Resource and habitat use of northern bottlenose whales in the Gully: ecology, diving and ranging behaviour

by

Sascha K. Hooker

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Resource and habitat use of northern bottlenose whales in the Gully: ecology, diving and ranging behaviour"

by Sascha Hooker

in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Dated: August 3, 1999

External Examiner ____________________
Robert D. Kenney

Research Supervisor ____________________
Hal Whitehead

Examining Committee ____________________
Sara Iverson

____
Ron O'Dor

____
Don Bowen

DALHOUSIE UNIVERSITY

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AUTHOR: Sascha K. Hooker

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Signature of Author

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ABSTRACT

Northern bottlenose whales (*Hyperoodon ampullatus*) show a concentrated distribution within the Gully, a submarine canyon off the coast of eastern Canada. Using data collected between 1988 and 1998, I have analysed the potential function of this local abundance in terms of foraging behaviour, movements and distributional preferences of these whales in the Gully.

Stomachs of northern bottlenose whales, which stranded in Nova Scotia and Quebec, contained a high proportion of the squid *Gonatus steenstrupi*. Fatty acid and stable isotope analysis of biopsy samples collected from free-ranging whales in the Gully were compared to results for samples of *Gonatus fabricii*. Results suggested that squid of this genus could form the bulk of bottlenose whale diet in the Gully. Isotopic nitrogen values suggest that bottlenose whales (mean 15.3 ‰ $\delta^{15}N$) occupy a trophic level of approximately 4.4.

The abundance and distribution of bottlenose whales varied between years, with yearly distribution shifting primarily along the main axis of the canyon. Bottlenose whale distribution was investigated in relation to fixed physical parameters (depth and slope), surface environmental characteristics (sea surface temperature and water clarity), and mid-water environmental characteristics (sub-surface biomass, depth and thickness of deep scattering layer). The distribution of bottlenose whales was found to show strongest correlation with water depth and deep-water biomass.

Two deployments of suction-cup attached time-depth recorder/VHF radio tags on bottlenose whales demonstrated the whales' exceptional diving ability, with dives approximately every 80 min to over 800 m (maximum 1453 m), and up to 70 min in duration. Sonar traces of non-tagged, diving bottlenose whales suggested that such deep dives are not unusual. Many of the recorded dives were to, or close to, the sea floor.

Photo-resightings and radio-tracking follows were used to investigate the pattern and scale of whale movements within the Gully over time intervals up to their residency period (approximately 10 days). Bottlenose whales showed little daily movement (~4 km/day) and maintained ranges of ~20 km^2 for time intervals between hours to days. This relative lack of movement is unusual for oceanic odontocetes and suggests that the canyon supports a profitable and stable food source for these whales. Geographic positions of individuals showed significant variation between years, but no range difference between whale age-sex classes. Within years, individuals showed some range separation particularly in years of highest whale abundance. Mature males showed consistent spatial orientation between years suggesting preferred relative locations.

Regular ultrasonic foraging clicks were recorded while whales were diving, and lower frequency, rapid and variable clicks were heard while whales were at the surface. The inter-click interval (0.4 s) and frequency (24 kHz) of clicks heard during dives were consistent with foraging at ranges of ~300 m on objects of diameter greater than 6 cm.

The estimated level of primary production required to support bottlenose whales in the Gully was much greater than could be produced within this area, suggesting that there must be significant energetic influx to the system. Identification of this input will aid in the development of a comprehensive conservation plan for bottlenose whales. The benthic nature of bottlenose whale foraging suggests that this foodweb would be especially sensitive to threats to the seafloor in the Gully.

LIST OF ABBREVIATIONS AND SYMBOLS

n.m.	nautical mile
knot	nautical mile per hour
km	kilometre
m	metre
cm	centimetre
mm	millimetre
yr	year
h	hour
min	minute
s	second
°C	degrees Centigrade
°	degree (e.g., of latitude, longitude)
'	minute (e.g., of latitude, longitude)
kg	kilogram
g	gram
mg	milligram
%	percentage
‰	parts per thousand
l	litre
ml	millilitre
µl	microlitre
Hz	hertz
kHz	kilohertz
dB	decibel
cal	calorie
J	Joule
C	carbon
N	nitrogen

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Two individuals have made a particular difference to the completion of this thesis. The first was Hal Whitehead, my supervisor, who selected me to be a part of his research team. I have thoroughly enjoyed my time in the lab and the opportunities it has provided, particularly the chance to study such a facinating and largely unknown species as the northern bottlenose whale. Hal persuaded me of my capability at sea and allowed me to captain his research vessel. For this, and for the wealth of sailing experience that I now have, I am very grateful. While allowing me a large amount of freedom to direct my own work, Hal has been helpful, supportive and willing to provide guidance when needed. I am especially grateful for his tutoring in terms of statistical analyses and programming. I have learnt a lot from him.

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PUBLICATIONS

Chapter 3 is partially based on the work published in:

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The review presented in Chapter 4 has been accepted for publication:

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CHAPTER ONE

Introduction

HABITAT AND RESOURCE USE

Knowledge of the habitat and resource use of a species is crucial to the design and implementation of any conservation or management strategy for that species. In order for a species to survive and propagate, it requires habitat, a food source, and mates. An understanding is therefore required of both the ecosystem of which a species is a part, and the particular niche of that species (Lindeman 1942, Hutchinson 1959). Elucidation of the links within an ecosystem further provide an indication of the stability of that ecosystem (MacArthur 1955).

In developing marine mammal conservation strategies, it is therefore useful to examine the functional role of a particular marine mammal in its ecosystem, to evaluate the potential impact of variation in prey populations or environmental change (Bowen 1997). Off the eastern coast of Canada, northern bottlenose whales (*Hyperoodon ampullatus*) appear to show two population centres, in the Gully, off Nova Scotia, and in Davis Strait off Labrador (Reeves et al. 1993). Their distribution off Nova Scotia is strongly focused above the Gully, a submarine canyon, and appears to be well defined by the physical aspects of that canyon (Figure 1.1). In contrast, other cetacean species, including those found year-round in the region, do not show such a well-defined habitat preference (Hooker et al. 1999).

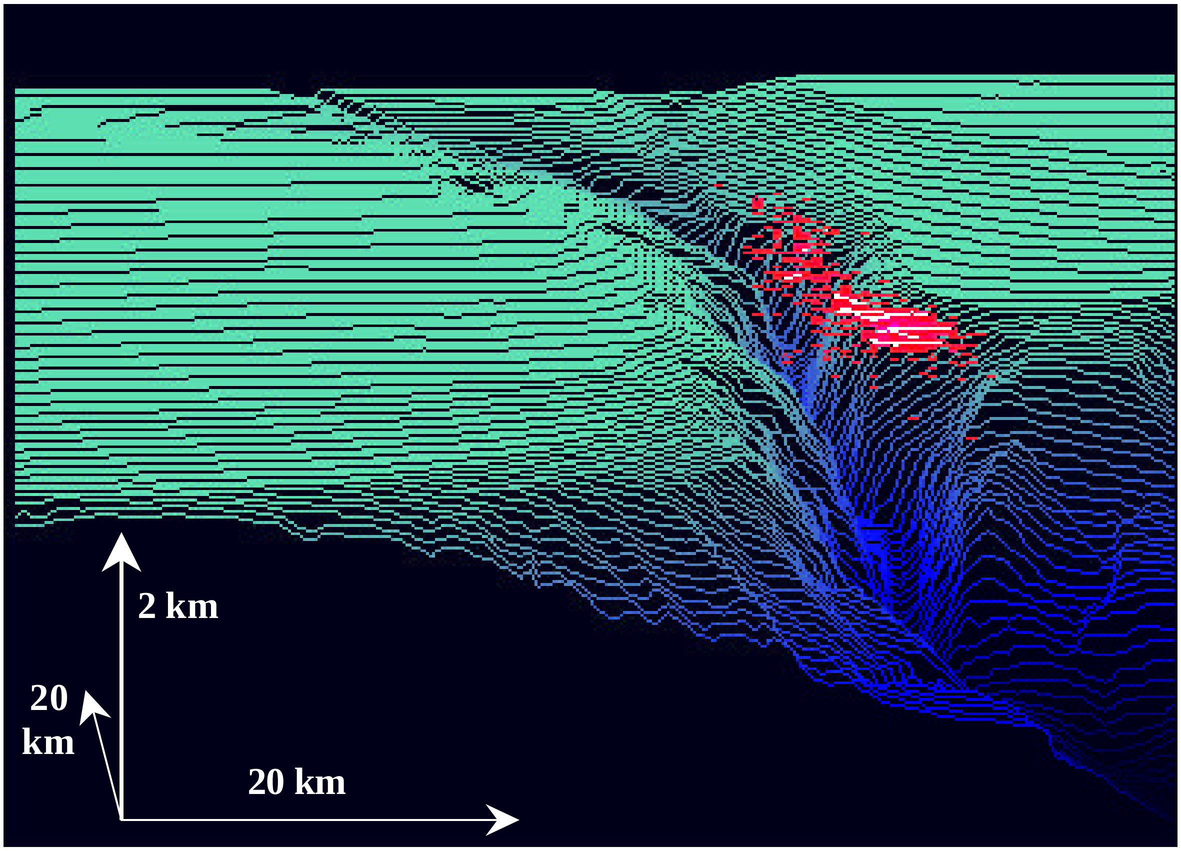

Figure 1.1. Three-dimensional representation of the Gully, a submarine canyon off the east coast of Canada, showing locations of bottlenose whale sightings 1988-1998.

Studies of cetacean habitat requirements and foraging ecology have been conducted over a great range of spatial scales. Most work on cetacean distribution and habitat requirements has been conducted over large scales (e.g., Reilly 1990, Payne and Heinemann 1993, Jaquet and Whitehead 1996). In the past, much of the work on cetacean feeding ecology also came from commercial harvesting over large scales, but more recent work on foraging behaviour has been over much smaller scales (e.g., Würsig 1986). In general, behavioural studies of many organisms tend to be conducted over much smaller scales than ecological studies, yet the matching of scales is likely to be most productive in assessment of the link between foraging behaviour and habitat use (Lima and Zollner 1996). This study investigates the small-scale habitat use and local foraging behaviour of bottlenose whales in the Gully. The ecological requirements of beaked whales are largely unknown, and in this respect, the work described in this thesis represents a case study of the foraging ecology of one population of beaked whale.

THE NORTHERN BOTTLENOSE WHALE, *HYPEROODON AMPULLATUS*

Phylogeny and systematics

The northern bottlenose whale is a member of the beaked whale family, Ziphiidae. Beaked whales are the least known family of large mammals (Wilson 1992). One species of beaked whale, Longman's beaked whale (*Mesoplodon (Indopacetus) pacificus*) is known only from two skulls in Australia and Somalia, and another unidentified species, *Mesoplodon* species "A", has only ever been observed at sea and so its skull morphology is still unknown (Jefferson et al. 1993). New species of beaked whales are still being discovered, for example, *M. peruvianus* and *M. bahamondii* were identified from skull specimens in Peru and Chile, respectively, only in the last decade (Reyes et al. 1991, 1995).

The current lack of knowledge of many beaked whale species stems from their distribution and behavioural characteristics. Beaked whales usually live in deep water, hence often far offshore beyond the reach of the primarily shore-based cetacean population studies. They dive for long periods and are therefore not often seen at the surface. Even when they are seen, many species are difficult to identify. Furthermore most species appear to be quite shy and do not readily approach boats.

Unlike many other beaked whale species, northern bottlenose whales are not shy of boats, and in fact will often approach slow-moving or stationary boats, apparently in curiosity, and will circle them for an hour or more (Gray 1882). This behaviour, together with their predictable distribution in certain locations, has allowed their study to advance at a greater rate than that of other beaked whale species.

There are two recognised species in the genus *Hyperoodon*: the northern bottlenose whale *Hyperoodon ampullatus* Forster, 1770; the southern bottlenose whale *Hyperoodon planifrons* Flower, 1882. A third putative bottlenose whale, found in the tropical Pacific may exist (Urban-R et al. 1994, Gallo-Reynoso and Figueroa-Carranza 1995, Pitman et al. 1999), although Pitman et al. (1999) suggested that this unidentified tropical bottlenose whale may be *Indopacetus pacificus*.

The known fossil record of beaked whales is sparse (Mead 1975, Whitmore et al. 1986, de Muizon 1991). Most fossil ziphiids have been identified based on partial remains of rostra (the extension of the skull that forms the beak). Ziphiids have in the past been grouped with the family Physeteridae into the superfamily Physeteroidea, based primarily on skull structure (Mead 1989b). However, beaked whales are currently assigned their own superfamily, Ziphoidea, and their phylogenetic placement in relation to Physeteroidea and Delphinoidea is uncertain (Rice 1998). Heyning (1997) placed sperm whales as the basal group of living odontocetes, whereas de Muizon (1991) placed sperm whales and ziphiids into the basal clade. Ziphiids and physeterids both have a high wax ester content in their blubber, which other odontocete families do not have (Litchfield et al. 1976), and both have similar heart shape and structure (Rowlatt 1981). Within the beaked whales, Moore (1968) linked *Hyperoodon* and *Mesoplodon* on the basis of similarities in their skull characteristics, but many authors feel that such an assignment was premature (Mead 1989b). The evolutionary relationships between the ziphiids are still largely unknown. Recent work using molecular techniques to identify beaked whale species (Henshaw et al. 1997, Dalebout et al. 1998) will likely provide some of these answers in the near future.

General characteristics

Northern bottlenose whales are recognised primarily by their long and tube-like snout, distinct from their melon. The dorsal fin is small and falcate, located approximately two thirds down the back. Their flippers are small and rounded. Flipper pockets or indentations in the body allow the flippers to be laid flat against the body surface. The flukes lack a median notch; in fact they often have a median projection rather than a notch.

Northern bottlenose whales are the third largest beaked whale species; Baird's beaked whale (*Berardius bairdii*) and Arnoux's beaked whale (*B. arnuxii*) are larger. Adult female bottlenose whales reach lengths of up to 8.7 m (Thompson 1846) and adult males lengths of up to 9.8 m (Benjaminsen 1972). There is sexual dimorphism in both size (adult males being slightly larger than adult females) and head shape (adult males develop an enlarged and flattened forehead). Gray (1882) illustrated the change in head shape between different age-sex classes. This change in head shape is reflected in the maxillary crests, which are much more developed in adult males than in females or juveniles. The function of these crests is largely unknown, although acoustic (Mitchell and Kozicki 1975) and intra-sexual competitive (Gowans and Rendell 1999) functions have been suggested.

The whaling industry

Much of what is known about bottlenose whales has come from data collected in conjunction with the whaling industry. There have been two main eras of large-scale commercial fisheries for the species – between 1890 and 1905 and between 1960 and 1970. Scottish whalers were the first to start a directed bottlenose whale hunt, taking 28 in Frobisher Bay in 1852. Then in 1877 the sealer “Jan Mayen” of Peterhead took 10 whales in Cumberland Sound (Southwell 1884). Within a few years of this, the Norwegians took up and essentially took over the fishery, such that by 1891 there were over 60 vessels employed (Gray 1941). Between 1882 and the 1920s about 60,000 bottlenose whales were caught (Holt 1977). Annual catches between 1890 and 1905 frequently exceeded 2500 whales, with a maximum of 3300 killed in each of 1891 and 1896 (Christensen 1984).

Between 1925 and 1955 the total annual catches dropped to 20 – 100 (Mitchell 1977). Then, in the 1960s the catches increased to more than 300 per year (Christensen 1984). Initially catches centred off Møre and Andenes, Norway and off the coast of Spitzbergen (Figure 1.2; Mead 1989b), but in 1962 the fishery shifted to Iceland, and in 1969 it expanded to the Davis Strait (Christensen 1975). Catches increased to a maximum of 700 in 1965 (Mitchell 1977), then declined again to 213 in 1971 and to 3 in 1973 (Christensen 1984). The stated reason for the closure of the fishery was economic as the value of bottlenose whales fell (Jonsgård 1977), although there is also evidence that the population was quite heavily depleted by this time (Mitchell 1977).

A whale fishery operating out of Blandford, Nova Scotia, also took bottlenose whales during this latter period. Eighty-seven whales were taken from the Gully area between 1963 and 1968 (Jahn et al. 1964, 1968, Reeves et al. 1993).

Bottlenose whales have also been taken in small numbers by coastal fisheries for many hundreds of years, in the Faroe Islands, Norway, Iceland and Greenland (Christensen 1984). Such fisheries have only taken a few hundred whales over 400 years (Bloch et al. 1996).

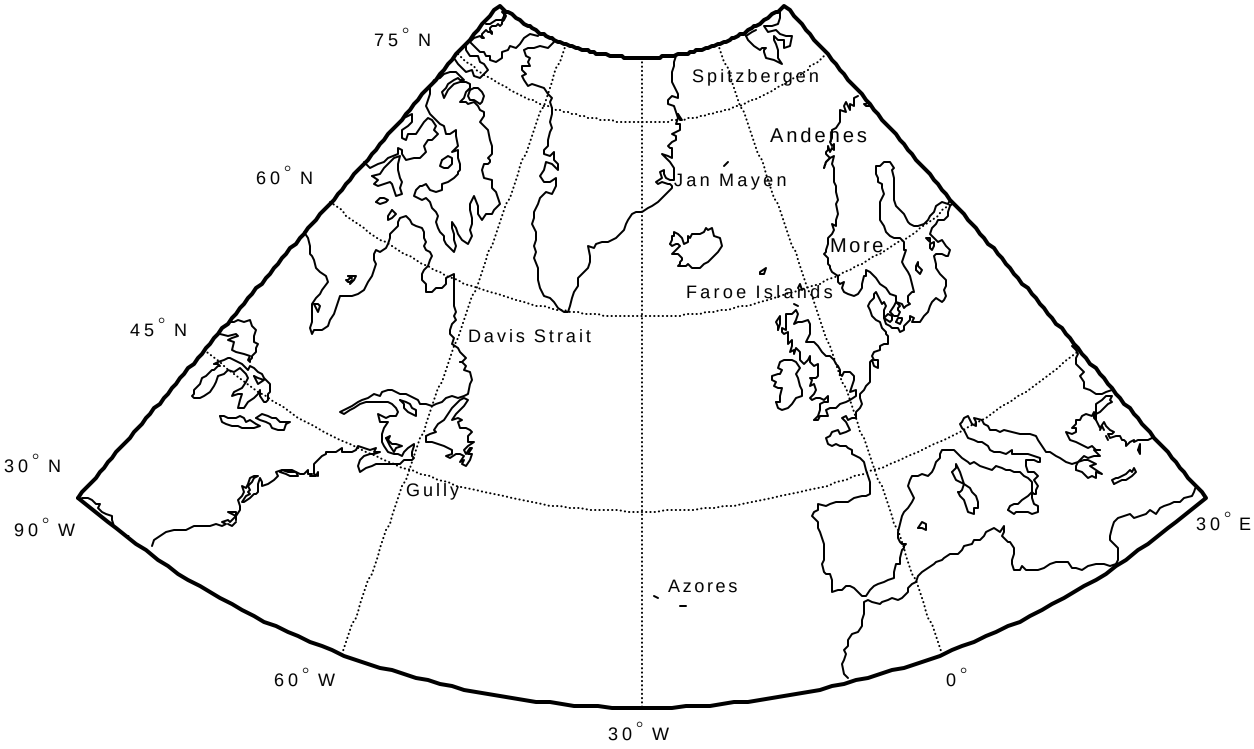

Figure 1.2. Map of the North Atlantic showing locations described in text.

Conservation status

In 1976, following the decline in numbers of bottlenose whales caught by whalers, the species was assigned the status of "vulnerable" (definition: taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating) by the IUCN (Mitchell 1976). It was later changed to the designation of "insufficiently known" (Klinowska 1991), and then to the designation "lower risk, conservation dependent" (definition: taxa that do not qualify for the vulnerable category only because of species-specific or habitat-specific conservation efforts, the cessation of which would result in the taxon qualifying for one of the threatened categories within a period of five years; Baillie and Groombridge 1996). In 1977, the International Whaling Commission considered the further exploitation of northern bottlenose whales and recommended Protection Stock status with zero catch limit (Klinowska 1991). On a national basis, the status of the Gully population of bottlenose whales was updated by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC) from “not at risk” to “vulnerable” in 1996 (definition: a species of special concern because of characteristics that make it particularly sensitive to human activities or natural events, Whitehead et al. 1997a).

Distribution

The northern bottlenose whale is found only in the North Atlantic from approximately the Gully to the ice edge of Davis Strait in the west, and from the Azores to the west coast of Spitzbergen in the east (Figure 1.2). Knowledge of its distribution is based primarily on whaling, stranding and occasional sighting data.

True (1910) reported strandings between Boston and New York, but the female specimen he reports from New York Bay has been questioned (Ulmer 1941, Mitchell and Kozicki 1975). The southernmost stranding record in the western North Atlantic appears to be from Rhode Island in 1867 (Mitchell and Kozicki 1975). A group of six bottlenose whales was sighted slightly further south than this (40° 46.2’N 66°59.0’W) during a NMFS assessment cruise in July 1996 (Waring et al. 1997) and there were several sightings in the Mid-Atlantic Bight region during the CETAP (Cetacean and Turtle Assessment Program) between 1979 and 1982 (Kenney et al. 1997).

In the eastern North Atlantic, bottlenose whales have been seen as far south as the Cape Verde Islands (15°N), and several strandings have been reported on the southwestern coasts of Europe (Ruud 1937). The species is occasionally observed off the Azores (Steiner et al. 1998). There are also a few older records of the species occurring in the Mediterranean sea (Clement 1881), although no recent records have been published.

Distribution of catches by whalers suggested at least six major population centres of bottlenose whales. Two of these were in the western North Atlantic – (1) in the Gully off Nova Scotia, and (2) in the Davis Strait off northern Labrador. The other four population centres were in the eastern North Atlantic – (1) west of Svalbard, Spitzbergen, (2) north of Iceland and around Jan Mayen, (3) around Andenes, Norway, and (4) around Møre, Norway (Figure 1.2; Benjaminsen and Christensen 1979). There is some concern that the easterly populations of bottlenose whales were much reduced, leading to the westward expansion of whalers and whaling (Mitchell 1977). The current distribution and abundance of bottlenose whales from these eastern populations is not well known. Sightings surveys between Norway and Greenland show few whales in the Norwegian Sea (Øien 1990), but the population around the Faroe Islands and Iceland still appears to be fairly healthy (Sigurjónsson et al. 1989, 1991). In the final years of whaling (1971-1975), observers recorded many bottlenose whales in the Davis Strait, Labrador (Christensen 1977).

Migration

Suggestions that bottlenose whales follow a yearly migration have come mainly from whalers. Bottlenose whales were thought to have a more northerly distribution during the spring and first part of the summer, starting to migrate south in July (Mitchell and Kozicki 1975). Catches in Svalbard took place primarily between April and June and those off Iceland took place between April and July (Benjaminsen 1972). The whaling high season in the Faroes was from 20 August to 20 September (Bloch et al. 1996). Almost all whaling was conducted between March and October, so little is known of winter distribution of these whales.

The major problem with using these data to infer migration pattern is the lack of any effort data with which to compare sighting or stranding results. Whalers may have often propagated their own beliefs claiming that whales were migrating when in fact it was they that were migrating and claiming that whales were "travelling" also. Strandings on the Atlantic shores of Europe and North America in the last months of summer or autumn were also cited as further evidence of southward migration (Ohlin 1893, Fraser 1953). A comparison of strandings data for the coasts of Britain and Ireland with those collected for maritime Canada do appear to show an increase in strandings during late summer and autumn (Table 1.1; Figure 1.3). However, such an increase in strandings should not be used to infer migration as the cause. Other explanations, such as an inshore movement following a food source, are equally plausible. Bottlenose whales are in fact also seen in the Azores during the summer months (Steiner et al. 1998), and were caught in largest numbers (10 from a total of 26) in June off Scotland (Thompson 1928), when, given the migration hypothesis, they would not be expected at these locations until much later in the year.

Counter to the southern migration hypothesis, a whale stranded in the Faroes in late August was found to contain a specimen of *Vampyroteuthis infernalis* in its stomach. The southern distribution of this squid suggested that this whale had recently been much further south in the Atlantic (Clarke and Kristensen 1980). Further to this, there has been no explanation provided as to why these whales would migrate south during mid-summer. Migrations in the northern hemisphere would generally be expected to move northward in spring and southward in autumn (as was originally suggested for bottlenose whale migration, Gray 1882), so the suggestion that bottlenose whales move south at the onset of summer as the waters begin to warm up seems somewhat counter-intuitive.

The Gully population of northern bottlenose whales appears to be fairly resident (Whitehead et al. 1997b). Whales have been observed in the Gully during most months of the year, and the same whales have been photo-identified there during winter months as during summer months (Whitehead et al. 1997b).

Table 1.1. Strandings of northern bottlenose whales in the western North Atlantic. Museum abbreviations: MANS, Museum of Academy of Natural Sciences, Philadelphia; MCZ, Museum of Comparative Zoology, Harvard University; NMC, National Museum of Canada, Ottawa.

Year	Date	live/dead/ whaled	Sex	Length (m)	Location	Reference / Notes
1867	Feb	whaled	female	8.23	Newport, Rhode Is. (41°30’N)	True 1910; Ulmer 1941; Mitchell and Kozicki 1975 skeleton MANS, Philadelphia
1869	Jan 29?	dead	male	7.61	North Dennis, Mass.	True 1910; Ulmer 1941; Mitchell and Kozicki 1975 skeleton MCZ 1207
1923	Oct	live	female male	Adult immature	Beverly Farms, Mass. (42°33’N)	skeletons MCZ 25361-2 Mitchell and Kozicki 1975
1940	4 Sept	live	female	6.73	Cap Martin, Gulf of St. Lawrence, QE	Sergeant and Fisher 1957
1953	27 July	whaled	male	~6.7	Dildo Arm, Trinity, Newfoundland	Sergeant and Fisher 1957
1968	12 Jan	dead	male	8.70	Sable Island, NS	Sergeant et al. 1970 nb. possibly whaled
1969	9 Oct	dead	male	6.15	Cobequid Bay, Bay of Fundy	Mitchell and Kozicki 1975 cranium NMC 42836.
1974	2 Feb	dead	male	~8.23	Sable Island, NS	B. Beck, pers. comm. cited in Mitchell and Kozicki 1975
1985	18 May	dead	male	5.25	Sable Island, NS	Lucas and Hooker In press
1987	8 Oct	live	female	5.48	Magdalen Islands	P. Beland, pers. comm.
1992	18 May	dead	female	~7.5	Sable Island, NS	Lucas and Hooker In press
1992	8 Oct	live	male	6	Sydney, NS	NSSN necropsy report
1994	6 Nov 9 Nov	live	female male (calf)	7.4 3.88	Montmagny, QE	GREMM; St. Hyacinthe vet college; Fontaine 1995
1997	8 Sept	live	male	6.6*	Sept-Iles, QE	L. Measures, Department of Fisheries and Oceans, pers. comm.

*measured curvilinearly

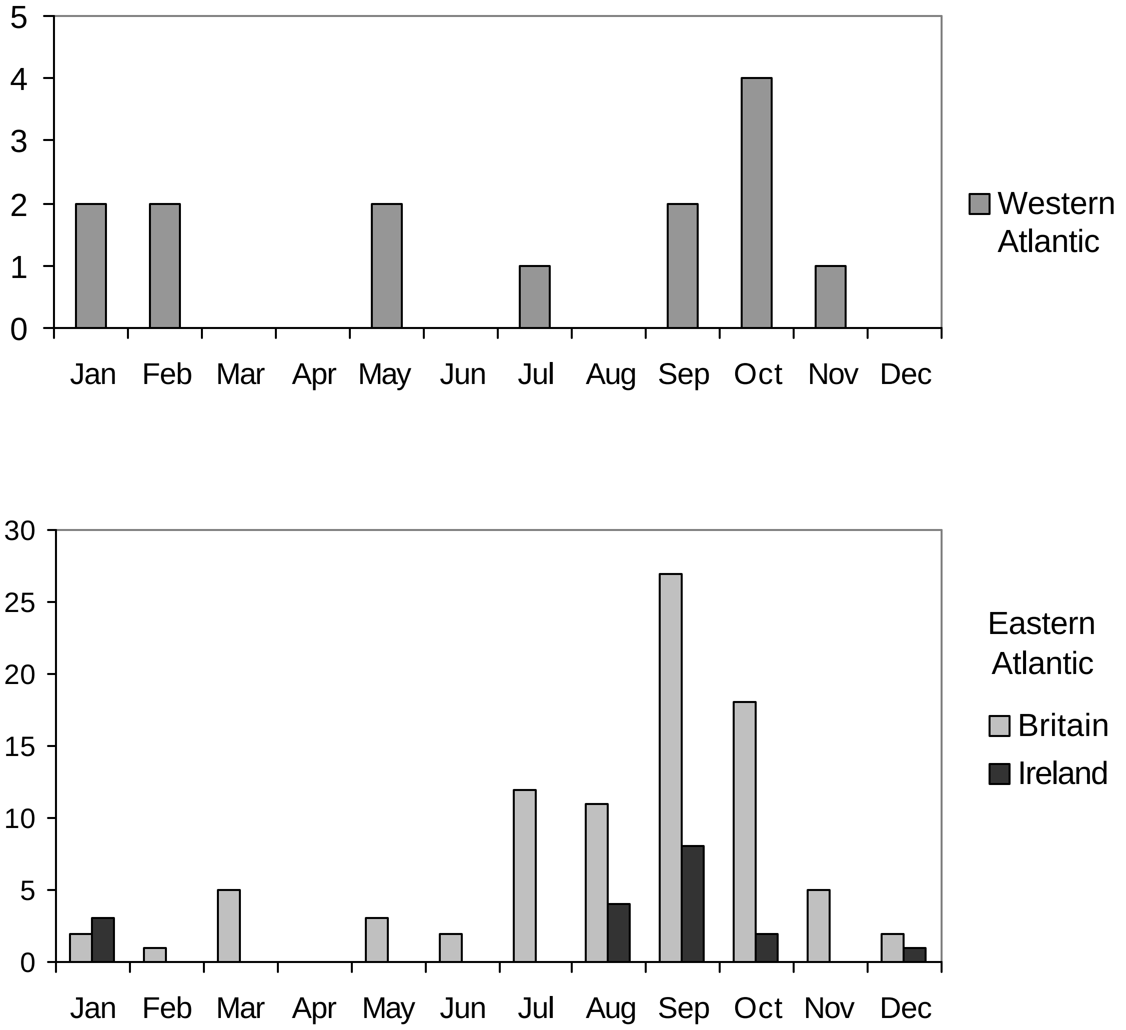

Figure 1.3. Comparison of stranding records on the coast of maritime Canada (above) and in Britain and Ireland (below). Sources for Canadian strandings are shown in Table 1. British strandings are from Harmer (1927), Fraser (1934, 1946, 1953, 1974), Sheldrick (1989); Irish strandings are from Berrow and Rogan (1997).

Prey

Knowledge of the diet of bottlenose whales has also come from both hunted and beach-cast animals. Stomach content analyses have shown that their primary prey is the squid species *Gonatus fabricii* (Benjaminsen and Christensen 1979, Clarke and Kristensen 1980, Lick and Piatkowski 1998). A variety of other squid, fish and even echinoderms have also been reported in the diet (Benjaminsen and Christensen 1979).

Predators and parasites

Norwegian whalers observed an attack by killer whales on a northern bottlenose whale, and also an attack on two harpooned bottlenose whales (Jonsgård 1968a). Jonsgård (1968b) described observed injuries to bottlenose whales such as one or both flippers missing and also some scars caused by tooth rakes from killer whales. Other potential causes of the tooth rakes observed may be other toothed whales (e.g., long-finned pilot whales, *Globicephala melas*) which have been observed accompanying bottlenose whales (personal observation; Gowans 1999). The tooth rakes observed appear too clean to represent shark attacks, but sharks may nevertheless be a threat, particularly for young calves.

Northern bottlenose whales occasionally support lice and barnacles. Gray (1882) observed lice around the fins and on the body surface. One of these was identified as *Platycyamus thompsoni*, which he noted had also been found previously on a bottlenose whale captured off the coast of England. Stalked barnacles (*Conchoderma auritum*) may be found attached to the teeth of adult males (Ohlin 1893). Mitchell and Kozicki (Mitchell and Kozicki 1975) also observed a barnacle (*Tubicinella* sp.) attached to the flanks of an animal stranded in Nova Scotia. Other commensal organisms include the diatom layer coating the skin surface of whales and thought to be responsible for the brown coloration observed (Gray 1941; M. Poulin, pers. comm.).

Population structure

There has been some suggestion of segregation between sexes of bottlenose whales, although these results were based primarily on observations from whaling vessels.

During May and June 1882, 203 bottlenose were caught in the bays and edge of the pack ice south of Jan Mayen, of which 96 were adult males, 56 were females and 51 were younger males (Gray 1882). Turner (1886) states that predominately females, often each accompanied by a calf, were taken on the coasts of western Europe. Of 26 bottlenose whales landed at Scottish whaling stations between April and September, 18 were females (Thompson 1928). Of 25 whales for which sex was recorded from catches in the Gully, 15 were female (Reeves et al. 1993).

The Gully population sex ratio is approximately 1:1 (Gowans 1999), and groups are encountered containing any mixture of age-sex classes. Juvenile whales may be seen with different escorts, although most associate primarily with their presumed mother (Gowans 1999). Most associations between individuals appear to be brief, although adult males sometimes form bonds which last for several years (Gowans 1999).

Life history

Christensen (1973) investigated the age of 53 females and 75 males caught off Labrador. The age of females varied between 1 and 27 (mean 9.8, based on yearly tooth growth layers) and males varied between 1 and 37 (mean 13.1 dentine growth layers). However, the accuracy of this technique decreases with age in some species (e.g., Bowen et al. 1983). The maximum age of animals has often been proved to be much older than that recorded from such samples, so these should be treated cautiously as indices of lifespan (c.f. Christensen 1982, Olesiuk et al. 1990). The majority of females were found to reach sexual maturity at ages from 8 to 12 years (Christensen 1973). Males appear to attain sexual maturity at 7.3-7.6 m (24-25 feet) in length, which corresponds to 10-12 years of age (based on tooth growth layers, Benjaminsen 1972).

Birth is thought to take place in late spring and summer (Benjaminsen 1972, Gowans 1999), following a gestation period of at least 12 months (based on figure in Benjaminsen 1972). Fetuses recorded from April-July were generally either newly conceived (0.3-0.7 m) or close to parturition (2.4-3.3 m), but the presence of intermediate fetus lengths may indicate some breeding year round (based on figure in Benjaminsen 1972). Christensen

(1973) interpreted the 1:1 ratio of pregnant to lactating females to indicate a 2-year breeding cycle. The largest fetuses recorded were 3.6 m (12 feet) in length (Benjaminsen 1972) and Benjaminsen (1972) suggested that the mean length at birth is approximately 3 m. Mead (1989b), however, suggested that since the smallest recorded calf was 3.5 m (Fraser 1934), the length at birth is more likely 3.5 m. However, this may vary for different populations as calves seen in the Gully appear to be smaller than this (Gowans 1999).

Genetics

There is some suggestion that the populations identified in the North Atlantic (the Gully, Labrador, Iceland, Faroes, Spitzbergen and Norway) may represent separate stocks (NAMMCO 1993). Evidence that the Gully population may be genetically distinct from the nearest population centre off the coast of Labrador is primarily based on the smaller (ca. 0.7 m) size of the Gully animals (Whitehead et al. 1997b), although there also appear to be differences in mitochondrial DNA haplotype frequencies between the two populations (M.L. Dalebout, pers. comm.).

THE GULLY

The Gully is the largest submarine canyon off the coast of eastern Canada (Figure 1.4). The canyon is approximately 40 km long (from the 500 m contour to the 2000 m contour down the centre of the canyon) and 5-10 km across (at the 500 m contour). The Gully has recently been proposed by the Department of Fisheries and Oceans (DFO) as a pilot marine protected area (MPA), the first in eastern Canada. The impetus for this is primarily the increasing interest in oil and gas production on the Scotian Shelf, and the attendant threats of disturbance, chemical and acoustic pollution to bottlenose whales.

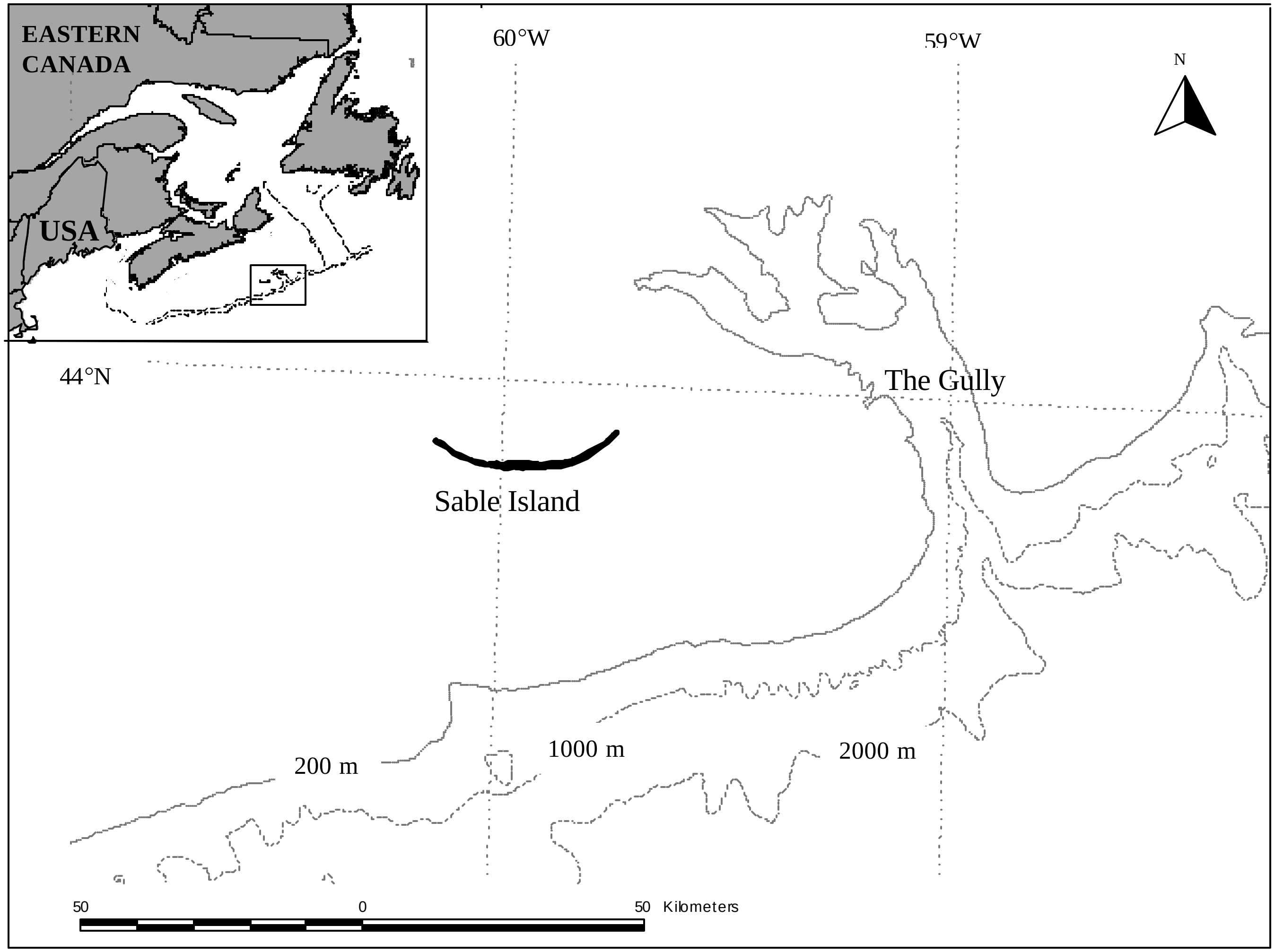

Figure 1.4. Map showing location of the Gully relative to eastern Canada.

Prior to its designation, a thorough review of the geology, physical, chemical and biological oceanography together with the vertebrate and invertebrate biomass using the Gully was commissioned (Harrison and Fenton 1998). This showed in general that much of the fauna and sub-surface biomass within the Gully was not significantly different in diversity or abundance to that found elsewhere on the Scotian Shelf, but that the geological structure of the region is unique and the diversity and abundance of cetaceans and finfish in the region are higher than elsewhere on the Scotian Shelf.

In particular, the area appears to be of special significance for bottlenose whales (Whitehead et al. 1997a). The area was known to whalers as a hotspot for bottlenose whales (Reeves et al. 1993), and bottlenose whales are still reliably found in the Gully and have been studied there since 1988 (Whitehead et al. 1997a, b; Figure 1.4). The population of bottlenose whales which uses the Gully, calculated from photo-resightings data between 1988 and 1997, numbers approximately 130 animals (95 % c.i. 100 – 170) (Gowans 1999). Over each summer, individuals appear to repeatedly enter and leave the Gully, spending on average 10 days (s.e. 5 days) in the Gully and 37 days (s.e. 26 days) outside the canyon (Gowans 1999). Where whales go outside the Gully is unknown, but the population differences between the area and Labrador (seen Genetics above) suggest that this may be a largely separate population inhabiting the Gully and surrounding area with little or no genetic mixing with other populations. At any one time there appear to be approximately one-third of the population (43 ± s.e. 10 animals) in the Gully (Gowans 1999).

THE INTER-RELATIONSHIP OF ECOLOGICAL PARAMETERS

The question most apparent from the review of biological features of the Gully concerns why the canyon, which is not obviously more productive than nearby ocean areas (Harrison and Fenton 1998), is favoured by bottlenose whales. Habitat choice is usually dependent on a trade-off between the benefit of resource gain and the threat of predation (Lima and Dill 1990). However bottlenose whales do not appear to have a particularly high predation pressure (see Predators), and sharks, which are thought to be their primary predators, are small and rarely seen in the Gully (pers. obs.). Although animals require a variety of resources for survival and to propagate, the paramount resource (without which, finding mates becomes superfluous) is food. To paraphrase Hutchinson (1959): in any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature.

This question of why bottlenose whales favour the Gully essentially involves determining both their habitat use and their foraging ecology. In order to answer this, I will use a multi-disciplinary approach such that each chapter of this thesis represents a stand-alone investigation into a different aspect of bottlenose whale ecology and behaviour (Figure 1.5). I will first discuss bottlenose whale diet by comparing results from stomach content analyses with those from analysis of biopsy samples from whales in the Gully. I will then use other behavioural characteristics to make inferences about the habitat characteristics of prey within the Gully. The study of bottlenose whale distribution in relation to habitat characteristics shows which features of the canyon appear most important to these whales and how these change with space and time. The study of bottlenose whale movements will show how individuals use the Gully both vertically, in terms of foraging depth, and horizontally, in terms of the spatial distribution and temporal use of the area. These will in turn help to define the searching strategies used to find their prey, and the spatial and temporal scales of foraging. Lastly, documentation of the acoustic repertoire used by bottlenose whales will allow further investigation of their foraging behaviour. These aspects of species ecology are inter-related and the study of each can be used in conjunction with the others to identify characteristics of the Gully and its ecosystem that are important to these whales.

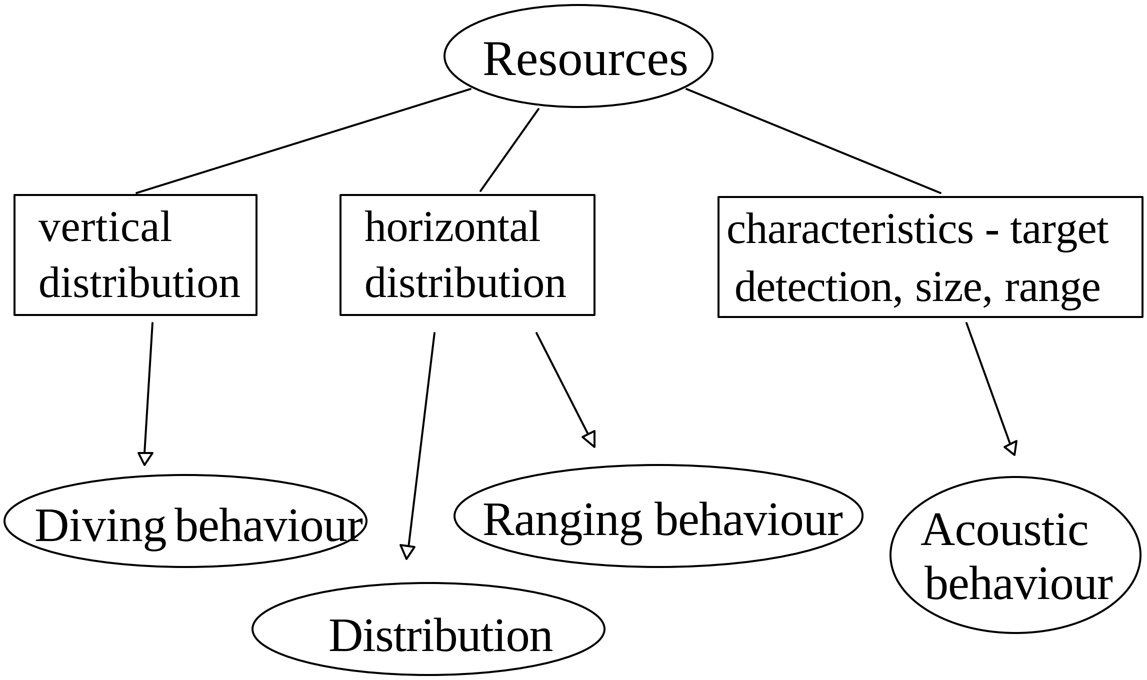

Figure 1.5. Schematic illustrating the effects of the distribution and characteristics of resources on the behaviour and distribution of a population of whales.

CHAPTER TWO

Diet and foraging ecology of northern bottlenose whales in the Gully: fatty acid and stable isotope analyses of biopsy samples

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ABSTRACT

The diet of bottlenose whales (*Hyperoodon ampullatus*) in the Gully, a submarine canyon off the coast of eastern Canada, was examined using fatty acid and stable isotope analysis of blubber and skin from biopsy samples and compared to results from stomach contents. Stomachs of two northern bottlenose whales, which stranded in Nova Scotia and Quebec, contained a high proportion of the squid *Gonatus steenstrupi*. Biopsy samples were collected from free-ranging bottlenose whales in the Gully during 1997: skin samples (n=17) were analysed for stable isotopes and blubber samples (n=16) for fatty acids. Blubber samples from stranded animals (n=3) were analysed to determine fatty acid stratification. These results were compared with those obtained from samples of adult (n=3) and juvenile (n=6) *Gonatus fabricii* from the Norwegian Sea. Adult squid showed significant differences from juvenile squid in both stable isotope and fatty acid composition. Blubber-biopsy fatty acid composition was similar to that of adult *Gonatus*, but was significantly different from that of juvenile *Gonatus* or other recorded prey species. Isotopic nitrogen values suggest that bottlenose whales (mean 15.3 ‰ δ^{15}N) and adult *Gonatus* appear to occupy a fairly high trophic level. The fatty acid composition of adult *G. fabricii* was unlike that previously recorded for other squid species, and its fat content was greater than that found for many other squid species. Results of fatty acid and stable isotope analysis suggest that *Gonatus* could form a major part of bottlenose whale diet in the Gully. However it is not known whether the fatty acid composition of *G. steenstrupi* from the western North Atlantic is similar to that of *G. fabricii* from the Norwegian Sea and thus conclusions remain limited.

INTRODUCTION

Knowledge of the diet of any species is fundamental to understanding its ecology. Among cetaceans there is a great deal of variation in patterns of feeding ecology: although mysticetes can tolerate long periods without food (during migration and breeding), odontocetes appear to require food year-round. The high-use of and apparent reliance on the Gully region by bottlenose whales (Chapter 1) is assumed to be a result of the food supply found there, but the prey of northern bottlenose whales in the Gully is essentially unknown. The first step in defining the ecological role of northern bottlenose whales in the Gully will therefore be to identify their primary prey.

Previously published data on the diet of northern bottlenose whales have come primarily from the northern North Atlantic and from either hunted or beach-cast animals. Ohlin (1893) reported that bottlenose whales are teuthophagous, feeding primarily on ‘cuttle-fishes’, but that the stomachs of some specimens contained an abundance of herring (*Clupea harengis*). There is wide agreement throughout the literature that the primary squid species found in the diet is *Gonatus fabricii* (Benjaminsen and Christensen 1979, Clarke and Kristensen 1980, Lick and Piatkowski 1998). However, there is some evidence of dietary differences between different populations of bottlenose whales. Benjaminsen and Christensen (1979) examined the stomach contents of bottlenose whales caught off Iceland (n=46) and Labrador (n=108). *Gonatus fabricii* was the major dietary component in both locations, but 50 % of whales off Labrador also contained fish remains, while only 10 % of those off Iceland had eaten any fish. Fish species identified in the stomachs of Icelandic whales included cusk (*Brosmius brosme*), lumpsucker (*Cyclopterus lumpus*), and redfish (*Sebastes* sp.). Stomachs of Labrador whales contained Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* sp.), rabbit-fish (*Chimaera monstrosa*), piked dogfish (*Squalus acanthias*), ling (*Molva molva*), and skate (*Raja* sp.). One Labrador whale also had deep-sea prawns (*Pandalus*) in its stomach. Three stranded bottlenose whales in the North Atlantic (one in the Faroe Islands and one in Jutland, Denmark, Clarke and Kristensen 1980; and one in Hiddensee Island in the Baltic Sea, Lick and Piatkowski 1998) contained predominately (or only) remains of *Gonatus fabricii* in their stomachs.

There are no published data on the diet of bottlenose whales from the Gully. However, some information is available from recent strandings of bottlenose whales in maritime Canada. An immature male bottlenose whale stranded in Sydney, Nova Scotia, on 19 October 1992, after being observed in the harbour for about 11 days prior to the stranding. The stomach was found to contain predominately beaks of the genus *Gonatus*, believed to be *Gonatus steenstrupi* (S.C. Smith, unpublished data; Table 2.1). The stomach contents of another immature male bottlenose whale, which stranded at Sept-Iles in the Gulf of St. Lawrence in September 1997, also contained predominately *G. steenstrupi* (L. Measures and S.C. Smith, unpublished data; Table 2.1). Of the squid species identified from these beaks, *Gonatus* is also the largest in mass (c.f. Clarke and Kristensen 1980). It is unknown how long squid beaks are retained in the stomach. Lick and Piatkowski (1998) suggested they may be retained for at least 3 days. Clarke and Kristensen (1980) suggested that these whales probably eat 4 % of their body weight each day, i.e., approximately 600 squid.

Table 2.1. Results of stomach content analyses of two northern bottlenose whales stranded in maritime Canada. Number of lower beaks of each species is shown; the percentage that this represents is shown in parentheses.

Squid	Sydney[1]	Sept-Iles[2]
Gonatus steenstrupi	720 (55)	1358 (87.2)
Taonius pavo	328 (25)	75 (4.8)
Teuthowenia sp.	223 (17)	
Histioteuthis reversa		116 (7.5)
Histioteuthis dofleini		5 (0.3)
Histioteuthis heteropsis		1 (0.1)
Histioteuthis sp.	11 (1)	
Chiroteuthis spp.	20 (1.5)	
Alloposus mollis	7 (0.5)	2 (0.1)
Total lower beaks	1309	1557
Total upper beaks	2533	3474

[1] immature male bottlenose whale, S.C. Smith, unpublished data.
[2] immature male bottlenose whale, L. Measures and S.C. Smith, unpublished data.

The general picture arising from these analyses suggests that the primary prey of bottlenose whales is either *Gonatus fabricii* or *G. steenstrupi* depending on geographic location. *Gonatus steenstrupi* was only recently distinguished as a separate species from *G. fabricii* (Kristensen 1981). Both species are found across the North Atlantic, although *Gonatus steenstrupi* has the more southern distribution of the two, and appears to be the more likely inhabitant at the latitude of the Gully (Kristensen 1981). Most *Gonatus* sampled near the Gully were not differentiated to species (Dawe and Stephen 1988).

