BALEEN WHALE DISTRIBUTIONAL PATTERNS AND THE POTENTIAL INFLUENCE OF BIOLOGICAL AND PHYSICAL PROCESSES

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Baleen whale distributional patterns and the potential influence of biological and physical processes

by

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"If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale. Because we are clever at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly."

J.A. Wiens, 1989

Abstract

Processes influencing baleen whale distribution have been traditionally inferred from correlations with behavioural, physical or biological variables. Such variables are often not directly linked to any particular process or mechanism, and hypotheses based on well established physical or biological models are rarely tested. In addition, the effects of measurement scale are seldom explicitly considered.

One way to incorporate reasoning about scale in descriptions of baleen whale distributional patterns is via a comparison of results obtained across a range of spatial and temporal scales. This approach was exemplified through a description of spatial and temporal patterns of humpback, finback and minke whale distribution in Placentia Bay, Newfoundland. A multi-scale comparison of results indicated that local patterns of abundance are unlikely to reflect large-scale, population trends. Spatial patterns of baleen whale distribution were found to be highly variable, and no consistent trends are apparent. Differences in the seasonal timing of humpback and finback abundance are considered to reflect the exploitation of different food resources elsewhere during the spring, and reiterate the importance of the timing of sampling.

Dimensionless ratios were then used to evaluate the relative importance of somatic growth, demographic and kinematic processes on northwest Atlantic humpback whale biomass concentration. Changes in humpback biomass concentration resulting from changes due to their own locomotory behaviour dominated over all other processes

across a wide range of spatial and temporal scales. A review of current research knowledge of northwest Atlantic humpbacks indicated that limited data on growth rates and age structure of the population, calf survival and recruitment are available.

An examination of humpback whale aggregative response to prey availability as a function of scale indicated that humpbacks were associated with prey at small (2.5-7.5 km) spatial resolutions. This suggests that whales may be continuously tracking prey. Maximum coefficients of association between whales and prey obtained at relatively small spatial scales (10-22.5 km) suggest that studies examining interactions between humpback whales and their prey can be conducted at relatively small scales, but repeated sampling may be necessary before any patterns can be detected.

Other authors have suggested that episodic oceanographic events influencing prey distribution may indirectly influence baleen whale distribution and movements. An examination of water temperature profiles obtained in Placentia Bay indicated the occurrence of a localized coastal upwelling event during the summer of 1994. This event coincided with observations of large patches of euphausiids and schools of mackerel, and also with the peak in humpback whale relative abundance. These findings are speculated to indicate a potential response of humpback whales to concentrations of prey resulting from changes in oceanographic conditions. Additional experiments are needed to confirm these observations.

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Chapter 1. Introduction

Studies examining baleen whale distribution have traditionally focused on descriptions of spatial and temporal patterns of abundance (e.g. Perkins and Whitehead, 1977; Balcomb and Nichols, 1978; Mayo, 1982; Whitehead *et al.*, 1982; Kenney and Winn, 1986; Edds and Macfarlane, 1987; Lynch, 1988; Hain *et al.*, 1992; Mattila *et al.*, 1994). This approach has evolved to incorporate behavioural (e.g. Wursig *et al.*, 1985; Straley, 1990; Smultea, 1994), physical (e.g. Kenney and Winn, 1987; Brown and Winn, 1989; Woodley and Gaskin, 1996) and biological (e.g. Volkov and Moroz, 1977; Whitehead *et al.*, 1980; Payne *et al.*, 1986; 1990; Smith *et al.*, 1986; Piatt *et al.*, 1989) variables in an attempt to identify mechanisms capable of generating observed patterns. While descriptions of baleen whale distribution in relation to biological and environmental features may provide indications of processes that potentially influence distributional patterns, such descriptions often aid little in resolving how these processes operate. Two related reasons can account for this limited ability of descriptive studies to identify mechanisms influencing baleen whale distribution. The first reason is that many of the variables examined are often not directly linked to a particular process or mechanism. For example, several studies (e.g. Whitehead and Moore, 1982; Winn *et al.*, 1986; Tershy *et al.*, 1990; Hain *et al.*, 1992) have shown that the distribution of various species of baleen whale falls within a characteristic range of water temperature conditions. However, these findings do not identify the specific mechanism linking water temperature to distributional patterns -- for instance, does it represent a physiological or

energetic constraint for the whales; is it simply a reflection of the range of temperatures tolerated by the various prey species; or does it reflect some other mechanism not yet hypothesized? A second reason is that specific hypotheses based on well-established physical and/or biological theories or models are rarely tested (Peters, 1991; Schneider, 1995). As a result, inferences about processes potentially influencing baleen whale distributional patterns are often based on conjectures rather than on a more rigorous, quantitative evaluation of data.

Linked to the problem of inferring processes from descriptions of distributional patterns and associated correlations with physical or biological variables is the effect of measurement scale. It is well recognized that the detection of patterns is often dependent on the scale of observation (Haury *et al.*, 1978; Wiens, 1989; Levin, 1992; Schneider, 1994c). Examples of scale-dependent patterns are illustrated in Figures 1.1 and 1.2. Figure 1.1 shows 80 solid circles representing organisms randomly distributed over a given area delimited by the squared contour line. At time = t_0, 20 out of 80 organisms are found within a circular area representing a smaller sampling resolution. The overall number of organisms within the larger area decreases to 40 at time = t_1, but 20 out of the 40 remaining organisms can still be found within the smaller circular sampling area. The overall decrease from 80 to 40 organisms would be detected if sampling was conducted across the larger area, but at the smaller spatial resolution the number of organisms would have remained the same (n = 20). Hence changes in the overall number of organisms

Figure 1.1: An example of scale-dependent pattern. Solid circles represent organisms randomly distributed over an area delimited by the squared line. A smaller sampling area is depicted by the circular line. At time = t_0, 80 organisms can be found within the larger sampling area, and 20 out of 80 organisms are located within the smaller circular area. The overall number of organisms decreases to 40 at time = t_1, but 20 out of 40 organisms can still be found within the smaller sampling area. Hence an overall decrease in the number of organisms would be observed at the larger sampling resolution, but no changes in abundance would be detected at the smaller sampling scale.

would be detected at large spatial scales, but not at smaller ones. This example mimics findings that decreases in abundance of fish populations often result in a contraction of their range, but local patterns of abundance remain unaltered (Schneider, 1994c).

A similar example is provided in Figure 1.2, but this time the overall number of organisms (n = 80) at times t_0 and t_1 remains the same. However, at the smaller spatial resolution the number of organisms decreases from 20 at time = t_0 to 5 at time = t_1. Sampling at the smaller spatial resolution would appear to indicate a decline in the number of organisms, but not at the larger spatial scale. This example is analogous to observed patterns of humpback whale (*Megaptera novaeangliae*) distribution in the Gulf of Maine, where annual variations in abundance occur at the local level (e.g. Payne *et al.*, 1990) but at a larger spatial scale the overall population does not exhibit the same trends (cf. Katona and Beard, 1990). These examples illustrate that explicit reasoning about scale is important in the detection of patterns, and also when inferences about processes generating such patterns are made.

The objective of this thesis was to incorporate reasoning about scale in descriptions of baleen whale distributional patterns, and to explicitly evaluate the potential influence of biological and physical processes on baleen whale distribution as a function of spatial and temporal scale. A traditional description of humpback, finback (*Balaenoptera physalus*) and minke (*B. acutorostrata*) whale spatio-temporal patterns of abundance in Placentia Bay, Newfoundland, Canada, is presented in Chapter 2. A multi-scale examination of results exemplifies the importance of scale in descriptive studies. In

Figure 1.2: A similar example of scale-dependent pattern as that described in Figure 1.1. At time = t_0, 80 organisms represented by solid circles can be found within the larger sampling area delimited by the squared line; 20 out of 80 organisms are located within the smaller circular sampling area. The overall number of organisms at time = t_1 remains the same, but only 5 out of 80 organisms are located within the smaller sampling area. In this case, small-scale sampling would appear to indicate a decline in the abundance of organisms, but a similar trend would not be observed at a larger sampling scale.

Chapter 3 dimensionless ratios (cf. Horne and Schneider, 1994b) are used to evaluate the potential influence of somatic growth, demographic and kinematic processes on the distribution of northwest Atlantic humpback whale biomass as a function of scale. Findings from Chapter 3 lead to an investigation of the scale-dependence of humpback whale aggregative responses to prey availability, carried out in Chapter 4. The degree of association between humpback whales and their prey is hypothesized to be low at small spatial scales given the high mobility of these whales, and is expected to increase as a function of measurement distance. Chapter 5 tests whether upwelling events influencing prey distribution can also be related to small-scale patterns of humpback whale distribution. A summary of findings from all chapters is provided in Chapter 6.

Chapter 2. Spatial and temporal patterns of baleen whale distribution in Placentia Bay, Newfoundland

2.1 Introduction

The description of baleen whale distributional patterns has been a topic of interest for over 30 years. Many of the initial studies were aimed at an understanding of movement patterns among traditional whaling grounds (e.g. Nemoto, 1959; Nasu, 1963; 1966; Chittleborough, 1965; Dawbin, 1966). More recently, descriptions of baleen whale distribution have been used to determine "high-use" areas and their importance for the protection and conservation of whale populations (e.g. Kenney and Winn, 1986, 1987; Smultea, 1994; Woodley and Gaskin, 1996); to assess potential impacts of human industrial activities (e.g. Sorensen *et al.*, 1984; von Ziegesar *et al.*, 1994; Borggaard, in prep.); and in the development of predictive models (e.g. Moses and Finn, 1995). A common feature in many of these studies is the lack of an explicit consideration of the effects of measurement scale.

The scale of investigation will often determine the range of patterns that can be identified, and it may also limit our ability to recognize mechanisms underlying such patterns (Wiens, 1989; Levin, 1992). For example, effects of habitat alterations (clearcutting and thinning) on avian population trends have been observed at the scale of small forest patches (hundreds of km^2), but not across regions (thousands of km^2; Virkkala, 1991). Explicit examinations of baleen whale distributional patterns as a function of spatial and temporal scale have not yet been attempted (cf. Schneider, 1994c).

An inherent difficulty in conducting multi-scale studies of baleen whale distribution is the broad range of scales encompassed by their life history attributes and movements. However, because the scale of investigation is implicit in most studies, a comparison of results obtained across a range of scales can be useful. In this chapter spatial and temporal patterns of humpback, finback and minke whale distribution in Placentia Bay, Newfoundland, Canada, are described. A multi-scale examination of results illustrates how inferences about processes generating observed patterns may benefit from the incorporation of reasoning about scale.

Waters off Newfoundland comprise an important feeding ground for humpback, finback and minke whales. During the summer months, these species can be found both in coastal (Perkins and Whitehead, 1977; Whitehead *et al.*, 1980; Piatt *et al.*, 1989) and offshore (> 100 km; Lynch, 1988) waters, feeding primarily on schools of capelin (*Mallotus villosus*; Mitchell, 1975; Piatt *et al.*, 1989). Limited previous studies examining their distribution have suggested a spatial segregation between minke, finback and humpback whales in inshore waters, with minkes being more frequently sighted closer to shore, and finbacks further offshore, than humpbacks (Perkins and Whitehead, 1977; Piatt *et al.*, 1989). Conversely, these species generally exhibited a temporal overlap in their occurrence, which has led several authors to suggest the possibility of competition (Lynch and Whitehead, 1984; Whitehead and Carlson, 1988; Piatt *et al.*, 1989). However, studies conducted off Newfoundland have been restricted to the east and northeast coasts, and few data are available from other locations. Also, as previous studies were conducted

during the 1970s and 1980s, it would be of interest to evaluate if any changes in baleen whale distributional patterns in Newfoundland waters have taken place during a period of oceanographic and biological changes in the early 1990s (Mann and Drinkwater, 1994).

2.2 Methods

2.2.1 Data collection

Boat surveys were conducted off the eastern coast of Placentia Bay, Newfoundland, Canada (Figure 2.1) during 1993 and 1994. Surveys were conducted on a daily basis, weather permitting, for a total of 28 days in 1993 (1 July-23 August) and 13 days in 1994 (13 June-21 July). Sampling methodology differed somewhat between years; therefore they will be described separately.

A preliminary study to determine the occurrence of baleen whales and oceanographic characteristics of the region was conducted in 1993 from a 7 m open boat. Effort was concentrated at the Cape St. Mary's region, an area of approximately 150 km^2 ranging from Patrick's Cove (46°57'N; 054°13'W) to the Bull and the Cow Rocks (46°46'N; 054°06'W; Figure 2.1). The range of the study area was delimited after a ten day period of exploratory surveys (1-10 July), based on the observed spatial limit for the distribution of whales in the area, and the feasibility of covering such area on a daily basis. Survey routes varied between days, but approximately the same area was covered on every day of effort. During all surveys, time and position at which changes in Beaufort and visibility conditions occurred were recorded. A Raystar 390 Global Positioning

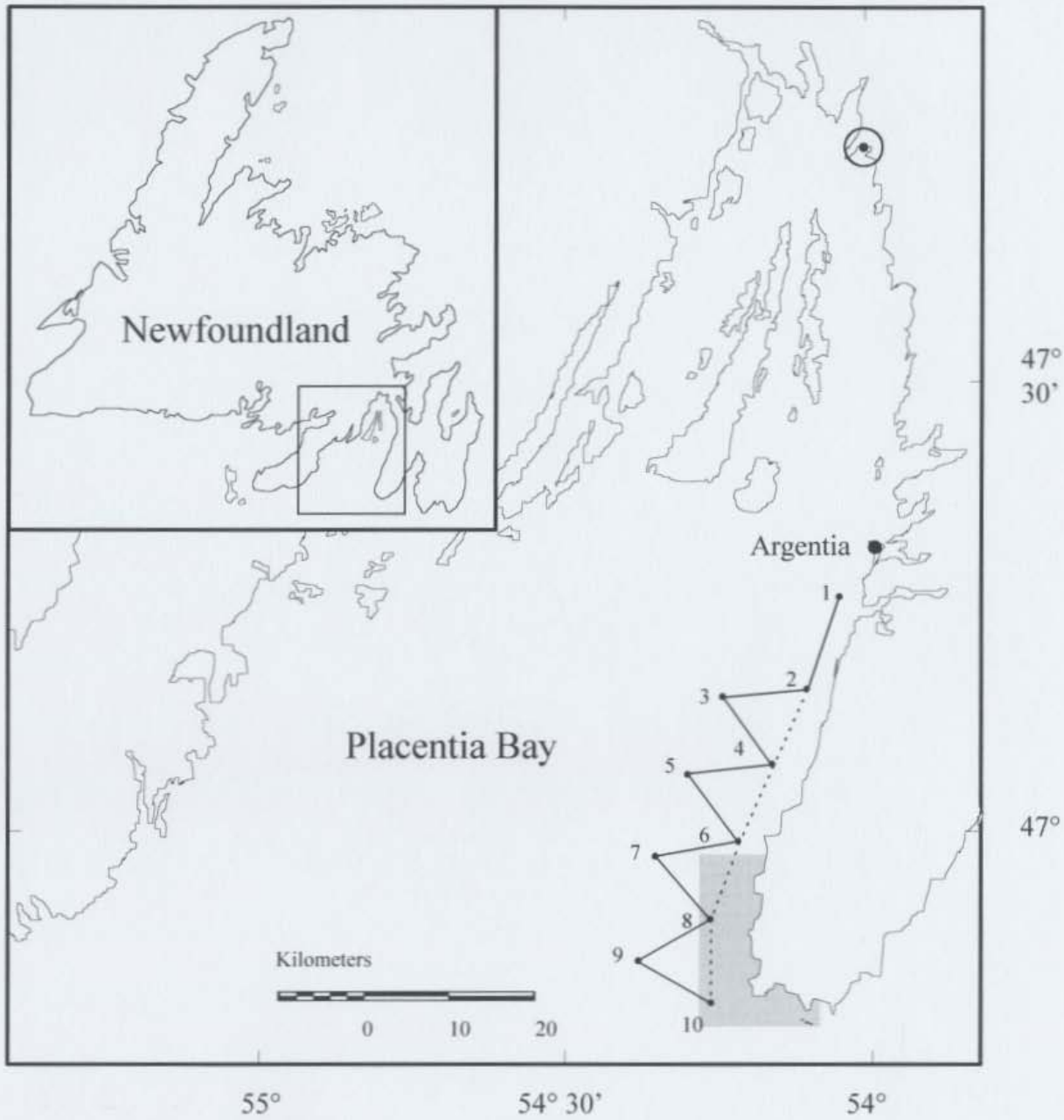


Figure 2.1: Study area in Placentia Bay, Newfoundland, Canada. The shaded area indicates 1993 sampling area; solid and dotted lines show transect routes surveyed during 1994; numbered solid circles within transect lines represent oceanographic sampling stations. The symbol ⊙ placed at the head of the bay indicates the location of a reference point used in calculations. The Argentia climatological station is shown approximately half-way along the eastern shoreline.

