

**The
Ventilation Characteristics of Different
Behaviours
in
Minke Whales (*Balaenoptera
acutorostrata*)
of the
St. Lawrence Estuary, Québec, Canada**

By

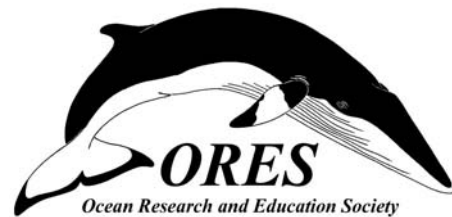
Matthew Curnier

2005

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A thesis submitted in partial fulfilment of the requirements for the degree of
Master of Science in Marine Mammal Science at the University of Wales,
Bangor.

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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STATEMENT 1

This dissertation is being submitted in partial fulfilment of the requirements for the degree of Master of Science in Marine Mammal Science.

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STATEMENT 2

This dissertation is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged in the text by explicit references. A full list of references is appended.

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Foreword

Two brilliant people have focused my natural enthusiasm for biology. At secondary school, I had the privilege of being taught by two of the best biology teachers, namely Mr and Mrs Smale. I have these two people to thank most for their continual support in my early biology career. Their energy in teaching and passion for their subject was my motivation for entering into the field of biology. Mr Smale, who held a zoology degree from Royal Holloway, encouraged me to study zoology with marine zoology at the University of Wales, Bangor. Sadly, Mr Smale died in December 2003. Throughout my studies and thesis I remember him as my inspiration.



Breaching Minke

Ursula Tscherter

*“I must go down to the seas again, for the call of the running tide
Is a wild call and a clear call that may not be denied”*

Sea-Fever

John Masefield

**The Ventilation Characteristics of Different Behaviours in Minke Whales
(*Balaenoptera acutorostrata*) of the St. Lawrence Estuary, Québec, Canada**

Abstract

In order to maximise the time submerged underwater, whales often breath with ventilations clumped together in short series, rather than being regularly spaced. The pattern in which whales come to the surface, respire, and dive again varies with behaviour and activity level. Minke whale (*Balaenoptera acutorostrata*, Lacépède, 1804) blow rates were investigated in the St Lawrence. 25-minute samples were collected from a RIB throughout the summer feeding seasons (June to October) of 1995 to 2005 from presumably undisturbed minke whales performing four different behaviours; 1) near-surface feeding (NS), at depths of 10-50m; 2) deep feeding (DF), at depths >50m; 3) travelling (TRV) and 4) surface feeding (SF). NS and DF samples were ascertained with SONAR. From these samples, various ventilation characteristics were calculated and statistically assessed: mean surfacing interval; dive duration; time between blows in a surfacing; surface duration; and the number of blows per surfacing. All ventilation characteristics were significantly different across the range of behaviours. Breathing patterns therefore serve as good indicators of behaviour. SF ventilation characteristics were investigated by assessing blow rates in relation to engulfment (strike) rates. Two distinct forms of SF were categorised: type 1 SF (where a simultaneous ventilation event occurs with the strike) and type 2 SF (where the feeding manoeuvre disallows a simultaneous ventilation). Type 1 SF had equal proportions of blows to strikes but type 2 SF had a much higher number of blows than feeding strikes. The St. Lawrence Estuary and the Saguenay Fjord had significantly different blow-strike rates; due to type 1 SF occurring solely in the Estuary and only type 2 SF being found in the Fjord. The environmental conditions are likely responsible for the preference of a particular feeding type in a given area. The blow/strike ratios were compared over the 11 years of study. The number of blows per feeding strike increased from 2000, peaking in 2003, suggesting a higher effort requirement for food capture. This likely reflects food shortage in the region.

Caractéristiques Ventilatoires lors de Différents Comportements chez les Petits Rorquals (*Balaenoptera acutorostrata*) de l'Estuaire du St. Laurent

Résumé

Afin de prolonger les périodes d'immersion les baleines ne respirent pas de façon régulière mais avec des phases ventilatoires regroupées et courtes. La fréquence avec laquelle les baleines remontent à la surface pour respirer avant de replonger varie avec leur comportement et l'intensité de leur activité. Une étude des rythmes respiratoires des petits rorquals (*Balaenoptera acutorostrata*, Lacépède, 1804) du St. Laurent sur une période de 11 ans (1995 à 2005) a montré quatre différents comportements chez le petits rorqual. Cette étude qui s'est déroulée pendant les saisons de recherches (de juin à octobre) avec des observations de 25 minutes a permis d'identifier les comportements suivants: 1) alimentation en profondeur basse (NS, profondeur de 10-50 m); 2) alimentation en profondeur (DF, profondeur de >50 m); 3) voyageur (TRV); et 4) alimentation en surface (SF). La distinction entre les comportements de NS et DF s'est faite avec l'aide d'un SONAR. Les variables ventilatoires mesurées et analysées statistiquement sont: l'intervalle moyen entre chaque remontée à la surface, la durée de plongée, la durée entre chaque souffle dans une séquence de surface, la durée d'une séquence de surface et le nombre de souffles dans une séquence de surface. Les données ont montré des différences statistiquement significatives selon les comportements et donc les modèles de respiration peuvent maintenant servir d'indicateurs de comportement. La relation entre les taux de souffles et les taux d'engouffrement de proie permet de distinguer deux types de caractéristiques ventilatoires en SF: SF type 1 (lors d'une respiration simultanée avec l'engouffrement) et SF type 2 (où la manœuvre d'engouffrement ne permet pas une respiration simultanée). Lors de SF type 1 le nombre de souffles est égal au nombre d'engouffrement alors que lors de SF type 2 le taux de souffles est nettement supérieur au taux d'engouffrement. Le ratio souffles – engouffrement diffère de façon marquée entre les observations faites dans l'estuaire du St Laurent et celles prises dans le Fjord Saguenay. L'hypothèse pour ce phénomène est que les différents types de SF sont plus favorisés dans certaines zones que d'autres à cause de facteurs océanographiques spécifiques à ces zones. Le SF type 1 ne fut observé que dans l'estuaire alors que dans le Fjord seul le SF type 2 fut observé. Le ratio de souffles contre engouffrement s'est modifié au cours des 11 ans d'études. Les résultats témoignent d'une augmentation de ce ratio après 2000 et ont atteint un maximum en 2003. Ces résultats suggèrent que les petits rorquals doivent fournir un plus grand effort pour la prise de nourriture sans doute due à la réduction de proies appropriées dans la région.

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1. INTRODUCTION

1. INTRODUCTION

1.1. The Minke Whale

1.1.1. *The Balaenopteridae and the Taxonomic Organisation of the Minke Whale*

The Mysticeti suborder (or baleen whales) are found within the order Cetacea and are classified into four families that currently comprise 13 tentatively recognised species (Table 1.1). Minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) are found within the family Balaenopteridae. (Bannister, 2002). Members of this family (also called rorquals, a corruption of a Danish word meaning 'tubed' or 'pleated' whale) are the most abundant and diverse of the living baleen whales (Berta & Sumich, 1999) and include the blue, fin, sei, Bryde's, minke, Antarctic minke, and humpback whales (Table 1.1) (Reeves et al, 2002). They are characterised by their sleek body form and the presence of numerous ventral pleats (or throat grooves) on the underside of the mouth (Bannister, 2002; Reeves et al, 2002). These ventral pleats may extend from the cranial margin of the lower jaw to the umbilicus. The rorqual whales also have relatively short baleen in comparison to other mysticete families; a dorsal fin positioned far back on the body; very long heads occupying between one-third and one half of the total length of the body; rapid swimming speeds, and a jaw line with virtually no arch (Reynolds et al, 1999; Bannister, 2002). The minke whale, as a group, is the smallest of the rorquals. Of all the baleen whales only the pygmy right whale (*Caperea marginata*) is smaller (Carwardine, 2000).

The shape of the rostrum is particularly typical of the minke whale. It is very narrow and pointed upon which is a single, longitudinal ridge. The species name describes this distinctive feature of minke whales as '*acutorostrata*' translates into 'sharp snout' (Reeves et al, 2002). The dorsal fin is relatively tall and falcate and is located comparatively forward on the posterior one-third of the body to those of other, larger rorquals (Carwardine, 2000; Fontaine, 2005).

Until relatively recently, only one species of minke whale was thought to exist, and were all referred to as the common minke whale or *B.acutorostrata*. In the last half of the 20th century, morphological and genetic evidence of a second species has accumulated and only came to full recognition in the late 1990s as the Antarctic minke whale *Balaenoptera bonaerensis* (Burmeister, 1867; Perrin & Brownell, 2002; Reeves et al, 2003; Zerbini & Castello, 2003).

Species	Common name
Balaenidae (right whales)	
<i>Balaena mysticetus</i>	Bowhead whale
<i>Eubalaena australis</i>	Southern right whale
<i>Eubalaena glacialis</i>	Northern right whale
Neobalaenidae	
<i>Caperea marginata</i>	Pygmy right whale
Balaenoptera (rorquals)	
<i>Balaenoptera bonaerensis</i>	Antarctic minke whale
<i>Balaenoptera acutorostrata</i>	Common minke whale
<i>B.a.acutorostrata</i>	North Atlantic minke whale
<i>B.a.scammoni</i>	North Pacific minke whale
<i>B.a</i> subspecies	Southern Hemisphere dwarf minke whale
<i>Balaenoptera borealis</i>	Sei whale
<i>Balaenoptera edeni</i>	Bryde's whale
<i>Balaenoptera musculus</i>	Blue whale
<i>Balaenoptera physalus</i>	Fin whale
<i>Megaptera novaeangliae</i>	Humpback whale
Eschrichtiidae	
<i>Eschrichtius robustus</i>	Gray whale

Table 1.1. Species and common name of members of the suborder Mysticeti, the baleen whales. Note that more than one common name may be used and recognised for particular species.

Asides these two clearly defined species of minke, the present convention is to recognise a further two or possibly three subspecies of the common minke whale; the North Atlantic minke whale (*B.a.acutorostrata*), the North Pacific minke whale (*B.a.scammoni* but formerly *B.a.davidsoni*), and the unnamed Southern Hemisphere dwarf minke whale (Perrin & Brownell, 2002; Reeves et al, 2003). Genetically, the dwarf minke whale is more closely related to the North Atlantic than to the North Pacific form (Perrin & Brownell, 2002). The taxonomy of the minke whale is unclear (Reeves et al, 2002) and many authors still withhold judgement about the best taxonomic arrangement until further studies have clarified the situation.

This research in this study was performed on the North Atlantic minke whale subspecies *Balaenoptera acutorostrata acutorostrata*.

1.1.2. Morphological Characteristics and Variations in Minke Whales

The Antarctic and common minke whale differ significantly in many external and skeletal features. Genetic analyses have demonstrated that these two species have been separated for several thousand years. Indeed, there is a greater degree of relatedness between the sei and Bryde's whales than there is between the two species of minke whale (Reeves et al, 2002).

The average length of the common minke whale in the North Atlantic at physical maturity has been estimated at about 8.5 - 8.8 m in females and 7.8 - 8.2 m in males (Armstrong & Siegfried, 1991) although a maximum measurement has been recorded at 12 m (Fontaine, 2005). An estimate for the North Pacific is 8.5 m in females and 7.9 m in males, whilst in Antarctic minke whales; females are thought to reach an average of 9.0 m at maturity and 8.5 m in males (Carwardine, 2000). The maximum length recorded for an Antarctic minke whale is 10.7 m (Reeves et al, 2002). The dwarf minke whale is on average about 2 m shorter than its Antarctic counterpart, reaching a maximum length of 7.8 m (Perrin & Brownell, 2002).

Minke whale baleen is small compared with that of other rorquals, reaching a maximum length of 20-30 cm and a width of 12 cm (Carwardine, 2000). There are apparent distinctions in baleen between species and subspecies. The colour of the baleen can differ geographically. The baleen of North Atlantic minkes has been described as creamy white, whilst North Pacific minkes have creamy yellow colour. In the dwarf subspecies, the baleen appears dark-grey or brown due to the development of a posteriorly positioned dark, narrow fringe. In the Antarctic minke whale, the baleen plates are black on the left beyond the first few plates and on the right they are white in the first third and black in the rear two-thirds of the row (Perrin & Brownell, 2002; Reeves et al, 2002)). The number of baleen plates also varies. The common minke whale usually has 230 to 360 baleen plates on each side of the mouth, although the Atlantic subspecies usually growing more than their Pacific relatives (Carwardine, 2000). The dwarf and the Antarctic minke whales generally have fewer baleen plates, between 200 to 300 plates (Reeves et al, 2002). Further differences in colouration can exemplify the distinctions between the various kinds of minke, such as the white band on the pectoral fin that is diagnostic of the species. It can be readily found in all Northern Hemisphere minkes. It is also retained in the dwarf subspecies but it is not so distinctive in *B. bonaerensis* (Figure 1.1) (Perrin & Brownell, 2002).

Even the number of ventral pleats differs according to the particular species/subspecies. The common minke whale has 50 to 70 ventral pleats that terminate just behind the pectoral fins (Carwardine, 2000, Fontaine, 2005). Conversely, the Antarctic minke whale has far fewer ventral pleats, between 22 and 38, which extends nearly as far back as the umbilicus (Reeves et al, 2002).

One of the skeletal characteristics showing differences between minke whales is the size, shape and particular cranial features of the skull. The skull itself is larger in *B.bonaerensis* than any of the *B.acutorostrata* (Perrin & Brownell, 2002).

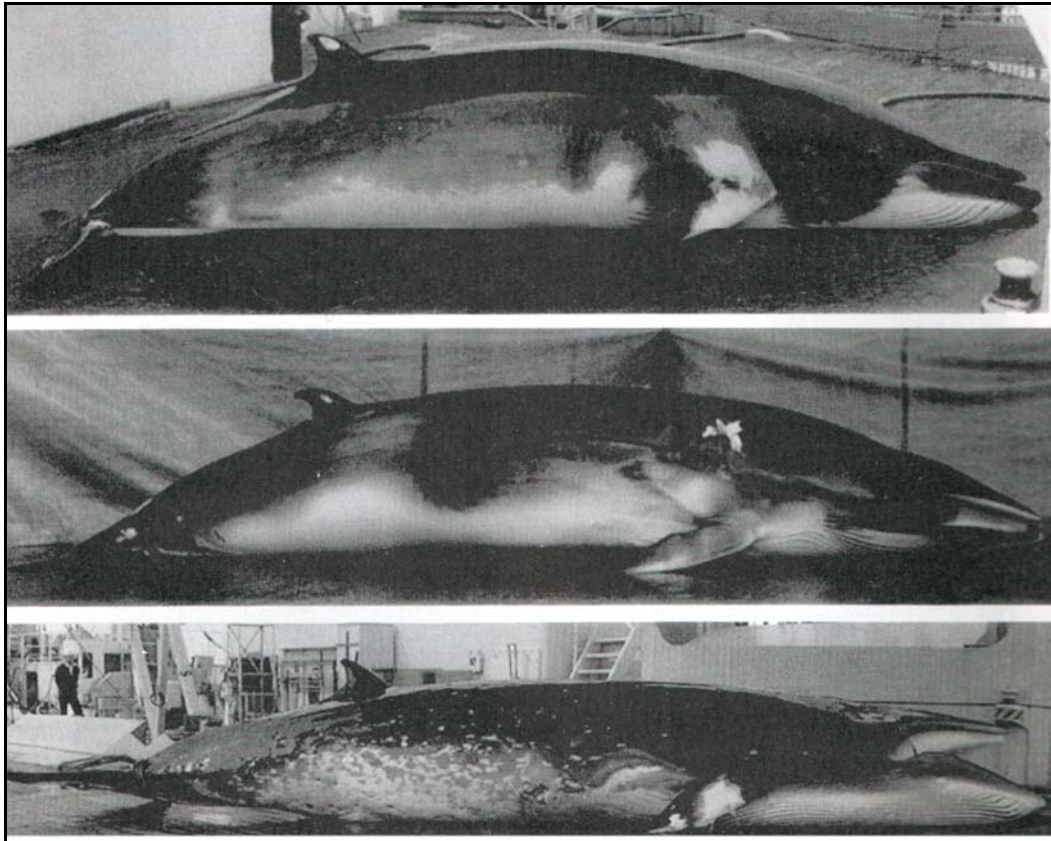


Figure 1.1. Differences between the minke whale species and subspecies. (Top) Dwarf minke whale (*Balaenoptera acutorostrata* subspecies); (Middle) Antarctic minke whale (*B.bonaerensis*), (Bottom) North Pacific minke whale (*B.a.scammoni*). Taken from Perrin & Brownell (2002)

1.1.3. Distribution, Range and Abundance

Minke whales are among the most widely distributed of all the baleen whales (Pierce et al, 2004). Generally, they inhabit warmer waters during winter and travel north to colder regions in the summer (Haug et al, 1995; Heithaus & Dill, 2002).

1.1.3.1. Common Minke Whale *B. acutorostrata*

In the North Atlantic, the common minke whale is found as far North as Baffin Bay in the Canadian Arctic, Denmark Strait, and Svalbard in the Barents Sea during the summer period (Figure 1.2) (Perrin & Brownell, 2002; Macleod et al, 2004). The wintering grounds are poorly known but extend at least to the Caribbean in the west of the Atlantic and the Straits of Gibraltar in the east, although anecdotal accounts have reported affinities of minke whales as far south as the Senegalese coast (Perrin & Brownell, 2002). There are thought to be 120,000 minke whales in the northeastern North Atlantic (Haug et al, 1995; Macleod et al, 2004), together with an estimated 60,000 minke whales in central North Atlantic. No overall estimate of minke whale abundance is available for the western North Atlantic, but there are thought to be at least several thousand minke whales present along the east coast of North America (Reeves et al, 2003) and photo-identification studies are being conducted to resolve this unknown (Tscherter, unpub.). In the North Pacific, the summer range extends to the Chukchi Sea, whilst in the winter the minke whales are found south to within 2° of the equator (Perrin & Brownell, 2002; Rudolph & Smeenk, 2002). In the North Pacific, two minke whale stocks are identified; one in the Sea of Japan and the other in the Sea of Okhotsk. There may be a population of 36,000 in these areas (Buckland et al, 1992).

1.1.3.2. Dwarf Minke Whale *B. acutorostrata* subspecies

The dwarf form is only found in the Southern Hemisphere, in primarily middle to lower latitudes and is best known from wintering areas off eastern Australia (extending its range as far north as 11°S), New Caledonia, southern Africa, and Brazil (7°S). It is found in the Atlantic Ocean all year round, moving to higher latitudes (at least 65°S) in the summer (Reeves et al, 2003). In the far south, the dwarf minke is seasonally sympatric with the Antarctic minke whale on the feeding grounds of the austral summer (Figure 1.2). Where there is sympatry with the Antarctic cousins, the dwarf minke will tend to occur in more coastal waters over the continental shelf (Perrin & Brownell, 2002).

1.1.3.3. Antarctic Minke Whale *B. bonaerensis*

Antarctic minke whales appear to have a circumpolar distribution in the Southern Hemisphere (Rudolph & Smeenk, 2002). They are found from 55°S to the ice edge during the austral summer and some have even been recorded to over-winter in the Antarctic. During the austral winter most retreat to breeding grounds at mid-latitudes 10-30°S off northeastern Australia, southern Africa and off the northeast Brazilian coast (Figure 1.2). In these areas, they occupy a more oceanic habitat than the dwarf minkes (Perrin & Brownell,

2002). The Antarctic minke whale may be the most abundant baleen whale species today, with a total population of several hundred thousand and very high densities during the summer feeding season. (Reeves et al, 2002; 2003).

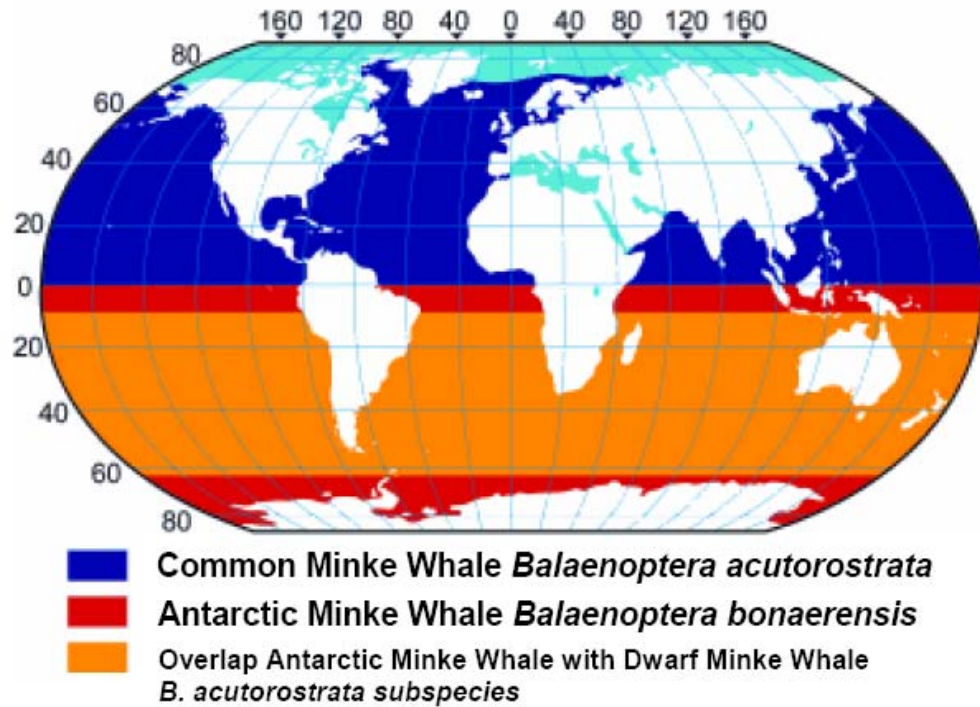


Figure 1.2. Map of the distribution of the three minke whale species/subspecies. These include the common minke whale *Balaenoptera acutorostrata*, the Antarctic minke whale *Balaenoptera bonaerensis* and the dwarf minke whale (unnamed *B. acutorostrata* subspecies). (ACS online 2004)

1.2. Ventilation; Rates and Differences

Apart from infrequent aerial displays such as surface feeding (see below) or breaching, the ventilatory behaviour of whales is certainly their most obvious activity. Whales are tied to the surface by the necessity to breathe: and thus all activities are consequently subjugated to ventilatory patterning in a manner more profound than for any terrestrial mammal (Dolphin, 1987). Although whales require oxygen as a resource from the surface, they often require to be submerged in order to feed, travel, communicate efficiently, socialise, mate, avoid predators and for many other reasons besides (Würsig et al, 1984; Dorsey et al, 1989). Therefore, and so as to allow greater periods underwater, the respirations of a whale are almost always clumped together in short series rather than regularly spaced. The pattern in which whales come to the surface, respire, and dive again varies with behaviour and activity level. These patterns are useful in characterising and discerning different behaviours and may be observable whilst those underwater are not (Dorsey et al, 1989).

