An Exploratory Investigation of Gray Whale (*Eschrichtius robustus*) Spatial Foraging Strategy and the Effect of Vessel Traffic

by

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ABSTRACT

Rapid expansion of the whale-watching industry in Tofino, British Columbia has raised concerns over the effect that increased vessel traffic may have on gray whale (*Eschrichtius robustus*) behaviour. This thesis studies the possible influence that vessel traffic may have on the spatial utilization patterns of summering gray whales in Clayoquot Sound near Tofino. The thesis formulates a spatial foraging model based on optimal foraging theory in patches and compares this with field observations. Observations made use of surface sightings of feeding whales resulting in a series of points. Exploratory analysis was conducted because of data uncertainty and a lack of a suitable sample size. The thesis concludes that observed gray whales appear to feed in a manner similar to the spatial foraging model and that these whales showed little evidence of spatial variability associated with the presence of vessel traffic. The thesis also demonstrates the effectiveness of exploratory analysis in evaluating spatial patterns in a behavioral study where data is limited.

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This work is dedicated to the memory of ***Gil Sherwin***
for your inspiration and kindness

Chapter 1

Introduction

"Considering the intelligence of cetaceans, and the gray whales' experience with the human race, I don't feel it is unreasonable to believe that these whales either noticed that recent generations of their kind were not being harassed in the eastern Pacific, or else this lack of harassment resulted in the loss of all memory of harassment at the hand of humans."
Roy Nickerson, The Friendly Whales, 1987.

"In 1613, when Galileo published the first telescopic observations of Saturn, word and drawing were as one. The stunning images, never seen before, were just another sentence element.

Saturn, a drawing, a word, a noun.

The wonderful becomes familiar and the familiar wonderful."
Edward R. Tufte, Envisioning Information, 1990.

"Admiral, there be whales in here. . .", *Star Trek IV: The Voyage Home, Paramount Pictures, 1986.*

1.1 Introduction

Non-consumptive wildlife-oriented recreation has expanded rapidly over the past few years as human evaluation of wildlife changes from resource extraction to a more benevolent appreciation for nature. Much of the recreation takes the form of wildlife viewing within the animal's natural habitat. New economies have been created based on providing services for people who wish to view wildlife. As with many new industries, wildlife viewing services have expanded exponentially as they attempt to catch up to the increasing demand for these services. As these activities continue to expand, there is increased concern over the impact that frequent human interaction with wildlife has on the well-being of the animals. This concern is not, however, totally because of a selfless concern for wildlife. Wildlife viewing industries are very much dependent on the availability of the resource (the wildlife) and an adequate demand for their services (wildlife viewers). Given a high demand for their services, wildlife viewer services have a self-interest in ensuring that wildlife remains available.

Tofino, British Columbia, Canada is an example of a tourist based community that has undergone rapid expansion of its wildlife viewing industry. Increased interest in observing whales in their natural habitat and an abundance of gray whales (*Eschrichtius robustus*) and potential sightings of killer whales (*Orcinus orca*) have created a thriving whale-watching industry in the community. Concern over this rapid expansion has led many to speculate as to the effect that increased human activity will have on the resource base.

Gray whales are the main attraction offered by the wildlife viewing operators in Tofino. The town's proximity to northward migration routes and availability of summer feeding grounds combine for an adequate supply of whales for viewing. Summer resident whales are subjected to the most intense human contact as the summer tourist trade peaks between July and August. Often fewer than ten whales will be subjected to periodically constant vessel traffic interaction during daylight hours. The industry itself is unregulated although there are guidelines established by the federal government concerning methods of approach and observing whales (Canada 1990).

In the interest of maintaining a healthy whale viewing industry for Tofino, it is vital that whales remain nearby. To ensure this, the impact of vessel interactions on the whale's normal spatial behaviour must be investigated. Identification of alterations in the whale's spatial utilization patterns in the presence of vessel activity can lead to the development of management strategies that might help avoid displacement of the resource.

Traditionally, behaviour studies have been undertaken to assess the impact of human activity on animals in general and whales in specific. This approach, however, is problematic for two reasons. Firstly, there is the danger that apparent animal behaviour can be misinterpreted by the observer resulting in incorrect conclusions about the impact. Secondly, marine mammal behaviour is difficult to interpret because of the lack of ability to observe the animal completely. Analysis of the whale's spatial utilization may provide a more objective approach to assessing human-whale impact but it, too, requires some level of behaviour interpretation.

Many studies have considered changes in terrestrial animal spatial utilization patterns due to human activity (eg. Dorrance *et al.* 1975, MacArthur *et al.* 1966, McLellan & Shackleton 1989, Rost & Bailey 1979) but few have considered similar impacts on whales (Baker *et al.* 1983, Malme *et al.* 1983, Myrberg 1990a). A lack of understanding of whale behaviour and difficulty in observation has contributed to this gap in wildlife impact assessment. Fortunately, much is known of the behaviour of grey whales (eg. Nerini 1984 for a review) that enable a model of whale spatial behaviour to be developed that can then be used to assess the impact of vessel traffic.

The following study considers the impact of vessel traffic and the effect that it might have on the gray whale's spatial foraging patterns. A generalized model of spatial behaviour is described then compared to observations made of foraging whales. I hypothesize that whales will exhibit behaviour consistent with the foraging model with and without the presence of boats. Deviations from the model, in association with the presence of vessel traffic, may be an indication of an effect on whale spatial foraging patterns from boats.

The underlying method makes use of exploratory analysis to represent the relationships between whale and boat interactions. This approach is justified given the inherent problematic nature of the data and the dynamic character of the habitat that the whales are found in. The approach is purposefully generalized given these difficulties. To give formal structure, hypotheses are generated and are used to guide the research by adjusting assumptions and identifying relationships. The subsequent goal is to identify further avenues of research that might lead to a better understanding of gray whale spatial behaviour and of the relationship between humans and whales.

The following thesis proceeds in four parts. The first surveys the literature on gray whale behaviour and formulates a spatial foraging model. The second and third sections outline the research method and results. The final section evaluates the results and discusses the implications for the management and the ultimate sustainability of the Tofino whale viewing industry.

Chapter 2

Background

2.1 Introduction

Gray whales draw the attention of many western Vancouver Island whale watchers through June, July and August since whales are generally easy to find during this period and since they have a reputation for exhibiting friendly behaviour towards boats (Nickerson 1987). This behaviour might include close encounters where people have the opportunity to touch surfaced whales. Recent increases in the popularity of whale watching in Clayoquot Sound off western Vancouver Island has prompted concerns over potential effects that vessel traffic may have on the normal behaviour of the whales. Most evidence relating to boat induced effects have been largely anecdotal and inconclusive (i.e., Reeves 1977 & Watkins 1986). Researchers have attempted to assess boat influences on behaviour through surface observations during vessel encounters (Baker *et al.* 1983) and by studying boat noise as a possible influence (Myrberg 1990a).

Absent from the published literature is a consideration of the relationship of the whales' spatial utilization patterns and the influence of vessel activity. Alterations in these patterns may range from interruption of short term feeding activity to whales moving to different feeding grounds. Such changes in spatial behaviour could have a potential effect on gray whale feeding efficiency. This might come about by altering the amount of time devoted to foraging or by increasing the costs of foraging through increased avoidance behaviour.

In the following section, the literature on gray whale feeding is summarized in order to provide a link to foraging theory that can then be used to assess the spatial behaviour of summering whales in Clayoquot Sound, British Columbia. The scale being considered is local, that is, *within* feeding patch behaviour versus *between* patch or migratory behaviour. The scale is argued to be appropriate given the nature of the general feeding behaviour, vessel traffic patterns and ease of data collection. The following discussion consists of three main parts. First, a summary of observed feeding behaviour of gray whales will be presented. Second, potential effects of human activity on whale behaviour will be outlined. The final part summarizes foraging theory and develops a spatial foraging model. The model is then applied to observed gray whale foraging patterns, the results of which are contained in the remaining chapters.

2.2 Literature Review

The gray whale's primary activity during the summer period is feeding (Darling 1977a; Darling 1977b; Guerrero 1989; Hatler & Darling 1974; Murison *et al.* 1984; Oliver *et al.* 1984). A considerable amount of research has been done on the feeding behaviour of the whales in addition to the types of prey that are consumed. The following discussion outlines the feeding characteristics of gray whales, in particular, where they feed, how they feed, and what they feed upon.

2.2.1 Part I - The Gray Whale Foraging Activity

Kim and Oliver (1989) summarize the geographical extent of gray whale foraging. They classify the feeding areas into three zones including the primary, secondary and tertiary feeding grounds. The primary and secondary feeding grounds are located in the Bering and Chukchi seas while the tertiary zone is found from waters off Alaska to Baja California (Kim & Oliver 1989). They also note that the feeding grounds off Vancouver Island are the most well developed south of the Bering Sea but are also significantly smaller than the primary and secondary grounds.

Researchers have not specifically addressed why some whales choose to exploit the feeding grounds off Vancouver Island rather than continuing on to the more productive Bering and Chukchi seas. It is believed, although not adequately documented, that the same individual whales return to the same secondary feeding sites year after year (Darling 1977a). Kim and Oliver (1989) note that as the gray whale population has been increasing, the occurrence of whales in the tertiary feeding grounds has also increased in frequency. This last point alone may indicate a response to increased intraspecific competition in the primary feeding areas. Research in ecology has shown that animals faced with increased intraspecific competition may disperse to other habitats to avoid the increased stress (Chepko-Sade & Halpin 1987).

Foraging gray whales have been observed feeding on a variety of prey. However they seem most often to make use of tube-dwelling amphipods and mysid crustaceans (Darling 1977a; Darling 1977b; Blokhin 1986a; Guerrero 1989; Kim & Oliver 1989; Johnson & Nelson 1984; Moore *et al.* 1984). Whales in and around Clayoquot Sound appear to feed frequently on benthic infauna (Oliver *et al.* 1984) and swarming mysid crustaceans (Oliver *et al.* 1984; Guerrero 1989). Guerrero (1989) also notes that herring eggs and small fish also are consumed (Guerrero 1989).

Gray whales appear to use an assortment of methods for exploiting prey. Initial research suggested that, when feeding on benthic organisms, whales scooped up large amounts of sediment and filter the prey through their baleen. Rice and Wolman (1971) claimed that the whales disturb bottom sediment first then feed on prey in the resulting turbid water. In the only study on a captive gray whale, Ray and Schevill (1974) documented suction feeding where the whale would turn on its side and suck squid from the bottom of the observation tank. In studies of gray whales in the Bering Sea and off the coast of Vancouver Island Oliver *et al.* (1983) observed feeding activity similar to that of the Ray and Schevill study. In addition, diver observations suggested that the primary sediment disturbance by the gray whales was by their tails contacting the bottom while feeding.

Since it is difficult to observe whales underwater most observations have been made from the surface, although some researchers have made use of divers, cameras and sonar with some success (Dolphin 1988; Johnson & Nelson 1984; Kim & Oliver 1989; Kvitek & Oliver 1981; Oliver *et al.* 1984; Oliver & Kvitek 1984, Avery & Hawkinson 1992). Surface respiration and swimming behaviours have been documented by several authors (Carl 1968; Gill & Hall 1983; Guerrero 1989; Mallonee 1991; Sumich 1983; Wursig *et al.* 1986). An early quantitative observation of diving behaviour was mentioned by Carl (1968) where a gray whale was observed feeding on benthic organisms for several hours. Results showed a succession of dives made up of a series of short submergences followed by one of longer duration. The longer dive usually lasted about twice as long as the preceding ones and was followed by two or more blows before re-submerging (Carl 1968). In another study, whales were observed having shorter surfacing times, shorter dive times and fewer blows per surfacing when feeding than at other times (Wursig *et al.* 1986). Whales were also noted to have an obvious association between increasing blow rates and feeding at greater depths (Houston & Carbone 1992). In a detailed observation of several whales off the coast of northern California, Mallonee (1991) documented the occurrence of 50 summering whales noting several different behaviours as well as locomotion associated with feeding.

Observations of gray whales feeding on mysids and other pelagic prey show that they employ engulfing and surface skimming methods (Nerini 1984). Murison *et al.* (1984) observed gray whales feeding on mysids off Vancouver Island. They concluded that different behaviour patterns can be expected when exploiting pelagic prey. In particular, Guerrero (1989) noted that whales change position little when exploiting mysids while analysis of respiration rates implied greater energy expenditures to capture this prey than when exploiting benthic organisms. She also noted that, despite the higher respiration rates for capture of mysids, rates were still lower than those observed when the whales were travelling.

Once gray whales begin feeding, it appears that few natural extrinsic factors, outside of variability in patch quality, affect their behaviour. Killer whales (*Orcinus orca*) are the gray whale's only natural predator. Transient killer whales have been known to harass, attack and, although rarely observed, kill gray whales (Guerrero 1989; Burrage 1964; Leatherwood 1974; Jefferson *et al.* 1991). Researchers off Vancouver Island have observed that gray whales will leave a feeding area if killer whales are present (Darling 1977a; Guerrero 1989). Gray whales may also employ hiding tactics by using shallow water, kelp beds, or the surf zone as protection (Burrage 1964; Jefferson *et al.* 1991).

In summary, most gray whales migrate to the northern feeding grounds in the Bering and Chukchi seas while some spend summers feeding off Vancouver Island and other areas along the west coast of North America. Primary feeding prey exploited by whales in Clayoquot Sound appears to be dense mats of amphipods and free swimming mysid swarms. While feeding, the whale's dive patterns tend to be regular with durations largely dependent on dive depth. Finally, if confronted by natural predators, gray whales will often employ an avoidance strategy that might include hiding in shallow water or kelp beds or by leaving the area where the threat is perceived.

2.2.2 Part II - Human Influences on Feeding Behaviour

The evidence pertaining to the influence of human activity on gray whales and whales in general is largely inconclusive. Difficulties in observing and interpreting whale behaviour make assessment problematic. Studies of terrestrial animals appear to have had greater success at evaluating human influence because of the greater ease of observation and definition of habitat conditions. The following section firstly considers some of the literature pertaining to terrestrial animals then secondly considers evidence relating specifically to gray whales.

Many animals have shown tendencies towards habituation of human activity. McLellan and Shackleton (1989) showed that grizzly bears (*Ursus horribilis*) tend to respond less to humans near places where human activity is relatively high (i.e. near roads or towns). They also noted that in areas where bears were not accustomed to human activity there was a greater chance of the bear to respond quite strongly (aggressively or greater avoidance effort) to an encounter. MacArthur *et al.* (1982) also found that mountain sheep (*Ovis canadensis*) respond little to existing human activity but that their sensitivity changes depending on how the animals were approached (i.e. from up slope rather than down slope). Schultz and Bailey (1978) found that elk (*Cervus elaphus*) adapted to human activity by minimizing encounters with humans without any apparent affect. Their study failed to show any statistically significant relationship between abundant tourist activity and normal behaviour, distribution and movements of elk.

