternative hypothesis 3:1, and appears to involve the interaction of a number of different patterns, which are likely to be a result of changing prey availability. There is certainly no evidence of a steady movement to the North, as was feared by members of the whale-watching industry. The whales' use of Cow Bay on alternate years appears to be consistent for the later four years of the five-year period described above, and continues for two more years, according to Dunham (1999), but with different parts of the Bay being utilized in some years than in others. The whales made some use of Cow Bay, Siwash Point and Rafael Point in 1998 and 1999, but mainly close to shore in probable mysid-feeding locations (Meier, in preparation). The whales' use of Rafael Point is unknown for 1991 and 1992, but the area was not exploited in 1993. In 1994 Rafael Point and Siwash Point were subjected to heavy use by the whales, and in 1995 foraging at these locations was somewhat less intense. Ahous Bay was used extensively by foraging whales only in 1991, while Grice Bay was used in 1995 after a hiatus of ten years, and again in 1996 (Dunham, 1999) and 1999 (Author pers. obs.).

If seasonal foraging patterns exist, it may be necessary to assess each site individually for a longer period of time than that covered by this study before the interactions between the various patterns can be interpreted. In order to better interpret the relative profitability of foraging locations, it is also necessary to obtain information about the foraging range of gray whales, since comparisons with foraging locations outside the study area could be affecting the whales' foraging decisions. A site-fidelity study using photo-identification has established that foraging whales remain in the study area for periods of time which vary from a few days to a few months (Tombach, in preparation). Once complete, the site-fidelity study should provide some valuable information which increases understanding of the whales' medium- and coarse-scale foraging decisions.

Depth does not appear to be a primary factor affecting the distribution of gray whales within the study area. Figures 28 and 29 show that their within-season use of Cow Bay does not follow the predicted shallow-to-deep progression. Since this is a departure from the suggested energetically efficient pattern, it is possible to interpret the whales' behaviour in terms of vessel-related behaviour modification. However, this interpretation is not satisfactory, since the whales do not escape vessel contact by feeding in different parts of Cow Bay. The most likely explanation is that whales ignore depth within a site, and treat each site as one patch, or as a small number of patches if more than one prey type is present.

Chapter 6: CONCLUSIONS

Gray Whale foraging behaviour in Clayoquot Sound varies with foraging location, and to a much lesser extent with vessel activity. The variation due to vessel activity is statistically significant, but is of such low magnitude that its biological significance is questionable.

The majority of the variability in the feeding behaviour of the gray whales in Clayoquot Sound cannot be accounted for by the factors considered in this study. However, prey type and water depth both appear to have an effect on the whales' ventilation patterns. Whales feeding on planktonic prey show significantly higher ventilation rates than whales feeding on benthic prey; whales foraging in deep water show longer feeding dive durations than whales feeding in shallow water on the same prey. In most cases the effect of prey type appears to be somewhat stronger than that of depth.

There is interaction between the effect of location and that of vessel traffic on the whales' behaviour. This means that the whales are affected by vessels differently in different locations. There is some evidence that the effects of vessels are stronger in shallow locations than in deep, but the overall picture is complex.

The whales in this study were observed for 280 hours under a variety of conditions. This large and comprehensive behavioural sample enables the flexibility and diversity of gray whale foraging behaviour to be measured more fully than it has been in other studies. Gray whale behaviour changes in response to prey type, feeding depth, and possibly other factors have not been identified, and the overall picture is more complex than was previously thought.

Gray whales are known to be diverse and opportunistic foragers, but this study and Dunham's (1999) provide evidence that they can subsist on non-benthic prey to a much greater extent than shown by earlier studies, sometimes feeding on planktonic prey for the majority of their feeding season. Others switched prey within seasons or from day to day. Again, this shows a level of behavioural flexibility that gray whales were not thought to possess. Instead of concentrating their foraging activities in dense prey patches within feeding sites, the data seem to indicate that the whales treat each feeding site as one patch. This means that their foraging decisions are likely to occur on a coarse scale rather than a finer, within-site scale. A follow-up study in which the whales' activity and the prey distribution are measured contemporaneously over the course of one or more feeding seasons would enable more detailed assessment of the tradeoffs involved in the whales' foraging decisions.