System (GPS: Raytheon Marine, Manchester, NH, USA) was used to determine positions.

While at sea two observers searched for whales in all directions. Strip width was determined by visibility conditions. When one or more whales were sighted, time and position were recorded before the boat changed course to approach the whale(s). Time and position at the sighting location were again recorded, and species and group size determined. A group was defined as two or more individuals remaining relatively close to each other (< 100 m) either performing the same behaviour in a somewhat synchronized manner, or behaving differently but remaining close to each other and usually heading in the same direction. Behavioural observations were conducted over periods ranging from 15 to 76 min (mean = 43 min), and an attempt was made to photographically identify all humpback whales sighted. Presence of potential prey was continuously monitored using a Raytheon V-820 colour echosounder (Raytheon Marine) with a beam angle of 40° and frequency set at 50 KHz. Whenever prey was detected in the echosounder, time and position were recorded. Identification of prey as capelin was based on: (a) the depth of the school in the water column (e.g. Piatt, 1990); (b) direct visual identification ; (c) observation of prey items carried by seabirds (black-legged kittiwakes (*Rissa tridactyla*), Atlantic puffins (*Fratercula arctica*), common murres (*Uria aalge*), and greater (*Puffinus gravis*) and sooty (*P. griseus*) shearwaters) in the vicinity of whales; and (d) the presence of spawning capelin at beaches along the shore. Identification of euphausiids and mackerel (*Scomber scombrus*) were based on direct visual observation from the surface.

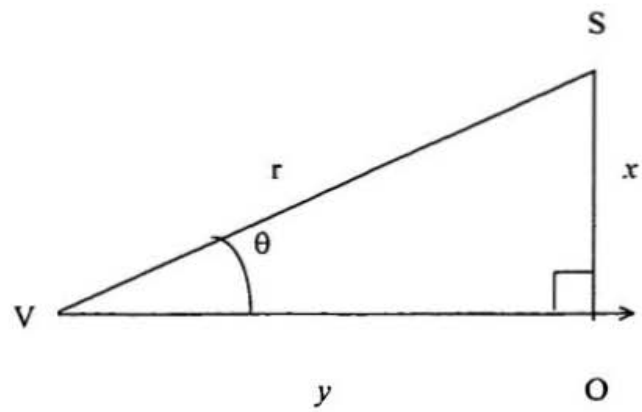
During 1994 fixed transects following triangular routes were conducted at an angle of 60° from the coast, covering an area of approximately 650 km^2 extending into the Cape St. Mary's region (Figure 2.1). The number and order of triangular legs completed varied between transects; hence transects differed in total length. Transects were continuous in space, but not always in time (see below). Survey design aimed at testing baleen whale responses to prey availability (Chapter 4) and oceanographic conditions (Chapter 5); hence the changes from the 1993 design.

Surveys were conducted from a 7 m open boat (June) and a 14 m longliner (July). Two observers searched for whales covering an angle of 180° at the bow of the vessel. Strip width (w) was determined by visibility conditions. When one or more whales were sighted, the vessel would approach the whale(s) to conduct behavioural observations. After these were completed, the vessel would then return to the trackline to resume the transect. A detailed log of the time and position of the vessel before leaving the transect to approach a sighting, during behavioural observations, and during the vessel's return to and resuming of the transect, was kept. Time spent conducting behavioural observations ranged from 13 to 130 min (mean = 48 min). However, when weather conditions were poor, and/or the time needed to complete the transects was limited, the vessel would not approach a sighting. In such cases, sighting angle was obtained using a compass, and sighting distance from the vessel estimated by the observers. Only sightings for which species were positively identified were included in the analyses. All remaining protocols were repeated as in 1993. Presence of potential prey was continuously monitored using a

Raytheon V-820 colour echosounder (June) and a Furuno FE-606 paper echosounder (July; Furuno Electric Co., Ltd., Nishinomiya, Japan), both with frequency set at 50 KHz. Beam angle was fixed at 40° and 28° for each sounder, respectively. Oceanographic casts were obtained at the end of each triangular leg using a Seabird SBE-19 conductivity-temperature-depth (CTD) recorder (Seabird Electronics, Inc., Bellevue, WA, USA).

Positions of sightings for which only sighting angle and distance were available were estimated as follows:

For each sighting, 23° 35' magnetic variation was subtracted from the track course so as to obtain true bearings. Sighting angle was then added to or subtracted from the true course, depending on whether the sighting occurred on the right or left side of the vessel, respectively. This calculation allowed for the estimate of sighting direction in true degrees. Sighting direction and the closest of four reference bearings (90°, 180°, 270° or 360°, in true degrees) to the sighting direction were used in a triangulation as follows:



where V = vessel position;

O = reference bearing (90°, 180°, 270° or 360°, true degrees);

(Canadian Hydrographic Services, Department of Fisheries and Oceans, Ottawa, Canada) and assigning the closest depth measurement to each sighting.

The along-shore distribution of sightings was determined based on the distance between each sighting and a fixed reference point located at the head of Placentia Bay (47°47'18" N, 54°30' W). Values (km) were obtained according to the formula:

$$1.852 \bullet 60 \bullet \arccos(\sin(Lat1) \bullet \sin(Lat2) + \cos(Lat1) \bullet \cos(Lat2) \bullet \cos(Long2-Long1)) \quad (2.1)$$

where Lat1 = latitude of sighting;

Long1 = longitude of sighting;

Lat2 = latitude of reference point; and

Long2 = longitude of reference point.

Sighting rates, defined as the number of whales sighted per hour of effort for each species, were calculated for each day of effort. Only searching effort, i.e. transect duration minus time spent conducting behavioural observations or returning to the track line, was used in the calculation of sighting rates. Resightings of photographically-identified humpback whales within the same day were discarded. As photo-identification effort for finbacks and minkes was limited, all sightings of these species within the same day were assumed to represent different individuals unless sighting locations overlapped. In such cases, the second overlapping sighting was discarded.

Time and position of all sightings, and oceanographic casts obtained in Placentia Bay during 1993 and 1994 are available from the Centre for Newfoundland Studies, Queen Elizabeth II Library, Memorial University of Newfoundland, St. John's, Newfoundland (Appendix I).

2.2.2 Data analysis

A preliminary analysis testing for the potential effects of sea state and visibility conditions on the number of whales sighted per hour of effort was carried out separately for each species and for each year (SAS, Inc., Cary, NC, USA). Visibility conditions were classified into 3 categories: 0-5 km; 5-10 km; and > 10 km. Variability in baleen whale sighting rates (log transformed) as a function of season (Julian day) was controlled statistically in the models, with Julian day being categorized into two-week intervals. Randomization tests (1 000 iterations) were conducted given the non-normality of residuals (see Crowley, 1992 for a review of resampling methods). A SAS routine (T. Bult, Department of Biology, Memorial University of Newfoundland, St. John's, NF, Canada) was used to randomly reassign values of the response variable to different treatments, without replacement. P-values were based on the distribution of F statistic values generated through randomization, and calculated as the probability of obtaining an F statistic equal to or more extreme than the one in the original analysis. Significance level (α) was set at 0.05. A significant effect of Beaufort and/or visibility conditions on

baleen whale sighting rates would determine the inclusion of these variables in any subsequent model.

Given the high correlation between distance from shore and depth of sightings ($r = 0.923$, $n = 210$), only depth was used in the analyses. Depth and distance of sightings from the head of Placentia Bay were then used to test for inter-specific differences in spatial patterns of distribution. Due to differences in the area surveyed in the two years, the variable year was controlled for in the models (GLM Proc, SAS, Inc.). Separate analyses for depth and distance of sightings from the head of the bay were carried out. Where a significant year effect was found, the same models were run on separate datasets for each year. Paired comparisons were used to determine which species differed with respect to depth or distance of sightings from the head of Placentia Bay.

Differences in the seasonal timing of abundance of humpbacks, finbacks and minke whales were examined using the number of whales sighted per hour as a function of species and Julian day (GLM Proc, SAS, Inc.). As it was not possible to compute sum of squares for all interaction terms when year was included as a variable in the model, separate analyses were carried out for each year. A significant interaction between species and Julian day would indicate inter-specific seasonal differences in baleen whale relative abundance. In these cases, paired comparisons (Sokal and Rohlf, 1981) were carried out to determine which species differed with respect to their timing of abundance.

Because the residuals from the above models did not fit either a normal, poisson or gamma distribution, randomization tests (1 000 iterations) were used to test for

significance. Randomized p-values were calculated as previously described, and significance level (α) set at 0.05.

2.3 Results

A total of 349 baleen whales were sighted in Placentia Bay during 1993 and 1994. Of these, 198 (56.73%) were humpback, 90 (25.79%) finback, and 61 (17.48%) minke whales (Table 2.1). The total number of whales sighted varied between years, with approximately 62% more sightings taking place in 1994.

No significant effect of Beaufort or visibility conditions on the number of humpbacks, finbacks or minke whales sighted per hour were obtained (Table 2.2). This result is likely a reflection of the low effort conducted under poor Beaufort or visibility conditions. Neither Beaufort nor visibility were controlled for in any subsequent model.

No significant differences in the along-shore distribution of humpback, finback and minke whale sightings were obtained ($n = 210$, $p = 0.217$). Sightings of the three species occurred over a similar range of distances, with mean ($\pm$ SD) distance values of 90.99 km ($\pm$ 15.62 km, $n = 108$) for humpbacks, 88.91 km ($\pm$ 20.66 km, $n = 51$) for finbacks, and 96.06 km ($\pm$ 13.89 km, $n = 51$) for minkes. Depth at sightings varied significantly with species ($n = 210$, $p = 0.001$), and also between years ($p = 0.003$). Inter-specific differences in the depth of sightings were not statistically significant when only 1993 sightings were analyzed ($n = 72$, $p = 0.378$), probably a result of sampling effort being concentrated closer to shore (ca. 5 km or less) in that year compared to 1994.

Table 2.1 - Humpback, finback and minke whale relative abundance in Placentia Bay, Newfoundland.

	Total no. of sightings (groups)			Total no. of whales			No. of whales sighted h^{-1}		
Year	Humpbacks	Finbacks	Minkes	Humpbacks	Finbacks	Minkes	Humpbacks	Finbacks	Minkes
1993	33	16	22	70	37	26	1.94	0.49	0.26
1994	74	35	29	128	53	35	2.89	0.63	0.67
Total	107	51	51	198	90	61	2.24	0.53	0.38

Note: The number of whales sighted h^{-1} for each species is based on average values for all days of effort in each year. Total number of whales sighted h^{-1} consists of average values for 1993-1994.

Table 2.2 - Randomized p-values (1 000 iterations) testing for the effects of Beaufort and visibility conditions on baleen whale relative abundance, controlling for Julian day.

		1993			1994		
Model terms	n	Humpbacks	Finbacks	Minkes	Humpbacks	Finbacks	Minkes
Beaufort	81	0.298	0.888	0.160	0.850	0.752	0.413
Julian day		0.001	0.212	0.045	0.088	0.074	0.677
Visibility	57	0.376	0.569	0.525	0.320	0.778	0.757
Julian day		0.001	0.222	0.081	0.124	0.145	0.681

Note: Visibility conditions were classified into three categories: 0 to 5 km, 5 to 10 km, and > 10 km. Julian day was categorized into two-week intervals.

However, a significant effect was obtained for the 1994 dataset ($n = 138$, $p = 0.002$). Further analyses of the 1994 data indicated that finbacks were sighted in shallower waters (mean depth ± SD = 43.28 m ± 38.62 m, $n = 35$) than humpbacks (76.90 m ± 45.34 m; $n = 74$, $p = 0.002$) or minkes (62.59 m ± 38.65 m; $n = 29$, $p = 0.048$). Because depth and distance from shore were highly correlated, this finding indicates that finbacks were generally sighted closer to shore than humpbacks and minkes. No significant differences in depth of humpback and minke sightings ($p = 0.150$) were obtained.

The timing of humpback, finback and minke whale relative abundance differed significantly as a function of Julian day in both years (Table 2.3; Figure 2.2). Paired comparisons indicated that in both years humpbacks differed significantly from finbacks in their timing of arrival ($n = 82$, 1993: $p = 0.017$, 1994: $p = 0.009$), the latter peaking in abundance later in the season than the former. Humpbacks differed significantly from minkes in their timing of arrival in 1993 ($n = 82$, $p = 0.003$), but not in 1994 ($n = 82$, $p = 0.281$). No significant differences in the timing of abundance of minkes and finbacks were observed in 1993 ($n = 82$, $p = 0.904$) nor in 1994 ($n = 82$, $p = 0.062$). The relative abundance of minke whales varied on a daily basis, but remained relatively consistent throughout the survey period in both years (Figure 2.2).

Prey was observed within the study area in 21 out of 28 days in 1993, and 10 out of 13 days in 1994. In 1993 prey consisted mostly capelin; during 1994 whales were seen foraging on capelin as well as euphausiids and mackerel.

Table 2.3 - Randomized p-values (1 000 iterations) testing for differences in the timing of baleen whale relative abundance, controlling for Julian day.

	p-values	
Model terms	1993	1994
Species	0.114	0.186
Julian day	0.001	0.663
Species × Julian day	0.011	0.020

Note: Julian day was categorized into two-week intervals.

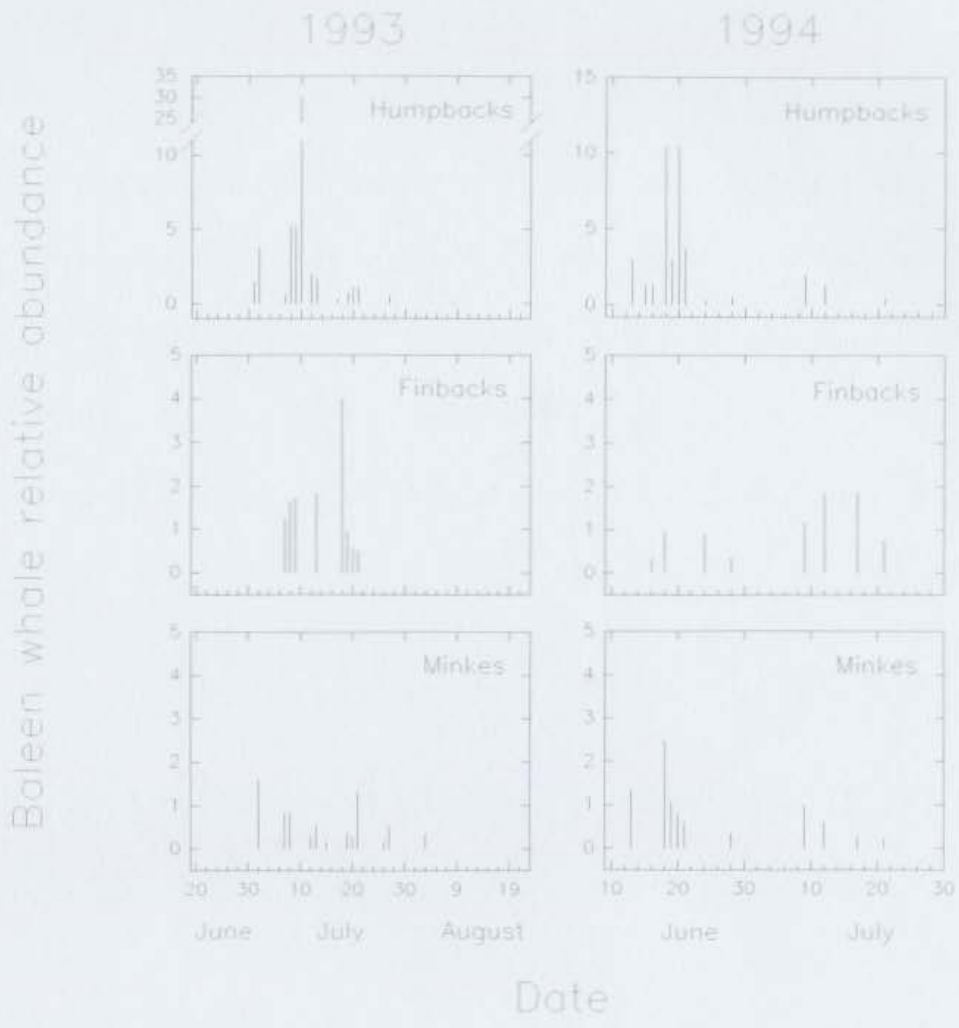


Figure 2.2: Relative abundance of humpback, finback and minke whales in Placentia Bay, Newfoundland, as a function of date. Data from 1993 is presented on the left column; 1994 data is shown on the right. Note that the scale of the x axis differs between years; the scale of the y axis differs between species.

