TROPHIC RELATIONSHIPS, SEASONAL DIVING ACTIVITY AND MOVEMENTS OF HARBOUR SEALS, *PHOCA VITULINA CONCOLOR*, IN THE ST LAWRENCE RIVER ESTUARY, CANADA

By

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ABSTRACT

An understanding of community structure and the ecological requirements of a species are desirable for responsible management practises/decisions. In the St Lawrence Estuary, the harbour, or common seal is the seal species that is most frequently observed from shore but, ironically, it is also the least abundant pinniped within the region. The number of harbour seals in the Estuary remains low despite decades of protection from hunting and the absence of other obvious anthropogenic factors which might limit their expansion. Reasons for their low population levels are unclear. Several other marine mammal species are found in the St Lawrence Estuary, and one hypothesis to account for the low number of harbour seals may be competition for food resources with these other species. However, given the scarcity of information on seasonal distribution, trophic relationships, and activity patterns of harbour seals in this region, it is difficult to evaluate this hypothesis. This information is lacking partly because of 1) the large amount of time that harbour seals, and pinnipeds in general, spend underwater and away from shore, 2) the difficulty of studying their foraging behaviour while they are in these areas, and 3) the difficulty of obtaining sufficient and unbiased information on their diet. In this thesis, recent techniques that overcome some of these limitations are used to examine the diet of harbour seals, trophic relationships in the Estuary community, their seasonal movements, diving and foraging behaviour, and preferred habitats to determine whether the competition hypothesis warrants further investigation.

The structure of the St Lawrence Estuary and Gulf communities was examined using stable carbon and nitrogen isotopes, with a special focus on trophic positions and relationships among harbour seals and the other marine mammal species in the area. Different body tissues were used to examine diet over variable periods of time for a number of marine mammal species. The analyses suggested that most harbour seals likely remain in the Estuary year-round, and occupy top trophic positions along with other marine mammal species. Harbour seals and hooded seals occupy the highest trophic positions. Grey seals, male beluga whales and Gulf harp seals were intermediate and Estuary harp seals and female beluga whales occupied the lowest trophic positions. These differences in trophic positions, along with subtle variations in diving behaviour and distributions among the different marine mammal species in the Estuary, may minimise overlap in food resource utilisation. Stable isotope analyses also showed that harbour seals are largely piscivorous by the time they are one year old, but that yearlings may feed at lower trophic levels than older seals.

Information on diving and foraging activity were obtained by deploying time-depth-velocity recorders and stomach temperature sensors or satellite transmitters on individual seals. The dive records of harbour seals were classified using a combination of principal components, complete linkage and K-means cluster analyses in order to examine diving behaviour. These combined methods were shown to be slightly more efficient than the use of a K-means cluster analysis alone. The analysis identified five dive types on the basis of dive depth and swim speed characteristics. Four dive types were U-shaped, while another was V-shaped. Dives associated with stomach temperature drops, indicative of feeding, were spread among all five dive types. However, most successful foraging took place during U-shaped dives where seals swam along the bottom at speeds near the minimum cost of transport with occasional bursts of faster swimming.

The analysis of diving records also indicated that harbour seals in the Estuary rarely performed deep dives. Despite considerable variation among individuals, 95% of dives were on average less than 23 m deep (range 5–50 m; $n = 20$ seals). Many dives were very shallow, with dives less than 4 m representing on average 51% of all dives (range 15–93%; $n = 13$ seals) and 35% of dives associated with foraging success (range 1–72%; $n = 11$ seals). Patterns of seasonal variation in diving behaviour were explored. Diving activity, depicted by diving rate and time spent diving, intensified while haul-out activity declined during winter. Haul-out frequency and time spent diving also varied according to the reproductive or moulting status of individuals. Except for a single breeding male, harbour seals hauled out on most days during summer. Most seals hauled out preferentially near daytime low tides and dove most intensively during twilight or night. Diving depths were generally shallower at night than during the day, which might be a consequence of feeding on vertically migrating prey. The analysis of stomach contents from seals ≤ 2 yrs-old ($n = 17$) indicated that capelin, herring, rainbow smelt, sand lance and winter flounder are eaten by harbour seals in the Estuary, at least on a seasonal basis. Adult females decreased diving activity, but did not cease feeding during early lactation. They may take advantage of the abundance of spawning capelin in bays located near their haul-out sites while they are nursing young pups. Adult males fed regularly during the pre-mating season when underwater display areas were likely being established. Juveniles decreased diving activity with the approach of the moult and intensified effort following its completion. When foraging success was examined in relation to overall diving activity, 5 of 7 juveniles had lower foraging success rates than adults. Four of the 5 less efficient juveniles fed at depths that were on average deeper than more efficient seals.

