

**Lateralisation of Minke Whales
(*Balaenoptera acutorostrata*)
whilst Surface Feeding in the St. Lawrence Estuary
(Quebec), Canada**



**Master Thesis in Marine Biology
by
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Abstract

Lateralised behaviour has been studied in different non-human species and also in marine mammals, but not in minke whales (*Balaenoptera acutorostrata*). This study examined if minke whales predominantly use one side of their bodies and to quantify this behaviour. Active behaviour of surface feeding was split in different body planes and analysed. This includes manoeuvres in lateral plane (1), where the whale is lying on its right or left side, manoeuvres in ventral plane (2), involving rolling back to either side into the dorsal-ventral plane, and in dorsal-ventral plane surfacings (3), rolling to the right or left side. In addition, different factors (tidal phases, feeding habitats, the orientations of the whale's body, influence of sunlight) were analysed whether the relative frequencies of the sides of lateralisation differed among the expected equally distribution of the different factors.

In lateral manoeuvres (N=1819) the 43 identified whales occurred more frequently on the right side (97.6%) than the left side (2.4%). In the ventral manoeuvres (N=585) the 41 identified whales rolled back over its right side more often (96.9%) then over its left side (3.1%). In the dorsal-ventral manoeuvres (N=146) the 9 identified whales exhibit a significant difference between the roll to the right side (95.2%) and rolling to the left side (4.8%). In all three manoeuvres the identified whales, which were lateralizing to the left side ((1)=11, (2)=7, (3)=3) were also lateralizing to the right side in other observations.

There is no significant correlation in all manoeuvres when comparing the relative frequencies of the sides of lateralisation in respect to tidal phases, feeding habitat, orientations of the whale's body and direction to the sunlight.

However, this study point out that the side of lateralisation in minke whales (N=54) is independent of the tidal phases, feeding habitats, orientations of the whale's body and sunlight. Therefore, I suggest that the reason of the right side preference is not due to the different environmental factors but instead the minke whales from the St. Lawrence Estuary exhibit the significant split of 95/5 toward the right side and this is a consistent behavioural asymmetry in surface feeding behaviour. This behavioural lateralisation is possibly related to an asymmetry of function in the brain like Clapham et al. (1995) also suggested for the humpback whales. However, not much is known about the brain of minke whales to allow final conclusions.



1. Introduction

Abiotic Factors

The dominant geophysical structure of the St. Lawrence Estuary is the Laurential Channel, a 200 - 300 m deep glaciated valley that originates along the continental shelf southeast of Newfoundland. The deep, U-shaped channel extends from the Gulf of St. Lawrence along the northern side of the estuary to the first sill, which is 50 m deep. In this area the narrow and deep (350 m) Saguenay River flows into the St. Lawrence Estuary. In the summer, the St. Lawrence Estuary is generally characterized by a three layer temperature structure with a warm (5 - 20°C) surface layer, which is 20 - 30 m deep and the salinity is between 18 - 31‰. This warm surface layer is overlying a cold intermediate layer with temperature from -1 to 2°C and the salinity is > 32‰. The third layer is around 4°C and salinity is > 33‰. The surface layer occurs from late spring to early fall as a result of freshwater outflow from the Saguenay River and St. Lawrence Estuary (Zeppelin 1998). The intermediate layer with a flow upstream is around 75 - 100 m deep and is formed by the advection of cold water from the Gulf of St. Lawrence during winter. The third and deepest layer consists of a warmer water mass and these waters originate in part from the Labrador Current. These last two colder layers spill over the sill into the Saguenay River and the deep basins of the upper Estuary. The coldest, intermediate layer raises nutrient rich waters to the surface, which creates an upwelling over the sills. This area around the Mouth of the Saguenay River is a “nutrient pump” because of the high levels of nutrients in the surface layer compared to other areas in the estuary.

Biotic Factors

The North Atlantic minke whales travel into the St. Lawrence Estuary from May through October primarily to feed on the abundance of capelin (*Mallotus villosus*) and euphausiids. Other species of baleen whales including finback whales (*Balaenoptera physalus*), blue whales (*Balaenoptera musculus*) and occasionally humpback whales (*Megaptera novaeangliae*) also utilize this optimal summer feeding ground. Several toothed cetaceans also feed in this area including Harbour porpoises (*Phocoena phocoena*), as well as the endangered population of belugas (*Delphinapterus leucas*) that inhabit these waters year round and sometimes even sperm whales (*Physeter macrocephalus*) (Zeppelin 1998).

Capelin are abundant between late April and early May along the north shore of the estuary (Bailey et al. 1977). Spawning occurs between mid-April and the end of June. Capelin gradually drift downstream to the Gulf from June through the middle of August. There is a year-round concentration of juvenile capelin at the confluence of the Saguenay River and St. Lawrence Estuary, which is supported by zooplankton production in the river (Bailey et al. 1977). The shallows at the Laurential Channel Head are known aggregation areas for juvenile capelin, where they often form dense shoals and concentration peaks along fronts in the upper water column (Bailey et al. 1977). Simard & Lavoie (1999) found that the Laurential Channel Head was the site of the richest krill aggregation then documented for the NW Atlantic. The mechanisms responsible for the generation of the aggregation act on a large range of scales, from metres to hundreds of kilometres and minutes to years (euphausiid life



cycle), involve dynamic processes linked to local topography (Lavoie et al. 2000). All of the above cited biotic factors potentially influence the distribution of minke whales within the study area.

Lateralisation

The preferred use of one limb/hand (handedness) over the other is one characteristic of lateralised behaviour patterns. The most familiar example of lateralised behaviour is the phenomenon of handedness in humans, approximately 90% of whom show a bias towards the right hand in fine-detail tasks such as manipulation (Annett 1972).

Although many animals (e.g. cats, rats, mice and monkeys) show a preference for the use of one paw, studies have suggested that such biases exhibit a 50/50 split among individuals at the population level (Warren 1987). A significant deviation from a 50/50 split is indicative of hemispheric specialization (Rogers & Bradshaw 1996), and is therefore informative about the evolution of the brain of the species (Galatius 2005). In cetaceans, functional cerebral asymmetries have been demonstrated in bottlenose dolphins (Kilian et al. 2000, von Fersen et al. 2000). Furthermore, selective breeding experiments in mice have failed to produce generations that show significant deviations from parity in such preferences (Collins 1969). This result has suggested that, while other species may exhibit such biases, they are determined by chance, and the preference for a particular paw is reinforced at the individual level by use. MacNeilage et al. (1987) reviewed the primate literature and concluded that significant population-level asymmetries of hand preference, similar to that found in humans, exist for a number of species and that primate handedness evolved as a precursor to human left- and right-hemisphere specialization. However, this theory has been the subject of considerable criticism and no consensus currently exist on the subject.

Several examples of lateralised behaviour patterns have been detected at the population level in cetacean species, e.g. bottom-feeding in gray whales (*Eschrichtius robustus*) (Kasuya & Rice 1970) and humpback whales (*Megaptera novaeangliae*) (Clapham et al. 1995), strand-feeding in bottlenose dolphins (*Tursiops truncatus*) (Hoese 1971) and several examples of asymmetric swimming-patterns in captive odontocetes (Ridgway 1986, Sobel et al. 1994). Using video recordings, Levermann et al. (2003) indicated a predisposition of walrus for the use of the right front flipper during feeding and that such lateralised behaviour, if truly apparent, is potentially important because its existence has significant implications for the evolutionary development of the brain.

With all this knowledge of lateralised behaviour patterns but nothing published about the minke whales, the aim of this study was to examine if minke whales also exhibit a preferred side of lateralisation whilst surface feeding and to quantify this behaviour. In addition, the question was whether any of several possible environmental or temporal variables such as tidal phases, feeding habitats or sunlight might influence any pattern of lateralisation.



2. Background

2.1. Evolution of Cetacean

Before the recent discoveries in Pakistan, one popular theory of cetacean evolution was that whales were related to the mesonychids, an extinct order of carnivorous ungulates (hoofed animals), which looked rather like wolves with hooves. These animals possessed unusual triangular teeth that are similar to those of whales. Mesonychids started slowly returning to the sea roughly 55 million years ago. The *Pachyaena*, an example of the extinct group of mesonychids, had four legs with paws and was to evolve into a hoof-shaped animal.



Figure 1. *Pachyaena*, an example of the extinct group of animals called mesonychids (www.nap.edu)

However, DNA analysis generated an alternative hypothesis. Whale DNA is more similar to that of the hippopotamids than to any other living animal. Therefore, a debate arose as to whether hippopotami (hippos) or mesonychids were the closest relatives of the whales.

The recent discovery of *Pakicetus*, the earliest proto-whale, has helped to settle the debate. The skeletons of *Pakicetus* demonstrate that whales did not derive directly from mesonychids. Instead, they are a form of artiodactyl (another type of ungulate) that began to go into the water after the artiodactyl family split from the mesonychids. In other words, the proto-whales were early artiodactyls that retained aspects of their mesonychid ancestry (such as the triangular teeth), which modern artiodactyls have since lost.

The pakicetids lived in the early Eocene, around 52 million years ago. They looked rather like dogs with long, thick tails. It is not known exactly how they lived, but they may have roamed the seashore or hunted in rivers. What links the pakicetids to whales is the structure of their ears, which contain an adaptation to underwater hearing that is possessed only by whales. It seems that the Pakicetids were amphibious carnivores which, thanks to their remarkable ears, were able to hear better in the water than other aquatic mammals. This adaptation began the journey that would lead to the evolution of the whale (www.en.wikipedia.org).

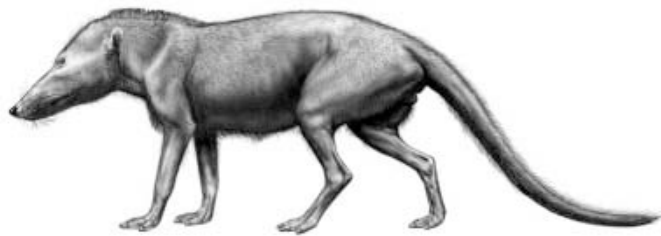


Figure 2. A reconstruction of *Pakicetus*. Illustration by Carl Buell.
(www.neoucom.edu)

The most remarkable of the recent discoveries in Pakistan has been *Ambulocetus*, an archaeoceti that lived about 50 million years ago and was found 1993. *Ambulocetus* looked like a three-metre long mammalian crocodile and was clearly amphibious, as its back legs are better adapted for swimming than for walking on land. It had long, powerful jaws with shark-like teeth, a small brain and the pelvis fused to the backbone like land-dwelling mammals but unlike whales.

Rodhocetus is another recent discovery. The meaning of the name is "Rodho"-whale, the local name of the region in Pakistan where the fossil was found. *Rodhocetus*, an extinct primitive Eocene whale, lived about 46 million years ago. Its principal adaptation was flukes (horizontal bars) on its tail, which enabled faster swimming. However, it retained substantial hind legs. Its pelvis was not fused to the backbone and it had a long, pointed snout with many sharp, triangular teeth.

Basilosaurus is a snake-like cetacean whose fossils was found in the 1830's and was initially mistaken for a lizard. It lived in the late Eocene about 40 - 35 million years ago and was 25 m in length with reduced hind legs and pelvis. *Basilosaurus* was a fully recognisable whale that lived entirely in the ocean. Although basilosaurids look very much like modern whales, they lacked the 'melon organ' that allowed their descendants to sing and use ultrasound as effectively as modern whales. They had small brains. This suggests that they were solitary and did not have the complex social structure of modern whales. Fossils have been found on the Atlantic coast of North America and in Eocene rock of Australia and Egypt (www.en.wikipedia.org).

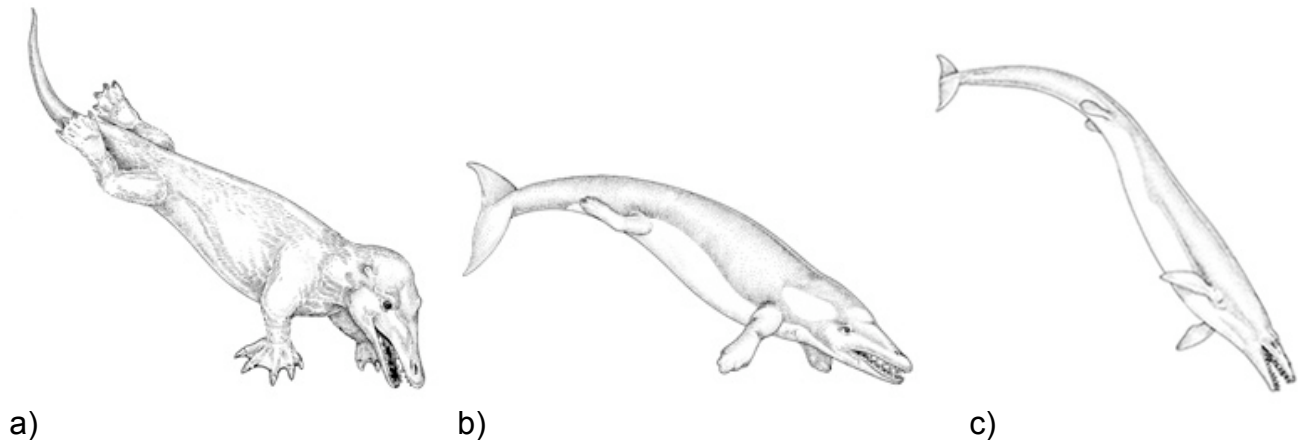


Figure 3. Development of the Archaeocetes: a) *Ambulocetus* b) *Rodhocetus* c) *Basilosaurus* (www.nap.edu)

2.2. Adaptations and Anatomy

The body form of all cetaceans has a number of common features. All cetaceans are streamlined and elongated. They lack external hind limbs and the forelimbs have been drastically modified into flippers. These flippers vary in size and shape, from small and almost unnoticeable in the sperm whale to long and conspicuous in the humpback whale. The hand and finger bones are enclosed within a connective tissue. Most cetaceans have a dorsal fin situated at or behind the centre of the back. It can be little more than a hump as in the humpback whale or very tall and erect as in the orca. The fluke and the dorsal fin consist of connective tissue without skeleton inside. For locomotion all cetaceans use the fluke as a natural propeller and they also swim with a dorsal-ventral bend technique (gallop). The key adaptation, however, is the layer of fatty tissue, or blubber, found immediately beneath the skin. The fur is degenerated and generally only a few whiskers still exist. The thickness of the blubber varies greatly among species. The blubber serves the functions of insulating the internal organs, storing energy and giving the streamlined form. Another adaptation is their precise navigation, which they need for their enormous migrations between the feeding grounds and breeding grounds.

