Aquatic Mammals 1988, **14.1**, 21–32

Feeding Techniques and Foraging Strategies of Minke Whales (*Balaenoptera acutorostrata*) In the St Lawrence River Estuary

E. M. Lynas* and J. P. Sylvestre†

**Ocean Research Information Society, 2 Sandbar Road, Pt Pickering, Ontario L1W 1A1, Canada*
†Société d'Etudes des Cétacés du Tadoussac, 4 Allée de la Forêt, 92360, Meudon la Forêt, France

Abstract

A total of nine parameters were measured on 2539 minke whale sightings drawn from a sample of 90 animals. Analyses indicate three main swimming patterns functionally related to: 1. travelling, 2. searching, and 3. feeding. Each was found to be distinguishable on a behavioural basis, and was significantly different ($\alpha = 0.05$) in at least one of four measured parameters. Feeding *per se* comprised sets of manoeuvres whose functional aspects were: 1. entrapment (sub-surface circles, ellipses, and hyperbolas), 2. engulfment (surface plunges and diverse lunges), and 3. entrapment/engulfment (near-surface diverse arcs). Aids to entrapment included the use of rock faces, current, and the air/water interface. Prey abundance, species (perhaps also size), and individual preferences appear to determine the choice of technique employed.

Two significantly different ($\alpha = 0.05$) feeding strategies were distinguished: 1. line fishing, and 2. patch fishing. These also were examined under two different hydrodynamic conditions: 1. turbulent shoal water, and 2. deep open water. In a 2 × 2 factorial analysis of equalized random samples, no significant interaction effects were evidenced between the strategy employed and the different hydrodynamic conditions. There were significant effects of strategy, however, with values for 'p' ranging from <0.025 to <0.005. No significant difference was found in the effort expended with each strategy as measured by the mean ratio of ventilations per set of manoeuvres in each feeding sequence.

Introduction

Minke whales (*Balaenoptera acutorostrata*) are the most common of three rorqual species (minke, finback, and blue) that frequent the St Lawrence feeding grounds. They arrive as early as the first week of May each year, and leave again beyond the end of October. Representative members of the species can be observed almost on a daily basis.

The minke spends approximately 61 per cent of its time during daylight hours feeding, and a further 36 per cent in activities directly related to that end (Lynas, 1986). Notwithstanding, the subject has received only incidental treatment in the literature.

Sergeant (1963), Mitchell & Kozicki (1975), and Perkins & Whitehead (1977) comment briefly on the fact that the minke shows a preference for coastal waters and follows migrating capelin (*Mallotus villosus*) around the bays and headlands of Newfoundland. Gaskin (1982) reports observing a minke feeding among herring (*Clupea harengus*) in a tidal streak off south-western Nova Scotia, rising to take one or two breaths every three to five minutes. He also makes a passing comment on the more 'flamboyant' behaviour of minke feeding among capelin at the confluence of the St Lawrence and Saguenay rivers. Elsewhere (1976), and in more detail, he illustrates a behaviour which we have come to term *oblique lunge feeding* (see below). In addition, Gaskin describes a feeding manoeuvre he observed among finback whales (*B. physalus*), which he calls 'plunge feeding'. We have observed exactly the same manoeuvre being executed by minke whales. The appelation fits very well with our attempt to unify our nomenclature; so we have made use of it in describing this manoeuvre.

Perhaps the paucity of references in the literature is due to the difficulty in amassing direct evidence of feeding taking place. It is time consuming. The point of observation is critical. Proximity to the animals is essential. Surface and near-surface movements of predator and prey alike often are both sudden and subtle.

Methods

Observations were carried out by the senior author during daylight hours from the *R. V. Beluga* (a 14 metre diesel-powered vessel) and/or from inflatable craft, with the help of from two to four assistants. First data were taken opportunistically near the end of the 1984 season, again when other work permitted across the season in 1985, and uniformly across the