Satellite telemetry and *in situ* tracking of individuals indicated that harbour seals are largely coastal. While away from their haul-out sites, they frequent river mouths, bays and near-shore areas where depths are usually less than 50 m. This distribution pattern was observed both during summer and winter, although ice formation in bays forced animals to abandon some near-shore areas during winter. Most harbour seals remained in the Lower Estuary throughout the year. However, 4 of 7 seals over-wintered in areas 65–520 km ($\bar{x}$ ± SD = 266 km ± 202) away from their summer haul-out areas. Heavy ice conditions may have contributed to the relatively large amplitude of movements observed in these animals.

Harbour seals appear to find both their necessary food resources and haul-out substrates within relatively small geographic areas throughout the year. They may overlap in their food resource utilisation with some other marine mammals from the Estuary, but direct resource competition is likely minimised by differences in distribution and feeding areas. The coastal nature of the harbour seal, its use of riverine resources and its position as a top predator in the Estuary community might increase its vulnerability to the development of man-made infrastructures and human activity and to the effects of contaminants that tend to bio-accumulate within the St Lawrence River Estuary ecosystem.

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CHAPTER 1

General Introduction

The structure and dynamics of ecological communities has preoccupied researchers since at least the 1920s (*e.g.* Elton 1927; 1958; Tansley 1935; Lindeman 1942; Hutchinson 1959; Hairston et al. 1960). However, systematic attempts to understand factors that determine the structure of food webs did not begin until the late 1960s (*e.g.* Paine 1969; DeAngelis 1975; May 1979; Pimm 1982; Cohen and Newman 1988; Paine 1988; Sprules and Bowerman 1988; Schoener 1989; Vadas 1990; Pimm et al. 1991; Jones and Lawton 1995; Polis and Strong 1996; Pahl-Wostl 1997).

A central theme within community food web studies has been the factors or species controlling population biomasses in communities (Lindeman 1942; Hairston et al. 1960; Pimm and Lawton 1978; Vadas 1990; Polis and Strong 1996; Tilman et al. 1998). Although it was readily obvious that species were not all equally important to community structure (Ray 1981; Huntly 1991; 1995), evidence emerged that some species, often called keystone species, may exert a disproportionate influence on community structure (Paine 1969; Grimm 1995). These keystone species may occur at any trophic position in food webs (Pimm et al. 1991). Numerous studies demonstrated the influence of the rate of primary production on ecological interactions and community structure — known as a bottom-up control (Lindeman 1942; Yodzis 1984; Iverson 1991). Keystone species may also be found at the other extreme of the food web and exert a so-called top-down control on community structure (Hairston et al. 1960; Strong 1992; Estes 1995). However, little attention has been paid to demonstrating possible effects of top predators in marine systems (Hairston et al. 1960; Fretwell 1977; Polis and Strong 1996; Pahl-Wostl 1997) mostly because of the difficult logistics associated with such studies (Estes 1995; Bowen 1997). Ecosystems are inherently complex and their behaviour is relatively hard to predict. Furthermore, reliable conclusions on the role of species in communities may often be obtained only by manipulating components of wild communities, which has inherent logistical and ethical limitations.

Marine mammals, as apex predators, may exert a top-down control on ecological interactions and represent important structural components in food webs (*e.g.* Laws 1985). The clearest example of the ecological significance of marine mammal predation in structuring ecosystems probably comes from the study of sea otters. Sea otters have been shown to maintain kelp beds and increase community diversity by controlling the abundance of sea urchins in near-shore communities (Estes and Duggins 1995; Kvitek et al. 1998). In contrast, killer whales, preying on sea otters would have the opposite effect on community diversity (Estes et al. 1998). Another example of this phenomenon has been suggested for harbour seals in the Seal lakes in northern Quebec. The fish community is dominated by lake trout (*Salvelinus namaycush*) in lakes where harbour seals are absent. However, in the Lower Seal Lake, where harbour seals are present, lake trout show signs of what has been interpreted to be heavy exploitation and brook trout is the dominant fish species (Power and Grégoire 1978). Other evidence for marine mammals functioning as important apex predators in communities comes from the Antarctic, where an increase in abundance of some krill-dependent pinnipeds (crabeater seal *Lobodon carcinophagus*), whales (minke whale *Balaenoptera acutorostrata*) and penguins (king penguin *Aptenodytes patagonicus*) has been reported following the near extirpation of blue whales (*Balaenoptera musculus*) (Parsons 1992). Although marine mammals might represent keystone species in the communities discussed above, it is unclear whether these reports reflect exceptions or *the rule* (Ray 1981; Bowen 1997). In some regions, marine mammals have been reduced by overexploitation to such low levels that they might have little influence on community structure (*e.g.* Livingston 1993; Estes et al. 1998).