A problem with dietary studies based on stomach contents of stranded bottlenose whales from various locations is that they may not accurately reflect the normal diet of whales in the Gully. A potential technique for investigating diet of living animals is to collect fecal samples (c.f. sperm whales *Physeter macrocephalus*, Smith 1992). However, despite considerable efforts, we have been unable to collect fecal samples from bottlenose whales in the Gully. Furthermore, stomach content or fecal analyses provide detail on only the most recent few meals and may be biased due to the increased likelihood of certain, less digestible dietary items (such as fish otoliths and squid beaks) being retained (Bigg and Fawcett 1985, Smith 1992, Gannon et al. 1998). Recently, two new techniques (fatty acid signature analysis and stable isotope analysis) have been used to analyse the dietary components of blubber and skin from biopsy samples (Iverson 1993, Michener and Schell 1994, Iverson et al. 1997). They are based on the principle that the relative amounts of fatty acids and the composition of stable isotopes from an animal's diet will be reflected in its tissues (Hobson 1990, Wada et al. 1991, Iverson 1993). One benefit of these analyses is their ability to provide information about longer-term diet.

Some specific fatty acids are generally conserved through the food chain so that their signatures will reflect those of the prey species (Iverson 1993). Marine prey species tend to have distinct fatty acid signatures, such that analyses can provide detailed information about the diet of marine predators (Kirsch et al. 1998). In marine mammals, the blubber layer is the most important site of fat storage and can be used to assess differences in diets of individuals (Iverson et al. 1997). Biopsy sampling of live cetaceans is widely used to collect skin and blubber samples (International Whaling Commission 1989).

However, such biopsies sample only the outer 1.5-2.5 cm of the blubber layer (often less than one quarter of the blubber thickness). In several cetaceans, the most metabolically active part of the blubber, where most active deposition and withdrawal of lipids likely takes place, appears to be the middle or inner layers adjacent to the muscle (Lockyer et al. 1984, Koopman et al. 1996). Therefore, to correctly interpret the fatty acid signatures observed in the outer blubber of bottlenose whales, it is first necessary to investigate the degree of stratification of fatty acids in the blubber layer. The extent of stratification can also be assessed by investigation of lipid class composition across the blubber layer.

Carbon and nitrogen both occur naturally in two stable isotopic forms: ^{13}C / ^{12}C and ^{15}N / ^{14}N. Many chemical and physical processes cause either an enrichment or depletion of the heavier isotope (Michener and Schell 1994). The usefulness of the stable isotope approach to foraging ecology is the stepwise enrichment in isotopes at each trophic level (Hobson 1990). This enrichment is about 3 ‰ for ^{15}N at each trophic level; analysis of ^{15}N differences between species therefore allows inferences about foodweb structure (Michener and Schell 1994). Trophic enrichment of ^{13}C is generally much lower (approximately 1 ‰); ^{13}C is generally more useful in assessing differences between ecosystems, e.g., inshore vs. offshore, benthic vs. pelagic, fresh water vs. marine (McConnaughey and McRoy 1979, Dunton et al. 1989, Ramsay and Hobson 1991, Michener and Schell 1994, Smith et al. 1996). The stable isotope compositions of different tissues may reflect different durations of dietary history: blood has the fastest turnover rate; skin has a faster turnover rate than muscle which in turn often has a faster turnover rate than blubber (Tieszen et al. 1983). Each of these will therefore in turn provide information on increasingly long-term dietary habits (Tieszen 1978, Owens 1987). Cetacean stable isotopes have previously been analysed primarily from dead animals, but it has recently been demonstrated that small amounts of skin from biopsies can be used successfully to provide dietary information (Todd et al. 1997).

Both fatty acid signature analysis and stable isotope analysis provide information about differences between individuals and populations, but can only be interpreted with regard to diet by comparisons with the results from their prey. To use the results from bottlenose whales to assess potential diet, fatty acid and stable isotope analyses need therefore also be conducted on samples of all suspected prey items (including the squid *Gonatus*). Deep-water sampling in canyon areas is methodologically problematic and was far beyond the scope of this study. However, limited data from the expected primary prey items can be used to make some inferences about bottlenose whale diet.

The aims of this study were therefore: (1) to investigate whether fatty acid results from blubber biopsies of bottlenose whales can be used to infer aspects of diet, and (2) to assess, using stable isotope analysis and fatty acid signature analysis, whether the squid *Gonatus* is potentially a major dietary component of bottlenose whales in the Gully.

METHODS

Sample collection

Full blubber samples, necessary to compare fatty acid differences across the blubber layer, were obtained from three whales which had stranded in eastern Canada (1992-1997; Table 2.2). All stranded whales were assessed as in reasonable body condition at the time of the stranding. The cause of death was not established for either of the juveniles; the calf was thought to have died following the loss of its mother.

Table 2.2. Stranded animals from which full blubber samples were used for analysis of blubber stratification. Percentage of fatty acid 14:1n-5 is shown for comparison with whale length.

Code	Date	Location	Sex/Age	Type	Length (m)	Age† (yr)	Outer blubber 14:1n-5 (%)
Ha-01-92	8-Oct-92	Sydney, NS [2]	immature male	live	6	~2	7.07
Ha-02-94	6-Nov-94	Tadoussac, QE [1]	juvenile male (suckling)	live	4.5	~1	9.65
Ha-97-01	8-Sept-97	Sept-Iles, QE [3]	immature male	live	6.6*	~3	4.75

Samples collected by: [1]Canadian Cooperative Wildlife Health Centre, College of Veterinary Medicine, University of Montreal, QE, Canada; [2] Nova Scotia Stranding Network, Halifax, NS, Canada; [3] Department of Fisheries and Oceans, Mont-Joli, QE, Canada.
† Approximate age estimated from length (from growth curve in Christensen 1973)
*measured curvilinearly, so length is slightly overestimated.

Full blubber cores were taken from the stranded animals and frozen in aluminium foil. A small (0.5 x 0.5 cm) full blubber core was then taken from each of these and was divided into inner (next to the muscle layer), middle, and outer (next to the skin) samples.

Biopsy samples (n=18) were collected from free-ranging northern bottlenose whales in the Gully (44°N, 59°W) on 16 July, 12-14 August and 16 August 1997. The biopsy dart was made up of a crossbow bolt to which a hollow, 2.5 cm long, 0.6 cm diameter solvent-cleaned stainless steel biopsy tip was attached. This tip contained a barbed dental brooch to aid in retention of the sample (c.f. Barrett-Lennard et al. 1996). A 12-m auxiliary sailing vessel was maneuvered alongside a whale at distances ranging from 5 to 15 m, and the dart was fired from a 67-kg draw crossbow (Barnett Wildcat XL) at the mid-lateral region near the dorsal fin of the whale. A stop collar, attached to the tip of the bolt, prevented penetration deeper than the biopsy tip and caused the bolt to rebound upon impact with the whale. The darts were designed to float and were collected using a dip net. Reactions to this procedure are discussed Appendix 1. Subsamples of blubber collected for fatty acid analysis were approximately 1.5 cm length x 0.2 cm diameter; subsamples of skin for stable isotope analysis were approximately 0.2 cm length x 0.4 cm diameter.

In the field we attempted not to sample the same animal twice (by keeping track of the scar characteristics of biopsied whales), and whenever possible a photographic record was kept of each biopsied whale. However, only 10 of the 17 animals sampled for fatty acids and stable isotopes were identified photographically (S. Gowans, unpublished data). Therefore, while I am confident that no animal was sampled twice within a period of a few days, there is a small chance that an animal sampled in July may have been sampled again in August. The sex of the biopsied animals was later identified from skin samples (M.L. Dalebout, unpublished data).

Samples of the expected prey species *Gonatus steenstrupi* were unavailable but samples of *Gonatus fabricii* were provided by Dr. H. Bjørke (Institute of Marine Research, Bergen, Norway). These were collected in the Norwegian Sea in July 1996 at depths of approximately 1100 m (see Bjørke et al. 1997) and were analysed for comparative purposes.

Fatty acid analysis

Three sets of analyses for fatty acid signatures were conducted: (1) using full blubber cores of stranded animals; (2) using outer blubber layer samples from live animals in the Gully; and (3) using *Gonatus* squid samples.

Full blubber cores from stranded bottlenose whales (Table 2.2) were divided into inner, middle and outer layers, the inner layer being that closest to the muscle, and the outer layer that closest to the skin. Blubber subsamples from biopsies were placed in solvent-rinsed glass vials filled with 2:1 chloroform: methanol with 0.01 % BHT (butylated hydroxytoluene). Homogenized samples of three adult *Gonatus* squid, and four juvenile squid were also subsampled and placed in solvent.

Fatty acid analysis of all samples was carried out by Dr. S.J. Iverson (Dalhousie University, Canada) following methods described in Iverson et al. (1997). In brief, lipids were extracted using a modified Folch extraction (Folch et al. 1957). Fatty acid methyl esters were prepared directly from the pure extracted lipid and then extracted into hexane. Analysis of fatty acid methyl esters was carried out using temperature-programmed gas liquid chromatography. Identifications of fatty acids and isomers were determined from various sources (Iverson et al. 1997). Individual fatty acids are expressed as weight percent of total fatty acids and are designated by shorthand IUPAC nomenclature of carbon chain length: number of double bonds and location (n-x) of the double bond nearest the terminal methyl group. Lipids from two blubber samples were also converted to fatty acid butyl esters to permit detection of isovaleric acid (for exact methods see Koopman et al. 1996), as this component can represent up to 27 % of total fatty acids in the outer blubber of some cetacean species (Koopman et al. 1996).

Lipid class composition of inner, middle and outer blubber from the stranded animals was analysed by H.N. Koopman (Duke University, USA), using Iatroscan (Quantitative thin layer chromatography with flame ionization detection, TLC-FID, see Ackman and Heras 1997 for details of the technique). Total extracted lipids from the Folch procedure were suspended in hexane at 15 mg/ml. One µl of sample was spotted onto each of three rods (Chromarod III – silica gel) and developed in a solvent system of 96:4:1 hexane:ethyl acetate:formic acid for 48 min. Following incubation, rods were dried and then analyzed by TLC-FID Iatroscan. Lipid class concentrations were calculated using standard curves, and converted into percentages of total lipid.

The fatty acid 14:1n-5 is thought to be synthesised and deposited in the outer blubber layer of some cetaceans as the animal ages (biopsied right whales (*Eubalaena glacialis*), S.J. Iverson, unpublished data; harbour porpoise (*Phocoena phocoena*), H.N. Koopman, unpublished data). However, it has also been found in foetal blubber from biosynthesis (Iverson et al. 1995). The proportion of this fatty acid was therefore noted in conjunction with the length and approximate age of the stranded animals (Table 2.2) to investigate any potential relationship.

Since results of fatty acid composition are presented as percentages, all data were arcsine squareroot transformed and analysed using MANOVA tests. Since my interest is in dietary interpretation of these results, the fatty acids selected for statistical comparison were those known to be of dietary origin (Iverson 1993; S.J. Iverson, pers. comm.), and/or present in fairly large quantities (>1 %) in either bottlenose whale or *Gonatus* samples (16:0, 18:0, 18:1n-9, 20:1n-11, 20:1n-9, 20:5n-3, 22:1n-11, 22:1n-9 and 22:6n-3 – hereafter referred to as "major fatty acids").

As a simplified means of viewing the similarities in fatty acid proportions between samples, a Pearson correlation coefficient was calculated for the major fatty acid proportions between all samples, and the mean correlation coefficient was calculated for each comparison type. This allows the similarity between samples of one type (e.g., adult *Gonatus*) to be viewed in conjunction with the similarity between samples of two different types (e.g., adult *Gonatus* and female bottlenose whales). Fatty acid compositions of two other potential prey species: herring (n=53) and redfish (n=19) from the Scotian Shelf (Iverson, Bowen and Ackman, unpublished data) were included for reference in these comparisons. This method provides an index of the similarity between one type of prey and another but is not suitable for formal hypothesis testing. To further explore the similarities and differences between samples, each sample was plotted for the first two principal components of the transformed major fatty acids listed above.

Stable isotope analysis

Skin samples were subsampled from the biopsies, wrapped in aluminium foil and placed in a liquid nitrogen-filled dry shipper. Analysis of these samples for stable isotopes of carbon and nitrogen was carried out by Dr. P. Ostrom (Michigan State University, USA). Samples were lipid extracted with an azeotropic mixture of chloroform and methanol using Soxhlet extraction and analysed using a Carlo Erba elemental analyser interfaced to a Prism (Micromass) mass spectrometer, following methods described in Todd et al. (1997). Homogenized samples of three adult *Gonatus* squid and whole samples of two juvenile squid were also analysed using the same procedure.

Heavier isotope concentrations are referred to as a ratio in δ notation in parts per thousand noted (‰), determined from: δX (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$. The carbon stable isotope ratios are expressed relative to the internationally recognised calcium carbonate standard known as PCB; the nitrogen stable isotope ratios are expressed relative to atmospheric nitrogen.

RESULTS

Bottlenose whale lipids and fatty acids

Bottlenose whale blubber lipids were dominated by wax esters throughout the blubber layer. Triglycerides occurred in small amounts in the middle layer, and slightly higher amounts in the outer layer (Table 2.3). Some differences in fatty acid composition were apparent between inner, middle and outer blubber layers (Figure 2.1a; Table 2.4). However, the small sample sizes (3 animals and 3 blubber locations) render statistical comparison of fatty acid composition between sites problematic.

Table 2.3. Mean lipid class composition of bottlenose whale blubber (n=3)

Blubber layer	Wax esters (%)	Triglycerides (%)	Free fatty alcohol (%)	Phospholipid (%)
inner	96.02	0.00	3.77	0.21
middle	92.70	6.13	1.00	0.18
outer	85.82	14.18	0.00	0.00

Table 2.4. Summary of fatty acid composition in bottlenose whales and *Gonatus* samples (mean (s.d.) are shown).

	Strandings			**Biopsies***	***Gonatus***	
Fatty Acids	inner n=3	middle n=3	outer n=3	n=16	Adult n=3	Juvenile n=4
8:0	0.00±0.00	0.00±.0.00	0.00±0.00	-	0.00±0.00	0.00±0.01
10:0	0.03±0.01	0.05±0.03	0.06±0.03	0.04±0.02	1.17±0.72	0.15±0.05
12:0	0.58±0.16	0.66±0.21	0.73±0.25	0.66±0.29	0.04±0.00	0.05±0.01
13:0	0.03±0.00	0.03±0.00	0.03±0.01	0.04±0.02	0.00±0.00	0.01±0.01
Iso14	0.12±0.04	0.18±0.05	0.25±0.05	0.11±0.04	0.01±0.01	0.05±0.03
14:0	5.42±1.15	5.08±1.65	4.83±1.63	3.20±0.32	0.88±0.90	2.99±1.04
Iso15	0.11±0.05	0.11±0.07	0.09±0.03	0.05±0.02	0.03±0.05	0.07±0.05
Anti15	0.05±0.01	0.05±0.00	0.05±0.01	0.03±0.01	0.02±0.03	0.04±0.02
15:0	0.10±0.02	0.11±0.01	0.10±0.02	-	0.04±0.06	0.30±0.03
Iso16	0.23±0.26	0.25±0.20	0.23±0.17	0.07±0.03	0.06±0.02	0.64±0.17
16:0	2.97±0.18	3.32±1.50	3.42±1.64	2.59±0.49	3.07±0.30	15.97±1.21
7Me16:0	0.10±0.03	0.15±0.01	0.17±0.03	0.16±0.02	0.08±0.06	0.31±0.04
Iso17	0.06±0.02	0.07±0.01	0.07±0.01	0.12±0.04	0.08±0.07	0.04±0.02
17:0	0.05±0.01	0.04±0.02	0.04±0.02	0.02±0.01	0.10±0.02	0.25±0.07
18:0	0.91±0.06	0.70±0.17	0.68±0.22	0.60±0.09	0.99±0.22	1.80±0.29
20:0	0.08±0.01	0.06±0.02	0.05±0.00	-	0.12±0.04	0.17±0.01
Total saturates	10.86 ±1.56	10.78±3.85	10.86±3.55	7.69±1.03	6.66±1.76	22.81±0.97
14:1n-9	0.17±0.01	0.17±0.03	0.16±0.04	0.44±0.26	0.19±0.06	0.10±0.04
14:1n-7	0.17±0.01	0.24±0.02	0.28±0.04	0.42±0.24	0.01±0.01	0.03±0.01
14:1n-5	2.38±0.61	4.35±1.34	7.16±2.45	3.57±0.98	0.04±0.06	0.14±0.02
15:1n-8	0.02±0.02	0.02±0.01	0.02±0.01	0.05±0.01	0.00±0.01	0.00±0.00
15:1n-6	0.03±0.01	0.04±0.01	0.05±0.01	0.07±0.01	0.01±0.01	0.00±0.00
16:1n-11	0.47±0.17	0.65±0.21	0.58±0.15	1.19±0.40	0.17±0.08	0.26±0.04
16:1n-9	0.52±0.12	0.67±0.10	0.61±0.02	1.21±0.73	0.16±0.02	0.28±0.07
16:1n-7	13.19±1.53	18.04±0.95	19.87±1.86	20.27±1.81	1.72±1.81	2.70±1.47
16:1n-5	0.19±0.19	0.38±0.50	0.22±0.24	0.04±0.02	0.08±0.05	0.05±0.01
17:1	0.22±0.03	0.27±0.03	0.25±0.03	0.23±0.12	0.12±0.09	0.18±0.06
18:1n-13	0.07±0.03	0.08±0.01	0.07±0.01	0.06±0.03	0.00±0.00	0.09±0.05
18:1n-11	2.89±0.96	2.71±0.51	2.26±0.54	5.15±1.71	1.75±0.77	0.43±0.04
18:1n-9	19.55±1.71	19.05±2.28	17.36±1.15	17.67±1.81	27.58±11.45	9.22±2.62

18:1n-7	1.74±0.50	2.24±0.24	2.14±0.14	2.79±0.38	2.89±0.50	2.71±1.46
18:1n-5	0.22±0.03	0.21±0.02	0.21±0.01	0.21±0.06	0.29±0.11	0.54±0.11
20:1n-11	13.19±3.68	7.28±1.44	6.24±1.84	7.23±1.10	1.85±0.38	0.83±0.07
20:1n-9	17.95±2.13	13.71±2.06	12.91±2.83	13.50±2.72	17.66±1.33	7.09±1.21
20:1n-7	0.69±0.15	0.45±0.06	0.47±0.11	0.41±0.20	0.64±0.09	0.19±0.08
20:1n-5	0.15±0.21	0.16±0.20	0.11±0.15	0.00±0.00	-	-
22:1n-11	10.16±1.83	13.02±5.53	9.37±1.79	12.06±1.82	20.24±5.23	4.87±2.22
22:1n-9	1.80±0.36	1.79±0.73	1.23±0.29	1.57±0.20	2.11±0.57	0.81±0.03
22:1n-7	0.15±0.02	0.12±0.01	0.10±0.04	0.11±0.03	0.28±0.08	0.09±0.02
24:1n-9	0.07±0.03	0.08±0.06	0.04±0.04	0.04±0.05	0.43±0.06	0.03±0.02
Total mono unsaturates	85.97±1.79	85.73±6.74	81.69±3.47	88.29±2.94	78.20±3.17	30.61±8.56
16:2n-6	0.04±0.01	0.05±0.01	0.05±0.01	0.12±0.02	0.02±0.01	0.01±0.01
16:2n-4	0.34±0.04	0.29±0.02	0.28±0.01	0.23±0.07	0.53±0.25	0.13±0.05
16:3n-6	0.24±0.04	0.33±0.06	0.34±0.10	0.69±0.20	0.04±0.07	0.11±0.11
16:3n-4	0.03±0.02	0.06±0.01	0.05±0.01	0.07±0.11	0.00±0.00	0.03±0.05
16:3n-1	0.07±0.06	0.10±0.09	0.08±0.08	-	0.01±0.02	0.14±0.02
16:4n-3	0.29±0.47	0.34±0.55	0.23±0.36	-	0.06±0.01	0.20±0.05
16:4n-1	0.00±0.01	0.02±0.01	0.02±0.02	-	0.01±0.01	0.04±0.03
18:2d5,7	0.31±0.53	0.33±0.55	0.22±0.35	0.00±0.00	0.00±0.00	0.03±0.01
18:2n-7	0.03±0.01	0.03±0.03	0.05±0.02	0.02±0.03	0.01±0.02	0.04±0.06
18:2n-6	0.87±0.19	1.03±0.14	1.03±0.18	0.73±0.15	1.24±0.23	0.86±0.20
18:2n-4	0.02±0.02	0.04±0.00	0.04±0.00	0.09±0.02	0.03±0.02	0.05±0.02
18:3n-6	0.04±0.01	0.05±0.01	0.06±0.01	-	0.04±0.01	0.05±0.02
18:3n-4	0.11±0.00	0.12±0.01	0.11±0.01	-	0.07±0.01	0.02±0.02
18:3n-3	0.16±0.05	0.27±0.03	0.31±0.06	-	0.34±0.19	0.48±0.13
18:3n-1	0.00±0.00	0.00±0.00	0.01±0.01	-	0.11±0.05	0.03±0.04
18:4n-3	0.04±0.02	0.19±0.02	0.24±0.09	-	0.58±0.33	0.45±0.22
18:4n-1	0.02±0.02	0.07±0.01	0.08±0.03	-	0.08±0.01	0.05±0.01
20:2n-9	-	-	-	-	0.11±0.05	0.04±0.01
20:2n-6	0.18±0.06	0.22±0.03	0.26±0.03	0.06±0.07	1.52±0.69	0.69±0.06
20:3n-6	0.05±0.02	0.07±0.03	0.09±0.01	0.01±0.02	0.17±0.07	0.05±0.02
20:4n-6	0.08±0.05	0.19±0.06	0.32±0.01	0.12±0.11	0.33±0.08	0.74±0.10
20:3n-3	0.11±0.12	0.08±0.04	0.07±0.02	0.00±0.01	0.27±0.01	0.54±0.22
20:4n-3	0.17±0.08	0.31±0.07	0.38±0.10	0.15±0.12	0.59±0.09	0.29±0.08
20:5n-3	0.30±0.29	1.01±0.40	1.59±0.17	0.71±0.94	3.39±0.59	14.56±1.35
22:2n-6	0.06±0.03	0.03±0.01	0.05±0.03	0.00±0.00	0.00±0.00	0.00±0.00
21:5n-3	0.03±0.02	0.04±0.04	0.07±0.02	0.02±0.04	0.19±0.04	0.21±0.04
22:4n-6	0.04±0.02	0.02±0.01	0.03±0.02	0.00±0.01	0.02±0.03	0.03±0.02
22:5n-6	0.19±0.32	0.09±0.05	0.11±0.09	0.01±0.03	0.03±0.03	0.09±0.04
22:4n-3	0.13±0.12	0.11±0.17	0.02±0.01	0.00±0.00	0.02±0.02	0.01±0.02
22:5n-3	0.20±0.17	0.33±0.24	0.69±0.04	0.17±0.35	0.30±0.18	0.62±0.07
22:6n-3	0.22±0.12	0.55±0.30	0.70±0.12	0.22±0.54	5.02±1.28	25.98±7.31
Total poly unsaturates	4.35±0.24	7.53±1.17	6.35±0.91	3.42±2.34	15.11±1.39	46.55±8.03

*Certain fatty acids are missing from analysis of the biopsy samples since thin layer chromatography was not conducted resulting in inability to read certain fatty acid peaks.

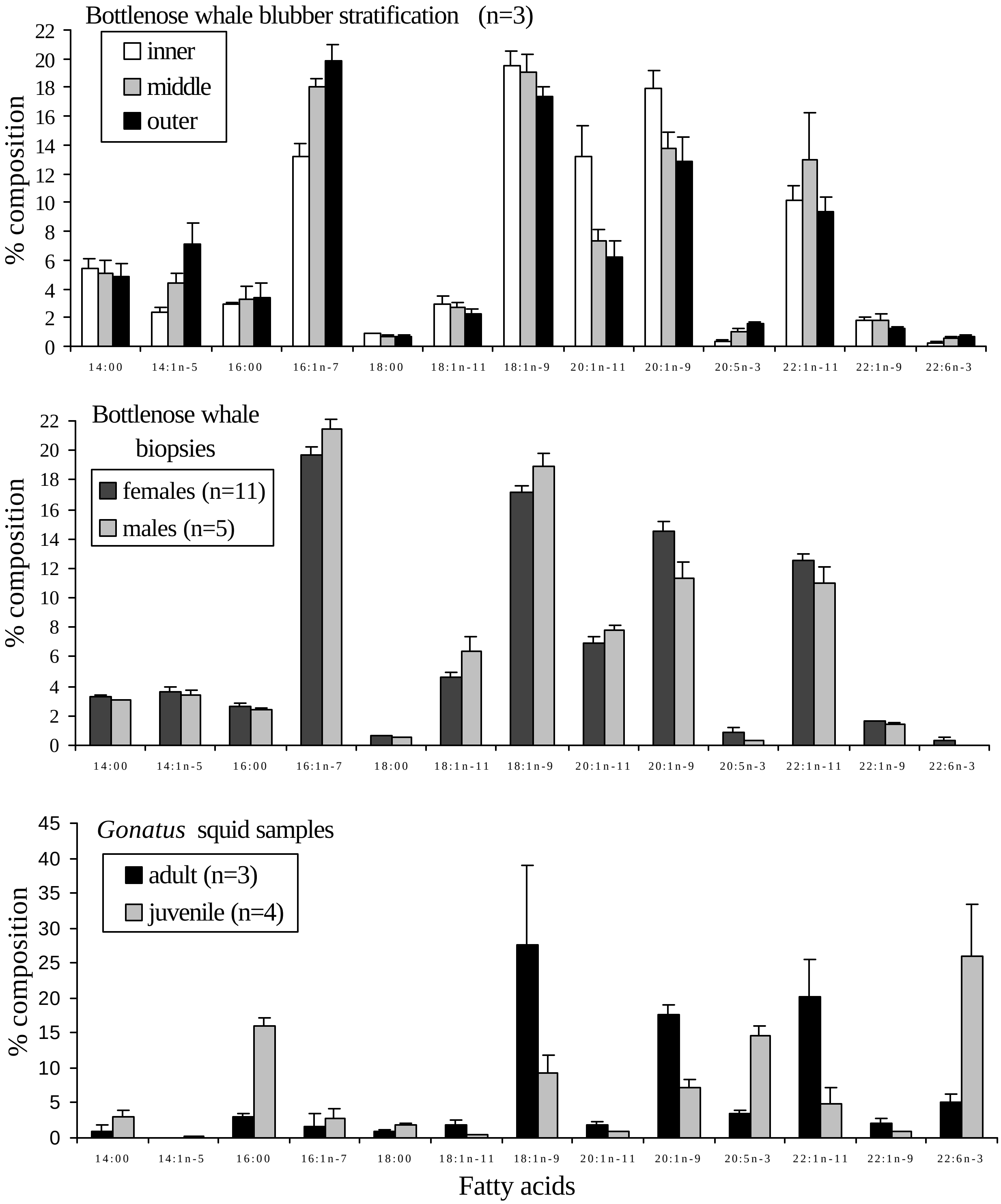

Figure 2.1. Percent composition of selected fatty acids (a) from the inner, middle and outer blubber layers of stranded northern bottlenose whales (n=3) sampled at a mid-lateral site below the dorsal fin, (b) from blubber biopsy samples of male and female free-ranging bottlenose whales, (c) from adult and juvenile *Gonatus fabricii*. (Standard error bars are shown.)

The trend toward increasing levels of 14:1n-5 with age found for other cetacean species is not clear in the stranded bottlenose whales sampled. In fact, the youngest (suckling) animal had the highest levels of 14:1n-5 (Table 2.2), which may reflect its proximity to birth. A larger sample of known age animals is needed to test this relationship further.

Eighteen biopsy samples were collected from bottlenose whales during June-August 1997. Of these, blubber from 16 samples was retained for fatty acid analysis and skin from 17 samples was retained for stable isotope analysis (Table 2.5). Unlike many other cetacean species (see Koopman et al. 1996), bottlenose whale blubber contained no isovaleric acid. The general fatty acid composition of the blubber biopsies was similar to that observed in the blubber fatty acids of stranded animals (Figure 2.1, Table 2.4). The proportions of major fatty acids from blubber biopsies were significantly different from those of the inner and middle blubber layers of stranded animals, but not from the outer layer (MANOVA: biopsies vs. inner F =22.1, $p < 0.001$; biopsies vs. middle F = 6.8, $p = 0.004$; biopsies vs. outer F = 1.9, $p = 0.182$). Although the lipid classes were stratified over the blubber layer, the differences in dietary fatty acids between blubber layers was much less than that recorded from other cetacean species (Figure 2.1a, Koopman et al. 1996) and suggests that biopsy samples (which contain only the outer blubber layer) may be used to infer some aspects of diet in this species.

Bottlenose whale stable isotopes

All biopsy samples had fairly similar levels of δ^{15}N ranging from 14.39 to 15.59 ‰ and of δ^{13}C ranging from –18.09 to –16.65 ‰ (Table 2.5, Figure 2.2). A problem with the first run of sample #18 (probably caused by a fault in the apparatus) gave unfeasibly high values of both δ^{13}C (-6.18 ‰) and δ^{15}N (40.21 ‰) but a second run of this sample gave reasonable results (shown in Table 2.5). Two samples (#3 and #13) were slightly anomalous for δ^{15}N and were therefore run a second time (Table 2.5). The small size of biopsy skin samples prohibited homogenization of samples, so the average value of these two runs was calculated to reflect the overall content of each sample. The overall means of biopsy sample stable isotopes were -17.38 ‰ δ^{13}C (s.e. 0.09, n=17) and 15.25 ‰ δ^{15}N (s.e. 0.08, n=17).

Table 2.5. Biopsy samples from northern bottlenose whales in the Gully showing known details for individual whales, stable isotope results and showing which samples were processed for fatty acid composition.

Sample	Date collected	ID	Year ID first seen	Sex	Stable isotopes		Fatty acid analysis
					$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	
3	16 July	1289	1990	f	-17.77	14.73	√
4	"	-	-	f	-17.45	15.19	√
5	"	-	-	f	-16.65	15.32	√
6	"	54	1988	f	-17.34	15.32	√
8	12 Aug	1000	1996	f	-17.15	15.12	√
9	"	1313	1997	f	-17.58	15.44	√
10	"	-	-	f	-17.36	15.03	-
11	13 Aug	1318	1997	f	-17.59	15.30	√
12	"	1315	1997	f	-17.24	15.04	√
13	"	619	1993	f	-17.19	14.39	√
14	14 Aug	-	-	f	-16.68	15.32	√
15	"	-	-	m	-17.29	15.59	√
16	"	480	1990	m	-17.74	15.59	√
17	16 Aug	1039	1996	m	-17.39	15.50	√
18	"	-	-	m	-17.06	15.51	√
19	"	1336	1997	f	-18.09	15.50	√
20	"	-	-	m	-17.86	15.39	√
Mean±s.e.					-17.38±0.09	15.25±0.08	

Bottlenose whale male-female differences

Male bottlenose whales had significantly higher levels of isotopic nitrogen than females (t-test, *p* = 0.002; males: 15.52 ± 0.04 ‰ $\delta^{15}N$, n=5; females 15.14 ± 0.09 ‰ $\delta^{15}N$, n=12; Figure 2.2). However there was no significant difference between levels of isotopic carbon between males and females (t-test, *p* = 0.514; males: -17.47 ± 0.33 ‰ $\delta^{13}C$, n=5; females: -17.34 ± 0.41 ‰ $\delta^{13}C$, n=12; Figure 2.2). There was also no significant difference between proportions of major fatty acids between males and females (MANOVA *p* = 0.321; Figure 2.1). However, k-means clustering into two groups based on major fatty acids divided the biopsy samples into groups according to sex with 87.5 % success: a group of five animals (four of which were male) and a group of 12 animals (11 of which were female). It appears therefore that there may be underlying dietary differences between male and female dietary fatty acids but that the sample sizes are too small to detect statistically significant differences.

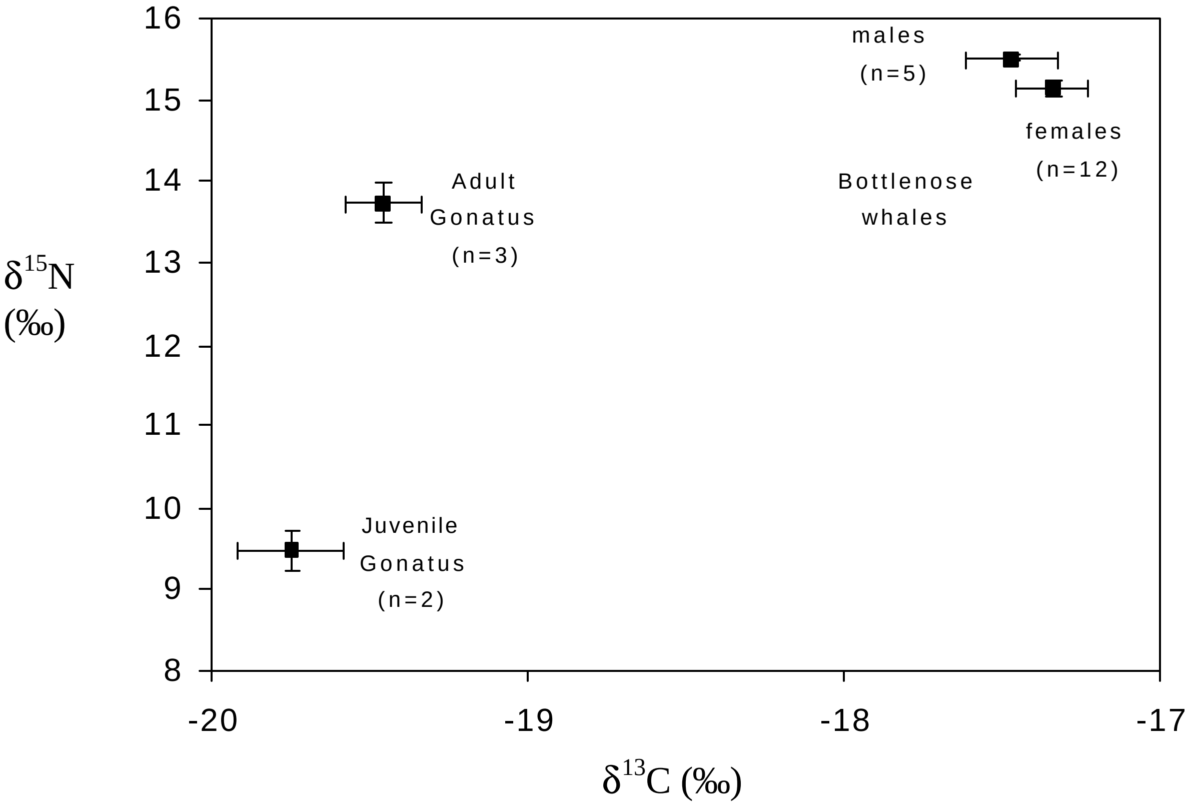

Figure 2.2. Carbon and nitrogen stable isotope ratios of bottlenose whale skin samples from the Gully and *Gonatus* squid samples collected in the Norwegian Sea. Bottlenose whale samples are shown separately for males and females. *Gonatus* squid samples are shown separately for adults and juveniles. (Standard error bars are shown.)

Gonatus fatty acids and stable isotopes

Nine samples of *Gonatus fabricii*, collected from the Norwegian Sea, were analysed. Three of these were adult squid: – two females (26.0 cm and 30.2 cm mantle lengths) and one male (21.5 cm mantle length). The small size of the six juvenile squid prevented subsampling so four were processed for fatty acids and two for stable isotopes (Table 2.6).

Table 2.6. *Gonatus* samples from the Norwegian Sea. Collection details (see Bjørke et al. 1997), stable isotope results, samples processed for fatty acid composition and lipid contents are shown.

Station and ID	Sex/Age	Mantle length (cm)	Weight (g)	Stable isotopes $\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Lipid (%)	Fatty acid analysis
276 1218-1	Adult female	26.0	179.12	-19.60	13.60	6.34	√
276 1216-2	Adult female	30.2	214.03	-19.22	14.23	7.26	√
280 0112-5	Adult male	21.5	83.28	-19.55	13.40	11.28	√
280 0112-6	Juvenile		3.94	-	-	5.73	√
280 0112-7	Juvenile		3.65	-	-	5.49	√
280 0112-8	Juvenile		n/a	-	-	3.40	√
280 0112-9	Juvenile		2.68	-	-	3.60	√
280 0112-10	Juvenile			-19.92	9.73	-	-
280 0112-11	Juvenile			-19.59	9.22	-	-

Juvenile *Gonatus* contained high levels of the dietary fatty acids 20:5n-3 and 22:6n-3, while adult *Gonatus* contained less of these but high levels of 20:1n-9 and 22:1n-11 (Figure 2.1c, Table 2.4).

The nitrogen isotope ratio of adult squid was significantly different from that for juvenile squid (t-test, $p = 0.002$; adults $\delta^{15}N$: mean 13.74 ‰, s.d. 0.43, n=3; juveniles $\delta^{15}N$: mean 9.47 ‰, s.d. 0.36, n=2; Figure 2.1, Table 2.6). The carbon isotope ratio of adult squid was not significantly different from that of juvenile squid (t-test, $p = 0.285$; Figure 2.2).

Comparison of fatty acids in *Gonatus* to those in bottlenose whale biopsies

Biopsy sample fatty acid signatures from bottlenose whales were different from those recorded for both adult and juvenile squid samples but were much more similar to adult squid than to juvenile squid (Figure 2.1, Table 2.4). When the fatty acid composition of each sample was correlated with that of every other sample, the mean correlation between bottlenose whale biopsies and adult *Gonatus* samples was fairly strong, whereas that between biopsies and juvenile *Gonatus* samples was negative (Table 2.7). Mean correlations between whale biopsies and the other potential prey, herring and redfish, were much weaker than those between whale biopsies and adult *Gonatus* (Table 2.7, Figure 2.1, Figure 2.3). Similarly a plot of all samples against the first two principal components of transformed major fatty acids shows the close similarity between bottlenose whale fatty acids and those of the two female *Gonatus* samples. The male *Gonatus* sample was at some distance from whale samples, but since only one adult male was sampled, this may be anomalous (Figure 2.4).

The differences in stable isotope results for bottlenose whale biopsies and *Gonatus* samples are shown in Figure 2.2. Bottlenose whales and adult *Gonatus* show a difference of approximately 1.5 ‰ $\delta^{15}N$ and 2.1 ‰ $\delta^{13}C$, while bottlenose whales and juvenile *Gonatus* show a difference of approximately 5.8 ‰ $\delta^{15}N$ and 2.4 ‰ $\delta^{13}C$.

Table 2.7. Mean correlation coefficients between samples. The fatty acid compostion of each sample was correlated with that of every other sample. The average correlation coefficient is presented for comparisons of each sample type to every other sample type (including comparisons between samples within each type, e.g. inner blubber of one whale with inner blubber of another whale). Values give an index of similarity between samples.

		Stranded samples			Biopsies		*Gonatus*			Other prey	
		inner (n=3)	middle (n=3)	outer (n=3)	female (n=11)	male (n=5)	adult female (n=2)	adult male (n=1)	juvenile (n=4)	herring (n=53)	redfish (n=19)
Stranded samples	inner (n=3)	0.953									
	middle (n=3)	0.899	0.907								
	outer (n=3)	0.924	0.946	0.959							
Biopsies	female (n=11)	0.925	0.951	0.957	0.971						
	male (n=5)	0.917	0.944	0.953	0.949	0.956					
Gonatus	female (n=2)	0.780	0.898	0.919	0.890	0.902	0.998				
	male (n=1)	0.606	0.746	0.703	0.789	0.689	0.731				
	juvenile (n=4)	-0.290	-0.265	-0.208	-0.225	-0.233	0.005	-0.026	0.921		
Other prey spp.	*herring (n=53)	0.050	0.141	0.203	0.382	0.146	0.289	0.522	0.574	0.720	
	*redfish (n=19)	0.229	0.318	0.375	0.397	0.314	0.484	0.646	0.543	0.743	0.716

* Iverson, Bowen and Ackman, unpublished data.

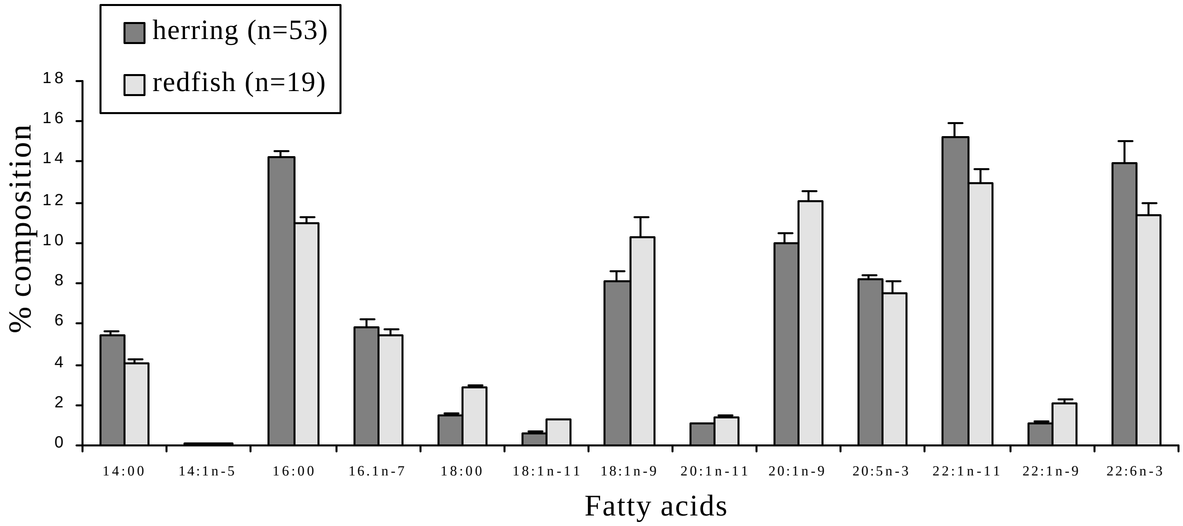

Figure 2.3. Percent composition of selected fatty acids from herring and redfish caught on the Scotian Shelf, Eastern Canada (Iverson, Bowen and Ackman, unpublished data).

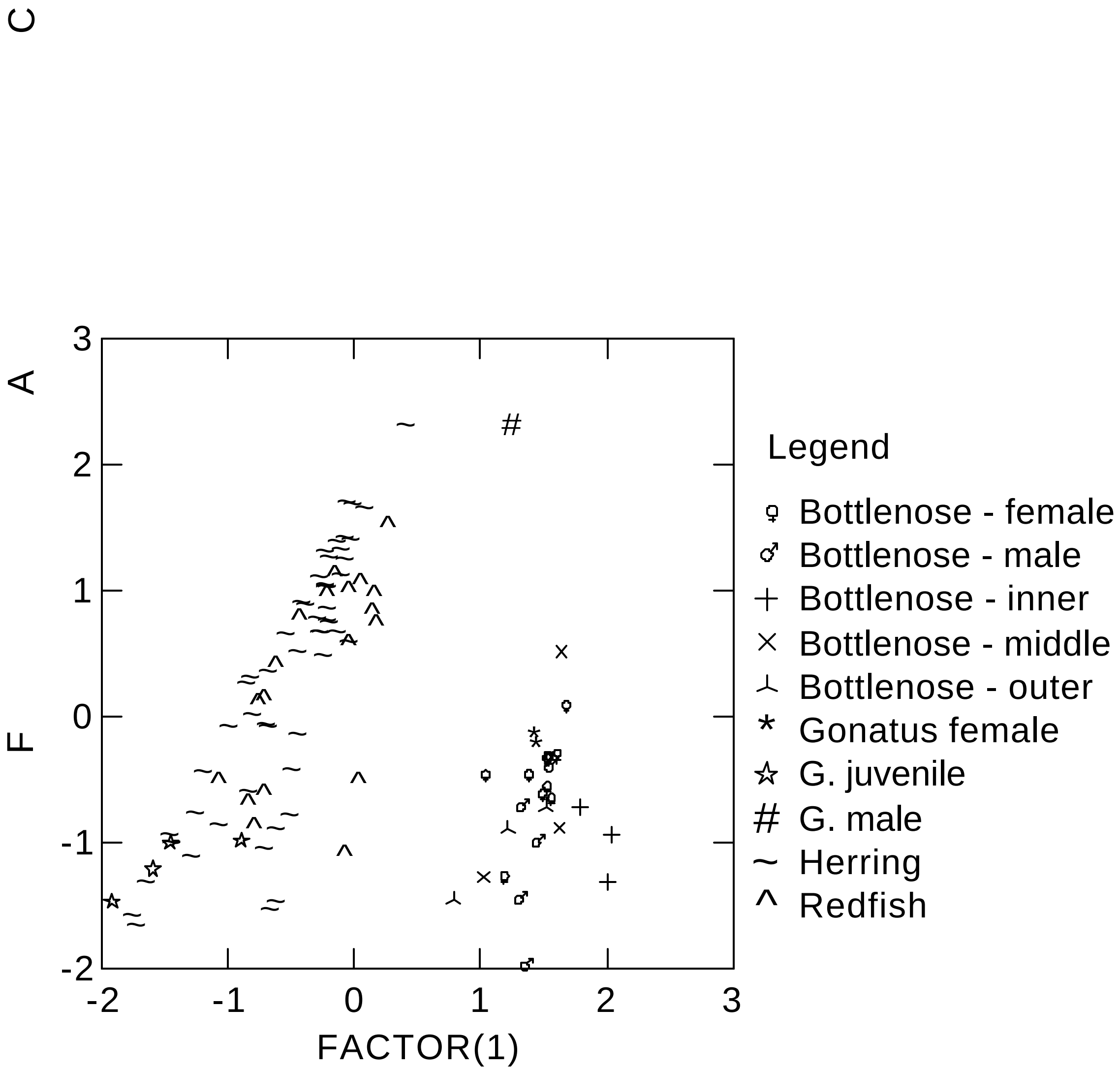

Figure 2.4. Principal component analysis using major fatty acids for all samples. Factor (1) explains 54 % of variance, factor (2) explains 19 % of variance.

DISCUSSION

Viability of using blubber biopsies for inferring aspects of diet

The blubber of most cetaceans investigated appears to show some stratification (e.g., balaenopterid whales, Ackman et al. 1975, Lockyer et al. 1984; sperm whales, Lockyer 1991; harbour porpoises, Koopman et al. 1996). Among these species longer chain unsaturated fatty acids, typical of diet, have been more prevalent in the inner blubber layer, suggesting that this layer is more metabolically active than the outer layer in terms of lipid deposition and fat storage. Northern bottlenose whales also showed differences in lipid class composition and fatty acid composition across the blubber layer (Table 2.3, Figure 2.1a). However, this stratification was less pronounced than in smaller cold-water cetaceans such as harbour porpoises and belugas (Koopman et al. 1996; S.J. Iverson, pers. comm.). The outer blubber layer in the three stranded animals contained dietary fatty acids in relatively similar proportions to those observed in the inner layer. In contrast, the outer layer of some cetaceans contains almost all short and medium-chain fatty acids with few or absent long-chain or polyunsaturated fatty acids (S.J. Iverson, pers. comm.).

The fatty acid composition of the blubber biopsies appeared to show a similar fatty acid composition to that recorded from the outer blubber layer of stranded animals (Figure 2.1; Table 2.7). These results suggest that biopsy samples can be used to investigate at least some relative aspects of diet, such as differences between individuals and demographic groups, for this species.

Bottlenose whale blubber

The high proportion of wax esters found in bottlenose whale blubber (Table 2.3) has been previously observed in beaked whales by Litchfield et al. (1976). Baird's beaked whale (*Berardius bairdii*) contained 98 % wax esters, dense-beaked whale (*Mesoplodon densirostris*) 99 % and northern bottlenose whale 94 % (Litchfield et al. 1976). The Physeteridae also have a high wax ester content, with sperm whales recorded at 60-85 %, and dwarf sperm whale (*Kogia simus*) at 42 % (Litchfield et al. 1976, Lockyer 1991). This prevalence of wax esters appears to be phylogenetically related, but its function is largely unknown.

The fatty acid analyses described here are based on the fatty acids released from triglycerides and wax esters in the blubber layer. In wax esters (a fatty acid plus a fatty alcohol), the fatty alcohol is not analysed. It is not known whether these alcohols are largely from diet or derived primarily from biosynthesis. However, I am assuming in discussing these results, that it is primarily the fatty acids which reflect diet.

Bottlenose whale blubber in the western North Atlantic appears to contain primarily monounsaturated fatty acids (Table 2.4). Lockyer (1991) identified many of the fatty acids among various sperm whale samples and found 18 % saturated, 60 % monounsaturated, and 1 % polyunsaturated fatty acids, with >16 % unidentified; thus giving a ratio of 3.4 unsaturated to saturated. This ratio was much higher in this study (~8).

The major fatty acids (in quantities >5 %) found in bottlenose whales were: 16:1n-7, 18:1n-9, 20:1n-11, 20:1n-9 and 22:1n-11. The first two of these, 16:1n-7 and 18:1n-9, can be produced endogenously through biosynthesis, although they are likely also to come from the diet (Iverson 1993). The latter three, 20:1n-11, 20:1n-9 and 22:1n-11 are likely to be primarily dietary in origin (Iverson 1993). Two of these monounsaturates (22:1n-11 and 20:1n-9) are believed to originate from the fatty alcohols contained in the wax esters of some copepods, from which they are carried up marine food chains (Pascal and Ackman 1976, Ackman 1980, Ackman et al. 1980, Iverson 1993).

***Gonatus* samples**

The fatty acid composition of *Gonatus fabricii* was found to be distinctly different between adult and juveniles (Figure 2.1c). Juvenile *Gonatus* contained relatively high quantities of the fatty acids 20:5n-3 and 22:6n-3, whereas adult *Gonatus* contained little of these but relatively high quantities of 20:1n-9 and 22:1n-11. Such a difference between adult and juvenile squid was also reflected in the δ^{15}N composition. Adult *Gonatus* contained much more δ^{15}N (mean δ^{15}N = 13.7 ‰, s.e. 0.25, n=3) than juveniles (mean δ^{15}N = 9.47 ‰, s.e. 0.25, n=2). This enrichment of 4.2 ‰ suggests that adult *Gonatus* are approximately 1.2-1.4 trophic levels higher than juvenile *Gonatus* (assuming trophic enrichment of 3.0-3.4 ‰ at each trophic level).

Gonatus is thought to have distinct ecological requirements at different life-stages, with juveniles (up to 3 cm pen length) living in the surface waters (to 80 m) and later showing ontogenetic descent to the sea floor. Juveniles prey on various zooplankton, primarily copepods and euphausiids, but also amphipods, pteropods and chaetognaths (Nesis 1965, Kristensen 1983). In contrast, copepods and euphausiids have never been recorded as prey of adult *Gonatus*. The major prey of adults instead consists mainly of amphipods, isopods and decapods (shrimps and mysids). At all ages, *Gonatus* will take the largest prey possible, for adults this includes fish and other squid. Cannibalism is also known (Kristensen 1983, 1984), and this would further raise the trophic level of cannibalistic individuals (Hobson and Welch 1995).

Previous studies of the fatty acid composition of squid have focused on shallow water squid species. The short-finned squid, *Illex illecebrosus*, from the North Atlantic was found to be high in the dietary fatty acids 20:5n-3 and 22:6n-3, but low in the fatty acids 20:1n-9 and 22:1n-11 (Kirsch et al. 1998). A similar pattern (high in 20:5n-3 and 22:6n-3) was also noted for unspecified small squid in Prince William Sound (Iverson et al. 1997). This pattern was also found for juvenile *Gonatus*, but not for adult *Gonatus* (Figure 2.1, Table 2.4). The lack of 20:5n-3 and 22:6n-3 is unusual in marine prey species (S.J. Iverson, pers. comm.).

Similarly, isotopic values reported for other squid species in the North Atlantic have tended to be fairly low: 11.9±0.1 ‰ δ^{15}N recorded for short-finned squid, *I. illecebrosus* (Hobson and Montevecchi 1991), and 12.2±0.2 ‰ δ^{15}N for the long-finned squid, *Loligo pealei* (Abend and Smith 1997). Most other published data on squid from the Pacific also tend to show low levels of isotopic nitrogen (neon flying squid, *Ommastrephes bartrami*, 11.7±0.4 ‰ $\delta^{15}N$, Gould et al. 1997; unspecified small squid 9.6±0.5 ‰ $\delta^{15}N$, Hobson et al. 1997; miscellaneous squid 11.6±1.9 ‰ $\delta^{15}N$, Gould et al. 1997). However, in the North Pacific a single sample of a large gonatid squid was found to contain 16.7 ‰ $\delta^{15}N$ (Hobson et al. 1997). The similar results found here, with adult *Gonatus* showing significantly higher isotopic nitrogen than juvenile *Gonatus*, suggest that this dietary and trophic difference may be consistent throughout the gonatid family.