Cetaceans have a poor sense of smell but use taste to detect chemicals in the water currents and touch for bonding or to maintain order within the pod. The cetaceans' eyes are set well back and to either side of its huge head. This means that cetaceans with pointed 'beaks' (such as dolphins) have good binocular vision forward and downward, but others with blunt heads (such as the sperm whale) can see to either side but not directly ahead or directly behind. The eyes shed greasy tears, which protect them from the salt in the water (www.en.wikipedia.org). Sight is quite good with many capable of binocular vision. Different areas of the retina are adapted for air and water vision. Most cetaceans both produce and detect sound. Cetaceans use sound in the same way as bats - they emit a sound, which then bounces off an object and returns to them. From this, cetaceans can discern the size, shape,



surface characteristics and movement of the object, as well as how far away it is. This is called echolocation, and with it cetaceans can search for, chase and catch fast-swimming prey in total darkness. Odontocetes (see 2.3.) have anatomical adaptations for producing/detecting ultrasonic clicks for echolocation. Sound waves travel faster through the water than in the air and so the external ear was no longer needed. The cetaceans' ear is no more than a tiny hole in the skin, just behind the eye. The inner ear, however, has become so well developed that cetaceans can not only hear sounds far away, but can also discern from which direction the sound comes.

The blowhole is located at the highest point of the head in order to facilitate breathing at the surface. This is energetically efficient because the movement of swimming does not need to be interrupted for breathing. Cetaceans are endothermic (warm-blooded) and viviparous. The calves are images of their parent and in the biological language they are termed precocial.

On the other hand, cetaceans have also retained some ancestral features. They still breathe with lungs and therefore have to go up to the surface. Cetaceans exchange 80 - 90% of lung volume as they breathe in and out, compared to 15% in humans, and exhale only 1.5% O₂ after a dive. Therefore, ventilation and respiration are extremely efficient (www.lifesciences.napier.ac.uk). Oxygen is not only stored in the lungs and in the blood, but also in muscles where it is bound to myoglobin. Myoglobin has a greater affinity for oxygen than blood haemoglobin and so oxygen in the blood is readily given up to the muscles when the blood passes through. Myoglobin gives the muscles their characteristic dark colour and makes muscle one of the main oxygen-storing tissues. About 82% of the oxygen is stored in body tissues (land mammals: 25%), about 9% in blood (land mammals: 41%) and also about 9% in the lungs (land mammals: 34%). Although not a lot of oxygen is stored in the blood, this oxygen is important because cetaceans have twice as high a concentration of red blood cells per unit volume of blood than land mammals. During deep dives the heart rate drops and the blood is restricted to the brain and heart. This condition is known as bradycardia.



In the next Figure, the anatomy of Odontocetes and Mysticetes with their scientific terms is visualized.

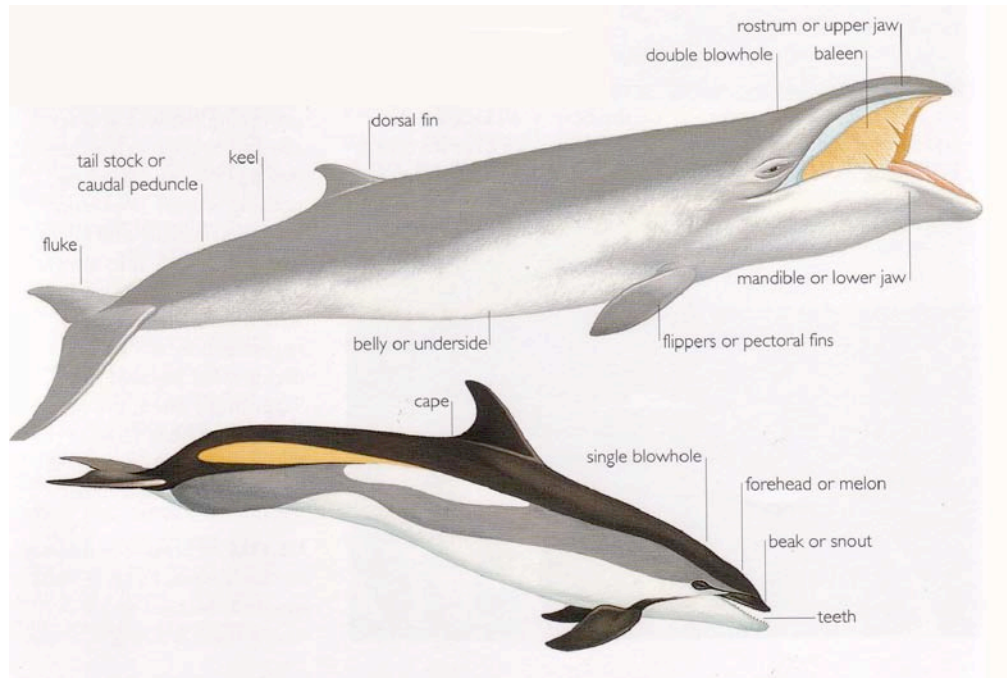


Figure 4. Anatomy of Odontocetes and Mysticetes (Carwardine et al. 2002)

2.3. Systematic

Whales, dolphins and porpoises belong to a single group of marine mammals known as the cetaceans. The world's present-day cetacean fauna consists of more than 80 species. They are classified in two distinct groups¹: The odontocetes, toothed whales, which possess teeth and includes the sperm whales, beaked whales, river dolphins, monodontids (beluga and narwhal), ocean dolphins and porpoises. The other suborder mysticetes, baleen whales, have no teeth but instead baleens. The vast majority of cetaceans are odontocetes with 70 species in all. Two morphological features distinguish the two suborders: Odontocetes have teeth, which are similar in shape and size (homodont) and a single blowhole (nostril), while mysticetes have baleens and two blowholes. Another major difference is that odontocetes locate prey by using echolocation, while the mysticetes do filter-feeding. Generally, cetaceans migrate between summer feeding grounds in polar waters and winter breeding grounds in warmer waters, where calving takes place. Some species stay in the same place all year round.

¹ In the last years new results in embryology, cytogenesis and molecular biology showed, that this two groups are not justify by phylogenesis. These suborders are because of the whales teeth or baleens.

Background



Table 1. Suborder Mysticetes and Odontocetes and their families (various internet sources, [blue](#)=indicates species that can be observed in the St. Lawrence Estuary)

Suborder Mysticeti (baleen whales or mysticetes)

Family	Scientific name	Common name (German, French)
Balaenidae (Glattwale)	<i>Eubalaena australis</i> <i>Eubalaena glacialis</i> <i>Eubalaena japonica</i> <i>Balaena mysticetus</i>	southern right whale (Südkaper) North Atlantic right whale (Atlantischer Nordkaper) North Pacific right whale (Pazifischer Nordkaper) bowhead whale (Gönlandwal)
Neobalaenidae (Zwergglattwale)	<i>Caperea marginata</i>	pygmy right whale (Zwergglattwal)
Eschrichtiidae (Grauwale)	<i>Eschrichtius robustus</i>	gray whale (Grauwal)
Balaenopteridae (Furchenwale)	<i>Balaenoptera acutorostrata</i> <i>Balaenoptera bonaerensis</i> <i>Balaenoptera borealis</i> <i>Balaenoptera edeni</i> <i>Balaenoptera musculus</i> <i>Balaenoptera physalus</i> <i>Megaptera novaeangliae</i>	Common minke whale (Nördlicher Zwergwal, Petit rorqual) Antarctic minke whale (Südlicher Zwergwal) sei whale (Seiwal) Bryde's whale (Brydewal) blue whale (Blauwal, Baleine bleue ou Rorqual bleu) fin whale (Finnwal, Rorqual commun) humpback whale (Buckelwal, Baleine à bosse)

Suborder Odontoceti (toothed whales or odontocetes)

Family	Scientific name	Common name (German, French)
Physeteridae (Pottwale)	<i>Physeter macrocephalus</i>	sperm whale (Pottwal, Chachalot)
Kogiidae (Zwergpottwale)	<i>Kogia breviceps</i> <i>Kogia sima</i>	pygmy sperm whale (Zwergpottwal) dwarf sperm whale (Kleinstpottwal)
Platanistidae (Flussdelfine)	<i>Platanista gangetica gangetica</i>	South Asian river dolphin (Ganges-Delfin)
Pontoporiidae (Flussdelfine)	<i>Pontoporia blainvillei</i>	franciscana (La-Plata-Delfin)
Lipotidae (Flussdelfine)	<i>Lipotes vexillifer</i>	baiji (Baiji)
Iniidae (Flussdelfine)	<i>Inia geoffrensis</i>	boto (Amazonas-Delfin)
Monodontidae (Gründelwale)	<i>Delphinapterus leucas</i> <i>Monodon monoceros</i>	white whale (Beluga, marsouin blanc) narwhal (Narwal)
Phocoenidae (Schweinswale)	<i>Phocoena phocoena</i> <i>Phocoena spinipinnis</i> <i>Phocoena sinus</i> <i>Phocoena dioptrica</i> <i>Neophocaena phocaenoides</i> <i>Phocoenoides dalli</i>	harbour porpoise (Kleiner Tümmler, marsouin commun, pourcil) Burmeister's porpoise (Burmeister Schweinswal) vaquita (Hafenschweinswal) spectacled porpoise (Brillenschweinswal) finless porpoise (Indischer Scheinswal) Dall's porpoise (Dall-Hafenschweinswal)



Delphinidae (Delfine)

<i>Steno bredanensis</i>	rough-toothed dolphin
<i>Sousa chinensis</i>	Indo-Pacific humpback dolphin
<i>Sousa teuszii</i>	Atlantic humpback dolphin
<i>Sotalia fluviatilis</i>	tucuxi
<i>Lagenorhynchus albirostris</i>	white-beaked dolphin
<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin
<i>Lagenorhynchus obscurus</i>	dusky dolphin
<i>Lagenorhynchus obliquidens</i>	Pacific white-sided dolphin
<i>Lagenorhynchus cruciger</i>	hourglass dolphin
<i>Lagenorhynchus australis</i>	Peale's dolphin
<i>Grampus griseus</i>	Risso's dolphin
<i>Tursiops truncatus</i>	Common bottlenose dolphin (Grosser Tümmler)
<i>Tursiops aduncus</i>	Indo-Pacific bottlenose dolphin
<i>Stenella frontalis</i>	Atlantic spotted dolphin
<i>Stenella attenuata</i>	pantropical spotted dolphin
<i>Stenella longirostris</i>	spinner dolphin
<i>Stenella clymene</i>	clymene dolphin
<i>Stenella coeruleoalba</i>	striped dolphin (Blau-Weisser Delfin)
<i>Delphinus delphis</i>	common dolphin (Gemeiner Delfin)
<i>Delphinus capensis</i>	long-beaked common dolphin
<i>Lagenodelphis hosei</i>	Fraser's dolphin
<i>Lissodelphis borealis</i>	northern right whale dolphin
<i>Lissodelphis peronii</i>	southern right whale dolphin
<i>Cephalorhynchus commersonii</i>	Commerson's dolphin
<i>Cephalorhynchus eutropia</i>	Chilean dolphin
<i>Cephalorhynchus heavisidii</i>	Heaviside's dolphin
<i>Cephalorhynchus hectori</i>	Hector's dolphin
<i>Peponocephala electra</i>	melon-headed whale
<i>Feresa attenuata</i>	pygmy killer whale
<i>Pseudorca crassidens</i>	false killer whale
<i>Orcinus orca</i>	Orca (killer whale) (Schwertwal)
<i>Globicephala melas</i>	long-finned pilot whale (Gewöhnlicher Grindwal)
<i>Globicephala macrorhynchus</i>	short-finned pilot whale (Indischer Grindwal)
<i>Orcaella brevirostris</i>	Irrawaddy dolphin

Ziphiidae (Schnabelwale)

<i>Tasmacetus shepherdi</i>	Shepherd's beaked whale
<i>Berardius bairdii</i>	Baird's beaked whale
<i>Berardius arnuxii</i>	Arnoux's beaked whale
<i>Mesoplodon pacificus</i>	Longman's beaked whale
<i>Mesoplodon bidens</i>	Sowerby's beaked whale
<i>Mesoplodon densirostris</i>	Blainville's beaked whale
<i>Mesoplodon europaeus</i>	Gervais' beaked whale
<i>Mesoplodon layardii</i>	strap-toothed whale
<i>Mesoplodon hectori</i>	Hector's beaked whale
<i>Mesoplodon grayi</i>	Gray's beaked whale
<i>Mesoplodon stejnegeri</i>	Stejneger's beaked whale
<i>Mesoplodon bowdoini</i>	Andrews' beaked whale
<i>Mesoplodon mirus</i>	True's beaked whale
<i>Mesoplodon ginkgodens</i>	ginkgo-toothed beaked whale
<i>Mesoplodon carlhubbsi</i>	Hubbs' beaked whale
<i>Mesoplodon peruvianus</i>	pygmy beaked whale
<i>Mesoplodon bahamondi</i>	Bahamonde's beaked whale
<i>Ziphius cavirostris</i>	Cuvier's beaked whale
<i>Hyperoodon ampullatus</i>	northern bottlenose whale
<i>Hyperoodon planifrons</i>	southern bottlenose whale



2.4. The Species in the St. Lawrence Estuary

2.4.1. Odontocetes

2.4.1.1. Beluga (*Delphinapterus leucas*)

The beluga is an arctic animal and therefore robust and blubbery. The head with its rounded forehead is small compared to the body. The forehead changes shape and the lips can appear rounded as they vocalise. The neck is unusually mobile because the cervical vertebrae are not fused and belugas readily turn or nod their heads. There is no dorsal fin, but instead a narrow ridge on the back where a dorsal fin would otherwise be. Belugas travel in groups of 5 to 20 and can be often seen in the Saguenay Mouth and River. The belugas in the St. Lawrence Estuary are from the most southern population. The body size ranges between 4.2 - 4.9 m in males and 3.9 - 4.3 m in females (Carwardine et al. 2002). Unfortunately, the belugas in the St. Lawrence Estuary have high contaminant burdens in their bodies and high cancer rates (Carwardine et al. 2002).



Figure 5. Beluga (Reeves et al. 2002)



2.4.1.2. Harbour porpoise (*Phocoena phocoena*)

A harbour porpoise can be recognised by its low dorsal fin and the absence of a beak. The blow is rarely seen but can be heard. They are found mainly in cool, coastal waters throughout the northern hemisphere. Harbour porpoises travel in groups of two to five and reach a maximum length of 1.5 m. They are the shortest-lived cetaceans, rarely surviving past the age of 12 years (Carwardine et al. 2002). They are subject to predation by large sharks and orcas.