An understanding of community structure and the identification and function of keystone species is desirable for responsible resource management. In eastern Canada, several groundfish stocks collapsed in the late 1980s (Gomes et al. 1995; FRCC 1997). Although overfishing is likely the proximate cause, changes in natural mortality due to increased predation pressure from marine consumers including marine mammals is regarded as a possible factor that may be influencing the slow recovery of some stocks (Myers and Cadigan 1995; Hammill and Stenson 1997; Myers et al. 1997; Dutil et al. 1998). However, the effect of a reduction in predation pressure on groundfish stocks is difficult to evaluate, given our limited understanding of the dynamics of interactions among groundfish, consumers and other community components.

In several regions, stocks which have collapsed in marine communities have been the marine mammals themselves (*e.g.* Laws 1994; Kjellqwist et al. 1995; Estes et al. 1998). Although overexploitation is often recognised as a major cause in the initial population decline, some populations fail to show signs of recovery despite protection from hunting for long periods of time and the absence of other obvious anthropogenic factors which might limit their expansion (see Knowlton et al. 1994; Merrick 1997; Frost et al. 1998). The high trophic position occupied by many marine mammals may put them in a vulnerable position if changes in the structure of communities occur. Large population declines in apex predators such as Steller sea lions (*Eumetopias jubatus*), sea otters, harbour seals (*Phoca vitulina*) and some species of seabirds (murres and kittiwakes) in the Bering Sea and Gulf of Alaska have been observed during the last few decades (Frost et al. 1994; Estes et al. 1998). Considerable effort has been mounted in this particular case to understand the community structure involved in this system (*e.g.* Hansen 1997; Frost et al. 1998). A decrease in the availability of preferred prey is regarded as a possible cause for the observed population declines. And, a high biomass of adult groundfish, which may outcompete these apex predators, may now be preventing their recovery (Merrick 1997). Community structure and ecological requirements of marine mammals are so poorly understood in most regions that their role(s) in population declines or lack of recovery often cannot be ascertained.

The harbour seal is found in many localities throughout eastern Canada, from Nova Scotia to Ellesmere Island. In 1973, this species was thought to number around 12,700 individuals in Atlantic Canada, 5% of which inhabited the St Lawrence River Estuary (Boulva and McLaren 1979). Harbour seal numbers in the Estuary were thought to be declining at the end of the 1970s (Boulva and McLaren 1979) and hence, culling programs ceased. According to recent censuses, the abundance of harbour seals in the Estuary remains low (Lesage et al. 1995a; V. Lesage, M.O. Hammill and K.M. Kovacs, unpubl. data). The specific demographic status of this species since they were afforded protection is unknown. However, there is evidence that harbour seal numbers are declining in other parts of their range in eastern Canada (Ellis 1998).

The harbour seal is a small phocid that lives in coastal waters. Urban development and increasing boating activity along both shores of the Estuary may be disruptive, particularly during the breeding and moulting seasons, *i.e.* May through early September (Boulva and McLaren 1979). Since the announcement of the creation of the Saguenay/St Lawrence marine park, which opened officially during the summer 1998, an increase in the marine recreational activities, including seal-watching, has been observed in areas important for this species (Michaud et al. 1997; Lesage, personal observation). There are concerns that these activities might affect marine mammals negatively. However, no decision can be made regarding access to these regions since the seasonal distribution of harbour seals, their preferred habitats and susceptibility to disturbance are poorly understood.

High contamination loads may affect the reproductive rates of harbour seals (Reijnders 1986; Brouwer et al. 1989; Ross et al. 1993) and may increase their susceptibility to viral infections (Dietz et al. 1989). Contaminant loads of harbour seals in the Estuary are high compared to those of other pinniped species and are as high as those observed in stranded St Lawrence beluga whales for some compounds (Bernt 1998). The sources of contamination of these harbour seals remain difficult to identify, given that their seasonal distribution and their diet are largely unknown.

Harbour seals may compete with the fishing industry or other species such as seabirds, large fish or other marine mammals for food resources. A wide diversity of species including several marine mammals are attracted to the St Lawrence River Estuary (Canada), which is one of the most productive regions of the world (El-Sabh and Silverberg 1990; Therriault 1991). Harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are seasonal visitors to the area during late fall and winter, whereas grey seals (*Halichoerus grypus*), harbour porpoises (*Phocoena phocoena*) and several mysticete whales such as minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*), blue whales (*Balaenoptera musculus*) and humback whales (*Megaptera novaeangliae*) visit the Estuary mainly in late spring, summer and early fall (Sergeant 1963; 1976; Sergeant and Hoek 1973; Mansfield and Beck 1977; Michaud 1991; Lavigueur et al. 1993; Lesage et al. 1995b; Gosselin and Hammill 1998). Harbour seals (*Phoca vitulina*) and beluga whales (*Delphinapterus leucas*) are the only year-round resident marine mammals in the Estuary.