The wide variety - spatially, temporally and behaviourally - of foraging strategies shown by gray whales in Clayoquot Sound between 1993 and 1995 indicates that it is difficult to predict which sites will be important to the whales in any given year. The implications of these findings are that all the sites in Clayoquot Sound for which there are records of gray whale foraging have ecological importance for the species. Protection of all such sites, and others outside the immediate study area where the whales may go to supplement their dietary intake, should be a management goal for this region. Activities which cause disturbance of the sea floor and the introduction of pollutants should be avoided in the areas where gray whales feed. Above-tidal regions should also be protected from disturbance, since the characteristics of the land (particularly soils and vegetation) are intimately tied to the health of the shallow subtidal regions in which the Clayoquot Sound gray whales forage (Karagatzides, in preparation).

Although there have been studies concerning whale energy budgets (Dolphin, 1988; Sumich, 1983), this is the most comprehensive study to attempt to describe whales' spatial foraging behaviour in relation to vessels. Patterned after Garner's (1994) exploratory study, the approach has the potential to be a powerful tool in assessing the impact of whale-watching boats on feeding gray whales. One of the most common concerns of whale-watching patrons is the industry's potential for disturbance or harrassment of the whale (Duffus, 1988). Most whale-watch operators are also highly anxious to avoid stressing whales, not least because their livelihood is dependent on the continuing presence of the whales in an area easily accessed from the tourist centre. More information is urgently needed on how boats should behave to achieve non-damaging use of the whale resource (Duffus & Dearden, 1992). The application of quantitative monitoring techniques based on assumptions of optimality may be the much-needed breakthrough in providing a practical basis for guiding or regulating boat behaviour.

The changes in the whales' behaviour correlated with the presence of whale-watching vessels are small relative to the changes correlated with foraging site. Although the whales' diving behaviour was statistically different in the presence of whale-watching vessels than in their absence, the extremely small magnitude of the differences calls into question whether statistical significance necessarily implies biological significance. Isolated incidents of disturbance occur every so often, but the data do not show a clear, continuous disturbance effect of the kind feared by the operators and passengers of the whale-watching vessels.

The possible effects of "agents of disturbance" such as whale-watching vessels can be expected to fall somewhere along a continuum ranging from "no significant change" to "biologically significant behavioural change" (see Figure 35). In order to assess "biological significance," it is necessary to find some way

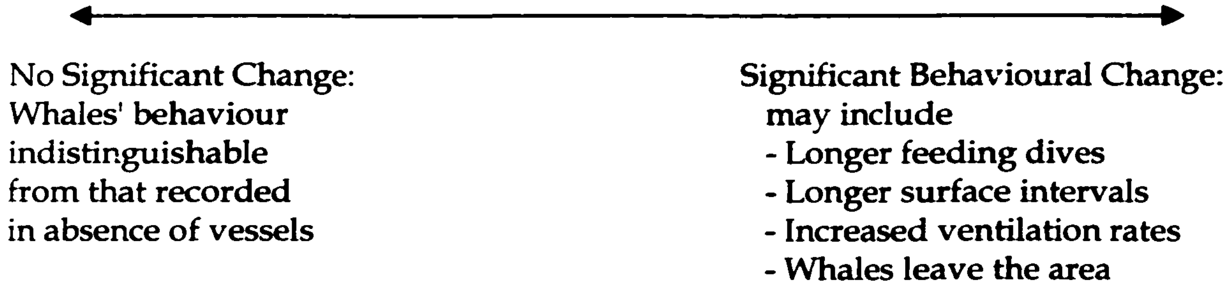


Figure 35: Theoretical Representation of Possible Effects of Disturbance on Gray Whale Foraging Behaviour

to measure the long-term health of the whales which forage in Clayoquot Sound. Site-fidelity studies which pinpoint certain whales which return to the area year after year (Tombach, in preparation) may lead to a solution to this problem.

While the inferior prey density in Clayoquot Sound represents a disadvantage for foraging gray whales, the relatively shallow depth at which the prey is found, and the reduction in travel time from the breeding grounds, represent advantages. It is not known why these particular whales tend to forage off Vancouver Island, rather than making the migration the entire distance to the primary and secondary feeding grounds. The possibility exists that the whales which summer in Clayoquot Sound are not representative of the entire population of gray whales, and caution should be used when extrapolating the results of this study to the general population. These whales may represent a relic population from a time during a past glacial maximum when the current "tertiary" feeding grounds were actually the primary - or only - feeding grounds available to them (Sumich, pers. comm. 2000).