Upon exhalation, the flow of air escaping from the lungs causes the drops of water that surround the blowhole to be blown upwards. A particularly large amount of water may be spouted in baleen whales, whose blowholes are located in rather deep folds. The water that is sprayed constitutes the blow that is typical for large whales (Berta & Sumich, 1999). Depending on the species, therefore, the blow can be highly visible. This feature allows the ventilatory behaviours of cetaceans to be easily recorded, measured and analysed. Nonetheless, surprisingly few studies have assessed ventilatory patterning according to their respective behaviours and activities in mysticete whales. The range of surfacing and respiration patterns in bowhead whales, *Balaena mysticetus*, has been examined with respect to their behaviour in the Beaufort Sea (Würsig et al, 1984; Dorsey et al, 1989). The ventilation characteristics of gray whales, *Eschrichtius robustus*, have also been examined in some detail, such as during migrations (Sumich, 1983). Other ventilation studies have been performed on right whales, *Eubalaena glacialis*. Within the Balaenopteridae, Dolphin (1987a; 1987b) assessed the ventilatory patterning of foraging humpback whales, *Megaptera novaeangliae*, in Alaska. Lagerquist et al (2000) performed a study on the diving characteristics of blue whales, *Balaenoptera musculus*. Jahoda et al (2003) measured and compared the ventilation rates in fin whales between two distinct behavioural states: wide range behaviours, such as travelling, and narrow range behaviours, such as feeding. Kopelman & Sadove (1995), however, were slightly more specific and targeted two particular behaviours by measuring the ventilatory rate differences between surface feeding and non-surface feeding fin whales. Lafortuna et al (2003) compared in detail the differences in ventilation characteristics between travelling and feeding whales and found that a general mechanism of control of breathing in cetaceans. The study suggested a constancy in tidal volume and ventilatory amplitude, whilst the respiratory frequency was highly variable. Investigations concerning the blow rate of minke whales were carried out predominantly in the late 1980s-early 1990s and focused primarily on overall blow rates,

usually given in number of blows per whale per hour or as mean surfacing intervals. Lynas & Sylvestre (1988) did superficially examine the ventilation rates in surface feeding minke whales. To the author's knowledge no other detailed analysis have assessed the differences of ventilation characteristics over a range of behaviour types.

However, it is not only behaviour that affects the ventilation rates of cetaceans. Leatherwood et al, (1982), after reviewing published comments and responses to questionnaires about ventilatory patterns of whales, summarised quite succinctly that diving and breathing patterns appeared to vary significantly with several different factors including 'time of day, season, geographical area, environmental conditions, number of individuals present, dominant behaviour of the group, age composition of the group, presence of the survey platform, and perhaps other factors...'

Minke whale surfacing rates and patterns have served as an integral part of research on this species (Joyce et al, 1990). The observations have a variety of applications. Respiration rates can help estimate the probability of observing a whale on the track line when conducting line transect surveys (i.e. $g(0)$) (Stern, 1992) and to estimate the associated probability of detecting an animal anywhere within the area of observation ($g(y)$). The reliability of whale population estimates made from "cue-counting" census surveys depends upon accurate and well-documented studies of ventilatory patterns to provide correction factors so as to readjust results for unobserved submerged animals (Leatherwood et al, 1982; Kopelman & Sadove, 1995). Moreover, since minke whales breath only once per surfacing, ventilatory information can be used to estimate metabolic rates of free-swimming whales by indirectly calculating the rates of oxygen consumption (Folkow & Blix, 1993). Finally, data on surfacing rates, ventilation patterns and diving behaviour are also important in assessing the reactions of whales to industrial disturbance such as shipping, oil exploration (Dorsey et al, 1989), as well as other potential sources of disturbance such as the invasive presence of vessels derived from the whale-watching industry.

1.3. Food, Feeding Techniques and Foraging Strategies

1.3.1. Food of the Minke Whale

All rorquals feed on euphausiids to some extent. Whilst some members of this family feed almost exclusively on krill, the minke whale has a much more diverse diet and has been described as the most ichthyophagous species within the Balaenopteridea (Macleod et al, 2004). Northern Hemisphere minke whales usually a more fish-based diet than *B. bonaerensis*. In the Antarctic, the minke whales' diet consists almost entirely of krill (*Euphausia superba*) (Bushuev, 1986; Armstrong & Siegfried, 1991). It is estimated that minke whales have a consumption rate of 212 kg d⁻¹ and 252 kg d⁻¹, for males and females, respectively translating to a total annual consumption of 35.5 x 10⁶ tonnes of krill (Armstrong & Siegfried, 1991). In the North Atlantic, they are known to take a huge range of pelagic shoaling and demersal fish species, in particular sand eel *Ammodytes* sp., herring *Clupea harengus*, mackerel *Scomber scombrus*, capelin *Mallotus villosus*, cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, sprat *Sprattus sprattus*, Norway pout *Trisopterus esmarkii* and saithe *Pollachius virens* (Markussen et al, 1992; Haug et al, 1995; Nøttestad et al, 2002; Macleod et al, 2004; Pierce et al 2004). Further, minke whales have been shown to switch and feed successfully from one prey type to another without compromising their body condition when one prey species is in insufficient supply (Linstrøm et al, 2002). Food consumption in the northeast Atlantic has been measured at 204 kg d⁻¹ and 277 kg d⁻¹, for males and females, respectively, which equates to a total annual consumption of 2.2 x 10⁶ tonnes of fish (Markussen et al 1992). Although Atlantic minkes are capable of taking a wide range of food types, capelin constitutes the main prey species of minke whales in the St. Lawrence (Figure 1.3).

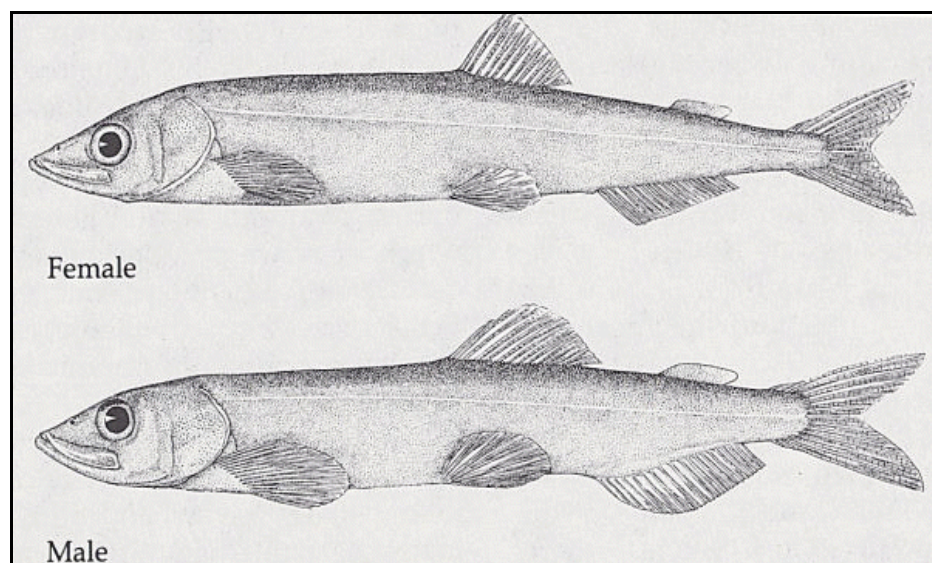


Figure 1.3. Capelin (*Mallotus villosus*); main prey species of the minke whale (*Balaenoptera acutorostrata*) in the St. Lawrence area. (McGill online, 2006).

1.3.2. Prey Capture in Minke Whales

Batch feeding is a tactic employed by baleen whales to consume a large number of prey items in a single feeding event. Mysticetes have evolved to be obligate batch feeders (Heithaus & Dill, 2002) and have developed three different strategies for efficiently feeding on large quantities of small prey items: sediment straining, as seen in the gray whales; skimming, displayed by the right and bowhead whales and lunging or gulping performed by rorquals (Croll & Tershy, 2002). These strategies are reflected in the morphology of the baleen, mouth, tongue and method by which the mouth is expanded (Berta & Sumich, 1999). The first method requires a short head with short, straight, coarse baleen in addition to only 3-5 ventral grooves. The second form of filter feeding necessitates long, fine-textured baleen arranged in a strongly arched rostrum. Skimming prey from the surface requires no throat distension and consequently ventral grooves are absent. Last, rorquals, that use the lunging or gulping feeding technique, have developed a suite of adaptations to do so. For example, the minke whale is a fast and streamlined swimmer with relatively short and coarse baleen (Hoelzel et al, 1989; Wells et al, 1999). The mouth of the minke whale is enormous and can extend posteriorly nearly half the total length of the body. Further, the lower jaw opens to almost 90° of the body axis (Figure 1.4). The minke whale is able to do this because of the well-developed coronoid process of the lower jaw, which serves principally as the insertion point of the temporalis muscle. A tendinous part of the temporalis, the frontomandibular stay, enhances and strengthens the mechanical linkage between the skull and the lower jaw and serves to optimise the gape during engulfment feeding (Berta & Sumich, 1999).

Water and prey enter the mouth by negative pressure produced by the backward and downward movement of the tongue and by the forward swimming motion of the whale. In this manner large volumes of water and fish (up to 70% of the animal's body weight) are engulfed. The muscular tongue, in concert with contraction of the ventral wall muscles of the mouth (and often accompanied by vertical surfacing behaviour in the minke) forces water out through the baleen and subsequently assists in swallowing the trapped prey (Figure 1.4). During feeding the tongue is capable of invaginating to form a hollow sac thereby increasing the potential volume of the buccal cavity (Berta & Sumich, 1999; Croll & Tershy, 2002).

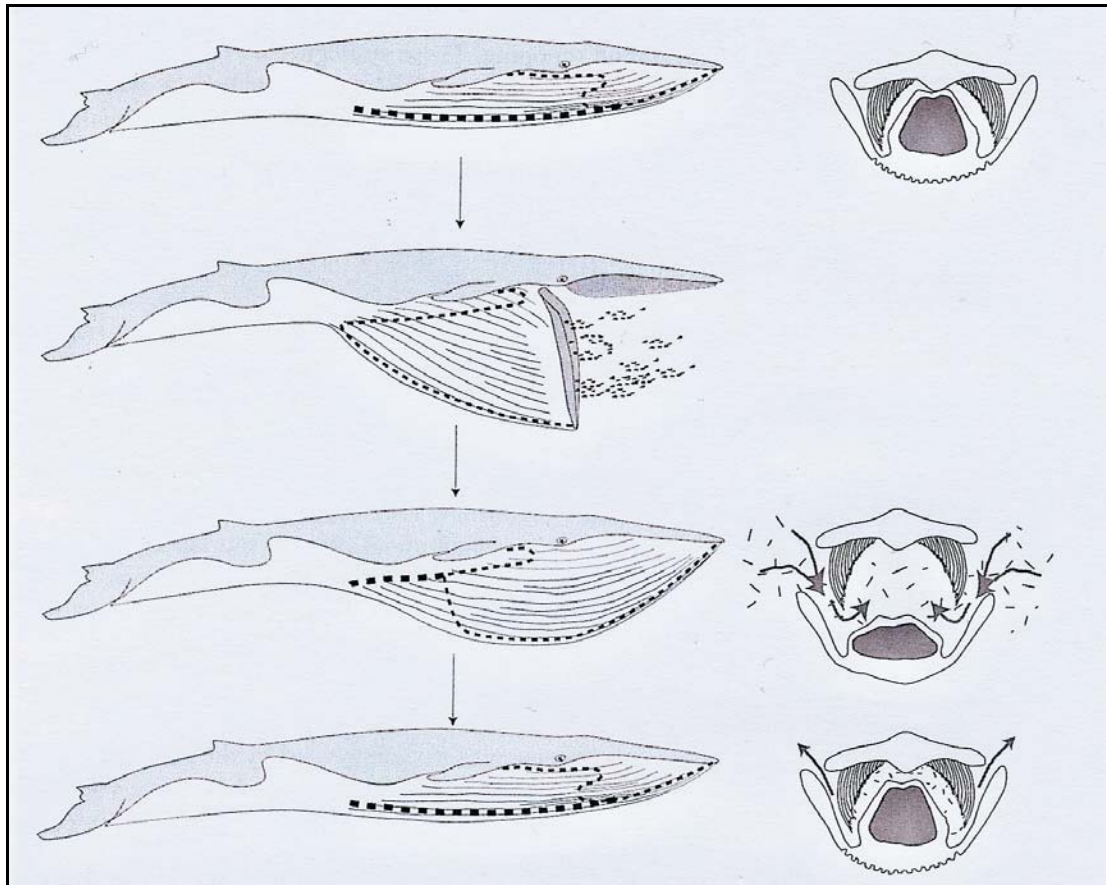


Figure 1.4. Lateral and cross sectional views of engulfment feeding of a baleen whale, illustrating the action of the tongue within the baleen basket. Taken from Berta & Sumich (1999).

1.3.3. Feeding Techniques of Minke Whales

The area of the St Lawrence serves as a summer feeding ground for the minke whale. As the most abundant of the three rorqual species that frequent this region (Edds & MacFarlane, 1987), these whales arrive as early as the first week in May each year, and leave again beyond the end of October (Lynas & Sylvestre, 1988). They spend approximately 61% of time during daylight hours feeding, and a further 36% in activities directly related to that end (Lynas, 1986). Despite this, the subject of feeding techniques has received only incidental treatment in the literature. The scarcity of references may be due to the difficulty in amassing direct evidence of feeding taking place, particularly as studies concerning feeding are time consuming, the point of observation is critical and proximity to the animal is paramount. A further difficulty is that the surface manoeuvres performed by minkes are both extremely rapid and subtle (Lynas & Sylvestre, 1988). However, Lynas & Sylvestre (1988) recorded in detail the feeding techniques and strategies of the minke whales:

The feeding patterns displayed by the minkes in the St Lawrence can be readily divided into two types: 1) Entrapment manoeuvres in which component behaviours serve to intercept, contain, or compress the prey, which comprise of sub-surface and near-surface

movements, and 2) engulfing manoeuvres, in which the prey is consumed or swallowed. These manoeuvres occur at the surface. A third category comprising near-surface movement with elements of surface movements also exists although its function is unclear. These movements are used on occasion for entrapment and engulfing and are thus termed entrapment/engulfing manoeuvres.

1.3.3.1. Entrapment Manoeuvres

Entrapment manoeuvres comprise circles, gyres, ellipses, figure-of-eights, hyperbolas and head slaps and underwater blows.

1.3.3.1.1. Circling

When circling the whale swims with its dorso-ventral axis at 90° to the horizontal and with its ventral surface towards the prey. The circles made by the animal may range from 1.5 to 2.5 times its own length in diameter. There are particular surface signatures indicating the behaviour of the animal under water. For example, the whale's fluke movements are visible at the surface as it mounts the water column. Further, the surfacing style of the minke whale may also be a demonstrative sign of this circling entrapment behaviour. The minke whale may surface in a 'chin-up blow' format, either laterally (becoming a 'lateral chin-up blow') or in a normal dorso-ventral plane (Thomson et al, 2003; pers. observ.) (Figure 1.5). At the culmination of this entrapment sequence, the whale performs an engulfing manoeuvre across the centre of the circle. It appears that the minke whale uses the pale-coloured ventral surface, powerful fluke beats, and the air-water interface as aids of entrapment.

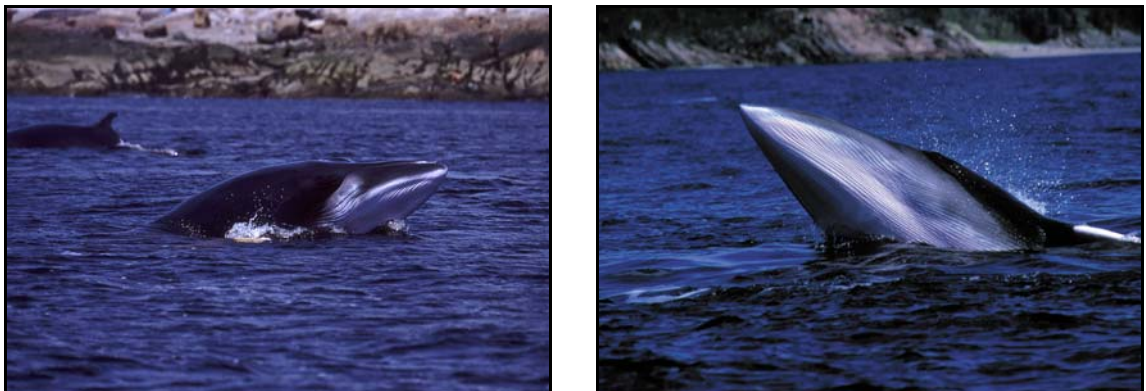


Figure 1.5. Entrapment manoeuvres of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). (Left) Chin-up blow. (Right) Lateral chin-up blow. Photos: ORES®.

1.3.3.1.2. Gyres

Gyres are similar with the exception that the whale creates a circle of much greater diameter although reduces this diameter with each circuit. This strategy may reflect prey that is initially quite widely distributed or there is a greater mass from which a segment has been cut.

1.3.3.1.3. Ellipses

Ellipses cover a much larger area, with decidedly long and short axes. The long axes can be in excess of 100 m. Surface traces are seldom apparent, and the main expressions of ellipses are the whale's pattern of surfacing and turns as it moves over the bottom while rotating about some locus. Ellipses are often sustained for lengthy periods of time and frequently include feeding circles within them, and generally include numerous engulfing manoeuvres.

1.3.3.1.4. Figure-of-Eights

Figure-of-eights are variants on ellipses and have a long axis of not more than six body lengths. The significant feature of figure-of-eights is that the minke whale will first turn in one direction, followed by the opposite direction, at either end of the long axis.

1.3.3.1.5. Hyperbolas

Hyperbolas involve at least one turn or semi-circuit at the conclusion of a short straight-line run, often associated with searching. Minke whales can be seen to deploy these hyperbolas parallel to rock faces, followed by an inward oriented engulfing manoeuvre. This type of entrapment manoeuvre is particularly common in the Saguenay Fjord, which is bordered by steep-sided rock faces.

1.3.3.1.6. Head Slaps and Underwater Blows

Similar to an oblique lunge (see below), the whale lunges at an angle of 30° to 45°, yet the throat is not expanded and there is no water purging out. At the highest point, the whale angles its head backwards and slaps it onto the surface of the water resulting in a huge splash accompanied by a loud sound (Thomson et al, 2003) (Figure 1.5). Often, after a regular surfacing, the minke whale will exhale strongly immediately after the blow holes have re-entered throwing a fountain of water into the air, coupled with a roaring sound (Thomson et al, 2003) (Figure 1.6). These entrapment behaviours are thought to cause the fish to corral closer together.



Figure 1.6. Entrapment manoeuvres of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). (Left) Head slap – the head is raised before forcefully slapping the chin down onto the surface of the water. (Right) Underwater blow – a strong exhalation soon after resubmerging. Photos: ORES®.

1.3.3.2. Engulfing Manoeuvres

Engulfing manoeuvres involve plunges and oblique, lateral, vertical and ventral lunges (Thomson et al, 2003). Lateral, vertical and ventral lunges have also been described for humpback whales (Wells et al, 1999). Fin whales have also been reported to perform oblique lunge strikes (Whitehead & Carlson, 1988).

1.3.3.2.1. Plunges

Plunges are performed in the dorso-ventral plane, with the body axis of the whale approaching the surface generally at an angle of not more than 30° . Rarely is more than the rostrum and part of the underlip visible as the minke exits the water but often the tops of the ventral grooves are seen in their distended form (Figure 1.7). Plunge feeding is the subtlest form of engulfing manoeuvre and is best observed from profile or from the front. This manoeuvre permits ventilation.



Figure 1.7. Engulfment manoeuvre of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). Plunge – a strike in the dorso-ventral plane with an emergence angle $<30^\circ$ Photos: ORES®.

1.3.3.2.2. Lunges

The lunges, unlike the plunge, are quite acrobatic and aerial displays of feeding. An oblique lunge is very similar in character to the plunge, but is performed at a steeper angle of approximately 45° and totally exposes the ventral grooves (Figure 1.8). Sometimes the whole body emerges in a flat porpoising-type leap. A more extreme version of the oblique lunge is the vertical lunge. The whale emerges at 90° to the plane of the water (Figure 1.8).

The minke usually reverses or sinks back into the water. Re-entry may aid in the purging action. These engulfment manoeuvres allow a ventilation.



Figure 1.8. Engulfment manoeuvre of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). (Left) Oblique lunge – a strike in the dorso-ventral plane with an emergence angle of approximately 45° . (Right) Vertical lunge – a strike in the dorso-ventral plane with an emergence angle of approximately 90° Photos: ORES[®].

Ventral and lateral lunges are similar in structure to the oblique lunge and share the same water-exiting angle of 45° . However, during a ventral lunge the minke will be in ventro-dorsal plane (i.e. with its dorsal surface closest the water), whilst in a lateral lunge the whale emerges and generally re-submerges laterally (i.e. with one flank closest the water) (Figure 1.9). No ventilation occurs during these strikes.

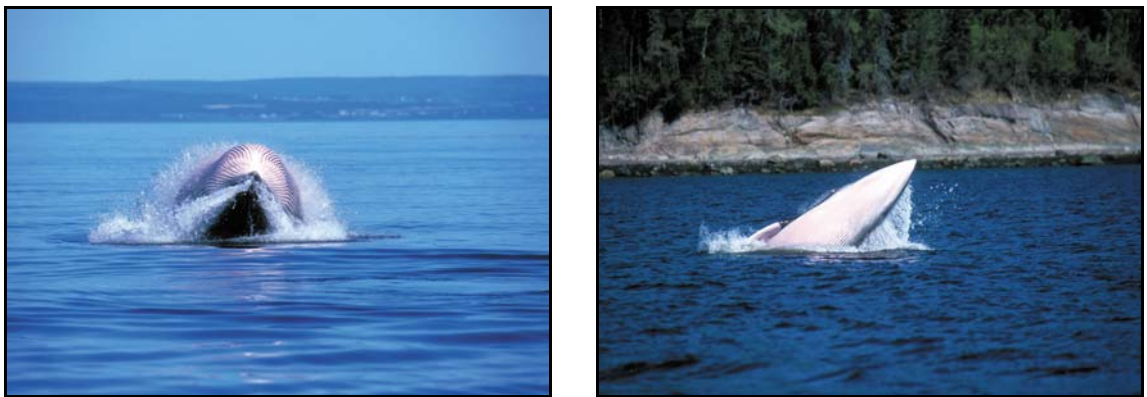


Figure 1.9. Engulfment manoeuvre of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). (Left) Ventral lunge – a strike in the ventro-dorsal plane with an emergence angle of approximately 45° . (Right) Lateral lunge – a strike in the dorso-ventral plane with an emergence angle of approximately 90° Photos: ORES[®].

1.3.3.3. Entrapment/Engulfing Manoeuvres

These manoeuvres consist of horizontal, ventral and lateral arcs (Figure 1.10).