Temporal differences in the arrival of finbacks and humpbacks in inshore waters off Newfoundland coincide with evidence that the two species forage at different trophic levels (Todd *et al.*, 1995). Analyses of carbon and nitrogen isotopes from tissue samples indicate that finbacks feed at a lower trophic level than humpbacks during the month prior to their arrival in Newfoundland (Todd *et al.*, 1995). It is possible that the later arrival of finbacks in Placentia Bay results from their exploitation of different food resources elsewhere during the spring. However, little is know about the distribution and movements of finbacks off Newfoundland during the fall, winter and spring, after they leave inshore waters (Hay, 1982). More detailed studies are needed to determine seasonal patterns of finback distribution off Newfoundland, and to verify whether prey availability and distribution can explain temporal patterns of finback abundance.

Food availability is generally thought to determine baleen whale distributional patterns (Murison and Gaskin, 1989; Payne *et al.*, 1990; Tershy, 1992), especially across small spatial scales (Kenney and Winn, 1986). It has also been suggested that physical processes influencing prey distribution may also correlate with whale distribution (Piatt *et al.*, 1989). Although it was not possible to quantify prey abundance in Placentia Bay, observations of prey schools and feeding whales and seabirds suggest that prey was readily available throughout the area. Piatt *et al.* (1989) reported that availability of prey in their study area largely exceeded the estimated whale consumption (average 0.59% of total capelin biomass). However, differences in whale abundance and spatio-temporal distributional patterns in Placentia Bay in comparison with those reported by Piatt *et al.*

al., 1989; 0.04-0.31; Lynch and Whitehead, 1984). Although fluctuations in the ratio of finbacks to humpbacks may result from variability in the number of sightings of either species, ratio values are consistent with observed patterns of relative abundance. Finback relative abundance in Placentia Bay (mean 0.53 finbacks h^{-1}; Table 2.2) was much higher than that reported between 1982-1985 (mean 0.11 finbacks h^{-1}, range 0.04-0.19; Piatt *et al.*, 1989).

Variability in the ratio of finbacks to humpbacks during the late 1970s (mean 0.38; range 0.16-0.74) and early 1980s (mean 0.19; range 0.04-0.31) has been attributed to a decline in the finback population (Lynch and Whitehead, 1984). However, no apparent decline in this population was observed during years of intensive harvesting (1967-1972; Hay, 1982), and it is unlikely that such a decline would take place after the stock was given legal protection. The suggestion that a decline in the finback population could result from competition with the sympatric humpback whale (Lynch and Whitehead, 1984) is also not supported by evidence from other regions. Off Iceland, an increase in the humpback population (Sigurjónsson and Gunlaugsson, 1990) did not appear to adversely affect the finback stock. Surveys conducted off the northeast U.S. also report large numbers of both humpbacks and finback whales within the same region (Payne *et al.*, 1990), with no indication that populations of either species are declining (e.g. Hain *et al.*, 1992; Katona and Beard, 1990). A more parsimonious explanation for the variability in the ratio of finbacks to humpbacks is change in the inshore abundance of finbacks resulting from changes in their distribution and movements. Studies conducted

off the northeast coast of the U.S. indicate that finback distribution is generally very fluid (Hain *et al.*, 1992). Inter-annual variability in their distribution and movements has been related to changes in the distribution and abundance of their prey (Payne *et al.*, 1990; Hain *et al.*, 1992). Inshore/offshore abundance of finbacks off Newfoundland has been correlated with the abundance of capelin (Whitehead and Carscadden, 1985). It is likely that fluctuations in the inshore abundance of finbacks off Newfoundland, as reflected in the ratio of finbacks to humpbacks, result from variable patterns of movement as observed elsewhere.

Minke whale relative abundance in 1993-1994 (0.26 and 0.66 minkes h^{-1}, respectively) was comparable to that observed in previous years at other locations (average 0.45 minkes h^{-1}, range 0.16-0.81, Piatt *et al.*, 1989). This population has generally been considered stable (Whitehead and Carscadden, 1985; Piatt *et al.*, 1989), although current population estimates are not available (Hay, 1982).

Evidence provided in this study, coupled with findings from studies conducted elsewhere, suggest that local patterns of humpback and finback abundance do not reflect large-scale, population trends. Both species exhibit variable patterns of distribution and movements (e.g. Whitehead and Carscadden, 1985; Payne *et al.*, 1990; Hain *et al.*, 1992; this paper), which are generally thought to reflect availability of prey. Hence inferences about population trajectories based on small-scale spatio-temporal patterns of abundance of these species should be treated with caution.

The relation between small- and large-scale patterns of minke whale abundance is not clear. Studies conducted off the west coast of North America have showed that individual minke whales exhibit a high degree of site-fidelity and residency (Dorsey *et al.*, 1990), and occupy distinct ranges (Dorsey, 1983). Preliminary investigations of photographically-identified minke whales off Newfoundland (Borggaard, in prep.) suggest similar patterns to those observed elsewhere. These findings imply in a relatively limited amount of movement by individual whales; however, inshore/offshore movements of minkes in response to capelin abundance have been documented (Whitehead and Carscadden, 1985). Until minke whale movements off Newfoundland are better understood, and a more refined assessment of population parameters carried out, inferences about the relation between local patterns of minke whale abundance and population trends remain speculative.

Previous studies off Newfoundland suggested a spatial segregation between humpback, finback and minke whales, with minkes being more frequently sighted closer to shore, and finbacks further offshore, than humpbacks (Perkins and Whitehead, 1977; Piatt *et al.*, 1989). The observed distribution of baleen whales in Placentia Bay, however, does not agree with this hypothesis. In 1993 a spatial overlap between humpbacks, finbacks and minke whales was observed; in 1994 finbacks were sighted significantly closer to shore than humpbacks and minkes. This finding suggests that small-scale spatial patterns of baleen whale distribution can be highly variable, and there are no consistent species patterns.

(1989) were observed despite the apparent availability of prey in both studies. Small-scale spatial variability in baleen whale abundance and distribution has been suggested to reflect a preference by the various species for different prey densities (Piatt and Methven, 1992). However, prey density alone does not explain distributional patterns of humpback whales in the Gulf of Maine (Payne *et al.*, 1986), making any comparisons between species problematic. Variability in baleen whale distribution off Newfoundland has also been correlated with strength of capelin year-classes (Whitehead and Carscadden, 1985), suggesting that processes influencing baleen whale distribution at larger spatio-temporal scales may be reflected in part across smaller scales.

Analyses of spatial and temporal patterns of humpback, finback and minke whale distribution in Placentia Bay indicated that local fluctuations in abundance do not necessarily reflect large scale, population trends. Spatial patterns of occurrence were highly variable, and appear to result from processes occurring at both small and large spatial scales. Differences in the timing of arrival of humpbacks and finbacks may possibly reflect the exploitation of different food resources prior to their arrival in inshore waters, but further studies are needed to verify this hypothesis. An important implication of observed differences in the timing of abundance of the two species is that timing of sampling should be taken into consideration when field studies are conducted.

Studies relating baleen whale distribution to biological (e.g. prey availability, population abundance) or physical (e.g. oceanographic events) processes have been conducted across a range of spatial and temporal scales (tens to hundreds of km; e.g.

Krieger and Wing, 1986; Smith *et al.*, 1986; Brown and Winn, 1989; Sigurjónsson and Gunlaugsson, 1990; Wishner *et al.*, 1995; Woodley and Gaskin, 1996). However, an explicit treatment of scale is still lacking (cf. Schneider, 1994b), and may in part explain discrepancies in results obtained from different studies. For example, initial studies examining seabird distribution did not detect a relationship between seabirds and their prey (cf. Schneider, 1994b). Subsequent work (e.g. Schneider and Piatt, 1986) showed that the association between seabirds and prey was stronger at some measurement distances, but weak or non-existent at others. Scale-dependent aggregative responses to biological or physical processes have been demonstrated for a variety of marine organisms, including plankton (Haury *et al.*, 1978; Weber *et al.*, 1986), fish (Rose and Leggett, 1990) and seabirds (Schneider and Duffy, 1985; Piatt, 1990). Understanding of baleen whale spatial and temporal distributional patterns, and the processes that are capable of generating such patterns, would likely be improved through the application of reasoning about scale in future studies of baleen whales.

Chapter 3. Evaluating the influence of biological and physical processes on northwest Atlantic humpback whale distribution

3.1 Introduction

The explicit use of spatial and temporal scale in analyses of population dynamics parallels the increase in evidence that distributional patterns of terrestrial (e.g. Virkkala, 1991; Kelt *et al.*, 1994) and aquatic (e.g. Schneider, 1989; 1990; Shackell *et al.*, 1994) organisms are dependent on the scale of observation. In aquatic environments, scale-dependent aggregation in response to physical or biological processes have been documented for zooplankton (Haury *et al.*, 1978; Weber *et al.*, 1986), fish (Fiedler and Bernard, 1986; Rose and Leggett, 1990) and seabirds (Schneider and Piatt, 1986; Piatt, 1990; Schneider, 1991). The potential influence of physical and biological processes on the distribution of large marine organisms, such as baleen whales, has not been quantified as a function of scale.

Baleen whales are highly mobile marine organisms whose life history and movements encompass a wide range of spatial and temporal scales. Examinations of whale distribution relative to oceanographic processes (e.g. Nasu, 1963; Volkov and Moroz, 1977; Brown and Winn, 1989; Tershy *et al.*, 1991) and prey concentrations (e.g. Nasu, 1966; Whitehead *et al.*, 1980; Bryant *et al.*, 1981; Whitehead and Carscadden, 1985; Winn *et al.*, 1986; Piatt *et al.*, 1989; Piatt and Methven, 1992) are numerous, yet measurement scales are seldom explicitly stated (e.g. Bryant *et al.*, 1981; Whitehead and Carscadden, 1985; Tershy *et al.*, 1991). These distributional studies are often conducted

at single spatial or temporal scales, and it is not clear if or how the influence of physical and biological processes on whale distribution varies across scales.

Horne and Schneider (1994a) have proposed the use of dimensionless ratios to assess the relative importance of biological and physical processes that potentially influence the distribution of biological quantities. This technique compares somatic growth, demographic, and kinematic rates via dimensionless ratios. Summary rate diagrams consisting of dimensionless ratio values plotted as a function of spatial and temporal scale can be used to indicate variance generating processes at any scale of interest, to identify potential research areas and appropriate sampling scales for field studies, and to limit the range of scales over which results can be generalized.

This technique was initially developed using capelin, a small, pelagic fish. As its application to larger, highly mobile marine organisms such as baleen whales has not been previously attempted, it was deemed desirable to select a well studied species. Knowledge of biological parameters, distribution and movements of northwest Atlantic finback and minke whales is limited. Therefore, in this chapter dimensionless ratios are used to evaluate the distribution of northwest Atlantic humpback whale biomass at spatial scales ranging from bays (10 km) to migration routes (1 000 km) and temporal scales ranging from hours to decades. Given the high mobility of humpbacks, changes in biomass due to their own locomotory behaviour are expected to dominate over other processes (e.g. growth, demographics) across most scales.

3.2 Methods

3.2.1 Dimensionless ratio analysis

Horne and Schneider (1994a) use dimensional reasoning and scaling arguments to evaluate the relative importance of biological and physical processes that potentially influence the distribution of any group of organisms. Their technique is comprised of four steps: a statement of the quantity of interest; the formation of dimensionless ratios combining biological and physical processes potentially influencing distributional patterns; the calculation of nominal ratio values; and the plotting of nominal ratio values as a function of spatial and temporal scale.

The quantity of interest in this case is the proportional rate of change in the concentration of humpback whale biomass in the northwest Atlantic. By focusing on biomass, rather than number of individuals or density, the relative contribution of processes occurring at the individual level (e.g. somatic growth) can be incorporated into the analyses. Rate of change in humpback biomass concentration $[B]$ is then a function of change in biomass due to recruitment and mortality ($\dot{N}$), somatic growth (M), active movement relative to the fluid ($\dot{V}_I$), and passive movement due to drift with currents ($\dot{V}_F$). Following Horne and Schneider (1994a) these are summarized as:

$$[\dot{B}] = \dot{N} + M - \dot{V}_I - \dot{V}_F \qquad (3.1)$$

The divergence theorem (Dutton, 1975) has been used to incorporate changes in biological quantities due to active ($\dot{V}_I$) or passive ($\dot{V}_F$) divergence (e.g. Schneider, 1991). Positive changes in biomass concentration result if organisms converge, whereas negative changes are expected if organisms diverge. Hence the kinematics terms ($\dot{V}_I$, $\dot{V}_F$) in Eq. 3.1 are negative.

Dimensionless ratios (cf. Taylor, 1974; Langhaar, 1980) were formed using terms in Eq. 3.1 to quantify the relative importance of each term on the change in humpback concentration as a function of spatial and temporal scale. Following the biological reasoning of Horne and Schneider (1994a) four dimensionless ratios were formed.

The first dimensionless ratio compares changes in biomass concentration due to somatic growth (M) to net changes resulting from demographic (N) and kinematic (V) processes:

$$\frac{M}{N-V} \tag{3.2}$$

Ratio values smaller than 1 are expected for long-lived species, which typically exhibit slow growth rates relative to the lifespan of the organisms. In such cases, changes in biomass due to demographics and kinematics exceed those due to somatic growth.

The second ratio evaluates the relation between demographic (N) and kinematic (V) processes:

$$\frac{N}{V} \tag{3.3}$$

Ratio values smaller than 1 are expected for highly mobile species where locomotion greatly exceeds passive drift with the fluid, resulting in a large value for the kinematics term.

The demographics ratio (N) compares changes in biomass due to recruitment ($\dot{N}_r$) to those due to natural ($\dot{N}_m$) and harvesting ($\dot{N}_f$) mortality:

$$\frac{\dot{N}_r}{\dot{N}_m + \dot{N}_f} \tag{3.4}$$

Ratio values smaller than 1 are expected for long-lived species, where the small mass of recruits relative to the remainder of the population, coupled with a low number of individuals entering the breeding population every year, result in small changes in biomass due to recruitment.

The kinematics (V) ratio compares changes in humpback biomass due to locomotory behaviour ($\dot{V}_L$) to those due to passive drift with the fluid ($\dot{V}_F$):

$$\frac{\dot{V}_L}{\dot{V}_F} \tag{3.5}$$

Individual motion is expected to dominate over passive drift across most scales given the high mobility of humpback whales. Drift with the fluid will only dominate at

times when humpbacks are not actively swimming (i.e. resting or "logging" at the surface; cf. Bredin, 1985; Helweg and Herman, 1994).

Values for each ratio were calculated at discrete spatio-temporal scales using published data, and nominal values (<1, 1, >1) plotted in rate diagrams as a function of spatial and temporal scale. Ratio values <1 indicate the predominance of process(es) in the denominator term, ratio values =1 indicate a potential interaction between process(es) in the numerator and process(es) in the denominator, and values >1 indicate that process(es) in the numerator predominate over process(es) in the denominator. Contour lines drawn on rate diagrams (cf. Figure 1a-d; Horne and Schneider, 1994a) mark spatial and temporal scales where dimensionless ratios change value. Ratio values and contour locations can be adjusted as additional data are obtained from field studies.

3.2.2 Data sources

As no direct rates of mass growth (M) are available for humpback whales (cf. Lockyer, 1981), measurements of length at age were used to estimate growth rates (Todd *et al.*, unp. manuscript). Rates of change in length at age were calculated for up to a maximum age of 48 years (Chittleborough, 1965). Average growth rates for the northwest Atlantic humpback population were obtained by assuming that at any one given time 31.6% of the population was comprised of immature individuals (less than five years of age; Clapham and Mayo, 1987b; 1990), and an uniform age class distribution within groups of immature and sexually mature individuals. The percentage of immature

(31.6%) and sexually mature individuals (68.4%) is based on birth rates of 7.9% year^{-1} (Clapham and Mayo, 1990) and the assumption of no calf mortality.

