FORAGING ECOLOGY OF HUMPBACK WHALES OFF NEWFOUNDLAND

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by

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ABSTRACT

Off the coast of Newfoundland humpback whales feed primarily on capelin which form schools of varying size, depth and age class. Observations were made on humpbacks foraging in six different prey situations, in each of which the distribution, abundance and behaviour of whales was related to bait characteristics. Whales were followed by boat and prey school information was provided by a paper printout depth sounder.

When whales were exploiting large deep immature or post-spawning capelin schools, dive times were positively correlated with depths to the top of the prey school and to the ocean floor in the immediate dive vicinity. Time spent at depth (filtering time) appears to be constant ($t = 2.3$ min) while dive time is proportional to prey depth. Surface times were positively correlated with dive times and with prey school and water depth and appear to function as a recovery period from foraging dives. When preying upon small concentrated schools of post-spawning capelin, water depth and vertical extent of prey school did not significantly predict either dive time or surface time. The time spent and the large amounts of directional change that occurred while whales were at the surface may function to reposition whales close to the prey school. When the concentrated post-spawning capelin schools dispersed into very small widely scattered schools, whales spent variable amounts of time at the surface travelling primarily in straight lines from school to school, diving only once into each pocket of bait. Surface and dive times were not correlated with vertical extent of prey or with water depth. Humpbacks were also observed to exploit small surface swarms of krill, using a foraging strategy distinct from that seen when feeding on capelin: a series of lateral lunges at the surface.

A dominant feature of humpback whale foraging is the formation of highly coordinated groups. It is hypothesized that coordination functions to minimize the disruptive effects that repeated dives of foraging whales may have on prey schools. When prey schools were large, whales foraged almost continuously and formed larger groups. Whales left small prey schools after 0.5 - 2.0 h exploitation to travel and to rest, possibly letting the school regroup before returning to forage. Group sizes were larger when whales were foraging than when not foraging. Local whale populations were greater and whales stayed longer where prey was more abundant.

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CHAPTER 1. INTRODUCTION

1.1 Populations and stocks of humpback whales

The humpback whales of the Northwest Atlantic are one of at least eight distinct stock units or sub-populations of humpbacks, six of which occupy the oceans of the southern hemisphere and two the oceans of the northern hemisphere, North Pacific and North Atlantic (Mackintosh 1965). All populations of humpback whales are migratory. Like most other baleen whales they breed in winter in sub-tropical or tropical waters (0° - 30° latitude) and then migrate to productive arctic or antarctic waters (50° - 70° latitude) where they spend the summer feeding (Mackintosh 1972, Dawbin 1964). The six South Pacific populations of humpbacks mingle on the three principal antarctic feeding grounds but appear to segregate into six or seven breeding units (Gaskin 1976). The sub-population which feeds in the North Pacific also consists of three separate breeding populations, each with distinct calving/breeding grounds (Herman and Antinoja 1977). Most of the Northwest Atlantic population however breed and calve off the West Indies but segregate into four feeding sub-stocks that use four different feeding grounds: 1) Gulf of Maine - south east Nova Scotia, 2) Gulf of St. Lawrence - Newfoundland and Labrador, 3) West Greenland and 4) Iceland (Whitehead et al. 1981; Katona et al. 1983; Martin et al. 1984).

An extensive program of fluke photography has elucidated these feeding sub-stocks. Photographs are taken of the ventral surface of the flukes and other distinctive areas of the animal, individuals are catalogued and sighting matches between and within breeding and feeding areas are sought (Katona et al. 1979, 1980; Katona and Whitehead 1981). Mark and recapture statistics are used on the fluke data to estimate population numbers. These suggest a Northwest Atlantic humpback population size of 3000 - 5000 animals (Katona et al. 1982; Whitehead 1982).

1.2 Feeding and breeding seasons

Seasonal migrations enable humpback whales to take advantage of the seasonally abundant food found in oceanic areas of high productivity (Nemoto 1957, 1964; Mackintosh 1970) and to bear calves in warm sheltered waters. Calving in tropical waters is probably adaptive for two reasons: 1) Calves have less blubber than adults and have a higher surface to volume ratio (and hence a faster rate of heat loss) so warm waters would prevent thermal stress (Whitehead and Moore 1982). 2) Calves may require shelter from heavy seas. Whitehead (1981) found that females with calves used protected areas near coral reefs. The migratory cycle is probably also related to the need to congregate during the mating period when males can display by means of a complex and beautiful song (Payne and McVay 1971; Tyack 1981) and compete for access to females (Tyack and Whitehead 1983; Baker and Herman 1984).

Humpback whales do not usually forage during the winter on the breeding grounds probably because adequate concentrations of prey are not available (Dawbin 1966; Baker 1978; Herman 1979; Whitehead and Moore 1982). The feeding season in northern waters is thus vital to Northwest Atlantic humpbacks since they need to obtain total annual energy requirements within a four to six month period. They can therefore be theoretically classified as energy maximizers (Schoener 1971), ie. their feeding time is limited so they should maximize energy obtained per time spent feeding. Humpback whales seem to be subject to few conflicting major selection pressures during the feeding season other than occasional predation by killer whales (Orcinus orca) (Whitehead and Glass 1985; pers. obs.). Almost all activity relating to mating and reproduction is confined to the wintering grounds. The need to forage efficiently thus will not be substantially compromised as it often is for other animals (Krebs et al. 1981), and most of the behaviour exhibited by humpback whales off Newfoundland could reasonably be assumed to be shaped by the need to feed efficiently.

1.3 Prey species

In comparison with many other species of whales, humpbacks are considered to be generalists, exploiting a wide variety of food types (Nemoto 1957, 1970; Slipjer 1962). Specificity of prey appears to depend partially on available stocks of forage species, although it is likely that prey preferences do exist. In the southern hemisphere they eat primarily euphausiids (Euphausiidae spp.) (Nemoto and Kawamura 1977). In the North Atlantic and North Pacific their diet is more varied (Slipjer 1962; Nemoto and Kawamura 1977). In the North Pacific the humpback whales' feeding range extends from the western rim of the North Pacific in the Sea of Okhotsk to the Gulf of Alaska on the eastern rim (Tomlin 1967), but some may feed off California rather than travel further north (Dohl 1983). Euphausiids are their major prey in the Northwest Pacific although schooling fish such as sardines (Sardinops spp.), herring (Clupea spp.), Atka mackerel (Pleurogrammus monopterygius) and saury (Cololabis saira) are also important (Nemoto 1957). Off Alaska humpbacks exploit euphausiids (Euphausia pacifica), herring (Clupea harengus), capelin (Mallotus villosus) (Jurasz and Jurasz 1979) and pacific sand lance (Ammodytes hexapterus) (Marine Mammal Commission 1980; Dolphin and McSweeny 1983). They may also take walleye pollock (Theragra chalcogramma) deliberately (W.Dolphin pers. comm.), or incidentally while exploiting krill (Jurasz and Jurasz 1979). Humpbacks have also been reported to exploit pandalid shrimp (Pandulus borealis), mysids (Mysiidae spp.) and amphipods (Amphipoda spp.) (Marine Mammal Commission 1980).

In the different feeding stock regions of the Northwest Atlantic humpback whales utilize different prey species, probably due to differences in prey availability among areas. Off the Gulf of Maine primary prey species are sand lance (*Ammodytes americanus*) and herring (Overholz and Nicolas 1979; Hain et al. 1982) and humpbacks may occasionally take pollock (*Pollachius virens*) (Watkins and Schevill 1979). Although capelin is the most important forage species for the Newfoundland - Labrador feeding stock (Mitchell 1973, 1975) humpbacks also exploit various species of krill (depending on what is available) and squid (*Illex illecebrosus*) (pers. obs.). Mackerel (*Scomber* spp.), sand lance and haddock (*Melanogrammus aeglefinus*) have also been found in stomachs (Mitchell 1973).

There are five major capelin stocks in the Northwest Atlantic : 1) Labrador - Northeast Newfoundland stock, 2) Northern Grand Banks - Avalon stock, 3) South Grand Banks (Southeast Shoal) stock, 4) St. Pierre - Green Bank stock, 5) Gulf of St. Lawrence stock (Carscadden 1983a, 1983b). All of these are probably exploited by whales to some degree although stocks 1), 2) and 3) are the largest (Carscadden 1978; Carscadden and Miller 1981) and are the most heavily exploited. The Northern Grand Bank - Avalon stock and the Southeast Shoal stock overwinter on the north part of the Grand Banks (Campbell and Winters 1973) and move inshore to spawn on Newfoundland beaches and on the Southeast Shoal of the Grand Bank respectively, in June and July (Carscadden 1983a, 1983b). Water temperature is a prime determinant of spawning time (Jangaard 1974). In inshore Newfoundland and Labrador spawning occurs in water temperatures of 5.5°C - 8.5°C (Templeman 1948) and on the Southeast Shoal in temperatures of 2.0 - 4.0°C (Pitt 1958). In inshore locations spawning occurs progressively later from southern to northern regions with the northward progressing rise in water temperature (Jangaard 1974). Spawning typically occurs in early June on the west and south coasts of Newfoundland, in late June to early July on the Southeast Shoal and the eastern Avalon Peninsula and in late July to early August in southern Labrador (Carscadden 1983a, 1983b; Leggett et al. 1984).

Capelin are probably subject to the greatest predation pressure during spawning for two reasons: 1) they are concentrated in shallow inshore areas where predators are abundant, and 2) spawning occurs at a time of year when some predators (seabirds, seals, whales) have increased food requirements. Spawning usually occurs at 3 - 4 years of age (Winters 1974). Less information is readily available on locations and migration of concentrations of immature capelin. Large feeding schools have been reported on the northern bank region of the Avalon Peninsula (Miller and Carscadden 1980, 1981) and in offshore waters from Labrador to northeast Newfoundland (Carscadden 1983b). Concentrations of immature fish may also move inshore to feed (Brown and Nettleship 1982) and may even overwinter in deep water fiords such as Trinity Bay (Winters 1970).

1.4 Baleen whale feeding

Baleen whales have been divided into skimmers, those that swim through surface concentrations of prey with the mouth open, passively sifting organisms, and swallowers (Nemoto 1957, 1970; Pivorunas 1979). Pivorunas (1979) puts only right whales (Balaenidae spp.) in the skimmer category while Nemoto (1957, 1970) includes sei whales (Balaenoptera borealis). Humpbacks, along with blue (B. musculus), fin (B. physalus), minke (B. acutorostrata) and Bryde's (B. edeni) whales are classified as swallowers. Prey and water are engulfed from dense schools or swarms and are temporarily held in the large buccal cavity formed by the mouth and expanded ventral grooves. Tongue pressure and contraction of the ventral grooves forces water out through the baleen; trapped prey are then swallowed (Nemoto 1970; Pivorunas 1979).

The different feeding mechanisms in skimmers and swallowers are correlated with morphological differences. Skimmers have very finely fringed long flexible baleen plates, deep pockets between the tongue and large lower lip or blubber flap to accommodate the ends of the baleen when the mouth is open and an arched rostrum to permit a wide gape (Nemoto 1957; Slipjer 1962; Pivorunas 1976, 1979). This anatomical design permits continued sifting while swimming through less dense layers of small sized prey items. Swallowers have shorter more rigid (to prevent deformation under water pressure) coarsely fringed baleen, a highly elastic sheet like tongue and a set of 20 - 100 ventral throat grooves; the latter two structures permitting extensive expansion of the bucccal cavity (Slipjer 1962; Nemoto 1970; Leatherwood et al. 1976; Katona et al. 1977; Pivorunas 1979; Watson 1981). The lower jaw has a reduced surface of articulation with the upper jaw so that it can drop forward and widen the whale's gape (Pivorunas 1976; Weinrich 1981). Swallowers or gulpers are thus morphologically adapted to quickly engulf large volumes of prey and water and upon closure of the mouth, to squeeze out the water, trapping the prey against the baleen. Because they are adapted to engulf rather than to sift through prey, swallowers require denser patches of prey than do skimmers (Nemoto 1957, 1970; Pivorunas 1979).

The diameter or fineness of the inner fringes on the baleen plates differs among swallowing type whales and varies with the size of prey items in the diet. Sei whales have very fine baleen fringes and typically utilize small sized prey such as copepods, Copepoda spp., and amphipods (Nemoto 1962, 1963; Kawamura 1974, 1978). They may feed in a manner similar to skimmers, sifting through surface prey, or may engulf prey from denser schools (Kawamura 1974; Katona et al. 1979). Species that eat primarily euphausiids (blue and fin whales) have coarser baleen fringes while the coarsest baleen is found in icthyophagous species (minke and humpback) (Nemoto 1957, 1970).

1.5 Humpback feeding behaviour

In summary then, humpbacks are swallowers with relatively coarse baleen, exploiting a wide variety of prey types, many of which are schooling fish. As a species they also possess a tremendously diverse repertoire of feeding behaviour and some unique morphological characteristics that both enable them to exploit many types of prey and to concentrate (and thus more efficiently engulf) prey from more dispersed sources. Different populations and sub-stocks of humpback whales exploit different prey species and therefore exhibit different foraging strategies.

Humpback foraging behaviour in the Gulf of Alaska has been extensively studied and described but quantitative data are scarce. Jurasz and Jurasz (1979) identify three basic feeding modes: lunge feeding, bubblenet feeding and flick feeding, with variations within each type. When lunge feeding the angle of the saggital plane of the whale to the water surface was observed to take three po[illegible]ions: vertical, lateral and inverted. Euphausiids, herring and capelin were exploited using lunge feeding and lunging speed increased with the swimming speed of the prey species (herring being the fastest, euphausiids the slowest). Groups of whales frequently coordinated lunges while swimming abreast in a diagonal line (echeloned).

Whales make bubblenets by exhaling gradually at depth while swimming in an arc. The rising bubbles form a ring or a closing spiral, the bubbles decreasing in size as the whale continues to exhale. The larger and more mobile the prey, the larger the initial bubbles in the ring (Jurasz and Jurasz 1979). Prey is condensed and contained as it is driven upward by the bubblenet (Earle 1979). The whale lunges through the center of the net as it reaches the surface or engulfs the aggregated prey just below the surface. Jurasz and Jurasz (1979) report the use of bubblenet feeding to exploit herring and euphausiids but not capelin. In flick feeding, observed only on euphausiid prey, the whale flicks the dorsal surface of its flukes down forcefully on the water surface as it dives, causing a splash and an internal wave. The wave moves forward and then after a few seconds the whale surfaces, mouth open, amidst the wave (Jurasz and Jurasz 1979). The whales were highly flexible in their choice of exploitation strategy, intermixing all these feeding modes and their variations (Jurasz and Jurasz 1979).

Dolphin and McSweeny (1981, 1983) have also studied humpback whales foraging off Alaska and have found correlations between both feeding strategy and respiration rates and the depth of prey schools. In addition they report the use of barriers such as rock faces, bubble curtains, the water surface and interfaces formed by abrupt temperature, density, salinity and velocity changes against which humpbacks herd prey (Dolphin and McSweeny 1981).

The various strategies used by humpback whales to exploit sand lance and herring in the Gulf of Maine have been described by Hain et al. (1979, 1982) and Watkins and Schevill (1979). Some of these such as echeloned lunge feeding, flick feeding (with the ventral side of the flukes here however) and bubblenets in the form of rows, circles and spirals are similar to those reported from the Gulf of Alaska. Hain et al. (1979, 1982) also report the use of bubble clouds, a single underwater exhalation of uniformly sized bubbles, to drive prey toward the surface. The whale may surface in the center of or beside the cloud and clouds may be produced in series or in multiples.

Off Newfoundland humpback whale feeding behaviour has been investigated by Davies and Harrison (1981) and Whitehead (1981). Whitehead (1981) discerned three types of feeding behaviour which were determined by the type of prey the whales were exploiting. These were 1) shallow water slow prey (probably capelin), 2) shallow water fast prey (perhaps squid) and 3) deep prey (capelin or plankton). The whales' basic behavioural strategies were similar in all three situations: whales dove into the sub-surface prey schools and little surface activity was seen. Lunging occurred on shallow water slow prey (capelin) only. Aspects of the basic sequence of behaviour that varied with prey type were: speed of movement at the surface (faster with fast prey), dive duration (longer with deep prey) and resurface duration in relation to dive location (whales travelled horizontally underwater with fast prey but resurfaced close to the dive area with deep prey) (Davies and Harrison 1981; Whitehead 1981). These studies were among the first that attempted to relate quantifiable aspects of whale feeding behaviour to measureable bait parameters.

Brodie (1977) and Edel and Winn (1978) suggested that the long white flippers, a morphological characteristic unique to humpback whales, might aid in prey capture. The flippers, because of their length, flexibility and range of motion would make humpbacks more manoeuvreable than other species of baleen whales (Edel and Winn 1978; Whitehead 1981) which may be important in exploiting fast swimming highly mobile prey (fish, squid) and for performing the complex feeding strategies hitherto described. They may also be used to herd fish. The white V and dark center formed by the humpbacks' outstretched flippers and body may induce fish that are near the proximal end of the flippers to avoid the light area and move towards the dark and into the whales' mouth (Brodie 1977). Brodie (1975) noted that where fish are a major component of the diet, humpback flippers are lighter in colour (e.g. Northwest Atlantic) than in areas where they eat mostly krill.

Previous research has thus demonstrated that humpback whales possess a wide repertoire of foraging behaviour that is highly variable, flexible and adaptable to the prey situation being exploited. Upon initial observation of humpbacks foraging in Newfoundland waters however, where capelin is the dominant prey species, this variability is not immediately apparent. There have been no unequivocal reports of the elaborate bubbling behaviour observed in other areas. Vertical and oblique lunging up through capelin schools (Davies and Harrison 1981; Whitehead 1981) and lateral lunging on krill (pers. obs.) are the only types of surface foraging behaviour documented to date. Whales are most often seen diving repeatedly into areas where prey aggregations probably exist.

While watching groups of humpback whales that were almost certainly feeding I had the impression that whales had a deliberate foraging strategy in spite of the absence of overt feeding behaviour. Diving behaviour was regularly patterned and confined to a restricted area, an apparent indication that a localized prey school was present. Questions arose as to how the whales were responding to the size, depth, extent, position, shape and movement of the prey school they were exploiting. I decided to measure visible aspects of behaviour that could be quantified (e.g. dive and surface time, direction, speed and distance of travel and group sizes) and investigate their relationship to bait parameters (such as those itemized above) measured with a depth sounder. I wished to investigate how foraging behaviour differed in different bait situations to see how behavioural variation in the quantifiable components of foraging behaviour might enable whales to more efficiently exploit various types of prey. I also wished to determine if the characteristics of foraging dives could be predicted from bait parameters and specifically which prey school features whales were responding to most strongly.

This study was initiated in 1979 and most data were collected in 1980 and 1981, before many of the previously described foraging behaviour findings were available. Completion of this work has in part corroborated the findings of other investigators, notably Whitehead (1981, 1983) and Dolphin and McSweeny (1983).

CHAPTER 2. METHODS

Boat-based observations of humpback whales were made off the coast of Newfoundland during the summers of 1979, 1980 and 1981. Work in 1979 served as a pilot study to perfect observational techniques. Whale groups were followed, behaviour was recorded, and movements were plotted on a map. Observations in 1980 and 1981 were an extension of 1979 methods with the addition of bait school information provided by a depth sounder.

2.1 Equipment

Groups of whales were followed with a 6 m fiberglass boat with a 35 hp motor. Whale behaviour was timed with a digital watch and observations were recorded verbally on a cassette tape recorder. A Si-tex Honda HE 30B paper printout echo sounder with a frequency of 50 KHz, a 40° cone beam transducer and a marking device was used for bait observations. One or more crew members were always present, primarily for safety, however in 1981 an assistant took compass readings, plotted whale and boat positions and measured boat speed.

2.2 Locations

Whales were observed in various locations, the choice of which was determined often by logistical factors in addition to a stable concentration of feeding whales. Logistical factors included available safe dock or mooring space, relatively short travel times to concentrations of feeding whales and shelter from heavy seas. The most productive study locations, from which most of the data for this study were drawn, are given in Figure 2.1 (see also Table 3.1).

2.3 Behavioural observation

An individual or a group of whales was followed for 1 - 5 h with the depth sounder on while behaviour was continuously recorded. Each watch of one whale group (or individual) was defined as an observation bout. Usually one, but occasionally two, observation bouts were done each day. In 1980 watches were seldom longer than 3 h. Watches ended either when 1) an adequate sample (2 - 5 h) of behaviour of that group feeding on a particular bait school was taken, 2) whales left the area, 3) weather changes, nightfall or motor trouble precluded further observation, or 4) whales ceased foraging and did not resume within about 1 h.

Groups were easily delineated. They moved as a unit, individuals travelled close together, usually within 15 m, and coordinated dives, surfacings and swimming directions. Groups were identified by the number of whales and by individual whale characteristics such as size (estimated length), dorsal fin shape, fluke pattern and other body

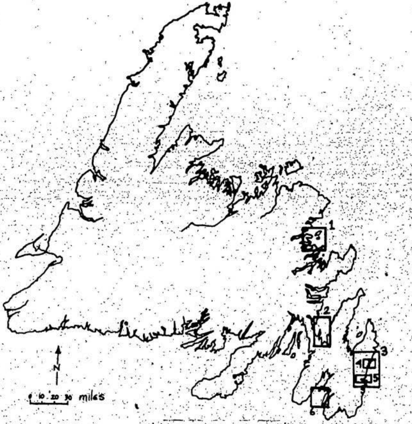


Figure 2.1

Map of Newfoundland showing study locations. 1.Varket Channel. 2.Trinity Bay. 3.Great Island - East Coast of the Avalon Peninsula. 4.Witless and Mobile Bays. 5.Cape Broyle Harbour. 6.St. Mary's Bay.

markings like scars or skin texture. Identifying humpback whales by these methods is standard practice (Katona et al. 1979; Katona and Whitehead 1981). In 1979 and 1980 fluke photographs were taken when possible.

Choice of study group was not random. On first encountering whales, groups of animals that seemed to be feeding were selected. Whales were not systematically observed if they were travelling, as indicated by movement at moderate speed in straight lines, or engaged in activities such as repeated breaching, lobtailing, rolling or flipper slapping (see Table 2.1). If after foraging for a while whales switched to other behavioural modes or states (travelling, resting, etc.) observation was usually continued to obtain information on time spent in other activities.

Decisions about whether whales were foraging (feeding) or not were based both on their behaviour and the presence of bait. Foraging behaviour when bait schools were deep (see Table 3.1) was characterized by repetitive dives and surfacings in one area and was thus easy to identify. When whales were diving but in the absence of prey they were considered to be not foraging. When bait was shallow and in small scattered schools, it was more difficult to discriminate between foraging and non-foraging behaviour. Here, non-foraging behaviour was distinctive. Travelling (see above) was also indicated by intervals between blows of more than 20 s as compared with a regular blow interval of about 10 s for surface movements while foraging. When

Table 2.1. Humpback whale behaviours referred to in the text. After Whitehead (1981).

BREACH	A leap from the water with more than half the body coming above the water surface. Whales often twisted while in the air to land on their backs.
FLIPPERING	Flipper visible above the water surface. Usually the whale would roll onto its side, lift the flipper vertically above the water, and allow it to fall back in, frequently slapping the water surface loudly. Whales sometimes flippered with both flippers when lying on their backs.
LOBTAIL	Thrash of the flukes onto the water surface. Usually the flukes would be lifted vertically above the water, and brought face down, ventrally or dorsally, onto it, often with great force.
LUNGE	A lunge from the surface showing less than half the body. Lunges could be vertical, horizontal, or any angle in between, and were conducted with the whale dorsally uppermost, ventrally uppermost, or on its side.
SPYHOP	Head of whale slowly raised above water.
TERMINAL DIVE	Whale disappears from the surface for at least 1.0 min, and usually for longer. Dives were typically preceeded by fluke-ups, tail arches or occasionally sideflukes.
FLUKE-UP	Flukes lifted to a vertical or less than vertical position while terminally diving. Movement ranged from flukes being dragged along the water surface, barely leaving it, to an almost vertical angle.
TAIL ARCH	Whale arches tail stock prior to terminal dive but flukes remain below the surface of the water.
SIDEFLUKE	Flukes visible above the water surface but oriented laterally rather than horizontally, as is usual. Whales sometimes propelled flukes forcefully sideways, other times they simply dove in a lateral position, rotated 180° about their long axis. In the latter case, often only half the fluke was seen.
LULL	Whale at surface moving very slowly or not at all.

resting whales also had longer intervals between blows and usually hung just below the surface with flippers extended, hardly moving at all. Absence of prey on the depth sounder was always taken to be indicative of no food and thus non-foraging behaviour. Overt feeding behaviour such as lunging was never seen without the presence of bait on the sounder.

Choice of groups for continued observation was also based on the ability to follow them. When whales were very dense, groups were easily confused after resurfacing. In such situations whale groups on the periphery of the dense concentrations were more easily followed.

In inshore Newfoundland waters humpback whale group sizes range from 1 - 10 but groups larger than 5 are rare (Whitehead 1983). I attempted to obtain a representative sample of the more common group sizes but this was not always possible. Often only certain group sizes were present in a location. A lot of time could not be spent locating and travelling towards groups of a specified size. It often took at least 30 min of observation to get to the point where the group could be reliably identified and consistently followed. Group sizes could change either by the time we got close enough for observations or soon after the observation bout began.

Whales were usually followed at a distance of 50 - 100 m. The boat did not visibly disturb them at these distances and the slow speeds, usually 1.5 - 3.0 knots, kept the engine noise low. On a few occasions we caused directional changes or premature fluke-ups if, for example, we suddenly increased speed to catch up to a fast moving group. These possibilities were always recorded. Very rarely whales would approach the boat or appear to look at us by spy hopping (see Table 2.1).

Behaviour was recorded for each individual in the group when possible. Resurface times and times of terminal dives were recorded to the nearest s. Terminal dives were identified by a fluke-up or a tail arch (see Table 2.1) and disappearance from the surface for longer than 1 min. Behaviour immediately prior to diving (down behaviour) was classified as fluke-up (Y), low fluke (LY), side fluke (SY), tail arch (TTA), or terminal dive with no fluke-up (TDNF).

While at the surface, the track of the group was monitored continuously by noting directions, distances and speeds of travel. Directional variables recorded include travel heading at the surface (true direction), terminal dive direction and resurface direction if observed. Swimming speeds were categorized (fast: >4 knots; moderate: 2 - 4 knots; slow: 0.5 - 2 knots) and recorded. Incidences of individual behaviours (Table 2.1) and the number of blows at the surface were noted. The information about travel distances, swimming speed and surface blows was not included in the computer analysis but it provided information about whether the whales were foraging and was valuable as general behavioural description.

Group data were also recorded when possible and included swimming conformation (arrangement of members of the group in space: in a horizontal line, whale A to the left, or one behind another etc.) and order of individual terminal dives. Repeat groupings, where the same whales were found together in the same group on successive or different days were recorded as were any repeat sightings of individuals.

2.4 Depth sounder data

When following whales the depth sounder was on continuously. Path traces of the whale group were done: when they resurfaced we would ~~go~~ to the area and then follow directly in their path. If they surfaced too far away we would simply head towards them and start to follow as soon as possible. The depth sounder was marked at the beginning of this path trace and at the end when the whales terminally dove, the location of which generally appeared as a circular calm patch or "footprint" on the water surface. After passing through the footprint where the whales went down, we usually continued travelling on the same bearing as the whales' terminal dive direction for approximately 50 - 100 m, the sounder would again be marked and we would wait for them to resurface. We sometimes went to the left or right of the predive direction at 30°, 45°, or 90° but this was not systematically done. Path tracing the foraging group provided a picture of the bait school the whales were presumably diving into. In addition to terminal dive areas the sounder was marked at the positions where whales lunged and occasionally where they turned or performed behaviours such as flipper slapping, rolling, breaching, etc.

To determine the approximate size, shape and position of fish schools fed on by whales we travelled back and forth repeatedly across the school at constant boat speed with the depth sounder on. We traversed across it in one direction until bait ended and then returned at a slightly different angle in order to cross the school at sucessively different points (Figure 2.2). This procedure is hereafter referred to as a bait school trace. We usually plotted our position in relation to landmarks or took compass bearings at turn points.

2.5 Bait identity

Depth sounder traces were the main source of information about bait identity. Additional evidence was provided by direct sampling of bait with a dip net or jigger, talking to fishermen about contents of cod (Gadus morhua) and bird stomachs, watching birds and collecting whale faeces. Traces were further verified by a capelin biologist and bioacoustician (D.Miller pers. comm.) and by capelin seiners. Representative figures of the depth sounder recordings of prey from the different study locations are included in the appropriate results section.

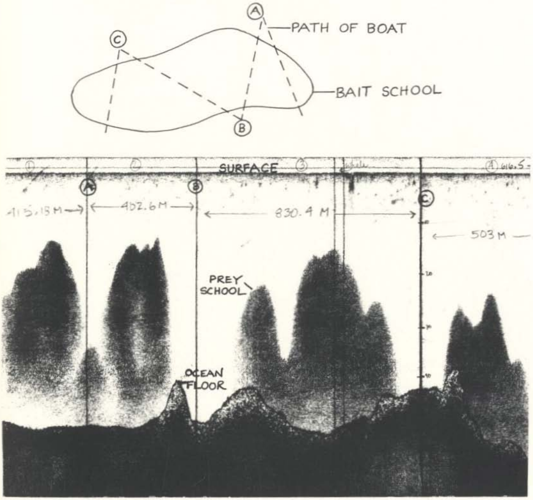


Figure 2.2

Schematic representation of a bait trace showing the outline of a prey school and the path of the boat (top). An example of resulting output on the depth sounder is also illustrated (bottom). The bait school was crossed four times at different places. Each single line on the trace indicates a turn point, the double line signifies the presence of a group of whales. Depth scale is 0-60 fathoms (0-109.7 m).

2.6 Map data

In some locations, when surrounded fairly closely (within 2 km) on at least two sides by land, plots of whale group movements were made on a map of the area. Terminal dive positions and sometimes resurface positions were plotted. In 1981 it was possible to make detailed plots of the paths taken by whales at the surface and to note spatial relationships of individuals within the group. Working in small bays such as Witless and Mobile Bays facilited plots accurate to within 200 m.

When landmarks were more distant a sighting compass was used to obtain bearings from the footprint location to three prominent points of land. It was not always possible to do this for every terminal dive but it was done quite regularly. This provided knowledge of the whales' approximate location (within 1 km) and large scale changes in location over the course of an observation bout.

2.7 Census data

In the smaller bays (Witless Bay, Mobile Bay, Cape Broyle Harbour) and in Varket Channel, the total number of whales in the study area were counted 1 - 8 times per day. In areas not sufficiently surrounded by land or where land was too far away to permit reliable sighting of all whales present, 5 min counts of all whales visible and their direction and distance from the boat were made 1 - 8 times per day (see Ramsey and Scott 1979). A second 5 min count was frequently repeated immediately after the first to provide another sample for that time period. Whale counts were made at times to coincide with observation bouts and when we moved to different locations within the study area.

2.8 Analysis

Because the depth sounder was marked at terminal dive areas, values of bait variables were available for each foraging dive. Knowledge of boat speed and paper speed permitted calibration of the horizontal axis of the depth sounder printout into m of water (Figure 2.3). The cross sectional area of bait 75 m to either side of the terminal dive mark, approximately 150 m around the footprint (Figure 2.3), was determined with a Zeiss MOP digitizer.

Continuous behavioural observations were partitioned into units consisting of a period of time spent at the surface plus the following dive time. Each case for computer analysis was structured around these behavioural units. Table 2.2 defines the variables that constitute a case. Behaviour occurring at the surface that could be quantified and categorized and measures of the actual time intervals (surface and dive time) were included as variables. Matched with each set of whale variables were the corresponding bait variables from depth sounder printouts. One case could thus be considered to be one dive by a whale or group of whales (see following) into a given set of bait characteristics with dive expanded to include the time spent and the behaviour occurring at the surface

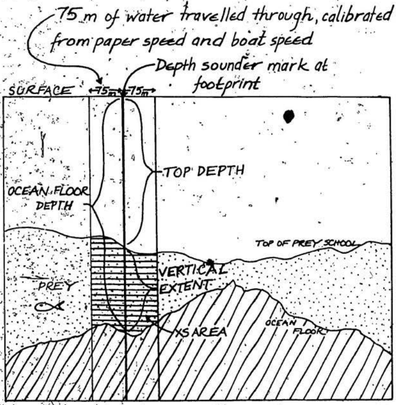

75 m of water travelled through, calibrated from paper speed and boat speed
Depth sounder mark at footprint
SURFACE
75m
75m
TOP DEPTH
OCEAN FLOOR DEPTH
TOP OF PREY SCHOOL
VERTICAL EXTENT
PREY
XS AREA
OCEAN FLOOR

Figure 2.3

Schematic depth sounder printout with mark at terminal dive location and illustrating bait variables.

Table 2.2. Variables used in the analysis.

CONTINUOUS WHALE VARIABLES

SURFTIME	Time spent at the surface in min.
DIVETIME	Time spent below the surface in min.
UNITIME	Surface time plus following divetime.
RATIO	Ratio of divetime to previous surftime.
GROSDIR	Total directional change at the surface in degrees. For example headings: E - S - W - S = 270°.
NETDIR	Magnitude of net change of direction at the surface. For example headings: E - S - W - S = 90°.
CLOCK	Net clockwise directional change at surface: E - S - W - S = 90°.
COUNTER	Net counterclockwise directional change at surface: E - S - W - S = 45°.

CONTINUOUS BAIT VARIABLES

FLRFP	Ocean floor depth at footprint in m.
FLRAV	Ocean floor depth averaged 150 m around, or 75 m to either side of the footprint.
TOPFP	Depth to top of bait school at footprint in m.
TOPAV	Depth to top of bait school averaged 150 m around footprint.
VEXTFP	Vertical extent of bait school at footprint in m.
VEXTAV	Vertical extent of school averaged 150 m around footprint.
AREA	Cross sectional area of bait school 150 m around footprint (m^2).

