Habitat Selection and Niche Characteristics of Rorqual Whales in the Northern Gulf of St. Lawrence (Canada)

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February 2008

A thesis submitted to McGill University in partial
fulfilment of the requirements of the degree of
Doctor of Philosophy

Abstract

Habitat selection influences the distribution patterns of animals and how they partition their ecological niches. However, studies of habitat selection seldom model temporal variability and focus primarily on terrestrial ecosystems where habitat patches change over comparatively long time scales. In marine ecosystems, ignoring the time-varying characteristics of habitats might lead to a poor understanding of ecological relationships.

Blue (*Balaenoptera musculus*), finback (*B. physalus*), humpback (*Megaptera novaeangliae*) and minke (*B. acutorostrata*) whales occur in sympatry in the Gulf of St. Lawrence (Canada) during the feeding season. I combined boat surveys with remote-sensing technology and computer ocean models to study habitat selection and niche characteristics of these rorqual whales for the years 1997-2002.

All four species responded to the temporal variability of their environment by selecting a combination of time-varying and static factors that differed from the available habitat and were likely linked with prey availability, namely shallow banks, steep seabed slope, cold and saline surface waters, deep and cold intermediate layer. Moreover, distribution of whale sightings was highly correlated with thermal fronts, a dynamic meso-scale process that increases biological productivity and aggregates prey.

Spatial distribution differed among species, likely reflecting differences in feeding strategies that could have evolved to alleviate inter-specific competition. There was clear spatial partitioning of the habitat use between species, and some separation in time. Fine-scale selection of dynamic variables appears to be the main mechanism facilitating co-occurrence. Minke whales had a specialised niche centred on shallow coastal waters. Deeper offshore waters and a colder intermediate layer characterised the niches of finback and humpback whales. The endangered blue whale had the narrowest niche, characterised by high salinity cold surface temperature and slow currents. This likely results from its specialised diet and may render it vulnerable to environmental change and competitive pressure.

In humpback whales, inter-individual variation was an important part of intra-population variation and contributed to the large niche width of that species. Individual specialisation, probably at the level of foraging techniques and diet preferences, could be an important mechanism for finer subdivision of the species' niche.

These findings greatly increase our understanding of habitat selection in rorqual whales, and encourage a wider use of dynamic environmental variables in future studies and management plans.

Résumé

La sélection de l’habitat influence la distribution des animaux et la manière dont ils coexistent. Cependant, les études prennent rarement en compte la variabilité temporelle et se penchent surtout sur les écosystèmes terrestres où les caractéristiques évoluent sur des échelles de temps relativement longues. Dans les écosystèmes marins en revanche, ignorer le caractère dynamique de l’habitat peut conduire à une mauvaise compréhension des relations écologiques.

Des rorquals bleus (*Balaenoptera musculus*), communs (*B. physalus*), à bosse (*Megaptera novaeangliae*) et des petits rorquals (*B. acutorostrata*) se rencontrent en situation de sympatrie dans le golfe du Saint-Laurent (Canada) durant leur saison d’alimentation. J’ai combiné des relevés en bateau avec des technologies d’échantillonnage à distance et des modèles informatiques du Saint-Laurent pour étudier la sélection de l’habitat et les niches écologiques de ces rorquals entre les années 1997 et 2002.

Dans ma zone d’étude, les quatre espèces répondaient à la variabilité temporelle de leur environnement en sélectionnant une combinaison de facteurs dynamiques et statiques qui différaient de l’habitat disponible et étaient liés à la disponibilité de leurs proies : bancs peu profonds, topographie sous-marine pentue, eaux de surface froides et salées, couche intermédiaire plus froide et plus profonde. De plus, la distribution des observations de baleines était hautement corrélée avec les fronts thermiques, un processus dynamique qui augmente la productivité biologique et regroupe les proies.

Les schémas de distribution spatiale différaient entre les espèces, reflétant probablement des différences de stratégie alimentaire apparues afin d’alléger la compétition interspécifique. Les quatre espèces semblaient se partager l’habitat dans l’espace et dans le temps, principalement au moyen d’une sélection à petite échelle des variables dynamiques. Les petits rorquals avaient une niche très spécialisée, centrée autour des eaux côtières peu profondes. Les niches des rorquals communs et à bosse se caractérisaient par des eaux plus profondes et plus loin des côtes, et par une couche intermédiaire plus froide. Le rorqual bleu, considéré en voie de disparition dans les eaux canadiennes, avait une niche caractérisée par de rares combinaisons de variables dynamiques, ce qui résulte sans doute de son régime alimentaire spécialisé et pourrait le rendre plus vulnérable aux changements climatiques et à la pression de la compétition.

Chez les rorquals à bosse, la variabilité inter-individuelle semble représenter une part importante de la variation intra-population. La spécialisation individuelle, vraisemblablement au niveau des techniques de chasse et du régime alimentaire, pourrait donc constituer un mécanisme permettant une division plus poussée de la niche de l’espèce.

Ces résultats améliorent considérablement notre compréhension de la sélection de l’habitat par les rorquals et soulignent l’importance d’inclure des variables environnementales dynamiques dans de futures études et plans de gestion.

Acknowledgments

One does not study big, wet, cryptic and temperamental animals for five years without getting dangerously indebted to a large number of people.

I would like to thank my academic supervisors, Dr. Dominique Berteaux and Dr. Murray Humphries. Dominique, you believed in me and in this project from the start; without your trust, your encouragement and your friendship, this project would not have existed. Murray, I want to thank you not only for your support and your open-mindedness, but also for broadening my scientific interests; the theoretical framework of this thesis owes a lot to your intellectual influence.

I want to thank Richard Sears for giving me the opportunity not just to do this project but also to fulfil a childhood dream. Richard, I still don’t know why, twelve years ago, you hired a well-mannered Parisian boy with no experience to work in your crazy research station, but I know I would not be doing this if it was not for you. You have been a mentor and a friend ever since, and I hope that this thesis will show you that your trust was not misplaced.

Thank you to Pierre Larouche from the Maurice-Lamontagne Institute for the satellite maps of surface temperature and for a very fruitful collaboration. Pierre, you were the first to provide me with environmental data and your trust was a huge encouragement. I am also incredibly indebted to François Saucier at ISMER for generously providing the environmental data on which three quarters of my analyses are based. By letting me benefit from your computer ocean model of the Gulf of St. Lawrence, you allowed me to propose a much more ambitious and thorough analysis of habitat selection, and to better model the complex relationships between whales and their environment.

I thank David Sergeant for his friendship, advice and encouragement over all my graduate years. Dave, I have enjoyed our exchanges thoroughly and I thank you for your interest in my research. I am also very

grateful to Rodger Titman for his continuous support, his kindness and his tutelage over the years. Rodger, you gave me a wonderful opportunity back when most doors were shut and I shall never forget it.

I want to thank all the interns and team members of the Mingan Island Cetacean Study. The cumulative result of their incredibly vast data collection effort is the only thing that makes projects like mine possible. For their support and friendship, thanks in particular to: Sylvie Angel, Alain Carpentier, Julien Delarue, Clothilde Kussener, Aude Lalis and Arnaud Tarroux. A special thought goes to Catherine Berchok, who taught me most of what I know about safely working at sea, including among other small things how to rescue somebody who falls overboard in ten-foot waves. Another thought goes to Daniel Grenier who welcomed me at the station with his generous, wise and calm nature, and who let me use his beautiful drawings in this thesis.

Of all my teammates, I have to give a special thank-you to Christian Ramp, for great times on the water and elsewhere (including various remote, isolated, foggy communities), and for useful advice on earlier drafts of the main chapters. Chris, Montreal is simply not the same without you. Also, your intimate knowledge of the humpback data allowed me to increase my sample size and avoid mistakes.

I want to thank everybody in the Wildlife Energetics and Ecology Lab at McGill for welcoming me and giving me a home in the department, and for reviews on numerous manuscripts: Quinn Fletcher, Stacey Jarema, Paul Jensen, Tricia Kerr, Manuelle Landry-Cuerrier, Meghan Larivée, Marianne Marcoux, Heather Milligan, Troy Pretzlaw, Sonja Ostertag, Jason Samson and Sarah Woods. Thank you for your warmth and friendship, for the stimulating discussions, and for all the cartons of chocolate milk.

I would like to thank Donna Hauser for trusting me with unpublished material and for fruitful exchanges about study designs and data collection. Thank you to Alain Caron from UQAR for statistical assistance

and many nudges in the right direction. Thank you to Louis Lefebvre for his sound advice while sitting on my comprehensive exam. Thank you also to Julien Martin for his patient statistical advice and for crash courses in how to use R. And many thanks to Marie Kubecki, who became my guardian angel from my very first day in the department and who had an answer to every single question I ever asked her.

Funding for this project was scarce, which is why I am all the more grateful for the generous support of the J.W. McConnell foundation and the Department of Natural Resource Sciences at McGill. I also received loans and scholarships from the “Programme d’Aide Financière aux Études” of the Quebec government.

Finally, I have benefited from incredible support from my family. Mum, dad, I have accomplished what I always dreamed of thanks to your open-mindedness and your encouragements at every step of the way. I also want to thank my godfather Jean-José Richer for his love and his generosity: Jojo, your financial support made a real difference when things got rough. And I thank Victor D-V for that extra little bit of motivation in the final year!

Camille, I simply cannot find the words to thank you enough for your loving, enduring support, your patience and your trust in me. You are a wonderful companion and an incredible mother to my son. I cannot wait to see what the future has in store for us.

Remarks on style and contributions to knowledge

This is a manuscript-based thesis. Chapters 2, 3, 4 and 5 have been written in manuscript format to facilitate publication in peer-reviewed journals. Therefore, some repetition occurs between chapters, especially in the literature reviews, methods and data sets.

Chapter 2 has been published as: Doniol-Valcroze T, Berteaux D, Larouche P, Sears R. (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. Marine Ecology Progress Series 335:207-216.

This thesis contains several elements that constitute original scholarship and contribute to the advancement of knowledge in its field. I was able to quantify habitat selection and niche partitioning of four cetacean species while considering not only the spatial variability but also the temporal dynamics of the available habitat. To my knowledge, this has not been achieved previously for any cetacean species.

Specifically, chapter 2 provides the first evidence of a direct link between the distribution of rorqual whales and the location of ephemeral surface thermal fronts that are believed to act as a fine-scale aggregation mechanism for prey.

Chapter 3 demonstrates for the first time that, in the marine environment, models of habitat selection with time-varying factors perform better than those that include only static factors. This was achieved using a constrained regression model that, to the best of my knowledge, had never been applied before to marine habitats.

Chapter 4 proposes the first description of niche partitioning by cetaceans with direct quantification of niche breadth and overlap in multi-dimensional environmental space.

Chapter 5 proposes the first quantification of individual variability in patterns of habitat use for any whale species. This was achieved by adopting a multivariate technique initially developed for the separation of species to the separation of individual niches.

The thesis also contributes to cetacean conservation efforts in the northern Gulf of St. Lawrence by describing for the first time the fine-scale distribution patterns and habitat associations of rorqual whales in this region. Such information is crucial to assess the biological requirements of these species and to identify areas of critical importance.

Contribution of Authors

Information from this thesis has been published or is currently in preparation to be submitted to peer-reviewed journals as co-authored manuscripts. This statement details the contributions of each co-author to the thesis.

Dr. Dominique Berteaux (Université du Québec A Rimouski) and Dr. Murray Humphries (McGill University) have provided academic supervision, statistical help and editorial assistance. Richard Sears (Mingan Island Cetacean Study) has provided the initial incentive for the project and support in the form of data and field logistics as well as general advice. Pierre Larouche (Institut Maurice-Lamontagne) has provided satellite maps of sea surface temperature and oceanographic expertise.

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1. General Introduction

1.1 Habitat selection and partitioning in a dynamic environment

A major goal of ecology is to understand how characteristics of the environment affect the distribution of organisms (MacArthur 1972). Habitat selection has a strong impact on these distribution patterns by influencing the use of habitat in both time and space. Differential habitat selection is also one of the principal mechanisms that allow species to coexist through partitioning of their habitat (Rosenzweig 1987). Studying habitat selection is therefore crucial to understand the ecology of species and the structure of communities. Habitat selection also has important implications for conservation and management, which depend on accurate information about the distribution of animals and the way these patterns change over time and space.

Studies of habitat selection have often focused on terrestrial ecosystems where habitat patches change over comparatively long temporal scales (Redfern et al. 2006). In marine ecosystems, habitats of mobile species can change over short time spans and fine[1] spatial scales (Bjørge 2002). This complexity poses unique challenges when trying to model species-habitat relationships. Studying habitat selection by marine mammals therefore generates additional challenges but can also improve our understanding of the general rules governing species distributions.

The Gulf of St. Lawrence in Eastern Canada constitutes a highly productive and complex system that contains some of the richest krill aggregations documented in the northwest Atlantic (Simard & Lavoie 1999). These large concentrations of food attract at least a dozen cetacean species to the area during the summer and autumn, including four species of rorquals (Sears et al. 1981): blue (*Balaenoptera musculus*),

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[1] In this study, I use the adjectives “fine” or “broad” to describe spatial scales, which place the term in the context of its ecological meaning (Levin 1992) and prevents confusion with the corresponding use of “large” and “small” by geographers (Corsi et al. 2000).

finback (*B. physalus*), humpback (*Megaptera novaeangliae*) and minke (*B. acutorostrata*) whales. Although the life histories of these whales are fairly well known (e.g. Fontaine 1998), there is very little information about their patterns of use, selection and partitioning of habitat at fine scales. The occurrence of these four sympatric and closely related species of rorqual whales in the St. Lawrence represents a rare opportunity to better understand mechanisms of habitat selection and coexistence in a complex, dynamic environment. Better and more spatially explicit research efforts are also needed to ensure protection and management of these species, which include the endangered blue whale.

The aim of this Ph.D. project is to study factors that influence fine-scale distribution of rorqual whales in the St. Lawrence, and specifically patterns of habitat selection and partitioning. To this end, I first review general literature on habitat selection and partitioning, whale feeding ecology and previous studies on distribution and habitat associations of marine mammals. I then build on this review to propose the central working hypothesis and objectives of this project. I briefly explain the study design and the data sets that are common to all the chapters of this thesis. Finally I describe an outline of the thesis and the links between the chapters.

1.2 Literature review

Determining factors that influence the distribution of organisms is one of the central questions in ecology (MacArthur 1972, Wiens 2002). According to theory, main determinants of the distribution of large mobile animals like whales are habitat selection and niche partitioning (Krebs 2001).

1.2.1 Habitat selection

The concept of habitat, is sometimes considered one of the few unifying concepts in contemporary ecology and yet lacks a clear and consistent definition (Block & Brennan 1993). It is sometimes synonymous with ecosystem or used to describe the entire physical environment of areas that differ qualitatively from one another (Whittaker et al. 1973). Here, I define *habitat* as the collection of resources and conditions present in an area occupied by or available to a given organism (Hall et al. 1997). Habitat is therefore organism-specific in the sense that it relates the presence of a species, population or individual to the area's physical and biological characteristics (Garshelis 2000).

In this habitat, animals seek resources that are best able to meet their requirements for survival (Manly et al. 2002). Some habitats therefore have a higher suitability for a given species (Fretwell 1972), which confers higher fitness in evolutionary time (Rosenzweig & Abramsky 1986). Choosing the right habitats thus has adaptive value (Levin 1968). Natural selection acts upon a set of behaviours that allow organisms to use physical cues as proximate indicators of beneficial habitats (Wiens 1985). Taken together, these behavioural choices constitute habitat *preferences*. Although sometimes synonymous with selection (Garshelis 2000), preference is better defined as the degree to which one habitat or resource is chosen over another if offered on an equal basis (Johnson 1980), which includes innate preferences for resources not actually available (Peek 1986).

Because the true preferences of animals are usually impossible to determine in the wild (i.e. without experimental manipulation), they are often inferred from habitat *selection* (Garshelis 2000), which is defined as the *process* of choosing resources based on habitat preferences, resulting in the disproportional use of some habitat components over others (Johnson 1980). For mobile animals, it is a hierarchical process that operates at the level of the individual (Krebs 2001) and involves a series of behavioural decisions about what habitat components to use, from broad spatial scales to the local microhabitat (Wiens et al. 1986).

Habitat cues, time lags produced by environmental variation and presence of conspecifics and other species are all factors that can affect occupancy at the local level, turning the selection template into *realized* habitat selection (Wiens 1985). The result of this process is *habitat use*: the non-random utilisation of a collection of physical and biological habitat components (Hall et al. 1997). In spatially explicit analyses, habitat use can be represented by a probabilistic function in which higher density of observations represents higher use of habitat (Marzluff et al. 2004).

Thus, habitat use is the consequence of the selection process, which itself results from innate preferences for resources that yield better fitness (Garshelis 2000). In the context of whale ecology, I interpret these definitions as follows: the whales' habitat is the entire set of conditions and resources in the area where whales are observed. Within this habitat, patterns of whale density in space and time allow delineation of areas with high habitat use, and measurement of their characteristics. Selection can be inferred by comparison of used and available habitat. Characteristics of used habitat are then assumed to be representative of the whales' actual habitat preferences.

1.2.2 Niche partitioning

Habitat preferences can be ascertained across any gradient of available resource or environmental characteristic. Collectively, these preferences correspond to the *ecological niche* of the species, which Hutchinson (1957) defined as a hypervolume in the n-dimensional space of all the environmental factors acting on the organism. The space within this hypothetical hypervolume would thus represent the range of conditions where a species could exist (Pianka 1981).

This *fundamental* niche is the set of resources an organism can use in the absence of competition and other biotic interactions (Hutchinson 1965). However, natural ecosystems are composed of assemblages of coexisting species which interact with one another (MacArthur 1958). Areas in which a species is found frequently are thus not necessarily representative of optimal habitat because of these intra- and inter-specific interactions (Van Horne 1983). Competition, which can occur between any two species that use the same types of resources and live in the same habitats, can limit their distributions (Levin 1968). Competition can result from common exploitation of limiting resources or from interference in gaining access to resources (Krebs 2001).

Competition is common in natural populations (Schoener 1986, Gurevitch et al. 1992). According to the competitive exclusion principle, two species with identical niches are in complete competition and cannot coexist (Gause 1936), which could lead to the rapid extinction of many species (Hardin 1960). However, species can minimise competition by shrinking or moving their niche along environmental gradients until they reach limiting similarity (MacArthur 1972). In practice, potential competitors accomplish this by segregating in time, space and environmental resources (Chesson 2000). The resulting set of habitat variables constitutes the *realized* niche: the observed patterns of resource use in the presence of competition (Hutchinson 1965).

This process of differential resource selection is known as niche or habitat *partitioning* and is one of the principal mechanisms that allow species to coexist (Rosenzweig 1981). Even small ecological differences (e.g. diet specialisation) can allow closely-related species to minimise competition (Lack 1940, MacArthur 1958). Environmental heterogeneity can also help species coexist even if their requirements are very similar (Hutchinson 1961).

Inter-specific competition is not the only interaction that can modify an organism's niche. For most animals, the presence of conspecifics can be an important element of the environment (Whitehead 1999) and can influence habitat selection (Thomas & Taylor 1990). Studies usually consider that conspecific individuals of a given population are ecologically equivalent (Bolnick et al. 2003). If individuals truly have identical niches, they find themselves in a situation of complete competition. In this case, the competitive exclusion principle often leads to the apparition of individual territories (Krebs 2001). When territoriality is not possible, individual variation and in particular foraging specialisations can constitute additional mechanisms for finer subdivision of niches (Roughgarden 1972) and thus reduction of intra-specific competition (Weiss 2006).

1.2.3 Feeding ecology of rorqual whales

Rorquals constitute one of the three families of baleen whales and include blue, finback, humpback and minke whales (Fig. 1-1). The diversity and global distribution of cetaceans reflect their success in modifying the terrestrial morphology, physiology, and behaviour of ancestral mammals to the marine environment (Berta & Sumich 1999). These adaptations have important consequences for their ecology in general and their distribution patterns and foraging strategies in particular.

Physical properties of the aquatic environment and the high productivity of marine habitats allow cetaceans to occupy the large end of the body size range of extant animals. This results in large energy requirements. Blue whales for instance have the highest prey demands of any predator that has ever existed (Rice 1978). This also results in a large disparity between their size and that of their prey (Berta & Sumich 1999). Baleen whales cannot feed directly on phytoplankton but are anatomically specialised to exploit small prey occurring at higher trophic levels (Kawamura 1980). Blue whales prey exclusively on euphausiids (Yochem & Leatherwood 1985) while other species of rorquals eat both small fish and zooplankton (Gaskin 1982). In the St. Lawrence, the trophic levels of the finback and humpback whales as determined by stable isotope analysis are low, which indicates a high contribution of zooplankton to their diet (Borobia et al. 1995). Rorqual whales use an engulfment feeding technique in which the mouth is enlarged by expansion of the throat grooves and invagination of the tongue to create a large ventral cavity (Lambertsen 1983). Water is then forced out through the baleen plates and the food items are trapped inside (Orton & Brodie 1987).

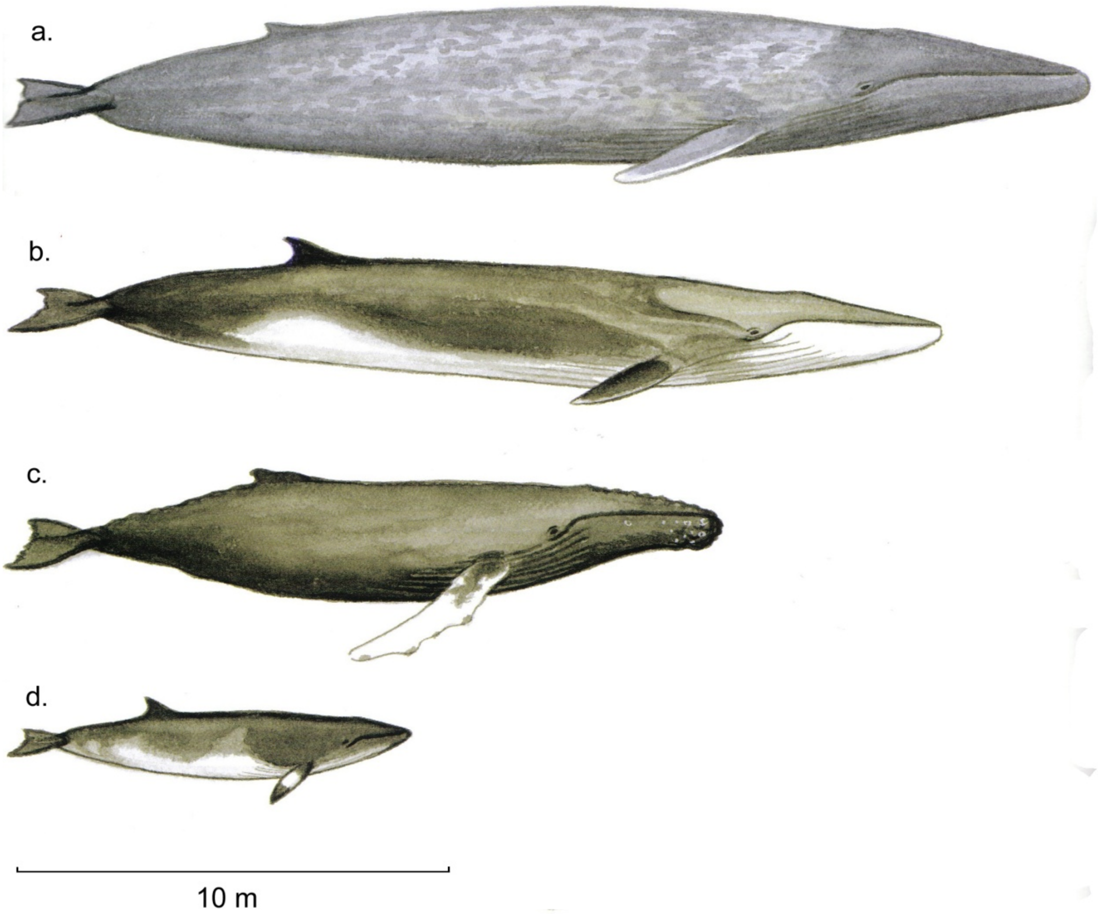

Figure 1-1. Comparative size, morphology and appearance of rorqual whales occurring in the Gulf of St. Lawrence: a. blue whale; b. finback whale; c. humpback whale; d. minke whale (drawings by Daniel Grenier)

This feeding strategy allows rorquals to capture schooling euphausiids or fish in large numbers during each feeding bout (Berta & Sumich 1999). However, for efficient exploitation these food patches must be predictable in terms of their seasonality and their approximate location (Georges et al. 2000). Broad-scale distributions of whales are thus direct consequences of the spatio-temporal patterns of marine primary productivity (Gulland 1974). The rate at which phytoplankton produces new organic matter from inorganic carbon is determined by nutrient availability, light intensity and temperature (White and Johns 1997). In temperate waters, mixing by winter storms adds nutrients to the surface layers, and increasing sunlight in spring triggers a phytoplankton bloom. Herbivorous zooplankton blooms a few weeks later, yieldinghigh primary production (Levinton 1982).

Coastal upwellings maintain this productivity by replenishing nutrients during the summer when they would otherwise be depleted by plankton grazing (Berta & Sumich 1999). This is a meso-scale process in which cold and nutrient-rich subsurface waters are brought to the surface, creating optimal conditions for plankton growth (Barber & Smith 1981). Coastal upwellings can be initiated by strong winds blowing surface waters offshore or by divergent current systems (Rose & Leggett 1988), and are often reinforced by interaction with local bathymetry (Ingram 1985). This phenomenon typically involves a horizontal spatial scale of 5-100 km and recruits water from 40 to 80 meters in depth (Barber & Smith 1981). The large biological production of these upwelling areas contributes to the high productivity of many marine ecosystems (Barnes & Hughes 1988).

These broad and meso-scale processes of marine productivity explain the general distributional patterns of baleen whales (Gulland 1974). However, rorquals need to find densely-clumped patches of prey to maximise their feeding efficiency (Piatt et al. 1989). Because they cannot feed directly on phytoplankton (Berta & Sumich 1999), they have to focus their foraging effort at finer scales in areas where consumers of phytoplankton concentrate at predictable locations (Marchand et al. 1999). Most of these local aggregations are generated by fine-scale three-dimensional dynamic processes occurring at the site of strong interactions between currents and bathymetric features (Denman 1976) or near sharp density interfaces (Olson & Backus 1985), such as fronts between differing water masses where convergent currents induce downwelling of surface waters (Wolanski & Hammer 1988).

There are several important differences between terrestrial and marine habitats. Marine systems are usually large, open and lack obvious geographical barriers, making it difficult to define habitat types (Rapoport

1994). The ocean is an exceptionally heterogeneous environment (Steele 1976, Haury et al. 1978), and marine resources exhibit patchiness over a large range of scales (Mackas & Boyd 1979). By providing buoyancy, the high density of seawater distributes organisms over a vast, fully three-dimensional environment (Carr et al. 2003). Aquatic systems also have a faster rate of response and a greater sensitivity to environmental variability than terrestrial ones (Steele 1985). These patterns combine to give rorqual foraging habitats their main characteristics: patchiness, three-dimensionality and variability in time (Mangel & Hofman 1999). Little is known of how rorqual whales make use of the dynamic nature of their habitat.