Data on humpback recruitment ($\dot{N}_r$), defined as the proportional number of individuals that reach sexual maturity and contribute to the reproductive biomass of the population in any given year, are restricted to the sighting history of nine individuals first photographed as calves. Of these, eight (89%) were resighted at least until the age of five (Clapham and Mayo, 1987a) and assumed to have reached sexual maturity (Clapham and Mayo, 1987b; 1990). This preliminary value should be treated with caution as it is based on resightings of individuals from only two cohorts (calves born in 1979 and 1980), and the small sample size results in the fate of a single individual potentially causing a large (> 10%) change in recruitment estimates. The possibility of higher mortality rates during the first few weeks after birth, prior to the calves' arrival at the feeding grounds (Clapham and Mayo, 1987a), and variability in resighting probabilities (Weinrich *et al.*, 1993) may also bias estimates of recruitment based on the sighting history of calves. To be conservative, crude birth rates (i.e., the proportional number of calves sighted in relation to the total number of whales sighted in any given year; cf. Clapham and Mayo, 1990) were used in place of recruitment. Crude birth rates were multiplied by the average mass of neonates (Winn and Reichley, 1985) and the resulting value divided by the proportional mass of immature and sexually mature individuals in the population. Average weights of individuals less than five years of age (10.46 t) were estimated by assuming that humpback whales attain 70% of their mature weight at puberty, as

documented for Antarctic balaenopterid whales (Lockyer, 1981). Average weights for mature individuals (27.02 t) were computed based on data in Ash (1953, *in* Lockyer, 1981).

In recent years, humpback harvesting mortality ($\dot{N}_r$) has been insignificant. Since the species was given legal protection in 1955, reported harvesting of humpbacks in the north Atlantic totaled 41 whales taken in Canadian waters between 1966 and 1971, a maximum of ten whales taken annually in West Greenland, and one to five animals caught every year in the West Indies prior to 1980 (Whitehead, 1987). An indirect source of harvesting mortality is entanglement of whales in fishing gear (Lien *et al.*, 1989; Volgenau, 1991; Lien, 1994). Therefore harvesting mortality has been replaced by entanglement mortality in the calculations. Lack of quantitative data on other sources of anthropogenic mortality (e.g. ship collisions; Wiley *et al.*, 1995) prevented their inclusion in estimates of humpback mortality rates.

Estimates of humpback survival ($\dot{N}_m$) based on resightings of photographically identified individuals from the Gulf of Maine (Buckland, 1990) were assumed to be representative of the northwest Atlantic population. As the fate of individuals not resighted cannot be determined, this estimate potentially incorporates mortality resulting from entrapments in fishing gear within that region. Therefore entrapment mortality within a feeding area was estimated as the average mortality for Newfoundland and Labrador (0.35% $year^{-1}$) and the Gulf of Maine (0.22% $year^{-1}$; Volgenau, 1991) minus entrapment mortality for the Gulf of Maine (0.22% $year^{-1}$), resulting in an entrapment

mortality of 0.065% year^{-1}. Estimates of entrapment mortality for the northwest Atlantic population consisted of mortality rates from Newfoundland and Labrador only (0.35% year^{-1}).

Estimates of humpback movement relative to the fluid ($\dot{V}_I$) were based on residence of the population at various spatial scales (e.g. length of stay in feeding grounds: Whitehead *et al.*, 1980: Mate, 1983; Clapham *et al.*, 1993). Migratory speeds at temporal scales of less than a year were estimated based on the migratory transit of photo-identified individuals between breeding and feeding grounds (Clapham and Mattila, 1988).

Observations of humpback whales at wintering areas near Hawaii suggest that whales rest during the early morning but the total time spent resting is not clear (cf. Figure 3; Helweg and Herman, 1994). Data on daily activity budgets for humpbacks in the feeding grounds and duration of these resting periods during migration are also lacking. Passive drift with the fluid ($\dot{V}_F$) was then estimated by assuming that humpbacks "sleep" (Allen, 1916 *in* Lockyer, 1981) or rest at the surface (Helweg and Herman, 1994) during one-fifth of the day. It was also assumed that they actively swim during at least half of these resting periods in order to remain approximately in the same location; hence being subject to drift with water currents for a total of one-tenth of a day. Estimates for passive drift with the fluid were obtained by multiplying average current speeds for the inshore branch of the Labrador Current (Helbig *et al.*, 1992), representing the major

current in a feeding area, and the Gulf Stream (Pickard and Emery, 1982), the major current in the migration route, by one-tenth. Even if total time spent resting was underestimated, values for drift will be small relative to changes in biomass resulting from active movement, and it will not changes order of magnitude results.

3.3 Results

The rate diagram of growth to population dynamics (Figure 3.1a) indicates the predominance of demographic and kinematic processes over somatic growth across all scales. Average growth rates of 7.19% $year^{-1}$ obtained for individuals less than five years of age, combined with growth rates of 0.30% $year^{-1}$ for the remaining of the population, result in average growth rates of 2.48% $year^{-1}$ for the entire northwest Atlantic population. This value is exceeded by changes due to recruitment (0.720% $year^{-1}$), natural (4.9% $year^{-1}$: Buckland, 1990) and entrapment (0.35% $year^{-1}$: Volgenau, 1991) mortalities combined with changes due to kinematics (5.15% $year^{-1}$). Ratio values smaller than 1 were also obtained at spatial scales of a feeding area or smaller, across all temporal scales. It was assumed that somatic growth rates at these scales (≤ feeding area) are comparable to estimated values for the northwest Atlantic population. However, if sampling is conducted over time periods during which humpback populations remain within an area of a bay, feeding area or migratory route, changes in humpback biomass concentration due to kinematics will approximate zero as there is no net movement. In

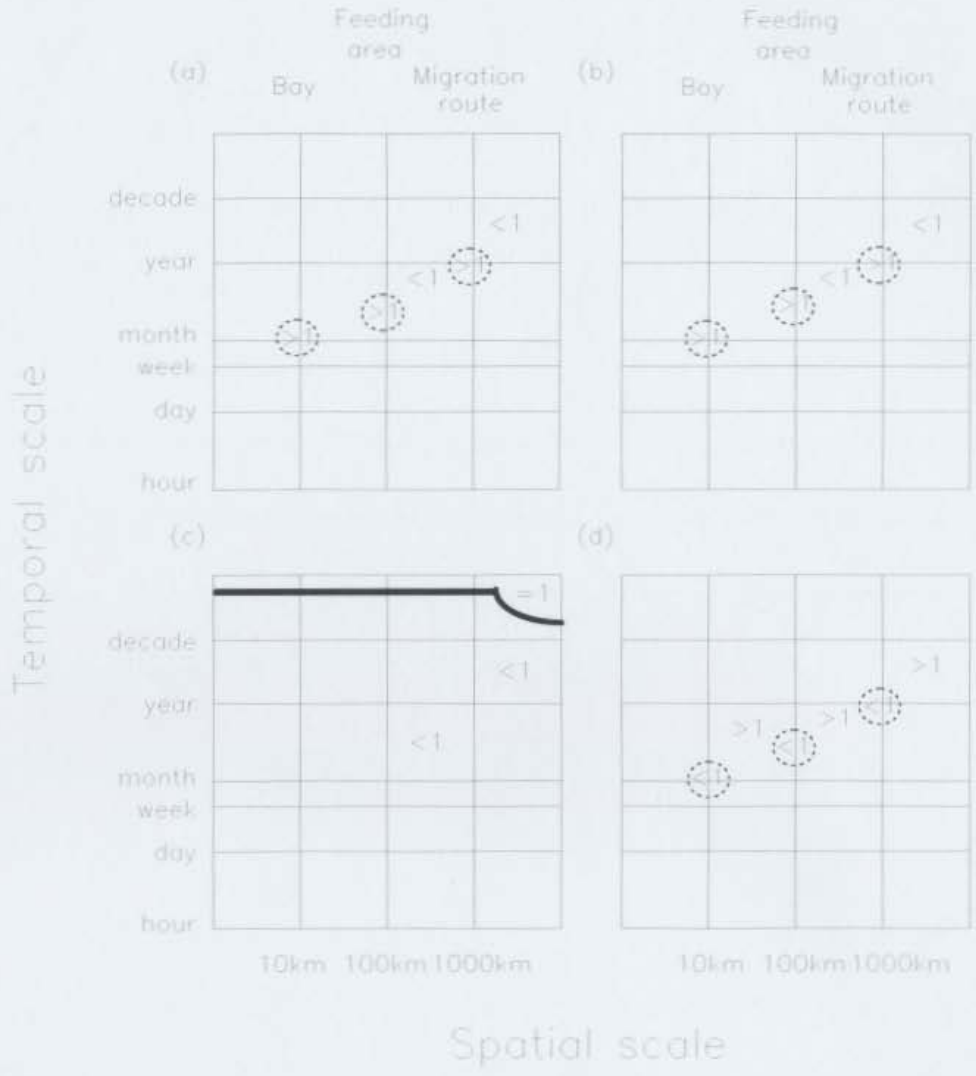


Figure 4.1: Rate diagrams of dimensionless ratio values for (a) growth to population dynamics ($\dot{M}/\dot{N}\text{-}\dot{V}$); (b) demographics to kinematics ($\dot{N}/\dot{V}$); (c) demographics ($\dot{N}_r/\dot{N}_m+\dot{N}_f$); and (d) kinematics ($\dot{V}_I/\dot{V}_F$). Dotted lines indicate shifts in ratio values when sampling is conducted during periods of residence times.

such cases, changes in biomass due to growth will exceed those due to population dynamics (Figure 3.1a, dotted lines).

The main feature of the demographics to kinematics ratio (Figure 3.1b) is the dominance of kinematics over demographics at spatial scales of bays to migration route across all time scales. Humpback residence times approximate one month at the scale of a bay (56 km; Whitehead *et al.*, 1980) and 5 months at the scale of a feeding ground (~ 700 km; Mate, 1983; e.g. Clapham *et al.*, 1993). On an annual scale, the northwest Atlantic humpback population completes a migratory cycle within the region. At these spatio-temporal scales humpback locomotory behaviour greatly exceeds drift with the fluid, and the resulting value for the kinematics term will be large. Changes in humpback biomass concentration due to demographics will only exceed those due to kinematics if sampling is conducted during periods of residence times, when there is no net movement ($V \sim 0$; Figure 3.1b, dotted lines).

The rate diagram of the demographics ratio (Figure 3.1c) indicates a balance between births and deaths at the larger spatio-temporal scales encompassing several generations. This result is speculative as long term (>> decade) trends in humpback recruitment and mortality are not available. Ratio values smaller than 1 were obtained at all other spatio-temporal scales, indicating the dominance of mortality over recruitment. At the spatial scale of a feeding ground or smaller, birth rates of 7.9% $year^{-1}$ (Clapham and Mayo, 1987a, 1990) combined with an average mass of 2 t for neonates (Winn and Reichley, 1985) result in changes in biomass due to recruitment on the order of 0.720%

year^{-1}. This value is exceeded by net mortality rates of 4.96% year^{-1} resulting from natural (4.9% year^{-1}; Buckland, 1990) and entrapment (0.065% year^{-1}; Volgenau, 1991) mortalities combined. Calf production on Silver Bank (median 7.85% year^{-1}; Whitehead, 1982), a measure of birth rate at the scale of the entire northwest Atlantic, results in rates of change due to recruitment similar to those obtained at the scale of a feeding area (0.725% year^{-1}), whereas the combined entrapment mortality for the northwest Atlantic is on the order of 0.35% year^{-1} (Volgenau, 1991). Assuming that survival rates based on mark-recapture of individuals within a feeding ground are representative of the northwest Atlantic humpback population, ratio values <1 are also obtained at the scale of migration routes.

The main feature of the rate diagram of the kinematics ratio (Figure 3.1d) is the dominance of active movement at spatial scales of a bay to migration route over time periods of residence in these areas. Humpback populations remain within an area of a bay (ca. 56 km) for approximately one month (Whitehead *et al.*, 1980), whereas length of stay in the feeding grounds (ca. 700 km; Mate, 1983) is of approximately 5 months (cf. Clapham *et al.*, 1993). On an annual basis and spatial scale of migration route (ca. 2 000 km), the vast majority of the northwest Atlantic population completes a migratory cycle between breeding and feeding grounds. At these spatio-temporal scales, changes in humpback biomass concentration due to locomotory behaviour greatly exceed those due to passive drift. Average current speeds of 0.1m s^{-1} or 1 296 km per 5 months for the inshore branch of the Labrador Current (Helbig *et al.*, 1992) result in changes due to drift

equal to (129.6 km/700 km)/5 months, or 18.51% per 5 months at scales of a feeding area or less. In contrast, changes in humpback whale biomass concentration due to active movement correspond to (700 km/700 km)/ 5 months, or 100% per 5 months, and ratio values are much greater than 1. Over periods of less than a year, average humpback migratory speeds of 2.78 km h^{-1} (Clapham and Mattila, 1988) exceed passive drift associated with the Gulf Stream (average surface speed of 1.5 m s^{-1}; Pickard and Emery, 1982), and ratio values are also much greater than 1.

3.4 Discussion

The importance of locomotory behaviour on the distribution of humpback whale biomass is implicit in most studies that have examined their distributional patterns and movements. Results presented in this paper confirm this expectation through a quantitative evaluation of the relative importance of various physical and biological processes that potentially influence the distribution of northwest Atlantic humpback whale biomass across a range of spatio-temporal scales. Changes in humpback biomass concentration due to demographics and kinematics exceeded those due to growth across all spatio-temporal scales (Figure 3.1a). Changes in humpback biomass distribution resulting from changes due to demographics (births, deaths) were exceeded by those due to kinematics (active and passive movement) at the scale of a bay to migration route and time scales of residence in these areas (Figure 3.1b). At these spatio-temporal scales,

kinematic ratio values greater than 1 (Figure 3.1d) indicate that changes in humpback concentration due to active movement exceeded those due to passive drift with the fluid.

A review of the northwest Atlantic humpback literature indicates that little data on growth and age structure of the population, calf survival and recruitment are available. In addition, in many cases it is not clear the range of scales over which conclusions can be generalized. For example, the only available estimate of survival rates for northwest Atlantic humpback whales is based on resightings of photographically identified individuals from the Gulf of Maine (Buckland, 1990). It is not known whether this estimate is representative of the northwest Atlantic population or other feeding aggregations.

Lack of data on northwest Atlantic humpbacks could potentially bias the results presented in this paper. One potential source of bias is the assumed population age structure used to estimate humpback growth rates. Baleen whales show a characteristic phase of rapid growth during the first two years of life (Lockyer, 1981), and average growth rates may vary substantially as a function of the proportion of young animals in the population. It is difficult to evaluate potential effects of this assumption given the lack of data on the age structure of the northwest Atlantic humpback population.

A second potential source of bias in growth estimates is the use of length at age from a sample of female humpbacks (Todd *et al.*, unp. manuscript). If humpback growth rates are similar to those of other balaenopterid whales, where females grow slightly faster than males (e.g. Lockyer, 1981), values used in this study potentially overestimate

growth rates for the northwest Atlantic humpback population. However, this potential overestimate does not alter the general results as population dynamics dominated over somatic growth across all scales even when using possibly inflated values (Figure 3.1a).

Another potential source of bias is the use of crude birth rates in place of recruitment. Not all individuals born in a given year survive until the age of attainment of sexual maturity (e.g. Clapham and Mayo, 1987a). Hence the use of crude birth rates likely represents an overestimate of the actual number of individuals entering the breeding population. Nonetheless, rate diagrams remain unaltered even if calf survival is low. Monitoring calf survival in the breeding grounds, combined with continuous monitoring after migration to feeding areas, are necessary before any reliable estimates of recruitment can be attempted.

An interesting by-product emerging from a review of the literature on northwest Atlantic humpbacks is a comparison of current population growth estimates based on mark-recapture techniques with those based on biological parameters. Population growth rates can be expressed as (Ricklefs, 1990):

$$N_t = N_{t=0} \bullet e^{rt} \qquad (3.6)$$

where N_t = population size after a given time = t;

$N_{t=0}$ = initial population size;

r = intrinsic rate of increase; and

t = time.