It is generally thought that squid are relatively low in fat content when compared to marine fish (Sidwell et al. 1974). However, samples of both adult and juvenile *Gonatus* were found to have relatively high lipid content, with higher fat content in adult squid than in juveniles (Table 2.6). The values observed here, ranging from 3.4 to 11.28 %, are much higher than found for other squid species but lower than for many fish (e.g., 2 % lipid in *I. illecebrosus*, 16 % lipid in Atlantic mackerel, *Scomber scombrus*, Kirsch et al. 1998). The adult females had much lower fat content than the adult male, possibly due to recent spawning (both females possessed spermatophores, Bjørke et al. 1997). Calorific values have previously been determined for some small *Gonatus steenstrupi* at 3.78 kJ/g wet weight, although it was noted that the calorific value of adults would be higher (Clarke et al. 1985). Clarke et al. (1985) suggested that it is the low-density oil in their livers (used for buoyancy) which elevate the calorific values of the Gonatidae.

Dietary information from biopsy samples

The fatty acid composition found for the Gully bottlenose whales was primarily high in the fatty acids 20:1n-11, 20:1n-9 and 22:1n-11 (Figure 2.1). Although I cannot compare the bottlenose whale biopsy samples with *Gonatus* samples from the Gully, *Gonatus* samples from the Norwegian Sea may serve as a general index of the underlying fatty acid signature for North Atlantic *Gonatus* species. Elsewhere ecosystem differences have been observed between locations for a particular species (Iverson et al. 1997). Likewise, regional differences between the eastern and western Atlantic may exist, but this could not be assessed.

The fatty acid composition of the bottlenose whale biopsy samples was more similar to that of the adult *Gonatus* than that of the juvenile *Gonatus* (Figure 2.1, Figure 2.4, Table 2.7). While this does not prove that *Gonatus* is a major prey item of bottlenose whales in the Gully, their fatty acid signatures are at least consistent with such a possibility. Other potential prey items recorded from bottlenose whale stomach contents elsewhere in the North Atlantic and available in the Gully are herring and redfish (Ohlin 1893, Benjaminsen and Christensen 1979). Although herring are also high in 20:1n-9 and 22:1n-11, they also contain high levels of 22:6n-3 and they do not contain such high levels of 20:1n-11. The overall fatty acid compositions of these species were therefore more different from those of the biopsied bottlenose whales than was the adult *Gonatus* composition (Figure 2.3, Table 2.7), suggesting that these are less likely to be major prey of Gully bottlenose whales. Similarly, no other prey species have yet been recorded with a fatty acid signature similar to that of bottlenose whales (S.J. Iverson, pers. comm.).

Isotopic nitrogen is most useful for making inferences about trophic level in the marine environment, and an approximately 3 ‰ δ^{15}N increase is generally thought to reflect a trophic level increase (Minagawa and Wada 1984). Bottlenose whales were found to have fairly high isotopic nitrogen at 15.3±0.1 ‰ δ^{15}N. The difference in ^{15}N between bottlenose whales and juvenile *Gonatus* (5.8 ‰) is therefore greater than that expected for dietary items. The difference between whales and adult *Gonatus* (1.5 ‰) is similarly less than would be expected from primary prey. This may simply be due to differences between *Gonatus* species and locations (*G. steenstrupi* in the Gully and *G. fabricii* in the Norwegian Sea), or it may reflect partial consumption of lower trophic level organisms.

There are few measurements of isotopic content of primary producers in the Gully region. On Georges Bank, particulate organic carbon samples ranged from 4.8 to 6.0 ‰ δ^{15}N and zooplankton from 6 to 9 ‰ δ^{15}N (Fry and Quinones 1994). However, whereas seawater organic nitrate δ^{15}N is generally 3-6 ‰, deep-sea particulate organic nitrogen generally has δ^{15}N ratios greater than 6 ‰ (Saino and Hattori 1987). The higher isotopic nitrogen found in adult *Gonatus* may therefore be due both to depth and to feeding at a higher level of the food chain.

Making inferences based on δ^{13}C values is more difficult since trophic enrichment is generally much less than for δ^{15}N. Furthermore, other factors come into play: δ^{13}C values are typically higher in coastal or benthic food webs than in pelagic food webs (McConnaughey and McRoy 1979, Dunton et al. 1989), and higher in lower latitudes than in higher latitudes (Burton and Koch 1999).

Comparison with published results for other odontocete species in the North Atlantic shows that bottlenose whales have a relatively high isotopic nitrogen content (Table 2.8, Figure 2.5). One minor flaw with such a comparison is that most of the published results for stable isotope contents are based on analysis of muscle tissue, and there may be tissue differences in isotopic values. For long-finned pilot whales (*Globicephala melas*) isotopic nitrogen was 0.5 ‰ higher and carbon was 0.75 ‰ lower in skin than in muscle (Tieszen et al. 1983, Abend and Smith 1997). Even taking these differences into account, it can be seen that bottlenose whales eat at a relatively high trophic level compared to most other odontocetes. The three odontocete species found to contain a higher ^{15}N ratio than bottlenose whales (Table 2.8, Figure 2.5) were the narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*) and the white-beaked dolphin (*Lagenorhynchus albirostris*). Narwhals are believed to be largely teuthophagous including *G. fabricii* (Hay and Mansfield 1989), while belugas are believed to feed on a wide range of prey items (Brodie 1989). Both narwhals and belugas are also deep divers and are thought to forage at times at the sea floor (Martin and Smith 1992, Heide-Jørgensen and Dietz 1995; A.R. Martin, pers. comm.). The diving behaviour of white-beaked dolphins is unknown; they are thought to be generalists and feed on various fish and squid species but there has been some suggestion that they may be benthic feeders (Reeves et al. 1999). The differences in ^{15}N values for Arctic beluga and the beluga stranded in Newfoundland may represent different diets between the Arctic and St. Lawrence populations (Brodie 1989). By comparison with other odontocetes, bottlenose whales also appear to have fairly high isotopic carbon levels. Whether this indicates high trophic level, or their presence in a benthic ecosystem, or both, is unclear (Table 2.8, Figure 2.5).

Table 2.8. Comparison of stable isotope results recorded from odontocetes in the North Atlantic (ranked according to ‰ $\delta^{15}N$).

Species	*n*	sample source	Location	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	Reference
beluga *Delphinapterus leucas*	6	muscle	Arctic	16.6±0.6	-18.1±0.5	Hobson and Welch 1992
white-beaked dolphin *Lagenorhynchus albirostris*	1	muscle	Newfoundland	16.2	-18.1	Ostrom et al. 1993
narwhal *Monodon monoceros*	4	muscle	Arctic	15.8±0.7	-18.0±0.4	Hobson and Welch 1992
northern bottlenose whale *Hyperoodon ampullatus*	17	skin	Gully	15.3±0.1	-17.4±0.1	*this study*
common dolphin *Delphinus delphis*	1	muscle	Newfoundland	14.8	-17.8	Ostrom et al. 1993
bottlenose dolphin *Tursiops truncatus*	9	teeth	Atlantic US	14.8±0.8	-13.9±0.4	Walker and Macko 1999
long-finned pilot whales *Globicephala melas*	6	skin	North Atlantic	13.9±0.1	-18.8±0.1	Abend and Smith 1997
beluga *Delphinapterus leucas*	1	muscle	Newfoundland	13.6	-17.6	Ostrom et al. 1993
common dolphin *D. delphis*	15	teeth	Atlantic US	12.4±0.8	-14.5±0.3	Walker and Macko 1999
pygmy sperm whale *Kogia breviceps*	12	teeth	Atlantic US	12.4±0.9	-12±0.5	Walker and Macko 1999
pygmy sperm whale *K. breviceps*	1	muscle	Newfoundland	11.9	-17.2	Ostrom et al. 1993
Sowerby's beaked whale *Mesoplodon bidens*	4	muscle	Newfoundland	11.7±0.6	-18.5±1.1	Ostrom et al. 1993
sperm whale *Physeter macrocephalus*	1	muscle	Newfoundland	11.1	-22.8	Ostrom et al. 1993

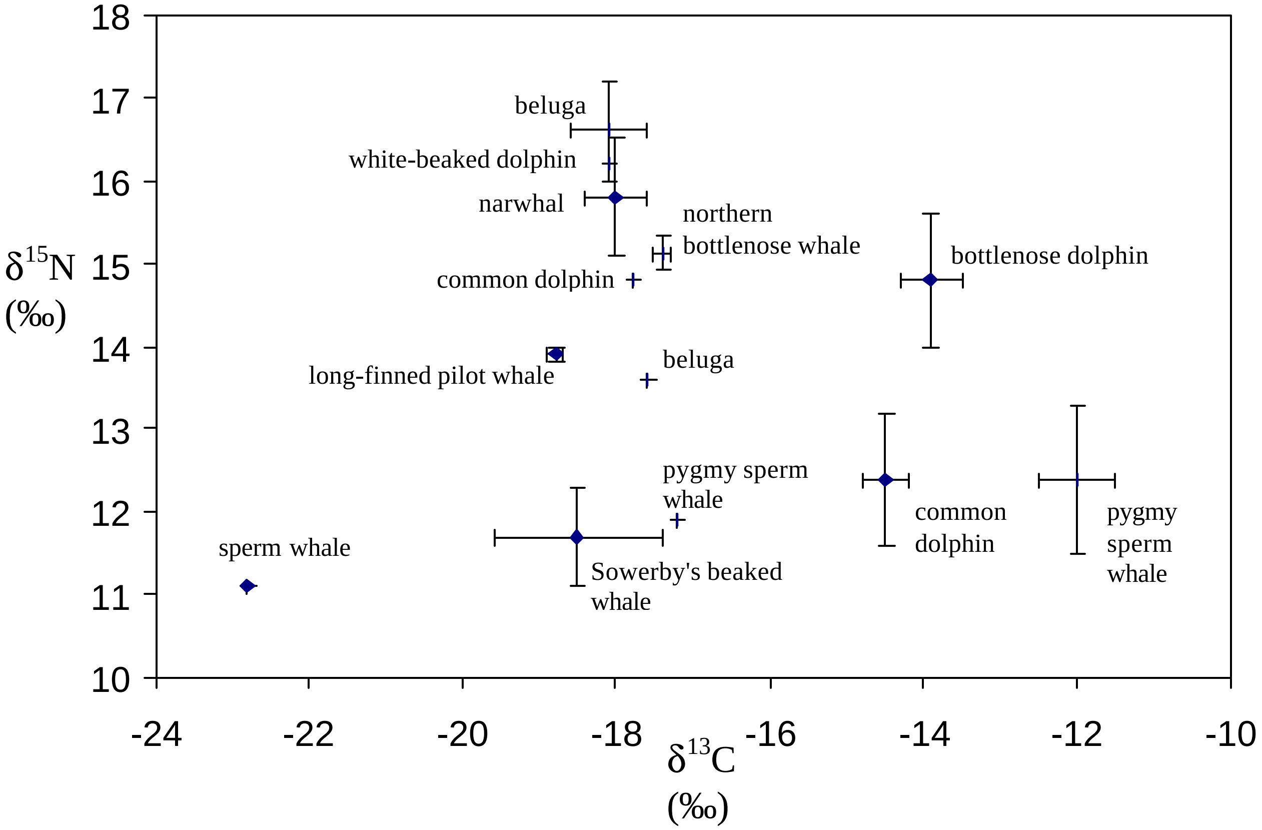

Figure 2.5. Stable isotope values of North Atlantic odontocetes (sources and sample sizes are given in Table 2.8).

Differences between male and female bottlenose whales were significant for isotopic nitrogen and appeared to show some differences in fatty acids, such that k-means clustering based on major fatty acids identified the two groupings with 87.5 % accuracy (Figure 2.1, Figure 2.2). Although samples were genetically identified as male or female, no techniques were available to assess age of these animals. This sample of males is therefore also likely to include juvenile males. Bottlenose whales are sexually dimorphic, such that adult males can be identified in the field based on their size and lighter coloured, flattened foreheads (Gray 1882). Two of the biopsied animals (#15 and #16) were identified in the field as large adult males, and another (#17) was identified photographically as a mature male (S. Gowans, pers. comm.). These samples also had the highest values of isotopic nitrogen (15.59 ‰ for the first two and 15.50 ‰ for the third respectively). While anecdotal, this is suggestive of trophic differences between adult males and other bottlenose whales in the Gully. A similar difference was found in δ^{15}N ratios for Steller sea lions, with adult males showing a higher trophic position than adult females, and adult females higher than juvenile males (Hobson et al. 1997). These authors suggested this was likely due to a differential reliance on certain food items or a difference in the size of prey taken. Similarly, a greater reliance on larger *Gonatus* would result in the slight increase in trophic level observed for the adult males. Alternatively other possible explanations include feeding at greater depth or in different locations. Bernard and Hohn (1989) found that lactating spotted dolphins (*Stenella attenuata*) switched their diet to flying fish rather than squid, and suggested that this might be due to water or nutrient requirements, the necessity to forage more often, or in order to forage closer to the surface. Similarly, Recchia and Read (1989) found that lactating female harbour porpoises ingested more fish and had a significantly higher total caloric intake than non-lactating females or mature males.

Conclusion

This study demonstrates the potential utility of biopsy samples for dietary studies in some cetacean species. The three different techniques investigated here: fatty acid and stable isotope analyses of skin and blubber biopsies, and stomach contents of stranded animals, all give complementary results. While none conclusively demonstrate that

Gonatus is a major dietary item of northern bottlenose whales in the Gully, there is general agreement between all three methods suggesting that *Gonatus* could be their major prey item. Furthermore the results present a strong case for selective feeding on adult rather than juvenile *Gonatus* (Figure 2.1, Figure 2.2).

However, the *Gonatus* samples investigated were from a different ecosystem from that of the Gully bottlenose whales and the comparison between the two is therefore only inferential. That said, the unique pattern of fatty acids found in bottlenose whale blubber from the Gully is not consistent with any other obvious prey species (S.J. Iverson, pers. comm.). The analysis of *Gonatus* specimens and other deep-water prey from the Gully region will provide further detail on the diet of bottlenose whales in the Gully.

CHAPTER THREE

The influence of biotic and abiotic oceanographic features on the distribution of northern bottlenose whales in a submarine canyon

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ABSTRACT

Bottlenose whales are regularly sighted above the Gully, a submarine canyon off Nova Scotia, and have been studied there between June and August in 1988-1998. Abundance and distribution of whale sightings during this study showed significant differences between years, but there was little difference between months. A comparison of the distribution of sightings with that of search effort for fixed physical parameters (depth and slope) and for surface environmental characteristics (sea surface temperature and water clarity) showed that depth appears to be the primary factor affecting whale distribution. Between 1993 and 1998, estimates of sub-surface biomass in the water column were measured along transect lines up the midline and laterally across the Gully. Whale density showed the strongest correlations with mid-water biomass and scattering layer depth. The correlation between whale density and environmental variables was studied over several spatial scales, to investigate the scale dependence of whale habitat preference with physical and environmental parameters. The correlations found tended to be stronger over larger scales, suggesting that these features were only loosely related to the positioning of the whales' primary prey. Overall, the relationship found between bottlenose whales and deep-water features of the water column suggests that whale distribution may be related to benthic or bathypelagic productivity. Annual variation in weather conditions has been suggested to cause variation in the benthic productivity of submarine canyons. The intensity of winter storm activity was correlated with whale distribution and negatively correlated with whale abundance at 1-2 year time lags, but sample size was small and any conclusions are premature at this stage.

INTRODUCTION

Not surprisingly, the distributions of many species of odontocetes (toothed whales) relate primarily to the distribution and abundance of their prey (see Kenney et al. 1996). However, little is known about the distribution or abundance of the prey of many odontocete species, and this is especially the case for the deep-water squid species, which are thought to be the primary prey of deep-diving cetaceans. Investigation of the physical and environmental determinants of cetacean distribution can therefore additionally provide detail on determinants of prey distribution. Previous research on the distribution of various cetacean species has shown some correlation with both fixed physical features (e.g., Hui 1979) and temporally variable oceanographic conditions (e.g., Tynan 1997). The distribution of cetacean species may be correlated with oceanographic features at various depths, ranging from surface phenomena such as sea surface temperature, water clarity, surface chlorophyll or biomass (Smith et al. 1986, Brown and Winn 1989), midwater effects such as sub-surface biomass, deep scattering layer or oxygen minimum layer (Reilly 1990, Griffin 1997, Fiedler et al. 1998), or, potentially, sea floor effects such as benthic productivity. However, although such correlations have been observed over large spatial scales (corresponding to the species distributional range or broad-scale patterns of distribution), there have been fewer studies of correlates over a small area (indicative of small-scale habitat use).

Little is known about the environmental factors which influence the distribution of northern bottlenose whales (*Hyperoodon ampullatus*). Northern bottlenose whales are found throughout the northern North Atlantic, from the ice-edge in the north to Rhode Island in the southwest, and to the Strait of Gibraltar in the southeast (Mead 1989b). Previous studies of northern bottlenose whale distribution have investigated catch locations on the whaling grounds, and suggested that whales appear to favour waters deeper than 1000 m (Benjaminsen and Christensen 1979). Off the eastern coast of Canada, northern bottlenose whales are routinely observed above a prominent submarine canyon, known as the "Gully" (Reeves et al. 1993, Whitehead et al. 1997a, b). Their distribution above the Gully appears to be highly localized, centred in a 12 x 8 km core area (Faucher and Whitehead 1991, Faucher and Weilgart 1992; Figure 3.1), suggesting a localized prey base. There is some evidence that whales feed in the Gully; bottlenose whales have been recorded to dive to near the sea floor, presumably in order to forage (Chapter 5) and are periodically observed to defecate near the surface (pers. obs.). Bottlenose whale diet is thought to consist primarily of squid of the genus *Gonatus* (see Chapter 2), but little is known concerning habitat preference of these or other potential prey species.

In this chapter I investigate the correlation between environmental characteristics of the Gully and bottlenose whale distribution, and examine the temporal variations in both whale distribution and environmental characteristics. While surface and mid-water oceanographic conditions are quite easily recorded, obtaining a measure of benthic biomass is much more difficult. I have used a lagged index of weather activity as a potential proxy for benthic productivity, since it is likely that this is one of the primary environmental features affecting the benthos within the canyon (Harding 1998). Storm events facilitate reintroduction of particulate organic carbon into the water column above the continental shelf (Harding 1998), and this organic material is deposited at approximately 1000 m depth on the shelf edge, co-incident with minimum current speeds (Walsh et al. 1988, Biscaye et al. 1994). Thus increased storm events will potentially lead at some time lag to an increase in organic material reaching the deep benthos. I therefore investigated bottlenose whale sighting rate with reference to the fixed physical features of the Gully (depth, slope), and variable oceanographic conditions at the surface (sea surface temperature [SST], water clarity [indicating surface primary productivity]), midwater (sub-surface biomass), and sea-floor (using a lagged index of storm activity). The elucidation of predator-prey dependency has been shown to depend to a large extent on the scale of measurement involved (Rose and Leggett 1990, Jaquet 1996b). At scales smaller than the aggregations of predator or prey, there may be little or even negative correlation in distribution between the two, whereas at scales larger than their aggregations, there will often be strong positive correlation (Rose and Leggett 1990). I have therefore also included an assessment of the influence of spatial scale on the correlation between whale density and surface and midwater environmental parameters.

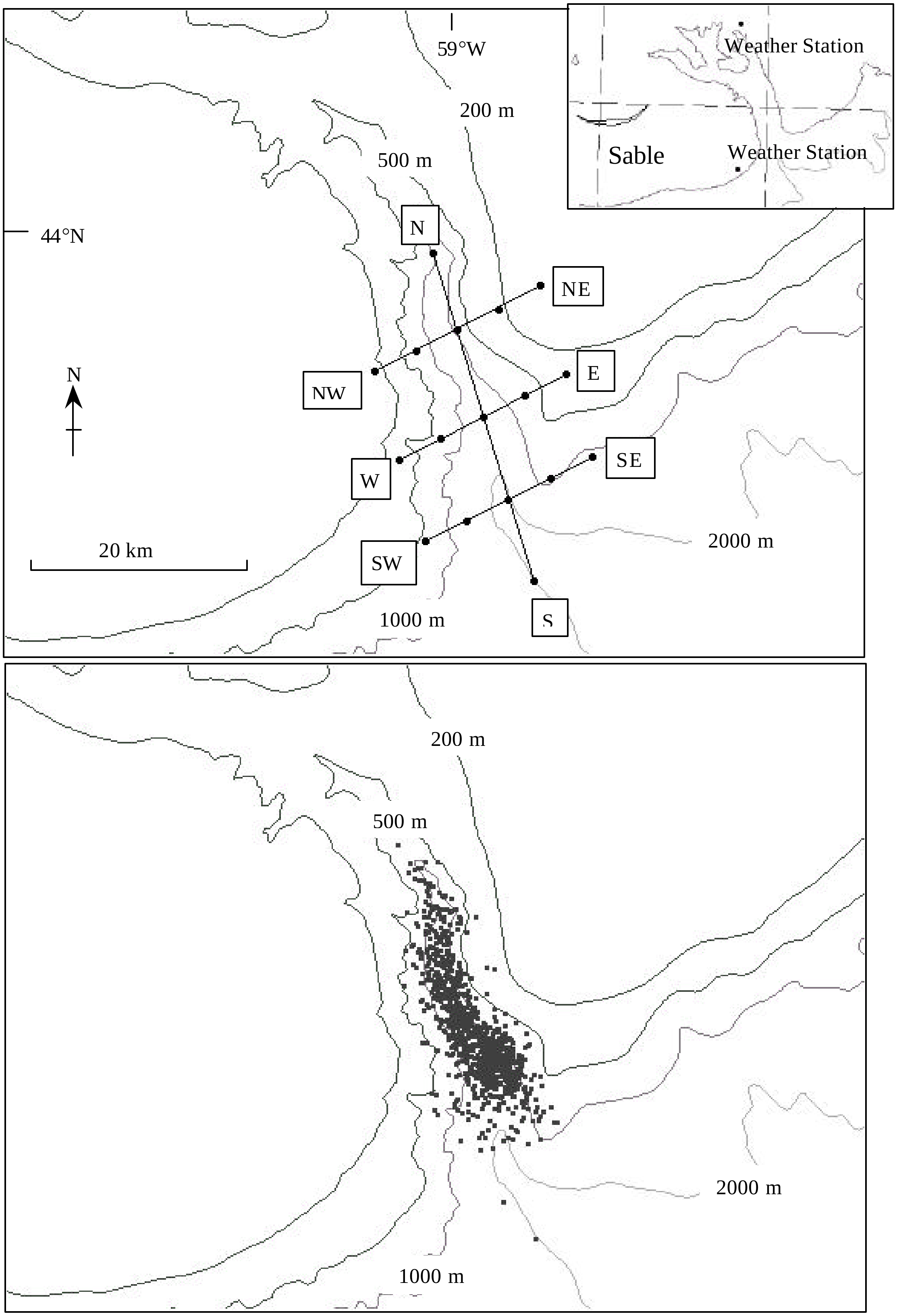


Figure 3.1. Upper map shows study area and transect lines and stations (——•——). Lower map shows bottlenose whale sightings 1988-1998.

METHODS

Fieldwork

Research was conducted each summer (June-August) from 1988 to 1990 and from 1993 to 1998, for varying periods of time (13-65 days; Table 3.1) using an auxiliary sailing vessel (10-12 m length). The position, date, time, Beaufort sea state and visibility were recorded for each sighting and every hour. Locations were recorded from Loran (SeaPort Loran-C, 1988-1990) or GPS (Trimble Transpak GPS, 1993-1996 and Garmin 65 Global Navigator, 1996-1998). Sea surface temperature was recorded every three hours (06h, 09h, 12h, etc). During daylight hours, the Gully area was searched in a non-systematic manner for northern bottlenose whales (hereafter referred to simply as "whales") by 1-6 crew members. The bearing and estimated distance of whales from the research vessel were noted and used to calculate each sighting position. A new sighting was defined as a whale or group of whales first spotted after at least 10 minutes without any whales in view. This definition was tested during VHF radio-tracking of tagged whales. If whales dived for longer than 10 mins they were generally very difficult to relocate visually but could be tracked by radio-signals emitted by the tags (Hooker and Baird 1999a).

Table 3.1. Yearly distribution of fieldwork in the Gully (43.5 – 44.5°N; 58.5 – 60°W).

Year	Dates	# hours in Gully	Daylight hours *	# sightings
1988	July 8-21, July 25-Aug 6	347	211	11
1989	July 16-30, Aug 1-15	362	225	58
1990	June 14-28, July 2-18, July 25-Aug 12	680	401	180
1993	July 10-23	242	149	70
1994	July 31-Aug 18	289	171	39
1995	Aug 20-Sept 2	128	76	12
1996	June 7-25, July 4-21, July 27-Aug 12, Aug 19 - Sept 2	1071	659	207
1997	June 7-23, July 1-19, July 24-Aug 6, Aug 10-27	1070	653	194
1998	July 12-31, Aug 6-23	685	387	151

*Daylight hours: 05:00 – 20:00

Four transect lines (each composed of five equidistant stations) were set up across the study area (Figure 3.1). A 32-km longitudinal transect (running approximately north-south) was set up to run up the centreline of the Gully, and three 17.5-km latitudinal transects (running approximately east-west) were set up perpendicular to this crossing the three central stations of the north-south transect (Figure 3.1). During most trips since 1993 these transects were sailed or motor-sailed during daylight hours at a speed of 4-6 knots (Table 2). The maximum distance strayed from the trackline during transects was approximately 500 m. SST and water clarity (depth of Secchi disk visibility) were recorded at each of five regularly-spaced stations along the transect. A Furuno sonar (60 kHz frequency) was used to record sub-surface biomass between stations. The sonar was set at a constant gain and at a vertical range of 600 m for all transects. The sonar image was recorded directly to video and transect station positions were marked by breaks in the video recording.

Table 3.2. Transect records in the Gully.

Year	Month	N-S	W-E	NW-NE	SW-SE
1993	July	x	x	-	-
1994	August	x	x	x	x
1995	August	x	x	-	-
1996	June	x	x	x	x
	July	x	x	x	x
	August	x	x	x	x
1997	June	x	x	x	x
	July	x	x	x	x
	August	x	x	x	x
1998	July	x	-	-	-
	August	x	x	x	x

The video recording of scattering layer biomass was later input to computer (using the software OPTIMAS). Since brightness indicated the intensity of scattering layer, biomass density was assigned a luminosity value (greyscale, 1-255) for every 10 m depth and every 50 m of trackline. For each 50 m of trackline, various indices were then calculated: overall mean biomass (the average luminosity value between 30-600 m), surface biomass (average luminosity between 50-300 m), mid-water biomass (average luminosity between 300-600 m), depth of the scattering layer (depth of maximum luminosity 30-600 m), and thickness of scattering layer (the total depth range for which luminosity is greater than 1.25 x average).

To determine the possible impact of time of day on sub-surface biomass, still photographs of the sonar display were taken hourly during a 24-hour period at the central station in the Gully. This procedure was repeated on three occasions (8-9 July 1996, 17-18 July 1996 and 2-3 August 1996).

Analyses

For any study of cetacean distribution, effort (i.e., a measure of the locations searched) is crucial in correcting the bias present in sighting locations (e.g., Kenney and Winn 1987, Polacheck 1987, Reilly 1990, Gowans and Whitehead 1995); this is especially so for data collected when a systematic or randomly determined search pattern was not used. Here I compare bottlenose whale sightings to effort in two ways: 1) comparing positions of sightings to hourly search positions (or 3-hourly search positions for sea surface temperature); 2) by defining areas over which to compare the sighting rate of whales in each 3 week trip with other measured environmental parameters. The effect of weather conditions (sea state and visibility) on sighting rate was assessed, and when necessary the data were restricted accordingly.

Variation in bottlenose whale abundance was investigated between years and calendar months using a goodness of fit G-test, which compared the relative distributions of effort and sightings, and by a loglinear model, which investigated the interactions between the categorical variables year, month and whale/effort abundance. The density of whales over the Gully area was mapped for each trip. Given the known preference of bottlenose whales for certain depths, regions were defined based primarily on depth and the corrected sighting density (i.e., the number of sightings per hour of search effort) was calculated and displayed for each region.

A digitized bathymetric vector map of the Gully region (Seabed Exploration Associates, Halifax, Canada) was used to interpolate depth for each 500 x 500 m cell of the region using the GIS software IDRISI. Depth values were used to calculate slope values for each cell (calculated as the maximum slope around each cell from the depth difference between it and neighboring cells). These depth and slope values were then assigned to sightings and hourly search positions which lay within these cells. The SST for each sighting was assigned as the closest 3-hour record. Investigation of the difference between consecutive readings shows an absolute mean difference of only 0.57°C (s.d. 0.6°C, *n* = 1111). The SST did not appear to be related to time of day at which the reading was taken (visual examination of difference between SST and daily mean SST showed no pattern in variation with time of day). The correlation between sighting rate (calculated as # sightings/ # search hours) within a gridcell (2 x 4 km around each transect station) and the Secchi depth recorded at that location for each trip was investigated.

A Kolmogorov-Smirnov goodness of fit test (K-S test; for variables: depth, slope, SST and Secchi depth) was used to test the hypothesis that the variables for sighting data had the same distribution as those for the effort data. Correlations between these variables for hourly records were tested using Spearman correlations (since variables were not all normally distributed). To check that there was no effect of habitat on whale group size (since the use of sightings masks the number of individuals present), regressions were performed for group size against each parameter (depth, slope, SST) for all sightings.

The mean biomass in the upper-water (50-300 m depth), mean biomass in the mid-water (300-600 m depth), overall mean biomass, depth of the primary scattering layer and thickness of scattering layers were calculated for set segments of each transect (2, 4, or 8 km). The presence of any positional, year or month effects (or interactions of these) for each of these indices were assessed using ANOVAs.

Whale sighting densities during the same research trip (sightings/search hours) were calculated for each segment of each transect (over an area extending to 2 km each side of the transect line). Such wide areas were necessary in order to capture a reasonable number of sighting and effort locations for each. Mean depth and mean slope for each area were calculated from the GIS software IDRISI. Spearman correlations were used to investigate the effect of each of these parameters on whale density. Table 3.3 summarises the parameters calculated for each section of each sonar transect.

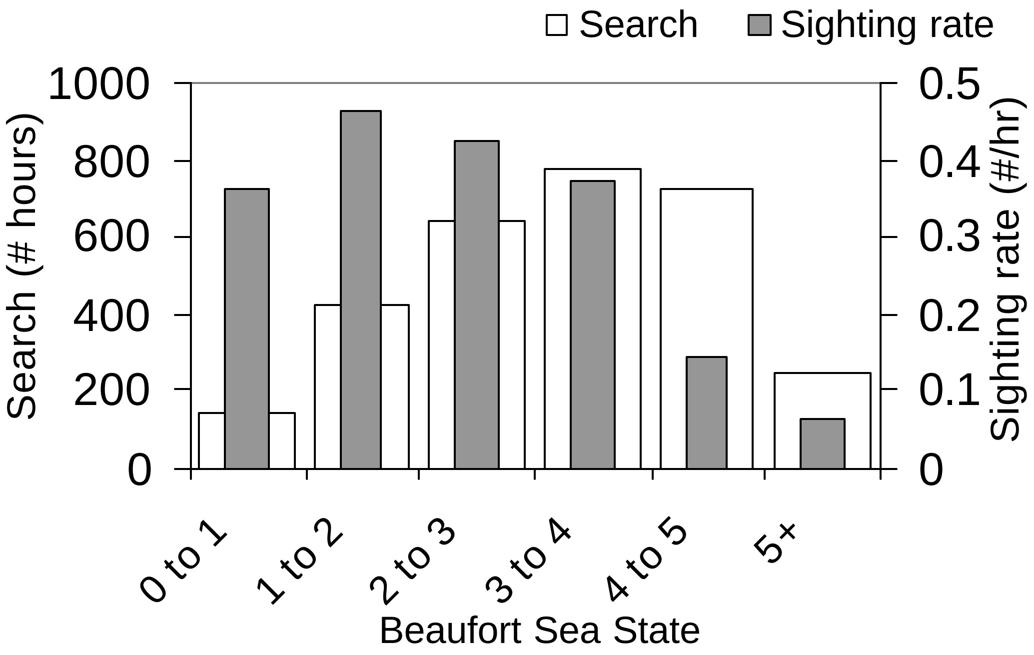
Table 3.3. Variables calculated for analyses of transect data.

Variable	Description	Units
SST	Sea surface temperature, interpolated between transect stations	°C
Secc	Secchi depth interpolated from results for transect stations	m
BiomU	Mean biomass index 50-300 m	-
BiomM	Mean biomass index 300-600 m	-
DepS	Depth of maximum scattering layer	m
Thick	Thickness of scattering layer	m
Biomass	Overall index of mean biomass	-
AvDep	Average depth of seafloor	m
AvSlop	Average slope of seafloor	°

Annual variation in wind speed and wave height data from two stations in the Gully were provided by Environment Canada (one station approximately 10 km west of the west transect station at 43°45'N 59°10'W, and the other just north of the 200 m isobath to the north of the Gully at 44°22.5'N 59°10'W, Figure 3.1). Differences between these stations were compared using a Pearson correlation. The number of 6-hour records of wave height greater than 8 m was used as an indicator of storm activity. This was plotted for each year and the periodicity of storm activity was compared (visually and using Pearson correlations) to annual changes in bottlenose whale distribution and abundance.

RESULTS

Sighting rate varied significantly with Beaufort sea state (G-test, G=232, p <0.001), but was relatively constant in sea conditions up to Beaufort force four (Figure 3.2; G-test, G = 10.5, n=8, p > 0.10). Similarly sightings were almost half as likely in visibility of less than 500m compared to good visibility (Figure 3.2). Tests presented below therefore use the restricted dataset (Beaufort <4, and visibility >500m), however the majority of displays use the full dataset.



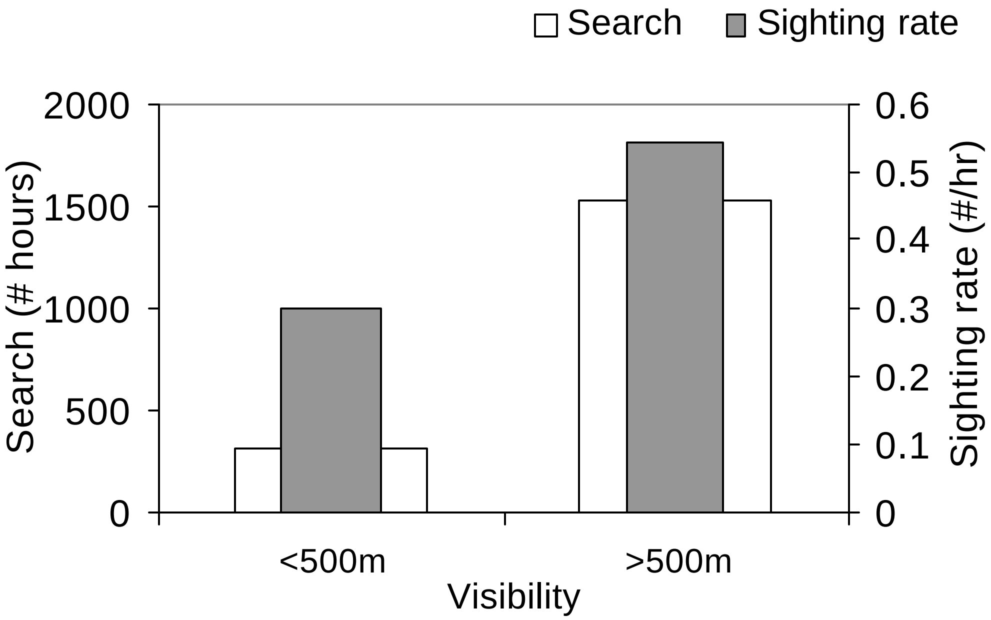


Figure 3.2. Variation of sighting rate (# sightings per hour) with sea state and visibility. Distribution of search effort (hours) is also shown.

Abundance

A direct comparison of sightings to effort (in good weather conditions) showed that there was a significant difference between number of sightings and effort expended between years (G-statistic 33.9, n=9, $p < 0.001$) and between months (G statistic 27.1, n=6, $p < 0.001$). 1988 was essentially a pilot research year and effort expended outside of the canyon area has likely resulted in an underestimate of sighting rate. There appears to have been relatively low bottlenose whale abundance in 1994 and 1995 (62 % and 74 % of the overall mean respectively), although these were the years of least search effort (resulting in less confidence in the calculated sighting density, Figure 3.3). There was also a significant interaction between year and month in terms of sightings versus effort (loglinear model, $p = 0.0054$; Figure 3.4). This suggests that there are variations in bottlenose whale density over each summer, but that these are not predictable by month (e.g., there is not always greater density in July).

Distribution

Temporal variation

Distributional changes in bottlenose whale sighting density were plotted visually using areas defined by depth, latitudinal divisions and the centreline of the Gully. Over 99 % of sightings were in waters deeper than 500 m, so only areas deeper than this were included. Visual investigation of these plots show that variation in distribution between years and months appears to have been primarily along the north-south axis of the Gully (Figure 3.4). This shift in distribution is more apparent when plotted against latitude for each year (Figure 3.5). Whales appear to have been distributed toward the south of the Gully in 1989-1993, in the north in 1994-1996, fairly evenly throughout the Gully in 1997 and in the north of the Gully in 1998.

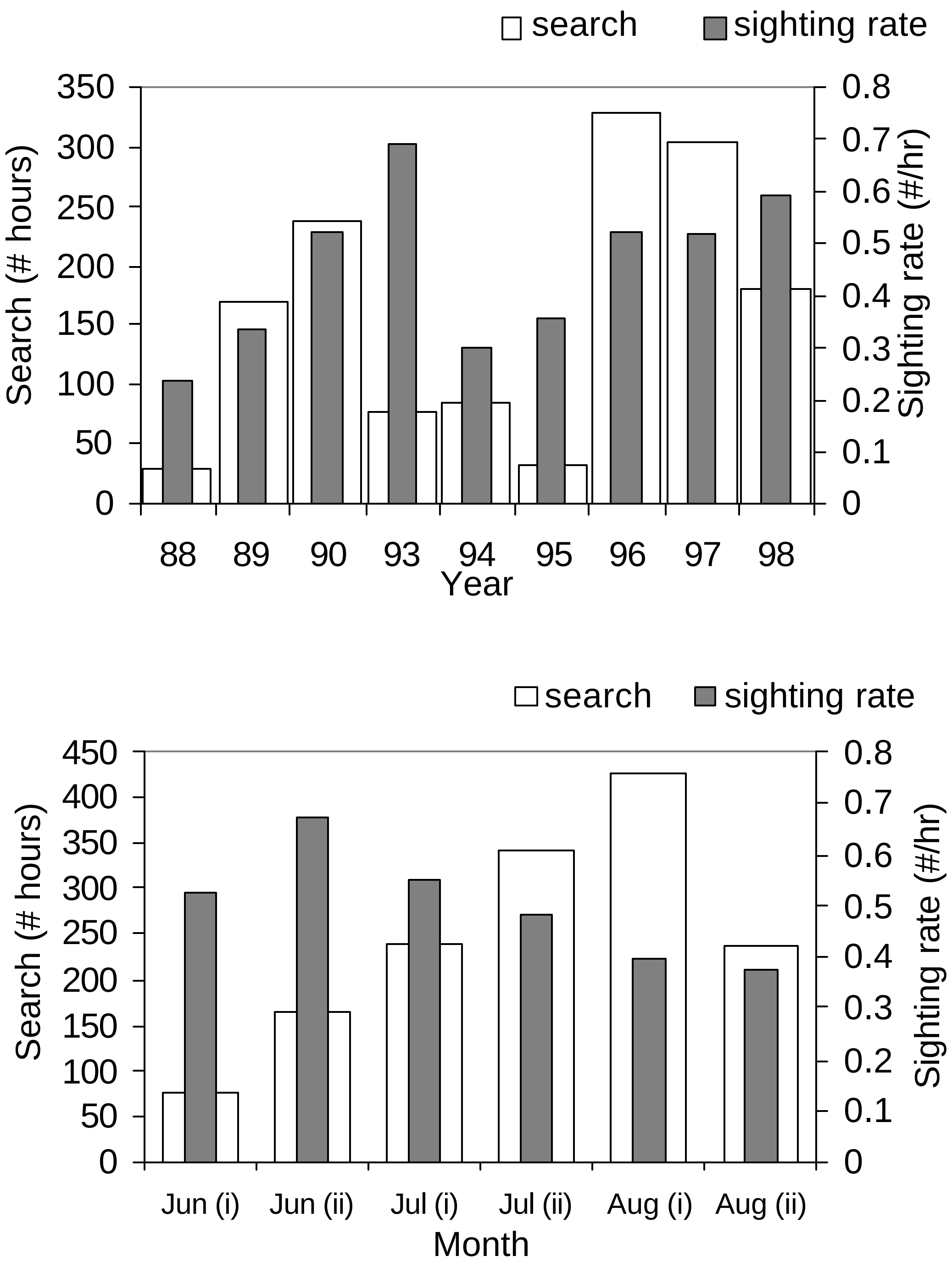


Figure 3.3. Temporal variation in bottlenose whale sighting rate during conditions of Beaufort sea state < 4 and visibility > 500m. Sighting rate (# sightings per hour effort) and search effort are shown (a) with year and (b) with half-month. Search effort is shown to provide an indication of confidence in the sighting rate. Months were split into two halves (1-15 days, 16-31 days) in order to provide increased resolution of temporal change over the summer months.

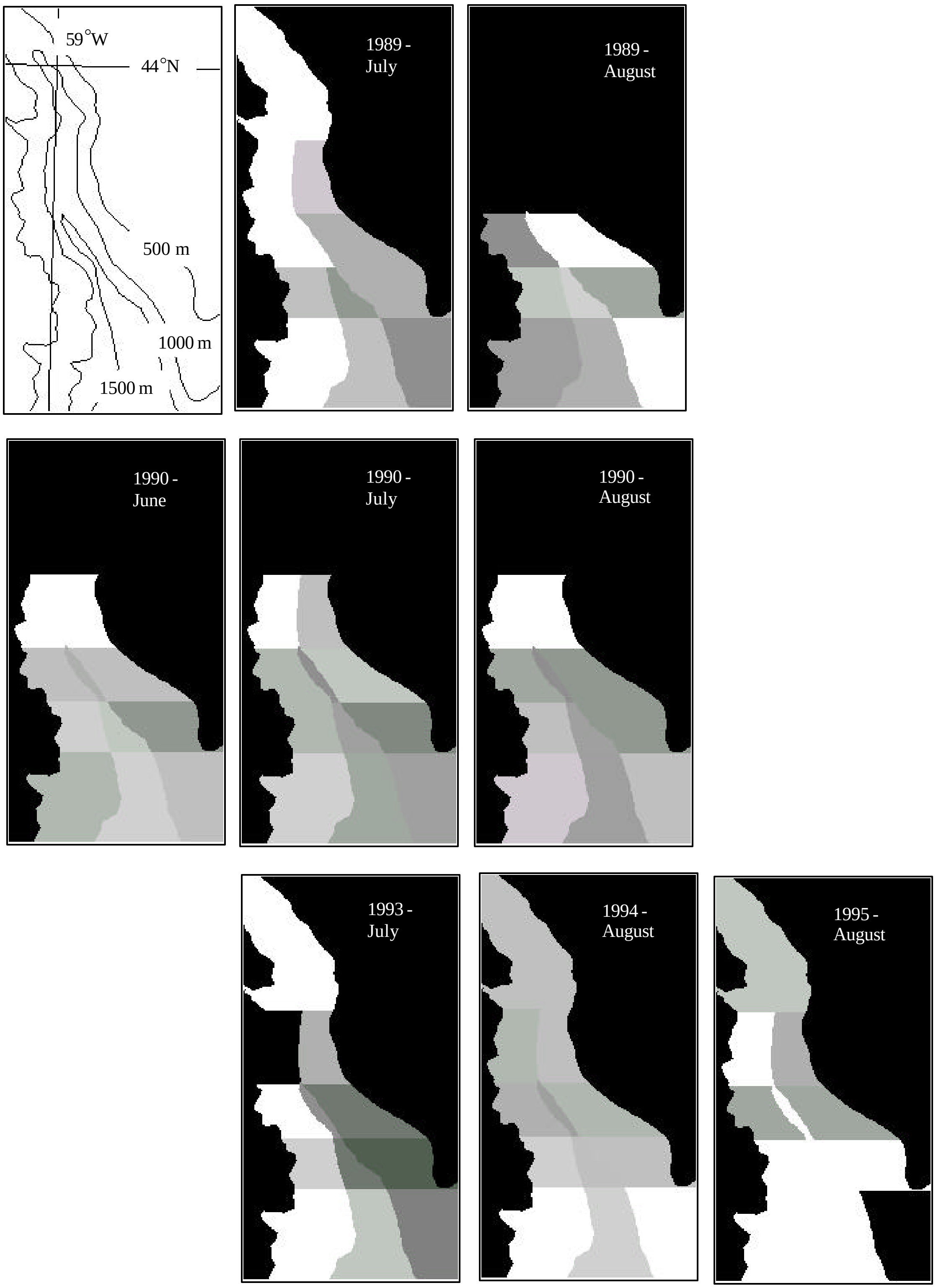


Figure 3.4. Variation in bottlenose whale density in the Gully recorded for each 2-3-week trip. First figure shows the template for all following figures. Black shows areas not calculated (outside 500m contour or areas of no search effort). White indicates areas of no sightings; relative darkness of grey indicates increase in sighting density.

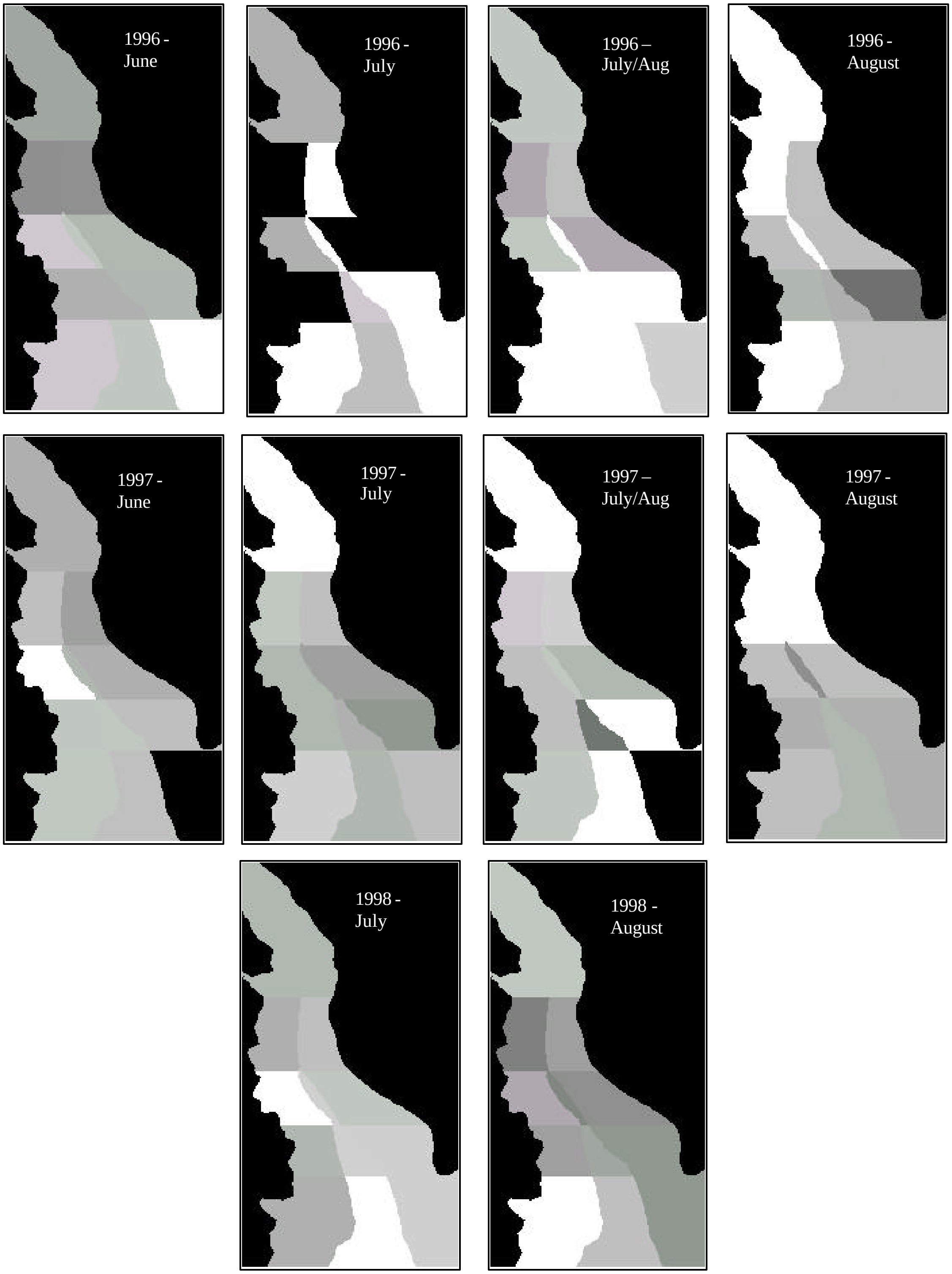


Figure 3.4 (cont). Variation in bottlenose whale density in the Gully recorded for each 2-3-week trip. First figure shows the template for all following figures. Black shows areas not calculated (outside 500m contour or areas of no search effort). White indicates areas of no sightings; relative darkness of grey indicates increase in sighting density.

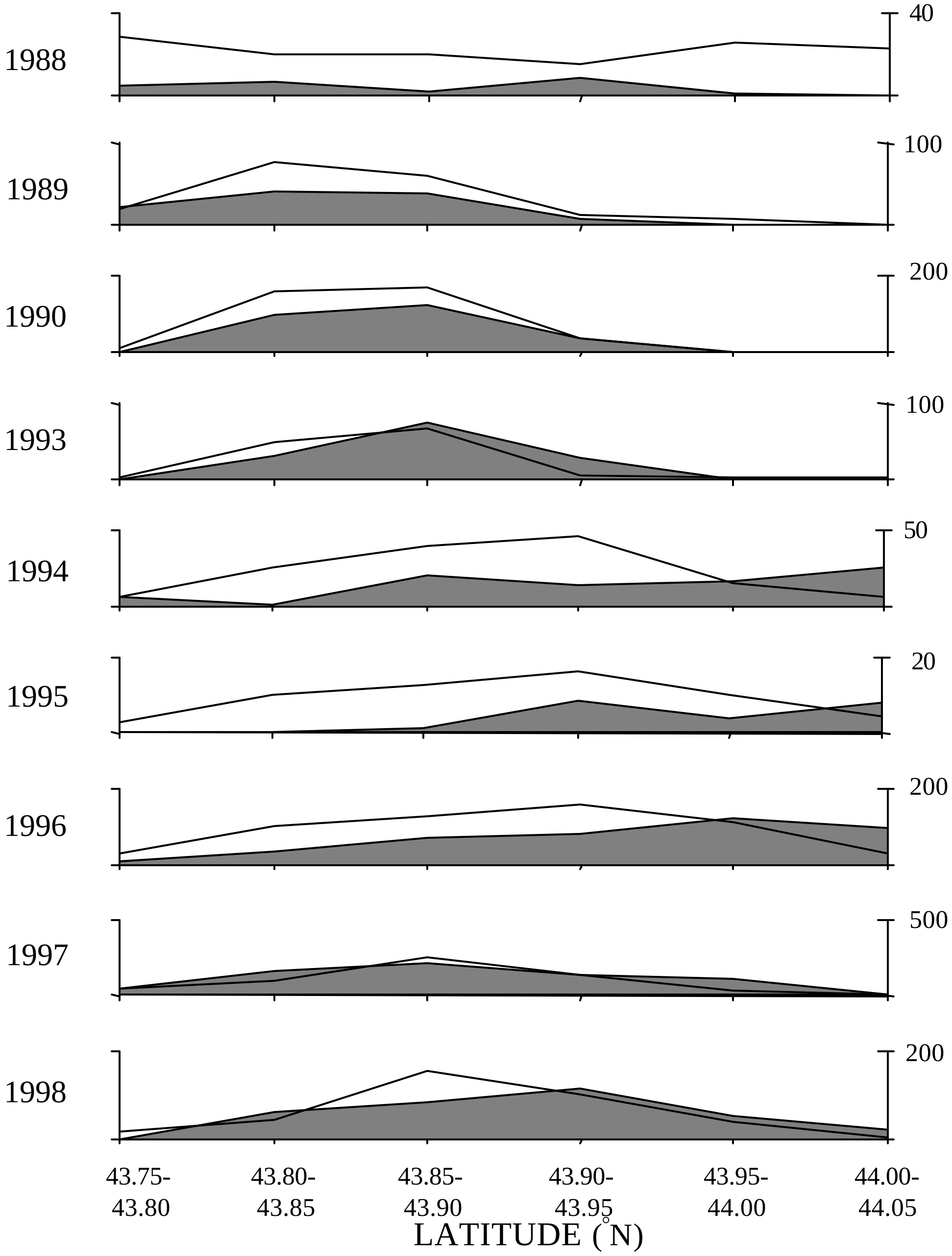


Figure 3.5.Yearly differences in sighting density along north-south gradient through the Gully. Shaded area shows sighting density (i.e., sightings/hour). Line shows distribution of search effort hours (scale shown on right).