1.2.4 Previous studies of whale-habitat relationships

There has been considerable incentive to study the distribution of whales, first by whalers and later by managers (Jaquet 1996). However, studying cetacean habitat selection can be extremely challenging as they spend most of their lives under water (Hastie et al. 2003). Collecting data on free-ranging animals at sea presents numerous logistic and financial challenges (Ingram et al. 2007). Also, the study of marine ecosystems requires methods for investigating patchiness and variability (Mangel & Hofman 1999). Because of these constraints, early studies of habitat use by whales usually chose easily accessible oceanographic variables and broad spatial scales, while de-emphasizing temporal variability (Bjørge 2002). Lately, new developments in remote-sensing (e.g. satellite data) and analytical tools (e.g. geographic information systems, spatial statistics, computer-intensive methods) have led to a rapid increase in the explanatory power of habitat selection models (Redfern et al. 2006).

As predicted by their feeding ecology, whales tend to have non-uniform distribution at a wide range of spatial scales (Jaquet 1996). These clumped distribution patterns were first linked to preferential use of certain water depths (Gowans & Whitehead 1995, Baumgartner 1997, Davis et al.

2002) and heterogeneous seabed topography (Hui 1985, Selzer & Payne 1988, Gowans & Whitehead 1995, Baumgartner 1997, Davis et al. 2002, Ingram et al. 2007). In particular, finback whales in the Bay of Fundy were associated with shallow regions of high topographic variation and well-mixed waters (Woodley & Gaskin 1996), and in the St. Lawrence estuary they were observed primarily along steep contours where biological productivity was believed to be high (Sergeant 1977).

Whale distribution patterns have also been linked to dynamic environmental variables, although usually at broad scales. The most important variables seem to be sea surface temperature (Brown & Winn 1989, Forney 2000, Baumgartner et al. 2001, Hamazaki 2002) and salinity (Selzer & Payne 1988, Forney 2000). Dynamic integrative processes, such as frontal systems, are more rarely studied but have been shown to influence the fine-scale distribution of some species (Mendes et al. 2002, Johnston et al. 2005b, Tynan et al. 2005). In the California Channel Islands, most blue whales were found in cold, well-mixed, productive waters resulting from upwellings, where they fed on dense aggregations of euphausiids both on the shelf and off the shelf edge (Fiedler et al. 1998). The relative importance of these ecological determinants appears to vary between regions and species, suggesting the need for studies of region-specific critical habitats (Hastie et al. 2005).

Whale distribution is directly associated with prey distribution patterns when these data are available (Woodley & Gaskin 1996, Jaquet & Gendron 2002, Baumgartner et al. 2003, MacLeod et al. 2004). Positive correlations have been found between the distribution of rorquals and their prey in coastal environments (Piatt et al. 1989). Fluctuations in abundance of rorqual whales in the Gulf of Maine were related to changes in abundance of their 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 the presence of sand eels (*Ammodytes* *americanus*) (Payne et al. 1986). The presence of finback and humpback whales off Newfoundland was correlated with peak abundance of capelin, *Mallotus villosus* (Whitehead & Carscadden 1985). In the North Pacific, blue whales seem to aggregate in locations and at times that correspond with peak euphausiid biomass (Burtenshaw et al. 2004).

1.2.5 Other factors influencing distribution of whales: niche partitioning and intra-population variation

The feeding ecology of rorquals and the characteristics of their environment have important ecological consequences for their community dynamics. First, their large size and the almost complete absence of predators in the Gulf of St. Lawrence (Wenzel & Sears 1988) mean that their distribution is unlikely to be affected by predation. Competition is therefore the main limiting factor for rorqual whales (Mangel & Hofman 1999), as it is for other medium or large piscivores (Schoener 1989).

Second, the combination of the high feeding requirements of rorquals and the patchiness of resources in marine environments means that the rich patches of food they are looking for are few and far between, and are also attractive feeding grounds for most other marine mammals (Mangel & Hofman 1999). Therefore, many species of cetaceans with similar ecological requirements have to coexist in direct sympatry on their feeding grounds (Bearzi 2005).

Third, whales live in a dynamic environment where favourable habitat conditions can change over small spatial and temporal scales (Redfern et al. 2006). The heterogeneous and unstable spatial distribution of their prey makes it impossible for rorquals to defend access to resource via territoriality (Davies 1978, Clapham 1993) and renders economic defence of specific areas unprofitable (Gosling & Petrie 1981). Finally, large mammals occupy larger home ranges than predicted by their energy needs, possibly because of their lower encounter rate with prey (Haskell et al. 2002). As home ranges become too large to be defendable, their overlap increases and so does the potential for both intra- and inter-specific competition (Jetz et al. 2004). Combined with the impracticality of territories, this means that rorquals are expected to have large overlapping home ranges and frequent neighbour interactions, both within and between species.

Little is known of inter-specific competition among rorquals. Examination of stomach contents showed that the diets of humpback and finback whales overlap greatly (Whitehead & Carlson 1988), creating the potential for competition. Nemoto (1959) hypothesised that the differences in diets and feeding strategies observed among rorquals in the northern hemisphere were the consequence of competition which had encouraged partitioning of available food resources. However, it is difficult to know if resources in the North Atlantic are limiting today, considering that whale populations have likely not recovered to their pre-whaling numbers (Boyce 2000). If resources are not limiting, rorquals might still suffer from interference competition, which occurs when the direct interaction of organisms hampers their ability to obtain the resource they seek (Krebs 2001).

Despite this strong potential for competition, very few studies have investigated the co-occurrence of rorqual whales and the mechanisms that allow them to use the same habitat and partition their resources (Parra 2006). The fine-scale distributions of finback and minke whales in the Bay of Fundy were not statistically correlated and were influenced by different environmental variables, suggesting some degree of habitat partitioning (Ingram et al. 2007). Theory predicts that environmental heterogeneity in space and time can promote species coexistence (Chesson 1985). The complex and dynamic spatial structure of their environment might thus offer whales many opportunities for niche partitioning. However, niche breadth and overlap in baleen whales have never been quantified.

Competition for common resources can also affect conspecifics and create intra-population variation in the form of individual specialisation

(Roughgarden 1972). Individual specialisation is usually considered rare and thus most studies pool data across individuals, preventing a detailed examination of individual strategies (Thomas & Taylor 1990). However, a recent review showed that individual variation is widespread and can profoundly affect a population's ecology (Bolnick et al. 2003). Such individual foraging specialisations have been observed in minke whales (Hoelzel et al. 1989) and could have evolved as a mechanism to mitigate intra-specific competition. Our knowledge of intra-population variation in whales remains very limited.

1.2.6 The Gulf of St. Lawrence

The Gulf of St. Lawrence is a semi-enclosed sea in the north-western Atlantic Ocean (Fig. 1-2). Together with the St. Lawrence Estuary, it constitutes a complex system receiving large inflows of both fresh water (from an extensive drainage basin) and sea water flowing from the Atlantic Ocean (White & Johns 1997). The dominant feature of the bottom topography is the Laurentian Channel that extends from the Scotian Shelf to Tadoussac in the Estuary and has a maximum depth of 535 m (Loring & Nota 1973). At the western end of the Laurentian Channel, intense tidal mixing is responsible for some of the richest krill aggregations documented in the northwest Atlantic (Simard & Lavoie 1999).

During summer and fall, the Gulf is a well stratified, three-layered system (Trites 1971). At the surface, heat from the sun creates a shallow layer of warm water with temperatures up to 20°C (Koutitonsky & Bugden 1991). The cold intermediate layer (CIL), a relic of winter cooling of the surface layer, extends below the surface layer from 30 to 125 m with core temperatures between 2° and -1°C (Gilbert & Pettigrew 1997). Variations of its thickness and depth have important implications for food availability (Lavoie et al. 2000). The deep layer underneath begins at about 125 m and continues to the bottom, with temperatures of 4-6°C (Trites 1971).

This stratified marine system causes nutrient depletion at the surface and higher concentrations of nutrients in deeper waters (Coote & Yeats 1979). In upwelling areas, strong winds, rapid changes in bathymetry and intense tidal action cause local disruption to this stratification, bringing these deeper, nutrient-rich waters to the surface (White & Johns 1997). These regions are associated with marked increases in biological productivity and support a high abundance of large zooplankton and juvenile fish, creating especially attractive conditions for whales, since these are their two main prey items (Simard & Lavoie 1999).

Figure 1-2. Map of Eastern Canadian waters indicating the location of the Gulf of St. Lawrence and the study area

Whaling records (e.g. Mitchell 1974) and field studies (Edds & Macfarlane 1987, Sears et al. 1990, Kingsley & Reeves 1998) indicate that portions of the Gulf are important seasonal feeding grounds for blue, finback, humpback and minke whales. Rorquals usually arrive in the St. Lawrence after the April ice break-up and most of them leave the Gulf by December or January (Sears et al. 1981). Although some information exists about the food habits and seasonal distribution of baleen whales at broad spatial scales (Mitchell 1974), little is known of their patterns of habitat use and selection. One fine-scale study showed that minke whale distribution in the Mingan Islands remained stable from year to year and was correlated with topography (Naud et al. 2003).

My study area is located in the northern Gulf of St. Lawrence, in the Jacques Cartier Passage between the Mingan Islands and Anticosti Island (Fig. 1-3). This region is characterised by heavy tidal mixing, wind-driven and topographically-induced upwellings with high levels of biological productivity during the summer (Koutitonsky & Bugden 1991). Aerial surveys have identified the Jacques Cartier Passage as the area with the greatest diversity of cetacean species in the whole Gulf and of particular importance for rorqual whales (Sears & Williamson 1982, Kingsley & Reeves 1998).

Areas of coastal upwelling create attractive conditions for foraging whales but are also the most at risk from human development (McIntyre 1999). The Gulf of St. Lawrence is no exception and like most cetaceans in Eastern Canadian waters, rorquals face numerous anthropogenic threats, among which detrimental health effects of toxic pollutants (Ross et al. 1996, Metcalfe et al. 2004), increasing pressure from whale-watching activities (Michaud & Giard 1998) and depletion of local resources through overfishing (DeMaster et al. 2001). Fishing activities in the Gulf include bottom trawling, which constitutes a major threat to coastal ecosystems (Turner et al. 1999). Other problems include collisions with ships and entanglement in fishing gear (Bergeron et al. 2002). For instance, 16% of blue whales identified in the St. Lawrence bear scars from collisions with ships and there are 3 reports of blue whales drowning due to fishing gear between 1979 and 2001 (Sears & Calambokidis 2002).

Global climate characteristics were shown to drive southern right whales (*Eubalaena australis*) population dynamics (Leaper et al. 2006) and numerous populations of cetaceans are believed to be at risk from the impacts of global climate change (Würsig et al. 2001, Frederiksen et al. 2006). The Gulf presents some characteristics of colder ecosystems (e.g. the cold intermediate layer); it is thus possible that rorquals in the St. Lawrence face similar threats to those in polar ocean ecosystems (Smetacek & Nicol 2005). Also, concern has been expressed about the effects of offshore oil exploitation (Hofman 1995, Berta & Sumich 1999).

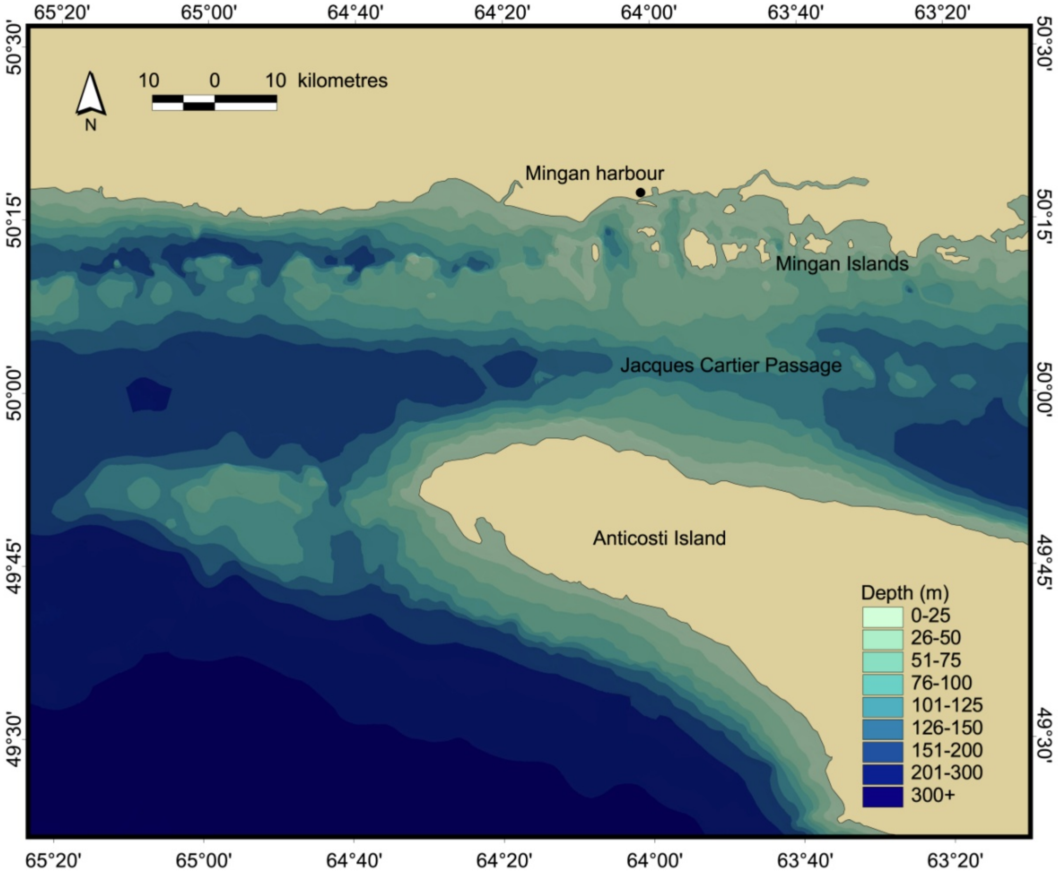

Figure 1-3. Map of the study area and main bathymetric contours

1.3 Rationale, objectives and hypotheses

1.3.1 Rationale

My rationale for conducting this project is two-fold. First, studying species occurrence can be used to test hypotheses concerning underlying ecological processes (Arthur et al. 1996).Recent progress in statistical and modelling techniques has improved our understanding of species-environment relationships (Guisan & Zimmermann 2000). However, these advances have focused primarily on terrestrial ecology (Redfern et al. 2006). This is an important shortcoming, because marine habitats differ in fundamental ways from their terrestrial counterparts: they are fully three-dimensional (Carr et al. 2003), lack clear separations between habitat types (Rapoport 1994) and exhibit greater sensitivity to temporal variability (Steele 1985). As a result, some theories developed on land may not apply to marine environments. For instance, most ecologists have studied homogeneous areas of habitat, as advised by MacArthur (1972).The importance of temporal variation is acknowledged in theory but rarely studied in practice and thus deserves more attention (Wiens 2002). I believe that studying mammals in marine environments can improve our understanding of the generality of these ecological theories.

Secondly, studies that quantify habitat use and selection can be used to assess the biological requirements of species (Arthur et al. 1996), to predict effects of habitat and climate changes (Thomas et al. 2004), to justify protection of key areas (Morrison et al. 1998) and to improve conservation planning (Wiens 2002). However, reserve design theory has been developed predominantly for terrestrial systems (Hixon et al. 2001). Rorqual whales in the Gulf of St. Lawrence are faced with severe anthropogenic threats, which have to be put in context of their whaling history. For instance, blue whale hunting in the North Atlantic has reduced the population size by an estimated 95% (Christensen 2006). Blue whale stocks show few signs of recovery since the whaling stopped, which has led to their current “endangered” status, but there is little information suggesting how to implement effective conservation measures (Sears & Calambokidis 2002). In light of these risks, it is important to consider the spatial and temporal aspects of whale distribution. Learning more about habitat selection in the Gulf of St. Lawrence can help identify and predict areas of greater ecological importance for rorquals. There may be ways to mitigate the overlap between these areas and human activities (e.g. shipping lanes, whale-watching, fishing), which could be very important for the conservation of marine mammals in Eastern Canada considering the predicted increase of anthropogenic environmental disturbance (Berta & Sumich 1999).

1.3.2 Objectives and hypotheses

My main objective is to attempt to determine the factors that influence fine-scale distribution of rorqual whales in the northern Gulf of St. Lawrence. Based on the literature review, I suggest several hypotheses. First, food resources are very patchy in the marine environment and therefore I expect a clear habitat selection signal (i.e. rorquals should select environmental characteristics that differ widely from those of the available habitat). Second, patterns of prey distribution and the lack of territoriality in rorquals imply that whales face potentially strong inter- and intra-specific competition. Finally, because marine habitats are very dynamic, I expect time-varying variables to be extremely important for both habitat selection and partitioning. Therefore, my overall working hypothesis is that the fine-scale distribution of rorqual whales is influenced by three non-exclusive processes: habitat selection, habitat partitioning among species and individual variation. From this, I draw several predictions, which I set out to test:

1. Rorquals associate with meso-scale frontal features which provide improved feeding opportunities by concentrating prey (chapter 2).

2. Rorquals respond to the dynamic nature of their environment by selecting rare combinations of both static and time-varying variables (chapter 3).
3. Coexisting rorqual species differ in habitat preferences (chapters 2, 3 and 4).
4. Coexisting rorqual species partition their niche in space and time (chapter 4).
5. Individual specialisations play an important role in intra-population variation (chapter 5).

1.4 Study design, data collection and scale

1.4.1 Study design

Understanding the occurrence of animals in space and time requires modelling of habitats (Wiens 2002). Garshelis (2000) defined three main types of habitat analyses: use-availability design (which compares the proportion of time an animal spends in each available habitat type), demographic response design (which compares population parameters in different habitats) and site attribution design (which compares sites used by an animal to unused or random sites). I chose a site attribution design based on the nature of my data and the difficulty of classifying marine environments into arbitrary habitat types. Because of the cryptic behaviour of whales, it is almost impossible to know if a certain area is truly “unused” by whales. Therefore, I chose to use random sites rather than unused sites to represent the available habitat.

Comparisons of used vs. available habitats can be performed in several ways, from simple univariate comparisons of categorical resources (Neu et al. 1974) to multivariate analyses of continuous variables and logistic regression (Manly et al. 2002). Multivariate analyses provide methods to study the joint relationships of intercorrelated variables. By analysing several variables simultaneously, they allow interpretations that would be impossible with univariate approaches (James & McCulloch 1990). They also offer the opportunity to summarise large data sets, which is especially useful in an exploratory study (Redfern et al. 2006).

Whatever the statistical method, studies typically assume that all habitats encompassed by a predetermined study area are available to all individuals. In the case of whales, because of the absence of physical barriers for large mobile animals in the marine environment, it can be reasonably assumed that the entire study area is available, except where water is too shallow. In most cases, the characteristics of available habitat are determined once and for all, and are not allowed to vary in time (Arthur et al. 1996). This approach has potential problems (Johnson 1980, Thomas & Taylor 1990) and does not accurately represent the dynamic, fast-changing nature of marine habitats. For instance, the available habitat in terms of water temperature may be different for a whale observed in June and another observed in August. Similarly, characteristics such as currents can change drastically over the tidal cycle and with them so does the definition of available habitat.

Unlike in terrestrial systems, defining discrete periods may not be practical for such rapidly changing habitats (Arthur et al. 1996). When dealing with time-varying variables, describing the characteristics of available habitat at the same time as used habitat can be difficult. Put simply, it is hard for researchers to be everywhere at the same time. Here, thanks to new technologies (satellite remote-sensing and ocean computer models), I use simultaneous measurements of the characteristics of both used and available habitats. For each whale sighting in my data set, I plotted a random point in the study area. These random points have the same date and time as the real sightings but have a different position; thus, they represent an alternative habitat that was available to the whale at the very moment of the sighting.

1.4.2 Data

The study of marine mammals presents two major challenges. First, whales spend most of their time underwater and thus it is difficult to observe how they use their habitat. However, as all cetaceans must return to the surface to breathe, habitat use can be inferred from their distribution at the surface (Hastie et al. 2003). Second, understanding marine ecosystems requires methods for investigating patchiness and variability (Mangel & Hofman 1999). For this project, I combined a data set of whale surface sightings with environmental data that described the entire study area for any moment in time.

Personnel from the Mingan Island Cetacean Study (MICS) conducted field work in the Jacques Cartier Passage from June to October 1996-2002 using rigid-hulled inflatable boats with outboard engines. This sampling effort represented an average of 60 surveys per year. Total distance covered in a day could be up to 220 km (mean = 112 km, SE = 34 km) and average surveying effort was 10 338 km (SE = 1022 km) per year. As part of a photo-identification study, boat surveys tried to cover the largest possible area every day and spent more time in areas where whales were frequently encountered. Although the sampling was neither random nor systematic, surveys incorporated a broad range of habitat variability and were performed blindly with respect to habitat characteristics (with the exception of distance to shore). Field work was highly dependent on weather conditions. Surveys were conducted when wind speed was ≤20 knots (37 km/h), sea state ≤4 on the Beaufort scale and visibility was ≥6 km. Due to prevailing westerly winds, more time was spent in the western half of the research area than in the eastern half. Animals were spotted at a distance of up to 5 km. The latitude and longitude of each sighting of blue, finback, humpback and minke whales were recorded with a GPS (precision ≤ 30 m) where the whale dove at the end of its surface sequence (i.e. its “footprint”).

When good quality pictures could be obtained, photo-identification techniques were used to keep only the individual's first sighting of the day in the analysis (Fig. 1-4). We chose the first sighting because it was recorded before the behaviour of the whale could have been modified by the approach of the boat and thus was the least biased observation.

Environmental variables came from three different sources. Static variables (depth, slope and distance from shore) were computed using a digital nautical chart in ArcView 3.1 (ESRI, Redlands, CA, USA). Dynamic variables were obtained from two data sets. First, differences in the physical properties of water masses are often associated with upwellings and frontal systems. When these features alter the properties of surface waters, information on their location and intensity can be collected by satellite (Georges et al. 2000). Thus, I used sea surface temperature maps obtained from satellite remote-sensing to identify temperature gradients and the location of strong thermal fronts (cf. section 2.3.2 and 2.3.3). Second, I used a three-dimensional coastal ocean model (Saucier et al. 2003) to obtain temperature, salinity and currents, as well as depth and minimum temperature of the cold intermediate layer (cf. 3.3.2).

Not all chapters in this thesis use the same sample size because they have different objectives or use different sources of data. In chapter 2, the availability of cloud-free satellite maps that corresponded to days with field surveys was the limiting factor. The data set in chapter 2 is therefore smaller than in chapters 3 and 4, for which the ocean model was able to provide data for virtually all whale sightings in the study period. However, the period covered by the ocean model only starts in 1997, preventing the use of 1996 field observations in chapters 3 and 4 (which was unfortunate considering that there were 20 blue whale sightings in 1996 and only 30 for the whole 1997-2002 period). Finally, in chapter 5, I investigate individual variability and thus I was limited to working with only one species (humpback whales) because the number of individually identified whales was too low to include the other three species.

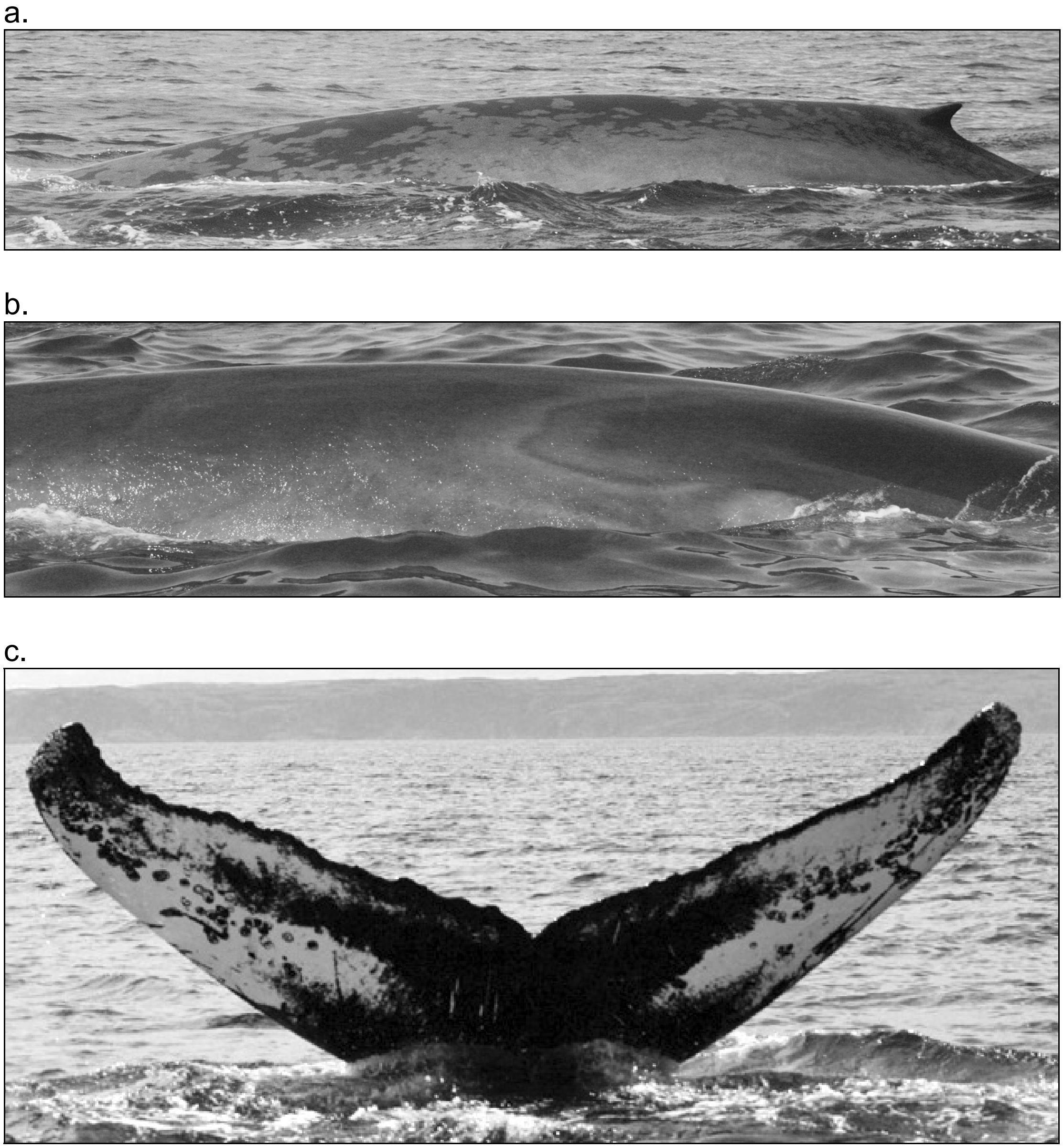

Figure 1-4. Examples of photo-identification pictures for three species of rorqual whales. Patterns of pigmentation are stable over time and specific to each individual; a. blue whale; b. finback whale; c. humpback whale (fluke). Photographs by Christian Ramp.

1.4.3 Scale

The scale of an ecological investigation strongly affects the interpretation of patterns and must therefore be chosen with care (Wiens et al. 1986). Habitat selection occurs at several levels and these levels act at corresponding scales (Heglund 2002). At the level of population dynamics (and the broader spatio-temporal scales), selection for specific habitats is reflected in differential reproductive rates (Levin 1968) and restricted by general aspects of an animal's physiology, ecology and behaviour (Wiens et al. 1986). Subsequently, selection is influenced by proximal forces that work at increasingly finer spatio-temporal scales (Heglund 2002).