All of these studies have consistently indicated a difference in animal reaction to humans between areas where hunting is permitted and areas where hunting is restricted.

Animals appear to be more sensitive to human activity where hunting is prevalent.

Animals also appear to be less responsive to human activity where the habitat allows escape. McLellan and Shackleton (1989) noted that grizzly bears in open areas have a stronger avoidance response to humans than when encountered in covered areas. Similar behaviour was noted in sheep (MacArthur *et al.* 1982) and elk (Schultz and Bailey 1978).

It is unclear how much of the human activity that takes place near and around gray whale habitat influences their behaviour. Recent concerns have focused on the effects of oil spills, noise from oil exploration and exploitation activity, fishing activities, and vessel traffic. Most of the studies conducted on the reaction of gray whales to oil spills have been associated with the Nestucca oil spill off Vancouver Island on December 23, 1989 (Harding & Englar 1989). In these studies, little evidence was found of ill effects from oil on migrating whales (Darling 1989a; Darling 1989b; Harding & Englar 1989). However, this may have been partly due to winter storms breaking up most of the oil before whales passed through the area (Darling 1989a).

Geraci and St. Aubin (1985) considered various effects of oil on many marine mammals including gray whales. They considered many impacts including fouling of whale baleen from various grades of oil. The study found that the degree of fouling varied between species of baleen whales and that gray whales appeared the least effected due to the broad spacing of their baleen plates (Geraci & St. Aubin 1985). The authors also found that plate spacing contributed to rapid cleansing during flush tests.

The major risk to gray whales occurs from the potential for ingesting sufficient amounts of oil while feeding on oil contaminated substrate (Baird & Guenther 1991). Several authors have indicated that despite this risk, marine mammals demonstrate abilities to detect and avoid oil (Baird & Guenther 1991; Geraci & St. Aubin 1985; Geraci *et al.* 1983; Smith *et al.* 1983).

Beyond potential influences from oil, noise from oil production and other industrial activity can effect whales. Gray whales, indeed all marine life, are subject to varying degrees of noise from different sources. The inherent background noise of the sea, both biological and non-biological, can affect how well an animal can hear and communicate (Myrberg 1990a). Myrberg (1990b) shows that certain levels of noise from oil drilling activity, seismic noise, ship traffic and other similar sources of industrial noise can reach levels where a whale will avoid noisy areas or exhibit aggravated behaviour.

Results of studies conducted on the effects of vessel traffic noise on whales vary among researchers. Dalheim *et al.* (1984) observed that certain frequencies of boat noise seem to attract gray whales giving an impression of "friendly" behaviour. Where this behaviour was observed, sound signatures were in frequency ranges that the whales use to communicate (below 2 kHz). Other effects of vessel traffic noise are largely anecdotal. In an analysis of 25 years of minke (*Balaenoptera acutorostrata*), finback (*Balaenoptera physalus*), right (*Eubalaena glacialis*), and humpback (*Megaptera novaeangliae*) whale observations in Cape Cod waters, Watkins (1986) found varying reactions to noise specifically when frequencies ranged from 15 Hz to 28 kHz. Most negative reactions to sounds occurred during sudden changes in acoustic intensity from nearby sources. In particular, " . . . reactions to sounds occurred when whales were within 100 m of the sources, or when sudden increases in received sound levels were judged to be in excess of 12 dB, relative to previous ambient sounds " (Watkins 1986: 255). Watkins also showed that when noise was constant whales either ignored the source or exhibited attraction to the noises depending on source frequencies. Research by Richardson *et al.* (1985) suggests that bowhead whales (*Balaena mysticetus*) react to sudden increases in boat motor and aircraft noise but only for very short periods without any apparent long term changes in whale behaviour. Baker *et al.* (1983) found that humpback whales exhibited significant movements away from the path of vessels at distances of about 8000 metres. However, the greatest tendencies to move away occurred when vessels were much closer.

The effects of direct vessel traffic other than noise are less substantiated. Reeves (1977) showed that several studies conducted on gray whale and vessel traffic interactions off California and Mexico have been inconclusive. Where negative effects were thought to have occurred one year, they failed to repeat themselves in others. Watkins (1986) implies that whales seem to ignore boat traffic unless a collision is apparent between the whale and the vessel. Reeves (1977) mentions that in the wintering grounds of Baja California gray whales were subject to purposeful harassment by angry Mexican fishermen that feared the whales were eating their fish stocks. Despite harassment, normal fishing boat activity does not appear to disturb the whales (Reeves 1977). Although Baird *et al.* (in press) in a recent survey of gray whale mortality due to fishing off the British Columbia coast, estimated that approximately two gray whales per year, representing 27% of the total estimated gray whale mortality in the area, are killed as a result of entanglement in fishing gear.

To summarize, terrestrial animal studies have shown that animals tend to become habituated to constant human activity. Where animals rarely encounter humans, they incline to react more strongly to an encounter. The degree to which an animal will react appears dependent on the speed and intensity of approaching noise sources and the availability of habitat in which to hide. Studies of whales are less conclusive because of difficulties in observation.

2.2.3 Part III - Optimal Foraging Theory and the Gray Whale

In order to assess the potential affect that vessel traffic might have on gray whale foraging behaviour, it is necessary to formulate a theoretical representation against which to compare observed behaviour patterns. The following section attempts to develop a foraging model based on optimal foraging in patchy environments as described by Charnov (1976). The assumption underlying this study of gray whales is that whales feed optimally and thus will display characteristics consistent with optimal foraging theory. This assumption is based on previous testing of the theory on other animals showing optimal foraging theory to be an adequate method of describing foraging behaviour (Emlen 1968; Schoener 1971; Krebs & Davies 1987; Pyke *et al.*, 1977; Norberg 1977; Stephens & Charnov 1982; Kamil & Sargent 1981; Dolphin 1988; Pianka 1988). Given this key assumption, the following discussion focuses on the spatio-temporal aspects of foraging theory as a method of assessing whale movements and thus the potential influence of boats on these movements. The section concludes with the formulation of an informal model of gray whale spatial foraging behaviour.

In virtually all studies of optimal foraging theory, the basic hypothesis is that ". . . animals forage to maximize their Darwinian fitness (i.e., contributions to the next generation) " (Pyke 1984:7). Subsequently, researchers have explored the nature of foraging behaviour in animals based on assumptions regarding the 'currency' of fitness. This currency is usually net energy gain although other researchers have shown that net gain of particular nutrients can also be considered a currency for maximizing fitness in some animals (Rapport 1971; Pulliam 1974; Lendrem 1986).

The strategies an animal employs in foraging, however, may not be directly linked to the desire to maximize the net benefit. For example, an animal that is at risk of predation may wish to avoid predation before foraging given that the risk of being killed is higher than the risk of starvation. Since foraging opportunities may often be limited, the types of food that the animal will choose are often higher in currency value (i.e., energy or nutrients) than if it were not at risk. Conversely, an animal that is not at risk of predation but is at risk of starvation (i.e., usually an animal incapable of storing enough energy or nutrients) will spend greater amounts of time foraging and be less concerned with particular food value. How an animal exploits a feeding patch will be largely dependent on the strategy it needs to employ to satisfy the considerations of the risk of predation or starvation.

Once an animal has located a patch, certain *within* patch behaviour should occur that minimizes the cost of exploitation, all other factors being equal. Pyke *et al.* (1977) indicate that extensive studies in entomology can be applied to the patch behaviour of other animals (Laing 1937, 1938; Putnam 1955; Mitchell 1963; Chandler 1969; Richerson & Borden 1972 in Pyke *et al.* 1977). Generally, if patch quality is not known then meandering will take place until prey is found. Once found, an animal will increase its turning rate to remain within the area of the prey (Pyke *et al.* 1977).

Outside of risk of predation, how long an animal stays within a patch is generally dependent on the net rate of return of energy or nutrients. In particular, when the density of prey gained from a patch falls below a certain level, an animal will tend to leave for a more profitable patch or switch to a secondary preferred food type. Charnov (1973, 1976 *et al.*, 1976) developed a model aiming to predict how an animal will decide to move or switch based on declining returns of foraging related to resource depletion. As an animal exploits a patch the net gain will slowly decline as the prey density becomes depleted. Eventually the animal will leave the patch when the net rate of energy gain is equal to or lower than what it would gain from the next closest patch. This point is known as the marginal value, explicitly defined as the point where " the marginal capture rate in the patch drops to the average capture rate for the habitat " (Charnov 1976: 132). In patchy environments, distance to the next patch is an important consideration since the net rate of return of another patch is reduced in proportion to the distance needed to travel to the new patch.

In gray whales and many other diving animals, the costs and potential benefit of switching to another patch is not limited to horizontal travel. Increased travel costs are also associated with vertical movements within the water column. This factor limits whales to the depth that they will feed since more energy is required to exploit deeper prey. Kramer (1988) adapts Charnov's 'marginal value theorem' (Charnov 1976) to develop models to predict energy returns in diving animals. He concludes that when the model is applied to diving animals that:

> . . . [the] principle predicts that with increasing distance to feeding sites or other areas of resource gain, the bout lengths of surface time and dive time will increase, as will percent time at the surface. . . (Kramer 1988:89).

In a further rendering of this model, Houston and Carbone (1992) showed that the relationship between depth and time spent in the foraging patch is not linear as implied by

Kramer (1988). They concluded that:

> . . .the optimal time for an animal to remain in a foraging area increases with increasing [depth] when [depth] is small but decreases with increasing [depth] when [depth] is large (Houston & Carbone 1992:263).

This model differs from Kramer's (1988) in that efficiency of oxygen consumption (net rate of energetic gain) is considered in addition to the proportion of time spent in the foraging areas (Houston & Carbone 1992).

In an example of diving efficiency in humpback whales, Dolphin (1988) has noted that the whales exhibited increased surface respiration in deeper water. He concludes that the deeper a whale travels the longer it must stay at depth to overcome the energy lost from the dive and that the optimal depth is a result of the proportional return from foraging at that depth (Dolphin 1988). Houston and Carbone (1992) noted that this conclusion may not be entirely valid since if a:

> . . . forager has knowledge of the distribution of prey and does not search while descending, the forager should always forage at the best depth, and variation in foraging depth will reflect variation in the best depth, perhaps as a result of changes in prey availability or changes in foraging costs as a result of environmental conditions (Houston & Carbone 1992:261).

Although the tendency for an animal should be to minimize the associated cost with exploiting its prey, it is not precluded from leaving a foraging patch for reasons other than loss of patch fidelity or increased costs of capture. Pyke *et al.* notes that:

> If the distribution of a resource does in fact change in space and time it may well be advantageous for an animal to spend time 'exploring' or 'being curious' to the detriment of immediate foraging efficiency, if the information so gained will enable it to switch its behaviour rapidly as conditions change (Pyke *et al.* 1977 in reference to Royama 1970).

Forkman (1991) in laboratory experiments with gerbils (*Meriones unguiculatus*) found that, when the availability of preferred food types was abundant, easily attainable and spatially stable, the gerbils would spend time searching for other food sources. When the conditions were changed so that food availability was less predictable (unpredictable quality, location, and ease of attainability), the gerbils became less explorative and more exploitative. Forkman also notes that behaviour will change based on whether an animal is satiated. He postulates that a hungry animal will tend to feed optimally while one that is satiated will tend to be more explorative thus feeding less optimally.

Little published work has been done on the application of optimal foraging theory to gray whale behaviour. Dolphin (1988: 2432) states that " . . . despite numerous descriptions of baleen whale feeding behaviour, few attempts have been made to integrate these observations with existing foraging theory. " Difficulties exist in determining energy and nutrient budgets for whales in addition to estimating the distribution and abundance of their prey given the lack of baseline studies and the nature of the habitat. Nevertheless, Dolphin (1988) demonstrates that it is possible to calculate estimates for feeding effort and prey availability for humpback whales through surface observations of diving and respiratory activity and by using echo sounders. The results provide an estimate of the costs and time and energy budgets for the whales.

Despite the lack of quantitative research into gray whale foraging behaviour, inferences can be made regarding what type of optimal foragers they are (i.e., energy maximizers, risk or cost minimizers). Larger whales tend to migrate annually and restrict their feeding to short summer periods in the higher latitudes (Gaskin 1982). Mating takes place during the winter months in lower latitudes resulting in a distinct temporal and spatial segregation between mating and feeding (Dolphin 1988). As a result, whales do little feeding during mating periods causing a net seasonal loss of energy. The seasonal short-fall must be met through the summer feeding period where energy returns are maximized. Since whales in general appear to have low risk from predation (Dolphin 1987; Baird *et al.* in press; Burrage 1964; Leatherwood 1974; Jefferson *et al.*, 1991) virtually all of their time during the feeding period is spent foraging (verses avoiding predators). In terms of the whale's fitness, the yearly migration cycle should balance where enough energy will be gained from foraging for the return migration and for mating.

This last point illustrates the importance of a consistent source of food for the whales during this period. If feeding ground quality was to fall to levels where greater search effort had to be expended to obtain food, whales could be in danger of reducing their fitness due to increased energy expenditures. The same would be true if the whales frequently encountered predators or were disturbed in some other way from their foraging activity.

It is the potential for such a disturbance that is the focus of this thesis. If evidence of avoidance behaviour can be observed then further study must address the implications of this behaviour on the total energetics of the whales. The result may be an alteration of the regional occurrence of some whales or reduced fitness in others. The remaining discussion formulates a spatial model of gray whale within-patch behaviour based on the previous outline of optimal foraging theory. The proposed model will be used to assess observations of gray whale foraging and to evaluate behaviour deviations due to potential influences from vessel traffic.

2.3 Foraging Patch Model

If gray whales forage in an optimal manner then certain predictions can be made regarding the expected observed behaviour. The focus here is on spatial components of patch exploitation, specifically horizontal and vertical movements through the patch. The following assumptions are made regarding gray whale foraging behaviour:

a) Observed gray whales are foraging in an optimal manner over the long term (the summer feeding season) in such a way that the net energy gain is maximized by minimizing energy expenditure;

b) In the shorter term (daily feeding patterns) a whale will tend to forage in a more optimal manner when not satiated than when it is satiated;

c) Whales that are foraging optimally will minimize diving depth;

d) Whales are feeding on stable quality foraging patches of finite return thus continued foraging will result in eventual depression of patch quality;

e) The foraging patch is geographically stable. Its boundaries are defined by the areas of continuous presence of amphipod mats where depth is not maximized. Where depth is maximized this becomes the outer patch boundary regardless of the presence of amphipod mats.

