Spatial distribution of rorqual whales in the Strait of Jacques Cartier, Gulf of St. Lawrence, Quebec, Canada

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Abstract

The spatial distribution of four species of rorqual whales was studied along the north shore of the Gulf of St. Lawrence during the months of June to October from 1989 to 2000. A research effort of 6511 hours at sea yielded 849 sightings of blue whales (Balaenoptera musculus), 5291 of finback whales (Balaenoptera physalus), 3822 of humpback whales (Megaptera novaeangliae) and 6489 of minke whales (Balaenoptera *acutorostrata*). Spatial and behavioural data were collected at sea using inflatable boats, and Global Positioning Systems (GPS) were used to obtain accurate positions. These data were plotted and analysed using a Geographic Information System (GIS) to test the hypotheses that patterns of distribution were not random, were associated with bathymetry and reflected specific differences in habitat use. The resulting maps illustrated the clustered distribution of rorqual whales linked to sea-bottom topography, probably associated with areas of local upwelling and increased productivity. Blue and fin whales shared almost the same distribution, humpback whales were found in slightly deeper, offshore waters whereas minke whales were more abundant in shallower waters. Little attention has been given until now to local patterns of distribution in the area and such information can be useful for practical management considerations. The results emphasise the importance of scale in ecological studies of marine mammals and the need for further research using additional oceanographic parameters, in order to better understand habitat selection.

Résumé

La distribution spatiale de quatre espèces de rorquals a été étudiée le long de la côte nord du golfe du Saint-Laurent durant les mois de juin à octobre, de 1989 à 2000. Un effort de recherche de 6511 heures a permis d'observer 849 occurrences de baleines bleues (Balaenoptera musculus), 5291 occurrences de rorquals communs (Balaenoptera physalus), 3822 occurrences de rorquals à bosse (Megaptera novaeangliae) et 6489 occurrences de petits rorquals (Balaenoptera acutorostrata). Les animaux ont été approchés en mer grâce à des embarcations pneumatiques à coque rigide et des appareils GPS. Ces données ont été analysées au sein d'un système d'informations géographiques (SIG) afin de tester les hypothèses suivantes : les schémas de distribution ne sont pas aléatoires, sont associés aux facteurs bathymétriques et reflètent les différences entre les espèces. Les résultats sous forme de cartes de distribution illustrent la répartition nonaléatoire des rorquals, associée aux régions sous-marines dont la topographie est plus accidentée. Rorquals communs et rorquals bleus partagent une distribution similaire, les rorquals à bosse se retrouvent dans des eaux légèrement plus profondes tandis que les petits rorquals sont plus abondants dans les eaux moins profondes. Peu d'attention avait été portée jusqu'à présent sur les schémas locaux de distribution dans la région. Ce type d'informations peut s'avérer utile pour des considérations de protection des espèces et d'aménagement du territoire. Les résultats mettent également en valeur l'importance du choix de l'échelle pour étudier les mammifères marins et le besoin de recherches supplémentaires utilisant davantage de facteurs océanographiques.

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Introduction

Until recently, little consideration was given to the spatial domain of whales. Most studies have focused on general ecology of cetaceans, especially on predator-prey relationships (e.g. Veit *et al.* 1993, Griffin 1997, Darling *et al.* 1998) and habitat preferences on a large scale (e.g. Whitehead & Carscadden 1985, Polacheck 1987). Fewer studies have tried to link environmental features directly with spatial and temporal distribution on a small or intermediate scale. This is related to the practical difficulty of studying these animals in the field, determining their exact position as well as environmental parameters. Early studies used whaling data (Uda & Nasu 1956, Uda & Dairokuno 1958) when appropriate. Other papers have tried to relate estimates of abundance to temporal variations in the environment or prey availability to compensate for the lack of accurate spatial data (Whitehead & Carscadden 1985, Payne *et al.* 1990).

Between the 1960s and today, new statistical methods and advances in geomatic technologies, especially from satellite and aerial imagery, have helped marine mammal scientists find spatial patterns and make predictions about movements and distribution of animals over broad areas. The ability to interpret spatially explicit data at various scales has important potential for studying habitat use. Progress in field techniques (e.g. photo-identification), newly available technologies like Global Positioning Systems (GPS), radio- or satellite-tracking devices and Geographic Information Systems (GIS), as well as the creation of long term databases have helped researchers to study relationships between the spatio-temporal distribution of whales and the characteristics of their habitat at a finer scale.

The Estuary and Gulf of St. Lawrence in Eastern Canada constitute a rich and complex system receiving large inflows of both fresh and sea water. The head of the Laurentian Channel, for instance, appears to be the site of the richest krill aggregation yet documented in the northwest Atlantic (Simard & Lavoie 1999). These aggregations of euphausiids and fish, especially capelin (*Mallotus villosus*), attract many species of whales to the area during the summer.

At least eighteen species of marine mammals can be encountered in the Gulf of St. Lawrence during the summer and fall (Sears *et al.* 1981), including four species of balaenopterid whales. Although biological and ecological information is available for most of these species (e.g. Fontaine 1998), as well as some data about their general distribution in the Gulf, there is very little information about exact movements, local patterns of distribution, and partitioning and use of habitat.

Land-based observations of whales in the St. Lawrence Estuary began as early as the mid-seventies (Mitchell *et al.* 1983, Edds & MacFarlane 1987). The proximity of whales to shore in the Estuary was convenient for land-based observation, which yielded general information about occurrence and behaviour of balaenopterid whales. However, these observations did not give accurate data on positions, habitat use and factors influencing spatial distribution. Moreover, such studies covered only a small area close to shore and did not yield information on distribution farther off shore. Radio tracking of whales helped study movements and behaviour over small periods of time (Ray *et al.* 1978; Michaud & Giard 1998). Aerial surveys that covered a much larger area were flown in 1982 (Sears & Williamson 1982) and more recently in 1995 and 1996 (Kingsley & Reeves 1998). They provided data on spatial distribution of cetaceans in the Gulf and abundance estimates but could not study variation in time. Studies combining land-based observation, local aerial surveys and boat transect lines began in the early 1980s and represented a larger research effort in both time and space (Sears 1979, Sears 1980, Sears *et al.* 1981, Sears & Williamson 1982, Sears *et al.* 1982).

Since then, the Mingan Island Cetacean Study (MICS) has accumulated a wealth of data, estimating abundance and inter-annual variation along the North Shore (Bérubé & Sears 1990). Distribution of minke whales (*Balaenoptera acutorostrata*) within the Mingan Islands archipelago was studied using MICS data (Naud 2000).

Learning more about the way baleen whales use their habitat in the Gulf of St. Lawrence can lead to better protection of their environment, management of the whale watching industry and management of the shipping activities in proximity to endangered species (e.g. blue whales, *Balaenoptera musculus*), a growing concern especially in the crowded St. Lawrence Estuary. This knowledge can help delineate areas that are important to some of the whale species at certain times of the year and highlight differences in the dispersion patterns of each species considered. Such information is potentially useful for practical management considerations and for generating hypotheses that might account for observed differences among species.

The results of a review of 36 studies, all concerned with habitat use or spatial distribution of cetaceans, are summarised in Table 1. Nine studies found correlations between cetacean distribution and higher variability of the underwater topography; four studied upwelling directly and found strong correlations with whale dispersal patterns. Of the 11 studies that used sea surface temperature as a factor, 9 found that cetaceans were more abundant in colder waters. None of the studies that used salinity found any correlation. Studies examining the productivity or the abundance of food items almost all yielded meaningful results, showing strong correlations between habitat use of whales and their food items. Because bathymetric data are readily available and easy to access, topography was chosen as the main factor in the present study. Topography is also the underlying factor behind most other oceanographic variables (Barber & Smith 1981).

The overall presence of whales in the Gulf of St. Lawrence from April to December is associated with the presence of large quantities of food (euphausiids, fish) (Simard & Lavoie 1999). Areas of high topographic relief are associated with local plumes of upwelling and therefore increased productivity (Longhurst 1981, Levinton 1982). These areas of upwelling are linked with aggregations of zooplankton or small fish and in turn often attract larger predators such as whales, which need to feed in areas where food is abundant and concentrated (Nemoto 1970). Prey species are not uniformly distributed. Foraging efficiency, therefore, should be maximised when effort is concentrated in areas where prey are concentrated. Cetacean food is probably concentrated in regions of high general productivity. Because undersea topography can have a major influence on productivity, cetacean distribution patterns may be associated with the topographic patterns of the ocean floor (Hui 1979).