Most of the marine mammal species found in the St Lawrence Estuary are to some extent piscivorous (Vladykov 1946; Lynas and Sylvestre 1988; Fontaine et al. 1994; Borobia et al. 1995; Hammill and Stenson 1997). Several species appear to exploit prey based on its abundance (*e.g.* Proust 1995; Tollit et al. 1997a; Lawson et al. 1998). Therefore, various marine mammal species may exploit similar resources. However, given that the habitat dimensions of the harbour seal and that of the other marine mammals found in the St Lawrence Estuary are poorly defined, our understanding of trophic relationships among these species and possible overlap in their resource utilisation remains limited.

There are three explanations for the general lack of information on spatial distribution and diet of marine mammals. First, these animals spend a considerable proportion of their life underwater and away from shore. Until the recent advent of self-contained time-depth recorders (end of the 1960s: Kooyman 1965) and radio (late 1970s: Pitcher and Calkins 1979) and satellite telemetry (end of 1980s: Stewart et al. 1989), these animals were inaccessible while in remote areas. Secondly, although insights into marine mammal diving behaviour have been gained through the use of time-depth-recorders and telemetry, the study of their foraging behaviour has been limited by our inability to monitor food intake in wild animals, and to confirm the association between particular dive types and actual feeding (*e.g.* Boness et al. 1994; Tollit et al. 1998). Therefore, foraging behaviour of live animals and regions important for such activities are often inferred from the interpretation of diving patterns and dive profiles (*e.g.* Le Boeuf et al. 1992; Boness et al. 1994; Boyd et al. 1995; Schreer and Testa 1996; Coltman et al. 1997; Tollit et al. 1998), from changes in body mass or chylomicrons in blood serum (*e.g.* Walker and Bowen 1993; Lydersen and Kovacs 1996) and, sometimes, from incidental observations of animals manipulating prey at the surface (*e.g.* Lydersen and Kovacs

1996). Thirdly, the rapidity of digestion, particularly in pinnipeds (Helm 1984; Markussen 1993), and the variable rates of digestion of hard parts depending on the prey ingested (Tollit et al. 1997b) and meal size (Marcus et al. 1998) often result in a large proportion of animals with empty stomachs or in biased estimates of diet composition. This limits the information gained from stomach contents or faecal sampling. Recently developed dietary assessment techniques that bypass the problems related to stomach content or faecal sampling and new technologies allowing the monitoring of foraging success in wild marine mammals show promise (*e.g.* Bjørge et al. 1995; Smith et al. 1996; Andrews 1998; Bekkby and Bjørge 1998).

An examination of the trophic position of harbour seals relative to that of other marine mammals found in the St Lawrence Estuary, as well as their diet, foraging areas and activity patterns would contribute to the evaluation of the potential for competition between harbour seals and the other marine mammal species. This study was designed to gain insights into some aspects of harbour seal foraging ecology in the St Lawrence Estuary. Specifically, Chapter 2 examines the structure of the St Lawrence Estuary and Gulf communities using a dietary assessment technique that employs stable isotopes ratios in tissues of organisms to infer their diet. Stable isotope signatures of harbour seals are compared with resident beluga whales as well as some seasonal residents in the Estuary that include grey, harp and hooded seals. These comparisons attempt to provide insight into the trophic relationships of harbour seals and the other components of this community. In Chapter 3, characteristics of harbour seals dives associated with foraging are examined using diving records obtained from time-depth-velocity recorders in combination with stomach temperature sensors. Harbour seal diving records are classified using a combination of multivariate statistical analyses. Dive types associated with successful foraging are identified by a drop in stomach temperature. In Chapter

4, the vertical and horizontal dimensions of harbour seal habitat and their seasonal variations are examined using satellite telemetry, time-depth-recorders and direct observations aided by VHF radio-telemetry. This information is combined with the sections on the characteristics of foraging dives (Chapter 3) and on the possible diets of harbour seals (Chapter 2) to examine the foraging behaviour of yearling and adult harbour seals in greater detail. Chapter 5 discusses the major findings from all of the components in this study, and highlight areas of research in harbour seal ecology or technological aspects used to study harbour seal biology that warrant further investigation.

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CHAPTER 2

Marine mammals and the community structure of the Gulf and Estuary regions of the St Lawrence (Canada)

Abstract

The community structure of both the Estuary and Gulf of St Lawrence regions were examined, with a special focus on the trophic position (TP) and relationship(s) among harp, hooded, grey and harbour seals as well as beluga whales. A multiple stable isotope and multiple tissue approach, used in conjunction with conventional dietary information, suggested that marine mammals occupied the highest trophic positions in the food webs of both communities and that they overlapped with one another to some extent trophically. Harbour seals and hooded seals occupied the highest TP, grey seals, male beluga whales and Gulf harp seals were intermediate, and Estuary harp seals and female beluga whales were at the lowest TP. A general pattern of increasing enrichment of ^{15}N or ^{13}C with age was observed in marine mammals (as well as fish), although yearlings showed a decreased enrichment compared to both younger and older age classes. Sex also influenced $\delta^{15}N$ values. Males were more ^{15}N-enriched than females, with the difference between the sexes increasing with age, and being most pronounced in species that are sexually dimorphic with respect to body size. Geographical location also influenced isotope abundance. Estuary organisms were generally ^{13}C-enriched relative to Gulf animals. $\delta^{13}C$ values were on average lower in short-term diet integrators (blood serum) than in longer-term diet integrators (red blood cells) of harbour seals captured in April–June in the Estuary, which suggests that they probably did not move outside

the Lower Estuary during the winter. Grey seals captured in the Lower Estuary did, however, show evidence of having been in the Gulf region some weeks or months before capture.