Each of these five assumptions will have an affect on the spatial behaviour of an animal feeding in this way. Assumption 'a' and 'b' address the issue of spatial variance. Under assumption 'a', a feeding whale should show little spatial variation over the feeding period if patches of adequate quality are available. This tendency arises from the effort to minimize energy expenditures. Although the seasonal tendency will be to minimize spatial variation, this does not preclude the whale from exhibiting less than optimal foraging behaviour over shorter term periods (Assumption 'b') resulting in greater spatial variability. Variance in an optimal forager will be constrained by the nature of the foraging patch

(Assumptions 'd' and 'e'). Depth will have a tendency to control the way in which the foraging patch is exploited (Assumption 'c') in particular, shallower areas will be exploited first. Deeper areas will be exploited as the quality of the shallower areas is depressed.

Under these assumptions, a foraging whale should progress through the patch in a row-prime order with depth maintained as the row constant. The whale should also turn often to remain in the patch while progressing to deeper areas of the patch as shallower areas become depleted (Figure 2.1). Theoretically, if a whale is observed from the beginning of patch exploitation to the end, the resulting series of observation points can be used to approximate the boundaries of the patch itself. It should be noted that the resulting seaward boundary would not necessarily be a physical patch boundary but an artifact of the whales optimal depth limit.

The above model explains how a whale should exploit a patch. However, it would be difficult to assess the model against actual observations. Natural variations in movements associated with the whales switching from exploitive to explorative behaviour alone would cause spatial variability to exceed the true patch boundaries.

Another problem relates to observation and observation period. To assess the model adequately would require knowledge of the location of the true patch boundary on the part of the observers. In addition, the observer would need to know when the whale entered the patch, when exploitation began, and when the animal left. This necessitates continuous monitoring of whale behaviour on the surface as well as at depth which is extremely difficult. Precise mapping of patch boundaries is also difficult but not

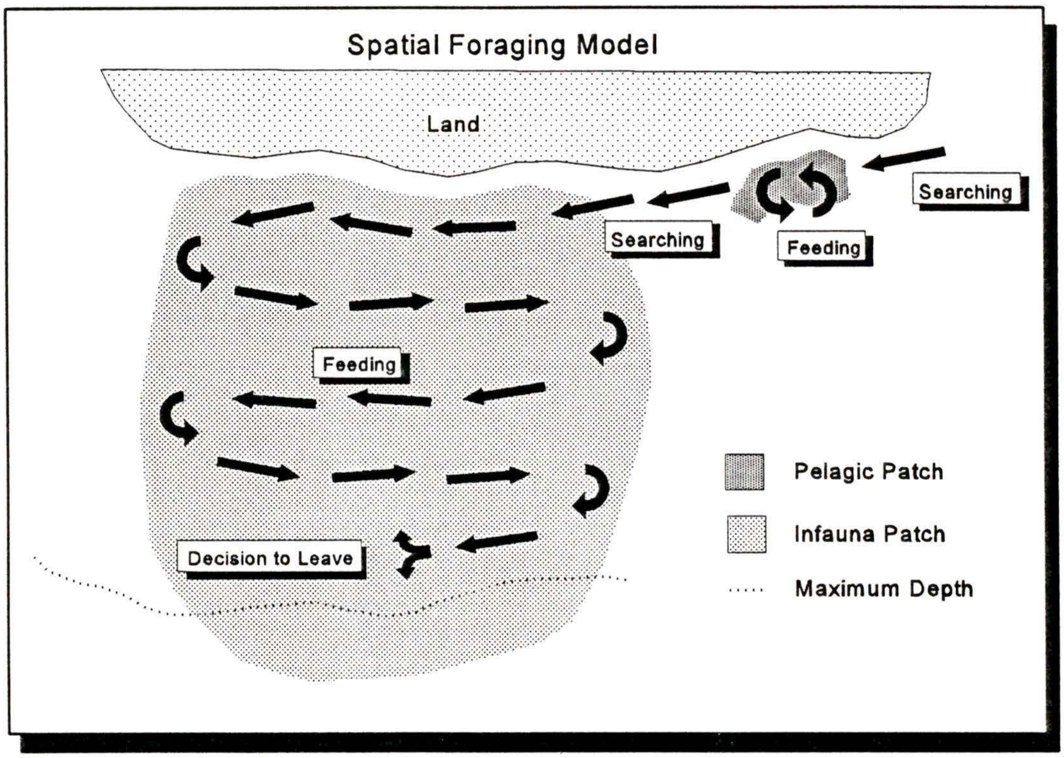


Figure 2.1. Model of gray whale spatial foraging strategy.

impossible by making use of diver sampling or remote sensing with side-scan sonar equipment (Johnson & Nelson 1984; Kvitek & Oliver 1981).

The constraints associated with proving this model can be overcome by considering spatial patterns in whale observations. Surface observations can be recorded and used as samples of spatial foraging patterns. Horizontal shifts in whale positions over time should show specific trends as the patch is exploited and if vessel traffic is influential. Conversely, analysis of depth associated with these observations should show similar trends.

Given the previously described model, I surmise that whales will exhibit spatial foraging behaviour, both horizontally and vertically, that are consistent with the model. Furthermore, deviations in spatial behaviour away from the model will be associated with the presence of vessel traffic, all other factors being equal.

In summary, a considerable amount of literature exists supporting optimal foraging theory. If gray whales are assumed to forage in this manner then certain predictions can be made regarding the expected spatial behaviour. Despite this, an animal that tends to forage in this manner may not do so continually. There may be natural variations in movements associated with switching from exploitive to explorative behaviour that are not attributed to changes in patch quality or location. If spatial patterns are studied from observations then comparisons can be made between spatial behaviour patterns with and without the presence of vessels. A correlation between deviations in spatial patterns and the presence of boats may indicate an alteration in gray whale's normal foraging behaviour.

Chapter 3

Methods

3.1 Introduction

The following chapter outlines the methods used to investigate gray whale spatial behaviour at two feeding sites in Clayoquot Sound during July and August, 1992. The approach is non-experimental, relying on field observations for analysis. Establishment of a control site or group was not possible given the site specific nature of the phenomena under study. Inherent in this type of analysis is also a large degree of uncertainty associated with observation error and the inability to observe whale activity underwater. Given these limitations, the methods used in analyzing data in this study rely on exploration of spatial pattern analysis. This type of analysis is used as a *first-step* in investigating trends in data before using traditional statistical techniques to assess significance (Tufte 1983; Tukey 1977; Hoaglin *et al.* 1983). Different methods of graphing data are used to display relationships and show possible associations or trends (Tufte 1983 provides excellent examples of these graphs). The goals are to verify initial hypotheses followed by further research and statistical testing, or the formulation of new hypotheses, or devise new research questions.

3.2 Study Area

The study area encompassed two gray whale feeding areas in Clayoquot Sound, British Columbia, Canada. The first is located off the southern side of Flores Island near the western extent of the Garrard Group at approximately 49° 14'N, 126° 08'W (Figure

3.1). This area includes the bay located between Siwash Cove to the west and the headland approximately 3.7 kilometres east and extends offshore to the estimated limit of sandy substrate types corresponding to approximately the thirteen-metre depth contour. This area is referred to as Cow Bay and has a total area of approximately 13.7 km^2.

The second site is located on the north-western side of Vargas Island including Ahous Bay out to the south eastern side of Blunden Island at approximately 49°10.5'N, 126° 02'W (Figure 3.1). Total area enclosed by this site is approximately 4.0 km^2.

These sites were chosen for several reasons. First, the sites historically have been frequented by whales during the entire summer period. Second, large kelp beds in Cow Bay may provide potential habitat for mysid swarms that are exploited by gray whales. Third, Ahous Bay is often sheltered from severe sea state conditions as compared to other areas. Fourth, there is an active whale-watching industry nearby (Tofino). Finally, opportunities existed to observe whales with varying levels of exposure to vessel traffic.

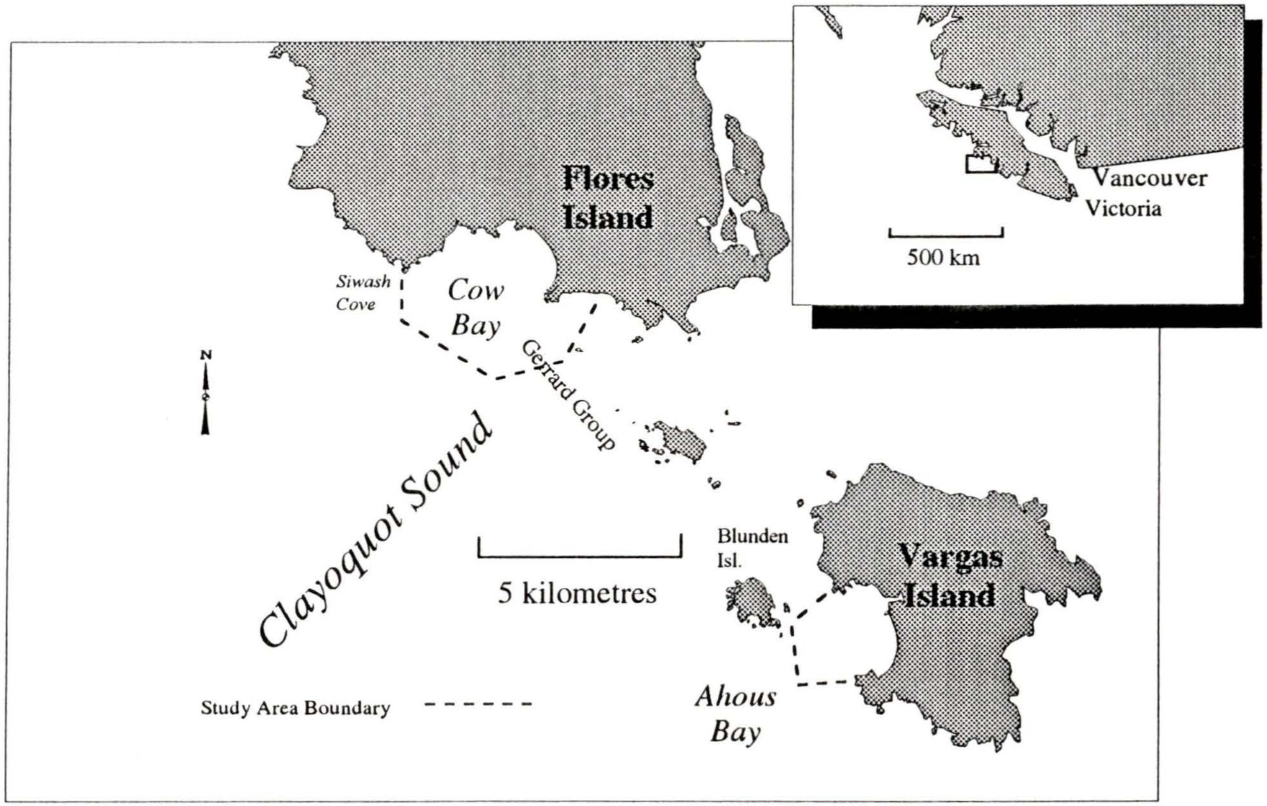


Figure 3.1. Study area.

3.3 Pilot Study

During the summer of 1991, a preliminary study was conducted in order to assess study area potential and data acquisition problems. Whale behaviour and position were observed from a 4.6 metre Zodiac between July and August. General notes on whale behaviour were recorded and positions were estimated and plotted on base maps. Notes also were taken on vessel activity including number of vessels in the area, behaviour, vessel type, and time spent observing whales. Experiences from this study (see Chapter 4 - Results) were applied directly to the design methods employed in the subsequent field season.

3.4 1992 Study - Whale Position and Behaviour

Observations of whale location and behaviour were made between July 6, 1992 and September 6, 1992. Data were collected by three field personnel from a 4.6 metre Zodiac with a thirty-five-horsepower engine. Operation of the engine was limited as much as possible to minimize potential observer influence while watching whales. Observation vessel distances from the whales averaged 100-200 metres. Relative proximity to the whales was required for accurate range estimating and identification of individual where possible. Observers focused on collecting data on a single whale rather than all whales in the study area. Notes were made of numbers of other individuals in the study area but positions were not recorded. Comments on whale identification were noted.

Whale position was determined using bearing and range estimates from the observation vessel position. Observation position was obtained using a Magellan portable marine Global Positioning System (GPS) receiver. Bearings were taken with an Autohelm digital flux compass while range was estimated by the observers.

Range estimation was problematic. Initially an optical range finder was used to estimate distance. Unfortunately, difficulties in focusing the instrument in variable sea conditions and on a surfacing whale proved impractical. As a result, distance to whales was estimated visually by the observers. Observers were trained by estimating 100 metre distances along a beach. An observer would walk along the beach while another would estimate distance. Actual distance was then measured using the optical range finder. Qualitative assessment of the observers ability to estimate range indicated an error of approximately 10 to 25 per cent depending on observer. How this level of accuracy translates into actual field estimates is difficult to establish since estimating distances on water tends to be more difficult than estimating distance on land. For the purposes of this study, distance estimates were assumed to be within 25 per cent error level assuming the worst case from the training session.

To assess performance of the GPS, daily position fixes were taken at the base camp at a fixed known point. Summary statistics were calculated to assess GPS accuracy (Table 3.1). Analysis confirms manufacture claims that GPS will be accurate to within twenty-five metres 90% of the time. On average over the study period, the GPS provided accuracy to within ten metres of the actual position.

Table 3.1. Summary of GPS readings for base camp to assess accuracy (N = 45).

	Degrees
Mean Longitude	126.06410518
Mean Latitude	49.26095355
Modal Longitude	126.064331
Modal Latitude	49.261002
Minimum Longitude	126.068993
Minimum Latitude	49.259998
Maximum Longitude	126.062660
Maximum Latitude	49.262833
Standard Deviation Longitude	0.000845
Standard Deviation Latitude	0.000420

Whale behaviour was classified through surface observation. Behaviour classes are based on an ethogram (behaviour classification) developed by Mallonee (1991) (Table 3.2). Dive durations were recorded where possible. Times were recorded in seconds from initial surface blow and every subsequent blow. Dive duration was established from when the whale showed a fluke (indicative of dive attitude) to the next blow. Where a fluke was not observed, dives were interpreted as extended periods where a blow was not observed.

Vessel data collected included vessel name and type, duration in the study area, general direction of approach and departure, and comments on boat behaviour. This data

Table 3.2. Ethogram of gray whale behaviour based on surface observations. (Adapted from Mallonee 1991).