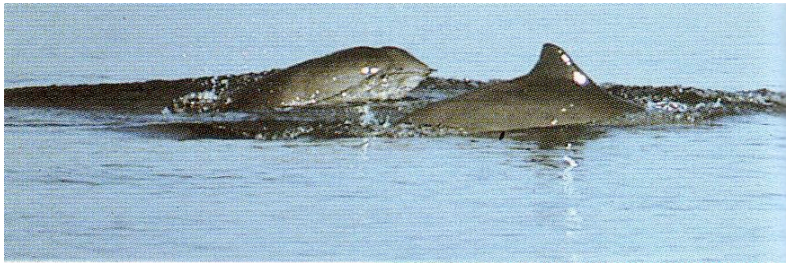


Figure 6. Harbour Porpoises (Carwardine et al. 2002)

2.4.1.3. Sperm Whale (*Physeter macrocephalus*)

The sperm whale, the largest of the toothed whales, has a low hump followed by a series of bumps leading to the fluke, which is thick. The head takes up a third of the body length. Males can reach up to 11 - 20 m and females up to 8.2 - 17 m (Carwardine et al. 2002). The lower jaw is narrow and the blowhole is set forward on the head positioned strongly to the left, which is an identification characteristic for the sperm whale. Before diving they lift their flukes and dive up to 3'000 m deep. This can last up to two hours (Carwardine et al. 2002). They eat squid, including giant squid (up to 12 m long), and larger fish. Their distribution is truly cosmopolitan, stretching from the Arctic to Antarctic and including most large gulfs and seas.



Figure 7. Sperm Whale (Reeves et al. 2002)



2.4.2. Mysticetes

2.4.2.1. Blue Whale (*Balaenoptera musculus*)

This is the largest living animal with the maximum measurement length of 33.3 m and a weight of 190 tonnes being recorded in a female in the southern hemisphere. The males are 1.5 - 3 m shorter than the females. A newborn blue whale measures at least 6 m and drinks 190 l of milk a day, putting on about 3.5 kg per hour or 90 kg a day (Carwardine et al. 2002). Blue whales have a mottled pattern that is highly variable and can be used to identify individuals. The tiny dorsal fin is set far back on the body and appears well after the blowholes when the whale surfaces. The triangular flukes are often raised during a dive. The blue whale is a wide-ranging species that occurs in all oceans and inhabits coastal, shelf and oceanic waters.



Figure 8. Blue Whales (Carwardine et al. 2002)

2.4.2.2. Fin Whale (*Balaenoptera physalus*)

This is the second largest living animal after the blue whale. The males reach 25 m and the females even 27 m. The female baleen whales are bigger than the males as you can see here. The fin whale has a dramatic asymmetry. The head is white on the lower right side and black on the lower left side. It often can be observed alone or in pairs in the St. Lawrence Estuary. Other common names for this species include finback and Common Rorqual. It is a cosmopolitan species, which also occurs in the Mediterranean Sea. The fin whales are among the fastest of all the large whales, capable of bursts of speed up to 25 knots (46 km/h).

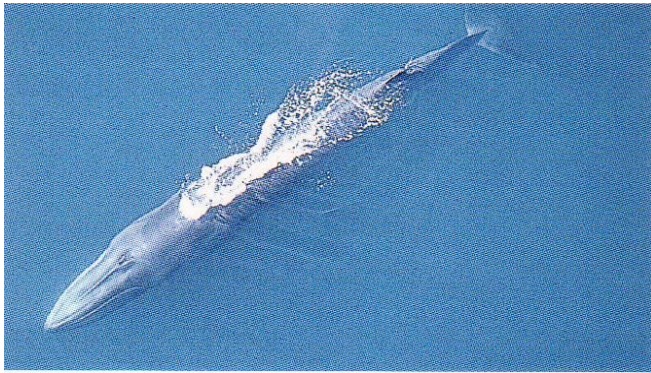


Figure 9. Fin Whale (Carwardine et al. 2005)

2.4.2.3. Humpback Whale (*Megaptera novaeangliae*)

The humpback whale has the longest flippers of any cetacean, which give this whale its scientific name. The translation is “big wing of New England” and the geographic reference is to the location where the first humpback whale was described. The flippers are narrow and approximately one-third the length of the body (up to 5 m). The dorsal fin is reduced to a fleshy hump, or hook, that sits on a sort of platform on the back. They have tubercles on the head. Humpback whales are found worldwide in all major oceans and are highly migratory. The migration of this species is the longest of any mammal, with some whales making a round-trip journey of 16'000 km (Reeves et al. 2002). Certain individuals, such as Tic-Tac-Toe, Le Souffleur and Siam, spend part of the summer in the St. Lawrence Estuary. Humpback whales are known for their acrobatic behaviours, including breaching, lobtailing and flipper slapping. The purpose of these behaviours is not always clear, but they all have different functions depending on the social or behavioural context. Another common behaviour of humpback whales is the bubble-feeding technique, where they blow “nets” of bubbles to concentrate and trap prey, mostly fish.



Figure 10. Humpback Whales surfacing with full mouth of fish from bubble-feeding (Reeves et al. 2002)



Figure 11. Breaching of a Humpback Whale (Carwardine et al. 2002)



2.4.2.4. Minke Whale (*Balaenoptera acutorostrata*)

There are two species of minke whales: The “common” minke whale (*Balaenoptera acutorostrata*) in the northern hemisphere, with the characteristic white band across the middle of the flippers, and the Antarctic minke whale (*Balaenoptera bonaerensis*) in the southern hemisphere, which lacks the white band across the flippers. There are two subspecies in the northern hemisphere: The North Atlantic minke whale (*B. a. acutorostrata*) and the North Pacific minke whale (*B. a. scammoni*). Some consider a dwarf form occurring in the southern hemisphere to be a third subspecies, but this form has not yet been assigned a scientific name and is referred to simply as *Balaenoptera acutorostrata subspecies*.

Because the North Atlantic minke whale (*Balaenoptera acutorostrata*) is the subject in my study, I will describe them a little more precisely.



Figure 12. The Minke Whale named Crab Claw from the St. Lawrence Estuary (© S. Koster)

Minke whales (*Balaenoptera acutorostrata*) as the smallest of the rorqual whales has 50 - 70 throat grooves, running from the chin to the mid-section. They have a characteristic white band on each flipper contrasting with its very dark grey top colour. Like all baleen whales, they have two blowholes and grow to be about 7 - 9 m in length, weighing about 6 - 9 tonnes. Females are about 0.6 m longer than males. Minke whales have a snout that is distinctively triangular, narrow and pointed. The skin is very dark grey above and lighter below. The life span of a minke whale can be over 20 years. Minke whales either travel single or congregated in small pods of about 2 - 3 whales. They arch their body prior to a dive but do not raise their flukes above the ocean surface. The baleen plates in the minke whale's jaw have about 300 pairs of short, smooth baleen plates. The largest plates are less than 30 cm long and 13 cm wide. The fine textured baleen bristles are fringed and are creamy-white with pure white bristles.

Minke whales are the most common of three rorqual species (minke, finback and blue) that frequent the St. Lawrence feeding grounds. They arrive as early as the first week of May each year and leave again after the end of October (Lynas 1986).



Minke whales are seasonal feeders and carnivores. They sieve through the ocean water with their baleens. They filter out small polar plankton, krill (euphausiids), and small fish such as capelin, cod and herring. The minke whale spends approximately 61% of its time during daylight hours feeding and a further 36% in activities directly related to that end (Lynas 1986). Most often the minke whales are observed whilst feeding in the St. Lawrence Estuary on capelin (*Mallotus villosus*), as the minke whales in the northern hemisphere mainly do (Hoelzel et al. 1989). During a feeding strike, it is sometimes possible to see fish jumping out of the water or even out of the mouth. This traditional whale feeding ground has become over the last decade one of the most important whale-watching sites in the world, attracting thousands of ecotourists annually.

Up until the 1930s, no one in the whaling industry bothered with minke whales because their larger relatives, such as fin whales and blue whales, were plentiful and brought a higher profit per catch. But when populations of the larger whales became seriously depleted, with several species brought close to extinction, attention turned to minke whales. By the time the International Whaling Commission's (IWC) moratorium on commercial whaling was passed in 1986, minke whales were the most important species for whaling in both the North Atlantic and the Antarctic. In 2004, Iceland agreed to catch "just" 25 minke whales because of the pressure from different organisations and governments (www.wwf.ch). Japan is still whaling under the banner of "scientific whaling" and Norway landed 3'172 minke whales between 1993 and 2000 (www.worldwildlife.org). The minke whale is listed on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix I (except the population of West Greenland, which is included in Appendix II), which prohibits international trade with all great whales.

2.5. Individual Identification of Whales

The identification of individual cetaceans using natural markings is a common tool for studying distribution, habitat use, population dynamics and behaviour. Natural features, such as dorsal edge marks (DEM) and shapes, lateral body pigmentation and scars, are used in the photo-identification. DEMs are an identification feature whose presence can be photographically documented irrespective of most environmental and lighting conditions and which allows the highest identification success rate by itself (Tscherter & Morris 2005). Changes in natural markings may result in misidentification when matching two photographs (Blackmer et al. 2000). Morris & Tscherter (2005) analysed temporal stability of DEMs used to identify minke whales in the summer feeding grounds of the St. Lawrence Estuary. DEMs such as nicks, dents and cut off tips are present on approximately 73% of all minke whales in the study area (Tscherter & Morris 2005) and these DEMs show a high temporal stability (Morris & Tscherter 2005).

For the propose of my master thesis 54 identified minke whales were observed performing entrapment and feeding manoeuvres. The whales are divided in different categories due to DEMs. The "dorsal kit" created by ORES includes the following categories:



- A) Dorsal Edge Marks dominate (DEM)
 B) Body Marks Dominant (BMD)
 C) Distinctive Dorsal Edge Shape (dDES)
 D) No Dorsal Edge Marks (nDEM)

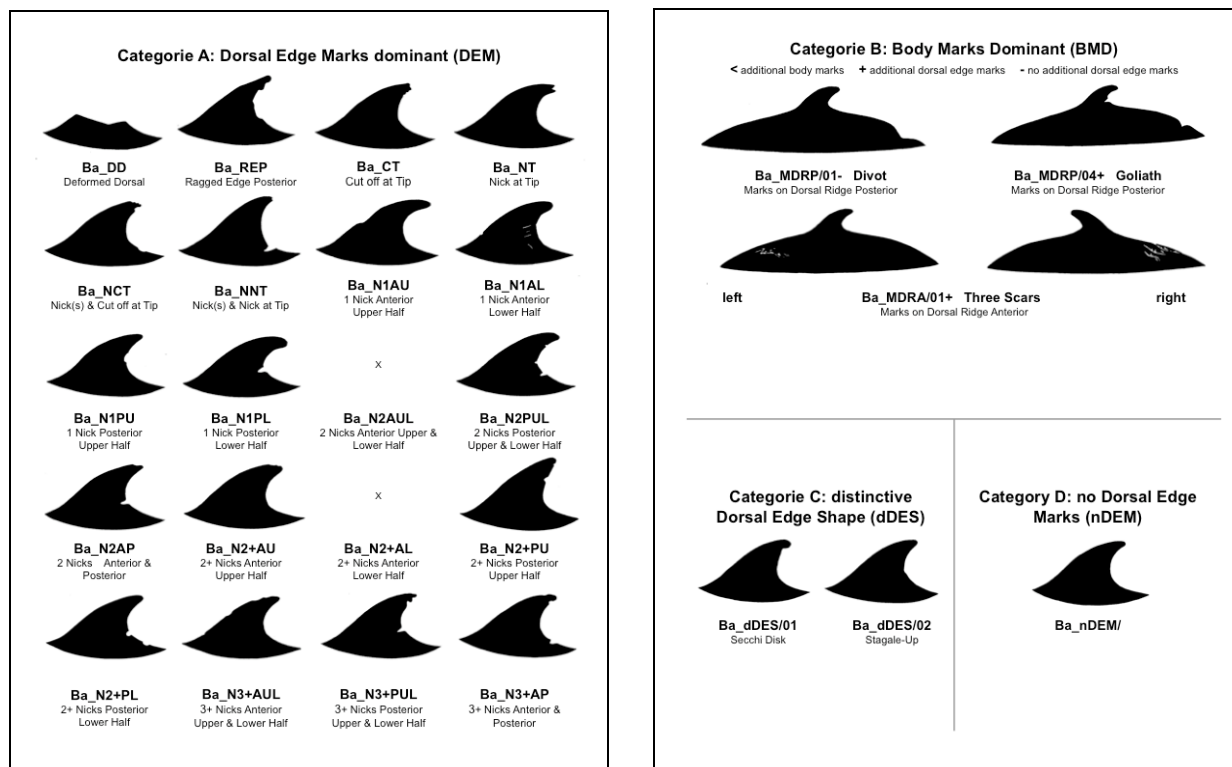


Table 2 & 3. "Dorsal kit" from ORES with the categories A to D. (The division leads to the identification code. Ba=*Balaenoptera acutorostrata*.)

These categories lead to the identification code, which gives every known minke whale a unique identification. This identification code first consists of Ba, standing for the species name *Balaenoptera acutorostrata*. After the underline the category code follows and the number of minke whale in this same category is indicated after the slash. Additionally, the ORES-Team gives the whales a name, which makes it easier to talk about the whale seen in the field (e.g. Loca=Ba_N1PL/21, the dorsal fin has one nick posterior in the lower half and Loca is the 21st individual in this category).

2.6. Marine Food Chain

All living things depend on each other to live. The food chain shows how some animals eat other animals to survive.

Each level of consumption in the marine food chain is called a trophic level. Phytoplankton is the first trophic level (I, Dinoflagelata, Diatoms, Coccolithophorida) of the marine food chain



followed by the small zooplankton (II, copepoda, larvae, bivalvia), which feeds on the phytoplankton. The small zooplankton is then eaten by bigger zooplankton (III) like krill, gastropoda and jellyfish, which all go on to be eaten by big fish and squid (IV, small nekton). The fifth trophic level, the bigger nekton, is tuna, swordfish, small sharks, penguins, seals and odontocetes. The last trophic level (VI) includes the orcas, white sharks, leopard seals and mysticetes.

But baleen whales skip a few steps to get closer to the phytoplankton level. They do not eat from the fifth trophic level, the big nekton, but from the third trophic level the krill, which in turns eat the phytoplankton from the first level. Also the sperm whales as a member of the sixth trophic level skip a step and eats squids from the fourth trophic level. By skipping of trophic levels the animals gain efficiency in producing biomass and this is visible in the large body mass.