The aim of the present study was to analyse the sighting records of rorqual whales from the MICS database and to describe the spatial distribution for each species by testing the following hypotheses:

- Spatial distribution of rorqual whales is not random
- Patterns of dense distribution are linked to sea-bottom topography
- Different species exhibit different dispersion patterns

Literature review

Production in oceanic ecosystems

Patterns of distribution of primary production in the oceans have been fairly well mapped out in broad general terms. Phytoplankton use light to synthesize organic matter from inorganic carbon and nutrients dissolved in fresh and marine waters. They are thus responsible for primary productivity. The rate at which phytoplankton produces new organic matter in the marine environment is determined by nutrient availability (especially nitrogen compounds), light intensity and temperature. The maximum potential level of primary productivity in a system also depends on additional factors such as the stratification of the water column (White & Johns 1997). Over much of the open oceans of the tropics and subtropics, both production and standing stock at all trophic levels are low. Much of the available nutrient material is locked up in living organisms. Any tendency of plants to increase is limited by grazing herbivores, which in turn are controlled by predation by larger animals. However, in temperate and subarctic waters, at the end of winter, the deep mixing of water by winter storms adds nutrients to the surface layers, and increasing sunlight in spring triggers a phytoplankton bloom which cannot be controlled by the herbivorous zooplankton. The latter in turn blooms a few weeks later. These waters (for instance, the North Atlantic in a band from New England to Iceland and Norway, and much of the Antarctic ocean) are therefore regions of high primary production (Gulland 1974, Levinton 1982).

In upwelling areas there is a somewhat similar, but more continuous, structure of unbalanced production, i.e., production in which the peaks of plant and herbivore production do not coincide. Coastal upwelling is a mesoscale process in which cool and nutrient-rich subsurface water is brought to the surface and moved away from vertical transport by horizontal surface flow. The forces that initiate the upwelling can be divergent current systems or steady offshore winds. Optimal conditions of nutrient supply are therefore provided by vertical transport into the euphotic layer, and optimal light conditions for phytoplankton are maintained in the stabilised horizontal divergent flow of the surface layer. The ocean responds on a timescale of 1-10 days, a horizontal spatial scale of 5-100 km and recruits water from 40 to 80 meters in depth (Barber & Smith

1981). The subsequent phytoplankton bloom is similar to the spring bloom in temperate or subpolar waters, which in turn supports a later zooplankton outburst, generally somewhat downstream of the initial upwelling. These upwelling areas are among the most productive seas in the world and support some of the richest fisheries (Gulland 1974).

Patchiness of organisms in pelagic ecosystems is often linked to hydrographic mechanisms, such as convergence in frontal systems and wind-driven or tidally driven processes, which favour the presence of aggregations at predictable locations and times (Marchand et al. 1999). Anchovies, for instance, are known to concentrate in submarine canyons and escarpments in the areas of upwelling (Mais 1974). There appears to be great diversity in phytoplankton patch size associated with the diversity of aggregationdispersion mechanisms, especially in tidally and topographically dominated continental shelf seas, with changes in the horizontal distribution usually associated with plumes of upwelled water (Longhurst 1981). Zooplankton patchiness occurs at all scales from centimetres to tens of kilometres in the horizontal plane and is dominated in the vertical plane by a layer of abundant biomass near the surface, with deeper layers containing sparser plankton (Gulland 1974). The combination of biological behaviour of euphausiids with persistent horizontal and vertical current systems, such as upwelling, gyres, twolayer circulation, shelf-break and coastal currents, has been invoked to explain the transport, maintenance, and accumulation of krill in many regions of the world. The mechanism involved is the interaction of the three-dimensional circulation with the vertical distribution and behaviour of euphausiids over a broad continuum of scales in both space and time. At large scales (>100 km, greater than months), the different vertical distributions of life stages and the diel vertical migration of the organisms combine with the current structure to retain the species in a given system and to generate a zonation with age as observed in the Gulf of St. Lawrence (Lavoie et al. 2000).

However, local aggregations are generated by meso- (5-100 km, days) or smallscale processes occurring at the site of strong interactions of the deep circulation with bathymetric features, such as continental or coastal shelf-breaks or edges, deep basins on shelves and channel or canyon heads, which often correspond to regions of upwarddomed isotherms. Especially in shelf regions, the effect of internal waves must be considered when trying to understand patchiness. Trains of internal waves in shallow seas can be generated by the passage of tidal streams over shallow banks in whose lee the waves originate, having different characteristics at different stages of the tide. These waves affect the coherence between the different linked variables such as temperature, chlorophyll, salinity and plankton. For instance, lack of correlation between chlorophyll and temperature variability in the Gulf of St. Lawrence was demonstrated in two simultaneous sets of horizontal tows separated vertically by only 4 meters (Denman 1976).

Baleen whale feeding grounds at high latitudes have been classified into three categories: 1) those that occur on ocean fronts between major water masses; 2) oceanic eddy grounds, either dynamic (tongues or salients formed on ocean fronts) or topographic (as a result of water mass deflection by islands, capes, promontories or other surface features); 3) areas of upwelling, either dynamic (induced by ocean gyre movement or by cyclones and anticyclones) or topographical (induced by sea mounts, subsurface ridges or edges of continental shelves) (Gaskin 1982). Our study area in the Gulf of St. Lawrence falls in the third category; it is a region of topographically induced upwelling.

The Estuary and Gulf of St. Lawrence

The Estuary and Gulf of St. Lawrence constitute a complex system receiving large inflows of both fresh and sea water. The fresh water originates from an extensive drainage basin. Sea water flows into the Gulf of St. Lawrence from the Atlantic Ocean through Cabot Strait and, to a lesser extent, the Strait of Belle Isle. The Gulf itself has a mean depth of 152 m, although 25% of it is shallower than 75 m. The dominant feature of the bottom topography is the Laurentian Channel which begins in the deep ocean beyond the Scotian Shelf and ends at Tadoussac in the Estuary. It has a maximum depth of 535 m. There are also two side branches of the Laurentian Channel within the Gulf: the Esquiman Channel and the Anticosti Channel (White & Johns 1997).

Various subregions of the Gulf have been proposed based on biological, hydrological and topographical characteristics, but an acceptable rationale for a single, comprehensive system of subdivisions has yet to be made. The most recent division of the Gulf was proposed by de Lafontaine et al. (1991), who considered the Gulf as having four subregions: the northwestern Gulf, the Gaspe current, the Magdalen shallows (southern Gulf) and the northeastern Gulf. The lowest levels of nutrients occur in surface waters

(top 30 m) during summer and fall after being depleted by a period of rapid phytoplankton growth. Dead biological material sinking in the water column dissolves or decays with the help of bacteria. This decay causes nutrients to be released back into the water column, a process called regeneration. A stratified marine system with limited vertical water exchange, such as what is found in large portions of the Gulf and Lower Estuary in the summer, causes nutrient depletion at the surface and higher concentrations of nutrients in deeper waters (Coote & Yeats 1979). The concentrations of nutrients in the intermediate and deep layers of the Gulf are approximately three times higher than those at similar depths in North Atlantic waters outside the Gulf. The deeper waters are depleted of dissolved oxygen because, as dead organisms sink, the release of nutrients by the breakdown of tissue is an oxygen demanding process. In the northeast Gulf, high oxygen values in the deep layer are thought to derive from the Labrador current waters, flowing through the Strait of Belle Isle, which have oxygen levels as high as 10 mg/l (D'Amours 1993).

Heat from the sun in the spring and summer causes a shallow layer of warm water to develop on the surface throughout the Gulf and the Lower Estuary, overlying cooler, deeper waters. Cooler air temperatures and stronger winds in the fall and winter cause the upper layers to lose heat to the atmosphere and to mix with deeper waters below (White & Johns 1997).

A particular feature of the St. Lawrence system is the presence, from April to December, of a cold intermediate layer (CIL) extending below the surface mixed layer down to over 150 m with core temperatures less than 0°C (Lavoie *et al.* 2000). The Gulf is considered to be a moderately stratified system, but there are often local disruptions to stratification, bringing deeper, colder, more saline waters to the surface. Main causes for these upwellings include rapid changes in bathymetry and intense tidal action. Internal tides bring cold, deep and highly saline waters to the surface and take warmer, low salinity water to deeper regions (White & Johns 1997).