Term	Definition	Probable Function
Transit	Forward movement from area to area	Travel
Milling	Forward and many directional changes within a restricted area	Searching Circling
Constant directional changes in movement within a restricted area	Bottom Feeding	
Plumbing	Sea floor disturbance resulting in surface mud patches and plumes	Bottom Feeding
Swim Slow	Minimal forward progress	Bottom Feeding
Swim Moderate	Constant forward progress	Travel
Swim Fast	Rapid forward progress with occasional white water	Unknown
Float	No forward Movement	Resting/orientation
Float then swim slow		Searching
Float then swim fast		Searching

was recorded when the whale-watchers were observing the same whale that was being tracked by the study team. Counts of total vessels in the study area were also maintained.

Efforts to inform whale watcher operators of whale occurrence status was kept to a minimum in an effort to reduce our influence on vessel occurrence. This was a difficult task since many operators, once they were used to the researcher presence, would ask for information. Normal vessel behaviour was also difficult to evaluate since operators appeared to follow prescribed whale-watching guidelines when our research vessel was present. We observed no evidence of purposeful harassment of whales despite alleged reports of such activity from other operators.

3.5 1992 Study - Substrate Sampling

Substrate samples were taken in Cow Bay on July 18, 1992 in an effort to obtain a qualitative assessment of patch quality. This information could be used to explain variability in whale observations associated with prey availability. Samples sites were chosen based on the 1991 whale sightings (Refer to Figure 4.1). Two transects were sampled across the mouth of the Bay to bisect areas where whales had and had not been observed feeding . Four stations along each of the two transects were sampled using a 15.24 cm^2 Ponar grab-sampler mounted on a 3.7 metre Zodiac. Three samples were taken at each site to yield a total of twenty-four substrate samples. Each sample was fixed whole in a 10% seawater formalin solution and later placed in a 70% ethanol solution for analysis.

3.6 Analysis

A base map of the two study areas was digitized from Canadian Hydrographic charts and imported into MapInfo® automated mapping software. Whale observations were numbered in sequence and a digital attribute data base created using Microsoft Excel® spreadsheet software. In addition to the observation sequence number, other attribute data included date of observation, whale identification, number of boats present, and relative depth at the observation point. Depth was determined with assistance from the Canadian Hydrographic Service at Sidney B.C. (M. Jennings pers.comm.). Resulting depths were not corrected for tides thus measures are a relative rather than absolute indication of feeding depth. Observation point location were entered directly into MapInfo and the attribute data attached to each point.

The resulting graphical data base was used to produce several plots for analysis. An initial plot of all observations was produced to show point distribution for each site. A second thematic shading plot was produced to show progression of observations over time for comparison to the foraging model outlined in Chapter 2. Observations were colour coded by date and joined with a corresponding line to show spatial progression. Observations were shaded with colour values that made it easy to distinguish earlier observations from later ones (i.e. dark red to light blue).

To assess vessel influence on foraging patterns, the graphical data base was used to indicate the extent of the observed foraging patch with and without boats. Observations without boats present were selected using MapInfo's query function. A polygon was then drawn around the selected observation as an analogue to feeding areas without boat influence. Polygons were drawn by connecting the shortest distance between outer points until closed (minimum enclosing polygon). The same was done for observations with boats. The resulting polygons were overlaid on the base map to show changes in patch distribution in the presence of vessel traffic.

To further assess model fit and the influence of vessel traffic, the data were also analyzed by changes in depth over time. Combination line and bar charts were produced of depth and number of boats present for each study site. A correlation analysis was done between the sequence number, depth and boats to indicate strength of relationships. Finally, dive durations were analyzed for differences between each site using confidence limits to assess the influence of feeding depth on dive duration.

The final stage of the analysis involved a qualitative assessment of patch quality in Cow Bay. Substrate material was analyzed for grain size composition while organisms were counted to assess abundance. Organisms were removed by passing each sample through a #30, 0.595 millimetre soil sieve. The sieve was used for convenience and availability and was adequate given that most other studies have used sieve sizes up to 1 millimetre for the initial sorting procedure (Kim & Oliver 1989; Oliver & Slattery 1985; Weitkamp *et al.* 1992). Organisms were separated from the remaining organic material using a photographic tray, hand held lens, pipette and tweezers. A general taxonomic classification (family and order) and census were performed using a stereoscopic dissecting microscope. Kozloff (1987) was used as a key to identifying invertebrates.

Substrate samples were dried in a Fisher Isotemp oven for 24 hours at 100°C then graded according to grain size. Sieves were chosen to represent general composition of sand grain ranging from medium sand (coarse sand was not present) to silt (Table 3.3). Samples were placed in stacked sieves and shaken in a Fisher-Wheeler sieve shaker for ten minutes. The volume of material in each sample was measured in a graduate cylinder to ±5 millilitres. Samples at each station were then pooled and a proportion of grain size composition was calculated.

Table 3.3. Sieve sizes used to grade substrate sample grain size.

Mesh #	Size (μm)	Description
50	0.297	Medium Sand
80	0.177	Fine Sand
100	0.149	Fine Sand
200	0.075	Very Fine Sand
400	0.038	Silt

Note: All sample grain sizes were less than 0.595 um or mesh #30.

A census of organisms in each sample was conducted then pooled for each station. An estimated number of amphipods per litre was calculated based on the pooled sample size for each station. Other organisms were not included in this part of the analysis because of their low occurrence.

3.7 Summary

Whale observations were made at two locations in Clayoquot Sound during the summers of 1991 and 1992. Several plots and graphs were produced to show the relationship of observations to the theoretical model described in Chapter 2 and the spatial influence of vessel traffic on whale foraging behaviour. A qualitative assessment of feeding patch quality was also conducted at one of the sites. Table 3.4 summarizes the types of analysis that were undertaken. The following chapter discusses the results of the analysis.

Table 3.4. Summary of analysis procedures.

Graphical Analysis

- Plots of all observations made at each study site.
- Plots of temporal progression for all observations classified according to date.
- Plots of observed feeding range with and without boats.
- Graph of depth progression of observations.
- Graph of depth progression and boat counts.

Statistical Analysis

- Correlation analysis between temporal progression (times sequence number), depth and boat presence.
- Confidence limits between mean dive duration between each study site.
- Census of organisms taken in substrate samples.
- Grading grain size of substrate samples.

Chapter 4

Results

4.1 Introduction

The following chapter describes the observations made during July and August 1991 and 1992. The pilot study season - July and August 1991 - allowed for familiarity of the study site and problems that would be encountered in sampling in subsequent seasons. Problems in data collection due to weather and inexperienced field crew resulted in data that are difficult to analyze using the methods developed here. For example, no effort was made to observe individual whales for the duration of the observation period. This resulted in problems in distinguishing whales when more than one whale was sighted. Additionally, the inability to distinguish whales caused problems in enumerating boat occurrence. Problems were further complicated with poorly designed data entry forms which did not provide convenient places to record boat - whale counts and positions, respectively. Finally, the field crews had difficulty in assessing position without navigational aids. Triangulation using a hand-held magnetic spotting compass proved too tedious to track numerous whale sightings. Crews resorted to estimating positions from visual cues along headlands and islands near where whales were sighted.

Despite the problems during the first field season, the resulting data indicated general feeding patterns and local areas where whales were feeding. A plot of the whale sightings was used to plan substrate sampling during the 1992 season (Figure 4.1). Whales were observed on 11 days during the two month period (Table 4.1). Although numerous observation days were lost to weather conditions, others were lost

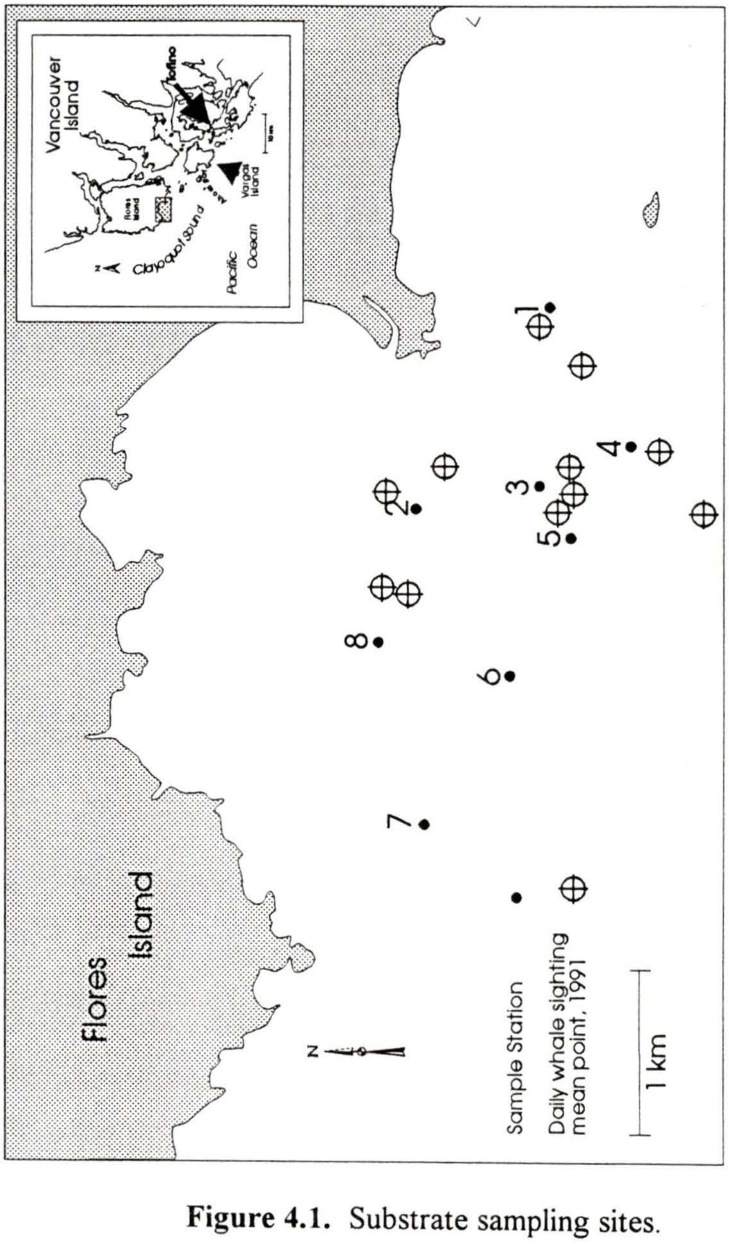


Figure 4.1. Substrate sampling sites.

due to a lack of whales in the study area. The first whale sighting did not occur until July 19. Comparatively, whales normally arrive in the area by late June to begin feeding in the Tofino area (Darling 1977; Guerrero 1988).

Table 4.1. Summary of 1991 pilot study observations, July and August 1991.

Date	Sightings†	Observation Period (minutes)
July 19	12	117
July 22	10	112
July 24	7	50
August 1	13	372
August 2	7	180
August 5	11	180
August 10	5	150
August 11	7	148
August 12	12	85
August 15	15	248
August 16	6	155
11 Days	105	1797

† *Sightings were recorded every 30 minutes due to difficulties in estimating position. Thus, these sightings do not correspond to dive intervals.*

4.2 1992 Field Season Results

Experience gained from the pilot study was applied to the sampling design for the following field seasons. Data collection and boat enumeration were simplified by concentrating observation effort on a single animal. Data forms were altered to allow for whale position and boat counts to appear together. Position information was improved through the use of a portable global positioning system and range estimation. Although weather conditions during the second field season had improved, whales again arrived later than expected (Table 4.2). Whales did not arrive into Ahous or Cow bays until late July. A total of 93 observations were made in Cow Bay while 187 were made in Ahous Bay (Table 4.3). Approximately seven individuals were observed during the study.

Table 4.2. Summary of gray whale observations in Clayoquot Sound, British Columbia from July 1 to August 31, 1992.

Date	# of Whales	# of Boats	Obs. Time (hours)	Whale I.D.
07/26	1	0	1.78	?
08/17	2	9	4.80	Hal
08/18	2	6	3.00	Dumpy
08/19	3	5	2.04	Dumpy
08/20	1	8	2.15	Dumpy
08/23	1	8	3.32	Dumpy
08/24	2	8	4.43	Plate
				Scarface
08/27	1	1	1.34	Scarface
08/28a	2	1	1.25	Plate
08/28b	2	2	1.50	?
08/29	3	8	4.18	Dumpy
08/31	4	6	1.13	?

n = 5 -7 Individuals

Table 4.3. Summary of daily observation counts at Cow and Ahous Bays

Date	Observations	
	Ahous Bay	Cow Bay
07/26		13
08/17	47	
08/18	26	
08/19	22	
08/20	20	
08/23		21
08/24		30
08/27		12
08/28		17
08/28	17	
08/29	44	
08/31	11	
Total	187	93

4.2.1 Observation Plots and Habitat Polygons

Plots of observations for both sites show a bimodal distribution (Figure 4.2 and 4.3). Analysis of observation progression indicates little temporal change at Cow Bay (Figure 4.4) although Ahous Bay suggests a temporal shift away from shore at later dates (Figure 4.5). Outlier observations to the north in Ahous Bay may be due to missed intermediate observations although field notes from this day suggest the whale was moving extensively across the bay.

Given the bimodal distribution of the data, plots of observed feeding patch range show two sets of polygons at each site (Figure 4.6 and 4.7). Each polygon represents an observed feeding patch (assuming that the whales were feeding) with or without vessel traffic present. Both plots indicate extensive overlap between polygons with and without traffic suggesting little influence from boat presence. Although there appears some interesting changes in aspect between polygons with boats and those without, there is not enough continuous data to evaluate the significance of this spatial trend.