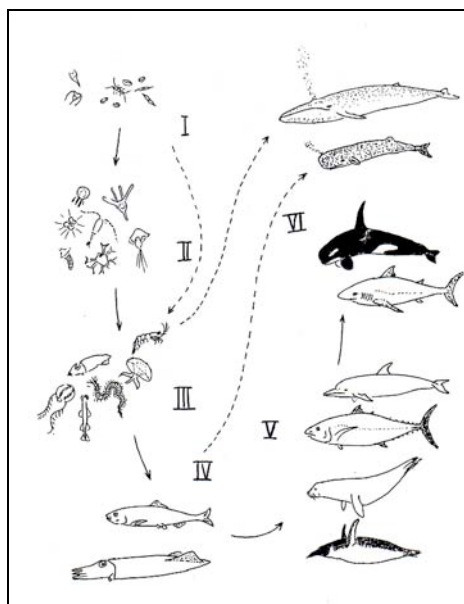


Figure 13. Marine Food Chain. (I=Phytoplankton (primary production), II=small zooplankton, III=zooplankton, IV=small nekton, V=bigger nekton, VI=big nekton (final consumer), Senn 1995)

2.7. The Whales' Food and Upwelling System of the St. Lawrence Estuary

The head of the Laurentian Channel in the St. Lawrence Estuary is an area where intense upwelling is maintained by the interaction of the tidal circulation with shallow topographic features obstructing the upstream flow during flood (Saucier & Chassé 2000). Complex local hydrodynamics spins out a simple pelagic trophic pathway involving zooplankton, capelin (*Mallotus villosus*) and whales. This region is the site of a rich and persistent zooplankton aggregation (Simard & Lavoie 1999) resulting from the pumping of krill by the strong estuarine circulation (Saucier & Chassé 2000) and its concentration-aggregation by the intense tidally driven upwelling and other hydrodynamic processes that are closely linked to



the local topographic features (Lavoie et al. 2000). The shallows at the head of the Laurential Channel are known aggregation areas for juvenile capelin, where they often form dense shoals and concentration peaks along fronts in the upper water column (Bailey et al. 1977, Marchand et al. 1999). With the outflow from the Saguenay River and the water from the St. Lawrence Estuary pushed up during high tide a riptide can be formed where a high concentration of food is caught in the different water masses and therefore a lot of minke whales can be seen whilst surface feeding in this area called Saguenay Mouth.

Local aggregations of both, krill and capelin, attract several species of baleen and toothed whales, which for centuries have gathered in this region during summer (Marchand et al. 1999). This capelin distribution and tidal dynamics closely match the local fin whale (*Balaenoptera physalus*) and minke whale (*Balaenoptera acutorostrata*) distributions (Simard et al. 2002).

2.8. Surface Feeding Behaviour of Minke Whales in the St. Lawrence Estuary

Most baleen whales can be classified into one of three general feeding categories: skimming, swallowing or both (skimming and swallowing). The strategies are consistent with anatomical features of the head, throat and baleen. The minke whale is typical of the swallowing category. All cetaceans swallow their prey whole. Anatomical features adapted to this strategy include the comparatively short baleen and an expanding buccal cavity. To employ this method, the whale swims into a concentration of prey, taking a large volume of water into the mouth and then expelling it, while trapping the prey on its fringed baleen.

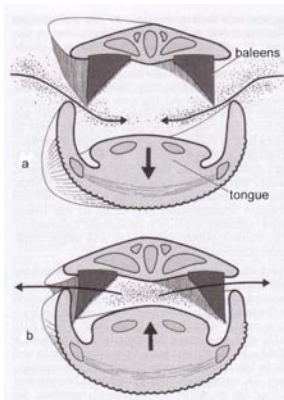


Figure 14. Filtration of prey with the baleens:
a) Phase of intake, mandibula down.
b) Phase of filtration, mandibula up.
(Westheide et al. 2004)



Figure 15. Southern right whale (*Eubalaena australis*) in the Muséum d'Histoire Naturelle in Paris (© S. Caviezel)

Entrapment and feeding manoeuvres are performed in different body planes: dorsal-ventral (back up - belly down), lateral (sideways), ventral-dorsal (belly up - back down) and vertical (head up - tail down). The following definitions of the entrapment and feeding manoeuvres (2.8.1. and 2.8.2.) are from Lynas & Sylvestre 1988, Thompson et al. 2003 and student preparation booklet from ORES.



2.8.1. Entrapment Manoeuvres

With multidirectional surfacing during a feeding cycle, the minke whale performs, besides numerous regular oxygen intake surfacings, different entrapment and entrapment-related manoeuvres to corral and concentrate the prey with:

2.8.1.1. Chin-up blow (c_upbl)

The whale surfaces dorsal-ventrally pushing its head well into the air, taking a breath and re-submerging. The white throat is not expanded but is clearly visible.



Figure 16. Chin-up blow in regular plane (© ORES - U. Tscherter)

2.8.1.2. Lateral Chin-up blow (Lc_upbl)

Similar to the Chin-up blow but lateral surfacing of the whale with the right flipper in the water (=right-side-down, RSD) or left flipper in the water (=left-side-down, LSD) and showing the opposite flipper in the air.



Figure 17. Lateral Chin-up blow with right-side-down (© ORES - U. Tscherter)



2.8.1.3. Head Slap (HS)

The whale lunges at an angle of 30 to 45°, but the throat is not expanded and no water purges out of the mouth. At the highest point, the whale bends its head back and slaps it onto the surface, which creates a huge splash and sound. Sometimes the whales start laterally and slap on one side (slap RSD or slap LSD).



Figure 18. Head Slap in regular plane (© ORES - U. Tscherter)

2.8.1.4. Underwater Exhale on the Dive (UWbl)

After a regular surfacing the whale exhales strongly right below the surface throwing a fountain of frothing water into the air, accompanied by a roaring sound.



Figure 19. Underwater Exhale on the Dive (© ORES - U. Tscherter)



2.8.2. Feeding (Engulfing) Manoeuvres

Strikes right in the water line are called arcs, compared to lunges where the whale's body partially leaves the water. The surfacing counts as a feeding manoeuvre when accompanied by any of the following: (1) visible distension of the throat, (2) an open mouth or (3) water or fish purging from the mouth.

2.8.2.1. Plunge

In this manoeuvre the body of the whale is in the dorsal-ventral plane, with its axis approaching the surface generally at an angle of less than 30 degrees. Only the rostrum, part of the under lip and frequently the baleens are visible at the surface. Afterwards water can be seen being purged from the animal's mouth and the grooves are expanded.

2.8.2.2. Oblique Lunge (OL)

The direction of this movement is similar to that of a plunge, except that the angle the whale's body makes with the horizontal plane is 45 degrees. The significant characteristic of the movement is that the whole head, including the ventral grooves, is exposed at the surface of the water.



Figure 20. Oblique Lunge (© ORES - U. Tschertter)

2.8.2.3. Vertical Lunge (VertL)

The body axis of the whale is perpendicular, or nearly perpendicular to the horizontal plane. The whale's head and thorax are thrust upward into the air. The whale then re-submerges either, simply by sinking below the surface while still in the vertical plane, or by tipping over on its side, or forward onto its belly.



2.8.2.4. Lateral Lunge (LL)

This manoeuvre is similar to an oblique lunge but the whale approaches the surface laterally at about 45 degrees. Like all lateral manoeuvres it can be RSD or LSD.



Figure 21. Lateral Lunge with right-side-down (© ORES - U. Tscherter)

2.8.2.5. Lateral Arc (LA)

A lateral arc is similar to a lateral lunge, except that the whale's body does not break the surface beyond exposing the tip of the fluke. Often the animal will roll into a dorsal-ventral position immediately following the arcing movement and ventilate before re-submerging. This lateral manoeuvre can also be RSD or LSD.



Figure 22. Lateral Arc with right-side-down (© ORES - U. Tscherter)



2.8.2.6. Ventral Lunge (VL)

The whale approaches the surface ventrally at about 45 degrees. The pink belly is visible and with good observation skills it is sometimes possible to determine the sex of the whale. The whale can do a roll back to the dorsal-ventral plane on the surface and this is termed rolling back left (or counterclockwise) over its right side and showing the left flipper in the air (=back-left-over-right-side, backLoRS) or rolling back right (or clockwise) over its left side and showing the right flipper in the air (=back-right-over-left-side, backRoLS). To make the side of the lateralised manoeuvre more clear the new abbreviations in this thesis are: backL-over-right-side (backLoRS) instead of only backL and backR-over-left-side (backRoLS) instead of only backR, which are the definitions of ORES.



Figure 23. Ventral Lunge with rolling back-right-over-left-side (© ORES - U. Tschertter)

2.8.2.7. Ventral Arc (VA)

A ventral arc differs from a ventral lunge only in the fact that the whale's body does not break the water surface. Following the arc, it may roll onto either side and in this way the tip of the fluke may be exposed. As described with the VL manoeuvre, the roll can be backLoRS or backRoLS.

2.9. Lateral Surface Feeding of Minke Whales

At a individual level, fast swimming predators, such as minke whales, will swim on their sides around the prey, using their speed and maybe the reflective colouration of their white bellies to surround, bunch and confuse small shoals of fish and force them up to the surface, where they are finally entrapped by the air (Lynas & Sylvestre 1988).

They use the entire manoeuvre described above. Often during or after a manoeuvre they take one side to entrap/feed or dive again as a lateralisation side. The preferred use of one limb/hand (handedness) over the other is one characteristic of lateralised behaviour already reported extensively in humans. As a background in research I investigated the topic of the side of lateralisation and found three different papers, which I would like to summarise in order to get a better understanding of this complex topic.



2.10. Published Papers on the Topic of Lateralisation

2.10.1. Do humpback whales exhibit lateralized behaviour?

Abstract: Lateralized behaviour has been documented in non-human species, although many observers believe that it occurs at the individual rather than the population level. Its occurrence in Humpback Whales, *Megaptera novaeangliae*, in Massachusetts Bay was investigated by examining active behaviour types in which preference could be given to one direction or side. These included head breaching (direction of spin), flippering (right or left) and tail breaching (direction of movement). In addition, persistent abrasions on the right or left jaw resulting from turns to one side during bottom feeding were noted (...). Overall, these data suggest that Humpback Whales exhibit some behavioural asymmetries, at least one of which is at the population level. This result suggests asymmetry of function in motor or somatosensory representations, although too little is known about the brain of this species to permit definitive conclusions (Clapham et al. 1995).

2.10.2. Feeding behaviour of wild walruses with notes on apparent dexterity of flipper use

Introduction: Based on observations of walruses in captivity and signs of predation left on the sea floor by free-living walruses, various types of feeding behaviour have been suggested in the literature. In this study, however, the underwater feeding behaviour of wild adult male Atlantic walruses (*Odobenus rosmarus rosmarus*) is documented for the first time in their natural habitat by scuba-divers. The video recordings indicated a predisposition for using the right front flipper during feeding. This tendency towards dexterity was explored further by examining a museum collection of extremities of walrus skeletons (Levermann et al. 2003).

Conclusion: In contrast to previous knowledge, flipper use seemed to be of high importance combined with muzzle use. A preference for use of the right flipper rather than the left was indicated. The observations of foraging behaviour in the wild in combination with measurements of limb skeleton asymmetry suggest that lateralized limb use occurs in the walrus. Although based on small sample sizes this is to our knowledge the first record of a piniped showing lateralized behaviour (Levermann et al. 2003).

2.10.3. Bilateral directional asymmetry of the appendicular skeleton of the Harbor porpoise (*Phocena phocena*)

Abstract: Directional asymmetry (DA) of the lengths, diameters, and masses of the scapula, humerus, radius, and ulna were analyzed on a sample of 213 harbor porpoises from Denmark and West Greenland. The levels of DA were consistent across yearlings and older animals, mature and immature animals, sexes, and populations. All investigated variables showed significant DA favoring the right side. (...) These DAs and the examples of lateralized behavior recorded in cetaceans point to the existence of lateralized use of the flippers at the population level in harbor porpoises and possibly other cetacean species (Galatius 2005).



These three papers show lateralisation in a pinniped and in cetaceans. Another publication exists where dolphins feeding out of water in a salt marsh is described by Hoese (1971), where he observed *Tursiops truncatus* out of the water on its right and sometimes left side.

With all this knowledge of lateralised behaviour pattern but nothing published about the minke whales, the aim of my master thesis was to examine if also minke whales in the St. Lawrence Estuary are exhibit one side of lateralisation whilst surface feeding and to quantify this behaviour. In addition, the question was if any of several possible environmental or temporal variables as tidal phases, feeding habitats or sunlight might influence any pattern of lateralisation.



3. Materials and Methods

3.1. Study Area

The study area is about 500 km² and located in the St. Lawrence Estuary and the adjoining Saguenay River. It is approximately delimited by 47°47'00" - 48°21'00" N latitude and 69°48'00" - 69°23'00" W longitude (Figure 24).



Figure 24. Map of East Canada with an overview of the St. Lawrence Estuary and the study area, which is indicated with the red box (ORES - U. Tschertter).

In this thesis the study area was divided into four feeding habitats according bathymetric and oceanographic features (Figure 25):

- the Laurential Channel Head (LCH) starting at Les Escoumins, a 200 - 300 m deep glaciated valley ending with a steep upward slope rising to a depth of 50 m at the mouth of the Saguenay River
- the Saguenay River (SR) from the line between Pointe Noir and Pointe d'Islet to Cap de la Boule
- the Saguenay Mouth (SM) from the line between Pointe Noir and Pointe d'Islet to K56 and La Toupie
- upper Estuary (upE) south of K54 to Baie des Rochers

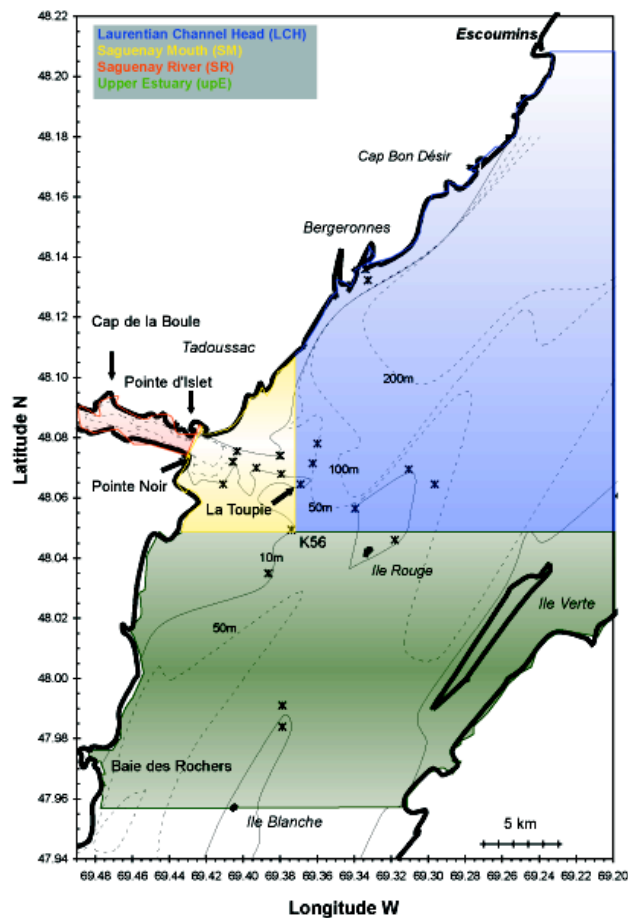


Figure 25. Map of the study area with the four feeding habitats and with respect to sea floor topography (adapted from ORES source, A. Boldt).