The northwestern Gulf, where the study area is located, supports a distinct community of phytoplankton consisting predominantly of large diatoms in spring and dinoflagellates in summer. It has a high abundance of large zooplankton (large *Calanus* copepods, euphausiids, chaetognaths and shrimps), relatively low abundance of fish eggs and larvae, and high abundance of juvenile fish (primarily capelin) (White & Johns

1997). There are many breeding seabirds and the region supports a high diversity of whales in the summer months. Krill abundance and distribution are highly variable on a time scale going from hours with the semidiurnal tidal cycle to years with the run-off cycle. Interannual changes in climate also affect these dynamics (Lavoie *et al.* 2000). The intrinsic characteristics of this krill aggregation are fundamental properties structuring, in time and space, trophic exchanges with predators, such as pelagic fish and baleen whales, food web dynamics, and mass energy transfer in the regional pelagic ecosystem. This complex aggregation/dispersion mechanism determines where and when the food meets the requirement of the predators feeding there (Simard & Lavoie 1999). The high abundance of both euphausiids and juvenile capelin makes the region especially attractive for whales, since these are their two main prey items.

Dispersal patterns of cetaceans

There has been incentive to study the spatial and temporal distribution of whales by the whaling industry for the past two centuries. Indeed, knowing where the whales were meant less time at sea and larger profits (Melville 1851). Whalers frequently exchanged information about catches and sightings. Consequently, by the 1840s, they had discovered almost all the major whaling grounds between 40° N and 40° S (Jaquet 1996). Plots of sightings and catches on maps of the world were made solely with the idea of understanding distribution and migrations of the animals and therefore increasing efficiency of the whaling industry (e.g. Townsend 1935 in Jaquet 1996). For a long time, whaling was the most abundant source of information available on whales and it still is the largest data set available on pre-whaling world-wide population distribution.

During the nineteenth century, whalers noticed that whales were not uniformly distributed throughout the oceans but were abundant in certain areas or "grounds" (Jaquet 1996). For example, as early as 1840, sperm whales (*Physeter macrocephalus*) were found to be numerous where there were powerful currents or where currents flowed in opposite directions (Bennett 1840). Correlations between sperm whale density and oceanic fronts were suggested by whalers. Sudden changes in sea surface temperature were an indication of a promising area for a new whaling ground (Ashley 1926). Most of the knowledge about sperm whale distribution gained during the Yankee period is summarised in Townsend's charts. Townsend undertook the colossal work of plotting 36

909 sperm whale catches from the logbooks of Yankee whalers (1761-1920) on world charts. They showed concentrations of kills coincident with areas of upwelling, for example along the equator, along the west coast of South America and South Africa, and off California. They also showed some concentrations of whales in the Sargasso Sea and around the Azores Islands, areas which are believed to be of poor primary productivity. Whaling data were also used to show that baleen whale abundance is correlated on a large scale with zones of primary productivity (Gulland 1974) and zooplankton productivity (Foerster & Thompson 1985).

Caution must be used when interpreting the results of the whaling data. First, they only concern species that were economically interesting. Secondly, they yield information about a species only when this species was actually being hunted. As soon as the industry shifted to another species, then so did the available data. Thirdly, they were biased in many ways, for instance toward big animals (e.g. male sperm whales rather than females and their calves). Townsend's charts suggest extensive southward movement of sperm whales at the onset of the northern winter and a reverse movement at the onset of the northern summer. However, these records do not account for the fact that whalers could not hunt successfully at high latitudes during the winter. It is possible that these apparent migrations are partly the consequence of whalers fishing in different latitudes at different times of the year.

As large organisms occupying the top level of the food chain and present in all waters world-wide (Rice 1998), marine mammals have a major influence on the structure and functioning of some marine communities (Estes 1979, Ray 1981). This has been acknowledged and even recorded into law: "... such species and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part" (US Marine Mammal Protection Act, 1972).

Marine mammals have adapted an essentially terrestrial morphology, physiology, and behaviour to the medium of the sea. They have done so widely and successfully; they are found in all seas and fill many different ecological niches. They have low reproductive rates and are K-selected by comparison with other animal groups (Ray 1981), although within their group lies a wide spectrum of strategies that relates to features of their habitat. The most important difference between the two main groups of cetaceans is their diet. Odontocetes (toothed whales) are usually top predators; the squids and fishes on which they prey are probably themselves second or third predators. Toothed whales are thus separated from primary production by several steps. Mysticetes (baleen whales), on the other hand, are trophically much nearer to primary production. For instance, the typical food chain of Antarctic rorquals is: diatoms to euphausiids to whales. Toothed whales are possibly less dependent on high biomass than baleen whales because they pursue individual animals and may therefore be able to harvest the available food over a much wider area than do baleen whales. On this basis (food) one might expect the rorquals to be confined to areas of high zooplankton biomass, but to be abundant in those areas, and sperm whales to be more widespread, though at a lower density (Gulland 1974).

Right whales (*Balaena glacialis*) have been the subject of many articles, probably because a significant proportion of the North Atlantic population aggregates in a relatively small place every year (the Bay of Fundy) and because they are easier to approach and study than the faster rorqual whales. Since their level in the food chain is quite low, most studies have hypothesised that there is a strong and straightforward relationship between their spatial distribution and plankton patches (or physical factors promoting the presence and abundance of plankton). It was shown that right whales need extremely dense patches of plankton to meet their energy requirements (Kenney et al. 1986). In the Bay of Fundy, they are associated with flat bottom topography, well stratified waters (Woodley & Gaskin 1996) and high copepod densities (Mayo & Marx 1989, Murison & Gaskin 1989). The same relationship was found for right whales in Cape Cod Bay, Massachusetts (Mayo et al. 1985) and in the Great South Channel off New England (Wishner et al. 1988). Using a model that included bathymetry and sea surface temperature, Moses and Finn (1997) were able to predict right whale habitat preferences and distribution in the same areas. But no correlation was found between the distribution patterns of right whales and satellite-derived sea surface thermal structure in the Great South Channel (Brown & Winn 1989).

Rorqual whales include blue whales (Balaenoptera musculus), finback whales (Balaenoptera physalus), humpback whales (Megaptera novaeangliae), sei whales

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(Balaenoptera borealis), Bryde's whales (Balaenoptera edeni) and minke whales (Balaenoptera acutorostrata). They are fast and agile swimmers. Except for the humpbacks, they are generally less known and studied than other cetaceans. They exhibit a wide range of feeding preferences, with sei whales preying mainly on copepods, blue whales preying on euphausiids and the other species eating both fish and euphausiids. Positive correlations between baleen whales and their prey have been recorded in a coastal environment (Piatt et al. 1989). Fluctuations in the abundance of rorqual whales in the southern Gulf of Maine were related to changes in their selected prey (Payne et al. 1990). A shift in the distribution of humpback whales occurred in response to a shift of their prey in the same area (Weinrich et al. 1997) and their spatial distribution on George's Bank was strongly correlated with presence of sand eels (Ammodytes americanus) (Payne et al. 1986). Fin whales are associated with shallow regions of high topographic variation and well mixed waters (Woodley & Gaskin 1996). Presence of finback and humpback whales off Newfoundland was correlated with peak abundance of capelin and with age-class of the fish (Whitehead & Carscadden 1985). Fin whales in the St. Lawrence estuary were observed primarily along steep contours where biological productivity is believed to be high (Sergeant 1977). Blue whale distribution in the California Channel Islands is related to areas of upwelling, positively correlated with productivity and negatively correlated with surface temperature (Fiedler et al. 1998). Minke whale distribution in the Mingan Islands remains stable from year to year, and is correlated with topography (Naud, 2000). Hoelzel et al. (1989) found no correlation whatsoever between minke whale habitat preferences and salinity, oxygen concentrations or temperature, but found a significant relationship with topography.

Differences among baleen whales should be interpreted in terms of trophic levels: blue whales resemble right whales in trophic level and their distribution is directly correlated with productive areas, abundance of prey, upwelling areas and temperature. Distribution of other rorquals such as finback, humpback and minke whales is associated with areas of high topographic variation inducing upwelling and mixing of waters. Their presence is related to depth and temperature only in a broad way and these two factors cannot be used effectively to predict small scale habitat use, probably because of their higher mean level in the food chain.

The importance of scale

The scale at which an investigation is done affects the interpretation of pattern. For instance, planktonic organisms may occur in large patches of 0.5 to 10 km diameter but spatial distribution may be random within the patches (Levinton 1982). Ecosystems also contain many spatial scales. For example, in the California Current, the communities of zooplankton and their predators exhibit characteristic spatial scales of 50 m for fish schools, 300 m for plankton aggregation, 1 000 m for gaps between plankton aggregation and 10 000 m for gaps between fish schools (Smith *et al.* 1989). The question of scale is therefore very important. If the relationship between the distribution of a predator and the is previse studied at too small a scale, co-occurrence will not be apparent as predators are seldom exactly aligned with their prey. On the other hand, if the system is studied at too large a scale, little will be learned of the small scale relationships.