1.3.3.3.1. Arcs

Ventral and lateral arcs are similar to ventral and lateral lunges, except that the whale's body only just breaks the surface of the water (Thomson et al, 2003). The whale turning sharply on its side (either side) and arching sharply to the left or right produces a horizontal arc. 97.6 % of the time, the whale performs these manoeuvres on the right side (Koster, 2006). The locus of the movement may be at a point dorsal or ventral to the animal. Only the non-pivotal pectoral fin and sometimes a fluke tip break the surface of the water as the animal turns through the horizontal plane.

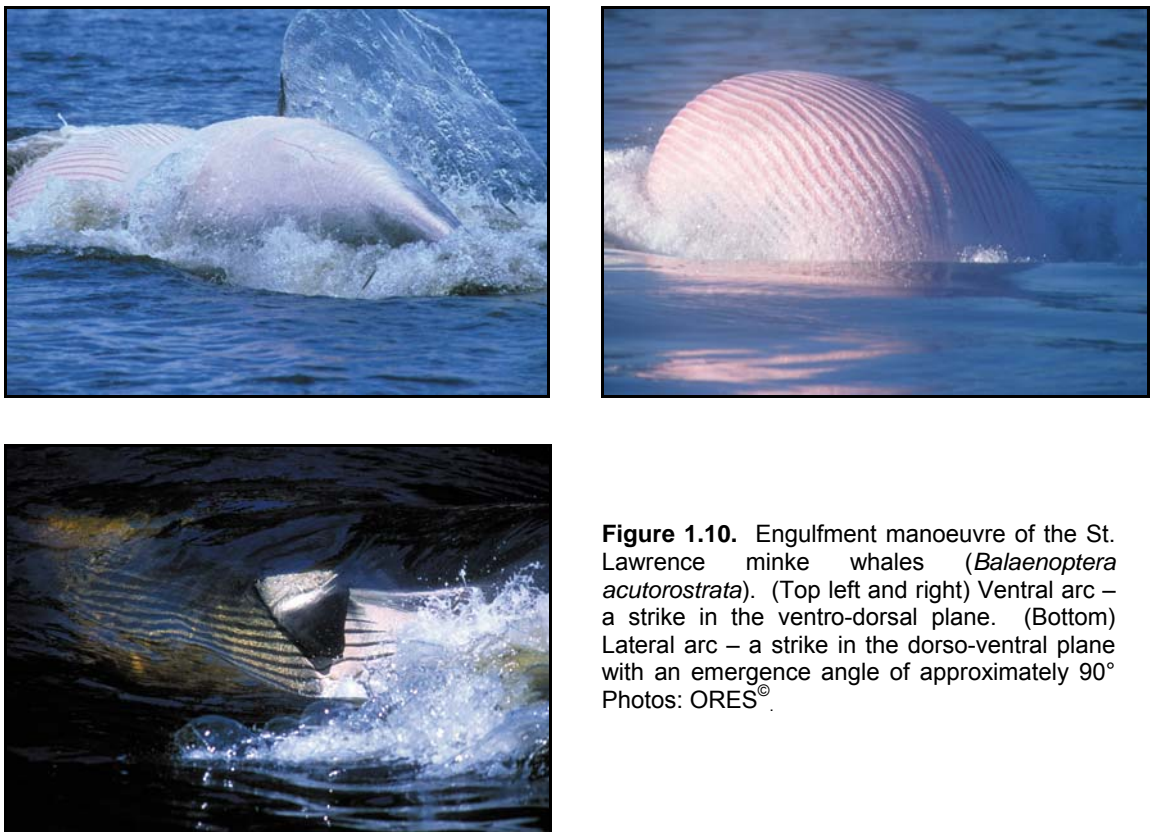


Figure 1.10. Engulfment manoeuvre of the St. Lawrence minke whales (*Balaenoptera acutorostrata*). (Top left and right) Ventral arc – a strike in the ventro-dorsal plane. (Bottom) Lateral arc – a strike in the dorso-ventral plane with an emergence angle of approximately 90° Photos: ORES®.

1.3.4. Foraging Strategies of Minke Whales

1.3.4.1. Bird Associated Fishing vs. Lunge Feeding

Wells et al, (1999) have outlined two broad feeding specialisations of the minke whale: lunge feeding or bird-association feeding. In the latter, the whales exploit concentrations of fish fry that have been 'prepared' by flocks of feeding gulls and diving birds from above and often by predatory fish and sharks from below. The bird association feeders take advantage of a concentrated prey resource but that is, however, ephemeral and consequently difficult to locate. Conversely, lunge feeders pursue a patchy resource that is consistent, abundant and that can be found relatively predictably both spatially and temporally. The trade-off here is

that the whales must actively corral and hunt the prey, suggesting higher energy expenditure. The strategies may enjoy equal pay-offs if the balance between a low rate of intake and low energy expenditure for a bird-association forager is similar to the high expense but high intake for the lunge feeder (Hoelzel et al, 1989).

1.3.4.2. Line Fishing vs. Patch Fishing

Bird associated fishing is not applicable to the minke whales of the St Lawrence and thus they feed mostly by lunging and are regularly seen actively concentrating the prey at the air-water interface. However, Lynas & Sylvestre (1988) have characterised two clear minke whale feeding strategies in this area; 1) 'line fishing', involving engulfing mouthfuls of prey scattered along a line (which is akin to the principals of bird-associated foraging) and 2) 'patch-fishing', a more intense and localised activity involving more concentrated prey.

Travelling and/or searching usually precede a line fishing feeding cycle, from which the animal launches into feeding. The feeding itself can be very brief, followed by resumption of travelling and/or searching. When line fishing, entrapments are usually in the form of hyperbolas and semi-circuits. A sudden horizontal arc in the direction of the prey usually marks the beginning of the feeding. Subsequent actions may involve no more than one or two entrapment series, followed by a single engulfing strike (see above). If this part of line fishing is more prolonged, circling, several ventilations and more than one engulfing strike may occur before the minke continues on its search for more food. The duration at any one location will depend on the concentration and quantity of prey. A likely reason for minke whales to employ this strategy is when the food availability is in the scale of mere mouthfuls.

Conversely, patch fishing involves a higher threshold of feeding activity within a confined area. Both entrapment behaviours (circling and elliptical movements) together with a whole range engulfing strikes, either in regular or irregular sequences, are characteristic of patch fishing strategy. For example, the whale may execute a whole series of entrapment manoeuvres (although individuals display preferences for a particular engulfing manoeuvre (Thomson et al (2003)), followed by a strike only to re-initiate the whole cycle. Alternatively, after entrapment a whole series of strikes (irregularly spaced in time) may ensue. This behaviour can last for more than 2.5 hours and may be interspersed by occasional respiration sequences, during which the whale leaves the striking area only to return to it upon a dive, leaving a trail resembling an inverted J. This behaviour is thought to combine the need for extensive gas exchange, possibly to repay a small oxygen debt after a period of high activity, with allowing the prey to regroup.

1.4. The St Lawrence Estuary and the Saguenay Fjord

1.4.1. The St. Lawrence Estuary

The Laurentian Channel is the main channel connecting the St. Lawrence system to the Atlantic and is approximately 1400 km in length (Figure 2.1). Its depth varies from 450 m at the entrance of the Gulf of St. Lawrence to 325 m near the head of the channel (Lavoie et al, 2000). At this point, the channel shoals over a distance of approximately 20 km to a barrier of banks, islands and narrow, shallow sills of less than 40 m in depth off Tadoussac (Simard & Lavoie, 1999) (Figure 1.11). This topographical feature separates the Saguenay Fjord, the deeper lower Estuary and the shallow upper Estuary (Gratton et al, 1988).

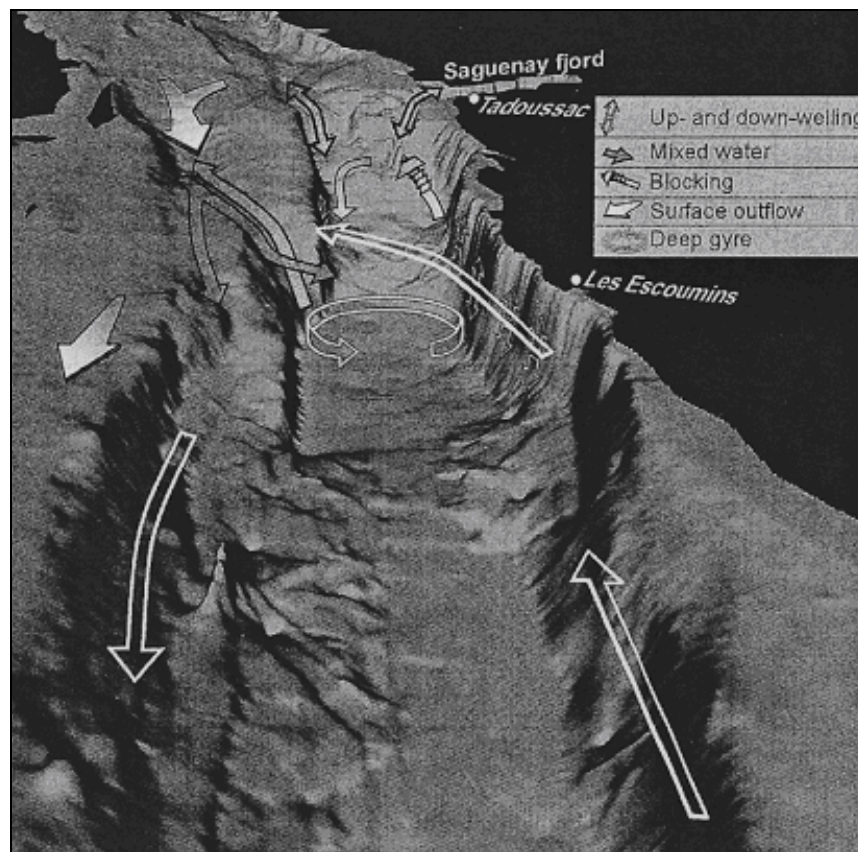


Figure 1.11. The bathymetry of the Laurentian Channel, showing shoaling of the bottom until Tadoussac, where the Laurentian Channel head forms. There are visible depths differences between the upper Estuary (upstream of the channel head) and the lower Estuary. The diagram displays the principal circulation characteristics in this region. Taken from Lavoie et al (2000).

The St. Lawrence has a characteristic three-water-layer system that appears seasonally. For example, from April through to December, a surface layer, stretching to a depth of 20 or 30 m with a temperature of 2-5°C and a salinity of 18 to 31 ‰ forms due to freshwater run-off and freshwater outflow from the Saguenay Fjord (Rainville & Marcotte, 1985). A cold intermediate layer (CIL) also forms extending below the surface mixed layer down to a depth of 150 m depth with core temperatures less than 0°C (Banks, 1966). These temperatures do range, however, between -1 - 2°C and coupled with a salinity of 32 ‰, makes a denser, heavier water mass than the surface layer. The CIL results from the advection of cold water from the Gulf of St. Lawrence during the winter period (Gratton et al, 1988). Finally, the lowest layer

consists of a warmer water mass with temperatures of 4°C and a salinity exceeding 33 ‰. This water mass that derives in part from the Labrador Current, is continuous and hence occupies the depths of both the lower St. Lawrence Estuary and the Gulf of St. Lawrence (Gratton et al, 1988). At the head of the Laurentian Channel, the interaction of the flooding tide with the rapidly shoaling bottom leads to strong upwelling of CIL and bottom waters over the sills on a twice-daily basis (Gratton et al, 1988; Ingram & El-Sabh, 1990; Lavoie et al, 2000). This results in cold surface waters between 2 - 7°C (Ingram & El-Sabh, 1990).

The tidal currents, rapid depths changes, freshwater input, the presence of two distinct water masses (St. Lawrence and Saguenay Fjord), leads to an extremely dynamic system. In turn, aggregations of krill species in this area are equally complex (Ingram & El-Sabh, 1990 but for extensive review see Simard & Lavoie, 1999; Lavoie et al, 2000). Euphausiids are known to form both large and small-scale, dense aggregations in multiple environment types (Simard & Lavoie, 1999). They are influenced by particular parameters, including water circulation, bottom topography, euphausiid behaviour, neap versus spring tide patterns, and nutrient availability (Ressler et al, 2005). The St. Lawrence appears to be the site of the richest krill aggregation yet documented in the northwest Atlantic with mean densities ranging from 6 - 73 ton km⁻² (Simard & Lavoie, 1999). In this case, circulation seems to be the major factor influencing this aggregation and distribution (Lavoie et al, 2000).

At the shoaling point, towards the Laurentian Channel head, there are intense vertical water movements. During the two hours preceding high water in the tide phase, the vertical upstream water flow reaches peak velocity and upwelling of both CIL and bottom oceanic water masses over the sills is maximal. During this time krill is advected upstream from the seaward portion of the lower Estuary. The upwelling raises and compresses the krill scattering layer vertically (Cotté & Simard, 2005). *Meganyctiphanes norvegica* are mainly found in the deep oceanic layer whilst *Thysanoessa raschi* occupy the CIL (Simard et al, 1986) and so during periods of intense upwelling, these krill species are advected closer to the surface (Lavoie et al, 2000). The head of the Laurentian Channel is therefore deemed to be a site of 'quasi-permanent rich krill aggregation' on a semi-diurnal time frame (Simard & Lavoie, 1999; Lavoie et al, 2000). However, on average, the abundance of krill at the head of the Laurentian Channel is lower and more variable than that further downstream due to the high variability of flow rate in this zone (Lavoie et al, 2000). Lavoie et al (2000) allude to the nature of krill contributing to their extensive aggregations in upwelling areas. As krill are negatively phototactic, they will actively swim downwards to remain in the safe dark zone when advected upwards. This reaction occurs at the 'barrier isolume', which is a threshold light intensity that initiates an avoidance behaviour in the euphausiid (Cotté & Simard, 2005). At the Laurentian Channel head, the rate of flow can become so intense that the krill present are unable to resist against it to maintain their vertical position and are consequently flushed into the upper Estuary and the Saguenay Fjord. By contrast, the downstream areas, for example the north shore between Les Escoumins and Cap de Bon Désir (Figure 2.2), have

vertical velocities of water, which are at a rate low enough for the euphausiids to maintain their relative position within the water column. The krill swimming down to maintain their light levels will aggregate at the slopes and gradually find themselves in denser waters. Whilst there is a mass movement downwards, euphausiids positioned at lower depths may not react as vigorously as those closer to the light barrier as their survival may not be as threatened by increasing light levels. This results in the effective 'piling up' of krill from those below, being advected upwards and not yet responding to increased light levels and those from above, migrating downwards in order to reach a darker, safer environment. Indeed, it is this mechanism that is cause for the presence of the highest biomass of euphausiids off the coast of Les Escoumins and Cap de Bon Désir (Simard & Lavoie, 1999). When the currents reverse to the ebb tide, the Saguenay and upper Estuary waters, pushed upstream by the flood, now flow over the CIL waters, which are pushed downstream and downwards (Marchand et al, 1999). The aggregation built up on the shallow area during flood is flushed back towards the Laurentian Channel, where currents shear vertically and flow is downstream at depth. The scattering layer of the euphausiids becomes more diffuse but still contains dense patches (Lavoie et al, 2000; Cotté & Simard, 2005).

1.4.2. The Saguenay Fjord

Geometrically speaking, the Saguenay is a classic fjord, due to its length of 170 km and narrow feature of 1-6 km and a typical U-shaped cross section. In addition, the Saguenay has a shallow 20 m deep sill at its mouth, which intersects the St. Lawrence Estuary near Tadoussac (Figure 1.12) (Schafer et al, 1990). An 80 m sill divides the Saguenay into two basins, occurring 18 km upstream of Tadoussac. The eastern most basin is relatively small but nevertheless reaches a maximum depth of 250 m. The basin to the west of this is much longer, extending to Lac Saint-Jean, and reaches a maximum depth of 275m. However, this western basin is beyond the limits of the study area and is therefore not very relevant to the present report but has been included for completeness. The river systems that discharge into the Fjord drain a basin that covers in excess of 78,000 km² and in turn contribute more than 5.0 x 10⁹ m³ of freshwater to the St. Lawrence system (Schafer et al, 1990).

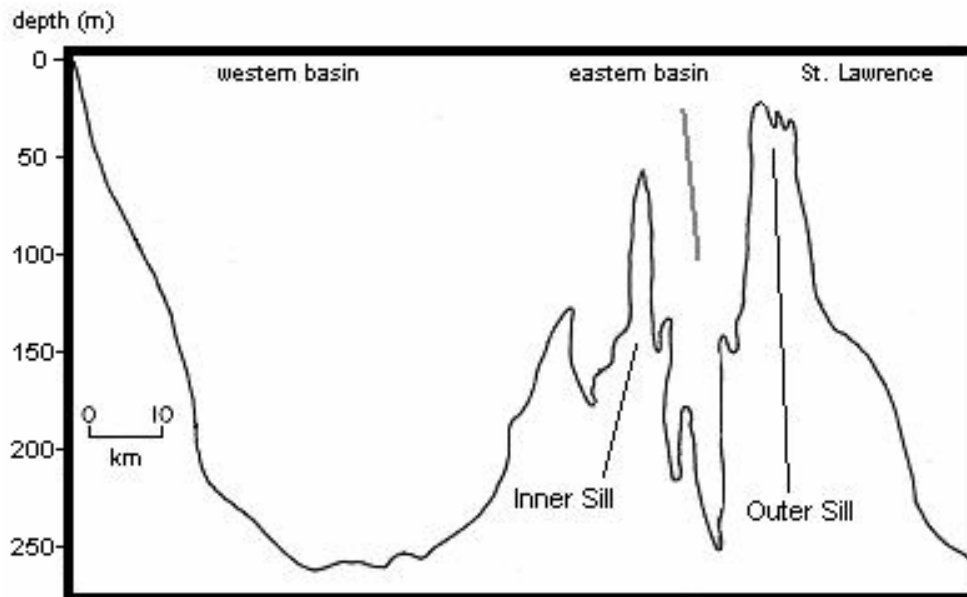


Figure 1.12. The bathymetric profile of the Saguenay Fjord showing the outer sill that separates the Saguenay Fjord from the St. Lawrence Estuary and the inner sill, which divides the Fjord into the eastern and western basins. Modified from De Ladurantaye et al (1984).

Drainville (1968) was the first to propose the hypothesis of water intruding into the deep basins of the Saguenay from the surface waters of the St. Lawrence Estuary at high tide. This, in turn enabled the explanation of elevated levels of particulate organic matter, high chlorophyll *a* concentrations, and rich phytoplankton densities in the deep basins of the Saguenay Fjord arriving in the surface waters of the St. Lawrence (De Ladurantaye et al, 1984). As mentioned, the effects of the intrusion of water coming from the Estuary are numerous and can be seen at the very beginning of the flood tide and lasts throughout the duration of the high tide period. Tides during spring can carry St. Lawrence Estuary water into the eastern basin at a rate of up to 1.5 to 2.0 m s^{-1} . The Estuary waters will occupy the whole water column above the sill and due to its higher density (resulting from high salinity ($>29 \text{ ‰}$) and of low temperature ($<1^\circ\text{C}$)) forms into a plume that rapidly descends the inside edge of sill. The arrival of this denser water mass shunts the deep Saguenay water vertically upwards, which will in turn re-descend, to its original position but in the next basin up the Fjord (De Ladurantaye et al, 1984). On the ebb tide, an important amount of the introduced water will return to the Estuary, although these are mainly low-density surface waters. Ebb flow rates may be in the order of 1.5 to 2.5 m s^{-1} . The ebb is at its strongest at the Saguenay mouth where flow rates can reach 3.0 to 3.6 m s^{-1} during the spring tides (Schafer et al; 1990). Tidal mixing together with internal waves reduces and almost eliminates stratification in the Fjord for most of the year (De Ladurantaye et al, 1984). The presence of gravel deposits rather than sandy, muddy sediments on the Fjord floor further reinforces the hypothesis of strong mixing (as this type of sediment suggests high near-bottom turbulence). Further evidence of vigorous mixing in this section of the Saguenay can be seen by the relatively vertical orientation of salinity and temperature contours and by comparatively uniform concentration distributions of suspended particulate matter (SPM) (De Ladurantaye et al,

1984; Schafer et al, 1990). The resulting water has an extremely opaque property, which together with the tannins leached from the surrounding land generates a very brown, low visibility and unclear water mass (pers. observ.). Indeed, if stratification does occur then a thin surface layer forms, known as the photic zone (5-10 m), which contains warm brackish water on top of a deeper layer (descending to 275m), which is characterised by cold, saline and well-oxygenated water. These bands of water can occur in the summer months from May to October (Schafer et al, 1990).

Many of the biological characteristics of the Saguenay Fjord marine fauna are a reflection of water mass conditions and circulation. The seasonal dynamics of the Fjord biota are characterised by four elements: 1) the late start of production processes; 2) the low level of primary production; 3) the persistently poor phytoplankton biomass; and 4) the absence of definite spring and summer blooms. The initiation of annual production processes is strongly interrelated with the intrusion of the nutrient-rich, saline waters from the St. Lawrence Estuary and the reduction of freshwater run-off during the summer. One of the most important elements that accompanies the influx of waters from the Estuary is zooplankton. The abundance, composition and structural distribution of zooplankton populations in the Saguenay are bound to this seasonal and semi-diurnal intrusion of surface waters from the St. Lawrence River Estuary (for detailed information see De Ladurantaye et al, 1984). It serves as an enrichment mechanism and is, in turn, responsible for the very high standing stock of zooplankton observed in the deep waters of the Fjord basin. Moreover, zooplankton in the Fjord is often found in much greater concentrations than in adjacent estuarine waters for a number of taxon (De Ladurantaye et al, 1984; Schafer et al, 1990). In fact, the zooplanktonic communities in the Saguenay consist primarily of highly abundant but small species whilst the planktonic fauna of the neighbouring estuary can be characterised by species that are less abundant but are larger in gross size (De Ladurantaye et al 1984).

1.4.3. Distribution of Capelin *Mallotus villosus*

Many authors have described instances where the distribution of krill will affect the distribution of upper trophic levels. Whilst this is certainly true in many cases, a direct trophic relationship based on prey density cannot fully explain the aggregation of fish in the St. Lawrence. The abundance and distribution of capelin (*Mallotus villosus*) in the St. Lawrence, is more associated with physical and biological processes as opposed to the distribution of their prey (krill) (Jacquaz et al, 1977; Marchand et al, 1999). Although fish can tolerate a wide range of temperatures, individuals are acclimated to a narrower temperature range in a given area and time (Bone et al, 1999). Whilst reacclimation to other temperature ranges is possible it is costly in both time and energy (Guderley, 1990) and so behavioural and avoidance responses are preferable. When capelin are exposed to temperature gradients, they tend to concentrate within the narrow thermal zones by changing their spatial distribution pattern. Capelin that occupy the upper water column at the head of the Laurentian Channel are most likely acclimated to the 2-5°C that characterises the surface water layer. When the CIL upwells in

the area during flood tide, fish seem to avoid the cold water (0°C) and, instead remain in the warmer waters bordering the CIL, to which they are acclimated (Marchand et al, 1999). First, the thinning of the warm surface layer caused by the cold-water upwelling may cause the capelin to concentrate near the surface, especially during the flood tide. When fish approach the air-surface interface, they may exhibit an anti-predator behaviour by swimming downwards to reduce exposure to visual predators (Laurila et al, 1998), probably enhancing the aggregation process. Second, when the CIL reaches the surface, fish probably avoid these cold waters by swimming away from it in a horizontal direction (Marchand et al, 1999). In the St. Lawrence the speed of propagation of these fronts has been measured at 40 cm s⁻¹, which corresponds to the swimming speeds that can be sustained for long time periods by the capelin (Videler, 1993). Such behaviour allows fish to remain within their acclimated temperatures and cope with the rapid changes that occur in this physically dynamic environment (Marchand et al, 1999). Indeed, it is not ambitious to foresee that capelin concentrating along the edge of the CIL might occasionally enter this cold intermediate layer for brief periods of time in search of food and then return to warmer waters that they normally inhabit. These brief excursions would not require energy expenditure on metabolic acclimation (Marchand et al, 1999).