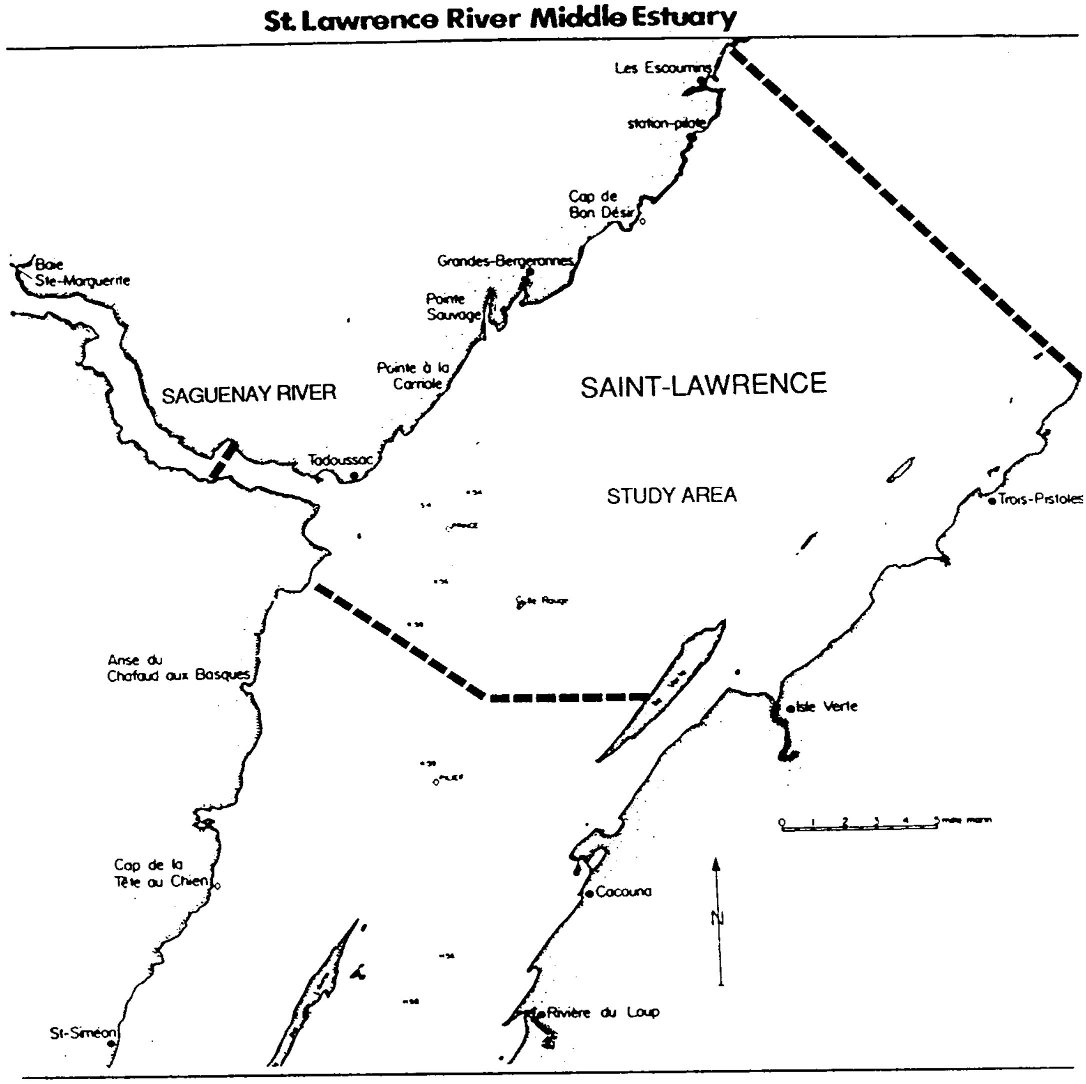

Figure 1. St. Lawrence River Middle Estuary.

season in 1986. Approximately 60 per cent of the data were collected during 1986. The primary sample comprised 90 individuals, resulting in 2539 sightings for analysis. Observations were carried out weather permitting, and generally in wind speeds of less than 20 knots.

Fifty-four per cent of the subjects were encountered in the heavy rips and shoal waters of the St Lawrence/Saguenay confluence. The balance occurred in the deep, open downstream water east of Pointe à la Carriole to just east of Les Escoumins (Fig. 1).

Subjects were selected *ad libidum* on the basis of every other animal (1st, 3rd, 5th, . . ., nth) encountered in the day, provided its identity could be maintained long enough to determine its patterns of behaviour. (In general, a 20 minute minimum was applied.) It then was included in the sample.

Time/frequency measurements were made to the nearest 100th of a minute with a Remax electronic, digital stopwatch on dive durations, surface durations, surface intervals, ventilation rates and respiration sequences for each subject. (Reaction time was assumed to be constant for each observer. Corrections were applied among observers.) Data on a nominal scale were taken of swimming patterns and feeding manoeuvres. Interval scale data (coordinates, bearings, and direction of movement) also were recorded for each subject, together with such secondary data as: current, tide, sea states, prey species seen in the surface waters, and feeding sea birds.

We attempted to quantify the presence of euphausiids in location to feeding animals with a Schindler-Patalas trap (discrete sampler), but problems with its deployment in heavy current rendered the effort quite useless. A Ray Jeff Mx-2500 chart recorder with a 200KHz transducer was used periodically to check for the presence of shoaling fish in the vicinity of animals exhibiting feeding behaviours. A strong sonar trace was assumed to be confirmation of the presence of fish rather than euphausiids.

Corroborative empirical observations were recorded by the junior author in the process of 97 whale-watching trips taken in 1985 and 1986 in co-operation with the La Cie de la Baie de Tadoussac.

We concluded that an animal's recorded sequence of behaviours was directly associated with feeding, if we observed one or more of the following events:

1. The animal's mouth in an open or closed state at or near the surface of the water with its ventral grooves simultaneously distended.
2. Water being purged from the sides of an animal's mouth at the surface.
3. In the case of an airborne manoeuvre (see below), contraction of the ventral grooves while purging.
4. Small shoaling fish seen jumping clear at the air/water interface ahead of the sudden eruption of a whale's head from the water.
5. Small shoaling fish seen spilling from the sides of an animal's mouth as it closed at the surface.
6. Small shoaling fish seen escaping back into the water across a whale's emerging body.
7. Gulls seen diving into the water beside an animal's head and capturing stunned prey items not taken by the whale.
8. Gulls seen wheeling and diving overhead, and diving sea birds, principally cormorants (*Phalacrocorax carbo*), fishing in the immediate vicinity of an animal otherwise exhibiting feeding behaviours.

Results

Swimming patterns

Three swimming patterns associated with feeding minke were differentiated on the basis of relative speed, direction of movement, and respiration patterns. The apparent functions of these are *travelling, searching*, and *feeding*. Travelling was characterized by relatively slower movement through the water, a longer surface interval between ventilations, and maximum ventilations per respiration cycle (surface duration). (Surface duration time and the number of ventilations were highly correlated: $r = 0.93$.) Directional movement generally was in a straight line. Searching involved fewer ventilations in a surface sequence, and an increase in diving duration. Speed was increased over travelling. A significant feature of this swimming pattern was its angular movement: a kind of zigzag, although generally in a common orientation with respect to the flow of tide and current. The behaviour appears to bring the whale into sensory contact with a greater volume of water. Feeding involved a mix of directional movement. Dives were of shorter duration, and swimming appeared vigorous. Ventilations between dives were minimized (one or two, generally), interspersed by extended surface periods involving 3 to 7 ventilations (Table 1).