The best scale to choose for a study is usually one that corresponds to the patch size of both predator and prey (Rose & Leggett 1990). If the relationship between the distribution of a predator and the distribution of its prey is studied at excessively fine scale, co-occurrence will not be apparent as predators are seldom exactly aligned with their prey (Levin 1992). However, ecosystems contain many spatial scales. For example, in the California Current, the communities of zooplankton and their predators exhibit spatial scales of 50 m for fish schools, 300 m for plankton aggregations, 1 000 m for gaps between plankton aggregations and 10 000 m for gaps between fish schools (Smith et al. 1989).

Ideally, whale-habitat studies should thus use a hierarchical scale framework that takes into account the relative influence of fine, meso- and broad scale processes (Redfern et al. 2006). For instance, Pribil and Picman (1997) showed that the relative importance of different habitat variables for seabirds depended upon the spatial scale of study. In practice, these patterns are generally studied on large spatial scales (10-100 of km) and rarely at finer scales (Allen et al. 2001), presumably because of the logistical difficulty in measuring and recording relevant environmental variables (Baumgartner & Mate 2005). Since studies over broad scales cannot be extrapolated to finer scales (Rose & Leggett 1990), this lack of fine-scale studies limits our understanding of meso- and fine scale processes such as fronts, eddies and other dynamic characteristics of the water column (Redfern et al. 2006).

I chose the scale of this study based on both biological considerations and logistical constraints (i.e. resolution of satellite maps and ocean model). With a scale of 5 km for the ocean model and 1.1 km for the satellite data, the scale of this study is located below the traditional definitions of meso-scale in marine studies (10-100 km) and investigates the upper range of fine-scale correlations (100 m – 5 km) (Redfern et al. 2006).

1.5 Outline of thesis

Based on the literature, the most likely primary determinants of whale distribution patterns are habitat selection, inter-specific competition and potentially intra-population variation such as individual specialisations. The different parts of this thesis address each of these factors.

Chapters 2 and 3 both focus on habitat selection. They aim to compare used vs. available habitats, to test whether habitats are used in proportion to their availability or if preference leads to disproportionate use of certain habitats. These two chapters differ in the variables considered and the philosophical approach. Chapter 2 takes a standard hypothetico-deductive approach to test the effect of one variable (distance to thermal fronts) on the distribution patterns of rorquals. This variable was chosen because of its integrative nature: it represents the end result of several dynamic ocean processes. Chapter 3 uses a multivariate approach in an inductive framework, in which numerous abiotic variables are studied simultaneously and models are compared using inference and information theory.

Habitat use and niche partitioning can be analyzed at several levels: the individual, the population or the community (Krebs 2001). Chapters 2 and 3 allow me to show that patterns of habitat use at the population level are representative of the selection process and characterise the ecological niche of each species. I then use these patterns of habitat use to investigate the differences between species (chapter 4) and among individuals (chapter 5). Thus, the analysis in chapter 3 aims to find the variables that best discriminate between used and available habitat for each species, as is needed to develop species-specific habitat models. In chapter 4, I try to find the variables that best separate the four species of whales from one another, as is required to address ecological hypotheses about their coexistence. Finally, chapter 5 gives some insight into the intra-population factors responsible for niche breadth and variation.

2. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence

This is the first of two chapters focusing on habitat selection (i.e. comparing used vs. available habitat). Here I use a subset of the whale data combined with satellite maps of sea surface temperature to test the ecological hypothesis that distribution of four species of rorqual whales is influenced by thermal fronts, a dynamic meso-scale process responsible for increased productivity and aggregation of prey.

This chapter has been published as: Doniol-Valcroze T, Berteaux D, Larouche P, Sears R. (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. Marine Ecology Progress Series 335:207-216.

2.1 Abstract

Distribution patterns of cetaceans have been linked to basic environmental features such as underwater topography and sea surface temperature, but the mechanisms underlying these relationships are poorly understood. Dynamic meso-scale processes like thermal fronts are prime candidates to link physiographic factors to whale distribution because they increase biological productivity and aggregate prey. However previous studies of large whales have found little evidence of such associations, possibly because they were not at the appropriate spatio-temporal scales. I quantified the relationship between SST fronts and the distribution of blue, finback, humpback and minke whales in the northern Gulf of St. Lawrence. I compared the distribution of 1078 whale sightings collected from boat surveys conducted in 1996-2000 to the locations of frontal areas determined from 61 satellite maps. The distributions of whales and thermal fronts were highly correlated (random resampling and Mantel tests of matrix similarity). Spatial distributions differed among species, likely reflecting differences in feeding strategies. Identification of surface fronts from satellite imagery thus effectively complemented field observations of whales. These findings increase our understanding of habitat quality in rorqual whales, and encourage a greater use of dynamic environmental variables in future studies of whale habitat use.

2.2 Introduction

Successful management of cetacean populations requires information on their foraging habitats (Bjørge 2002). Therefore, a growing number of studies quantify relationships between habitat use and basic environmental features in order to generate predictive models of marine mammal distribution (e.g. Gregr & Trites 2001, Hamazaki 2002). Model predictors are often chosen based on their availability, although choice of variables should rather derive from ecological theory (Gregr 2004). Common predictors of cetacean distribution include sea surface temperature, distance to shore, and underwater topography (e.g. Hoelzel et al. 1989, Woodley & Gaskin 1996), but the mechanisms linking these variables to patterns of habitat selection have only been investigated recently (e.g. Croll et al. 2005). Nevertheless, identifying cause–effect relationships in ecological models is critical (Hilborn & Mangel 1997).

The distribution of rorqual whales on their feeding grounds is mostly related to the abundance and patchiness of krill (Murase et al. 2002) and fishes (Whitehead & Carscadden 1985). Patchiness of organisms in coastal ecosystems is often caused by the dynamic features of meso-scale oceanographic processes like fronts, eddies and upwellings (Olson & Backus 1985). These processes usually involve spatial scales of 1 to 10 km and temporal scales of 1 to 10 d (Hofmann & Powell 1998). In most cases, when these upwellings reach the surface, one of their manifestations is a thermal gradient between warm surface waters and cold upwelled waters. Such meso-scale oceanographic processes increase biological productivity and aggregate zooplankton species (Olson & Backus 1985), thus influencing the distribution of several pelagic fish species (Fiedler & Bernard 1987, Podesta et al. 1993).

Gaskin (1987) predicted that these transition zones between tidally mixed and thermally stratified areas could be an important feature of North Atlantic right whale (*Eubalaena glacialis*) habitat in the lower Bay of Fundy. This hypothesis was supported by some anecdotal evidence (Murison & Gaskin 1989) but not by quantitative results (Woodley & Gaskin 1996). Similarly, Baumgartner et al. (2003) suggested that spatial and interannual variability in right whale occurrence on the Scotian shelf may be associated with SST gradients, but Baumgartner & Mate (2005) found no evidence that tagged right whales associated with such fronts. Several cetacean species do concentrate near meso-scale features and coastal upwelling areas (Benson et al. 2002, Davis et al. 2002) but specific information on rorqual whales is very scarce. Hamazaki (2002) showed that rorqual abundance was related to areas with higher monthly probability of front occurrence but this relationship was never investigated spatially, nor at a finer time-scale.

Long-term studies of rorqual whales in the northern Gulf of St. Lawrence (Quebec, Canada) have shown that distribution of blue, finback, humpback and minke whales is linked to areas of heterogeneous sea-bottom topography (T. Doniol-Valcroze & R. Sears unpubl. data). Naud et al. (2003) found a similar relationship for minke whales studied in a subset of the same research area, and therefore this link appears strong across several spatial scales (1 to 10 km grid cells). However, these studies also showed significant variation in time (e.g. within and between years) that could not be explained by static bathymetric factors. Satellite remote sensing shows that surface temperature in the St. Lawrence is strongly influenced by tidal mixing and upwellings and can change quickly (Thibault et al. 2002). Such meso-scale processes could provide additional explanation for the temporal variability observed in whale habitat use. Because these upwellings can be induced by local changes in sea-bottom topography (Hui 1985, Marchand et al. 1999), the resulting thermal fronts may constitute an important link between physiographic factors and whale distribution patterns.

Here I consider the influence of a dynamic oceanographic feature on habitat selection of rorqual whales through the use of biological (whale sightings) and physical (satellite-derived SST) data collected at fine spatial and temporal scales. I test the hypothesis that spatio-temporal distribution of four species of rorqual whales in the northern Gulf of St. Lawrence is related to thermal fronts. More specifically, I predict that whales should be found closer to SST fronts than expected under a random scenario, and that differences between species should reflect species-specific feeding strategies.

2.3 Material and methods

2.3.1 Study area

I worked on the North Shore of the Gulf of St. Lawrence, in the Strait of Jacques Cartier between the Mingan Islands and Anticosti Island. This region of the Gulf is characterised by wind-driven upwellings during the summer, heavy tidal mixing and high levels of biological productivity (Koutitonsky & Bugden 1991). Aerial surveys show that the North Shore shelf has the greatest cetacean species diversity of the entire St. Lawrence (Kingsley & Reeves 1998).

2.3.2 Data collection

Personnel from the Mingan Island Cetacean Study conducted field work from June to October 1996 to 2000 (as described in section 1.4.2) to obtain data on the distribution of blue, finback, humpback and minke whales in the study area.

Satellite data were received from the National Oceanic and Atmospheric Administration (NOAA), processed by the Remote Sensing Laboratory of the Maurice Lamontagne Institute and then published using the St. Lawrence Observatory web site (www. osl.gc.ca). Raw data received each day from the ‘advanced very high resolution radiometer’ (AVHRR) were transformed into SST maps covering the entire Gulf of St. Lawrence using Terascan™ software. Images were geo-referenced automatically using coastline recognition. Temperatures were calculated using a split-window algorithm (McClain et al. 1985).

2.3.3 Data mapping and identification of thermal fronts

For this analysis, I used data obtained on days for which a good quality satellite map of SST was available (with no clouds masking the study area) and for which weather conditions permitted field surveys. For each of these observation days, a GIS coverage was built by plotting the sightings on a map projected in Universal Transverse Mercator with a central meridian of –63° longitude, using ArcView 3.1 software with the ‘spatial analyst’ and the ‘animal movement’ extensions (Hooge & Eichenlaub 1997). Satellite images of SST were incorporated into the GIS as raster (cell-based) layers. Pixels measured 1.132 km and were calibrated to temperature values in intervals of 0.256°C. Fronts are usually defined as ‘narrow regions where horizontal gradients are large’ (Mann & Lazier 1991) but definitions vary with respect to the strength of the gradient. For Ullman & Cornillon (1999), each front represented a change in SST >0.375°C km^{-1}. In contrast, Marchand et al. (1999) observed fronts in the Estuary of the St. Lawrence with typical temperature gradients of 2 to 5°C over a few kilometres. I identified temperature gradients on each SST map by applying a Laplace filter to a series of circular matrices of 3 pixels in diameter. The centre pixel of each matrix returned data on the range of temperature values across that matrix. This edge-detection filter can identify fronts in any direction. Preliminary analysis showed that the average temperature gradient in the data set was 0.58°C km^{-1} (SD = 0.65). Gradients of 1.88°C km^{-1} thus represented two standard deviations above the mean. Based on this, I decided to define SST fronts as gradients of 2°C km^{-1}, which represented only the strongest temperature gradients.

2.3.4 Statistical analyses

I used a random resampling approach (Manly et al. 2002) to test the null hypothesis that whale sightings were distributed randomly with respect to thermal fronts. For each year, I drew the minimum convex polygon (MCP) containing 95% of the effort tracks. I used a land mask to remove the shape of the landmasses and created a buffer of 500 m around the shorelines to ensure that the polygon represented available habitat for whales (Fig. 2-1). For each observation day, I plotted random points within the MCP representing the study area of that year, in equal number to whale sightings. This ensured that random points fell in areas that were well covered by the survey effort. I then calculated the Euclidean distance to the closest front for each of the random points and whale sightings. For each species, I pooled the data by month and by year and compared the average distances for random points and whale sightings using an ANOVA. I used post-hoc t-tests to compare each species with the random sample separately.

Resampling tests do not address the fact that environmental variables are usually correlated with each other as well as spatially autocorrelated (Schick & Urban 2000). Parametric tests assume independence between data points but, in this case, because of spatial autocorrelation, two sightings that are close to each other have more similar characteristics than sightings that are further apart. Data cells are therefore not independent and this can increase Type I errors (some relationships appear significant when they are not). As recommended by Schick & Urban (2000), I used Mantel tests to assess the correlation between whale locations and environmental variables while at the same time taking into account the spatial autocorrelation of these variables. Mantel tests differ from standard parametric regression techniques in that the dependent variables are dissimilarity matrices, and the test measures the degree of pairwise similarity between sets of data (Mantel 1967). Significance is evaluated via permutation procedures. A simple Mantel test asks whether locations that are similar in terms of the predictor variable (distance to front) are also similar in terms of the dependent variable (whale presence or absence). A partial Mantel test also considers space (geographic location) as a predictor variable, testing whether samples that are close in space have similar values for other variables. The power of this test is its ability to take into account effects of confounding variables (Legendre & Legendre 1998). The Mantel r^2 is based on the normalised value r of the Mantel statistic z. This standardised value rescales the statistic to the range of a conventional correlation coefficient bounded on [–1,1].

I constructed 6 dissimilarity matrices, all of them generated from the positions of all random points and whale sightings; one matrix was constructed for space (Euclidean distance between sightings), one for the distance to fronts, and one for each species of whale. For the distance to fronts, I used the D15 dissimilarity index, which has the advantage of normalising the distance by the largest difference across the study area (Legendre & Legendre 1998). For whales, I used group contrast matrices, where similar sites (i.e. two random points or two whale sightings) had a contrast value of 0, and dissimilar sites (i.e. at the intersection of a random point and a whale sighting) had a contrast value of 1. I then used simple and partial Mantel tests for each combination of these matrices, using 10 000 iterations to assess significance. I performed analyses using the R package for multivariate and spatial analysis, Version 4.0 (Casgrain & Legendre 2001).

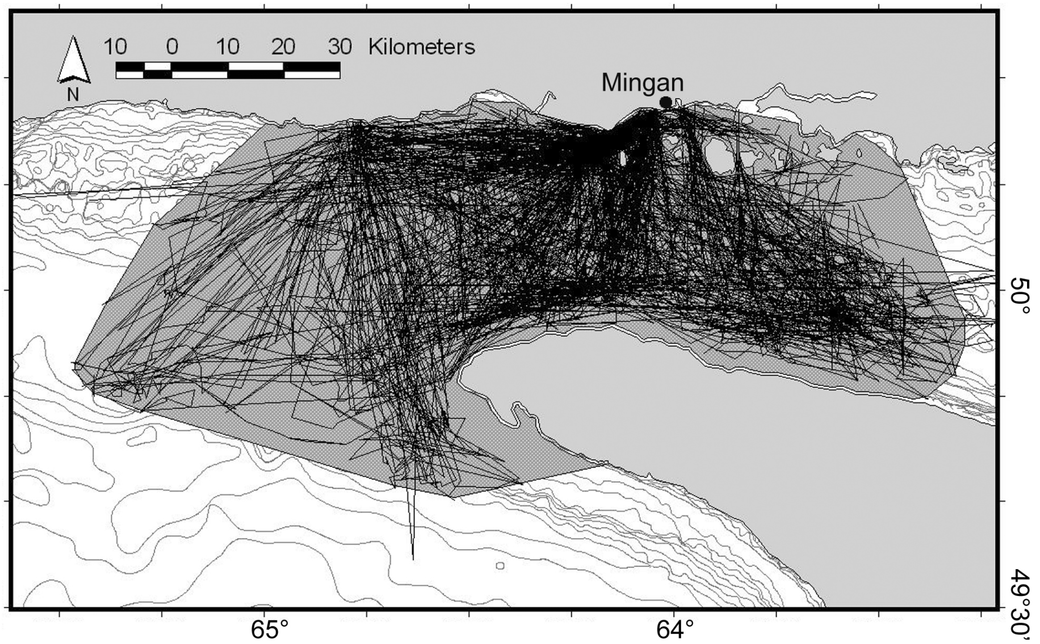

Figure 2-1. Map of the study area showing the track lines used during boat surveys over the 1996-2000 period (black lines) and the marine part of the minimum convex polygon containing 95% of the survey tracks (grey shading).

2.4 Results

2.4.1 Observation days and whale sightings

SST images were available on an irregular basis due to the frequency of images with heavy cloud cover obscuring the region; 61 observation days matched both requirements of a good quality satellite map and weather conditions permitting field surveys. These days were distributed homogeneously over the five years of the study but not over the four months of the field season (Table 2-1). June and August were consistently under and over-represented, respectively, in the analysed data set. The 61 observation days available for analysis represented 1078 sightings of rorquals: 27 blue, 321 finback, 419 humpback and 311 minke whales. These are the first sightings of the whales seen on each day. Sightings from different dates can include the same individuals. Fig. 2-2 shows that whale sightings were not distributed homogeneously within the survey effort.

Table 2-1. Distribution across years and months of suitable observation days in the northern Gulf of St. Lawrence between 1996 and 2000. Observation days suitable for analysis satisfied two requirements: availability of a good satellite map of sea surface temperature and weather conditions permitting field surveys.

	June	July	August	September	all months
1996	1	4	5	3	**13**
1997	0	2	3	4	**9**
1998	2	3	4	2	**11**
1999	3	2	5	5	**15**
2000	1	3	6	3	**13**
all years	**7**	**14**	**23**	**17**	**61**

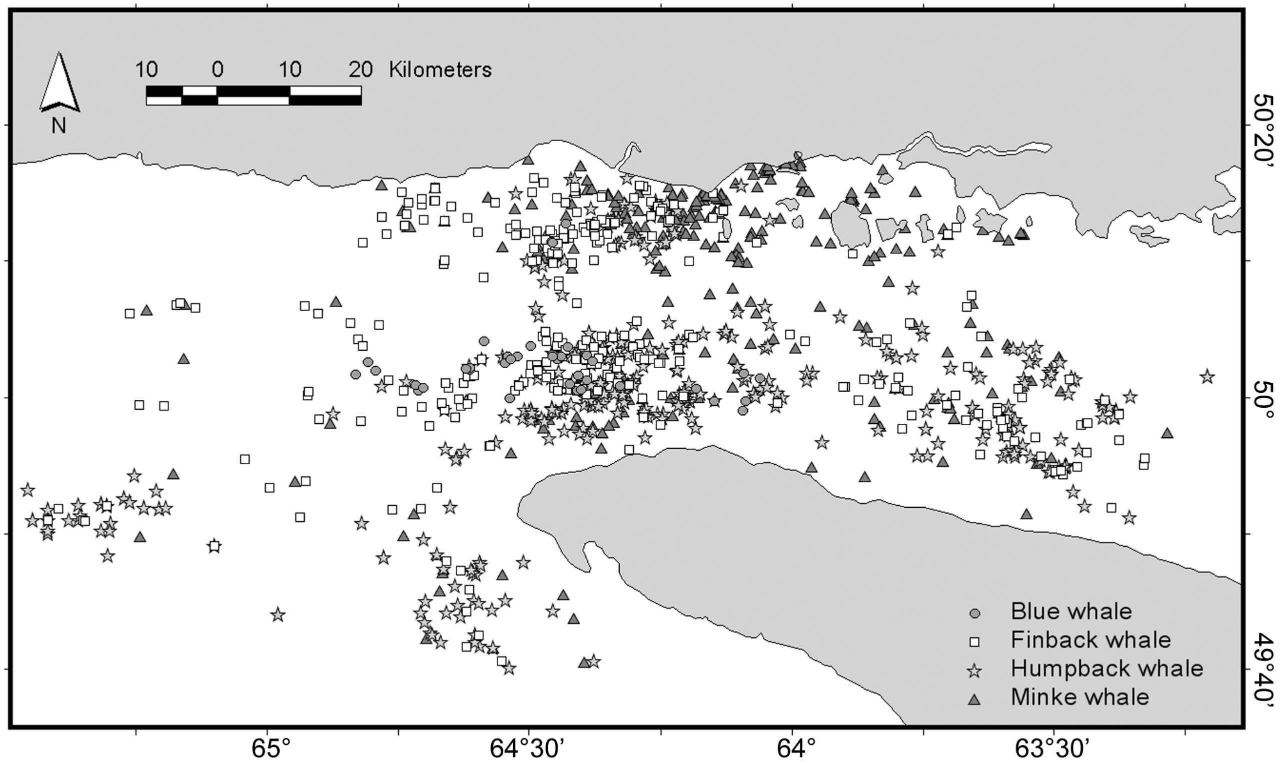

Figure 2-2. Map showing the distribution of blue (n=27), finback (n=321), humpback (n=419) and minke whale (n=311) sightings used in the analysis of habitat selection by rorqual whales over the 1996-2000 observation period.

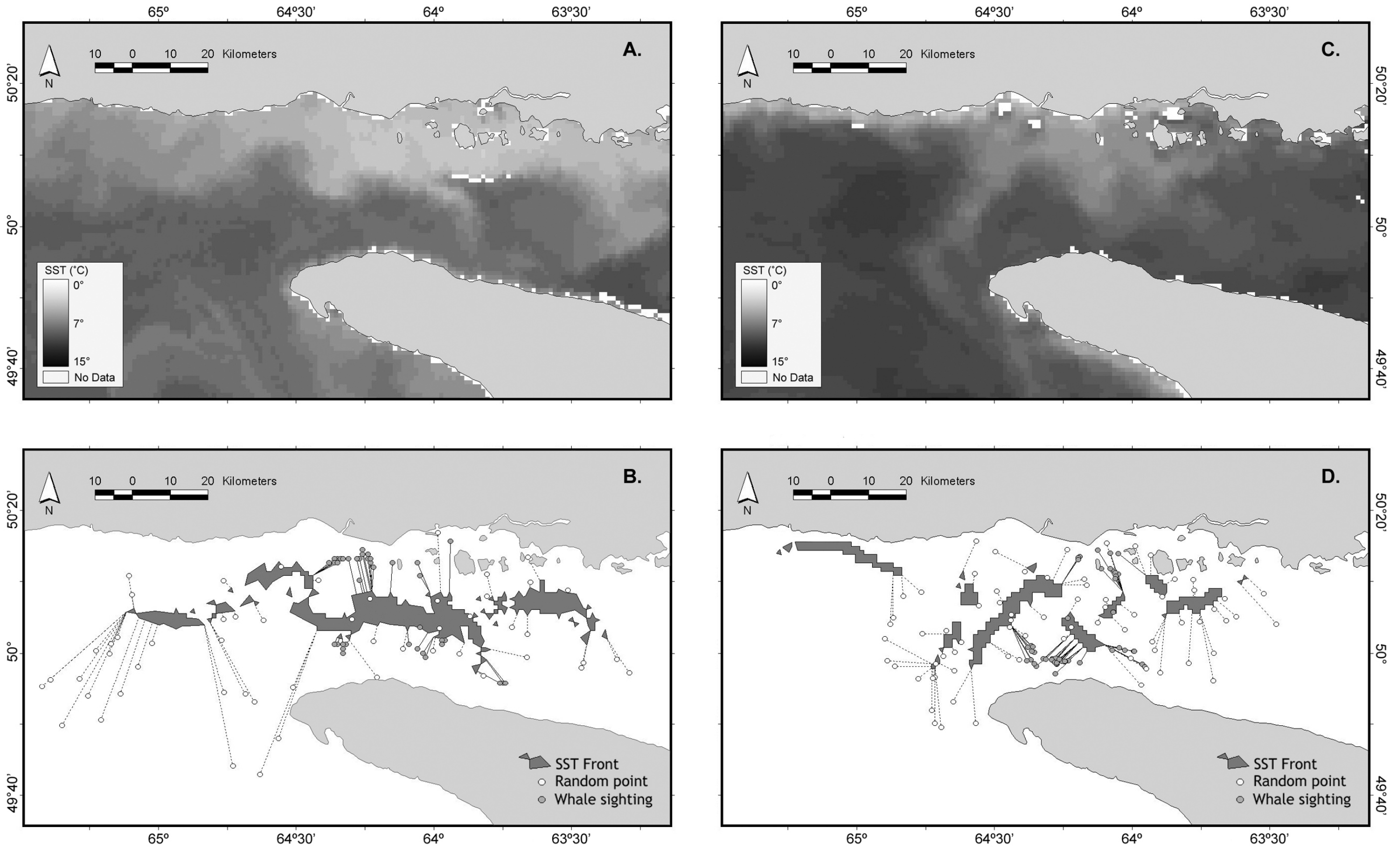

Figure 2-3. Maps showing sea surface temperature, location of frontal areas, whale sightings (shaded circles), random points (open circles) and the shortest straight lines linking sightings or random points to the closest thermal front. A) SST map dated September 02, 2000 and B) associated SST fronts typical of upwellings induced by westerly winds; C) SST map dated August 23, 2000 and D) associated SST fronts typical of tidally induced upwellings.

2.4.2 Distribution of whales with respect to thermal fronts

Temperature gradients observed in satellite maps were often steep (frequently >2°C km^{-1}) indicating the occurrence of strong meso-scale oceanographic processes. Whales were located closer to thermal fronts than expected from a random distribution (ANOVA, $F_4 = 7.45$, $p < 0.001$). I illustrate this relationship and the temporal variability of surface fronts in Fig. 2-3. The pattern of SST and frontal areas on 2 September, 2000 (Fig. 2-3 A,B) is characteristic of a wind-induced upwelling with fronts lying in a general east–west axis. The configuration on 23 August, 2000 (Fig. 2-3 C,D) shows the typical result of tidal forces with discontinuous irregular fronts, some of them in a north–south axis. Post-hoc t-tests showed that the relationship between whales and thermal fronts was not the same for all species: the difference between whale sightings and random points was statistically significant for blue ($t_{84} = 8.41$, $p < 0.001$), finback ($t_{640} = 5.91$, $p < 0.001$) and humpback ($t_{836} = 6.87$, $p < 0.001$), whales but marginally non-significant for minke whales ($t_{620} = 1.79$, $p = 0.08$). On average, blue whales were the closest to the fronts, followed by humpback, finback, minke whales and random points. This order remained remarkably stable over the 4 months of the study (Fig. 2-4), except in July when finback whales were found slightly closer to the frontal areas than humpback whales. Each species was farther away from the fronts in June than in any other month, which was also true of the random points.

Simple Mantel tests between space and the other matrices showed strong spatial autocorrelations for all species of whales as well as for the SST fronts (Table 2-2). Simple Mantel tests also showed significant correlations between the SST front matrix and all 4 whale matrices, confirming the results of the resampling test: points that were similar in terms of whale presence were also similar in their distance to the frontal areas. A partial Mantel test showed that there was a significant effect of the distribution of SST fronts on distribution of blue (Mantel partial $r^2 = 0.19$, $p < 0.01$), finback ($r^2 = 0.13$, $p < 0.05$) and humpback ($r^2 = 0.12$, $p <$

0.05) whales even once spatial autocorrelation was accounted for, but not in the case of minke whales ($r^2 = 0.07$, $p = 0.11$). This indicates that the correlation observed between SST fronts and minke whales in the simple Mantel test might have been due to their strongly autocorrelated spatial structure, whereas the spatial component was not the only explanation for the correlation found with the 3 other rorqual species.