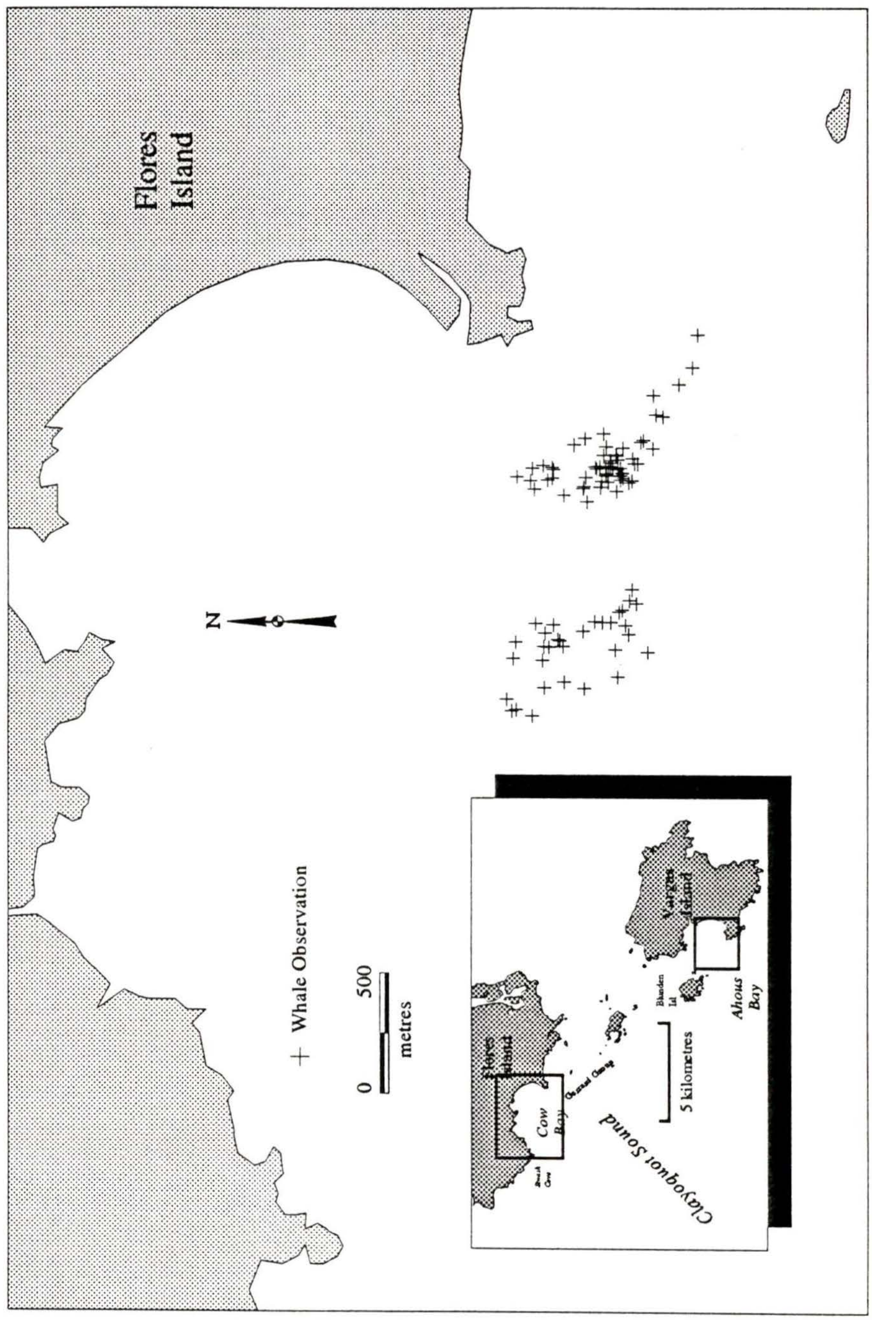


Figure 4.2. Distribution of observations at Cow Bay. Observations of two to three individuals over 5 observation periods.

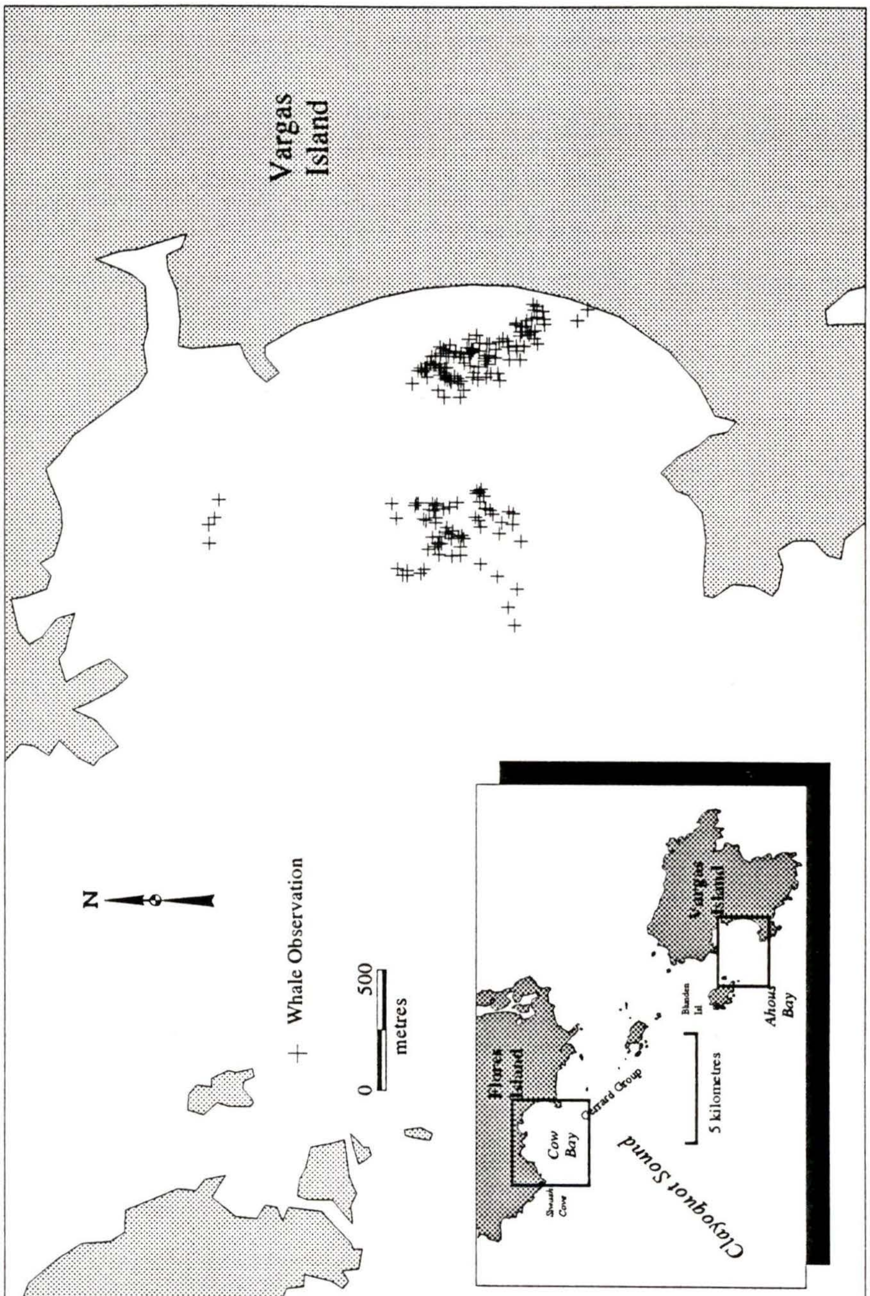


Figure 4.3. Distribution of observations at Ahous Bay. Observations of two to three individuals over 7 observation periods.

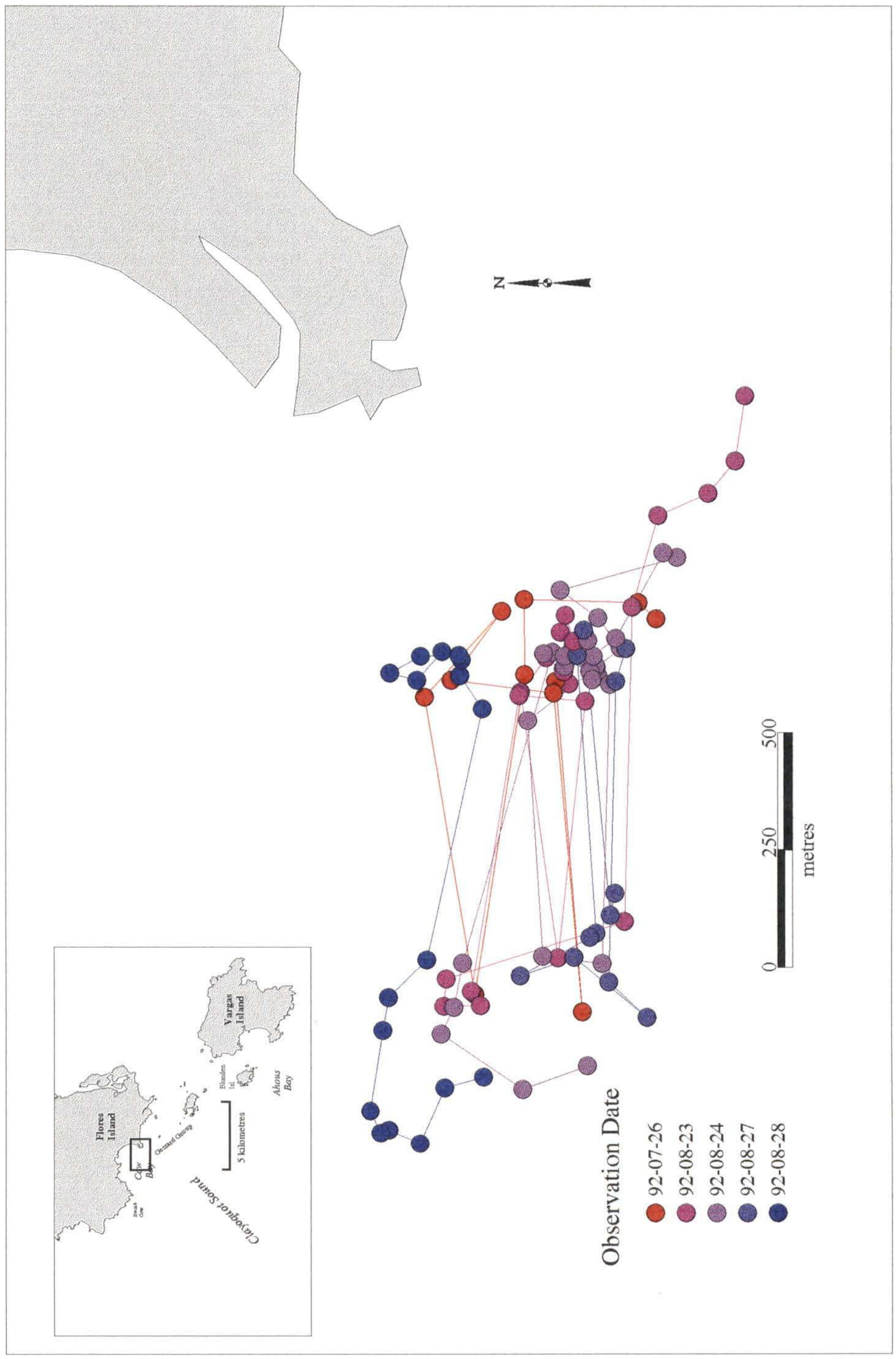


Figure 4.4. Temporal distribution of observations at Cow Bay.

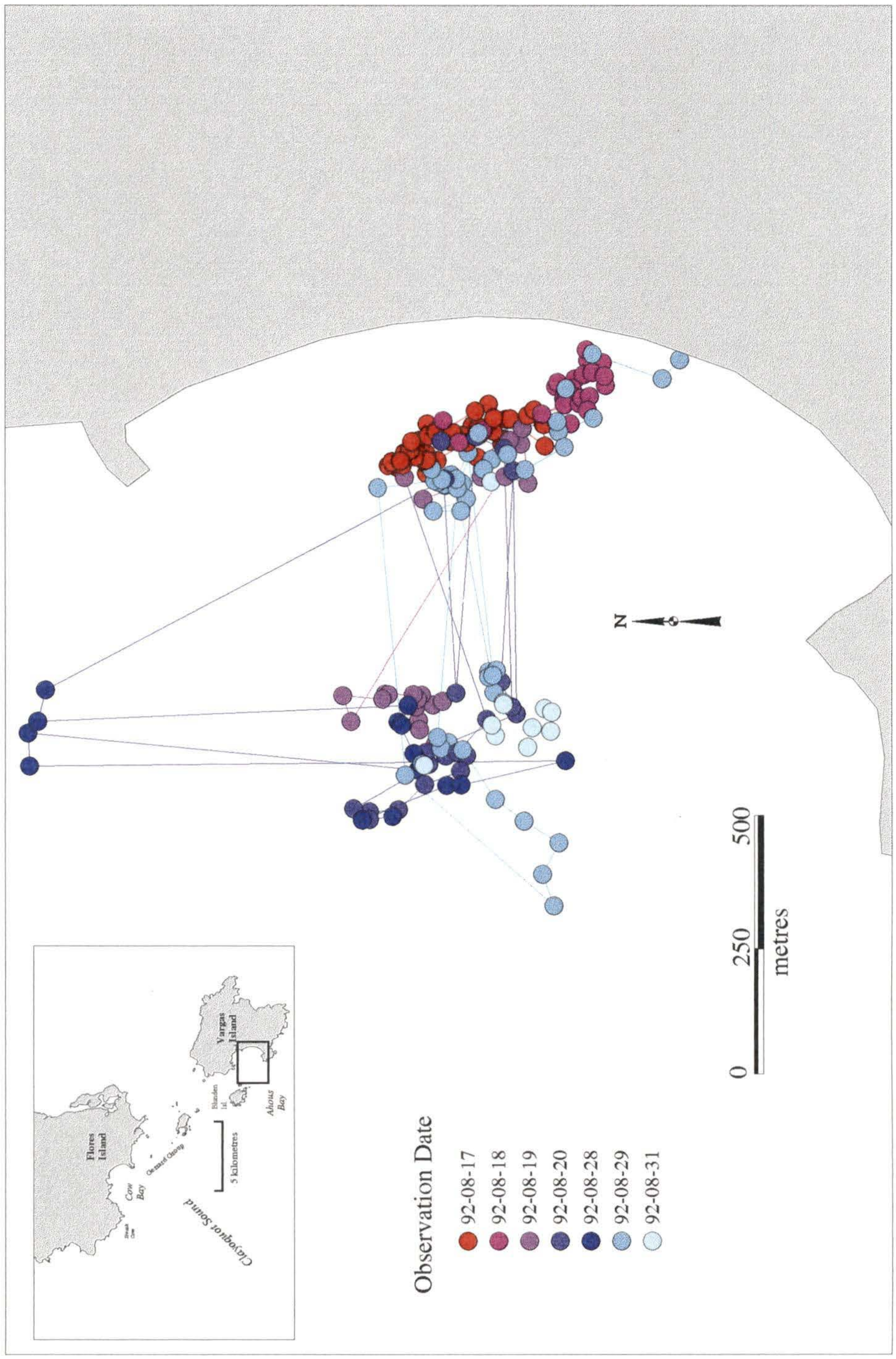


Figure 4.5. Temporal distribution of observations at Ahous Bay.