Since the intrinsic rate of increase corresponds to the proportional change in population size after a given time = t, then:

$$r = \ln\left(\frac{N_t}{N_{t=0}}\right) \bullet t^{-1} \qquad (3.7)$$

If t = 1 year, the number of individuals in the population after 1 year (N_t) will correspond to the number of individuals at an initial time t = 0 ($N_{t=0}$) plus the proportional net number of individuals entering the population in any given year, or:

$$N_t = N_{t=0} + (\text{number of births - number of deaths}) \qquad (3.8)$$

If $N_{t=0}$ = 5 505 (Katona and Beard, 1990), and current annual estimates of crude birth rates (median 7.85% year^{-1}: Whitehead, 1982: 7.9% year^{-1}; Clapham and Mayo, 1990), natural (4.9% year^{-1}; Buckland, 1990) and entrapment mortality (0.35% year^{-1}; Volgenau, 1991) for the northwest Atlantic humpback population are applied to Eq. 3.8, $N_t \cong$ 5 651 individuals. Using these values of $N_{t=0}$ and N_t in Eq. 3.7 result in annual population growth rates of 2.6% year^{-1}. This value is somewhat comparable to rates of increase obtained for south Pacific humpbacks (4.6% year^{-1}; Chittleborough, 1965), but is considerably lower than the most recent estimate obtained for the western north Atlantic population using mark-recapture techniques (9.4% year^{-1}; Katona and Beard, 1990). One possible explanation for the higher rate of increase obtained using mark-recapture methods is increased efficiency in sampling (Hammond, 1990). Increased sampling effort and area coverage over time may result in a large number of previously non-identified

individuals being sampled from the population. Since this large number of "new" individuals is a reflection of increased effort, it will likely exceed the actual number of animals being recruited into the population. If mark-recapture models based on this increasing number of "new" individuals are used to estimate population size, such estimates will correspondingly exhibit a large rate of increase over time -- reflecting increased sampling effort rather than intrinsic rates of increase. It has been suggested that this increase in effort and area coverage will eventually minimize heterogeneity of capture (Hammond, 1990). At the present time, however, estimates of recruitment and survival based on long-term monitoring of individually photo-identified whales (e.g. Clapham and Mayo, 1987a; 1990) may provide a more reliable method for the estimate of population parameters.

A second possible explanation for the observed discrepancy in population growth estimates is that such estimates reflect the low precision of the techniques used. Confidence intervals for population growth estimates based on mark-recapture methods are very broad (cf. Katona and Beard, 1990), encompassing population growth rates of 2.6% $year^{-1}$ reported in this paper. Hence it may be argued that population growth rates based on mark-recapture methods do not truly differ from those based on biological parameters. If this is the case, the broad range of values obtained when using different techniques illustrates the need for a more careful interpretation and application of population growth estimates for both conservation and management.

Dimensionless ratios are not predictors of distributional patterns resulting from physical or biological processes. They are a tool that can be used to summarize current knowledge of spatial and temporal dynamics of population biomass, facilitating a critical evaluation of current knowledge and the identification of research areas where data are lacking. In addition, dimensionless ratios can be used in the identification of processes potentially influencing distributional patterns and appropriate sampling scales for future studies (cf. Hatcher *et al.*, 1987). In the case of northwest Atlantic humpback whales, their own locomotory behaviour dominates over all other processes across the range of spatio-temporal scales typically encompassed by field studies (e.g. bays to migration route, weeks to decade). In comparison, rates of change in biomass resulting from somatic growth and demographics are small. These findings suggest that the relative importance of somatic growth and demographic processes may only be apparent across very large temporal scales encompassing the life-span of these organisms.

Chapter 4. Humpback whale aggregative response to prey availability

4.1 Introduction

It is widely recognized that humpback whale distribution and movements within their feeding grounds are directly coupled to the availability of their preferred prey. Studies demonstrating an association between whales and prey are numerous, and encompass spatial resolutions ranging from that of a bay (tens of km; e.g. Whitehead *et al.*, 1980; Bredin, 1985; Piatt *et al.*, 1989) to oceanic regions (thousands of km; e.g. Nemoto, 1959). However, explicit comparisons of patterns across scales have not been attempted, and it is still not clear whether the degree of association between whales and prey depends on spatial scale.

Scale-dependent predator-prey interactions have been documented for a variety of aquatic organisms (e.g. Schneider and Piatt, 1986; Weber *et al.*, 1986; Schneider, 1989; Rose and Leggett, 1990). These findings reiterate the importance of the choice of measurement scale in the design of research studies. Examinations of the degree of association between predators and their prey as a function of scale may also serve to clarify mechanisms underlying observed patterns. For example, Horne and Schneider (1994b) failed to detect an association between cod (*Gadus morhua*) and capelin across a range of spatial scales. An investigation of the foraging energetics of the predator (cod) demonstrated that their bioenergetic characteristics were likely the most importance factor determining cod-capelin spatial distributions (Horne and Schneider, 1994b).

In this Chapter, the degree of association between humpback whales and prey, primarily capelin (cf. Chapter 2; Piatt *et al.*, 1989), is evaluated as a function of spatial and temporal scale. Whale counts and fish scores obtained during transects conducted in Placentia Bay, Newfoundland, are used to calculate correlation coefficients between whales and prey at spatial resolutions ranging from 2.5 km to 40 km. The degree of association between whales and prey was expected to be low at small spatial scales given the high mobility of humpback whales. As spatial resolution increases, sampling effort within a given spatial scale will also increase. Hence it was hypothesized that the strength of association between whales and prey would increase as a function of spatial resolution.

4.2 Methods

The dataset used in this study is the same as that described in Chapter 2. However, due to methodological differences between 1993 and 1994 surveys, and a greater area coverage per day of effort during the latter (cf. Figure 2.1), only data from 1994 transects were included in the analyses. A total of 13 transects of varying lengths were examined (Table 4.1).

As the vessel's speed varied within and between transects, the distance between transect legs and duration of each leg were used to estimate speed. Time spent conducting behavioural observations were not included in computations. Transects were then divided into 2.5 km bins based on the estimated speed of the vessel during each leg. Prey scores (presence or absence) were assigned to each bin. Sighting angle (θ) and distance from the

Table 4.1 - Date, vessel, start time, end time and length of transects conducted in Placentia Bay, 1994. Time is in Newfoundland Standard Time (GMT minus 2.5 h).

Date	Vessel	Start Time	End Time	Length (km)
June 13	open boat	12:30	18:28	47.5
June 15†	open boat	8:17	10:03	30
June 16†	open boat	7:27	14:23	87.5
June 18†	open boat	7:19	9:15	30
June 19	open boat	10:00	14:58	50
June 20†	open boat	7:47	11:28	20
June 21	open boat	8:42	16:01	102.5
June 24†	open boat	8:25	14:49	77.5
June 28†	open boat	7:56	13:10	82.5
July 09	longliner	6:21	14:49	105
July 12	longliner	7:52	17:07	80
July 17†	longliner	7:10	13:17	85
July 21†	longliner	6:59	13:08	82.5

Note: † indicates transects not included in the analyses due to a low number (≤ 1) of 2.5 km bins containing sightings.

vessel (r) were used to estimate perpendicular (x) and parallel (z) distances of sightings from the transect line (Buckland *et al.*, 1993):

$$x = r \bullet \sin(\theta) \qquad (4.1)$$

$$z = r \bullet \cos(\theta). \qquad (4.2)$$

Values of z were used to determine the bin to which each sighting was assigned. Humpback sightings for which $x > 2$ km were not included in the analyses. Whale counts and prey scores (presence or absence) at the minimum measurement distance (= bin size) of 2.5 km were further combined into measurement distances of up to half of a transect's length, or a maximum of 40 km. Eight transects (15-16, 18, 20, 24, 28 June; 17, 21 July) with a low (≤ 1) number of bins containing sightings were not included in the analyses.

Pearson's product-moment correlation (Sokal and Rohlf, 1981) was used to measure the degree of association between humpbacks and prey. Correlation coefficients (r) between whales and prey were computed for each measurement distance, and Monte Carlo randomization methods (Crowley, 1992) used to test for significance. A SAS routine (SAS, Inc., Cary, NC, USA) was used to randomly reassign whale counts to measurement bins and compute values of r based on the randomized counts. 1 000 randomizations were carried out for each measurement distance within each transect. Due to the small sample size, it was not possible to test all coefficients at larger measurement distances. The observed correlation coefficients were considered significant if they exceeded 950 out of 1 000 values of r obtained through randomization (i.e. a

p-value < 0.05). To investigate the scale-dependency of the association between whales and prey, the difference between the maximum and minimum significant correlation coefficients was computed for each transect and compared with 1 000 values obtained through randomization. A significant difference ($p < 0.05$) between coefficients obtained at different measurement distances would indicate scale-dependency.

4.3 Results

Capelin was the most common prey in Placentia Bay, being observed in the study area during 6 out of 13 transects (21, 28 June; 9, 12, 17, 21 July). Identification of prey as capelin was most commonly based on direct visual identification during observations of feeding whales and seabirds. Large patches of euphausiids and schools of mackerel were also seen on two days each (18-19 June and 19-20 June, respectively). On three days (15-16, 24 June) no prey was detected in the echosounder. Humpback whales were observed feeding on all three prey species seen in the study area.

The total number of humpback whales sighted varied between transects (Table 4.2). Humpback counts were higher in June than in July, indicating an apparent decrease in abundance over time.

Whales were significantly associated with prey at the minimum measurement distance of 2.5 km in 3 out of the 5 transects analysed (Figure 4.1). In these transects, presence of prey explained over 50% of the variation in whale counts (Figure 4.2). Measurement distances of maximum significant correlation values differed between

Table 4.2 - Humpback whale counts obtained during transects conducted in Placentia Bay, 1994. Whale counts include sightings within 2 km of the transect line only.

Date	Number of 2.5 km bins containing sightings	Number of whales
June 13	5	10
June 15†	1	2
June 16†	1	9
June 18†	1	1
June 19	4	13
June 20†	1	4
June 21	2	6
June 24†	0	0
June 28†	0	0
July 09	2	10
July 12	2	5
July 17†	0	0
July 21†	0	0

Note: † indicates transects not included in the analyses due to a low number of bins (≤ 1) containing sightings.

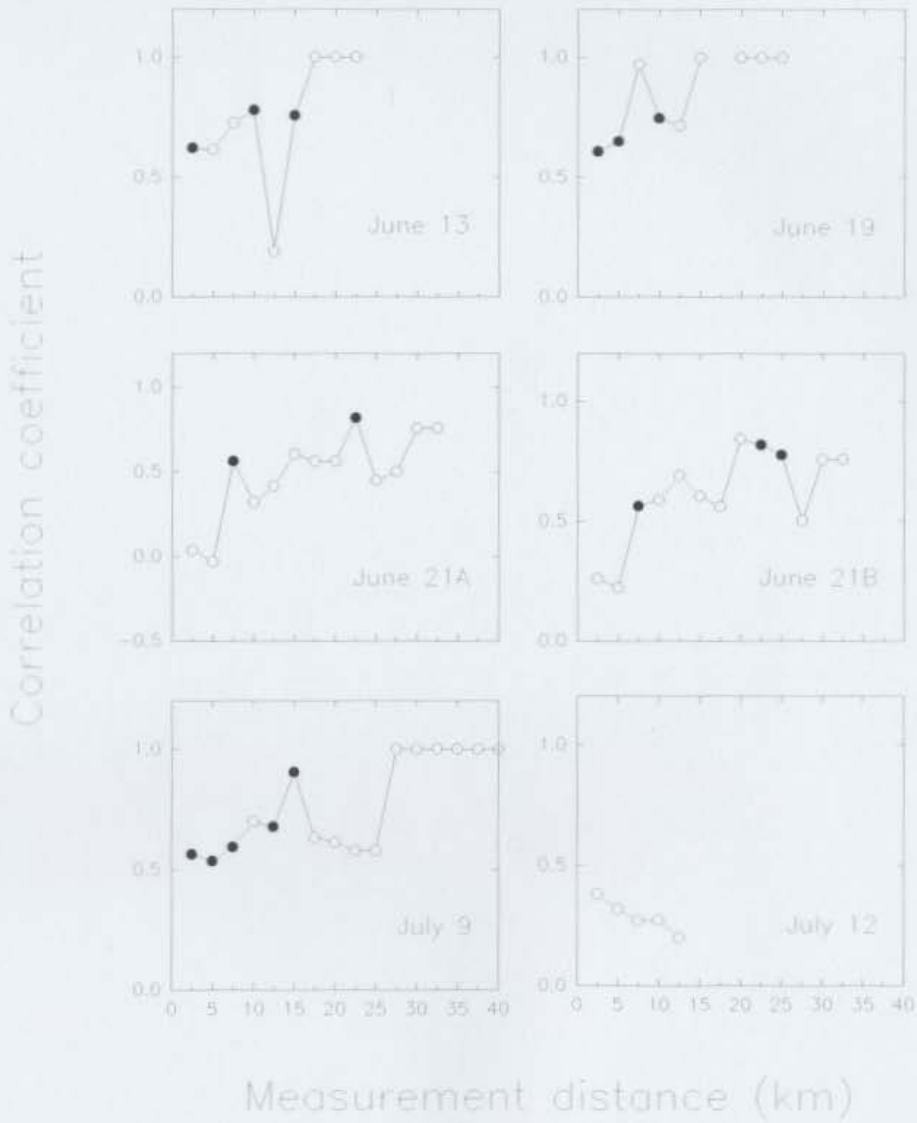


Figure 4.1: Pearson's product-moment correlation coefficient between humpback whales and prey as a function of measurement distance. Solid circles indicate p-values < 0.05; clear circles indicate p-values ≥ 0.05 or coefficients not tested for significance. Transect dates followed by "A" indicate prey scores based on echosounder observations from the trackline only; "B" indicates prey scores based on echosounder observations obtained while off transect (i.e. during behavioural observations).

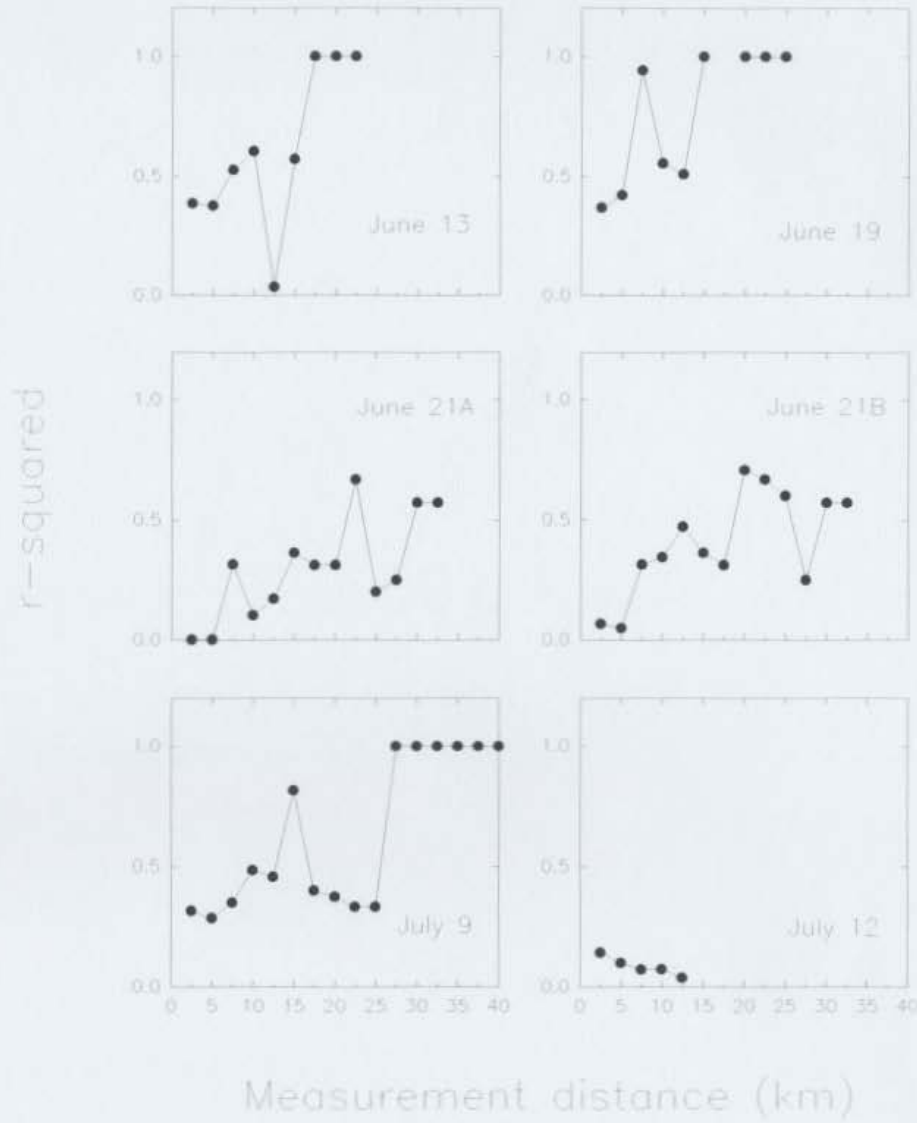


Figure 4.2: r-squared values based on coefficients of association between humpback whales and prey, plotted as a function of measurement distance. Transect dates followed by "A" indicate prey scores based on echosounder observations from the trackline only; "B" indicates prey scores based on echosounder observations obtained while off transect (i.e. during behavioural observations).

transects, ranging from 10-22.5 km. Only in one transect (12 July) no significant correlations were observed.