Each of the above is best thought of as part of a continuum. An exception to this generalization occurs when a whale is travelling in an apparently predetermined way towards a particular location. In such instances the animal was observed to remain in a travelling mode when it encountered another feeding whale. Conversely when a searching animal encountered another feeding whale, it too would begin feeding (presumably if sufficient prey was available), or having investigated, soon resume its original course.

Feeding patterns

Feeding patterns are readily divided into two main types: 1) those in which the component behaviours serve to intercept, contain, or compress the prey comprising sub-surface and near-surface movements—designated *entrapment manoeuvres*, and 2) those in which the prey is consumed or swallowed, and are made up of surface movements—designated *engulfing manoeuvres*. A third type of near-surface behaviour comprises movements which reflect some surface manoeuvres, the function of which is not entirely clear. Although we have seen them being employed as engulfing manoeuvres on occasion, they also may be used for entrapment. Accordingly, we have designated them *entrapment/engulfing manoeuvres*.

None of the above, of course, precludes the existence of other sub-surface manoeuvres used either for entrapment or engulfment which have no surface or near-surface manifestations that can be observed.

Entrapment manoeuvres

Entrapment manoeuvres comprise circles, gyres, ellipses, figure-of-eights, and hyperbolas. When circling the whale swims with its dorso/ventral axis at 90° to the horizontal and with its ventral surface towards the prey. Circles are from 1.5 to 2.5 times the animal's length in diameter. The trace from the whale's fluke movements is evident at the surface as it mounts the water column. At the culmination of

Table 1. Comparison of Minke Whale swimming patterns

	Feeding		Searching		Travelling
Number of Ventilations/	2.27 (1.17)		3.22 (1.40)		6.44 (2.41)
Dive	µ1	=	µ2	≠	µ3
Surface Duration*	0.35 (0.32)		0.44 (0.38)		1.33 (0.71)
	µ1	=	µ2	≠	µ3
Surface Interval*	0.20 (0.07)		0.20 (0.07)		0.25 (<0.01)
	µ1		≠		µ3
Diving Duration*	1.36 (0.77)		3.76 (2.13)		3.67 (2.06)
	µ1	≠	µ2	=	µ3
N of Dives	1918		410		211

*Durations are given in minutes.
( )Standard deviations.
µ1 Multiple comparison of means (Tukey) $\alpha = 0.05$.

the movement, the whale performs an engulfing manoeuvre across a chord or diameter of the circle. It appears to use its light coloured ventral surface, powerful fluke beats, and the air/water interface as aids to entrapment. Gyres are similar but vary in that the whale very obviously begins a circle of much greater dimensions and steadily reduces its diameter with each circuit. The movement may reflect prey that is loosely distributed, or a greater mass from which a segment is being cut.

Ellipses cover a much larger area, with decidedly long and short axes. The long axis can be in excess of 100 metres at times. Surface traces seldom are apparent, and the main manifestations are the whale's pattern of surfacing and turns as it moves over the bottom while rotating about some locus. Ellipses often are sustained for lengthy periods of time. They may include feeding circles within them, and generally they include numerous engulfing manoeuvres. Figure-of-eights are variants of ellipses that have a long axis of not more than six body lengths. Their significant feature is that the whale turns first in one direction and then in the opposite, at either end of the long axis.

Hyperbolas involve at least one turn or semi-circuit at the conclusion of a short straight-line run, often in association with searching. They sometimes are deployed parallel to rock faces, followed by an inward oriented engulfing manoeuvre.

Engulfing manoeuvres

Engulfing manoeuvres involve plunges and oblique, lateral, vertical, and ventral lunges. Lateral, vertical, and ventral lunges are similar to those that have been described for humpbacks by Jurasz & Jurasz (1979), and described and summarized for finback and blue whales by Gaskin (1982). 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°. (Interestingly, Williamson (1972) has measured the angle of surfacing in a captive minke at 25° to the plane of the water.) Rarely is more than the rostrum and part of the underlip visible as the whale exits the water. Often the tops of the ventral grooves are seen in their distended form. Plunge feeding is the most subtle form of engulfing manoeuvre. It is observed well only when the whale is seen in profile or from straight ahead. For this reason its frequency may have been under-estimated in this study. An oblique lunge is similar in character to a plunge, but it is performed at a steeper angle (approximately 45°) and exposes the ventral grooves entirely. Sometimes the whole body emerges in a flat porpoising-type leap. Re-entry may aid the purging action.

Entrapment/engulfing manoeuvres

Entrapment/engulfing manoeuvres consist of horizontal, lateral and ventral arcs. Lateral and ventral arcs are similar to lateral and ventral lunges, except that the whale's body does not break the surface of the water. A horizontal arc is executed by the whale turning on its side (either side) and arcing sharply to the left or right. The locus of the movement may be at a point dorsal or ventral to the animal. Only the non-pivotal flipper and sometimes a fluke tip break the surface of the water as the animal turns through the horizontal plane. All three manoeuvres have been observed with both distended and quiescent ventral grooves.

Feeding strategies

Line fishing. A typical feeding cycle may begin either with a travelling or searching pattern, from which the animal swings into feeding activity *per se*, comprising first entrapment and then engulfing manoeuvres. In the case of activity originating from a searching pattern, the feeding activity can be very brief, following which the animal takes up searching once more in the same general direction. Several similar sequences of similar or varying duration may follow one another as the whale moves up current or down along a line of upwelling. This type of behaviour we have called *line fishing*.

When line fishing, near-surface entrapment mainly takes the form of hyperbolas and semi-circuits. The beginning of feeding frequently is telegraphed by a sudden horizontal arc in the direction of the prey. Subsequent action may involve no more than one or two entrapment turns (either direction, or first one way, then the other) followed by a single engulfing manoeuvre of either plunge, lunge or arc varieties. Somewhat more extensive episodes include brief circling, several ventilations and more than one engulfing manoeuvre before the whale moves on. The duration would appear to be related to the amount and dispersal of the prey. No sonar pulses have been recorded near line fishing whales, but this probably has more to do with our inability to detect the item, rather than with the presence or absence of prey. It is not difficult to conceive of line fishing as a strategy used when feeding is a matter of mere mouthfuls among widely scattered prey items.