The best scale to choose is usually one that corresponds with the patch size of aggregations of both predator and prey (Rose & Leggett 1990). Foraging whales can spread over several kilometres (Jaquet & Whitehead 1999) and patch size for typical prey species (euphausiids, fishes, squids) is about a few kilometres (Berkes 1976, Rose & Leggett 1990). Jaquet and Whitehead (1999) argue that, on feeding grounds, most marine mammals can be studied at spatial scales of 5-45 km. North Atlantic right whales are closely associated with copepod abundance over a spatial scale of 5 km by 5 km in the gulf of Maine, and at the same scale, right and finback whales can be associated with different depth profiles (Woodley & Gaskin 1996). Short-finned pilot whales (*Globicephala macrorhyncus*) were encountered significantly more often in areas of high relief than in areas of low relief over a spatial scale of 11 km off southern California (Hui 1985).

Most distribution studies of cetaceans have correlated the presence of whales with some biological or physical aspect of their habitat at a very large scale. Since relationships between distribution of a predator and distribution of its prey are invariably scale-dependent (Rose & Leggett 1990, Jaquet & Whitehead 1999), studies over large scales cannot be extrapolated to smaller scales. Knowledge concerning environmental factors influencing whale distribution over spatial scales of less than 100 km is still very limited.

Many apparent contradictions can be explained by studying spatial distribution at different scales. For instance, temperature was shown to influence right whale distribution in a study at intermediate scale (Moses & Finn 1997). However there was no significant correlation in a study at small scale (Brown & Winn 1989), which can be explained by the time and space lag between temperature and its effect on prey density.

Methods

Study area

The study area was located on the North Shore of the Gulf of St. Lawrence, between the Mingan Islands and the northern side of Anticosti Island (Fig. 1). This region of the Gulf is the site of wind-driven upwelling during the summer, heavy tidal mixing and is associated with high levels of biological productivity (Koutitonsky & Bugden 1991, Rose & Leggett 1988) (Fig. 2). The area is characterized by a varied topography made up of numerous sediment types, with depth ranging from 1 to 300 m (Fig. 3). It is also characterized by the presence of many rivers, which enhance productivity. Rivers of the Quebec North Shore contribute up to 14% of the fresh water supply to the St. Lawrence (Koutitonsky & Bugden 1991). Areas with similar characteristics, such as the estuary of the Saguenay River and the Strait of Belle Isle, have been found to be of importance to marine mammals as well (Kingsley & Reeves 1998). Research along the Quebec North Shore since 1979 has established that it is frequented regularly by abundant populations of cetaceans (Sears et al. 1981). Aerial surveys flown in 1992, 1995 and 1996 showed that the North Shore shelf was the most productive area, with the greatest species diversity (Sears & Williamson 1982, Kingsley & Reeves 1998). The animals arrive in the Gulf of St. Lawrence in spring after the ice break-up (usually in April) and range along the North Shore to feed (Sears et al. 1981). Most of them leave the study area by December or January.

Collection of data at sea

Field work was conducted by personnel from MICS from June to October for the years 1989 to 2000 inclusively. Location and behaviour of whales were collected at sea using rigid-hulled inflatable boats of various sizes (but mostly 4.5 to 8 metre long) with outboard engines of 40 to 200 horsepower. The total distance covered in a day could be up to 220 km.

Animals were spotted at a distance of up to 7.5 km (4 nm) in good conditions, thanks to their spouts or raised flukes. Whales were approached when surfacing, and notes were taken concerning their position (latitude and longitude using a GPS), number and composition of group, heading and behaviour. Photo-identification techniques were used to identify individuals (as described in Hammond. 1990 and Sears *et al.* 1991) using 35 mm cameras with zoom lenses and black and white film. Each species had its particular markings, as described below. Photo-identification prevented us from counting the same individuals several times within the sampling period, therefore preventing some sightings from being given too much weight.

Behaviour patterns can be hard to recognise and their interpretation is strongly experience-related. They were classified into broad categories according to standard cetacean ethograms. The lack of an explicit protocol for sampling is termed *ad libitum* sampling and it typically entails scoring "as much as one can" or whatever is most readily observable of the behaviour of an animal or a group of animals (Mann 1999). *Ad libitum* observations suffer from a variety of potential biases: different individuals may be more or less visible and some behaviour may be more salient and more readily recorded than others. Such biases indicate that *ad libitum* data are probably not appropriate for estimating rates of behaviour or for comparing rates across subjects or across studies (Mann 1999). However, only feeding behaviour is relevant to this study. Feeding behaviour can be seen and recognised as such only if happening at the surface. The animal appears at the surface, sometimes in sudden lunges, exhibiting one of the following characteristics: mouth is still open, mouth is closed but ventral pouch is inflated, mouth is closed and water is being forced out through the baleen plates. Since it is only the occurrence or non-occurrence of feeding behaviour that was used in this study, and not its rate or frequency, the biases of *ad libitum* sampling should not have had any effect.

The distribution of the research effort in space was highly dependent on weather conditions, which had to be good enough both for safety and efficiency of research. Overall, going to sea and working with the animals was possible if wind speed was below 20 knots (37 km/h), sea state below 4 on the Beaufort scale, and visibility was at least 5.5 km (3 nautical miles). Since it was safer to head into the direction of the wind in case it picked up later, so that one returns with it and not against it, winds dictated the general direction of travel (east or west) every day as well as the amount of time (and therefore the range) that could be spent on the water under safe boating conditions. Because of that, effort was not homogenous in space. Prevailing winds during the summer and fall are westerlies and southwesterlies, and thus more time was spent in the western half of the research area than in the eastern half. However, most research days involved trying to cover the largest possible area, crossing the Strait of Jacques Cartier towards Anticosti Island and thus surveying areas of very different underwater topography: banks and islands along the North Shore, mid-passage canyon between the North Shore and Anticosti, and the edge of the Anticosti northern shelf. Moreover, both halves of the research area present similar topographical characteristics. Thus, there should not be any bias in the statistical analysis (unlike if, for instance, one half consisted mainly of flat sea bottom and the other half had greater relief).

Species studied

<u>Blue whale</u> (*Balaenoptera musculus*)

The largest animal ever to have lived on Earth, blue whales reach a maximum length of 28 m in the St. Lawrence and a mass of about 130 tons. They feed exclusively on euphausiids (krill). In the St. Lawrence, their main prey items are *Meganyctiphanes norvegica* and *Thysanoessa raschii* (Yochem & Leatherwood 1985). They are mostly solitary but can be found in pairs. We photo-identified them using the mottling on their flanks and back (Sears *et al.* 1991) and have identified 372 individuals in the western North Atlantic over the last 22 years.

<u>Finback whale</u> (Balaenoptera physalus)

Second largest whale (mean length is 21 m, mean weight is 60 tons), finbacks in the St. Lawrence feed on both euphausiids and several fish species (especially capelin). Commonly found in groups of 2-12 individuals, it is believed they use cooperative group foraging techniques. Fin whales were photo-identified using the dorsal fin and pigmentation patterns on the right side of the head (Agler 1992). There are 520 individuals in our catalogue.

<u>Humpback whale</u> (*Megaptera novaeangliae*)

Humpback whales are medium sized whales (mean length is 15 m, mean weight is 45 tons) that feed mainly on fish in the St. Lawrence, possibly using cooperative group hunting techniques. Humpback whales have been well studied and are probably better known than any of the species observed. Individuals were identified using patterns of black and white pigmentation on the underside of the fluke (Hammond 1990). To date, our catalogue contains 530 animals.

Minke whale (Balaenoptera acutorostrata)

Smallest of the baleen whales (mean length is 9 m, mean weight is 8 tons), minke whales are solitary hunters and feed mostly on fish such as capelin and sand lance but also on euphausiids. Limited photo-identification has been conducted on this species.

Statistical methods

Observations consisting of a list of sightings came directly from the MICS database. Each sighting had the following information: date, time, year, month, week, latitude, longitude, depth, species and whether feeding behaviour was recorded or not.

A map projected in Universal Transverse Mercator with a central meridian of -63 degrees of longitude, showing coordinates in decimal degrees and distance units in kilometres was used for plotting the data. Latitude and longitude of the sightings were converted from degrees/minutes/seconds to decimal degrees, and then plotted directly on

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the map, using GIS ArcView 3.1 software with the Spatial Analyst extension, as well as the Animal Movement extension (Hooge & Eichenlaub 1997). Plots showed the distribution of whales in the study area, each dot representing a sighting. A map was produced for each species, as well as for sightings for which feeding behaviour was recorded (all species combined). Data were separated into twelve different layers, each corresponding to one of the twelve years of effort, so that counts of sightings could be done separately for each year.