If the whales are not changing their behaviour "significantly" (in biological terms) in the presence of whale-watching vessels, there are two possible explanations for this. The first is that our assumptions about the whales' energy

currency are flawed and that, as a result, we are missing something from our measurements. Further study of the gray whales' prey and habitat choices (Dunham, 1999; Tombach, in preparation; Meier, in preparation) may make it possible to determine more accurately what to measure. It is possible that the effects of stress could be physiological rather than behavioural, in which case it would be highly informative to compare such indicators as heart rate or the levels of certain hormones in the presence and absence of vessel traffic. There are serious practical problems with this type of approach, including the lack of accessibility of large cetaceans for the installation of monitoring devices, and the fact that such an installation would be likely to itself be a source of stress.

The second, and simpler, explanation is that the whales are not disturbed by whale-watching vessels. Until further data are forthcoming, it makes sense to recommend that the whale-watching vessels continue to adhere to their current guidelines, particularly in the shallower of the feeding areas. If possible, these guidelines should be elevated to the level of regulations. There are numerous benefits to be gained from having relevant, meaningful whale-watching regulations in place. The current self-policing system which exists among whale-watching vessel operators in Clayoquot Sound is vulnerable to selfish, profit-motivated business owners who encourage their drivers to approach the whales more closely than do the current group. In addition, the aforementioned educational potential of the whale-watching experience would be greatly increased if the public is shown a natural world to be respected rather than a sideshow. In addition, if whale watching can become completely "non-consumptive," causing no ill effects to the resource it uses, all involved can benefit: whales, tourists, operators and other beneficiaries of the industry. Finally, if a workable system of regulations can be developed, it may serve as an example to other "ecotourism" industries and encourage them to design and implement similar regulations.

There is some cause for concern that many small short-term behavioural changes, such as the small increases in feeding dive duration observed in this study, may add up to a larger long-term impact on the whales. Continued monitoring of their site fidelity and spatial use of the study area would be useful in assessing whether Clayoquot Sound continues to be a profitable foraging location for them.

As is often the case with studies of natural systems, controlled conditions are difficult to approximate. This study's assessment of the potential of vessels to influence whales is limited to recording the number of boats present. There is no doubt that the study of whale/boat interactions would be greatly enhanced if it were possible to quantify the actions of vessels rather than making a simple count of the boats in the area. The measurement of underwater motor noise would initially seem to be a possible solution, but due to the nature of sound propogation through water, the sound produced by a given configuration of boats would vary widely depending on the boats' (and whales') position in the bay, with the ocean conditions, and with the other variables that influence sound propagation. The problem of how to measure vessel activity in more detail is one to which considerable energy could be devoted in the future.

The behavioural changes detected by this study which are associated with whale-watching vessel numbers are interpreted as being biologically insignificant to the whales. Since other, biologically significant changes associated with other external factors were, by comparison, easily found using the same methods, the data presented here can be seen as baseline data for a situation in which gray whales are effectively not impacted by whale-watching vessels. Another study of the same type, after a period of ten years or after the number of whale-watching vessels in the water has increased measureably, would be a valuable follow-up to the baseline study. It is likely that whale-watching helps to foster public sympathy towards whales; therefore, in a sense, whales and whale-watching are interdependent. Recent years have seen tremendous growth in the whale-watching industry on Vancouver Island and elsewhere. In the absence of quantitative studies describing whale-vessel interactions, this study serves as a starting point for further exploration of this complex issue.

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Appendix 1

(a) Hours of research effort for each site and year of the study.

	Ahous Bay	Cow Bay	Rafael Point	Siwash Point	Grice Bay	Total:
1993	11.5	87.5				99
1994			39.5	4.5		44
1995	22	62.5	7.5	19.5	17.5	129
Total:	33.5	150	47	24	17.5	272

(b) Number of Dive Cycles recorded for each site and year of the study.

	Ahous Bay	Cow Bay	Rafael Point	Siwash Point	Total:
1993	80	1413			1493
1994			1062	62	1124
1995	465	766	224	118	1573
Total:	545	2179	1286	180	4190

Appendix 2

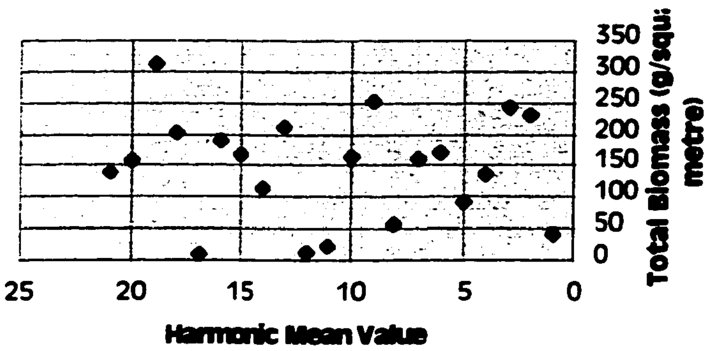
The raw data collected and used in this study is archived at the University of Victoria Whale Research Laboratory. Please contact the Whale Research Laboratory with any requests to obtain this data:

Whale Research Laboratory
University of Victoria
Department of Geography
P. O. Box 3050
Victoria, B. C. V8W 3P5
Canada

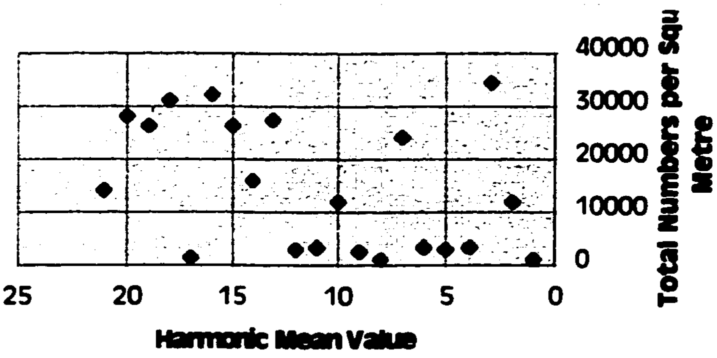
Appendix 3

Whale Activity and Prey Characteristics

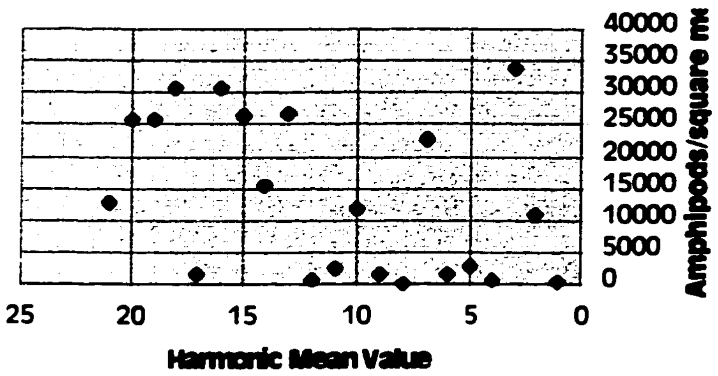
These graphs show the Harmonic Mean as a measure of whale activity at each of the sites where benthos was sampled in Ahous Bay in the summer of 1995. No correlations were apparent between whale activity and prey characteristics.



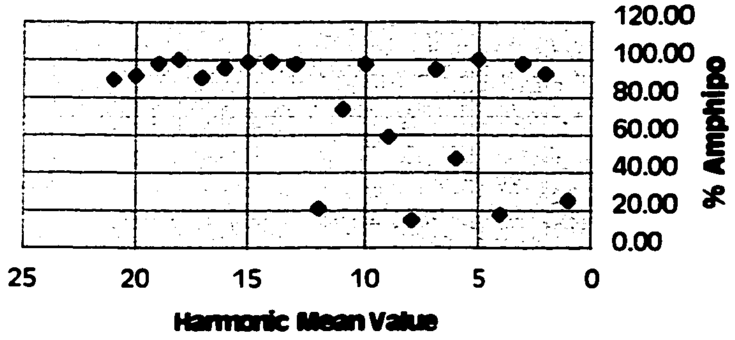
a. Total Biomass (grammes per square metre) plotted against harmonic mean activity value



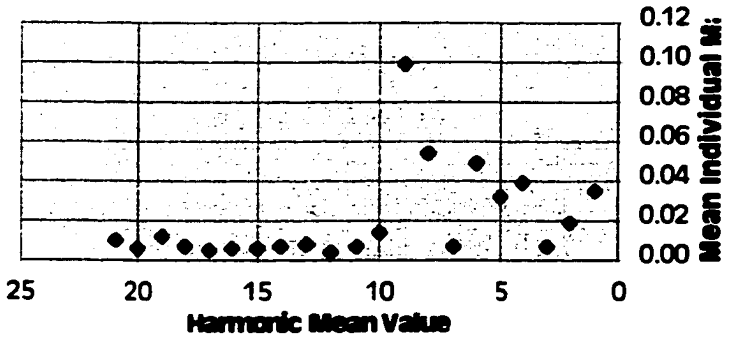
b. Total number of individuals per square meter plotted against harmonic mean activity value



c. Total number of amphipods per square meter
plotted against harmonic mean activity value.



d. Percentage amphipods
plotted against harmonic mean activity value



e. Mean individual mass of organisms
plotted against harmonic mean activity value