Although statistically significant, most Mantel correlations were low. However, because of the randomisation technique involved, the magnitude of Mantel correlations are often comparatively small, even when highly significant statistically (Dutilleul et al. 2000) and should be interpreted with caution (Schick & Urban 2000). The coefficient I used in the Mantel tests assumed that the functional relationships between species and habitat variables were linear. Although I did not test this assumption, a re-analysis of the minke whale data using a Spearman nonparametric coefficient in the Mantel test (Legendre & Legendre 1998) yielded similar results and conclusions.

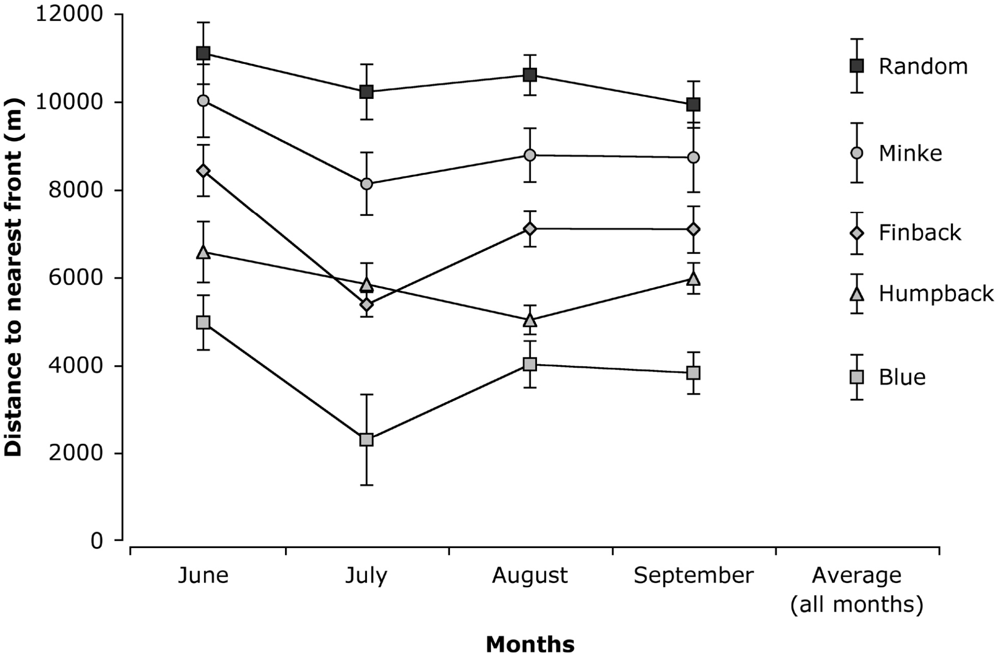

Figure 2-4. Mean distances between whale sightings or random points and the nearest frontal area for years 1996-2000. Error bars represent 1 SE.

Table 2-2. Mantel r coefficients and p values for results of simple and partial Mantel tests between dissimilarity matrices representing space, distance to nearest front and presence/absence of each species of whale during a 5-year study in the northern Gulf of St. Lawrence (1996-2000). The left column represents spatial autocorrelation. The middle and right columns show the correlations between whale distribution patterns and sea surface temperature fronts.

	Space (Simple test)	Fronts (Simple test)	Fronts (Partial test)
Fronts	0.35 ($p<0.001$)	-	-
Blue	0.14 ($p<0.01$)	0.25 ($p<0.01$)	0.19 ($p<0.01$)
Finback	0.21 ($p<0.01$)	0.22 ($p<0.01$)	0.13 ($p<0.05$)
Humpback	0.07 ($p<0.01$)	0.16 ($p<0.01$)	0.12 ($p<0.05$)
Minke	0.49 ($p<0.001$)	0.11 ($p<0.05$)	0.07 ($p=0.11$)

2.5 Discussion

I combined a large data set of whale sightings with satellite images of SST to show that whale distribution was unambiguously dependent on frontal areas. Blue, finback and humpback whales were closer to thermal fronts than expected under a random scenario, whereas minke whales were not. This important patterning effect of the SST fronts on the distribution of whales was robust enough to be maintained even once spatial autocorrelation was taken into account. To my knowledge, this fine-scale spatial relationship between fronts and rorqual whales is shown here for the first time, but is similar to a larger scale relationship between humpback whales and a coastal upwelling front in the California Current System (Tynan et al. 2005).

My results suggest that frontal areas create attractive foraging conditions for rorquals. Most fronts in the St. Lawrence result from tide- or wind-induced upwellings (Koutitonsky & Bugden 1991). These upwellings increase biological productivity (Olson & Backus 1985), which might alone explain the attractiveness of such areas to large whales. However, the location of SST fronts can change quickly from day to day. Because I worked at the time-scale of single days, I believe that the link I observed between whale and front distribution cannot be explained solely by this increased productivity. Another explanation is that temperature gradients created by these upwellings can have a herding effect on krill and fishes along their edge. Krill forced upwards by the upwelling try to swim down to avoid the more intense light levels at the surface and their concentration increases, making them easier prey for their predators (Lavoie et al. 2000). Similarly, when capelin are exposed to temperature gradients, they concentrate within narrow thermal zones by avoiding the colder water (Marchand et al. 1999). Therefore, concentrations of krill and capelin can be expected at SST fronts, where cold waters limit their distribution. At the head of the Laurentian Channel for instance, location and timing of some capelin aggregations in the upper water column are predictable (Simard et al. 2002). Thus, whales have a higher probability of detecting dense patches of food and can minimise their foraging and travelling times by exploiting frontal areas. I believe that this herding effect and the predictability of such concentrations of prey items are the main reasons for the relationship I observed at such a small time-scale.

A potential source of bias in my study comes from the nature of the sampling design. Habitats where whale densities were highest were likely to have been oversampled because field operations aimed at maximising whale encounters, rather than ensuring that habitats were sampled equally or randomly. An artificial relationship between whales and frontal areas could thus have been created if field workers were cuing on frontal areas to find whales. This, however, was not the case, since field personnel were not informed about the position of fronts when leaving from the research station in the morning. In addition, potential biases when collecting data from platforms of opportunity are minimised by broad spatial and temporal coverage that incorporates a range of habitat variability (Evans & Hammond 2004, Redfern et al. 2006), as was the case in this study. Like other studies based on platforms of opportunity or catch data (e.g. Weinrich et al. 2000, Gregr & Trites 2001, Clapham et al. 2004), I thus assumed that if any strong ecological association did exist, I would be able to detect it despite the limitations of my design. It is also important to note that I compared used to available habitat, rather than used to unused habitat, so that I never assumed that unsampled habitat contained no whales. This approach is the most conservative way to estimate habitat selection (Manly et al. 2002).

My results were consistent throughout the research season despite a potential seasonal bias in the sampling methods. In June, temperature gradients are smaller because spring warming of the waters has not yet occurred. Thermal fronts might then be harder to detect using surface temperature and some of them might not reach the threshold value of 2°C km^{-1}. A smaller number of fronts at the surface would make all points appear farther away from the frontal areas and this could explain why mean distances to the nearest front were higher in June than in any other month. Because this was true for all species and for random points as well, I do not believe this is a biological difference.

Rorquals are sometimes observed feeding along front lines (R. Sears & T. Doniol-Valcroze pers. obs.). In this study, most whales were observed closer to the fronts than expected under a random scenario but they were not directly on top of the frontal areas. Two hypotheses could explain this spatial lag. First, the fronts are not straight lines under the surface. They can deviate from a vertical line, and can sometimes originate several kilometres away from where they are detected at the surface. Thus the actual aggregation of prey items may be a certain horizontal distance away from the surface manifestation of the front. Second, aggregation of passive dispersing prey species by fronts may take time to develop (Olson & Backus 1985, Podesta et al. 1993). This lag could explain the difference between the distribution of fronts measured by satellite and the distribution of whales observed from boats a few hours before or after.

I believe the spatial and time lags mentioned above could explain why some studies of large baleen whales did not find relationships between whales and SST fronts. Such studies usually examine the value of the temperature gradient at the exact location of the whale sighting and not the distance to the nearest front (Baumgartner & Mate 2005). In addition, they often use SST maps that have been averaged over several days (Hamazaki 2002). Alternatively, it is possible that different species (e.g. rorquals vs. right whales) show specific associations with thermal fronts, that study areas differ in the relative importance of thermal fronts to whales, or that results depend on the way thermal fronts are defined and identified. For these reasons, I believe that SST fronts constitute a complementary proxy for food availability, but that they might not be suitable in all cases. However, the benefits of this proxy are that it is one step closer to actual prey availability than many other oceanographic variables, and that it suggests plausible mechanisms for the observed spatial relationships.

Blue whales were found closer to SST fronts than any other whale species and, once spatial autocorrelation was taken into account, minke whales were not associated with fronts. I suggest two non-exclusive hypotheses to explain these differences among rorquals. First, blue whales are specialists and feed exclusively on krill (Yochem & Leatherwood 1985). In contrast, humpback and finback whales have a more omnivorous diet in my study area, with some overlap between the two species (Borobia et al. 1995). Because euphausiids are capable of less active horizontal movements (Haury et al. 1978), their aggregation patterns are probably more influenced by the concentrating effect of fronts than are those of fishes (Lavoie et al. 2000). Marchand et al. (1999) observed that the distribution patterns of capelin in the estuary of the St. Lawrence did not coincide exactly with the krill distribution, but the two total biomasses were significantly correlated. This could explain why humpback and finback whales, which feed on both krill and fishes, were observed farther away from the fronts and were not significantly different from each other. This hypothesis could only be tested with data on prey items at each sighting location. It would also be useful to know more about the diving profiles of the different species using data-recording tags.

Second, in my study area, minke whales use shallower waters on average than other rorquals, their distribution is strongly linked to heterogeneous bottom relief (T. Doniol-Valcroze & R. Sears unpubl. data) and they prefer certain substrates like underwater sand dunes (Naud et al. 2003). Similarly, minke whales (as well as some finbacks) studied in the Bay of Fundy were attracted to high-vorticity regions of eddy habitats (Johnston et al. 2005a). These results could reflect distinctive hunting techniques for which underwater topography and tidally-induced features are important (Hoelzel et al. 1989), explaining why the relationship between fronts and minke whales was very weak. This hypothesis could be tested with a multivariate model that would include all of these variables and compare their relative importance for minke whales. Overall, these observations suggest a finer degree of habitat partitioning among rorqual species on their feeding grounds than had been previously suspected.

The spatial autocorrelation values for the four species (Table 2-2) show that the whales with the least amount of spatial structure are the ones most highly correlated with fronts. In contrast, minke whales are the most spatially autocorrelated, yet there is no observed relationship to fronts, which emphasises the need to identify other variables which could be contributing to these spatial patterns. I also observed that using partial instead of simple Mantel tests slightly diminished the significance of the relationship with fronts, suggesting that the spatial autocorrelation present in the data could represent the effect of other, unknown, variables.

In conclusion, this study confirms that habitat selection by rorqual whales cannot always be explained solely by looking at the absolute values of environmental parameters. These results show that SST fronts can have a strong influence on the distribution of rorquals and could explain part of the temporal variability that cannot be addressed by static factors. I strongly encourage other studies of habitat use by marine mammals to include such dynamic variables in their models, especially when data on prey distribution are not available. I also found significant differences between the four rorqual species in relation to the frontal areas, indicating a fine degree of habitat partitioning that deserves more research. I believe these results can help identify habitats important to whales and can prove critical for management decisions.

3. Multivariate analysis of habitat selection by rorqual whales in the Gulf of St. Lawrence: importance of dynamic variables

This is the second of two chapters focusing on habitat selection. The first used a standard hypothetico-deductive approach to test the effect of one variable (distance to thermal fronts), which was chosen because of its integrative nature. This result confirmed the importance of dynamic processes. Since many studies of cetaceans, including previous studies in the northern Gulf of St. Lawrence, showed that static factors (e.g. bathymetry) also influence distribution patterns, I wanted to examine the relative importance of static and dynamic factors. In this chapter I take a different philosophical approach by using multivariate statistics in an inductive framework. I use a much larger data set of whale sightings and numerous abiotic variables to explore whale-environment relationships in the context of multiple working hypotheses, with particular emphasis on the importance of time-varying variables.

This chapter includes work from the following manuscript: Doniol-Valcroze T, Berteaux D, Sears R. Habitat selection in dynamic environments: rorqual whales in the Gulf of St. Lawrence. In prep.

3.1 Abstract

In studies of habitat selection, temporal variability is seldom modelled because of the difficulty to sample used and available habitat simultaneously. However, when dealing with mobile animals in a marine system, ignoring the time-varying characteristics of habitats might lead to a poor understanding of ecological relationships and diminished predictive power. I modelled habitat selection by rorqual whales in the Gulf of St. Lawrence using paired logistic regression to account for the dynamic nature of the environment and provide a true picture of availability. For each of 2145 sightings collected from boat surveys (1997-2002) and an equal number of random locations representing available habitat, I obtained environmental characteristics using a computer ocean model. All four species of rorquals responded to this temporal variability by selecting time-varying factors that differed from the available habitat. Models that included only static variables performed consistently worse than those including both static and dynamic ones. St. Lawrence rorquals were selecting for factors traditionally linked with prey availability: shallow banks, steeper seabed slope, slower current velocities, cold and saline surface waters. There were differences between species, which I interpret as differences in diet and hunting strategies.

3.2 Introduction

The study of habitat selection is a primary goal of ecologists. However, most models of habitat selection have been developed primarily for mobile animals with well-defined home ranges or for static locations that are important elements of a species' natural history (e.g. dens, nests). These studies typically make two assumptions: that an animal's entire home range is available for selection and that most habitat characteristics change slowly with time (e.g. seasonally) or not at all (Arthur et al. 1996). Compton et al. (2002) examined the consequences of violating these assumptions for animals with low mobility and large home ranges (wood turtles). However little is known of animals with ill-defined home range and high mobility in a fast-changing environment.

Recent developments in habitat modelling have seen an increasing use of computer-intensive methods to integrate a large number of explanatory variables (Guisan & Zimmermann 2000). Such complex distribution models can improve our understanding of species' ecology and can provide better predictive power for management decisions, especially in the context of environmental change. However these developments have focused primarily on terrestrial systems in which habitat patches are mostly two-dimensional and habitat changes over relatively long temporal scales (Redfern et al. 2006). In contrast, marine ecosystems are fully three-dimensional (Carr et al. 2003) and very dynamic (Steele 1985). Thus, habitats of mobile marine species can change dramatically over both short time spans and small spatial scales (Bjørge 2002).

This complexity poses unique challenges when trying to model species-habitat relationships. Methods that allow for fluctuating habitat (e.g. Arthur et al. 1996, Hjermann 2000) typically require mapping habitat into discrete categories. Defining such habitat types for marine environments is usually not practical, if not impossible. Most marine animals are expected to respond to the complex and dynamic three-dimensional nature of their environment, but for logistical reasons studies of marine species frequently use simple descriptions of the habitat. Ecologists can reduce the complexity of marine habitats by looking only at two-dimensional surface patterns or static variables (e.g. underwater topography, Hui 1985), by using a broad time scale (e.g. monthly maps of ice dynamics, Ferguson et al. 2000) or by choosing species with relatively restricted home ranges (e.g. dolphins, Heithaus & Dill 2002). However, increasing availability of oceanographic data now allows more sophisticated approaches, and recent studies have begun to use multivariate approaches to understand the relationship between baleen whales and their environment (e.g. Tynan et al. 2005, Friedlaender et al. 2006).

Rorqual whales of the Gulf of St. Lawrence (Quebec, Canada) provide an excellent system for studying habitat selection patterns of large mobile animals with no well-defined home range and a changing habitat. Blue, finback, humpback and minke whales are regular visitors to this area during the summer and have been studied extensively over the last 25 years (Sears et al. 1981). Previous studies of habitat selection in the Gulf of St. Lawrence have focused mostly on single variables such as underwater topography (Doniol-Valcroze 2001) and distance to the nearest surface frontal area (Doniol-Valcroze et al. 2007). However, taken alone these variables had little explanatory power. New sources of oceanographic data can now be used to propose fine-scale, time-explicit models of habitat selection.

Here I use a wide range of habitat characteristics to examine resource selection when availability changes through time. My objectives were to quantify the relative influence of environmental variables on the fine-scale distribution of the four rorqual species. Food resources in marine habitats are very patchy and change quickly through time (Mangel & Hofman 1999). Therefore my working hypothesis was that whales exhibit strong selection towards combinations of variables that differ from the available habitat and correspond to transitory favourable conditions. Specifically, I made the following predictions. First, whales should respond to the dynamic nature of their environment and therefore models of selection including dynamic variables should perform better than models based solely on static variables. Second, preferences for favourable sets of conditions should remain stable through time despite inter-annual variations in environmental conditions. Third, because differential habitat selection is one of the principal mechanisms that allow species to coexist (Rosenzweig 1981), I expect species-specific patterns of habitat selection that reflect differences in diets or foraging strategies. I test these hypotheses using a combination of long-term data on whale sightings, a newly available ocean model of the Gulf of St. Lawrence (Saucier et al. 2003), and a suite of conditional fixed-effects models (paired logistic regression) comparing the characteristics of used and available habitats measured synchronously.

3.3 Methods

3.3.1 Data collection

Personnel from MICS collected data on the distribution of blue, finback, humpback and minke whales (cf. section 1.4.2) from June to October 1997-2002 in the Northern Gulf of St. Lawrence (Fig. 3-1).

Environmental variables (Table 3-1) were obtained from a digital nautical chart in ArcView 3.1 (ESRI, Redlands, CA, USA) and from a three-dimensional coastal ocean model with realistic tidal, atmospheric, hydrologic and ocean forcing (Saucier et al. 2003). The model inputs are near-surface atmospheric measurements, radiation and precipitation as well as tidal data and observed temperature and salinity at different depths through the open boundaries. The model computes a fully prognostic solution for currents, temperature, salinity and turbulent energy. Its grid has 5 km horizontal resolution, 5 m vertical resolution and 5 min time-steps. Model predictions and accuracy were validated through comparisons with *in situ* measurements and adequately reproduced circulation patterns in the Gulf (Saucier et al. 2003). In Saucier and Chassé (2000), the model results were compared with 51 current meter records and showed that over 80% of the observed current component hourly variance could be reproduced from the model-derived harmonics. Similarly, there was good agreement between observed and modelled tidal amplitude. I used some of the predicted variables directly (temperature, salinity, currents) and computed depth and minimum temperature of the CIL from the horizontal temperature profiles.

Table 3-1. Environmental variables used in the analysis of habitat selection by rorqual whales in the Gulf of St. Lawrence. Static variables were computed from a digital nautical chart. Dynamic variables were obtained from a three-dimensional coastal ocean model (Saucier et al. 2003).

Variable	Description (units)	Range
Static variables		
depth	Water depth (m)	4 - 218
distance	Distance from nearest shore (km)	0.5 - 54
slope	Mean value of seabed slope within 3 km (°)	0 - 2.95
Dynamic variables		
SST	Water temperature in the surface layer (°C)	0.32 - 14.50
salinity	Salinity of the surface layer (p.s.u.)	19.2 - 32.1
h.currents	Speed of horizontal current in the surface layer (m s-1)	0 - 1.59
v.currents	Maximum speed of vertical current in the water column (cm s-1)*	-0.31 - 0.45
depth.CIL	Depth of the cold intermediate layer (at the coldest point) (m)	45 - 85
temp.CIL	Water temperature of the cold intermediate layer (at the coldest point) (°C	0.21 - 1.85

* negative values indicate downward current

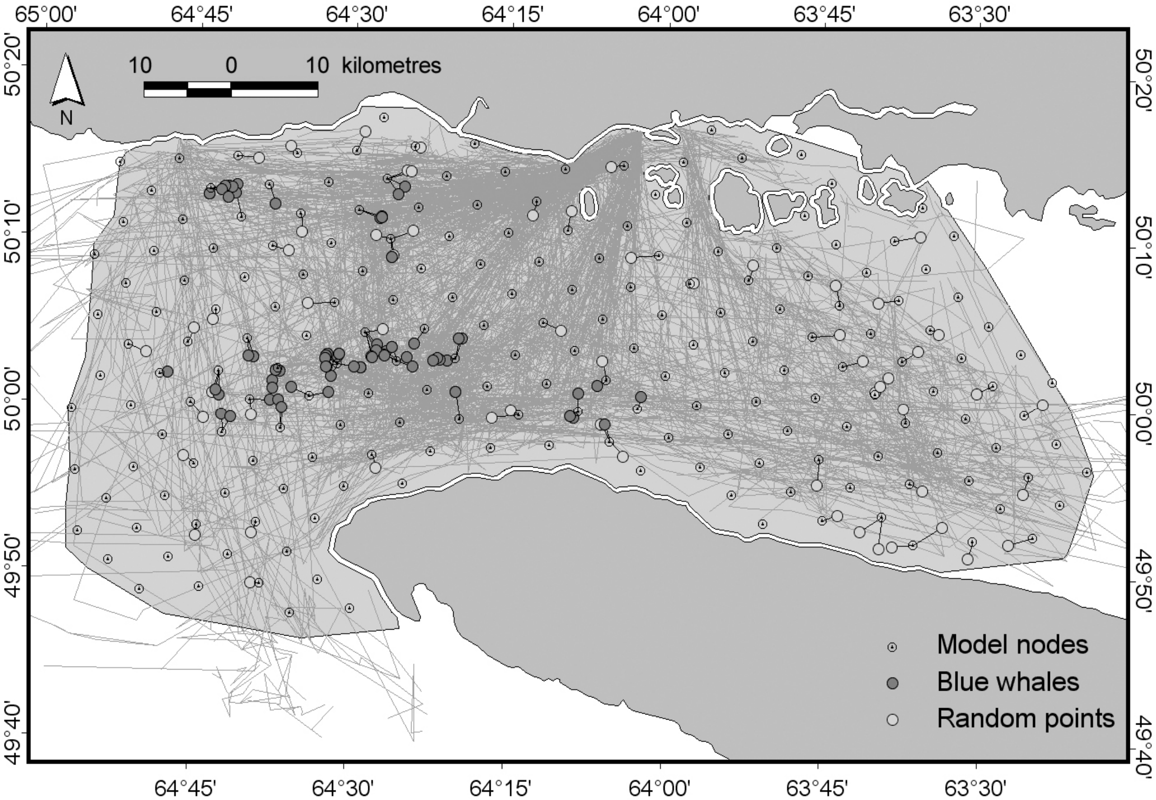

Figure 3-1. Map of the northern Gulf of St. Lawrence (Quebec, Canada) showing the effort tracks used to sample whale distribution (grey lines). Blue whale sightings and random points are plotted for illustration, as well as the shortest distance linking sightings and random points to nodes of the ocean model. The grey shaded area is the combination of all Minimum Convex Polygons containing 95% of the effort tracks for each year of study (1997-2002) and constitutes the area where random points were plotted to represent available habitat.

3.3.2 Defining available habitat

For each year, I drew the minimum convex polygon (MCP) containing 95% of the effort tracks. I used a land mask to remove the shape of the landmasses and created a buffer of 500 m around the shorelines to ensure that the polygon represented available habitat for whales. For each whale sighting, I created a random point within the corresponding MCP (Fig. 3-1). I used the ocean model to derive the environmental variables of the location where the whale was observed and the random location at the same date and time, which provides the only valid comparison between the dynamic characteristics of used and available habitat.

3.3.3 Habitat selection modelling

Multivariate approaches are recommended for an exploratory approach of habitat selection based on a large number of environmental variables (Garshelis 2000). Resource selection models based on comparisons between used and available habitat typically use discriminant function analysis or logistic regression (e.g., Mladenoff et al. 1995, Baumgartner et al. 2001). However, both techniques pool together all the sightings on one side and the random locations on the other, thus losing the dynamic link between pairs of simultaneous observations. Following the suggestion by Compton et al. (2002) for species with movement patterns that violate the assumptions of traditional habitat selection models, I used paired logistic regression (Hosmer & Lemeshow 1989). This conditional fixed-effects model compares use with availability at the same time and therefore comes closer to modelling the choices that animals are making (Compton et al. 2002). Paired logistic regression is comparable to a paired t-test. For each variable and for each sighting, values at random points were subtracted from the values of associated whale sightings. I then used these differences as predictor variables in a standard logistic regression, with the intercept being excluded from the model. The resulting models constitute resource selection functions (RSF) that can be used to infer the choices made by each species towards combinations of environmental variables (Manly et al. 2002).

3.3.4 Model selection

In the case of models containing multiple variables, an information-theoretic approach is recommended over stepwise significance testing because it usually yields better models and leads to clearer understanding of predictor variables (Greaves et al. 2006). To assess habitat selection for each species, I fitted and compared a set of paired logistic regression models. Each of these models can be considered a specific, biologically meaningful hypothesis regarding resource selection (Burnham & Anderson 2002). In the context of multiple working hypotheses, it is important to carefully select variables that have a potential ecological influence (Anderson et al. 2000). My choice of variables was based on theoretically plausible relationships and on the results of preliminary univariate analyses (paired t-tests). In order to avoid over fitting my models with collinear variables, I restricted the models to have no two variables with a Pearson's correlation coefficient >0.5. I assessed goodness-of-fit of each model by testing its residual variance as a chi-square statistic. I then used Akaike's Information Criterion AIC (Burnham & Anderson 2002) to compare their relative likelihood. I compared the ranking of models that included only static variables or only dynamic variables with those that included both static and dynamic variables to evaluate the importance of time-varying processes.

3.3.5 Inter-annual variability

In the St. Lawrence, inter-annual changes in climate can affect the dynamics of prey distribution (Lavoie et al. 2000). I do not know whether rorqual whale habitat preferences remain constant from year to year or if they adapt to different environmental conditions. Therefore, I investigated inter-annual variability in habitat selection patterns. For all the variables included in the best model of each species, I compared the selection scores (observed minus available) across years. Large inter-annual differences in sample size and variance precluded a meaningful analysis using a parametric ANOVA, so I compared the medians using a non-parametric Kruskal-Wallis test (Zar 1999). All statistical analyses were done using R v2.4 computer software (S. Urbanek & S.M. Iacus, Foundation for Statistical Computing 2006).

3.4 Results

3.4.1 Static and dynamic models of habitat selection

I obtained habitat characteristics for a total of 2145 whale sightings (Table 3-2) and an equal number of random locations. For all four species, models of habitat selection that included dynamic variables (SST, salinity, horizontal and vertical currents, temperature and depth of the CIL) performed better than models based solely on static variables (depth, slope, distance to shore) (Table 3-3). For blue whales, the best model contained only dynamic variables, suggesting marginal importance of static factors. For finback and humpback whales, the best models included both static and dynamic variables, and dynamic-only models performed better than those containing only static variables. For minke whales, the best models also combined both types of variables but in this case static-only models performed better than dynamic-only ones.

For blue and minke whales, the best models adequately fitted the data (goodness-of-fit chi-square, $p > 0.50$) and explained an important proportion of the original variance (Adjusted McFadden's R^2 34% and 40% respectively, Table 3-4). However, for humpback and finback whales, none of the models in the candidate set adequately fitted the data (goodness-of-fit chi-square, $p < 0.001$), and even the best models described only a small proportion of the variance (<10%).