An underlying assumption to most spatial distribution studies is that a habitat which is occupied by whales and dolphins on their feeding ground is used by them mostly for feeding purposes. Previous results from the Cetacean and Turtle Assessment Program (CETAP) have shown that the distribution of sightings of a particular species where definite feeding behaviour was observed tended to closely mirror the overall sighting distribution for that species (Kenney & Winn 1986). Even if some sightings in a study do include whales that were just travelling from one place to another, the vast majority of sightings were for whales aggregating at a certain place for feeding or social purposes. Thus, during the statistical analysis, the few sightings of travelling animals should have little weight compared to the density of animals that aggregate for feeding purposes.

<u>Effort</u>

Effort was tested both for between-year and within-year variation. Total effort per day, expressed in hours, was averaged for each year and the means were compared with ANOVA. The research season was separated into two-week periods and average time spent on the water per research day was calculated for each of these two-week periods. The means were then tested for homogeneity using ANOVA.

Distribution of depths

The "depth" of a sighting does not represent the depth at which the animal was diving. It represents the depth of the sea floor at the location of the sighting. Depths can indicate what kind of habitat animals are using (shallow waters vs. deep waters) and may be directly linked to the presence/abundance of favourite prey species. Differences between mean depths of sightings for each species can represent differential use of the environment and habitat preference, and were tested using ANOVA.

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Test for spatial randomness

The data were subjected to a test of complete spatial randomness (CSR) which acts as a dividing hypothesis to distinguish between random, uniform and aggregated patterns (Diggle 1983). We have used the sample mean of the nearest neighbour distances as a way to measure and analyse the average distance from an individual to its nearest neighbour. This test is powerful against both aggregated and random alternatives. The advantage compared to a simple Chi-square test using values expected from a Poisson distribution in a grid is that the nearest neighbour test does not use a grid, and therefore is not sensitive to grid size.

The expected average distance from an individual to its nearest neighbour in a random distribution, r_{e} is

$$r_e = \frac{1}{2\sqrt{L}}$$

where L is the number of individuals per unit area. If the measured distance r is greater than r_e , then a tendency toward uniformity is demonstrated; if r is less than r_e , there is aggregation. An index of difference from a random pattern is obtained by dividing the observed mean by the expected mean: $R = r/r_e$. R indicates how clustered or dispersed points are within the study area. An R value of less than 1 indicates a tendency towards a clumped (clustered) pattern. An R value of 1 indicates a random distribution. An R value > 1 indicates an organized (uniform) pattern. The computer script used (Hooge & Eichenlaub 1997) also applies a simple test of significance for deviation from randomness, using the standard error of the expected difference to calculate the normal deviate, z and compares it with the proportion of the normal curve (Zar 1999).

Kernel densities

In addition to plotting data, a probabilistic model known as the adaptive-kernel method (Worton 1989) was used to provide a more visually explicit image of the spatial distribution of whales. Kernel methods are used to calculate the distribution of use: "the two-dimensional relative frequency distribution for points of location of an animal over a period of time" (Seaman & Powell 1996). This definition refers to the animal's home range. However, if we use positions for several individuals of the same species instead of

positions for only one individual, then we obtain a distribution map showing the density of sightings. The Spatial Analyst expansion to ArcView yields maps showing the kernel density of sightings in the form of different shades of colour and thereby provides identification of core areas (i.e. zones of greater density). Advantages of this method are that it does not make any assumption about the statistical distribution (it is nonparametric) and it can have more than one core area (Worton 1989; Sauer *et al.* 1999).

Contour Index and scales

Hui (1979) stated that maximum depth, minimum depth and absolute depth change are inadequate measures of topographic elements influencing food supply. A Contour Index (CI) was formulated that incorporates into a single number both the change in depth and the maximum depth at a given point. A grid of squares was laid on the map of the study area (Fig. 4). The CI, a dimensionless number ranging from 0.01 to 99.99, indicates the percent change in depth in each grid and is defined as CI = 100(M-m)/M where m = the minimum depth and M = the maximum depth within the grid square (Hui 1979). Grids that included a shoreline were assigned a minimum depth of 1 fathom (1.83 m). CI values were computed using a nautical chart and assigned to each grid square (Fig. 5). The range for CI was divided into five equal classes (1-19; 20-39; 40-59; 60-79; 80-99) and each grid was assigned to one of the classes according to its CI value (Table 2). The distribution of CI values was then compared to the expected distribution if sightings were independent of topography. The number of sightings expected to occur in each CI class if whales were randomly distributed with respect to the CI classes was calculated as follows: Ei = Ot Li/Lt, where Ei is the expected number of sightings in CI class I, Ot is the total number of observations, Li is the number of grid squares occurring in CI class I and Lt is the total number of squares. The expected distributions were compared to the observed distributions by using Chi-Square analysis. Contour Index has the advantage of being easy to compute for all scales once grid size is decided.

This analysis was conducted at three different spatial scales: small (67 grid squares of 9.25 x 9.25 km), intermediate (17 grid squares of 18.5 x 18.5 km) and large (4 zones of about 1450 km²), which can help determine at which scale the spatial distribution has a biological meaning (Diggle 1983).

The chi-square test was run for each year and for each scale.

Heterogeneity Chi-Square

Pooling of homogeneous data can result in a more powerful analysis (Zar 1999). Therefore, in addition to performing the twelve separate chi-square tests (one for each year), all values were totalled and a chi-square test was performed on these totals. In pooling these values, it is assumed that all twelve data sets came from the same statistical population, which would mean that whales behaved the same way with respect to topography every year. This was tested by a procedure called heterogeneity chi-square analysis, which uses the difference between the total of individual chi-square values and the chi-square for the total data. This difference is itself a chi-square value, with 1 degree of freedom.

Results

Twelve years of field work from 1989 to 2000, involving 1023 days of observation, yielded 6511 hours of effort at sea. This research effort produced 849 sightings of blue whales, 5291 of finback whales, 3822 of humpback whales and 6489 of minke whales (for a total of 16 451 sightings). Sightings for which surface feeding behaviour was actually observed numbered 1097.

Effort

Between years

Total time spent on the water per year ranged from 432.62 to 705.50 hours with an average of 563.64 hours. Average effort time per research day ranged from 6.63 to 7.91 hours with an average of 7.31 hours and was very homogenous (no statistical difference between years; p>0.25).

Within year

Within year

Average effort per day for each two-week period ranged from 5.77 to 8.39 hours. ANOVA revealed that biweekly effort means were not homogenous (p<0.001) with a peak during July and early August due to better weather conditions and longer days.

Mean depths

Depths for all sightings followed a normal distribution with a mean of 113.96 m and a standard deviation of 41.76 (Table 2). There was no need to log-transform the data (Fig. 5). When sightings were sorted by species, means for blue, finback, humpback and minke whales were 107.63, 109.09, 120.84 and 64.18 metres respectively. ANOVA showed there was a significant difference among the four species (P<0.001). Pairwise comparisons showed that the mean depths for humpback and minke whales were significantly different from the other species, but that the difference between finback and blue whales was not significant.

Despite normality of the data, the big difference in sample size and variance for the blue whale makes the comparison with the other three difficult. However, a non parametric test (Kruskal Wallis) yielded the same results (P<0.001). Finback and blue whales appear to be using the same depth profiles, whereas humpback whales seem to prefer slightly deeper waters on average and minke whales use shallower waters. However, this does not mean that the blue whales and finbacks use the same locations in space.

Spatial distribution

Results for the nearest neighbour test from the Animal Movement extension for ArcView (Hooge & Eichenlaub, 1997) are summarised in Table 4. For all species as well as for sightings with feeding behaviour, the null hypothesis of complete spatial randomness was rejected. Spatial distribution of the four species of whales in the study area was neither random nor uniform: it was clumped and selective.

Figures 6-10 show the spatial distribution of each species in the study area, in the form of both distribution plots and kernel densities of sightings. Each dot on the plots represents one sighting, although at this scale several dots can be hidden beneath one

another. For this reason and because the plots become confusing when there are too many dots in the same area, it is clearer to use the densities of sightings for interpretation.