More prolonged periods of entrapment and engulfing manoeuvres, uninterrupted by other than very brief searching runs blend into a second general strategy we have designated as *patch fishing*.

Patch fishing

This type of feeding strategy involves sustained activity in a relatively confined area over the bottom. It includes extensive circling and/or elliptical manoeuvres. Engulfing may be mixed among plunges, lunges, and arcs, either in regular or irregular sequences. An animal may, for example, execute several entrapment manoeuvres (circuits of a circle or ellipse) followed by an engulfing movement, at the conclusion of which the whale begins another series of entrapment and engulfing manoeuvres. Alternately, entrapment may be followed by several engulfing manoeuvres in an irregular sequence with mixed lunges, plunges, and arcs being employed. These behaviours may extend for time periods of slightly less than half an hour to more than 2.5 hours, interspersed by occasional respiration sequences of from three to seven ventilations during which the whale moves away from the area of its last strike, only to turn back towards it upon diving. This manoeuvre resembles an inverted letter *J*. It may combine the need for more extensive gas exchange with allowing the prey to coalesce.

Often an animal displays a preference for a particular engulfing manoeuvre, utilizing it almost exclusively. Similarly, on the occasions when two animals are working the same large patch (although independently), each may display a preference for particular but different engulfing manoeuvres.

Where feeding bouts were of shorter duration, their termination was more often signalled by a searching pattern. Frequently this would evolve into another bout of patch fishing at a nearby location. Extended bouts were more often found to be terminated by a travelling pattern and the total relocation of the animal.

Patch fishing, in four cases where the integrity of the whale's identity could be maintained, was initiated at the culmination of travelling behaviour that extended from 1.7 to approximately 3 nautical miles.

In shoal waters whales were often observed feeding in heavy current between reefs just in front of, or just behind, an area of rip where the tide was pushing up over the river current or vise versa. On such occasions the whales appeared to be taking advantage of the opposing water masses, perhaps by coming up behind prey that had oriented itself in the direction of the dominant force on either side of the tidal rip.

Analyses

In an examination of 869 feeding dives, patch fishing was the dominant strategy employed in 78.25 per cent of all observations, versus 22.75 per cent line fishing. (Percentages after correcting for observation time were 64.74 and 35.26, respectively.) Moreover, patch fishing (corrected) was characterized by a greater number of feeding manoeuvres of all types per feeding bout (Table 2). Line fishing was almost equally divided between open waters (0.52) and shoal waters (0.48); whereas, patch fishing was more prevalent in shoal waters (0.65) than in open waters (0.35).

Randomly drawn equal samples ($N=40$) of the normalized ($x'=\sqrt{x+0.5}$) data revealed significant differences ($\alpha=0.05$) in surface and sub-surface manoeuvres between the two strategies (Table 2), and in near-surface manoeuvres between line fishing in open water and shoal water patch fishing (*Tukey's test*). Variability resulting in significance or lack of significance in the latter data, we believe, is attributable to the difficulty in detecting near-surface manoeuvres.

Interaction effects between the strategy employed and the different hydrodynamic conditions were tested in 2×2 factorial analyses of variance. No

Table 2. Mean manoeuvres per feeding bout (corrected) Minke Whale using two fishing strategies under two different hydrodynamic conditions

	Patch fishing				Line fishing		
	Shoal water		Open water		Shoal water		Open water
Near-Surface	1.07 (2.72)		0.51 (0.60)		0.21 (0.43)		0.22 (0.55)
	$\mu 1$	=	$\mu 2$	=	$\mu 3$		
	$\mu 1$			$\neq$			$\mu 4$
Surface	3.56 (4.31)		3.57 (3.88)		1.21 (1.48)		1.72 (1.49)
	$\mu 1$	=	$\mu 2$	$\neq$	$\mu 3$	=	$\mu 4$
Sub-Surface	8.16 (8.48)		7.14 (7.23)		1.25 (2.50)		1.90 (3.60)
	$\mu 1$	=	$\mu 2$	$\neq$	$\mu 3$	=	$\mu 4$

( ) = Standard deviations.
$\mu 1$ = Multiple comparison of means (Tukey) $\alpha = 0.05$.
N of Bouts = 103.
N of Animals = 73.

Table 3. Surface and near-surface manoeuvres of Minke Whales using two fishing strategies (proportions)

Manoeuvre	Line fishing	Patch fishing	Cumulative
Arcs:			
Horizontal	0.09	0.07	0.07
Lateral	0.05	0.02	0.03
Ventral	0.07	0.07	0.06
Unidentified	0.03	0.04	0.04
(Total)	(0.24)	(0.20)	(0.20)
Lunges:			
Ventral	0.16	0.19	0.19
Vertical	0.05	0.05	0.05
Oblique	0.11	0.15	0.15
Lateral	0.07	0.18	0.17
Unidentified	0.03	0.03	0.02
(Total)	(0.42)	(0.60)	(0.58)
Plunges	0.34	0.20	0.22
(Total surface)	(0.76)	(0.80)	(0.80)

significant interaction effects were evidenced. The tests did confirm significant effects of strategy for surface and sub-surface manoeuvres, with values for 'p' of <0.025 and <0.005, respectively.

A measure of the energy expended with each strategy was sought by comparing the mean ratio of ventilations per feeding dive in each case. The two strategies were not found to be significantly different in their energy demands. We are not entirely satisfied with this relative measure, however. It does not take into account the variable conditions under which a whale may be working, nor its breathing efficiency, nor as Kramer (in press) suggests the depth to which it is diving.