3.4.2 Inter-annual variability

Patterns of selection for blue whales were stable from one year to another. I found no inter-annual differences for salinity (Kruskal Wallis, p=0.12), vertical currents (p=0.46) and temperature of the CIL (p=0.12). Spatial distribution patterns of minke whales change very little from one year to another (Doniol-Valcroze 2001). Accordingly, I found no statistically significant difference in habitat selection for static variables such as depth (p=0.17), distance (p=0.13) and slope (p=0.18). In contrast, I found inter-annual differences for dynamic variables (SST, salinity, depth and temperature of CIL, all p<0.001). In contrast, finback whales' selection for static variables changed from year to year (depth and slope, all p<0.001) whereas their selection for some dynamic variables remained constant (horizontal currents, p=0.29; temperature of CIL, p=0.40). In the case of humpback whales, selection for both static and dynamic variables showed strong inter-annual variability (all p<0.01).

Table 3-2. Number of sightings per year of each species of rorqual whales in the northern Gulf of St. Lawrence (1997-2002).

Year	Blue	Finback	Humpback	Minke
1997	0	35	55	312
1998	4	214	99	149
1999	0	45	159	196
2000	3	115	107	212
2001	11	102	72	71
2002	12	77	41	54
total	30	588	533	994

Table 3-3. Paired logistic regression models of habitat selection by rorqual whales in the Gulf of St. Lawrence (1997-2002), ordered by AIC.

Species	Model	AIC	Δ AIC
Blue whale			
	temp.cil + v.currents + salinity	33.32	0.00
	temp.cil + h.currents + v.currents + salinity	35.27	1.95
	depth + distance + slope + temp.cil + v.currents + salinity	35.91	2.59
	sst + temp.cil + h.currents + v.currents + salinity	37.21	3.89
	temp.cil + salinity	37.37	4.05
	depth + distance + slope + temp.cil + h.currents + v.currents + salinity	37.77	4.45
	temp.cil + h.currents + salinity	38.72	5.40
	distance + slope	38.96	5.64
	sst + temp.cil + depth.cil + h.currents + v.currents + salinity	39.19	5.87
	depth + distance + slope + sst + temp.cil + h.currents + v.currents + salinity	39.70	6.38
	depth + distance + slope	40.12	6.80
	v.currents + salinity	40.62	7.30
	h.currents + v.currents + salinity	40.68	7.36
	depth + distance + slope + sst + temp.cil + depth.cil + h.currents + v.currents + salinity	41.66	8.34
Finback whale			
	depth + meanslope + tempcil + h.currents + salinity	771.45	0.00
	depth + distance + meanslope + tempcil + h.currents + salinity	772.07	0.62
	depth + distance + meanslope + tempcil + h.currents + v.currents + salinity	773.43	1.98
	depth + distance + meanslope + tempcil + depthcil + h.currents + v.currents + salinity	775.20	3.75
	depth + distance + meanslope + sst + tempcil + depthcil + h.currents + v.currents + salinity	777.09	5.64
	h.currents	785.69	14.24
	tempcil + h.currents	786.56	15.11
	h.currents + salinity	786.80	15.35
	sst + h.currents + salinity	787.10	15.65
	sst + tempcil + h.currents + salinity	787.23	15.78
	tempcil + h.currents + salinity	787.27	15.82
	sst + tempcil + h.currents + v.currents + salinity	788.94	17.49
	sst + tempcil + depthcil + h.currents + v.currents + salinity	790.92	19.47
	distance	798.35	26.90
	distance + meanslope	798.48	27.03
	depth + distance + meanslope	798.86	27.41
Humpback whale			
	depth + meanslope + sst + depthcil + h.currents	693.43	0.00
	depth + meanslope + sst + depthcil + h.currents + salinity	694.72	1.29
	meanslope + sst + depthcil + h.currents	695.24	1.81
	depth + meanslope + sst + depthcil + h.currents + v.currents + salinity	695.97	2.54
	meanslope + sst + depthcil + h.currents + salinity	697.23	3.80
	depth + distance + meanslope + sst + depthcil + h.currents + v.currents + salinity	697.48	4.05
	sst + depthcil + h.currents	697.6	4.17
	sst + depthcil + h.currents + v.currents	698.84	5.41
	depth + distance + meanslope + sst + tempcil + depthcil + h.currents + v.currents + salinity	699.48	6.05
	sst + tempcil + depthcil + h.currents + v.currents	700.72	7.29
	sst + tempcil + depthcil + h.currents + v.currents + salinity	702.68	9.25
	depth + meanslope + depthcil + sst	703.23	9.80
	depth + meanslope + depthcil + h.currents	710.5	17.07
	depth + meanslope	727.50	34.07
	depth + distance + meanslope	729.50	36.07
Minke whale			
	depth + distance + slope + sst + temp.cil + depth.cil + salinity	746.14	0.00
	depth + distance + slope + sst + temp.cil + depth.cil + v.currents +salinity	746.90	0.76
	depth + distance + slope + sst + temp.cil + depth.cil + h.currents + v.currents + salinity	748.75	2.61
	depth + distance + slope + sst + depth.cil + temp.cil	749.93	3.79
	depth + distance + slope + sst + salinity	757.30	11.16
	slope + distance	760.50	14.36
	depth + distance + slope + depth.cil	763.18	17.04
	depth + distance + slope + temp.cil	764.86	18.72
	depth + distance + slope	766.46	20.32
	depth + slope	792.00	45.86
	depth	845.90	99.76
	distance	874.77	128.63
	sst + temp.cil + depth.cil + h.currents + salinity	886.41	140.27
	sst + temp.cil + depth.cil + salinity	895.70	149.56
	sst + depth.cil + temp.cil	898.47	152.33
	slope	1097.72	351.58

3.4.3 Characteristics of selected habitats

Coefficients of the best models (Table 3-4) showed that rorqual whales exhibited clear habitat selection for numerous variables, both static and dynamic. However, species differed not only as to the value and sign of the coefficients but also as to which variables were most influential. All species except blue whales were influenced to some extent by water depth, slope and distance to shore: minke and finback whales both used shallower waters than the average available habitat (Figure 3-2). Minke and humpback whales both selected for higher slope, but minke whales preferred waters relatively closer to shore whereas humpback whales used more offshore waters.

Relationships with dynamic variables were more complex. The characteristics that most influenced the distribution of blue whales were downward vertical currents and a colder CIL (Figure 3-2). Minke whales were found in colder, less saline waters whereas the other three species preferred higher salinity than the average conditions. Humpback and finback whales chose areas with slower horizontal currents. Influence of the cold intermediate layer was found in the best models of all four species: in particular, finback whales selected for colder CIL and humpback whales for a deeper CIL.

Table 3-4. Coefficients of the best paired logistic regression models of habitat selection for each species of rorqual whales.

Variable	Blue	Finback	Humpback	Minke
depth		-0.0084***	0.0034□	-0.0096**
distance				-0.057***
slope		-0.28*	0.35*	0.56***
sst			0.18***	-0.083*
salinity	0.75□	-0.18*		-0.082*
h.currents		-2.12***	-1.20***	
v.currents	-15.28**			
depth.CIL			0.014**	-0.015***
temp.CIL	-2.51**	-0.44*		0.03*
Goodness-of-fit	0.55	<0.001	<0.001	0.99
Adjusted McFadden's R^2	34%	7%	8%	40%

□$p < 0.1$ *$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

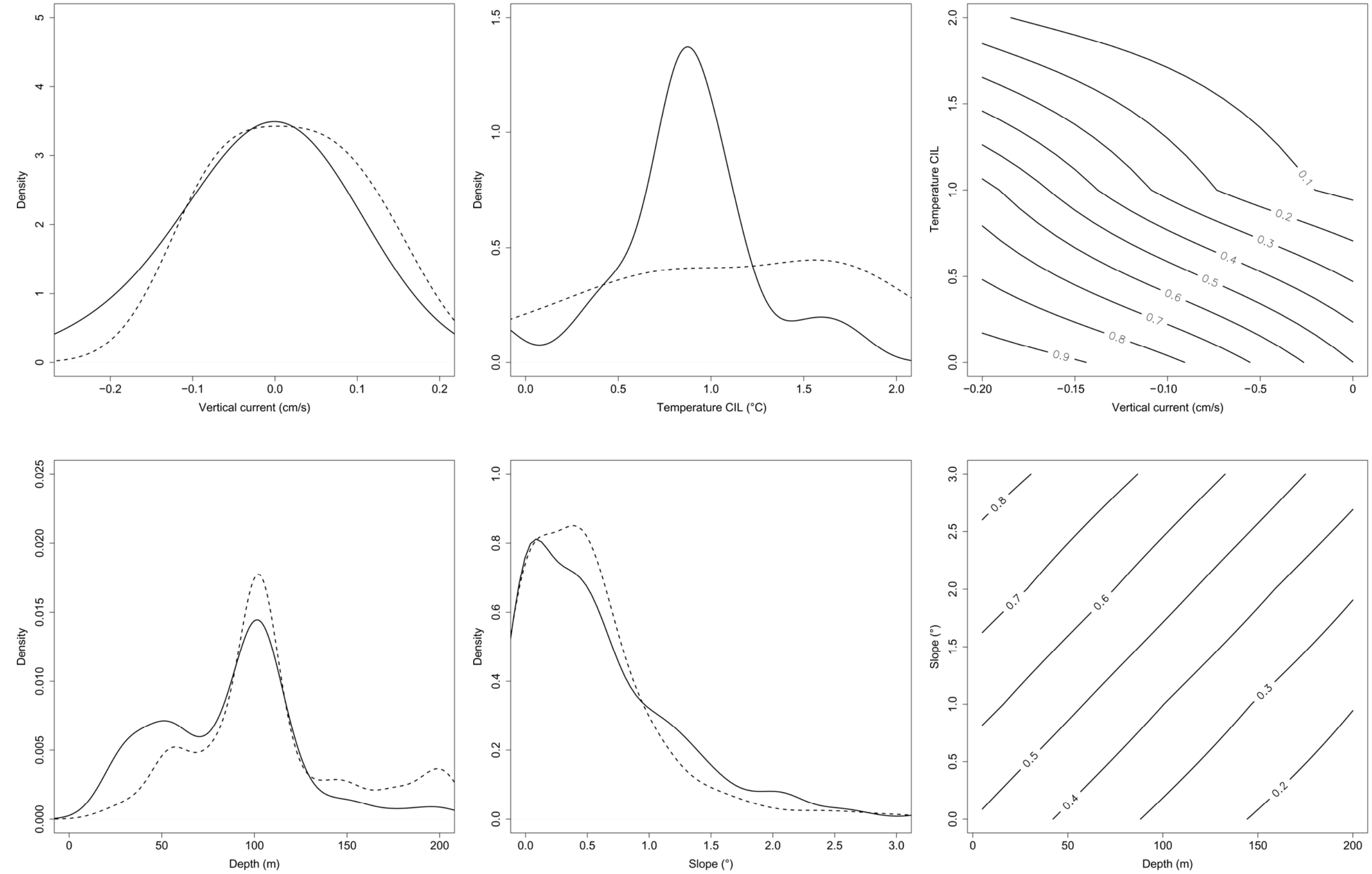

Figure 3-2. Left and centre: Density plots of used (solid line) and available (dashed line) habitat for important environmental variables in models of habitat selection by blue (top) and minke (bottom) whales. Density is in number of sites per 0.033 units of each variable for blue whales and 0.001 for minke whales. Right: Selection function surface of use probabilities for combinations of these variables.

3.5 Discussion

3.5.1 Habitat selection in dynamic environments

I modelled habitat selection of rorqual whales in the Gulf of St. Lawrence using environmental characteristics at whale sightings and paired random locations where habitat was measured simultaneously. Rather than pooled techniques such as discriminant analyses and standard logistic regression, I used paired logistic regression to compare use with availability at the same time and thus to control for confounding factors (Compton et al. 2002). My results show that all four species of rorqual whales respond to the dynamic nature of their environment by selecting for time-varying variables that differ from the available habitat. Models that included only static variables performed consistently worse than those which included dynamic variables, which emphasises the importance of considering time-changing habitat characteristics when dealing with fluid and dynamic environments.

While I successfully modelled habitat selection for blue and minke whales, my models for humpback and finback whales did not fit the data adequately and did not show strong explanatory power. My method assumed that random points correctly represented habitat that was available for each animal (Garshelis 2000). Both existing knowledge and my own field observations show that whales can easily travel the entire span of the study area in a few hours. Thus it seems reasonable to assume that any location in the area delineated by the effort MCP was available to each individual, and that whale locations resulted from an active selection process. Another potential source of bias in the study comes from the sampling design. Habitats where whale densities were highest were likely over-sampled because field operations aimed at maximising whale encounters, rather than ensuring that habitats were sampled equally or randomly. However, by comparing used to available habitat (rather than used to unused habitat) I never assumed that unsampled habitat contained no whales. This approach is the most conservative way to estimate habitat selection (Manly et al. 2002). In addition, I sampled a large range of different habitats, with broad spatial and temporal coverage, which minimises biases in data collected from such platforms of opportunity (Evans & Hammond 2004). This design allowed me to successfully detect selection towards frontal areas in the previous chapter (see also Doniol-Valcroze et al. 2007).

If my methods modelled habitat selection appropriately, there must be other reasons for the unexplained variance. I note that in a similar study of habitat selection in the Bay of Fundy, general additive models explained 42% of the total deviance for minke whale distributions but only 14% for finback whales (Ingram et al. 2007), which is remarkably similar to my results and hints at common explanations for this modelling difficulty. It is possible that fluid habitats are inherently difficult to model with a single spatio-temporal scale (Redfern et al. 2006). Whales might have already selected the general area based on preferences for certain variables and thus would not exhibit preference for these characteristics within the area. Conversely, some selection may take place at a finer scale than I was able to model. It is also possible that the variables available in this analysis were not good proxies for the actual processes underlying resource selection. Without a good knowledge of the mechanisms linking the variables to the distribution and abundance of prey items, it is difficult to address this question.

Finally, the low r^2 could indicate the importance of other factors like social dynamics. In sociable animals, habitat selection by individuals may be influenced by the behaviour and distribution of conspecifics (Ersts & Rosenbaum 2003). Such influence would not be explained by the environmental variables. Here, I suggest it was not a coincidence that the modelling worked best for solitary species (blue and minke whales) but not as well for species that form groups (finback and humpback whales). Similarly, strong individual variation has been shown in some whale species (Hoelzel et al. 1989) and could be another reason for the unexplained variance. For all species except humpback whales, I did not have enough sightings per individual to model this variability but I feel that this subject warrants more research and thus I explore intra-population variation among humpback individuals in chapter 5.

3.5.2 Constancy of habitat selection

Blue whale exhibited stable and strong selection patterns for rare combinations of dynamic variables (i.e. their selection towards dynamic variables did not change from year to year). This, combined with the relatively high R^2 of the best model for this species, gives me confidence that I was able to infer the actual preferences of this species towards rare transitory conditions that likely favour feeding on euphausiids. Patterns of habitat selection for minke whales were also stable for static variables, whereas they changed from year to year with respect to dynamic variables. My interpretation is that minke whales select their habitat primarily based on static descriptors that provide advantageous foraging conditions. This also translates into consistent spatial distribution patterns, although not knowing the identity of individual minke whales prevents me from measuring actual site fidelity.

In contrast, finback whales exhibited strong inter-annual variation in their spatial patterns as well as their selection for static variables such as depth and distance to shore, but their selection for fine-scale dynamic variables was remarkably stable. This suggests that, unlike minke whales, finback are actively looking for habitats characterised by dynamic processes, and that their overall selection for certain static characteristics of the seabed might be mere consequences of the anchoring of dynamic processes in static factors. Finally, the habitat variables in my best model of humpback habitat selection were shown to change from year to year. Combined with low goodness-of-fit and explained deviance, this confirms that I was not able to adequately model the true habitat preferences of humpback whales at this scale.

3.5.3 Species-specific selection patterns

Whale distribution is thought to be determined by physical oceanographic features and the effects of these features on prey abundance (Redfern et al. 2006). However, when data on prey items are directly available, whales are consistently and predictably associated with prey distribution (Simard et al. 2002, Friedlaender et al. 2006). Thus, rorqual whales may be able to locate their prey directly or to identify physical features and oceanographic processes that enhance prey aggregation (Croll et al. 2005, Friedlaender et al. 2006). Overall, these results showed that St. Lawrence rorquals were selecting for factors traditionally linked with prey availability: shallow banks, steeper seabed slope, lower CIL temperature, cold and saline surface waters characteristic of upwelling areas. Most species also selected areas with slower current velocities. This situation is similar to that of finback and minke whales in the Bay of Fundy, which forage in low-velocity eddy regions where euphausiids and herring accumulate at predictable locations (Johnston et al. 2005a).

However, there were marked differences between species, which could be due to differences in diet and hunting strategies. Blue whale habitat was essentially influenced by dynamic variables, in particular by higher salinity, strong downward currents and a colder CIL. These conditions likely correspond to frontal areas where convergence of different water masses induce downwelling and create slicks where euphausiids aggregate in large numbers (Wolanski & Hammer 1988). This interpretation agrees with the result of the previous chapter that blue whales were found consistently closer to thermal fronts than other species. In contrast, minke whale habitat selection was strongly influenced by static factors: shallow coastal waters with heterogeneous topography. This is likely a consequence of minke whale being found predominantly in the

Mingan Archipelago where they hunt for small fish (Naud et al. 2003). The best model for minke whales also contained significant coefficients for colder SST and lower salinity, which are characteristic of the archipelago where constant upwelling keeps surface temperature lower than in the surrounding area and the strong influence of rivers lowers salinity.

Models of habitat selection for humpback and finback whales were harder to interpret, in part because of their poor performance. Several models with different variables performed similarly in terms of AIC, which made it difficult to identify the most important factors. It is clear that these two species were influenced by a more complex combination of both static and dynamic variables. This intermediate situation between blue and minke whales could be a consequence of a broader diet that includes both krill and fish (Borobia et al. 1995). Overall, these species-specific patterns suggest a higher degree of habitat partitioning among these closely related sympatric species than previously suspected and encourage further research on the community dynamics in the area (cf. Chapter 4).

3.5.4 Implications

My results have several implications. I suggest the important roles of both static and dynamic factors can be interpreted in terms of scale. Static factors like physiographic features may be responsible for an area's general appeal to rorquals by creating beneficial preliminary conditions for prey presence and abundance. Dynamic ocean processes, which might be anchored in static factors (Yen et al. 2004), would in turn be responsible for the distribution of prey in dense concentrations that are appealing to rorquals, and the predictability of such aggregations. Dynamic factors may therefore be better suited to explain distribution and habitat selection at a finer scale in both time and space. In this view, static factors could prove useful to characterise potential habitat for management purposes while dynamic factors would be necessary to better predict daily movements and distribution. However, these dynamic factors themselves might be difficult to obtain ahead of time (the ocean model could not), making actual prediction nearly impossible.

Temporal variability in habitats is seldom modelled because of the added complexity and the difficulty to sample the available habitat simultaneously. However, ignoring the dynamic nature of habitats might lead to lack of understanding of ecological relationships, and nowhere does this seem truer than for mobile marine species like cetaceans. Although I looked at the three-dimensional characteristics of the habitat selected by whales, I have still limited my study to the two-dimensional surface location of the animals themselves. The next logical step would be to use newly available technologies to record the precise location of whales in the water column and examine their real-time patterns of habitat use in their three-dimensional environment. Combined with careful definition of available habitat and conditional fixed-effects models, these data could provide a better understanding of ecological relationships within the complex and time-varying habitats of the marine environment.

4. Niche partitioning by four sympatric rorqual whale species in the Gulf of St. Lawrence: mechanisms facilitating coexistence

In chapters 2 and 3, I showed that distribution patterns of each population of rorqual whales in the northern Gulf of St. Lawrence resulted from a selection process towards certain habitat characteristics. I also showed that there were differences between species, suggesting a mechanism of habitat partitioning. Here, based on these patterns of habitat use, I characterise the ecological niches of each species in space, time and multivariate environmental space, and investigate their overlap and their differences. In other words, while chapter 3 aimed at finding the variables that best discriminated between used and available habitat for each species, here I try to find the variables that best separate the four species of whales from one another, as is required to address ecological hypotheses about their coexistence.

This chapter includes work from the following manuscript: Doniol-Valcroze T, Berteaux D, Humphries M, Sears R. Coexistence in dynamic habitats: niche partitioning by sympatric rorqual whales. In prep.

4.1 Abstract

The patchy distribution of resources in marine environments often forces baleen whales to coexist on their feeding grounds. Four species of rorquals with overlapping diets occur in sympatry in the Gulf of St. Lawrence (Quebec, Canada), but nothing is known of the mechanisms that allow them to partition their habitat. I combined 50,000 km of boat surveys and a computer ocean model to quantify space use, habitat preferences and niche breadths for the years 1997-2002. There was clear spatial partitioning of the core areas between species, and some degree of separation in time. Multivariate ordination techniques allowed me to identify combinations of variables that best separated the four niches. Minke whales had a specialized niche centred on shallow coastal waters. The niches of finback and humpback whales were characterized by deeper, offshore waters and a colder intermediate layer. These differences probably reflect species-specific diets and foraging strategies. The endangered blue whale had the narrowest and most marginal niche, characterized by rare combinations of dynamic variables (high salinity, cold surface temperature, slow currents). This is likely a consequence of its very specialized diet and might render it vulnerable to environmental change and competitive pressure. Important niche overlap between rorquals suggests strong potential for past or present competition. I propose fine-scale selection of dynamic variables as a mechanism facilitating co-occurrence of the most ecologically similar species.

4.2 Introduction

The fundamental niche of a species is usually defined as differential preferences along habitat gradients in environmental space (Hutchinson 1965). However, in the presence of competition, coexistence of species is dependent on the ability of each species to partition resources, temporally or spatially, within a particular area, which results in the realized niche (MacArthur 1972). Theory also predicts that environmental heterogeneity in both space and time can promote species coexistence (Chesson 1985). This has been examined in a variety of theoretical models (Chesson 2000). In practice, however, empirical studies of temporally explicit community dynamics are rare (Johnson 2000). Understanding the role of local environmental variation on competitive coexistence in patchy environments remains a major challenge in spatial ecology (Amarasekare 2003).

Resource partitioning is generally studied between sympatric members of a group of species having some general similarity in their trophic roles (Schoener 1986). Many species of whales have similar trophic levels and co-occur in the same habitat (direct sympatry) on their feeding grounds (Bearzi 2005). This is likely a result of the patchy nature of resources in the marine environment and the high feeding requirements of baleen whales. Also, whales live in a fast-changing dynamic environment where favourable habitat conditions can change over fine spatial and temporal scales. Yet, very few studies have investigated the co-occurrence of baleen whales and the mechanisms that allow these species to use the same habitat and partition their resources.

In response to the increasing availability of oceanographic data, multivariate approaches have been used to understand the relationship between competing cetacean species and their environment. Reilly and Fiedler (1994) used canonical correspondence analysis to separate dolphin species in the eastern tropical Pacific. Baumgartner et al. (2001) used linear discriminant analysis to study cetaceans in the Gulf of Mexico. Both studies, however, were performed at a large spatial scale and could not investigate local patterns of resource partitioning. Parra (2006) showed that slight differences in habitat preference maintained the coexistence of two sympatric Australian dolphins at a local scale. None of these studies considered time partitioning and time-varying variables as potentially important mechanisms to facilitate coexistence, nor did they quantify niche breadth and specificity.

The community of rorqual whales in the Gulf of St. Lawrence (Canada) provides an excellent system for studying the fine-scale community interactions of sympatric mobile predators in a dynamic environment. Blue, finback, humpback and minke whales in this area are regular visitors during the summer and have been studied extensively over the last 25 years (Sears et al. 1981). Examination of stomach contents of finback and humpback whales show that these two species eat a wide and overlapping range of food types, mainly schooling fish and euphausiids (Whitehead & Carlson 1988) supporting the possibility of competition. I previously compared their space use patterns to show species-specific differences that suggest habitat partitioning (Doniol-Valcroze 2001). However, limitations of the available environmental data prevented a detailed study of habitat partitioning. New sources of oceanographic data now make it possible to investigate fine-scale habitat preferences for each species, and allow a comparative examination of the relative importance of static and dynamic oceanographic factors.

Knowledge of niche relationships between co-existing species is required to understand community structure and species-specific requirements, and to provide valuable information for management purposes. I used a six-year multivariate dataset to explore community dynamics of sympatric rorquals on their feeding ground. Based on the overall similarities in diet and habitat of the four species in the study area, my working hypothesis was that substantial niche overlap between rorqual species has promoted the evolution of partitioning mechanisms to facilitate co-occurrence. I tested this hypothesis through three specific objectives: 1) to quantify overlap of their spatial and temporal distributions; 2) to quantify characteristics, width and overlap of niches in environmental space; and 3) to evaluate how fine-scale use of dynamic variables can allow several species to use the same spatial locations and further partition their habitat.

4.3 Methods

4.3.1 Study design

When analyzing the coexistence of competing, mobile organisms, an ideal situation would be to know the locations of all individuals in the study area simultaneously as well as their diet, and thus to assess interactions and competition between species in real-time. In practice, this is not a realistic situation when collecting data on free-ranging whales. In my sampling design, I could only know of the position of the whales that were in the vicinity of the research boat at any given time. Thus, I had to infer niche overlap and partitioning of rorquals by pooling all sightings together and looking for similarities and differences in their overall patterns of habitat use.

Potential competitors can avoid competition by ecological segregation in time, space or food resources (Schoener 1986). Therefore I analysed spatial, temporal and habitat-based niche dimensions separately. First I quantified overlap in spatial distribution patterns then examined overlap in time. While it would have been ideal to study space and time simultaneously, the sample sizes became too small for meaningful analyses once I split my data set by month and year. Secondly, I wanted to measure niche width and separation. Such measures are usually made in discriminant space (Green 1974, Dueser & Shugart 1979), but these spaces are sensitive to the most abundant species (Van Horne & Ford 1982). Because I had large differences in number of sightings among species, I chose a recent technique of constrained ordination that is not sensitive to sample size heterogeneity: the Outlying Mean Index (Doledec et al. 2000).

Finally, I wanted to evaluate how fine-scale temporal heterogeneity allowed rorquals to further partition their habitat. If selected habitat characteristics depended only on where the animals were observed in space, I would expect e.g. humpback sightings located in the core area of finback whales to be associated with the same characteristic as those selected by finback whales rather than the usual characteristics of the humpback niche. If, however, rorquals can use dynamic variables to co-exist at the same locations by selecting for different characteristics, I would expect them to exhibit consistent habitat selection patterns no matter where they are in space.

4.3.2 Data collection

A full description of the data collection methods is provided in sections 1.4.2 and 3.3.1. Briefly, personnel from MICS collected data on the distribution of blue, finback, humpback and minke whales from June to October 1997-2002 in the Northern Gulf of St. Lawrence. Each whale sighting was associated to a series of static and dynamic environmental variables (Table 3-1), obtained from a digital nautical chart and from a three-dimensional coastal ocean model (Saucier et al. 2003).