Blue whale sightings are more numerous in two main areas: on the series of banks located along the North Shore and on the northwestern Anticosti shelf (Fig. 6). Finback whale sightings are more numerous and widespread than blue whales, but the density map reveals three main areas of concentration: the banks along the North Shore, the northwestern and the northeastern Anticosti shelve (Fig. 7). Overall, it is a distribution very similar to that of the blue whale. Humpback whales are less abundant than blue and finback whales along the North Shore. They make similar use of the northwestern and northeastern Anticosti shelves, but they are also found in significant numbers on the southwestern Anticosti plateau and on Parent Bank, ten kilometres to the west of Anticosti Island (Fig. 8). Minke whales have a strikingly different distribution. Although found along the North Shore and along the northern side of the Anticosti shelf, they are mainly concentrated in the Mingan archipelago (Fig. 9). Sightings for which feeding behaviour was observed are mainly distributed along the North Shore and north of Anticosti (Figs. 10).

Expected distributions were compared to observed distributions according to CI class using Chi-Square analysis. Data met the necessary conditions (no class had less than five observations) of this parametric test for goodness of fit (Zar 1999). At small and intermediate scales, aggregations of rorqual whales in the study area did not occur uniformly among CI classes, for all species combined as well as for each species taken separately (Tables 4 and 5, P<0.001). However, the results vary according to species.

At the smallest scale, sightings of rorqual whales were less abundant than expected in the low CI class (20-39), slightly more abundant than expected in the average CI class (40-59) and more abundant than expected in the high and very high CI classes (60-99). For blue, fin and humpback whales, sightings were less numerous than expected in the lowest (20-39) and highest (80-99) CI classes, and more numerous than expected in the average and high CI classes (40-79). Sightings of minke whales were much less than expected in the low and average CI class (20-59), close to expected values in the high CI class (60-79), and much higher than expected in the highest CI class (80-99). Sightings for which surface feeding behaviour was observed were less numerous than expected in low, average and high CI classes (20-79) and more abundant than expected in the highest CI class (80-99).

Similarly, at intermediate scale, sightings of rorqual whales were less abundant than expected in the average CI classes (40-79), and more abundant than expected in the highest CI class (80-99).

At large scale, CI for each grid square fell in the same range. Because of this, no test for goodness of fit could be done, even when subdividing the CI into smaller classes (e.g. classes of 5 or 10). Instead, total number of whales per grid square as well as average number of whale per research day and per grid square were compared using an ANOVA and found to be statistically different (p<0.001).

Heterogeneity test

Pooled and independent chi-square tests for each year all yielded the same results. Heterogeneity chi-square was not statistically different from zero (p>0.25), showing that there was no between-year variability and that we were justified in pooling all years together. Data for each year thus came from the same statistical population, which means that the whales behaved the same way with respect to topography each year.

Discussion

Spatial distribution and topography

Distribution of rorqual whales in the study area was neither random nor uniform but clustered. Whales spend the summer and fall in the Gulf of St. Lawrence for foraging and feeding purposes (Sears 1980, Simard & Lavoie 1999). Distribution of their main prey items (euphausiids and small fish) is patchy (Simard & Lavoie 1999), so finding that distribution of whales was patchy was reasonable to expect. Results show that the average depths where these aggregations occur fall between 60 and 110 m. Feeding behaviour and diving capabilities of baleen whales indicate that most activity occurs within the upper 100 m of the water column on the feeding grounds (Gaskin 1982), which is consistent with the mean depths obtained in this study and therefore with the idea that these clustered patterns are associated with feeding. Moreover, the distribution of sightings for

which feeding behaviour was observed mirrored the overall distribution of the four species very closely, involving the same core areas and yielding the same statistical results.

The four species of rorqual whales were found mostly over areas of high topographic variability. This preference was shown at both small and intermediate scales but was not apparent at a larger scale. Levels of statistical significance for the Chi-Square tests were very high (p<0.001), which can be explained in part by the large sample size. Also, results were consistent over the last 12 years. Thus they can be accepted with confidence. These results are similar to those obtained for finback and right whales (Hoelzel *et al.* 1989, Woodley & Gaskin 1996) and for minke whales (Naud 2000), although at different scales. They can also be compared to studies of odontocetes (Hui 1979, 1985, Watts & Gaskin 1985, Jaquet & Whitehead 1996) that show similar correlations between topography indices and spatial distribution.

In the study area, higher topographic variability (higher CI) is associated with the presence of banks and shelves (along the North Shore and west of Anticosti Island), or with the edge of the northern shelf of Anticosti. These are areas of upwelling (Rose & Leggett 1988). Rapid declines in nearshore sea temperatures of up to 10°C within a few days occur during the summer. These upwellings can be induced on a permanent basis by the Labrador current coming into contact with the underwater topography of the Mingan Islands, on a periodic basis in the case of tidally induced upwellings, or they can be episodic in the case of wind-induced conditions. Examination of satellite images of sea surface temperature confirm that nearshore bands of cold water occur periodically during the summer and the presence of patches showing high levels of primary productivity is further evidence of upwelling along the North Shore (Rose & Leggett 1988). The predominant westerly and southwesterly winds over the region also favour upwelling along the Shore.

Under all circumstances (current-, tide- or wind-induced), the effects of these local upwellings are similar. These dynamics regulate local primary production processes and the transport of energy through their influence on krill and fish migration (Rose & Leggett 1988). Upwellings enhance the abundance of krill along the slope of the shore. Krill forced in shallow areas, such as the shelves bordering the Quebec North Shore or

Anticosti concentrate near the bottom when swimming down to avoid the more intense light levels at the surface. By being more conspicuous and unaccustomed to higher light levels, the krill become easier prey for their predators, notably baleen whales and both bottom and pelagic fishes (Simard & Lavoie 1999).

When fish are exposed to temperature gradients, they tend to concentrate within narrow thermal zones by changing their spatial distribution pattern. They display behavioural thermoregulation through preference and avoidance responses. Capelin have a lower temperature limit well over 0° C during both spawning and feeding periods and aggregate in response to rising cold intermediate waters during strong upwelling events (Ings *et al.* 1997). When the Cold Intermediate Layer (CIL) upwells, capelin avoid the cold water (<2°C) and instead remain in the warmer waters bordering the CIL to which they are acclimated. The thinning of the warm surface layer caused by the cold-water upwelling may cause the capelin to concentrate near the surface in the warmer water. When fish approach the surface, they may swim downwards to reduce exposure to visual predators (Appenzeller & Legget 1995), likely enhancing the aggregation process. Then, when the CIL reaches the surface, fish swim away from it horizontally (Marchand *et al.* 1999). Therefore, concentrations of capelin can be expected at upwelling fronts, where cold waters limit both their vertical and horizontal distribution.

Many fronts associated with fish aggregations are regularly observed in the upstream portion of the shallow waters bordering the Laurentian Channel (Marchand *et al.* 1999). Bottom topography coupled with tidal forcing plays a major role in the formation and location of such fronts (Ingram 1985). Marchand *et al.* (1999) showed that at the head of the Laurentian Channel, the location and timing of some capelin aggregations in the upper water column are predictable. For predators, there is a high probability of detecting dense capelin concentrations in frontal areas at such times.

Frontal systems and upwelling are known to affect distribution patterns of whales by influencing the distribution of their prey (e.g., finbacks, Viale 1991; minke whales, Gaskin 1982). Whales and seabirds capitalize on these predictable barriers by developing strategies of capture that optimise their feeding success. Thus, a key factor making the area attractive for marine mammals is the aggregation of krill and its link with other abundant prey species, especially capelin. The need of cetaceans for highly concentrated food is well documented (Nemoto 1970; Brodie et al. 1978). Predators use many cues to

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minimize search effort for food. For animals relying on large concentrations of prey, such as schools of fish and baleen whales, aggregations of food at a wide range of scales minimize energy lost in searching activity. Dense patches are of little interest if they are not embedded in an area where the probability of encountering other dense patches is also high. Feeding grounds are such areas where rich food patches are strongly autocorrelated (Kawamura 1980). There is high risk in leaving a feeding ground as well as displacement cost. This should impose limits to short- to mid-term displacements during the feeding season and favour a certain degree of site fidelity. This type of predator concentrates in a decreasing food environment, up to a point where they have to leave to find a new feeding ground unit. The mesoscale assemblage of feeding ground units then becomes important (Simard & Lavoie 1999). Whales have the advantage of being informed of the locations of these feeding grounds through infrasound calls from distant individuals.

In the case of sperm whales, movements of groups of females are related to feeding success. When feeding success is high, groups zigzag back and forth over areas a few tens of kilometres across, whereas when success is low, they move in straight lines at speeds of about 100 km/day. Residence time within an area a few tens or hundreds of kilometres across is therefore highly variable and strongly correlated with feeding success. Such movement patterns can lead to a system of density-dependant habitat selection in which animals tend to distribute themselves geographically so that feeding success is roughly equal everywhere (MacCall 1990).