Introduction

Marine mammals are generally top predators in marine ecosystems. Over the last century, major changes in their biomasses have been documented in various parts of the globe (Mohn and Bowen 1996; Hammill and Stenson 1997; Sydeman and Allen 1999). However, little is known about their role in structuring marine ecosystems (Bowen 1997). This may be due in part to the fact that they tend to be large animals whose ecological needs often exceed the temporal and spatial scales used to define community boundaries. Information on diet composition and trophic relationships of community components are needed to help understand the role of marine mammals in ecosystem dynamics.

The harbour seal is a small phocid that is widely distributed throughout the northern hemisphere. In 1973, harbour seals in eastern Canada were thought to number around 12,700 individuals, 700 of which inhabited the St Lawrence River Estuary (Boulva and McLaren 1979). Little current information is available on the overall abundance of harbour seals in Atlantic Canada, but a few recent censuses indicate that their numbers remain low in the Estuary (Lesage et al. 1995a; Lesage and Hammill, unpublished data) and might be declining in other parts of their range in eastern Canada (Ellis 1998). Several other marine mammal species are observed in the St Lawrence Estuary, either as permanent residents (*e.g.* beluga whales) or as seasonal visitors (*e.g.* harp and grey seals). Over the last two decades the abundance of some species such as harp and grey seals has increased markedly (Mohn and Bowen 1996; Stenson et al. 1999) and some overlap in habitat or food resource utilisation between seal or marine mammal species may occur. The existence of actual competition is extremely difficult to confirm, because it requires information on whether consumption of prey by one species limits access or availability of this prey to another species. However, an initial step toward exploring competition within communities is to examine diet composition and trophic relationships, and to obtain information on how individual species forage in order to obtain sufficient food resources.

Most feeding studies are based on diet reconstructions from scats or stomach contents. These approaches permit the taxonomic identification of ingested items using hard parts, but are limited by the rapidity of digestion and the differential presence or erosion of hard parts within prey species (Helm 1984; Tollit et al. 1997; Marcus et al. 1998). Consequently, both of these approaches provide information only about the animal's most recent meals and, therefore, repeated sampling in different regions and at different times is needed to obtain an understanding of diet composition.

Insights into trophic relationships and feeding habits of marine mammals may be gained from an approach that uses ratios of naturally occurring isotopes, often isotopes of nitrogen and carbon, in specific tissues (*e.g.* Hobson and Welch 1992; Ostrom et al. 1993; Muir et al. 1995). This method is based on the demonstration that stable isotope ratios in tissues of animals are correlated with those in their diet (Tables 2.1, 2.2). When nitrogen (N) is assimilated, ^{14}N is preferentially excreted and consumers become enriched in ^{15}N relative to their food (Minagawa and Wada 1984). Because ^{15}N-enrichment from one trophic level to the next is relatively predictable, N isotopes can serve as indicators of a consumer's trophic position relative to that of species occupying lower trophic positions, *e.g.* primary producers. For carbon (C), the trophic fractionation of ^{13}C is typically small compared to that of ^{15}N, resulting in no, or relatively small, enrichment in the heavier isotope (^{13}C) along the food chain. Although this makes C a less reliable index of trophic position, it is still useful to the study of diet through its use as a tracer of sources of primary productivity. Primary producers vary in their isotopic C signatures according to: their origin (terrestrial or aquatic); C pool used and concentration (CO_2 in air, dissolved CO_2 or HCO_3^- in water); prevailing C pathways (C_3 vs C_4 plants); and the condition of the surrounding environment (well mixed or stagnant) (Smith and Epstein 1971; Osmond et al. 1981; France 1995; Fry 1996). These properties assist in discriminating between animals which obtain their resources from terrestrial *vs* aquatic, benthic *vs* pelagic or inshore *vs* offshore environments (Ramsay and Hobson 1991; Doucett et al. 1996; Smith et al. 1996; Page 1997).