CATEGORICAL VARIABLES

DWNBEHAV	Down behaviour: fluke-up, low or side fluke, no fluke-up.
FORAGE	Foraging or not foraging
LUNGE	Number of surface lunges for each period of time spent at the surface.
HOUR	Hour of day.
TYPE	Type of bait school: deep capelin, shallow capelin or krill.
PLACE	Study location.
DATE	Date of observation.
GPSIZE	Size of followed whale group.

prior to diving. Two types of each bait variable, at the footprint and averaged 150 m around the footprint (Figure 2.3 and Table 2.2), were included in the analysis. It was originally thought that the average value would be less arbritrary, however values of each were habitually very similar.

Two data sets were created: one for individual whales and one for whale groups. For the individual data set, one surface - dive bout or case exists for each dive for each whale in the group. For the group data set, one case is one surface - dive bout for the group as a unit. Because each individual whale is represented in the individual data set, whale variables (e.g. times and directions) are valid. Bait variables alone, unless in conjunction with whale variables, will be invalid because for large groups bait variables will be over represented by a factor of the number of whales in the group. In the group data set each case represents one dive into one bait situation by a foraging unit (whale group); it is the set of all bait situations whales foraged on (dove or lunged into). Whale variables are invalid because individuals are not represented. Use of the group or individual data set in a particular analysis depended on the focus of each research question. The group data set was used for all all analyses involving bait variables only.

All analysis was done with the SPSS statistical package (Nie et al. 1975). Multivariate analyses of variance were done to determine the effect of each categorical variable (DATE, PLACE, TYPE, FORAGE, GPSIZE, DWNBEHAV, LUNGE, see Table 2.2) on: 1) all continuous variables, 2) continuous whale variables only, 3) bait variables only. This was done as a prerequisite to finer tests of significance that require the existence of an overall effect, such as multiple comparison tests.

Non-significant multivariate analysis of variance results precluded further testing. If results of multivariate analysis of variance were significant, the effect of each categorical variable on each continuous variable was examined using one-way analysis of variance. When one-way results were significant the Newman-Keuls multiple comparison test was performed to reveal significantly different groupings among levels of the categorical variable. Levels of significance were 0.05 unless otherwise stated.

To examine the effect of bait characteristics on surface and dive times step-wise multiple regression analyses were done using the individual whale data set. Both bait and whale variables (except for the dependent time variable) and then bait variables alone were used as independent variable sets in two step-wise regression analyses. Results from the first analysis will demonstrate the relationship of each time variable to other whale variables as well as bait variables, results from the second will depict each time variable solely as a function of bait variables. Both types of each bait variable, at the footprint and averaged 150 m around the footprint, were originally entered into the regression equation. To correct for multicollinearity, which results from the combination of such pairs of highly correlated independent variables, regressions were rerun removing variables that were very highly correlated with each other (r>0.940). In the deep prey locations this necessitated using only the footprint value of each bait variable, in the shallow prey locations only the variable of ocean floor depth averaged 150 m around the footprint needed to be removed.

Durbin-Watson tests were run for each separate multiple regression to monitor autocorrelation effects. The test procedure is not exact though, if the calculated statistic falls between the upper and lower test bounds, the results are inconclusive (Nie et al. 1975). Analyses that were found to be autocorrelated when every case of the data set was used were rerun using only the first case from each hour to remove the continuity of cases in time. In order to smooth out some of the variability inherent in the dive by dive data set, a set of multiple regression analyses was performed on an aggregated data set consisting the mean value of each variable for each hour of observation.

2.9 Effort

Table 2.3 delineates the size of each data set broken down by study location. As a measure of effort, the number of observation bouts and average bout length for each place is also included. This is much less than the total time spent at sea as considerably more time was spent in logistical activities such as finding whales, travelling to where whales were, finding an appropriate group to follow, tracing bait schools, etc.

Table 2.3

The number of cases in the whale group and individual data sets, the number of observation bouts (continuous periods of observation) and the total time spent in observation bouts in each study location. No group data set exists for St. Mary's Bay krill feeding as whales were acting individually for most dives. They did not coordinate activities and move as a foraging unit as groups did in most other study locations.

	Group Data (no. of dives)	Individual Data (whales x dives)	Number of Observation Bouts	Total Hours of Observation
		DEEP CAPELIN		
VARKET CHANNEL	139	226	9	14.2
TRINITY BAY	193	592	14	24.8
GREAT ISLAND	120	225	6	16.5
DEEP BAIT TOTAL	452	1043	29	55.5
		SHALLOW POST SPAWNING CAPELIN		
WITLESS MOBILE	139	221	4	14.3
CAPE BROYLE	60	99	3	6.8
SHALLOW BAIT TOTAL	199	320	7	21.1
		KRILL		
KRILL NO LUNGING		27	2	2.3
KRILL LUNGING		36	1	2.2
KRILL TOTAL		63	3	4.5

CHAPTERS 3 - 10. RESULTS

Results will first be presented for each study location which represent different bait, and therefore foraging, situations (See Table 3.1, Figure 2.1). The deep capelin foraging locations are presented first (Chapters 3 - 5), then shallow capelin locations (Chapters 6 and 7) and finally krill feeding (Chapter 8). Chapter 9 will summarize the effects of the categorical variables (FORAGE, GPSIZE, DWNBEHAV) on continuous whale behavioural variables and on bait variables within each bait type (deep capelin, shallow capelin, krill). Foraging behaviour in the different bait situations will then be compared (Chapter 10).

Table 3.1. Study locations and their bait characteristics.

VARKET CHANNEL BONAVISTA BAY	July 30 - August 19, 1980. Deep immature capelin. Whales and bait were in Varket Channel between Willis and Bessy Island to the north and Morris and Ship Island to the south for the duration of the study period.
HEAD OF TRINITY BAY	August 21 - September 22, 1980. Deep immature capelin. For the first half of the study period whales and bait were just off Collier Point and Chapel Head, they later moved north and west along the east side of the Bellevue Peninsula and then west until they were southeast of Bull Island.
SOUTHERN SHORE WITLESS AND MOBILE BAYS	July 8 - 10, 1981. Very small schools of post-spawning capelin. Bait schools were scattered throughout Witless Bay but were locally concentrated in Mobile Bay.
CAPE BROYLE HARBOUR	July 11 - 17, 1981. Small shallow schools of immediately post spawning capelin. Bait was initially concentrated off Gentleman Pt.; it then dispersed along the southern shore of the outer part of Cape Broyle Harbour.
EAST OF THE AVALON PENINSULA OFF GREAT ISLAND	July 18 - 26, 1981. Deep and midwater post spawning capelin. Bait schools were located east of La Manche to southeast of Great Island, being found progressively more northward throughout the study period.
ST. MARY'S BAY KRILL FEEDING	June 24 - July 5, 1981. Krill, Euphausiidae sp. Whales were lunging and feeding on small surface swarms of krill west of Gaskiers and Point La Haye.

CHAPTER 3. VARKET CHANNEL

Behavioural observations of humpback whales were carried out in and near Varket Channel, Bonavista Bay from 30 July to 19 August 1980. Whales and bait were present in Varket Channel (Figure 3.1) throughout this period. On two days we travelled around Willis Island into Willis Reach and observed whales feeding off the northeast tip of Willis Island and just north of Great Black Island.

3.1 Bait schools

Figure 3.2 shows the locations of bait schools throughout the study period as determined from bait traces and from path traces of whales feeding on the schools. From these traces, the east school (30 July, 3, 10 August, labelled east, Figure 3.2) seems to be distinct from the west one. Following a northwest gale on the night of 10 August the west school moved farther south. Small schools (2, 7, 12, 15 August) were separate from large ones seen on the same date but were similar in appearance on the depth sounder printouts.

Sounder printouts of typical prey schools from Varket Channel are presented in Figure 3.3. Bait was deep and likely consisted of immature capelin or possibly immature herring. Fishermen found immature capelin in the stomachs of cod taken off Bessy Island on 1 - 2 August but aside from this there was little fishing in the immediate study area.

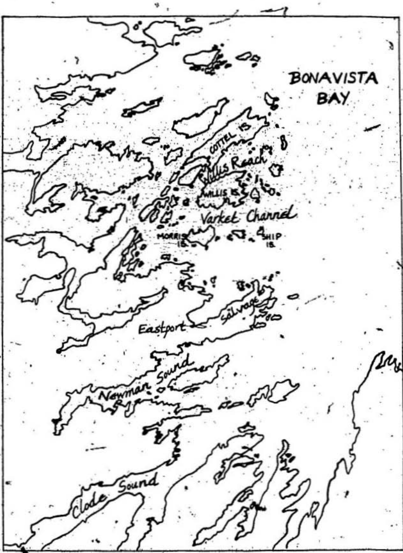


Figure 3.1

Varket channel study area. Throughout the study period (2-19 August) whales were located primarily in Varket Channel although some were also seen in the east part of Willis Reach.

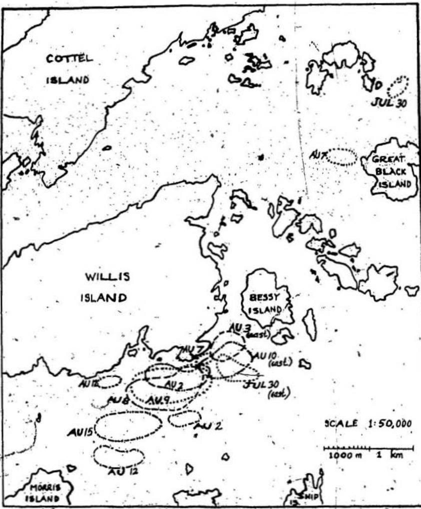
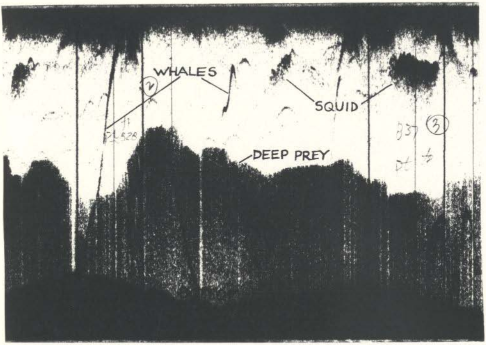


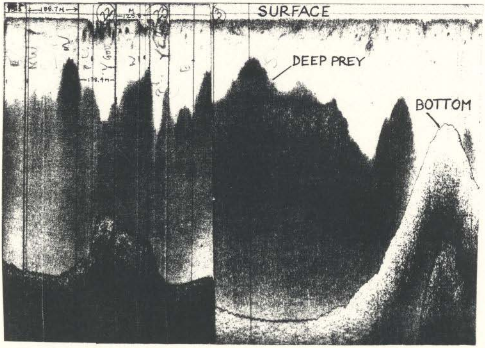
Figure 3.2

Locations of prey schools that observed groups of whales were utilizing on different days of the study period in Varket Channel.

Figure 3.3

Depth sounder traces of (probably) immature capelin from Trinity Bay (top) and Varket Channel (bottom). Small squid schools can be seen above the deeper bait in the top figure. Squid schools, verified by jigging, consistently occupied this position in the water column and were coarser grained in trace appearance. The top trace also shows whales emerging from (far left) the deep prey schools. Depth scale is 0-60 fathoms (0-109.7 m).


WHALES
SQUID
DEEP PREY
②
③


188.7M
138.4M
125.
SURFACE
DEEP PREY
BOTTOM
③

On 2 - 3 August the bait school was quite vertically extensive, in some locations just 10 - 30 m below the surface. Gannets (*Sula bassanus*) and terns (probably *Sterna hirundo* and *S. paradisaea*) were observed diving in areas where bait was close to the surface and coming up with small (10 cm) fish that had dark dorsal parts and looked like immature capelin. Attempts to take underwater photographs of the school and to jig something when the depth sounder indicated a location directly over bait were unsuccessful.

Mean depths to the top of the bait school, to the ocean floor, and of the vertical extent of the bait school for this location are presented in Table 3.2. Figure 3.4 depicts daily variation in the mean depths of the top of the bait school and of the ocean floor. The vertical distance between the two curves (top depth - floor depth = vertical extent) gives only an approximation of the mean daily vertical extent of fish for two reasons. Because all of the variables are calculated independently for each dive, the mean daily top depth subtracted from the mean daily ocean floor depth is not necessarily the mean daily vertical extent of fish. Fish schools were usually but not always on the bottom so this would also produce the discrepancy. A more accurate illustration of the mean daily variation of the vertical extent of fish schools at terminal dive locations is given in the lower portion of Figure 3.4.

Table 3.2

Mean values of bait variables averaged over the entire study period in locations where prey schools were deep. All depths are in m, XS AREA is in m . (*) indicates a significant difference ($p<.05$) between values for foraging and non-foraging dives.

	TOP DEPTH			FLOOR DEPTH		
	all dives	forage dives	non forage dives	all dives	forage dives	non forage dives
TRINITY BAY	76.4	76.0	*105.5	127.7	127.6	129.2
VARKET CHANNEL	91.9	90.1	*124.9	150.9	155.3	125.7
GREAT ISLAND	95.4	92.9	*113.7	124.1	125.2	116.5
DEEP BAIT AVERAGE	86.1	84.3	*116.1	133.8	134.5	120.8

	VERTICAL EXTENT			XS AREA		
	all dives	forage dives	non forage dives	all dives	forage dives	non forage dives
TRINITY BAY	43.1	43.5	* 18.3	6170	6220	*2600
VARKET CHANNEL	43.0	45.4	* 1.3	5970	6300	* 60
GREAT ISLAND	24.2	27.2	* 2.9	3450	3900	* 260
DEEP BAIT AVERAGE	38.1	40.1	* 4.0	5400	5680	* 490

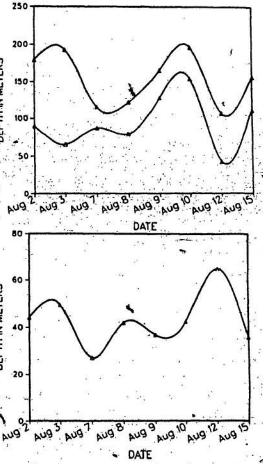


Figure 3.4

Upper: Mean depths to the top of the bait school and to the ocean floor on each day of observation in Varket Channel. The X axis represents the water surface, the line closest to it the top of the bait school and the uppermost line the ocean floor. The area between the lines thus represents prey school extent and the area below the lower line the water depth above the prey school. Lower: Daily variation in vertical extent of prey is also illustrated in the lower graph (more accurately).

Changes in floor depth with date correspond to different school locations within Varket Channel. For the most part top depths closely parallel floor depths, resulting in fairly constant vertical extents (Figure 3.4). The vertical extent of prey schools was not significantly different over date except for on 2 - 3 and 12 August when schools were more extensive.

3.2 Census data

The total number of whales in the study area per day and mean daily group size as determined from census counts are given in Table 3.3. Also included is a rank of fish school size (1=largest; 10=smallest) for each day, approximated from the area covered by each school in Figure 3.2. The correlation coefficients between sucessive pairs of these variables are (n=10 except for the first coefficient where n=11):

total whales per day and mean daily group size $r = .866$
total whales per day and rank of school size $r = -.680$
mean daily group size and rank of school size $r = -.690$

All correlation coefficients were significant ($p<0.05$). The average group size was more strongly related to the total number of whales in the study area than to the rank order of the prey school size. The relationships between school size and the two demographic variables (total whale population and average group size) were of a similar magnitude. Since the largest school was ranked 1 the latter

Table 3.3

Census data from Varket Channel. During censuses whales were counted by groups (e.g. 2+3+1+4 etc.) so that for each census taken there was a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of the mean group size for each census taken.

Date	Total Whales	SD	Average Group Size	SD	Rank Fish School Size
30 JULY	7.0	1.4	2.1	0.34	7
31 JULY	6.3	1.1	2.2	0.45	-
2 AUG	6.8	0.9	1.7	0.10	3
3 AUG	6.0	0.5	1.6	0.07	6
7 AUG	6.0	1.0	1.8	0.51	9
8 AUG	8.3	1.6	2.5	0.92	2
9 AUG	8.0	1.0	2.6	0.55	1
10 AUG	8.0	1.1	2.5	0.28	4
12 AUG	4.0	1.2	1.3	0.12	8
15 AUG	3.0	0.8	1.6	0.30	5
19 AUG	3.0	0.5	1.5	0.50	10
OVERALL MEAN	6.0	1.9	1.94	0.46	

two correlations are negative.

Throughout most of the study period a resident population of whales inhabited Varket Channel. The small size of the population and prolonged observation of the same whales enabled us to become familiar with them. Table 3.4, compiled from drawings of whales seen on sucessive days also shows evidence for preferred groupings.

3.3 Behavioural description

Typical feeding behaviour in this bait situation consisted of one or more whales diving down into bait and resurfacing 2.5 - 5.0 min later, usually within 500 m of the down position. Dives were usually preceded by fluke-ups. Whales typically spent 1.5 - 4.0 min at the surface, routinely travelling 200 - 800 m and seldom turning more than 90°. There was little variability in surface and dive times: they were both quite regular in duration.

Group behaviour was highly coordinated. Individuals within a group swam close together (<15 m apart), frequently abreast in a line. They usually turned together so that all whales constantly swam in the same direction. Whales dove together as a unit or serially; intervals between dives of members of the same group were usually less than 10 s. Resurfacings were also well coordinated but the small whale (<7 m, Groucho) frequently came up noticeably earlier (1 - 2 min) than the rest of the group, rejoining them afterwards. Whales moved most rapidly when resurfacing, sometimes

Table 3.4

Repeated sightings of recognized whales throughout the study period in Varket Channel. A small resident population enabled us to become familiar with the whales. Initial small groupings are enclosed in round brackets. Smaller groups sometimes merged to form larger groups, signified by square brackets.

30 JULY	(Black, White)	Groucho	
31 JULY	(Loner, Spike)		
2 AUG	(Line, Groucho)	(Loner, Spike)	
3 AUG	Black	(Loner, Spike)	(Rusty, Scotch)
7 AUG	Groucho		
8 AUG	[(Spike, Line, Loner, Groucho) (Black, White)] (Rusty, Scotch)		
9 AUG	[(Spike, Line, Loner, Groucho) (Black, White)] (Rusty, Scotch)		
10 AUG	[(Spike, Line, Loner, Groucho) (Black, White)] (Rusty, Scotch)		
12 AUG	Sharpee		
15 AUG	Black	Sharpee	Groucho

explosively breaking the water surface and blowing loudly. Swimming speed decreased after the first few blows and often continued to do so until whales were lulling (see Table 2.1) or moving very slowly (<1 knot). A moderate increase in speed sometimes occurred immediately prior to terminal dives.

Whales foraged almost continually except for a few instances of travelling. For example, on 2 August a group of two moved from the large fish school south to the smaller one and subsequently back again. In this location, when whales were foraging and travelling, blow intervals were usually about 10 s. Resting, with blow intervals of 30 s or more, was not observed.

3.4 Behavioural analysis

<u>Continuous whale variables</u>. Values of whale behaviour variables averaged over the entire study period in Varket Channel are given in Table 3.5. Variation in time variables by date is illustrated in Figure 3.5. Surface times were significantly longer, and hence the dive time to surface time ratio smaller, on 8 - 10 August. As a consequence of spending longer periods of time at the surface, directional changes were significantly greater on these days. Dive times and unitimes also follow this trend and correspond to greater bait and ocean floor depths on 9 - 10 August (see Figure 3.4). Both surface and dive times were significantly shorter on 12 August than on all other days of the study period (Figure 3.5). Correspondingly, ocean floor depths

Table 3.5

Average values (and SD) of whale behavioural variables for the study period (2 - 19 August, 1980) in Varket Channel, broken down into foraging and non-foraging dives. Time variables are in min, directional variables in degrees, TRATE in degrees/min. No significant differences between foraging and non-foraging dives were found.

	OVERALL		FORAGING DIVES		NON FORAGING DIVES	
	Mean	SD	Mean	SD	Mean	SD
SURFTIME	2.67	1.26	2.70	1.28	2.05	0.70
DIVETIME	3.83	1.26	3.83	1.26	3.90	1.29
UNITIME	6.50	2.15	6.53	2.17	5.95	1.38
RATIO	1.70	0.87	1.68	0.88	2.14	0.90
GROSDIR	76.2	76.6	75.9	76.8	82.5	–
NETDIR	60.3	62.1	59.8	61.9	72.5	69.1
CLOCK	40.9	54.9	40.9	54.7	42.5	64.1
COUNTER	-34.9	58.4	-34.7	58.6	-40.0	57.1
OVERALL DIRN	6.2	83.7	6.2	83.4	2.5	95.8
TRATE	31.4	37.4	31.3	37.6	34.3	31.5

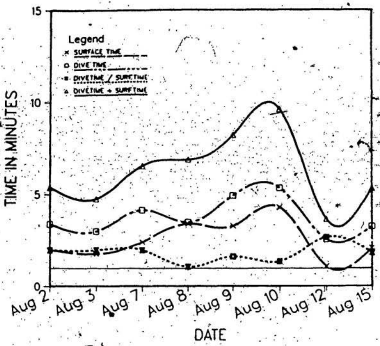


Figure 3.5

Daily means in surface and dive times in Varket Channel. Mean values of unitime (dive time plus preceding surface time) are depicted by the uppermost line. The mean daily dive time to surface time ratio is illustrated by the dotted line. 1.0 is referenced to illustrate ratio values greater or less than 1.0. Foraging dives from the individual whale data set were used to compile this figure.

and depths to the top of the bait school on 12 August were significantly shallower (Figure 3.4).

Categorical variables. Frequencies of different group sizes and down behaviours for this study location are summarized in Table 3.6. These categorical variables are broken down by foraging and non-foraging dives, hence the number of occurrences of each type of dive is also given.

Single whales were followed more often than other group sizes but this does not reflect their abundance (see Table 3.3). As mentioned (Section 2.3), all group sizes could not be randomly sampled during all observation bouts. Observed groups of whales in this location foraged almost continually; only 7 non-foraging dives were identified. Non-foraging dives occurred with group sizes of 1 - 2 only. Whales raised their flukes before most dives.

Multiple regression analysis. Results from the two separate multiple regression analyses, the first depicting the relationship of each time variable to other whale variables as well as bait variables, and the second, depicting each time variable solely as a function of bait, are presented in Table 3.7. Table 3.8 illustrates the first order correlation coefficients between pairs of variables.

Both combinations of dependent variables, whale plus bait and bait only, were significantly linearly correlated with each time variable. All time measures were most strongly related to the depth of the bait school (TOPAV, TOPFP) even when whale variables were included in the

Table 3.6.

Frequencies of various group sizes and down behaviours for Varket Channel broken down by foraging and non-foraging dives. Group size frequencies were determined from the group data set so they represent the number of dives of groups of size n. Down behaviour frequencies were calculated from the individual data set so they represent the actual occurrences of each behaviour.

	FORAGING DIVES		NON-FORAGING DIVES		OVERALL TOTAL	
	Number	column %	Number	column %	Number	column %
GROUP SIZE						
singles	89	67.4	4	57.1	93	66.9
small (2-4)	41	31.1	3	42.9	44	31.7
large (5-8)	2	1.5	-	-	2	1.4
	132	100	7	100	139	100
DOWN BEHAVIOUR						
fluke-up	188	87.1	9	90.0	197	87.2
LY or SY	4	1.8	-	-	4	1.8
no fluke	24	11.1	1	10.0	25	11.0
	216	100	10	100	226	100

Table 3.7

Multiple regression results from Varket Channel with different time measures used as dependent variables. The independent variable list contains both whale and bait variables in the upper section of the table, bait variables only in the lower section. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the dependent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	27.5	TOPAV	29.0	TOPAV	35.9
	GPSIZE	40.0	SURFTIME	34.0	GPSIZE	41.6
	DIVETIME	44.3	VEXTFP	35.1 (-)	VEXTFP	43.0
	AREA	45.1 (-)	AREA	36.9 (-)	GROSDIR	44.2
					TRATE	51.1
Total proportion of variance accounted for	46.9		38.7		51.8	
Durbin-Watson test	no autocorrel		no autocorrel		inconcl p<.05 no auto p<.01	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	27.0	TOPAV	36.4	TOPAV	41.6
	FLRAV	28.2	VEXTFP	37.6 (-)	AREA	42.3 (-)
	AREA	30.8 (-)	AREA	38.8 (-)	TOPFP	42.8
					FLRAV	43.3
Total proportion of variance accounted for	31.3		39.6		44.5	
Durbin-Watson test	inconcl p<.05 inconcl p<.01		inconcl p<.05 inconcl p<.01		autocor p<.05 inconcl p<.01	

Table 3.8. First order correlation coefficients between pairs of variables in the Market Channel dive by dive data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	UNITIME	RATIO	TRATE	GROSDIR	NETDIR	GPSIZE
SURFTIME	1.00000**	0.45644**	0.85481**	-0.66424**	-0.18422**	0.18479**	0.15702*	0.42021**
DIVETIME	0.45644**	1.00000**	0.85190**	0.13397	-0.01958	0.22075**	0.19508**	0.09867
GROSDIR	0.18479**	0.22075**	0.23751**	-0.14887*	0.80448**	1.00000**	0.89384**	0.08466
NETDIR	0.15702*	0.19508**	0.20620**	-0.13236	0.72122**	0.89384**	1.00000**	0.10394
FLRFP	0.16241*	0.32167**	0.28321**	-0.08846	-0.02278	0.06025	0.04751	-0.13242
FLRAV	0.15819*	0.31792**	0.27853**	-0.09020	-0.02074	0.05855	0.04490	-0.12975
TOPFP	0.46580**	0.50061**	0.56614**	-0.22331**	-0.10273	0.14985*	0.12366	0.10269
TOPAV	0.48467**	0.53882**	0.59953**	-0.24581**	-0.07171	0.19532**	0.16850*	0.11316
VEXTFP	-0.16136*	-0.14477*	-0.17941*	0.02764	-0.00641	-0.08895	-0.04076	-0.07018
VEXTAV	-0.15355*	-0.16580*	-0.18708**	0.01472	-0.01744	-0.10746	-0.05764	-0.04644
AREA	-0.08360	-0.16932*	-0.14796*	-0.04907	-0.04153	-0.09798	-0.06082	0.02061
GPSIZE	0.42021**	0.09867	0.30488**	-0.38202**	-0.10989	0.08466	0.10394	1.00000
UNITIME	0.85481**	0.85190**	1.00000**	-0.31283**	-0.11985	0.23751**	0.20620**	0.30488**
RATIO	-0.66424**	0.13397	-0.31283**	1.00000**	0.12973	-0.14887*	-0.13236	-0.38202**
TRATE	-0.18422**	-0.01958	-0.11985	0.12973	1.00000	0.80448**	0.72122**	-0.10989

	FLRFP	FLRAV	TOPFP	TOPAV	VEXTFP	VEXTAV	AREA
SURFTIME	0.16241*	0.15819*	0.46580**	0.48467**	-0.16136*	-0.15355*	-0.08360
DIVETIME	0.32167**	0.31792**	0.50061**	0.53882**	-0.14477*	-0.16580*	-0.16932*
GROSDIR	0.06025	0.05855	0.14985*	0.19532**	-0.08895	-0.10746	-0.09798
NETDIR	0.04751	0.04490	0.12366	0.16850*	-0.04076	-0.05764	-0.06082
FLRFP	1.00000**	0.99775**	0.49816**	0.49539**	0.15305*	0.16093*	0.09266
FLRAV	0.99775**	1.00000**	0.49811**	0.49753**	0.14431*	0.15391*	0.08323
TOPFP	0.49816**	0.49811**	1.00000**	0.94012**	-0.54940**	-0.51697**	-0.47267**
TOPAV	0.49539**	0.49753**	0.94012**	1.00000**	-0.46668**	-0.48425**	-0.43150**
VEXTFP	0.15305*	0.14431*	-0.54940**	-0.46668**	1.00000**	0.96615**	0.92346**
VEXTAV	0.16093*	0.15391*	-0.51697**	-0.48425**	0.96615**	1.00000**	0.94959**
AREA	0.09266	0.08323	-0.47267**	-0.43150**	0.92346**	0.94959**	1.00000**
GPSIZE	-0.13242	-0.12975	0.10269	0.11316	-0.07018	-0.04644	0.02061
UNITIME	0.28321**	0.27853**	0.56614**	0.59953**	-0.17941*	-0.18708**	-0.14796*
RATIO	-0.08846	-0.09020	-0.22331**	-0.24581**	0.02764	0.01472	-0.04907
TRATE	-0.02278	-0.02074	-0.10273	-0.07171	-0.00641	-0.01744	-0.04153

regression equation. When whale variables were removed from the regression however, the explained variance of each time variable decreased by approximately 10%. Regression results using only footprint values of bait variables to control for multicollinearity were quite similar to those using the full set of bait variables (Appendix 1, Table A3.1).

Each time variable differed in its capacity to be predicted by bait variables (Table 3.7). Unitime, the combination of dive time plus surface time, was better predicted than either surface time or dive time alone. Surface time showed the weakest relationship with immediate bait variables. The vertical extent and cross sectional area of bait at the dive area were negatively related to dive and surface times (Table 3.7).

Analyses that were found to be autocorrelated when every case of the data set was used (see Table 3.7) were rerun using only the first case from each hour. Two sets of analyses remained autocorrelated or were inconclusive when tested (Appendix 1, Table A1.1). When data were reanalyzed the independent variables accounted for a greater proportion of variance of each time variable (Table A1.1) than was accounted for in the initial regression analysis (Table 3.7).

A set of multiple regression analyses were performed on an aggregated data set consisting of the mean value of each variable for each hour of observation. Whale behaviour (hourly means of dive and surface times) was more closely related to the average depth and extent of fish schools and average ocean floor depth for each hour (Appendix 1, Table A1.2). The bait variables accounted for approximately double the variance of each time measure when hourly means were used. Results of both reanalyses were similar to the initial analysis in that the depth of the bait school (TOPAV, TOPFP) was most strongly related to all time measures (Tables A1.1, A1.2). When only footprint values of bait variables were used as independent variables in these aggregated regressions the total amount of variance of the dependent time variables accounted for decreased by 2 - 12% (Appendix 3, Table A3.2). Relationships between pairs of variables that were evident in the table of first order correlation coefficients (Table 3.8) were more strongly expressed when the data set of hourly means was used to compute them (Appendix 2, Table A2.1).

CHAPTER 4. TRINITY BAY

A large concentration (15 - 30) of humpback whales was in the head of Trinity Bay (Figure 4.1) from mid August to mid October 1980. Observations were carried out from 21 August to 17 September; adequate foraging behaviour data were obtained on 11 of the 15 days we were able to work at sea. On the other four days concentrations of whales and bait were noted.

4.1 Bait schools

Figure 4.2 delineates locations and approximate boundaries of bait schools and concentrations of foraging whales throughout the study period. These were determined by noting positions where whales and prey schools were concentrated and also from systematic bait traces of the schools. Precise boundaries of cohesive prey schools are plotted (shaded) for 22, 30 August and 2, 17 September only. Schools were not discrete and well delineated (as they were in Varket Channel); very extensive areas of bait were frequently broken by pockets or ridges devoid of bait and often seemed to actually consist of two or three separate fish schools, perhaps intermingling at points or splitting and merging periodically. The bait aggregations in Trinity Bay were generally twice as large as those in Varket Channel. Outlines of discrete fish schools (22, 30 August and 2, 17 September) illustrated in Figure 4.2 are larger than those in Figure 3.2, which is 1.6x the scale of Figure

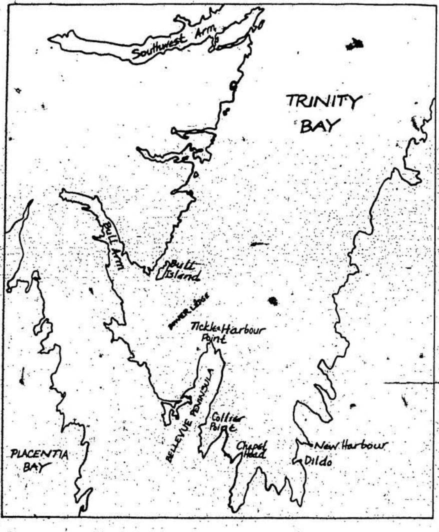
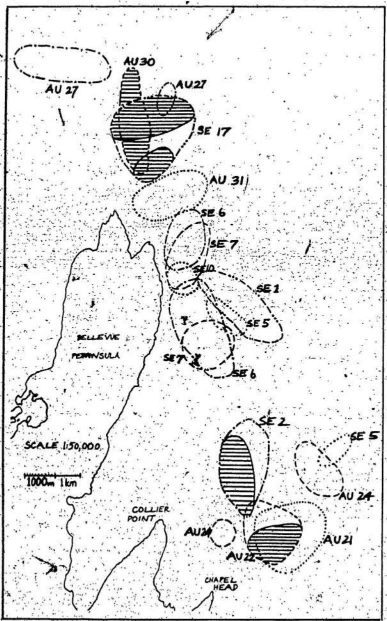


Figure 4.1

Lower part of Trinity Bay. Whales were located north of Chapel Head and Colliers Point during the early part of the study period (21 Aug - 2 Sept) and later (5-17 Sept) were north, northeast, and northwest of Tickle Harbour Point.

Figure 4.2

Locations of prey schools that observed groups of humpback whales were utilizing on various days in Trinity Bay. Shaded areas within outlines of whales and bait concentrations for particular days (22,30 Aug, 2,17 Sept) represent cohesive continuous fish schools as determined from bait traces. On some days whales and bait were present in two separate areas.


AU 27
AU30
AU27
SE 17
AU 31
SE 6
SE 7
SE10
SE 1
SE 5
BELLEVUE
PENINSULA
SE7
SE 6
SE 2
SE 5
SCALE 1:50,000
1000m 1km
AU 24
COLLIER
POINT
AU24
AU21
AU22
CHAPEL
HEAD

4.2, and additional concentrations of bait and whales also existed on these days.

Depth sounder printouts of typical prey schools from this study area are presented in Figure 3.3. The bait schools the whales were foraging on were almost certainly deep immature capelin. Fishermen from Chapel Arm were finding immature capelin in cod stomachs throughout the first half of the study period. On 2, 6 and 7 September we observed gulls (<u>Larus</u> spp.) and Black-legged Kittiwakes (<u>Rissa tridactyla</u>) diving into the turbulent water where whales had just surfaced and coming up with small (8 cm) fish that looked like immature capelin in their beaks.