In the present study, no correlation between topography and whale distribution was found at large scale. Contour Index as defined by Hui (1979, 1985) was used at a small scale (similar to the small scale in the present study) and has never been used at large scale. When computed for the large scale, values of relative depth change were all very high and fall in the same category, making comparisons difficult. Hui's measure of topographic variability might therefore be ill-suited for large scales in coastal regions. It may also be that the topography of our research area was too homogenous at this scale. However, distribution of sightings was not homogenous even though topography was. Therefore, the patterns that were observed at small and intermediate scales were not present at a large scale. It is likely that the scale of local phenomena of upwelling and their influence on whales is too small to be detected at the large scale.

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The present study considers only summer and early fall distribution (June to October). It is noteworthy that most of the data available on plankton and nekton in the Gulf and Estuary of the St. Lawrence have been collected during summer surveys, thus limiting our understanding of the effects of winter conditions (White & Johns 1997). Although this is a major deficiency in our knowledge of the Gulf and Estuary system, it does not have an impact on this study. Within-year variations were not taken into account. Spatial distribution was studied in relation to topography, a factor that does not vary with time. The effects of topography on whale dispersal patterns are believed to be a result of the interactions between topography and movements of water masses. These movements can result from constant events such as the Labrador current, periodic events such as time of tides and tidal amplitude, or episodic parameters such as direction and strength of winds. Therefore, if such data are compared with whale distribution on a small enough time scale, correlations should be expected. One difficulty of obtaining such data is that local factors within the Gulf often mask normal monthly and yearly variation for parameters such as temperature and salinity (White & Johns 1997).

Effort from year to year was very even, which allowed us to compare the different years; if there had been any between-year difference in the spatial distribution, it could not have been attributed to heterogeneity of effort over the twelve years of research. Within-year effort was not homogenous, with more time spent on the water during the months of July and August. Since within-year variation was not investigated in this study, it is assumed that this does not affect the results or their interpretation.

Differences in distribution patterns

The distribution maps outline differences in the dispersal patterns of the four species. Unlike minke whales, blue, fin and humpback whales appear to avoid shallow areas, despite their high Contour Index. Blue whales have only rarely been seen within the Mingan Archipelago in 22 years (Sears, personal communication). Adult humpbacks are rarely seen among the islands but juveniles sometimes occur there, perhaps because of their smaller size, although social factors such as exclusion from hunting with the large groups of adults may also be involved. Finback whales are also rare within the islands, but on several occasions (especially in July 1995 and July 2000), large groups came into the shallow waters of the archipelago to feed. Although found in all areas where the other
species are found, it is clear from the distribution maps, the mean depths and the CI test results that minke whales use shallow waters more than their larger relatives. They seem to concentrate mainly within the Mingan Islands. Their presence close to shore and in the archipelago explains why they have the highest CI use of all species.

Shallow areas appear to be avoided by the three larger species and not by the smallest one. The minke whales' smaller size and greater agility could allow them to exploit a more varied habitat. Different hunting techniques may also explain this difference. Minke whales use the shape of the sea bed to their advantage when hunting, using submarine trenches, shelves and walls as well as the incline of the beach to herd their prey (Hoelzel *et al.* 1989). Their presence in the archipelago can be linked to its very variable topography which aids their hunting. This is likely more important for minke than for blue whales which do not hunt fish, and for fin and humpback whales which use cooperative techniques.

Competition, not predation, is the main limiting factor for medium or large piscivores (Hairston *et al.* 1960, Schoener 1989). Considering their level in the food chain, rorqual whale distribution patterns are likely more influenced by competition than by predation. Field observations confirm this as in 22 years of research in the study area, predation upon blue, fin or humpback whales has never been witnessed. Predation on minke whales by killer whales, on the other hand, has been observed eight times (MICS, unpublished data; Wenzel & Sears, 1988). Nevertheless, observations of killer whales in the Gulf of St. Lawrence are increasingly rare and are now exceptional anywhere but in northeast Gulf and the strait of Belle-Isle (MICS, unpublished data). Predation was virtually absent from the study area and therefore can be dismissed as an intermediate scale distribution factor for these species.

Interspecific competition occurs when two or more species inhibit or interfere with one another as a result of the common use of resources (Schoener 1989). Minke whales may prefer to forage in the islands where competition from larger rorquals is almost nonexistent. Development of hunting techniques adapted to shallow conditions may reduce overlap of these animals' realised niches and therefore competition. Overall, there was significant overlap in whale distribution patterns and no data on what the animals were eating for each specific sighting, thus making it impossible to test an hypothesis of competitive displacement in this study.

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Conclusion

Zooplankton aggregations lead to predator concentrations, especially for pelagic fish and whales during their feeding season. Understanding these locally rich areas, where large scale production is concentrated and transferred to higher trophic levels, is essential for a comprehensive view of the ecosystem. With the help of new technologies, recent studies have put more emphasis on understanding the factors controlling spatio-temporal distribution of cetaceans at small and intermediate scales. In this study, 12 years of sighting data from the Mingan Island Cetacean Study were plotted and analysed for four species of rorqual whales.

Rorqual whales in the study area had a clustered distribution linked to areas of highly variable topography, believed to be associated with local phenomena of upwelling. These upwelling areas appear important not only because of increased productivity and therefore food availability but mostly because they are responsible for aggregations of both krill and fish. The concentrations of food probably maximise foraging and feeding efforts of the whales.

Correlations between topography and whale distribution were found at small and intermediate scales (9.25 - 18.5 km grid squares) but were lacking at a larger scale, possibly because the large scale used in this study (1450 km^2) did not correspond to patch size for aggregations of both predators and prey, and therefore did not reveal small scale relationships.

Distribution maps showed differences between species, of which the most important was the presence of minke whales in shallow waters that appear to be avoided by the larger species. Although differences in size, diet, hunting techniques or competitive displacement can be proposed as responsible for these specific dispersal patterns, these hypotheses remain speculative and untested.

Overall, it is possible to use topography to explain why rorqual whales in the study area choose certain locations and to predict other sites of interest to them. However, it is harder to explain why one of these sites is chosen over another on a daily basis. More research is needed to understand what other environmental factors influence whales in their choice of feeding sites among all the sites of potential interest. Other areas in the St. Lawrence (Estuary, Gaspesie, Strait of Belle-Isle) should be studied in a similar way to provide comparisons and help to confirm or refute the findings of this work. Twodimensional numerical models of the M, tide in the Gulf and Estuary of the St. Lawrence are available (e.g. Pingree & Griffiths 1980) and could be used to predict frontal regions separating areas of well-mixed waters from areas showing pronounced summer stratification. Marked increases in biological productivity may be associated with upwelling and mixing in these regions. Satellite images can be useful for predicting the location of such mesoscale fronts between water masses, given the cold signature of the intermediate layer. The 1-km² resolution should be sufficient to predict the locations of large fish concentrations that attract predators (Marchand et al. 1999). Future studies involving long-lived satellite tags and acoustic studies of spatial distribution capable of identifying individuals and behaviour should provide useful insights. Also, extensive databases of oceanographic and biological data (temperature profiles, salinity, chlorophyll densities, productivity estimates, movements and distribution of food items) with a fine resolution in both time and space would be very helpful to detailed ecological studies of cetaceans.