The tidal upwelling-downwelling dynamics, together with the fish's ability to redistribute vertically that is responsible for the upstream retention of capelin at the Laurentian Channel and the maintenance of large-scale aggregations (Simard et al, 2002). The surface outflow from the Saguenay entrance at the end of ebb can help bring back the previously upwelled capelin over the shallows and extend their distribution away from the slope. This horizontal displacement could be associated with a dive to the top of the zooplankton scattering layer in order to close the vertical loop and maintain retention (Simard et al, 2002). Therefore, large fish aggregations often form and are retained, around and at the head of the Laurentian Channel. Concentrations in this zone are commonly an order of magnitude larger than the densities found in the surrounding areas (Marchand et al, 1999).

Both Jacquaz et al (1977) and Bailey et al (1977) describe a strongly seasonal pattern of distribution of capelin in the St. Lawrence Estuary. They dictate that there is an influx of capelin from the Gulf in beginning of November that continues throughout the winter months. It is thought that this is a contranatal migration towards the spawning areas in the upper Estuary and hence the high concentrations of capelin occurring here in April. After this there is a return to more downstream parts of the Estuary during the spring and summer to feed on euphausiid krill (Vésin et al, 1981). A major exception to the seasonal distribution pattern is the year-round occurrence of juvenile capelin in and near the mouth of the Saguenay Fjord (Bailey et al 1977). De Ladurantaye et al (1984) report that zooplankton biomass in the lower Saguenay remains relatively stable at greater depths, which may provide a food resource for a limited number of juveniles in the area throughout the year. This population of capelin, in turn, contributes, significantly to the beluga whales (*Delphinapterus leucas*), that reside on a

semi-permanent basis in the Saguenay and the confluence area with the St. Lawrence, as well as baleen whales, namely the minke whale (*Balaenoptera acutorostrata*) and the fin whale (*Balaenoptera physalus*) (Michaud & Giard, 1997; 1999; Simard et al, 2002; Fontaine, 2005).

1.5. Aims

The purpose of the present study is threefold. First, is to obtain a mean surfacing interval for the minke whale population in the summering grounds (Edds & MacFarlane, 1987) of the St. Lawrence River Estuary. To the author's knowledge no estimation of breathing rates has ever been documented for minke whales in this area or indeed for the northwest Atlantic. Second, is to examine the variation of surfacing intervals over a range of behaviours. A further aim, in conjunction with this, is to analyse the ventilation patterns and compare them between different behaviours. Statistical comparisons of the breathing patterns across the range of activities aims to assess whether these are sufficient to enable suitable categorisation of behaviours according to their breathing regimes in future ethological studies. The St. Lawrence represents a summer feeding ground for minke whales. Therefore, the third objective is to investigate in greater detail the nature of surface feeding behaviour. The primary purpose here is to explore any relationships between the number of blows performed by the whale and the number of striking manoeuvres and whether these vary on a temporal or spatial scale. This study also aims to address any factors that may be responsible for such associations and their variations.

2. MATERIALS AND METHODS

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2.1. Study Area

The area of study is in the St Lawrence River Estuary and the Saguenay Fjord (Figure 2.1) and is found within the waters of the Saguenay-St. Lawrence Marine Park. The boundaries of the study area stretch downriver to Les Escoumins and upriver to Baie des Rochers (Figure 2.2). It extends to several kilometres up the Saguenay Fjord and to the south coast of the St Lawrence River Estuary (Figure 2.2). This consists of a total area of approximately 500 km² and is delimited by the latitudes 47°97'00"-48°21'00" N and the longitudes 69°48'00"-69°23'00" W.



Figure 2.1. Map of the study area, inside the red cage, located in the middle estuary of the St. Lawrence, Québec, Canada. The dark blue in the Estuary represents the Laurentian Channel.

2.2. Data Collection

Ventilation-rate data of minke whales have been collected for several decades by ORES (Ocean Research and Education Society; Québec, Canada) in order to attain baseline information on the behaviour of these whales. For the present study, data from 1995 to 2005 field seasons (June to October) have been employed, comprising a total of 11 years of data. The research teams consisted of an experienced boat driver, a photographer, a primary and secondary observer and a minimum of four other supporting observers, arranged equally around the boat to achieve full, 360° visual coverage of the surrounding waters. The platforms used for data collection comprised of two small, highly manoeuvrable RIBs (Rigid Inflatable Boats) of 6 m in length using four-stroke outboard engines.

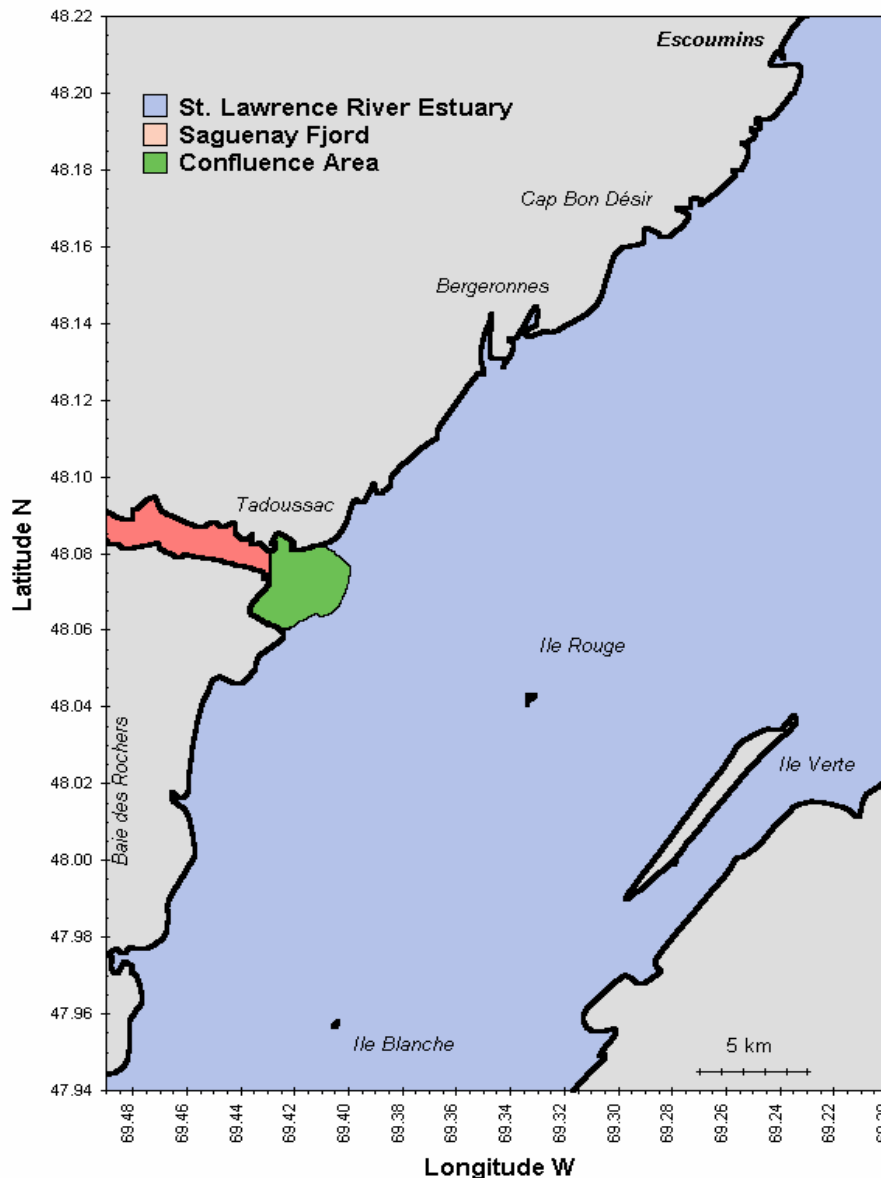


Figure 2.2. The outer limits of the study area. The study area itself has three distinct environments; the St. Lawrence River Estuary; the Saguenay Fjord, the St. Lawrence-Saguenay Confluence area.

The experiments were only conducted when sighting conditions were considered good and when the sea states were equal to or less than 3 on the Beaufort scale. Transects were run daily both up and downriver as well as into the Saguenay Fjord throughout the field season. When a minke whale was sighted within 1 km of the transect, the boat approached the whale to within 30 m and turned to match the speed and direction of the whale, if necessary. This distance was maintained to allow for identification photographs to be taken. Identification photographs were taken with *Nikon 90FX* single-lens reflex (SLR) cameras fitted with a 300 mm fixed focal lens and 400 diapositive films at shutter speeds of 1/500 s to 1/1000 s. After suitable photographs were taken (usually within the first few surfacings), the boat kept to

within 100 m of the specimen for the data acquisition, but observation distances ranged between 10 and 150 m. The starting point for the experiments was at the exhalation prior to a dive.

The supporting observers were responsible for calling out sightings. The primary observer was responsible for timing intervals between blows in a hr: min: sec format and passing this information to the secondary observer who recorded the times of exhalations and other behavioural notes. Where possible, a GPS (Global Position Satellite; Magellan 5000DLX) reading was also recorded by the secondary observer for each dive (denoted by the whale arching its tailstock and also leaving a signature 'footprint' or 'dive puddle'). If more than one animal was present in the immediate vicinity, the most easily recognisable animal was chosen for the ventilation sample. When it was possible to distinguish both animals in a pair by distinctive colouration or dorsal fin shape, respiration data was collected for both. However, if too many whales were present in a given area no experiments were started. Similarly, if an experiment had been started but too many whales arose, causing confusion over the target individual, the sample was discarded and not used in the analysis. The desired sampling period was 25 min. Sequences of less than 25 min duration were removed from the dataset. It is possible that not all surfacings in a sequence were seen and noted. To minimise this possibility, the RIBs continued in the same direction and speed as the whale during long dives in order to be close to the whale when it surfaced. In addition, effort was also made to locate footprints or puddles of undetected surfacings after the first observed surfacing in a sequence. Sequences where it was thought that surfacings may have been missed were omitted from the analysis. 376 samples remained in the dataset for analysis.

2.3. Definition and Categorisation of Minke Whale Behaviours

The samples were categorised into four groups of behaviours as follows: Whales were considered to be surface foraging (SF, n=192) if they exhibited lunging activity (oblique, lateral, vertical or ventral) with distended ventral grooves or open mouthparts exposed to the air, or if they exhibited arching activity (lateral or ventral) with distended ventral grooves visible just under the surface (up to 10 m). This was accompanied by purging of water from the mouth.

Animals that were feeding below the surface were noted as depth feeders. In order to ascertain the depths of their activity, profiles of prey scattering layers in the water column were run opportunistically (generally when wind speeds were < 10 knots) among foraging whales, using a 192 kHz transducer with an 8° angle coupled to a Lowrance X16 echo graph chart recorder, with an output power of 1600 watts (225 rms).

Near-surface (NS, n=59) foraging was defined by tight elliptical surface swimming patterns and slight to pronounced dorsal or caudal arches, coupled with shallow diving angles < 30°~ over prey patches (< 50 m deep). Strong dorsal arches (rounding out) and diving angles

$>30^\circ$, over prey patches (> 50 m) were considered to be indicators of foraging at depth and this behaviour was categorised as deep feeding (DF, $n=75$). Lastly, whales displayed travelling (TRV, $n=50$) behaviour and this was seen by clear displacement of the animal on a direct course.

2.4. Manipulation and Analysis of Data

For each sample, several ventilation characteristics were calculated (Figure 2.3):

1. Surfacing interval. The surfacing interval is the time taken between blows, in which the whale is submerged. For ease of data management and representation of results, the mean surfacing interval for each sample was calculated. Mean surfacing intervals were then obtained for each behaviour (Appendix A) from which boxplots were constructed. However, in direct statistical comparisons, all surfacing interval values from each sample were used.
2. Dive duration. All dive durations (Figure 2.3, a)) from all samples were pooled together and categorised into their respective behaviours. In most samples, a dive is clearly apparent within the data, but in cases that were not so evident, an arbitrary time of 60 sec was used to define the dive.
3. Time between blows in a surfacing. This is the number of blows in a clustered series of ventilations within a surfacing prior to a dive (Figure 2.3, b)).
4. Surface duration. This is calculated by summing all the surfacing intervals within a clustered series of blows (Figure 2.3, c)).
5. Number of blows in a surfacing. The number of exhalations produced in each ventilation cluster was pooled together for each of the different behaviours.

Because the dive profile of SF animals does not possess a visually discernible structure as that shown in Figure 2.3, only surfacing intervals were calculated for these samples.

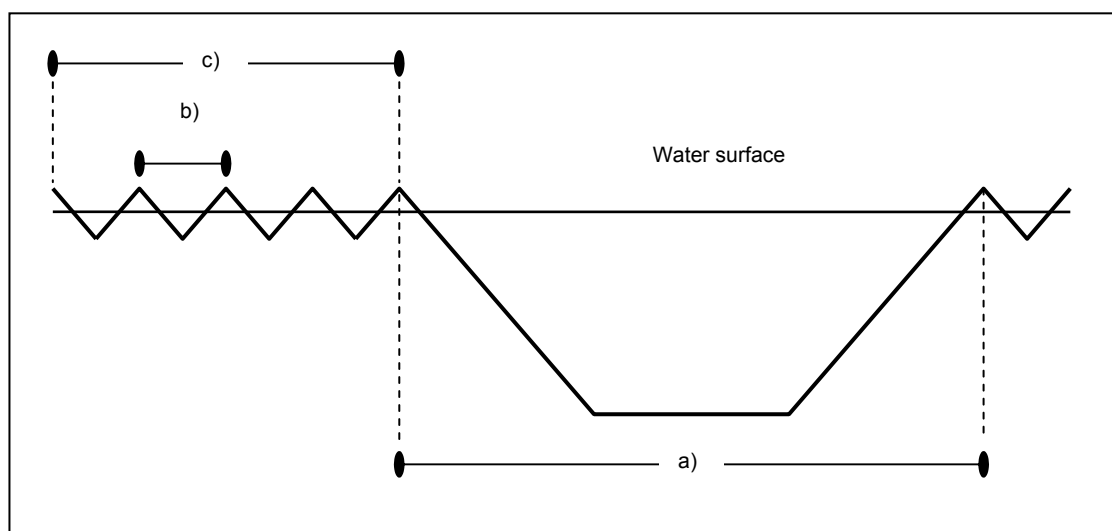


Figure 2.3. Schematic demonstrating the profile of a minke whale's dive path, applicable to near surface (NS), deep feeding (DF), and travelling (TRV) animals. a) dive duration; b) time between blows within a surfacing; and c) surfacing duration.

In order to calculate an overall surfacing interval for minke whales in the St. Lawrence, the computed mean surfacing interval for each behaviour was averaged.

For a more in-depth analysis of SF breathing ecology a higher number of samples were used. For this analysis all samples that had four, or more dive cycles were employed, resulting in a 236-sample dataset. From these samples, the number of blows and the number of strikes within the sample and divided it by the time duration of that sample, calculated blow rate and feeding strike rate. These values permitted direct blow to strike ratios to be determined. The number of blows in a given sample was divided by the number of strikes within that same sample to generate a single ratio value of number of blows per feeding strike.

This dataset was then divided according to several grouping variables. First, the samples were organised according to whether the feeding strike permitted a simultaneous ventilation event (see 1.3.3.2 Engulfing Manoeuvres pp 15). Those that allowed a breathing event were termed Type 1 SF (n=68). Samples where the engulfment manoeuvres did not permit a breathing event were called Type 2 SF (n=152). In samples where there was a mix of the two feeding types, grouping into a category was only permitted if one feeding type had double the number of the opposing feeding strike type. If this criterion was not satisfied, then the sample was discarded. (Only 11 samples were discarded). Second, the samples were organised according to their location within the study area. Samples either occurred in 1) the St. Lawrence River Estuary (n=108); 2) the Saguenay Fjord (n=63); or 3) the St Lawrence-Saguenay Confluence area (n=62) (Figure 2.2). Last, the samples were divided into their respective years; 1995 (n=12); 1996 (n=18); 1997 (n=15); 1998 (n=13); 1999 (n=16); 2000 (n=11); 2001 (n=31); 2002 (n=10); 2003 (n=60); 2004 (n=34); and 2005 (n=16).

2.5. Statistical Analysis

The statistical analysis was conducted using SPSS version 12.0. All data sets were assessed for normality in order to determine what form of statistical analyses to use. The chosen non-parametric test to ascertain significant differences in the ventilation characteristics between each behaviour was the Kruskal-Wallis test. It is effectively the equivalent of the parametric one-way analysis of variance test and is based on the assumption that samples are taken from populations with the same median (Pallant, 2001). Thus, this test uses the median value and not the mean. The data collected in this study contains a number of extreme values and causes a certain degree of skewing. Therefore, this particular test is appropriate for the present data set as such values will not influence the results generated by this non-parametric test, as would be the case with parametric tests. It also allows the direct comparison between three or more datasets. Boxplots were also produced for each ventilation characteristic, enabling the significant differences between the behaviour categories to be viewed visually. Graphs of the frequency distribution of ventilations (ventilation profiles) were produced from the above results. These profiles display the temporal occurrence of ventilations.

In the investigation concerning SF, the relationship between blow rates and strike rates were examined by creating a scatter plot. Again, non-parametric analyses of variance were employed, first to assess statistical distinctions in blow and strike rate between the two types of SF (Mann Whitney U test as only 2 datasets are compared here); second to compare the strike and blow rates between the different zones in the study area (Kruskal-Wallis test); and third to test for any significant changes in the blow and strike rates throughout the 11 years of study (Kruskal-Wallis test). Boxplots were constructed showing the difference of blows per strike throughout the years. Boxplots were created to demonstrate the inter-year differences in the number of blows per feeding strike and also for each type of SF.

The following level of analysis comprised of bivariate correlations that were run using a Pearson product moment coefficient. These tested for the presence and subsequently strength and direction of linear relationships between the two continuous variables; blow rate and strike rate. Correlation coefficients were then obtained for groups of variables: first, for the two types of SF and second, for the three different zones in the study area. The generated results were tested for to see if significant differences occurred between the correlation coefficients (e.g. test the difference for significance in the correlation between strike rate and blow rate in type 1 and type 2 SF, and also between the St. Lawrence Estuary, the Saguenay Fjord and St. Lawrence-Saguenay Confluence area (Appendix F)). First it was necessary to convert the obtained r values into z scores from which the observed value (z_{obs} value) were calculated using Equation 1 (Pallant, 2001).

$$z_{obs} = \frac{z_1 - z_2}{\sqrt{\frac{1}{N_1 - 3} + \frac{1}{N_2 - 3}}}$$

Equation 1

If the z_{obs} values obtained were between -1.96 and +1.96 then there is no statistically significant difference between the correlation coefficients. The decision rule, therefore, is:

- o If $-1.96 < z_{obs} < 1.96$: correlation coefficients are not statistically significant.
- o If $z_{obs} \leq -1.96$ or $z_{obs} \geq 1.96$: correlation coefficients are statistically significantly different (Pallant, 2001).

The final level of statistical analysis employed was the linear regression. Regression is used to explore the relationship between one continuous dependent variable and a number of independent variables or predictors (also continuous). It allows a more complex exploration of the interrelationship between a set of variables and whether one set of variables is able to predict a particular outcome i.e. how effectively a dependent variable (strike rate) is able to predict an independent variable (blow rate). Linear regressions were presented graphically.

3. RESULTS

3. RESULTS

3.1. Tests of Normality

The dataset for all five ventilation parameters were assessed for normality using a Kolmogorov-Smirnov statistic. A summary of these can be found in Table 3.1. This test revealed that all the datasets obtained within this study violated the assumption of normal distribution with one exception: the dive duration in DF (Table 3.1). Therefore, non-parametric statistics could be used to determine any differences in ventilation parameters between the various behaviours.

Ventilation Characteristics	Behaviours							
	NS		DF		TRV		SF	
	D	p	D	p	D	p	D	p
Surfacing Interval	0.322	0.000*	0.483	0.000*	0.242	0.000*	0.195	0.000*
Dive Duration	0.086	0.000*	0.041	0.070	0.144	0.000*	-	-
Time between Blows in a Surfacing	0.191	0.000*	0.158	0.000*	0.168	0.000*	-	-
Surface Duration	0.119	0.000*	0.064	0.000*	0.130	0.000*	-	-
Number of Blows per Surfacing	0.139	0.000*	0.132	0.000*	0.173	0.000*	-	-

Table 3.1. The results of the Kolmogorov-Smirnov tests (statistic and probability values) to assess if the datasets of the ventilation characteristics of all behaviours are normally distributed. * shows significance above the $p = 0.05$ level.

The SF datasets were analysed for normality, again using a Kolmogorov-Smirnov statistic, as summarised in Table 3.2.

SF variable	Result of Normality	
	D	P
Blow rate	0.052	0.200
Strike rate	0.148	0.000*
Number of blows per feeding strike	0.112	0.000*

Table 3.2. The results of the Kolmogorov-Smirnov tests (statistic and probability values) to assess if the datasets of the blow rate, strike rate and number of blows per feeding strike demonstrate normal distribution. * shows significance above the $p = 0.05$ level.

Tests showed that only the scores within blow rates had normal distribution, whilst the strike rate and the number of blows per feeding strike datasets had significant results above the $p = 0.05$ level. Analyses could be performed using non-parametric statistics to determine if any further trends or patterns occurred in SF behaviour of minke whales.

3.2. Mean Surfacing Interval

The mean surfacing interval recorded in this study for minke whales of the St. Lawrence River Estuary and Saguenay Fjord region was determined as 54.786 sec (range 1-749 sec).

3.3. Ventilation Characteristics

For a summary table of mean surfacing intervals refer to Appendix A. To view the scores for all the other ventilation characteristics refer to Appendix B, C, D, and E.