Schools of squid (<u>Illex illecebrosus</u>) were also present throughout the study period but were readily discernible on the depth sounder from schools of immature capelin. They were much less horizontally and vertically extensive and were closer to the surface. Individual squid as separate echo sounder targets could also be more clearly seen (Figure 3.3). We identified such schools by jigging squid from them on 24 August and 2 September. Pilot whales (<u>Globicephala melaena</u>) were frequently seen in the vicinity of schools of squid, probably feeding on them, but on only one occasion (10 September) did we confirm that humpbacks were foraging on squid.

Bait and ocean floor depths for this location averaged over the duration of the study period are summarized in Table 3.2. The depth of bait schools on a given date paralleled ocean floor depth (Figure 4.3). Variation in depth with date reflects changes in location of the principle bait concentrations that whales were feeding on. Bait and whale concentrations were in deeper water at the beginning of the study period (Figure 4.2), they gradually moved into shallower water alongside the Bellevue Peninsula in early September. On 17 September they had again moved into deeper water north of the Bellevue Peninsula.

The vertical extent of fish schools that whales were feeding on varied irregularly throughout the study period (Figure 4.3) in spite of the general correlation of bait school depth with ocean floor depth. As previously mentioned the distance between the two curves in Figure 4.3 only approximates the mean daily vertical extent of bait (see Section 3.1).

On 30 August the fish school on which whales foraged was significantly more extensive than schools on every other day of observation except for 1 and 7 September (Figure 4.3). Fish schools on these latter two days were not significantly more extensive than on other days, however. On 30 August whales were also foraging in significantly deeper water (Figure 4.3) than on any other day of observation.

4.2 Census data

Unless it was foggy or seas were very rough whales

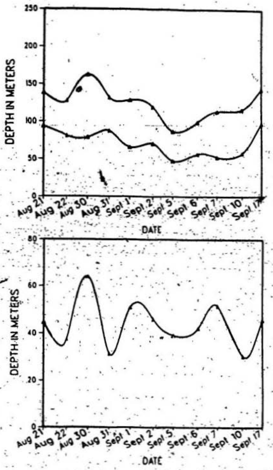


Figure 4.3

Upper: Mean depths to the top of the bait school and to the ocean floor on each day of observation in Trinity Bay. The X axis represents the water surface, the line closest to it the top of the bait school and the uppermost line the ocean floor. The area between the lines thus represents prey school extent and the area below the lower line the water depth above the prey school. Lower: Daily variation in vertical extent of prey is also illustrated (more accurately) in the lower graph.

could be seen if they were present to the east, south and west due to the dark backdrop of land, however, precise estimates of group sizes were difficult to obtain for distant groups. Sightings to the north were far less reliable. Because of these factors census results (Table 4.1) from this study location are not as accurate as those from Varket Channel.

There was a significant correlation between the total daily humpback whale count and mean daily group size (r=0.626). Throughout the entire study period 4 - 8 fin whales and 1 - 5 minke whales were seen each day. Groups of pilot whales were repeatedly sighted. On 21 August and on 5 and 17 September schools of 10 - 20 white-sided dolphins (Lagenorhynchus acutus) were observed.

There was a persistent population of 15 - 35 humpback whales in the bottom of Trinity Bay from mid August to mid September (Table 4.1) and at least 20 whales were still present in mid October 1980 (D. Chabot pers. comm.). Because of the large population it was difficult to remember many individual whales, hence conclusive evidence is lacking that the same whales were present for the duration of the study period. Some whales were very distinctive in fluke pattern however, and it was necessary to follow them for only a short period of time to become familiar with them. These individuals had residence times in the study area for 1 - 2 weeks.

Table 4.1

Census data from Trinity Bay. During censuses whales were counted by groups (e.g. 2+3+1+4 etc.) so that for each census taken there was a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of the mean group sizes for each census taken.

Date	Total Whales	SD	Average Group Size	SD	Number of Counts
21 AUG	26.7	6.0	2.89	0.12	3
22 AUG	18.2	4.3	1.88	0.36	5
24 AUG	17.0	1.0	2.10	0.13	2
27 AUG	20.4	2.8	2.08	0.04	5
30 AUG	24.8	4.9	2.79	0.80	4
31 AUG	19.0	3.0	1.87	0.35	3
1 SEP	17.0	1.0	2.10	0.10	2
2 SEP	24.0	5.5	1.85	0.33	4
5 SEP	21.2	3.9	2.54	0.38	5
6 SEP	21.7	1.4	2.15	0.54	6
7 SEP	25.3	4.5	2.23	0.67	3
10 SEP	14.0	-	1.60	-	1
17 SEP	29.5	3.5	2.25	0.15	2
OVERALL MEAN	21.4	4.5	2.18	0.37	

4.3 Behavioural description

Although fish schools in Trinity Bay were shallower (Table 3.2) and larger than those in Bonavista Bay (Varket Channel) they were similar in appearance on the depth sounder (Figure 3.3) and in vertical extent and were probably also immature capelin. Feeding behaviour of whales in this study location closely resembled that exhibited in Varket Channel.

On 31 August a group of 3 whales stopped foraging and rested for approximately 1 h although they were over a fish school when resting began. The group remained intact and individuals were horizontally aligned for most of the time. They moved extremely slowly or lay still just below the surface, blowing at 30 s - 2 min intervals. Eventually they moved or drifted away from the fish school but after 15 min were once again over bait and still resting. They continued to rest while over a prey school for 40 min, finally diving at the far end of the school that they had just moved across. Typical foraging behaviour was resumed at this point.

Generally it was difficult to tell if or how whales were responding to the geometry of the prey schools they were exploiting. Other times it was quite obvious they were diving in a systematic way in relation to the shape of the school and its position over specific bottom characteristics. On 27 August 3 whales were foraging on a long narrow fish school oriented north - south along the east side of Bower Ledge, between Bull Island and Tickle Harbour Point (Figure 4.1). The whale group persistently surfaced travelling east, turned in a U shape at the surface and dove west into the school, possibly driving capelin against the bottom ridge and facilitating prey capture.

Although schools of squid were present throughout the study period, only once were whales observed preying on them. On 10 September two whales were noticed lunging forward through the surface of the water and rolling to the side immediately after, a behaviour not previously or subsequently seen in whales supposedly utilizing deep bait. Individual squid could be seen leaping from the water in the wake of lunging whales. Small schools of the type from which squid had been jigged earlier were located just below the surface where the whales had lunged. Eventually 5 whales congregated in the area of squid abundance but no coordinated lunging occurred. Whales lunged for a period of only 10 min but two animals continued to exploit local squid schools for another 5 min using an alternate foraging strategy. This consisted of circling around a small concentration of squid, turning to face the school and diving into it with flukes raised.

At 1700 h on 5 September an unusual example of cetacean behaviour was observed where three species of whales appeared to be chasing a fast moving fish school. Approximately 30 white-sided dolphins, 20 humpback and 8 fin whales coalesced into a conspicuous and somewhat frenzied group. The dolphins were ahead of, and seemed to be leading, the rorquals, the whole group travelling rapidly in wide circles of 1 km or more in diameter. Group structure was dynamic. Sometimes large numbers of humpbacks moved as a unit, horizontally aligned and raising their flukes in synchrony. Shortly after fluking the whales would surface together and repeat the procedure. Other times all whales converged in a ring and coordinated as small groups, 3 or 4 whales swimming close together and fluking up simultaneously towards the center of the ring. Blows were frequently loud and forceful and spyhops, rolls and sideflukes (see Table 2.1) were prevalent. A concentration of gulls and terns circled above the commotion, diving periodically.

By 1800 h the dolphins had departed (they could no longer be heard on the hydrophone) and the baleen whales were dispersing into groups and moving more slowly. There was no conclusive depth sounder evidence for the existence of a fast moving fish school but it could easily have been missed as we did not venture into the midst of the pandemonium. The whales could have been chasing squid, as they are known to be one of the fastest moving of marine creatures (Norris and Dohl 1983) and are utilized by white-sided dolphins (Watson 1981). When shoals of mackerel (*Scomber scombrus*) were seen near Varket Channel on 7 August, whales did not actively pursue them.

4.4 Behavioural analysis

Continuous whale variables. Mean values of whale behavioural variables in this study location are given in Table 4.2. Both dive times and surface times were significantly shorter from 5 - 7 September (Figure 4.4) when bait schools were closer to the surface and in shallower water just east of the Bellevue Peninsula (Figures 4.2, 4.3). Although surface times for 10 September conform to this pattern, dive times were significantly longer on this date than on any other day. During the observation bout on 10 September, which comprised only four sequential dives, whales were foraging on small subsurface schools, possibly of squid. It was later on this date that whales were seen lunging at the surface amidst squid schools.

Correspondingly, the mean dive time to surface time ratios for each day had similar values of 1.5 - 2.4 except on 10 September when the mean ratio was significantly larger due to the long dive times (Figure 4.4). Except for 21 - 22 August, dive times were longer when whales were foraging on bait schools at greater depths, farther from shore (30 - 31 August, 1, 17 September) (Figure 4.2, 4.3).

Categorical variables. Frequencies of different group sizes and down behaviours broken down by foraging and non-foraging dives are depicted in Table 4.3. Small groups of 2 - 4 whales were most abundant. Groups larger than 5 were less common and were followed on three days only: 21, 22 August and 6 September. Single whales were rarely followed.

Table 4.2

Average values (and SD) for whale behavioural variables for (21 Aug - 17 Sept, 1980) in Trinity Bay broken down into foraging and non-foraging dives. Time variables are in min, directional variables are in in degrees, TRATE is in degrees/min. * denotes significant differences between values for foraging and non-foraging dives (p<.01 except DIRN, p<.05).

	OVERALL		FORAGING DIVES		NON-FORAGING DIVES	
	Mean	SD	Mean	SD	Mean	SD
SURFTIME	3.14	3.62	2.85	1.13	*16.93	20.57
DIVETIME	4.59	1.41	4.57	1.40	* 5.73	1.32
UNITIME	7.73	4.02	7.42	1.99	*22.65	20.24
RATIO	1.81	0.95	1.83	0.94	0.95	0.79
GROSDIR	83.3	82.3	82.5	80.4	120.0	149.0
NETDIR	68.0	62.5	67.8	62.3	75.0	70.6
CLOCK	43.4	61.7	43.5	62.0	35.6	49.3
COUNTER	-39.0	55.2	-38.1	53.4	*-84.4	105.6
OVERALL DIR	4.3	83.1	5.4	83.0	*-48.8	70.4
TRATE	28.7	27.1	29.2	27.2	* 6.8	5.5

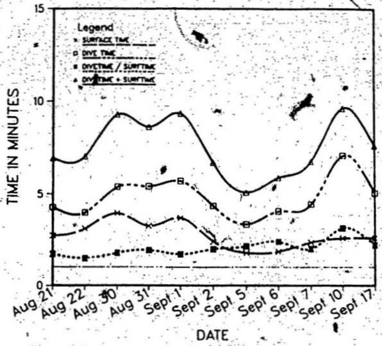


Figure 4.4

Daily means in surface and dive times in Trinity Bay. Mean values of unitime (dive time plus preceding surface time) are depicted by the uppermost line. The mean daily dive time to surface time ratio is illustrated by the dotted line. 1.0 is referenced to illustrate ratio values greater or less than 1.0. Foraging dives from the individual whale data set were used to compile this figure.

Table 4.3

Frequencies of various down behaviours and group sizes from Trinity Bay broken down by foraging and non-foraging dives. Group size frequencies were determined from the group data set so they represent the observed number of dives of groups of size n. Down behaviour frequencies were calculated from the individual data set and represent actual occurrences of each behaviour.

	FORAGING DIVES		NON-FORAGING DIVES		OVERALL TOTAL	
	Number	column %	Number	column %	Number	column %
GROUP SIZE						
singles	9	4.7	-	-	9	4.7
small (2-4)	165	86.8	4	100.0	169	87.1
large (5-8)	16	8.5	-	-	16	8.2
	190	100	4	100	194	100
DOWN BEHAVIOUR						
fluke-up	511	88.3	12	100.0	523	88.5
LY or SY	29	5.0	-	-	29	4.9
no fluke	39	6.7	-	-	39	6.6
	579	100	12	100	591	100

Observed groups of whales foraged almost continuously; they switched to non-foraging behaviour only three times after observation had begun. Non-foraging (resting) whales spent considerable periods of time just floating at the surface, hence the long surface times for non-foraging dives (Table 4.2). Most dives were preceded by fluke-ups (Table 4.3).

Multiple regression analysis. Results from multiple regression analyses on the dive by dive data set are presented in Table 4.4. Similar to the results from Varket Channel, there was a reduction in the proportion of explained variance of each time measure when bait variables only were included in the regression equation. This was most marked when bait variables were regressed on surface time. Not surprisingly, a large portion of the variance of surface time accounted for by the independent variables was attributable to the directional variables: how much, in what direction and how fast whales turned while at the surface (Table 4.4). Directional variables accounted for very little (5%) of the variability of dive time, however. Surface time was slightly better predicted by bait variables in the immediate dive area than was dive time (Table 4.4). Unitime, the combination of dive time and surface time, was more strongly correlated with bait variables (Table 4.5) and accounted for more of their variance than either surface time or dive time alone (Table 4.4), as was the case in Varket Channel (Tables 3.7, 3.8). When only footprint values of bait variables were included in order to control

Table 4.4

Multiple regression results from Trinity Bay with different time measures used as dependent variables. In the top section of the table the independent variable list contains both whale and bait variables, in the lower section, bait variables only. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the independent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	15.5	SURFTIME	5.3	FLRAV	12.6
	TRATE	55.2	GPSIZE	7.1(-)	GROSDIR	16.2
	FLRAV	57.7	FLRAV	8.1	TRATE	29.2
	DIVETIME	59.2	VEXTFP	9.2(-)	VEXTFP	31.1(-)
	TOPAV	59.9	TOPAV	13.1	TOPAV	32.7
	NETDIR	60.4	VEXTAV	15.2(-)	VEXTAV	33.4(-)
			AREA	16.3(-)	GPSIZE	34.2(-)
Total proportion of variance accounted for	60.9		17.7		35.5	
Durbin-Watson test	no autocorrel.		inconcl	p<.05	autocor	p<.05
			inconcl	p<.01	autocor	p<.01

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative ~~proportion of~~ variance accounted for	FLRAV	14.6	FLRAV	3.9	FLRAV	12.6
	VEXTAV	16.0(-)	VEXTFP	5.6(-)	VEXTFP	15.0(-)
	~~AREA~~	~~17.1~~	TOPAV	9.9	TOPAV	17.5
	FLRFP	17.3	VEXTAV	11.3	VEXTAV	18.0(-)
			TOPFP	12.0	TOPFP	18.5
Total proportion of variance accounted for	17.4		12.7		18.7	
Durbin-Watson test	inconcl	p<.05	autocor	p<.05	autocor	p<.05
	inconcl	p<.01	inconcl	p<.01	autocor	p<.01

for multicollinearity, the proportion of variance of dive time accounted for by the independent variables decreased by 32 - 34%, while that of both surface time and unitime decreased by just 3 - 10% (Appendix 3, Table A3.3).

Regression analyses were run using the hourly means of each variable in an effort to remove autocorrelation. Some sets of analyses remained autocorrelated but in all variable combinations that were reanalyzed, whale diving behaviour (time measures) was better predicted by bait school characteristics than when the data set containing every dive was used (see Appendix 1, Table A1.4). This also occurred when regressions were rerun using the first dive of every hour (Table A1.3). Whale diving behaviour was less well predicted when only footprint values of bait variables were included in the aggregated (hourly means) regression analysis. The accountable variance of the time variables decreased from 3 - 17% (Appendix 3, Table A3.4) but there was no consistent pattern (i.e. among time variables) to the decrease.

Table 4.5 depicts the first order correlation coefficients between pairs of variables. Relationships between pairs of variables were the reverse of those found in Varket Channel in two notable ways. 1) Time spent at the surface was more highly correlated with the depth to the top of the bait school and to the ocean floor than was dive time. 2) Floor depths were more highly correlated with both surface and dive times than were top depths.

Table 4.5. First order correlation coefficients between pairs of variables in the Trinity Bay dive by dive data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	TOPFP	TOPAV
SURFTIME	1.00000**	0.23119**	0.39377**	0.31687**	0.37804**	0.38204**	0.24842**	0.25608**
DIVETIME	0.23119**	1.00000**	0.08561	0.07398	0.19159**	0.19819**	0.07621	0.05490
GROSDIR	0.39377**	0.08561	1.00000	0.91944**	0.28562**	0.28301**	0.04246	0.05786
NETDIR	0.31687**	0.07398	0.91944**	1.00000**	0.24586**	0.24168**	-0.00369	0.01521
FLRFP	0.37804**	0.19159**	0.28562**	0.24586**	1.00000**	0.99703**	0.49377**	0.51494**
FLRAV	0.38204**	0.19819**	0.28301**	0.24168**	0.99703**	1.00000**	0.49089**	0.51071**
TOPFP	0.24842**	0.07621	0.04246	-0.00369	0.49377**	0.49089**	1.00000**	0.98310**
TOPAV	0.25608**	0.05490	0.05786	0.01521	0.51494**	0.51071**	0.98310**	1.00000**
VEXTFP	-0.01691	-0.07437	0.13769**	0.18887**	0.24916**	0.25129**	-0.50852**	-0.46456**
VEXTAV	-0.01529	-0.03280	0.13141**	0.17775**	0.25621**	0.26148**	-0.46225**	-0.45515**
AREA	0.01106	-0.05160	0.12575**	0.17619**	0.23769**	0.24354**	-0.48913**	-0.47974**
GPSIZE	0.03405	-0.12553**	0.01624	-0.03711	-0.12802**	-0.12191**	-0.01572	-0.03434
UNITIME	0.72602**	0.83689**	0.28205**	0.23056**	0.34811**	0.35503**	0.19363**	0.18288**
RATIO	-0.59855**	0.46152**	-0.22852**	-0.19963**	-0.16497**	-0.16414**	-0.14661**	-0.17347**
DIRN	0.16272**	0.03746	0.15825**	0.12433**	0.05006	0.05248	0.01950	0.02150
TRATE	0.00861	0.03072	0.85417**	0.84285**	0.14292**	0.13925**	-0.03437	-0.02177

	UNITIME	RATIO	DIRN	TRATE	VEXTFP	VEXTAV	AREA	GPSIZE
SURFTIME	0.72602**	-0.59855**	0.16272**	0.00861	-0.01691	-0.01529	0.01106	0.03405
DIVETIME	0.83689**	0.46152**	0.03746	0.03072	-0.07437	-0.03280	-0.05160	-0.12553**
GROSDIR	0.28205**	-0.22852**	0.15825**	0.85417**	0.13769**	0.13141**	0.12575**	0.01624
NETDIR	0.23056**	-0.19963**	0.12433**	0.84285**	0.18887**	0.17775**	0.17619**	-0.03711
FLRFP	0.34811**	-0.16497**	0.05006	0.14292**	0.24916**	0.25621**	0.23769**	-0.12802**
FLRAV	0.35503**	-0.16414**	0.05248	0.13925**	0.25129**	0.26148**	0.24354**	-0.12191**
TOPFP	0.19363**	-0.14661**	0.01950	-0.03437	-0.50852**	-0.46225**	-0.48913**	-0.01572
TOPAV	0.18288**	-0.17347**	0.02150	-0.02177	-0.46456**	-0.45515**	-0.47974**	-0.03434
VEXTFP	-0.06208	-0.03347	-0.02162	0.14055**	1.00000**	0.96963**	0.94216**	-0.00888
VEXTAV	-0.03178	-0.00186	-0.01727	0.13392**	0.96963**	1.00000**	0.96091**	0.02650
AREA	-0.03025	-0.03150	0.01559	0.10918*	0.94216**	0.96091**	1.00000**	0.00835
GPSIZE	-0.06957	-0.08030	0.10624*	-0.04425	-0.00888	0.02650	0.00835	1.00000
UNITIME	1.00000	-0.01054	0.11802**	0.02656	-0.06208	-0.03178	-0.03025	-0.06957
RATIO	-0.01054	1.00000	-0.08487	0.02112	-0.03347	-0.00186	-0.03150	-0.08030
DIRN	0.11802**	-0.08487	1.00000	0.02984	-0.02162	-0.01727	0.01559	0.10624*
TRATE	0.02656	0.02112	0.02984	1.00000	0.14055**	0.13392**	0.10918*	-0.04425

When the aggregated (hourly means) data set was used to compute the coefficients, variables were in general more highly correlated (Appendix 2, Table A2.2). The relationship between dive time and depth to the top of the bait school which was, as one would initially expect, quite strongly positive in Varket Channel (Tables 3.8, A2.1), was almost nonexistent in the Trinity Bay results (Tables 4.5, A2.2).

CHAPTER 5. GREAT ISLAND

The small shallow schools of post spawning capelin that were localized in the small inshore bays of the southeast coast of the Avalon Peninsula (Figure 5.1) in early July moved offshore and into deeper water about mid July. Whales were observed foraging on these late post spawning schools from 18 - 26 July, 1981. After 30 July the large deep schools had dispersed and most whales had left the area. Strong southwest winds precluded continuing behavioural observations during the last week of July.

5.1 Bait schools

Figure 5.2 depicts the concentrations of capelin and whales on various dates throughout the study period in this area. It is not known if whales were foraging in the vicinity of Great Island before 17 July. When we travelled from Witless Bay to Cape Broyle Harbour on 11 July looking for other foraging whales, none was seen outside of the small inshore bays (Witless and Mobile Bays, Cape Broyle Harbour). On 17 July whales were seen off North Point and Brigus Head but heavy swell prevented us from following foraging groups. Whales and prey schools moved progressively north throughout the latter half of July (Figure 5.2).

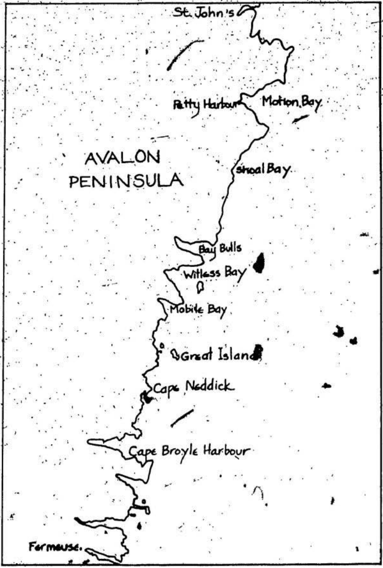
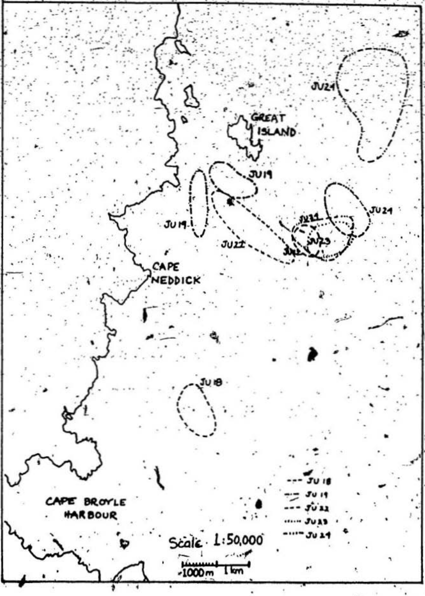


Figure 5.1

East coast of the Avalon Peninsula, south of St. John's. On 25-26 July behavioural observations were carried out in Shoal Bay and Motion Bay, areas not included in the following enlarged map (Figure 5.2).

Figure 5.2

Locations of concentrations of whales and bait throughout the study period in the Great Island study area. Outlined areas do not represent actual perimeters of fish schools except for the most westerly school on 19 July. On some days (19,22,24 July) whales were foraging on prey in two or more locations.


JU24
GREAT ISLAND
JU19
JU24
JU19
JU23
JU22
JU23
JU22
CAPE NEDDICK
JU18
--- JU 18
-·- JU 19
--- JU 22
······ JU 23
-····- JU 24
CAPE BROYLE HARBOUR
Scale 1:50,000
1000m
1km

After 19 July concentrations of prey were usually composed of smaller intermingling sub-schools (see Figure 5.3). Because of this composite structure it was difficult to assess the size of capelin aggregations here as compared to Varket Channel and Trinity Bay. In general they were smaller than in both other deep bait locations. Smaller patches of bait were frequently spread over a larger area than that occupied by the concentrated schools in Varket Channel. When observations were first begun here schools were larger and more cohesive (Figure 5.3) and small surface schools of capelin were present above the deeper schools. Common murres (Uria aalgae) and Atlantic puffins (Fratercula arctica) were regularly seen with capelin in their beaks.

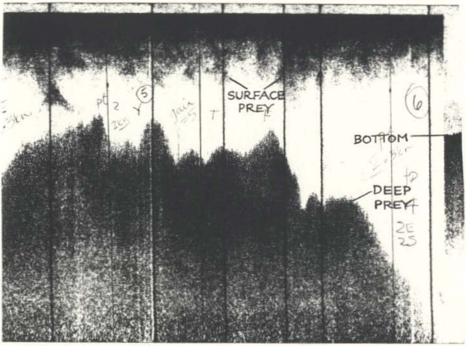
Average bait and ocean floor depths for this location are summarized in Table 3.2. As the study period progressed prey schools were found in shallower water (Figure 5.4), although not necessarily closer to land (Figure 5.2), and they decreased markedly in vertical extent (Figure 5.4). The depth of bait schools themselves did not change significantly throughout the study period (Figure 5.4). The larger post spawning capelin schools seen here sometimes extended to the ocean floor and at other times were located midway between the surface and bottom (see Figure 5.3) especially after 22 July.

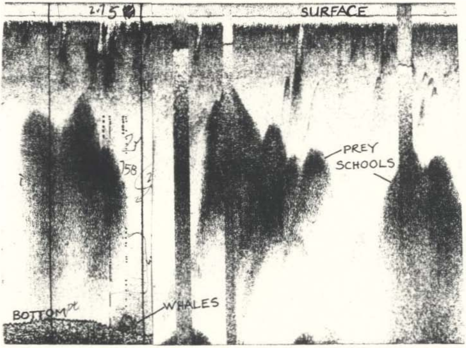
5.2 Census Data

Although we worked progressively further north (Figure

Figure 5.3

Representative depth sounder printouts from the Great Island study area. The upper school is from early in the study period (18-19 July) when schools were larger and more cohesive. The lower figure is typical of the composite schools observed later (21-26 July). Depth scale is 0-60 fathoms (0-109.7 m).


5
SURFACE
PREY
6
BOTTOM
DEEP
PREY
2E
2S


2.15
SURFACE
158
PREY
SCHOOLS
BOTTOM
WHALES

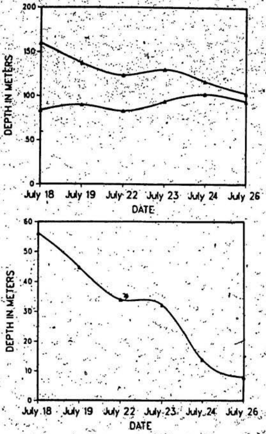


Figure 5.4

Upper: Mean depths to the top of the bait school and to the ocean floor on each day of observation in the Great Island study area. The X axis represents the water surface, the line closest to it the top of the bait school and the uppermost line the ocean floor. The area between the lines thus represents prey school extent and the area below the lower line the water depth above the prey school. Lower: Daily variation in vertical extent of prey is also illustrated (more accurately) in the lower graph.

5.2). 6 - 9 humpback whales were present within visible radius every day that work at sea was possible (Table 5.1). There was no significant correlation between total whales and mean daily group size (r=0.394).

We did have to keep moving north in order to find suitable concentrations of foraging whales to observe but in spite of changes in our position the visible population size remained the same. The distribution of humpbacks may have shifted north or there may have been a relatively stable density off this region of the coast and we were moving north through it. The former seems the more likely for a number of reasons. On 24 July when we travelled as far as Fermeuse to look for whales, none was seen further south than Cape Neddick (see Figure 5.1). On 25 July the local whale population was located from Bay Bulls to Shoal Bay, no whales were seen from Cape Broyle Harbour to Bay Bulls. A bait trace done on this date south east of Great Island, where whales were foraging the previous day, indicated only a very small amount of prey still present in the area. On 26 July whales and bait were concentrated off Shoal Bay although areas further south than Bay Bulls (Figure 5.1) were not surveyed. No prey - whale aggregations are plotted for this date. In response to highly significant reduction in the amount of prey available, (as reflected in the vertical extent of fish schools at whale terminal dive areas, Figure 5.4), the apparent local whale population decreased slightly (Table 5.1) but not significantly.

Table 5.1

Humpback whale counts from the Great Island study area. During censuses whales were counted by groups so that for each census taken there was a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of the mean group sizes for each census taken.

Date	Total Whales	SD	Average Group Size	SD	Number of Counts
18 JUL	6.3	0.0	2.20	0.00	1
19 JUL	6.8	1.0	2.27	0.54	4
22 JUL	7.0	0.0	1.75	0.00	1
23 JUL	6.2	0.4	1.72	0.36	6
24 JUL	6.0	0.0	1.50	0.00	2
26 JUL	5.3	0.6	1.75	0.23	3
OVERALL MEAN	6.3	0.6	1.87	0.30	

On each day of the study period 1 - 3 minke whales were seen and, except for 18 July, 1 - 7 fin whales were seen. On 25 July 15 - 20 white-sided dolphins were observed south of Shoal Bay.

Because of the small number of humpbacks in the area we could usually keep track of both individuals and groups over the course of a day. A whale with a very distinctive dorsal fin and unusual back markings near the fin was first seen on 19 July and resighted on 22 and 23 July. A pair of whales (Tom and Rosie) was repeatedly seen together on 23 July and the same pair was then followed for 6.5 h on 24 July. A whale initially sighted and followed with Tom and Rosie on 23 July was subsequently seen off Shoal Bay on 26 July. Residence time in this location thus appears to be at least 3 - 4 days. No whales followed earlier in July in Witless and Mobile Bays or Cape Broyle Harbour were later recognized outside these bays in this study location.

5.3 Behavioural description

Whale foraging behaviour here was comparable to that observed in the other two deep bait locations. Whales did not forage as continuously however, 14% of all dives observed were categorized as non-foraging. Non-foraging dives include instances of travelling (from one localized concentration of capelin to another on 23 and 24 July), resting (one whale of a pair rested while the second continued to exploit the prey school below), and leaving or losing bait schools. In the latter instance two whales seemed to either inadvertently lose or deliberately leave a prey school as they continued to dive in the surrounding area but not into bait.

Small surface aggregations of capelin were widespread throughout the study area from 18 - 24 July. Whales selectively utilized only the deeper schools except on 24 July when a pair of animals apparently foraged on shallow bait for 2 h. The pair dove repeatedly into small shallow capelin schools; no deeper schools were present immediately below.

5.4 Behavioural analysis

Continuous whale variables. Mean values of whale behavioural variables for this study location are presented in Table 5.2. Figure 5.5 depicts variation in time variables with date. Times spent at the surface were significantly longer on 19 July than on any other day. Hence the mean dive time to surface time ratio was smallest and the magnitude of directional change at the surface was largest on this date. The rate of directional change was also greatest on 19 July. In addition to longer surface times, this would also account for greater amounts of directional change. Mean dive times for each day do not correspond to mean daily bait or ocean floor depths (Figures 5.4, 5.5).

Table 5.2

Average (and SD) values of whale behavioural variables for the study period (July 18 - 26, 1981) in the Great Island study area broken down into foraging and non-foraging dives. Time variables in min., directional variables in degrees, TRATE in degrees/min. * in the non-foraging dives column denotes significant differences from values for foraging dives. ($p<.01$ for all variables except DIRN where $p<.05$)

	OVERALL		FORAGING DIVES		NON-FORAGING DIVES	
	Mean	SD	Mean	SD	Mean	SD
SURFTIME	3.54	3.15	2.91	1.24	* 8.33	6.85
DIVETIME	4.77	1.57	4.92	1.46	* 3.59	1.92
UNITIME	8.31	3.14	7.83	1.76	*11.92	6.80
RATIO	1.86	1.16	2.00	1.12	* 0.77	0.81
GROSDIR	77.8	75.1	74.8	71.8	104.2	94.1
NETDIR	60.7	54.3	60.2	55.5	66.7	44.8
CLOCK	38.0	52.5	34.7	49.2	* 65.8	68.3
COUNTER	-40.0	54.6	-40.3	56.0	-38.3	44.5
OVERALL DIR	-2.0	74.5	-5.5	74.9	* 27.5	66.7
TRATE	23.6	22.0	24.8	22.5	* 13.5	14.1

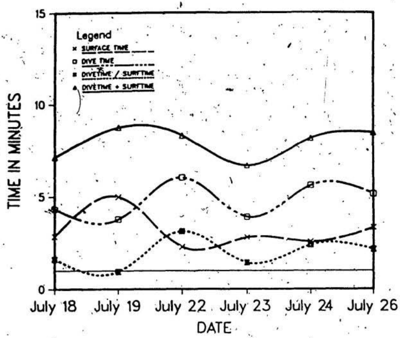


Figure 5.5

Daily means in surface and dive times in the Great Island study area. Mean values of unitime (dive time plus preceding surface time) are depicted by the uppermost line. The mean daily dive time to surface time ratio is illustrated by the dotted line. 1.0 is referenced to illustrate ratio values greater or less than 1.0. Foraging dives from the individual whale data set were used to compile this figure.

Categorical variables. Frequencies of different group sizes and down behaviours broken down by foraging versus non-foraging dives are reported in Table 5.3. Small groups of 2 - 3 whales were most common, although single whales comprised approximately one third of all groups followed. Group categories were delineated differently for this location (group sizes of 4 included with large rather than small groups) to avoid the problem of empty cells in further analysis. No groups larger than 5 were seen in this location. For only four dives of all those observed in this location were group sizes larger than 4 (two dives of a group of 4, two dives of a group of 5). These large groups were always observed on foraging dives, only single whales and small groups displayed non-foraging behaviour. As in both other deep bait locations, most dives were preceded by fluke-ups.

Multiple regression analysis. Multiple regression analysis results for the data set containing all dives are summarized in Table 5.4. As in other deep bait locations the removal of whale variables from the independent variable list decreased the proportion of variance of each time measure that the independent variables account for. This was most evident with surface time, a large part of the variance of which was due to the directional variables. Unlike results from Varket Channel and Trinity Bay, surface time was not significantly correlated with bait variables at all (Table 5.4).