The stable isotope approach also provides a better estimate of the contribution of invertebrates to the diet than stomach content or faecal analyses. It bypasses the problems associated with the high frequency of empty stomachs found in marine mammals and estimates the assimilated, not just ingested, food. Furthermore, because the turnover time of isotopes is a function of a tissue's metabolic rate, the analysis of tissues with variable metabolic rates can provide information on diet integrated over a few days (*e.g.* blood plasma, liver) or a few months (*e.g.* red blood cells or muscle) (Tieszen et al. 1983; Hobson and Clark 1992b; Hilderbrand et al. 1996). This diet assessment method is relatively non-invasive and adds some flexibility to a sampling regime, in terms of both frequency and timing, since information on an animal's diet while in a particular region can be obtained a few weeks after its departure by sampling a long-term diet integrator such as red blood cells. The use of stable isotopes may also provide information on the time elapsed since an animal moved out of an area if C signatures of primary producers differ between the current and previously occupied regions.

However, the stable isotope approach is limited because it cannot specifically identify which species from a given trophic level were consumed. Creating models that estimate the relative contribution of different prey to the diet of a consumer requires some basic knowledge of potential prey species. In addition, because of the rapidly increasing complexity of the calculations, models generally assume that no more than 2 or 3 prey species are important (Gearing 1991; Ben-David et al. 1997). The stable isotope approach also requires determination of the enrichment in ^{15}N and ^{13}C at each trophic level (trophic enrichment factor, TEF). TEFs may vary depending on the tissue used (DeNiro and Epstein 1978; 1981; Tieszen et al. 1983; Hilderbrand et al. 1996; Hobson et al. 1996). They have been determined for muscle tissue and for whole individuals of a variety of species, including seals, fed a known diet. TEFs for ^{15}N appear to be relatively constant among many species, usually ranging from 2.9–3.8‰, with the exception of seals whose ^{15}N TEF in muscle tissue is somewhat low (Table 2.1). TEFs in ^{13}C are more variable between studies (Table 2.2), but the failure to extract the ^{13}C-depleted lipids from samples may account for some of this variability (Parker 1964; Gu et al. 1996). Animals fed a similar diet may differ by 1–3‰ in their stable C or N isotope ratios (DeNiro and Epstein 1978; 1981; Minagawa and Wada 1984; Hobson and Clark 1992a,b). In seals, this variation is usually < 1‰ when captive conspecifics are studied (Hobson et al. 1996), but this variability has not been examined between species. TEFs in ^{13}C and ^{15}N have been determined in seals for several tissues, including red blood cells, muscle and hair, but not for blood serum, a tissue which may be quite useful when examining short-term changes in diet.

Both conventional and stable isotope approaches have some limitations when used independently. However, their simultaneous use provides a powerful tool to study diet composition and trophic relationships within a community (Sydeman et al. 1997; Hobson et al. 1997; Burns et al. 1998). In this study, we examine the trophic structure of the St Lawrence Estuary and Gulf communities and explore the relationships between harbour seals (*Phoca* *vitulina*) and three other pinniped species (harp seals *Phoca groenlandica*, hooded seals *Cystophora cristata*, and grey seals *Halichoerus grypus*) and the beluga whale *Delphinapterus leucas*, using a multiple stable isotope (C and N) and multiple tissue (blood red cells and serum, and hair) approach. Information on potential prey is available from conventional dietary analysis; this information will be used to discuss the significance of trophic relationships identified using stable isotopes.

Materials and methods

Study area – The Estuary and Gulf of St Lawrence

The St Lawrence River system, located in a temperate-subarctic climate in eastern Canada, is one of the most productive regions of the world (Figure 2.1; El-Sabh and Silverberg 1990; Therriault 1991). The Estuary is naturally divided into two regions, hereafter called the Upper and Lower Estuary. The Upper Estuary is relatively shallow and moderately saline (10–25‰) due to discharges from the St Lawrence River. It is a well-mixed and turbid area where phytoplankton abundance is usually low except at the head of the Estuary near Ile d'Orléans (Painchaud and Therriault 1985). In contrast, the Lower Estuary is characterised by deeper waters, high salinities (> 25 ‰) and pronounced stratification during summer (Painchaud and Therriault 1985). The Labrador current enters the Lower Estuary via the Laurentian Trough and meets a sill at the confluence of the Saguenay River, creating a year-round upwelling of cold, mineral-rich waters in the photic zone of the Lower Estuary. However, high flushing rates and strong stratification in the spring delays the phytoplankton bloom in the Lower Estuary until early summer, reducing its productivity relative to similar estuaries in temperate regions (Therriault and Levasseur 1985).

Terrestrially-derived C, freshwater phytoplankton and salt marsh plants might be important C sources for a few organisms from the Upper Estuary, since sediments of terrestrial origin, as well as salt marsh and riverborne planktonic diatoms are found nearly exclusively in this region (Tan and Strain 1983). As one moves into the Lower Estuary and Gulf, salt marshes disappear, salinity increases and sediments gradually become dominated by marine sources, indicating a negligible contribution of freshwater phytoplankton, salt marsh plants and terrestrial C compared to that of marine particulate organic matter (POM), macroalgae or benthic microalgae. The Gulf of St Lawrence, which begins near Pointe-des-Monts, is characterised by high salinities (> 28‰) and unusually high levels of biological production relative to open seas. It is considered to be an inland sea because its internal current circulation limits exchange with the western North Atlantic (Therriault 1991).