3.2. Data Collection

The data was collected during five consecutive field seasons (June through October) from 2001 through to 2005. The research teams consisted of an experienced boat driver and a photographer, a time and a record keeper, and additional dedicated observers to ensure a 360-degree visual scan of the area. The data was taken from two small highly-maneuvrable inflatable crafts using 4-stroke outboard motors. Observations were carried out weather permitting and generally in wind speeds of less than 20 knots. Transects downriver and upriver were run daily throughout the study season. When a surface feeding minke whale was sighted within 1 km of the transect, the boat approached within 30 m of the whale. When the boat was within close proximity of the whale, a latitude and longitude position of the whale was recorded using Global Position Satellite (GPS) and these positions were divided into the four feeding habitats as explained above (see 3.1.). By using single lens reflex cameras fitted with 300 mm lenses and diapositive films exposed at shutter speeds of 1/500 to 1/1000 s identification photographs were taken. Other data such as entrapment and



feeding (engulfing) manoeuvres in different body planes with side of lateralisation were recorded. Times of surface feeding events were used along with Canadian Hydrographic Tide Tables to determine time of closest high tide and divide into 4 categories. High tide (HT) was defined as one hour before the exact local high tide until two hours after local high tide following by after HT (aHT), low tide (LT) and before HT (bHT) in the same intervals of hours. The orientation of the whale's body (towards the shores, upriver or downriver) was determined as the whale was breaking the surface. The orientation of the subject in relation to the sunlight whilst performing entrapment and feeding manoeuvres was defined as positive, when the whale's belly was oriented towards the sunlight, as negative, when the whale's belly was oriented away from the sunlight or as neutral, when the whale's belly was oriented parallel to the sunlight. As a field-aid I developed a "sun kit" to allow a fast and correct decision on the boat about the correct recording of this data type "sun" (see Appendix 7.1.). A further categorisation of the sunlight into two categories (noon and afternoon) was used to figure out if the different angles of the sun influenced the whale's orientation relative to the sunlight. This could occur because of the different angles of incidence and the different resulting reflection of the sunlight off the bright belly of the whale. In one category the sun is at a steep angle of about 70° in the position $\pm 25^\circ$ S at noon (11^{00} - 13^{00}) and in the other category the sun is at a flat angle of about 50° in the position SW to W in the afternoon (15^{00} - 17^{00}). Although using data from manoeuvres after five o'clock could have given an even clearer view on possible effects of the different angles, I chose this time period as it was the latest time window possible that still allowed me to analyse an equal amount of noon and afternoon data (noon: N=51, afternoon: N=60). The angles were determined by measuring the angle between the sun and the horizon using a triangular and a stable platform during different days and then the means were calculated. The surfacing was counted as feeding manoeuvre when accompanied by any of the following: (1) visible distension of the throat, (2) an open mouth or (3) water or fish purging from the mouth.

3.3. Investigated Manoeuvres

Entrapment and feeding manoeuvres were differentiated on the basis of the orientation of the whale's body and occurred either in:

- (1) Lateral manoeuvre: An entrapment or feeding manoeuvre when the whale was lying on either side of its body. If the whale was lying on the right side, this was termed right-side-down (RSD) or lying on the left side, this was termed left-side-down (LSD).
- (2) Ventral manoeuvre: A feeding manoeuvre where the whale approached the surface ventrally. The pink belly was visible. The roll back to dorsal-ventral was termed rolling back left (or counterclockwise) if the whale rolled over its right side and held the left flipper in the air (backLoRS) or rolling back right (or clockwise) if the whale rolled over its left side and held the right flipper in the air (backRoLS).
- (3) Dorsal-ventral manoeuvre: An entrapment or feeding manoeuvre where the whale was in the dorsal-ventral plane with its axis approaching the surface. The whale can submerge with a roll to either side (roll to the right=rollR or roll to the left=rollL).



In the background information chapter (see 2.8.) the single manoeuvres are described (ordered so all entrapment manoeuvres are first, followed by all feeding (engulfing) manoeuvres).

3.4. Data Analysis

The data was used to determine whether minke whales exhibit a side of lateralisation and if the minke whales' sides of lateralisation frequencies in different body planes differed among tidal phases, feeding habitats (i.e. topographic or oceanographic features), orientation of the whale's body and incidence of sunlight.

The data was analysed in the following order: A) Comparison of the right and left side frequency, B) Individually identified minke whales and their preferred side of lateralisation C) Relative frequencies of the side of lateralisation with respect to the tidal phases, D) Relative frequencies of the side of lateralisation with respect to the feeding habitats, E) Relative frequencies of the side of lateralisation with respect to the orientation of the whale's body and F) Relative frequencies of the side of lateralisation with respect to the sunlight and angles of the sun.

Chi-squared tests after Pearson was used, but if the sample size was smaller than five the Fisher-exact tests was employed to test for deviations of observed from expected relative frequencies derived under the null-hypothesis of equal relative frequencies in different tidal phases, feeding habitats, orientation of the whale's body and incidence of sunlight and angles of the sun. The relative frequencies were used due to the fact that the number of outings varies in the different tidal phases and unequal coverage of the feeding habitats. The photo-identification of the minke whales in the study area revealed that several individual are present when running the surveys. This suggests that the data collected in the study was from multiple whales and was therefore random.

The statistical analysis was conducted using SPSS Version 13.0. for Windows.



4. Results

Surfacing behaviours of 54 identified minke whales with known side of lateralisation were observed on 2'550 entrapment and feeding manoeuvres over the course of the study from 2001 to 2005.

4.1. Side of Lateralisation (A) and Individually Identified Minke Whales (B)

In all three analysed manoeuvres a strong preference to the right side was observed (Figure 26). In the lateral manoeuvre the whales lay more often on their right side, in the ventral manoeuvre more rolls back to the dorsal-ventral plane over its right side occurred and in the dorsal-ventral manoeuvre the whales submerged more with a roll to the right side. These results were calculated with 1819 manoeuvres in lateral plane of 43 identified whales, 585 manoeuvres in ventral plane of 41 identified whales and 146 manoeuvres in dorsal-ventral plane of 9 identified whales. In all three manoeuvres the identified whales, which were lateralizing to the left side (lateral=11, ventral=7, dorsal-ventral=3), also lateralised to the right side during other observations. Two whales, Crowsfoot=Ba_N1AL/01¹ and Pazza=Ba_N2+PU/11, performed more left side manoeuvres in the five analysed years. This was observed during samples² on each whale. Only one minke whale (Loca=Ba_N1PL/21) showed all three manoeuvres at least once to the left side. Two minke whales (Artiste=Ba_dDES/12 and Shooting Star=Ba_MDRP/06) performed lateral and dorsal-ventral manoeuvres to the left side but were never seen exhibiting a ventral manoeuvre over the left side. One minke whale (Broken=Fin Ba_DD/02) performed lateral and ventral manoeuvres to the left side but was never seen in a dorsal-ventral manoeuvre to the right or left side (Table 4). All three manoeuvres fluctuated between being split 71/29 and 100/0 to the right side over the during of the five conductive field seasons (Table 5).

¹ identification code, Ba= *Balaenoptera acutorostrata*, see Background 2.5 for further information.

² sample=during at least 30 minutes all blows and manoeuvres are recorded from the same whale.

Results

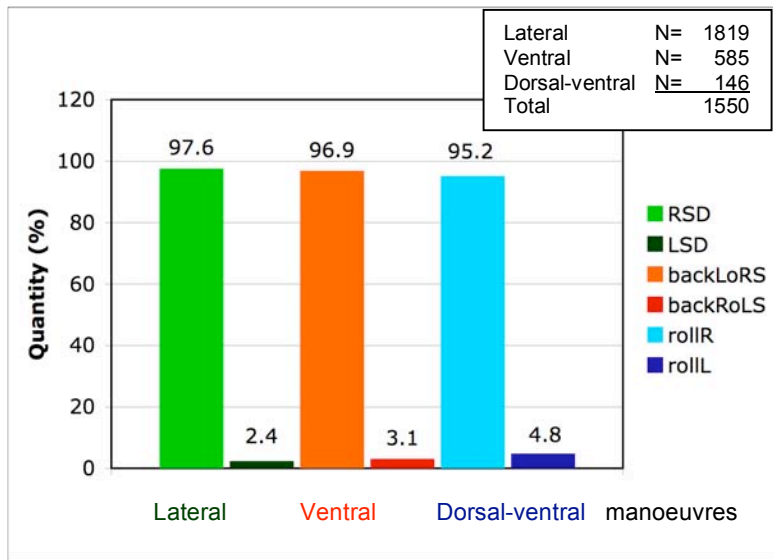


Figure 26. Side of lateralisation in the lateral, ventral and dorsal-ventral manoeuvres. (RDS/LSD= right-side-down/left-side-down in lateral manoeuvres, backLoRS/backRoLS= rolling back over its right/left side in ventral manoeuvres, rollR/rollL= roll to the right/left side in dorsal-ventral manoeuvres. Numbers of examined manoeuvres are given in the box at the right upper corner.)

Table 4. Observed numbers of the side of lateralisation in the three manoeuvres for identified individuals.

Name	Manoeuvres					
	Lateral		Ventral		Dorsal-ventral	
	RSD	LSD	backLoRS	backRoLS	rollR	rollL
Artist	198	1	8	-	19	3
Broken Fin	12	2	3	1	-	-
Loca	271	10	48	1	54	1
Shooting Star	82	4	7	-	2	2
Boomerang	3	-	30	5	-	-
Bubbler	4	2	-	-	-	-
Crowsfoot	1	*4	2	-	-	-
El International	387	3	12	-	37	-
Dopey	1	-	6	2	5	-
Graffigne	5	1	5	1	-	-
Hibou	7	-	1	1	-	-
Pazza	1	*4	1	-	-	-
Piccola	13	2	15	-	-	-
Requin	33	5	9	-	-	-
Three Scars	-	-	1	1	-	-
(Various identified whales)	448	-	154	-	15	-
NA	245	1	210	6	7	1
nDEM	65	4	55	-	-	-
Total	1776	43	567	18	139	7

In each manoeuvre the side of lateralisation is given: RDS/LSD=right-side-down/left-side-down in lateral manoeuvres, backLoRS/backRoLS=rolling back over its right/left side in ventral manoeuvres, rollR/rollL= roll to the right/left side in dorsal-ventral manoeuvres. Every animal with at least one left side manoeuvre is listed alphabetically. In the upper part of the table are the animals with left side manoeuvres in more than one manoeuvre. The third last row of data (Various identified whales) summarizes information for identified individuals without any left side manoeuvre. NA=not available, the minke whale could not be identified. nDEM=no Dorsal Edge Mark and therefore more than one possible individual. *observed during one sample.

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Table 5. Observed numbers of the side of lateralisation in the three manoeuvres over the five field seasons.

Year	Manoeuvres								
	Lateral		Split	Ventral		Split	Dorsal-ventral		Split
	RSD	LSD	R/L	backLoRS	backRoLS	R/L	rollR	rollL	R/L
2001	313	12	96/4	29	1	97/3	5	2	71/29
2002	91	1	99/1	18	0	100/0	12	0	100/0
2003	671	16	98/2	116	3	98/2	86	4	96/4
2004	380	4	100/0	195	4	98/2	14	0	100/0
2005	321	10	97/3	209	10	95/5	22	1	96/4
Total	1776	43	98/2	567	18	97/3	139	7	95/5

In each manoeuvre the side of lateralisation is given: RDS/LSD=right-side-down/left-side-down in lateral manoeuvres, backLoRS/backRoLS=rolling back over its right/left side in ventral manoeuvres, rollRoLS/rollLoRS=roll to the right/left side in dorsal ventral manoeuvres. The split was calculated and approximated to 1% whereas right (R) first and left (L) is second.

4.2. The Different Factors (C to F)

There was no significant difference for all manoeuvres when comparing the relative frequency of the side of lateralisation with respect to tidal phases (Fisher exact test=1.258-4.434, df=3, p=0.210-0.765, Table 6, a. Tidal Phases). Comparison between the relative frequency of the side of lateralisation and the feeding habitats showed no significance in lateral manoeuvres (Fisher exact test=3.608, df=3, p=0.302), but differed significantly in ventral and dorsal-ventral manoeuvres (Fisher exact test=7.199 and 13.858, df=3, p=0.050 and 0.002, respectively, Table 6, b. Feeding Habitats).

Table 6. Observed numbers of manoeuvres in the tidal phases and feeding habitats.

Man- oeuvres	Side	a. Tidal Phases					Statistics				b. Feeding Habitats					Statistics			
		HT	aHT	LT	bHT	Total	Fisher	df	p		LCH	upE	SR	SM	Total	Fisher	df	p	
Lateral	RSD	637	381	287	471	1776					151	117	595	913	1776				
	LSD	17	5	11	10	43					3	3	9	28	43				
	Total	654	386	298	481	1819	*4.434	3	0.210		154	120	604	941	1819	3.608	3	0.302	
Ventral	backLoRS	231	101	84	151	567					170	117	58	222	567				
	backRoLS	8	6	1	3	18					11	3	0	4	18				
	Total	239	107	85	154	585	3.533	3	0.309		181	120	58	226	585	7.199	3	0.050	
Dorsal- ventral	rollR	34	49	13	43	139					2	7	83	47	139				
	rollL	1	2	1	3	7					3	0	3	1	7				
	Total	35	51	14	46	146	1.258	3	0.765		5	7	86	48	146	13.858	3	0.002	

Side: RDS/LSD=right-side-down/left-side-down in lateral manoeuvres, backLoRS/backRoLS=rolling back over its right/left side in ventral manoeuvres, rollR/rollL=roll to the right/left side in dorsal ventral manoeuvres. Tidal Phases: HT=high tide, aHT=after high tide, LT=low tide, bHT=before high tide. Feeding Habitats: LCH=Laurential Channel Head, upE=upper Estuary, SR=Saguenay River and SM=Saguenay Mouth. Statistics: Fisher exact-test (Fisher) was used, df=degrees of freedom, p-value (p) was given as exact significant, 2-sided. *was calculated with the chi-squared-test. Due to varying numbers of outings in the different tidal phases and unequal coverage of the feeding habitats (Morris, pers. comm.), the numbers are not comparable between the tidal phases or feeding habitats (only within each tidal phase or feeding habitat).