4.3.3 Spatial and temporal overlap

I plotted whale sightings in ArcView 3.1 (ESRI, 1995) and used the Animal Movement Analyst extension (Hooge & Eichenlaub 1997) to estimate a fixed kernel utilization distribution for each species. The kernel method uses a probabilistic model to calculate the two-dimensional relative frequency of sightings (Worton 1989). Kernel ranges of 50% and 95% probability of occurrence were calculated using smoothing parameters calculated via the least squares cross-validation procedure (Seaman & Powell 1996). This method does not make any assumption about the statistical distribution and it can have more than one core area (Sauer et al. 1999).

I chose the 95% contour to represent the range of each species within the study area because it contained most of the locations where the whales were observed but excluded potential outliers. The 50% contour was chosen to represent the core areas of habitat use because higher and lower values resulted in few very large or multiple very small density peaks that did not seem to represent ecologically meaningful areas of importance. These threshold values have been used by other researchers (e.g. Parra 2006) and therefore facilitate comparisons between studies.

I calculated the percent of area overlap between each species' core area and representative range and those of the three other species. I also examined the temporal distribution of sightings throughout the season to determine the abundance peaks of each species, and tested for differences among species using a one-way ANOVA.

4.3.4 Niche characteristics and width

I used a MANOVA to test for overall differences between species based on habitat variables. My choice of variables was based on theoretically plausible relationships and on the results of habitat selection analyses in Chapter 3. I then used the Outlying Mean Index (OMI) to quantify the marginality and niche width of the four species (Doledec et al. 2000). Like discriminant analysis, this ordination technique detects which ecological factors provide the best separation of species based on their niche characteristics. OMI addresses both linear and non-linear response from species to the environment and thus requires fewer assumptions than discriminant analysis. This technique also calculates the mean of each species for each variable and plots them as gravity centres on axes that maximise species separation. The origin of the axes represents the gravity centre of a theoretical ubiquitous species uniformly distributed among habitat conditions in the data set. The distance of the gravity centre of each species to the origin is called the marginality. The total inertia given by the analysis measures how well the environmental variables separate the four niches. A Monte-Carlo test with 1000 permutations was used to test for the significance of environmental variables on niche separation. I performed niche analyses in the ADE-4 package for R (Chessel et al. 2006).

4.3.5 Spatial overlap and dynamic variables

To evaluate whether dynamic variables could explain why more than one species used the same spatial locations at different times, I focused on sightings of a given species that were located within another species' core area, then evaluated whether, at the time of the sighting, the location had dynamic characteristics similar to those generally preferred by the intruding species or by species typically encountered in this core area. I performed a second OMI analysis with only the temporally dynamic variables. I calculated the mean canonical scores of the four rorquals on a single principal component axis. For each species, I then selected the sightings that were located spatially within another species' core area. I plotted the canonical scores of these sightings and used a one-tailed t-test (Zar 1999) to test the prediction that canonical scores were closer to the mean characteristics of their species' own core area than to those of the other species.

4.4 Results

4.4.1 Survey effort and space use patterns

The sampling effort for 1997-2002 represented an average of 10,000 km per year (Fig. 4-1). I observed a total of 2145 whale sightings for which I obtained habitat characteristics from the ocean model. Of these, 30 were blue whales, 588 finback, 533 humpback and 994 minke whales. Rorquals were observed throughout the study area but each species showed clear aggregations at certain core areas, as represented by the 50% kernel contours (Fig. 4-2). Although rather ubiquitous, minke whales concentrated mostly in shallow coastal waters and were the only species commonly found within the Mingan Archipelago. Blue whales in contrast were usually found in deeper waters and their core area was far offshore in the centre of the Jacques Cartier passage. Finback and humpback whales had two core areas of habitat use, but while finback whales used both offshore and inshore waters, humpback whales were predominantly found farther offshore.

4.4.2 Spatial and temporal overlap

Overlap of representative ranges (95% kernel) among all four species was considerable (20-89%, Table 4-1). The largest overlap occurred between finback and blue whales as the finback range overlapped with 89% of the blue whale range. All four species clearly aggregated in core areas of habitat use (Fig. 4-2). Overlap indices for these core areas were much smaller (0-57%, Table 4-2). Minke whale habitat use was very different from the other species, showing no overlap with blue and humpback whales and very little overlap with finback whales. In contrast, humpback and finback whales displayed large overlap with one another, essentially using the same core areas.

There were differences between the four species in terms of temporal distribution. Humpback whales were almost never observed early in the season (before mid-July) and finback whales were rarely seen later than September. Blue and minke whales could be seen throughout the season. The average sighting dates differed significantly between species (ANOVA, $F_{3,2141}$=321.57, p<0.001). Despite large temporal overlap, the abundance of the three more numerous species did not peak at the same time but rather followed a temporal sequence through the season (Fig. 4-3). Finback sightings peaked in mid-July while humpback sightings peaked in the second half of August. Minke sightings first peaked in June but remained abundant throughout the rest of the season. Blue whale sightings were spread more evenly throughout the field season but in much lower numbers.

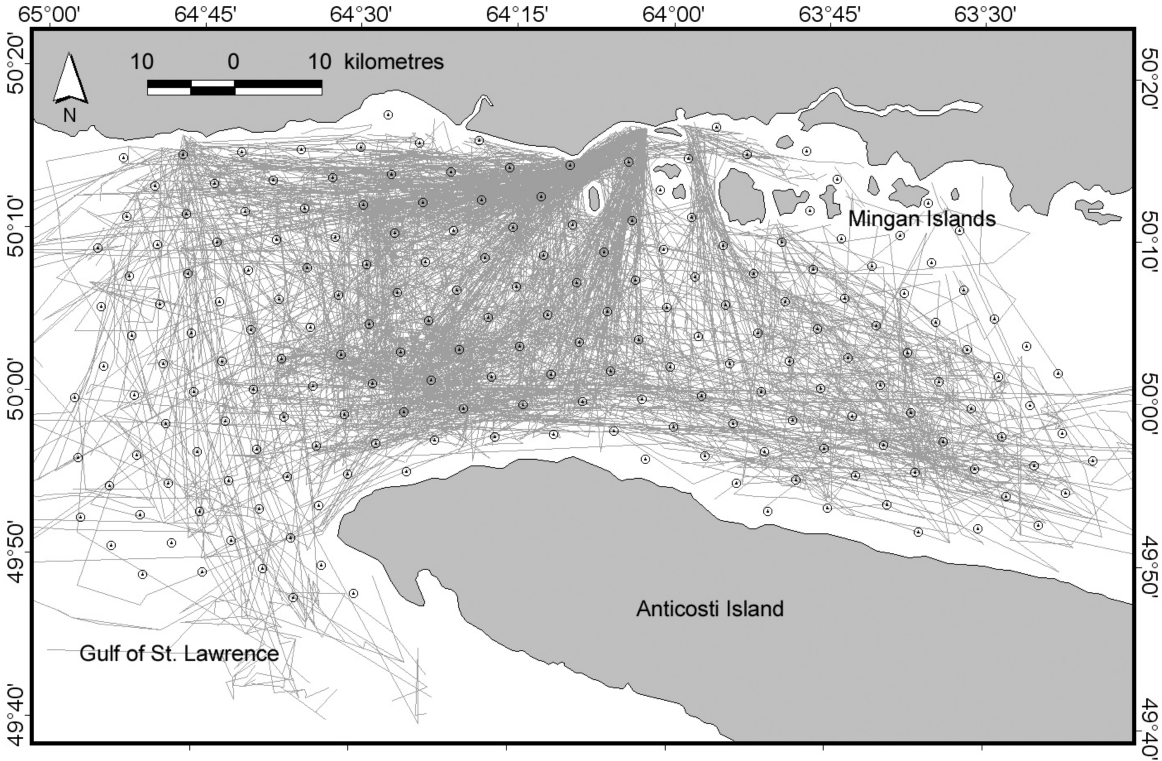

Figure 4-1. Map of the northern Gulf of St. Lawrence (Quebec, Canada) showing the effort tracks used to sample whale distribution (grey lines) for the period 1997-2002 and nodes of the computer ocean model (open circles) used to determine habitat characteristics.

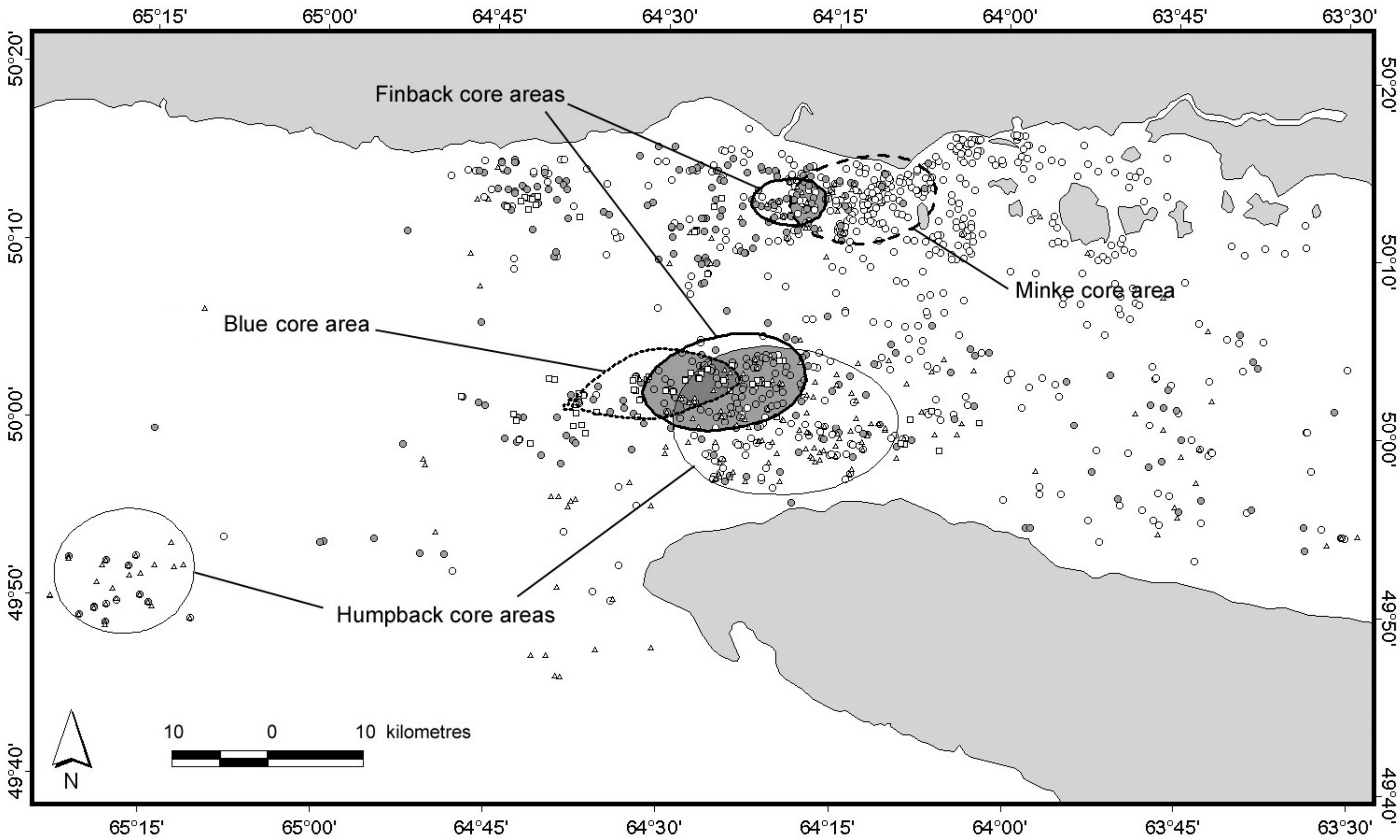

Figure 4-2. Distribution, core areas and spatial overlap of blue (squares, n=30), finback (closed circles, n=588), humpback (triangles, n=533) and minke whale (open circles, n=994) sightings in the northern Gulf of St. Lawrence for the period 1997-2002 (note that at this scale many sightings are superposed). Shaded areas correspond to overlap between two species (light grey) and three species (dark grey).

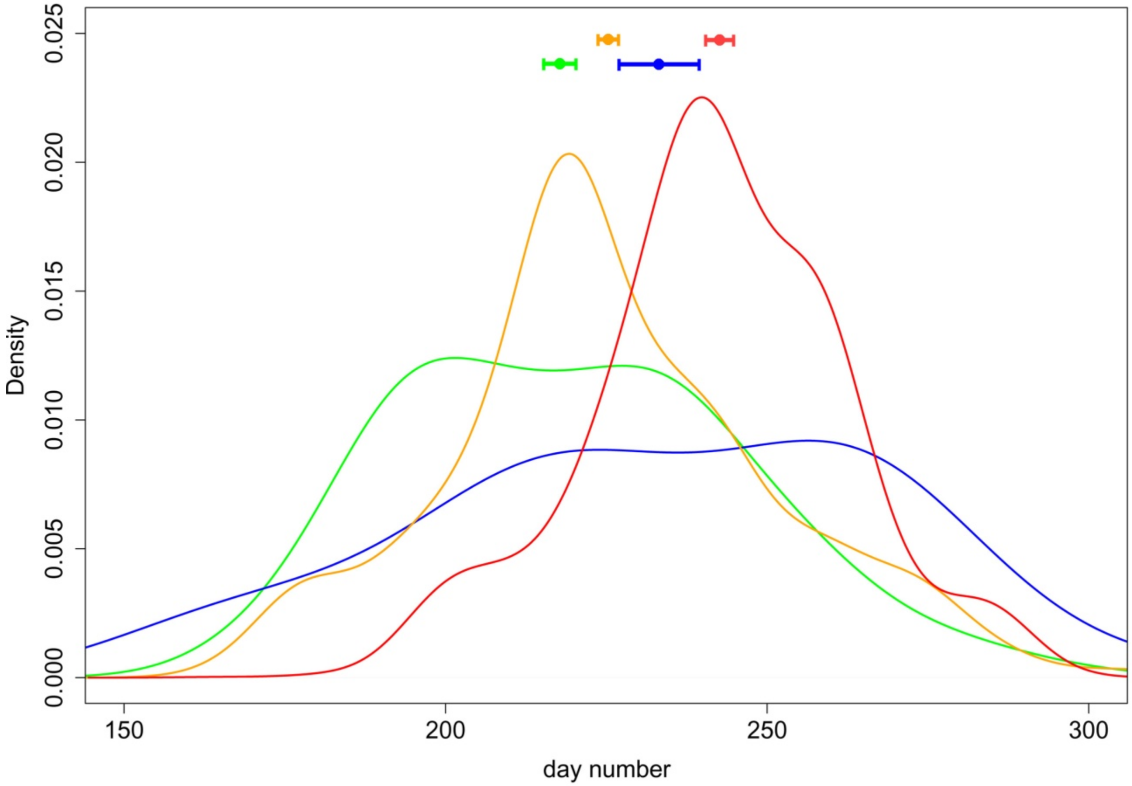

Figure 4-3. Temporal distribution of blue (blue), finback (orange), humpback (red) and minke (green) whale sightings for the years 1997-2002 pooled together. Density is in number of sightings per 0.033 days for blue, 0.002 days for humpback and finback, and 0.001 days for minke whales. Differential peaks of abundance between species are clear in the study area, located in the northern Gulf of St. Lawrence, Canada. Horizontal bars on top indicate means and 95% Bonferroni intervals for each species.

Table 4-1. Percentage of a species' representative range (95% kernel) contained in the range of another species.

	in blue range	in finback range	in humpback range	in minke range
Blue	100	89	68	46
Finback	40	100	65	54
Humpback	20	43	100	36
Minke	21	55	55	100

Table 4-2. Percentage of a species' core range (50% kernel) contained in the core of another species.

	in blue core	in finback core	in humpback core	in minke core
Blue	100	53	24	0
Finback	28	100	57	8
Humpback	5	21	100	0
Minke	0	12	0	100

4.4.3 Niche characteristics and width

There were differences in habitat characteristics used by the four species of rorquals (MANOVA, Wilks' Lambda = 178.3, $p < 0.001$). These differences resulted in some degree of niche separation between species (OMI ordination, Fig. 4-4). The variables that best discriminated among species were distance to shore, depth, temperature and depth of the CIL, slope and salinity (Monte-Carlo randomization tests, all $p < 0.001$).

When read as a measure of the marginality of a species' niche, the Outlying Mean Index (OMI, Table 4-3) indicates that blue whales used habitat characteristics that differed most from the average conditions (OMI=11.5). They also had the smallest tolerance value, a measure of niche width. Blue whale niche was characterised by higher salinity and lower temperatures typical of upwelling conditions as well as a deeper, colder CIL, deeper waters and flatter topography. In contrast, finback niche was closer to that of a hypothetical ubiquitous species (OMI=1.9) and had a wider niche. Humpback and minke whales had intermediate marginality values with large niche widths, but humpback niche was characterised by deeper waters farther from shore, whereas minke whales were found in shallower waters, closer to shore and with more heterogeneous topography.

4.4.4 Spatial overlap and temporal separation via dynamic variables

The number of sightings observed within another species' core area mirrored closely the results of spatial overlap (Table 4-4). For instance, no blue whales were observed in the minke core area but a large proportion of finback whale sightings were located within the core areas of humpback whales. Differences in canonical scores showed that when minke and humpback whales were observed in other species' core areas, the current dynamic characteristics of those areas were similar to the conditions that prevail in their own core areas (Fig. 4-5). Finback whales, on the other hand, were selecting for temporal variables that were similar to those of the species in which core area they were observed (i.e. when finback whales sightings were in humpback core area, their dynamic characteristics were more similar to those of humpback core than finback core). No differences were detected for sightings of any species in minke core and for blue whale sightings in any other core (all $p > 0.5$) but samples sizes for these categories were small.

Table 4-3. Niche marginality and width of blue, finback, humpback and minke whales in the northern Gulf of St. Lawrence (based on outlying mean index and tolerance in a discriminant space defined by nine environmental variables).

	marginality (OMI)	width (tolerance)
Minke	5.5	18.1
Blue	11.5	12.4
Finback	1.9	16.6
Humpback	8.0	21.5

Table 4-4. Number of sightings (and proportion of total sample size) of each species observed in the core area of another species.

	in blue core	in finback core	in humpback core	in minke core
Blue	-	26 (87%)	16 (53%)	0 (0%)
Finback	95 (16%)	-	166 (28%)	17 (3%)
Humpback	20 (4%)	71 (13%)	-	5 (1%)
Minke	9 (1%)	71 (7%)	101 (10%)	-

4.5 Discussion

I examined spatial distribution and fine-scale niche attributes of rorqual whales in the northern Gulf of St. Lawrence between 1997 and 2002, and showed that the realized niches of sympatric populations of rorquals could be separated to some extent by patterns of habitat use. Theory predicts that animals most often segregate in space (by using different habitats), less often in diets and rarely in time (Schoener 1986). Here I discuss each of these factors and then examine how their combinations might allow rorquals to partition their niches.

4.5.1 Partitioning in space and habitat characteristics

I observed considerable spatial overlap among all four species but some degree of specialisation at the level of their core areas of habitat use. For instance, there was clear spatial partitioning of habitat between blue and minke whales, as they used very different core areas. Similarly, while there was overlap of habitat descriptors, multivariate ordination techniques allowed me to identify variables that best separated the four species. Minke whales had a specialised niche centred on shallow coastal waters, which is similar to the observed separation between minke and finback whales in the Bay of Fundy (Ingram et al. 2007). The niches of finback and humpback whales were wider and characterised by deeper, offshore waters and a colder intermediate layer. Blue whales had the narrowest and most marginal niche, characterised by rare combinations of dynamic variables (high salinity, cold surface temperature, slow currents). Selection of different habitats based on spatial location and static descriptors allows minke whales to separate their niche from the other three species, but seems insufficient to prevent competition between blue, finback and humpback whales.

4.5.2 Diet specialisation

Differences between niche widths and positions could also be interpreted in terms of diets. The narrow niche of blue whales could be a consequence of their specialist euphausiid-based diet and their need for very dense concentrations of food (Yochem & Leatherwood 1985). Also, their niche was entirely nested within the other species' niches, showing that these rare conditions are also sought by other rorquals and therefore could indicate tremendous potential for interspecific competition. The larger niches of finback and humpback whales are likely a consequence of their more omnivorous diet, and the part of the niche that does not overlap with that of blue whales could correspond to conditions favouring the hunting of fish (Whitehead & Carlson 1988). Small differences between humpback and finback whales could correspond to different proportions of euphausiids and fish in their diet. Indeed, fatty acid analysis performed on humpback and finback whales in my study area showed a small but significant difference between these two species' diets and argues in favour of niche separation via slight differences in diet (Borobia et al. 1995).

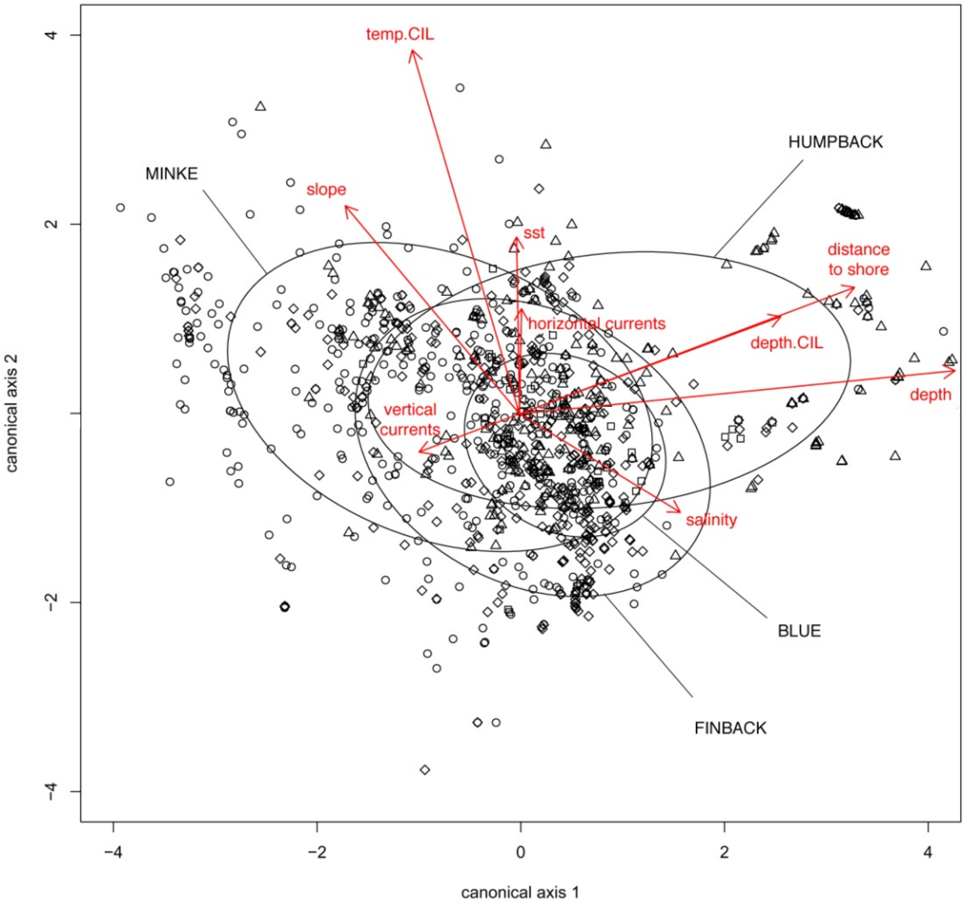

Figure 4-4. Plot of blue (squares), finback (diamonds), humpback (triangles) and minke (circles) whale sightings on OMI axes. Red arrows show canonical weights of local-scale environmental variables. Ellipses contain 75% of the sightings of each species and represent ecological niches.

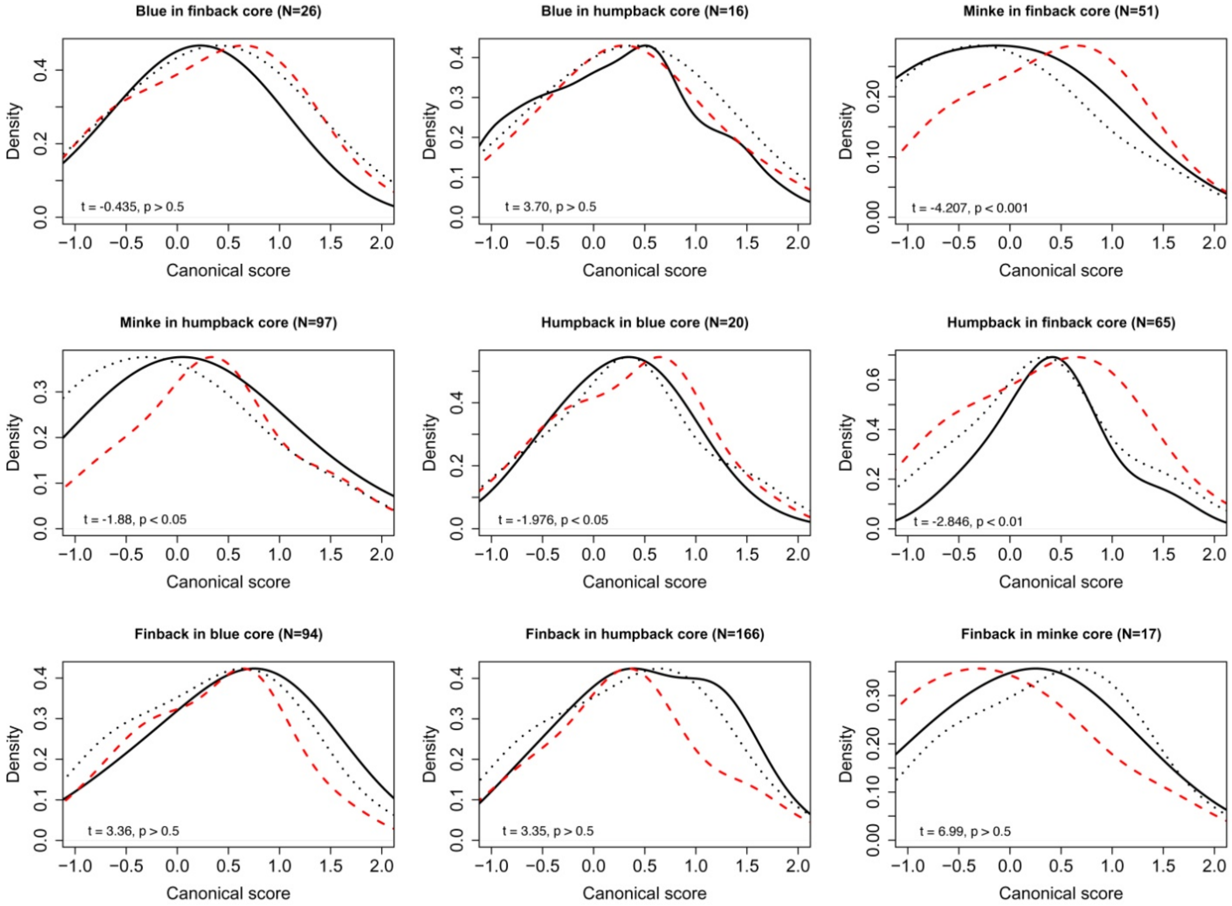

Figure 4-5. One-axis OMI analysis with dynamic variables only. For each combination of species A observed in the core area of species B, the canonical scores of these particular sightings of A (solid line) are compared to the overall niche of A (dotted line) and of B (red dashed line); *t*-test results indicate the probability of statistically significant deviance from the mean score of species B. Three combinations are not represented because their sample size was too low (< 10). Kernel densities are in number of sightings for each 1/N fraction of canonical score unit.