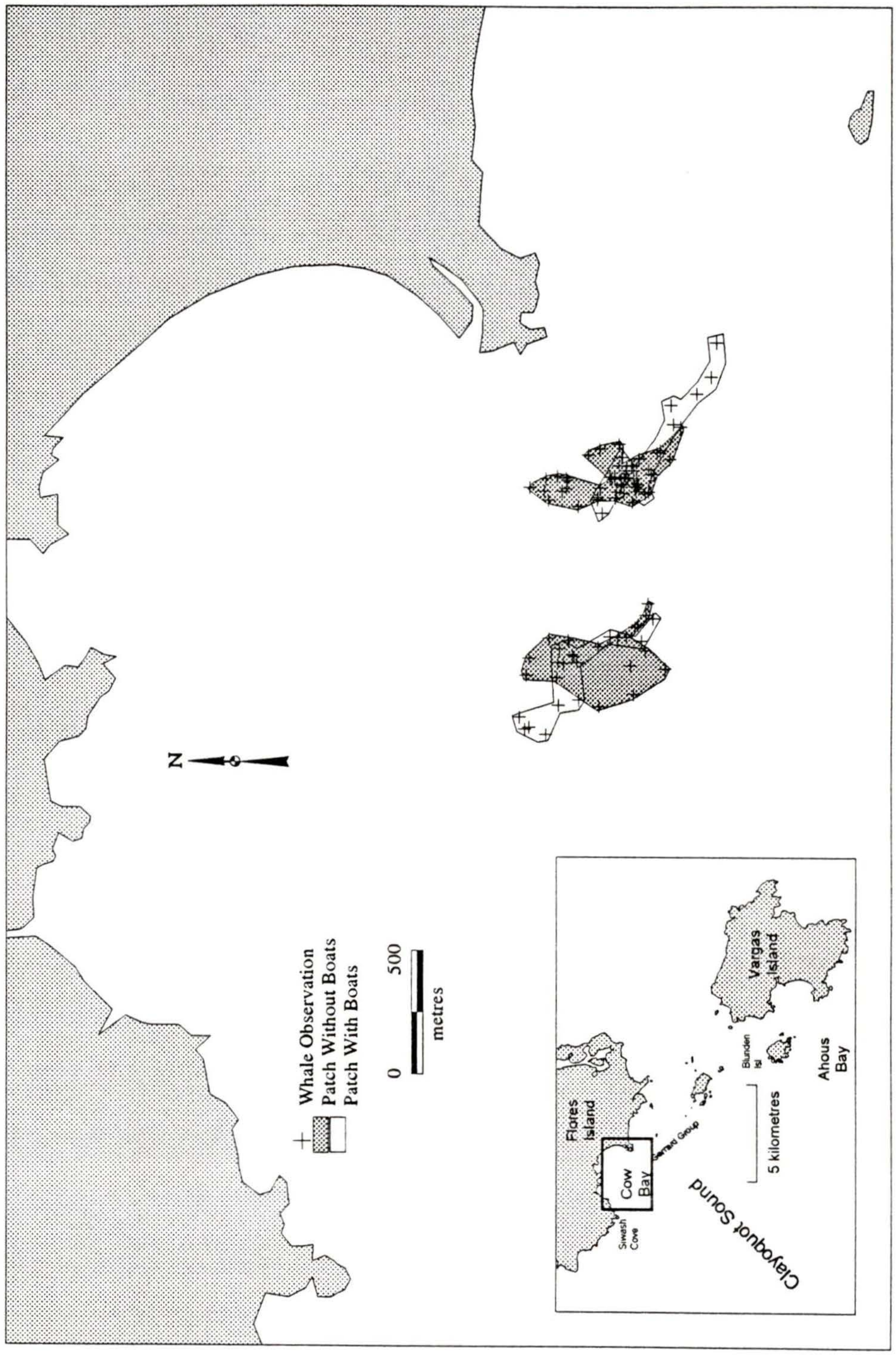


Figure 4.6. Observed feeding patch with and without boats at Cow Bay.

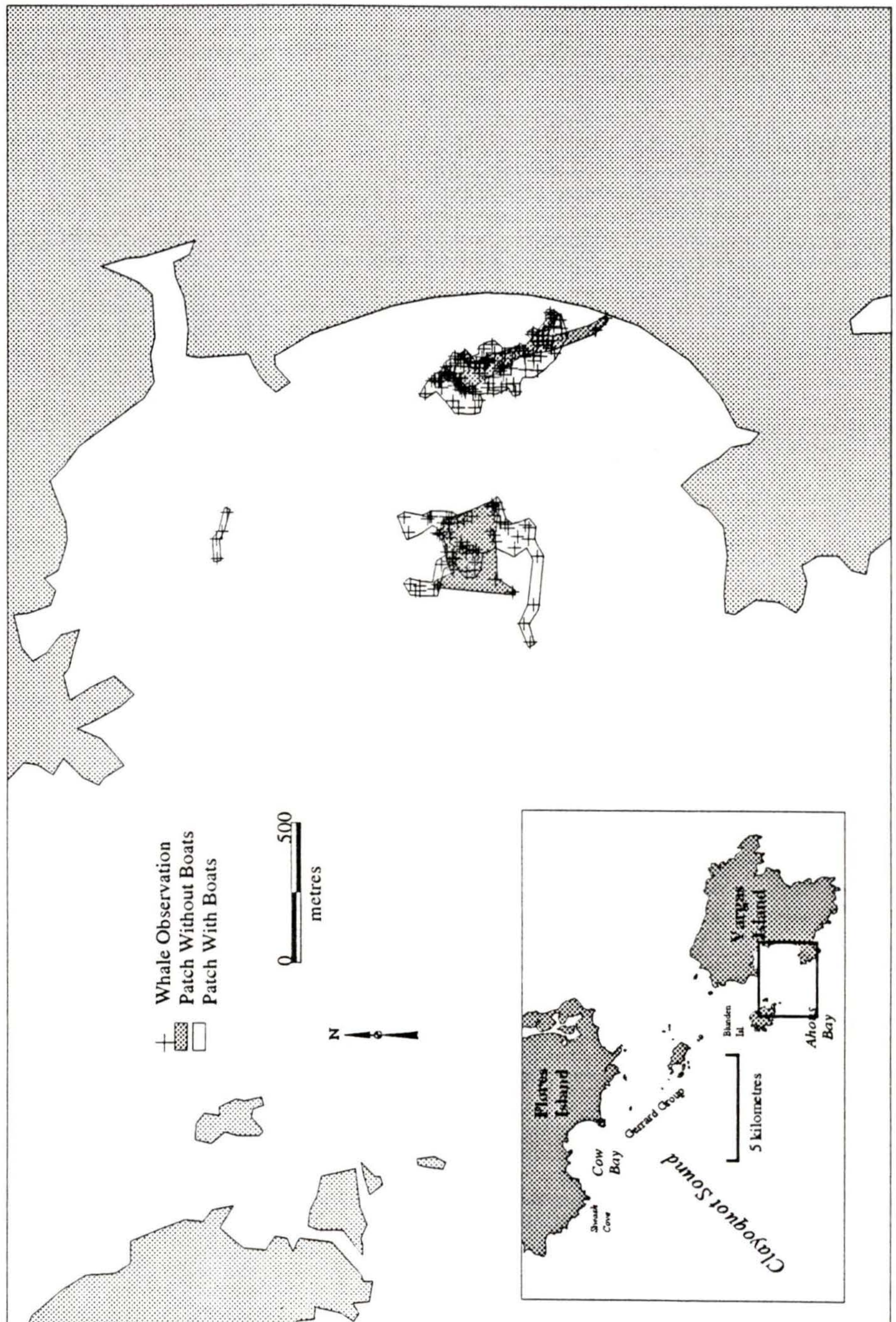


Figure 4.7. Observed feeding patch with and without boats at Ahous Bay.

4.2.2 Depth Progression and Depth - Boat Correlation

Graphs of depth progression over the observation period show that whales in Ahous Bay began feeding in very shallow waters and showed little variation for the first few days of observation (Figure 4.8). Later observations indicated a much broader range of depth variation although depths between 8 and 12 metres and <2 metres appear to dominate (Figure 4.8 and Table 4.4). In comparison, depth progression for Cow Bay were fairly consistent during the observation period (Figure 4.9). Depth variation was slight despite the horizontal bimodal distribution of the data points (Table 4.5).

Graphs of depth and boat progression suggest that depth variations were independent of vessel presence (Figures 4.10 and 4.11). Ahous Bay whales were subjected to the highest frequency of vessel encounters between the two study sites. There appears little association between variations in depth and the presence of boats despite a broad range of vessel encounter rates (Figure 4.10). Although Cow Bay had considerably lower vessel encounters, observations made in the presence of boats seemed to have little to no affect on the feeding depth observed (Figure 4.11).

Table 4.4. Summary statistics for feeding depths at Ahous Bay.

Measure	Depth (m)*
Mean	4.23
Standard Error	0.35
Median	0.70
Mode	0.30
Standard Deviation	4.80
Variance	23.01
Kurtosis	-1.60
Skewness	0.57
Range	12
Minimum	0.3
Maximum	12.3
Count	187

**Depth values are chart depths representing relative rather than absolute feeding depths.*

Table 4.5. Summary statistics for feeding depths at Cow Bay.

Measure	Depth (m)*
Mean	14.80
Standard Error	0.22
Median	15
Mode	15
Standard Deviation	2.16
Variance	4.66
Kurtosis	5.66
Skewness	-2.19
Range	11.5
Minimum	6.8
Maximum	18.3
Count	93