3.3.1. Mean Surfacing Intervals

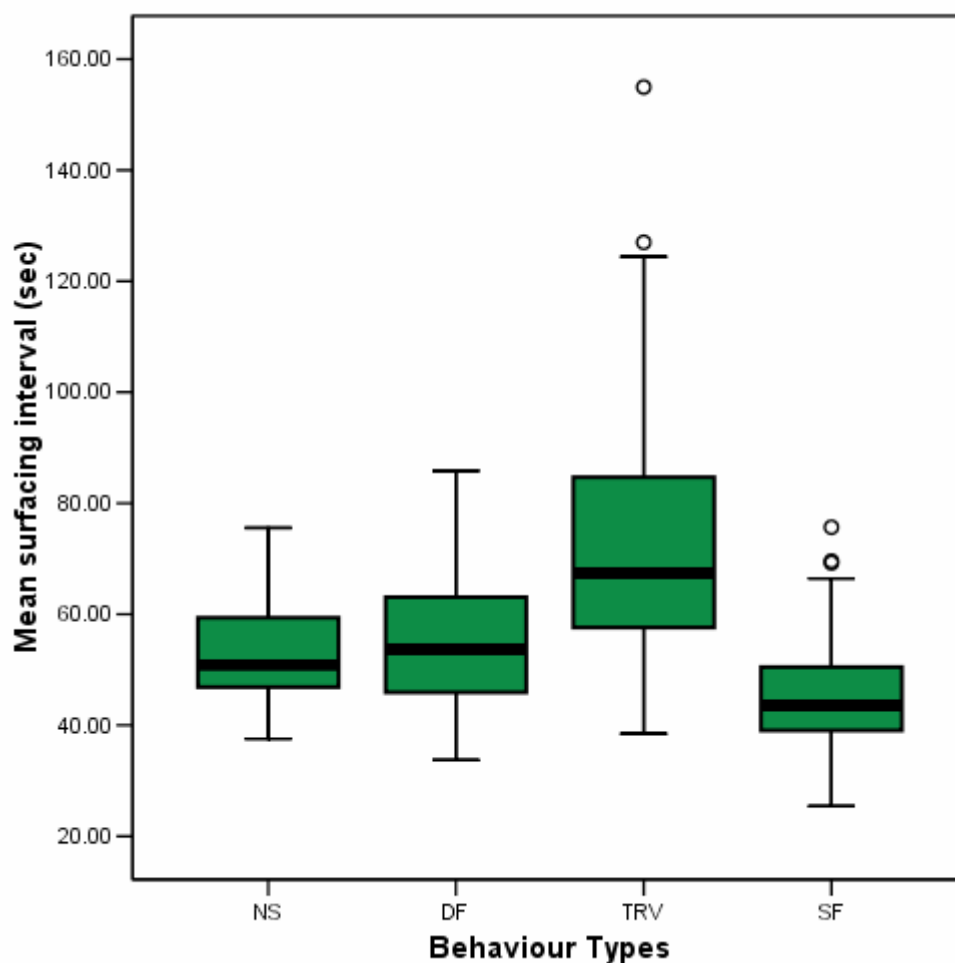


Figure 3.1. Boxplot showing the mean surfacing intervals across the four different behaviours, including NS (near-surface feeding), DF (deep feeding), TRV (travelling), and SF (surface feeding).

The results of the Kruskal-Wallis test show that surfacing intervals are statistically significantly different across the range of behaviours ($H_3 = 744.411$, $p = 0.000$). This significant difference is graphically portrayed in Figure 3.1. The mean surfacing interval for NS and DF are remarkably similar: 52.034 (range 2-449 sec) and 52.495 sec (range 2-588 sec), respectively. The mean surfacing interval for a travelling whale is longer than any other behaviour at 71.162

sec (range 2-749 sec). SF animals have the lowest mean surfacing interval of 43.452 sec (range 1-543 sec).

3.3.2. Dive Duration

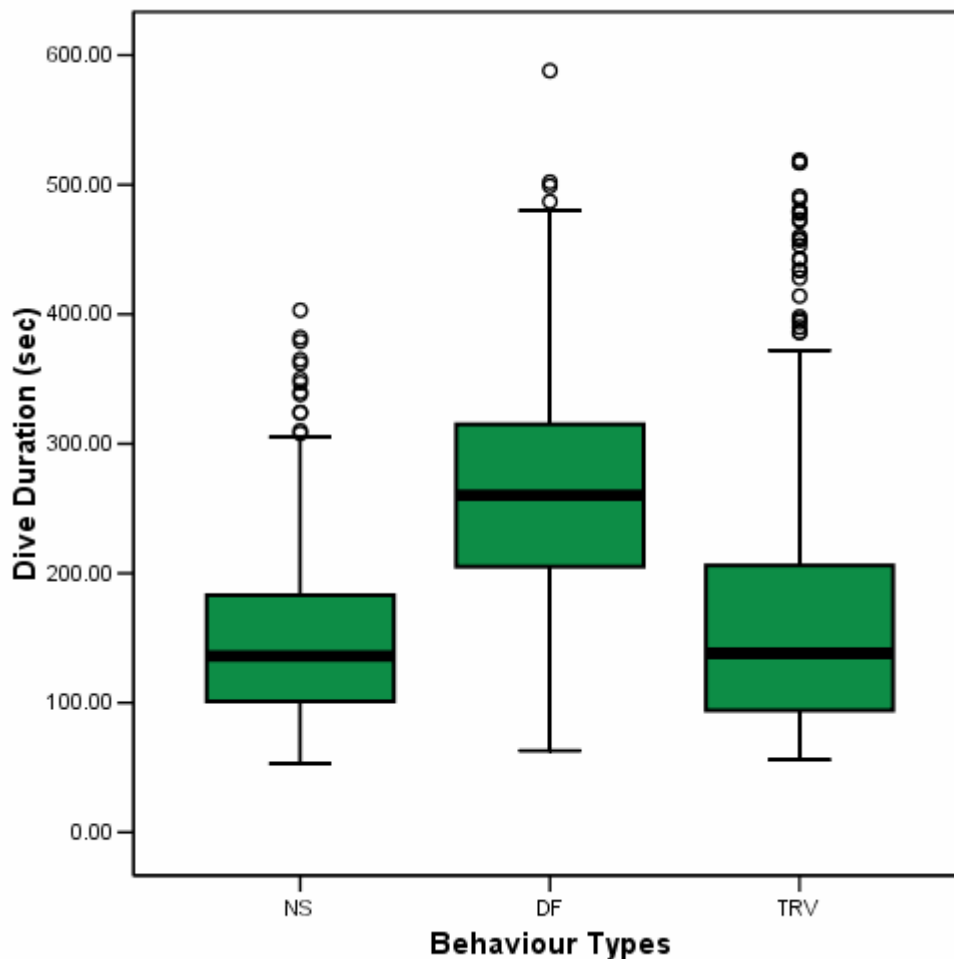


Figure 3.2. Boxplots showing the range of dive duration scores across three behaviours, including NS (near-surface feeding), DF (deep feeding), and TRV (travelling).

The dive durations vary considerably across all three behaviours and show significant differences between them ($H_2 = 456.745$, $p = 0.000$). On average, NS will show dive durations of 149.679 sec (range 60-449 sec), which is similar to that of TRV, 168.413 sec (range 56-749 sec). DF dive durations are longer than either of the previous behaviours at 266.186 sec (range 63-588 sec). The differences and range of dive durations for the behaviours is illustrated in Figure 3.2.

3.3.3. Time Between Blows in a Surfacing

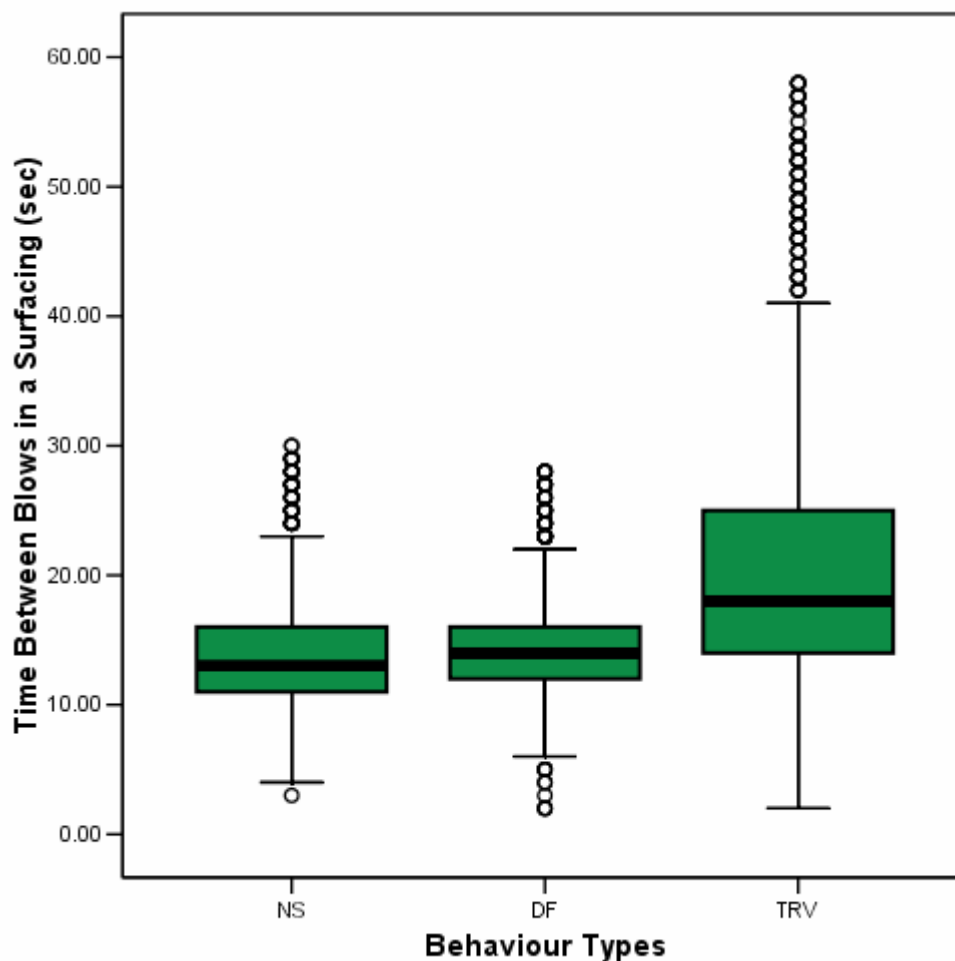


Figure 3.3. Boxplots showing the time between blows within a surfacing across three behaviours, including NS (near-surface feeding), DF (deep feeding), and TRV (travelling).

The ventilation characteristic of time between blows in a surfacing shows difference at a statistically significant level between all three behaviours ($H_2 = 504.765$, $p = 0.000$). The mean time between blows in a surfacing was 15.101 sec, 14.466 sec, and 21.026 sec for NS, DF and TRV, respectively. The significant difference lies between TRV, and the feeding behaviours, NS and DF. TRV has a much higher time span between blows within a surfacing than that of NS or DF, which have relatively similar inter-blow times (Figure 3.3). However, it is of note that DF does have tendency to show shorter inter-blow durations within a surfacing. The range of scores for this characteristic is relatively similar between NS, DF, and TRV: range 3-58 sec, 2-59 sec, 2-59 sec, respectively.

3.3.4. Surface Duration

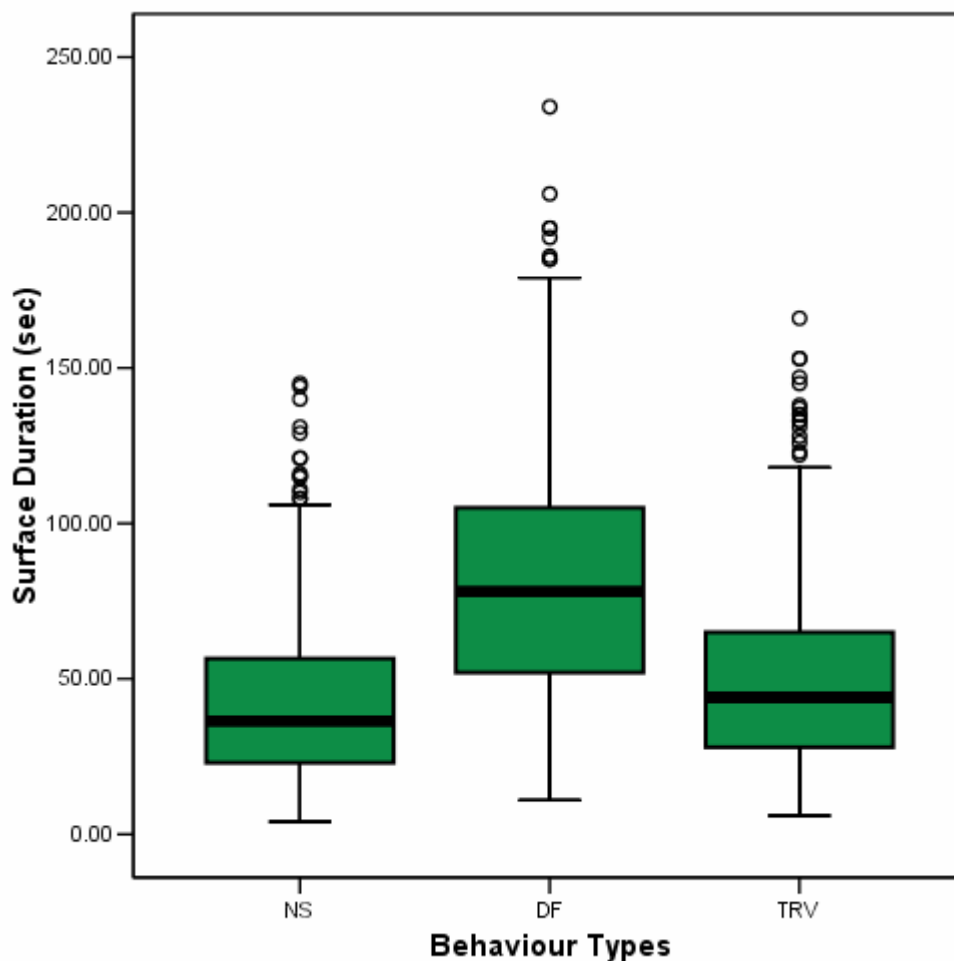


Figure 3.4. Boxplots showing the surface duration (time between the first and last blow in a series of ventilations) across three behaviours, including NS (near-surface feeding), DF (deep feeding), and TRV (travelling).

The boxplot in Figure 3.4 illustrates that the surfacing duration in DF activity is significantly longer than that of both NS and TRV ($H_2 = 293.543$, $p = 0.000$). The mean surfacing duration for DF is 82.194 sec, whilst for NS and TRV the mean values obtained were 44.667 sec, and 52.881 sec, respectively. The ranges of surfacing durations are similarly large for all three behaviours; NS (4-288 sec); DF (11-292 sec); TRV (6-392 sec).

3.3.5. Number of Blows per Surfacing

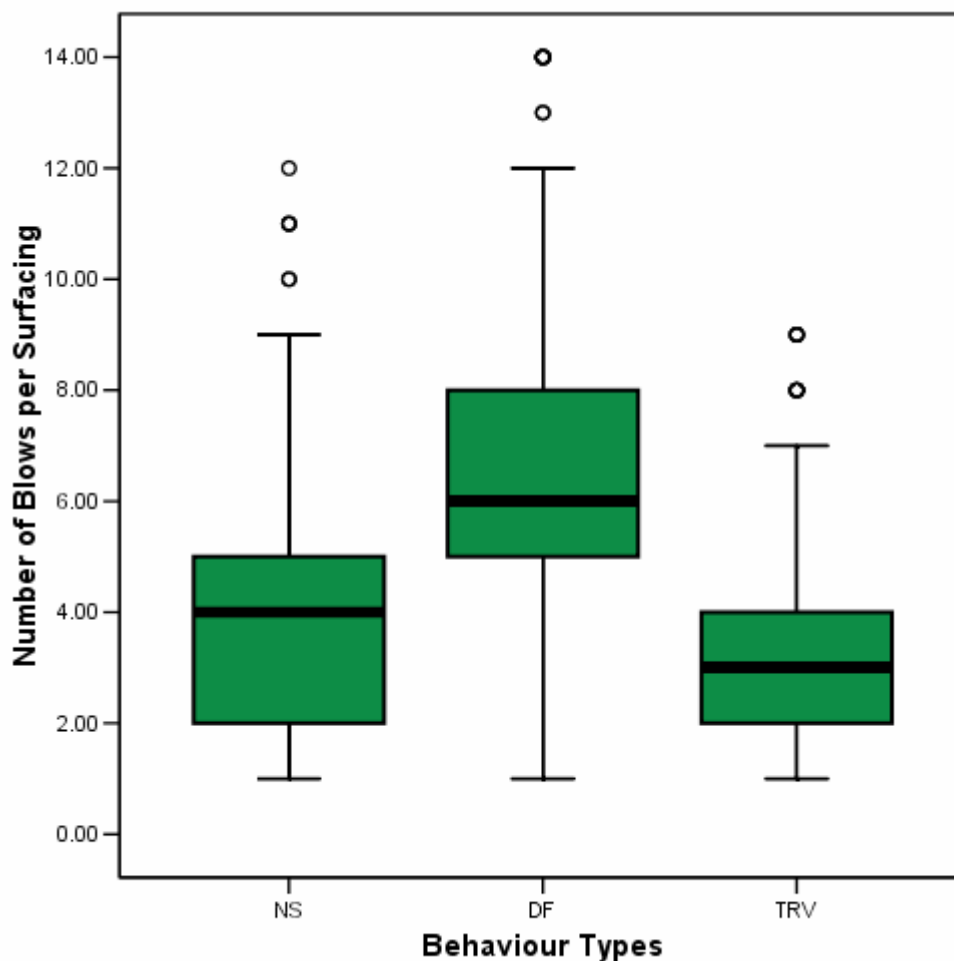


Figure 3.5. Boxplots showing the number of blows performed in a surfacing across three behaviours, including NS (near-surface feeding), DF (deep feeding), and TRV (travelling).

The number of blows performed in a surfacing by a whale varies significantly between the three kinds of behaviour ($H_2 = 614.797$, $p = 0.000$) as demonstrated in Figure 3.5. The mean number of ventilations in a surfacing in DF behaviour is 6.605, although these did range from as little as 1, up to 18 blows per surfacing. The means for both NS, 3.636, and TRV, 2.939 are again much lower by comparison. The upper range is also less in NS (1-12 blows per surfacing) and TRV (1-9 blows per surfacing) than in DF.

3.4. Ventilation Profiles

The means calculated for each ventilation parameter were used to reconstruct profiles of the breathing patterns that are typical of each behaviour type. Figure 3.6 and 3.7 show the temporal distribution of individual surfacings.

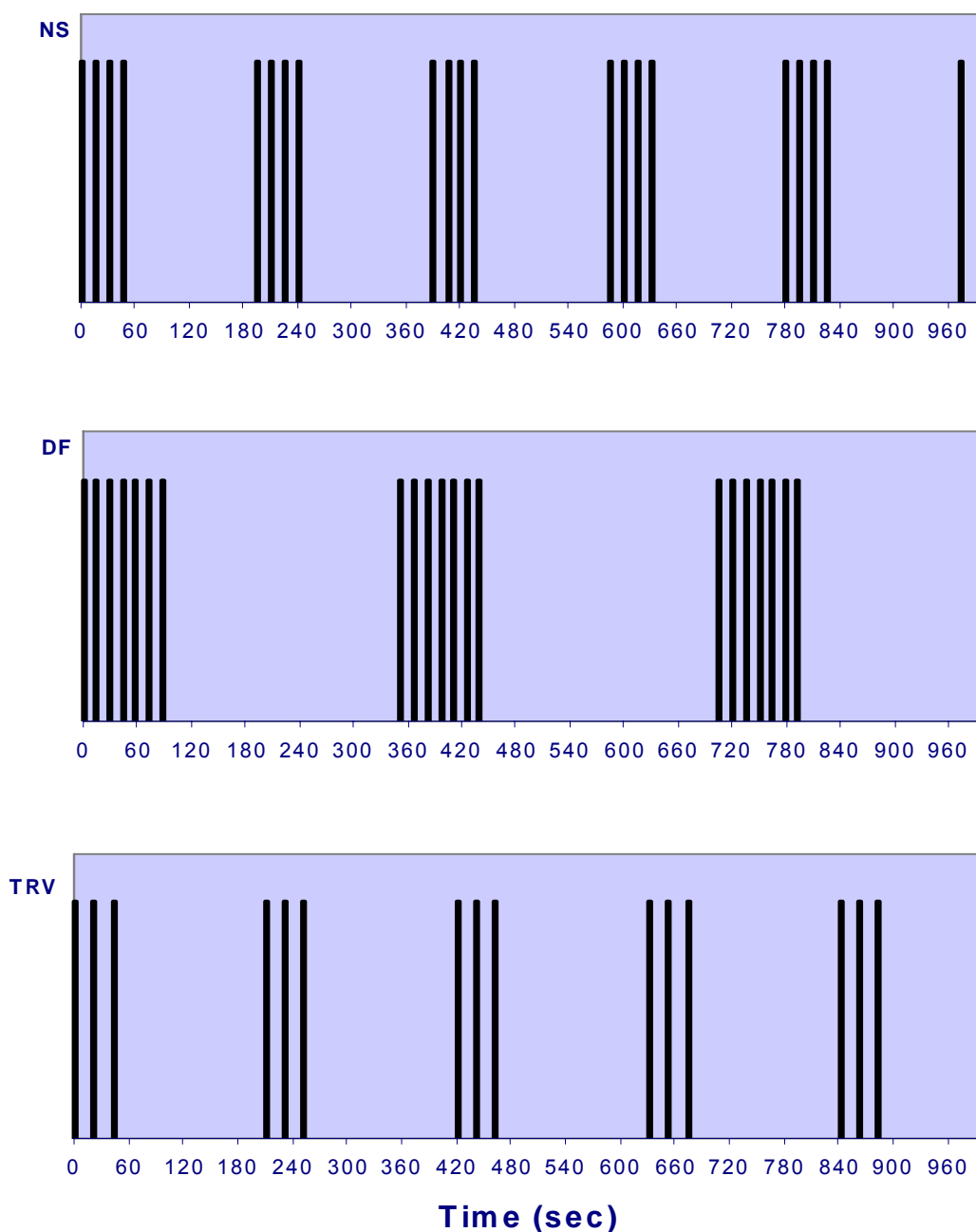


Figure 3.6. The ventilation profiles of NS (near-surface feeding), DF (deep feeding), and TRV (travelling) behaviours showing the temporal pattern of blows (black bars) based on means calculated from the ventilation characteristics (see 3.3 Ventilation Characteristics).