The relative frequency of the side of lateralisation with respect to the orientation of the whale's body was equally distributed (Fisher exact test=1.824-5.561, df=3, p=0.120-0.659, Table 7, a. Orientation) and therefore the minke whales did not differ the orientation related to the side of lateralisation whilst surface feeding. In all three manoeuvres the whale's belly was oriented towards the sunlight (positive) more frequently (Figure 27). These analyses were calculated with 514 lateral manoeuvres of 28 identified whales, 28 ventral manoeuvres of 8 identified whales and 17 dorsal-ventral manoeuvres of 3 identified whales. However, the data

Results



for lateral and ventral manoeuvres shows no difference between the relative frequency of the side of lateralisation and the direction with respect to the sunlight (Fisher exact test=2.594 and 1.014, df=3, p=0.099 and 0.432, respectively, Table 7, b. Sunlight). The data for dorsal-ventral manoeuvres had no roll to the left side and therefore no analysis could be done. By analysing the angles of the sun at noon and afternoon and the direction of the whale's belly with respect to the sunlight (positive or negative) in all three manoeuvres the distribution was not significantly different from the expected equal distribution (Fisher exact test=0.313-2.305, df=1, p=0.149-1.000, Table 8). As a control, the data from overcast weather was analysed with respect to the whale's orientation. This was equally distributed to all possible orientations and therefore no preference to one direction was given without possible influence of sunlight (N=101, $\chi^2=4.70$, df=3, p=0.195).

Table 7. Observed numbers of manoeuvres with different orientation of the whale's body and the sunlight.

Man-o-euvres	Side	a. Orientation					Statistics			b. Sunlight			Statistics		
		North shore	downriver	South shore	upriver	Total	Fisher	df	p	pos	neg	Total	Fisher	df	p
Lateral	RSD	209	369	146	205	929				317	188	505			
	LSD	3	4	5	5	17				8	1	9			
	Total	212	373	151	210	946	3.708	3	0.287	325	189	514	2.594	3	0.099
Ventral	backLoRS	124	52	62	110	348				19	5	24			
	backRoLS	2	1	2	5	10				4	0	4			
	Total	126	53	64	115	358	1.824	3	0.659	23	0	28	1.014	3	0.432
Dorsal-ventral	RS	30	42	7	6	85				12	5	17			
	LS	1	1	0	3	4				0	0	0			
	Total	31	43	7	9	89	5.561	3	0.120	12	5	17	NA	NA	NA

Side: RDS/LSD=right-side-down/left-side-down in lateral manoeuvres, backLoRS/backRoLS=rolling back over its right/left side in ventral manoeuvres, rollR/rollL=roll to the right/left side in dorsal ventral manoeuvres. Sunlight: positive (pos)=the whale's belly was oriented towards the sunlight, negative (neg)=the whale's belly was oriented away from the sunlight. Statistics: the Fisher exact-test (Fisher) was used, df=degrees of freedom, p-value (p) was given as exact significant, 2-sided.

Table 8. Observed numbers of manoeuvres with respect to the angles of the sun at noon (N=51) and afternoon (N=60).

Manoeuvres	Sunlight	Sunangles		Total	Statistics		
		Noon (11 ⁰⁰ -13 ⁰⁰)	Afternoon (15 ⁰⁰ -17 ⁰⁰)		Fisher	df	p
Lateral	pos	8	8	16			
	neg	8	4	12			
	Total	16	12	28	0.778	1	0.459
Ventral	pos	0	1	1			
	neg	1	3	4			
	Total	1	4	5	2.305	1	0.149
Dorsal-ventral	pos	20	33	53			
	neg	14	11	25			
	Total	34	44	78	*0.313	1	1.000

Sunlight: positive (pos)=the whale's belly was oriented towards the sunlight, negative (neg)=the whale's belly was oriented away from the sunlight. Angles of the sun (Sunangles): defined as angle between the water surface and the sun, which was compared between noon (11⁰⁰-13⁰⁰) and afternoon (15⁰⁰-17⁰⁰), steep and flat angle, respectively. Statistics: the Fisher exact-test (Fisher) was used, df=degrees of freedom, p-value (p) was given as exact significant, 2-sided. *was calculated with the chi-squared-test.

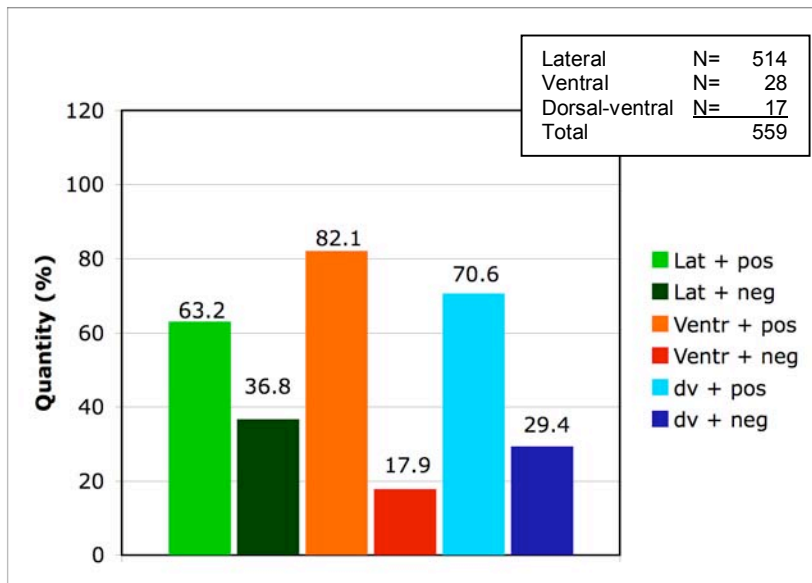


Figure 27. Direction to the sunlight in lateral (lat), ventral (ventr) and dorsal-ventral (dv) manoeuvres. (The sunlight was termed positive (pos) if the whale's belly was oriented towards the sunlight and negative (neg) if the whale's belly was oriented away from the sunlight. Numbers of examined manoeuvres are given in the box at the right upper corner.)



5. Discussion and Conclusion

5.1. Side of Lateralisation and Individually Identified Minke Whales

Side of lateralisation (A)

This study clearly demonstrates the minke whales' preference for the right side in all three examined manoeuvres whilst surface feeding in the habitat of the St. Lawrence Estuary. The findings parallel those of Hoese (1971), who found a strong preference for right-side-down orientation among bottlenose dolphins (*Tursiops truncatus*) that feed by chasing prey and temporarily stranding themselves on shoreline banks. In addition, Clapham et al. (1995) examined jaw abrasions resulting from turns to one side during bottom feeding and active behaviour types in which a preference could be given to one direction or side in humpback whales (*Megaptera novaeangliae*). They noted that 80% of individuals showed abrasion on only the right jaw. One of the three active behaviour types, the flippering, showed a bias (77.3%) towards one direction, generally the right side. Additionally Kasuya & Rice (1970) found parallels while examining jaw abrasions and baleen wear in the bottom-feeding gray whale (*Eschrichtius robustus*) and noted that 80% of individuals showed a clear right side bias.

Individually identified minke whales and their preferred side of lateralisation (B)

It is important to know that all identified minke whales in this study that were observed lateralizing to the left side also performing the manoeuvres to the right side during other observations. No minke whale in the study area performed the manoeuvre(s) exclusively to the left side. The whale named Crowsfood performed four LSD manoeuvres in lateral plane and two rolls back right from ventral to dorsal-ventral plane in one sample in 2003. Crowsfood was only seen once again that season, performing a RSD manoeuvre. We therefore know that Crowsfood performed manoeuvres to both sides but unfortunately, this individual never appeared again after 2003, and so closer examination of its behaviour was impossible. The whale named Pazza was also sampled and was observed performing four LSD manoeuvres and one RSD manoeuvre in 2001. Again, Pazza never appeared in later seasons to verify its behaviour. Therefore, it is not possible to conclude that these two minke whales do exhibit a preference to the left side. Only one minke whale (Loca) performed all three manoeuvres at least once to the left side. This is unusual but not astonishing considering that it was also Loca who invented the Chin-up blow in 1999 and the Head Slap in 2000 as new entrapment manoeuvres (Tscherter, pers. comm.). This minke whale seems to try different manoeuvres in new forms and to different sides, which amazes the researchers. Loca was also seen doing Head Slaps not only in the dorsal-ventral plane but also by surfacing dorsal-ventrally and slapping to one side and once even slapping backwards. The repertoire of invented manoeuvres is quite big and changes slightly over time (Tscherter, pers. comm.). But nevertheless even this minke whale still performed the majority of manoeuvres to the right. A transition in side would require a very long training time in order to become as efficient as the usual side. During the time in which the manoeuvre is trained to the new side, the energy balance for the new variation would be negative, and a



transition to the other side would only occur when executing the manoeuvre to this side became more profitable. But why use energy to learn a different variation of a manoeuvre the animal is already accustomed to performing? There are no disadvantages in using only the familiar right-hand side. I suppose that because the number of manoeuvres performed to the left does not increase from year to year, the minke whales do not benefit from training it, but they have the possibility to perform manoeuvres to the left. In the animal kingdom, to survive is all that counts and for whales in feeding grounds like the habitat of the St. Lawrence Estuary, the priority is to get as much food as possible in order to increase the blubber layer. This energy will be used in the coming winter while the whales are forced to fast due to the thin food supply in the winter habitats and it is especially important for females, who will need a lot of energy for giving birth and nursing the newborn.

Conclusion

I conclude that there is no benefit in surface feeding to the left for those individuals who perform left side manoeuvres. The right side is still predominant. The results of this study suggest a consistent behavioural asymmetry in surface feeding behaviour. This split of 95/5 is particularly significant, because it appears to represent the behaviour of lateralisation at population level, with the degree of the split almost equal to the 90/10 division of right/left handedness seen in humans (Annett 1972).

5.2. The Different Factors

5.2.1. Tidal Phases

Relative frequencies of the side of lateralisation with respect to the tidal phases (C)

The tidal phases did not influence the side of lateralisation in any examined manoeuvres (lateral, ventral or dorsal-ventral). Although Gibbins (2003) showed that surface feeding was most frequent during high tide, the split of 95/5 to the right side still existed in all tidal phases. Therefore, the relative frequency of the side of lateralisation did not alter with the change in tidal phases. The Atlas of Tidal Currents from the St. Lawrence Estuary shows that there are different currents (in each feeding habitat) at high tide and low tide. While for example the current is almost zero before high tide (bHT) in the Laurential Channel Head, in the Saguenay Mouth an upriver current already exist (see Appendix 7.2., Figure 29, 30, 31). In contrast, after high tide a strong downriver current is created by the water in the Saguenay River and the tidal force in the Laurential Channel Head and in the Saguenay Mouth (see Appendix 7.2., Figure 32, 33, 34). I suppose that there is no disadvantage in using the left side manoeuvre. However, the fact that using the right side is more familiar makes it more beneficial and this effect is independent of changes in current speeds caused by tidal phases.



5.2.2. Feeding Habitats

Relative frequencies of the side of lateralisation in the feeding habitats (D)

The relative frequency of the side of lateralisation in the lateral manoeuvres was not significantly different in the feeding habitats. This indicates that minke whales do not use one side more often depending on the feeding habitat. The split of using the right side more often still exists in all feeding habitats. The significant result for the relative frequency of the side of lateralisation in ventral and dorsal-ventral manoeuvres in the different feeding habitats was based on 18 and 7 left side manoeuvres, respectively, whereas the lateral manoeuvre results were based on 43 manoeuvres. The results from the ventral and dorsal-ventral manoeuvres were a small sample size and therefore I suggest approaching this result with caution. A closer look at the data shows that the sample size of five in the dorsal-ventral manoeuvres in the Laurential Channel Head was responsible for the significant result. With more samples the analysis should be redone. The data from the ventral manoeuvre should also be checked by collecting more data and analysing again. The four habitats have different bathymetric and oceanographic features, but this does not affect the relative frequency of the side of lateralisation. Only the type of manoeuvre is affected by the conditions of the different feeding habitats. For example, entrapment manoeuvres are often observed in the Saguenay Mouth and River but rarely in the St. Lawrence Estuary. I suppose that due to the topographic features, different current patterns are formed in the different habitats and therefore the whales adapt their foraging behaviour. Due to the cold water in the deep Laurential Channel Head, the plankton is more abundant and attracts whales. The passively floating plankton is distributed by the current. Because the entrapment manoeuvre is used to corral the prey, I conclude that in the Saguenay Mouth and River the prey is more disperse and therefore such manoeuvres are needed. However, the feeding habitat influences only the type of manoeuvre, but not the side to which it is performed.

5.2.3. Orientation of the Whale's Body

Relative frequencies of the side of lateralisation with respect to the orientation of the whale's body (E)

The orientation of the whale's body was not correlated with the relative frequency of the side of lateralisation. This means that the relative frequency of the side of lateralisation can not be used as an indication of the orientation of the whale's body. The orientation maybe depends on the tidal phase (strength of currents) within the feeding habitat (direction of currents differ in the feeding habitats). Due to the small sample size of 17 LSD, the different orientations of LSD could not be analysed.



As an excursion, I like to mention a study implemented by U. Tscherter which analysed the orientations of the minke whales during a cue count ¹ in 2003. The minke whales orientated mainly NW performing OL and PL. This orientation was against the current during outgoing tide. This orientation could be an indication that the minke whales use and profit from the current (Tscherter, pers. comm.). With more data, maybe including lateral manoeuvres, this observation could be assured.

Although in the cue count from 2003 the manoeuvres (OL and PL) were against the current, in this master thesis the closer look at the orientation (and the maybe linked current flow) and the relative frequency of side of lateralisation was not correlated. However, the familiar use of the right side was dominant in all orientations.