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Reference	Species	Scale	Торо	UpW	Temp	Salt	Prey	Prod
Brown & Winn 1989	Bg	S			0			
Darling et al. 1998	Er	Ι					+	
Davis et al. 1993	Pm	L						+
Fieldler et al. 1998	Bm	S/I		+	+		+	+
Foerster & Thompson 1985	Cetacea	I		+			+	
Gaskin 1968	Ds	L			+			
Griffin 1997	Ds	S/I						+
Griffin 1999	Pm	S/I			+			+
Gulland 1974	Myst, Pm	L		+				+
Hui 1979	Ds	S	+					
Hui 1985	Dd, Gm	S	+					
Jacquet & Whitehead 1999	Pm	S	0				0	
Jaquet & Whitehead 1996	Pm	L	+		8			+
Karczmaki et al. 2000	Ds	S	+					
Kenney & Winn 1987	Cetacea	S	0					
Kenney &Winn 1986	Cetacea	Ι					+	
Kingsley & Reeves 1998	Lac	I	+					
Mate & Stafford 1994	Lac	I	+					
Mayo & Marx 1989	Bg	S					+	
Moses & Finn 1997	Bg	I	+		+			
Murison & Gaskin 1989	Bg	S					+	
Nemoto 1959	myst	L					+	
Payne et al. 1986	Mn	Ι					+	
Payne et al. 1990	Myst	Ι					+	
Piatt et al. 1989	Myst	S					+	
Polachek 1987	Ds,Pm	L			+			
Reilly & Fielder 1994	Ds	L			+	0		
Selzer & Payne 1988	Dd, Lac	I	+					
Silber et al. 1994	Cetacea	1	·		0			
Smith & Whitehead 1993	Pm	Ι		+	+			
Smith & Gaskin 1983	Рр	Ι					+	
Tershy et al. 1991	Cetacea	Ι			+			
Watts & Gaskin 1985	Рр	S			+		+	
Weinrich et al. 1997	Mn	I						+
Whitehead & Carscadden 1985	Myst	L					+	
Woodley & Gaskin 1996	Bg, Bp	S	+				+	

 Table 1:
 Review of 36 studies showing correlation between environmental factors and cetaceans distribution

Species Key:

Ba: Minke whale (Balaenoptera acutorostrata)
Bg: North Atlantic right whale (Balaena glacialis)
Bm: Blue whale (Balaenoptera musculus)
Bp: Finback whale (Balaenoptera physalus)
Cetacea: Cetacean species
Ds: Dolphin species
Er: Gray whale (Eschrichtius robustus)
Gm: Short-finned pilot whale (Globicephala melas)
Mn: Humpback whale (Megaptera novaeangliae)
Myst: Mysticete species
Odon: Odontocete species
Pm: Sperm whale (Physeter macrocephalus)

Pp: Harbour porpoise (Phocoena phocoena)

Scale Key:
L: Large
I: Intermediate
S: Small

Factors: Topo: Topography UpW: Upwelling Temp: Temperature Salt: Salinity Prey: Prey items Prod: Productivity

Results:

+ : Correlation found 0: No correlation found

 Table 2:
 Minimum, maximum and mean depths of rorqual whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)

	Blue whale	Fin whale	Humpback whale	Minke whale	All species
Number of sightings	849	5291	3822	6489	16 451
Minimum depth (m)	24.128	3.8	8.2	1.9	1.9
Maximum depth (m)	206.016	297	239.4	297	297
Mean depth (m)	107.63	109.09	120.84	64.18	113.96
Standard deviation	40.709	36.526	34.804	41.133	41.76

 Table 3:
 Results of the nearest neighbour test for Complete Spatial Randomness on rorqual whale sightings from the Gulf of St. Lawrence (data collected between 1989 and 2000)

Blue whale	Fin whale	Humpback whale	Minke whale	All species	Sightings with feeding
849	5291	3822	6489	16 451	1097
0.561907	0.800565	0.915766	0.790343	0.638924	0.211028
-10.02234	-27.8781	-10.0351	-29.6092	-32.7926	-63.4775
0.001	0.001	0.001	0.001	0.001	0.001
	Blue whale 849 0.561907 -10.02234 0.001	Blue whaleFin whale84952910.5619070.800565-10.02234-27.87810.0010.001	Blue whaleFin whaleHumpback whale849529138220.5619070.8005650.915766-10.02234-27.8781-10.03510.0010.0010.001	Blue whaleFin whaleHumpback whaleMinke whale8495291382264890.5619070.8005650.9157660.790343-10.02234-27.8781-10.0351-29.60920.0010.0010.0010.001	Blue whaleFin whaleHumpback whaleMinke whaleAll species84952913822648916 4510.5619070.8005650.9157660.7903430.638924-10.02234-27.8781-10.0351-29.6092-32.79260.0010.0010.0010.0010.001

Table 4: Results of the Chi-Square tests comparing expected and observed number of rorqual whale sightings in each of the Contour Index classes at small scale (data collected in the Gulf of St. Lawrence between 1989 and 2000)

		Blue whales Finback whales				Humpback whales			N	Minke whales			All species			Feeding behaviour			
CI Class	Nb of grids	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²
0.01-19.99	0	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a
20.00-39.99	10	125	55	39.2	776	295	298.15	561	254	168	952	84	791.42	2413	688	1233.16	161	18	127.01
40.00-59.99	14	170	218	13.55	1058	1502	188.86	764	1225	278.17	1298	588	388.37	3290	3533	17.95	219	134	32.99
60.00-79.99	13	158	253	57.12	988	1340	125.41	713	1060	168.88	1211	1140	4.16	3071	3793	169.74	205	66	94.25
80.00-99.99	30	396	323	13.45	2469	2154	40.19	1784	1283	140.7	3028	4677	898.02	7677	8437	75.24	512	879	263.06
Total	67	849	849	123.32	5291	5291	652.61	3822	3822	755.75	6489	6489	2081.97	16451	16451	1496.09	1097	1097	517.31
X ² for pooled data (df=3, tabulated X	a^2 at a = 0.001 is	16,266)		123.32		_	652.61			755.75		:	2082			1496.09			517.31
X ² for independent (df=3, tabulated X	t tests a^2 at a = 0.001 is	16,266)		122.71			649.2			753.27			2079.18			1492.9			516.21
Heterogeneity X ² (df=1, tabulated X	a^2 at a = 0.05 is 3	.841)		0.61			3.41			2.48			2.82			3.19			1.1

Table 5: Results of the Chi-Square tests comparing expected and observed number of rorqual whale sightings in each of the Contour Index classes at intermediate scale

		Blue whales			Blue whales Finback whales					Humpback whales N			Minke whales			ecies	Feeding behaviour			
CI Class	Nb of grids	Exp	Obs	X ²	Exp	Obs	X^2	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²	Exp	Obs	X ²	
0.01-19.99	0	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	
20.00-39.99	0	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	0	n/a	0	· 0	n/a	
40.00-59.99	2	100	20	64	622	321	145.66077	450	221	116.53556	763	215	393.58322	1935	777	693.004651	129	24	85.465116	
60.00-79.99	2	100	83	2.89	622	589	1.7508039	450	479	1.8688889	763	313	265.39974	1935	1464	114.646512	129	79	19.379845	
80.00-99.99	13	649	746	14.497689	4047	4381	27.56511	2922	3122	13.689254	4963	5961	200.68588	12581	14210	210.924489	839	994	28.63528	
Total	17	849	849	81.387689	5291	5291	174.97669	3822	3822	132.0937	6489	6489	859.66884	16451	16451	1018.57565	1097	1097	133.48024	
X ² for pooled data (df=3, tabulated X	a^{2} at a = 0.001 is	16,266)		81.388			174.98			132.09			859.67			1018.576			133.48	
X ² for independent (df=3, tabulated X	t tests r^2 at a = 0.001 is	16,266)		80.63			171.23			130.11			855.98			1015.23			132.71	
Heterogeneity X^2 (df=1, tabulated X	a^2 at a = 0.05 is 3	.841)		0.758			3.75			1.98			3.69			3.346			0.77	

Figure 1: Map of Atlantic Canada showing the location of the study area

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Figure 2: Map of the Gulf of St. Lawrence showing zones of maximum primary production and nutrient concentrations in surface water (adapted from Koutitonsky & Bugden 1991)



Figure 3: Map of the northern Gulf of St. Lawrence showing submarine topography

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Figure 4: a. Map of the study area showing the grid squares used for the calculation of the Contour Index values at small scale
b. Map of the study area showing the grid squares used for the calculation of the Contour Index values at intermediate scale
c. Map of the study area showing the grid squares used for the calculation of the Contour Index values at large scale



Figure 5: Histograms of the depths of rorqual whale sightings, sorted by species (data collected in the Gulf of St. Lawrence between 1989 and 2000)

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All species







0.2

0.1

____0.0 300 Proportion per Bar

300

200

100

0 L 0

Count









100 200 Depth (m)



Figure 6: a. Distribution plot of blue whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)
b. Density of blue whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)



Figure 7: a. Distribution plot of finback whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)
b. Density of finback whale sightings (data collected in the gulf of St. Lawrence between 1989 and 2000)


Figure 8: a. Distribution plot of humpback whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)
b. Density of humpback whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)



Figure 9: a. Distribution plot of minke whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)
b. Density of minke whale sightings (data collected in the Gulf of St. Lawrence between 1989 and 2000)



Figure 10: a. Distribution plot of rorqual whale sightings for which feeding behaviour was observed (data collected in the Gulf of St.
Lawrence between 1989 and 2000)
b. Density of rorqual whale sightings for which feeding behaviour was observed (data collected in the Gulf of St. Lawrence between 1989 and 2000)