Table 5.3

Frequencies of various group sizes and down behaviours for the Great Island study area broken down by foraging and non-foraging dives. Group size frequencies were determined for the group data set so they represent the observed number of dives of groups of size n. Down behaviour frequencies were calculated from the individual whale data set so they represent actual occurrences of each behaviour.

	FORAGING DIVES		NON-FORAGING DIVES		OVERALL TOTAL	
	Number	column %	Number	column %	Number	column %
GROUP SIZE						
singles	28	27.2	8	57.1	36	30.8
small (2-4)	71	79.0	6	42.9	77	65.8
large (5-8)	4	3.8	-	-	4	3.4
	103	100	14	100	117	100
DOWN BEHAVIOUR						
fluke-up	159	82.0	17	63.0	176	79.6
LY or SY	7	3.6	4	14.8	11	5.0
no fluke	28	14.4	6	22.2	34	15.4
	194	100	27	100	221	100

Table 5.4

Multiple regression results from Great Island with different time measures used as dependent variables. The independent variable list contains both whale and bait variables in the upper part of the table but only bait variables in the lower part. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the dependent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.01	All	p<0.01	All	p<0.01
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	14.0	TOPFP	9.1		
	TRATE	47.4	SURFTIME	14.0(-)	GROSDIR	8.4
	DIRN	49.5(-)	DIRN	14.6(-)	TRATE	24.9
	NETDIR	51.4	NETDIR	15.4(-)	TOPAV	29.7
	VEXTAV	51.6(-)	TRATE	19.0	DIRN	30.1(-)
	VEXTFP	53.1(-)	TOPAV	19.7	VEXTAV	30.2(-)
	FLRFP	53.1	AREA	20.2(-)	AREA	31.3(-)
	FLRAV	54.6	VEXTFP	25.5(-)		
	TOPAV	54.7	VEXTAV	26.1(-)		
Total proportion of variance accounted for	55.1		27.8		31.6	
Durbin-Watson test	inconcl	p<.05	autocor	p<.05	autocor	p<.05
	no auto	p<.01	autocor	p<.01	autocor	p<.01

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		All	p<0.01	All	p<0.01
1st variables entered and cumulative proportion of variance accounted for	TOPAV	0.5	TOPAV	7.9	TOPAV	8.2
	TOPFP	1.5	VEXTFP	8.7(-)	AREA	9.3(-)
	VEXTFP	1.8	AREA	15.8(-)	VEXTFP	11.9(-)
	AREA	3.3(-)	FLRFP	16.1	VEXTAV	12.5(-)
	VEXTAV	3.8	FLRAV	18.0	TOPFP	12.8
	FLRFP	3.8	TOPFP	18.4	FLRFP	13.0
	FLRAV	6.3	VEXTAV	18.9(-)	FLRAV	14.1
Total proportion of variance accounted for	6.3		18.9		14.1	
Durbin-Watson test	autocor	p<.05	autocor	p<.05	autocor	p<.05
	autocor	p<.01	autocor	p<.01	autocor	p<.01

Dive time showed the strongest relationship with immediate bait variables. Unitime, the combination of dive time and surface time, showed characteristics of both in its capacity to be predicted by independent variables. It was better predicted than dive time but not as well predicted as surface time when directional variables were included, due to the strong effect of directional variables on surface time. When bait variables only were used in the equation, unitime was less well predicted than dive time due to the weak relationship between surface time and bait characteristics (Table 5.4).

The proportion of variance of surface and dive time accounted for by the independent variables dropped by 3 - 13% when only footprint values of bait measures were included in order to control for multicollinearity. The prediction of unitime by bait variables only (whale variables excluded from the analysis) dropped by 60% when the set of bait variables included just footprint measures (Appendix 3, Table A3.5). Regression results with only footprint bait measures were, however, qualitatively similar to results that include both types of bait variable, in that the same variables emerged as the best predictors of whale diving behaviour.

Regression analyses were rerun using the hourly means of each variable in an effort to remove autocorrelation (Appendix 1, Table A1.6). This was not entirely sucessful, but as for other deep bait locations, whale behaviour (time variables) was better predicted by bait variables when this data set was used. Surface time, however, still did not show a significant correlation with bait variables alone. Similar results were obtained when regressions were run using data composed of only the first dive of every hour (Table A1.5). Only the regression of dive time on bait variables alone remained autocorrelated. When this data set was used time spent at the surface was significantly related to all immediate bait variables except the vertical extent of bait at the whales footprint. Regression results on the aggregated data set using only the footprint measures of bait variables were similar to those from the dive by dive data set.

Tables 5.5 and A2.3 portray the first order correlation coefficients for the dive by dive and hourly mean data sets respectively. The interrelationships among variables were similar to those from other deep bait locations in a number of ways. Dive time was negatively related to the vertical extent and cross sectional area of the prey school in the immediate dive vicinity. Relationships evident between variables in the dive by dive data set were more strongly expressed in the aggregated data set. Time spent at the surface and group size were slightly positively correlated in the dive by dive data set, while in the aggregated data set the correlation was substantially stronger, both here and in Trinity Bay. (There was a slight increase in the correlation coefficient in Varket Channel.) Larger groups seem to spend longer periods of time at the surface. Contrary to the results from other deep bait locations,

Table 5.5. First order correlation coefficients between pairs of variables in the Great Island dive by dive data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	~~SURFTIME~~	~~DIVETIME~~	~~GROSDIR~~	~~NETDIR~~	~~FLRFP~~	~~FLRAV~~	~~TOPFP~~	TOPAV
SURFTIME	1.00000**	-0.20685**	0.37482**	0.35438**	0.05850	0.04979	0.04379	0.07502
DIVETIME	-0.20685**	1.00000**	-0.07714	-0.12034	0.03480	0.03948	0.30220**	0.30124**
GROSDIR	0.37482**	-0.07714	1.00000**	0.91991**	0.03547	0.02969	0.06744	0.05884
NETDIR	0.35438**	-0.12034	0.91991**	1.00000**	0.09727	0.09139	0.09443	0.09117
FLRFP	0.05850	0.03480	0.03547	0.09727	1.00000**	0.99882**	0.17622*	0.23481**
FLRAV	0.04979	0.03948	0.02969	0.09139	0.99882**	1.00000**	0.17418*	0.22968**
~~TOPFP~~	~~0.04379~~	~~0.30220**~~	~~0.06744~~	~~0.09443~~	~~0.17622*~~	~~0.17418*~~	~~1.00000**~~	~~0.96202**~~
TOPAV	0.07502	0.30124**	0.05884	0.09117	0.23481**	0.22968**	0.96202**	1.00000**
VEXTFP	0.02647	-0.22259**	0.03768	0.07067	0.54619**	0.54730**	-0.62484**	-0.55651**
VEXTAV	0.00232	-0.19282**	0.03368	0.05613	0.55910**	0.56163**	-0.61082**	-0.56021**
AREA	-0.01463	-0.13849	0.02029	0.03710	0.55678**	0.55758**	-0.59848**	-0.54736**
GPSIZE	0.13625	-0.03082	0.14883*	0.15154*	0.25565**	0.25795**	-0.05055	-0.02356
UNITIME	0.77277*	0.46112**	0.28990**	0.24334**	0.07563	0.07077	0.23576**	0.26345**
RATIO	-0.52270*	0.66447**	-0.35880**	-0.35857**	-0.17519*	-0.17088*	0.08437	0.07332
~~DIRN~~	~~0.07755~~	~~-0.15329*~~	~~-0.08217~~	~~-0.10794~~	~~-0.20577**~~	~~-0.21643**~~	~~-0.19034**~~	~~-0.19816**~~
TRATE	-0.00467	0.03485	0.83508**	0.80491**	-0.03507	-0.04180	0.04248	0.00931

	UNITIME	RATIO	DIRN	TRATE	VEXTFP	VEXTAV	AREA	GPSIZE
~~SURFTIME~~	~~0.77277**~~	~~-0.52270**~~	~~0.07755~~	~~-0.00467~~	0.02647	0.00232	-0.01463	0.13625
DIVETIME	0.46112**	0.66447**	-0.15329*	0.03485	-0.22259**	-0.19282**	-0.13849	-0.03082
GROSDIR	0.28990**	-0.35880**	-0.08217	0.83508**	0.03768	0.03368	0.02029	0.14883*
NETDIR	0.24334**	-0.35857**	-0.10794	0.80491**	0.07067	0.05613	0.03710	0.15154*
~~FLRFP~~	~~0.07563~~	~~-0.17519*~~	~~-0.20577**~~	~~-0.03507~~	0.54619**	0.55910**	0.55678**	0.25565**
FLRAV	0.07077	-0.17088*	-0.21643**	-0.04180	0.54730**	0.56163**	0.55758**	0.25795**
TOPFP	0.23576**	0.08437	-0.19034**	0.04248	~~-0.62484**~~	~~-0.61082**~~	~~-0.59848**~~	~~-0.05055~~
TOPAV	0.26345**	0.07332	-0.19816**	0.00931	-0.55651**	-0.56021**	-0.54736**	-0.02356
~~VEXTFP~~	~~-0.12039~~	~~-0.20510**~~	~~-0.01396~~	~~0.00287~~	1.00000**	0.98777**	0.95936**	0.23742**
VEXTAV	-0.12298	-0.17609*	-0.02333	-0.00237	0.98777**	1.00000**	0.96784**	0.22727**
AREA	-0.10311	-0.13869	-0.00789	-0.00215	0.95936**	0.96784**	1.00000**	0.23967**
GPSIZE	0.10358	-0.15404*	-0.16466*	0.02594	0.23742**	0.22727**	0.23967**	1.00000**
~~UNITIME~~	~~1.00000**~~	~~-0.04301~~	~~-0.02911~~	~~0.01837~~	-0.12039	-0.12298	-0.10311	0.10358
RATIO	-0.04301	1.00000**	0.00747	-0.09548	-0.20510**	-0.17609*	-0.13869	-0.15404*
DIRN	-0.02911	0.00747	1.00000	-0.03582	~~-0.01396~~	~~-0.02333~~	~~-0.00789~~	~~-0.16466*~~
TRATE	0.01837	-0.09548	-0.03582	1.00000**	0.00287	-0.00237	-0.00215	0.02594

surface time and dive time were negatively correlated in this study location.

CHAPTER 6. SOUTHERN SHORE

The data set for this location includes observations of whales exploiting small scattered schools of post spawning capelin in Witless and Mobile Bays from 8 - 11 July, 1981, and in Cape Broyle Harbour on 16 July when prey schools were similar to those exploited in Witless and Mobile Bays (Figure 6.1).

6.1 Bait schools

Prey schools in this location consisted entirely of capelin. The existence of seabird colonies on nearby islands depends on capelin as a food resource and puffins, murres, and kittiwakes with capelin in their beaks were a common sight. We observed capelin leaping from the water ahead of lunging whales and dead capelin were frequently seen floating at the surface. Throughout the study period fishermen were finding capelin in the stomachs of cod and of seabirds accidently caught in fishing nets (J.Piatt pers. comm.). Capelin were primarily at the post spawning stage; spawning occurs in middle to late June in this location (Leggett et al. 1984).

Patches of post spawning capelin were dispersed throughout Witless and Mobile Bays although areas of proportionally greater prey density did exist (Figure 6.1). Bait schools extended from the surface downwards except on 10 July when a small dense bottom school was present in

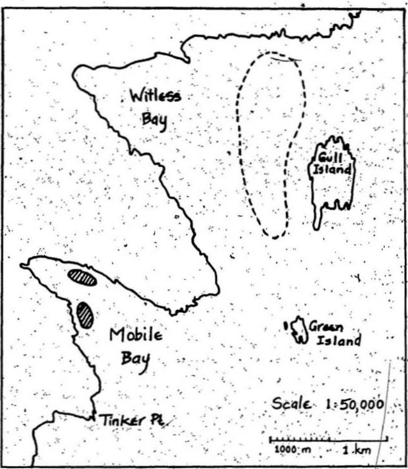


Figure 6.1

Southern Shore study area, excluding Cape Broyle Harbour (see Figure 5.1). Small post spawning capelin schools were distributed throughout Witless Bay and the inner portion of Mobile Bay. Crosshatched areas in Mobile Bay represent concentrated prey schools. The outlined area of Witless Bay delineates the region whales foraged in during the observation bout on 10 July.

Mobile Bay (Figure 6.2). This concentrated type of school is similar in configuration to those seen later in Cape Broyle Harbour from 11 - 14 July (see following, Figure 7.2) and likely precedes the dispersed school stage, seen both here and after the more concentrated schools in Cape Broyle Harbour broke up (16 July).

Mean values of bait variables and of ocean floor depths for this study location are given in Table 6.1. Significant differences in ocean floor depths among days reflect the various observation locations. Floors were deepest in Cape Broyle Harbour (16 July) and shallowest close to shore in Witless and Mobile Bays (8 July, Figure 6.1). The vertical extent of prey schools was significantly less when they were in shallow water close to shore (8 July in Witless and Mobile Bays) and significantly greater in deeper water farther from shore (10 July, Witless Bay; 16 July, Cape Broyle Harbour; Figure 6.1). Graphs of variation in bait variables over the course of the study period were considered inappropriate for this foraging situation since we observed whales in different bays on each day. Hence, a continuous picture of bait changes over time in one area, as compiled for the deep bait study locations, is unavailable.

6.2 Census data

Four humpback whales were present in each of Mobile and Witless Bays on 4 July so food resources in this location had been exploited prior to the onset of behavioural observation. Only 2 - 5 humpback whales were present on

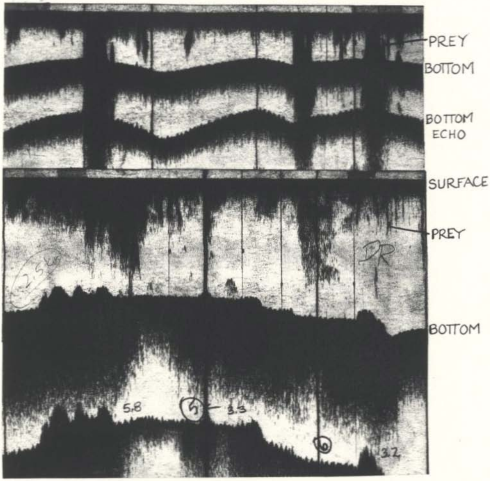


Figure 6.2

Depth sounder printouts of concentrated post-spawning capelin schools from Mobile Bay (top) and of more scattered surface capelin schools from Witless Bay (bottom). Depth scale is 0-30 fathoms (0-54.6 m).

Table 6.1

Mean values of bait variables averaged over the entire study period in locations where prey schools were shallow. All depths are in m, XS AREA is in m. (*) indicates a significant difference ($p < .05$) between values for foraging and non-foraging dives. Contrary to the table of values for deep bait, no set of values for top depth exist for these areas as bait was at or just below the surface. No dives were classified as non-foraging when whales were lunging on krill.

	FLOOR DEPTH			VERTICAL EXTENT		
	all dives	forage dives	non forage dives	all dives	forage dives	non forage dives
WITLESS BAY	35.9	36.7	30.8	9.3	9.7	* 6.8
CAPE BROYLE	38.7	37.6	48.6	9.7	10.0	6.6
SHALLOW BAIT AVERAGE	36.7	37.0	34.7	9.4	9.8	* 6.7
KRILL LUNGING	38.2	38.2	-	10.6	10.6	-
KRILL NO LUNGE	75.6	69.6	* 85.2	3.3	4.0	* 3.7
KRILL AVERAGE	57.9	51.4	* 85.2	7.4	8.3	* 3.7

	CROSS SECTIONAL AREA		
	all dives	forage dives	non-forage dives
WITLESS BAY	1040	1080	* 740
CAPE BROYLE	1180	1230	* 730
SHALLOW BAIT AVERAGE	1080	1120	* 730
KRILL LUNGING	1080	1080	-
KRILL NO LUNGING	390	440	* 290
KRILL AVERAGE	710	810	* 290

each day of observation (Table 6.2). Group sizes were small, the mean group size over the entire period was 1.83 ± 0.19. There was no significant correlation between total whales in the study area and group size, although the direction of the relationship was negative (r= -0.812). Group sizes were larger when fewer whales were present. Minke whales were seen each day except 10 July; no fin whales were seen. On 11 July no whales were seen in Witless Bay; only 2 were present in Mobile Bay. No information on whether whales continued to forage in these small bays after 11 July is available as observations were subsequently carried out in Cape Broyle Harbour.

Two individually identified whales followed in Mobile Bay on 8 July were again observed together and followed on 10 July in Witless Bay. One of the pair was later seen on 12 July in Cape Broyle Harbour. Residence time in these small bays was thus at least 2 - 4 days and individual whales exploited resources in more than one bay.

6.3 Behavioural description

Groups of whales selectively utilized the concentrated aggregations of capelin in Mobile Bay (Figure 6.1) but only for limited time periods. On 11 July 2 whales foraged on a dense area of bait in Mobile Bay for only 0.5 h before they left the prey school and proceeded to travel leisurely away from the area of bait and up the north shore of the bay. The foraging strategy used to exploit the small subsurface schools dispersed throughout this study area was termed

Table 6.2

Humpback whale counts from the Southern Shore study area. During censuses whales were counted by groups so that for each census taken there was a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of all mean group sizes for each census taken. No count was done in Mobile Bay on 10 July; no whales were present in Witless Bay on 11 July.

Date	Place	Total Whales	s.d.	Average Group Size	s.d.	Number of Counts
8 JU	Mobile	5.0	0.0	1.78	0.19	3
8 JU	Witless	4.0	0.8	2.00	0.41	4
10 JU	Witless	5.0	0.0	1.81	0.64	3
11 JU	Mobile	2.0	0.0	2.00	0.00	3
OVERALL MEAN		4.0	1.4	1.90	0.12	13

"cruise and munch" behaviour. Whales travelled slowly in fairly straight lines, often following the shore and terminally diving periodically. Terminal dives were not always marked by fluke-ups; disappearance from the surface for 1 min or more was a more reliable indicator. Whales travelled in groups but did not habitually coordinate dives, surfacings, direction of movement or lunges. It was repeatedly noted that horizontally and vertically more extensive patches of bait were present at the surface in the immediate vicinity of the footprint than in the area either preceding or following it.

When foraging on the dense capelin schools behaviour contrasted distinctly with cruise and munch strategy. Whales circled extensively while they were at the surface, dives were oriented toward the school and forward lunges were occasionally seen. No lunges were observed when whales were using cruise and munch foraging mode.

It was apparent that whales became aware of where the concentrated capelin schools were located. On 8 July in Mobile Bay we observed a pair of whales that were alternately exploiting two areas of high bait density, travelling directly back and forth between them (Figure 6.1). The same pair later left the dense aggregation of bait on the northeast side of the bay, crossed the bay and travelled up the southwest shore, foraging on small dispersed capelin schools (cruise and munch). As they proceeded out of the bay bait became very sparse and they stopped foraging: they travelled very slowly, blowing only once/min, out of the bay and around Tinker Point into the adjacent cove. After circling around the cove they re-entered the bay, continuing in non-foraging mode. They headed straight for the dense area of bait they had left about 1 h earlier and resumed foraging.)

The greater part of the data set for this study location consists of cruise and munch foraging on small dispersed capelin schools. Data collected on 8 and 10 July in Witless Bay and 16 July in Cape Broyle Harbour consists entirely of cruise and munch behaviour. Only observations from 8 July in Mobile Bay contain sequences of foraging on concentrated bait schools.

6.4 Behavioural analysis

Continuous whale variables. Mean values of whale behavioural variables broken down by foraging and non-foraging dives are presented in Table 6.3. When both foraging and non-foraging dives were included, surface times were significantly longer on 8 July in Mobile Bay but this reflects the effect of the long times spent at the surface during non-foraging dives (Table 6.3). When foraging dives only are considered, no significant daily differences in surface time existed. Dive times were significantly longer on 16 July when whales were feeding in the deeper waters of Cape Broyle Harbour.

Table 6.8

Average values of whale behavioural variables for July 8 - 11,16, 1981 in the Southern Shore study area broken down into foraging and non-foraging dives. Time variables in min, directional variables in degrees, TRATE in degrees/min. ** in the non-foraging dives column denotes significant differences from values for foraging dives at p<.01; * at p<.10.

	OVERALL		FORAGING DIVES		NON-FORAGING DIVES	
	Mean	SD	Mean	SD	Mean	SD
SURFTIME	3.88	4.79	2.64	2.08	**12.41	8.33
DIVETIME	2.16	1.14	2.21	1.14	* 1.80	0.90
UNITIME	6.04	4.89	4.85	2.47	**14.21	8.50
RATIO	1.43	1.94	1.46	1.58	** 0.37	0.73
GROSDIR	98.0	143.6	75.5	104.7	**253.5	247.7
NETDIR	63.7	71.6	55.5	62.0	**120.4	102.7
CLOCK	47.8	81.0	38.2	67.9	**113.3	124.5
COUNTER	-53.0	88.1	-40.2	63.3	**-141.8	159.1
OVERALL DIR	-5.3	78.9	-2.0	76.0	* -28.5	94.4
TRATE	34.1	57.1	35.9	60.5	21.2	20.2

Whales turned least at the surface on 16 July when foraging on small dispersed bait schools up and down the south coast of Cape Broyle Harbour. On 8 July, when the data set includes sequences of foraging on concentrated capelin schools in Mobile Bay (Figure 6.1), slightly greater amounts of surface directional change occurred, but not significantly greater than on other days except for 16 July.

Categorical variables. Frequencies of various sizes of followed groups and of different down behaviours, partitioned by foraging and non-foraging dives, are displayed in Table 6.4. Group sizes were small (2 - 3 whales) in 85% of all dives observed. Although lone whales were always present (Table 6.2), very few were followed. Groups of four whales were rare and no larger groups were seen. Only 66% of all dives were preceded by fluke-ups.

Multiple regression analysis. As for the deep bait locations, a large part of the variance of surface time is attributable to directional variables (Table 6.5). Bait variables alone account for only 2% of surface time variance. When dive time is used as the dependent variable however, almost all of its total explained variance is due to bait variables; only 2% is attributable to directional variables. Predictably, results with unitime as the dependent variable show characteristics of both the dive time and surface time results and are intermediate between them. When the regression equation equation includes only the footprint measures of bait variables to correct for multicollinearity the degree of prediction of dive time

Table 6.4

Frequencies of various group sizes and down behaviours for the Southern Shore study area broken down by foraging and non-foraging dives. Group size frequencies were determined for the group data set so they represent the observed number of dives of groups of size n. No groups larger than 4 were observed. Down behaviour frequencies, calculated from the individual whale data set, represent actual occurrences of each behaviour.

	FORAGING DIVES		NON-FORAGING DIVES		OVERALL TOTAL	
	Number	column %	Number	column %	Number	column %
GROUP SIZE						
singles	4	3.4	1	4.8	5	3.6
small (2-3)	105	89.0	17	80.9	122	87.8
medium (4)	9	7.6	3	14.3	12	8.6
	118	100	21	100	139	100
DOWN BEHAVIOUR						
fluke-up	129	66.8	17	60.7	146	66.0
LY or SY	25	13.0	5	17.9	30	13.6
no fluke	39	20.2	6	21.4	45	20.4
	193	100	28	100	221	100

Table 6.5

Multiple regression results from the Southern Shore with different time measures used as dependent variables. The independent variable list contains both whale and bait variables in the top row and bait variables only in the bottom row. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the dependent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.01		All p<0.01		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	35.7	FLRFP	26.9	GROSDIR	21.8
	TRATE	50.0	FLRAV	36.0	TRATE	36.8
	NETDIR	52.6	SURFTIME	37.2	FLRFP	44.6
	DIVETIME	53.5	VEXTAV	38.2	FLRAV	47.9
	VEXTAV	54.1	VEXTFP	39.2	NETDIR	49.8
Total proportion of variance accounted for	55.0		40.0		50.4	
Durbin-Watson test	no autocorrel		no autocorrel		no autocorrel	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		All p<0.01		All p<0.01	
1st Variables entered and cumulative proportion of variance accounted for	VEXTAV	0.9	FLRFP	27.2	FLRFP	4.2
	AREA	1.7	FLRAV	36.3	FLRAV	6.9
	VEXTFP	1.8	VEXTAV	37.2	VEXTFP	7.3
	FLRFP	1.9	VEXTFP	38.3	AREA	7.9
	FLRAV	2.0	AREA	38.4	VEXTAV	7.9
Total proportion of variance accounted for	2.0		38.4		7.9	
Durbin-Watson test	no autocorrel		no autocorrel		no autocorrel	

dropped by 25% for the bait plus whale variables analysis, 30% for the bait variables only analysis. Although the prediction of unitime dropped by 50% for the bait variables only analysis when just footprint measures are used, bait measures account for a very small proportion (4 - 8%) of the variance of unitime anyway (Appendix 3, Table A3.7). Regression results were qualitatively similar after re-analysis to control for multicollinearity. No individual regression analyses were autocorrelated.

Correlation coefficients between pairs of variables (Table 6.6) further emphasize the above relationships. Surface time is well correlated with the directional variables (GROSDIR, NETDIR) and not with bait variables. Dive time is well correlated with bait variables, especially floor depth, but not with directional variables. Relationships of unitime with bait and directional variables are intermediate between those for dive time and surface time.

Table 6.6. First order correlation coefficients between pairs of variables in the Southern Shore data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	VEXTFP
SURFTIME	1.00000**	0.09790	0.59752**	0.53282**	-0.04312	-0.04942	-0.09662
DIVETIME	0.09790	1.00000**	-0.08283	-0.10439	0.51841**	0.42794**	0.25915**
GROSDIR	0.59752**	-0.08283	1.00000**	0.82799**	-0.22672**	-0.20845**	-0.17986*
NETDIR	0.53282**	-0.10439	0.82799**	1.00000**	-0.21676**	-0.19469*	-0.12708
FLRFP	-0.04312	0.51841**	-0.22672**	-0.21676**	1.00000**	0.96907**	0.49694**
FLRAV	-0.04942	0.42794**	-0.20845**	-0.19469*	0.96907**	1.00000**	0.48546**
VEXTFP	-0.09662	0.25915**	-0.17986*	-0.12708	0.49694**	0.48546**	1.00000**
VEXTAV	-0.09868	0.34088**	-0.14347	-0.10260	0.50332**	0.48436**	0.84782**
AREA	-0.05238	0.26288**	-0.07266	-0.04499	0.40198**	0.38870**	0.78910**
GPSIZE	0.05198	-0.06955	0.10038	0.16548*	-0.07875	-0.07610	-0.03555
UNITIME	0.88927**	0.54225**	0.46640**	0.40187**	0.20185*	0.15495	0.03753
RATIO	-0.30810**	0.14284	-0.16288*	-0.17770*	-0.05220	-0.05785	-0.05319
DIRN	0.11892	-0.07511	0.13431	0.17778*	-0.08399	-0.07776	0.04544
TRATE	-0.15564	-0.16983	0.33519**	0.40082**	-0.16771*	-0.15461	-0.12783

	DIRN	TRATE	VEXTAV	AREA	GPSIZE	UNITIME	RATIO
SURFTIME	0.11892	-0.15564	-0.09868	-0.05238	0.05198	0.88927**	-0.30810**
DIVETIME	-0.07511	-0.16983*	0.34088**	0.26288**	-0.06955	0.54225**	0.14284
GROSDIR	0.13431	0.33519**	-0.14347	-0.07266	0.10038	0.46640**	-0.16288*
NETDIR	0.17778*	0.40082**	-0.10260	-0.04499	0.16548*	0.40187**	-0.17770*
FLRFP	-0.08399	-0.16771*	0.50332**	0.40198**	-0.07875	0.20185*	-0.05220
FLRAV	-0.07776	-0.15461	0.48436**	0.38870**	-0.07610	0.15495	-0.05785
VEXTFP	0.04544	-0.12783	0.84782**	0.78910**	-0.03555	0.03753	-0.05319
VEXTAV	0.03237	-0.10740	1.00000**	0.90755**	-0.04520	0.07336	-0.05534
AREA	0.08616	-0.04366	0.90755**	1.00000**	-0.02941	0.07660	-0.08236
GPSIZE	-0.15212	0.02900	-0.04520	-0.02941	1.00000*	0.01192	-0.26368**
UNITIME	0.06588	-0.20945	0.07336	0.07660	0.01192	1.00000**	-0.19447*
RATIO	-0.02442	0.08451	-0.05534	-0.08236	-0.26368**	-0.19447*	1.00000**
DIRN	1.00000	0.04553	0.03237	0.08616	-0.15212	0.06588	-0.02442
TRATE	0.04553	1.00000	-0.10740	-0.04366	0.02900	-0.20945**	0.08451

CHAPTER 7. CAPE BROYLE HARBOUR

Groups of humpback whales were observed foraging on a dense aggregation of post spawning capelin in Cape Broyle Harbour from 11 - 14 July, 1981. After 14 July the concentrated prey dispersed into small schools scattered along the south shore of Cape Broyle Harbour. As bait schools on 16 July in Cape Broyle Harbour were distinct from those observed earlier in this location, but were similar to schools exploited by whales in Witless and Mobile Bays (Southern Shore study area), observational data from 16 July in Cape Broyle Harbour are included with the Southern Shore data set.

7.1 Bait schools

Prey schools in this location consisted entirely of capelin (see Section 6.1). Capelin were primarily at the post-spawning stage; spawning typically occurs during the first week of July in this location (K.Frank, pers. comm., Leggett et al. 1984).

From 11 - 14 July, post-spawning capelin were concentrated primarily off Gentleman Point, although small surface schools were also dispersed along the south shore of Cape Broyle Harbour (Figure 7.1). Schools were most dense on 11 July, becoming progressively more scattered until by 16 July no local dense aggregations existed (Figure 7.2). From 16 - 18 July small surface schools of capelin were

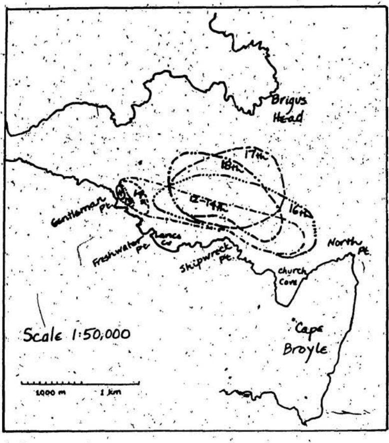
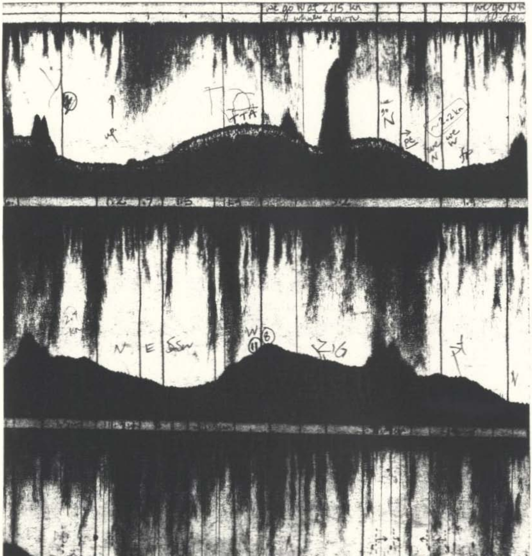


Figure 7.1

Locations of prey schools in Cape Broyle Harbour, 11-18 July, 1981. Numbers within outlined areas refer to limits of prey on that day. In addition to the concentrated schools of capelin off Gentleman Point from 11-14 July, small scattered surface schools extended along the south shore of the bay (12-14). Outlined sections from 16-18 July refer to areas of small scattered surface schools only, concentrated schools were no longer present after 14 July.

Figure 7.2

Depth sounder printouts of bait schools from Cape Broyle Harbour. Upper: Concentrated prey from 11 July when dense bottom schools were present. Middle: Trace from 13 July when bottom schools were less extensive and concentrated. Lower: Printout from 14 July by which time bottom schools had completely disappeared. All traces from the area of Gentleman Point (see Figure 7.1). Depth scale is 0-30 fathoms (0-54.6 m).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dispersed in the outer part of the harbour (Figure 7.1).

From 11 - 13 July surface aggregations of prey extended downwards to meet small dense bottom schools (Figure 7.2). By 14 July no bottom concentrations were present although condensed surface schools were still localized near Gentleman Point. By 16 July, in addition to being more diffuse, surface schools were also less vertically extensive.

Mean values of ocean floor depth and prey school extent averaged throughout the study period for Cape Broyle Harbour are provided in Table 6.1. Bait schools exploited by whales were found in progressively deeper water as the schools dispersed and moved further from shore. No significant daily differences in the vertical extent of schools were present, however.

7.2 Census data

The number of whales present in the bay decreased from 11 - 17 July (Table 7.1). Group sizes were small ($X=1.43 \pm 0.24$) and no groups larger than 4 were observed. There was no significant correlation between total daily whale count and mean daily group size. No humpback whales were seen here after 17 July and after 20 July the area was no longer monitored for whales. Each day 2 - 6 minke whales were present but no other species of cetaceans were noted. A pair of whales followed on 13 July was observed again and followed on 14 July, indicating stable groupings and

Table 7.1

Humpback whale counts in Cape Broyle Harbour. During censuses whales were counted by groups so that for each census taken there was a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of all mean group sizes for each census taken. No whales were present after 17 July.

Date	Total Whales	SD	Average Group Size	SD	Number of Counts
11 JU	6.7	0.6	1.67	0.14	3
12 JU	8.0	-	1.33	0.52	1
13 JU	7.0	0.8	1.50	0.18	4
14 JU	5.7	0.6	1.58	0.38	3
16 JU	5.3	1.0	1.50	0.14	4
17 JU	3.0	-	1.00	-	1
OVERALL MEAN	5.9	1.7	1.43	0.24	

residence times of at least two days.

7.3 Behavioural description

Whales exploited the concentrated prey school off Gentleman Point for 0.5 - 2.0 h at a time, circling extensively at the surface in the vicinity of the school. They dove into the school from all directions, exhibiting no significant preference for inshore directions (southeast to west northwest) (Figure 7.1).

On two of the four days of observation, whales proceeded to exploit the small scattered schools along the south coast of Cape Broyle Harbour (Figure 7.1) after leaving the Gentleman Point school, using cruise and munch foraging mode. They then entered what was considered to be a non-foraging behavioural mode similar to that seen in Witless and Mobile Bays. This consisted of lying almost motionless at the surface or moving very slowly (<0.5 knot) and blowing at 1 min intervals (compared to 10 s between blow intervals when foraging on the dense prey school). On the other two days whales appeared to stop foraging immediately. On 14 July a pair of whales left the Gentleman Point prey school, travelled leisurely out to North Point (see Figure 7.1), and then returned directly to the school after 1 h to resume foraging.