**Depth values are chart depths representing relative rather than absolute feeding depths.*

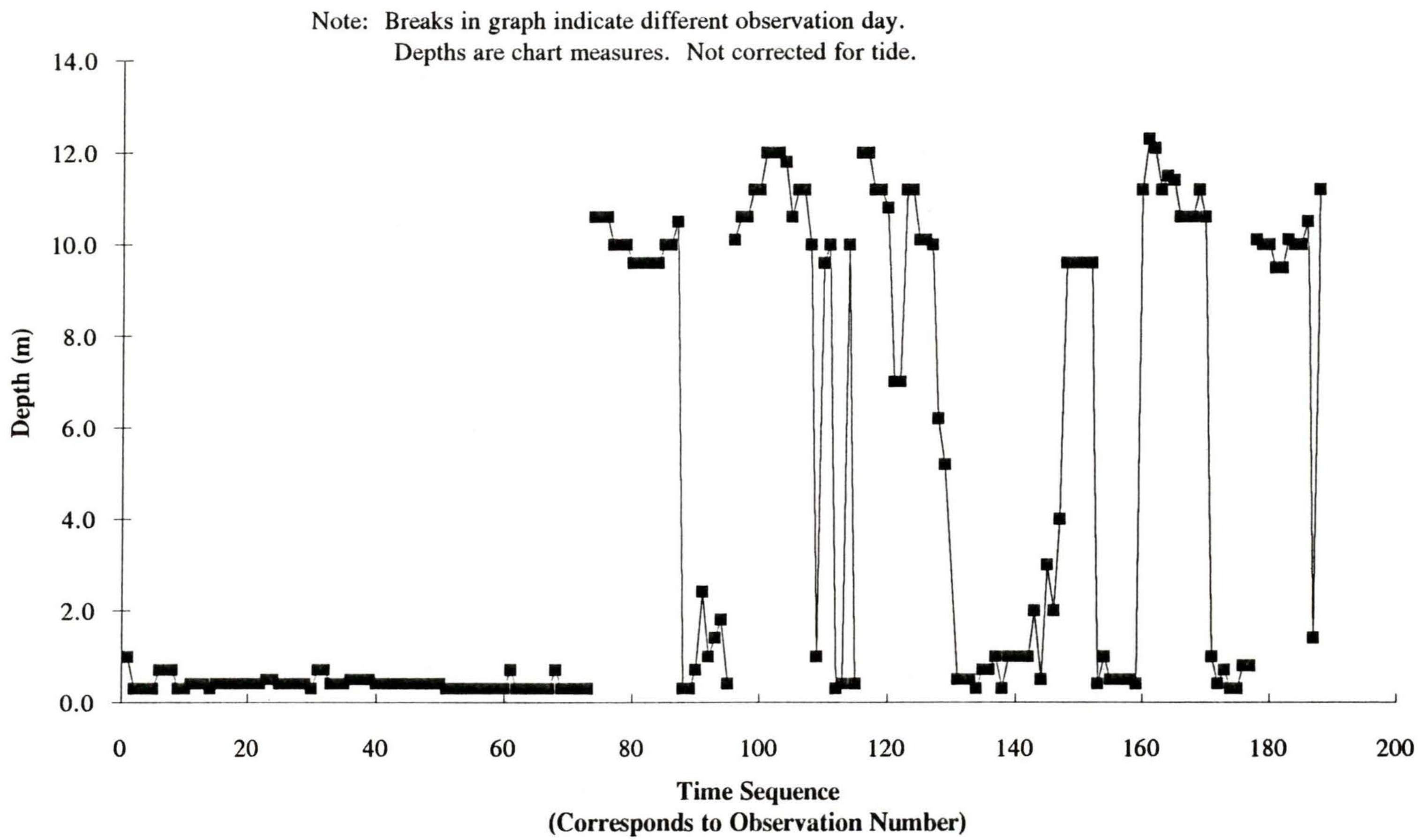


Figure 4.8. Depth progression for observations in Ahous Bay

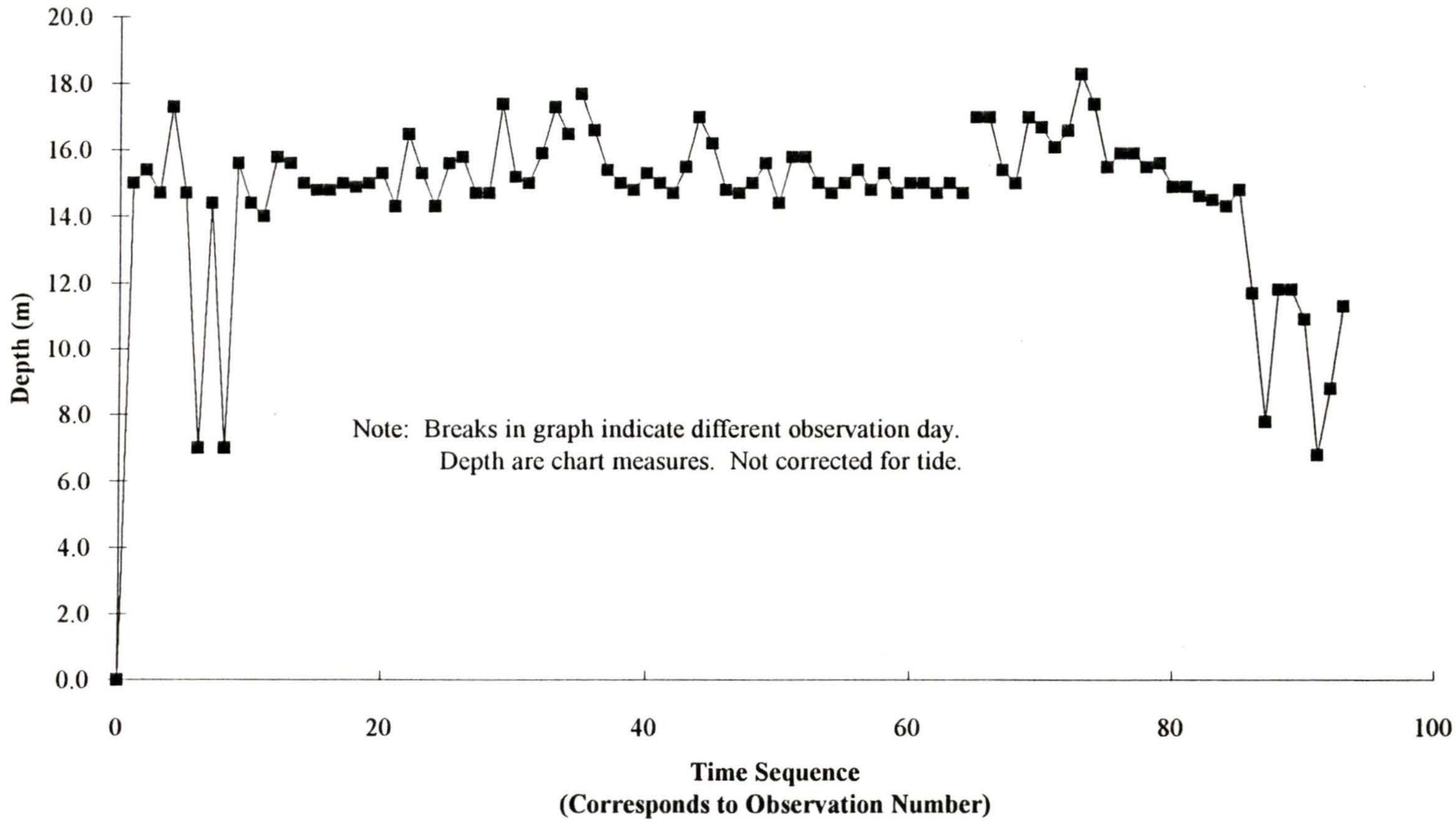
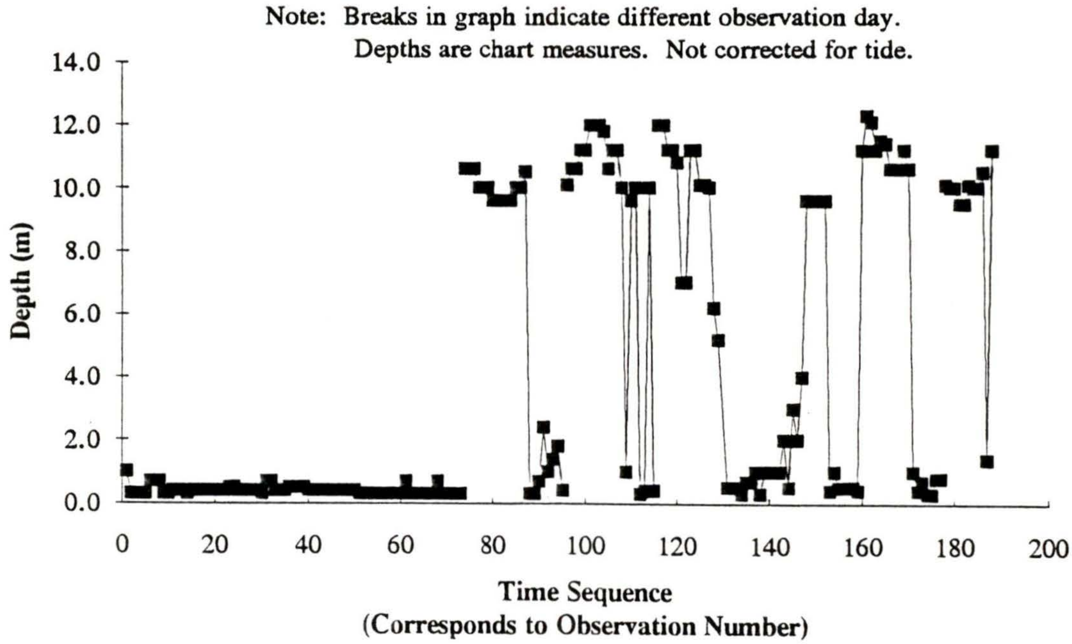


Figure 4.9. Depth progression for observations in Cow Bay



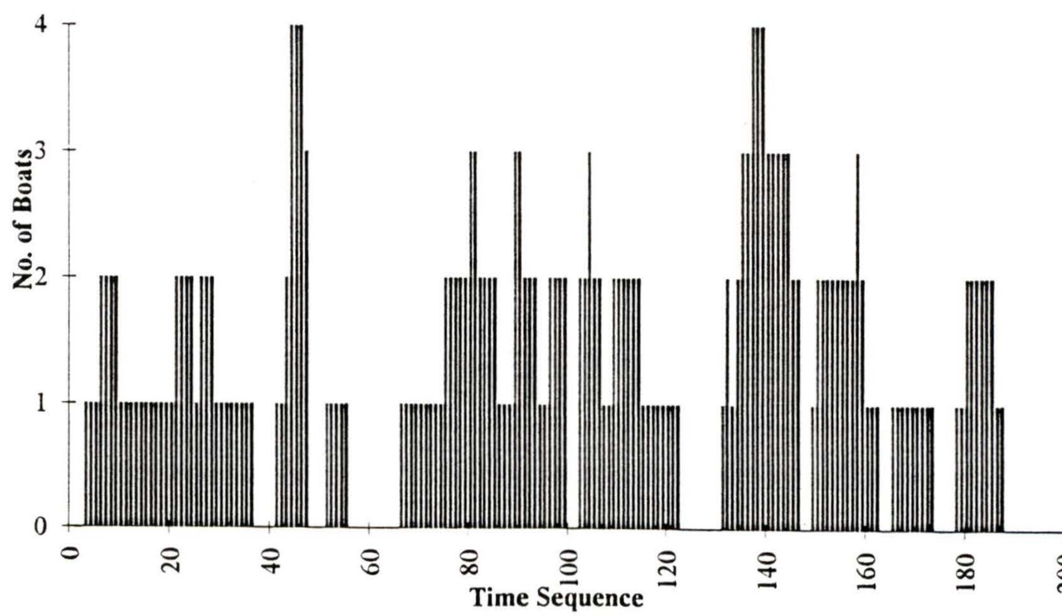
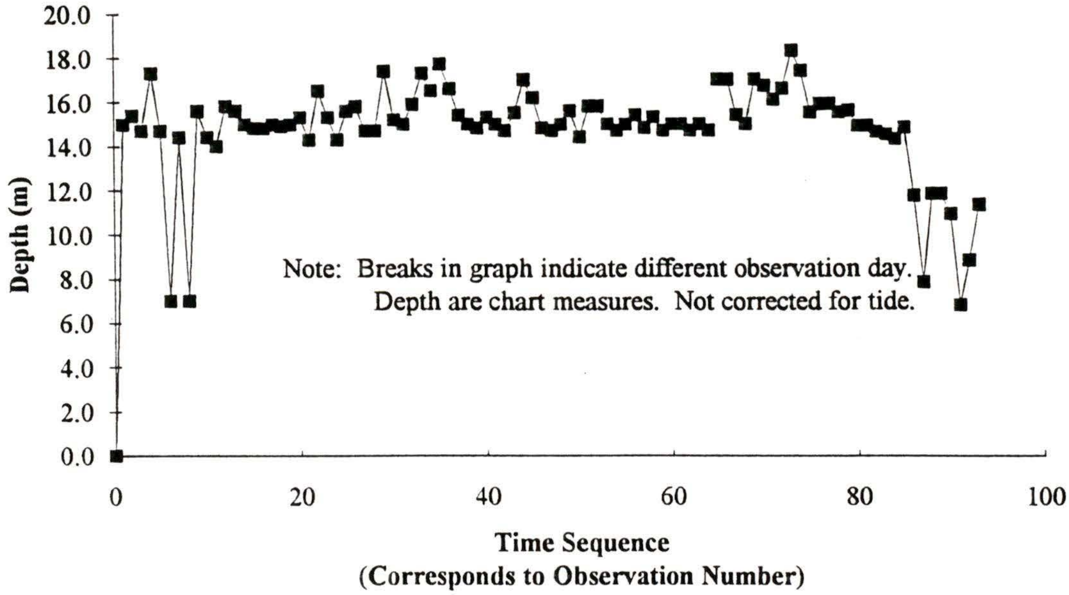


Figure 4.10. Depth of observations and associated vessel counts at Ahous Bay



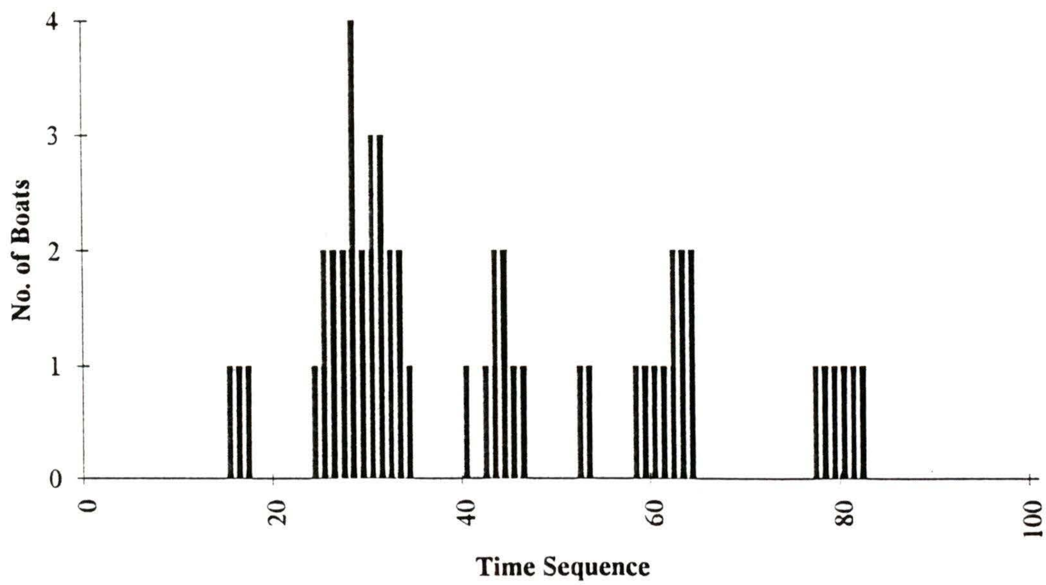


Figure 4.11. Depth of observations and associated vessel counts at Cow Bay

As might be expected, correlation analysis between time sequence, depth and boat presence showed little to no association at either site (Table 4.6). Association between time sequence and depth for Ahous Bay was the strongest with a correlation coefficient of 0.49, $p<0.05$ suggesting a trend to deeper water over time.

Table 4.6. Summary of correlation coefficients (r) between boats, depth and time sequence for Cow and Ahous Bays, 1992 field season ($p<0.05$).

Ahous Bay	Sequence Number	Boats	Depth
Sequence No.	1		
Boats	0.10	1	
Depth	0.49	-0.02	1
Cow Bay			
Sequence No.	1		
Boats	-0.17	1	
Depth	-0.10	0.18	1

Finally, a difference-of-means test for dive durations between the two study sites indicated that observations at Cow Bay were significantly higher than those observed at Ahous Bay ($t=1.96$, $p<0.05$, see Table 4.7).

Table 4.7. Confidence limits for analysis of dive duration, Cow Bay and Ahous Bay, 1992.

	Ahous Bay (minutes)	Cow Bay (minutes)
n	145[†]	77[†]
Mean	4.33	5.68
Standard Deviation	1.97	1.35
Variance	3.86	1.83
Upper Limit	4.65	5.98
Lower Limit	4.0	5.37

[†] *Number of dives does not correspond to the actual number of observations made since at least two observations are necessary to time one dive. This applies only at the beginning of a sequence of observations.*

4.2.3 Substrate Sampling

Some difficulty was encountered when sampling substrate. Due to the size and weight of the Ponar grab sampler (15 cm^2) it was difficult to obtain a high level of penetration into the dense sandy substrate. Resulting samples were quite small yielding pooled sizes ranging from a low of 835 millilitres to a high of 1250 millilitres (Table 4.8). Although Gammaridean Amphipoda made up the majority of all samples, several other organisms were found including molluscs (class Bivalvia and Gastropoda), polychaetes, isopods (suborder Flabellifera), decapods (family Cancridae), polyclads (order Polycladida), and Cumacean crustaceans (order Cumacea) (Table 4.9). Station 7 had the highest occurrence of amphipods with an estimated 1376 individuals per litre of substrate while station 2 had the lowest with 89 individuals per litre (Table 4.8).

Table 4.8. Summary of substrate sample obtained at Cow Bay, Clayoquot Sound, British Columbia, Summer 1992.

Station	Dry Sample (ml)	Amphipods per litre
1	860	367
2	650	89
3	1250	230
4	950	175
5	835	126
6	1225	776
7	1160	1376
8	1140	696
Mean	896.7	426
Standard Deviation	203.0	415.9

Table 4.9. Summary of species collected at Cow Bay, Clayoquot Sound, British Columbia, Summer 1992 for all samples combined.

Species	Number Observed
Amphipoda Gammaridea	4 271
Mollusca Bivalve	97
Polychaeta	31
Mollusca Gastropoda	6
Isopoda Flabellifera	6
Decapoda Camcridae	2
P. Polycladida	4
Cummacea	1

Substrate composition showed some variation in grain size ratios between sites (Figure 4.12). Virtually all sand was found to have between 0.177 and 0.075 mm grain size. Most samples contained small amounts of sand greater than 0.297 mm (medium sand) while very little grain size less than 0.038 mm (silt) was found in the samples. Sites 1 and 2 showed the highest proportion of fine grain sand with over 85% of the sample consisting of grain size between 0.297 and 0.177 mm. Sites 4 and 7 had the most even composition between grain size.