Surface and near-surface engulfment was found to be dominated by lunge-type manoeuvres. Proportionally, these were 0.42 and 0.60 for line and patch fishing respectively. More arc-type movements were employed during line fishing bouts: 0.24 versus 0.20, and plunges were recorded more often also when whales were line fishing (0.34) than when patch fishing (0.22) was observed (Table 3).

Discussion

The minke whale's proclivity for a relatively solitary existence, also noted by others (Gaskin, 1976; and Perkins & Whitehead, 1977), makes it a good subject for study, in as much as individual behaviours are readily isolated, provided observations are made at close range. Given the variety of manoeuvres associated with feeding activity that we have been able to identify, it is clear that individuals in pursuit of prey have at their disposal a number of techniques and, at least, two foraging strategies.

We have suggested that the choice of technique(s) an animal makes reflects in part its individuality. But inclination appears to give way to need quickly enough when the situation demands. This is well-illustrated by the behaviour of a photo-tagged whale (not part of our sample) which performed 62 engulfing manoeuvres while patch fishing, in just under 90 minutes, 52 of them (0.84) in the ventral mode. Observed on a second occasion during 36 minutes of line fishing followed by 25 minutes of patch fishing, only 2 of 9 (0.22) were in the ventral mode when line fishing, versus 11 of 11 in that mode patch fishing.

The efficacy of one of these manoeuvres over another is unclear to us, but we note that only 2 of the 5 surface engulfing moves employed (plunge and oblique lunge) at all resemble the traditional view of engulfing as described and summarized by Pivorunas (1979) and Lambersten (1983): that is, movements in the dorso/ventral plane. Together they represent less than half (0.46) of all surface manoeuvres in our sample. In addition, if as we suspect, most lateral and ventral arcs are the same, functionally, as lateral and ventral lunges, performed with less vigour or slightly lower in the water column, then their selection over dorso/ventral movements is apparent. Similar manoeuvres have been described (although not necessarily quantified), as we have pointed out, for finback, humpback and blue whales; so they must have a certain utility. We have noted for example that lateral and, to a lesser extent, ventral lunges when they are the culmination of circling are more likely to be across a chord or tangental to the circle. It may be that since the whale is already in a lateral position while circling, lateral or ventral lunges are faster, more efficient means of engulfment. The ventro/dorsal position (white above, dark beneath) also may make the striking whale more difficult for the prey to detect.

On only five occasions during our study were we able to confirm that minke were feeding on euphausiids. Four of the cases did not meet the criteria for a valid sample, but in all observations only plunge and oblique lunges were observed being employed. This could be a response to smaller prey items, slower prey items, or a greater concentration of prey items. But without a valid sample it is merely speculative.

We have already characterized line fishing as a matter of mouthfuls among scattered prey items. Patch fishing, on the other hand is a more localized and intensive activity. This is reflected in the increased number of surface and sub-surface manoeuvres per bout in our sample, and by an increased time spent in the same body of water. Certainly, the processes of entrapment and engulfment are more systematic during patch fishing. This suggests the availability of a greater concentration or a more exploitable concentration of prey items, or both. Similarly, we note that the ratio of entrapment to engulfing manoeuvres approaches 1 : 1 for line fishing, while for patch fishing it approaches 2 : 1. It is possible to view the latter in terms of the whale being *on* the prey, so to speak, more of the time. If (with the reservation already expressed) simultaneously the cost in energy to the whale of the extra manoeuvres is not significantly different, then patch fishing may represent an optimal foraging strategy for the minke. An operational scenario for such a strategy might consist of the opportunistic searching out of large concentrations of prey items and/or travelling to those known locations where at a certain time large concentrations are to be found, or where such concentrations of prey as exist are most easily exploited, and then systematically parcelling out, entraping and engulfing the same.

Gaskin (1982) characterizes the minke as the most ichthyophagous of the *Balaenoptera*, Nemoto (1970) states that whales that swallow (or gulp) their prey (which include the minke) need very heavy concentrations of food organisms to be able to feed. These conditions are met with in the St Lawrence. From May through August spawning and spent capelin pass through the estuary towards the Gulf, and in the region of the Saguenay confluence a population of juvenile capelin exists year-round (Bailey *et al.*, 1977). Although we have not obtained instantaneous traces of whales diving to their prey as has Dolphin (1987) for humpbacks in Alaska, in our opportunistic sampling we have obtained simultaneous sonar traces of swimming minke and dense prey concentrations at depths up to 19 metres in shoal waters. These coincide well with our numerous observations of entrapment and engulfing behaviour and lateral search swimming seen in the surface segment of the water column.

We do not mean to suggest by the foregoing that minke whales do not seek out prey items that are deeper in the water column. Whales have been observed making selections among varying prey concentrations, however (Watkins & Schevill, 1979), and it is reasonable to deduce that they make selections among prey items at varying depths as well. What we are suggesting is that in an optimal strategy (all other things being equal), because it is bound to the upper stratum in any case, a whale is likely first to seek out available concentrations that are closest to the surface.

Kramer (in press) presents an interesting model that applies the marginal value theorem to air breathing by aquatic animals. Oxygen is seen as a limited resource available at the surface, and its acquisition follows a curve of diminishing returns. He proposes a relationship among surface duration, diving duration, and diving depth (or horizontal distance), such that for deeper dives the percentage of time spent at the surface should increase, while the under water proportion decreases with increasing depth because oxygen for these longer dives is acquired at a lower average rate. Conversely, shallower dives mean less time spent at the surface in proportion to the amount of time spent underwater. In line with our previous reasoning, if prey is available close to the surface, then an optimal strategy would maximize the time there. This may explain why in our data (Table 1) the surface to dive time ratios for feeding and searching tend to be lower than for travelling. Work presently underway on diving depths may provide further evidence of this trend.