Although correlations between whales and prey generally increased as a function of measurement distance (Figure 4.1), differences between maximum and minimum correlations were not significant in any of the transects analysed. Comparable results were obtained when coefficients based on prey scores from the transect line only (Figure 4.1A) and those based on echosounder observations obtained while off-transect (Figure 4.1B) were tested (see below).

Due to the relatively narrow beam angle of the echosounders used, the effective prey sampling width was much smaller than the potential maximum whale sighting distance in relation to the transect line. At a depth of 50 m, for example, beam angles of 40° and 28° result in a maximum prey sampling width of 25 and 12.5 m directly underneath the vessel, respectively. In contrast, humpback sightings up to 2 km from the transect line were recorded. This mismatch in prey and whale sampling resolution could potentially underestimate the degree of association between whales and prey. If, for example, a whale was sighted at a distance of 1 km from the trackline during any given 2.5 km bin, but prey was not detected in the echosounder, a prey score of zero (prey absent) would be assigned to that bin. A low correlation between whales and prey would then be obtained, even though prey could be present in the immediate vicinity of the sighting but was not detected by the echosounder.

Transects during which the vessel approached whale sightings to conduct behavioural observations were used to investigate the potential effects of the difference in prey and whale sampling widths. Correlation coefficients based on prey scores obtained during transects only were compared to those based on prey scores obtained in the immediate vicinity of a sighting. Of the five transects (13, 19-21 June; 12 July) during which at least one 2.5 km bin contained a sighting and behavioural observations were also conducted, only in one (21 June) was prey detected in the vicinity of a sighting but not on the transect line. During this transect, correlation coefficients based on prey scores obtained in the vicinity of sightings were generally greater across most measurement distances than those based on prey scores from the transect line only (Figures 4.1, 4.2). This finding suggests that the degree of association between whales and prey could have potentially been underestimated in other transects that were not evaluated. Overall, however, the detection of prey on the transect line appeared to be a good indicator of the occurrence of prey within 2 km from the trackline.

A relatively high number of 2.5 km bins contained no whale sightings, reflecting their patchy distribution. Due to this high number of zeros, it was assumed that variability in the time spent on each bin (= effort) would not affect correlation coefficients between whales and prey as a large number of zeros would still be obtained if whales counts within each bin were standardized by effort. To ensure that this was the case, Pearson's product-moment correlation coefficients were recalculated using whale counts standardized by effort (i.e. searching time within a given bin). These values were then

compared to the original coefficients used in the analyses. A GLM Proc (SAS, Inc.) was used to test for differences between original and standardized coefficients, controlling for measurement bins within each transect. Due to the non-normality of the residuals, a randomization test (1 000 iterations) was used to calculate p-values. No significant differences between original and standardized coefficients were obtained (n=104, p = 0.373). Hence variability in effort within each bin did not affect estimates of the degree of association between whales and prey.

4.4 Discussion

Analyses of humpback whale counts and the occurrence of prey on repeated transects conducted off Placentia Bay indicate that whales were significantly associated with prey at small spatial resolutions. Significant coefficients of association between whales and prey at the minimum measurement distance of 2.5 km were observed in three out of five transects (Figure 4.1). In one other transect (21 June) a significant correlation was obtained at a measurement distance of 7.5 km. However, the degree of association between whales and prey did not significantly increase as a function of measurement distance.

Significant associations between whales and prey at small (2.5 km) spatial resolutions were somewhat surprising. Behavioural observations conducted in Placentia Bay indicated that not all whales were feeding when sighted, suggesting that continuous feeding does not account for the observed association between whales and prey at small

spatial scales. Low correlations between seabirds and fish at small spatial resolutions have been suggested to result from seabirds drifting away from fish schools while sitting on the water in between foraging bouts (Schneider, 1994c). Observations of humpback whales during a resting period immediately after a feeding bout indicate that they move or drift away from fish schools during short time intervals, but remain in the vicinity of prey throughout most of the time spent resting (Bredin, 1985). These findings suggest the possibility that humpback whales are continuously tracking their prey over small spatial scales.

The absence of a significant increase in the degree of association between whales and prey as a function of measurement distance is consistent with evidence from previous studies relating whale distribution to the availability of prey. For example, Piatt *et al.* (1989) reported that capelin abundance explained 63% of the variance in whale abundance at a coastal area (ca. 10-20 km) off Newfoundland. Significant correlations between humpback whales and capelin on the order of 0.8 were also observed during transects ca. 56 km in length (Whitehead *et al.*, 1980). Thus unlike less mobile marine vertebrates (e.g. Piatt, 1990), humpback whales are associated with their prey over a wide range of spatial scales.

Measurement distances of maximum significant correlation between whales and prey were variable between transects, ranging from 10-22.5 km. Variable scales of maximum association have also been documented for seabirds foraging on capelin (Piatt, 1990) and cod feeding on capelin (Rose and Leggett, 1990). However, as it was not

possible to test coefficients at larger spatial scales, and given that associations between whales and prey at scales of tens of km have been reported (e.g. Piatt *et al.*, 1989; Whitehead *et al.*, 1980), it is likely that stronger correlations will be detected at larger spatial scales.

Weak correlations obtained in other studies of predator-prey interactions has led to the suggestion that aggregations of predators in response to concentrations of prey may only be observed over a limited range of scales (Horne and Schneider, 1994b). However, significant correlations between whales and prey reported in this study span spatial scales over almost an order of magnitude (2.5-22.5 km), and are also likely to be observed at greater spatial resolutions. It might be speculated that the large range of scales over which whales were significantly associated with prey reflects high energetic requirements resulting from a prolonged period during which they fast or reduce feeding. Humpback whales undergo annual migrations between feeding regions at higher latitudes and breeding grounds in warm, tropical waters. They are generally thought to fast (Winn and Reichley, 1985) or feed very little while on the breeding grounds. Lockyer (1981) estimated that Antarctic humpback whales returning from their breeding grounds double their weight during the feeding season. As daily activity budgets and feeding rates of northwest Atlantic humpback whales are not available, the suggestion that metabolic requirements influence their aggregative response remains to be verified.

This study has shown that humpback whales were significantly associated with prey across a range of spatial scales (2.5-22.5 km), but the strength of this association did

In this equation, D_a corresponds to the air density relative to that of the water (0.001), and C_{10} is the drag coefficient (0.002) estimated for the Avalon Channel (Csanady, 1982).

Computations of the critical wind impulse necessary to raise the pycnocline to the surface were carried out by Schneider and Methven (1988) and Schneider (1994a). Since the thermocline coincides with the pycnocline during the summer, the critical wind impulse is also related to changes in water temperature conditions and movement of the thermocline.

5.3 Results

Average water temperatures of the upper 10 m generally reflected the seasonal warming trend of the upper layer (Figure 5.1). As not all oceanographic stations were sampled over continuous and/or overlapping periods of time, it was not possible to investigate the coherence in daily fluctuations in temperature between all stations. However, stations 1 and 2 (cf. Figure 2.1) were continuosly sampled between 15-16 and 18-21 June. An examination of average water temperatures in the upper 10 m obtained at these stations indicated a slight decrease in temperatures on 20 June (Figure 5.2). This event also appeared to be detected at other stations located within 5 km from shore (stations 6 and 10; Figure 5.2). Temperature and density (sigma-*t*) profiles obtained on 19-20 June at station 2 show that both thermocline and pycnocline rose during this period (Figure 5.3).

Chapter 5. Humpback whale aggregative response to localized upwelling

5.1 Introduction

Previous studies relating humpback whale distribution to oceanographic features have commonly described surface isotherms and water mass structures typical of areas in which these whales are found (e.g. Nasu, 1963; Dawbin, 1966; Whitehead and Moore, 1982), identified associations between the presence of whales and the seasonal warming trend of surface waters (e.g. Whitehead, 1981), or failed to detected any relationships (e.g. Piatt *et al.*, 1989). Observed associations between whales and oceanographic conditions within their feeding grounds are generally explained in terms of the effects of such features on the distribution of the various prey species (e.g. Volkov and Moroz, 1977). Any direct influence of water temperatures on whales is unlikely given the vast range of temperature gradients found throughout their distributional range (e.g. Dawbin, 1966), and the variability in size/blubber thickness among species that are found within a similar range of water temperature conditions (e.g. Whitehead, 1981).

Humpback whales feed primarily on capelin during their stay on Newfoundland's feeding grounds, but various other prey items such as euphausiids (Mitchell, 1975), mackerel, sand lance, haddock (*Melanogrammus aeglefinus*) and squid (*Illex illecebrosus*; Bredin, 1985) may also be taken. Off eastern Newfoundland, coastal distribution and movements of capelin have been related to the occurrence of wind-induced upwelling events (Schneider and Piatt, 1986; Schneider and Methven, 1988;

Schneider, 1989), although such relation may only be detected during extreme events (Schneider, 1994a). These findings led Piatt *et al.* (1989) to suggest that episodic oceanographic events influencing prey distribution may also indirectly influence baleen whale distribution and movements. The observed association between humpback whales and prey across relatively small (2.5-7.5 km) spatial scales (Chapter 4) corroborates this idea, and further suggests that whale aggregative responses to coastal oceanographic events may be detected at small spatial scales.

In this chapter the relative abundance of humpback whales in Placentia Bay is investigated in relation to oceanographic conditions. Water temperature profiles obtained in Placentia Bay during 1994 are used to examine the occurrence of coastal upwelling, and compared with observations of whale abundance and prey availability.

5.2 Methods

Humpback whale daily relative abundance, observations of prey and water temperature profiles obtained as described in Chapter 2 were used in the analyses; only data from 1994 were included.

So as to obtain continuous temperature and density profiles of the water column, temperature readings obtained at sampling speeds of less than 0.25 m s^{-1} were deleted. A two-bin running average was performed to smooth the profiles and to minimize variability in contiguous readings; only the downcasts were used. A SAS routine (SAS,

Inc.) was used to calculate average water temperatures of the upper 10 m for each cast. The depth (m) of the 5 °C isotherm for each cast was tabulated.

Hourly measurements of wind speed and direction for the months of June and July were obtained from the Argentia climatological station (Atmospheric Environment Service, Environment Canada, St. John's, Newfoundland), located approximately half-way along the eastern shore of Placentia Bay (cf. Figure 2.1). These measurements were used to calculate the along-shore (W_y) and cross-shore (W_x) wind components:

$$W_y = - W \bullet \cos (A - 20) \qquad (5.1)$$

$$W_x = - W \bullet \sin (A - 20) \qquad (5.2)$$

where W = wind speed (km h^{-1}); and

A = wind direction (true degrees).

As the orientation of the coastline runs at an angle of approximately 20° from true North, this value was subtracted from the recorded wind direction. Positive values of W_y are obtained in the northern direction parallel to the coastline; positive values of W_x correspond to the eastward direction.

The impulse (I) imparted on the water by the wind corresponds to (Schneider and Methven, 1988):

$$I = T \bullet u^2_t \qquad (5.3)$$

where T equals the time period of interest (s), and u^2_t is the friction velocity:

$$u^2_t = D_a \bullet C_{10} \bullet W_t \bullet W. \qquad (5.4)$$

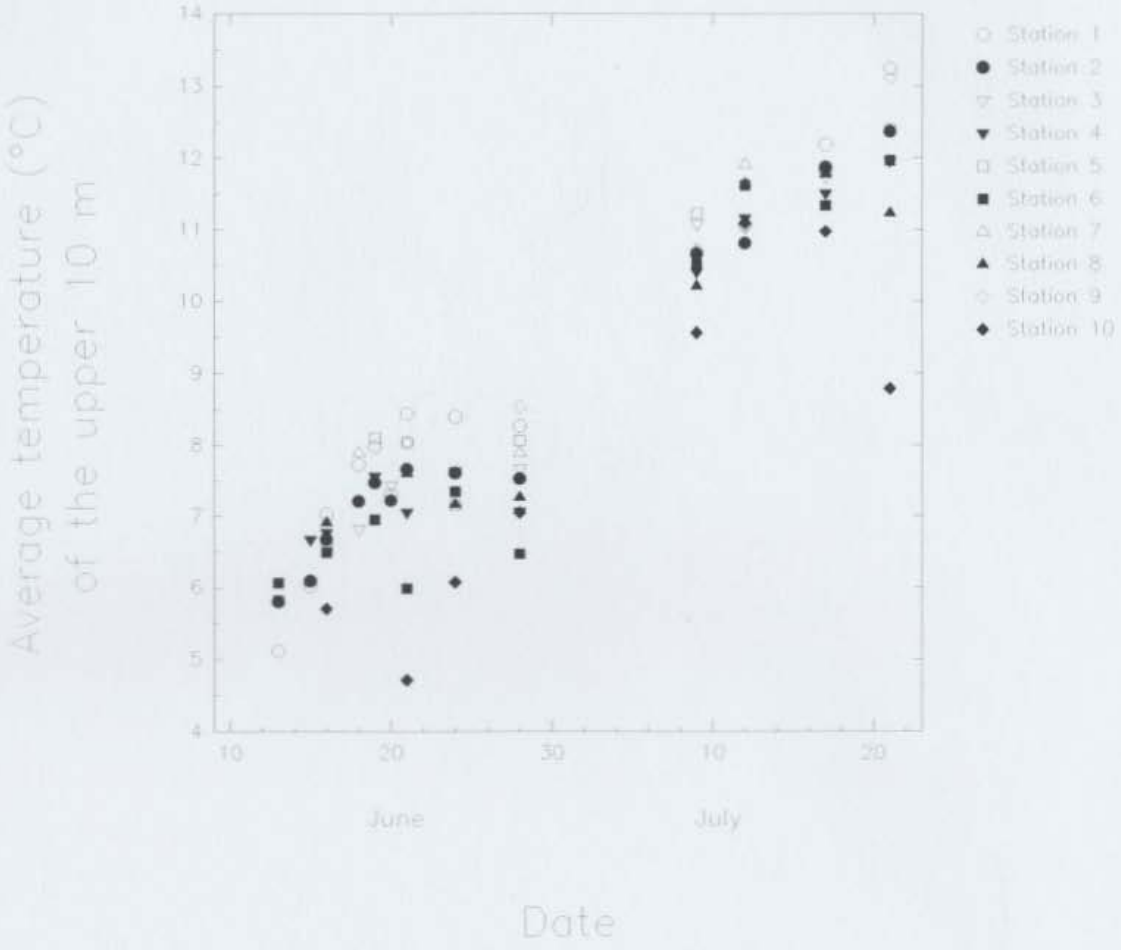


Figure 5.1: Average water temperatures of the upper 10 m obtained at oceanographic stations in Placentia Bay (cf. Figure 2.1) between 13 June-21 July.