Field collections

Marine mammals

Carbon and nitrogen isotopic signatures were obtained from 285 marine mammals frequenting the St Lawrence system: 112 harbour seals; 35 grey seals; 57 harp seals; 44 hooded seals; and 37 beluga whales (Table 2.3). Harbour and grey seals were live-captured in the Estuary by deploying a gill net near their haul-out sites. Most were captured in the Lower Estuary at Bic and Pointe Mitis during May–October 1995–1997 (Figure 2.1). A few individuals were captured at Ile Blanche, an island located at the limit of the Upper and Lower Estuary. Some grey seals (January) and harp seals (March), and all hooded seals (March) were live-captured on the ice in the southern Gulf during their respective breeding periods. Some of these animals actually may have spent some time in the Estuary prior to their capture. Harp seals were also collected as part of the annual hunt in the Lower Estuary near Godbout in February. Beluga samples were obtained from beached carcasses in either the Estuary or Gulf of St Lawrence.

Live-captured seals were immobilised with an intramuscular injection of Telazol® (Tiletamine and Zolazepam, Fort Dodge® Laboratories, Iowa) at a dose of 0.5–1.0 mg per kg of body mass and weighed using one or two 200 ± 0.5 kg Salter spring scales suspended from a portable tripod. A lower incisor was extracted for age determination. A blood sample was taken from the extradural vein and hair was clipped from the mid-dorsal region. Animals sampled after death were also weighed and a sample of muscle tissue and a tooth (canine for seals; any tooth for beluga whales) were collected. Blood serum and clotted cells were separated by centrifugation and frozen separately at -20°C. Other samples were also stored at -20°C until analyses.

Other components of the Estuary and Gulf communities

Samples from species other than marine mammals (n = 533) were obtained from both the Estuary and Gulf of St Lawrence as part of ongoing research programs within the Department of Fisheries and Oceans. POM was collected using 4-L Niskin bottles at the depth of maximum chlorophyll production and obtained by filtering water through pre-combusted Whatman GF/C filters. Zooplankton was collected concomitantly from vertical tows using a 1-m diameter by 3-m long Bongo net with 333 µm mesh. Zooplankton were kept alive overnight to allow clearance of gut contents and were separated according to size and species. Zooplankton, larger invertebrates and fish were stored at -20°C until analyses. Depending on animal size, either a muscle sample (fish and larger invertebrates including decapods) or the entire organism (other crustaceans) were used for analyses.

Laboratory experimentation

Tissues were collected from seals held in four different facilities in order to examine diet–tissue fractionation factors (*i.e.* TEF) for both C and N isotopes, and variability in isotopic signatures among conspecifics and species. These included harbour and grey seals from the Québec Aquarium (QC) and University of Guelph (ON), harbour seals from Shippagan (N.B.) and harp seals from Memorial University (Nfld). All animals were either born in captivity or had been held in captivity for at least two years prior to sampling. Except for harp seals whose diet was a mixture of herring and capelin, all animals were fed a constant diet of herring throughout their life in captivity. Blood was obtained from routine collections. Serum was separated from clotted cells by centrifugation and each tissue was frozen at -20°C. Two mixed hair samples were collected during the annual moult when two tanks were cleaned each of which contained two harbour seals. Specimens of herring and capelin were also collected from the different facilities for isotope ratio analysis. TEF values for harp seals are presented, but because they were not fed a constant diet of herring, these animals were excluded from the calculation of overall mean fractionation factors for the different tissues.

Chemical analyses

Prey samples and marine mammal blood and muscle tissues were freeze dried for 36 to 48 h and homogenised. Hair was cleaned, using a detergent and an ultrasonic bath, and rinsed several times in distilled water before being dried in an oven at 60°C. The hair was then soaked in ether, rinsed in distilled water and allowed to air dry. The smaller plankton (*e.g.* copepods) were not acid washed because carbonates have no observable effect on their $\delta^{13}C$ values and this procedure may alter $\delta^{15}N$ values (Gearing et al. 1984; Goering et al. 1990). However, carbonates may inflate $\delta^{13}C$ values by about 0.4‰ in slightly larger organisms such as krill (Bunn et al. 1995). Therefore, a correction factor was used for the C signatures of krill and species of comparable size such as *Caprella* sp and *Gammarus* sp.