Lunging occurred on each day of behavioural observation in this study area. Whales usually approached the surface of the water at an angle of approximately 45°, and could be seen closing their mouths at the surface. During most lunges whales were in a normal vertical position (dorsal upwards) although occasional side lunges were noted. Lunges were seen only in the vicinity of the Gentleman Point school except for one instance. On 16 July whales that had been previously exploiting scattered capelin schools off Church Cove using cruise and munch strategy, suddenly started lunging after dark. Depth sounder traces from lunge areas showed that surface schools had condensed and dropped slightly in the water column (Figure 7.3). Although whales travelled in groups they did not habitually coordinate dives, surfacings, lunges or direction of travel.

7.4 Behavioural analysis

Continuous whales variables. Mean values of whale behavioural variables for all dives, foraging dives, and non-foraging dives are summarized in Table 7.2. No time variables were significantly different among various days of the study period. Whales turned significantly less and at a slower rate at the surface on 14 July when bait schools had begun to disperse. Greater amounts and faster rates of surface directional change occurred on 11 and 13 July when the Gentleman Point bait school was still highly localized.

Categorical variables. Frequencies of followed group sizes and down behaviours are given in Table 7.3. No single whales were followed although they were seen each day (Table 7.1). Groups of 4 were rare and when they did occur were ephemeral. The data set contains only two dives of groups

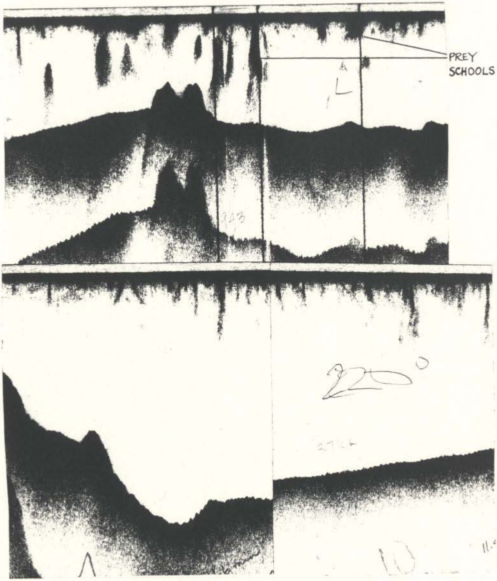


Figure 7.3

Depth sounder printouts from 16 July in Cape Broyle Harbour. The top trace shows fish schools observed in an area where whales were forward lunging after dark (2140 h). The lower trace depicts typical schools exploited by whales throughout the day. Depth scale is 0-30 fathoms (0-54.6 m).

Table 7.2

Average (and SD) values of whale behavioural variables for 11 - 14 July, 1981 in Cape Broyle Harbour broken down into foraging and non-foraging dives. Time variables in min., directional variables in degrees, TRATE in degrees/min. ** in the non-foraging dives column denotes significant differences from values for foraging dives at $p< .01$, * at $p< .10$.

	OVERALL		FORAGING DIVES		NON-FORAGING DIVES	
	Mean	SD	Mean	SD	Mean	SD
SURFTIME	4.23	3.02	3.72	2.28	** 8.72	4.86
DIVETIME	2.67	1.04	2.65	1.04	2.82	1.04
UNITIME	6.89	3.27	6.37	2.53	**11.54	5.22
RATIO	1.10	1.25	1.17	1.29	* 0.42	0.24
GROSDIR	132.3	113.5	126.4	112.7	184.5	113.1
NETDIR	96.8	85.1	91.8	83.6	*141.8	89.4
CLOCK	58.4	80.6	53.6	79.0	*101.3	86.3
COUNTER	-73.2	76.9	-72.6	75.5	-78.8	92.6
OVERALL DIR	-14.8	108.7	-19.0	104.9	-22.5	139.5
TRATE	34.7	27.4	36.1	28.5	22.4	14.1

Table 7.3

Frequencies of various group sizes and down behaviours for Cape Broyle broken down by foraging and non-foraging dives Group-size frequencies were determined for the group data set so they represent the observed number of dives of groups of size n. No groups larger than 4 were observed. Down behaviour frequencies were calculated from the individual whale data set so they represent actual occurrences of each behaviour.

	FORAGING DIVES		NON-FORAGING DIVES		OVERALL TOTAL	
	Number	column %	Number	column %	Number	column %
GROUP SIZE						
singles	-	-	-	-	-	-
small (2-3)	52	96.3	6	100.0	58	96.7
medium (4)	2	3.7	-	-	2	3.3
	54	100	6	100	60	100
DOWN BEHAVIOUR						
fluke-up	21	23.6	-	-	21	21.2
LY or SY	12	13.5	4	40.0	16	16.2
no fluke	56	63.9	6	60.0	62	62.6
	89	100	10	100	99	100

of this size. Only 24% of all dives were preceded by fluke-ups. Terminal dives without any flukes raised were most common.

Multiple regression analysis. Most of the variance of surface time (75%) was attributable to directional variable variance, bait variables were not significantly correlated with surface time and account for only 3% of its variance (Table 7.4). Bait variables were not significantly related to dive time either and accounted for just 8% of its variance. 9.4% of the variance of dive time is due to directional variable variance. Multiple regression results for unitime, the combination of dive time plus surface time, were intermediate between results for each of the component variables. Regressions that were rerun to correct for multicollinearity were quantitatively and qualitatively similar except in one instance. There was a 75% decrease in the proportion of variance of dive time accounted for by both bait and whale variables, when the only bait measures were those at the footprint.

Some tests for autocorrelation were inconclusive. In two analyses where this occurred (bait variables only regressed on time variables) results were not significant, so regressions were not redone. In the regression of surface time on bait and whale variables combined, the relationship between directional variables and surface time was so obvious (and expected) that retesting to confirm the absence of autocorrelation was considered unnecessary.

Table 7.4

Multiple regression results from Cape Broyle Harbour with different time measures used as dependent variables. The independent variable list in the top row contains both whale and bait variables and in the bottom row, bait variables only. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the dependent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.01		p<0.05 except GPSIZE, NETDIR not signif.		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	40.3	DIRN	4.4	NETDIR	35.7
	TRATE	72.8	AREA	7.3	TRATE	56.2
	DIRN	74.9	GPSIZE	8.5	GROSDIR	65.2
	VEXTFP	75.2	NETDIR	9.7	VEXTFP	65.7
	AREA	75.7	GROSDIR	13.8	FLRAV	66.3(-)
	FLRFP	75.9(-)	VEXTAV	14.8	GPSIZE	66.6
			FLRAV	15.5		
			FLRFP	17.3		
Total proportion of variance accounted for.	76.0		17.3		67.0	
Durbin-Watson test	inconcl p<.01 inconcl p<.05		no autocorrel		no auto p<.01 inconcl p<.05	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		none		none	
1st Variables entered and cumulative proportion of variance accounted for	VEXTAV	1.6	AREA	3.7	VEXTAV	3.5
	FLRFP	2.1(-)	FLRAV	4.8	VEXTFP	3.6
	AREA	2.6	FLRFP	7.6	AREA	3.6
	FLRAV	2.9(-)	VEXTAV	7.8	FLRFP	3.7(-)
	VEXTFP	3.2	VEXTFP	7.9	FLRAV	5.4(-)
Total proportion of variance accounted for	3.2		7.9		5.4	
Durbin-Watson test	no auto p<.01 inconcl p<.05		inconcl p<.01 inconcl p<.05		no autocorrel	

Correlation coefficients between pairs of variables for this study location (Table 7.5) further reflect the above results. Surface time was strongly correlated with the amount of surface directional change (GROSDIR, NETDIR) but negatively correlated with all other variables. Dive time was not strongly correlated with any variables. Surface times, because they were longer and more variable than dive times in this study location, were the more influential component of unitime. Unitime was thus more strongly correlated with surface time than with dive time.

Table 7.5. First order correlation coefficients between pairs of variables in the Cape Broyle Harbour data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	VEXTFP
SURFTIME	1.00000**	0.03577	0.63451**	0.59786**	-0.09454	-0.09203	0.12474
DIVETIME	0.03577	1.00000**	0.03604	0.14949	0.05849	0.06549	0.12856
GROSDIR	0.63451**	0.03604	1.00000**	0.88062**	-0.30986**	-0.30694**	0.14484
NETDIR	0.59786**	0.14949	0.88062**	1.00000**	-0.28093*	-0.27864*	0.21201
FLRFP	-0.09454	0.05849	-0.30986**	-0.28093*	1.00000**	0.99919**	-0.21004
FLRAV	-0.09203	0.06549	-0.30694**	-0.27864*	0.99919**	1.00000**	-0.21466
VEXTFP	0.12474	0.12856	0.14484	0.21201	-0.21004	-0.21466	1.00000**
VEXTAV	0.12777	0.17502	0.27815*	0.35359**	-0.20537	-0.20377	0.78731**
AREA	0.10587	0.19190	0.24965*	0.31182**	-0.20807	-0.20686	0.76958**
GPSIZE	0.03802	0.11765	-0.11743	-0.07395	-0.04057	-0.04008	0.02024
UNITIME	0.91151**	0.44362**	0.58386**	0.59768**	-0.06071	-0.05557	0.16478
RATIO	-0.68245**	0.39402**	-0.41671**	-0.33478**	0.05394	0.05270	0.02722
DIRN	-0.04717	0.21015	0.04715	0.00685	0.11027	0.11801	0.11404
TRATE	-0.14728	-0.04742	0.52990**	0.42930**	-0.29632**	-0.29959**	0.08608

	DIRN	TRATE	VEXTAV	AREA	GPSIZE	UNITIME	RATIO
SURFTIME	-0.04717	-0.14728	0.12777	0.10587	0.03802	0.91151**	-0.68245**
DIVETIME	0.21015	-0.04742	0.17502	0.19190	0.11765	0.44362**	0.39402**
GROSDIR	0.04715	0.52990**	0.27815*	0.24965*	-0.11743	0.58386**	-0.41671**
NETDIR	0.00685	0.42930**	0.35359**	0.31182**	-0.07395	0.59768**	-0.33478**
FLRFP	0.11027	-0.29632**	-0.20537	-0.20807	-0.04057	-0.06071	0.05394
FLRAV	0.11801	-0.29959**	-0.20377	-0.20686	-0.04008	-0.05557	0.05270
VEXTFP	0.11404	0.08608	0.78731**	0.76958**	0.02024	0.16478	0.02722
VEXTAV	0.14892	0.19212	1.00000**	0.96653**	-0.01867	0.18661	0.02666
AREA	0.11460	0.17862	0.96653**	1.00000**	0.01504	0.17392	0.04616
GPSIZE	0.01598	-0.20383	-0.01867	0.01504	1.00000	0.08251	0.01359
UNITIME	0.04418	-0.15159	0.18661	0.17392	0.08251	1.00000**	-0.44986**
RATIO	0.03312	0.19557	0.02666	0.04616	0.01359	-0.44986**	1.00000**
DIRN	1.00000**	-0.07459	0.14892	0.11460	0.01598	0.04418	0.03312
TRATE	-0.07459	1.00000**	0.19212	0.17862	-0.20383	-0.15159	0.19557

CHAPTER 8. KRILL FEEDING

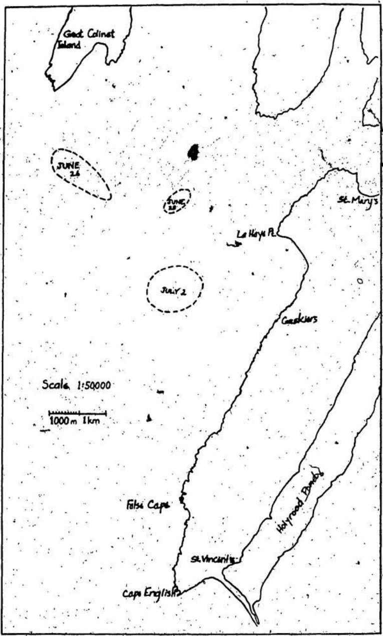
From 25 June - 2 July, 1981, humpback whales were observed feeding on krill (Thysanoessa raschii) at the head of St. Mary's Bay. We observed whales laterally lunging into surface swarms of krill on 25 - 26 June and 2 July. On 26 and 28 June whales were exploiting krill by simply diving into small patches of it. The data set for this study location consists of whales using both foraging strategies. Although whales periodically travelled in groups when feeding on krill, for the most part they fed separately and only a limited amount of coordination occurred. Hence, no group data set was created for this study location.

8.1 Bait schools

Figure 8.1 shows locations of concentrations of (Thysanoessa raschii) and of behavioural observation bouts for this study location. Samples of (Thysanoessa raschii) were collected on 26 June and 2 July in the vicinity of lunging whales. Brick red faeces, diagnostic of krill in the diet, were frequently seen and a sample was obtained on 28 June and 2 July. Only surface traces were seen on the depth sounder (Figure 8.2), and these were quite different from printouts of surface capelin schools (Figures 6.2 and 7.2). Brown faeces, the colour typically seen when whales were consuming capelin, was also seen on 28 July, however, the whale could have been earlier foraging on schools of capelin off St. Vincent's (Figure 8.1). Humpback and minke

Figure 8.1

Locations of observations of humpback whales foraging on krill on different dates in St. Mary's Bay. Outlined areas do not delineate exact perimeters of prey schools, just general areas where krill feeding occurred.


Great Colinet Island
JUNE 26
JUNE 28
St. Mary's
La Haye Pt.
JULY 2
Gaskiers
Scale 1:50000
1000m 1km
False Cape
Holyrood Pond
St. Vincent's
Cape English

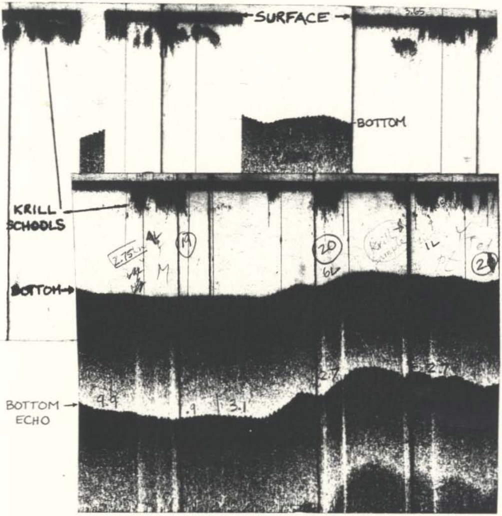


Figure 8.2

Depth sounder printouts from 26 June (top, 0-30 fathoms, 0-54.6m) and 2 July (bottom, 0-60 fathoms, 0-109.7 m) in St. Mary's Bay. On 26 June whales were simply diving into the patches of krill shown on the upper printout. Whales were laterally lunging at the surface into the krill schools portrayed in the lower trace. The upper trace is 2x the scale of the lower trace so krill swarms appear as large as those in the lower trace but they were actually smaller.

whales were observed exploiting schools of spawning capelin off St Vincent's from 22 June - 4 July.

Mean depths of krill schools and of ocean floors during observation bouts are provided in Table 6.1. Ocean floors were significantly shallower and the vertical extent and area of krill swarms were greater on 2 July when whales were laterally lunging. Because whales lunged into bait and then dove, not necessarily where they had just lunged, bait variables have slightly different names for this study location. The suffix -eat refers to bait variables at the lunge location for data from 2 July and at the dive location for data from 26 and 28 June (where whales were presumably diving into areas of prey they were about to exploit). The suffix -fp (footprint) refers to bait variables at the dive location for lunging data from 2 July, and bait variables averaged 150 m around the footprint for data from 26 and 28 June (suffix -av from other study locations).

8.2 Census data

At the beginning of the study period there was a sharp increase in the whale population, followed by an abrupt decline after about one week (Table 8.1). On 24 June no whales were sighted, and on 2 July only four were sighted north of False Cape (see Figure 8.1). Group sizes were small; single whales were sighted more frequently than other group sizes and the largest group size recorded was 3. There was no significant correlation between daily total whale count and mean daily group size.

Table 8.1

Humpback whale counts from St. Mary's Bay. During censuses whales were counted by groups so that each census yields a total number of whales in visible radius plus a mean group size for n groups. Total whales for each date is the mean total from all counts for that day. The average group size for each date is the grand mean of all mean group sizes for each census. No whales were present on 24 June and no groups larger than 3 were ever seen.

Date	Total Whales	SD	Average Group Size	SD	Number of Counts
25 JUN	9.0	-	1.50	0.55	1
26 JUN	11.3	0.2	1.28	0.15	7
28 JUN	12.0	-	1.20	0.42	1
2 JUL	4.0	1.0	1.33	0.34	3
OVERALL MEAN	9.1	3.6	1.33	0.13	

Only one individual whale was resighted. A whale previously followed on 26 June was seen west of Cape English on 2 July. Pods of white-beaked dolphins (Lagenorhynchus albirostris) were seen on 25 and 28 June and minke whales were occasionally sighted.

8.3 Behavioural description

In this study location the unique aspect of humpback whale foraging behaviour was the lateral surface lunging. During lunges whales were completely on one side when breaking the water surface. They typically moved quite slowly for 4 - 10 s with the jaws open and buccal grooves greatly expanded. Closure of the jaws was generally accompanied by rotation to normal swimming position (dorsal upwards).

We noted two principal patterns of movement at the surface during bouts of lunging. The most frequent of the two was a repeated series of zig-zags. The whale would blow once or twice in one direction, moving 20 - 40 m at the surface, turn abruptly, making a 45° - 90° angle with its previous direction of movement, and lunge, travelling through another 20 - 40 m. The other common movement pattern at the surface formed the shape of a lollipop. The whale moved 100 - 200 m in a straight line and then started to lunge and travel in a circle. Generally a complete circle was made, the whale returning to the approximate point where it diverged from its straight line path. It took 3 - 4 lunges to close the circle. Occasionally whales would laterally lunge immediately upon surfacing, as is typical of forward lunges used to capture capelin, observed in Witless and Mobile Bays and Cape Broyle Harbour.

Two whales feeding in the same vicinity would sometimes coordinate for a number of lunges and then resume lunging separately. Coordination occurred in two forms. Usually whales moved together in the same direction at the surface, lunging in unison side by side. Occasionally, however, cooperating whales lunged in opposite directions but passed close to each other with jaws agape. Coordinated lunges were most common in the zig-zag pattern of surface movement.

Only one instance of the possible use of bubbling behaviour to concentrate prey was recorded. A whale exhaled at depth, creating two patches of numerous large bubbles at the surface.

On 28 June a single whale proceeded to travel steadily south after cruise and munch foraging on small patches of krill. This travelling sequence (10 dives) comprises the only non-foraging dives for this study location.

8.4 Behavioural analysis

Continuous whale variables. Table 8.2 depicts means of whale variables for this study location partitioned by a number of factors. Since foraging behaviour during the observation bout on 2 July (containing lateral lunging) was distinct from that observed on 26 and 28 June (cruise and munch) variable means are first partitioned by date. Means

Table 8.2

Average values of whale behavioural variables from observations of humpback whales feeding on krill in St. Mary's Bay. Time variables in min, directional variables in degrees, TRATE in degrees/min. Variable means are first partitioned by date. Means for 2 July are divided into lunging and non-lunging dives, those for 26 and 28 June into foraging and non-foraging dives. All dives from 2 July were designated as non-foraging. Three comparisons are depicted: 1) lunging with non-lunging dives from 2 July, 2) lunging dives from 2 July with foraging dives from 26 and 28 June, 3) foraging with non-foraging dives from 26 and 28 June. * denotes mean values significantly different from non-lunging dives on 2 July, + denotes mean values significantly different from non-foraging dives on 26 and 28 June ($p < .05$).

	2 JULY		26 and 28 JUNE	
	lunging	non-lunging	foraging	non-foraging
SURFTIME	3.78	*1.34	3.28	$^{+}$1.24
DIVETIME	3.5[illegible]	4.06	4.51	$^{+}$2.84
UNITIME	7.37	*5.39	7.79	$^{+}$4.08
RATIO	1.71	*4.06	1.58	$^{+}$2.98
GROSDIR	$^{+}$306.8	*22.5	*31.8	20.3
NETDIR	$^{+}$198.9	*22.5	*30.4	13.5
CLOCK	$^{+}$204.0	*4.1	*22.5	13.5
COUNTER	$^{+}$-109.5	*-18.4	*-9.3	-6.8
DIRN	$^{+}$94.5	*-14.3	*13.2	6.8
TRATE	$^{+}$77.2	*21.2	*13.1	16.0

for 2 July are divided into dives with and without surface lunges, those from 26 and 28 June are divided into foraging and non-foraging dives.

Four comparisons were made between sets of variables: 1) Lunging dives with non-lunging dives from 2 July, 2) Foraging dives with non-foraging dives from 26 and 28 June, 3) Lunging dives from 2 July with foraging dives from 26 and 28 June, and 4) non-lunging dives from 2 July with non-foraging dives from 26 and 28 June. All multivariate analyses of variance of the effect of each factor of comparison on all whale variables combined were significant except the last: non-lunging dives from 2 July were no different from non-foraging dives on 26 and 28 June.

In the comparison between surface bouts that contained lunges on 2 July, and those that did not, differences were striking. When lunging, whales spent longer times at the surface and turned significantly more and at a faster rate. Whales virtually travelled in straight lines and spent less than 1.5 min at the surface when they did not lunge (Table 8.2).

Considering only the cruise and munch foraging data (26 and 28 June), non-foraging dives (from a travelling sequence, see previous) were significantly different from foraging dives on all time measures (Table 8.2). The basic unit of whale behaviour (unitime), was shorter in duration during travelling; the whale spent significantly less time both at the surface and diving.

In the third comparison, that of lunging dives on 2 July with foraging dives on 26 and 28 June, only directional variables were different (Table 8.2). Whales turned more extensively and at a faster rate when lunging laterally at the surface amid swarms of krill (2 July) than when simply diving into patches of krill (26 and 28 June). Lunging dives comprise the only instance in this entire study where whales demonstrated any significant clockwise or counterclockwise directional tendency. When lunging, whales turned predominantly clockwise.

<u>Categorical variables</u>. Single whales were followed most often (Table 8.3) (and were most abundant, see Table 8.1). The majority of dives were preceded by fluke-ups (92%).

Of the period of observation involving lateral lunging (2 July), a number of results are of note. Almost 70% of the dives included surface lunges (Table 8.3). Ocean floors were significantly shallower when lunging occurred than when whales did not lunge. Bait was more extensive on lunging dives, although not significantly so. When lunging dives only are considered, the number of times whales lunged at the surface was significantly linearly correlated ($p<0.01$) with time spent at the surface ($r=0.72$) and with the cross sectional area of the krill school 75 m to either side of the center of the lunge area ($r=0.64$). An average of 1.3 ± 0.6 lunges/min surface time occurred and the mean number of lunges per surface bout was 3.2 ± 2.3.

Table 8.3

Frequencies ~~of various~~ group sizes and down behaviours and of the number of foraging and non-foraging dives that occurred during observation of humpback whales feeding on krill in St. Mary's Bay. No groups larger than 2 were followed. The lower portion of the table depicts the number of dives containing various numbers (0-9) of surface lunges. The percentage of dives with no lunges at the surface and with one or more surface lunges is also given.

	FORAGE		GROUP SIZE		DOWN BEHAVIOUR		
	forage	non-forage	single	pair	fluke	LY SY	no fluke
NUMBER	52	10	52	10	47	11	4
PERCENT	83.9	16.1	83.9	16.1	75.8	17.7	6.5

NUMBER OF DIVES WITH n LUNGES AT THE SURFACE ON JULY 2

# LUNGES	0	1	2	3	4	5	6	7	9
# DIVES	11	9	4	1	1	6	1	1	1
PERCENT	34.4				68.6				

Multiple regression analysis. When both bait and whale variables were included in the regression equation, almost all of the variance of surface time was explained (Table 8.4). Directional variables accounted for 70% and bait variables just 24% of surface time variance. Bait variables alone were not significantly linearly correlated with surface time.

Compared with surface time, much less of the variance of dive time was due to the directional variables (20%) and more was due to bait variables (33%). All bait variables were significantly linearly correlated with dive time. Bait and whale variables combined predicted unitime at a level intermediate between that for surface time and dive time, however, unitime was better predicted by bait variables alone than either surface time or dive time was.

When regressions were rerun to control for multicollinearity the proportion of variance of dive time accounted for by both bait and whale variables decreased by 27%, that accounted for by bait variables alone decreased by 15%. There was a 15% decrease in the variance of unitime accounted for by bait plus whale variables and a 43% decrease when bait variables alone were used. Regression results with surface time as the independent variable were not substantially affected and all results were qualitatively similar after re-analysis.

Table 8.4

Multiple regression results from krill feeding in St. Mary's Bay with different time measures used as dependent variables. The independent variable list in the top row contains both whale and bait variables and in the bottom row, bait variables only. Independent variables are listed in the order of entry into the regression equation along with the proportion of variance of the time variable that each variable plus all variables entered on preceding steps account for. (-) indicates a negative relationship between that variable and the dependent variable.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.01		All p<0.01		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	49.5	FLRFP	23.1	GROSDIR	24.3
	TRATE	84.7	GPSIZE	30.2	FLRFP	53.3
	FLRFP	90.6	AREA	39.8	TRATE	70.7
	FLREAT	91.9	VEXTFP	41.4	FLREAT	72.7
	GPSIZE	92.5	SURFTIME	43.4	DIRN	77.7
	VEXTFP	92.8	DIRN	44.9	NETDIR	81.1
	DIRN	93.1	FLREAT	47.2		
			NETDIR	48.5		
			GROSDIR	51.4		
Total proportion of variance accounted for	94.1		52.4		81.5	
Durbin-Watson test	no autocorrel		autocor p<.01 autocor p<.05		autocor p<.01 autocor p<.05	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		p<0.01 except VEXTEAT p<0.05		p<0.01 except FLRFP not sig.	
1st Variables entered and cumulative proportion of variance accounted for	AREA	6.7	FLRFP	23.1	FLRFP	7.6
	FLRFP	11.3	AREA	30.0	AREA	27.2
	FLREAT	18.4	FLREAT	31.4	FLREAT	36.2
	VEXTFP	22.3	VEXTFP	32.9	VEXTFP	42.1
	VEXTEAT	23.6	VEXTEAT	32.9	VEXTEAT	42.6
Total proportion of variance accounted for	23.6		32.9		42.6	
Durbin-Watson test	no autocorrel		inconcl p<.01 autocor p<.05		no auto p<.01 inconcl p<.05	

As surface times were highly variable, regression lists with surface time as the dependent variable were not autocorrelated, whereas those with dive time as the dependent variable were highly autocorrelated (dive times were more consistent). The number of cases in the dive by dive data set used in the regression analyses (foraging dives only) for this study location was 41. Regression analyses on a data set of hourly means or one containing only the first dive of every hour, in an effort to remove autocorrelation, would thus remove too many cases to remain statistically valid.

First order correlation coefficients between pairs of variables (Table 8.5) are another indication of the relationships among variables elucidated in Table 8.4. Surface time was highly correlated with the amount of directional change at the surface, weakly correlated with the amount of bait at the dive or lunge area and negligibly correlated with the ocean floor depth. Dive time was substantially correlated with the ocean floor depth at the dive or lunge area but negligibly correlated with the degree of surface directional change or vertical extent of prey. Unitime, showing characteristics of both component variables, dive time and surface time, was moderately correlated with directional change and ocean floor depth. Within bait variables, krill schools were more extensive when ocean floors were shallower.

Table 8.5. First order correlation coefficients between pairs of variables in the krill feeding data set. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLREAT	FLRFP	VEXTEAT
SURFTIME	1.00000**	-0.07740	0.70324*	0.45194**	-0.02589	-0.01709	0.20635
DIVETIME	-0.07740	1.00000**	-0.17033	-0.19388	0.47743**	0.48043**	-0.14865
GROSDIR	0.70324**	-0.17033	1.00000**	0.84828**	-0.48668**	-0.49051**	0.73766**
NETDIR	0.45194**	-0.19388	0.84828**	1.00000**	-0.47388**	-0.48416**	0.76488**
FLREAT	-0.02589	0.47743**	-0.48668**	-0.47388**	1.00000**	0.99834**	-0.68426**
FLRFP	-0.01709	0.48043**	-0.49051**	-0.48416**	0.99834**	1.00000**	-0.68655**
VEXTEAT	0.20635	-0.14865	0.73766**	0.76488**	-0.68426**	-0.68655**	1.00000**
VEXTFP	0.10102	-0.06048	0.41137**	0.59970**	-0.32796**	-0.33890**	0.58692**
AREA	0.26245	-0.12062	0.71400**	0.77511**	-0.64766**	-0.66184**	0.87481**
GPSIZE	0.20730	-0.15506	0.04815	0.12712	0.23311	0.22004	-0.17915
UNITIME	0.79835**	0.53860**	0.49143**	0.26483	0.26649	0.27575*	0.08460
RATIO	-0.58206**	0.47404**	-0.39866**	-0.36668**	-0.04296	-0.03720	-0.09877
DIRN	0.23045	0.09691	0.34673**	0.50358**	-0.17139	-0.18577	0.31163*
TRATE	0.09498	-0.08384	0.72028**	0.76163**	-0.48623**	-0.49549**	0.81979**

	DIRN	TRATE	VEXTFP	AREA	GPSIZE	UNITIME	RATIO
SURFTIME	0.23045	0.09498	0.10102	0.26245	0.20730	0.79835**	-0.58206**
DIVETIME	0.09691	-0.08384	-0.06048	-0.12062	-0.15506	0.53860**	0.47404**
GROSDIR	0.34673*	0.72028**	0.41137**	0.71400**	0.04815	0.49143**	-0.39866**
NETDIR	0.50358**	0.76163**	0.59970**	0.77511**	0.12712	0.26483	-0.36668**
FLREAT	-0.17139	-0.48623**	-0.32796**	-0.64766**	0.23311	0.26649	-0.04296
FLRFP	-0.18577	-0.49549**	-0.33890**	-0.66184**	0.22004	0.27575*	-0.03720
VEXTEAT	0.31163*	0.81979**	0.58692**	0.87481**	-0.17915	0.08460	-0.09877
VEXTFP	0.21521	0.53826**	1.00000**	0.72553**	-0.00474	0.04884	-0.23134
AREA	0.36765**	0.69977**	0.72553*	1.00000**	-0.03145	0.14895	-0.16034
GPSIZE	0.03597	-0.04417	-0.00474	-0.03145	1.00000**	0.08153	-0.33522*
UNITIME	0.25329	0.02963	0.04884	0.14895	0.08153	1.00000	-0.20557
RATIO	-0.09961	-0.13365	-0.23134	-0.16034	-0.33522*	-0.20557	1.00000
DIRN	1.00000**	0.28318*	0.21521	0.36765**	0.03597	0.25329	-0.09961
TRATE	0.28318*	1.00000**	0.53826**	0.69977**	-0.04417	0.02963	-0.13365

CHAPTER 9. EFFECTS OF CATEGORICAL VARIABLES

9.1 Introduction

The effects of the categorical behavioural variables (FORAGE, GPSIZE, DWNBEHAV) on other whale behavioural variables and on bait variables were examined within each study location and for each bait type (deep capelin, shallow capelin, krill). Results of these interactions will be first presented for different bait types. The degree to which each study location fits the general pattern within that bait type will be subsequently described.

9.2 MANOVA

Multivariate analysis of variance results for the two types of capelin schools are depicted in Table 9.1. The effect of each categorical variable on 1) all continuous variables, 2) continuous whale variables only, and 3) bait variables only for both foraging and non-foraging dives is indicated. Non-significant multivariate results for a categorical variable precluded finer analysis. For deep capelin all multivariate analyses were significant except for the effect of group size on bait variables. For shallow capelin, only forage had a significant overall effect on all combinations involving continuous whale variables. The effect of group size on bait variables was marginally significant. When whales were foraging on krill no multivariate analyses of the effects of group size and down behaviour on each of the three different combinations of

Table 9.1

Results of multivariate analysis of variance for pooled deep capelin data (upper section) and pooled shallow capelin data (lower section). The effect of each categorical variable was determined over each of three different combinations of continuous variables, firstly for all dives and then for foraging dives only. Group size categories for deep capelin were 1, 2-4, 5-8, those for shallow capelin were 1, 2-3, 4. Individual data were used for any tests involving whale variables. Group data were used for the tests involving bait variables. Figures refer to significance levels for each test.

	Whale and Bait Variables		Whale Variables only		Bait Variables only	
	overall	forage	overall	forage	overall	forage
			DEEP CAPELIN			
FORAGE	0.0001	--	0.0001	--	0.0001	--
GPSIZE	0.0001	0.0001	0.0001	0.0001	0.145	0.118
DWNBEHAV	0.0001	0.0001	0.026	0.013	0.0001	0.0001
			SHALLOW CAPELIN			
FORAGE	0.0001	--	0.0001	--	0.069	---
GPSIZE	0.070	0.060	0.615	0.743	0.048	0.052
DWNBEHAV	0.143	0.053	0.477	0.121	0.102	0.198

variables were significant. The effects of foraging/non-foraging and lunging/non-lunging on both whale and bait variables have been presented for krill feeding data (Section 8.4).

9.3 Deep capelin

Table 9.2 illustrates the results of multiple comparison tests between different levels of down behaviour (fluke-up, LY or SY, no fluke-up) and group size (1, 2-4, 5-8). When whales did not raise their flukes prior to diving, dive times were shorter and hence the dive time to surface time ratio smaller. In the Great Island study area the pattern of results was identical to that seen for the data from all deep capelin foraging situations combined. There was a non-significant trend toward the same pattern in the Trinity Bay results but results from Varket Channel did not reveal the above pattern.

Single whales spent less time both at the surface and diving than groups and while at the surface they travelled in straighter lines (Table 9.2). Results from two individual study locations, Varket Channel and Great Island, conformed to the overall pattern for the pooled deep capelin data, while the effects of group size on other whale variables in Trinity Bay did not contribute to the overall deep capelin pattern.

Table 9.2

Deep Capelin, variables significantly different over various group sizes (top row) and down behaviours (bottom row). Results from one way analyses of variance (ANOVA) indicate the overall effect of group size on individual variables. Significantly different group sizes or significantly different groupings among levels of down behaviour elucidated by results from multiple comparison tests are illustrated by a space between groupings.