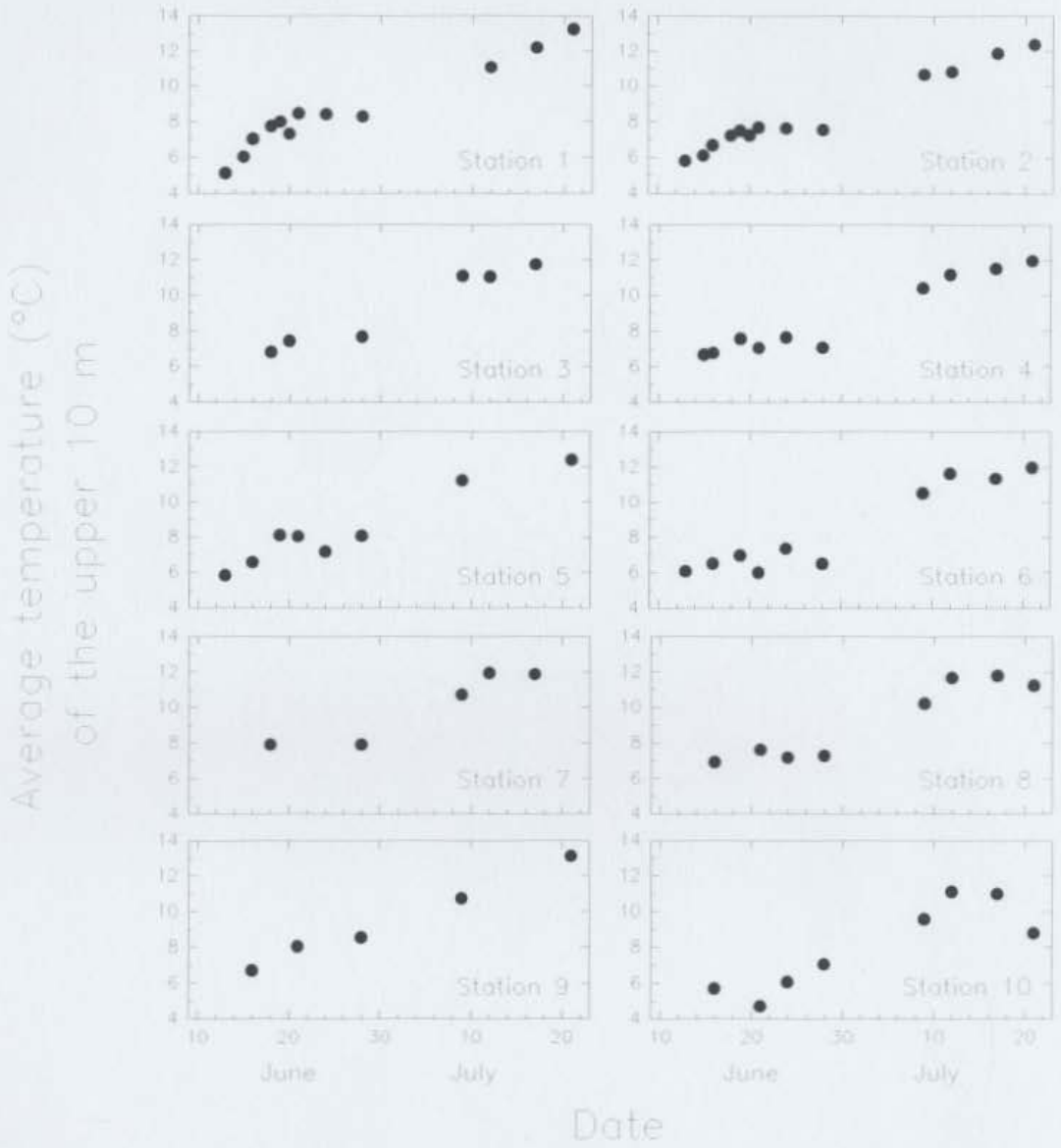


Figure 5.2: Average water temperatures of the upper 10 m obtained between 13 June-21 July at ten oceanographic stations located in Placentia Bay (cf. Figure 2.1).

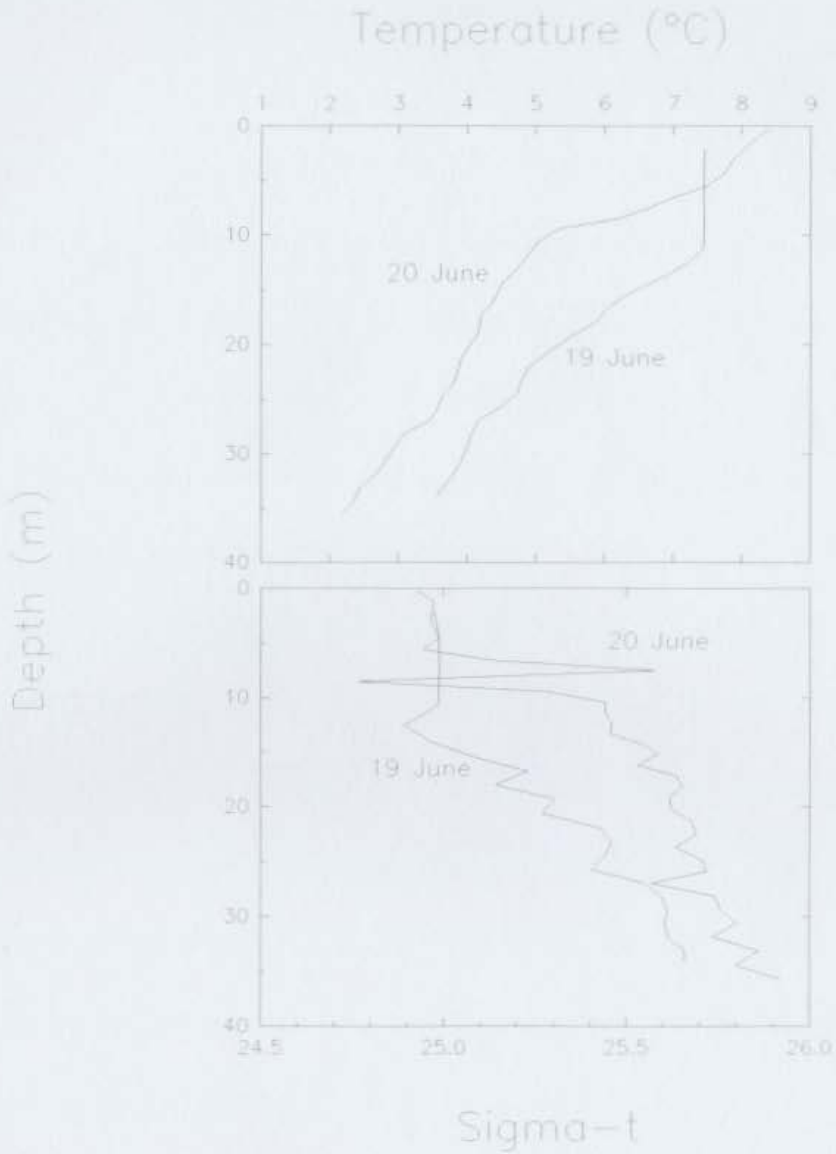


Figure 5.3: Water temperature and density (sigma-*t*) profiles obtained at station 2 (cf. Figure 2.1) on 19-20 June.

The depth of the 5 °C isotherm was variable between stations (Figure 5.4). Again, given that not all stations were sampled on a continuous basis, a comparison of changes in depth of the 5 °C isotherm between all stations was not possible. However, beginning on 18 June a gradual surfacing of the 5 °C isotherm was observed at stations 1 and 2 (Figure 5.5); a similar trend appears to occur at stations 6 and 10. By 20 June, the 5 °C isotherm had risen to about 10 m at stations 1-2. The observed drop in average temperatures of the upper 10 m, coupled with the surfacing of the 5 °C isotherm and the rising of the thermocline and pycnocline between 18-20 June, suggest that a localized upwelling event occurred during this period.

However, wind speeds throughout June and July never reached the thoretical critical value at which the thermocline could be raised to the surface (Figure 5.6). The maximum wind impulse during this period corresponded to 2.29 $m^2 s^{-1}$ obtained at a single 6 h interval. This value is lower than the critical value of 2.5 $m^2 s^{-1}$ required over a continuous period of 30 h so that a surfacing of the pycnocline could be observed (Schneider and Methven, 1988). Given the absence of any substantial wind events, the observed changes in oceanographic conditions during 18-20 June are not due to the direct effects of upwelling favourable winds.

One potential explanation for the localized upwelling observed on 20 June is that relaxation of downwelling favourable winds on 19-20 June generated internal waves. Downwelling favourable (southwest) winds prevailed throughout the week prior to 20

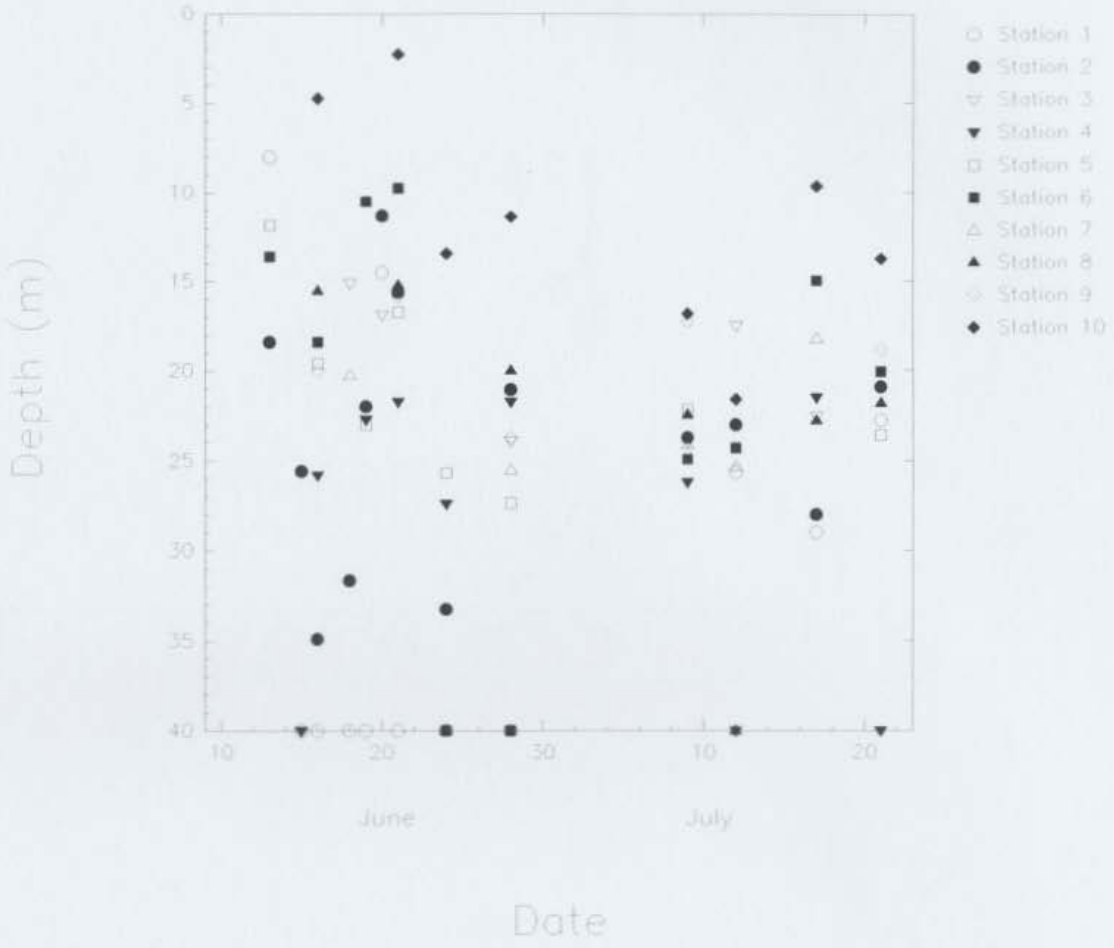


Figure 5.4: Depth of the 5 °C isotherm recorded at oceanographic stations in Placentia Bay between 13 June-21 July. Symbols placed at the maximum depth (40 m) indicate days for which water temperatures throughout the water column exceeded 5 °C.

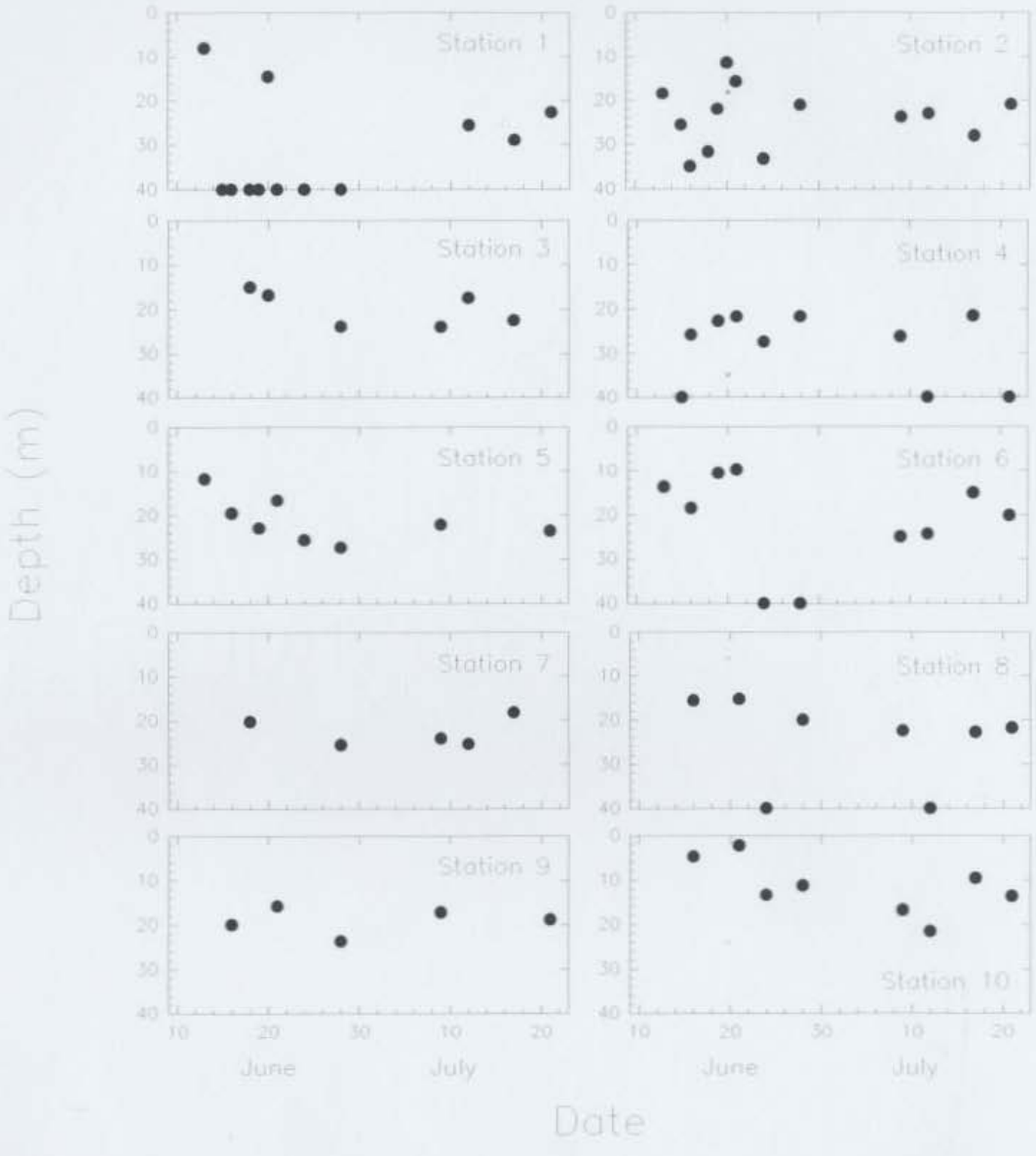


Figure 5.5: Depth of the 5 °C isotherm recorded between 13 June-21 July at ten oceanographic stations located in Placentia Bay (cf. Figure 2.1). Solid circles placed at the maximum depth (40 m) indicate days for which water temperatures throughout the water column exceeded 5 °C.

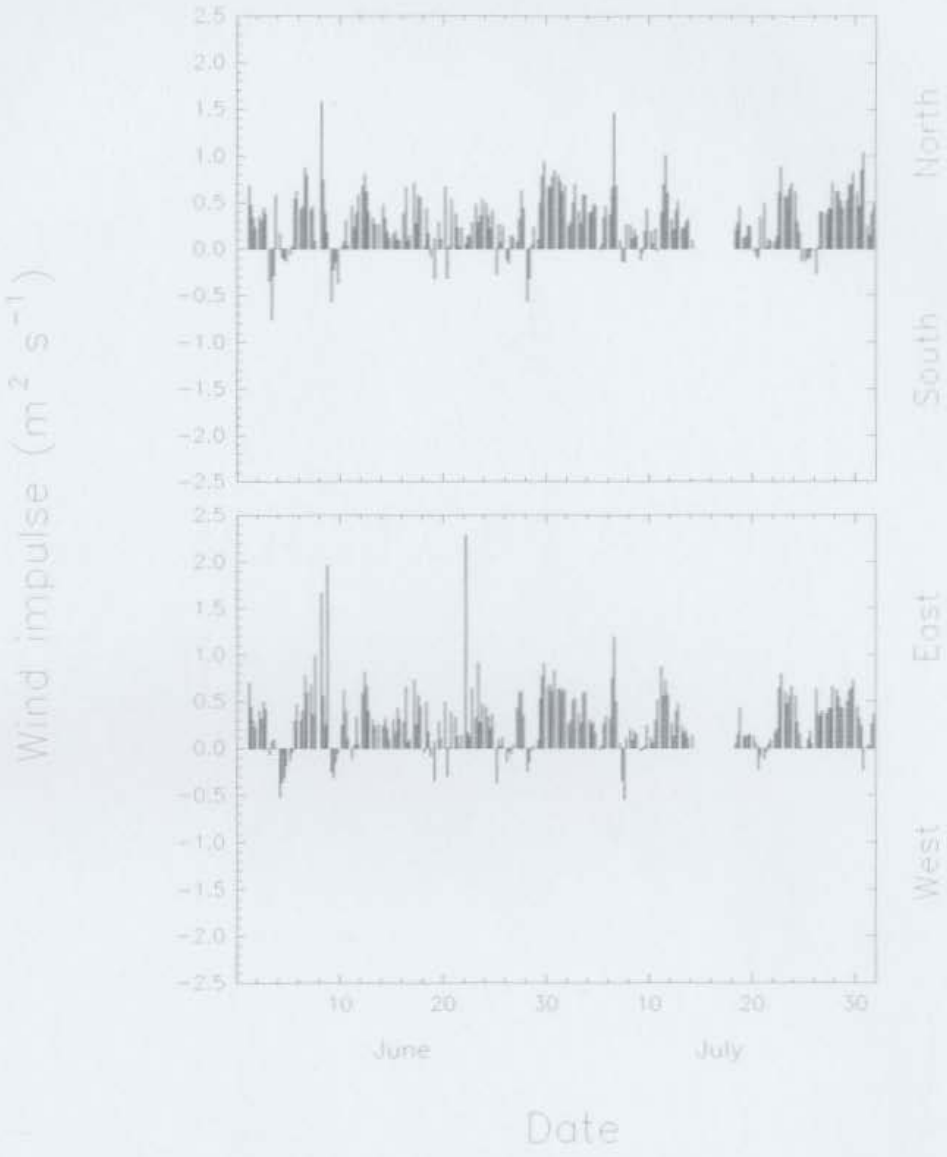


Figure 5.6: Cross- and long-shore wind impulse during June and July based on wind measurements obtained at the Argentia climatological station (Atmospheric Environment Service, Environment Canada, St. John's, Newfoundland).