Fixed physical features – depth and slope

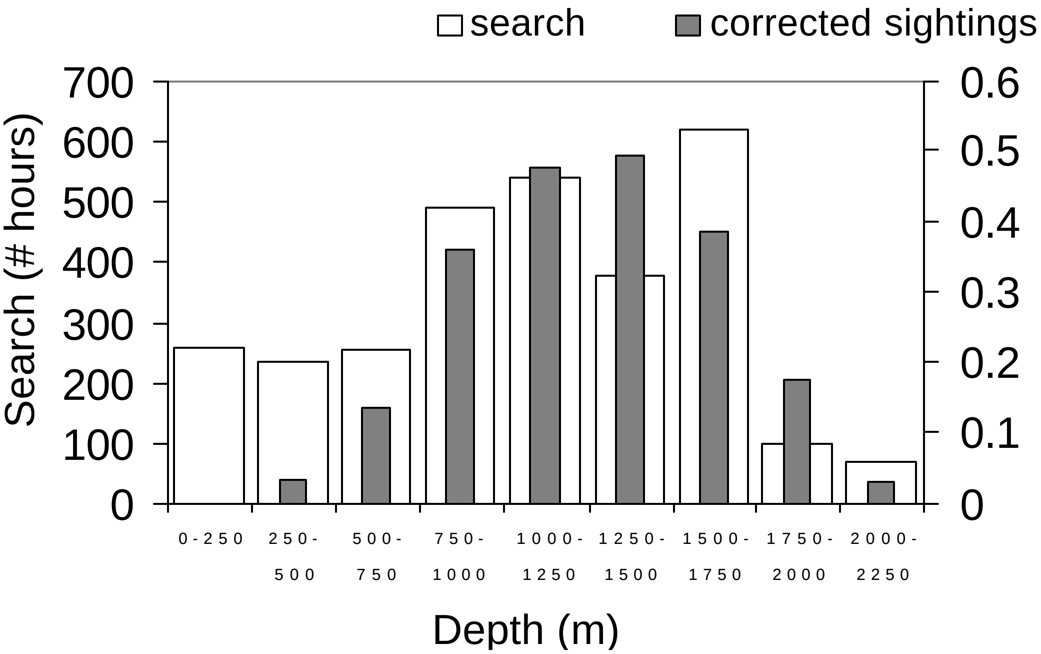
A direct comparison of sightings to effort showed that depth and slope for sightings were significantly different from those of search locations (Table 3.4, Figure 3.6). Depth and slope were correlated ($r = 0.268$). The interaction between depth, slope and sightings or effort was found to be significant (loglinear model, $p < 0.001$). The relative importance of slope or depth were investigated in turn. The effect of slope given the effect of depth was investigated using a general linear model (dependent variable: slope; categorical variables: sighting/effort and depth category) but was not significant ($p = 0.073$). The effect of depth given that of slope (dependent variable: depth; categorical variables: sighting/effort, slope category) was found to be significant ($p = 0.001$). There was no relationship between the group size of each sighting and the depth or slope in which that sighting was observed (regression: for depth $r = 0.004$; for slope $r = 0.018$). The possibility that the eight sightings observed in water shallower than 500 m might be due to the poorer positioning capability of the Loran was investigated, but since seven of these were recorded (since 1994) using GPS, this does not appear to be the case.

Table 3.4. Average parameter values for all sightings of bottlenose whales in the Gully. Kolmogorov-Smirnov (K-S) tests of sighting rate uniformity for parameters shown (restricted to sea state <4, and visibility >500m).

Variable	mean (s.d.) range (n=922)	K-S value	*p*	n (sighting, search)
Depth	1200 m (300) 280-2000	0.213	< 0.001	922, 2944
Slope	14.9° (7.7) 0-35	0.142	< 0.001	922, 2944
SST	15.0°C (4.0) 5-18	0.053	0.152 (ns)	922, 1822

Surface oceanographic features – sea surface temperature and Secchi depth

There was no significant difference between the distributions of sea surface temperatures of sightings and those of search locations (Table 3.4). There was also no significant effect of water clarity (Secchi depth) on sighting rate at station locations for each trip (Pearson correlation: $r = -0.04$). Secchi depths ranged from 8.5 to 20 m (mean 14.5 m, s.d. 2.2 m).



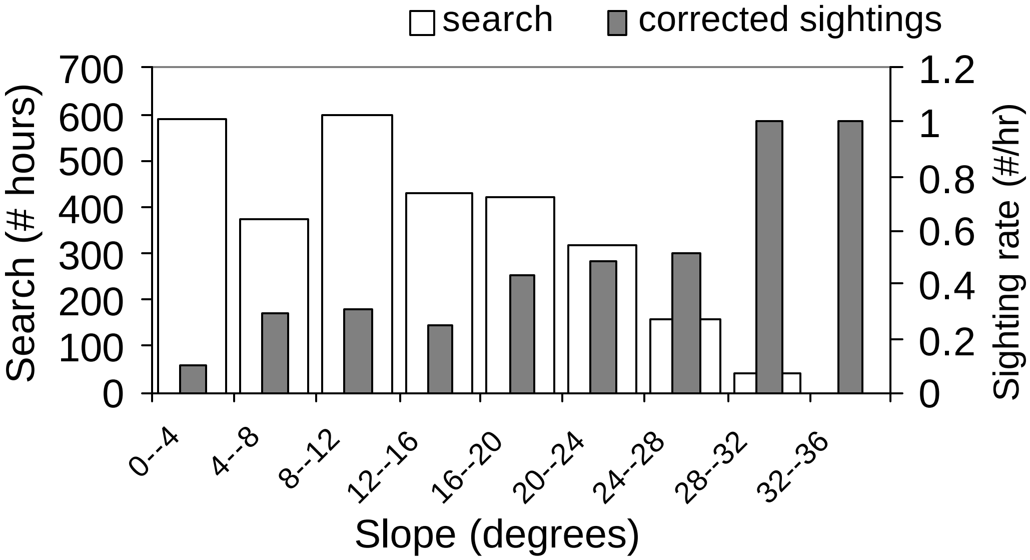


Figure 3.6. Variation in bottlenose whale sighting rate (number of sightings per hour of search effort) (a) with depth and (b) with slope. Search effort is shown for each depth or slope category to provide an indication of confidence in sighting rate.

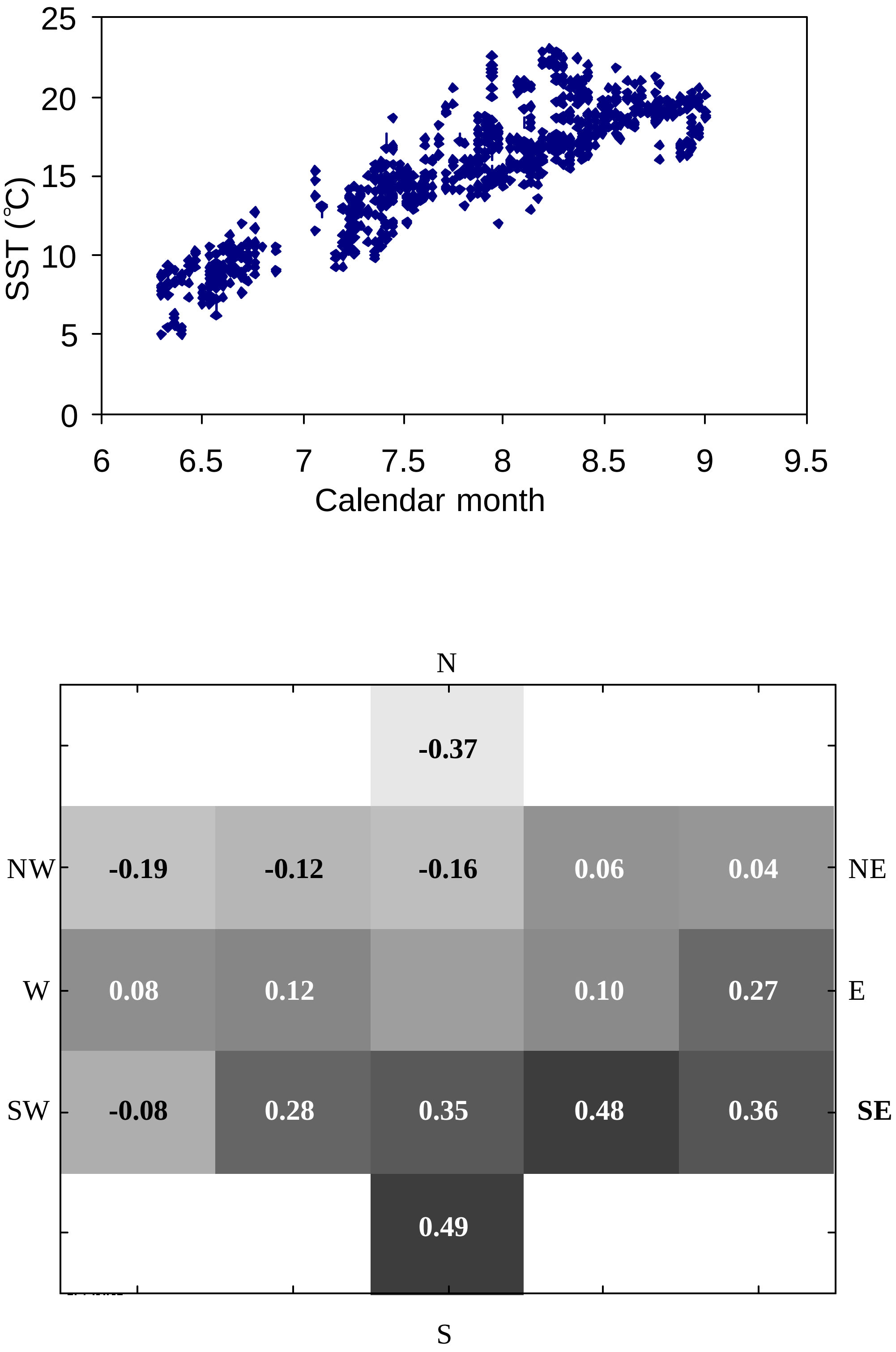
Sea surface temperature was significantly correlated with calendar month (Pearson correlation $r = 0.86$) but there was no correlation between Secchi depth and calendar month (Pearson correlation $r = 0.172$). There was also a significant relationship between whale group size and both month and SST, with larger groups sighted later in the summer at warmer sea surface temperatures (regression: decimal month $r = 0.187$, $p < 0.001$; SST $r = 0.253$, $p < 0.001$).

Sea surface temperature readings tended to vary in a consistent manner along each transect. Calculation of the average differences in temperature between stations (normalising all to zero at the centre station) showed a fairly consistent pattern of temperature difference across the Gully, regardless of monthly or yearly variation in absolute temperature. The northwestern part of the Gully was roughly 0.8°C cooler than the southeastern edge (Figure 3.7). Secchi depths recorded were much more variable and tended to show no such consistent pattern along transects (average coefficient of variation of Secchi depth of each transect 9.4 %).

Sub-surface biomass

The photographic records of hourly scattering layer variation at the central transect station were slightly confounded by up to 800 m spatial variation between records. However, in general little change was observed in scattering layer depth between approximately 7am and 6pm, the time in which transects were conducted (Figure 3.8), suggesting that the collection of transect data over the approximately 2-4 hour timespan of each transect was unlikely to have affected the results. A diurnal migration of the deep scattering layer towards the surface was observed during the night (Figure 3.8).

Investigation of the five biomass variables (50-300 m biomass, 300-600 m biomass, overall biomass, depth of primary scattering layer and thickness of scattering layers) showed little or no relationship with transect position for any of the four transects. The major exceptions were the depth and thickness of the scattering layer for the NW-NE transect (Table 3.5).



			N			
			-0.37			
NW	-0.19	-0.12	-0.16	0.06	0.04	NE
W	0.08	0.12		0.10	0.27	E
SW	-0.08	0.28	0.35	0.48	0.36	**SE**
			0.49			
			S			

Figure 3.7. (a) Scatterplot showing variation of sea surface temperature in the Gully over the summer. (b) Average differences in sea surface temperature at transect stations (see Figure 1) across the Gully. Temperature differences are given in °C relative to the central transect station.

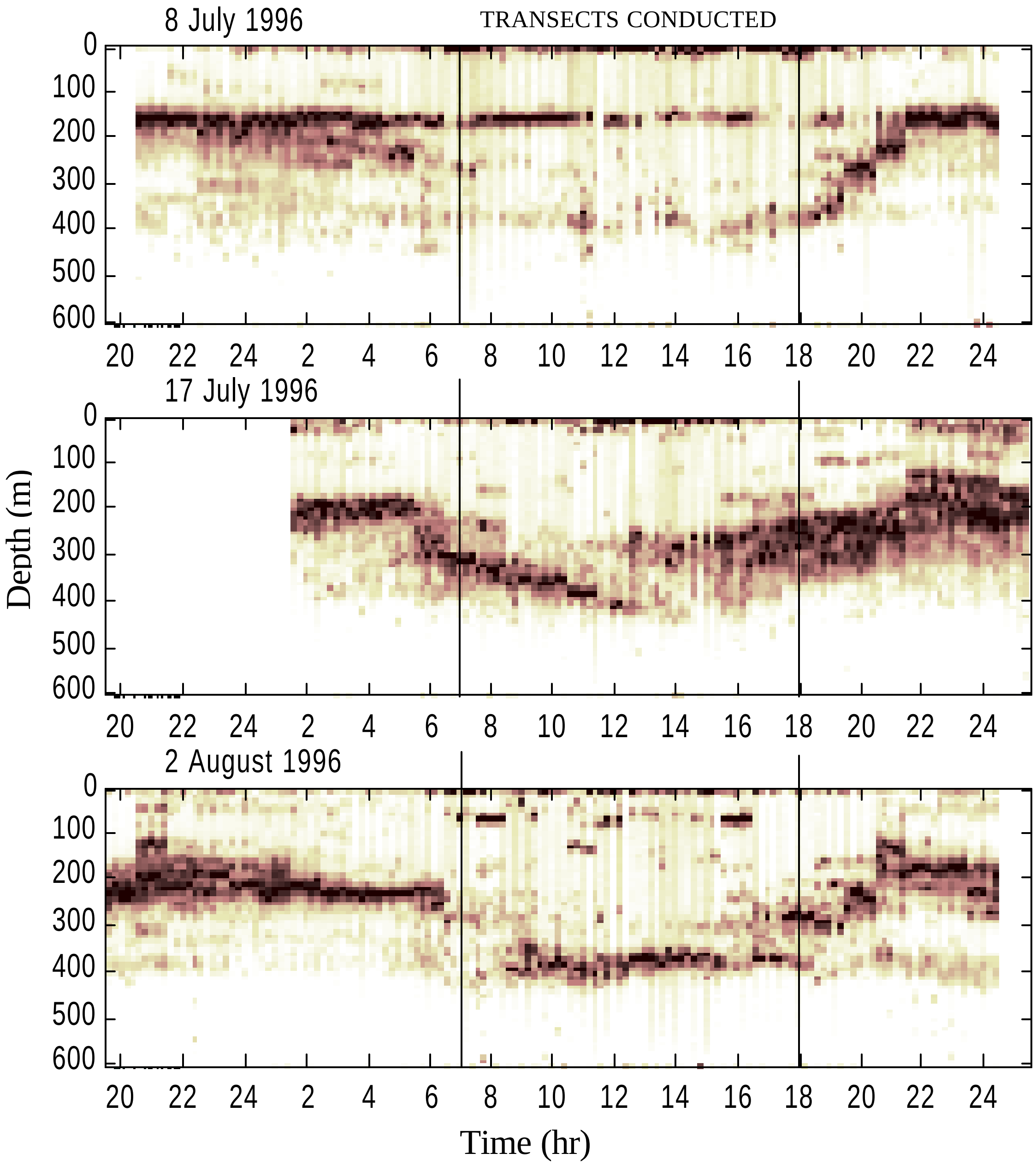


Figure 3.8. Daily variation in sub-surface biomass, based on still photographs taken of the sonar display at the central station of the N-S transect on three separate occasions in 1996. Dark areas show areas of highest biomass.

Investigation of the pattern of these variables across this transect showed that the relationship was probably related to the shallow depths at the sides of the transect, i.e., the scattering layer would become non-existent or shallower over shallow water depths.

All biomass factors in all transects varied significantly by year (Table 3.5, Figure 3.9). Depth of scattering layer was related to month for all transects except the NW-NE; upper water biomass was related to month within the N-S and NW-NE transects (Table 3.5). The general trend in these cases was for depth of the scattering layer to increase to a maximum in July or August and for the upper-water biomass to drop in July (Figure 3.10).

Table 3.5. Variation of biomass variables with space and time. P-values are shown for ANOVA of each biomass variable with area, year and month and interactions of these. Significant effects are shown in bold. (See Table 3.3 for variable abbreviations.)

Transect	Factor	Single effect			Interaction	
		area	year	month	area*year	area*month
N-S	biomS	0.171	**<0.001**	**0.001**	0.478	0.999
(*n*=160)	biomM	0.354	**<0.001**	0.552	0.784	0.919
	depS	0.937	**<0.001**	**<0.001**	0.347	0.455
	biomass	0.739	**<0.001**	**0.034**	0.902	0.925
	thick	0.232	**<0.001**	0.001	0.696	0.966
NW-NE	biomS	0.564	**<0.001**	**0.012**	1.000	0.996
(*n*=64)	biomM	0.295	**0.016**	0.880	0.515	0.872
	depS	**<0.001***	**0.003**	0.999	0.223	0.949
	biomass	0.765	**<0.001**	0.055	1.000	0.942
	thick	**<0.001***	**0.048**	0.763	0.950	0.999
W-E	biomS	0.813	**<0.001**	0.06	0.920	0.999
(*n*=80)	biomM	0.911	**<0.001**	0.228	0.775	0.996
	depS	0.732	**<0.001**	**0.019**	0.321	0.999
	biomass	0.980	**<0.001**	0.236	0.998	1.000
	thick	0.667	**<0.001**	0.391	0.973	0.999
SW-SE	biomS	0.661	**<0.001**	0.262	0.881	0.959
(*n*=64)	biomM	0.816	**<0.001**	0.459	0.076	0.998
	depS	0.945	**0.003**	**0.001**	0.963	0.702
	biomass	0.914	**<0.001**	0.987	**0.015**	0.998
	thick	0.990	**<0.001**	0.733	0.355	1.000

*change in deep scattering layer depth is due solely to sea floor depth

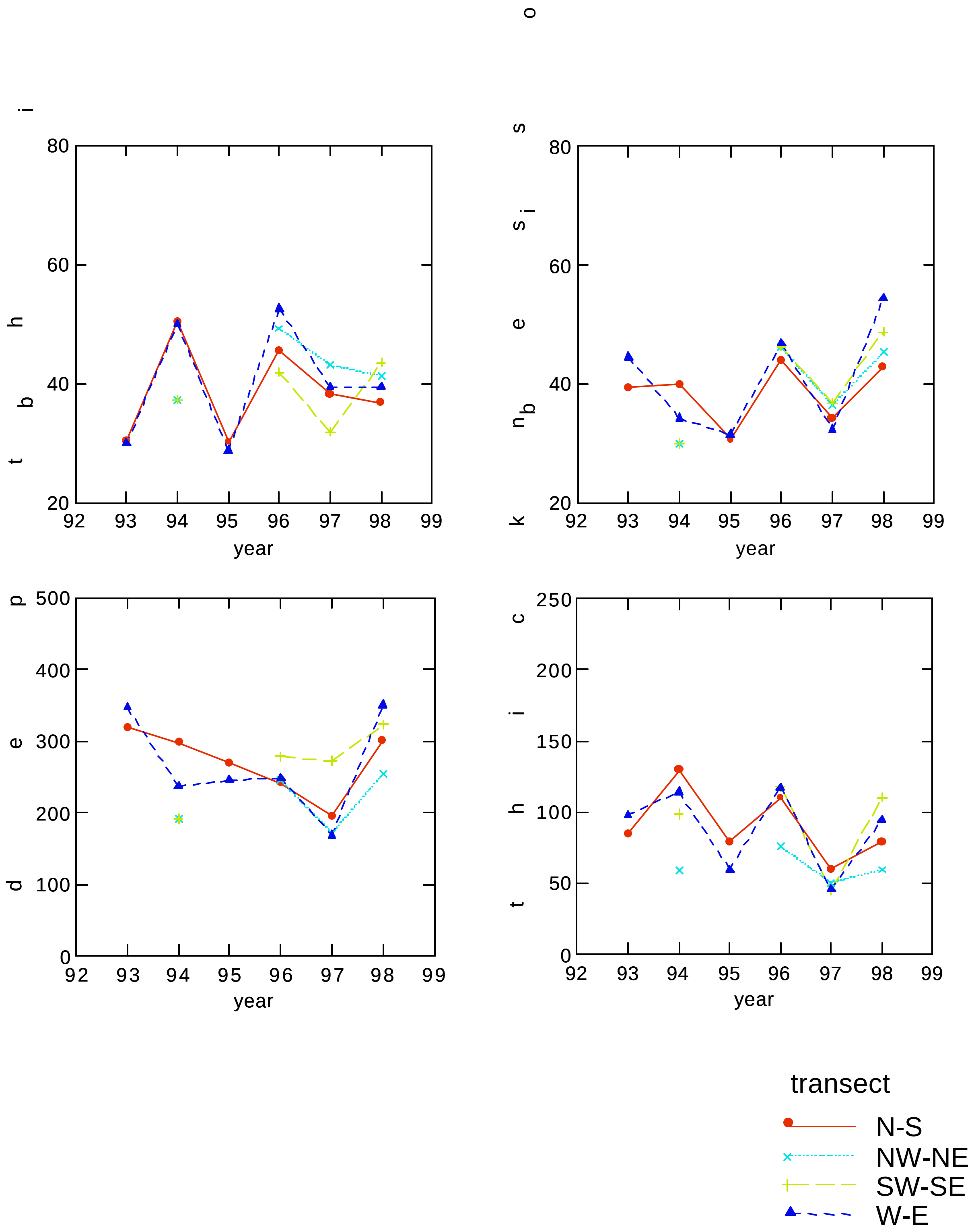


Figure 3.9. Interannual variation in sub-surface biomass parameters.

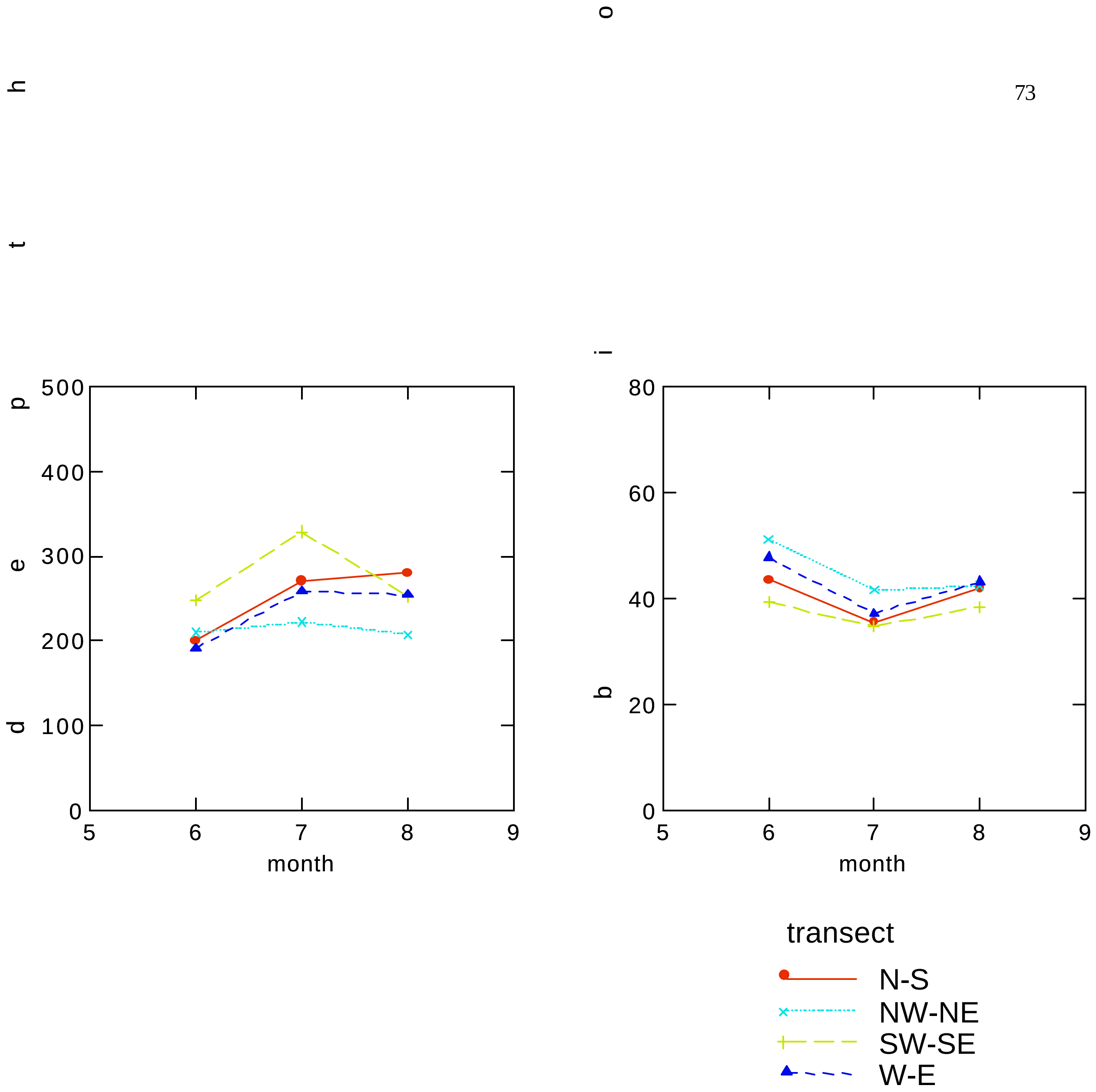


Figure 3.10. Monthly variation in sub-surface biomass parameters.

Correlation with bottlenose whale abundance

Bottlenose whale sighting density showed strong correlations with sea floor depth and slope over a range of scales (Table 3.6), but also showed some correlation with various indicators of sub-surface biomass (depth of the scattering layer and the mid-water biomass). Examination of different transects and between different spatial scales also revealed some interesting trends (Table 3.6). There was a larger correlation between whale density and mid-water biomass along the N-S transect at increasing spatial scale, a much smaller correlation over the E-W transect and no correlation over the NW-NE or SW-SE transects. This suggests that over a large scale, whales were found north or south within the canyon according to mid-water biomass. The depth of scattering layer was also strongly positively correlated with whale density. Over the N-S transect the strongest correlation was seen at a scale of 4 km. This is also the case for the NW-NE transect, although such correlations were much reduced for the E-W transect and the SW-SE transect. Overall biomass appeared to have little correlation with whale density except over large spatial scales.

Table 3.6. Spearman correlation coefficients between bottlenose whale sighting density and various parameters at varying spatial scales (see Table 3.3 for explanation of parameter abbreviations). Stronger correlations are shown in bold.

Transect	Scale (km)	SST	Secc	BiomS	BiomM	DepS	Thick	Bio-mass	Av Dep	Av Slop	n
N-S	2	-0.043	-0.140	-0.107	**0.265**	**0.275**	0.068	0.097	**-0.462**	**0.447**	111
N-S	4	-0.054	-0.193	-0.132	**0.285**	**0.293**	0.026	0.097	**-0.598**	**0.569**	65
N-S	8	-0.041	-0.182	-0.077	**0.366**	**0.286**	**0.210**	0.147	**-0.714**	**0.701**	35
NW-NE	2	**0.242**	0.176	0.068	-0.025*	**0.395**	**0.398**	-0.141	**0.710**	**0.699**	54
NW-NE	4	**0.205**	**0.260**	0.080	0.024*	**0.418**	**0.477**	-0.075	**0.772**	**0.772**	31
W-E	2	0.036	-0.034	-0.161	0.165	**0.204**	0.140	0.075	**0.637**	**0.747**	47
W-E	4	0.123	0.099	0.042	**0.224**	0.183	0.190	**0.234**	**0.541**	**0.833**	24
SW-SE	2	-0.015	0.056	-0.178	0.020	0.138	-0.212	-0.092	0.193	0.139	50
SW-SE	4	0.017	0.065	-0.148	0.014	0.009	-0.163	-0.032	0.198	**0.244**	30

* n=31 (2 km scale); n=8 (4 km scale) for NW–NE transect calculation of Biom2 (due to shallow depths over much of the transect)

As expected, there was a negative correlation between depth and whale density along the N-S transect since whales were primarily distributed toward the north (shallower) end of this transect line. Likewise, there was a positive correlation with depth for the NW-NE and W-E transects since whales were primarily found in the center of the canyon (i.e., the deepest part). The increase in the strength of correlation with increasing scale for both depth and slope suggests that while depth and slope were reasonable predictors of whale distribution, whales were associated with bathymetric features over scales of 4-8 km.

Annual variation in weather conditions

Interannual variability in weather conditions on the Scotian Shelf appeared to result in a fairly cyclical pattern of storm frequency with several years of few storms (i.e., few records of waves >8 m) and occasional years of much higher storm frequency (Figure 3.11). There was good correspondence between results at both stations (Pearson correlation $r = 0.84$).

Pearson correlations of bottlenose whale sighting rate at varying time lags (0 to 3 years) showed the strongest negative correlation ($r = -0.281$) between sighting rate and the previous year's winter storm activity. Although there was a tendency for bottlenose whale sighting rate to decrease in the year after high winter storm activity, this relationship was not clearly apparent (Figure 3.11). However, mean bottlenose whale latitude (see Figure 3.5) also showed the strongest positive correlation with storm activity at a time lag of one year ($r = 0.627$) or two years ($r = 0.742$). The modal bottlenose whale latitude showed the same trend. The greatest winter storm activity was recorded during 1993 and 1994, following which there was also a distributional change of bottlenose whales towards the northern part of the Gully during 1994-1996 (Figure 3.4, Figure 3.11). However, samples sizes are small and these results should be treated with caution.

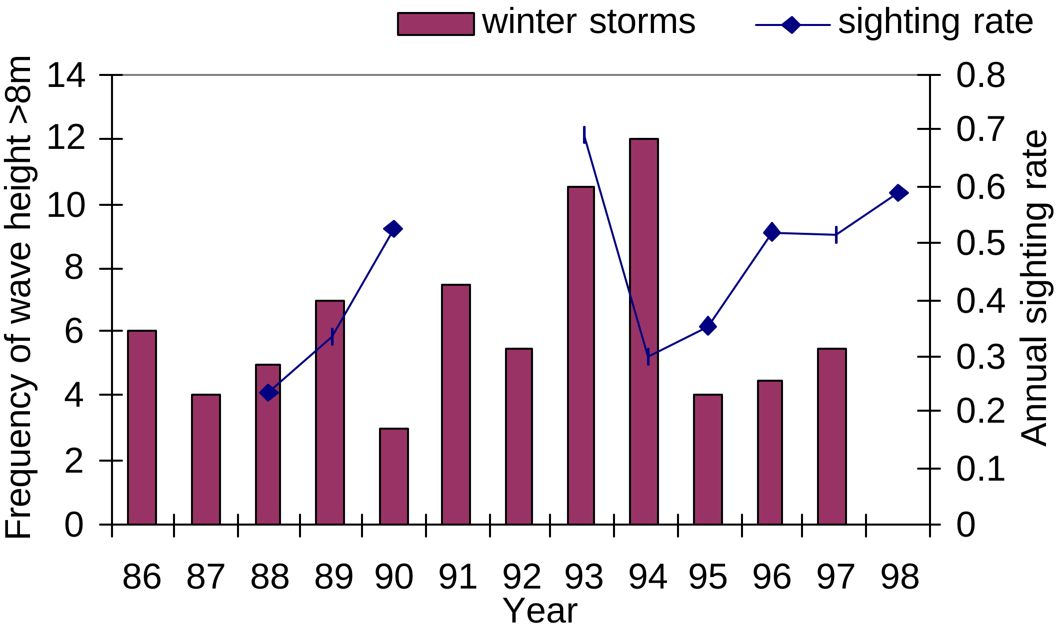


Figure 3.11. Mean yearly variation in winter storm activity on the Scotian Shelf at two stations close to the Gully (data provided by Environment Canada). Bars show the average number of days of wave height greater than 8 m from the preceding October to March of the year shown. The superimposed line shows the sighting rate for each year (from Figure 3.3).

DISCUSSION

This study is the first quantitative treatment of the environmental factors affecting the distribution of any beaked whale species and one of the first to detail the fine scale habitat use of an offshore species. The factor best correlated with whale distribution above the Gully appears to be depth, with the whales showing a preference for depths of between 750 and 1750 m (Table 3.4, Figure 3.6). Previous studies describing sighting locations of bottlenose whales elsewhere in the North Atlantic describe a similar pattern, although without consideration of effort, sighting densities cannot be assessed and such results are essentially circumstantial. Whales observed off the coast of Norway at Møre and Andenes appeared to have a fairly localised distribution at a steep rise in bathymetry (Benjaminsen 1972). Off the coast of Norway (Benjaminsen 1972), and off the coast of Labrador (Benjaminsen and Christensen 1979), the majority of whales were caught in water deeper than 1000 m with only occasional catches in water as shallow as 200 m and up to 80 km from the nearest 1000 m contour (Benjaminsen 1972). In the Gully the majority of sightings were in water deeper than 500 m but there were occasional sightings in shallower water depths (to a minimum of 280 m).

Of the environmental parameters measured, bottlenose whale density showed some correlation with mid-water parameters (depth of scattering layer, 300-600 m biomass and scattering layer thickness), but no correlation with surface environmental parameters (sea surface temperature or water clarity, Table 3.6). The frequency of the sonar used (60 kHz) corresponds to target sizes of greater than or equal to approximately 2.5 cm (Fletcher 1992). The primary constituents of this scattering layer, based on this size and the depth range of 200-300 m, were likely to have been shrimps and euphausiids. The primary prey of bottlenose whales is thought to be the squid *Gonatus*, adults of which are found close to the sea floor (Kristensen 1983). However, juveniles of this squid (pen length < 3 cm) are found in large shoals in the uppermost 80 m of the water column above deep water, although they have also been caught occasionally as deep as 1000 m (Kristensen 1983). The juveniles show ontogenetic descent to depth, taking larger prey as they grow (Nesis 1965, Kristensen 1983, Bjørke et al. 1997). Adult *Gonatus* feed on other squid and crustaceans, and so would be expected to show some correlation with the biomass of these organisms within the water column. Submarine canyons have previously been found to contain increased densities of sub-surface biomass (Hudon et al. 1993), but there has been little documentation of squid density around canyon areas, presumably due to problems of sampling in topographically diverse areas.

There was some variation in whale abundance and distribution within the Gully between months and years (Figure 3.3, Figure 3.5). During 1994 and 1995 there were both low abundances of whales, and whale distribution appeared to shift northward within the Gully (Figure 3.3, Figure 3.5). Although there was a general decrease in sighting rate with calendar month (Figure 3.3b), this may not be due to changes in overall whale density, since there was a concurrent increase in group size with calendar month.

The fact that bottlenose whale distribution is strongly correlated with depth and weakly correlated with sub-surface biomass, but shows no correlation with surface oceanographic parameters, suggests that bottlenose whales (and hence also their prey) are distributed primarily according to deep water phenomena. Evidence that bottlenose whales may be benthic foragers was noted by whalers, who observed a limey mud on the beaks of some animals and starfish in the stomach contents of others (Ohlin 1893). In the Gully, bottlenose whales have been recorded diving repeatedly to depths to, or close to, the sea floor, presumably in order to forage (Hooker and Baird 1999a). The yearly variation in bottlenose whale abundance was negatively correlated at a one-year time lag with high winter storm activity (Figure 3.11). There was also a correlation between high winter storm activity and the yearly latitudinal distribution of bottlenose whales at a 1-2 year time lag (Figure 3.5, Figure 3.11). A possible explanation for the negative correlation between winter storm activity and bottlenose whale abundance is that the high winter storm activity causes increased transport of material to the benthos and increased benthic productivity both in the Gully and on the shelf edge. There would therefore be increased foraging opportunities for the whales not only in the Gully but also on the shelf edge, thus resulting in a smaller population density of whales within the Gully. Within the Gully, such a change also appears to cause a northerly distributional shift. The lowest residency times of individual whales in the Gully were also found during 1990 (Gowans, 1999), the summer following lowest winter storm activity with a high density of whales. However, storm activity is at best likely only a poor proxy of changes in benthic biomass, and until more is known about the benthic fauna in the Gully and its spatial and temporal variation, it will be difficult to draw any further conclusions. Other physical parameters may also show a cycle of variation similar to that observed for bottlenose whale distribution. For example, shifts in the Gulf Steam (such as the northerly shift observed between 1994 and 1996, Taylor et al. 1998) may cause changes in sea floor currents and the deep-water biomass within the Gully.

It has previously been observed that cetacean biomass along the northeastern U.S. continental shelf edge was lower above submarine canyon areas than elsewhere (Kenney and Winn 1987). The results presented here show the strong apparent preference of northern bottlenose whales for the centre of the Gully submarine canyon (Figure 3.1). Hooker et al. (1999) also showed that this preference was exhibited by some other odontocete species, particularly sperm whales (*Physeter macrocephalus*) and striped dolphin (*Stenella coeruleoalba*) in the Gully. The difference between Kenney and Winn's (1987) study and the results obtained for the Gully is likely a consequence of the different scale of study. Directed study of odontocete distribution within each canyon area may reveal different features of habitat use compared to broad-scale studies encompassing a wide-range of canyon sizes, features and across a range of latitudes. It is also possible that Gully is not strictly comparable to other smaller submarine canyons. Whitehead et al. (1998) have suggested that the Gully may be oceanographically unique, extending further inland at the 500 m contour and forming a larger "cut" in the shelf edge than other submarine canyons along the eastern seaboard of North America. Such a large scale feature would be more likely to alter current flows and potentially might therefore favour prey distribution and attract cetaceans more than other smaller canyons.

Submarine canyons are thought to function as conduits of sediment to the deep ocean (Gardner 1989a). In a study of Baltimore Canyon, a downslope current was found in the upper canyon waters (275 m) while an upslope current was found in the lower canyon waters (600 m). Such a current flowing in the Gully would account for the slightly cooler temperatures observed at the northern transect station (Figure 3.7). The deposition of organics found above shelf waters is maximal at about 1000 m (Walsh et al. 1988, Biscaye et al. 1994), and would also be expected to occur at a greater volume in submarine canyons due solely to their increased shelf area (essentially consisting of an infolded shelf). Consistent with this hypothesis, Haedrich et al. (1980) found that the diversity and abundance of fauna in canyon slope areas was greater between 40 and 1290 m, but was reversed in waters deeper than this. Since the Gully is the largest canyon on the Scotian Shelf, high rates of organic deposition resulting in high diversity and abundance of fauna at depth would be expected.

A further oceanographic mechanism thought to bring nutrient-rich water from depth into nearer-surface waters is via internal waves (Cooper 1947). Internal waves have been studied in Baltimore Canyon (Gardner 1989b), where it was found that resuspension of sediment occurred predominantly in the canyon axis between 200 and 600 m depth, with little evidence of resuspension within the canyon axis deeper than 1000 m, or on the canyon walls or adjacent continental slope. Resuspension events were relatively frequent, primarily corresponding with the semidiurnal tide, after which it is thought that the sediment-laden water would move seaward. The resuspension caused by internal waves might therefore strip these depths of benthic biomass and account for the paucity of sightings to the north of the 1000 m contour up the Gully canyon axis (Figure 3.1).

The benthic fauna of the Gully is also thought to include a fairly high abundance of deep-sea corals (Breeze et al. 1997, Breeze and Davis 1998). These corals may grow to several metres in size and have been found between depths of 200 and 1000 m. Within the Gully they have primarily been found in waters to the north of the core area for northern bottlenose whales, but this is likely to reflect poor search effort since the majority of reports come from fishermen who tend to fish only in water shallower than 400 m (Breeze et al. 1997). The presence of corals generally reflects areas of hard substrate with moderate current flow, but not areas of high turbidity.

The 750-1500 m depth preference shown by bottlenose whales in the Gully (Figure 3.6) presumably reflects a high prey population in these waters, but the lack of correlation with biomass measured by sonar (to 600 m) suggests that their prey inhabits waters deeper than this, i.e., bathypelagic or benthic. Markle et al. (1988) investigated the fish and crustacean fauna of the Scotian Slope and found that decapod crustaceans were found at greater diversity and higher density at depths greater than 600 m, with caridean shrimps (*Acanthephyra* spp.) numerically dominant between 800 and 1200 m. Markle et al. (1988) noted that while these shrimps are usually considered pelagic, their results suggested that they are at least diel members of the bottom community. Since adult *Gonatus* are known to feed primarily on crustaceans or other squid (including other *Gonatus*), this presents a plausible explanation for the food chain governing bottlenose whale distribution in the Gully. It should be noted, however, that this remains a hypothesis.

Conclusion

This study has shown a general correlation of bottlenose whale distribution in the Gully with deeper-water features of the water column. However, further data are needed on the diet of bottlenose whales in the Gully and continued monitoring of their distribution is needed in order to further investigate the relationship between whale density and benthic biomass.

CHAPTER FOUR

Diving and ranging behaviour of odontocetes: a methodological review and critique

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ABSTRACT

Movements can be analysed in terms of horizontal or vertical dimensions, but cetacean movement is ultimately three-dimensional, and it is the integration of analyses of both horizontal and vertical movements that will provide the most insight about an animal's behaviour. Current field techniques can provide simultaneous information on both diving (vertical movements) and ranging (horizontal movements). I discuss techniques and analyses for diving and ranging studies, together with the advantages and disadvantages of each technique. Ranging studies using VHF or satellite-linked radio-tags have evolved alongside studies of diving behaviour using time-depth recorders, and problems associated with deployment and attachment techniques apply to both. The diving and ranging behaviour of twelve species of odontocete has been studied using time-depth recorders or acoustic transponders with VHF- or satellite-tags. However, differences in sampling techniques used, and summary statistics presented, have made comparisons difficult. I review these issues and suggest measures that should be presented in future studies of diving and ranging. In general, studies should be consistent in their presentation of the basic measures and statistics, and provide enough information for the reader to assess the limitations of the data.

INTRODUCTION

Information on three-dimensional ranging of animals can provide insights into many aspects of their behaviour and ecology, including the mating system, diet, and daily and yearly energy budgets (Harris et al. 1990, Boyd et al. 1991, de Leeuw 1996). Cetaceans spend the vast majority of their time beneath the water's surface, where they are invisible to observers, and the lack of ranging information in three dimensions has limited a comprehensive study of their ecology.

The term “diving” has been used to describe two different aspects of the behaviour of marine mammals. Some authors use “diving behaviour” to describe the pattern of surfacing (i.e., dive durations without information on dive depths, e.g., Leatherwood and Ljungblad 1979, Mate et al. 1994, 1995), while others use it to describe sub-surface behaviour of marine mammals (i.e., always including information on depths as well as duration of dives, e.g., Martin and Smith 1992, Westgate et al. 1995). Throughout this review I use the term “diving” to refer to the sub-surface behaviour of marine mammals, involving information on the depths of dives. In the past, information on diving behaviour of many cetaceans could only be obtained from incidental reports of whales taking line out when harpooned (e.g., Gray 1882), from whales entangled in deep sea cables (e.g., Heezen 1957), or from experiments with trained captive animals (e.g., Ridgway et al. 1969, Bowers and Henderson 1972). Knowledge of the diet of a species has also been used to infer dive depth (Fitch and Brownell 1968, Clarke 1976, Bernard and Hohn 1989), but while dietary information can be extremely useful for interpretation of studies of diving, it should not be used in lieu of them. Such techniques alone have provided either snapshots of behaviour or insights into the probable dive depths of some species, but cannot replace detailed description of diving behaviour.

More recently, researchers have been able to follow diving animals using ship-board echosounders or sonar systems, and have managed to track animals through all or part of their dives (Lockyer 1977, Gordon 1987, Papastavrou et al. 1989, Mano 1990, Kriete 1995, Simila 1997, Hooker and Baird 1999a). This technique is problematic for many odontocetes, because such systems may be audible to the study animal, potentially affecting the behaviour observed. In addition, this technique is only feasible for fairly large animals, which show relatively consistent movements. Among odontocetes, sonar-tracking has only been successful with sperm whales, *Physeter macrocephalus* (Lockyer 1977, Papastavrou et al. 1989), killer whales, *Orcinus orca* (Simila 1997), and partially successful with northern bottlenose whales, *Hyperoodon ampullatus* (Hooker and Baird 1999a, Chapter 5). With a smaller species, the bottlenose dolphin (*Tursiops truncatus*), short sequences of sonar recordings have been used to calculate swim speeds (Ridoux et al. 1997), but no vertical movement information could be recorded using this system.

Studies of ranging behaviour have also been subject to various limitations (Scott et al. 1990). "Discovery" tags were used during the whaling era to mark individual animals. These were labelled metal cylinders fired into the blubber of large whales (among odontocetes these were primarily sperm whales, ziphiids, killer whales, and occasionally pilot whales, *Globicephala* spp.) and later recovered from animals caught in a fishery. However, the potential of these tags to ascertain movements was limited to only the deployment and recovery points, and whales were often tagged and recovered during the same whaling season and on the same whaling grounds (Brown 1975). Other remotely deployed marking techniques such as spaghetti tags (vinyl covered strands of wire connected to a dart tip) suffered problems due to a high shedding rate (Sergeant and Brodie 1969, Scott et al. 1990). Paint-marking has also been tested on bow-riding dolphins (Watkins and Schevill 1976) but marks were only short-term (lasting up to 24 hours). Marking of captured animals (freeze-branding, fin notching, rototags or Petersen-type disk tags) has been fairly successful, but due to the effort involved in capture operations, sample sizes are usually limited, and fairly extensive effort is required to obtain resightings (Evans et al. 1972, Scott et al. 1990). The use of resighting data based on photographs of natural markings bypasses the logistics involved in applying marks, but also require extensive field effort, and can be biased by a number of factors, including uneven distribution of survey effort or animal distribution and variable recapture probabilities of individuals (Hammond et al. 1990). Some tracking information has previously been obtained by following cetaceans acoustically using hydrophone arrays, but this is problematic if the animals cease to vocalise at any time (Watkins and Schevill

1977). While groups of animals can be followed in this manner (e.g., Whitehead and Gordon 1986), following one animal is often impossible for periods longer than minutes, unless it is alone or is the only animal vocalising (Watkins and Schevill 1977).

The development of miniature instrumentation such as radio transmitters and time-depth recorders (TDRs) has opened up opportunities for following and recording both the diving and the ranging behaviour of aquatic animals (Evans 1971, Kooyman et al. 1976, Frost et al. 1985, Mate 1989, Scott et al. 1990, Anon. 1992b, Stone et al. 1994, Watkins et al. 1996). However, attachment of these devices to cetaceans is not simple. Unlike land-mammals, sea mammals cannot simply be collared. Pinnipeds can be captured fairly easily while hauled out on land, and instruments can be attached with glue and later recovered when the animals return to land to breed or moult (e.g., Le Boeuf et al. 1986). Live-capture operations for cetaceans, on the other hand, are either fairly complicated or impossible. Consequently, for many species, instruments must be remotely deployed. The high epidermal shedding rate and furless skin of cetaceans prohibits simple attachment with glue. Initial attachment of instrumentation to cetaceans involved harness backpacks (Norris et al. 1974), but these were found to cause problems of chafing and increased drag and have largely been discontinued for all but short-term deployments. Instead, instruments are now usually either pinned or sutured to the dorsal fin or ridge, or attached via suction-cups (although for male narwhals, *Monodon monoceros*, the tusk can be used for long-term attachment, Heide-Jørgensen and Dietz 1995). The relative ease of long-term attachment and recovery of instrumentation on pinnipeds has allowed studies of their diving and ranging behaviour to advance at a much greater rate than those of cetaceans (Butler and Jones 1997). It has been only recently that researchers have begun to use tags to investigate the diving and ranging behaviour of cetaceans in detail.

Previous comparative reviews of marine mammal ranging behaviour have focused primarily on diving behaviour, investigating the link between diving and body size across species (Boyd and Croxall 1996, Schreer 1997, Schreer and Kovacs 1997), modelling various aspects of diving behaviour (Kramer 1988, Houston and Carbone 1992, Thompson et al. 1993, Carbone and Houston 1996), tests of these models (Boyd et al.

1995), or reviews of the behavioural and physiological implications of diving (Boyd 1997, Butler and Jones 1997, Kooyman and Ponganis 1998). There have been few comparative reviews of ranging behaviour among marine mammals, but those of other mammal species have investigated the link between home range size, group size and body weight (e.g., primates, Clutton-Brock and Harvey 1977; carnivores, Gittleman and Harvey 1982). Technique-oriented reviews have described the various field methods used to study ranging behaviour in cetaceans (Scott et al. 1990), or compared the analytical techniques used to study home range (Harris et al. 1990). Analysis of three-dimensional home-ranges (e.g., Koeppl et al. 1977) appears to be rare. While cetacean ranging is three-dimensional, these animals are bound to the water surface by the necessity to breathe, and as such are probably not suited to such three-dimensional home range analyses. Nevertheless, studies of both diving and ranging complement each other in providing an accurate picture of animal movements. For future comparative work on diving and ranging, some consistency in presentation of data will be required between species. This chapter is the forerunner to such work and endeavours to point out the current inconsistencies in data collection and presentation for studies of odontocete diving and ranging.

In this review, I discuss the techniques available for studying diving and ranging of odontocetes, together with the advantages and disadvantages of each, the results that each technique can provide, and the analytical techniques available.

DIVING METHODOLOGY

To date, diving studies (providing information on dive depths) have been reported for 12 species and 20 populations of odontocetes (Table 4.1), which should provide some basis for interspecific comparison. However, differences in techniques, sampling regimes, and data retrieval present immediate obstacles to such comparison.

Table 4.1. Studies of odontocete diving behaviour showing the device used, together with the deployment and attachment methods, number of individuals tagged (*n*) and the sex of these when known. Devices include TDR with attached VHF transmitter (VHF-TDR), satellite-linked TDR (SL-TDR), VHF radio-linked TDR (RL-TDR), and acoustic transmitter. VHF or satellite tracking carried out in conjunction is shown in parentheses.