SURFTIME		DIVE TIME		RATIO		GROSS DIRECTIONAL CHANGE	
SIGNIFICANCE OF ANOVA							
0.0001		0.0001		0.0005		0.0001	
Gpsize	Mean	Gpsize	Mean	Gpsize	Mean	Gpsize	Mean
1	2.24	1	3.82	5-8	1.58	1	51.8
		5-8	4.11				
2-4	2.95			2-4	1.83	2-4	83.5
5-8	3.04	2-4	4.64			5-8	86.6
				1	2.06		

DIVE TIME		RATIO	
SIGNIFICANCE OF ANOVA			
0.008		0.0001	
Dwnbehav	Mean	Dwnbehav	Mean
no Y	4.05	no Y	1.43
Y up	4.50	Y up	1.86
LY or SY	4.70	LY or SY	2.01

For all deep capelin data combined, when whales were not foraging they spent significantly longer periods of time at the surface (t=8.92 min for non-foraging dives, t=2.86 min for foraging dives) and thus had smaller dive time to surface time ratios (Table 9.3). Amounts of non-foraging surface directional change were not significantly different from those for foraging whales, non-foraging whales turned at a significantly slower rate however (Table 9.3). Results from Trinity Bay and Great Island (Tables 4.2 and 5.2) support this overall pattern. In Varket Channel whales considered to be foraging did not behave statistically differently from those considered not to be foraging (Table 3.5).

All bait variables were significantly different between foraging and non-foraging dives (Table 3.2). Non-foraging dives occurred in shallower water but depths to the top of the bait school were greater. There was markedly less bait present when whales were considered to be not foraging however this was an artifact of foraging/non-foraging criteria (see Section 2.3). The effect of forage on bait variables from each of the deep capelin study locations paralleled that demonstrated for pooled deep capelin data (Table 3.2).

9.4 Shallow capelin

Only bait variables were significantly different among the levels of group size (1, 2-3, 4; Table 9.1). Ocean floors were significantly deeper and bait schools more vertically extensive when group sizes were small (2-3 whales). Floors were shallower and there was less bait present when groups were comprised of single whales or 4 whales. Although group size did not have a significant effect on bait variables combined (from multivariate analysis of variance) in either of the individual shallow capelin study locations, data from the Southern Shore study area showed a non-significant trend similar to that seen for the pooled shallow capelin data.

Forage did not have a significant overall effect on combined bait variables from the pooled shallow capelin data (Table 9.1) but whale variables were highly significantly different between foraging and non-foraging dives (Table 9.3). When not foraging, whales spent longer periods of time at the surface and thus ratios of dive time to surface time were smaller. As a consequence of longer surface times greater amounts of directional change occurred, even though non-foraging whales turned at slower rates. Differences between foraging and non-foraging dives in both individual shallow capelin foraging situations (Tables 6.3 and 7.2) contributed to the effect of forage in the pooled shallow capelin data.

Table 9.3

Average values of whale behavioural variables from pooled deep capelin data and pooled shallow capelin data, broken down into foraging and non-foraging dives. * in the non-foraging dives column denotes significant differences from values for foraging dives (p<.05 except for TRATE for shallow capelin, p<.10). Time variables in min, directional variables in degrees, TRATE in degrees/min.

	DEEP CAPELIN		SHALLOW CAPELIN	
	foraging	non-foraging	foraging	non-foraging
SURFTIME	2.86	*8.92	2.98	*11.44
DIVETIME	4.47	4.34	2.35	2.07
UNITIME	7.33	*13.26	5.33	*13.50
RATIO	1.83	*1.18	1.56	*0.39
GROSDIR	79.8	100.7	91.5	*235.3
NETDIR	64.7	67.0	66.9	*126.1
CLOCK	41.4	50.1	43.1	*110.0
COUNTER	-37.8	-50.6	-50.4	*-125.2
DIRN	3.6	-0.5	-15.1	-7.3
TRATE	28.7	*15.9	36.0	*21.5

CHAPTER 10. COMPARISON OF STUDY LOCATIONS

10.1 Bait schools

Figure 10.1 and Table 10.1 summarize the prey school characteristics of each study location. Prey extent was similar in the two deep immature capelin situations (Varket Channel, Trinity Bay) but schools of deep post-spawning capelin (Great Island) were less extensive. The prey school - water depth profile was similar in three of the shallow bait situations. In Saint Mary's Bay when whales were diving rather than lunging into small patches of krill and where there was a high proportion of non-foraging dives, prey schools were markedly less extensive in relation to water depth.

10.2 Time variables

Figure 10.2 depicts mean surface and dive times for each study location for foraging dives. Surface times were longest in Cape Broyle Harbour, although not significantly longer than those in both krill feeding situations in St. Mary's Bay or in the Great Island study location (Student-Newman-Keuls multiple comparison tests). Dive times were significantly shortest in the Southern Shore study area. Dive times in Cape Broyle Harbour were significantly longer than those in the Southern Shore study area but significantly shorter than those in all other study locations. Dive times were longest when bait schools were deep (Varket Channel, Trinity Bay, Great Island) and when

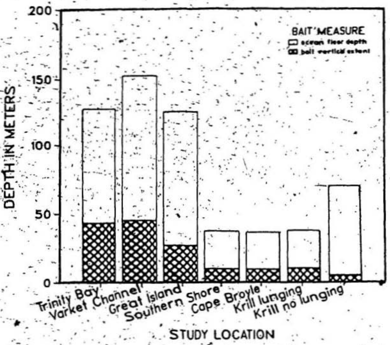


Figure 10.1

Bait and ocean floor depths for each study location. The shaded area of the bar represents the portion of the water column occupied by prey. The open area represents 1) water depth above the prey school for deep bait locations - first 3 bars, or 2) water depth below surface prey schools for shallow bait locations - last 4 bars. The line dividing light and dark portions of the bar identifies 1) mean depths to the top of the prey school on deep bait locations or 2) depths to which prey schools extend in shallow bait locations.

Table 10.1

Differences in various bait school characteristics among study locations.

DEEP SCHOOLS

	TRINITY BAY	VARKET CHANNEL	GREAT ISLAND
SIZE/ ABUNDANCE	largest	intermediate	smallest
DEPTH (m)	75 - 125	90 - 150	95 - 125
VERTICAL EXTENT (m)	45	45	25
AVAILABILITY	stable over obs period	decreasing slowly	decreasing rapidly
SPECIES/ AGE CLASS	immature capelin	immature capelin	post-spawning capelin

SHALLOW SCHOOLS

	WITLESS MOBILE	CAPE BROYLE	SMB KRILL
SIZE/ ABUNDANCE	intermediate	largest	smallest
DISPERSION	dispersed-patchy	concentrated	dispersed-patchy
VERTICAL EXTENT (m)	10	10	7
FLOOR DEPTH	35	40	60
AVAILABILITY	decreasing slowly	dispersing-decreasing abundance	increase then decrease in abundance
SPECIES/ AGE CLASS	post-spawning capelin	post-spawning capelin	krill

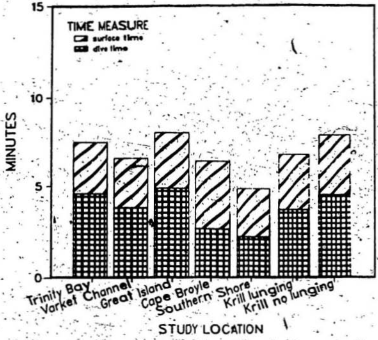


Figure 10.2

Average surface (top light section) and dive times (lower dark section) for the different study locations. The total height of the bar for each study location represents mean unitime. Dive times were significantly shorter when whales were foraging on shallow capelin schools (Cape Broyle Harbour, Southern Shore).

whales were preying on krill.

The mean ratios of each dive time to the preceding surface time for the different study locations are presented in Figure 10.3. Ratios were smallest in the shallow bait locations, (but not significantly smaller than those for Varket Channel and krill non-lunging) where dive times were shortest and surface times longest. The largest dive time to surface time ratios occurred when whales were lunging on krill. These were significantly larger than ratios in Cape Broyle Harbour only.

10.3 Directional variables

The total amount and rate of surface directional change in each study location is portrayed in Figure 10.4. Whales turned significantly more at the surface when lunging on krill than when using any other foraging strategy in any other bait situation. Directional changes when whales were foraging on small concentrated post spawning schools (Cape Broyle Harbour) were significantly less than when they were lunging on krill but significantly greater than in all other prey conditions. Rates of surface directional change were similar in all bait and foraging situations except where whales were laterally lunging at the surface to exploit swarms of krill, when turning rates were significantly greater.

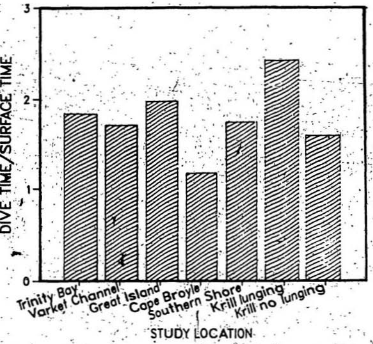


Figure 10.3

Mean dive time to surface time ratios for the various study locations. Ratios were smallest when whales were exploiting small concentrated shallow capelin schools in Cape Broyle Harbour and largest when lunging on krill in Saint Mary's Bay.

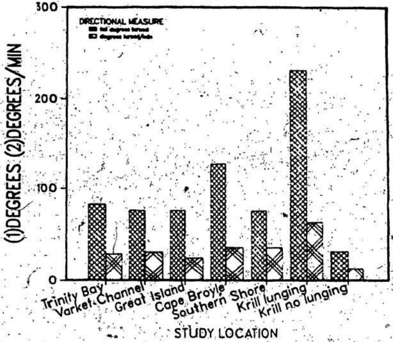


Figure 10.4

Mean total surface directional change (left dark bar) and rate of directional change (right light bar) for each study location, Both the rate and amount of surface directional change were significantly greater when whales were lunge feeding on krill.

10.4 Categorical variables

Figure 10.5 depicts the percentages of foraging and non-foraging dives at each study location. In both deep immature capelin foraging situations (Trinity Bay, Varket Channel) less than 5% of all dives were classified as non-foraging. A larger proportion of non-foraging dives (10 - 16 %) occurred in other study locations. When whales were lunging on krill (2 July) no dives were classified as non-foraging, although there was no significant difference between non-lunging dives from 2 July and non-foraging dives observed on 26 and 28 June when whales were simply diving into patches of krill (see Section 8.4).

The percentage of various group sizes followed in the different study locations is illustrated in Figure 10.6. Group sizes larger than 5 were only observed where bait schools were large and deep (Trinity Bay, Varket Channel, Great Island); no groups larger than 4 were observed when whales were exploiting small shallow fish schools.

Fluke-ups preceded greater than 80% of all dives when whales were exploiting large deep fish schools and when they were laterally lunging on krill (Figure 10.7). The proportion of dives preceded by fluke-ups was less when whales were preying upon small shallow capelin schools or simply diving into swarms of krill.

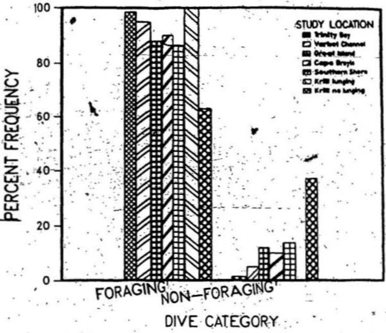


Figure 10.5

The percent frequency of foraging and non-foraging dives in each study location. When whales were lunge feeding on krill all dives were classified as foraging dives. The percent frequency totals 100% for each study location rather than for each dive category.

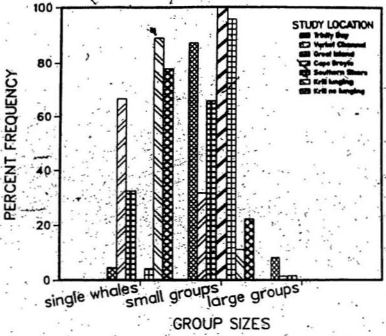


Figure 10.6

Percent frequency of different categories of group size in each study location. The percent frequency totals 100% for each study location rather than for each group size. The data from Varket Channel is biased in that a larger proportion of single whales were followed. No single whales or large groups were followed in Cape Broyle Harbour although these group sizes did occur.

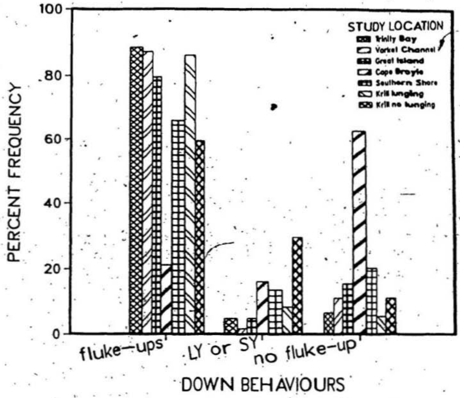


Figure 10.7

The percent frequency of various down behaviours in each study location. Fluke-ups preceded ≥ 80% of all dives when whales were exploiting large deep fish schools and when lunging on krill. Few fluke-ups were observed when whales were foraging on shallow bait schools.

Average group sizes and total whale populations from census counts and an estimated rank of bait abundance for each study location are presented in Table 10.2. Group sizes from census counts in each study location were significantly correlated with bait abundance but not with mean total whale population. Table 10.2 also depicts mean sizes of followed groups of foraging and non-foraging whales in each study location. The size of these groups is not a representative sample of all group sizes present in the population as whale groups followed were not chosen randomly (see Section 2.3), but they do reflect the different sizes of foraging and non-foraging groups. Foraging groups were significantly larger than non-foraging groups over all study locations and in deep bait locations ($p<.05$) but were not significantly different in shallow bait locations.

Table 10.2

The average total humpback whale population, group sizes and an estimated rank of bait abundance (calculated over the entire study period) for each study location. The Spearman rank correlation coefficient between total population and rank of abundance was 0.314 (n.s); between census group size and bait abundance was 0.970 ($p < .01$). The Pearson correlation coefficient between census group size and total population was 0.447 (n.s.). Foraging groups were significantly larger than non-foraging groups over all study locations and in deep bait locations ($p < .05$) but were not significantly different in shallow bait locations only.

STUDY LOCATION	RANK OF BAIT ABUNDANCE	MEAN GROUP SIZE (CENSUS)	MEAN TOTAL POPULATION (RANGE)	MEAN GROUP SIZE FORAGING	MEAN GROUP SIZE NON-FORAGING
Trinity Bay	1	2.18	21.4(14 - 30)	3.07	2.56
Varket Channel	2	1.94	6.0(3 - 8.3)	1.64	1.43
Great Island	3	1.87	6.3(5.3 - 7)	1.97	1.70
Cape Broyle Hr	4	1.90	4.0 (2 - 5)	2.24	2.10
Witless and Mobile	5	1.43	5.9 (3 - 8)	2.33	2.42
St.Mary's Bay	6	1.33	9.1 (4 - 12)	1.23	1.00

CHAPTER 11. DISCUSSION

11.0 Introduction

The results of this study showed that humpback whales vary their foraging behaviour in response to different prey situations. That response will be discussed within the broad conceptual framework of optimal foraging theory. Feeding time for humpback whales is limited: they have to obtain total yearly energy requirements within a four to six month feeding season. They can thus be theoretically classified as energy maximizers (Schoener 1971; Hixon 1982), maximizing energy intake per unit time spent feeding. The potential requirement to maximize energy intake within the feeding season should influence all aspects of their foraging ecology, from distribution and group structure in feeding areas to choice of, and strategies for exploiting, prey schools.

Theories of optimal foraging do provide a useful conceptual framework for comparing and qualitatively examining whale foraging behaviour, however, such an approach may be in error. Food may be abundant enough for humpback whales that they are not strongly constrained to be energy maximizers or to forage "optimally". Although it is assumed throughout this discussion that the criterion humpback whales are optimizing is energy intake per unit foraging time, the need to optimize may not substantially shape foraging behaviour.

In the first discussion section I consider whether each bait situation is truly different from the whales' point of view and what bait characteristics may influence choice of prey and patch (prey school) in humpback whales off Newfoundland. The second section discusses how prey characteristics determine whale distribution, length of stay in feeding areas and group sizes. The third section considers how humpback whales may find prey schools and what may be the best strategies for exploiting different prey configurations. The ability to predict whale behaviour from bait characteristics is discussed in the final section.

11.1 Humpback whales as efficient predators

11.1.1 Bait schools

Food resources exploited by humpback whales in the Northwest Atlantic are patchy in distribution. Prey schools or patches occur in highly localized areas with vast intervening stretches of ocean devoid of suitable schools of prey. According to optimal foraging theory, animals should respond to various parameters of patchily distributed prey. These include: 1) patch quality or profitability, 2) distribution of patches (inter-patch distance), 3) the number of different patch types (or prey types) available and the relative profitabilities of each type and 4) the average overall rate of energy return for a particular habitat composed of a given resource distribution (Pyke et al. 1977; Krebs 1978; Morse 1980).

This study sampled only some of the possible resource parameters that optimally foraging whales should respond to. These include prey abundance, type and age class; duration of prey availability; and prey school size, depth, vertical extent and degree of dispersion. Relative prey abundance was estimated from both size and dispersion of prey schools. (Prey school densities as determined from sounder printouts were not considered in the estimation of bait abundance since many variables such as sounder gain level, target strength and orientation and distance to target (D.Miller pers. comm.) can affect printout quality.) Table 10.1 outlines the bait factors that were sampled and the nature or value of each factor in the different study locations.

In this study, (as in most field studies of foraging) prey school parameters that foraging whales probably respond to are confounded. Thus Table 10.1 does not consist of mutually exclusive categories. Prey species and age class probably determine most other school parameters (e.g. size, stability, dispersion, depth) in addition to themselves influencing aspects of prey behaviour relevant to whales (e.g. the reaction of the school to a whale feeding dive). Although some parameters such as school size, species composition and distribution could be reasonably and comparatively (across study sites) estimated, none was precisely measured.

Since no study locations were identical on all prey school parameters (Table 10.1) each different study location was theoretically a different bait situation. In Varket Channel and Trinity Bay, the two most similar areas, and in which whale feeding behaviour was superficially the same, prey school and ocean floor depths were significantly different (Table 3.1) and the horizontal area covered by schools in Trinity Bay was usually greater than in Varket Channel (Figures 3.2, 4.2). Bait variation across areas facilitates correlation between differences in whale foraging behaviour and prey school characteristics.

11.1.2 Prey choice in humpback whales

As energy maximizers humpback whales should choose a prey type that maximizes energy return per unit foraging time. Comparative energy value of different prey types is only one component of prey choice that contributes to the maximization of energy return. All other things being equal (e.g. search and handling time (Pyke et al. 1977), nutrient values (Pulliam 1975)), predators should prefer the energetically richest type of prey. Comparative energy and fat content of the various prey species exploited by Northwest Atlantic humpback whales are given in Table 11.1. Based on energy value alone, humpback whales should prefer mackerel (Table 11.1), yet the primary prey species of the Newfoundland feeding stock of humpback whales is capelin. Krill ranks a distant second behind capelin in importance (Mitchell 1973). Factors other than the energy value of the

Table 11.1

Comparative energy value and fat content of prey species utilized by humpback whales off Newfoundland. Values for herring from Adams (1975) are based on cleaned fish and could be overestimates, values for krill (Euphausiidae spp.) are from Lockyer (1976), all other values are from Montevecchi et al. (1984). Energy values are for wet weight. Immature and adult capelin have similar energy and lipid content except for ovid females which are slightly higher (Montevecchi and Piatt 1983).

SPECIES	KJ/g	% LIPID
Mackerel	10.3	18.6
Sand lance	7.3	8.9
Capelin	4.2	8.3
Squid	4.3	6.0
Krill	4.6	1.0 - 4.0
Herring	9.2	13.6

prey item obviously determine choice of prey type. While the abundance of local prey stocks has an influence, other factors are related to the need to minimize the energetic costs of foraging and thus maximize net energy return.

11.1.3 Patch choice in humpback whales

As it is net energy return that is critical, predators should strive to keep the energetic costs of foraging low. They should thus minimize time spent, and therefore energy used in searching for and handling (subduing, killing, consuming) a prey item. Since humpbacks swallow mouthfuls of multiple prey items from patches or schools of prey, they should choose patches (prey schools) that enable them to minimize handling costs and to maximize net energy intake. The profitability of a given patch type is usually measured by the energy return per unit time spent foraging (handling time) in the patch (Krebs 1978). For humpback whales handling time could be viewed as the energy used per unit weight of food swallowed, since humpbacks do not need to subdue or kill prey. Various characteristics of prey schools would affect handling time thus determining patch profitability and influencing patch choice. After a brief theoretical introduction, further discussion will focus on qualitative aspects of prey schools that might enable humpback whales to minimize the energetic costs of foraging.

Theories of patch choice usually assume animals have prior knowledge of the existence and location of good and poor patches (Pyke et al. 1977). Studies showed that animals tended to avoid searching for patches in areas already searched and concentrated search effort in areas found through previous experience to be profitable (Pyke et al. 1977). Work has thus focused on optimal strategies for allocating time and effort to an array of patches of differing quality and on how changes in patch quality over time affect behavioural optima.

This emphasis has resulted in predictions of theoretically optimum strategies for dealing with patchily distributed resources. Two predictions that pertain to this study are: 1) animals should concentrate foraging effort in the most profitable patches and spend sucessively less time in less profitable patches (Krebs 1978), and 2) animals should leave a patch when their rate of energy return from the patch drops to the average rate of return for the local habitat (Charnov 1976).

Some observations that do not fit the predicted optima have emerged from these studies. Rather than spend all of their time in the most profitable patches, animals allocated time to sampling sub-optimal patches (Zach and Smith 1981). This would enable predators to track habitat quality and might be especially important in unpredictable environments where habitat quality varied with time. If this occurs the only way to maximize energy return is to monitor this change in quality, so that foraging effort is continuously (over the long term) applied in the most profitable patches. Thus rather than maximize their short term energy gain, which would result if predators behaved as predicted and allocated foraging effort on the basis of patch quality only, sampling may be a reflection that animals tend to maintain a long term foraging optimum (Pyke et al. 1977).

11.1.4 Prey school characteristics important to whales

Prey behaviour. Species and age class of schools of prey determine their antipredator behaviour, which in turn influences the profitability, and hence choice of such schools for humpback whales. Antipredator behaviour includes predator detection, evasive tactics and the speed of escape of prey. The presence and degree of development of antipredator behaviour in their prey and the ability of whales to counter these tactics may determine whether a given prey type is exploited,

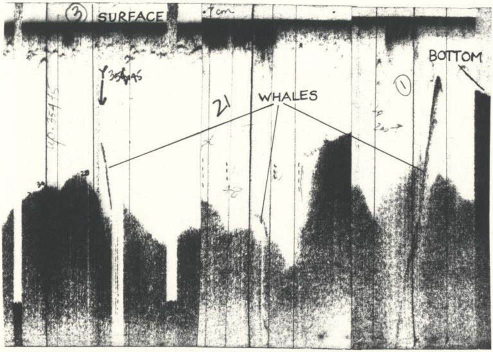
Schooling itself has been viewed as an antipredator device, reducing the probability of detection by predators (Cushing and Harden-Jones 1968; Hamilton 1971; Treisman 1975). It is unlikely, however, that this is an important function of fish schools, as most schools may be continually within the range of predator detection (Pitcher and Partridge 1979; Pitcher et al. 1979; Pitcher 1980; Partridge 1982). Whales for example select schooled prey, are probably quite efficient at detecting its whereabouts and are capable of extensive exploitation once schools are found. Selection has thus resulted in the evolution of a spectrum of antipredator tactics produced by fish schools (Pitcher 1979, 1982; Partridge 1982).

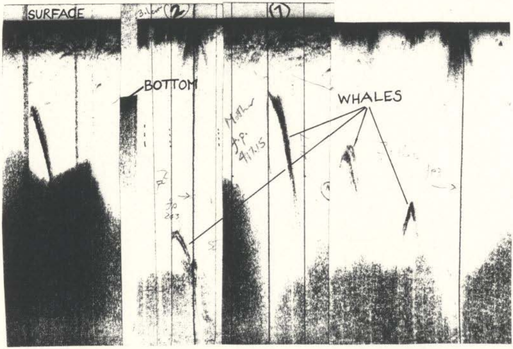
Fish schools of various species have been reported to split or explode centrifugally and reform after disruption (Pitcher 1979, 1982). Schooled capelin split and scatter at the point where a diver passes through them (G.Martel, pers. comm.) and foraging whales have been reported to produce this effect (Watkins and Schevill 1979). Evidence that humpbacks elicit this response in bait schools was provided by traces of prey schools splitting as whales dove into them (Figure 11.1) (see also Whitehead 1981). Krill probably have a less sophisticated set of antipredator behaviour than fish species exploited by humpback whales. (Mauchline and Fisher 1969) report that krill avoid rapidly towed collecting devices more strongly than if they are collected slowly. The speed of escape of prey is thus a component of antipredator behaviour.

Evasive manoeuvres by prey ahead of foraging whales would effectively decrease the density of the school and reduce the energy return per feeding dive. As antipredator tactics of prey and capture techniques of predators co-evolve, whales could be expected to have evolved feeding strategies to deal with evasive behaviour. Some of these may include the various bubble feeding techniques that passively concentrate prey and thus preempt evasive reactions of prey to penetration by whales (Jurasz and Jurasz 1979; Hain et al. 1982) or cooperative feeding and herding strategies. Many whales approaching a prey school

Figure 11.1

Depth sounder printouts of humpback whales entering prey schools. Ascending or descending whales are depicted by diagonal trace lines. Gaps or dips in otherwise continuous traces of prey may indicate local disruption of the school by whales. Depth scale is 0-60 fathoms (0-109.7 m) for trace sections depicting the surface, 60-120 fathoms (109.7-219.4 m) in sections depicting the ocean floor.


③
SURFACE
.7 cm
BOTTOM
①
21
WHALES


SURFACE
3.1cm
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BOTTOM
WHALES

together in a row may offset tendencies of the school to split at one point (which many schools tend to do (Pitcher 1979)). This is similar to Norris and Dohl's (1980) view that synchronous diving in odontocetes and pinnipeds may function as a strategy of food capture by confusing schooled prey and thus short-circuiting antipredator escape manoeuvres. As many of the schools exploited by whales in this study were beyond the limit of light penetration non-visual stimuli would be required for detection of both predators and prey. As a whale advances toward a prey school and suddenly opens its mouth a powerful inertial stream of water and prey would fill the buccal cavity (Pivorunas 1979) so evasive tactics may need to precede this point of contact.

Selective use of deep capelin schools in Trinity Bay in spite of the presence of squid schools may be partly related to rapid escape manoeuvres by squid as they are one of the fastest moving of marine creatures with burst speeds of up to 55 km/h (Norris and Mohl 1983). Humpback whales are only occasional predators of squid off Newfoundland yet squid are periodically quite abundant and are extensively exploited by pilot whales (Sergeant 1962). Humpbacks rarely take mackerel which are also available off Newfoundland, probably due to the speed at which shoals of mackerel travel.

<u>Prey school density</u>. The size or weight of individual prey items is a vital corollary to their relative energy values to predators that take one prey item at a time. As humpbacks are bulk feeders, gulping multiple prey items

suspended in water, prey taken in per mouthful or per unit volume of water is of more consequence than energy value per weight of prey. Lockyer (1976) and Nemoto and Kawamura (1977) consider prey school density to be a major factor in food selection by whales. Upon energetic analysis, Lockyer (1976) considered krill densities of 500 g/m to be well below the minimum required for efficient feeding, but that one hour of feeding on krill densities of 2 kg/m (densities in which whales have been reported to feed, (Mackintosh in Lockyer 1976) would be sufficient to meet daily energy requirements of fin whales.

Little information is readily available on comparative densities of different prey species. Zaferman (1972) measured the density of offshore post-spawning capelin schools in the Bering Sea using underwater stereoscopic photographs. Average school density was 15.7 fish/m with a range of 9.0 - 18.0 fish/m . Using an estimate of 25.0 g for the weight of single capelin (J.Piatt, D.Miller pers. comm.) this yields an average energy density of 225.0 - 457.5 g/m . Depth sounder traces have been used to measure the volume and hence energy density of capelin schools off the east coast of the Avalon Peninsula (J.Piatt unpub. data) using the formula : volume = 3.14 h w/4 (h=vertical extent of fish school, w=width of school at crossing point, Forbes and Naaken 1972).

Pitcher (1979) and Partridge and Pitcher (1980) caution against the use of two-dimensional representations from sounders and photographs for determining volumes and densities of fish schools for a number of reasons. Sounders tend to average gaps and edges and thus include space not actually occupied by fish. The volume of schools can change markedly: if fish are frightened by fishing gear or are swimming at faster speeds they pack more densely (Pitcher 1979, 1980; Pitcher and Partridge 1979). These authors found cyclical changes in volume of up to 100% (50%/min). Volume and hence density measurements could be orders of magnitude different from those experienced by whales. In addition, fish school shapes closely approximate an oblate spheroid rather than a sphere (Partridge et al. 1980), as the formula used by Forbes and Nakken (1972) assumes.

Much progress needs to be made before school densities and whale requirements can be reliably estimated. Lockyer (1976) used a basal swimming speed of 5 km/h to calculate daily and seasonal energy requirements (and hence minimum required prey school densities) for krill-eating fin whales but the energetics of humpbacks feeding on capelin are not directly comparable. In addition humpbacks possess a variety of behavioural mechanisms for concentrating prey from more dispersed sources (See Chapter 1). Whales did prefer the concentrated schools to the dispersed surface schools of post spawning capelin in Witless Bay, Mobile Bay and Cape Broyle Harbour (see below), however, the denser schools were also larger.

Changes in patch profitability and habitat quality can occur due to depletion and subsequent renewal of resource patches (Zach and Falls 1976a). Repeated feeding passes of humpback whales may disrupt dense cohesive prey schools thus causing a decrease in patch quality with an increase in whale foraging time. How quickly schools of a given type recover from disruption would influence their profitability as well as the quality of a habitat composed of schools of that type.

On 8 July in Mobile Bay humpback whales were exploiting two small concentrated patches of capelin, foraging on one for less than 1.0 h and then travelling directly to the other (Section 6.3). This suggests that disruption may occur rather quickly, decreasing patch profitability and prompting the whales to move to the alternate patch. It was apparent the whales could remember where the resource patches were but not so apparent that they could assess renewal time. After foraging on the dense schools humpbacks started to exploit the small scattered surface capelin schools. This may be a reflection of a slow rate of renewal (repacking) of the concentrated schools, forcing the whales to exploit the less profitable smaller dispersed patches of prey. The whales seemed preferentially to use the larger schools before the dispersed schools. Zach and Falls (1976b) found that ovenbirds (Seiurus aurocapillus) learned the distribution of patch densities, concentrating foraging effort in and returning to good patches, but nonetheless, sampling lower density patches, similar to the way whales seemed to do here.

In Cape Broyle Harbour also, whales usually left the prey school near Shipwreck Point after 0.5 - 2.0 h of foraging time, possibly as a result of a decrease in profitability due to a decrease in density from continued exploitation. Whales foraged on the smaller less dense scattered surface schools on only two of four days, suggesting that these small schools were of marginal profitability, since on the other two days whales rested, ignoring the small schools. In Mobile Bay whales ceased exploiting small scattered schools and rested before returning to the dense patches, also suggesting marginal profitability of these schools in comparison to dense ones. Rest periods could also simply be a reflection of the need for rest or could represent a digestive pause. It should be noted, however, that only one such pause/rest was observed when prey schools were large enough to permit continued foraging (Section 3.3, 4.3). Davies and Harrison (1981) also found that whales rested while waiting for schools to regenerate, that resting time increased with previous exploitation time and that lengths of stay in prey schools were greater after longer rest periods.

On the short term, depletion of prey abundance within the dense concentrations of capelin in Mobile Bay and Cape Broyle Harbour did not seem to be a factor prompting whales to leave the schools. Over three days of observation exploitation of these schools was repeated and continuous and schools were still present after this time.

Prey school size. Larger prey schools enable whales to minimize the costs of foraging in a number of ways. Resources are more abundant in larger patches; whales could forage for a longer period of time in each patch before depleting it. Longer foraging times per patch mean that foraging costs in terms of searching for and travelling to new patches are less. Larger schools may be less susceptible to complete disruption from repeated feeding passes of whales. This would also extend foraging time as whales could continue to forage on adequate densities by moving to new areas within the patch, rather than having to leave and find new patches or wait for the current school to regroup (as whales in Mobile Bay and Cape Broyle Harbour seemed to do). For bulk feeding cetaceans like humpbacks there probably exists a minimum school size below which exploitation is not profitable.

Whales had the most obvious choice between different sized prey schools off Great Island where both large deep and small shallow post spawning capelin schools were present (see Figure 5.2). Humpbacks used the large deep schools except on one occasion when a pair of whales left a deep school to forage on the small surface schools. In Trinity Bay small schools of squid were routinely present above the large deep immature capelin schools. Squid schools were ignored except in one instance. Here, however, prey species (and thus antipredator tactics) may have strongly influenced patch choice and was confounded with school size. Preferential use of larger (more concentrated) schools over smaller (more dispersed) schools in Witless Bay, Mobile Bay, and Cape Broyle Harbour (see previous) was very likely also a function of school size, as was the exodus of whales from Cape Broyle Harbour as the prey concentration dispersed.

Prey abundance. The role of food abundance in determining humpback whales' selection of capelin as their primary prey species has two aspects. First, providing they are profitable, animals should exploit abundant patch types more frequently as they would encounter them more often. The Newfoundland feeding stock of Northwest Atlantic humpback whales probably have a reasonably high encounter rate with capelin schools as capelin is the most important and abundant forage species of the region (Carscadden 1983a, 1983b). In addition (see Section 11.3.1) Northwest Atlantic humpback whales travel along routes where they are likely to frequently encounter capelin schools, (e.g. The Grand Banks, inshore Newfoundland).