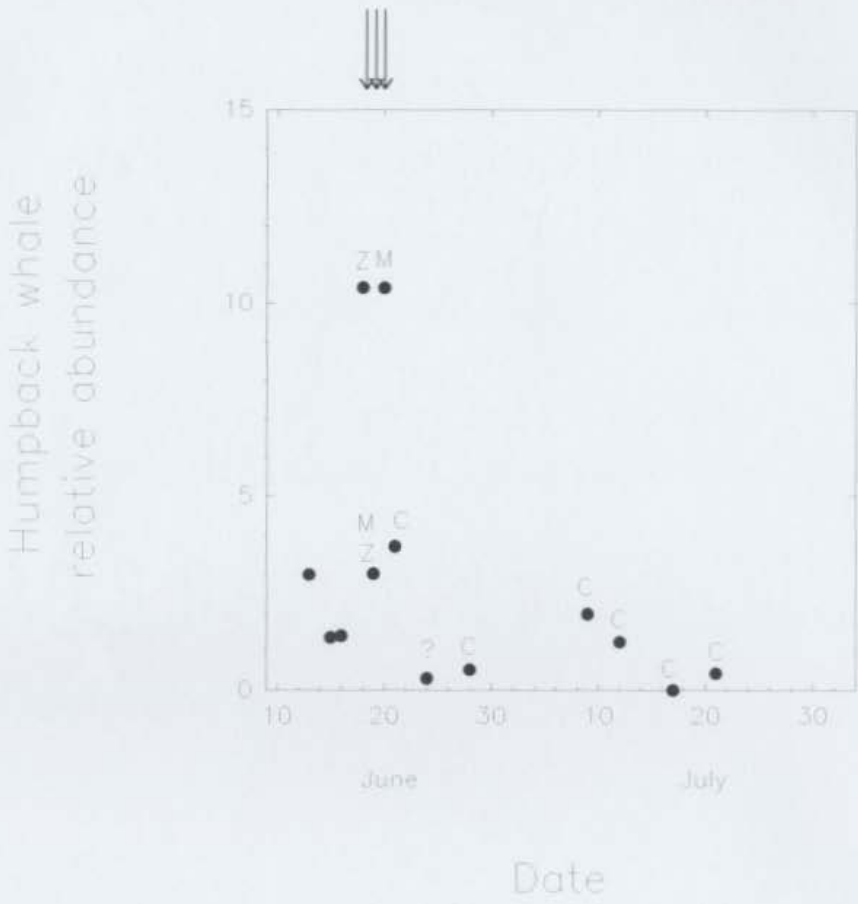


Figure 5.7: Humpback whale relative abundance (solid circles) and observations of prey recorded in Placentia Bay between 13 June-21 July. Z = zooplankton; M = mackerel; C = capelin; ? = unknown. The arrows indicate dates when localized upwelling was observed.

June, and relaxed on the 19-20th (Figure 5.6). As a result, it is posssible that internal waves were created, resulting in the displacement of the thermocline and pycnocline.

Prey was not observed in the study area prior to 18 June (Figure 5.7). On 18 June, large patches of euphausiids were observed; the following day both euphausiids and schools of mackerel were seen in the study area. On 20 June, only mackerel were seen. The presence of euphausiids and mackerel coincided with the onset of oceanographic changes. Capelin was not observed in the study area until this oceanographic event started to relax (21 June).

Humpback whales were sighted in Placentia Bay on every day of effort: only in one day (17 July) no whales were seen (Figure 5.7). Peak in humpback relative abundance coincided with changes in oceanographic conditions and the presence of zooplankton and mackerel.

5.4 Discussion

The observed drop in average water temperatures of the upper 10 m, coupled with the surfacing of the 5 °C isotherm recorded in Placentia Bay during 18-20 June, suggest that localized upwelling occurred during this period. The observed rising of both thermocline and pycnocline on 19-20 June also suggests that changes in water temperature were due to the occurrence of localized coastal upwelling. Previous studies off the east coast of Newfoundland have documented cold water mass replacements within 6 km from the coast (Schneider, 1989; Schneider and Methven, 1988; Schneider,

1994a) which have been generally attributed to wind-induced upwelling. However, given the absence of upwelling favourable winds during the time period of this study, it is unlikely that the observed changes in oceanographic conditions in Placentia Bay resulted from wind-driven water transport. A variety of factors such as tidal processes, local forcing and internal waves (Schneider and Methven, 1988) can potentially generate small-scale variability in coastal oceanographic conditions, but more refined data collection would be necessary before any inferences could be made.

Irrespective of the mechanism(s) causing the observed changes in oceanographic conditions, observations of patches of euphausiids during 18-20 June suggest the possibility that such patches were concentrated during localized upwelling. Prasad and Haedrich (1993) report the beginning of the spring phytoplankton bloom off Newfoundland occurring in mid-April, and peaking in early May. By mid-summer (i.e. early June), euphausiid biomass has already been accumulated (Robinson *et al.*, 1993). Changes in the horizontal distribution of large zooplankton within a deep lacustrine system have been associated with episodic wind events (Jones *et al.*, 1995). While the influence of small-scale, episodic oceanographic events such as localized upwelling on the coastal distribution of marine zooplankton patches has not been explicitly tested, it is possible that a similar pattern to that observed in lacustrine systems may also be observed in coastal marine environments.

Observations of schools of mackerel concurrently with the occurrence of patches of euphausiids agree with knowledge about their feeding habits. Although mackerel may

feed on a variety of prey species, zooplankton comprises the main item in their diet (Scott and Scott, 1988; C. Hood, Whale Research Group, Memorial University of Newfoundland, St. John's, Newfoundland, pers. communication). Whether the overlap in occurrence of schools of mackerel and patches of euphausiids represents a direct response by the former to aggregations of the latter cannot be ascertained.

Local changes in humpback whale abundance as a function of local changes in prey availability have been previously documented in Newfoundland waters (Bredin, 1985; Piatt *et al.*, 1989). Significant associations between humpbacks and prey obtained at small (2.5-7.5 km) spatial scales suggest that these whales are actively tracking prey (Chapter 4). It might be speculated that the coincidental peak in humpback whale relative abundance with a coastal upwelling event (Figure 5.7) potentially indicates an indirect response by the whales to the effects of oceanographic conditions on prey distribution. However, this suggestion is based on observations made during a single oceanographic event, and it is possible that the high abundance of humpbacks during this period simply reflects their timing of arrival (cf. Chapter 2). Additional experiments are necessary to confirm the hypothesis that humpback whales may respond to small-scale oceanographic events influencing prey distribution.

Chapter 6. Summary

Descriptions of baleen whale distributional patterns provide a starting point for the investigation of the potential influence of biological and physical processes on their distribution and movements. A better understanding of the mechanisms underlying observed patterns may be achieved by an incorporation of the idea that the detection of patterns depends on the scale of observation. This has been exemplified through a comparison of spatial and temporal patterns of humpback, finback and minke whale distribution in Placentia Bay, Newfoundland, with those obtained at differing scales. Results indicated that local patterns of humpback and finback abundance are unlikely to reflect large-scale, population trends; that their small-scale spatial distribution was highly variable; and that they differ with respect to their timing of abundance. These findings reiterate the idea that the effects of measurement scale on baleen whale distributional patterns should be taken into consideration when inferences about mechanisms generating such patterns are made.

A logical next step is the use of a quantitative framework to more explicitly evaluate the potential influence of well-established biological and physical processes on the distribution of baleen whales as a function of scale. Dimensionless ratios summarizing somatic growth, demographic and kinematic processes were used to compare the relative importance of these processes on the distribution of northwest Atlantic humpback whale biomass across a range of spatio-temporal scales. Humpback whale locomotory behaviour was expectably the dominant process across all scales

examined. Given the slow growth rates and long life-span of humpbacks, the potential influence of growth and demographic processes is speculated to be apparent only over large (>> decade) temporal scales.

Prey availability and distribution is generally recognized as the most important factor determining patterns of humpback whale distribution and movements within their feeding grounds. Explicit examinations of predator-prey spatial distributions as a function of scale may help clarify mechanisms determining the dynamics of such interactions. An examination of the degree of association between humpback whales and their prey as a function of scale showed that they were associated at relatively small spatial scales, but the strength of this association did not increase with measurement distance. From a behavioural perspective, these findings suggest the possibility that humpback whales are actively tracking prey, which is speculated to be a direct result of their high energetic requirements. With respect to the design of future studies, it is suggested that investigations of humpback whales in relation to prey availability and movements may be conducted at relatively small spatial scales, but repeated sampling may be necessary given the variability in the degree of association between whales and prey over different transects.

Given observed associations between humpback whales and their prey over small spatial scales, episodic oceanographic events known to influence prey distribution over relatively small scales could potentially be related to local patterns of whale abundance. The occurrence of an upwelling event was recorded in Placentia Bay, and observations of

prey availability and humpback whale relative abundance suggest a possible relationship between oceanographic changes and prey and whale distribution. However, additional experiments are necessary to confirm this observation.

Many more questions stem from the few answers provided in this study. The role of growth and demographic processes on the distribution of humpback whale biomass, and the spatio-temporal scales at which these processes operate, is one of them. A second question pertains to the influence of prey characteristics (e.g. behaviour and movements) on observed spatial patterns of humpback whale distribution. More especifically, how does the aggregative response of humpback whales to prey availability vary as a function of different prey species? It might be speculated that scales of association between whales and less mobile prey, such as sand lance, might differ from the ones observed in this study. An examination of this prediction could provide much insight into the foraging behaviour of humpback whales, and the specific mechanisms influencing such behaviour.

Perhaps some of the most interesting questions relate to a comparison of findings between species. Humpbacks, finbacks and minke whales differ in terms of their behaviour, mobility, and natural history attributes. Whether such differences are reflected in their distributional patterns, and in their relation with biological and physical variables, remains to be investigated.

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Appendix I. Oceanographic information

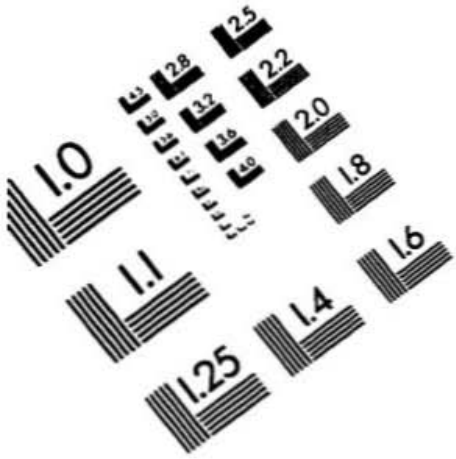
Oceanographic casts and information on whale sightings obtained in Placentia Bay, Newfoundland, during the summers of 1993 and 1994 are available from the Centre for Newfoundland Studies, Queen Elizabeth II Library, Memorial University of Newfoundland, St. John's, Newfoundland, Canada. All data are contained in text files stored in 3¼ diskettes (IBM format).

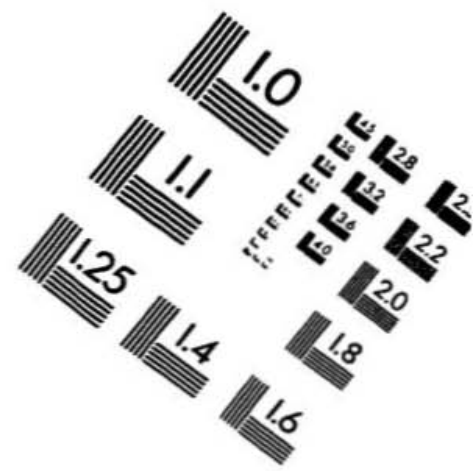
Baleen whale sighting information consists of species, date, time and location of sightings. Oceanographic casts and information on dates, times, location and initial processing of oceanographic casts are available. Below is a sample of oceanographic data:

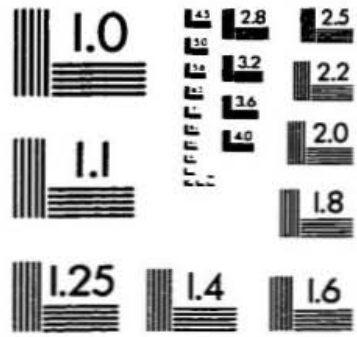
Cast #: 94072106
Date: 21 July 1994
Time: 12:21 PM (Newfoundland Daylight Savings time)
Latitude: 46° 51' 074" N
Longitude: 054° 19' 029" W

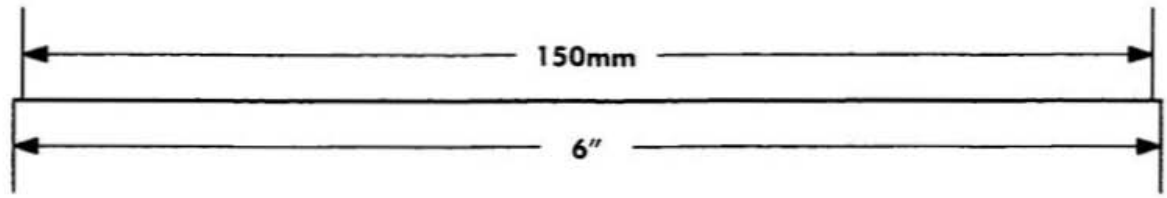
Conductivity (Siemens/m)	Pressure (decibars)	Temperature (°C)	Depth (m)	Salinity (PSU)	Sigma-*t* (kg m^{-3} - 1 000)
3.890581	0.538	13.9415	0.534	32.24	24.0678
3.838629	1.522	13.388	1.509	32.2231	24.1665
3.780912	2.997	12.8793	2.972	32.111	24.1798
3.757607	4.652	12.6721	4.613	32.0656	24.1847
3.767034	6.127	12.6102	6.076	32.2075	24.3064
3.759838	7.603	12.5843	7.54	32.1605	24.275
3.743908	9.078	12.5647	9.002	32.025	24.1738
3.735268	10.599	12.5375	10.511	31.9653	24.1327
3.688434	11.94	12.4025	11.841	31.6327	23.9006
3.564967	13.371	11.4071	13.26	31.2822	23.8109
3.437552	14.802	10.0044	14.679	31.2178	23.9999
3.27242	16.233	8.0094	16.098	31.2637	24.3398
3.161887	17.575	6.2742	17.428	31.6476	24.8714

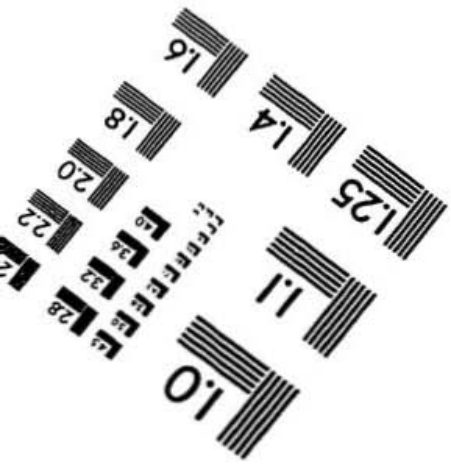
IMAGE EVALUATION
TEST TARGET (QA-3)











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