5.2.4. Sunlight

Relative frequency of the side of lateralisation with respect to the sunlight (F)

Because in all three manoeuvres the minke whales directed their bright bellies more frequently towards the sunlight, the assumption can be made that they somehow benefit from doing this. The sunlight reflecting off the whales' bright belly may throw the capelin into confusion and cause them to swim closer together, thus creating a denser patch of prey (hypothesis of Lynas N. and Tscherter U.). The minke whale can benefit by feeding on more prey with one strike. But the analysis of the relative frequency of the side of lateralisation in the lateral and ventral manoeuvres did not correlate with the influence of the sunlight. I propose that the manoeuvre towards the sunlight is independent of side because the side of lateralisation does not give a benefit of feeding on more prey, only the reflection of the sunlight. The entrapment manoeuvres themselves (either to the right or to the left side), which lead to the catching of dens prey, and the use of the currents are the driving force and not the side of lateralisation.

When analysing whether the angles of the sun at noon and afternoon might have an influence on the orientation of the whale's belly with respect to the sunlight, I could still find more positive orientations, both at noon (sun at a steep angle of about 70°) and afternoon (sun at a flat angle of about 50°). The fact that there are more manoeuvres with a positive direction at noon and in the afternoon indicates that the whale orientates towards the moving sunlight. Another reason could be that the two angles are not far enough apart to compare. Therefore no difference can appear. During the two hours the sun moves about 45° and the two angles are only about 20° apart ($\pm 25^\circ$ S at noon (11⁰⁰-13⁰⁰) and SW to W in the afternoon (15⁰⁰-17⁰⁰)). A new analysis using additional data from late afternoon observations that is perhaps compared with the existing morning data could verify these results.

¹ A cue count is a method applied by ORES for counting the surfacing of many whales. Too many whales performing too many manoeuvres make it impossible to record all the different data points simultaneously. After the whales are identified with photographs, the cue count starts and for example in the cue count from 2003 the time, feeding strike type and the orientation of the whale were recorded. The whales are no longer identified for each manoeuvre. In other cue counts different data can be measured as for example blow data if required.



I still propose that handedness is the driving force and therefore the sunlight has no effect on the side of lateralisation. Another possible explanation is that due to the sunlight in the first few meters under the surface of the sea the visibility is about 5 - 10 m, as I discovered while scuba diving at Cap Bon Désir and talking to resident people. I could see krill and schooling fish about the size of capelin while diving. Because cetaceans have quite good sight, minke whales locate their prey maybe also visually. Visuospatial processing in cetacean has right eye superiority and according to Kilian et al. (2000) this suggests a left-hemispheric dominance for the processing of visuospatial information. If the whale is feeding on its right side, the superior right eye can be needed to detect prey. This effect of the limited visibility whilst surface feeding in the light-flooded upper layer and right side preference of the minke whales is maybe linked to the right eye superiority. Minke whales are rarely observed surface feeding with open eyes (Tscherter, pers. comm.). They most probably close their eyes while breaking the surface, having located the prey beforehand. I ascribe this to an acquired reflex to protect their eyes. This aspect of minke whale behaviour from an underwater view is worthy of further study. The underwater filming would present a challenge. Firstly, the visibility of maximally 10 m is not much for filming, secondly, the water in the St. Lawrence is quite cold and thirdly, the current can be very strong.

Conclusion

However, this study points out that the side of lateralisation is independent of the tidal phases, feeding habitats, orientation of the whale's body and sunlight. I suggest that the lateralisation to one side is therefore not due to different environmental factors but instead, the minke whales from the St. Lawrence Estuary exhibit the significant split of 95/5 toward the right side and this is a consistent behavioural asymmetry in surface feeding behaviour. This phenomenon was also observed in other studies of gray whales, bottlenose dolphins and humpback whales as cited above. Clapham et al. (1995) indicated that this behavioural lateralisation is possibly related to an asymmetry of function in the brain. This behavioural lateralisation pattern is widely dispersed throughout the animal kingdom and therefore I conclude that it developed early in evolution and is anchored in their genes.



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Minke Whale photography on front page made by Ursula Tscherter, © ORES
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7. Appendix

7.1. “Sun kit”

The “sun kit” is a field-aid. It allows a fast and correct decision on the boat. The orientation of the whale’s body with respect to the sunlight indicates if the data type “sun” is positive, negative or neutral (towards, away from or parallel to the sun). The “sun kit” consists of two discs of which the upper one is transparent and rotates against the other. On the lower disc the orientations (N, E, S, W) are indicated. On the upper disc a yellow dot indicates the sun’s position and in each quadrant the key for the “sun data” is written for each manoeuvre and direction.

Example: Situation: 1) The sun is to the SW.

2) The whale was oriented W

3) The whale is performing a manoeuvre in a lateral plane right-side-down like Lateral Chin-up blow, Lateral Lunge, Lateral Arc

Sun kit: 1) Put the yellow dot on the upper disc over the inscription SW on the lower disc

2) Look at the point on the “sun kit” where W is written

3) In the quadrant in which W now lies the data for the manoeuvre can be read off: RSD manoeuvres are positive towards the sun (written in green).

If the manoeuvre were LSD it would be negative to the sun (away from the sun). If the manoeuvre were in normal plane, with the whale’s body and the sun in the same orientation: the manoeuvre would be neutral (parallel to the sun); this is indicated in black.



Figure 28. “Sun kit”



7.2. Atlas of Tidal Currents

(Canadian Hydrographic Service, 1997, St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières)

Times of surface feeding events were used along with Canadian Hydrographic Tide Tables to determine time of closest high tide and divide into 4 categories. High tide (HT) is defined as one hour before the exact local high tide until two hours after local high tide following by after HT (aHT), low tide (LT) and before HT (bHT) in the same intervals of hours. Therefore every tidal phase consist of three hours.

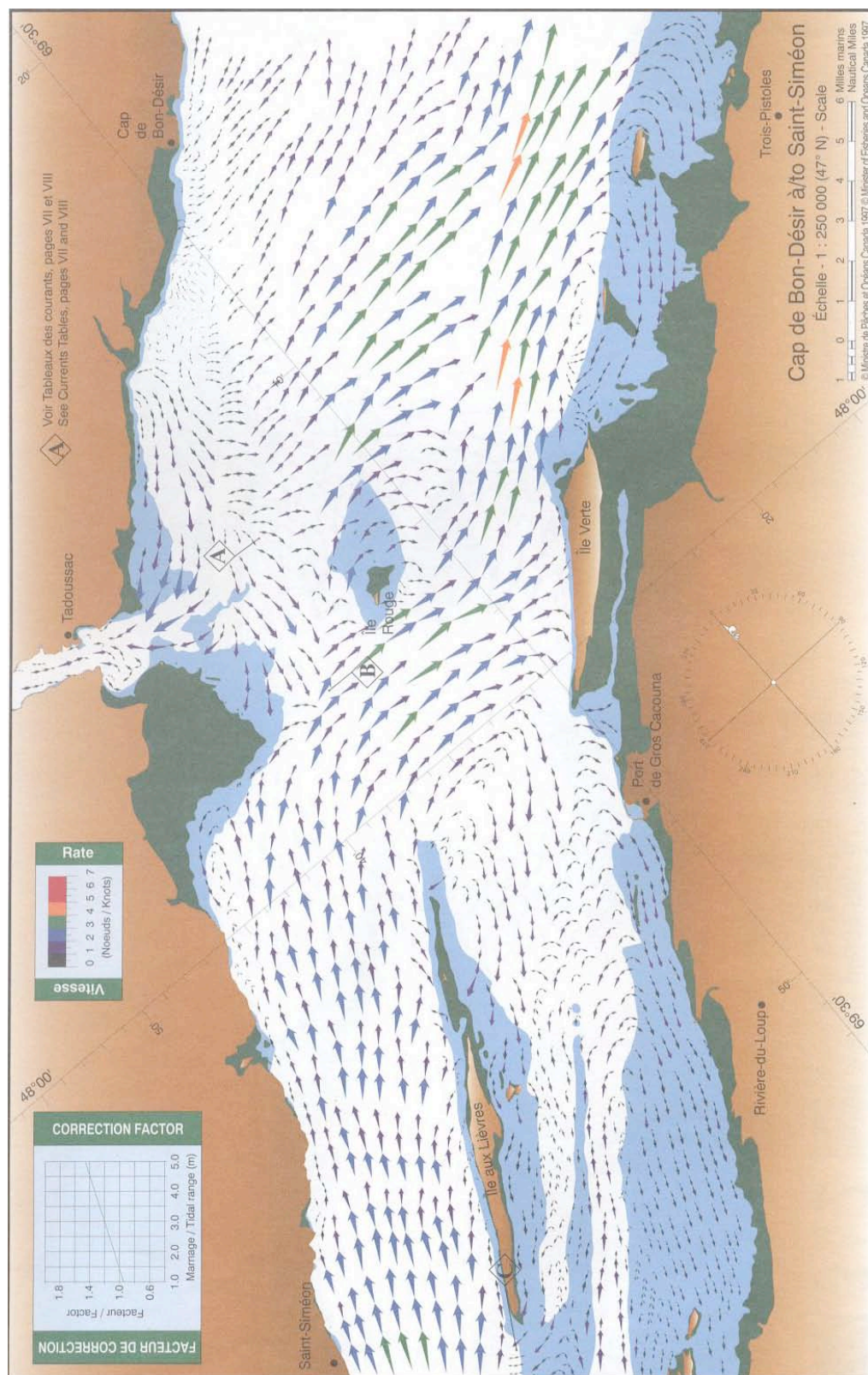


Figure 29. Map of the currents at the first hour before high tide (bHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)

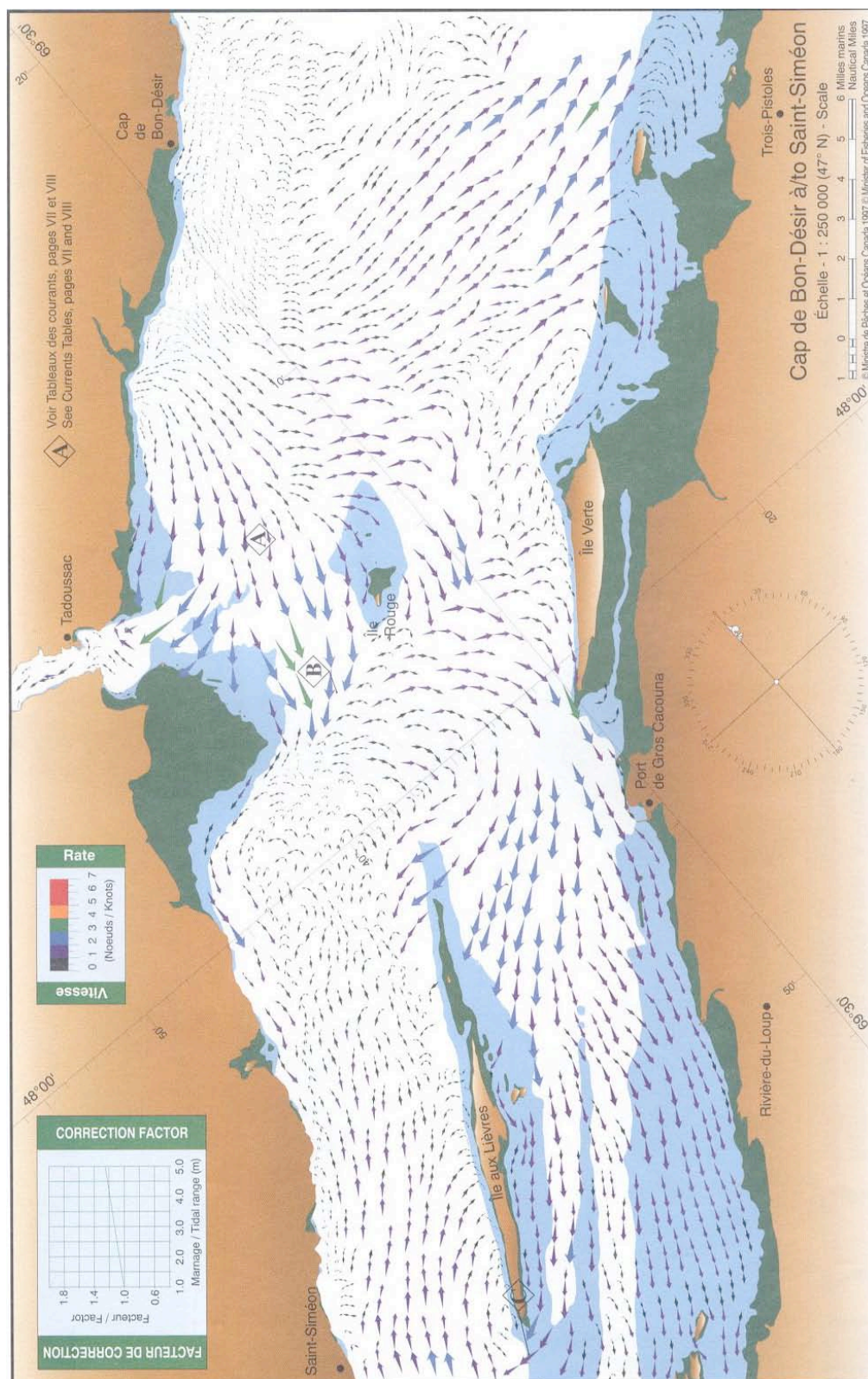


Figure 30. Map of the currents at the second hour before high tide (bHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)