All three behaviours show a similar blow cycle structure incorporating a cluster of ventilations in quick succession punctuated by a long submergence period. However, these ventilation profiles do demonstrate marked differences in the temporal distribution of these surfacing events according to the various behaviours. In summary, NS behaviour is typified by approximately four blows in each surfacing, which are spaced apart by intervals of approximately 15 sec, giving a mean surface time of about 44 sec. These bouts of blows are

interspersed by dives of 149 sec before the cycle begins again. In DF, the whales' surfacing period is much extended and lasts a mean of 82 sec. During this time a high number of blows may be performed, averaging a number of seven, with intervals of approximately 14 sec; a marginally faster rate than in NS. The dive time of this behaviour is significantly longer than either NS or TRV at 266 sec. TRV samples do have commonality with NS in terms of breathing regimes. The surfacing series in TRV consists of approximately three blows, giving a surface duration of about 53 sec, which is then followed by a dive of 168 sec. The time between the blows is much longer than in either of the feeding behaviours at 21 sec. TRV behaviour is characterised by long periods of submergence with a minimal number of surfacings. It can be concluded therefore, that each behaviour exhibits significantly different ventilation regimes from each other in all breathing characteristics, including the surfacing intervals, the dive duration, the time between blows within a surfacing, the surface duration and the number of blows per surfacing.

The prerequisite for ventilation characteristics to be calculated is a distinct blow-series-and-dive structure. Whilst NS, DF behaviours, and TRV to a lesser extent, adhere to this format keenly, SF behaviours do not. Therefore, the construction of SF breathing patterns has not been assessed in the same way as for the other three behaviours. However, for completeness the ventilation profiles for both feeding styles have been included. These two examples have been recorded directly from the field (Figure 3.7).

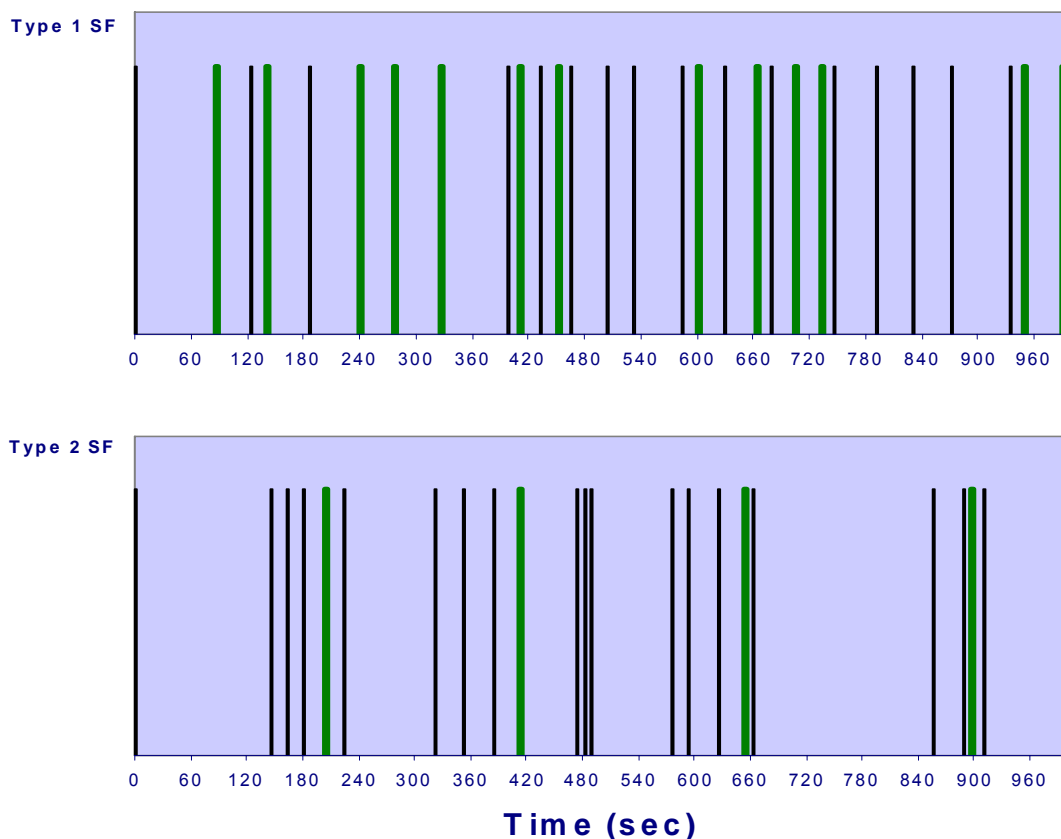


Figure 3.7. The ventilation profiles of type 1 and type 2 surface foraging behaviour, showing the pattern and timing of blows (black bars) with engulfing manoeuvres (green bars). There is no ventilation occurring during the feeding strikes of type 2 SF.

It is possible to observe the rather more regular and consistent pattern of ventilations displayed by the type 1 surface feeder. Here, the blows and striking manoeuvres are spaced apart at relatively equal time intervals and one feeding strike is often followed by a series of others. The noticeable difference between type 1 and type 2 SF is the occurrence of strikes. Type 2 SF rarely involves a consecutive series of engulfment manoeuvres as in type 1. Moreover, where the number of blows may be similar to or equal to the number of strikes in type 1 SF (strikes to blows = 13:16, in this example), the number of blows in a type 2 surface feeder greatly exceeds the number of strikes (strikes to blows = 4:18). This difference is shown by clustering of blow rates in association to strike rates (strikes/min) between the two SF strategies in Figure 3.9 and is also represented in Figure 3.12.

3.5. Surface Feeding Ventilation Characteristics

A Pearson's product-moment correlation coefficient statistic was used to determine if there were any correlations between the blow rate and strike rate of surface feeding minke whales (Table 3.3.).

SF variable	Strike rate (strike/min)
Blow rate (blow/min)	$r = -0.375$ $p = 0.000^{**}$

Table 3.3. Correlation coefficient (r) and probability value (p) obtained from the Pearson's correlation test used to determine any correlation between strike rate (strikes/min) and blow rate (blows/min) in surface feeding minke whales. ** indicates results which are significant at the $p = <0.01$ level.

Results of the Pearson's correlation test (summarised in Table 3.30) revealed that a strong negative correlation exists between the blow rates and strike rates during SF activity. This correlation is statistically significant ($p = 0.000$). A scatter plot of the trend between blow and strike rate can be found in Figure 3.8.

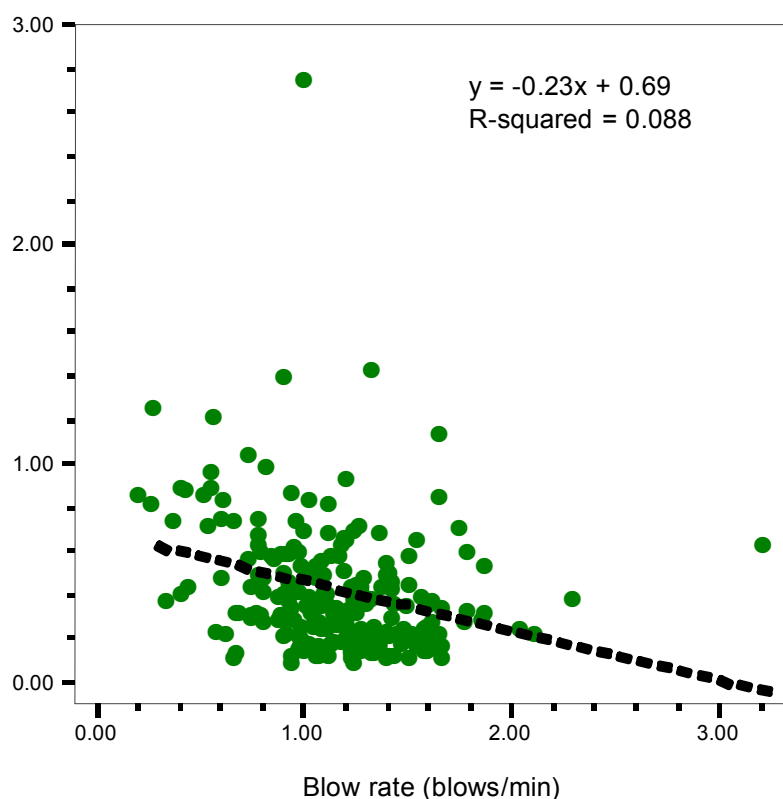


Figure 3.8. Strike rate (strikes/min) plotted against blow rate (blows/min) for all SF samples. The trend line equation and R-squared values are shown on the plot.

The negative relationship dictates that as the blow rate increases, the strike rate decreases. A linear regression also revealed that a significant functional relationship exists between the blow rate (blows/min) and strike rate (strikes/min) in SF minke whales (linear regression, $F_{1,234} = 22.497$, $r^2 = 0.088$, $p = 0.000$).

To examine more closely the nature, the variations and potential causes of this blow and strike rate relationship, Pearson's correlation coefficient tests were used to determine if any

correlations were present between the blow and strike rates with the different types of feeding strategy, the locations within the study area and temporally across the 11 years of study. A summary of the results of these tests can be found in Table 3.4.

SF variable	Type of SF	Area	Year
Blow rate	$r = 0.533$	$r = 0.295$	$r = 0.127$
	$p = 0.000^{**}$	$p = 0.000^{**}$	$p = 0.051$
Strike rate	$r = -0.507$	$r = -0.261$	$r = -0.031$
	$p = 0.000^{**}$	$p = 0.000^{**}$	$p = 0.634$

Table 3.4. Correlation coefficients (r) and probability values (p) obtained from the Pearson's correlation test used to determine correlation between strike rate (strikes/min) and blow rate (blows/min) in surface feeding minke whales. ** indicates results which are significant at the $p < 0.01$ level.

Results showed a significant correlation between blow and strike rates in relation to the different modes of surface feeding and also with regards to the area in which surface feeding occurred ($p = 0.000$ for all). There was no significant correlation between blow and strike rates with respect to the years ($p = 0.051$ and 0.634 , respectively). However, there was very nearly a significant correlation between blow rates and year at the $p < 0.05$ level.

3.5.1. Types of SF

A non-parametric analysis of variance (Mann-Whitney U test) was employed to assess any differences between the blow rates and strike rates of type 1 SF to those of type 2 SF. The results reveal that there was a significant difference in the blow rate between type 1 and type 2 SF ($W_{71, 154} = 1813$, $p = 0.000$). The test also showed significant difference in the strike rates between both these categories of SF ($W_{71, 154} = 1878$, $p = 0.000$). The differences in blow and strike rates between SF types is represented by clustering in the scatter plot shown in Figure 3.9.

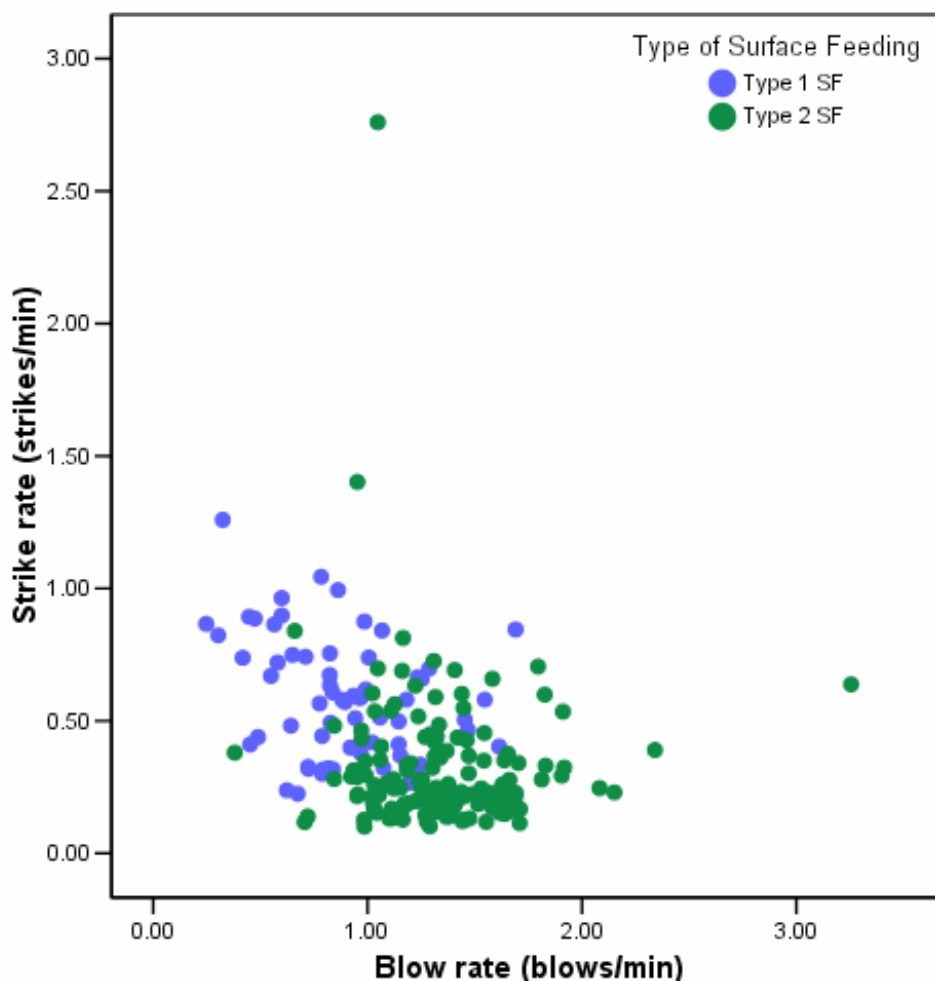


Figure 3.9. Strike rate (strikes/min) plotted against blow rate (blows/min) for all SF samples and showing clustering according to their location within the study area.

Figure 3.9 shows that blow rates are higher in type 2 SF than in type 1. Conversely, the opposite is true for strike rates, which are higher in type 1 than in type 2 SF. The blow rates in type 1 SF are relatively similar to their corresponding strike rates. By comparison, the blow rates in type 2 SF are much higher than their corresponding strike rates. This means that for a given number of strikes there is a much higher proportion of associated blows in type 2 SF than there is in type 1 SF.

Correlations were then sought, within the different types of feeding strategies. Again, Pearson's correlation tests were employed. A summary of the results can be found in Table 3.5.

SF variable	Strike Rate	
	Type 1 SF	Type 2 SF
Blow rate	$r = 0.360$ $p = 0.003^{**}$	$r = -0.085$ $p = 0.298$

Table 3.5. Correlation coefficients (r) and probability values (p) obtained from the Pearson's correlation test used to determine correlation between strike rate (strikes/min) and blow rate (blows/min) in relation to the type of surface feeding. ****** indicates results which are significant at the $p = <0.01$ level.

Only in type 1 SF is there a significant correlation between blow rate and strike rate ($p = 0.003$), whilst the correlation is not statistically significant in type 2 SF ($p = 0.298$). The correlation seen in type 1 SF dictates that as blow rate increases, the strike rate also increases. When testing the statistical significance of the difference between the two correlations coefficients of type 1 and type 2 SF the overall z observed value produced was -3.095 (Appendix F). This number is above the threshold value of -1.960 for significance (outlined in 2.2. Statistical Analysis pp 36). Therefore, the correlation coefficients between strike rate and blow rate for type 1 and type 2 SF are significantly different from one another.

A linear regression revealed that a significant functional relationship exists between the blow rate (blows/min) and strike rate (strikes/min) only in type 1 SF minke whales (linear regression, $F_{1,69} = 4.3087$, $r^2 = 0.059$, $p = 0.042$). Linear regression in type 2 SF did not show a significant relationship between blow rate (blows/min) and strike rate (strikes/min) (linear regression, $F_{1,163} = 0.866$, $r^2 = 0.005$, $p = 0.353$). A scatter plot of the trend between blow and strike rate for both types of SF can be found in Figure 3.10.

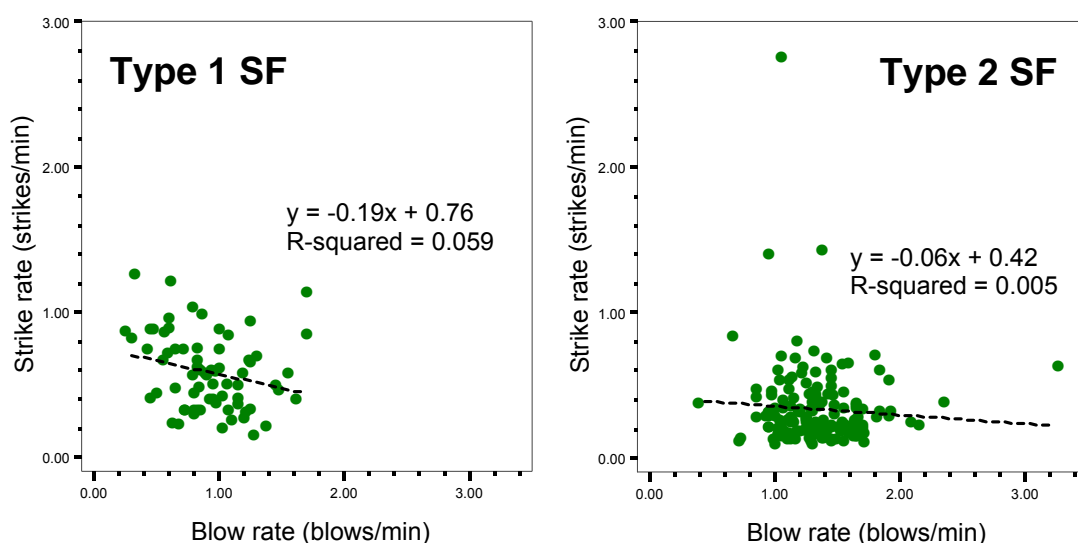


Figure 3.10. Strike rate (strikes/min) plotted against blow rate (blows/min) for type 1 SF and type 2 SF. The trend line equation is and R-squared values are shown on the plot.

3.5.2. SF in the Different Areas

A Kruskal-Wallis analysis of variance was used to test for any differences between the blow rates and strike rates across the three different areas within the study perimeter. The blow rates were significantly distinct between the study areas ($H_2 = 50.349$, $p = 0.000$), as were strike rates ($H_2 = 58.096$, $p = 0.000$). The differences in blow and strike rates between areas is represented by clustering in Figure 3.11. The main pattern observed in Figure 3.11 is the distinction of blow and strike rates between the St. Lawrence Estuary and the Saguenay Fjord. There is no apparent clustering of blow and strike rates within the confluence area.

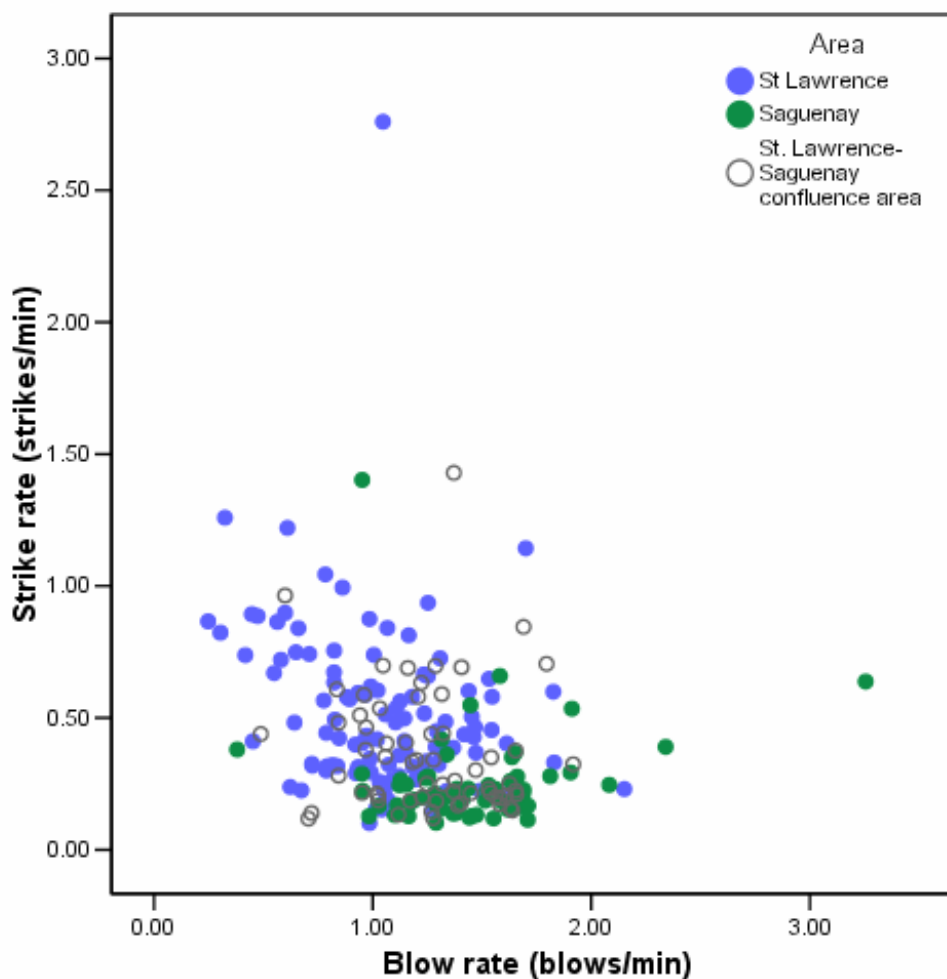


Figure 3.11. Strike rate (strikes/min) plotted against blow rate (blows/min) for all SF samples and showing clustering according to their location within the study area, including the St. Lawrence, the Saguenay Fjord and the St. Lawrence-Saguenay confluence area.

Correlations were sought between blow and strike rate within the different areas. Again, Pearson's product-moment correlation tests were employed. A summary of the results can be found in Table 3.6.

SF variable	Strike rate		
	St. Lawrence	Saguenay Fjord	Saguenay-St. Lawrence confluence
Blow rate	$r = -0.267$ $p = 0.005^{**}$	$r = 0.106$ $p = 0.410$	$r = -0.136$ $p = 0.293$

Table 3.6. Correlation coefficient (r) and probability value (p) obtained from the Pearson's correlation test used to determine correlation between strike rate (strikes/min) and blow rate (blows/min) with regards to the different areas in which SF took place. ****** indicates results which are significant at the $p = <0.01$ level.

Only in the St. Lawrence is there a significant correlation between the blow rate and strike rate ($p = 0.005$), whilst in the other two regions the correlations that exist are not statistically significant: $p = 0.410$ in the Saguenay Fjord and $p = 0.293$ in the confluence area. The correlation that is found between blow and strike rate in the St. Lawrence is a negative one. This is to say that as the blow rates decrease, then the strike rates increase. When the correlation coefficient values were assessed for statistical differences (Appendix F), the z observed value was -1.197 . This value does not exceed the critical value of -1.960 and thus the difference between the correlation coefficients between blow and strike rate in relation to the separate areas was not significant. When the correlation coefficients were analysed for their differences using only the values for the St. Lawrence and the Saguenay Fjord, the resulting z observed value exceeded the threshold limits of non-significance ($z_{obs} = -3.584$). Therefore, the correlation coefficients between blow rates and strike rates are statistically significantly different between the St. Lawrence Estuary and the Saguenay Fjord.