Acknowledgements

We wish to thank La Cie de la Baie de Tadoussac for providing the junior author with access to the whales. For their help in gathering and processing data we particularly thank Karen Benzing, Dr W. Pomper, Virginie Chadenet and Edward Raftery. Dr T. Dickinson, Dr I. W. Carlisle and Virginie Chadenet provided valuable assistance and criticism at various stages in the preparation of the manuscript. Deidra Lynas displayed considerable patience in documenting various observations photographically. Additional private funding was provided by C. Kurtz and J. Kitchen.

References

Bailey, R. F. J., Able, K. W. & Leggett, W. C. (1977). Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St Lawrence estuary. *J. Fish. Res. Board Can.* **34,** 2030–2040.

Dolphin, W. F. (1987). Ventilation and dive patterns of humpback whales *Megaptera novaeangliae* on their Alaskan feeding grounds. *Can. J. Zool.* **65,** 83–90.

Gaskin, D. E. (1976). The evolution, zoogeography and ecology of cetacea. *Oceanogr. Mar. Biol. Ann. Rev.* **14,** 247–346.

Gaskin, D. E. (1982). The Ecology of Whales and Dolphins. Heinemann, Lond., 459 pp.

Jurasz, C. M. & Jurasz, V. P. (1979). Feeding modes of the humpback whale *Megaptera novaeangliae* in Southeast Alaska. *Sci. Rep. Whales Res. Inst.* **31,** 69–83.

Kramer, D. L. (198?). The ecology of air breathing by aquatic animals. *Can. J. Zool.* In press.

Lambertsen, R. H. (1983). Internal mechanism of rorqual feeding. *J. Mamm.* **64(1),** 76–88.

Lynas, E. M. (1986). Minke whale time/activity budgets (preliminary analysis). Report to the Ministry of Fisheries & Oceans, Quebec: Whale Research Activities St Lawrence River Estuary, 1986. 37 pp.

Mitchell, E. & Kozicki, V. M. (1973). Supplementary information on the minke whale (*Balaenoptera acutorostrata*) from Newfoundland fishery. *J. Fish. Res. Board Can.* **32(7),** 985–994.

Nemoto, T. (1970). Feeding patterns of baleen whales in the ocean. *In Marine Food Chains* (ed. J. H. Steele), pp. 241–252. University of California Press, Berkely.

Perkins, J. & Whitehead, H. (1977). Observations on three species of baleen whales off Northern Newfoundland and adjacent waters. *J. Fish. Res. Board Can.* **34,** 1436–1440.

Pivorunas, A. (1979). The feeding mechanisms of baleen whales. *American Sci.* **67,** 432–440.

Sergeant, D. E. (1963). Minke whales *Balaenoptera acutorostrata* Lacapede, of the Western North Atlantic. *J. Fish. Res. Board Can.* **20(6),** 1489–1504.

Watkins, W. A. & Schevill, W. E. (1979). Aerial observations of feeding behaviour in four baleen whales *Ebualaena glacialis, Balaenoptera borealis, Megaptera novaeangliae*, and *Balaenoptera physalus. J Mamm.* **60,** 155–163.

Williamson, G. R. (1972). The true body shape of rorqual whales. *J. Zool. London.* **167,** 277–286.

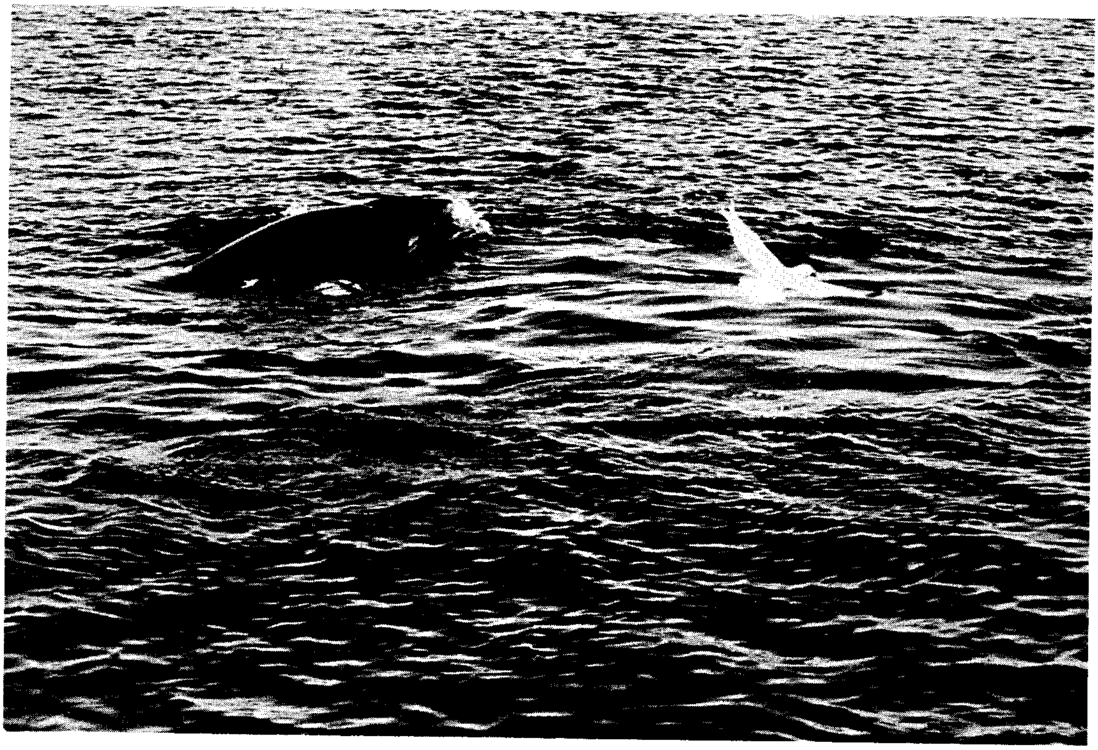

Figure 2. Plunge feeding. Note exposed baleen. At right the gull has a prey left behind by the whale.