FAMILY/ Species	**Location**	**Deploy**	**Attach**	**Device**	***n***	**sex**	**Study**
PHOCOENIDAE							
Harbour porpoise (*Phocoena phocoena*)	Bay of Fundy, Canada	incidental catch, herring weir	pinned to dorsal	VHF-TDR SL-TDR	7 8	3m 4f; 7m 1f	Westgate et al. 1995 Read and Westgate 1997
	Hokkaido, Japan	incidental catch, set net	pinned to dorsal	TDR	2	2f	Otani et al. 1998
	San Juan Is., WA, USA	directed gill-net	suction-cup	VHF-TDR	1	1f	M.B. Hanson unpublished
Dall's porpoise (*Phocoenoides dalli*)	San Juan Is., WA, USA	remote by pole or capture by hoop-net	suction cup or pinned to dorsal	VHF-TDR; VHF-TDR, (satellite, VHF)	1 7	-	Hanson and Baird 1998 Hanson et al. 1998; R.W. Baird & M.B. Hanson unpublished
DELPHINIDAE							
Common dolphin (*Delphinus delphis*)	Southern California, USA	capture by purse seine net	pinned to dorsal	RL-TDR	3	-	Evans 1971, 1974
Heaviside's dolphin (*Cephalorhynchus heavisidii*)	St. Helana Bay, South Africa	capture by hoop-net	pinned to dorsal	SL-TDR (VHF)	3	2m 1f	Sekiguchi et al. 1998
Pantropical spotted dolphin (*Stenella attenuata*)	E. Tropical Pacific	capture by purse seine net	pinned to dorsal	VHF-TDR	11	-	Scott et al. 1993, 1995
	Hawaiian Is., USA	remote by pole	suction cup	VHF-TDR	4	-	R.W. Baird unpublished
Atlantic spotted dolphin (*Stenella frontalis*)	Gulf of Mexico, USA	rehabilitated	pinned to dorsal	SL-TDR	1	m	Davis et al. 1996
Short-finned pilot whale (*Globicephala macrorhynchus*)	Hokkaido, Japan	remote by crossbow	suction-cup	VHF-TDR	2	-	R.W. Baird & M. Amano unpublished

FAMILY/ Species	**Location**	**Deploy**	**Attach**	**Device**	***n***	***sex***	**Study**
Killer whale (*Orcinus orca*)	*residents* – Haro Strait, WA, BC; SE Alaska	remote by crossbow or pole	suction-cup	VHF-TDR	34	17m 13f	Baird 1994; Baird et al. 1998, R.W. Baird unpublished
	transients - WA, BC; SE Alaska	remote by crossbow or pole	suction-cup	VHF-TDR	6	4f	Baird, 1994; Baird et al., 1998, R.W. Baird unpublished
MONODONTIDAE							
Beluga (*Delphinapterus leucas*)	Cunningham Inlet, NWT Canada	capture by hoop-net	pinned to dorsal ridge	SL-TDR	13	2m 11f	Martin and Smith 1992; Martin et al. 1993; Smith and Martin 1994; Martin et al. 1998
	Eastern Devon Is., NWT Canada	capture by hoop-net in shallows	pinned to dorsal ridge	SL-TDR	6	2m 4f	Heide-Jorgensen et al. 1998; Richard et al. 1998
Narwhal (*Monodon monoceros*)	Baffin Island, NWT, Canada	driven into nets in shallows	pinned to dorsal ridge	SL-TDR	3	3f	Martin et al. 1994
	Melville Bay, northwest Greenland	driven into nets	tusk mounted / pinned to dorsal ridge	SL-TDR	9	5m 4f	Heide-Jorgensen and Dietz 1995
ZIPHIIDAE							
Northern bottlenose whale (*Hyperoodon ampullatus*)	The Gully, E. Canada	remote by crossbow	suction-cup	VHF-TDR	2	-	Hooker and Baird 1999
PHYSETERIDAE							
Sperm whale (*Physeter macrocephalus*)	Caribbean Is.	remote by crossbow or gun	dart	acoustic	2	2m	Watkins et al. 1993

**Not represented: Kogiidae, Platanistidae, Iniidae, Pontoporiidae

The terminology used to describe different equipment and techniques can be confusing. To minimise this, I use the following:

- TDR: instrument which records depth (and possibly other parameters) with associated information on the time at which depth recordings were taken
- DD-TDR: download data TDR (needs to be recovered to download)
- SL-TDR: satellite-linked TDR, transmits (limited) dive data to satellite-receiver
- RL-TDR: VHF radio-linked TDR, transmits (limited) dive data to a VHF receiver
- VHF-TDR: tag containing VHF transmitter and DD-TDR, VHF transmitter is solely for location of TDR.

Techniques

Three methods are currently used to obtain diving behaviour data from tags.

(1) Attachment of a time-depth recorder (DD-TDR) which stores the data to be downloaded later to a computer.

These tags record depth information (and often other information such as velocity, temperature and light-levels) at user-defined intervals until the tag is recovered or until its memory is full. The tag must be recovered for the data to be transferred to a computer for analysis. Therefore animals must either be recaptured, or a buoyancy mechanism and VHF transmitter to locate the tag are required (or, in some cases, tags may be recovered after washing ashore without the need for such a locating transmitter e.g., Otani et al. 1998).

(2) Attachment of a time-depth recorder which transmits the data remotely via (a) VHF signals to a nearby receiver (RL-TDR), or (b) by UHF signals to a satellite (SL-TDR).

Data-transmitting TDRs (either RL-TDR or SL-TDR) require the tag antenna to be above the water surface for transmission. Since cetaceans generally surface for periods of seconds only, this places severe restrictions on the transmission time available. Data collected on-board the TDR must therefore be summarised prior to transmission. For VHF radio-transmission, the receiver must be within range to pick up good signals from the tag (commonly 4-10 km; this range depends on the power of the transmitter and height of the transmitting and receiving antennas, among other factors). For UHF radio-transmission, a receiving satellite must be passing overhead (see Mate 1989 for details of Argos satellite paths). Furthermore, the reliability of the uplink depends on whether environmental and atmospheric factors degrade the transmitter signal.

(3) Attachment of an acoustic transponder tag which can be interrogated sonically, or which transmits continuously.

Acoustic transponder tags may transmit data continuously at a pulse rate dependent on depth (Goodyear 1993), or can be interrogated at intervals (Watkins et al. 1993). One problem with acoustic tags is that, generally, the signals can only be received from less than 2 km away (Goodyear 1993, Watkins et al. 1993). This distance is dependent on the frequency used and the environmental conditions. Lower frequencies can be received at greater distances, but the signals would be more likely to lie within the hearing range of the animal, potentially affecting its behaviour. This is generally a greater problem for odontocetes than mysticetes, due to the former's presumed higher frequency hearing range.

The major differences in these techniques result from limitations of data sampling and data retrieval. In general, two data-storage/retrieval regimes are used in time-depth recorder studies: storage of the raw depth data, or on-board summarising or processing of data into a format thought to be representative of each dive. Associated with these are two respective data retrieval methods: recovery of the tag and the stored data, or remote retrieval of data from the tag while still deployed.

Sampling regime

The collection of data at regular intervals over each dive can potentially provide a large amount of data over a short time-span. This method gives the most detailed picture of dive profiles, often providing a second by second account of the study animal's depth. This method also allows the user to scan the data for potential errors, which would be impossible to detect if only certain parameters (such as maximum depth) were collected for each dive. For example, if the maximum recorded depth is at the limit of the depth sensor's range, it is impossible to know whether the animal went deeper than this. Viewing the dive profile would help determine whether the animal went beyond the range of the sensor, whereas if only maximum depth is recorded the means to check this is lost and must be inferred from the distribution of depth values (Heide-Jørgensen and Dietz 1995). Furthermore, it is only possible to correct for temperature-related depth shifts when the entire dive profile can be viewed (e.g., see Figure 4.1). Viewing such a profile, it is apparent that the surface is recorded at increased depth immediately after ascent from a deep dive (from much cooler waters), and then gradually shifts back to zero metres over a period of time spent in warmer surface waters.

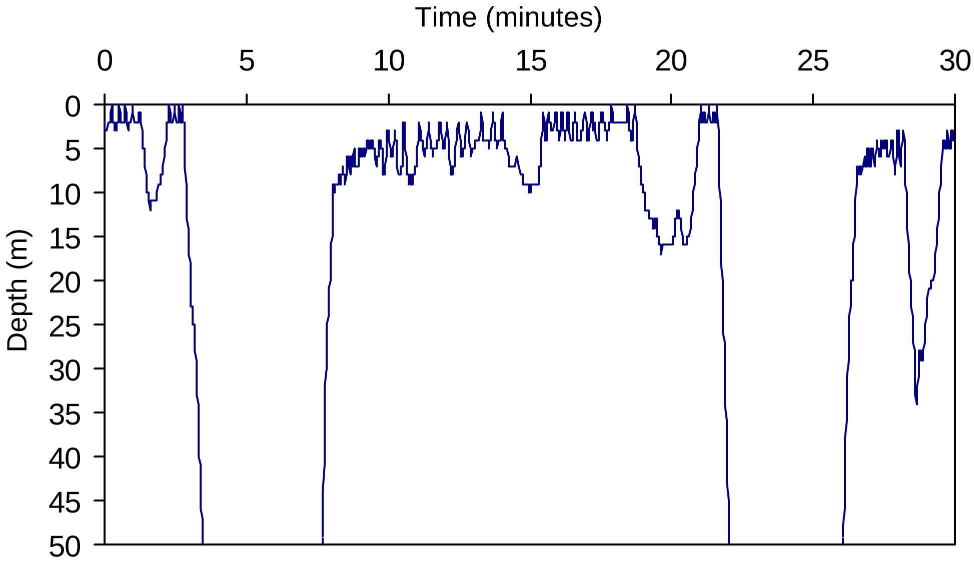

Figure 4.1. Dive profile showing temperature-related shifts in depth readings. After ascent from a deep dive the cold temperature, which the tag was exposed to, causes an offset in the depth measurement such that the surface is recorded as 10 m depth. This depth offset gradually returns to zero as the tag warms up over 5 min. This temperature-related shift in depth measurements potentially prohibits accurate assessment of dive durations or amount of time spent at different depths, particularly for tags where dive profiles cannot be observed in detail. Profile from short-finned pilot whale, Hokkaido, Japan, sampling rate 1 second, resolution 1 m; R.W. Baird and M. Amano, unpublished data. Note only the top 50 m of depth readings are shown; this TDR recorded depth to 237 m and the two long dives (~ 4 min) went to over 200 m.

The collection of summary statistics for each dive, in contrast, provides a much coarser resolution of data over the same time period. There is some debate as to the best method to summarise dives such that the least amount of information is lost (Anon. 1992a). Currently summary statistics are often generated as frequency distributions of dives within certain depth and duration ranges. For example, summary statistics recorded for satellite-tagged narwhals included: maximum depth during 24 hours, number of dives deeper than a predefined value in various depth categories in four six-hour sampling periods, and frequency of dives in six duration categories for each six-hour period (from Heide-Jørgensen and Dietz 1995). However, without prior information on a species' diving behaviour, the definition of these ranges may not be optimal.

Histogram summary statistics are useful for asking specific behavioural questions in terms of broad categorisation of results (e.g., are there differences in summary dive parameters between the four six-hour time periods?). One recent study showed broad-scale similarity between biological data recorded using histogram summary statistics and those obtained from downloading raw dive data (Burns and Castellini 1998). However, summary statistics provide no information on the behaviour of the animal during these dives, or on the animal's descent and ascent rates, as can be gained from the dive profile. Because dive information is obtained within broad user-defined limits, researchers are unable to look at dive shapes (Schreer and Testa 1995), or to investigate dive features such as the correlation of dive depth and duration. Furthermore, short-term changes in diving behaviour (e.g., crepuscular activity) would easily be overlooked using long periods over which summary data are calculated.

Data retrieval

Tag recovery (and downloading of archived data) provides the potential to store only a fixed amount of data (usually governed by the finite memory capability but potentially also the limited battery life of the tag). This finite capacity leads to a trade-off between sampling rate and total sampling time, at least for long-duration attachments (Boyd 1993). There are also problems in comparisons between studies using different sampling rates as this can affect the resolution of dive shape obtained (Schreer 1997), and can also provide quite varying results for measures such as time spent at the surface and the number of shallow dives. A higher sampling rate will always provide the most detailed data, and will be of most value for fine-scale analysis of feeding ecology. However, at minimum a sampling rate should be used which provides a good representation of dive shape.

Using satellite-linked data retrieval, it is only possible to send small amounts of data at each uplink. The number of uplinks will be affected by the number of satellite passes and the behaviour of the study animal. The number of satellite passes is latitude-dependent, with at least three satellite passes at the equator and up to 27-30 at high latitudes, from between two and three satellites per day (Mate 1989, A.R. Martin, personal communication). Species which surface for short periods, or which show very little of their back (or tagged surface) above the water, will have fewer viable uplinks. Martin et al. (1993) describe the problems found in using this method to study beluga whales: *"The constraint on the amount of data that can be sent and received within the ARGOS system proved to be a considerable limitation in this project and will inevitably be so in any study of marine mammals using ARGOS. A maximum of 256 bits of data can be sent in a transmission, and the probability of any such transmission coinciding with a satellite pass, and therefore potentially being received by the satellite (termed an 'uplink'), is small. Even then, many uplinks are corrupted, often by the animal submerging during the propagation of the signal itself."*

The major advantages of this method are its potential for longer sampling time (up to months), allowing a great deal of information to be gained from one study animal, and the range at which monitoring can be conducted. However, increased sampling time is not equivalent to increased sample size, which is based principally on the number of animals sampled (Machlis et al. 1985). Increased sampling time is likely to increase the probability of detecting the extremes within the data, such as the maximum depth or the maximum dive time (Link and Sauer 1996), and to detect long-term periodic variation. However, mean or modal values are better indicators of routine dive depths or durations than are maximum values, and are of more value in comparisons between different studies. The other major advantages of the data-transmission method are that the tags do not have to be recovered in order to access the data, and simultaneous monitoring of more than one animal is far simpler than when each animal needs to be tracked either acoustically or by VHF. However, the increased cost of this method may necessitate a small sample size.

In general, recovered TDRs tend to use regular and frequent sampling and are often deployed for only short intervals and so are not limited in terms of data storage. As these tags are retrieved they may also be deployed multiple times on several individuals. Satellite-linked TDRs are used to collect longer-term but limited data, so researchers can either collect summary statistics on all dives, or more complete information on a selected sample of dives prior to the uplink (e.g., Martin and Smith 1992, Martin et al. 1993). These tags are generally not recoverable and therefore cannot be reused.

Each potential study (taking into account the species, habitat, available funding, boats, experience of researchers, questions to be asked) should be assessed in its own right and a decision made on that basis as to the methodology to be used. For investigations of new species or populations it may be valuable to sample depth values (and other variables) at frequent intervals, in order to ascertain some of the basic dive characteristics for several individuals in a species/population. These detailed data can then be used to define dive types and an optimal sampling regime for use in longer-term studies.

RANGING STUDIES AND SPATIO-TEMPORAL SCALE

For the purposes of this review, a comprehensive assessment of ranging behaviour is not practical, and a good review of the topic is available in Scott et al. (1990). My aim instead is to discuss the study of ranging in conjunction with the study of diving behaviour. The same radio-tracking mechanisms used for telemetry or for recovering dive-recording tags are used to follow (VHF radio-telemetry) or remotely track (satellite-linked radio-telemetry) animals. I will compare these with the other commonly used field technique - re-identification of individuals using photo-identification. The major problem involved in studies of ranging is scale (i.e., the spatial and temporal resolution at which behaviour is measured). An animal's behaviour may appear very different if viewed over a scale of seconds compared to one of years, or over a range of a few metres compared to one of thousands of kilometres. To understand behaviour, observation should take place at a similar scale to the behaviour being studied (Levin 1992, McConnell and Fedak 1998). Individual locations recorded by photo-identification are usually opportunistic in space and time. A more detailed view of a particular animal's behaviour is obtained by focal following of one individual or group (see review of methodology in Mann 1999). Photo-identification and focal sampling (VHF radio-tracking and satellite-linked radio-tracking) operate over different scales, with potential implications for interpretation or comparison of results (Table 4.2). However, not all techniques are equally applicable to all species for reasons discussed below.

Table 4.2. Measurement of ranging behaviour.

Type of tag	Temporal scale (study duration)	Sampling rate	Accuracy	Disadvantages	Advantages
Photography of natural marks	months - decades	highly variable (hours - years)	~ 100 m (using GPS or LORAN)	biased by distribution of effort in space and time	inexpensive for inshore species; large sample sizes; simultaneous behavioural data can be collected
VHF tags	up to months	each surfacing or every few surfacings	~ 100 m - 1 km (dependent on tracking distance)	small sample sizes; tracking may be difficult in some areas, e.g., offshore; moderate cost	simultaneous behavioural data can be collected
Satellite tags	up to months	approx 1-3 times per day, dependent on satellite coverage	~1 – 10 km + (measure of accuracy available with each satellite pass)	high cost; small sample sizes	does not require field effort post-deployment

For cetaceans which are relatively slow-moving and are found in small groups, photo-identification of natural or man-made marks may be used to identify individual animals, and to provide movement information when an individual is re-sighted in different locations. (This technique is more difficult for offshore cetaceans both due to increased cost and logistically, with cetaceans such as oceanic dolphins found in groups of several hundred.) As many odontocetes cannot be followed easily between surfacings, photo-identification can provide only a series of snapshots of animal positions. In addition, these locations are highly dependent on boat position, and unless coverage is uniform in space and time, will not accurately represent the animal's ranging behaviour (Kenney and Winn 1987, Whitehead et al. in press). While detailed movements within a certain study area over a long timescale may be obtained, the possibility of the study animals making long-distance movements to unsampled areas cannot be refuted (e.g., the short-term movements of right whales, *Eubalaena glacialis*, out of areas in which they are usually encountered, Mate et al. 1997).

For some populations, animals can be followed in real time on the basis of their marks (e.g., killer whales, Baird and Dill 1995; sperm whale groups, Whitehead and Gordon 1986; some bottlenose dolphin populations, Mann and Smuts 1998). However, for species that have unreliable markings or that make long, unpredictable dives, radio-telemetry provides a means for tracking animals. VHF radio-tracking can potentially give the most detailed information about animal movement at small spatial and temporal scales, allowing researchers to track animal location during every surfacing bout, either visually or by using a groundtruthed signal strength and bearing from a known position. From this, it is possible to calculate rates of movement for each surfacing, or over short time periods of hours to a few days (for methods see White and Garrott 1990, Turchin 1998). However, this type of radio-tracking is often logistically constrained over larger scales, due to boat size or fuel limitations, or, in the case of shore-based studies, when animals swim out of receiver range.

Satellite-linked radio-tracking usually provides a less-detailed but longer-term and larger-scale picture of animal movements. Coverage of Argos satellites varies depending on geographic area, with more frequent satellite passes (and thus more potential locations) at higher latitudes (Mate 1989). This technique is more suitable for monitoring long-distance movements, providing on average one or two reliable locations per day from dorsal ridge or dorsal fin attached transmitters (Dietz and Heide-Jørgensen 1995, Davis et al. 1996). The accuracy of these positions can be quite variable however (Burns and Castellini 1998). The Argos manufacturers are attempting to introduce various improvements for their next generation of equipment (Taillade 1998). These include improving satellite coverage, increasing data volume transmission capability, improving satellite receiver sensitivity to reduce platform power requirements or enhance transmission performance, and to allow control of platforms remotely by allowing two-way communication with the transmitter through the satellite receiver (Taillade 1998).

DEPLOYMENT AND ATTACHMENT TECHNIQUES

The major problem with using TDRs or radio transmitters on odontocetes has been tag attachment. There are two major deployment techniques: capturing the study animal and attaching the tag, or remotely-deploying the tag (Table 4.1). Associated with these are two attachment techniques: penetrating - pinning through the dorsal fin or using a barb/hook attachment to the blubber, or non-penetrating - using suction-cup attachment to the skin surface (Table 4.1).

Capturing odontocetes is only feasible for smaller to midsize species (Asper 1975, Walker 1975). Methods of capture include hoop-netting smaller species (e.g., Dall’s porpoise and Heaviside’s dolphin), purse-seine netting midsize species (e.g., pantropical spotted dolphin), and drive captures for larger species (e.g., belugas and narwhals). The expense and logistical difficulty of such operations encourage the use of penetrating tags since these usually have longer-term attachments than suction-cup tags. Furthermore, long-term attachment is needed to ensure that “normal behaviour” can be recorded after a potential recovery period. Some odontocetes have been tagged after incidental capture in herring weirs or other fisheries (Westgate et al. 1995, Read and Westgate 1997, Otani et al. 1998), although such samples may be biased. While this is feasible for coastal fisheries, the logistics of getting researchers to incidentally caught (but living) animals offshore may be problematic (Otani et al. 1998).

Tags may be remotely deployed by crossbow (or a shotgun, Watkins 1993) or by using a long pole (Baird 1994, 1998, Stone et al. 1994, Schneider et al. 1998). Pole deployment is relatively simple for large, slow-surfacing or bowriding species (Stone et al. 1994, Giard and Michaud 1997, Hanson and Baird 1998), but is problematic for odontocete species which do not bowride, such as killer whales or northern bottlenose whales. Crossbow-deployed tags are usually more successfully applied using penetrating barb attachments than using suction-cup attachments, as the latter have a high chance of bouncing off. However, remote deployment of penetrating tags is unsuitable for many small odontocetes, due to relatively thin blubber layers and thus the increased chance of harming the animal (see diagram in Goodyear 1993). For larger odontocetes, whose capture is not feasible, remotely deployed suction-cup tags are therefore gaining popularity, despite deployment difficulties. Typically these remain attached for hours (a mean of 9.75 hours for 41 deployments on killer whales; R.W. Baird, unpublished data), though such attachments have held for up to 38 hours on a harbour porpoise (M.B. Hanson, unpublished data), and up to 3 days on a fin whale (Giard and Michaud 1997, Baird 1998). One suction-cup system has recently been designed to be used on captured small cetaceans, and involves a moulded dorsal-fin design using multiple small suction cups and velcro straps (Shippee et al. 1995).

SUMMARISING DIVING AND RANGING BETWEEN STUDIES

To date, TDR studies have been “published” (in theses or peer-reviewed literature) on the diving behaviour of nine odontocete species (Table 4.1), almost all of which have also used either satellite or VHF tracking simultaneously with collection of dive data. I discuss some of the inconsistencies in data collection, analysis, and presentation among these. Suggestions for future studies are made to minimise these differences, making comparisons between studies both more appropriate and more feasible.

Definition of diving behaviour

The nature of cetacean adaptation is that much behaviour (including travelling behaviour) is sub-surface. Cetaceans presumably travel below the surface due to the potential energetic advantages of reduced drag there (Hertel 1966, Law and Blake 1994). During surfacing bouts, most cetaceans travel and make shallow dives between breaths. In order to investigate these two behaviours separately, it is therefore necessary to differentiate between deep diving, and respiratory or travelling dives at the surface. Inclusion of surfacing bouts can potentially cloud the analysis of behavioural function since several dive classes are combined in analyses. Furthermore, wave action and zero-offset drift make it difficult to determine if these shallow "dives" are real.

Many authors subjectively define a dive as deeper than twice the value of error or resolution of the depth sensor (this appears to have originated from the design of analysis programs by the TDR manufacturer Wildlife Computers, Redmond, WA, rather than from any objective definition). TDRs were first developed for use on seals, which often stay continuously at the surface of the water between dives, and for which such a cut-off dependent on sensor-resolution is useful. It is apparent that use of tags with different depth resolution would give very different estimates of measures such as "time spent at surface" or "mean depth of dives" using this criterion. Deep, foraging dives of cetaceans are usually followed by a surfacing bout of shallower dives, the purpose of which may be to replenish oxygen stores or travel. The use of this 2x resolution value provides a cut-off point for what is underwater and what is at the surface, but is likely to affect interpretation of results to a large degree. To infer "foraging" behaviour from all dives greater than this value (which are likely to incorporate both foraging and surfacing dives) is therefore potentially a misrepresentation. Likewise, the size of the study species will probably influence the depth of surfacing bouts. A harbour porpoise may remain above 2 m during surfacing bouts, whereas a killer whale or bottlenose whale is likely to submerge deeper than this solely due to its body size.

There has been a good deal of interest in how to classify dives (Anon. 1992a, Schreer and Testa 1995, Schreer 1997). While these studies have usually been concerned with delineating more categories than deep versus surface, the issue is still to find an objective criterion for differentiating between dive types, in this case shallow, short dives during respiration bouts, and longer, deeper dives which serve other functions (e.g., foraging).

Various methods have been used in both cetacean and pinniped studies to discriminate surface from deeper dives. An example dataset of 24 hours of diving data (recorded at 1 sec intervals to 1m resolution using a Wildlife Computers Mk 6 TDR) from a southern "resident" killer whale in Haro Strait, WA (R.W. Baird, unpublished data) is used to demonstrate differences between these methods (Figure 4.2).

1. Elimination of any dives less than twice the depth sensor resolution from analysis and presentation (Figure 4.2a). This criterion often appears to be used by default. Satellite-linked TDRs, for which post-hoc investigation of dives is limited, require the use of a simple definition of this type (e.g., Heide-Jørgensen and Dietz 1995, Davis et al. 1996). This cutoff has also been used for TDR studies (although the presence of a variety of dive types may be noted, e.g., Baird 1994, Westgate et al. 1995).
2. Subjective grouping of "diving" behaviour according to certain dive characteristics (Hindell et al. 1991, Martin and Smith 1992, Le Boeuf et al. 1993, van Dam and Diez 1996). A result of this is that criteria such as "foraging dives are considered to be those of more than 1 min at maximum depth" are applied (e.g., Hindell et al. 1991) (Figure 4.2b). Martin and Smith (1992) use a similar subjective definition and present information for flat-bottomed dives deeper than 150m. However, this weights dive statistics toward deeper and longer dives, whereas studies including "respiration" dives are weighted toward shallow, short dives.
3. Investigating the multimodal nature of a three-dimensional plot of depth and duration can be used to discard shallow, short-duration dives (Boveng et al. 1996) (Figure 4.2c). Independent histograms of either duration or depth can be used, but tend not to represent the data as clearly.
4. Investigating the cumulative time spent in dives of different durations and using the bimodality of this to distinguish between long and short dives (Figure 4.2d). This weights the duration of dives according to the time involved, presenting a perspective on the investment rather than solely the number of dives in duration categories.
5. Use of multivariate statistical analyses such as cluster analysis or artificial neural networks to identify groupings within the data (Schreer and Testa 1995, Schreer

1997) (Figure 4.2e). Considerable care must be taken as to how many groupings are defined within the data, however.

6. Use of a log-survivorship plot of dive or surface durations (Fagen and Young 1978, Gentry and Kooyman 1986, Beavers and Cassano 1996) (Figure 4.2f). This technique is used for identifying bouts of behaviour, and can therefore be used to separate a bout of respiration dive types from deeper dives. A break or inflection in the slope of the log survivor function represents a change in probability of the event, signalling the presence of bouts within the data.

These techniques range from completely subjective (#2) to almost completely objective (#5 and #6) means to identify dive type. Among published odontocete diving studies there are very few explanations or definitions for the delineation of foraging dives. For the dataset shown (Figure 4.2), it is interesting to note that four of the six methods give relatively similar mean dive depths for “long” dives (and relatively similar sample sizes), while the other two methods produce widely divergent results. Twice the resolution of the depth sensor, for the example data (Figure 4.2a), does not appear to be sufficient when sensor resolution is relatively precise as it lumps many short, shallow dives into the “long, deep” dive category. At the other extreme, standardised cluster analysis into two clusters appears to group many intermediate depth and duration dives with surfacing dives (Figure 4.2e), and so includes only very long and very deep dives in the “long, deep” dive category (see Schreer (1997) for more detailed discussion of statistical clustering techniques). The log-survivorship function shows quite clearly that there appear to be at least three behavioural types (Figure 4.2f), the first of which, the 45-s cutoff, is likely to define surfacing dives. The other techniques were relatively straightforward and give quite similar results. Interpretation of results should clearly be conducted with great care.

The primary recommendation, which follows from this, is the explicit categorisation of dives by statistical or graphical investigation of dive type. At minimum, dives should be separated into those involved in respiratory bouts and those more likely to represent foraging behaviour.

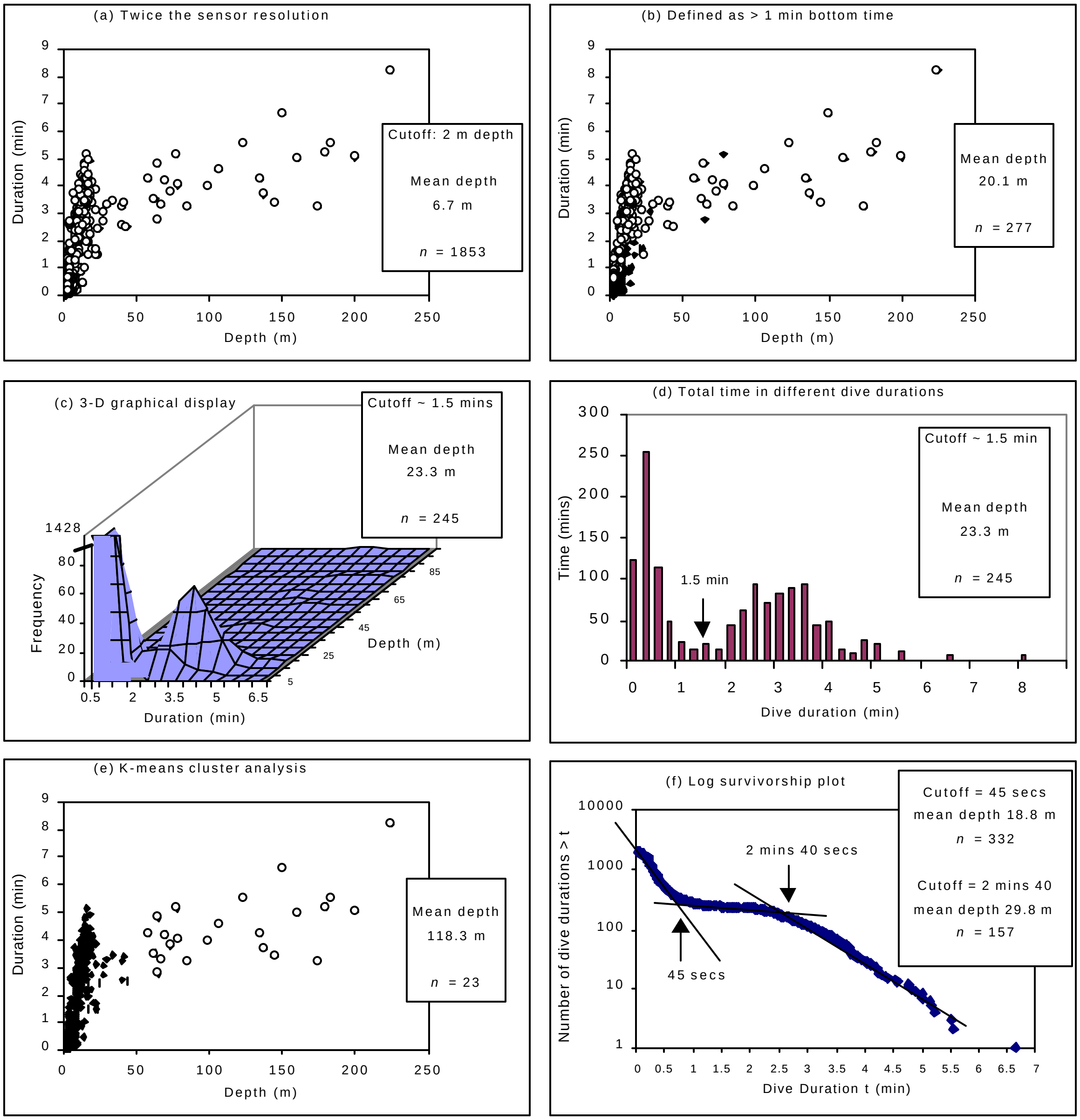

Figure 4.2. Examples of different methods used to categorise dives, illustrated using data from a single southern resident killer whale, British Columbia (R.W. Baird, unpublished data). (a) using twice the data resolution, (b) using a subjective definition such as more than 1 min at maximum depth, (c) using a three-dimensional frequency histogram of depth and duration, (d) using the bimodality of a plot of cumulative time spent in dives of different durations, (e) using cluster analysis, (f) using a log-survivorship plot of dive durations. Values given in boxes represent mean dive depth of “long, deep” dives, and give the number of such dives recorded with each technique. For (a), (b), and (e) open circles show dives of the definition given.

Presentation of ranging data

There does not appear to be any standard method for display of ranging data. The three-dimensional nature of cetacean ranging data (point locations, x and y, at sequential time, t) renders visual analysis difficult since this is usually done in two dimensions. Data are therefore generally either displayed statically in time, in terms of a spatial representation of (x, y)-locations, or features of movement, such as distance travelled, are plotted against time (White and Garrott 1990). Mammalian movement has generally been analysed spatially by investigating plots of movements and describing home range, following the definition given by Burt (1943) as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for the young”. However, many cetaceans do not appear to hold "home ranges" in the same manner as terrestrial mammals, and presentation of home range is likely less useful. Turchin (1998) suggested a method of displaying movement data following the theoretical framework of random movement (diffusion) models. Ranging behaviour can be interpreted by displaying mean squared displacement against the time lag over which that displacement is calculated. Although not as biologically intuitive as net displacement, net squared displacement is the more useful test statistic due to its relationship to the rate of population spread (diffusion rate). For example, random movement would result in a straight line relationship between squared mean displacement and time lag (Turchin 1998; see Chapter 6).

Data resolution

Sampling rate for detailed TDR records varies both within and between studies. Westgate et al. (1995) use a sampling rate of 1-3 seconds for research on harbour porpoises. While this variation in rate does not have a large effect on the recorded depths and durations of deep dives, it may cause some error in accuracy. Otani et al. (1998) use a sampling rate of 10 seconds for the same species and it can be seen that the distribution of dive durations they recorded is quite different to that observed by Westgate et al. (compare fig. 3, Otani et al. 1998, to fig. 2, Westgate et al. 1995). Many of the short surface respiration dives appear not to have been recorded using a 10-second sampling rate (see Otani et al. 1998). Schreer (1997) showed that sampling rate can also affect dive shapes. The sampling interval should be small enough both to allow resolution of the dive profile and to identify all surface intervals accurately (see Boyd 1993 for more detailed discussion of this problem). A 10-second sampling rate for narwhals, which have a mean dive duration of 5 min (Heide-Jørgensen and Dietz 1995), is likely to produce far more accurate results than a 10-second sampling rate for harbour porpoise, which have a mean dive duration of 1 min (Otani et al. 1998).

The resolution of ranging data also affects the resultant data. Animal movements are continuous, but records of ranging data are typically collected by noting position at regular or irregular time intervals. A good review of the effects of oversampling and undersampling of movements is available in Turchin (1998). Oversampling is rarely a problem in marine mammal studies, due to the logistics of gaining position data on animals over short time intervals. The straight-line distance assumed between locations is an underestimate of the continuous distance the animal travelled, and the longer the intervals between recorded locations, the more biased the estimates of distances travelled and the speeds will be. Dietz and Heide-Jørgensen (1995) showed that swim speed will be underestimated if calculated over intervals longer than 0.5-5 hours. The most detailed (but usually somewhat impractical) measurement of movement is to record the velocity of the animal and view this in conjunction with the dive profile. Movements recorded over longer time intervals can provide longer-term ranging information, for example, core-areas and long-term ranges.

The primary inconsistency in presentation of ranging statistics by different authors is to present a single rate of travel (calculated based on the sampling interval - per minute/ hour/ day). However if animals are not travelling in straight lines, the sampling interval will have a large effect on this estimated rate of travel, and yet these estimates are often used interchangeably in the literature. In some studies both are presented where one is merely a multiple of the other (e.g., Davis et al. 1996). For the majority of temperate latitude satellite-tracking data, locations tend to be sampled approximately once or twice a day and so the rate of travel is better presented as average daily movement than as hourly movement. A solution to this is to present these data graphically, showing how displacement varies with time interval (see methodology suggested above). In this manner displacement over various time intervals, ranging from the sampling interval up to the study duration, can be displayed.

The sampling interval from which diving and ranging data are calculated should be explicitly stated in all studies. Sampling interval is crucial, both for interpretation of results and for comparison between studies.

Sample size, sampling duration and representativeness

A further obstacle in the comparison presented here, which applies to both diving and ranging studies, is differences caused by sample size and “quality” of study animals. Some studies include a number of individuals sampled for periods up to months (Heide-Jørgensen and Dietz 1995, Westgate et al. 1995, Read and Westgate 1997), while others are of a single rehabilitated study animal (Davis et al. 1996) or animals sampled for only short periods, i.e., 1-30 hours (Baird et al. 1998). The representativeness of studies of rehabilitated animals to the behaviour of free-ranging wild animals may be questionable. However, it is possible that attachment of any tag, regardless of the condition of the study animal, may cause behavioural modification (e.g., Schneider et al. 1998).

Sample size and duration of sampling affect the maximum values of variables, e.g., the maximum dive depth ever recorded, or maximum speed ever recorded, more so than they affect mean or modal dive depth or duration (see Link and Sauer 1996). While these measures can provide an indication of the potential of a species, their strong dependence on sample size prohibits fine-scale inter-specific and inter-population comparisons of diving behaviour for datasets of widely differing sample sizes.

Differences in diving or ranging summary measures with increased duration and sample size have not been investigated. The number of samples required to obtain a reliable mean foraging depth could be investigated visually by plotting standard error of the mean depth for increasing number of dives or number of individuals (using jackknife – sampling with omission, or bootstrap – sampling with replacement, analyses, Efron and

Gong 1983, Krebs 1989). A similar method is used to test the number of fixes required to obtain an accurate measure of home range size (Voigt and Tinline 1980).

Comparative studies

In addition to the general problems described above resulting from differing methodologies and definitions, there are differences between studies in the data presented. I will summarise the measures commonly used and note some of the differences in calculation and presentation of these values by different authors.

The terminology used for dive parameters can be confusing; I have used the definitions:

- dive depth = maximum depth of each dive
  - mean dive depth = mean (maximum depth of dives)
  - modal dive depth = mode (maximum depth of dives)
- modal depth = depth at which most time is spent
- bottom time = time at >85 % maximum depth of dive
- daily maximum depth = maximum depth recorded each day

When comparing diving behaviour between species using detailed TDR records, the dive depth and duration are probably the most common and important summary measures for each dive. Mean or modal values of dive depth and duration are most useful for comparisons between individuals or species (Machlis et al. 1985). An indication of the rate at which dives are performed (the number of dives per day) is a crucial gauge of the energetic expenditure involved. Further to these, the percentage of time spent at the surface (or the percentage of time spent at depth) provides an indication of the time constraints of foraging. Presentation of modal depth is important to assess an animal's use of the water column. Categorization of dive shapes and presentation of the proportion of time spent at the “bottom” of dives (bottom time) may provide information on the function of dives (Asaga et al. 1994). Ascent and descent rates together with other dive parameters (duration, max. depth, and bottom time) can provide some information on the energetics of diving. Whether or not the species is diving to the sea floor is an important consideration for inter-population differences, since this may be highly dependent on location rather than on a species' capability. Finally, an overall summary for all individuals of mean values may be of most use in making broad comparisons between species and populations.

While this list sounds quite straightforward, the presentation of these data by different authors varies. Many authors provide detailed statistics for each animal studied (see Westgate et al. 1995), while others (e.g., Watkins et al. 1993) fail to provide many of the basic dive statistics suggested above. Others present description of dive types rather than quantification of these types (e.g., Baird 1994), or provide ranges of dive parameters with no other information to describe the distribution of these parameters (e.g., Martin and Smith 1992).

Data-downloading TDR studies usually provide mean dive depth recorded, while satellite-linked TDR studies usually provide a histogram of dive-depths. Studies using satellite-derived data often also present the mean of daily maximum depths, and it is worth noting that this is not necessarily the same as the daily mean of dive depths and cannot be used as a substitute. Most, but not all, studies provide results for dive rate (the number of dives observed per day), but do not separate this into the rate of dives of different classes, such as the rate of long, deep diving. Ideally, the dive rate should be provided for the classes of dives (depending on the dive definition used) for which basic statistics such as mean depth or duration are given.

Few studies calculate the proportion of bottom time for each dive and present a mean of this. Instead many authors provide mean bottom time and mean dive duration (essentially discarding information about dive shape; e.g., Westgate et al. 1995). However, calculating mean proportion of the dive at the bottom from these is not accurate:
(mean bottom time) / (mean dive duration) $\neq$ mean (bottom time / dive duration).

For example, if one dive has total dive duration of 10 min with bottom time of 8 min

i.e., BT/DT = 0.8,

while a second dive has total dive duration of 5 min with bottom time of 1 min i.e., BT/DT = 0.2,

then (mean bottom time)/(mean dive duration) = 4.5 / 7.5 = 0.6 (1)

whereas mean (bottom time/dive duration) = mean (0.8, 0.2) = 0.5 (2)

The mean proportion of a dive spent at the bottom, averaged over all dives (2) is more indicative of the "average" dive shape and is less susceptible to bias from dives of longer duration. This is therefore the more reliable calculation method of the two.

In assessing the proportion of time animals spend at the surface, a wide range of depths (1 m, 2 m, 5 m, 8 m, 10 m) have been used to define "surface". This value, calculated from a frequency histogram of the number of depth values recorded within certain ranges, is often determined for use in sighting surveys and so may be defined by reference to the clarity of the surface waters. Alternatively, authors may use "2x instrument resolution". In order to simplify comparisons with other studies, an indication of time spent at different depth ranges would be helpful (e.g., Table 4.3). This allows readers to assess the differences in sightability at the surface depending on various factors such as water clarity or surface chop. Further information regarding time spent at depth is also important for consideration of depth-specific threats (such as impact of certain fishing methods, acoustic impacts, etc). Westgate et al. (1995) used an alternative definition of surface time as the sum of the interdive times between dives of deeper than 2 m, divided by the total deployment time. Using the program Dive Analysis (Wildlife Computers, Redmond, WA), this definition is identical to a calculation of time spent at < 2m depth since the maximum depth of the surface (2 m) is used to define the start and end points for dives.

Table 4.3. Time at surface showing differences in definition of surface, based on same data as used in Figure 4.2, from a single southern resident killer whale, British Columbia (R.W. Baird, unpublished data)

Depth Interval	Percentage time at each depth layer	Cumulative percentage time between surface and layer
0 – 2 m	12.8	12.8
2 – 4 m	30.8	43.6
4 – 6 m	9.4	53.0
6 – 8 m	7.1	60.0
8 – 10 m	12.7	72.7

Finally, for comparisons between populations it is important to consider whether diving is bottom-limited. Results from narwhal and beluga studies (Martin and Smith 1992, Martin et al. 1993, 1994, Heide-Jørgensen and Dietz 1995, Heide-Jørgensen et al. 1998; A.R. Martin, pers. comm.) suggest that diving behaviour (especially maximum dive depths) depends to a large extent on the bottom depth of the area in which the studies are conducted. This is likely to be the case for many dive studies (e.g., Baird 1994), thus reporting bottom depth is important for comparisons between studies.

INTEGRATING DIVING AND RANGING

The two major resources that marine mammals need for survival are air and food. Animals will therefore optimize their diving behaviour in order to gain the maximum food under limitations of oxygen requirements (Kramer 1988). However, the spatial ranging behaviour of animals will be unaffected by oxygen requirements since oxygen is uniformly distributed at the surface, so we would expect ranging behaviour instead to be governed by maximisation of prey. Such correlation between movements and the profitability of foraging has been shown for sperm whales (Whitehead 1996a, Jaquet and Whitehead 1999). The integration of studies of diving and ranging can therefore provide information concerning the dimensions, concentration and patchiness of prey aggregations, and will allow a more detailed description of the foraging ecology of an animal than studies of either diving or ranging alone.

CONCLUSIONS

Due to the logistical difficulty of deploying time-depth recorders or radio-tags and the often limited attachment durations, studies of the diving and ranging patterns of odontocetes have not progressed at the same rate as those of pinnipeds. Perhaps because so few publications have resulted from this work, and by so few investigators, there is currently little accord in the way data are collected or summary measures reported. I have tried to identify some of the important considerations to keep in mind when designing and undertaking studies of the diving and ranging behaviour of odontocetes, particularly those using time-depth recorders. I have made a number of recommendations on which techniques and sampling regimes are appropriate depending on the questions being asked and the logistical constraints of the system being studied. My suggestions for standardisation between studies in terms of data analysis and presentation are summarised in Table 4.4. In particular, an objective discrimination between dive types of cetaceans is needed in order that dive statistics are not biased by the frequent shallow dives of a surfacing bout, and, if more than one dive-type for deep dives is identified, statistics should be presented for each dive-type. Studies using different sampling rates and sensor resolutions will not be strictly comparable. Factors important for management considerations include the proportion of dive at bottom and the modal depth, which are important for assessment of depth-specific (e.g., acoustic) impacts to a particular species, and the percentage of time at the surface which is important in establishing correction factors for population census analyses. Movement data should be presented over various time intervals ranging from the sampling interval up to the scale of the study duration. I hope that the adoption of some or all of these recommendations in future studies will aid the comparison of data collected by different investigators, on different populations and species of odontocetes.

Table 4.4. Suggestions regarding data analysis and presentation for future studies (see text for additional explanation).

Sampling rate	Differences in sampling rate will cause differences in results. Higher sampling rate will provide more precise results.
Sample size	Individual and seasonal variation may be a problem. Sample size is based on the number of individuals sampled, although the duration of the sampling period will affect the ability to detect temporal trends in the data.
Presentation of ranging data with varying time interval	Mean squared displacement and RMS (root mean squared) displacement should be plotted over varying time intervals to examine movement rate and pattern visually.
Definition of dive	There is a need to differentiate objectively between “respiration” dives and other dives. Possibilities include: - definition of foraging (although subjective) - cluster analysis - three dimensional frequency histogram: depth and duration - log-survivorship plot of dive duration - bimodal plot of cumulative time spent in dives of different durations
Presentation of dive statistics	Dive statistics (independently for dive-types): dive duration (mean, mode, max), dive depth (mean, max.), proportion of time at bottom, ascent rate, descent rate, modal depth. - summary results should be presented for each animal - numerical data description (mean, SD)
Dive rate (# dives/day)	Present dive rate (for each dive-type).
Proportion of dive at bottom	Presentation of mean proportion of dive at bottom will provide information on general dive shape.
Percentage of time at surface	Present the proportion of time at various depths (dependent on sampling resolution e.g., such that time (%) in top 2, 4, 6, 8, 10 m of the water can be assessed).
Are dives depth limited?	Dives to sea floor are likely to differ between sites, thus bottom depths in the study area should be given.
Representativeness	Representativeness of deployments should be discussed. Taggability of animals may vary such that data are not obtained from a random sample of the population, especially for studies of rehabilitated animals.

CHAPTER FIVE [†]

Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae)

ABSTRACT

Using suction-cup attached time-depth recorder/VHF radio tags, I have obtained the first diving data on northern bottlenose whales (*Hyperoodon ampullatus*), the first such data on any species within the family Ziphiidae. Two deployments in 1997 on northern bottlenose whales in a submarine canyon off Nova Scotia demonstrated their exceptional diving ability, with dives approximately every 80 min to over 800 m (maximum 1453 m), and up to 70 min in duration. Sonar traces of non-tagged, diving bottlenose whales in 1996 and 1997 suggest that such deep dives are not unusual. This combined evidence leads me to hypothesize that these whales may make greater use of deep portions of the water column than any other mammal so far studied. Many of the recorded dives of the tagged animals were to, or close to, the sea floor, consistent with benthic or bathypelagic foraging. A lack of correlation between dive times and surface intervals suggests that the dives were predominately aerobic.

[†] *This chapter has been previously published in:*
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INTRODUCTION

Beaked whales (the Ziphiidae) are one of the least known mammalian groups. All beaked whales are considered to be deep divers, based predominantly on their deep-water distribution and long dive times (Mead 1989a), but there is little direct evidence of dive depths to support this claim (Schreer and Kovacs 1997).

There has been some speculation that the northern bottlenose whale (*Hyperoodon ampullatus*) may be one of the deepest diving mammals (Gray 1882, Benjaminsen and Christensen 1979). Ohlin (1893) reported seeing 500 fathoms (900 m) of line taken out by a harpooned bottlenose whale in less than two minutes, while Gray (1882) reported that harpooned animals remained submerged for two hours and came to the surface “as fresh as if they had never been away”. Ohlin (1893) also reported the possibility of benthic feeding, based on the presence of sea stars (echinoderms) in the stomachs of some animals and mud on the beaks of others. However, dive profiles have not previously been obtained for this or any other species of beaked whale. Here I present the first detailed information on the diving behaviour of beaked whales, based primarily on deployments of time-depth recorders (TDRs) on two northern bottlenose whales in the Gully, a submarine canyon off the coast of Nova Scotia.

METHODS

Fieldwork was conducted between June and August in 1996 to 1998 from a 13-m auxiliary sailboat in the Gully, 370 km east of Halifax, Nova Scotia (approximate position: 43°N, 59°W). Northern bottlenose whales are consistently found in this canyon and have been studied there since 1988 (Whitehead et al. 1997a, b). Differentiating adult males from adult females in the field was based on their sexual dimorphism in size and head shape (Gray 1882, Mead 1989b).

Suction-cup attached tags were deployed on free-swimming whales using a crossbow (Baird 1998). Each tag contained a time-depth recorder (TDR) and a VHF radio-transmitter, and floated upon release from the whale. TDRs were built by Wildlife Computers, Redmond, WA, USA (tag no. 1) and by AGO Environmental Electronics Ltd, Victoria, BC, Canada (tag no. 2). Tag no. 1 recorded depth (every 1 s at 4 m accuracy) and velocity (every 5 s), while tag no. 2 recorded only depth (every 15 s at 20 m accuracy). Upon recovery of the tags, data were downloaded into a PC for analysis. Depth sensors of tags were calibrated both before and after tag attempts. The velocity sensor of tag no. 1 was based on rotation of a paddle wheel.

Drift in the depth values for tag no. 1 was corrected using the software ‘Zero-Offset Correction v. 1.26’ (Wildlife Computers), and data were then processed using ‘Dive-Analysis v. 4.08’ (Wildlife Computers), to produce summary statistics for each dive. Depth values from tag no. 2 were imported into Excel® (Microsoft) and drift was corrected by eye and using surfacing data (the times when radio-signals were audible). These data were then processed using Excel macros, adhering to the same principles as those used by ‘Dive-Analysis.’

In addition to the TDR study, we used a hull-mounted fish-finding sonar system (Furuno® Model CH-14; 60 kHz) set at a range of 600 m to track non-tagged whales as they dived. Sonar recordings were taken when there were no other whales in the immediate area. The research vessel was manoeuvred above the position where the whale began its dive, approximating the whale’s speed and heading. When speed and direction were judged correctly, an echo from the whale was received on the sonar, usually within a minute of the whale having left the surface. Once this was achieved, we would attempt to maintain the echo on screen during the whale’s descent by observing changes in the sonar image and consequently manoeuvring the boat in that direction. When we lost the echo on screen, a still photograph was taken to record the trace. These photographs were later digitised (CalComp Drawing Board™) and the differences in depth and time between the start and end positions of the dive descent were used to calculate the descent rate of the whale.

One possible error affecting the measurement of dive depths using this method is caused by the 15° vertical beamwidth. This could cause an image to be displayed when the whale was at 7.5° off the vertical plane, i.e., not directly under the research vessel. The maximum error incurred by this is $((1 - \cos 7.5°)/\cos 7.5) = 0.9$ % (c.f. Papastavrou et al. 1989). Depth values will therefore be slightly underestimated in some cases, resulting in a maximum of 0.8 % underestimation in descent rate.

RESULTS

Attempts to deploy the tags were made 84 times during 30 days between 1996 and 1998, with five successful tag attachments. Tags were recovered in three of these attachments and the data from two were successfully downloaded. The deployment in 1996 of a 500-m TDR (rated for less than the diving capacity of these whales) resulted in TDR failure, and VHF transmitter failure was probably responsible for one or both of the losses at sea in 1998. The first successful data recovery was from a tag (no. 1) deployed at 15:41 on 9 July 1997, on an adult female-sized whale ("individual 1") in a group of five animals, including one infant and one juvenile-sized whale. Individual 1 was observed with the juvenile and infant during all of its surfacings. The tag fell off after 2 h 33 min during a bout of high-speed swimming, 20 min after two groups joined (a total of eight whales). The second successful data recovery was from a tag (no. 2) deployed at 14:56 on 24 August 1997 on a sub-adult sized whale ("individual 2"), in a group of three animals. This tag fell off after 27 h 56 min, at which time individual 2 was in a group of five animals.