Linear regressions were performed to assess the relationship between blow and strike rates that occurred in the three different zones of the study area. Only in the St. Lawrence was the relationship between blow rate and strike rate significantly functional (linear regression, $F_{1,106} = 8.131$, $r^2 = 0.071$, $p = 0.005$). In the other two areas, the Saguenay Fjord and the St. Lawrence-Saguenay confluence area, the relationship between blow and strike rates were not significant (linear regression, $F_{1,61} = 0.688$, $r^2 = 0.011$, $p = 0.410$ and $F_{1,63} = 1.101$, $r^2 = 0.018$, $p = 0.298$, respectively). The scatter plots of the trend between blow and strike rates in the three different areas can be found in Figure 3.12.

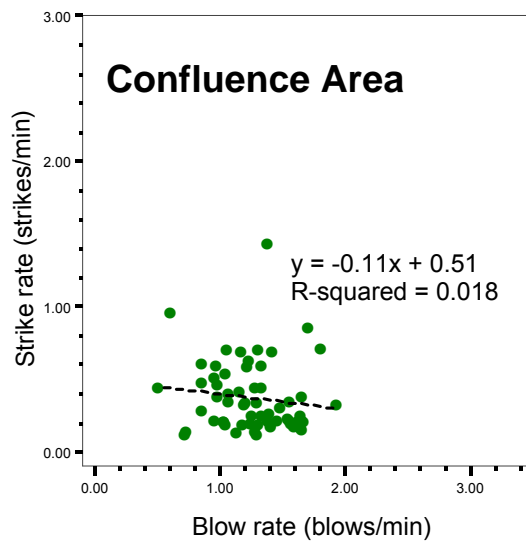
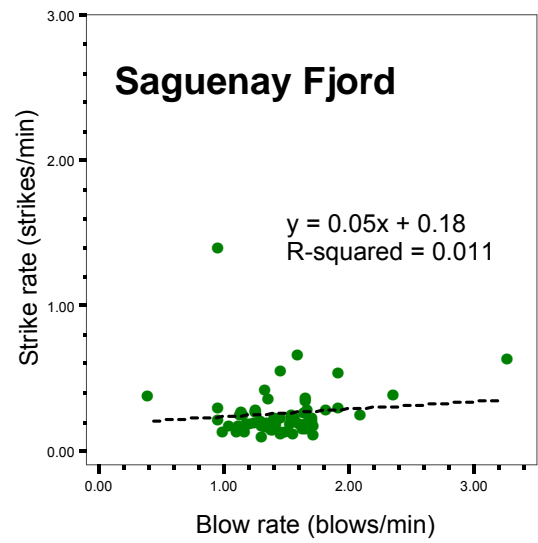
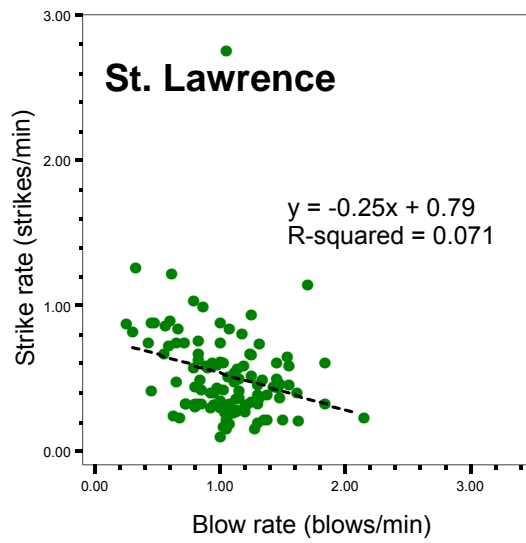


Figure 3.12. Strike rate (strikes/min) plotted against blow rate (blows/min) for the three different zones within the study area: the St. Lawrence, the Saguenay Fjord and the St. Lawrence-Saguenay confluence area. The trend line equation and R-squared values are shown on the plot.

3.5.3. Years

The results from the Pearson's test in Table 3.3 demonstrated that there was no correlation between blow or strike rates over the 11 years of study. The number of samples within each year was too small to analyse within-year correlations between blow and strike rates.

Therefore, in order to compare blow rates and strike rates over time, these two continuous variables were combined to make one dataset: the number of blows per strike. A Kruskal-Wallis analysis of variance was used to test for any differences of blows per strike ratio across the years of the study period. Significant differences in the number of blows per feeding strike were found between different years ($H_{10} = 45.653, p = 0.000;$). This is also represented in Figure 3.13.

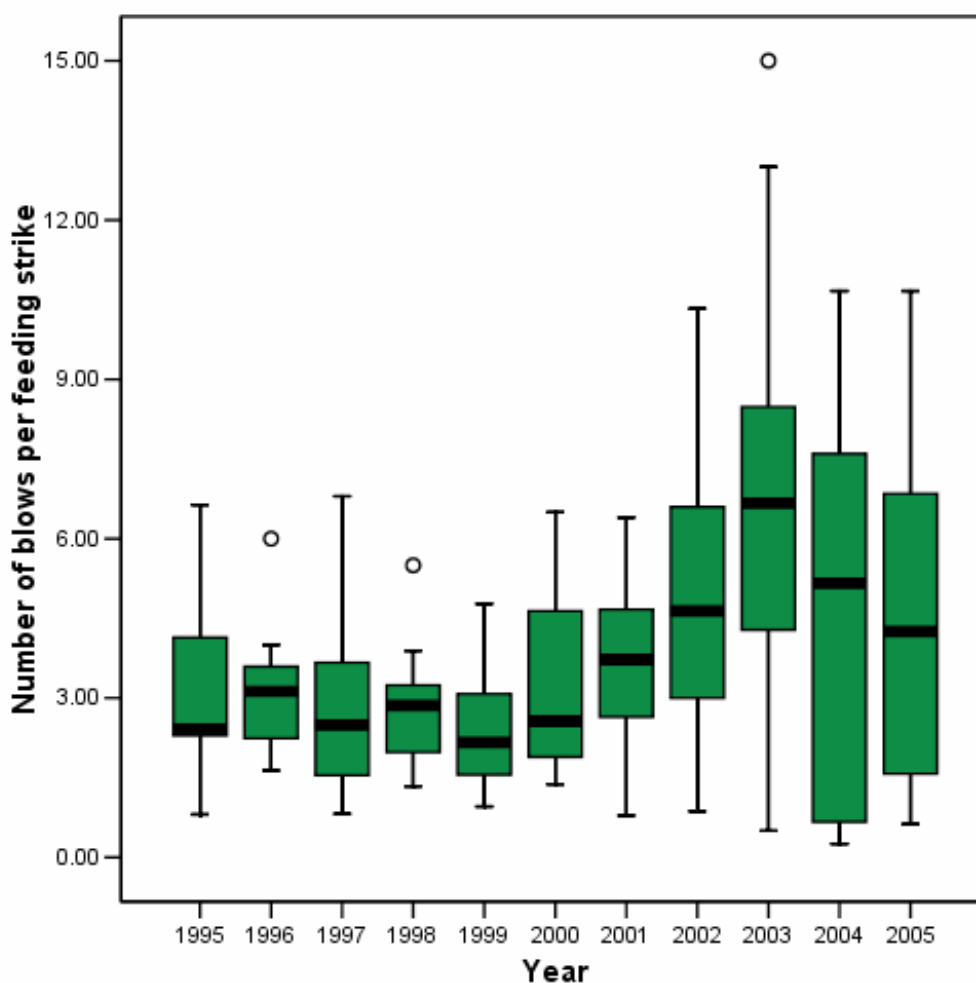


Figure 3.13. Comparison of the number of blows for every strike over the 11 years of study.

From 1995 to 2000 the number of blows per feeding strike remains relatively constant, as shown in Figure 3.11. The mean number of blows per strike from 1995 to 2000 are 3.203, 3.123, 2.801, 3.265, 2.261 and 3.313, respectively. . In subsequent years, the ratio shifted towards an increase in the number of blows until it peaked in 2003 with a mean number of 6.57 blows for every strike. After 2003, there is a gradual decline in the number of blows per feeding strike. However, the ratios do not return to the pre-2000 level.

Because Figure 3.13 comprises data from both types of feeding strategy, the number of blows per feeding strike for type 1 and type 2 SF have been plotted separately, as shown in figure 3.14.

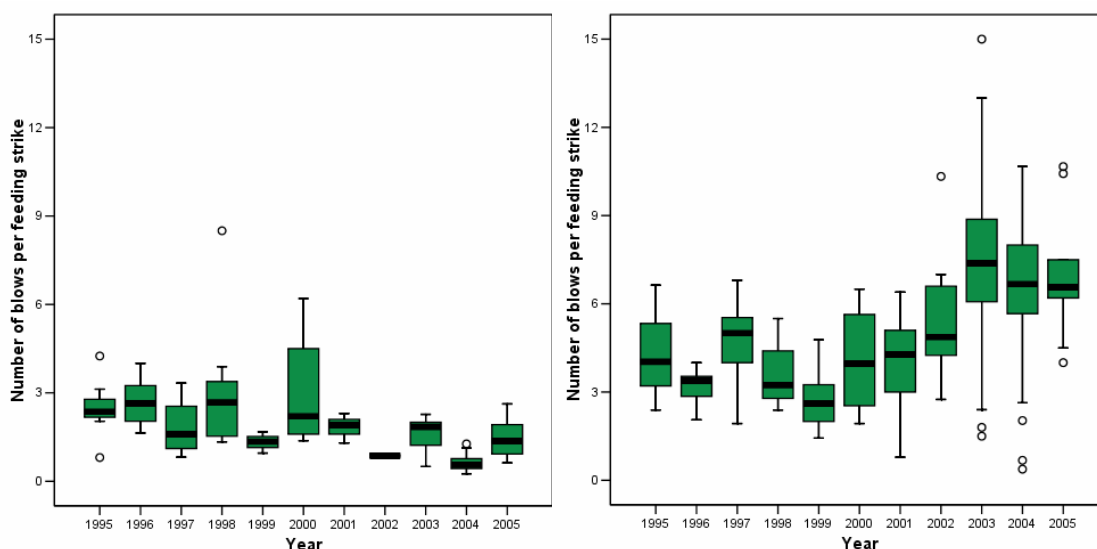


Figure 3.14. The number of blows per strike over the 11 years of study for a) type 1 SF and b) type 2 SF.

The number of blows per feeding strike remains relatively constant in the first 6 years of the study in type 1 SF, as shown in Figure 3.14. However, unlike the pattern in Figure 3.13, the blow to strike ratio decreases, so a fewer number of blows are occurring for each strike. By contrast, type 2 SF shows a similar pattern to that in Figure 3.13 of a greater number of blows per feeding strike as from the year 2000, which again peaks in 2003 and then decreases gradually in 2004 and 2005.

Pearson's tests were performed to assess whether a correlation was present between the number of blows per feeding strike and the years. This was done for all SF samples combined as well as for both feeding strategies individually. A summary of the results can be found in Table 3.7.

SF Variable	Year
Number of blows per feeding strike	
All SF	$r = 0.333$ $p = 0.000^{**}$
Type 1 SF	$r = 0.345$ $p = 0.003^{**}$
Type 2 SF	$r = 0.458$ $p = 0.000^{**}$

Table 3.7. Correlation coefficients (r) and probability values (p) obtained from the Pearson's correlation test used to determine any correlation between the number of blows per feeding strike and the year, from 1995 to 2005. ****** indicates results which are significant at the $p = <0.01$ level.

These correlation coefficients reflect the results in Figure 3.13 and 3.14. The number of blows per strike for all SF shows a strong, positive, and significant correlation with years ($p = 0.000$). The same is true in type 2 SF ($p = 0.003$), although the relationship here is stronger ($r = 0.333$ and $r = 0.458$, All SF and type 2 SF, respectively). This indicates that from the years 1995 through to 2005, the number of blows for each feeding strike increases. In type 1 SF, the number of blows per feeding strike displays a strongly negative relationship with years, which again is significant ($p = 0.000$). It is assumed that as the years progress, the number of blows per feeding strike diminishes.

3.6. Summary

A number of observations, patterns and correlations were found to be significant from the results of this study. These have been summarised below:

- o Minke whales had a mean surfacing interval of 54.786 sec in the St. Lawrence River Estuary and Saguenay Fjord region.
- o Minke whales had highly variable breathing patterns according to their behaviour.
- o The highest mean surfacing intervals were found in TRV behaviour and the lowest were found in SF animals.
- o NS behaviour was typified by dive durations of 149 sec, time between blows of 15 sec, surface durations of 50 sec and 4 blows in a surfacing.
- o DF behaviour was typified by dive durations of 266 sec, time between blows of 14 sec, surface durations of 82 sec and 7 blows in a surfacing.
- o TRV behaviour was typified by dive durations of 168 sec, time between blows of 21 sec, surface durations of 53 sec and 3 blows in a surfacing.
- o SF behaviour did not comply with the blow-series-and-dive ventilation pattern.
- o Two types of SF were identified: type 1 SF where the engulfment manoeuvres include a simultaneous gas exchange; and type 2 SF, where the engulfment strikes do not permit a ventilation event.
- o A significant negative relationship was found between blow rates and strike rates of SF minke whales. As blow rates decreased, strike rates increased.

- o Significant differences in blow rates and strike rates existed between the 2 types of SF and between the different zones within the study area.
- o (The differences in correlation coefficients of blow rates and strike rates between the two SF types were statistically significant. The differences in correlation coefficients of blow rates and strike rates between the three zones within the study area were statistically significant).
- o Significant positive correlations between blow and strike rates were found in type 1 SF and in animals SF in the St. Lawrence Estuary. As blow rates increased, strike rates increased.
- o No significant correlations between blow rates and strike rates were found in type 2 SF or in SF taking place in the Saguenay Fjord or the confluence area.
- o There were significant differences in the number of blows per feeding strike over the years of study. As the years progressed, the number of blows per surface feeding strike increased. This was true in type 2 SF. The number of blows per surface feeding strike in type 1 SF decreased from 1995 to 2005.

4. DISCUSSION

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4.1. Mean Surfacing Interval

The minke whale ventilation studies performed in the St. Lawrence River Estuary and the Saguenay Fjord throughout the summer seasons of 1995 through to 2005 resulted in a range of surfacing intervals of 1 to 749 sec and a mean of 54.786 sec. The mean surfacing intervals obtained from this study are some of the lowest for minke whales yet published (Table 4.1).

Mean Surfacing Interval (sec)	Location	Author
74.600	Norwegian waters	Folkow & Blix, 1993
68.300	Icelandic waters	Gunnlaugsson, 1989
68.703	Norwegian waters	Joyce et al, 1989
54.628	Icelandic waters	Joyce et al, 1990
95.816	Antarctic waters	Joyce, 1982
80.600	-	Øen, 1990 (unpub)*
85.714	Norwegian waters	Øien et al, 1990
93.264	Monterey Bay, California	Stern, 1992
66.100	Isle of Mull, Scotland	Stockin et al, 2001
75.000	Antarctic waters	Ward, 1988

Table 4.1. Mean surfacing intervals of minke whales obtained from other studies. * quoted by Stockin et al (2001).

The results of this study are comparable to the mean blow interval of 54.628 sec measured by Joyce et al (1990), in an Icelandic minke whale. However, similarities between the results from the present study to minke surfacing intervals of other studies are otherwise few. For example, minke whales around the Isle of Mull, Scotland had a mean surfacing interval of 66.100 sec (Stockin et al, 2001). Similarly, Gunnlaugsson (1989) found blow intervals of 68.300 sec in Icelandic minke whales, whilst Norwegian minke whales were found to have surfacing intervals of 68.703 (Joyce et al, 1989). Data for the Isle of Mull minke whales were collected from commercial whale watching boats whose primary objective was to target relatively active animals, such as surface feeding minke whales (Tetley, pers. comm.). Although this would favour shorter surfacing intervals, the methodology has probably derived inter-surfacing durations that are based on a narrow range of behaviours and thus may not be truly representative of actual blow rates. Most of the experiments performed by Gunnlaugsson (1989) were conducted in shallow waters and in animals that were apparently feeding. Breathing rate data from animals in deeper waters were only collected from one minke whale in this study. It is possible that the blow-rhythms obtained in this study are of animals, which are relatively easy to keep track of (due to surface foraging activity) and again may not be representative of the whole population (Gunnlaugsson, 1989).

The mean surfacing interval of surface feeding minke whales from this study is 43.452 sec. Near surface and deep feeding behaviours have blow intervals of 52.034 sec and 52.495 sec, respectively. If it is the case that the majority of the blow samples collected in the above studies are from feeding individuals, then there are still considerable ventilatory rate differences between these values and those of the present study. This may demonstrate geographical variation in blow rates between minke whales in the eastern North Atlantic and those of St. Lawrence area. It is possible that different feeding strategies employed by minke whales in these two regions are responsible for the differences in surfacing rates. In areas such as Scotland, bird associated foraging is a prevalent feeding method (Hoelzel et al, 1989; Wells et al, 1999). Here the whales exploit concentrations of fish fry that have been 'prepared' and concentrated at the air-water interface by flocks of feeding gulls and diving birds from above and often by predatory fish and sharks from below. The bird association feeders are advantaged in two ways: first, whales may detect feeding birds audibly and are effectively 'summoned' to the feeding area and second, on arrival, there is a ready concentrated prey resource that needs no further entrapment. Consequently, the level of physical activity in this feeding strategy is low. Conversely, the main form of surface feeding analysed in the St. Lawrence is that of patch fishing, which requires a high expenditure of energy in order to corral the prey into high concentrations before engulfment commences (Lynas & Sylvestre, 1988). This activity is of such an intense nature that it is not unreasonable to suppose that patch-feeding whales accrue oxygen debts. Consequently, in order to repay this debt, high levels of gas exchange are required, which may explain the lower surfacing intervals observed in this study in comparison to other areas. Stockin et al (2001) stated that minke whales, did not show extensive aerial behaviour and that the most conspicuous visual cue is the blow. Therefore, it is feasible to suggest that even in lunge feeding (the more energetic feeding strategy and one more akin to patch-fishing) the activity may be less acrobatic and thus less intense allowing more prolonged blow intervals than in the St. Lawrence.

Other studies have even longer surfacing intervals (Table 4.1). Minke whales off the coast of Norway have been recorded having surfacing intervals of 85.714 sec (Øien et al, 1990), 80.600 sec (Øien, unpublished data), 74.600 sec (Folkow & Blix, 1993) and 95.816 sec (Joyce, 1982). Øien et al (1990) acquired blow rates from two whaling vessels and a sightings survey vessel. No significant differences were found between the surfacing intervals collected by the whaling vessels and by the sightings survey vessel. The authors therefore deduced, that it was difficult to derive any firm conclusions as to whether the search for and chasing of these whales altered minke whale behaviour in terms of changes in the ventilation rates. However, fin whales show a shift to avoidance behaviour when disturbed by even small vessels. This behavioural change is characterised by higher surface velocities and lower blow-rates (Jahoda et al, 2003). As minke whales were being chased during these studies, it is likely that the breathing rates recorded by Øien et al

(1990) are biased downwards due to the surfacing rates associated with avoidance. Many of the above studies have based their surfacing rates on a small number of individual animals over a short period of time (Øien, unpublished data; Folkow & Blix, 1993) This possibly gives rise to the lengthier blow intervals than in the present study. Stern (1992) measured the blow rates of minke whales in Monterey Bay, California and derived extremely high mean surfacing intervals of 93.264 sec. In the methodology, Stern (1992) inferred that samples were collected from whales that were majority travelling with predictable direction, speed and ventilation patterns. This was to the exclusion of more erratic behaviours in an attempt to remove any data that were deemed to incorporate blow rates of disturbed whales due to the presence of the vessel. Travelling animals in the current report had the highest surfacing intervals of all other behaviours recorded and although still much lower (71.162 sec), it corresponds well that blow intervals are notably high in Stern's study. It may be the case, that in excluding apparently more active behaviours, the blow intervals recorded by Stern (1992) are biased upwards. Folkow & Blix (1993) were able to monitor and track the behaviour of whales at night during which they appeared to 'sleep' for certain lengths of time, swimming very slowly and just barely breaking the surface in order to breathe. These bouts of resting will have contributed substantially to lengthening surfacing intervals. The investigation by Joyce (1982) was performed in the Antarctic. Antarctic minke whales feed predominantly on euphausiid krill, which presumably involves less intense activity than predation on shoaling fish as no entrapment is required. Therefore, longer surfacing intervals may be expected. Moreover, this study reported difficult environmental conditions (the angles of sun with respect to the animals and the vessel) that caused blows to become effectively invisible to the observer. Consequently, artificially long surfacing intervals are likely reported due to the substantial probability of missed blows (Joyce, 1982).

Another factor that possibly affects surfacing intervals is the depth of water in which the whales are found. Some authors have suggested that higher surfacing rates are likely to occur in shallower areas, such as sheltered fjords and coastal regions, whilst low rates of ventilation are probable in more pelagic habitats (Øien et al, 1990). Many Icelandic minke whalers have noticed this trend (Gunnlaugsson, 1989). The difference in the vertical distribution of prey is likely responsible, in part, for the different dive-surfacing rhythms seen between inland and oceanic areas (Gunnlaugsson, 1989). The water depths of the St. Lawrence region may be shallower than those of other studies. The dynamics of this area are such that high concentrations of food are found at surface or near surface. These factors combined may contribute to a remarkably short mean surfacing interval.

Studies have been performed using various methods, which may, in part, be accountable for the wide variety of results for surfacing intervals. Some investigations have used solely visual observations to obtain minke whale blow rates (Joyce, 1982; Gunnlaugsson, 1989; Joyce et al, 1989; Øien et al, 1990; Stern, 1992), whilst others have based data collection

mainly from radio telemetry devices (Joyce et al, 1990; Folkow & Blix, 1993). Although authors argue that the results obtained by the two methods are not significantly different (Stockin et al, 2001) it does add a further limitation in terms of data comparability (Lagerquist et al, 2000). For example, 1) the whale may respond to being tagged by changing its normal surfacing pattern; 2) the whale may react to the vessel and alter its ventilation pattern; 3) more signals than surfacings are a possibility, especially if the radio antennae clears the water surface without the minke taking a breathe; 4) visual observations may underestimate surfacing rates as observers may miss blows, which would be recorded using radio telemetry; 5) if more than one whale is present confusion may arise as to which whale produces the blow in visual observations; and 6) there may be differences in surfacing behaviour between the period during which visual observations are taken (day) and radio tag sampling (both day and night). For greater discussion refer to Joyce et al, (1990).

The methods employed to obtain mean surfacing intervals in the present study do have inherent limitations. Because blow rate data were primarily sought from different behaviours, blow samples were not always collected in an objective fashion therefore causing the final dataset to have an inaccurate behavioural composition i.e. the dataset may have a higher number of samples from one particular behaviour type over another. Subsequently, the mean surfacing intervals of four behaviours (near surface feeding, depth feeding, travelling and surface feeding) were pooled together and averaged to obtain an overall mean surfacing interval for minke whales in the St. Lawrence. This assumes that minke whales partake in these four activities alone, each of which constitutes 25% of the whales' time budget. This means that no low blow rate activities, such as resting, standby and possibly search mode, have been incorporated into the final surfacing interval, causing a bias towards short blow intervals. Seeing as the three behaviours (NS, DF and SF) are all high-energy activities, and together constitute 75% of the whales' time budget, the overall mean surfacing interval is likely disproportionately high. These factors may contribute strongly to shorter mean surfacing intervals than those recorded in other studies. Therefore, the overall mean blow intervals derived from this study are not a fully accurate representation of overall blow rates of minke whales in this area.