4.5.3 Time and dynamic variables

Partitioning also occurred in time, particularly between minke, finback and humpback whales which all arrived and peaked in the study area at a different time. For instance, while humpback and finback whales exhibited the least amount of spatial and niche separation, they showed a significant separation in their temporal distribution. This suggests that for these two ecologically similar species, separation in time could be another important mechanism facilitating co-occurrence.

Time is rarely used for partitioning by terrestrial animals (Schoener 1986) and can only be used as a resource dimension when there is renewal of prey over time (Pianka 1981), or if it leads to reduced competition (Polis 1984). In the northern St. Lawrence, coastal upwellings maintain biological productivity during the summer by replenishing nutrients in the surface layer (Rose & Leggett 1988). By arriving in the study area at different times, rorquals might be able to alleviate competition and still have access to large concentrations of prey. However, because of the patchiness of prey and the short length of the feeding season, I believe that rorquals have few opportunities to partition their habitat in time and space (i.e. there is only a limited number of places that can meet their feeding requirements and this only during a short period of time).

On the other hand, the three-dimensional, dynamic nature of the marine environment seems to offer more opportunities for partitioning of niches. Theory tells us that environmental heterogeneity can help species coexist even if their requirements are very similar (Hutchinson 1961). Therefore, complex and time-changing spatial structures such as those found in the oceans might offer competitors more opportunities for habitat partitioning than terrestrial habitats would. This idea is further supported by my analysis of the fine-scale selection process within each species' core area. For instance, when minke and humpback whales were located in another species' core, they were selecting for dynamic variables that were still characteristic of their own usual niche (i.e. their habitat preferences for dynamic variables were consistent whatever their spatial location). To my knowledge, this fine-scale use of the dynamic characteristics of the aquatic habitat by top predators is shown here for the first time and gives us a unique insight into partitioning mechanisms available to mobile marine animals.

Habitat selection is often viewed as a hierarchical process in which an organism first chooses a habitat and then makes subsequent decisions about the use of different patches (Orians & Wittenberger 1991). The decision of whether to forage in a certain habitat or to continue searching is often made quickly, usually on the basis of rather general features of the environment (MacArthur et al. 1966). These results suggest that rorqual whales make preliminary choices as to what constitutes good foraging habitats based on static factors such as underwater topography but are ultimately interested in the dynamic variables that presumably drive prey abundance and concentration. They probably base these decisions on the anchoring of dynamic processes in static elements. For instance, areas of heterogeneous topography are known to induce temporally and spatially predictable upwelling (Yen et al. 2004). This hierarchical process explains how I can observe such large spatial overlap between species and yet clear habitat preferences based on fine-scale time-varying variables. It also suggests that the ability of different species to coexist in a region might be affected not only by the distribution of patches in space but also in time.

4.5.4 Competition in rorqual communities

Ecological theory predicts a positive relationship between interspecific overlap in resource use and the intensity of interspecific competition (Munday et al. 2001). These results would therefore suggest a high potential for competition among St. Lawrence rorquals. But overlap in use of resources is only one requirement for competition to occur; the resource must also be limiting. A high degree of niche overlap may indicate that competition is not intense but limited or incomplete (Colwell & Futuyma 1971) or that resources are superabundant (Gordon & Ilius 1989). Alternatively, low overlap of resources and high specialisation, such as what I observed for blue and minke whales, may reflect evolutionary divergence and may be indicative of past rather than present competitive interactions (Ilse & Hellgren 1995). Are resources in the St. Lawrence currently limiting despite potentially lower numbers of rorquals than before the whaling era? Unfortunately, I do not know if whales in the North Atlantic are food-limited (Clapham & Brownell 1996). If resources were not limiting on these feeding grounds, then observed patterns of habitat partitioning could be the ghost of competition past.

Nevertheless, my results have several implications. The endangered blue whale was by far the most specialised of all four species, both in terms of marginality and niche width. Its narrow preferences for rare combinations of dynamic environmental variables might explain its scarcity and suggests that this species might be very vulnerable to any future environmental change. I found that marked differences in habitat use could be one of the principal factors maintaining the coexistence of the least similar species (e.g. blue and minke). This suggests that the diversity of habitat characteristics in a given area helps maintain cetacean species diversity even at such a fine scale, which might be useful to consider for successful management purposes. I also found that using dynamic variables in the analysis considerably enhanced my ability to discriminate among species. Despite the difficulty of obtaining such data, I encourage future studies of marine communities to include them when feasible.

4.5.5 Conclusions

Small ecological differences can allow closely related species to minimise competition and thus coexist (MacArthur 1958). Fine-scale selection of dynamic variables seems to be the main mechanism facilitating the coexistence of rorquals on their feedings grounds. My results suggest that rorqual whales are searching in both space and time for suitable habitats in a patchy, time-varying environment. This study highlights the importance of considering multiple interacting species in studies of cetacean habitat use and selection. Additional studies of dietary and habitat overlap of these rorqual species, in both sympatric and allopatric situations, are required to better understand the way in which whales may partition their resources in a dynamic environment.

5. Influence of individual specialisation on intra-population niche variation of humpback whales in the Gulf of St. Lawrence

In chapter 4, I characterised the ecological niches of each rorqual species studied and estimated their width. Humpback whales had the widest niche of all four species, implying that they had a broad range of habitat preferences for the variables I measured. This makes it more difficult to model their distribution than for a species with narrow habitat preferences, which could explain in part the low explanatory power of the habitat selection models in chapter 3. This large intra-population niche variation can result from a combination of inter- and intra-individual variation. In turn, inter-individual variation can result from differences between sex and age classes as well as individual specialisation. In this chapter, I try to determine the relative importance of sex and individual specialisation on the intra-population variation of humpback whales. I focus on humpback whales because they exhibit the widest ecological niche but also because sample sizes of sexed and individually identified whales were too low in the other three species to include them in the analysis.

This chapter includes work from the following manuscript: Doniol-Valcroze T, Berteaux D, Humphries M, Sears R. Intra-population niche variation in humpback whales on their feeding grounds: occurrence and influence of individual specialisation. In Prep.

5.1 Abstract

Individuals in a population are not ecologically equivalent. Patchiness of resources and environmental variability can lead to individual specialisation in order to reduce intra-specific competition. However, individual variability is rarely quantified for niche characteristics other than diet. Large whales are expected to experience strong neighbour effects because of their large overlapping home ranges. Using 612 sightings of identified individuals and a computer model of habitat characteristics for the years 1997-2002, I investigated sources of intra-population variation in a population of humpback whales from the Gulf of St. Lawrence to determine the importance of individual specialisation. Multivariate analyses showed that individual variability was an important part of intra-population variation and contributed to the large niche width of the species. While there was no evidence of segregation by sex, individual specialisation, probably at the level of foraging techniques and diet preferences, appears to be an important mechanism for finer subdivision of the species' niche.

5.2 Introduction

According to niche theory, inter-specific competition for resources has a major influence on community structure (Schoener 1986) but it is not the only interaction that can modify an organism's niche. Intra-specific competition is a significant component in the evolution of niche widths (Polis 1984). For most animals, the presence of conspecifics can be an important element of the environment (Whitehead 1999) and can influence habitat selection (Thomas & Taylor 1990). Components of a single population may show differences in feeding ecology between sexes and age groups (Schoener 1967), polymorphic individuals (Roughgarden 1972) and even individuals apparently identical in all aspects except feeding behaviour (Polis 1984). Individual-specific differences in resource use effectively increase the niche width of a species or a population and thus allow finer subdivision of niches (Roughgarden 1972).

Ecologists acknowledge the importance of intra-population variation by working with large sample sizes to obtain a representative average for a given population and by taking into account individual identity in statistical analyses. Yet until recently, individual variability was rarely quantified for niche characteristics other than diet (Bolnick et al. 2003) and was usually considered rare (e.g. by Schoener 1986). Most habitat studies used to pool data across individuals, preventing a detailed examination of individual selection strategies (Thomas & Taylor 1990). However, inter-individual variation is now considered widespread and can profoundly affect a population's ecology (Durell 2000, Bolnick et al. 2003). The reduction of intra-specific competition through resource partitioning has been observed for species over a wide range of spatial scales, especially when resources are limited and environmental variability is high (Perry 1996, Bowen et al. 2002, Field et al. 2005). Thus in dynamic and patchy environments such as marine habitats, individuals that have evolved behaviour specialisations to reduce the impacts of intra-specific competition may have a selective advantage (Field et al. 2005).

Large mammal species require larger home ranges than suggested by their energy needs, possibly because of their lower encounter rate with prey (Haskell et al. 2002). As home ranges become too large to be defendable, their overlap increases and so does the potential for neighbour interactions and intra-specific competition (Jetz et al. 2004). Whales on their feeding grounds theoretically represent an extreme case of this situation, even though they do not have clearly defined home ranges. Satellite tracking of blue whales shows that the range of their movements during the feeding season can commonly encompass their entire feeding ground (Mate et al. 1999). If this is representative of other rorquals, we expect large overlap of space use patterns and therefore strong interactions with conspecifics (e.g. direct or scramble competition).

This in turn could lead to strong intra-population variation, whether in the form of segregation by sex and age (Schoener 1986) or individual specialisation (Roughgarden 1972). For instance, individual minke whales in the San Juan Islands use one of two possible hunting techniques and tend to feed in specific areas that differ in their bottom topography (Hoelzel et al. 1989). Our knowledge of inter-individual variation in other baleen whales remains very limited.

The population of humpback whales in the Gulf of St. Lawrence (Canada) provides a good system for studying the occurrence of individual variability in large marine mammals. Long-term studies have yielded individual identification and sexing of numerous animals (Ramp et al. in prep) and computer ocean models have been developed to describe the fine-scale environmental characteristics of their habitat (Saucier et al. 2003). However, previous studies in the St. Lawrence and elsewhere have used environmental variables such as surface temperature, salinity, depth and slope of the sea bed to describe humpback whale habitats, and showed that their explanatory power was weak (e.g. Gregr & Trites 2001, Chapter 3 of this thesis). Individual variability could increase intra-population variation, thus making it harder to adequately model habitat selection using the mean of selected habitat characteristics. Large inter-annual variability in environmental characteristics may also impact our ability to understand whale-habitat relationships.

Here I studied intra-population variation in humpback whales based on nine habitat variables. My first objective was to determine the relative importance of intra- and inter-individual variation. I quantified the contribution of segregation by sex, individual variability and inter-annual variation to the total niche width. Individual variability can arise from individual-specific patterns of habitat selection (i.e. individual specialisations) or can reflect the occurrence of site fidelity or territoriality. Therefore, my second objective was to determine the source of inter-individual variation by testing for site fidelity among years. Because of the mobile nature of their prey, site fidelity and defence are unlikely to be beneficial for rorqual whales (Clapham 1993). Therefore, I predict that humpback whales will exhibit no site fidelity on their feeding grounds and thus that inter-individual variation will reflect genuine differences in habitat preferences.

5.3 Methods

5.3.1 Study design: defining individual specialisation

To examine the occurrence and extent of individual specialisation, I used the framework initially provided by Roughgarden (1972). The total variance of a given habitat characteristic represents the total niche width (TNW) and can be partitioned in two components: the within-individual component (WIC) and the between-individual component (BIC) (Fig 5-1). Inter-individual variation is important when BIC/TNW is large compared to WIC/TNW. In turn, BIC has four main components: differences between sexes, age classes, morphological groups and individual strategies. An individual specialist is therefore defined as “an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete morphological group” (Bolnick et al. 2003). There is no threshold value to determine which individual is a specialist. It is recommended to consider instead the degree of specialisation, represented by BIC/TNW when all other components have been removed (Bolnick et al. 2002).

Of the four components of BIC, only sex and individual specialisations can be tested for rorqual whales (I do not have data on age groups and there are no known morphological groups in whales). Here, I first test for differences between sexes and individuals and quantify the contribution of these factors to the total niche width. Secondly, I test for between-years variations because it can contribute to both BIC and WIC and thus be an important confounding factor. I then examine the size and marginality of each individual niche to better understand the degree and results of specialisation. Finally, I investigate whether site fidelity is responsible for the observed inter-individual variation or if these differences represent actual specialisations.

5.3.2 Data collection

Data collection took place from June to October 1997-2002 and followed the same procedures as those outlined in previous chapters (cf. 1.4.2). Photo-identification techniques were used to recognise individuals based on the unique pigmentation markings on the ventral side of their flukes (Katona & Whitehead 1981). To avoid bias due to following different individuals for unequal periods of time, I kept only each individual's first sighting of the day in the analysis. Crossbows and specially designed arrows were used to biopsy free-ranging individuals and obtain skin samples (Palsbøll et al. 1991). Molecular analyses were conducted on these samples to determine sex by using sets of primers specific to either the ZFY or ZFX sequence found on the sex chromosome (Bérubé & Palsbøll 1996). Static and dynamic variables were obtained from the same sources as in chapters 3 and 4 (cf. 3.3.1).

5.3.3 Inter-individual differences

I tested for overall differences in habitat characteristics between sexes and among individuals using a two-factor, mixed-effects, nested MANOVA, with the nine habitat characteristics as dependant variables. Sex was treated as a fixed categorical factor and individual identity (ID) as a random categorical factor nested within sex. Repeated sightings of each individual served as replicates. I only used individuals for which I had 5 or more sightings (from different days). If the MANOVA showed a significant effect, follow-up univariate two-factor ANOVAs were run for each habitat characteristic. Within each of the two-factor ANOVAs, separate investigation of F-ratios allowed me to determine the proportional role of each factor (sex and ID). Tests were based on type III sums of squares so that the effect of each factor was evaluated after the variance due to the other factors had been removed (Zar 1999), i.e. I tested for the effect of ID once the effect of sex had been taken into account. Levene's test was used to determine whether variances were equal. Where necessary, I transformed the data using a natural log or square-root transformation. Because transformations did not always yield normality, I also used nonparametric Kruskal-Wallis tests to check for differences between medians and for possible outliers.

For each ANOVA that revealed differences among individuals, I then calculated BIC/TNW by comparing between-group variance to total variance (Bolnick et al. 2002).

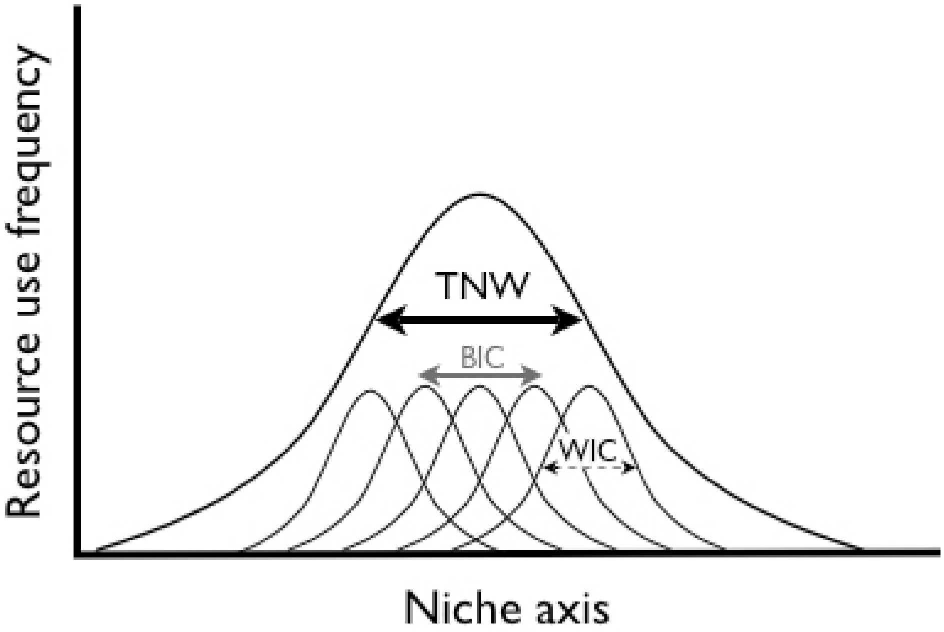

Figure 5-1. Schematic diagram of individual niches within a population's niche. The total niche width (TNW) is the variance of total resource use of all individuals and is subdivided between the between-individual component (BIC) and the within-individual component (WIC), such as TNW=BIC+WIC. In a population of individual specialists, WIC is small in proportion to BIC. Redrawn from Bolnick et al. (2003).

5.3.4 Inter-annual variability

Determining the temporal consistency of individual variation is important to avoid misleading interpretations (Bolnick et al. 2003). In chapter 3, habitat selection patterns of humpback whales showed strong inter-annual variability. This is a potentially confounding factor and I wanted to quantify its contribution to the total intra-population variation. First, I plotted humpback whale sightings in ArcView 3.1 (ESRI, Redlands, CA, USA) and used the Animal Movement Analyst extension (Hooge & Eichenlaub 1997) to estimate a 50% fixed kernel utilization distribution for each year. This 50% probability contour is a graphical representation of the core area of habitat use for all individuals in a given year and allows for visual inspection of inter-annual variability.

I then performed a second two-factor, mixed-effects, nested MANOVA, this time with year as a fixed categorical factor and ID nested within years. Again, I quantified the proportional contribution of both factors to the total variance using type III sums of squares. If I detected differences between years, I then tested for remaining inter-individual differences within each year.

5.3.5 Individual niche width

I quantified the marginality and niche breadth of each individual using the Outlying Mean Index (OMI), a technique habitually used to separate species in community ecology (Doledec et al. 2000). Here I used individuals as groups instead of species. Like discriminant analysis, this ordination technique finds which combination of ecological factors provides the best separation of groups and plots the gravity centres of each group in environmental space. The OMI is the distance between the gravity centre of each group and the origin. In this case, the origin can be interpreted as the gravity centre of the whole population and thus the OMI represents the marginality of each individual. The tolerance represents the breadth of each individual niche. The total inertia given by the analysis is a measure of how well the environmental variables separate the groups. A Monte-Carlo test with 1000 permutations was used to test for the significance of environmental variables on niche separation. I performed niche analyses in the ADE-4 package for R (Chessel et al. 2006).

5.3.6 Site fidelity

I conducted a site fidelity test for each individual seen in three different years or more. For each year, I first computed an average representative location based on the harmonic mean (which mitigates the impact of outliers) of all the sightings for that year, using the Animal Movement extension to ArcView (Hooge & Eichenlaub 1997). I then compared the geographic distance of these mean locations between years to distances between points randomly plotted in the study area using a Monte-Carlo test with 1000 iterations. I tested if distances between the areas used each year by a certain individual were smaller or larger than those expected in the absence of site fidelity.

5.4 Results

The field effort yielded 676 sightings of 75 sexed, identified individual humpback whales. Of these, 45 individuals were sighted 5 or more times and were kept for the analysis, for a total of 612 sightings. The sex-ratio was unbalanced (15 males and 30 females) but individual males were sighted almost as often as individual females (11.2 and 14.8 sightings per individual, respectively).

5.4.1 Differences between individuals and sexes

The analysis of the habitat characteristics associated with these sightings detected significant overall differences among individuals (MANOVA, Wilk's Lamdba = 0.34, $p<0.001$) but not between sexes (MANOVA, Wilk's Lamdba = 0.96, $p=0.97$). Follow-up univariate analyses indicated a statistically significant effect of depth (ANOVA, $F_{44,567}=4.36$, $p<0.001$), distance to shore (ANOVA, $F_{44,567}<3.62$, $p=0.001$), slope (ANOVA, $F_{44,567}=1.54$, $p<0.05$), SST (ANOVA, $F_{44,567}=1.55$, $p<0.05$), temperature of the CIL (ANOVA, $F_{44,567}=2.14$, $p<0.001$) and salinity (ANOVA, $F_{44,567}=1.49$, $p<0.05$) but no effect of currents and depth of the CIL. Dividing this effect between the two factors (sex and individual) confirmed that there were differences between individuals but no differences due to sex once individual variability had been taken into account (Table 5-1). Inter-individual differences accounted for a large part of the total niche width for depth (BIC/TNW= 25%) and distance (22%), and to a lesser extent for slope (11%), SST (11%), temperature of the CIL (15%) and salinity (10%).

We had significant deviation from normality for some variables, probably because of the small sample sizes for each individual. The nonparametric comparisons of medians confirmed the results for all variables except salinity (Kruskal-Wallis statistic = 23.52 $p>0.5$). Further examination of the data showed that no one individual was responsible but that there was a significant difference in salinity of habitat used between the years 1997-98 and the years 1999-2002 (Kruskal-Wallis statistic = 231, $p < 0.001$) and that this difference accounted for most of the variability pertaining to salinity.

5.4.2 Inter-annual differences

There were large differences in patterns of space use from one year to another (Fig. 5-2). Examination of 50% kernel contours showed that core areas of habitat use varied widely as to their geographic location between the years 1997 and 2000, and then remained more stable for the years 2000-2002. Results from the mixed ANOVA with individuals nested within years show that large inter-annual variability in habitat characteristics was responsible for an important part of the variance (Table 5-2). Even once this variability was taken into account, there was still important individual variability within each year for depth, distance and SST but not for the other variables. However, subdividing my data set by years resulted in some very small sample sizes and numerous individuals which were seen only once in a given year. Therefore, results from this test should be interpreted with caution. Only 2000 and 2001 had enough sightings allowing me to perform a meaningful ANOVA with at least 3 observations by individual and homogeneous variances. Within both years, statistically significant individual differences were found with respect to depth, distance and SST (all $p < 0.05$).

5.4.3 Individual niche width

I tested several OMI models and chose the one that best separated the 45 individuals, based on total inertia (Doledec et al. 2000). The best model showed that there were significant differences between individuals (Monte-Carlo randomization test, $p<0.01$), and that a combination of depth, distance and SST as discriminating variables provided the most satisfying explanation for this variation, confirming the results of the ANOVAs. I plotted the gravity centre and the ellipse containing 75% of the sightings of each individual humpback whale and observed considerable overlap of individual niches (Fig 5-3). The different sizes of the ellipses made it obvious that individuals differed with regard to niche width as well as niche position.

There was a wide range of values for OMI (1.3 to 78.4) and tolerance (1.7 to 71.2) among individuals (Table 5-3). Some individuals were specialised around the mean (low OMI and tolerance, e.g. H067) while others were specialised in more marginal conditions (high OMI, low tolerance, e.g. H165). Several individuals had niches that did not overlap with one another (e.g. H496 and H511) or that did not include the origin. Many individuals seemed to be generalists (high tolerance), among which most mirrored the population mean (low OMI, e.g. H141) while a few seemed to favour different habitats (high OMI, e.g. H163). The OMI was higher for males (mean=24.2, SD=21.9) than for females (mean=18.8, SD=20.2) but the difference was not statistically significant (*t*-test, t=-0.82, p > 0.25). There was no statistical difference between the mean tolerance for males and for females (males: mean=30.3, SD=16.5; females: mean=31, SD=16.5, *t*-test, t=0.15, p > 0 .50).

5.4.4 Site fidelity

Of 45 individuals, 34 were seen in three or more years. I found large inter-annual variability in mean locations, which mirrored the yearly habitat use patterns of the entire population shown in Fig. 5-2. For all 34 individuals, the distances between yearly mean locations were not smaller than those obtained between random points (one-tailed Monte-Carlo test, 1000 iterations, p > 0.50), indicating no site fidelity from one year to another within the study area.

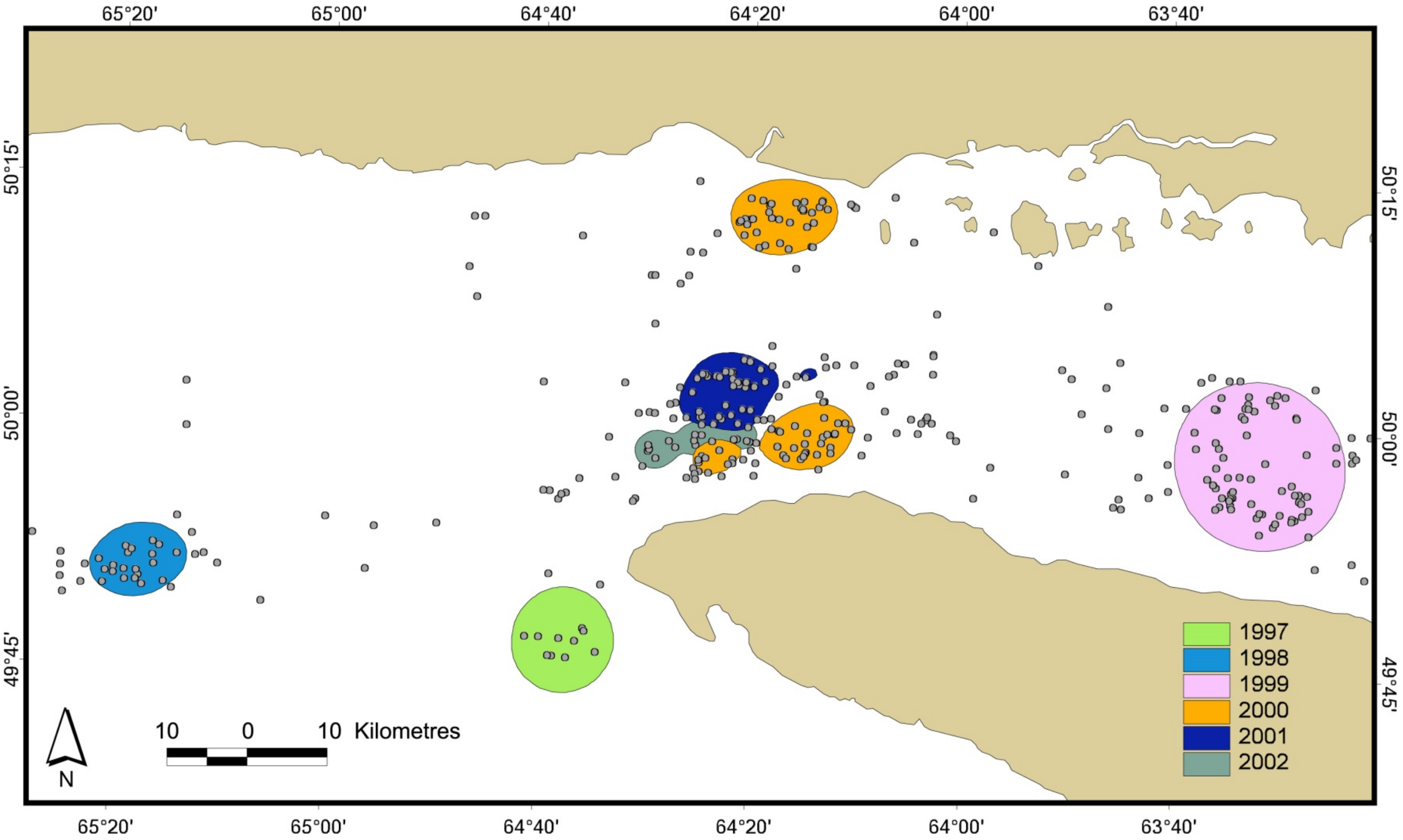

Figure 5-2. Map of northern Gulf of St. Lawrence showing the distribution of 676 humpback whale sightings (circles) and the 50% kernel contours representative of the core areas of spatial distribution for each year of study. Inter-annual differences in habitat use are clearly visible for the years 1997-2000.