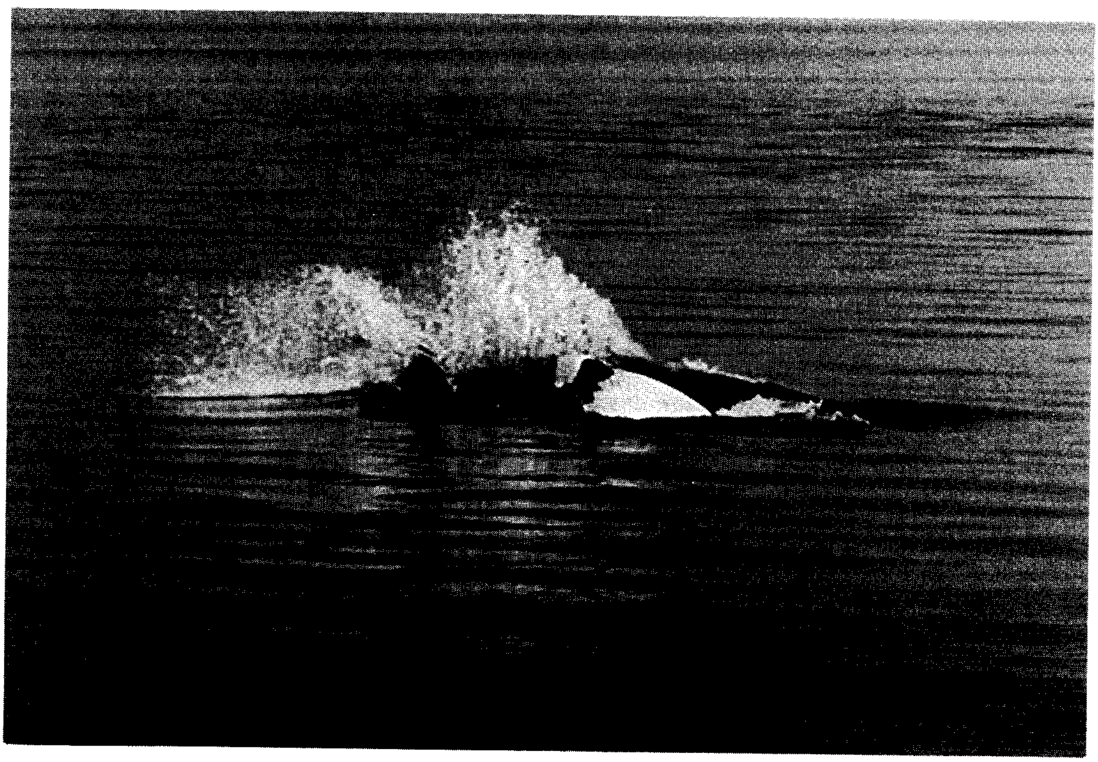

Figure 3. Lateral Lunge feeding.

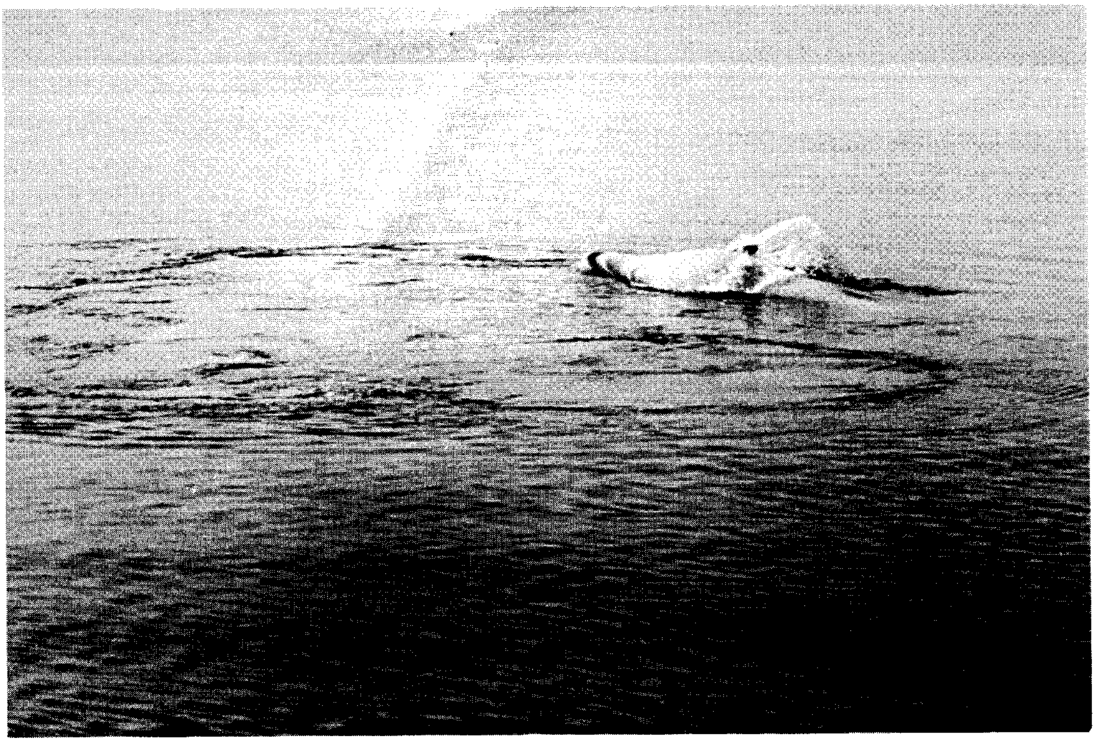

Figure 4. Ventral Lunge feeding. Note the feeding circle traced on the water surface.