4.2. Ventilation Characteristics

As marine mammals are constrained to the surface for oxygen (Würsig et al, 1984) they have evolved particular adaptations that optimise oxygen uptake relative to their time spent at the sea surface (Kramer, 1988), which in concert with their ventilatory rhythms allows the animal to extend underwater periods. This rhythm usually takes the format of a series of clustered breaths between periods of extended submergence or apnoea. This structure is highly flexible according to the behaviour, as demonstrated by the results herein.

Diving animals show a preference for aerobic metabolic pathways as it avoids the deleterious effects of the accumulation of anaerobic end products such as lactate, which need to be metabolised and thus prolonging recovery times. If an animal makes an aerobic dive, it must return to the surface before its O₂ reserves in the blood, muscles and other tissues are exhausted (Sumich, 1994; Carbone & Houston, 1996; Croll et al, 2001). The aerobic dive limit (ADL) is defined as 'the maximum breath-hold that is possible without an increase in the blood lactic acid concentration during or after a dive' (Kooyman et al, 1980). If dive durations are a simple function of the amount of O₂ an individual can carry in their bodies, then a diver can be expected to remain submerged until its oxygen stores are nearly exhausted (Boyd, 1997). However, many natural divers, particularly cetaceans, show a submergence time that is much shorter than that expected from their potential dive durations (Croll et al, 2001). Theoretically, it is optimal for divers to return to the surface prior to all O₂ reserves being used up, providing the time taken to replenish O₂ at the surface increases in an asymptotic fashion of time spent at the surface (Kramer, 1988). This is to say that upon arrival at the surface there may be a brief lag in which animals expire before inspiring, and then oxygen is replenished quickly in the lungs, followed by an increase of O₂ in the blood and muscular tissues. The initial rate of re-oxygenation is greatest in the earlier parts of the surfacing but as the oxygen stores of the body are recharged over the course of several breaths, the partial pressure differentials between those of the internal body and those of the external environment decline. Consequently, the rates of diffusion decrease and the net oxygen gain is reduced, producing a curve of diminishing returns (Kramer, 1988; Lynas & Sylvestre, 1988; Butler & Jones, 1997). Not only, therefore, is it more beneficial for the animal to return to the surface before it becomes fully de-oxygenated but it appears that optimal oxygen stores on uptake are also less than maximum. Consequently, the greatest rate of re-oxygenation can be achieved if the animals spend short times at the surface. This will also maximise the proportion of time spent submerged but this would require a behaviour that consists of a succession of short dives. Thus near-surface feeding minke whales, exploiting prey at relatively shallow depths (10-50 m), exploit this ventilation format. In this way they are able to spend more time foraging by making short dives that are less than the maximum potential dive duration. In deep feeding animals, foraging at depths in excess of 50 m, travel time to and from the feeding site itself becomes a gradually increasing component of the diving time budget. Therefore, the strategy employed by NS animals is not applicable. Consequently, as the distance increases, the amount of time spent at the surface should also increase together with amount of oxygen carried in the lung, blood and muscles (Figure 4.1). These behavioural responses (in the form of ventilatory regulation) to physiological demands may help explain why the ventilation characteristics of dive duration and surface duration are significantly longer in deep feeding minke whales than those foraging at shallower, near-surface depths.

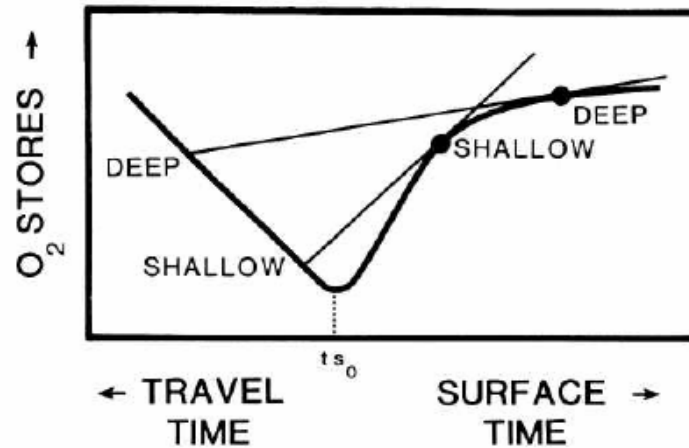


Figure 4.1. The effect of dive depth on optimal surface time. At shallow water depths, the time and oxygen stores expended on travel to and from the surface are small, and the optimal (indicated by the dot) is small. For deeper dives, the cost of travel in time and oxygen are greater, and longer surface times maximise the net rate of oxygen gain. (Figure taken from Kramer, 1988).

Apnoea in diving mammals does bring physiological costs, which come in the form of hypoxia (low oxygen-tissue levels as well as low oxygen-body water levels) and hypercapnea (where high blood-carbon dioxide partial pressures occur as a result of increased metabolism and perpetuated by hypoventilation). If a high metabolic rate is associated with the underwater activity, such as feeding and corralling/entrapping prey, as is the case for St. Lawrence minke whales then the high rate of O_2 utilisation and CO_2 production will hasten the development of hypercapnic hypoxia. This means that the ventilatory threshold will be reached sooner. The question can then be posed as to how minke whales feeding at depths greater than 50 m are able to maintain repeated aerobic dives, extend their underwater time span, and simultaneously avoid the effects of hypercapnea. The answer lies in hyperventilation. Hyperventilation reduces the blood- CO_2 pressure and recharges the body's oxygen stores. DF whales will use proportionally more O_2 and produce greater amounts of CO_2 than NS animals. It stands to reason, therefore, that an increased number of ventilations per surfacing are required to maintain the appropriate O_2 - CO_2 balance in order to permit a continued aerobic diving schedule in DF animals. Whilst aerobic metabolism most certainly predominates during NS dives, it is possible that DF whales may switch to an anaerobic metabolism due to the length of time submerged and the high energetic and metabolic costs associated with entrapment and feeding. Again, this would further explain the higher surface duration and higher number of blows per surfacing in DF than NS animals.

As minke whales surface for one breath at a time only they are constrained to the surface for a set amount of time in order to allow an appropriate number of ventilations to fully readjust their body O_2 and CO_2 stores after a long dive. Given that it takes more time to liberate CO_2 than it does to take up O_2 (Boutilier et al, 2001), it can be questioned as to whether these animals would ever forego full readjustments of their CO_2 levels. By rapidly charging themselves with O_2 , in order to delay hypercapnea, the whales could potentially

cut the surface period short, whilst still diving aerobically and 'put up with' the added CO₂ burden, and eventually offload this build-up at a later date by spending longer periods at the surface (i.e. during a resting period). It is possible to see the advantage of this quick upload of O₂, particularly in both NS and DF minke whales where returning to the site of food is of high priority and temporarily outweighs the benefits of adjustment of body gas partial pressures. This may, in part, help explain the slight difference in time between blows in a surfacing between NS and DF minke whales. Although not significantly different, DF demonstrated more rapid ventilations in a surfacing than NS. Whilst the urgency to return to the food might be greater in the DF (due to increased distance and time away from the prey), the ventilations may serve more as an 'O₂ snatch'. However, this difference in the inter-blow intervals in a surfacing is more likely associated with a depth feeding whale wanting to minimise its time away from the food source. A DF whale requires more time at the surface, than an NS whale, to allow a greater number of respirations in order to readjust the body gas quotas and stave off the development of hypercapnea. In this scenario, breathing and feeding are incompatible, so the whale may be trying to reduce the time away from the food source by reducing the time between blows, which still enables an adequate time span to re-oxygenate its body tissues. There is a lower limit to reducing the time between blows in as far as increased surface blow rates is probably to the expense of tidal volume (Dolphin, 1987b; Lafortuna et al, 2003).

It is not unreasonable to envisage similarities in the nature of travelling whales (as defined in this study) to a migrating behaviour. Dorsey et al (1989) observed a significantly different pattern of breathing in migrating bowhead whales than those in summer feeding grounds. Würsig et al (1984) observed that the overall surfacing intervals, number of blows per surfacing, surface duration and dive time all tended to be longer in a travelling whale. These observations are different to those of the present study, with the exception of overall surfacing intervals, which was longest in TRV animals. In contradiction with Dorsey's findings, travelling minke whales had the lowest number of ventilations of all other behaviours. The main focus in travelling is efficiency of displacement. Lafortuna et al (2003) noticed that travelling fin whales represented an optimised locomotor performance by maximising the distance travelled with respect to the water surface and minimising hydrodynamic drag. Lafortuna et al (2003) outlined ways in which drag can be reduced: First, drag becomes minimal beyond a depth of more than three times the body diameter of the swimming organism (Sumich, 1983; Lafortuna et al, 2003). Second, by avoiding the air-water interface hydrodynamic performance is further enhanced (Würsig et al, 1984). Therefore, it is optimal for a travelling whale to remain at depths equivalent to three body widths (3-5 m in the case of the minke whale) and to minimise the number of surfacings. This is coherent with the ventilatory behaviours seen in travelling minke whales. The inter-blow interval in a surfacing is remarkably longer than those seen in either NS or DF. Although it may be ideal for a travelling minke to remain at depths of 3-5 m, the need to maximise time at this depth may not be as pressing as in NS or DF, which may help explain

the distinctly lengthened time between blows during surfacings of TRV animals. Sumich (1983) also suggested that the short breath holds (blow intervals within a surfacing) serve to maximise the utilisation of O₂ from the inspired air. Because of the shallow depths occupied by a travelling whale, oxygen uptake is not of primary concern, which may be one reason as to why these whales exhibit a less conservative blow series and dive structure.

In the same way surface feeding minke whales do not adhere to such a precise ventilation series and dive structure, as do the other behaviours. Being so close to the surface, oxygen as a resource is no longer a limitation and thus the whales are not confronted with the trade-off of breathing versus feeding. No longer restrained by maintaining an aerobic internal function or optimising time at the surface and/or depths, the constraint of the blow series and dive is lifted. In the same way, engulfment manoeuvres in type 2 SF do not permit a simultaneous breathing event and so the whale may not be as 'free' in terms of oxygen uptake as in type 1 SF. For this reason, type 2 SF may appear to organise their ventilation structure such that it has a slight tendency for the blow-series and dive integrity that is not observed in type 1 SF. The same phenomenon was observed in surface feeding bowhead whales (Dorsey et al, 1989). Whilst feeding on zooplankton near the surface, the whales were found to breath freely and unconstrained by the usual dive pattern.

Most studies examining surfacing intervals of whales have needed to make a distinction between short duration dives (in this study termed 'time between blows in a surfacing'), and longer terminal dives (in this study termed 'dive duration') (Würsig et al, 1984; Dolphin, 1987a; 1987b; Dorsey et al, 1989; Kopelman & Sadove, 1995; Jahoda et al, 2003). Since the intervals between blows form a continuum, it is often difficult to distinguish between intra-cluster dives and true dives. Many researchers have chosen arbitrary inter-blow intervals as breakpoints (Dolphin, 1987b; Chu, 1988; Michaud & Giard, 1997; this study). A more accurate method of deciphering true dives from blows intervals within a surfacing is by using the log-survivorship analysis model (Stone et al, 1992; Kopelman & Sadove, 1995). In log-survivorship analysis the data is converted from a frequency distribution to a survivorship table and plotted semi-logarithmically with the abscissa being time and the ordinate being the logarithm of the number of intervals > time (Kopelman & Sadove, 1995). Breakpoints can then be distinguished by significant changes in the slope of the log-survivorship function. This gives a diving interval based on actual data and removes the need for 'choosing' a breakpoint interval, which may cause biases in later results. Although it is quite easy to see the differences in intervals between the dive durations and the inter-blow durations for DF, and to a lesser extent for NS whales, it is less apparent in TRV animals that demonstrate a less predictable ventilation pattern. Using log-survivorship analyses would more accurately separate out true dives from inter-blow durations and thus a more precise breathing regime for travelling minke whales could be determined. Further, the log survivorship method could be applied to the surfacing intervals of SF, which may

reveal a structure to the ventilation patterns of this behaviour type that may not otherwise be seen.

Minke whales in this area do not appear to be affected by the presence of boats (such as the research vessel) whilst performing activities such as SF, NS or DF. This is possibly due to the intensity of their foraging activity required to entrap their prey. However, it is during the less energetically demanding behaviours such as travelling that the whales are more susceptible to disturbance and may be more likely to show avoidance behaviour (Tscherter, pers. comm.). Many studies have shown that disturbance of whales result in evasive behaviours that reduce the surfacing intervals (Jahoda et al, 2003). Although some sampled whales may have been disturbed by the presence of the vessel, this occurred in only a few number of cases and thus their impact on ventilation rates are likely negligible. This area of the St. Lawrence has a high level of shipping activity and a very large whale watching industry (Michaud & Giard, 1999), which tends to suggest that whales have habituated to the presence of so many vessels. This means that the effects on the whales' breathing regimes due to disturbance by boat presence are minimal.

Although the categorisation process was straightforward in the vast majority of cases, particularly for SF, NS and DF, this was not necessarily the case for TRV whales. Whales that may have been travelling in a 'search mode' or travelling as part of line fishing behaviour will have been included into the TRV category. Although, these animals were still travelling by definition, the objective of their behaviour may be different. In a true traveller (akin to travelling seen in migration) the main intention is displacement from one area to the other, whilst in search mode or line fishing; the main aim is not a shift in location but seeking out food. These differences in behaviours will probably be reflected in the surfacing and ventilation arrangement. For example, Dolphin (1987b) observed that searching-browsing behaviours included those with erratic swimming patterns, such as rapid, apparently non-oriented changes in speed and direction as well as highly variable ventilation and dive patterns. As the present study has overlooked these differences, the results of travelling behaviour will be a combination of true travelling and possibly searching and line fishing behaviours. Therefore, future work should focus on how to visually define these behaviours in the field allowing for subsequent improved ventilatory assessment.

4.3. Surface Feeding Ventilation Characteristics

This study has revealed clear differences between the blow rates and strike rates of type 1 and 2 SF. The correlation coefficients of blow and strike rates between the two different feeding strategies are also significantly different. It is interesting to note also that there are significant differences in the blow and strike rates between different zones in the study area, particularly between the St. Lawrence Estuary and the Saguenay Fjord. It is apparent that the St. Lawrence generally has lower blow rates and strike rates that are relatively equivalent. In the Saguenay blow rates are much higher than the corresponding strike

rates. The principal reason for the differences in blow and strike rates between zones is mainly due to the different occurrence of feeding types that occur within these areas. Whilst in the St. Lawrence, there is a mix of feeding types, no type 1 SF sample has ever been documented so far in the Saguenay Fjord. Only type 2 SF samples have been recorded.

Thus, the question to address here is why there are such distinct differences in the breathing regimes between type 1 SF and type 2 SF. As previously mentioned, the feeding strikes in type 2 SF do not permit a simultaneous ventilation, whilst those of type 1 SF do. Without this limitation, type 1 SF are able to perform a continuous series of engulfment manoeuvres, whilst type 2 SF will need to intersperse feeding strikes with a series of respirations. Further, it appears that entrapment of prey is highly associated with type 2 SF, whereas it does not seem to be such a prevalent feature of type 1 SF, although this still remains to be tested. Therefore, as entrapment is such an energetic activity, it follows that type 2 SF requires a higher ventilation rate per strike than in type 1 SF. At this point, the impression given is that type 2 SF is more energetically costly and reaps fewer benefits due to lower strike rates than type 1 SF. It may thus be regarded as a less favourable feeding strategy. However, in order for both these strategies to be successful, they must enjoy relatively equal pay-offs.

There are two main ideas addressing this issue. The first hypothesis is that whilst entrapment manoeuvres are relatively easily identified in type 2 SF, they are not apparent in type 1 SF. It may be that entrapment activities in type 1 SF are thought to occur at greater depths, and are not visible to the observer at the surface. In this way type 1 SF may have similar energetic demands as those of type 2 SF (Tscherter, pers. comm.). This suggestion, however, does not explain the predominance of type 1 SF in the St. Lawrence and only type 2 SF being seen in the Saguenay. The second thought, therefore, proposes that as Saguenay waters do not allow for extensive visibility and baleen whales are predominantly visual predators (Heithaus & Dill, 2002), the minke whale in the Fjord will shoal the capelin towards the surface, in order to enhance potential visibility of the prey. In this way the whales maximise the chance of food intake. By contrast, the water has greater clarity in the St. Lawrence, allowing the minke whale to immediately and repeatedly engulf prey on localised food patches, without the requirement of prior entrapment. In this way, type 1 SF develops (Tetley, pers. comm.). However, this latter idea does not account for the presence of type 2 SF in the St. Lawrence. Both these suggestions need further testing in order to help explain the differences between the two surface feeding types as well as their occurrence in the three zones of the study area.

It may be the case that the bulk of type 1 SF occurs at high tide when large-scale upwellings at the Laurentian Channel and neighbouring areas are maximal. These systems cause the concentration of euphausiids and, in turn capelin. In this instance, type 1 SF may be the most favourable strategy to exploit a prey resource that is limited in terms of time i.e.

tidal changes. The dynamics of the St. Lawrence are such that it is able to support a high number of feeding minke whales in a localised area. In such an active locale, adopting the entrapment-style strategy of type 2 SF may not be suitable as corralling prey is not likely feasible in such a busy situation. Further, the presence of several whales may have an impact on the prey such that several shoals of fish are isolated and concentrated as a result. The author is not suggesting any form of conscious cooperative functioning in these whales, but that their presence merely has additional benefits in terms of ease of prey consumption. The three-layer system found in the St. Lawrence may further confine prey. High concentrations of capelin also occur in frontal zones of the confluence area.

Therefore, as entrapment is not necessary in these scenarios, it follows that type 1 SF is the more favourable method to employ here. Type 2 SF may then be used in the St. Lawrence or confluence area at times when the food source is not quite so aggregated (non-high tide periods) and when fewer minke whales are present. Some studies of foraging behaviour have suggested that individuals using the same strategy may show consistent preference for a particular, smaller-scale feeding technique (Lynas & Sylvestre, 1988; Weinrich et al, 1992; Thompson et al, 2003). The Saguenay represents an environmental patch of relative constancy with no stratification or processes resulting in naturally aggregated food patches (De Ladurantaye et al, 1984; Schafer et al; 1990). This dictates that the entrapment-style of type 2 SF is still necessary. Minke whales in the Fjord show a high degree of site fidelity and tenacity (Lynas et al, 2004) and are thus able to enhance their feeding performance within their specific micro-scale environment. Therefore, minke whales feeding in this area are more efficient at food acquisition, even though the energy expended to obtain it is seemingly higher than in their type 1 SF counterparts. In this way both type 1 and type 2 SF strategies would enjoy equal pay-offs. Unfortunately, the present study was not able to pursue this conjecture in any further detail.

The final investigation regarding the ventilation characteristics of SF was the inter-year differences in the number of blows per feeding strike. The number of blows per strike remained relatively stable from 1995 through to the year 2000 but then increased and peaked in 2003. 2004 and 2005 saw a gradual decrease in the number of blows per strike, but did not return to pre-2000 levels. If the blow to strike ratio serves as an indication of foraging success then these results suggests that the quantity of food available for the minke whales was diminishing after the year 2000 and more 'work' was required for food acquisition. Not all years have the same proportion of type 1 and type 2 SF. Therefore, these were separated to remove any impact this may have in the results. Interestingly, they showed opposite trends. Whilst type 2 SF demonstrated a similar pattern to overall SF blow ratios with years, type 1 SF saw a reduction in the number of blows per feeding strike with years. Whilst type 1 SF seemingly represents improved foraging success from 2000 onwards (due to a decreasing number of blows per strike), type 2 SF apparently shows decreasing foraging success. These are confounding results.

Some indices have suggested that capelin abundances in eastern Canadian waters have been low since the 1990s, whilst other analyses have suggested strong capelin classes since about 1992 (Rose & O'Driscoll, 2002; Baird, 2003). Carscadden & Vilhjálmsson (2002) stated that acoustic abundance estimates of capelin revealed dramatic fluctuations from year to year seeing as this species has high mortality and short life spans. Although there is controversy about the current status of capelin stock off eastern Canada (Rose & O'Driscoll, 2002; Baird, 2003), anecdotal information has observed a decrease in the amount of food available for large marine mammals. This corresponds to fewer of the larger members of the Balaenopteridae, such as fin and blue whales, returning to the St. Lawrence feeding grounds (Thompson et al, 2003). Minke (and humpback whales) are distinct from other mysticetes, in that they show a threshold response to prey availability, only using a habitat once prey density has reached a particular level (Heithaus & Dill, 2002). As minke whales continue to return to the St. Lawrence area, capelin must be present in sufficient quantities. If prey are becoming a limiting resource, yet still supporting a proportionally high number of minke whales, a greater effort will be required to entrap the prey. Therefore there is an increase in the number of blows per feeding strike over the years seen in type 2 SF. Where multiple whales feed (around the Laurentian Channel at high tide), intraspecific competition may become a rising concern in terms of foraging. The whales may therefore be attempting to maximise food intake by increasing the number of strikes (although the yield per mouthful is likely lower). Hence the number of blows per feeding strike in type 1 SF decreases.

5. CONCLUSION

5. CONCLUSION

Mean surfacing intervals of 54.786 sec were found in minke whales of the St. Lawrence Estuary area. Although surfacing intervals of animals in summering grounds are expected to be shorter, due to the high activity associated with feeding, this result is considerably lower than those of equivalent studies. This is likely due to the method of data acquisition. This study has also shown that the ventilation regimes of minke whales are very variable according to behaviour and intensity of activity. Such distinct ventilation patterns could prove useful in categorisation of minke whale behaviour in future ethological studies.

Two types of surface feeding were identified in this study: type 1 SF (where strikes permit a simultaneous ventilation) and type 2 SF (where the feeding manoeuvre disallows a simultaneous ventilation). Whilst type 1 SF had similar number of blows per strike, type 2 SF had a higher number of blows than feeding strikes. Analyses of blow and engulfment (strike) rates demonstrated significant differences between the St. Lawrence Estuary and the Saguenay Fjord, which were, in turn, related to the principal distribution of the SF types. Type 1 SF was only ever found in the St. Lawrence whilst the Saguenay saw exclusively type 2 SF. The preference for the use of a particular feeding type is likely due to the environmental differences presented by each area. Further, the blow to strike ratios analysed over the course of the 11 years of study revealed an increasing number of blows per feeding strike, suggesting an increased effort associated with prey capture. This is likely to be related to overall reductions in the quantity of food in the region.

The information presented in this report adds to the relatively scarce literature on the ecology of minke whales in the St. Lawrence. It also points to areas where methods can be improved and also provokes further questions, which can be pursued in future research. It is important that studies concerning ventilation rates, habitat use and feeding strategies are continued, so as to enhance ways in which the whales and their environments are conserved, managed and protected.

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8. APPENDICES

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