Second, this selection has occurred over an evolutionary time scale. Baleen whales have evolved to exploit, and hence currently require, locally superabundant resources. The very characteristics of capelin (its local superabundance: the formation of large dense schools), make it the ideal prey choice for humpback whales. Disruptions in the availability of their usually superabundant prey, however, may influence prey choice in humpbacks. The decrease in the abundance of capelin on the Southeast Shoal of the Grand Banks prompted many humpbacks to choose alternate prey (inshore capelin stocks) during the years of this study (1979 - 1981) (Whitehead 1981).

11.2 Distribution and abundance of whales and prey

The correlation of aggregations of various species of baleen whales with concentrations of their prey has been well documented (see Nemoto 1959, 1963). Historically, the distribution of humpback whales around the coast of Newfoundland parallels the distribution of capelin both spatially and temporally (Mitchell 1974; Whitehead et al. 1980). This study relates local levels of whale abundance with local levels of prey abundance; whales were more numerous where prey was more abundant (Table 10.2). The rank estimate of prey abundance is an over-simplification based on a subjective evaluation of the relative amounts of prey in each study location. Thus, although the trend to larger local whale populations with increasing bait abundance did occur, the correlation coefficient was not significant.

In Varket Channel the daily local whale population was significantly correlated with prey abundance, as indicated by the rank of daily prey school size (Section 3.2). (This indication would be valid as virtually all resources here were contained within one large and one smaller fish school.) In Cape Broyle Harbour the local whale population decreased as the concentrated school of post spawning capelin dispersed (Table 7.1). A change in resource distribution (from one large school to many small schools) was the more dominant feature of bait change (rather than an overall decrease in prey abundance), making the habitat less profitable to the whales and perhaps prompting them to leave the area.

Results from Varket Channel and Cape Broyle Harbour demonstrate that humpback whales monitor habitat profitabilities on a daily basis. This was not evident however in the Great Island study area. Local whale populations decreased only slightly in response to a marked decline in the vertical extent and area of fish schools on depth sounder printouts (Table 5.1, Figure 5.5). There are two possible reasons for this. The distribution of humpback whales around Newfoundland shifts north as the summer progresses (Whitehead et al. 1982). Whales migrating north from Placentia Bay and St. Mary's Bay could be passing this section of the coast at approximately this date and could account for a stable visible population over the course of a week of observation in spite of changes in our position and the apparent decrease in prey. In addition, vertical extent of schools on the depth sounder is only one measure of bait abundance; there may have been enough bait spread over a wider area to maintain the local whale population at the level recorded.

The sharp influx and subsequent decline of the local whale population in the head of St. Mary's Bay (Table 8.1) may have been due to rising and falling prey availability. *Thysanoessa raschii*, one of the commonest euphausiids in inshore Newfoundland waters (Richard 1986), typically forms large sub-surface swarms and is an important food for whales.

(Mauchline and Fisher 1969; Mauchline 1980). Migration to the surface to breed in late June or early July (Lindley 1980) may result in an increase in the size and density of swarms which could be temporarily quite profitable for whales. Alternatively, swarms may have been present before and after the influx of humpbacks. The whales may have entered the area simply as a continuation of their northward progression up into St. Mary's Bay searching for food, they may have exploited krill swarms because they were there and then left the area to continue migrating north.

Not only did numbers of humpbacks parallel habitat profitability but local whale aggregations tracked movements of bait within the study areas. This was most evident in Trinity Bay where fish schools and whale concentrations moved in tandem extensively throughout the head of the bay during the study period (Figure 4.2). If whales exploited these prey schools continuously night and day (which is likely), they would obviously be expected to move with the schools. Individual whales or groups that left prey schools to rest (see Goodyear 1982) would probably have little difficulty finding them again due to their proximity and the sounds of other foraging humpback whales (Chabot 1984).

On a scale of days and hours it was evident that humpback whales could remember where previously exploited and profitable prey schools were located. Whales left and later returned directly to schools in Mobile Bay and Cape Broyle Harbour. Whales were also observed to travel back and forth between two schools in Varket Channel and Mobile

Bay. This is entirely consistent with data from many other species demonstrating the ability to remember the location of profitable food sources (see Pyke et al. 1977; Morse 1980; Zach and Smith 1981).

11.2.1 Lengths of stay in feeding areas

Repeated sightings of very distinctive individuals in a study location permitted a rough estimate of how long whales might remain in different feeding areas. It was found that individual whales remained longest in areas where food was most abundant. Residence times ranged from a maximum of two weeks in Trinity Bay, 8 days in Varket Channel, 5 days off Great Island to only 2 - 4 days in the small bays of the eastern Avalon (Sections 3.3, 4.3, 5.3, 6.3, 7.3, 8.3). In Trinity Bay individual whales may have in fact remained longer than the observed maximum resighting interval of two weeks as prey schools were present in this location for two months. In other locations individual residence times were only slightly shorter than the duration of time any humpback whales continued to exploit prey in the area.

Studies have shown that animals are able to assess changing patch profitabilities; ie. when it is no longer profitable to forage in a patch. (See Section 11.1.3, Krebs et al. 1974; Charnov 1976; Krebs 1978). This would provide a mechanism of assessing when to leave a habitat containing patchily distributed prey. Residence times in a feeding area depend on the predator's ability to assess the profitability of the current habitat and on knowledge and expectations of profitability in other habitats. Feeding stock divisions demonstrate that Northwest Atlantic humpback whales return to the part of the ocean they fed in during the previous summer (Katona et al. 1983) so it is not extreme to hypothesize that they may remember separate feeding locations (habitats) within their feeding stock area. Whitehead et al. (1982) cite evidence that a few individual humpbacks returned to the same section of coastline in two successive years. Memory of feeding areas may provide whales with alternatives by which to assess their current location. Previous discussion (Section 11.1.3) has demonstrated that humpbacks do seem to assess the profitability of their current habitat.

The position of a particular feeding location on the general migration route to and through a feeding stock area (see Chapter 1) may also influence how long whales stay. If the concentration of prey is deep in a bay and remote from other prey concentrations (for example Varket Channel) whales may stay longer and exploit local resources more extensively. In this situation the cost of searching for and travelling to a new habitat would be greater than for feeding habitats along the general travel route, such as those along the east coast of the Avalon Peninsula. Whales may move at a faster rate through areas along migration routes, exploiting prey aggregations less extensively.

11.2.2 Preferred groupings

Whitehead et al. (1982) and Whitehead and Glass (1984) found no evidence for significant amounts of repeated or continuous groupings of individual humpback whales observed off Newfoundland over periods longer than 24 h. The only evidence for preferred groupings in my data occurred in Varket Channel (Table 3.3). Small isolated concentrations like those in Varket Channel may have an increased tendency to form repeated groups. Resident whales could become familiar with each other and certain individuals may form efficiently working feeding groups from which they exclude newcomers. As whales are not known to form kin groups during the feeding season, (unlike other species that form exclusive foraging groups e.g. wolf packs, (Zimen 1974)), group formation on the basis of foraging advantages would occur.

Although obvious agonistic behaviour is rarely observed in summer during the feeding season (in contrast with during the breeding season), Whitehead (1981) found that behaviour such as flippering, side-flukeing and defecation occurred more often during group splitting and joining suggesting that there is some tension when group size changes. Vocalizations seemed to be louder and more frequent during group encounters (Chabot 1984; pers. obs.). Behavioural mechanisms for excluding joiners may therefore exist.

In most situations a tendency opposing group preference may be more adaptive. Different individual humpback whales would have different amounts and types of information about the location of profitable feeding habitats and of profitable prey schools within those habitats (see Giraldeau

1984). This "information pool" would be enhanced in locations where many different individuals are sequentially entering and leaving the area (Ward and Zahavi 1973). High immigration and emigration rates would occur in feeding locations situated along migration or travel routes such as Bay de Verde (Whitehead et al. 1982) or the east coast of the Avalon Peninsula (this study). An individual could potentially obtain more information about where to find food if it joined with a greater number of different whales than with the same whales repeatedly. This sort of information transfer has been hypothesized (Giraldeau 1984), and evidence for it has been found in other species, for example great tits, Parus major (Krebs et al. 1972), great blue herons, Ardea herodias (Krebs 1974), and communally roosting species (Ward and Zahavi 1973).

11.2.3 Functions of humpback whale feeding groups

A dominant feature of humpback whale foraging is the formation of groups (see Nemoto 1964; Dawbin 1966; Davies and Harrison 1981; Hain et al. 1982; Jurasz and Jurasz 1979; Norris and Dohl 1980; Whitehead 1983). For group living to evolve there must be a selective advantage for each member of the group and for feeding groups there must be sufficient food for all group members (Brown 1975). Individuals feeding in groups can benefit in a number of ways. Group living enables predators to cooperate in capturing prey thereby improving capture success (Schaller 1972; Norris and Dohl 1980) and increasing the size range of prey available (Pimlott 1974). Animals may form feeding aggregations to gain protection from predators (Hamilton 1971; Treisman 1975)) or to benefit from increased ability to locate food due to information provided by other group members (Ward and Zahavi 1973).

Foraging aggregations will be selected for by patchily distributed food resources simply as a response to resource distribution. Thus the distribution of humpback whales around Newfoundland is aggregated. Within these aggregations, however, humpbacks form cohesive coordinating groups. Groups of foraging humpbacks coordinate dives, surfacings and swimming directions and even blow in synchrony (see Davies and Harrison 1981). That there is enough food for all group members and that resources are patchily distributed are not sufficient explanations for the high degree of coordination seen in feeding groups, for many individual whales could feed separately on the same fish school and theoretically obtain the same share of resources.

A selective advantage to group coordination in humpback whales could be to reduce the disruption of prey schools that may result from repeated passes of feeding whales through them. Disruption or short term dispersion of cohesive prey schools would be a disadvantage to humpback whales as it would reduce the amount of prey taken per foraging dive. Three or five mouths entering the school together from the same direction of approach would be less disruptive than if each whale dove into the school at a different location from different directions and at different times.

Evidence that grouping has a function directly related to foraging was that whales grouped to feed but dispersed when not feeding: foraging groups were significantly larger than non-foraging groups (Table 10.2). The above result was also found by Whitehead (1981). In addition, foraging group sizes were larger with larger prey schools but non-foraging group sizes were similar in large or small (deep or shallow) prey school situations (Table 10.2). When prey schools were small and would not support large whale groups (hence would not require coordinated feeding dives) less group coordination was observed (Section 6.3, 7.3). Whitehead (1981) measured indices of coordination among group members and found that coordination increased while the whales were feeding at depth, suggesting that the principal function of coordination (possibly to reduce prey school disruption) occurs under water.

Group coordination may represent a form of cooperative prey capture in humpback whales. Prey concentration with bubbles (Jurasz and Jurasz 1979; Hain et al. 1982) or against interfaces (Dolphin and McSweeny 1981) may be more efficient if it is done by coordinating groups. The high degree of coordination seen in groups of diving or lunging humpback whales (especially echeloned lunging, see Jurasz and Jurasz 1979) may indicate cooperative herding of prey aggregations, perhaps similar to the beater effect where predators form lines or semicircles to drive or flush prey (Wittenberger 1981). Fleeing prey avoid one predator only to encounter its neighbour.

11.2.4 What determines humpback whale foraging group sizes ?

Depending on the function of the group, different and often conflicting selection pressures determine group sizes in animals (e.g. competition for food or mates, predation pressure) and individual group members may have different preferred or optimal group sizes (Bertram 1978; Wittenberger 1981). Optimal group sizes assume individual group members "choose" group size to increase their fitness, however, resource distributions or demographic factors can offset adaptive processes influencing group size (Wittenberger 1981).

The hypothesized function (Section 11.2.3) of coordinating groups of humpback whales was to reduce disruption of cohesive schools of prey or to possibly facilitate cooperative herding of prey. A number of concepts concerning optimal group sizes are thus relevant to humpback whale foraging groups. 1) The size of such functional groups of animals is generally that which best performs or "optimizes" their evolutionary function (Pulliam 1973). 2) "The concept of optimal group size has most relevance in species where groups are temporary associations, probably for feeding." (Bertram 1978, p.96). 3) If group size is determined by immigration or emigration from the group rather than by birth or death rates then it would more closely reflect the adaptive choices of individuals (Wittenberger 1981).

Humpback whale foraging group sizes, then, may be those which permit the least disruption of prey schools. When a fish school is large a few large groups of whales would be less disruptive than many small groups as this would decrease the number of foraging passes through the school. For the least disruption, group sizes should be as large as the prey school would allow, given the potential constraints of coordinating very large groups. If, however, many large prey schools were available (a situation not observed in this study) group coordination to reduce school disruption would not be as necessary. Groups should be small when fish schools are small for two reasons. Small prey schools would not support large groups of whales because they would not be large enough to accomodate many whale mouths at the same time. In addition small schools might not contain sufficient food for all members of the foraging group.

In this study humpback group sizes did increase with increasing school size. Whales fed singly or in groups of two when they were utilizing small surface swarms of krill. They formed small groups when capelin schools were small and large groups when schools were larger (Table 10.2). Whitehead (1983) found that maximum feeding group size was correlated with the horizontal size of inshore prey schools. On the Grand Banks humpbacks formed very large groups of 12 - 40 animals earlier in the season when pre-spawning capelin schools were large and compact but after spawning as the schools dispersed into smaller units humpbacks fed in smaller groups (Whitehead et al. 1982; Whitehead and Glass

1984).

A larger number of whales could be expected to exploit a larger prey school as resource abundance within the school would be greater. Group sizes may thus be larger simply as a result of there being more whales in the immediate area. Whitehead (1983) found that group sizes were correlated with the local whale population. A similar correlation occurred in this study in two locations only, Varket Channel and Trinity Bay (Tables 3.2, 4.1). When study locations are compared there appears to be no consistent relationship between local whale population and mean group size. Group sizes were only slightly larger in Trinity Bay than in Varket Channel yet there were 3.5 times more whales, on average, in Trinity Bay. (The size of prey schools on a given day in Trinity Bay ranged from being approximately equal to, to twice as large as those in Varket Channel.) In Witless and Mobile Bay, group sizes were larger when fewer whales were present. When whales were exploiting krill in St. Mary's Bay, average group sizes were smaller than those in all other study locations, yet there were more whales present during part of the observation period than in all areas except for Trinity Bay (Table 10.2). Individual patches of krill were smaller than most capelin schools seen, supporting the hypothesis that group size is determined partly by prey school size.

11.3 Foraging behaviour strategies

11.3.1 Search strategies

Investigations of evolutionary strategies of optimal search in predators have yielded two observations applicable to humpback whales: 1) non-random search is more efficient at locating prey (Krebs 1978) and 2) animals use specific sites and locations as cues to find prey (Morse 1980; Zach and Smith 1981). Because of the highly patchy nature of their prey humpbacks require an efficient means of locating resource patches.

Food searching behaviour in Northwest Atlantic humpback whales involves 1) a northward migration to the feeding grounds of that particular foraging sub-stock, 2) travel to areas of high prey availability within the feeding grounds, 3) movement within areas of high productivity, and 4) movement from prey school to prey school. Humpbacks demonstrate non-random movement and/or the use of geographic or oceanographic cues in all four components of prey search. Although the latter two components are not evolutionary strategies per se since they may be learned, they are facets of prey search and will be included in this section of the discussion.

Feeding stock site fidelity (Katona et al. 1983) and the annual return to particular feeding grounds in Northwest Atlantic humpback whales (see Chapter 1) undoubtedly entails the use of oceanographic cues and insures that humpbacks will at least be in the vicinity of concentrations of their prey. Humpbacks are a coastal species, travelling along continental shelves and shorelines (Chittleborough 1965; Dawbin 1966). Such non-random routes would eventually result in encounter with prey as these are areas of high productivity. In the Northwest Atlantic shelf and coastal travel would lead whales to the capelin concentrations of the Grand Banks and inshore Newfoundland.

There are three sites of predictably high prey availability within the Newfoundland feeding sub-stock's foraging area: the Grand Banks, inshore Newfoundland and off Labrador. Humpbacks travel among these locations moving predominantly from south to north both between and within sites (Whitehead et al. 1982; Whitehead and Glass 1984). Some individual whales also demonstrated a tendency to return to particular sections of coastline in successive years (Whitehead et al. 1982). Oceanographic cues are probably used to travel and return to these sites of high prey abundance. Directional movement (south to north) may decrease the likelihood that sites are revisited or are visited after other whales had exploited them.

Once in areas where suitable bait schools are likely to be found, humpbacks are still faced with the task of finding highly localized concentrations of prey. A number of cues could be used to do this. Individuals may hear the vocalizations of other foraging whales over distances of 2 - 4 km (Chabot 1984). At smaller distances whales may detect sounds made by schools of fish or krill (Myrberg 1981) or perceive an acoustic shadow produced by fish schools located off beaches with surf noise, such as St Vincent's. Neurophysiological evidence suggests that humpbacks have excellent hearing (Herman and Tavolga 1980) and as sound travels well in water it is an ideal channel to use in prey search strategies. Although prey schools also emit smells (Kleerekoper 1969) it is unlikely that olfactory stimuli are used by mysticetes as they possess only remnants of the neuroanatomical structures involved in olfaction (Quay and Mitchell 1971). Mysticetes probably have a gustatory sense and could possibly locate prey by tasting excretions and other chemical substances produced by prey (Herman and Tavolga 1980).

On a finer scale, whales need to know when to dive: when bait is below them (for deep schools) or immediately ahead of them (for small dispersed shallow schools). The humpbacks observed in this study certainly did seem to know this. When they were foraging on schools too deep to see, the whales would often not be directly over a bait school while they were at the surface (indicated by the absence of prey traces on the depth sounder). When we reached their footprint after the terminal dive a bait school would begin in the immediate dive vicinity. This happened so frequently as to suggest that whales knew when they were over bait and it would be worth their while to dive. Similarly, when foraging on small shallow schools of capelin, whales would be swimming at the surface with no substantial schools present on the echo sounder, they would dive and when we reached the footprint a small capelin school would invariably be present. It makes adaptive sense for humpbacks whales to be able to detect when they were over or about to encounter prey schools as such knowledge would minimize unproductive dives. Hearing fish schools probably occurs when schools are deep while both sight and sound may be used to detect shallow schools. Humpbacks also feed at night (pers. obs.), an indication that senses other than vision play an important role in prey detection.

11.3.2 Exploitation strategies

Humpback whales in this study exhibited three principal behavioural strategies for exploiting the three broad prey type categories. When utilizing medium to large single concentrated prey schools (such as those in all deep bait locations and in Cape Broyle Harbour) humpbacks performed a repetitive sequence of foraging dives into the school. When bait was distributed in small shallow scattered schools (capelin in Witless and Mobile Bays and krill) whales moved from school to school using a cruise and munch foraging strategy. A series of lateral surface lunges were used to exploit larger patches of krill at the surface. Whales also occasionally lunged into capelin or squid. Variations within each strategy were apparent however, and correspond to variation in prey school characteristics within each main prey type. Others (Jurasz and Jurasz 1979; Whitehead 1981; Hain et al. 1982) have also found that humpbacks exhibit considerable variation within broad categories of foraging behaviour. As foraging behaviour was partitioned into a number of components, how variation in each of these components enables whales to efficiently utilize each prey situation will be discussed.

Dive and surface times. In the deep capelin situations (Varket Channel, Trinity Bay, Great Island) dive times were longer when prey and water depths were greater, both between and within (day to day variation) places. Since dive time could be considered to be a component of handling time (see Section 11.1.3), all other things being equal (density, size, species composition, etc.) deeper schools require a greater handling time component and may thus be more costly to exploit. When whales were feeding close to the surface on shallow capelin schools (Cape Broyle Harbour, Southern Shore) (Table 9.3, Figure 10.2) dive times were approximately half as long as those from deep capelin (Table 9.3, Figure 10.2). Given an average school depth for deep capelin of 80.0 m (Table 3.1), an average dive time of 4.5 min (Table 9.3) and an ascending and descending rate of 0.77 m/s (Whitehead 1981), this indicates that humpbacks spend about 1.0 min (65.5 s) ascending and descending and 2.33 min at depth, which is approximately the dive duration for shallow prey (2.35 min, Table 9.3). These findings are almost identical to those of Whitehead (1981). It seems then that filtering time is fairly constant but handling time is partially a function of prey depth.

When whales were utilizing the small concentrated post-spawning capelin schools in Cape Broyle Harbour surface times were longest and large amounts of surface directional change occurred. Whales may have needed to reposition themselves over the small school after diving through it and resurfacing distant from it. When humpbacks were laterally lunging amid krill swarms surface times were also long and whales moved relatively slowly. This is obviously a reflection that the filtering or consuming phase of foraging occurred at the surface.

The strategy of cruise and munch foraging on small scattered capelin schools in Witless Bay, Mobile Bay and Cape Broyle Harbour was characterized by highly variable surface times (SD = mean, Table 6.3). Variable surface times are a reflection of unpredictable travel times between prey schools. In deep immature capelin situations (Trinity Bay and Varket Channel) surface times were much less variable and were significantly positively correlated with following dive times (Tables 3.8, 4.5, A2.1, A2.2). Whitehead (1981) found similar correlations, with surface times more strongly correlated with the previous dive time than the following dive time. This suggests that when whales are foraging on deep prey surface times function as a recovery from foraging dives. The longer (and the more energetically costly) the foraging dive, the longer the recovery phase at the surface. In neither shallow capelin situations (Tables 6.6, 7.5), nor when whales were exploiting krill (Table 8.5), were surface times significantly correlated with dive times, suggesting that when whales are not making deep foraging dives surface times do not function as a recovery phase.

The mean ratios of dive times to preceeding surface times in the different bait situations reiterate dive and surface time differences (Section 10.2, Figure 10.3). Ratios were largest (2.50, Figure 10.3) when whales were lunging on krill. This was mostly the effect of non-lunging dives which were characterized by short surface times followed by long dive times. Whales typically alternated lunging and non-lunging dives, a long non-lunging dive preceeding a lunging bout at the surface. Long dives prior to lunging bouts may indicate that whales dove deep in order to gain momentum: they usually resurfaced with substantial force before beginning to lunge. Whales may also have been spending a long time at depth in order to accurately locate a krill swarm and orient so they would resurface adjacent to one and could lunge into it immediately without losing momentum.

<u>Movement patterns at the surface</u>. Foraging movement patterns of animals should vary with differences in resource patch characteristics (Morse 1980). In this study there were four main variations in resource patches: large superabundant patches (deep capelin), smaller concentrated patches (in Cape Broyle Harbour), dispersed very small patches (cruise and munch capelin) and resources that were thinly dispersed over a wide area (krill). Movement patterns of humpback whales were correlated with each of

these resource distributions.

When humpbacks were exploiting large deep capelin schools, directional changes at the surface were only about 90°. Large schools enabled whales to travel in fairly straight lines for 100 - 500 m at the surface and remain over bait, thereby permitting exploitation of different locations within the school and possibly minimizing disruption. Surface directional changes were significantly greater than those for deep capelin when whales were foraging on small concentrated schools of post-spawning capelin in Cape Broyle Harbour. After surfacing whales needed to circle to stay close to the bait school; straight line travel for only 200 m would position whales well away from the school (Figure 7.1). Foraging dives into remote locations within the school were not possible. Watkins and Schevill (1979) also noted that greater amounts of surface turning were required when humpbacks were preying on small active fish schools but that larger prey schools did not require circling.

The significantly greatest amounts of surface directional change observed when humpbacks were laterally lunging on krill reflect the swimming patterns during lunging (zig-zag or lollipop, Section 8.3), patterns which may increase the amount of krill taken per lunging bout. Humpbacks were also observed by Lockyer (1976) to zig-zag back and forth through krill at the surface. Whales turned at similar rates when feeding on capelin schools either deep or just below the surface, however, when lunging on krill rates of turning were significantly greater. Turning at a faster rate may enable humpbacks to remain within the krill patch and thus to filter more of it per lunging bout.

During cruise and munch foraging, the small amounts (80°, Table 6.3) of surface directional change observed reflect the humpbacks' general strategy of movement: travelling throughout the bay in broad zig-zags possibly searching for pockets of capelin. An observation that has emerged from studies of optimal patterns of movement in predators is that once a resource patch has been found movement patterns shift from meandering ones with small directional changes to ones that keep predators in the vicinity of the resource patch (ie. area restricted search, see Smith 1974a, 1974b; Pyke 1978). This was observed with the small concentrated school in Cape Broyle Harbour and with krill. Whales probably had no need to stay in the vicinity of the very small schools utilized during cruise and munch foraging however, as they were likely not profitable enough for extended exploitation. Whales thus moved from school to school.

Foraging time. Animals should cease exploiting a resource patch when energy return declines to the average for the habitat (Charnov 1976). A variety of studies have attempted to elucidate the behavioural mechanisms by which predators assess when it is optimal to leave a patch. If they are optimal foragers, the amount of time humpback whales continue to forage on a single prey school should depend on how school profitability changes over time, on the availability of alternate schools and the ease of finding and travelling to new schools. In rich habitats where resource patches are abundant and finding and travelling to an undepleted new patch is easier, predators should leave patches sooner (Charnov 1976).

Since foraging whales deplete and probably disperse prey schools, profitability would decline with increasing exploitation time. Larger schools would be expected to decline in profitability more slowly than small schools for two reasons: 1) they are depleted more slowly because they contain more biomass initially and 2) longer exploitation times are necessary to completely disrupt them since whales could successively dive into different locations within the school, letting previously exploited sections recover (Section 11.1.4). Humpbacks whales foraged almost continuously on the very large deep capelin schools in Varket Channel and Trinity Bay (Figure 10.5). A significant decline in profitability of these very extensive schools must occur very slowly as whales were rarely observed to cease foraging on a school. In Trinity Bay we only once observed a group of whales stop foraging to rest but other individuals continued to exploit the same prey school, and in Varket Channel a pair of whales once left a prey school and travelled to another.

Off Great Island where schools were smaller and less vertically extensive, especially as the study period progressed (Figure 5.3 and 5.5), a greater proportion of non-foraging behaviour occurred. A decline in both the horizontal and vertical dimensions of school size would markedly decrease the volume of prey available to humpbacks and hence accelerate the effects of school disruption and depletion from continued foraging. Whales left individual capelin schools off Great Island to rest, to travel to another school and to exploit another source of prey (small pockets of capelin at the surface). These observations suggest that the deep schools off Great Island decline in profitability, prompting whales to cease exploiting them.

In Cape Broyle Harbour where the single concentrated capelin school was much smaller than Great Island schools, humpbacks foraged continuously on the school for only 0.5 - 2.0 h, suggesting that patch quality had declined to sub-optimal levels after this period of time. This decline seemed to be initially due to disruption rather than depletion as whales returned directly to the school after it recovered (see Section 7.3). In this study area periods of non-foraging thus alternated with foraging periods. Effects of depletion on foraging time were difficult to assess as dispersal of the school over the course of the study period coincided with an exodus of humpback whales from the bay. The high proportion of non-foraging dives that were observed during cruise and munch foraging on scattered capelin schools in Witless and Mobile Bays occurred when humpbacks left or lost the areas of high school density. The encounter rate with resource patches dropped and whales switched to resting or travelling behaviour.

The non-lunging dives interspersed between lunging dives during krill lunge feeding were not significantly different from (non-foraging) travelling dives that occurred after cruise and munch foraging on krill (Table 8.2). The non-consumatory phase of humpback whale foraging behaviour during lunge feeding is thus more prolonged and consists of an entire behavioural unit or dive (surface plus dive time) rather than just the time spent at the surface as when whales make foraging dives into sub-surface bait. This may reflect the need for a rest or recovery period after a series of energetically costly lunges or may be time required for repositioning prior to the onset of another lunging bout. Whales sometimes travelled at the surface towards a krill swarm just before starting to lunge however (lollipop pattern of movement), and lunging dives did occasionally occur in succession, so rest and/or repositioning were not always required.

Non-foraging behaviour in humpback whales is distinct from foraging behaviour (Table 9.2, Sections 9.3, 9.4) and different types of non-foraging behaviour are distinct from each other. Resting was characterized by long surface times where whales lay almost motionless at the surface or moved leisurely in meandering paths. Whales turned greater amounts (due to longer times at the surface) but they did so more slowly. During non-resting travelling whales moved unidirectionally and spent shorter periods of time both at the surface and diving (Table 8.2). Foraging group sizes were larger than non-foraging group sizes (Table 10.2). The categorization of humpback whale behaviour into foraging and non-foraging is thus possible on the basis of measureable traits and on the presence of available prey.

11.4 Predicting foraging behaviour

Major goals of the multiple regression analysis were to determine whether immediate bait characteristics could account for or predict the basic unit of whale foraging behaviour (surface and dive times), specifically which bait variables had the strongest effect on whale behaviour, and whether whale behaviour was better predicted in some bait situations than others.

11.4.1 Deep capelin

Whale behaviour was best predicted when bait schools were deep. This is primarily because two of the bait variables measured in this study and used in the regression analysis (depth to the top of the bait school and ocean floor depth) strongly influence depth of dive and hence dive time. Surface time variance was also significantly predicted by bait variables when prey schools were deep (except in the Great Island study area). If surface time functions as a recovery period from a foraging dive (Section 11.3.2) this would be expected: bait and floor depths influence dive time which in turn influences surface time.

When prey schools were deep bait variables alone significantly predict whale diving behaviour, the inclusion of other whale variables in the regression equation (most of which were surface behaviours) had little effect on the proportion of variance of dive time accounted for. The proportion of variance of surface time accounted for was substantially reduced, however, when whale variables were excluded from the regression equation and only bait variables were used. The time whales spend at the surface is, as expected, positively correlated with what they do there - principally with how much and how fast they turn and with group size (see Section 5.6).

Of all the bait variables the vertical extent of the prey school in the immediate dive vicinity is least strongly correlated with dive and surface times. There are a number of reasons for this. The time descending to and ascending from prey schools may be the main component of dive duration with time spent at depth being less variable (Section 11.3.2). Therefore depth to prey but not vertical extent of prey more strongly determines dive and surface times. Even if filtering time did vary with prey school density or abundance whales may enter prey schools horizontally or diagonally so vertical extent of bait may not be relevant to filtering time. A minimum vertical prey extent may be necessary, however, to offset the disruptive effect of foraging dives and to make deep foraging dives worthwhile.

There was no consistent pattern to the effect on regression results of the removal of highly correlated bait variables to control for multicollinearity. It could be expected that the removal of some bait variables would most strongly affect the prediction of dive time but this only occurred in the Trinity Bay dive by dive regression results. One of each pair of bait variables was still enough to significantly predict whale diving behaviour in all deep prey study locations although to a lesser degree. In the Great Island study location reductions in the degree of prediction of both surface time and dive time may have interacted to produce a substantially greater reduction in the prediction of unitime, as it is the composite of the two other time variables. It is unclear why this should happen only in the Great Island results, however.

Dive by dive data sets were highly autocorrelated when whales were utilizing deep prey schools (Tables 3.7, 4.4, 5.4). This is indicative of the repetitive and predictable nature of humpback deep bait foraging behaviour. It is also indicative of the constancy of bait school characteristics through the duration of an observation bout. Dive times were not very variable from one dive to the next because whales were utilizing the same prey school, the depth of which remained fairly constant. Prey schools moved little during observation bouts hence ocean floor depths also did not change.

Greater proportions of surface and dive time variance were accounted for and correlation coefficients were stronger when aggregated data were used in the analysis (Appendices 1 and 2). Whales probably do not match each surface and dive time to the bait school characteristics immediately below them, but on a broader time scale, over a longer period of time, a more consistent correspondence between prey parameters and predatory behaviour might emerge. This appears to have been the result. Cases in the aggregated data set were mean values of variables for each hour of observation. Case to case variability (within variable variance) in the data is substantially reduced and existing relationships between variables emerge more strongly.

11.4.2 Shallow capelin

Contrary to results from deep capelin foraging, in shallow capelin locations surface time was neither related to dive time nor to bait variables (Tables 6.5 and 7.5). This supports the idea that when foraging on shallow capelin surface time is not a recovery period from a foraging dive but may have other functions (repositioning, letting prey regroup, school to school travel, see Section 11.3.2). Shallow capelin foraging data sets were not highly autocorrelated. This reflects the whales' behaviour (less regularly patterned) and supports the above predictions about the function of surface time during shallow capelin foraging. Surface times were highly variable between dives

(SD > mean, Tables 6.3, 7.2) probably because the duration varied according to its immediate function.

When prey schools were shallow only two bait measures were available, ocean floor depth and prey extent/area. There was no measure of top depth, the variable that most strongly influenced dive time when prey schools were deep. In the Southern Shore study area dive time was significantly predicted by bait variables (Table 6.5) but this was not the case in Cape Broyle Harbour (Table 7.4). It seems unlikely that the vertical extent of small pockets of capelin would influence dive time to any degree, for reasons similar to those for large deep capelin schools (see above). Ocean floor depths and vertical extents of prey schools were positively correlated in Witless and Mobile Bays; the two variables acting together (or ocean floor depth alone) may contribute to longer dive times.

Re-analysis with the reduced bait variable set to control for multicollinearity caused a greater reduction in time variable prediction when prey schools were shallow than when they were deep. This was consistently so with dive time, where bait variables, rather than whale variables, were the main predictors. As for the Great Island study location, in all shallow prey situations there was a substantial decrease in the prediction of unitime by bait variables alone (footprint values only). Reduction in the degree of prediction of both surface time and dive time may be compounded for unitime since it is a composite of the other two time variables.

11.4.3 Krill

Results from multiple regression analysis when whales were feeding on krill are similar to those for shallow capelin foraging: dive time but not surface time was significantly predicted by bait characteristics at the dive area. Both types of krill feeding data were used in the multiple regression analysis: that of whales lunge feeding on surface swarms of krill and also that of whales diving into small patches of krill (cruise and munch). In the former data set surface time could be expected to be related to bait variables as the consumatory phase occurs while whales are at the surface. During cruise and munch foraging, however, dive time could be expected to be predicted by bait variables. Multiple regression analysis for the two types of foraging were not done separately due to small data sets and pooled data set results are not clearly interpretable. Ocean floor depth seems to most strongly influence dive time (Table 8.4). This would be expected during cruise and munch foraging but during lateral lunging water depth may limit the depth (and thus time) of pre-lunging positioning or momentum gaining dives.