A total of 56 sonar recordings were obtained over 20 days during 1996 and 1997. Forty-seven of these contained a trace of a single whale; however nine showed two whale traces, resulting in a total of 65 traces.

Reactions of the whales to tag deployment appeared to be minimal, generally consisting of a flinch and a fast but shallow dive (see Appendix 1). Velocity data from individual 1 were high for 2 min after tag deployment (although the same velocity was observed later during apparently normal behaviour), then dropped to levels maintained throughout the majority of the tag attachment (Figure 5.1). In general, bottlenose whales showed no obvious reaction to the research vessel when under power beyond distances of 15-20 m, and distances greater than this were maintained for the majority of the tag attachments. There was also no apparent difference in the surface behaviour of whales when the sonar system was transmitting (S. Al-Omari, unpublished data).

I considered the whales to be “diving” when the maximum dive depth was greater than 40 m (corresponding to twice the depth resolution of tag no. 2). Both tagged whales spent similar proportions of their time diving (70 % and 62 % respectively, for individuals 1 and 2) and both spent similar proportions of dives at greater than 85 % of maximum depth, indicating general consistency in dive shape (Figure 5.2, Table 5.1). Dives fell into two discrete types based on the bimodal distribution of the cumulative time spent in dives of different durations (not shown). A *k*-means cluster analysis of standardised variables (dive duration, maximum depth, bottom time, ascent and descent rates) also verified these groupings. These two types could generally be considered as “short duration and shallow” and “long duration and deep” (Table 5.1).

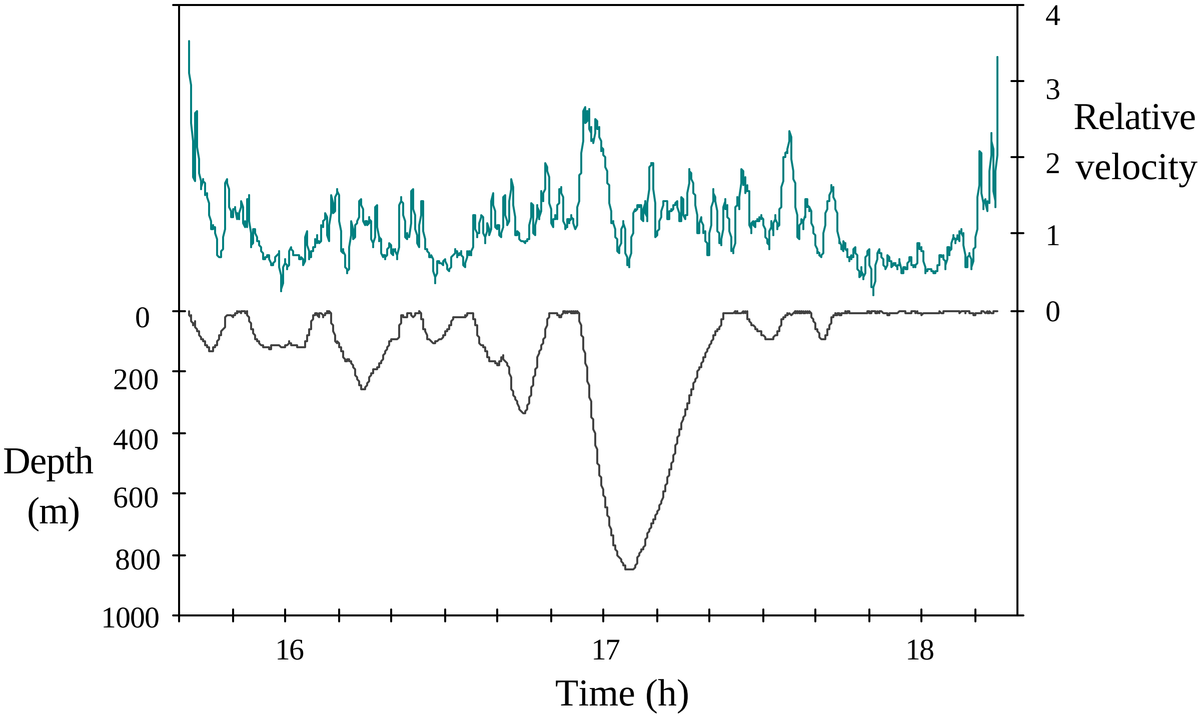

Figure 5.1. Dive and velocity profiles for individual 1. The lower graph shows depth while the upper graph shows relative velocity (uncalibrated) over the same time period.

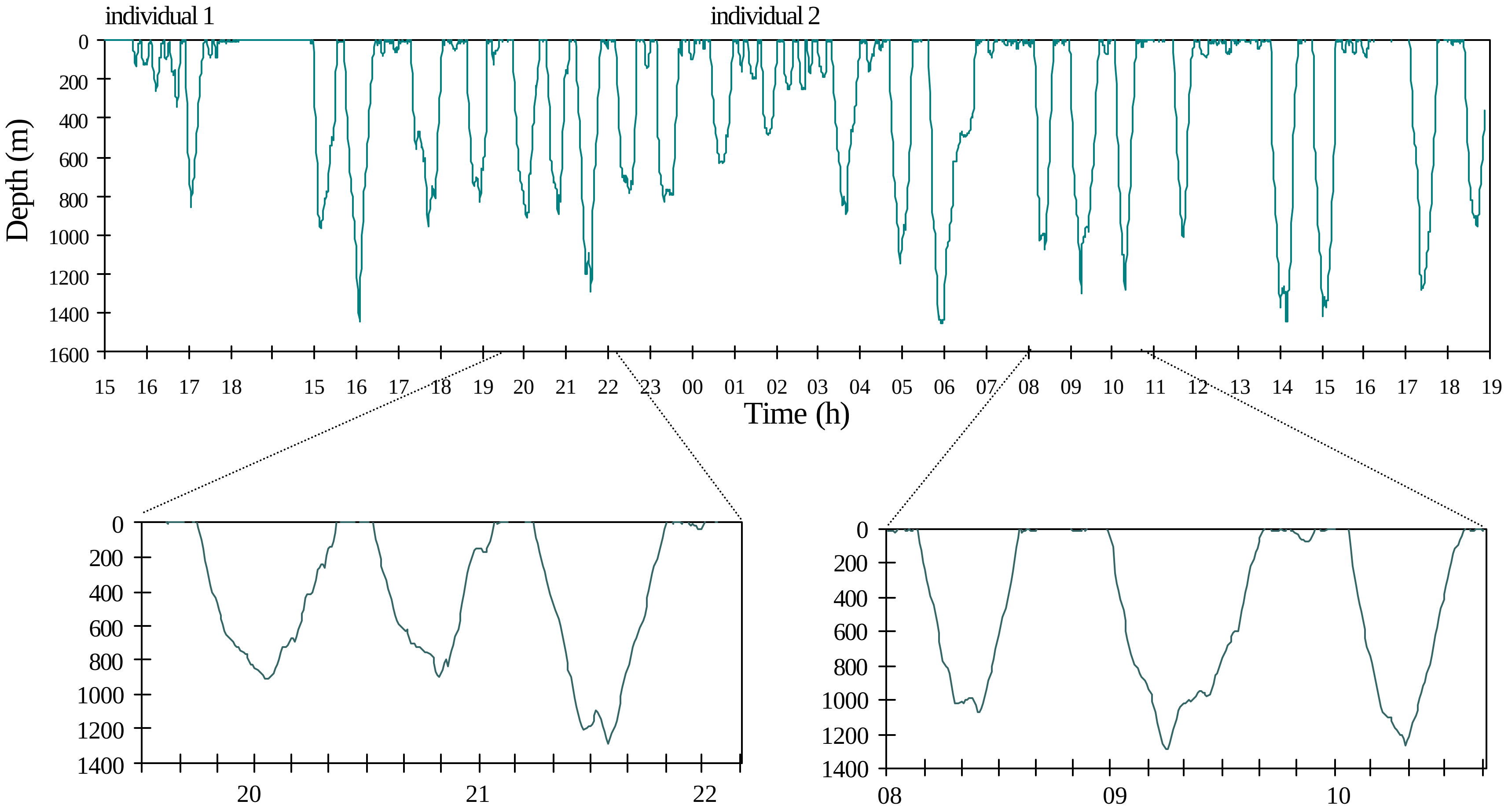

Figure 5.2. Dive profiles for individual 1 (2.5 hours) and individual 2 (28 hours) showing regular dives to depths exceeding 800 m. The time-scale is expanded for two sections of the dive profile of individual 2 in order to show dive shape in greater detail (to the same scale as shown in figure 5.1).

Table 5.1. Values of dive variables for short and long-duration dives for each individual (mean (s.d.) and range are shown for all categories except the single deep dive of individual 1, for which the recorded values are shown)

divetype	individual	*n*	duration (min)	maximum depth (m)	time at depth >85% maximum depth (min)	descent rate (ms^{-1})	ascent rate (ms^{-1})	percentage of dive at 85% maximum depth
short, shallow	1	7	11.17 (3.91) 6.00 – 16.23	166 (93) 96 - 332	3.16 (2.45) 1.30 - 8.58	0.73 (0.21) 0.45 - 1.10	0.56 (0.34) 0.30 - 1.30	27.5 (14.4) 14.9 – 58.0
	2	26	8.83 (3.40) 1.75 - 15.50	108 (65) 41 - 257	2.77 (1.85) 0.25 - 7.00	0.61 (0.43) 0.21 - 2.13	0.67 (0.36) 0.12 - 1.36	30.1 (13.2) 3.0-56.0
long, deep	1	1	29.48	852	7.02	1.93	0.80	23.8
	2	22	36.98 (9.4) * 25.25 - 70.50	1060 (273) 493 - 1453	9.72 (3.10) 5.00 - 17.00	1.33 (0.32) 0.60 - 1.93	1.11 (0.36) * 0.46 - 1.78	27.4 (10.6) 11.6 - 50.8

*Although there were 22 long-duration dives recorded for individual 2, the last dive has not been included in some calculations, since the tag fell off part way through the dive, while the animal was ascending.

The average depth of dives of individual 2 in the long duration cluster was 1,065 m (n = 22, range 493-1453 m), while only one dive of individual 1 to 852 m was classified in this category (Table 5.1). Using all dives, there was a strong relationship between the maximum depth of a dive and the duration of that dive (Pearson correlations: individual 1, $r = 0.943$, $p < 0.001$; individual 2, $r = 0.930$, $p < 0.001$). Dive duration was not significantly correlated with the following surface interval for either whale (Pearson correlations: individual 1, $r = -0.004$, $p = 0.993$; individual 2, $r = -0.126$, $p = 0.4$). Furthermore, even when recovery time is assumed to include all time between deep dives (including time spent on shallow dives), there was no significant relationship (Pearson correlation: individual 2, $r = 0.134$, $p = 0.572$).

Over all of the dives, average descent rates were not significantly different from average ascent rates (paired t-test, individual 1, $p = 0.16$; individual 2, $p = 0.38$). However, the long dives of individual 2 had significantly faster descent rates (mean 1.32 ms^{-1}) than ascent rates (mean 1.11 ms^{-1}; paired t-test, $p = 0.026$, Table 5.1). Descent and ascent rates were found to vary with depth during deep dives (>850 m), such that descent rates showed a general deceleration with depth (ANOVA, $p < 0.001$), while ascent rates were relatively constant overall but appeared to show a slight (but non-significant) deceleration in the final 250 m before reaching the surface (Figure 5.3). The difference between descent and ascent rates was only found to be significant between the initial descent (mean 1.84 ms^{-1}) and the final ascent (mean 1.31 ms^{-1}) in the top 250 m of dives (paired t-test, $p = 0.005$, $n = 12$; Figure 5.3). Average descent rate and average ascent rate were found to be correlated with the depth of dive (Pearson correlations: individual 2, descent $r = 0.72$, $p < 0.001$, $n = 48$, ascent $r = 0.57$, $p < 0.001$, $n = 47$), with a trend for both to increase with increasing dive depth. When this analysis was restricted to deep dives, only descent rate was significantly correlated with depth of the dive (Pearson correlation: individual 2, $r = 0.431$, $p = 0.045$, $n = 23$); neither overall ascent rate and nor the final ascent rate (during the final 250 m) showed any correlation with dive depth.

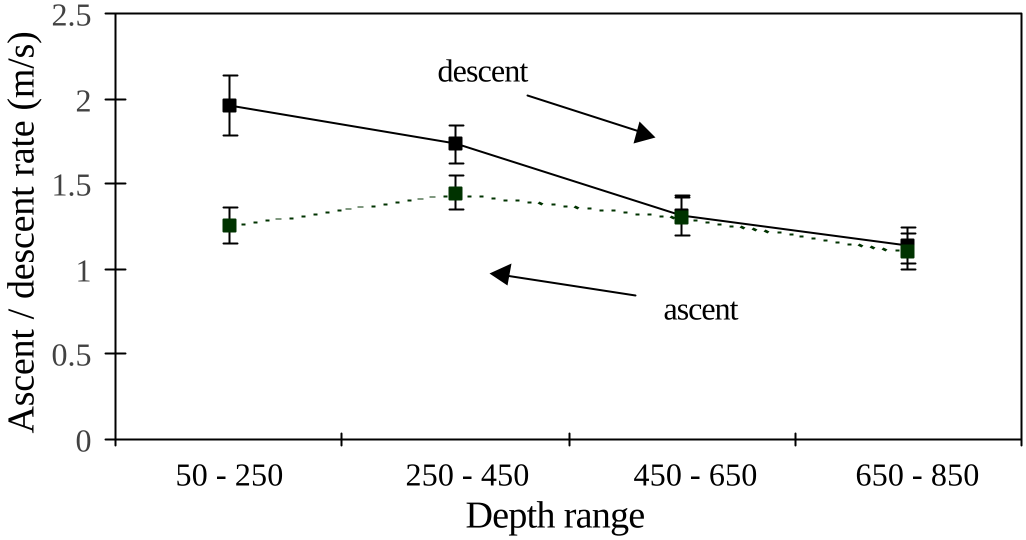

Figure 5.3. Variation in descent rate (solid line) and ascent rate (broken line) calculated over 200 m depth intervals during deep dives. Average descent and ascent rates (± s.e.) are shown for descents between 50 m and 850 m for dives to greater than 850 m.

The deepest sonar trace observed was to approximately 550 m, which was almost the limit of the sonar range used (600 m). Although most traces were lost before this depth, no traces were observed to level out (suggesting that these represented the initial descent of deeper dives). The sonar dive traces (of greater than 80 m descent) showed a mean descent rate of 1.87 ms^{-1} (s.d. 0.35, range 1.12 to 3.03, $n = 23$). The average start and end depths for these traces were 150 m and 340 m. This is comparable to the TDR-measured descent rates during the same depth range for long deep dives (individual 1: 2.45 ms^{-1}; individual 2: mean 2.04 ms^{-1}, s.d. 0.75), but is much greater than the descent rates observed for shallow short dives (Figure 5.4).

Accurate determination of sea-floor depths at locations of tagged whales was problematic, due to steep gradients in bottom depth in the submarine canyon. However, when the research vessel was close to the tagged animals, the maximum bottom depth was approximately 1500 m. Individual 1 was observed to move into shallower waters (750 m) just prior to the tag falling off and thus the final dive of 852 m may have been to, or close to, the sea floor (Figure 5.1). The maximum depth of the canyon between the tag deployment and recovery site for individual 2 was also 1500 m. Given the dramatic changes in sea-floor depth changes over short horizontal distances, it seems likely that individual 2 was diving close to, or to, the sea floor for many of the dives recorded (Figure 5.2).

Eleven of the sonar recordings showed more than one trace of a whale within the same recording. Of these, two recordings showed one animal descending while another animal was stationary or moving slowly horizontally just under the water surface, five showed one animal descending and then approximately a minute “behind” this, a second animal descending. Four of the sonar recordings showed two traces within 20 m or a few seconds of each other at depths of between 150 m and 300 m.

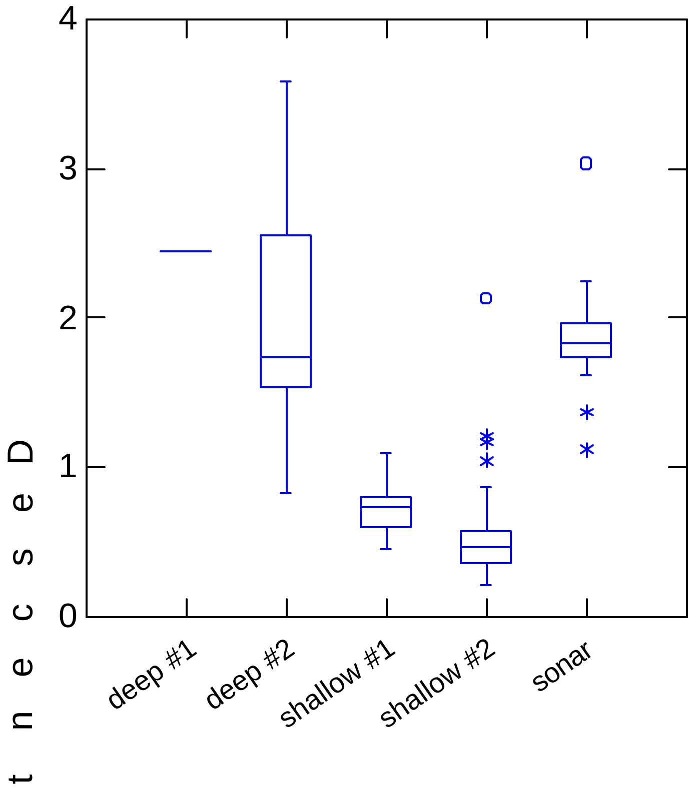

Figure 5.4. Box-plot comparison of the initial descent rates of dives. Long, deep dives and short, shallow dives are shown for individual 1 and individual 2. This shows that rates recorded for sonar dive traces of non-tagged whales are more comparable to the initial descents of deep dives than the descent rates of shallow dives. Box plot shows the median (centre line), the upper and lower quartiles (edges of the box), the range (ends of the bars or symbols); asterisks show outlier further than 1.5 x interquartile range from either quartile, circles show outlier further than 3 x interquartile range from either quartile.

DISCUSSION

These results show that bottlenose whales are capable of diving to great depths and that they may do so on a regular basis. Individual 2 dived approximately every 80 min to depths of greater than 800 m and at times as deep as 1450 m; the dives of individual 1 showed a similar profile, with one dive to 852 m during the 153 min deployment (Figure 5.1, Table 5.1). Descent rates calculated from sonar dive traces of non-tagged whales appeared to be more similar to the descent rates of deep dives than those of shallow dives of the tagged animals (Figure 5.4). This provides some support for the hypothesis that such deep diving recorded by the TDRs was not unusual, and that the dive parameters obtained using tag deployments are probably a reasonable representation of the diving behaviour of this species in the Gully region.

Other marine mammals have only occasionally been recorded to dive to similar depths. The deepest depths documented using TDRs or acoustic transponder tags have been from a northern elephant seal (*Mirounga angustirostris*) diving to 1500 m (DeLong and Stewart 1991), a southern elephant seal (*Mirounga leonina*) diving to 1200 m (Hindell et al. 1991), a sperm whale (*Physeter macrocephalus*) diving to 2000 m (Watkins et al. 1993), and narwhals (*Monodon monoceros*) on occasion diving to depths greater than 1000 m (Heide-Jørgensen and Dietz 1995). Regardless of these, the maximum depths ever recorded are not good representations of normal diving behaviour, and discussion of routine dive depths is more useful (Kooyman and Ponganis 1997, Schreer and Kovacs 1997). Routine dive depths for these deep-diving species have been reported as 400-600 m for sperm whales (Papastavrou et al. 1989, Watkins et al. 1993), and 350-700 m for northern and southern elephant seals (Le Boeuf et al. 1988, DeLong and Stewart 1991, Hindell et al. 1991). The regularity of dives of northern bottlenose whales to depths in excess of 800 m (Figure 5.2) exceeds the recorded frequencies of dives to such depths for other mammals recorded thus far.

The area in which the whales were tagged is a submarine canyon, which varies in depth dramatically over a few kilometres (Hooker et al. 1999). It is likely that the deeper dives recorded were often to, or near to, the sea floor. The diet of northern bottlenose whales is thought to be primarily the squid *Gonatus fabricii* (Benjaminsen and Christensen 1979, Clarke and Kristensen 1980, Lick and Piatkowski 1998), although its congener *Gonatus steenstrupi* is more likely to be found in the Gully (Kristensen 1981, Chapter 2). Mature *Gonatus* in the North Atlantic live around the sea-floor on continental slopes (Kristensen 1984, Moiseev 1991) and have recently been observed to spawn at depths of approximately 1000 m (Bjørke et al. 1997). Unfortunately the squid biota of the Gully is not well-known, but the dive depths observed here are consistent with what is known of the vertical distribution of the genus *Gonatus*. The lack of any distinct bursts of speed at depth (Figure 5.1) tend to suggest that these whales may forage in a fairly passive manner, consistent with recent suggestions of suction-feeding in beaked whales (Heyning and Mead 1996). The observation of more than one trace on some of the sonar images suggests that at least some of the spatial cohesion and co-ordination shown by groups at the surface (pers. obs.) may be retained during dives.

The lack of correlation between dive duration and surface time suggests that these whales are not reaching their aerobic dive limit (Kooyman et al. 1980, Boyd 1997, Kooyman and Ponganis 1998). Based on their large body size and the low velocities exhibited during diving (Figure 5.1), it seems likely that the aerobic dive limit for these whales is quite high (Williams et al. 1991, Kooyman and Ponganis 1998). It has been suggested that the shorter, shallower dives between long, deep dives may also function for recovery (Castellini et al. 1988, Kooyman et al. 1992), but a relationship between dive duration and such an extended surfacing period was not observed here, although small sample size may have prohibited the detection of such a relationship.

The effects of pressure on diving mammals are most dangerous during ascent, when the decrease in pressure may cause decompression sickness (the bends), or shallow-water blackout, a reduced concentration of oxygen in the arteries resulting in a decrease in the amount of oxygen reaching the brain (Kooyman 1988, 1989, Kooyman and Ponganis

1997). Relative pressure changes are greatest near the surface and the slight decrease in ascent rate shown by northern bottlenose whales during the final phase of ascent could potentially be a response to this. Martin and Smith (1992) also observed a decrease in ascent rate of beluga whales (*Delphinapterus leucas*) within 140 m of the surface and suggested that this might serve a physiological function, reducing the rate at which gas bubbles appear in the blood or tissues. Deep-diving pinnipeds such as elephant seals show the opposite trend, i.e., an increase in ascent rates near the surface (e.g., Fletcher et al. 1996) although ascent rate was found to be less flexible than the descent rate to experimental changes in buoyancy (Webb et al. 1998).

These data are based on only two TDR deployments and a small sample of sonar dive traces, and clearly more data are needed on the diving behaviour of this and other species of beaked whales to substantiate further these results. However, from the data presented here, it appears that bottlenose whales may make regular dives to greater depths than any other diving mammal yet studied.

CHAPTER SIX

Pattern and scale of northern bottlenose whale movements in the Gully: limited horizontal displacement in a profitable area

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ABSTRACT

Movement patterns of northern bottlenose whales in the Gully were investigated using photo-identification resightings (1988-1997) and radio-tracks of individuals (1996-1998) in order to assess the pattern, scale and function of movements and habitat use. Resightings of photographed individual whales over durations of 10 days (approximately their residency period within the Gully) suggested that whales show a 4 km daily displacement in location. No further increase in movement was apparent over timescales from 2-10 days, during which time they appear to range over a 20 km^2 area. There were no differences between rates of movement for different age-sex classes, or between different years. Tracking by VHF radio-signals was problematic for this species due to the long duration of dives and the brevity of surfacing bouts. Although this method allowed single individuals (n=5) to be followed, the sparse data collected was comparable in sampling interval to that collected opportunistically from photographs. Radio-tracking data showed movements of approximately 2 km per hour and 5-10 km per day, in good correspondence with movements measured using photo-resightings. Photo-resightings were also used to investigate variations in individual positions within the Gully. Positions varied significantly for different years. Within years, individuals showed some separation of ranges, particularly in years of high whale abundance, but there was no separation between age-sex classes. Between years, mature males showed consistent spatial orientation relative to one another, suggesting preferred locations possibly related to mating opportunities. By comparison with other odontocetes, the relative lack of movement observed for these whales in the Gully is unusual and suggests that the canyon supports a profitable food source for these whales.

INTRODUCTION

Data on the pattern and scale of animal movements are critical to conservation issues. Analysis of movement patterns can indicate individual spatial use, territoriality, and residency (White and Garrott 1990), in addition to patterns of resource dispersion and the profitability of foraging (Brown and Orians 1970, Whitehead 1996a, Jaquet and Whitehead 1999). The ranging behaviour of animals also has implications for a wide diversity of behavioural and life-history traits, such as predator defense, group-living, mating system, social structure and even communication (Geist 1974, Emlen and Oring 1977, Macdonald 1983, Ostfeld 1990). The study of movements of northern bottlenose whales (*Hyperoodon ampullatus*) within the Gully should therefore provide further detail on bottlenose whale foraging ecology and the pattern and scale of their resources. Investigation of the movement and spatial use of different age-sex classes will further allow an examination of any social or ecological differences in spatial patterning.

The study of movement has both temporal and spatial components, but many analytical techniques focus on either one or the other. Spatially, studies often investigate range-use, identify hotspots and calculate home-range estimates. Temporally, many mammal movement studies investigate the rate of travel. An alternative method of movement analysis, which encompasses both the temporal and spatial nature of movement, is to apply a diffusion approximation (Turchin 1998). Diffusion approximations to describe individual movements (random walk models) have been used by population biologists for nearly a century (Levin 1992). Turchin (1998) advocates the use of diffusion rate (D), the temporal rate of spatial population spread, as the most valuable index of movement. Since it incorporates both the mean and the variance of the distribution of dispersal distances, this has benefits over more standard measures of movement, such as mean distance moved (Turchin 1998). When animals are tracked and their locations are recorded, the diffusion rate can be estimated from:

$$\hat{D} = \frac{\sum l_i^{\,2}}{4\sum t_i} \tag{1}$$

where l_i are the distances and t_i is the time interval between fixes (Turchin 1998).

Following from this, a useful analytical approach for the analysis of movement is to plot squared displacement against time (Turchin 1998). Qualitatively different movement patterns (such as straight line movement, uncorrelated random movement, or a discrete range) result in different expected curve shapes. Straight line movement would result in the line of net squared displacement against time curving upwards; random movement would result in a linear relationship; and a discrete range would result in an asymptote. This method of analysis can be applied to radio-tracking data and to mark-recapture data and will be used here to compare the two.

One of the problems with the use of photo-resighting data is that data are often collected haphazardly in space and time, i.e., sampling is neither uniform nor random. If the probability that an animal is re-identified is dependent on its movement, for example if sampling does not cover the entire habitat, then a plot of displacement squared against time will be misleading (Turchin 1998). Whitehead (submitted) shows how maximum likelihood methods can be used, incorporating the photographic records themselves as a measure of the sampling effort, to generate corrected movement statistics.

In this chapter I will investigate: (1) how radio-tracking and photo-resightings compare in analysis of bottlenose whale movements, (2) the displacement rate of bottlenose whales within the Gully, (3) differences in displacement rate and range use of different age/ sex classes of whales, and over different years.

METHODS

Research was conducted in the Gully (approximately 44°N, 59°W) between 1988 and 1997, primarily from 10-12 m auxiliary sailing vessels. The majority of research effort has taken place during the summer months, but short trips have been conducted at other times of year (Table 6.1).

Table 6.1. Dates of fieldwork in the Gully

Year	Dates	Research Vessel
1988	July 8 – 21, July 25 – August 6	*Elendil*
1989	July 16 – 30, August 1 – 15	*Elendil*
	October 1	*Lady Hammond*
1990	February 10 – 11	*Alfred Needler*
	June 14 – 28, July 2 – 18, July 25 – August 12	*Elendil*
1991	July 24 – 25	*All Seven*
1992	July 26 – 27	*Divecom III*
1993	July 10 – 23	*Balaena*
1994	July 31 – August 18	*Balaena*
1995	August 20 – September 2	*Balaena*
1996	June 7 – 25, July 4 – 21, July 27 – Aug 12, Aug 19 - Sept 2	*Balaena*
1997	April 22 - 24	*Alfred Needler*
	June 7 – 23, July 1 – 19, July 24 – Aug 6, Aug 10 - 27	*Balaena*

Photo-identification

Northern bottlenose whales were approached to within 10-15 m and photographs were taken of the dorsal fin and surrounding flank area. A catalogue of identified individuals has been set up and maintained (Gowans 1999). Whenever possible in the field, photographs of the melon profile of a whale were taken in conjunction with a photograph of its dorsal fin. Bottlenose whales are sexually dimorphic in head shape and these photographs were later used to assign one of three age-sex classes: mature male, subadult male, or female / immature male (Gray 1882, Gowans 1999). Location data were recorded approximately every 20 min, using radio and satellite positioning. A Loran (SeaPort Loran-C) was used from 1988 to 1992 and GPS (Trimble Transpak or Garmin 65 Global Navigator) from 1993 to 1997. Loran data were accurate to approximately 400 m and GPS data to approximately 200 m. This spatial resolution, combined with the temporal resolution of photographic identifications (approximately 5 min), means that movements could be calculated from these data at timescales of a minimum of one hour.

Movements between all photo-resightings were calculated over a range of time intervals using the SOCPROG suite of Matlab programs (H. Whitehead, 1999; available from http://is.dal.ca/~hwhitehe/social.htm), either directly (using equation 1) or using likelihood techniques, which estimated the diffusion rate by maximising the likelihood of the patterns of identifications and re-identifications in space and time using Poisson error (Whitehead submitted). Three measures of movement were displayed with time interval: estimated diffusion rate, mean squared displacement and the root mean squared (RMS) displacement. Standard errors for these parameter estimates were obtained by jackknifing, omitting consecutive 10 hour periods in turn (Efron and Gong 1983).

As some of the markings used to identify individuals are known to change with time, the quality of the photo and the distinctiveness of an animal's marks will affect the likelihood of an animal being reidentified over long timescales (Gowans 1999). For timescales greater than one year, the data were restricted to comparisons of only reliably-marked individuals with both left and right sides of the dorsal fin identified using good quality photographs (see Gowans 1999). Over timescales smaller than this, all identifications of all individuals were used (since whales can be accurately re-identified within a single field season using any mark type, Gowans 1999).

Radio-tracking

Between 1996 and 1998, radio-transmitters (148 and 164 MHz) were deployed on northern bottlenose whales in the Gully (as described in Hooker and Baird 1999a and Appendix 1). Once tags were attached, we attempted to maintain close proximity (<500m) to the tagged whale, and positions were recorded from GPS (Garmin 65 Global Navigator).

VHF radio-signals do not transmit through seawater and so localisation of signals could only be attempted when the tag cleared the water surface as the whale surfaced to breathe. Tracking at these times was conducted primarily using a handheld antenna, since the long dive durations of bottlenose whales, combined with the relatively short transmitting interval, made the use of an automatic direction finder difficult.

Individual ranges

The positions of all identified individuals (limited to those with reliable marks and linked identifications from both left and right sides of the dorsal fin) were used to investigate differences between individuals in ranging patterns. Since individual positions were likely to be autocorrelated within each day, these data were reduced to two non-autocorrelated datasets: (1) the average position of each individual in each year and (2) the average position of each individual each day. The first dataset was used to test for differences between years in positions of individuals, and within each year, for differences between age-sex classes. The second dataset was used to test for individual differences in location within each year. In addition, this test was also repeated for each age-sex class in turn, to investigate whether individuals in some age-sex classes separated themselves spatially while others did not. All tests were performed using MANOVAs (using latitude and longitude as dependent variables).

Since individual locations varied according to year, and individuals appeared to separate themselves spatially, the presence of consistent relative spatial differences between individuals was also investigated. The average position of each individual in each year was used to calculate the overall mean yearly position, and the variation of each individual position from this was calculated. Differences between individuals of each age-sex class in these relative locations were investigated using the data for all years.

RESULTS

Movement analysis using photo-identification data

A total of 682 identified individuals have been recorded in the Gully bottlenose whale photo-catalogue. This catalogue is based on markings observed on both left and right sides of the animal in the area around the dorsal fin (see Gowans 1999, for details). Although whenever possible left and right side photos are matched on the basis of scars on the dorsal fin profile, there are undoubtedly instances where left and right photographs are not matched, or where an individual was assigned a new identification in different years on the basis of unreliable marks. It is therefore likely that a number of individuals are represented more than once in the catalogue. A total of 113 individuals were reliably marked and could be identified from photographs of either the left or right side of the dorsal fin. These individuals were found to be re-identifiable with good accuracy between years (Gowans 1999), and many of these have been re-identified over multiple years (Table 6.2, Table 6.3). For example, of the 15 reliably-marked animals identified in 1988, at least one has been seen during every year since then (Table 6.3).

Table 6.2. Number of years in which reliably-marked individuals, identifiable from both left and right sides, have been identified from good quality photographs.

# years	Individuals (total 113)	Percentage
1	28	25
2	41	36
3	19	17
4	11	10
5	9	8
6	2	1.5
7	3	2.5

Table 6.3. Total number of photographic identifications in year of the study, the number of these that showed reliable markings and were identifiable on both left and right sides, and the number of these reliably-marked individuals resighted (using only good quality photographs) from previous years.

Year	# IDs	# IDs	# Resightings (reliably -marked)							
	total	reliable	1988	1989	1990	1991	1993	1994	1995	1996
1988	32	15								
1989	170	52	12							
1990	260	72	14	40						
1991	8	5	1	0	4					
1993	82	23	4	8	16	2				
1994	85	20	3	7	12	1	7			
1995	25	11	1	4	6	0	3	6		
1996	136	45	6	19	25	2	13	9	8	
1997	140	50	5	19	24	1	15	10	10	30

**1992 is not included since there were no photo-identifications of animals.

Over intervals of approximately 40 days, the diffusion rate, calculated from movements of identified individuals, drops to approach zero (Figure 6.1a). This reflects the time at which the slope of squared displacement versus time interval approaches zero (Figure 6.1b). The further increase in squared displacement and RMS displacement over timescales of 2+ years (Figure 6.1b,c) reflects the distributional changes in bottlenose whale sighting locations observed between years (Chapter 3).

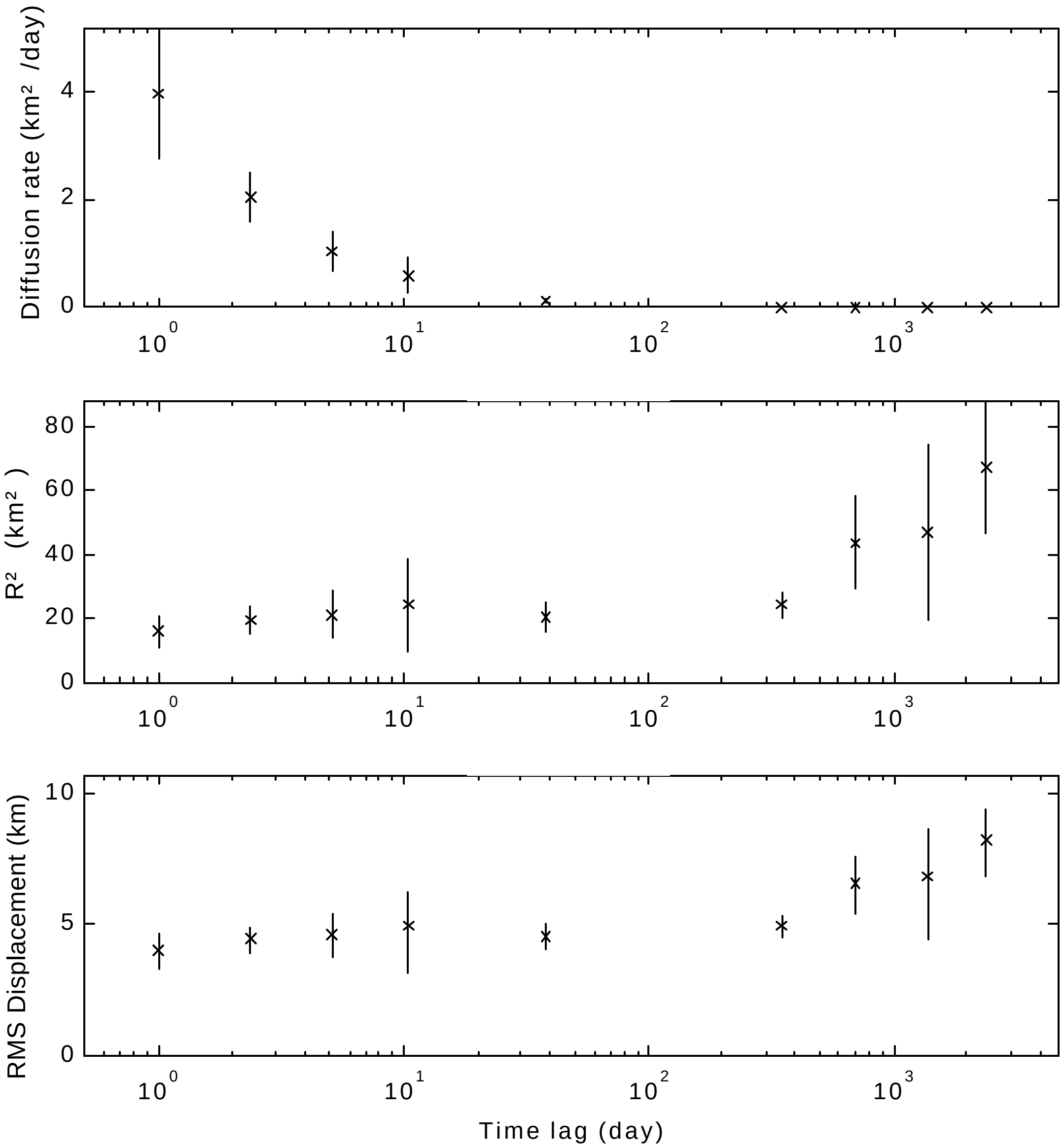


Figure 6.1. Movement parameters calculated over time lags of 1 day to several years (see text for details).

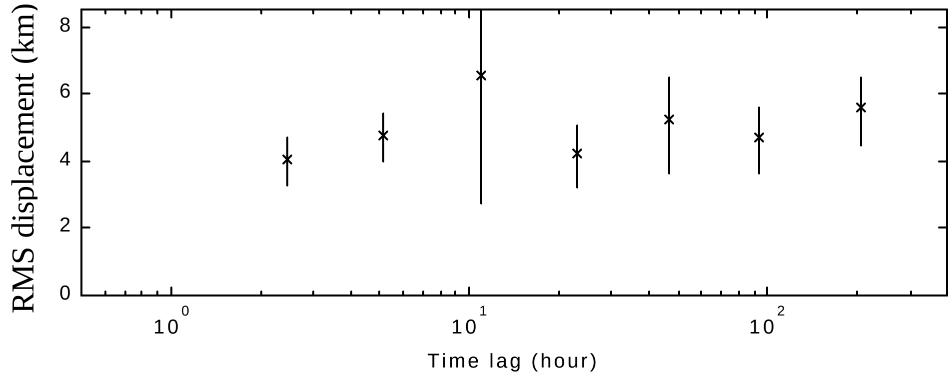
The likelihood and direct methods were found to give almost identical results, demonstrating that the observed pattern of bottlenose whale resightings is similar to that of search effort, i.e., the probability of sampling an animal is relatively constant over the area in which that animal is likely to be found, given that the animal is within the Gully. For all further analyses at smaller timescales the method of direct calculation rather than likelihood calculation was used.

Over smaller timescales of 2 hours to 10 days, bottlenose whales show an initial increase and then a levelling-off of distance moved (Figure 6.2). Movements were approximately 3-4 km over two hours (Figure 6.2), and there did not appear to be any difference in movement rates between different age-sex classes or in different years (Table 6.4). The orientation of the Gully and distribution of whales (Chapter 3) suggested that whales might be moving primarily north-south within the Gully. This was investigated by conducting one-dimensional analyses using the latitudinal or the longitudinal component of position data in turn. Over periods from hours to days there was greater movement north-south (5 km) than east-west (3 km, Table 6.4, Figure 6.3).

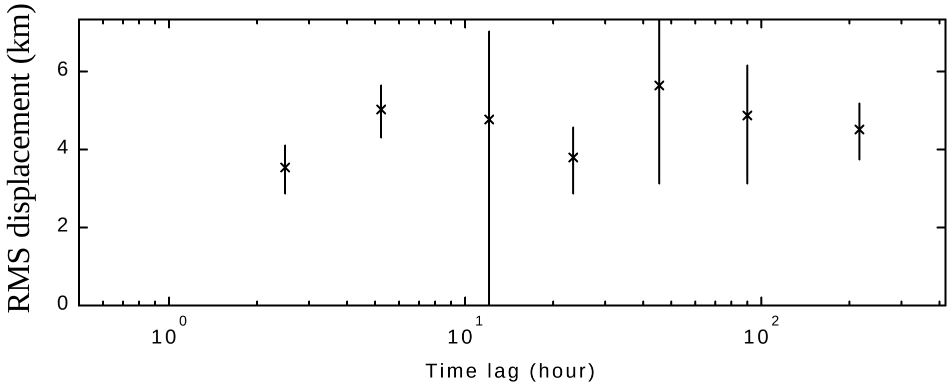
Table 6.4. Rates of movement calculated for different sub-samples of the dataset: for all data (all years, all individuals), for individuals categorised by age-sex classes, for years of greatest field effort, and for latitude and longitude separately (all years, all individuals).

Data	*# IDs*	2 hr Diffusion Rate (km^2/hour) mean (s.e.)	Daily squared displacement (km^2) mean (s.e.)
All data (1988-1997)	682	1.41 (0.25)	17.34 (4.02)
1989	170	1.08 (0.41)	18.63 (9.00)
1990	260	1.39 (0.72)	7.96 (2.09)
1996	136	0.88 (0.42)	25.60 (8.08)
1997	140	0.72 (0.18)	11.03 (1.96)
Female/Immature	107	1.69 (0.59)	20.07 (7.41)
Subadult male	25	1.28 (0.44)	11.76 (7.45)
Mature male	33	1.20 (0.29)	16.25 (9.28)
Latitude	682	1.53 (0.36)	12.15 (2.47)
Longitude	682	0.92 (0.30)	4.70 (1.09)

Females and immatures



Subadult males



Mature males

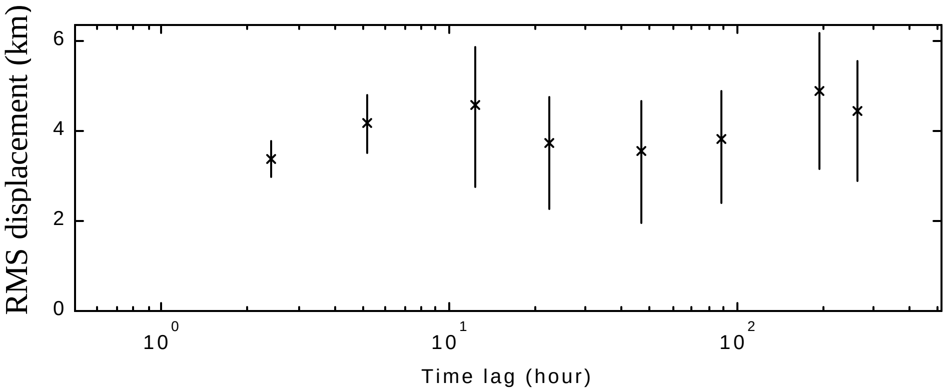


Figure 6.2. Movement parameters calculated over time lags of 2 hours to 10 days for different age-sex classes.

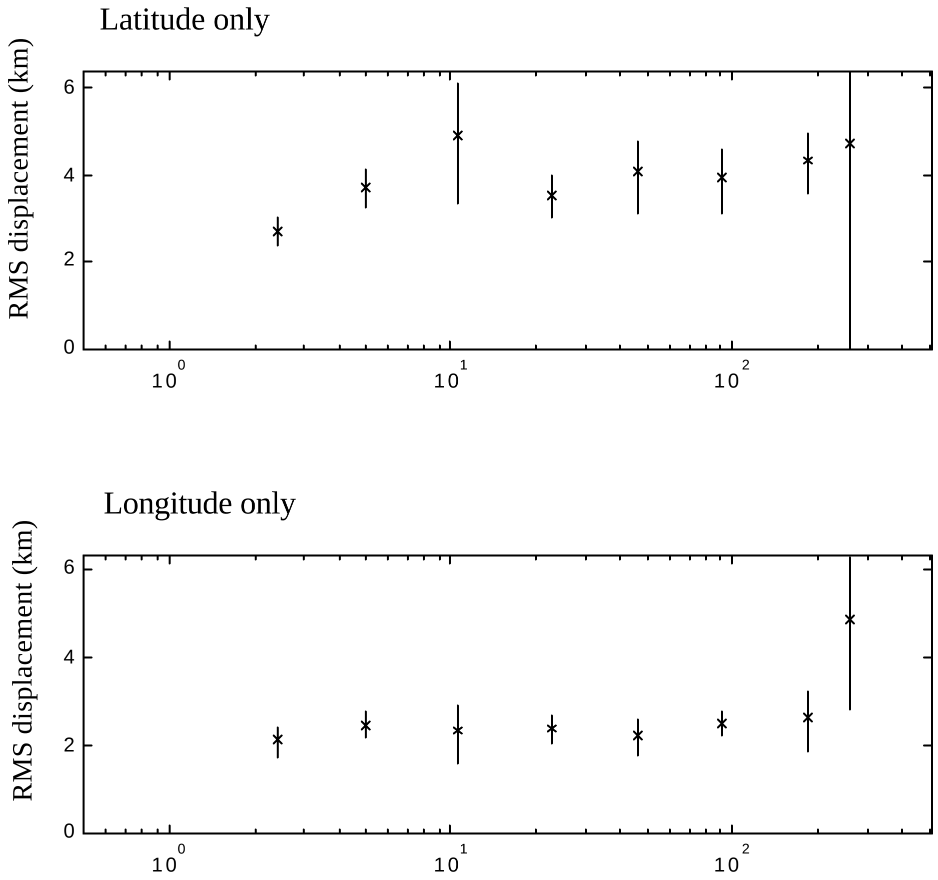


Figure 6.3. One-dimensional movement rates calculated for latitude changes and longitude changes over time lags of 2 hours to 10 days.

Radio-tracking

Five tags were deployed on northern bottlenose whales, for intervals ranging from 2.5 to 28 hours (Table 6.5, Figure 6.4). Various problems were encountered in attempting to follow the tagged animals. The most serious included VHF transmitter malfunction (#4), and possible tag malfunction (#5). Other difficulties encountered included the tag slipping down the body of the whale such that the tag did not clear the water surface when the whale surfaced (#1), difficulty obtaining a "fix" on an animal during the short duration of surfacing bouts and the short duration of each surfacing, and difficulty in spotting the tagged animal when a large number of groups surfaced at the same time (#3).

Table 6.5. Deployment and tracking durations of radio-tagged whales

Date	#	Time on	Time off	Duration (hr:min)	Comments
Aug 25, 1996	1	18:20	23:36	4:06	tracked for only 10 mins, presume tag slipped (such that antenna did not clear water surface during surfacing bout)
Jul 9, 1997	2	15:41	18:14	2:33	tracked for duration of deployment
Aug 24, 1997	3	14:56	18:52 (next day)	27:56	close tracking for last 2.5 hours of deployment
Aug 9, 1998	4	06:55	not retrieved	> 9:52	audible for 2 hours (in fog), 4 hours silent, heard again and relocated but transmitter failed, last seen at 16:47
Aug 15, 1998	5	17:53	not retrieved	> 14:33	close tracking for 3 hours, 3 hours silent, heard sporadically until 8:26.

Despite the difficulties encountered in following tagged animals, the position data obtained (from when tagged whales were seen) are useful in examining movements over short timescales.

Over the timescales that tagged animals were tracked (up to 1.5 days), distance squared followed an approximately linear relationship with time interval (Figure 6.5; regression of log of distance squared against log of time interval was significant, slope = 0.89, s.e. 0.13, $r = 0.638$, $p < 0.001$; regression excluding data for >8 hour time-interval had identical slope, s.e. 0.17, $r = 0.530$, $p < 0.001$).

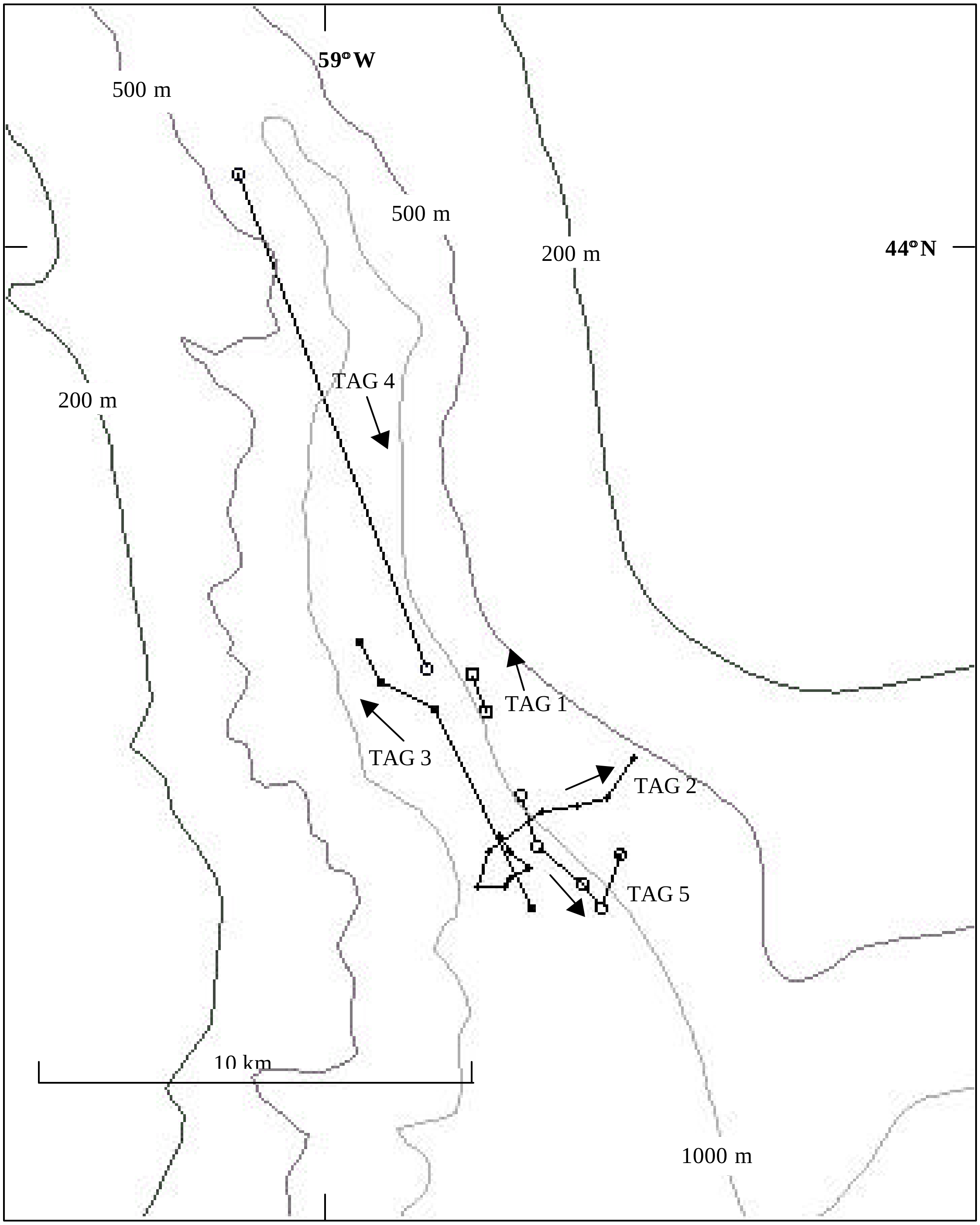


Figure 6.4. Movements of radio-tracked animals (see Table 6.5 for details).