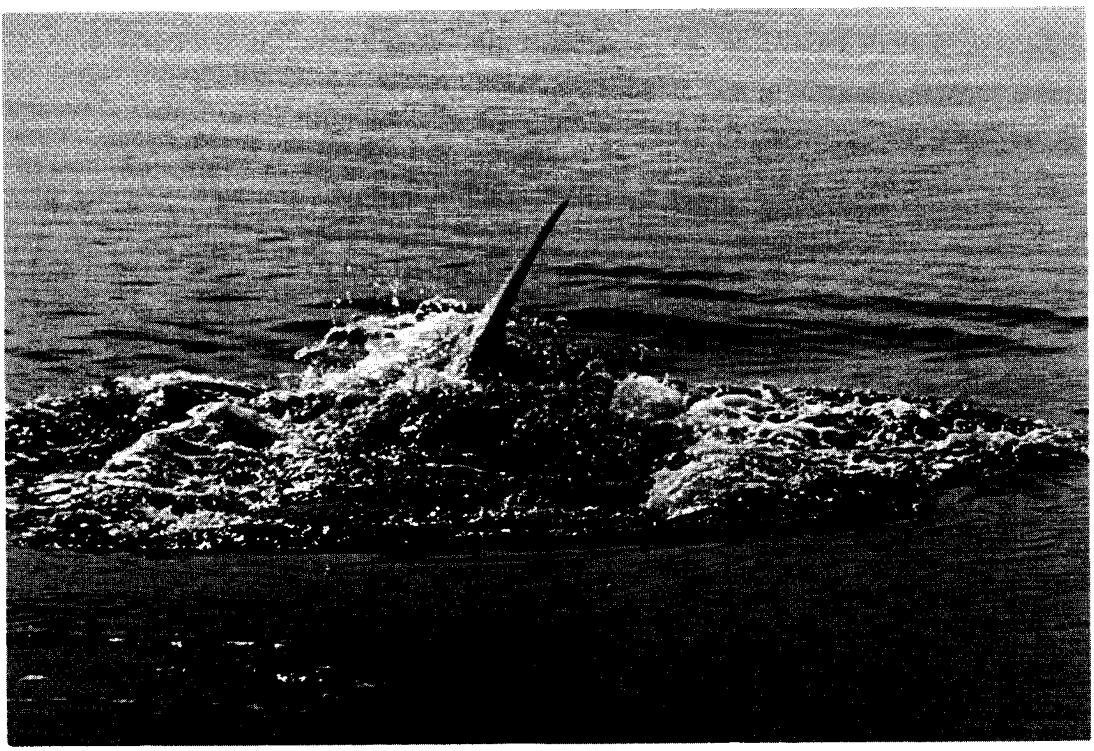

Figure 5. Culmination of a Lateral Arc. A fluke-tip breaks the surface.

Figure 6. Termination of an Oblique Lunge action.

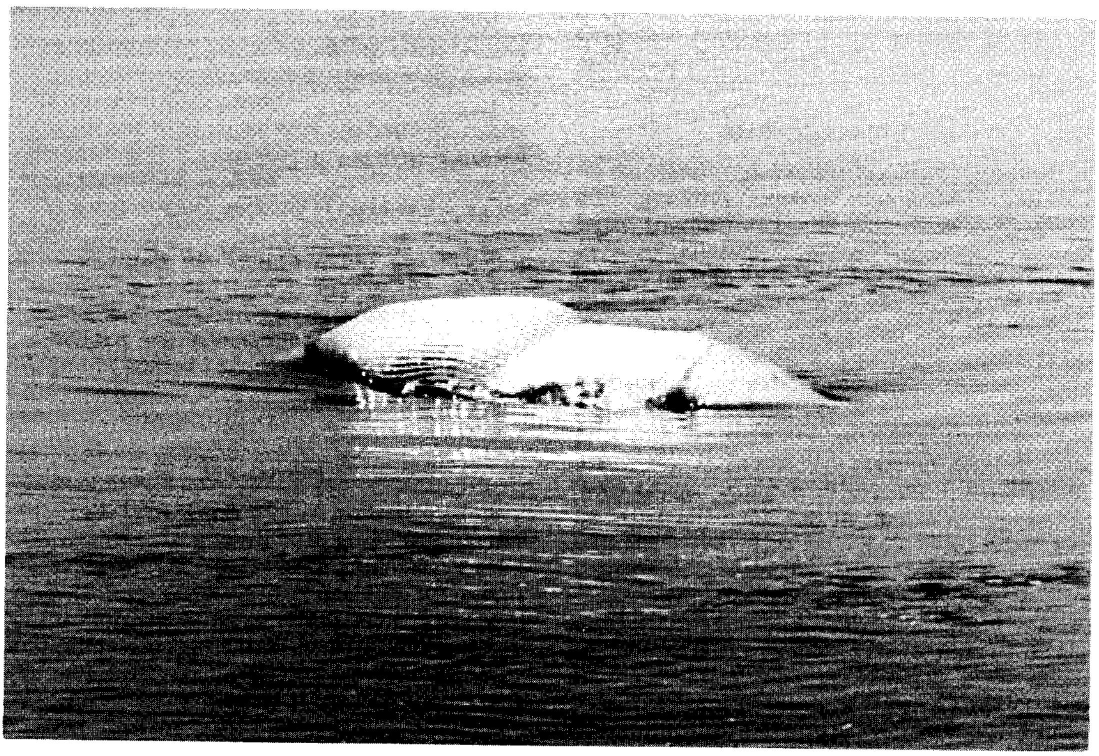

Figure 7. Ventral Lunge feeding. Note the fully distended ventral grooves.

Figure 8. Vertical Lunge feeding.