11.5 Implications for further research

Since foraging behaviour of humpback whales is closely related to the immediate prey situation, they appear to be quite efficient foragers. Discussing humpback foraging behaviour in terms of optimal foraging theory is only useful to a point and does have drawbacks. Such discussion helps generate predictions about prey school characteristics that might influence foraging behaviour and ideas about why whales respond demographically and behaviourally the way they do. Generating predictions that are testable is virtually impossible though, as the nature of the predator-prey system is not at all conducive to experimental manipulation. In addition the assumptions of optimality theory itself have been criticized (see Maynard Smith 1978; Krebs et al. 1981). It is very likely that humpbacks learn to exploit both novel and familiar prey in an opportunistic and flexible manner, also making the application of optimality theory less legitimate.

The behaviour of various types of prey schools seems to strongly influence choice of both prey type and exploitation strategy (see Chapters 1 and 11). Thus perhaps the most interesting and promising aspect of future research is further investigation of how humpback whale feeding influences behaviour of prey aggregations. Questions that might be addressed include how krill and fish schools of different species react to repeated disruption, and which species respond to bubbles or the approach of light objects (ie. flippers). Such a focus might determine why humpback whales use a particular foraging strategy on a particular type of prey, whether prolonged foraging really does disrupt prey schools and if foraging group coordination could function to minimize prey disruption.

Knowledge of particular aspects of whale foraging ecology (some of which this study attempted to address) such as the locations of prey aggregations and of important feeding areas and which are the preferred or most heavily exploited prey species is important. Such knowledge permits assessment of the vulnerability of a cetacean population to changes in prey availability that might result from human exploitation or environmental damage.

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APPENDIX 1

Table A1.1

Varket Channel multiple regression analysis on the data set composed of only the first dive of every hour. This was done to remove autocorrelation from analyses in Table 3.7.
Two multiple regressions were performed using unitime as the dependent variable. The first analysis included both bait and whale measures as independent variables, in the second, bait variables only were used. SURFTIME and DIVETIME wer[illegible] regressed on bait variables only.

DEPENDENT VARIABLE	SURFTIME		DIVETIME	
Bait Variables Significant	All	p<0.01	All	p<0.01
First variables entered and cumulative proportion of variance accounted for	TOPFP	57.9	FLRFP	45.7
	AREA	67.8(-)	TOPAV	56.8
	TOPAV	68.9	VEXTAV	59.5(-)
	FLRFP	69.2	VEXTFP	64.2(-)
	VEXTAV	69.2	FLRAV	66.6
Total proportion of variance accounted for	69.2		67.1	
Durbin-Watson test	no autocorre[illegible]		inconcl p<.05 inconcl p<.01	

DEPENDENT VARIABLE	UNITIME		UNITIME	
Significant Variables	All	p<0.01	All	p<0.01
First variables entered and cumulative proportion of variance accounted for	TOPAV	55.5	TOPAV	55.5
	FLRFP	65.7	FLRFP	65.7
	GPSIZE	75.6	VEXTAV	67.8(-)
	GROSDIR	78.6	TOPFP	74.0
	FLRAV	80.0		
Total proportion of variance accounted for	86.4		75.7	
Durbin-Watson test	no autocorrel		autocor p<.05 autocor p<.01	

Table A1.2

Varket Channel, results from multiple regression analysis on the aggregated data set consisting of the hourly means of each variable. This was done in an attempt to remove autocorrelation from analyses in Table 3.7. In the first row of equations independent variables include both whale and bait measures, in the second row, bait variables only are included. See Table 3.7 for more explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All $p<0.001$		All $p<0.001$		All $p<0.001$	
1st variables entered and cumulative proportion of variance accounted for	TOPAV	53.1	TOPAV	73.8	TOPAV	75.2
	GPSIZE	72.1	GROSDIR	81.2	GPSIZE	81.2
	DIRN	74.2	VEXTAV	82.2 (-)	GROSDIR	83.0
	NETDIR	75.5	SURFTIME	83.1	NETDIR	83.9
	DIVETIME	77.4	GPSIZE	83.7	AREA	84.7
	FLRFP	78.0	TOPFP	84.1	VEXTFP	86.4 (-)
	TOPFP	78.5			TOPFP	86.7
Total proportion of variance accounted for	81.1		85.0		87.1	
Durbin-Watson test	no autocorrel		no autocorrel		inconcl $p<.05$ no auto $p<.01$	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All $p<0.001$		All $p<0.001$		All $p<0.001$	
1st variables entered and cumulative proportion of variance accounted for	TOPAV	53.1	TOPAV	73.8	TOPAV	75.2
	FLRFP	59.3	VEXTAV	74.2 (-)	FLRFP	77.0
	TOPFP	60.1	~~FLRAV~~	~~74.3~~	AREA	77.3 (-)
	AREA	62.0 (-)	AREA	74.7 (-)	VEXTFP	78.8 (-)
	VEXTFP	68.2 (-)			VEXTAV	79.1 (-)
Total proportion of variance accounted for	68.7		74.8		79.4	
Durbin-Watson test	no autocorrel		no autocorrel		no autocorrel	

Table A1.3

Trinity Bay multiple regression analyses on the data set composed of only the first dive of every hour. This was done in an attempt to remove autocorrelation from analyses in Table 4.4. Both whales and bait measures were used as independent variables in the first row of equations, bait variables only were used in the second row. See Table 4.4 for further explanation.

DEPENDENT VARIABLE	DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001
First variables entered and cumulative proportion of variance accounted for	AREA	16.9	VEXTAV	16.9(-)
	GPSIZE	29.7	GROSDIR	38.0
	FLRAV	35.6	TRATE	51.9
	TOPFP	44.2	GPSIZE	60.3(-)
	SURFTIME	46.5	FLRAV	62.1
	VEXTFP	47.1(-)	TOPAV	64.6
	NETDIR	47.6		
	GROSDIR	50.5		
Total proportion of variance accounted for	51.7		65.4	
Durbin-Watson test	no autocor inconcl	p<.01 p<.05	autocorr inconcl	p<.05 p<.01

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	FLRFP	11.9	VEXTAV	19.1(-)	VEXTAV	16.9(-)
	VEXTFP	18.8(-)	FLRAV	30.5	FLRFP	35.7
	FLRAV	20.0	TOPAV	41.5	TOPAV	39.9
	VEXTAV	20.2(-)	VEXTFP	42.1(-)	VEXTFP	40.9(-)
					TOPFP	41.4
Total proportion of variance accounted for	23.9		42.6		41.6	
Durbin-Watson test	inconcl no auto	p<.05 p<.01	inconcl no auto	p<.05 p<.01	autocor inconcl	p<.05 p<.01

Table A1.4

Trinity Bay multiple regression analysis on the aggregated data set consisting of the hourly means of each variable. Independent variables include both whale and bait measures in the first row of equations, bait variables only are included in the second row. See Table 4.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.001		All p<0.001		All p<0.001	
1st variables entered and cumulative proportion of variance accounted for	FLRFP	30.3	SURFTIME	19.3	FLRFP	21.9
	GROSDIR	41.1	GPSIZE	30.6	GROSDIR	25.8
	TRATE	74.4	TOPAV	36.2	TRATE	44.6
	DIVETIME	77.2	AREA	42.9	GPSIZE	49.9
	NETDIR	79.8	FLRFP	49.4	VEXTFP	53.9(-)
	TOPFP	82.0	TOPFP	50.6	TOPAV	60.9
	TOPAV	83.2			TOPFP	64.2
Total proportion of variance accounted for	85.3		52.3		64.9	
Durbin-Watson test	no autocorrel		autocor p<.05 autocor p<.01		autocor p<.05 autocor p<.01	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All p<0.001		All p<0.001		All p<0.001	
First variables entered and cumulative proportion of variance accounted for	FLRFP	30.3	FLRAV	8.0	FLRFP	21.9
	VEXTFP	30.9	TOPAV	13.7(-)	VEXTFP	24.8(-)
	AREA	35.5	VEXTFP	31.3(-)	TOPAV	35.9
	VEXTAV	35.8	AREA	31.8	AREA	36.1
	TOPFP	35.9	TOPFP	32.5(-)	VEXTAV	36.2
Total proportion of variance accounted for	36.9		32.9		36.2	
Durbin-Watson test	inconcl p<.05 inconcl p<.01		autocor p<.05 autocor p<.01		autocor p<.05 autocor p<.01	

Table A1.5

Great Island, multiple regression analysis on the data set composed of only the first dive of every hour. This was done in an attempt to remove autocorrelation from the analyses in Table 5.4. Both whale and bait measures were used as independent variables in the first set of equations, independent variables included bait variables only in the second set of equations.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	$p<0.01$ except GPSIZE $p<0.05$		All $p<0.01$		All $p<0.01$	
			DIRN	29.5 (-)		
1st variables entered and cumulative proportion of variance accounted for	GPSIZE	14.6	GROSDIR	39.9 (-)	GPSIZE	9.9
	TOPAV	24.2	AREA	47.6 (-)	TOPAV	30.0
	DIRN	33.4	TOPFP	54.4	TRATE	36.3 (-)
	AREA	36.1	VEXTAV	59.2 (-)	NETDIR	63.8
	NETDIR	38.5	NETDIR	60.9 (-)	FLRFP	64.6
	TRATE	64.1 (-)	GPSIZE	62.4 (-)	FLRAV	72.8
	FLRFP	69.1	TOPAV	62.9	AREA	74.2
	FLRAV	79.3	TRATE	63.3 (-)	DIRN	75.4
	VEXTEP	81.0	FLRAV	64.4	GROSDIR	78.0
			FLRFP	67.4		
			VEXTFP	73.3 (-)		
Total proportion of variance accounted for	82.3		73.4		79.8	
Durbin-Watson test	no autocorrel		no autocorrel		no autocorrel	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	$p<0.05$ except VEXTFP n.s.		$p<0.01$ except AREA, VEXTAV $p<0.05$		$p<0.01$ except FLRFP, FLRAV, AREA $p<0.05$	
1st variables entered and cumulative proportion of variance accounted for	VEXTFP	4.6	TOPFP	22.4	TOPAV	9.3
	VEXTAV	23.5	TOPAV	25.6	TOPFP	15.8
	TOPFP	26.1	AREA	27.6 (-)	VEXTFP	16.9
	TOPAV	37.8	VEXTFP	35.0 (-)	VEXTAV	34.6
	AREA	37.9	FLRFP	37.9	AREA	34.9
	FLRFP	38.1	FLRAV	43.6	FLRAV	35.0
	FLRAV	46.9			FLRFP	39.8
Total proportion of variance accounted for	46.9		44.3		39.8	
Durbin-Watson test	no autocorrel		autocor $p<.05$ autocor $p<.01$		no autocorrel	

Table A1.6

Great Island, multiple regression analysis on the aggregated data set consisting of hourly means of each variable. In the top row of equations, independent variables include both whale and bait measures. Equations in the second row contain bait variables only in the independent variable list. See Table 5.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.01		All p<0.01		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for			DIRN	34.8(-)	TOPAV	23.8
			GPSIZE	47.5(-)	GROSDIR	35.4
	GROSDIR	44.8	TOPAV	50.3	TRATE	49.7
	TRATE	85.4	SURFTIME	54.2(-)	DIRN	55.3(-)
	NETDIR	87.0	FLRAV	55.4	FLRAV	58.5
	AREA	87.7	AREA	60.3(-)	AREA	62.2(-)
	VEXTFP	87.8	VEXTFP	61.7(-)	TOPFP	63.4
			TOPFP	65.5	VEXTFP	66.9(-)
			VEXTAV	68.8(-)	VEXTAV	70.6(-)
Total proportion of variance accounted for	89.0		70.0		71.0	
Durbin-Watson test	inconcl p<.05 no auto p<.01		no autocorrel		no autocorrel	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		All p<0.01		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for	VEXTFP	1.0	TOPFP	31.0	TOPAV	23.8
	VEXTAV	7.5	AREA	31.3(-)	TOPFP	28.4
	FLRAV	8.3(-)	VEXTFP	37.0(-)	FLRFP	33.9
	TOPAV	17.3(-)	VEXTAV	39.3(-)	AREA	42.6(-)
	TOPFP	18.2(-)	TOPAV	44.8	VEXTAV	46.4(-)
Total proportion of variance accounted for	18.6		45.4		46.4	
Durbin-Watson test	autocor p<.05 inconcl p<.01		autocor p<.05 inconcl p<.01		no autocorrel	

APPENDIX 2

Table A2.1. First order correlation coefficients between pairs of variables in the Varket Channel data set of hourly means. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	TOPFP	TOPAV
SURFTIME	1.00000**	0.68630**	0.24655	0.21126	0.24461	0.24767	0.69161**	0.72891**
DIVETIME	0.68630**	1.00000**	0.54438**	0.50695**	0.51417**	0.51040**	0.79372**	0.85885**
GROSDIR	0.24655	0.54438**	1.00000**	0.95740**	0.06760	0.06283	0.25253	0.33500*
NETDIR	0.21126	0.50695**	0.95740**	1.00000**	0.06165	0.05679	0.23106	0.31614*
FLRFP	0.24461	0.51417**	0.06760	0.06165	1.00000**	0.99957**	0.64773**	0.60671**
FLRAV	0.24767	0.51040**	0.06283	0.05679	0.99957**	1.00000**	0.64287**	0.60303**
TOPFP	0.69161**	0.79372**	0.25253	0.23106	0.64773**	0.64287**	1.00000**	0.94125**
TOPAV	0.72891**	0.85885**	0.33500*	0.31614*	0.60671**	0.60303**	0.94125**	1.00000**
VEXTFP	-0.43049**	-0.35574*	-0.20596	-0.13368	-0.19914	-0.19283	-0.65284**	-0.47573**
VEXTAV	-0.47217**	-0.43848**	-0.28617	-0.21205	-0.16278	-0.15611	-0.66387**	-0.57359**
AREA	-0.29102	-0.37103*	-0.29691	-0.20052	-0.32386*	-0.31664*	-0.62430**	-0.47917**
UNITIME	0.91098	0.92519	0.43736**	0.39772**	0.41922**	0.41868**	0.81098**	0.86738**
DIRN	0.03762	-0.06267	0.28779	0.18331	-0.29462	-0.29566	-0.20554	-0.17199
RATIO	-0.71121**	-0.07890	0.07043	0.06417	0.10840	0.10261	-0.26751	-0.26124
TRATE	-0.22175	0.18558	0.79913**	0.76139**	0.01515	0.01107	-0.16118	-0.07644
GPSIZE	0.48482**	0.08778	0.10182	0.13624	-0.25625	-0.25027	0.03821	0.06879

	DIRN	RATIO	TRATE	GPSIZE	VEXTFP	VEXTAV	AREA	UNITIME
SURFTIME	0.03762	-0.71121**	-0.22175	0.48482**	-0.43049**	-0.47217**	-0.29102	0.91098**
DIVETIME	-0.06267	-0.07890	0.18558	0.08778	-0.35574*	-0.43848**	-0.37103*	0.92519**
GROSDIR	0.28779	0.07043	0.79913**	0.10182	-0.20596	-0.28617	-0.29691	0.43736**
NETDIR	0.18331	0.06417	0.76139**	0.13624	-0.13368	-0.21205	-0.20052	0.39772**
FLRFP	-0.29462	0.10840	0.01515	-0.25625	-0.19914	-0.16278	-0.32386*	0.41922**
FLRAV	-0.29566	0.10261	0.01107	-0.25027	-0.19283	-0.15611	-0.31664*	0.41868**
TOPFP	-0.20554	-0.26751	-0.16118	0.03821	-0.65284**	-0.66387**	-0.62430**	0.81098**
TOPAV	-0.17199	-0.26124	-0.07644	0.06879	-0.47573**	-0.57359**	-0.47917**	0.86738**
VEXTFP	0.04672	0.33510*	0.17419	-0.09884	1.00000**	0.94259**	0.92544**	-0.42636**
VEXTAV	0.01862	0.33055*	0.12958	-0.05387	0.94259**	1.00000**	0.91416**	-0.49503**
AREA	0.07233	0.14032	-0.01056	0.06828	0.92544**	0.91416**	1.00000**	-0.36226*
UNITIME	-0.01591	-0.41583**	-0.01046	0.30275	-0.42636**	-0.49503**	-0.36226*	1.00000
DIRN	1.00000**	-0.14766	0.19710	0.03767	0.04672	0.01862	0.07233	-0.01591
RATIO	-0.14766	1.00000**	0.44570**	-0.65002**	0.33510*	0.33055*	0.14032	-0.41583**
TRATE	0.19710	0.44570**	1.00000**	-0.21867	0.17419	0.12958	-0.01056	-0.01046
GPSIZE	0.03767	-0.65002**	-0.21867	1.00000**	-0.09884	-0.05387	0.06828	0.30275

Table A2.2. First order correlation coefficients between pairs of variables in the Trinity Bay data set of hourly means. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	TOPFP	TOPAV
SURFTIME	1.00000**	0.43879**	0.51148**	0.42846**	0.55047**	0.55006**	0.29052**	0.30134**
DIVETIME	0.43879**	1.00000	0.15112	0.08001	0.28326**	0.28327**	-0.01338	-0.03546
GROSDIR	0.51148**	0.15112	1.00000**	0.95172**	0.37615**	0.37187**	-0.08135	-0.04273
NETDIR	0.42846**	0.08001	0.95172**	1.00000**	0.31274**	0.30910**	-0.12157	-0.09003
FLRFP	0.55047**	0.28326**	0.37615**	0.31274**	1.00000**	0.99886**	0.54633**	0.56320**
FLRAV	0.55006**	0.28327**	0.37187**	0.30910**	0.99886**	1.00000**	0.54973**	0.56560**
TOPFP	0.29052**	-0.01338	-0.08135	-0.12157	0.54633**	0.54973**	1.00000**	0.99071**
TOPAV	0.30134**	-0.03546	-0.04273	-0.09003	0.56320**	0.56560**	0.99071**	1.00000**
VEXTFP	0.11086	-0.09265	0.46019**	0.49957**	0.33244**	0.32664**	-0.31961**	-0.28004**
VEXTAV	0.12443	-0.06675	0.46099**	0.50942**	0.34301**	0.33926**	-0.29371**	-0.27765**
AREA	0.17403*	-0.07452	0.48600**	0.53395**	0.33236**	0.32747**	-0.33173**	-0.30378**
UNITIME	0.79844**	0.89136**	0.35937**	0.26981**	0.46765**	0.46744**	0.13779	0.12844
DIRN	0.34926**	0.06280	0.27733**	0.15418	0.07387	0.07909	-0.06470	-0.02397
RATIO	-0.52429**	0.44353**	-0.31173**	-0.31655**	-0.24507**	-0.24722**	-0.28274**	-0.30990**
TRATE	0.07809	-0.01711	0.84781**	0.88351**	0.17001	0.16597	-0.18238*	-0.16188
GPSIZE	0.03726	-0.31998**	0.09270	0.05119	-0.27302**	-0.27531**	-0.15129	-0.14963

	DIRN	RATIO	TRATE	GPSIZE	VEXTFP	VEXTAV	AREA	UNITIME
SURFTIME	0.34926**	-0.52429**	0.07809	0.03726	0.11086	0.12443	0.17403*	0.79844**
DIVETIME	0.06280	0.44353**	-0.01711	-0.31998**	-0.09265	-0.06675	-0.07452	0.89136**
GROSDIR	0.27733**	-0.31173**	0.84781**	0.09270	0.46019**	0.46099**	0.48600**	0.35937**
NETDIR	0.15418	-0.31655**	0.88351**	0.05119	0.49957**	0.50942**	0.53355**	0.26981**
FLRFP	0.07387	-0.24507**	0.17001	-0.27302**	0.33244**	0.34301**	0.33236**	0.46765**
FLRAV	0.07909	-0.24722**	0.16597	-0.27531**	0.32664**	0.33926**	0.32747**	0.46744**
TOPFP	-0.06470	-0.28274**	-0.18238	-0.15129	-0.31961**	-0.29371**	-0.33173**	0.13779
TOPAV	-0.02397	-0.30990**	-0.16188	-0.14963	-0.28004**	-0.27765**	-0.30378**	0.12844
VEXTFP	-0.01024	-0.17737*	0.42779**	-0.02049	1.00000**	0.97905**	0.96010**	-0.00617
VEXTAV	-0.05298	-0.17319	0.44814**	-0.00575	0.97905**	1.00000**	0.96125**	0.01810
AREA	0.04416	-0.21514*	0.45046**	0.01960	0.96010**	0.96125**	1.00000**	0.03783
UNITIME	0.21820*	0.03266	0.02805	-0.19574*	-0.00617	0.01810	0.03783	1.00000
DIRN	1.00000	-0.24115**	-0.01427	0.30000**	-0.01024	-0.05298	0.04416	0.21820**
RATIO	-0.24115**	1.00000**	-0.06762	-0.26904**	-0.17737*	-0.17319	-0.21514*	0.03266
TRATE	-0.01427	-0.06762	1.00000	0.01468	0.42779**	0.44814*	0.45046**	0.02805
GPSIZE	0.30000**	-0.26904**	0.01468	1.00000**	-0.02049	-0.00575	0.01960	-0.19574*

Table A2.3. First order correlation coefficients between pairs of variables in the Great Island data set of hourly means. ** indicates significant correlations at p<.01, * indicates significance at p<.05.

	SURFTIME	DIVETIME	GROSDIR	NETDIR	FLRFP	FLRAV	TOPFP	TOPAV
SURFTIME	1.00000**	-0.41626**	0.66896**	0.63319**	-0.07046	-0.08024	-0.08843	-0.01076
DIVETIME	-0.41626**	1.00000**	-0.36036*	-0.42027**	0.20151	0.20457	0.55658**	0.55214**
GROSDIR	0.66896**	-0.36036**	1.00000**	0.96374**	0.00764	-0.00592	-0.11435	-0.06735
NETDIR	0.63319**	-0.42027**	0.96374**	1.00000**	-0.01052	-0.02098	-0.19229	-0.13877
FLRFP	-0.07046	0.20151	0.00764	-0.01052	1.00000**	0.99927**	0.42925**	0.51179**
FLRAV	-0.08024	0.20457	-0.00592	-0.02098	0.99927**	1.00000**	0.43158**	0.50956**
TOPFP	-0.08843	0.55658**	-0.11435	-0.19229	0.42925**	0.43158**	1.00000**	0.96809**
TOPAV	-0.01076	0.55214**	-0.06735	-0.13877	0.51179**	0.50956**	0.96809**	1.00000**
VEXTFP	0.10144	-0.36453*	0.14360	0.19575	0.42752**	0.42367**	-0.58190**	-0.47796**
VEXTAV	0.07334	-0.33377*	0.10562	0.14962	0.44250**	0.43966**	-0.56749**	-0.47645**
AREA	0.06768	-0.20634	0.13106	0.16253	0.47867**	0.47098**	-0.45867**	-0.37418*
UNITIME	0.57148**	0.50825**	0.30778	0.22012	0.11465	0.10815	0.41781**	0.48748**
DIRN	0.25271	-0.58999**	0.35778*	0.46029**	-0.33308*	-0.34161*	-0.57739**	-0.54445**
RATIO	-0.72545**	0.80932**	-0.60650**	-0.59402**	0.01359	0.02071	0.28049	0.23355
TRATE	0.18985	-0.13655	0.82406**	0.77513**	0.04858	0.03667	-0.02754	-0.02480
GPSIZE	0.50189**	-0.42769**	0.49370**	0.51292**	-0.00623	-0.00379	-0.32928*	-0.33832*

	DIRN	RATIO	TRATE	GPSIZE	VEXTFP	VEXTAV	AREA	UNITIME
SURFTIME	0.25271	-0.72545**	0.18985	0.50189**	0.10144	0.07334	0.06768	0.57148**
DIVETIME	-0.58999**	0.80932**	-0.13655	-0.42769**	-0.36453*	-0.33377*	-0.20634	0.50825**
GROSDIR	0.35778*	-0.60650**	0.82406**	0.49370**	0.14360	0.10562	0.13106	0.30778
NETDIR	0.46029**	-0.59402**	0.77513**	0.51292**	0.19575	0.14962	0.16253	0.22012
FLRFP	-0.33308*	0.01359	0.04858	-0.00623	0.42752**	0.44250**	0.47867**	0.11465
FLRAV	-0.34161*	0.02071	0.03667	-0.00379	0.42367**	0.43966**	0.47098**	0.10815
TOPFP	-0.57739**	0.28049	-0.02754	-0.32928*	-0.58190**	-0.56749**	-0.45867**	0.41781**
TOPAV	-0.54445**	0.23355	-0.02480	-0.33832*	-0.47796**	-0.47645**	-0.37418*	0.48748**
VEXTFP	0.19650	-0.30131	0.04189	0.37756*	1.00000**	0.99418**	0.92368**	-0.23254
VEXTAV	0.16915	-0.26931	0.01176	0.36676*	0.99418**	1.00000**	0.93105**	-0.23148
AREA	0.15062	-0.16894	0.04179	0.27674	0.92368**	0.93105**	1.00000**	-0.12194
UNITIME	-0.29255	0.04371	0.05578	0.08956	-0.23254	-0.23148	-0.12194	1.00000**
DIRN	1.00000**	-0.415[illegible]**	0.21201	0.12698	0.19650	0.16915	0.15062	-0.29255
RATIO	-0.41566**	1.00000**	-0.28039	-0.47259**	-0.30131	-0.26931	-0.16894	0.04371
TRATE	0.21201	-0.28039	1.00000**	0.25242	0.04189	0.01176	0.04179	0.05578
GPSIZE	0.12698	-0.47259**	0.25242	1.00000**	0.37756*	0.36676*	0.27674	0.08956

APPENDIX 3

Table A3.1

Varket Channel, results from multiple regression analysis using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. This was done in an attempt to remove the effects of multicollinearity from analyses in Table 3.7. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 3.7 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	27.0	TOPFP	31.2	TOPFP	39.7
	GPSIZE	39.7	SURFTIME	35.5	GPSIZE	44.9
	DIVETIME	43.6	GROSDIR	37.1	VEXTFP	46.8 (-)
	TRATE	45.0 (-)	VEXTFP	38.9 (-)	GROSDIR	48.5
	GROSDIR	51[illegible]	AREA	42.4 (-)	TRATE	54.6 (-)
	DIRN	53.9			DIRN	55.3
					AREA	56.2 (-)
Total proportion of variance accounted for	54.6		42.7		56.3	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	26.6	TOPFP	30.2	TOPFP	38.8
	FLRFP	28.1	VEXTFP	32.1 (-)	VEXTFP	40.1 (-)
	AREA	30.4 (-)	AREA	35.5 (-)	FLRFP	41.2
Total proportion of variance accounted for	30.5		35.3		41.9	

Table A3.2

Varket Channel, results from multiple regression analysis on the aggregated data set (hourly means of each variable) using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. The effects of autocorrelation and of multicollinearity are thus removed from this analysis. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 3.7 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	47.8	TOPFP	63.0	TOPFP	65.8
	GPSIZE	68.9	GROSDIR	75.6	GPSIZE	73.2
	DIVETIME	72.2	VEXTFP	81.1(-)	GROSDIR	77.8
			SURFTIME	83.2	AREA	81.8(-)
					NETDIR	84.2
Total proportion of variance accounted for	73.0		83.3		84.2	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	TOPFP	47.8	TOPFP	63.0	TOPFP	65.8
	FLRFP	55.0	VEXTFP	67.6(-)	AREA	69.2(-)
	AREA	59.7(-)				
Total proportion of variance accounted for	60.0		67.8		69.3	

Table A3.3

Trinity Bay, results from multiple regression analysis using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. This was done in an attempt to remove the effects of multicollinearity from analyses in Table 4.4. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 4.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.001		All p<0.001		All p<0.001	
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	13.9	SURFTIME	4.5	FLRFP	11.9
	TRATE	54.4(-)	GPSIZE	6.4(-)	GROSDIR	15.5
	FLRFP	56.6	FLRFP	7.4	TRATE	28.3
	DIVETIME	58.0	VEXTFP	8.6(-)	VEXTFP	30.1(-)
	NETDIR	58.5	TOPFP	11.0	TOPFP	31.3
	TOPFP	59.0			NETDIR	31.8
	GPSIZE	59.2				
Total proportion of variance accounted for	59.3		12.1		32.3	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All p<0.001		All p<0.001		All p<0.001	
1st variables entered and cumulative proportion of variance accounted for	FLRFP	13.7	FLRFP	3.6	FLRFP	11.9
	VEXTFP	14.7(-)	VEXTFP	5.3(-)	VEXTFP	14.1(-)
	AREA	15.5	TOPFP	8.1	TOPFP	16.3
					AREA	16.9(-)
Total proportion of variance accounted for	15.6		8.3		16.9	

Table A3.4

Trinity Bay, results from multiple regression analysis on the aggregated data set (hourly means of each variable) using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. The effects of autocorrelation and of multicollinearity are thus removed from this analysis. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 4.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	FLRFP	30.3	SURFTIME	19.3	FLRFP	21.9
	GROSDIR	41.1	GPSIZE	30.6(-)	GROSDIR	25.8
	TRATE	74.8	TOPFP	34.9(-)	TRATE	44.6
	DIVETIME	77.2	AREA	41.4(-)	GPSIZE	49.9(-)
	NETDIR	79.8	FLRFP	46.9	VEXTFP	51.8(-)
	TOPFP	82.0			TOPFP	59.0
Total proportion of variance accounted for	82.0		47.1		59.0	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	All	p<0.001	All	p<0.001	All	p<0.001
1st variables entered and cumulative proportion of variance accounted for	FLRFP	30.3	FLRFP	8.0	FLRFP	21.9
			TOPFP	12.1(-)	VEXTFP	24.8(-)
			VEXTFP	29.8(-)	TOPFP	35.2
Total proportion of variance accounted for	30.3		30.5		36.4	

Table A3.5

Great Island, results from multiple regression analysis using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. This was done in an attempt to remove the effects of multicollinearity from analyses in Table 5.4. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 5.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All p<0.001		All p<0.001		All p<0.001	
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	14.0	TOPFP	8.9	FLRFP	8.5
	TRATE	47.4(-)	GPSIZE	13.8(-)	TRATE	25.0
	DIRN	49.5	SURFTIME	17.0(-)	TOPFP	29.1
	NETDIR	51.4	DIRN	18.4		
Total proportion of variance accounted for	52.0		25.4		30.7	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		All p<0.001		All p<0.01	
1st variables entered and cumulative proportion of variance accounted for			TOPFP	8.9	TOPFP	5.5
			AREA	11.4(-)		
			FLRFP	15.3(-)		
			VEXTFP	16.2		
Total proportion of variance accounted for			16.3		5.7	

Table A3.6

Great Island, results from multiple regression analysis on the aggregated data set (hourly means of each variable) using only footprint values for bait variables. Values of bait variables averaged 150 m around the footprint are not in the equation. The effects of autocorrelation and of multicollinearity are thus removed from this analysis. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 5.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME	DIVETIME	UNITIME
Independent Variables Significant	All p<0.001	All p<0.001	All p<0.001
1st variables entered and cumulative proportion of variance accounted for	GROSDIR 44.8 TRATE 85.4 NETDIR 87.0	DIRN 34.8(-) GPSIZE 47.5(-)	TOPFP 17.5 GROSDIR 30.3 TRATE 46.8 DIRN 53.1(-)
Total proportion of variance accounted for	87.0	47.5	54.0

DEPENDENT VARIABLE	SURFTIME	DIVETIME	UNITIME
Bait Variables Significant	none	All p<0.01	All p<0.01
1st variables entered and cumulative proportion of variance accounted for		TOPFP 31.0	TOPFP 17.5
Total proportion of variance accounted for		31.5	17.5

Table A3.7

Southern Shore, results from multiple regression analysis removing pairs of highly correlated variables from the equation. This was done in an attempt to correct for the effects of multicollinearity from analyses in Table 6.5. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 6.5 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	$p<0.001$	All	$p<0.001$	All	$p<0.001$
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	35.7	FLRFP	26.9	GROSDIR	21.7
	TRATE	50.0(-)	SURFTIME	28.3	TRATE	36.8(-)
	NETDIR	52.6	VEXTAV	29.4	FLRFP	44.6
	GPSIZE	53.5(-)	VEXTFP	30.7	NETDIR	46.3
	DIVETIME	54.2				
	VEXTAV	55.1				
Total proportion of variance accounted for	55.1		30.7		46.3	

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Bait Variables Significant	none		All	$p<0.001$	FLRFP	$p<0.01$
1st variables entered and cumulative proportion of variance accounted for			FLRFP	26.9	FLRFP	4.1
Total proportion of variance accounted for			26.9		4.1	

Table A3.8

Cape Broyle, results from multiple regression analysis removing pairs of highly correlated variables from the equation. This was done in an attempt to correct for the effects of multicollinearity on analyses in Table 7.4. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 7.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME	DIVETIME	UNITIME
Independent Variables Significant	All p<0.001	All p<0.01	All p<0.001
1st variables entered and cumulative proportion of variance accounted for	GROSDIR 40.3 TRATE 72.8(-) DIRN 74.9(-)	DIRN 4.4	NETDIR 35.7 TRATE 56.1(-) GROSDIR 65.2
Total proportion of variance accounted for	74.9	4.4	65.3

DEPENDENT VARIABLE	SURFTIME	DIVETIME	UNITIME
Bait Variables Significant	none	none	none
1st variables entered and cumulative proportion of variance accounted for		AREA 3.7	VEXTAV 3.5
Total proportion of variance accounted for		3.7	3.5

Table A3.9

Krill feeding, results from multiple regression analysis removing pairs of highly correlated variables from the equation. This was done in an attempt to correct for the effects of multicollinearity from analyses in Table 8.4. In the upper section of the table both whale and bait measures are included as independent variables; in the lower section, bait variables only are included. See Table 8.4 for further explanation.

DEPENDENT VARIABLE	SURFTIME		DIVETIME		UNITIME	
Independent Variables Significant	All	p<0.01	All	p<0.01	All	p<0.01
1st variables entered and cumulative proportion of variance accounted for	GROSDIR	48.5	FLRFP	22.1	GROSDIR	23.7
	TRATE	84.6	GPSIZE	29.8(-)	FLRFP	57.7
	FLRFP	90.2(-)	AREA	38.1(-)	TRATE	69.6
Total proportion of variance accounted for	90.2		38.1		[illegible]9.6	

DEPENDENT VARIABLE	SURFTIME	DIVETIME		UNITIME	
Bait Variables Significant	none	All	p<0.01	All	p<0.05
1st variables entered and cumulative proportion of variance accounted for		FLRFP	22.1	FLRFP	6.8
				AREA	24.1
Total proportion of variance accounted for		26.9			