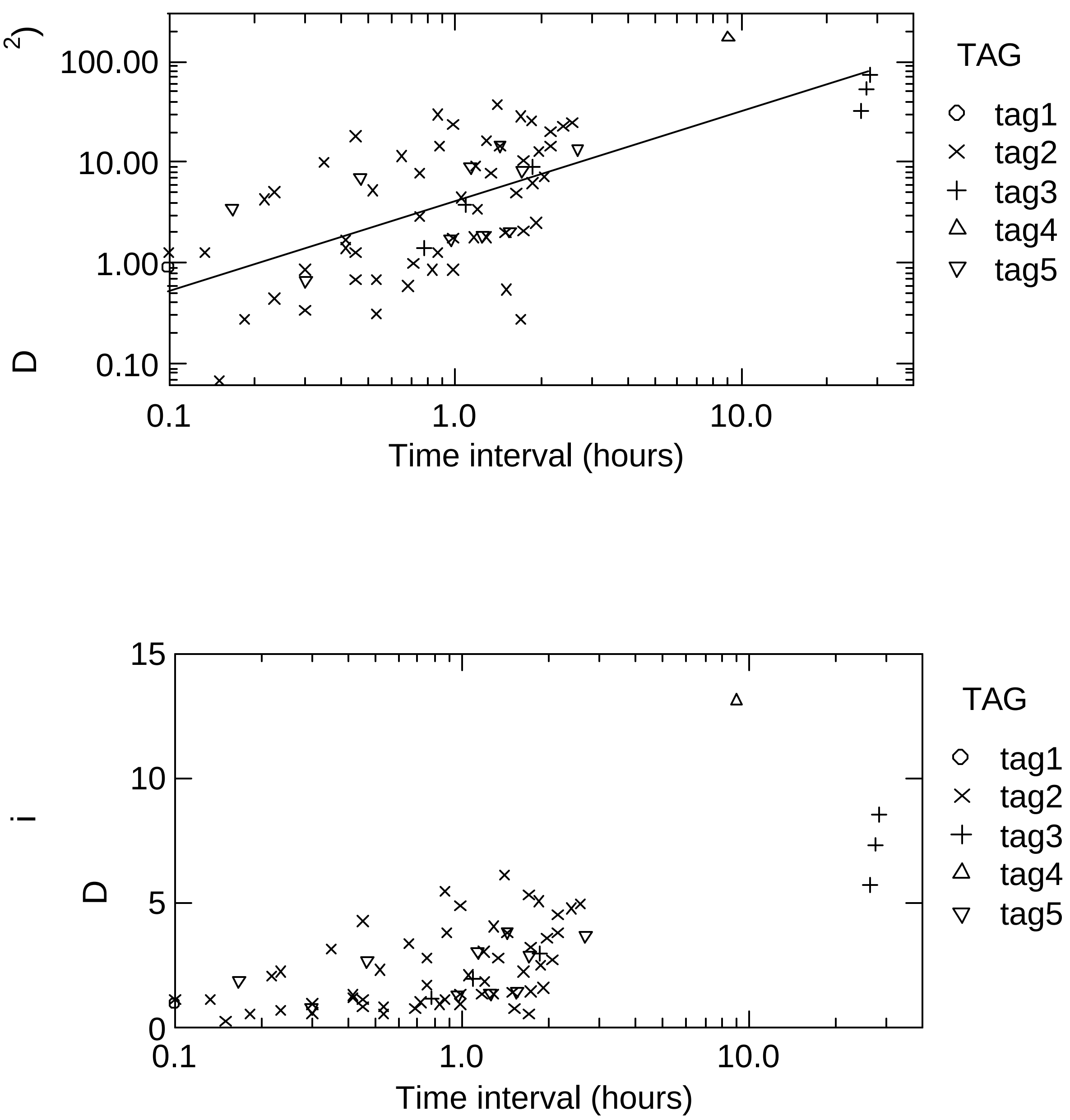


Figure ~~6~~.5. Squared distance (log scale) and distance with time-interval (log scale) calculated from results of radio-tracking. Regression line of logged distance squared against logged time interval is shown, r=0.638; slope=0.89

A linear relationship between distance squared and time interval (log-log plot slope of approximately 1.0, Figure 6.5) demonstrates that movement can be modelled as random and the estimate of diffusion (equation 1) is useful over these timescales. The few locations recorded from tag 3 at a 1 day timescale also lie close to this regression line, suggesting random movement. That from tag 4 lies above this line however, suggesting more directed movement, and may represent an animal leaving the Gully area.

For the tags which were successfully recovered and from which time-depth data were retrieved (tag 2 was on individual #1 and tag 3 on individual #2 of Chapter 5 respectively), the distance travelled during each dive can also be investigated. Over many of the dives the distance travelled appeared to increase with dive duration (Figure 6.6). The two apparent outliers were recorded from very short dives during a period of high speed swimming. However, these data were recorded for only two individuals and sample sizes were small.

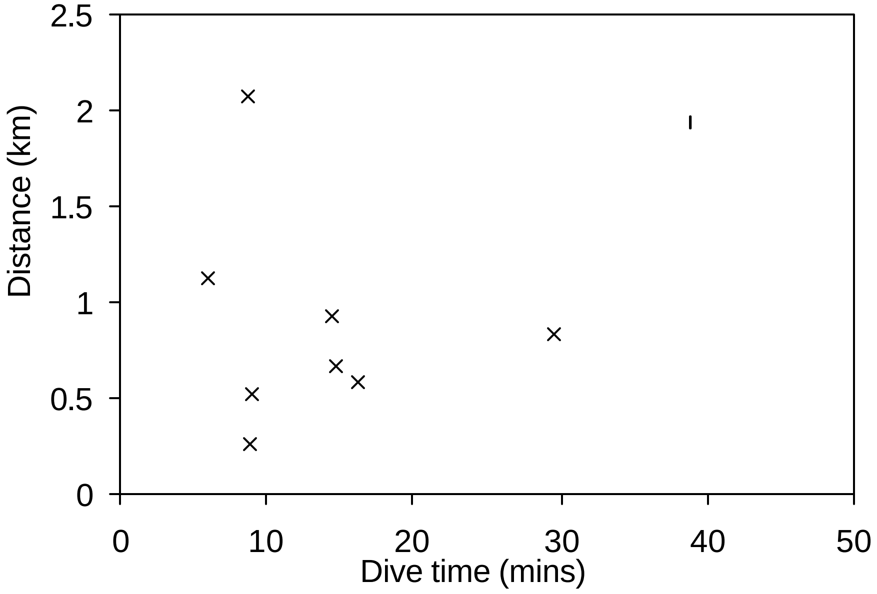


Figure 6.6. Relationship of distance moved to dive duration (x shows data recorded from first successful TDR deployment, #2; ◊ shows data recorded from the last dive of the second successful TDR deployment, #3).

Individual ranges

There were significant differences between years in the average location of individuals (MANOVA, F = 29.5, $p < 0.001$, 9 years). Variation, calculated as the square root of the summed variances in latitude and longitude, was approximately 5 km. Examples of changing locations of individuals between years are shown for six animals seen on more than 15 days each (Figure 6.7). Within each year, the positions of individuals of different age-sex classes showed no significant differences (MANOVAs for each year, $p > 0.05$).

Within years, there appeared to be some separation between individuals in the Gully in terms of preferred ranges (Table 6.6). Individuals generally appeared to show some range separation during 1990, 1996 and 1997 (Table 6.6). This effect was also seen between individuals within each age-sex class (Table 6.6). Since these were the years of greatest field effort, they have the greatest power to detect significant differences. However, these were also the years of longest field effort, so in order to check that a significant individual effect was not in fact caused by differences in sightings between months, the test was repeated including month as a factor. Although for two years (1990, 1997) month had a significant effect ($p < 0.05$), there was a significant individual effect for all three years even including month as a factor ($p < 0.05$).

There were significant differences between individuals in relative spatial orientation between years (variations from the mean yearly location, MANOVA F = 1.263, $p = 0.026$). Significant differences were found between mature male relative locations but not between those of other age-sex classes (Table 6.7). This separation between mature males was based on the consistent relative orientation of individuals from other individuals, whereas the separation between females/immatures and between subadult males was not of consistent orientation (e.g., always to the north or south of the average position). Plots of individual male sightings for the years of most field effort show this tendency toward constant relative location from year to year (Figure 6.8). For example, male #950 was observed to the north of other males in 1996 and 1997, whereas #480 had a central location in relation to other males.

Table 6.6. Results of MANOVA to test individual differences in sighting positions for all individuals and within each age-sex class (dependent variables: latitude and longitude, independent categorical variables: year and individual). Variation was calculated as the square root of variance in latitude plus longitude for relevant individuals.

	Year	*# IDs*	*n*	variation (km)	F-statistic	p-value
All animals	1989	25	77	1.61	0.999	0.489
	1990	50	172	2.08	1.468	**0.010**
	1993	10	29	2.45	1.595	0.114
	1994	6	13	2.36	0.665	0.737
	1996	29	95	4.77	1.947	**0.001**
	1997	31	88	2.96	1.694	**0.008**
Female/Immature	1989	6	14	1.39	0.790	0.640
	1990	14	53	1.90	2.052	**0.008**
	1993	6	17	2.72	2.365	**0.049**
	1996	7	23	3.31	1.677	0.123
	1997	13	41	2.24	2.360	**0.005**
Subadult male	1989	5	15	1.15	0.962	0.494
	1990	11	49	1.90	1.717	**0.049**
	1996	5	22	3.42	2.011	0.077
	1997	3	7	2.57	1.150	0.418
Mature male	1989	4	18	1.54	0.462	0.830
	1990	10	29	2.04	2.872	**0.003**
	1996	8	23	3.10	2.446	**0.021**
	1997	6	15	1.52	1.235	0.341

Table 6.7. Results of MANOVA to test individual consistency in relative location. Variations of individual positions from the mean yearly position were tested for individual differences within each age-sex class (dependent variables: latitude and longitude, independent categorical variable: individual).

	# IDs	*n*	F-statistic	p-value
Female/Immature	31	93	0.896	0.679
Subadult male	15	38	0.852	0.669
Mature male	18	54	1.850	**0.015**

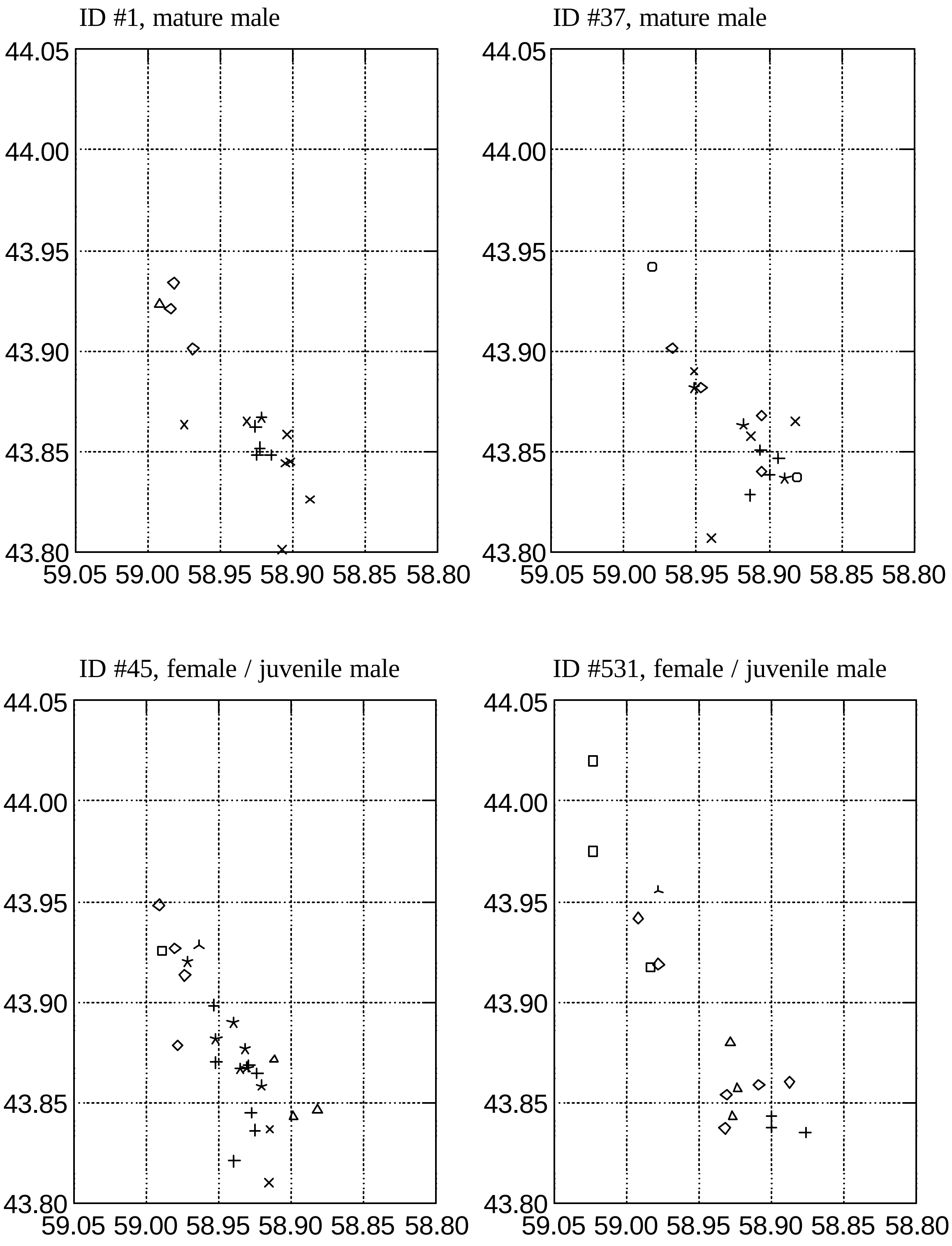
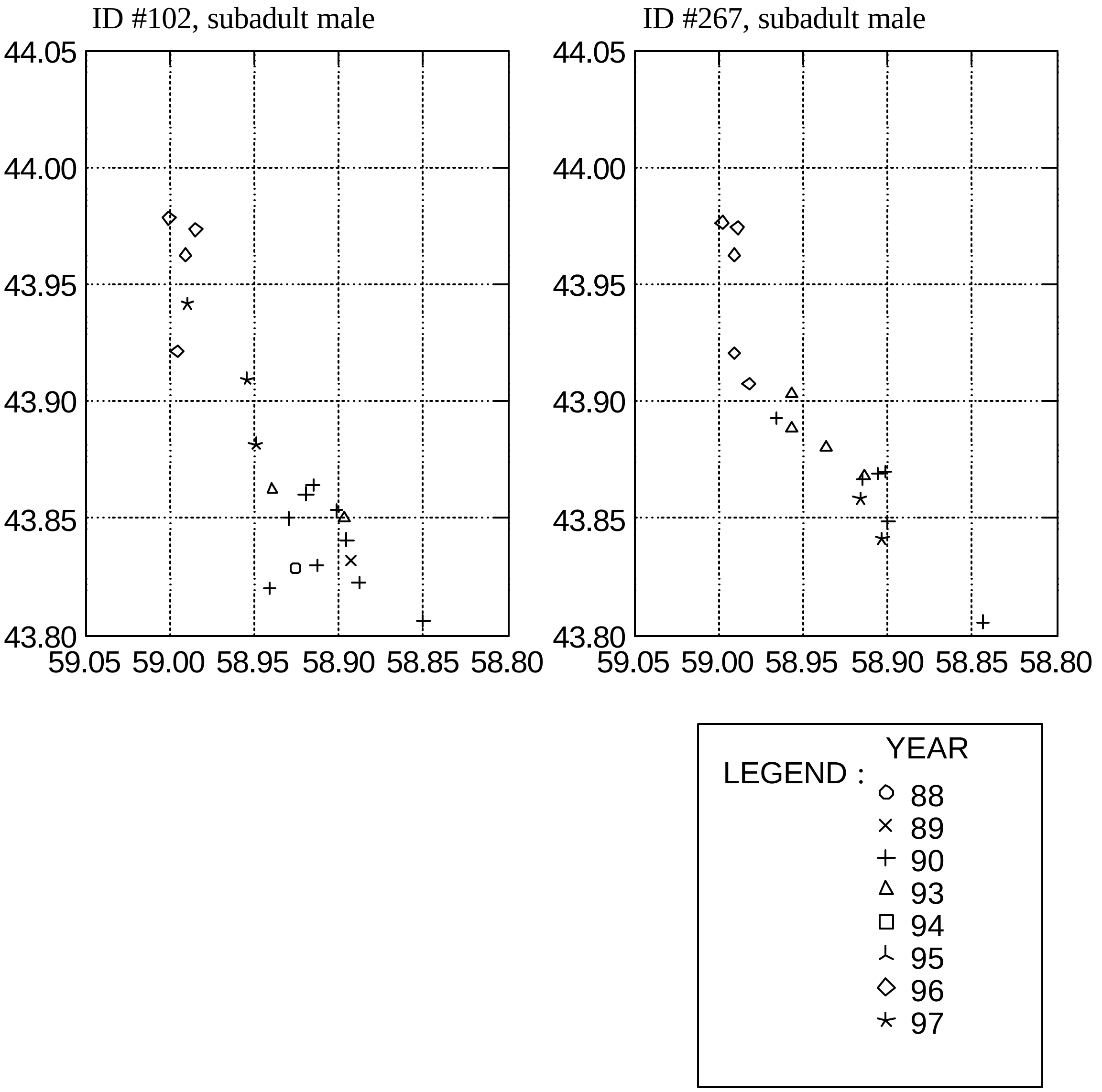
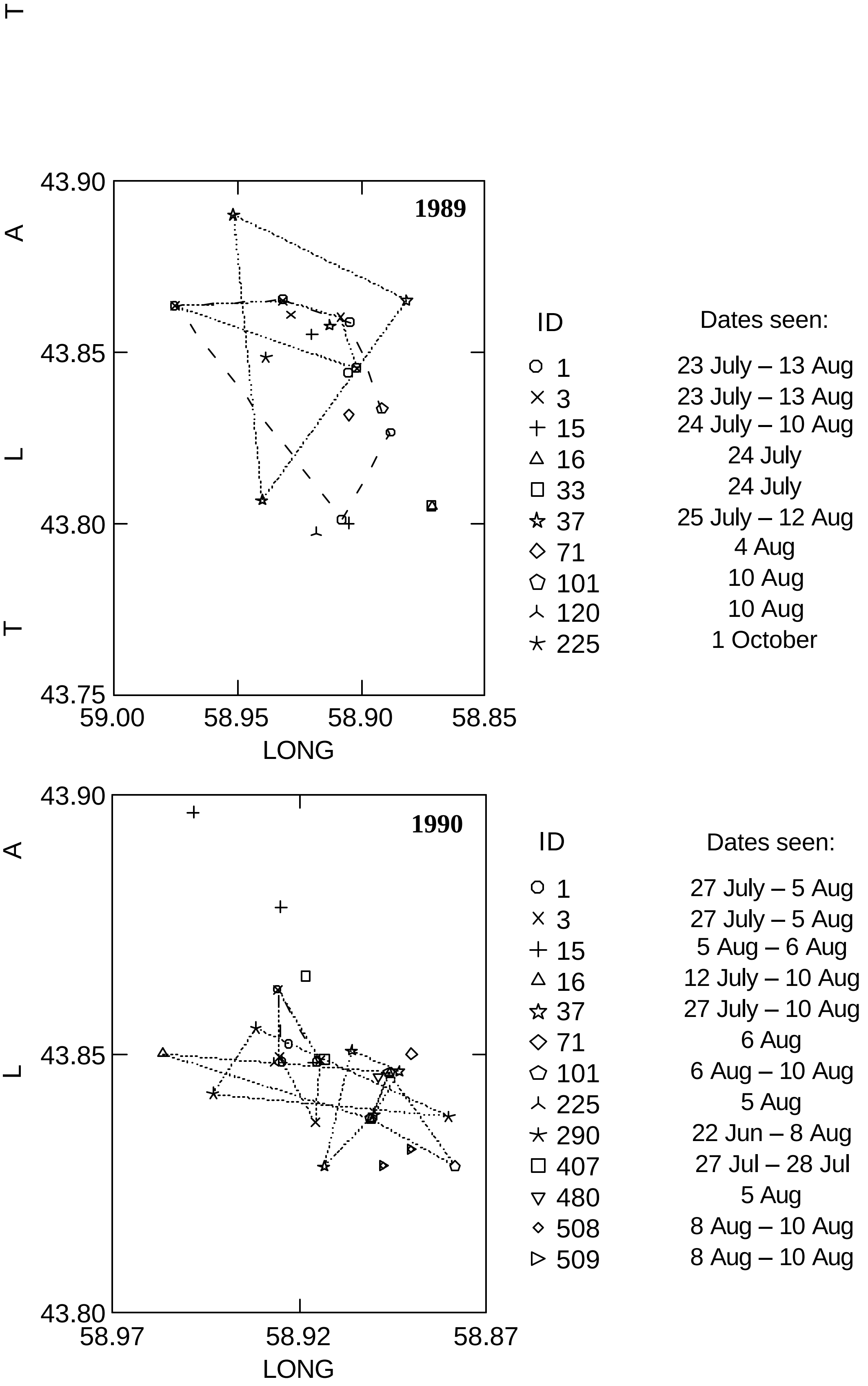


Figure 6.7 (continued overleaf). Locations of six individuals seen in total on more than 15 days, spanning at least 4 years. Two mature males, two subadult males and two female/juvenile males are shown.


ID #102, subadult male

ID #267, subadult male

Figure 6.7 (cont). Locations of six individuals seen in total on more than 15 days, spanning at least 4 years. Two mature males, two subadult males and two female/juvenile males are shown.



ID	Dates seen:
○ 1	23 July – 13 Aug
× 3	23 July – 13 Aug
+ 15	24 July – 10 Aug
△ 16	24 July
□ 33	24 July
☆ 37	25 July – 12 Aug
◇ 71	4 Aug
⬠ 101	10 Aug
⅄ 120	10 Aug
✶ 225	1 October

ID	Dates seen:
○ 1	27 July – 5 Aug
× 3	27 July – 5 Aug
+ 15	5 Aug – 6 Aug
△ 16	12 July – 10 Aug
☆ 37	27 July – 10 Aug
◇ 71	6 Aug
⬠ 101	6 Aug – 10 Aug
⅄ 225	5 Aug
✶ 290	22 Jun – 8 Aug
□ 407	27 Jul – 28 Jul
▽ 480	5 Aug
⋄ 508	8 Aug – 10 Aug
▷ 509	8 Aug – 10 Aug

Figure 6.8. Male ranges shown for years of highest number of sightings. First and last dates seen are shown for each individual.

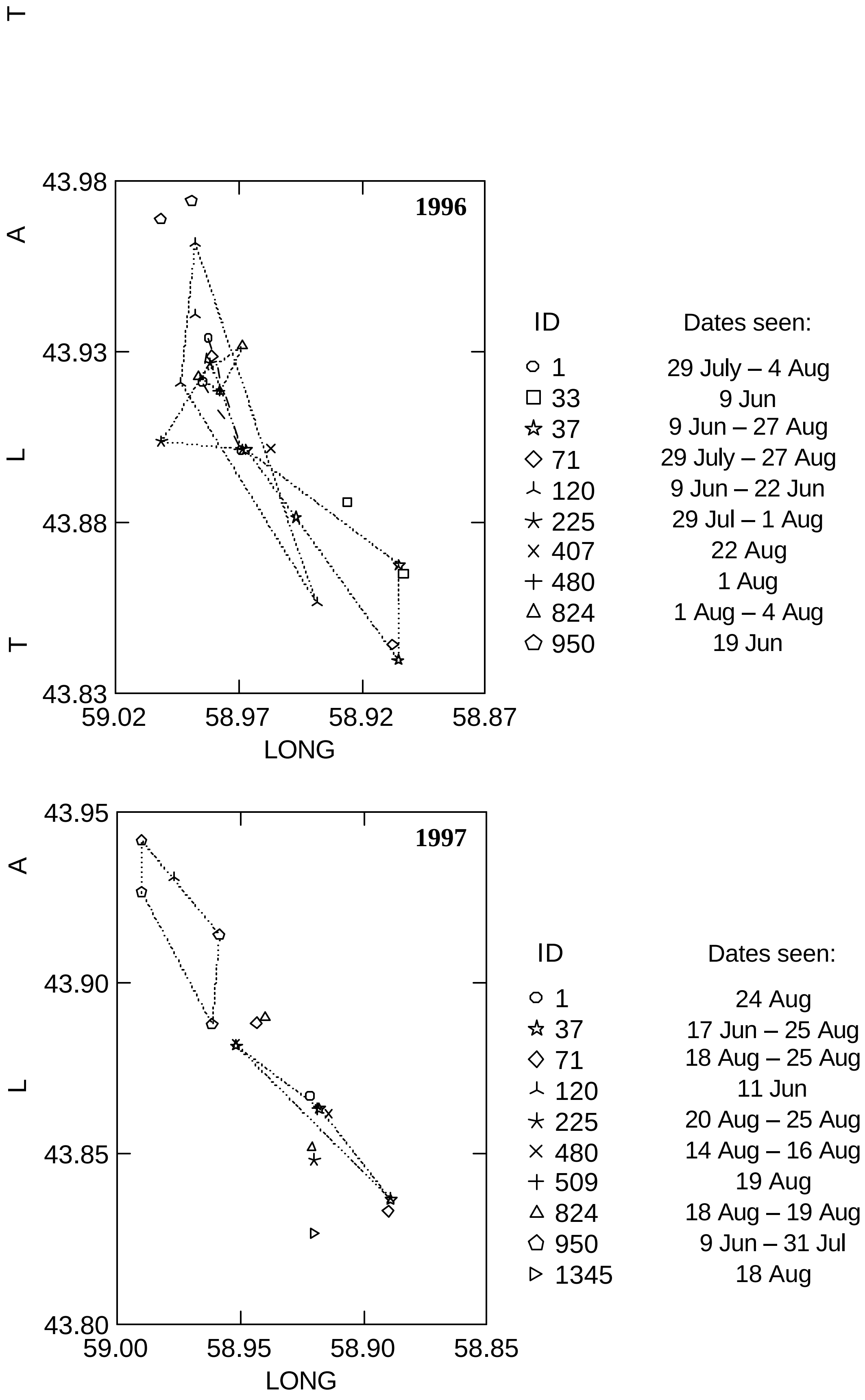


Figure 6.8 (cont). Male ranges shown for years of highest number of sightings. First and last dates seen are shown for each individual.

DISCUSSION

In general, radio-tracking provides finer scale resolution of individual movements than can be obtained from photo-resightings (Chapter 4). However, for northern bottlenose whales, radio-tracking could rarely be used to gain positions of the tagged animal for all surfacings and often animals could only be loosely tracked and were resighted only every 2-8 hours. In this respect, radio-tracking provided little increase in movement resolution compared to photoidentification data for this species. Photo-identification analyses showed that individual bottlenose whales appear to be resident within the Gully for time-periods of approximately 10 ± 5 days (Gowans 1999). At temporal scales of less than this, movements of animals within the Gully can therefore be well described by photo-identification data. Over temporal scales greater than this, one must make the proviso that while movement within the Gully can be investigated, this is done without reference to the potential movements of animals out of the area.

Results calculated over short timescales (2 hours – 2 days) using photo-resighting data and radio-tracking data were largely consistent. Over timescales of 2 hours, photo-resightings showed RMS distances of 3 km while radio-tracking suggested movements of 2-3 km (n=3). However, over timescales of 1-2 days photo-resightings suggested movements of 4-5 km (n=682; Figure 6.2), while radio-tracking suggested movements over 1-2 days of 5-10 km (n=2; Figure 6.5). This provides some suggestion (although based on a small sample) that animals, presumably when leaving the Gully, may show daily displacements greater than those observed within the Gully. Over longer timescales (1-10 days), the asymptote shown by the RMS displacement plots (Figure 6.2) at approximately 4-5 km, suggests that animals range over an area approximately 20 km^2 within the Gully over intervals spanning 1-10 days (also seen in Figure 6.1).

Since we were not sampling whales at every surfacing for collection of photo-identification data, it could be argued that this pattern of movement within a 20 km^2 area reflects the movements of the study vessel, rather than the movements of the whales. I do not believe this was the case for several reasons. (1) The distribution of bottlenose whales within the Gully appears to be fairly isolated, despite sampling outside the core area (Chapter 3). (2) Whales show residency periods of approximately 10 days within the Gully (Gowans 1999) and therefore measurement of movement within this timeframe should accurately reflect whale movement within the Gully study area. Within 10-day sampling intervals, animals therefore appear to have a discrete range within the Gully, much of which they cover in a single day. (3) The agreement between calculations of movement parameters using direct or likelihood methods suggests that the movement rates calculated were not biased by search effort. The agreement between movements calculated from photo-resightings and from radio-tracking also supports this.

The total Gully area over which bottlenose whales have been seen is approximately 20 km x 5 km (Chapter 3). Within each 10-day period, each individual ranges over approximately 20 km^2 of this, but these ranges appear to change between years (Figure 6.1). Read and Westgate (1997) point out that the scale of measurement of movements is likely to influence range estimates. Harbour porpoise (*Phocoena phocoena*) ranges were calculated at 210 km^2 from radio-tracking over periods of up to 22 days (Read and Gaskin 1985), but were found to be much larger (ca. 50000 km^2) from satellite-tracking over 212 days (Read and Westgate 1997). Nevertheless, over short timescales bottlenose whales in the Gully appear to reside within a relatively small range, a little smaller than the range of 85 km^2 calculated for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (Wells et al. 1980).

The daily movements of bottlenose whales within the Gully were also much less than those found for a variety of other cetacean species (Table 6.8). Daily displacements are likely to be partially affected by the study method (if search effort is not uniform) and by the timescale of the study, since animals may show very different daily displacements during certain time-periods. The species shown in Table 6.8 were all recorded over broadly similar timescales using methods which, for the most part, were either of relatively uniform search effort, or used methods to account for variability in search effort, such that their daily displacements should be comparable. Oceanic species, such as sperm whales and spotted dolphins, appear to cover wide areas spanning about 50 km daily, whereas more coastal species such as bottlenose dolphins and harbour porpoises cover much smaller distances spanning about 15 km daily. By comparison with these, bottlenose whales in the Gully move very little. Whitehead (1996a) and Jaquet and Whitehead (1999) showed that movements of sperm whales over periods of days correlate with their foraging success. Similarly, the small amount of movement shown by bottlenose whales in this study may be related to a profitable food source in the area.

Table 6.8. Published mean daily movement (24-hour displacement) of odontocetes.

Species	24-hr displacement (km)	*n*	method	timescale	Source and Location
Bottlenose whales *Hyperoodon ampullatus*	~4	113*	photo-id	days - 3 mo	*this study,* within the Gully
Sperm whales *Physeter macrocephalus*	~50	1800*	photo-id	days - 3 mo	Whitehead, submitted, South Pacific
Pantropical spotted dolphins *Stenella attenuata*	55[†]	26	tag retrieval	2 hr – 2 d	Perrin et al. 1979, Eastern Tropical Pacific
Dusky dolphins *Lagenorhynchus obscurus*	19.2 (s.d. 1.79)	10	radio-tag – shore / ship	1-15 d	Würsig 1982, Golfo San José, Argentina
Harbour porpoises *Phocoena phocoena*	26.0 (s.d. 13.9)	8	satellite-tag	2-212 d	Read and Westgate 1997, Bay of Fundy
Common dolphins *Delphinus delphis*	~15[‡]	1	radio-tag from ship	up to 23 hr	Evans 1971, Santa Catalina Is., CA, USA
Bottlenose dolphin *Tursiops truncatus*	23.7 (s.e. 2.4)	1	satellite-tag	25 d	Mate et al. 1995, Atlantic
Atlantic white-sided dolphin *Lagenorhynchus acutus*	~40[‡]	1	satellite-tag	6 d	Mate et al. 1994, Atlantic

* calculated from photo-id of population
[†] based on regression equation of displacement against time (for 2-48 hr returns)
[‡] value calculated from the data presented

If the Gully is so profitable however – then why do animals leave? The answer to this presumably lies in the per capita profitability of foraging. Optimal foraging theory and marginal value theorem predict that an individual will experience diminishing returns as the number of whales in the Gully increases. Although the Gully may be much richer than another foraging area, as more individuals enter the richer patch an individual will eventually do better in terms of individual net gain in the poorer patch. A resulting "ideal free distribution" (IFD) will then result (Krebs and Davies 1991). One of the assumptions of "ideal free distribution" is that individuals have perfect knowledge of the relative availabilities of resources. However, animals are unlikely to have perfect information and may move between patches in order to make sampling decisions, or for other reasons. Experimenters commonly report movement of animals between patches even after an equilibrium has been reached (see review in Hugie and Grand 1998). Hugie and Grand (1998) show that when non-IFD movements are incorporated into an IFD model, the equilibrium will often resemble that for IFD conditions. Movements of bottlenose whales in the Gully, showing a discrete range over the 10-day duration that whales are found in the Gully (Gowans 1999), therefore fit such a model, with individuals continually entering and leaving. Furthermore, this suggests that fluctuations in prey density take place over timescales of approximately 10 days.

While the results presented here describe the movement of whales within the Gully, we do not know how whales behave when they leave this area. It has been previously suggested that northern bottlenose whales may move fairly large distances in a short time period. The good condition of a beak of the cephalopod *Vampyroteuthis infernalis* in the stomach of a northern bottlenose whale stranded in the Faroe Islands suggests that this whale had travelled at least 1000 km (from more southerly regions where this cephalopod is found) within a few days (Clarke and Kristensen 1980). Another stranded bottlenose whale (in Hiddensee in the Baltic) contained *Gonatus* beaks, and *Gonatus* (and bottlenose whales) are generally distributed at least 1000 km away in the Norwegian Sea (Lick and Piatkowski 1998). Southern bottlenose whales (*Hyperoodon planifrons*) live-stranded and caught off South Africa contained squid usually found in the Antarctic and sub-antarctic (Sekiguchi et al. 1993). Likewise, diatoms found on the skin of one of these whales also suggested that it had recently moved into warmer waters (Nemoto et al. 1980). However, the apparent differences in genetic structure (M.L. Dalebout, pers. comm.) and size (Whitehead et al. 1997b) of bottlenose whales in the Gully from those off Labrador suggest that movement outside the Gully is not of the scale at which population mixing would occur.

Among mammals, female distribution is largely determined by access to resources, while male distribution (during the breeding season) is largely determined by access to females (Davies 1991). The displacement rates observed here were similar for different sex/age classes. Likewise the residency rates of different age-sex classes were found to be the same (Gowans 1999). This is difficult to interpret, however, since it could be due to the fact that all animals are foraging in the Gully, or could be because males are tracking individual female movements. Among sperm whales, males have been found to rove between groups of females (Whitehead and Arnbom 1987). If this were the case here, and males were using the Gully as a source of females rather than of food, they might be expected to show different rates of movement than females, or to stay in the Gully for different periods of time.

Individuals within all age-sex classes appeared to show locational differences in the Gully during some years (Table 6.6). The years during which animals had preferred ranges coincided with those during which highest whale abundance was recorded (Chapter 3). As would be expected, these years were also those in which the highest number of individuals was recorded and there was generally the greatest spread of individuals (as reflected by the variation of individual position from the mean, Table 6.6). Since MANOVAs generally have less power to detect differences with increasing number of groups tested, the separation in ranges found does not appear to be an artefact of the number of individuals tested. These results are consistent with the idea that the Gully contains an important foodsource for bottlenose whales but that there is some variation in abundance of prey between years. In years of high prey abundance with more animals in the Gully, it appears that there may be some spatial separation between individuals.

Within age-sex classes, only mature males showed consistent differences in relative location between years (Table 6.7). Since both males and females were distributed over the same area, and yet females showed no preference for relative location between years, such relative spatial preference seems unlikely to be related to foraging. Males probably have mating opportunities during the summer in the Gully. Fetus lengths recorded by whalers suggested a loosely-defined mating-season (with occasional mating year-round) and an approximate one-year gestation (Christensen 1973), and, since very young infants have been observed in the Gully during the summer months (Gowans 1999), bottlenose whales are also likely to mate at this time. Such relative spatial differences between mature males may therefore be based on preference for relative spatial locations which provide different mating opportunities as females enter and leave the Gully. Recent evidence of male-male conflict provides some anecdotal behavioural support for potential competition between males in the Gully (Gowans and Rendell 1999). However, male bottlenose whales have also been suggested to form coalitions (Gowans 1999; also visible in Figure 6.8).

Conclusion

The relatively small daily displacements observed for bottlenose whales in the Gully suggest that the Gully is a productive foraging location for these whales. Bottlenose whale use of the Gully as a foraging area appears to fit what would be expected from an ideal free distribution. Following from this, the residency period of 10 days for whales in the Gully would be expected to reflect the timescale of variation in prey abundance. Age-sex classes of whales showed no difference in movement parameters or locations within the Gully, suggesting that functional use of the area is similar for all whales, while yearly shifts in distribution but lack of difference in movement parameters between years suggest that this is likely related to foraging. However, mature males appeared to have preferred relative locations within the canyon which may be related to concurrent mating opportunities.

CHAPTER SEVEN

Acoustic behaviour of northern bottlenose whales - click characteristics and implications for foraging

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ABSTRACT

Sounds produced by northern bottlenose whales were recorded in the Gully, a submarine canyon off Nova Scotia. The predominant sounds heard were clicks; in 428 minutes of recordings no whistles were heard which could unequivocally be attributed to bottlenose whales. There appeared to be two major types of click series, initially distinguished by large differences in received amplitude, but which also differed in a number of other characteristics. Loud clicks (produced by whales nearby at the surface) were rapid, with short and variable inter-click intervals (mean 0.07 s; CV 71 %). The spectra of these surface clicks were variable and often multimodal, with peak frequencies ranging between 2 and 22 kHz (mean 11 kHz, CV 59 %). Clicks received at low amplitude (produced by distant whales, presumably at depth) appeared to have consistent inter-click intervals (mean 0.40 s, CV 12.5 %). Clicks produced at depth also had generally unimodal frequency spectra with a mean peak frequency of 24 kHz (CV 7 %) and 3 dB bandwidth of 4 kHz. Echolocating animals are thought to wait for the echo of a first click before emitting a second, such that inter-click intervals reflect the approximate distance searched by an animal. The inter-click intervals recorded from distant whales suggest a search distance of 300 m, comparable to that of sperm whales. Click frequency should be related to the size of the object being investigated; a 24 kHz frequency would be optimal for an object of approximately 6 cm, consistent with the size range of their primary prey species, the squid *Gonatus*.

INTRODUCTION

Very little is known of the acoustic repertoire of any of the beaked whales. Winn et al. (1970) described the first recorded sounds for any species of beaked whale. These were recorded during a four-hour encounter with northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully, Nova Scotia. This recording contained primarily single pulse clicks in intermittent series, but also discrete-frequency whistles, sweep-frequency chirps and possibly also burst-pulse modulated tones. Two other studies of the acoustic behaviour of free-ranging beaked whales have been opportunistically conducted on Baird's beaked whale (*Berardius bairdii*) and Arnoux's beaked whale (*Berardius arnuxii*). These species were also found to produce frequency-modulated whistles, burst-pulse clicks, and discrete clicks at times produced in quite rapid series (Dawson et al. 1998, Rogers and Brown 1999).

A few other sounds have been recorded from stranded beaked whales. Caldwell and Caldwell (1971) recorded pulsed chirps or whistles audible in the air from a stranded subadult male Blainville’s beaked whale (*Mesoplodon densirostris*) while the animal was lying in the surf. A stranded Gervais' beaked whale (*M. europaeus*) was also found to produce clicks of variable repetition rate (Caldwell and Caldwell 1987). Bonde and O’Shea (1989) attempted to record sounds from a stranded Sowerby’s beaked whale (*M. bidens*) but were unable to discern any vocalisations. Lynn and Reiss (1992) reported both pulsed sequences and whistles from two stranded young male Hubb's beaked whales (*M. carlhubbsi*).

In this chapter, the sounds recorded from northern bottlenose whales in the Gully are described and discussed, primarily with respect to the foraging behaviour of these whales. Assuming that such clicks are for echolocation, the inter-click interval and frequency of clicks recorded is used to infer information on the size of prey and the ranges over which foraging takes place (cf. Goold and Jones 1995 for sperm whales, *Physeter macrocephalus*).

METHODS

Acoustic recordings were made in the presence of northern bottlenose whales in the Gully, Nova Scotia (approximately 44°N, 59°W) during June-August in 1988-1990, 1995 and 1997. Whales were approached using 10-12 m sailing vessels, and recordings were made both while whales were at the surface close to the research vessel, and during the minutes after whales had left the surface. The recording equipment used consisted of an omnidirectional hydrophone (Celesco LC-32 at approximately 15 m depth, 1988-90; or Vemco VCHLF hydrophone at approximately 3 m depth, 1995 and 1997), an Ithaco 453 preamplifier and a Nagra IV-SJ tape recorder. High-pass rolloff filters (1 kHz) in the preamplifiers were used to minimise wave noise. Preliminary recordings in 1988 and 1989 were made at 19 cm/s, but during 1989 it was discovered using a bat detector (Ultra Sound Advice, S-25, 15-200 kHz) that the whales were also making sound in the ultrasonic range (Faucher and Whitehead 1991). Only recordings made at 38.1 cm/s are analysed here. The frequency response of the Nagra was flat up to 40 kHz, the LC-32 hydrophone was flat at 1-80 kHz, and the VCHLF hydrophone was flat at 1-25 kHz and rolled off to 35 kHz.

In order to maximise the likelihood that recordings were of bottlenose whales, tape segments were selected such that there had been no dolphins sighted within an hour before or after the recording. Signals from these tapes were viewed at 1/2 speed using a Multigon Industries Uniscan II spectrum analyser. From these, sixteen tape segments with high signal to noise ratio and for which either only one or very few whales were vocalising at one time were chosen for more detailed analysis. Ten click sequences from each segment (selected such that there was least ambiguity that clicks were from the same animal) with at least 10 seconds between each were digitised at 8 bits and analysed using the software Canary 1.1. Tapes were played at 1/8 speed (4.75 cm/s) with a computer sampling rate of 44 kHz, providing an effective analysis range of 1 - 176 kHz. To avoid aliasing, a Krohn-Hite Band-Pass Filter (Model 330N, Krohn-Hite, Cambridge, Mass, USA) was used with the low pass filter set at 80 kHz.

The inter-click interval was defined as the time between the maximum amplitude of the first pulse of the first click to the maximum amplitude of the first pulse of the next click, determined both audibly (by amplitude and frequency) and visually (primarily by amplitude of the waveform) to be from the same animal. The duration of the click was determined from the onset of the click to the point at which the signal decayed to the level of noise. A click quality value was assigned such that high-quality clicks were those more likely to represent signals recorded along the beam axis of the vocalising whale (Au 1993). The frequency spectrum (amplitude versus frequency) was calculated for each high-quality click. The region of the waveform over the duration of the click was used to calculate its quadratic spectrum (4096 point FFT, frame length 4096 pt, time frame 16 pt, Hamming window, frequency resolution 5.4 Hz). The peak frequency, 3 dB bandwidth, the number of peaks and the secondary peak frequency (if greater than one third of the amplitude of the first peak frequency) were noted. The majority of clicks were observed to have a multiple pulse structure, the second and consecutive pulses of which appeared to be reflections of the first, presumably on account of the shallow hydrophone depth or the proximity of the research vessel to the hydrophone (Figure 7.1). All measurements were made using only the first pulse of each click.

RESULTS

During preliminary analysis of the acoustic tapes, 428 minutes of tapes containing bottlenose whale sounds were monitored for selection. No whistles were heard in these recordings which could be unequivocally attributed to bottlenose whales. Although distant whistles were heard, these were generally within an hour of a dolphin sighting. No whistles were heard that were of an amplitude as great as that heard concurrently for bottlenose whale clicks.

Two classes of click series were distinguished by large differences in amplitude. The magnitude of this difference was great enough that clicks could be categorised to type without ambiguity. The first class (hereafter termed "distant" clicks) was heard at low amplitude, and was heard at times when whales were not at the surface. The second class (hereafter termed "nearby" clicks) was heard at much greater amplitude, often while whales were at the surface near the research vessel (Table 7.1). Distant clicks tended to be very regular (i.e., low coefficient of variation) in inter-click interval (Table 7.2, Figure 7.1). Nearby clicks were often emitted in rapid succession, often speeding up and then slowing and stopping (Figure 7.2).

Table 7.1. Recording sequences used, shows co-ordination between occurrence of regular clicks with diving behaviour.

Tape	Date	Local Time	Behaviour	distant	nearby	# whales
S27	11/8/89	15:15 - 15:18	diving	√		4 (then 2)
S28	11/8/89	19:36 - 19:42	milling at surface		√	5 (6)
S30	11/8/89	20:32 - 20:36	at surface	√		5
S31	11/8/89	20:51 - 20:57	at surface (5m away)		√	3
S34	12/8/89	15:14 - 15:19	diving	√		- (2)
X10	6/7/90	15.36 - 15.44	surface/ diving	√		2 (then 4)
X11	6/7/90	15.46 - 15.49	surface/ diving		√	2 (4)
X17	7/7/90	17.39 - 17.44	diving (some at surface)	√	√	4 (5)
X31	30/7/90	09.04 - 09.12	surface		√	3 (7)
X44	8/7/90	12.56 - 12.59	surface		√	2 (9)
BB1	29/8/95	17.30 - 17.35	long dive	√		- (4)
T2	12/6/97	09:59 - 10:03	diving	√		- (2)
T3	16/6/97	11:02 - 11:04	diving	√		- (then 3)
T3	16/6/97	11:09 - 11:10	at surface (10 m away)		√	3
T4	7/7/97	11:54 - 11:56	diving	√		- (3)

Note # whales: number given is number of whales at the surface, number in parentheses is the number of whales recorded during that sighting.

Differences between the two click types were investigated for all features measured. The two click types were significantly different in their inter-click intervals (ANOVA including tape segment as a main effect, F = 39.5, $p < 0.001$; Table 7.2, Figure 7.3a). Nearby clicks were found to have significantly different inter-click intervals between recording sessions, but distant click inter-click intervals did not differ significantly between recording sessions (surface clicks: ANOVA F = 2.55, $p = 0.029$; deep clicks: ANOVA F = 1.81, $p = 0.087$).

Distant clicks

Nearby clicks

Figure 7.1. Example waveforms showing the difference between distant and nearby clicks.   Expanded plots show the echoes often associated with each click.

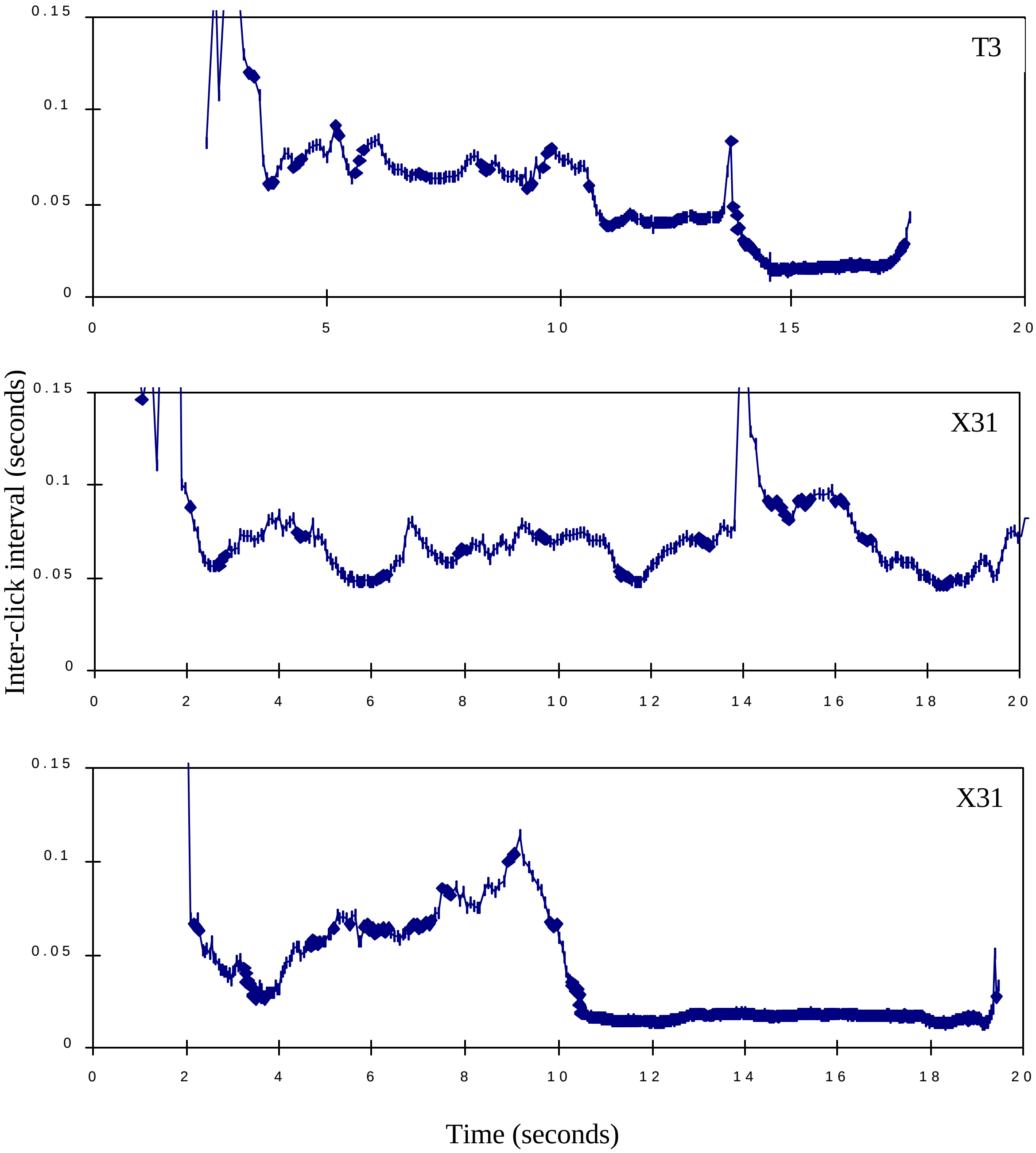

Figure 7.2. Examples of the sequential temporal variation in inter-click intervals during three series of nearby clicks. Sessions during which recordings were made are shown.

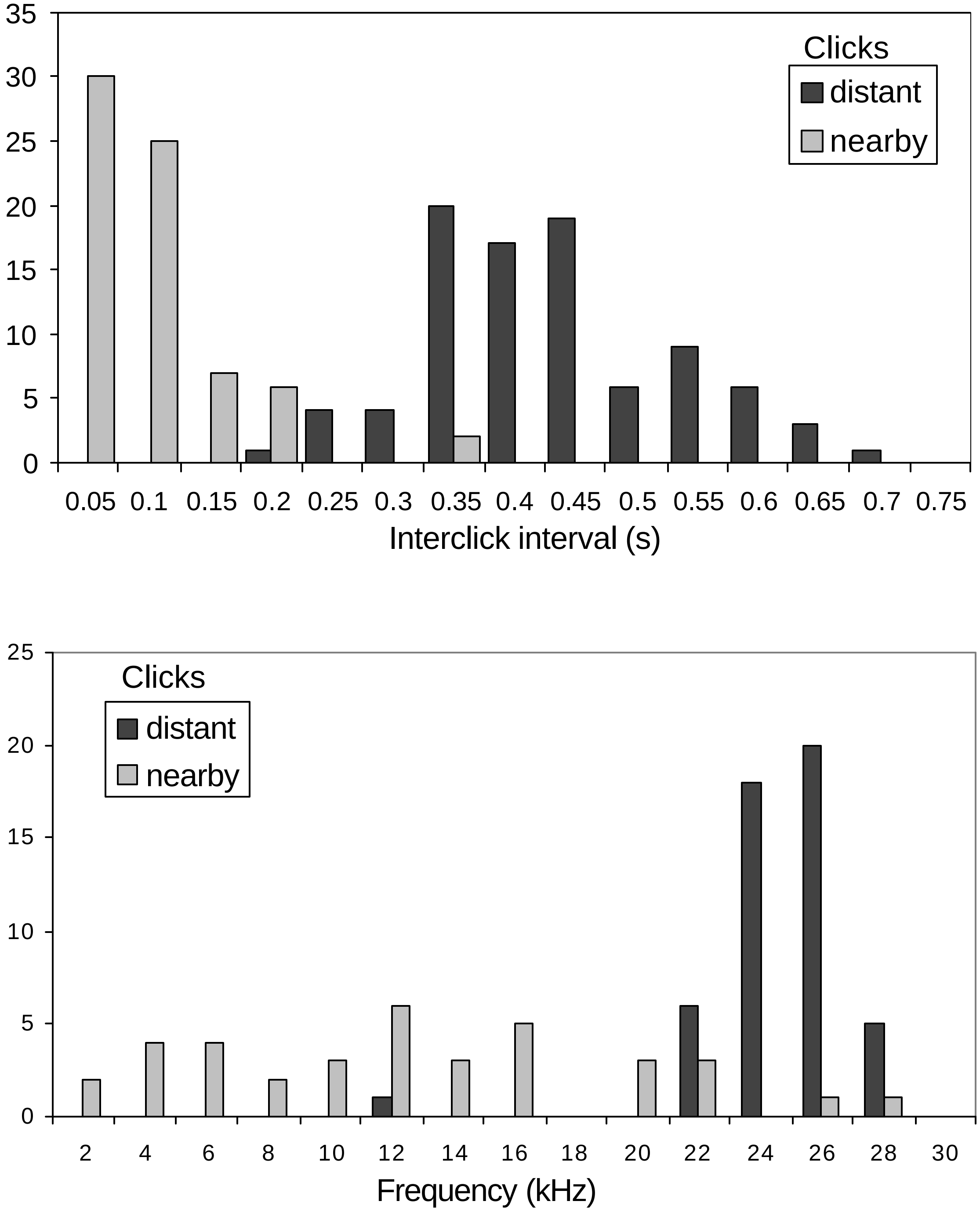

Figure 7.3. Frequency histograms showing (a) interclick intervals of distant and nearby clicks. (b) peak frequencies of distant and nearby clicks. Interclick intervals (n=160) are shown for all clicks regardless of quality. Peak frequencies are only shown for high quality clicks (n= 87), since frequency appeared to be affected by click quality.