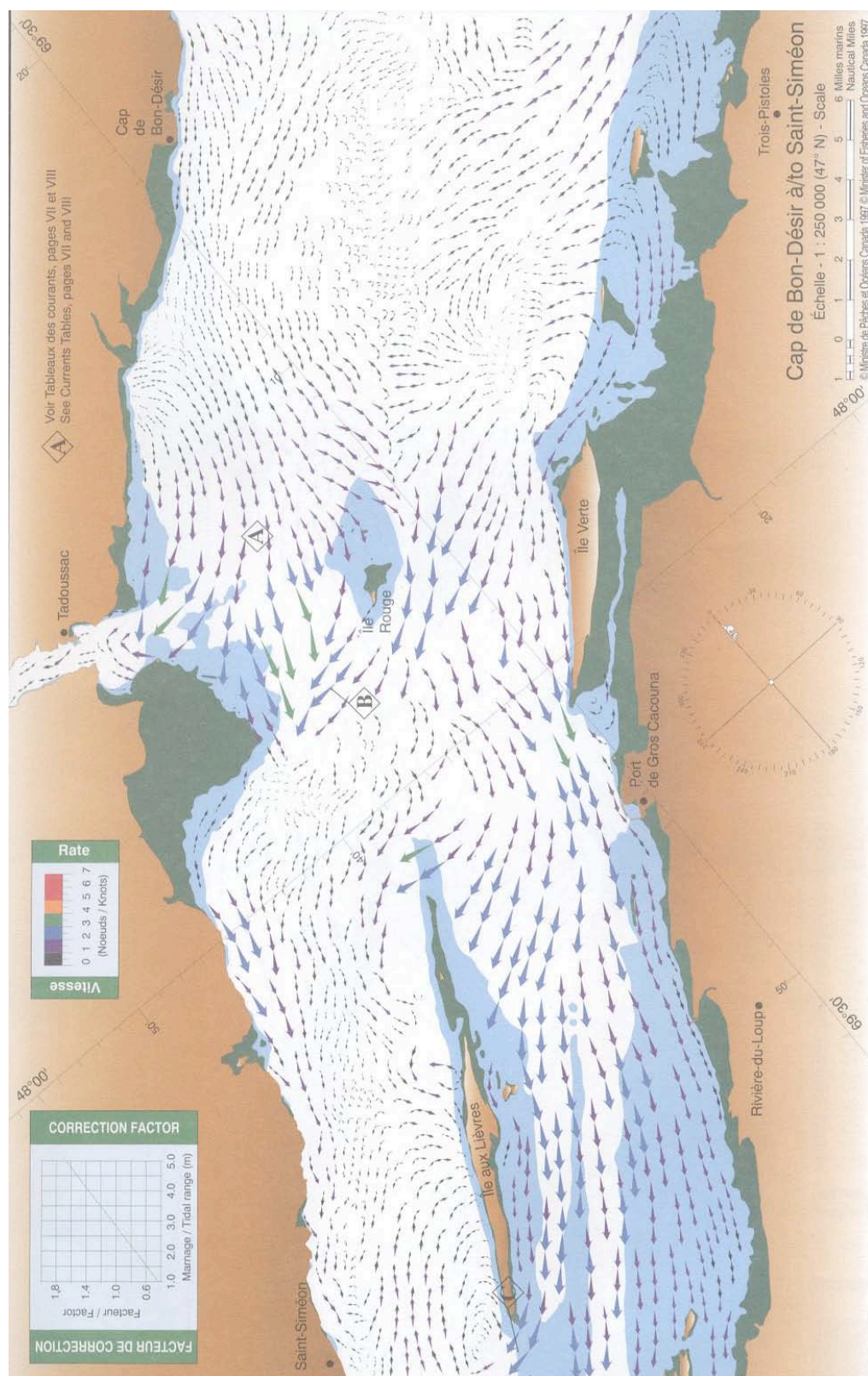


Figure 31. Map of the currents at the third hour before high tide (bHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)

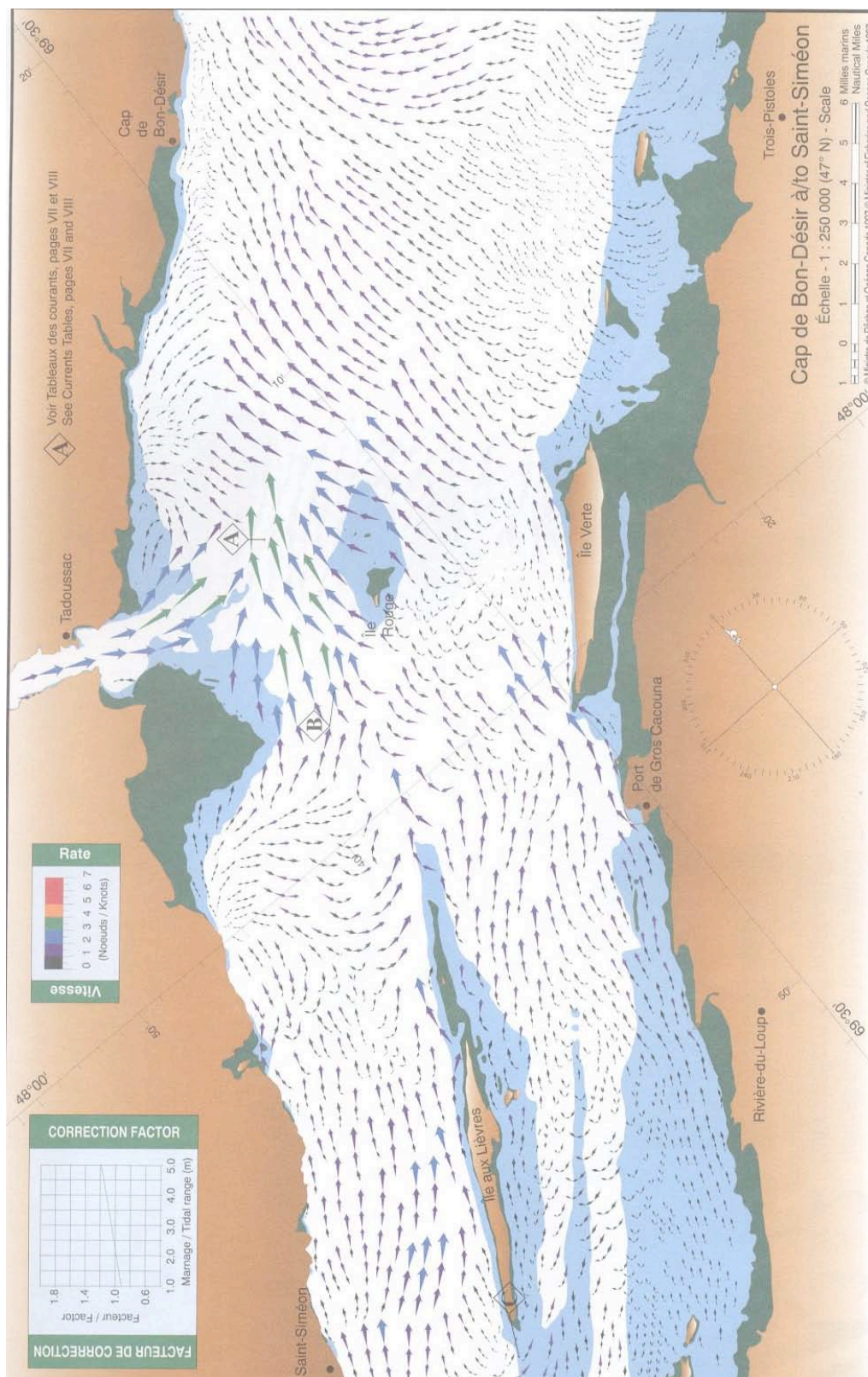


Figure 32. Map of the currents at the first hour after high tide (aHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)

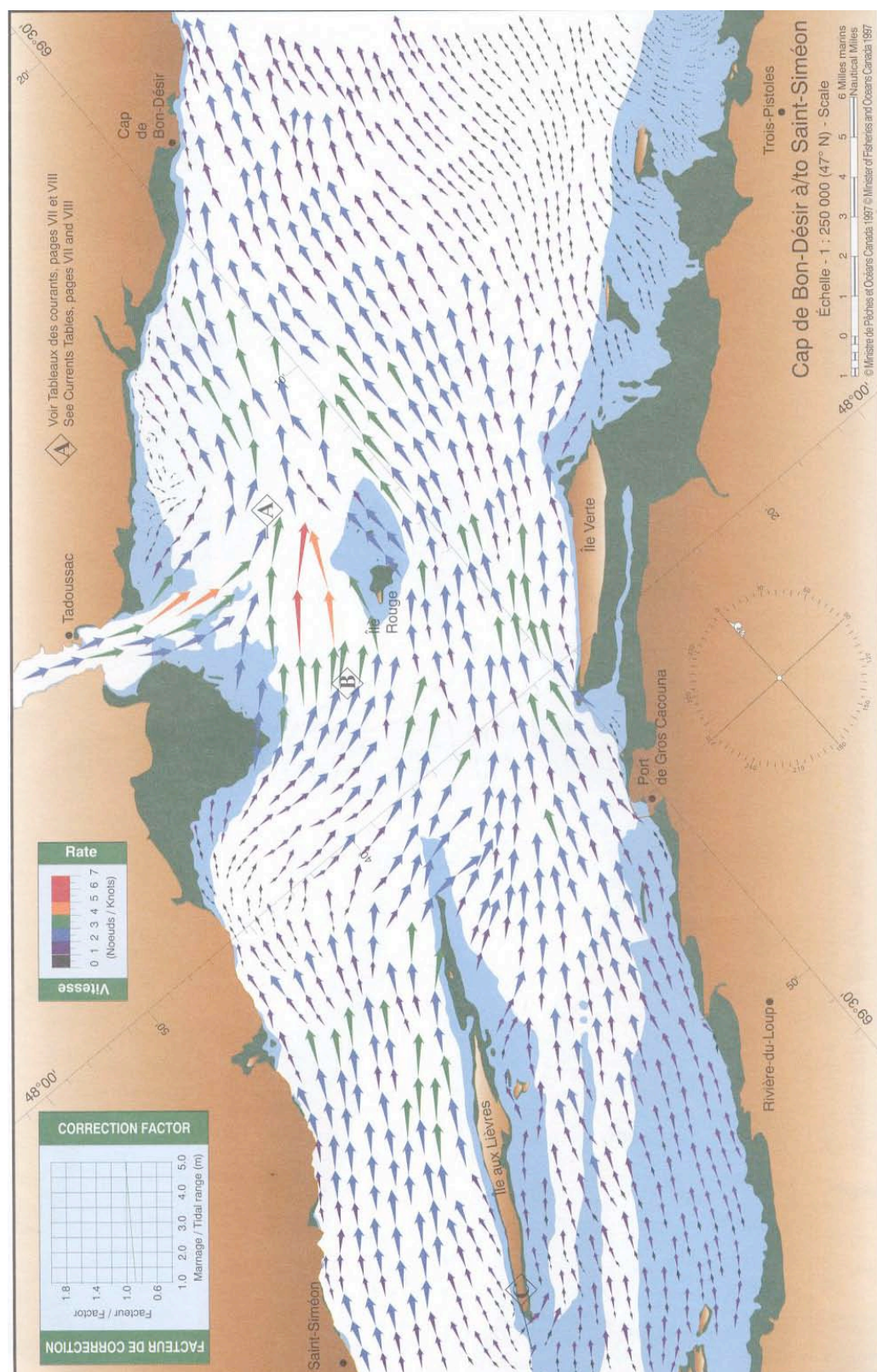


Figure 33. Map of the currents at the second hour after high tide (aHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)

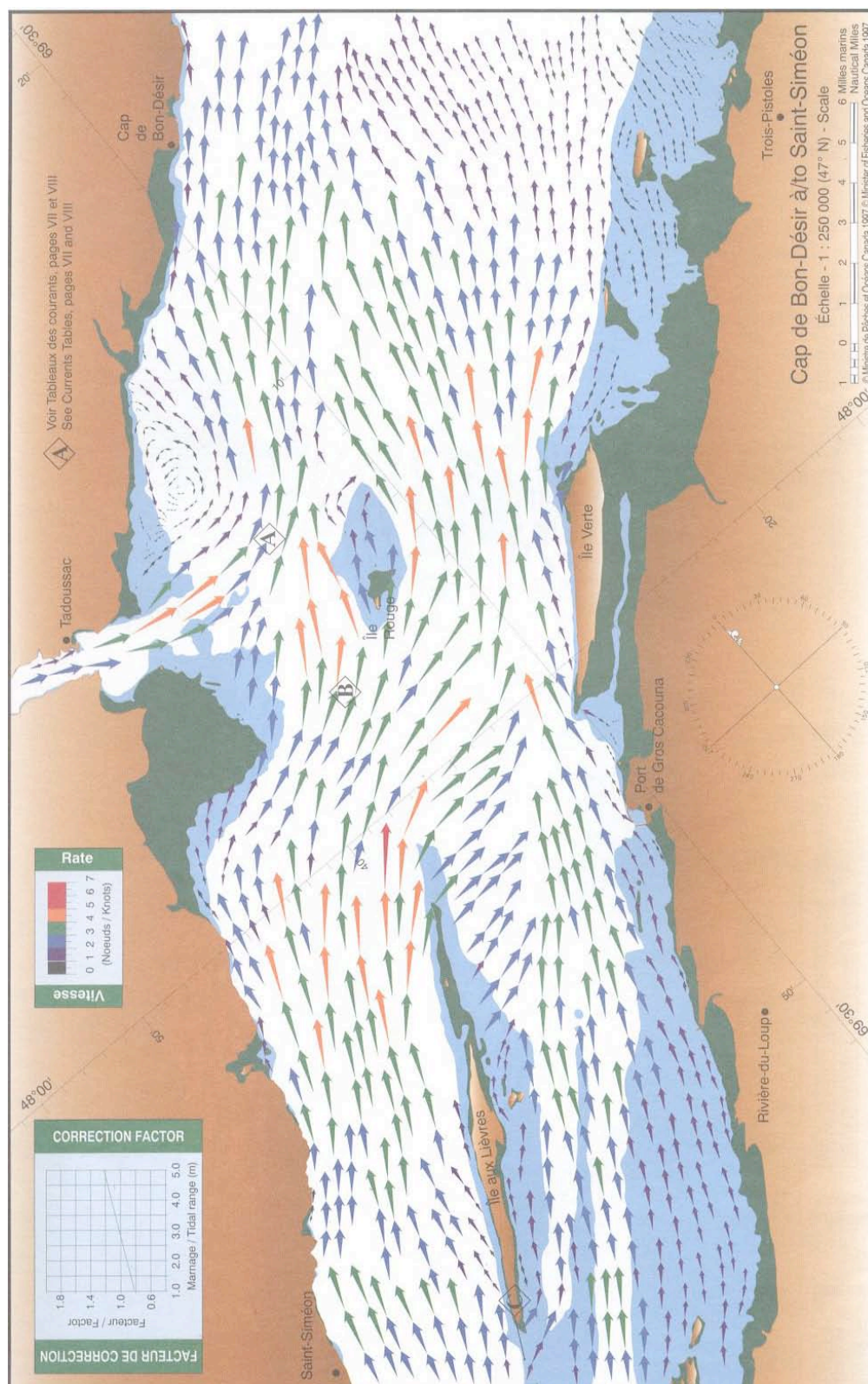


Figure 34. Map of the currents at the third hour after high tide (aHT) in the St. Lawrence Estuary from Cap de Bon-Désir to Trois-Rivières (Atlas of Tidal Currents, 1997)