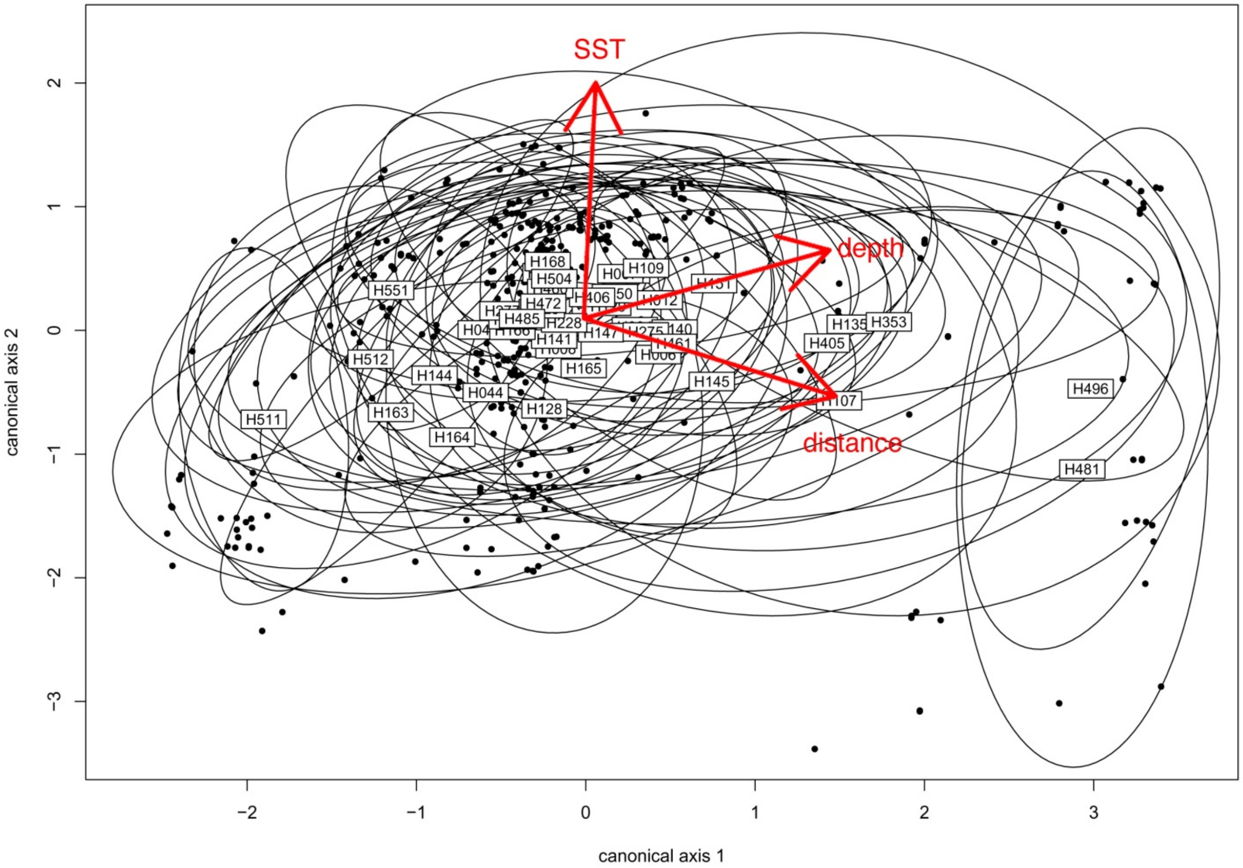

Figure 5-3. Plot of 676 sightings of 75 individually identified humpback whales on OMI axes. Red arrows show canonical weights of local-scale environmental variables. Ellipses contain 75% of the sightings of each individual and represent individual niches.

Table 5-1. Analysis of variance for static habitat characteristics of 45 individually identified humpback whales. 'Sex', sex of each individual; 'ID', individual identity, nested within 'Sex'; 'Residual', within-individual variance in observations; 'SS', sum of squares (type III); 'df', degrees of freedom; 'BIC/TNW', proportion of total variance explained by differences among individuals.

Variable	SS	df	F	p	BIC/TNW
Depth					
Sex	2688	1	0.6	0.44	
ID(Sex)	243445	43	4.46	<0,001	25%
Residual	720525	567			
Distance					
Sex	108959	1	0.25	0.62	
ID(Sex)	2.3E+07	43	3.66	<0,001	22%
Residual	8.3E+07	567			
Slope					
Sex	0.016	1	0.06	0.81	
ID(Sex)	13	43	1.57	< 0.01	11%
Residual	109	567			
SST					
Sex	4.5	1	0.53	0.47	
ID(Sex)	404	43	1.57	< 0.01	11%
Residual	3382	567			
Temp.CIL					
Sex	0.66	1	1.63	0.21	
ID(Sex)	22.69	43	2.19	<0,001	15%
Residual	126	567			
Salinity					
Sex	0.84	1	0.47	0.49	
ID(Sex)	84	43	1.52	< 0.01	10%
Residual	728	567			

Table 5-2. Analysis of variance for static habitat characteristics of 45 individually identified humpback whales. 'Year', year of observation; 'ID', individual identity, nested within 'Year'; 'Residual', within-individual variance in observations; 'SS', sum of squares (type III); 'df', degrees of freedom; 'BIC/TNW', proportion of total variance explained by differences among years and individuals.

Variable	SS	df	F	p	BIC/TNW
Depth					
Year	245273	5	45.46	< 0.001	30%
ID(Year)	197417	161	1.41	0.003	24%
Residual	388016	445			
Distance					
Year	6091630	5	351	< 0.001	24%
ID(Year)	5927620	161	1.16	0.013	23%
Residual	1.4E+07	445			
Slope					
Year	96.1	5	11.43	< 0.001	47%
ID(Year)	25.53	161	0.87	0.84	13%
Residual	80.7	445			
SST					
Year	692.9	5	26.99	< 0.001	20%
ID(Year)	958.4	161	1.49	0.0007	28%
Residual	1773.5	445			
Temp.CIL					
Year	54.52	5	80.41	< 0.001	42%
ID(Year)	21.61	161	0.98	0.54	17%
Residual	54.5	445			
Salinity					
Year	281.83	5	77.97	< 0.001	40%
ID(Year)	122.7	161	1.14	0.15	17%
Residual	297.22	445			

5.5 Discussion

5.5.1 Occurrence and extent of inter-individual variation

Ecological theory predicts increasing overlap in space use and increasing neighbour effects with increasing body size (Jetz et al. 2004). Here, I investigated the habitat use patterns of 45 individually identified humpback whales. I observed large overlap in space and niche characteristics but also found clear evidence of individual variability for some of the environmental variables. This individual variability was shown both in multivariate niche space (MANOVA and OMI) and when considering one variable at a time (ANOVAs) and it remained even after taking into account the effects of sex and inter-annual variability. By using complementary techniques, I showed that this variation occurred not only over ranges of environmental characteristics (i.e. some individuals preferred shallow waters while others preferred deeper waters) but also in terms of niche marginality and width (i.e. some individuals were more specialised than others).

Bolnick et al. (2003) recommend going beyond whether individual specialisation is simply present or absent and emphasise the need for quantification that can be compared between studies. In my study, inter-individual variability accounted for 24% of the total niche width for water depth, 23% for distance to shore and 28% for SST, even after inter-annual differences were taken in account. This is comparable to the higher range of values found in their review (Bolnick et al. 2003), which ranged from 0% to 70% with only 15 out of 49 studies scoring above 25%. Obviously, such measures need to be compared with care. Many of the values from other studies represent variation in diet rather than habitat, and studies can differ in methodology, sample size and time scale. However, these results suggest that humpback whales exhibit more individual variability than most other species, and certainly encourage further research.

Table 5-3. Results of Outlying Mean Index analysis for 45 individually identified humpback whales. 'omi' can be read as a measure of the marginality of each individual's niche, and 'tol' as a measure of niche width.

Individual ID	Sex	omi	tol
H002	f	14.8	25.5
H004	f	2.3	71.2
H006	m	5.7	48.6
H007	m	12.8	24.9
H008	f	4.3	42.5
H009	f	6.9	23.2
H012	m	16.7	49.8
H042	f	14.3	53
H044	f	16.5	44.8
H067	f	7.9	16.5
H069	m	2.2	38.1
H107	m	41.3	21.6
H109	f	14.9	21.7
H128	m	18.9	52.8
H129	m	2.6	12.3
H135	f	32.5	23.8
H140	f	7.9	51.7
H141	f	2.2	42.3
H144	f	27.9	44.7
H145	m	19.2	25.6
H146	m	37.5	17.1
H147	f	1.3	15.9
H150	f	5.8	24.8
H151	m	16.6	59.3
H163	m	50.4	31.9
H164	f	33.9	33.9
H165	m	5.4	21
H166	f	20	15.6
H168	f	57.1	14.7
H228	f	3.4	27.6
H263	f	8.1	43.3
H275	f	4.8	36.9
H277	f	10	29.4
H288	f	78.4	1.7
H329	f	3	30.9
H353	f	57.3	19
H406	f	4.2	47
H460	f	11.4	21.3
H461	f	6.5	47.1
H472	f	9.2	33.6
H485	m	7.7	31.6
H504	m	49.3	17.6
H511	m	76.6	1.9
H512	f	47.3	16.3
H551	f	50.3	10

5.5.2 Mechanisms of inter-individual variation

Differences among individuals in terms of bottom topography, distance to shore and SST are difficult to interpret without detailed behavioural observations. For instance, I do not know if they correspond to actual preferences for different habitat characteristics or if they reflect specialisation in terms of diet or hunting strategies. Future research on inter-individual variation in diet and trophic level is needed to address this question, and stable isotope or fatty acid analyses offer great potential in this regard (Iverson et al. 2004, Marcoux et al. 2007). Theoretically, these individual differences in habitat use could also result from site fidelity (i.e. individuals are restricted to different core areas that differ in their site-specific characteristics). Here I did not find any evidence of individual site fidelity from one year to another. On the contrary, I observed that humpback whales exhibited strong inter-annual variability in their spatial patterns, both collectively and at the individual level. These results suggest that individuals were not restricted to a specific location and that their habitat selection patterns were consistent wherever they moved to.

5.5.3 Causes of inter-individual variation

Niche theory predicts that environments with variable, patchy resources will promote the evolution of specialist feeding behaviours to reduce intra-specific competition (Schoener 1986, Bolnick et al. 2002) by allowing finer subdivision of the population's niche (Polis 1984). In this study, several individuals, both males and females, combined a narrow niche (low tolerance) with marginal habitat preferences (high OMI), which corresponds to the definition of such individual specialists (Bolnick et al. 2003). In the context of ideal free distribution (Fretwell 1972), these differences in habitat selection could reflect genuine individual differences at the level of habitat preferences (Garshelis 2000). However, two main factors could contribute to inter-individual variation other than individual specialisation: segregation by sex and age groups (Partridge & Green 1985, Bolnick et al. 2003).

I did not detect a difference between males and females in patterns of habitat use despite the fact that segregation by sex is known to occur on the North Atlantic feeding grounds (Weinrich & Kuhlberg 1991). It is possible that non-random associations between individuals or sex-related grouping do occur in the area but do not translate into different distribution patterns (i.e. males and females may segregate when they form groups but these groups use the same areas with the same habitat characteristics).

One individual specialist, H511, was described as a juvenile (based on its size) when it was observed in 2000. Individual variation often results from differences between age classes (Schoener 1986) and therefore it is possible that his marginal niche was due to its belonging in a different age class. Sexually immature humpback whales are sometimes observed on the outskirts of adult groups in breeding areas (Mattila et al. 1989). Similar segregation by age has been reported for humpback whales during their migration and on feeding grounds in the North Atlantic (Baraff & Weinrich 1993, Swingle et al. 1993). Because of the difficulty of reliably estimating the age class of these animals and the rarity of juveniles, I could not investigate segregation by age. Therefore, I cannot rule out the possibility that immature humpback whales use a different habitat on their feeding grounds.

Even in the absence of segregation by sex or age class, inter-individual variation could also be a consequence of social structure. For instance, social hierarchies can force individuals to use sub-optimal habitats (Partridge & Green 1985). Humpback whales form groups on their summer feeding grounds (Whitehead 1983), which are not random as to sex and age class (Weinrich & Kuhlberg 1991). Some of these associations are stable over long periods of time and exhibit clear individual preference in the choice of partner (Weinrich 1991). These non-random associations likely influence distribution patterns, in which case my results may reflect group rather than individual specialisations. A detailed analysis of association indices and group composition is needed to explore the impact of social structure on habitat use.

5.5.4 Temporal consistency of inter-individual variation

Inter-annual variability of habitat characteristics was an important driver of intra-population variation. However, within the constraints of this yearly variability, I could still detect individual-specific preferences for both static and dynamic variables. It is possible that individual specialisations of humpback whales remained constant from one year to the next, but that inter-annual changes in environmental variables forced them to move to different locations to find their preferred habitat characteristics.

It is legitimate to ask if the distribution patterns of Fig. 5-2 could have been biased by inter-annual differences in sampling effort. Because the main research objective of MICS personnel was photo-identification, field effort usually aimed at maximising encounters with whales rather than ensuring equal sampling of the study area. This made the spatial effort dependent on the location of whales rather than the opposite. Moreover, boat surveys tried to cover the largest possible area every day while searching for whales, and sampled a broad range of habitats. The whole study area was sampled efficiently every year and inter-annual differences were minimal. I am therefore confident that patterns of space use by humpback whales result from actual habitat preferences.

5.5.5 Conclusions

Individual specialisation remained apparent even after accounting for all other sources of intra-population and inter-individual variation. Individual variability of niche characteristics other than diet has never been shown for baleen whales and only rarely for other mammals (Bolnick et al. 2003). I believe that analysing the causes and consequences of intra-population variation can shed more light on the complexity of cetacean habitat preferences. For instance, my own models of habitat selection performed poorly for humpback whales (cf. chapter 3). Similarly, environmental variables had weak predictive power for this species in the Pacific (Gregr & Trites 2001). These results indicate that individual variability could be partly responsible for these difficulties in modelling habitat use of whales at the population level. I suggest that considering whale populations to consist of ecologically equivalent individuals could be misleading. If intra-population variation is commonplace, it may have non-trivial impacts on management issues by masking the importance of marginal habitats for some individual specialists.

6. General discussion and synthesis

The aim of this thesis was to improve our understanding of the ecology of large whales on their feeding grounds and in particular the factors influencing their distribution patterns at fine-scale. There is a lack of knowledge about how large marine predators select and partition their habitat, due in part to the difficulty of surveying a wide range of rapidly changing dynamic characteristics simultaneously. Since upper-level predators have important impacts on the structure and function of marine ecosystems (Estes et al. 1998), it is important to understand the mechanisms underlying patterns of habitat use and coexistence.

I studied whale-habitat relationships at several levels. First I examined how patterns of habitat selection for fine-scale environmental variables resulted in different ecological niches for each species (chapter 2 and 3). Then I quantified the width and marginality of these niches and studied how they interacted with one another (chapter 4). Finally, for one species, I looked at how inter-individual variation contributed to the total niche width (chapter 5). I believe this study of rorquals in the Gulf of St. Lawrence has generated data with important relevance to both ecological theory and conservation biology.

The results are synthesised below. I draw conclusions from the chapters of this thesis, both separately and taken together as a single, hierarchical study of habitat selection by rorqual whales in the northern Gulf of St. Lawrence. First, I synthesise the major contributions to our understanding of habitat selection and coexistence in rorqual whales on their feeding grounds. I also discuss the occurrence of intra-population variation in humpback whales and the possible implications if the findings are representative of a more general phenomenon. Second, I discuss the implications for successful management of rorqual whales in the Gulf of St. Lawrence and elsewhere on their feeding grounds. Finally, I describe promising directions for future research.

6.1 Habitat selection

Despite the difficulties of studying mobile animals in aquatic environments, I found it was possible to better understand the distribution of rorquals by carefully comparing the characteristics of the habitat used by whales to those of the surrounding habitat. I used remote-sensing technology and computer models of ocean processes to describe the dynamic characteristics of the habitat simultaneously with whale sightings. In particular, I attempted to model the complexity of marine environments by using both univariate and multivariate approaches and by including in my models both static and dynamic factors that were representative of three-dimensional processes (e.g. fronts, upwelling, characteristics of the cold intermediate layer).

Frontal areas constitute natural mechanisms that increase biological productivity and aggregate prey species (Wolanski & Hammer 1988). As such, they can be seen as an integrative process representing the combined effect of numerous environmental variables. In chapter 2, I found that their surface manifestation (SST fronts) had an important influence on the distribution patterns of blue, fin and humpback whales and that these species were selecting areas closer to these fronts than the rest of the available habitat. These results encourage further research on other similar integrative processes, because their interpretation may be easier than numerous, semi-correlated variables. In particular, future research should focus on the three-dimensional nature of these phenomena, because it is likely that whales and their prey respond to processes that affect the entire water column.

The results of chapter 3 confirm the importance of such dynamic processes. All four species of rorquals responded to the temporal variability of their environment by selecting time-varying characteristics that differed from the available habitat. I showed that the best models of habitat selection were those that included both static and dynamic variables. St. Lawrence rorquals were selecting for factors traditionally linked with prey availability: shallow banks and steeper seabed slope, but also slower current velocities, cold and saline surface waters, as well as certain characteristics of the cold intermediate layer.

When combined, the results of chapters 2 and 3 show that blue, finback and humpback whales are found close to SST fronts and in areas of slow-moving horizontal currents and downward vertical currents. This combination suggests that large rorquals and in particular blue whales exploit the low-velocity side of front lines and convergence areas, where prey usually accumulate. This was also the case for finback and minke whales in the Bay of Fundy (Johnston et al. 2005a). Time lags between SST maps and the actual sightings of blue whales, as well as the 5 km spatial scale of the ocean model, did not allow me to verify this hypothesis. However, tracking of individual whales combined with simultaneous recording of fine-scale environmental conditions could be used to gain further insight into the real-time choices of these whales.

Temporal variability is seldom modelled in studies of habitat selection. However, taken together, chapters 2 and 3 suggest that rorquals respond strongly to the dynamic nature of their environment and that ignoring the time-varying characteristics of marine habitats may lead to a poor understanding of ecological relationships. These results emphasise the importance of variables that relate not simply to biological productivity but also to mechanisms of food aggregation. It is likely that the most important variables in my selection models act together rather than separately. Static factors like physiographic features seem to create beneficial preliminary conditions for prey presence and abundance. Dynamic ocean processes, which are likely anchored in static factors (Yen et al. 2004), are in turn responsible for the fine-scale distribution of prey in dense concentrations that appeal to rorquals, and the predictability of such aggregations.

6.2 Niche partitioning

Differential habitat selection is one of the principal mechanisms that allow species to coexist (Rosenzweig 1981). While studying habitat selection, I found that the four species of rorquals used different combinations of environmental characteristics, indicating a finer degree of habitat partitioning on their feeding grounds than previously thought. Rorquals did not just differ as to their position on the axis of each variable; the relative importance of each variable also seemed to vary among species. This prompted me to conduct a finer study of the overlap between the four species' niches. While chapters 2 and 3 focused on the variables that distinguished used from available habitat, chapter 4 focused on the variables that best separated the different species from one another.

Understanding how species co-exist remains one of the main challenges in ecology (Tokeshi 1999). Differential use of space and segregation in time are usually proposed as mechanisms that promote coexistence. While many species of cetaceans co-occur in space and time, little is known of their ecological interactions and the strategies for coexistence in a rapidly changing, patchy environment. It was already known that rorquals in the Gulf of St. Lawrence often occurred in sympatry and had overlapping diets. However, I found that there was strong overlap in space use at fine scale, which suggested a potential for strong inter-specific competition. While I do not know whether resources are currently limiting in the St. Lawrence, I observed patterns of partitioning in time and niche characteristics that could result from a shaping effect of competition at one point in these species' evolutionary past.

I propose that fine-scale habitat selection, in particular towards dynamic variables, is one of the major mechanisms that allow these rorquals to co-exist. These results highlight the importance of considering the community context in studies of cetacean habitat use and selection. When studying one species at a time, the potential effects of competition on distribution cannot be assessed.

6.3 Intra-population variation

Individual variability is rarely quantified for niche characteristics other than diet (Bolnick et al. 2003). However, results from the previous chapters led me to hypothesise that large intra-population variation may be responsible for part of the unexplained variability in my models. In particular, I noted that the poorest models concerned the species that form groups on their feeding grounds (finback and humpback whales). Social behaviour can have important implications when analysing habitat selection (Ersts & Rosenbaum 2003). While I lacked the data to investigate the true effects of social structure on distribution patterns, I investigated other sources of intra-population variation such as segregation by sex and individual specialisation.

The population of humpback whales in the northern Gulf of St. Lawrence provided a good system to test these hypotheses, thanks to numerous observations of identified individuals of known sex. While I found little sign of segregation by sex, I found clear evidence of individual variability in habitat selection. By using complementary techniques, I showed that this variation occurred not only over the values of environmental characteristics but also in terms of niche marginality and breadth (i.e. some individuals were more specialised than others).

I propose that individual specialisation in humpback whales, probably at the level of foraging techniques and potentially diet preferences, can be an important mechanism for finer subdivision of the species' ecological niche. I do not know if these apparent specialisations truly occur at the level of individuals or if they are the results of preferences of groups to which these individuals belong. In either case, these results suggest that humpback whale populations are not ecologically homogeneous.

If these patterns were found to be common among cetaceans, they could have profound impacts on our understanding of whale-habitat relationships. At least in the case of humpback whales, I suggest that stronger than expected inter-individual variation is responsible for a large part of intra-population variation and thus for my difficulty in successfully modelling habitat selection. I suspect that a similar process exists for finback whales but, at present, lack the data needed to test this hypothesis.

6.4 Management considerations

One of the aims of this study was to improve our ability to conserve and manage populations of rorqual whales in Eastern Canadian waters. The Gulf of St. Lawrence in particular is a hotspot of diversity for cetacean species as well as an important waterway under considerable human use. Overlap between whales and human activity creates numerous conservation threats, including entanglement in fishing gear, collisions with ships and environmental pollution.

My main conclusions as to the importance of time-varying variables and the complexity of whale-environment relationships may improve our understanding of ecological processes but are less satisfying in terms of management. Indeed, management is often based on static maps of habitat quality or suitability (Garshelis 2000), or models that can predict distribution patterns based on habitat characteristics (Corsi et al. 2000). My results, on the other hand, suggest that management based on static definitions of habitats are likely ineffectual, and that accurate maps of habitat quality may be very difficult to produce unless the dynamic nature of marine environments is taken into account.

However, my results can shed some light onto the scales of habitat selection by rorqual whales and therefore improve the design of protected areas and other conservation measures. I showed that dynamic factors seemed better suited to explain distribution at fine spatio-temporal scale than static ones. My interpretation is that static factors may prove useful to characterise potential habitat for management purposes while dynamic factors are necessary to better predict daily movements and distribution.

However, these dynamic factors themselves might be difficult to obtain ahead of time (it was not possible with the ocean model I used), making actual prediction nearly impossible. Because dynamic factors are often anchored in static ones, conservation may benefit from better understanding the link between static characteristics and dynamic processes (e.g. Simard et al. 2002, Johnston et al. 2005a), which can allow managers to continue focusing on static descriptions of important habitats.

While it is unclear whether rorqual whales are food-limited in the North Atlantic, it is generally assumed that inter-specific competition is not an important factor for the recovery of blue whale stocks (NMFS 1998). The results of this study cast some doubt on this assumption. The niche of the blue whale, as defined by the available habitat variables, was the narrowest and the most marginal of all four species. When plotted in multivariate environmental space, it was completely nested within the combined niches of the other three rorqual species. Similarly, it exhibited great overlap in space and time with the other species, especially with finback whales. Even if resources are not limiting, it is likely that blue whales can experience interference competition as they try to exploit the densest patches of euphausiids. Also, the apparent reliance of blue whales on rare transitory combinations of time-varying variables suggests a potentially higher sensitivity to environmental change and may help to explain their decline or shift from certain areas.

6.5 Future work in the Gulf of St. Lawrence

In recent years, studies of cetacean species at different scales have considerably improved our understanding of their distributions (Redfern et al. 2006). However, there often remains large uncertainty over the factors influencing habitat selection (Bailey & Thompson 2006). This is especially true in this study for the processes driving the distribution of finback and humpback whales, which I could not model satisfactorily. Further work is needed at both broader and finer scales than those examined in this thesis. The Estuary and Gulf of St. Lawrence constitute an exceptionally well-suited system for such studies because sympatric species of whales are found in diverse regions with different characteristics.

A multi-scale analysis of habitat selection in the whole St. Lawrence system, comparing patterns of habitat use between and within areas, may be of particular interest. This will allow a truer representation of the hierarchical nature of habitat selection. It will also answer important questions as to the generality of my findings. If results are similar among regions, it will allow managers to extrapolate to other areas and facilitate conservation planning. If on the contrary there is large variability from one region to another in the relative importance of environmental characteristics for rorqual whales, it will show the necessity of collecting local data for local management plans.

Factors that influence the real-time decisions by foraging whales (e.g. prey encounter rates, distribution of food patches, presence of conspecifics) are hard to predict and difficult to put into models of habitat selection. I believe further insights could be obtained by analysing movement patterns at a finer spatio-temporal scale using telemetry techniques (e.g. tracking with satellite tags). Analysed with state-space models, these data would also make it possible to study the real-time decisions that guide movements and habitat selection.

Although I looked at the three-dimensional characteristics of the habitat selected by whales, I have still limited this study to the two-dimensional surface location of the animals themselves. The next logical step is to use newly available technologies to record the precise location of whales in the water column and examine their real-time patterns of habitat use in their three-dimensional environment. Combined with careful definition of available habitat, these data could provide a better understanding of ecological relationships within the complex and time-varying habitats of the marine environment.

Because large whales seek areas of high biomass, their distribution typically mirrors that of their prey (Baumgartner et al. 2003, MacLeod et al. 2004). However, whale and prey distribution are rarely compared directly because data on prey are seldom available at the right spatio-temporal scales (Redfern et al. 2006). Studies often use abiotic variables as proxies for prey distribution but lose explanatory power because of the space and time lags that occur between physical factors (e.g. bathymetry, temperature) and ecological processes (e.g. aggregation of prey). Our understanding of habitat selection by rorqual whales in the Gulf of St. Lawrence would benefit greatly from a direct comparison between their patterns of habitat use and the distribution of their prey, obtained by direct measurement or by computer simulation (e.g. Sourisseau et al. 2006).

If the distribution of prey changes for reasons other than normal oceanographic processes, the distribution of whales may change accordingly. In this eventuality, I would be unable to explain such changes based on the variables examined in this project. Any major spatial or temporal shift in whale distribution patterns could therefore indicate a change in the community structure and biomass of their prey (Tynan 2004). For instance, bottom-up controls have been found in marine food webs across four trophic levels (Frederiksen et al. 2006). Similarly, open-ocean systems can experience trophic cascades with reciprocal predator-prey effects (Ainley et al. 2006). The St. Lawrence has experienced severe changes in its trophic structure with, among other factors, the depletion of the stocks of Atlantic cod (*Gadus morhua*). The consequences of this collapse are mostly unknown, but it would be worthwhile to analyse changes over time in the abundance and distribution of whales in the whole Laurentian system. Negative impacts of prey collapse on a whale population may take years to detect through population level studies, and by the time they are detected it may be too late to act. This makes habitat selection studies important in detecting early signs of major changes in whale populations.

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