Click duration was not significantly different between click types (ANOVA, $p = 0.6$). There were also no significant differences between click durations from different recording sessions (ANOVA, distant clicks $p = 0.42$; nearby clicks $p = 0.18$). However, variability of nearby click durations was much greater than that of distant clicks (CV 105 % cf. CV 20 %; Table 7.2). Click duration was significantly negatively correlated with primary click frequency such that clicks of increased duration tended to be of lower frequency (Pearson correlation, $r = 0.38$, $p < 0.001$).

Table 7.2. Characteristics of click types. Mean (s.d.) are shown for good quality clicks for each recording session and the overall grand mean (of tape means) shows variability between sessions. (Each session probably contains replicates of one or more individuals.)

Tape	# high-quality clicks	Inter-click interval (s)	Duration (ms)	Peak frequency (kHz)	3dB bandwidth (kHz)
Distant					
S27	9	0.46 (0.08)	0.34 (0.08)	24.97 (0.98)	4.16 (0.81)
X34	8	0.41 (0.08)	0.32 (0.03)	25.19 (0.93)	4.73 (0.88)
X10	5	0.43 (0.10)	0.50 (0.41)	20.86 (5.97)	3.41 (1.46)
X17	9	0.45 (0.05)	0.34 (0.04)	22.36 (0.68)	4.96 (0.53)
BB1	7	0.43 (0.10)	0.37 (0.10)	22.80 (0.99)	3.93 (0.64)
T2	3	0.33 (0.04)	0.30 (0.05)	23.97 (0.23)	4.32 (0.81)
T4	6	0.33 (0.10)	0.36 (0.05)	25.50 (1.12)	3.99 (0.34)
T3	5	0.38 (0.02)	0.28 (0.05)	25.37 (0.21)	4.29 (0.09)
Overall		**0.40 (0.05)**	**0.35 (0.07)**	**23.88 (1.71)**	**4.23 (0.48)**
Nearby					
T3	2	0.02 (0.01)	3.32 (2.18)	4.36 (2.52)	0.44 (0.33)
S28	5	0.05 (0.02)	0.51 (0.29)	21.32 (5.07)	3.91 (3.08)
S31	7	0.04 (0.03)	0.56 (0.15)	16.07 (4.07)	2.74 (1.13)
X44	3	0.03 (0.01)	2.52 (0.96)	4.77 (2.95)	0.49 (0.07)
X17	4	0.14 (0.04)	0.49 (0.07)	13.30 (4.61)	2.72 (0.66)
X11	7	0.13 (0.10)	6.08 (9.40)	6.73 (4.68)	2.19 (0.72)
X31	9	0.06 (0.01)	0.63 (0.12)	9.00 (4.71)	3.25 (1.00)
Overall		**0.07 (0.05)**	**2.02 (2.13)**	**10.79 (6.36)**	**2.25 (1.33)**

The peak frequencies of clicks when whales were nearby was significantly different from those when they were distant (Figure 7.3; ANOVA including tape segment as a categorical variable, $p < 0.001$, F = 65.02). The frequency of distant clicks was more consistent (21-25 kHz) than that of nearby clicks (4-21 kHz) but frequency varied significantly with tape segment for both click types (ANOVAs: distant clicks, $p = 0.001$, F = 4.223; nearby clicks, $p < 0.001$, F=9.15; Figure 7.4). A higher proportion of distant clicks (84 %) than nearby clicks (57 %) were unimodal in frequency.

DISCUSSION

Winn et al. (1970) previously recorded the sounds of bottlenose whales in the Gully. Their recordings were primarily conducted while whales were at the surface near their research vessel, and during their 4-hour encounter they recorded discrete frequency whistles, sweep frequency chirps and burst pulse tones. In the recordings described here, no whistles were heard which could be ascribed with certainty to bottlenose whales. Although whistles were heard during many recordings, these were generally of low amplitude, and dolphins or pilot whales (*Globicephala melas*) were often sighted within half an hour of the recording. Winn et al.'s (1970) recording was made in a similar situation: they noted that they were following pilot whales when they found a group of bottlenose whales and that the pilot whales continued out of range of the recording system. The frequency of whistles they recorded (primarily 3-6 kHz; see their figure 1) are in fact similar to those described for long-finned pilot whales (Busnel and Dziedzic 1966). However, more recordings during which no other animals are vocalising, will be required before it can be stated with certainty that bottlenose whales do not whistle.

The nearby clicks of whales noted here appeared very similar to those documented by Winn et al. (1970) as possible burst-pulse tones (compare their figure 3 with figure 7.1 of this study). No distant clicks were noted by Winn et al. (1970). This was presumably because their analysis would have been focused on the loudest whales, i.e., those nearby rather than any at depth.

(a)

(b)

Figure 7.4. Examples of waveform and frequency spectrum of a good quality distant click (a) and a nearby click (b).

The inter-click interval of 0.4 s (i.e., 2.5 s^{-1}) found for distant clicks of northern bottlenose whales at depth is slightly faster than the click rates of 0.5 - 2 s^{-1} of sperm whales (Backus and Schevill 1966, Whitehead and Weilgart 1990, Goold and Jones 1995). Click interval is thought to depend principally on the range at which searching is taking place or the distance of the object on which an animal is echolocating. Animals appear to wait for the return of an echo before the next click is emitted (Au 1993). The inter-click interval of 0.4 s corresponds to a target range of 300 m (speed of sound in water ~ 1500 ms^{-1}). This may therefore be the range at which searching takes place underwater. Both sperm whales and northern bottlenose whales are teuthivorous deep divers (Rice 1989, Watkins et al. 1993, Hooker and Baird 1999a; Chapter 2), so their foraging behaviour is likely to be similar. The mean interclick interval of nearby clicks (0.07 s) corresponds to a distance of 52 m. This approximately reflects the distance the whales were from the research vessel when these sounds were recorded, suggesting that these sounds may have been directed at the research vessel.

The average peak frequency of northern bottlenose whale clicks recorded while whales were at depth was 24 kHz (Table 7.2). This is much higher than the frequencies of sperm whale clicks, for which Goold and Jones (1995) found that males used peak frequencies at 400 Hz and 2 kHz and females used frequencies at 1.2 and 3 kHz. The higher frequencies of northern bottlenose whales are more similar to frequencies (22-25, 35-45 and some 80+ kHz) found for Baird's beaked whale (Dawson et al. 1998). For 1989 and 1990 our recording system could detect sounds up to approximately 40 kHz (the response of the Nagra), whereas in 1995 and 1997 our recording system was limited by the VCHLF hydrophone which had a flat response to 25 kHz and rolled off to 35 kHz. Results from both recording systems were comparable, increasing our confidence of approximately 1-35 kHz sampling. It remains unknown whether bottlenose whales also produce sound at frequencies higher than this.

For echoes of the highest possible signal strength, an animal should use a wavelength comparable with the size of the object being sought (Fletcher 1992). This may not be the case while foraging, but assuming it is (especially while searching, in order to maximise the range), then a frequency of 24 kHz would be optimal for a target size of ~6.25 cm ($\boldsymbol{n}$(water) = 1500 ms^{-1}; $\boldsymbol{n} = f\lambda$, $\lambda = 1500 / 24{,}000$).

Northern bottlenose whales in the Gully are thought to feed predominately on the squid *Gonatus steenstrupi* (Chapter 2). *G. steenstrupi* are slightly smaller than *G. fabricii* and may grow to a mantle length of greater than 10 cm (Kristensen 1981). This fits with the implication from click frequencies that bottlenose whales are searching for animals of approximately 6 cm size. Furthermore, the high fat content of the liver of *Gonatus* may present a good acoustic reflection (T.K. Kristensen, pers. comm.). A fairly constant rate of clicking was heard for distant clicks, suggesting that increased click rate with decreasing target range may be unnecessary for these whales. Potential explanations for this are their targets may be largely immobile, or that bottlenose whales use vision in the final stages of prey capture. Bioluminescence is found among many deepwater (400-1200 m) squid, and is especially common in oegopsid squid (suborder Oegopsina), including the genus *Gonatus* (Hanlon and Messenger 1996), although photophores have not been noted on *Gonatus steenstrupi* (T.K. Kristensen, pers. comm.).

The difference in frequencies of clicks at the surface to those at depth appears unusual, and counter to that expected given the poor transmission of high frequencies in the sea. There appears to be little documentation available concerning changing frequency according to behaviour in cetaceans. Dawson (1991) described changing spectral characteristics with different behaviour for Hector’s dolphin (*Cephalorhynchus hectori*), although dolphins changed the number of peak frequencies within the main frequency range, rather than the primary frequency range. Belugas (*Delphinapterus leucas*) have been found to shift their clicks to higher frequencies and intensities when moved to a noisier environment (Au et al. 1985). It is thought that higher frequencies may be a by-product of the use of higher intensities (Au et al. 1985). It is therefore possible that bottlenose whales shift frequency at depth in order to generate higher intensity clicks, possibly in order to stun their prey (Norris and Møhl 1983) or to cause them to bioluminesce. Alternatively this may simply reflect different targets and bottlenose whales facultatively change frequencies in order to optimise the target reflection.

Among odontocetes, the melon is thought to focus the echolocation clicks produced. Bottlenose whales have a fat body (analagous to the melon) which lies between two maxillary crests (Heyning 1989). In adult male bottlenose whales, these maxillary crests become much enlarged and the fat body becomes more fibrous in nature (Heyning 1989, Mead 1989b). It is unclear whether the differences in facial anatomy between mature male bottlenose whales and females or juveniles would affect the sound produced. Differences in click characteristics observed in different tape segments are consistent with individual differences but further work cataloging sounds of different age-sex classes is needed before it is clear whether different age-sex classes produce different sounds.

The frequency recording range used here (1-35 kHz) prohibited detection of sounds at frequencies above approximately 35 kHz. However, although the full acoustic repertoire of this species remains unknown, this study demonstrates that bottlenose whales are producing sound within the 2-26 kHz range, and that they may use such sounds for foraging or for some form of spatial referencing. As such, the potential impact of foreign sounds in this (or higher) frequency range into the Gully region might affect their foraging capabilities. Of further concern is our lack of knowledge of acoustic pathways and sound decay within such a topographically diverse structure as a submarine canyon. It is possible that such a feature might act much as an acoustic resonance chamber, and that any noise entering this system would be more of a problem than in open ocean areas.

CHAPTER EIGHT

Synthesis: bottlenose whale ecology in the Gully and potential implications for conservation and behaviour

The primary goal of this thesis has been to describe the habitat use and foraging ecology of northern bottlenose whales in the Gully. Each chapter has in turn shed new light on these topics. I will briefly review the general results and will discuss these in the context of the Gully ecosystem, the conservation implications arising from this, and the behavioural implications of bottlenose whale ecology.

HABITAT AND RESOURCE USE

Foraging

Several of the chapters in this thesis suggest that foraging is the primary reason why bottlenose whales concentrate in the Gully. Although their distribution in the Gully could potentially be for another function such as breeding, measurement of diving behaviour has shown that whales travel repeatedly to, or near to, the sea floor, presumably to forage there (Chapter 5). Changes in the distribution of whales within the Gully varied between years (Chapter 3), while whales maintained much the same ranging behaviour (Chapter 6), further indicating that whales are probably using the area primarily for foraging. If the presence of whales in the Gully functions primarily in a social context, we would not expect to see changes in distribution between years. However changes in prey distribution from year to year would be expected to result in the type of changes observed in whale distribution. The acoustic behaviour of distant whales (i.e., regular clicks presumably functioning for echolocation) is also consistent with foraging at depth (Chapter 7).

Prey specificity

The diet of bottlenose whales elsewhere in the North Atlantic has previously been recorded to consist largely of one particular squid species, *Gonatus fabricii* (Clarke and Kristensen 1980, Lick and Piatkowski 1998). Stomach contents of bottlenose whales stranded in Nova Scotia and Quebec suggest that the major prey in this region is the congener *G. steenstrupi*. Dietary analysis of skin and blubber samples from whales in the Gully was consistent with a diet of adults of the genus *Gonatus* (Chapter 2). Adult *Gonatus* are found near the sea floor of continental shelves (Kristensen 1981, 1983). As such, their vertical distribution is consistent with the dive records obtained (Chapter 5). Furthermore, the click characteristics which are produced by distant whales (presumably those at depth) are consistent with the size range of adult *Gonatus* (Chapter 7). *Gonatus* specimens have been recorded from nearby areas off the Scotian Slope (Dawe and Stephen 1988), but their abundance and behaviour in the Gully is essentially unknown.

Individual energetic requirements

Since it appears that bottlenose whales feed primarily on adult *Gonatus* in the Gully, it is possible to calculate the energetic impact that these whales have on this squid species, in terms of the number of squid taken per day. This can also be related to the number of squid which must be taken per dive, providing further insight into the potential foraging strategies of these whales.

Given an assumed average weight of a bottlenose whale of 4700 kg (Kenney et al. 1997), and the relationship between basal metabolic rate (BMR) and body weight (W, in kg), $BMR = 70\ W^{0.75}$ (following Kleiber 1961, p 251), the basal metabolic rate of a bottlenose whale is approximately 40,000 kcal/day. In order to calculate consumption rate, BMR must be scaled for a variety of factors such as assimilation efficiency and active metabolism. Following Kenney et al. (1997) I have used a correction factor of 2.5, which leads to a consumption rate of 100,000 kcal/day.

The body composition of *Gonatus* contains approximately 8 % lipid (Chapter 2) and can be assumed to contain 20% protein (common for squid; S.J. Iverson, pers. comm.).

Using energetic conversions of 39.3 kJ/g for fat and 23.6 kJ/g for protein (Blaxter 1989), the energetic content of *Gonatus* is 7.8 kJ/g. The energetic content of a small (18.16 g) specimen of *Gonatus steenstrupi* was measured as 3.78 kJ/g (Clarke et al. 1985). Clarke et al. (1985) noted that this was likely to be an underestimate of the calorific value of adult *Gonatus*, which have an increased lipid content, and suggested that adults would probably have calorific values of greater than 4.53 kJ/g. Assuming the energetic content calculated above (7.8 kJ/g), an average adult squid weighing approximately 180g (Chapter 2) would therefore provide 1400 kJ, or 335 kcal (1 cal = 4.184 J).

The bottlenose whale consumption of 100,000 kcal/day (calculated above) would therefore be obtained from approximately 300 squid per day, or 12 squid per hour. When viewed in conjunction with results from the TDR deployments, which show foraging dives approximately every 80 minutes (Chapter 5), the number of squid eaten per dive must be of the order of 15-20 squid. The dive record does not show multiple changes in depth and velocity which might be expected from individual chases, suggesting that prey capture may consist of multiple individuals at one time. Consistent with this, *Gonatus* have been noted to have a tendency to shoal (Kristensen 1983).

Required primary productivity

Forty bottlenose whales, approximately one third of the population, were calculated to be in the Gully at any one time, based on the lagged re-identification rate of individual whales (Gowans 1999). We can therefore investigate the potential of the Gully to support this proportion of the bottlenose whale population by calculating the level of primary production required.

The area used by these whales is approximately 25 km x 8 km, i.e., 200 km^2 (Chapter 3, Chapter 6). Since an average whale removes 100,000 kcal per day (calculated above), the total daily energetic requirement of the bottlenose whale population in the Gully is $100{,}000 \times 40 / 200 \times 10^6$ kcal/m^2/day, or 0.02 kcal/m^2/day.

The nitrogen stable isotope ratio (15.25 ‰ δN^{15}) for bottlenose whale blubber (Chapter

2) can be used to estimate the trophic level of these whales. Assuming that primary productivity is at approximately 5 ‰ (trophic level 1) and trophic enrichment is approximately 3 ‰ (Fry 1988), bottlenose whales occupy a trophic level of 4.4. This is consistent with the potential foodchain: bottlenose whales – adult *Gonatus* – shrimps/ mysids/ fish/ other squid – zooplankton – phytoplankton (note: this is undoubtedly an oversimplification of the system but illustrates that a trophic level of between 4 and 5 appears consistent with what is known of oceanic foodchains). Transfer efficiency from one level of the foodchain to the next was assumed to be approximately 10 % (Pauly and Christensen 1995). The primary productivity required to sustain bottlenose whales at this level would therefore be $0.02 \times 10^{3.4} = 50.2$ kcal/m^2/day. Primary production required was converted from energy to carbon by 13.3 kcal/g C (Platt 1969), resulting in a total primary production of 3.8 g C/m^2/day (1400 g C/m^2/year).

Estimates of primary productivity range from 0.28 g/m^2/day (103 g/m^2/year) in open ocean, to 2.7 g/m^2/day (973 g/m^2/year) in upwelling systems (Pauly and Christensen 1995). Overall primary production on the Scotian Shelf was measured at 0.28 gC/m^2/day (102 gC/m^2/yr) and that on the Scotian Slope was 0.35 gC/m^2/day (128 gC/m^2/yr, Mills and Fournier 1979). Primary production in the Gully does not appear to be anomalously high by comparison with the rest of the Scotian Shelf and shelf break (Harrison and Fenton 1998). It therefore appears that the level of predation caused by 40 northern bottlenose whales within 200 km^2 could not be sustained by primary production in this area. It therefore appears that the Gully must be receiving energetic input from outside of a purely vertical foodchain.

Investigation of the assumptions involved in this calculation also supports this conclusion. (1) Other predators were not included in this model, so the productivity requirements represent the minimum to support the Gully ecosystem (based only on bottlenose whale consumption). (2) Specific prey composition of bottlenose whales was not included in the model, since calculations are based instead on trophic level of bottlenose whales. (3) The area requirements used in the model were overestimated (leading to an underestimation of productivity requirements). The 8 x 25 km area used is the total area in which bottlenose whales have been observed over the 10 years of their study in the Gully. (4) The abundance of bottlenose whales in the Gully may not be so great during the winter months. Some bottlenose whales have been observed in the Gully year-round (Whitehead et al. 1997b) but the calculation of 40 bottlenose whales in the Gully at any time (Gowans 1999) was based on research between June and August. If there are fewer bottlenose whales in the Gully during winter months, this might reduce the yearly energetic requirements by up to a factor of 2-3. Therefore, given the low magnitude and direction of these potential errors, the Gully ecosystem must be receiving some energetic input to support the bottlenose whale population there.

Other aspects of bottlenose whale foraging ecology also suggest that the Gully contains a greater prey abundance for these whales than the surrounding shelf edge areas. The concentrated distribution of whales within the Gully (Chapter 3), and the small extent of their movements (Chapter 6), also suggests the presence of a rich and profitable food source. Variation in bottlenose whale use of the area from year to year is relatively small (Chapter 3) suggesting that the system is relatively stable and dependable. The distribution pattern of bottlenose whales appears to vary between years much more than within each year, but this does not seem to affect the ranging behaviour of whales within the area (Chapter 3, Chapter 6), suggesting that although there is a general shift in the location of prey, its stucture (in terms of patchiness and scale) remains similar.

There are many potential explanations which could account for the apparent influx of material into the Gully allowing it to support this quite stable, high biomass of prey. *Gonatus* may grow elsewhere and migrate into the Gully. One possibility is that deep ocean currents bring nutrients or squid prey into the Gully. A southward flowing deep-water current has been suggested to run underneath the northward flowing surface current in the North Atlantic (Dickson et al. 1990). This deep current, if it passes the Gully, could entrain nutrients from the deep ocean. Harding (1998) has also suggested that the Gully may receive benthic input from the Scotian Shelf during times of high storm activity (see Chapter 3). Additionally, the benthic habitat structure, possibly the deep-sea corals within the Gully (Breeze and Davis 1998), may provide refugia for these squid and encourage a local abundance.

Seasonality of spawning and hatching are unclear for *Gonatus*. Egg masses and adult squid were collected at depths of 1000 m off Andenes, Norway during the month of July (Bjørke et al. 1997). Kristensen (1984) examined 7000 juvenile *Gonatus* from west Greenland and concluded that two populations exist, which differ in the time of breeding; the Davis Strait population hatches in spring and early summer, while the Disko Bugt population hatches in autumn and early winter. It is therefore possible that the Gully may be used by different populations which spawn at different times of year, so providing a fairly constant year-round prey supply. Okutani et al. (1995) observed a female gonatid cephalopod carrying egg masses on the arms. Seibel et al. (in press) describe brooding females, eggs and hatchlings of *Gonatus onyx* captured between 1250 and 1750 m off southern California, and suggest that eggs may require nine months to develop. Since Bjørke et al. (1997) have almost always recorded adult female *Gonatus* and eggs in the same trawl, they suggested that such behaviour may also be found among North Atlantic *Gonatus*. It would seem quite likely that spawning females, since they would presumably lose mobility, would seek some kind of refugia in which to spawn.

Resource use

The distribution of bottlenose whales in the Gully therefore appears to be based on a discrete and relatively plentiful food source found at depth in the central part of the Gully canyon. The reason that other cetaceans are not so consistently abundant in the area (Hooker et al. 1999), is presumably that this deep-sea food source is largely unavailable to species unable to perform such deep dives. Exceptions include sperm whales (*Physeter macrocephalus*) and other beaked whales (*Mesoplodon* spp.). Sperm whales appear to show a more northerly distribution within the Gully compared to that of bottlenose whales (Hooker et al. 1999). Vertically mounted sonar records show that sperm whales dive to approximately 215-415 m, often to the ocean floor, in this part of the Gully (Whitehead et al. 1992). Stomach contents of sperm whales in the Gully have not been recorded, but those of sperm whale taken by whalers from the Scotian Shelf contained primarily monkfish, *Lophius americanus* (V. Kozicki pers. comm. cited in

Mullins et al. 1988). By contrast, sperm whales in the eastern Atlantic appear to feed primarily on *Gonatus* (Clarke 1997). These differences in distribution, diving behaviour, and prey between the two species are suggestive of habitat and resource partitioning within the Gully. Less can be said regarding potential competition between bottlenose whales and other beaked whales, since these have been seen in the Gully only rarely. However four recent sightings of *Mesoplodon bidens* were slightly to the south of the usual distribution of bottlenose whales (Hooker and Baird 1999b).

Interpretation of this work is limited by the scale at which the study was conducted. I have analysed the foraging behaviour, movements and distributional preferences of animals within the Gully over the spatial scale of the canyon. While this provides a detailed account of the ecology of whales within the Gully, we do not know where the whales go when they leave the Gully and what they do during that time. Only one-third of the Gully population is thought to be in the Gully at any one time (Gowans 1999). Comparative data on the behaviour and movements of whales from the Gully population while outside of the canyon would therefore be valuable in assessing the behavioural choices made by whales in terms of movement and habitat choice. Furthermore, within the canyon itself, while this thesis has addressed bottlenose whale foraging ecology in the Gully, this has highlighted numerous other questions, particularly concerning the ecology of bottlenose prey within this ecosystem.

THE GULLY ECOSYSTEM AND ITS CONSERVATION

The ecosystem has been described as the basic unit of ecology (Evans 1956) and is often advocated as the unit for conservation (Agardy 1994, Jones 1994). However, the ecosystem concept tends to break down on close scrutiny, in an analogous fashion to the species concept. In both cases the boundaries of an ecosystem or species are problematic to define at a small scale.

The scale at which an ecosystem is defined is rarely taken into account in the design of conservation plans. Theoretically, an ecosystem should encompass all the linkages between species within a defined habitat. However, particularly in the ocean, the spatial boundaries of an ecosystem are often nebulous. For example, the Gully ecosystem was suggested as a potential marine protected area by the strategic identification of a high use area for bottlenose whales and other cetaceans (Hooker et al. 1999). However, this area does not encompass the range of any one bottlenose whale over the lifespan of that individual, or probably even over much shorter periods of time. Thus it is debatable whether the area encompasses an adequate representation of the habitat-area needs for a sizable proportion of the species' population (Bingham and Noon 1998, Buchanan et al. 1998). Likewise, in order to fully protect the ecosystem, all the species within that ecosystem should be adequately protected over their lifespan. As shown above, there appears to be a significant energetic influx to the Gully ecosystem, which supports the bottlenose whale population there. In order to provide a rigorous conservation strategy for the Gully, the source of this influx should be identified and protected.

Furthermore, this thesis has primarily identified only the top linkage within the bottlenose whale foodweb in the Gully, that between whales and squid. We are still largely unable to describe the myriad of other linkages and dependencies between species in this system. However, two features of this apex linkage suggest certain recommendations concerning conservation of the Gully. The prey specificity shown by bottlenose whales and their apparent reliance on the benthic/bathypelagic environment, suggest that any deleterious effects to this system should be minimised. Bottlenose whales appear to feed primarily on adult *Gonatus* (Chapter 2), and the year-round presence of whales in the area (Whitehead et al. 1997b) suggests year-round prey availability. The strong prey specificity shown by bottlenose whales elsewhere is cause for concern. The linkages within a system are thought to reflect the stability of that system (MacArthur 1955), and a strong reliance on a certain prey species suggests that this system may not be stable to perturbations. It is also cause for concern that the bottlenose whale ecosystem, although containing pelagic links within the food chain, appears to rely on benthic structure. The trophic links within this system appear to be pelagic, in that *Gonatus* feed on crustaceans, fish and other squid (Kristensen 1983). However, adult *Gonatus* are found at the sea floor (Kristensen 1983) and bottlenose whales and their prey appear to show a strong dependency on bathymetric features (Chapter 3). This raises concerns about the potential impact of human activities at various levels within the water column, but especially activities which cause changes in current patterns, deposition of matter, or other changes to the sea floor.

Oceanic foodwebs have rarely been fully categorised and so conservation based on this concept is problematic. For example, the effect of removing large whales from the Antarctic ecosystem caused unforeseen consequences in the increase of crabeater seal (*Lobodon carcinophagus*), minke whale (*Balaenoptera acutorostrata*) and many penguin populations (Laws 1985). In fact, even if all linkages within one foodweb are identified, changes in another may have unforeseen effects. The decline of the Steller sealion (*Eumetopias jubatus*) in the Bering Sea ecosystem seems to have resulted in prey switching of killer whales (*Orcinus orca*) and has had cascading effects through the sea otter (*Enhydra lutris*) foodweb (Estes et al. 1998).

The vulnerability of marine species to extinction is becoming more apparent as increasingly more case-studies are described (Roberts and Hawkins 1999). Species particularly at risk include those that are long-lived, with infrequent reproduction, a small range or reliance on particular habitat (Roberts and Hawkins 1999). Northern bottlenose whales in the Gully show many of these traits. The small size of this population and its dependence on this habitat suggest the necessity of a marine protected area for the region (Hooker et al. 1999). Threats to the ocean have in the past primarily affected continental shelf areas (e.g., pollution, dumping, dredging, etc), but threats to open ocean ecosystems are increasing at an alarming rate and open ocean conservation should be placed at a high priority (Mills and Carlton 1998). The Gully, at the junction between the continental shelf and the deep-sea, may be vulnerable to threats from both regimes. From the deep ocean, sounds may be carried within the deep sound channel and could enter and resonate within the Gully, potentially interfering with the ability of whales to echolocate (Chapter 7). On the continental shelf, any damage to the sea floor would likely disrupt the transport of benthic material from the shelf (Harding 1998), alter benthic habitat in the Gully, and consequently disrupt the foodweb.

BEHAVIOURAL IMPLICATIONS

The ecology of species within many animal groups has been shown to affect the social system of that species (Geist 1974, Jarman 1974, Macdonald 1983). The ecology of bottlenose whales appears at first sight to be similar to that of sperm whales, in that both species are deep-divers which feed primarily on squid (Clarke 1980, Watkins et al. 1993). However, the social system of bottlenose whales (although not fully elucidated) does not appear to match that of sperm whales (Table 8.1).

Table 8.1. Comparison of ecological and social differences between bottlenose and sperm whales.

	Sperm whales	Bottlenose whales, the Gully
ECOLOGICAL		
Diet	squid (often large, low energy content, Clarke 1980)	squid (primarily *Gonatus*, Chapter 2)
Diving	deep (~ 500 m, Papastavrou et al. 1989)	deep (~ 1000 m, Chapter 5)
Ranging	range over 1000s of kms (Whitehead submitted)	show high reliance on small area above the Gully (Chapter 3, Chapter 6)
SOCIAL		
Groups	stable matrilineal units, weak male bonds (Whitehead et al. 1991)	weak female bonds, but some strong male bonds (Gowans 1999)
Mating system	roving male (Arnbom and Whitehead 1989)	possible site preference by males (Chapter 6)
Co-operation	care of young (Whitehead 1996b)	not clear (Gowans 1999)

The primary difference between the ecological structures of these two species appears to involve the localised, plentiful, benthic food source for bottlenose whales within the Gully, compared to the pelagic food source of sperm whales, widely dispersed in space and time (Jaquet 1996a). Whether this difference in spatial scale of movement and foraging is responsible for the differences in sociality between these species will require further comparative work among other cetacean species, in terms of the nature and spatial scale of prey distribution and its relationship to social structure.

APPENDIX ONE

Behavioural reactions of northern bottlenose whales to biopsy and tagging procedures

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ABSTRACT

The potential cost to an animal of invasive or intrusive biological sampling should be established when such techniques are first used. Biopsy sampling (for genetic, toxicological and dietary analyses) and deployment of suction-cup attached time-depth recorders (to monitor diving behaviour) were undertaken with northern bottlenose whales (*Hyperoodon ampullatus*). Both techniques involve the physical impact of an object fired from a crossbow. Reactions of bottlenose whales to both these procedures were generally low-level, with stronger responses to hits than to misses. There was no statistical difference in response to tag versus biopsy hits, although more than just the target animal would often respond to tagging attempts. The prior behavioural state of the whales appeared to influence the reaction to both hits and misses: whales logging at the surface tended to show stronger reactions. Sea state appeared to affect the level of reaction to misses: whales were more likely to respond to a miss in calm sea conditions. No avoidance of the research vessel was observed following a tag or biopsy attempt; in most cases whales re-approached the research vessel within several minutes. Preoccupation level may be an important factor to consider in impact assessment for any activity on cetaceans.

INTRODUCTION

The non-lethal firing of projectiles at whales is gaining popularity, both in order to obtain skin and blubber samples (e.g., Lambertsen 1987), and to attach data-recording or transmitting devices (e.g., Mate and Harvey 1983, Goodyear 1993, Baird 1998, Mate et al. 1998). Data collected using these techniques are often important for management and conservation purposes, but may come at some cost (usually a behavioural disturbance) to the individuals involved. This cost may vary for different species or populations (see e.g., Schneider et al. 1998), and thus the impacts should be assessed each time such a study is conducted.

Projects to deploy data-recorders and to collect skin/blubber biopsies were recently undertaken on northern bottlenose whales in the Gully, Nova Scotia. Biopsy samples were collected for three primary purposes: 1) to assess whether the bottlenose whale population using the Gully is genetically distinct from populations elsewhere in the North Atlantic (see Whitehead et al. 1997a, b); 2) to measure contaminant levels in this population prior to the onset of nearby oil and gas exploitation (see Hooker et al. 1999); and 3) to identify dietary indicators in the skin and blubber (Chapter 2). Suction-cup attached time-depth recorders were used to record the diving behaviour of northern bottlenose whales (Hooker and Baird 1999a; Chapter 5), providing information on foraging behaviour and the use of depth. Such information is important in assessment of potential threats to the species, as acoustic or contaminant effects may vary with depth.

Reactions of various species of cetaceans to biopsy darting have been previously discussed (e.g., International Whaling Commission 1989, Whitehead et al. 1990, Brown et al. 1991, Weinrich et al. 1991, Barrett-Lennard et al. 1996, Weller et al. 1997). In general, a "startle" response has been observed to biopsy darting, although the level of reaction varied between species, and also between populations and individuals. The reaction of cetaceans to suction-cup tagging has been found to vary dramatically. Whereas reactions of killer whales (*Orcinus orca*) and Dall's porpoises (*Phocoenoides dalli*) to the technique were minor (Baird 1994, Hanson and Baird 1998), those of bottlenose dolphins (*Tursiops* sp.) were strong and relatively long-lasting (Schneider et al. 1998). Neither the tagging or biopsy techniques had previously been used on northern bottlenose whales. This paper compares the reactions of bottlenose whales to both techniques, and investigates factors affecting the behavioural reactions observed.

METHODS

Field research took place in the Gully, a submarine canyon on the Scotian Shelf (approximate position: 44°N, 59°W). All tagging or biopsy attempts were made from a 12 m auxiliary sailing vessel, operated under power at slow speeds (1-4 knots). Whales were approached and observed for varying time periods prior to the tag/biopsy attempts.

The biopsy dart used had a 2.5-cm long (0.6 cm diameter) cylindrical punch fitted with a dental broach (a barbed filament to hold a sample in place - c.f. Barrett-Lennard et al. 1996), attached to the end of a standard crossbow bolt (total weight 28.5 g). A cylindrical stopper set 2.5 cm back from the tip of the punch caused the bolt to rebound on impact from the whale. Bolts were fired from a 67-kg draw crossbow (Barnett WildCat XL) at a range of 5-15 m. Samples were usually taken from the flank area near the dorsal fin. The floating dart was recovered and the skin and blubber sample was removed. This was then sub-sampled for various analyses requiring either skin or blubber or both.

The tags used included a 7.5-cm diameter rubber suction cup (designed for roof-racks, Canadian Tire) to which the body of the tag (20 x 4 x 5 cm) was attached, and from which a 40-cm antenna extended. The syntactic foam housing of the tag contained a time-depth recorder (Wildlife Computers or AGO Environmental Electronics) and a VHF radio-transmitter (Advanced Telemetry Systems or Telonics). The total unit weighed approximately 340 g. Tags were attached to a modified crossbow bolt (weight approximately 25 g) and were deployed using the same crossbow as described above (Figure A1.1).

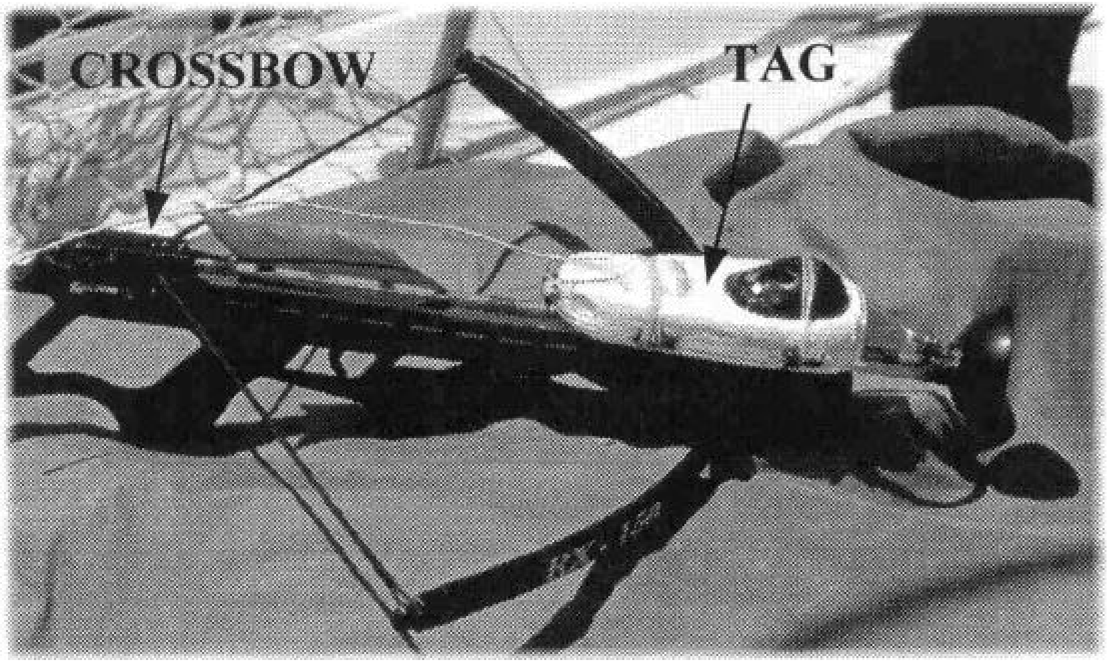

Figure A1.1. Suction-cup attached time-depth recorder/VHF radio tag ready to be deployed from the crossbow.

The group size and behavioural state of the whales pre-biopsy/tag attempt were noted. Group size was defined as the number of animals within five body lengths (chain rule, c.f. Smolker et al. 1992) of each other. Behavioural state was assigned as one of: logging (lying still or moving slowly in one direction at the surface), milling (moving slowly in no consistent direction), or travelling (moving in a consistent direction at greater than 2 knots). Whenever possible video footage was obtained of each tag or biopsy attempt, and this was used to confirm the consistency of behavioural categories assigned by different observers in the field for both the pre-attempt behaviour and the reaction. Attempts were classified as hit or miss, with hit defined as contact with the whale; hits were further subdivided as to whether they were successful, i.e., whether biopsies obtained a sample or whether tags attached to the whale for more than 30 seconds. Sea state (Beaufort scale calculated from wind speed) was recorded every hour; sea state at the time of the biopsy/tag attempt was interpolated from these. Categories of reaction types were defined following Weinrich et al. (1991):

(1) No reaction: whale continued its pre-attempt behaviour
(2) Low-level reaction: whale modified its behaviour slightly, but in a mild fashion, e.g., immediate dive or flinch
(3) Moderate reaction: whale modified its behaviour in a more forceful manner, e.g., tail slap, acceleration and fast dive, but gave no prolonged evidence of behavioural disturbance
(4) Strong reaction: whale modified its behaviour in a succession of forceful activities, e.g., successive percussive behaviours (breaches, tail slaps, head outs)

For animals in groups, whenever possible, it was noted whether a reaction was only observed for the target animal, or whether the whole group showed a reaction.

RESULTS

Forty-seven biopsy attempts were made on northern bottlenose whales in 1996 and 1997 (Table A1.1). Of these, 27 attempts hit the whale and 20 of these were recovered containing a skin and blubber sample. Six attempts hit but were not successful (either due to a low hit near the water line, or the sample may have fallen out). One dart sunk after hitting the whale. Video footage was taken of 18 biopsy hits, 15 of which were successful, and 11 biopsy misses. Eighty-four tagging attempts were made between 1996 and 1998 (Table A1.1). Twenty-nine attempts hit the whale but only 6 successfully attached (one for only 30 seconds). Video footage was taken of 15 tag hits, 3 of which were successful attachments, and 34 tag misses.

Table A1.1 Number of whales showing different reaction-types to tag and biopsy deployments (% shown in parentheses).

		Reaction		
Event	None	Low-level	Moderate	Total
Tag-hit	2 (7)	19 (65)	8 (27)	29
Biopsy-hit	3 (11)	20 (74)	4 (15)	27
Tag-miss	33 (60)	21 (38)	1 (2)	55
Biopsy-miss	16 (80)	3 (15)	1 (5)	20

The majority of whales showed no or low-level reactions to both tag and biopsy attempts (Table A1.1). Reactions were observed for 93 % of tag hits and 89 % of biopsy hits. Fewer reactions were observed for misses than for hits (40 % reacted to tag misses; 20 % reacted to biopsy misses, Table A1.1). Reactions (categorized as none, low or moderate) were significantly greater for hits than for misses ($G_2 = 50.30$, $p < 0.001$). Reactions to tag hits were not significantly different than reactions to biopsy hits ($G_2 = 1.72$, $p = 0.63$). Of the 6 successful tag hits, 2 animals showed a moderate reaction giving a hard tail flick, acceleration and dive, 1 animal accelerated and dove, and 3 showed a fast dive or a flinch.

The type of reaction shown by the target animal to a hit was significantly related to the behavioural state prior to the tag or biopsy attempt (comparison for all hits of behavioural state (logging vs. milling/travelling) and reaction (none/low vs. moderate) $G_1 = 4.04$, $p = 0.044$). Low-level reactions were most common for travelling or milling whales, whereas logging whales were more likely to show stronger reactions, especially to tag hits (Figure A1.2). There was also a similar relationship between behaviour and reaction to misses, although whales rarely showed a moderate reaction to a miss (comparison of behavioural state (as above) and reaction (none vs. low/moderate) $G_1 = 4.02$, $p = 0.045$).

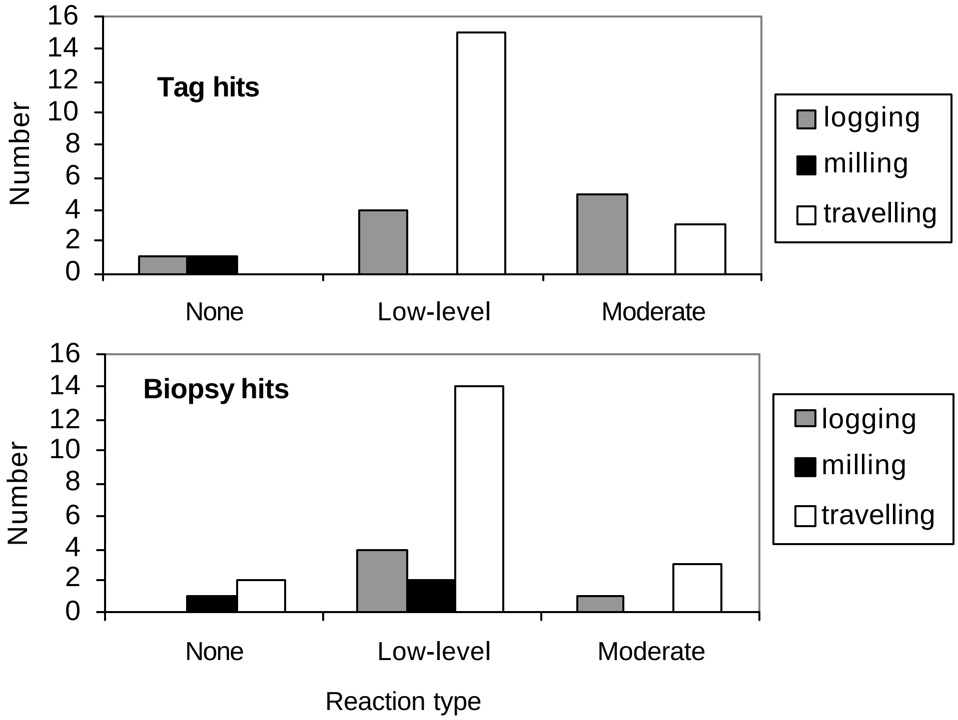

Figure A1.2. Relationship between behavioural state and reaction type for tag hits and biopsy hits. Number of reactions of each reaction-type is shown for each pre-biopsy behavioural category.

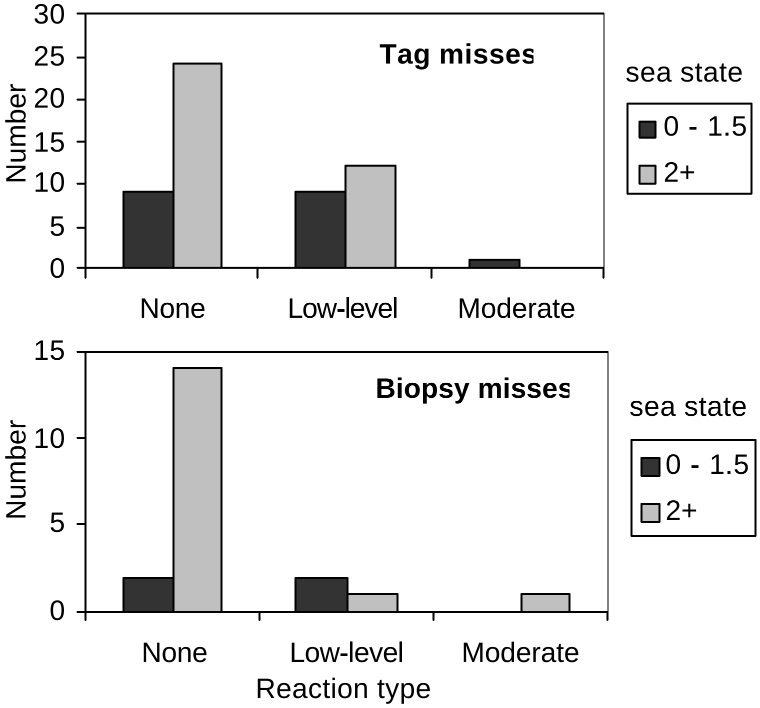

Figure A1.3. Relationship between sea state and reaction type for tag and biopsy misses. Number of reactions of each reaction-type is shown for the two sea state categories.

No statistically significant relationship was found between group size and reaction type of the target animal after hits (G_1 = 1.37, p = 0.24), although, anecdotally, moderate reactions to biopsy darting were observed only from whales in small groups (<3 animals). There was an effect of sea state on reaction type, but only for missed shots (comparison of sea state (≥ Beaufort 2 with < Beaufort 2) for reaction (none or some) G_1 = 4.38, p = 0.036, Figure A1.3). This effect was much greater for tag misses (G_1 = 6.80, p = 0.009) than for biopsy misses (G_1 = 2.41, p = 0.12, although this test may be somewhat inaccurate due to low sample size).

Of all occasions for which it was recorded, all animals in a group reacted to a tag hit (n = 3), and often all animals in a group reacted to a tag miss (group reaction n = 9; only target animal reaction n = 4). In contrast, biopsies appeared to primarily affect the target animal and group reactions were seen much less often (only target animal reaction n = 10, group reaction n = 4). No avoidance of the research vessel was seen after a tag or biopsy attempt. For most missed attempts and for a few tag or biopsy hits, animals remained at the surface. If animals temporarily made a shallow dive, they usually returned to the research vessel within a few seconds or were re-photographed within a few minutes of the tag or biopsy attempt (for 85 % of all attempts whales returned to the surface and remained with the research vessel at least five minutes).

Gender-related differences in the levels of reaction have been previously noted for at least one species of cetacean (Brown et al. 1994). The gender of the biopsied whales in this study was ascertained genetically (M.L. Dalebout, unpublished data), allowing me to investigate any difference in reaction. No significant difference between the reactions of males and females was found, although samples sizes were small (G_2 = 2.1, p = 0.35; Table A1.2).

Table A1.2 Gender of biopsied whales (*n* = 20) and respective reactions.

	Reaction			
Gender	None	Low-level	Moderate	Total
Male	0	5	2	7
Female	2	9	2	13

DISCUSSION

The response rate of northern bottlenose whales to biopsy hits in this study (89 %) was greater than that found for right whales (19.4 %), *Eubalaena glacialis* (Brown et al. 1991), or humpback whales (50 %), *Megaptera novaeangliae* (Weinrich et al. 1991), but was similar to that recorded for other odontocetes. A 100 % response rate was found for sperm whales, *Physeter macrocephalus* (Whitehead et al. 1990) and for bottlenose dolphins (Weller et al. 1997), and an 81 % response rate was found for killer whales (Barrett-Lennard et al. 1996). Reactions of bottlenose dolphins were described as an observable short-term change in behaviour (Weller et al. 1997); momentary shakes or accelerations were observed for killer whales (Barrett-Lennard et al. 1996), whereas sperm whales showed strong startle reactions, occasionally involving defecation (Whitehead et al. 1990).

Reactions of northern bottlenose whales to suction-cup tag deployment were generally low-level. Whales reacted to 93 % of tag hits and 40 % of tag misses. Baird (1994) documented only minor reactions by killer whales to crossbow deployed suction-cup attached tags with 52 % reaction to hits and 26 % reaction to misses. Reactions of short-finned pilot whales (*Globicephala macrorhynchus*) to crossbow-deployed tags consisted of a tail flick and fast dive (Baird, personal observation). Similar variation in reaction has been observed to pole-deployed suction-cup tags. Dall's porpoise and pantropical spotted dolphins (*Stenella attenuata*) showed relatively little reaction to suction-cup tags deployed by pole (Hanson and Baird 1998; Baird, personal observation), whereas bottlenose dolphins show prolonged and intense reactions to tag attempts and attachment, reacting to 100 % of hits and 71 % of misses (Schneider et al. 1998). The scale of reaction of northern bottlenose whales appears to lie in the middle of this range.

Contrary to expectations (based on the weight of the object hitting the whale), reactions to tag hits were similar to reactions to biopsy hits. A potential explanation for this is the variation in "tag hit" under our definition: some of the tag hits were glancing blows and so may have had little striking impact whereas others were direct hits. In contrast, the impact of the biopsy dart was more consistent (i.e., there were virtually no glancing hits for biopsy darts).

As many authors have pointed out, evaluating the long-term reaction to tag attachment is important in determining whether their presence affects the recorded behaviour (White and Garrott 1990, Walker and Boveng 1995, Croll et al. 1996). Data were recovered from two of the six successful tag attachments and one of these tags was equipped to recorded velocity (Hooker and Baird 1999a). The whale's initial reaction to tag deployment was a rapid acceleration and dive. The velocity record showed this initial increase but dropped within the first two minutes to levels observed for the rest of the deployment (Hooker and Baird 1999a). The general behaviour of the whales (dive times and surface intervals) was also consistent with that observed from non-tagged whales. Thus it appears that the whale's behaviour was modified for only a few minutes in a short-term reaction to the tagging procedure.

A criticism of previous studies examining the impact of biopsy darting has been that the effect caused by the close approach of the research vessel can be confounded with the effect of the biopsy itself (Brown et al. 1994). In this study, the behaviours observed for whales when first sighted were maintained during the approach of the research vessel for photo-id or immediately prior to the impact of the stimulus, so I am confident that the observed reactions were to the stimulus rather than the research vessel.

MANAGEMENT IMPLICATIONS

The major cue to which bottlenose whales react appears to be the physical impact of the tag or biopsy, as reaction to hits was much greater than reaction to misses (Table A1.1).

Whales also appear to react to an acoustic cue, evidenced by their stronger reactions to tag misses in calm sea conditions (when the hit would be more audible above background levels). The primary factor affecting the reaction of bottlenose whales to either tag or biopsy stimulus appears to be the behaviour of the whale at the time of the stimulus. Such a result is not surprising as it essentially reflects the preoccupation of the whale: the relative stimulus of a biopsy or tag is less for whales involved in travelling or milling than for whales lying still at the surface. Similar reasoning may explain why reactions of migrating humpback whales were generally lower than those of whales on feeding or breeding grounds (Brown et al. 1994), and why mothers or primary escorts of humpback whales (thought to be involved in breeding activity) show little reaction on the breeding grounds (Clapham and Mattila 1993). Such results have wide implications for monitoring the effect of various activities (e.g., noise pollution) on cetaceans, as the likelihood and level of reaction may vary depending on preoccupation.

In terms of future biopsy and tagging studies on northern bottlenose whales, deployment of tags or biopsy darts on travelling individuals appears to minimize the impact. In practice, deployments were also often more accurate when whales were travelling, due to the predictability of surfacing pattern, the relatively constant heading and the larger exposed flank area.

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