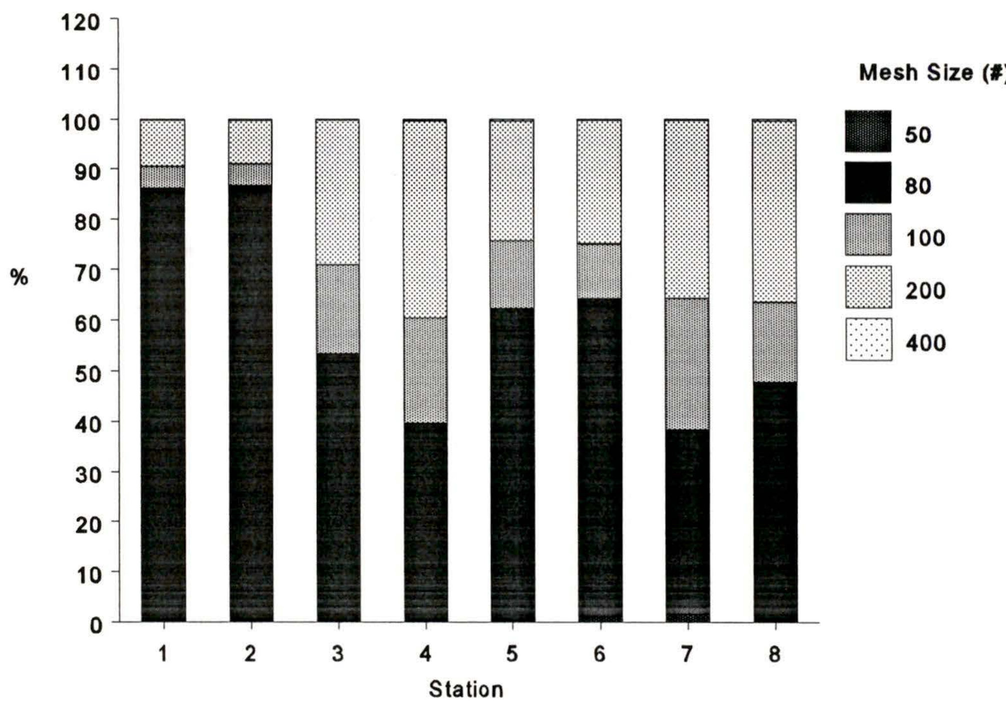


Figure 4.12. Substrate grain size per cent composition with mesh 50 = 0.297μ (medium sand), mesh 80 = 0.177μ (fine sand), mesh 100 = 0.149μ (fine sand), mesh 200 = 0.075μ (very fine sand), and mesh 400 = 0.038μ (silt).

An overlay of observations in Cow Bay and the substrate sample sites indicate which sites whales were found most often (Figure 4.13). Despite high occurrences of amphipods at station 7, the whales were observed more frequently between sites 2, 3, 5, and 6.

4.3 Summary

Whale observation data collected during the 1992 field season indicated bimodal spatial distributions at both study sites. Although there appears a temporal progression of observations from shallow to deeper waters in Ahous Bay, no such pattern appears in Cow Bay. Observations in Cow Bay show a fairly consistent feeding depth throughout the observation period. Comparison of observed patch range with and without vessel traffic showed a high degree of overlap. An apparent change in aspect was observed when boats were present, however, there were too few observations to test the significance of this trend. Additionally, there appeared no association between vessel presence and fluctuations in feeding depths at either site. Results of the substrate analysis showed large occurrences of amphipods at some sites. Whales, however, were not observed feeding in these areas. Problems associated with sampling substrate in this study forego any detailed analysis of patch quality beyond qualitative assessment. The following chapter discusses the results of this study within the framework of foraging theory and addresses areas future directions for research.

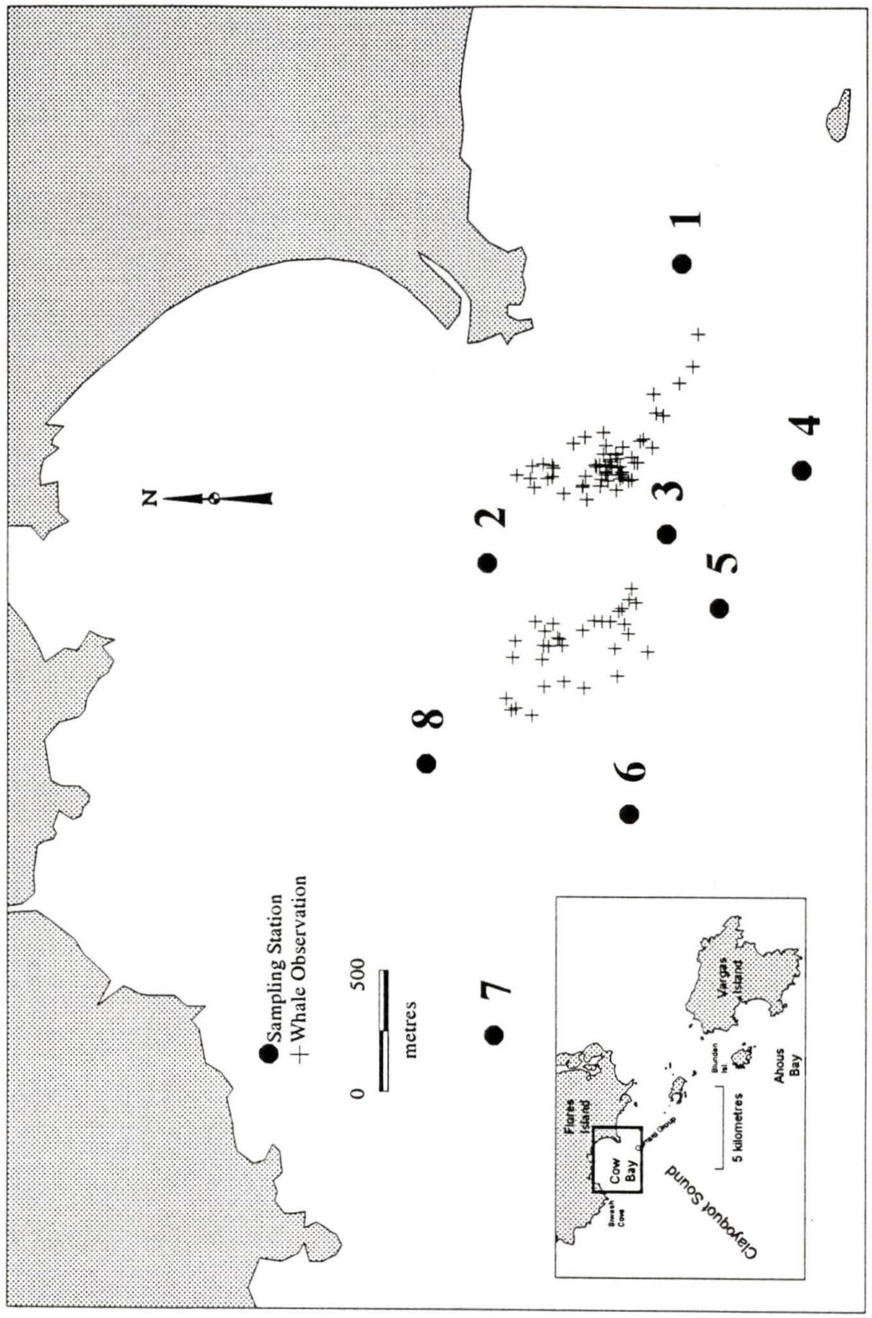


Figure 4.13. Cow Bay observations compared to substrate sampling sites

Chapter 5

Discussion

5.1 Introduction

In Chapter 2, I surmised that whales will exhibit behaviour that is consistent with a spatial optimal foraging model with or without the presence of boats. Deviations from the model, in association with the presence of vessel traffic, may be an indication of an effect on whale spatial foraging patterns from boats. Results from this study show deviations in spatial foraging behaviour but it cannot be directly attributed to the presence of boats. The following discussion addresses aspects of the results and places them within a theoretical framework. Improvements to the research are offered and future research questions are suggested.

5.2 Late Occurrence of Whales

In the course of any field study, a researcher assumes that the period chosen for study is representative of the normal occurrence of the phenomena. Unusually late arrival of whales in the study area during both field seasons suggests that these years were anomalous thus may not be representative. Based on previous observations and reports from whale watching operators, gray whales settle into a summer feeding pattern usually by the end of June. The apparent erratic appearances of the whales over the past couple of years has led to speculation by local residents and whale watching operators about the cause. Many feel that the rapid expansion of the whale watching industry is causing a delay in the whale's appearance as they avoid intensive vessel activity.

Others have speculated that the whale's erratic behaviour is due to the occurrence of an oil spill. In 1989, an oil spill may have affected the substrate, particularly in Ahous Bay, thus tainting the food supply. Darling (1989a, 1989b) and Harding and Englar (1989) found little evidence of an effect on the whale migration at the time nor was any oil found in the substrate of Ahous Bay. In addition, whales were observed feeding in Ahous Bay in the summer of 1990 (S. Bondi, charter operator, 1992, pers.comm.) thus suggesting little effect from oil.

A probable cause for the unusual spatial behaviour of the whales may have been the occurrence of an El Nino event during late 1990 and early 1991 and an unusually persistent event in 1992 (R. Thomson & H. Freeland, Institute of Ocean Sciences, pers.comm.). Mysak (1986) noted that changes in sea temperature and associated plankton productivity causes a northward deflection in salmon migration. Barber and Chavez (1983) observed that changes in sea temperature associated with El Nino results in shifts in areas of high shrimp production. The effect may be similar for mysid and amphipod production. Blooms in these species would result in other foraging areas becoming more productive. As a result, whales may stay in those areas longer. Further study on regional utilization of feeding areas would provide insight into this phenomena.

5.3 Observation Point Distribution

A whale feeding in the manner described in the foraging model should show a progression from shallow to deeper water as shallow portions of the feeding patch become depleted (Assumptions 'c' and 'd' in Chapter 2). Additionally, uniform patch quality should yield a uniform progression of observation points from shallow to deeper areas (Assumptions 'd' and 'e'). This was not observed in this study nor was an association evident between the bimodal distribution of the observations and the presence of boats. It is likely that some other factor is responsible for the bimodal distribution of observation at each of the two study sites.

A bimodal distribution could occur if the assumption regarding patch uniformity is not valid. Substrate sampling suggests that this may be the case. However, given difficulties in substrate sampling, it is not practical to conclude that the bimodal distribution in Cow Bay is due exclusively to variable patch quality in this study. Recent diver observations in Cow Bay (summer 1993) suggest that amphipod mats are dense and wide spread in this area (A. Bass, pers. comm.).

Ahous Bay shows similar characteristics. Guerrero's (1989) observations of Ahous Bay indicated wide spread amphipod mats throughout the area. Consistent substrate composition and hydrography (low relief and gradual slope) do not support a conclusion of high variability in patch quality. Additionally, Kim and Oliver (1989) studies in the Bering Sea showed that amphipod patch quality tended to be consistent over broad areas.

If patch quality is uniform in both areas then other factors must be responsible for the observation distribution. It is possible that patch quality may vary due to intervening factors such as the presence of many large crustaceans (crabs or sand dollars) or differences in substrate composition. This needs to be evaluated with diver observations or large grab sampler to detect their presence.

5.4 Depth Analysis

Closely associated with the spatial distribution of observations is the depth whales are feeding. A depth minimizing strategy during foraging should result in a progression from shallow to deeper areas of the patch over time. This was not the case for Cow Bay. However, Ahous Bay showed a weak tendency toward this pattern. In the case of Cow Bay, consistent depths may show a depth minimizing strategy as lateral movements did not translate into changes in foraging depth. Conversely, in Ahous Bay, depth minimizing strategy is suggested early on, followed by highly variable foraging depths that is consistent with search or avoidance behaviour. The patterns at either site could not be attributed to the presence of boats.

Variability in depths at Ahous Bay is, however, consistent with what might be expected where an animals has depleted one area and forced to search for other areas to forage. Again, details of patch quality and uniformity would help to confirm this assertion. The foraging depth pattern observed in Cow Bay, although apparently less variable than Ahous Bay, may be an artifact of observation time. A greater number of observation days may have yielded a similar pattern as was found at Ahous Bay.

5.5 Future Study

Perhaps the most significant question to arise from this study is the issue of patch choice and prey dynamics. Observations from 1991, 1992, comments from other operators, and from the latest ongoing study in the area show that whales exploit different areas of Cow Bay regularly. What then leads to the whale's choice to exploit one area of the bay and not another? An answer to this question would provide valuable information regarding whale foraging strategies specifically pertaining to habitat preference.

It is necessary to gain more understanding of the gray whale's dive patterns. Dive depth recording would show whether whales are diving directly to the bottom, do searching or move from one area to another underwater. This would give insight into searching strategies and possibly help to explain bimodal trends in surface observations. Additionally, partial dives in the presence of vessel traffic may be an indicator of avoidance behaviour.

Along with time depth recording information, more continuous positioning data are required. Field observations are too dependent on weather and sea state for accurate observation. Do whales change their feeding behaviour in different sea state conditions? Do whales continue to feed at night? Radio or satellite tagging of whales would provide continuous twenty-four hour coverage of whale positions for several days rather than a few hours. Continuous monitoring would also provide details of whale activity free from the influence of vessel traffic for long periods. Tracking should also be undertaken on several different whales to account for variability between individuals.

It is likely that the presence of field observers had an effect on whale-watcher operator behaviour. Despite numerous accounts of whale harassment, we observed very few of these incidents. Observation methods that are not so prevalent to operators would probably provide better information about operator activity. At worst, however, researchers appear to play a significant role in enforcement of federal government whale-watching guidelines, be it incidentally.

Finally, more observation data are required to further apply the analysis techniques outlined in this study. Admittedly, the volume of data collected was far too small to make conclusive statements regarding whale foraging behaviour. The study does show, however, the efficiency of the analysis and its application to data with high levels of uncertainty. Patterns become apparent that help to formulate new questions and guide future research.

5.6 Conclusion

This study used exploratory analysis in an effort to identify relationships between vessel presence and gray whale foraging patterns. Hypotheses were used to give a formal structure to the generalized analysis. This served to guide the research and identify new questions that, when addressed, will lead to a better understanding of the influence of vessel traffic on whale behaviour.

Results of this study were not able to confirm an alteration in gray whale spatial foraging patterns in the presence of boats. Surface analysis of whale movements are only valuable as an initial evaluation of whale behaviour. Further study must focus on understanding and mapping the dynamics of the prey that gray whales feed upon to explain associated surface behaviour. Additionally, study of gray whale dive patterns during feeding may indicate more subtle avoidance strategies such as partial dive and travel sequences. Radio or satellite tags would provide better position information without potential influences from an observation vessel.

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January 31, 1994

Date