Lipids were extracted from all samples other than marine mammal tissues (Bligh and Dyer 1959) because lipids may affect $\delta^{13}C$ values (Kling et al. 1992; Gu et al. 1996). $\delta^{15}N$ values are not affected by lipids (Rau et al. 1991; Hesslein et al. 1993). The effect of not extracting lipids from muscle, blood serum and red cells on marine mammal isotopic signatures was explored. The lipid content in muscle (± SD = 7.1% ± 1.5; *n* = 10 beluga whales and 11 harp seals) or red blood cells (± SD = 3.9% ± 0.9; *n* = 10 hooded, 10 grey, 10 harp, and 10 adult and 10 nursing pup harbour seals) did not vary significantly between groups (muscle: *one-way* ANOVA on ranks, $F_{1,19} = 0.17$; red blood cells: *one-way* ANOVA, $F_{4,45} = 2.18$; $P > 0.05$ for both tissues). However, serum of nursing harbour seal pups (± SD = 16.4% ± 2.7; *n* = 10) contained significantly more fat than that of adult harbour seals (± SD = 12.6% ± 1.5; *n* = 10; one-way *ANOVA*: $F_{1,18} = 4.53$; $P < 0.05$). The lipid content of a sample was predictable from its C:N ratio (*n* = 73 marine mammals, $r^2 = 0.89$, $P < 0.0001$, Figure 2.2) and was calculated for each marine mammal sample. Lipids are lighter in $\delta^{13}C$ by ~ 6‰ relative to protein (McConnaughey and McRoy 1979). Assuming that lipids and proteins are the two major constituents of muscle, blood serum and red cells, fat-free $\delta^{13}C$ values were estimated by adding 6‰ x $\%_{fat}$ to the measured $\delta^{13}C$ values (Alexander et al. 1996).

Fur was analysed only for the 1995 harbour seal samples and serum was analysed only for Estuary harbour and grey seals due to financial limitations. Red blood cells and muscle were the tissues chosen for comparative analyses among the different species because these tissues integrated diet over relatively long periods (≥ 2–3 months: Tieszen et al. 1983; Hobson and Clark 1992a; Hilderbrand et al. 1996).

Samples were analysed at the Environmental Isotope Laboratory (University of Waterloo, Waterloo, ON) using an Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1108). By convention, ^{13}C and ^{15}N isotope abundance are expressed in delta notation (‰), relatively to the PeeDee Belemnite (PDB) and atmospheric nitrogen (AIR) standards, respectively:

$$\delta X = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N, and R_{sample} is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. R_{standard} represents the ratios for their respective standards. Replicates using laboratory standards indicated an analytical error of ± 0.3‰ and ± 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. Deviations observed between replicates using samples in this study were on average 0.2‰ for both $\delta^{15}N$ and $\delta^{13}C$ ($n = 168$).

Subdivision of marine mammal and fish species into classes

Ages of the marine mammals were determined to the nearest year by counting growth layer groups of sectioned teeth (Brodie et al. 1990; Bernt et al. 1996). Pups were defined as nursing pups if they were captured before July 10, a date corresponding to the date of first births and peak of pupping (25 May–June 1) + mean duration of lactation (24 d) + ~ 2 wk post-lactation fast (Muelbert and Bowen 1993). Weaned pups were defined as pups captured after July 10 until they were ~ 5 months old.

When ≥ 5 specimens of a given species of fish or large invertebrate were collected, $\delta^{13}C$ and $\delta^{15}N$ values were linearly regressed against length to determine whether size affected C or N isotope ratios. Each species for which a significant ($P < 0.05$) effect of size on either $\delta^{13}C$ or $\delta^{15}N$ values was detected were segregated into length classes to increase group homogeneity of $\delta^{13}C$ or $\delta^{15}N$ values (usually to SD < 0.5‰). The within-group standard deviation (WGSD) was used as a segregation criterion. The limit for a length class was defined as the length at which WGSD was minimal. To identify this (these) limit(s), observations for a given species were sorted in ascending order of length. At first, only the smallest individual was included in group 1, other observations being in group 2. WGSD was calculated for each group when group size was > 1. The second smallest animal was then added to group 1, WGSD was re-calculated, and so on until all observations were contained in group 1. When the limit between the two length classes was identified, observations with lengths above this limit were re-sorted in ascending order and the process was repeated until no further segregation was possible (*i.e.* until WGSD remained similar to total SD). In most instances when size affected both $\delta^{13}C$ and $\delta^{15}N$ for a given species, length classes identified using C or N isotopes corresponded. However, an adjustment of length classes was required in a few instances. The consequences of choosing length classes based on one isotope or the other on WGSD was examined; the combination which resulted in the smallest increase in WGSD was retained.

The isotopic model

To examine the trophic structure of the Estuary community, $\delta^{15}N$ signatures were converted to trophic position, *TP*, using:

$$TP = 1 + (D_m - POM) / TEF$$

where $D_m = \delta^{15}N$ value in a consumers tissue, $POM = \delta^{15}N$ value of particulate organic matter, and TEF = trophic enrichment factor in ^{15}N for a particular tissue (Hobson and Welch 1992). This latter value was set to 3.4‰ for all community components except marine mammals, which represents the average TEF obtained for muscle tissue or whole animals of a variety of freshwater or marine species other than seals (Table 2.1). We used TEF obtained from the aquaria animals for blood serum and red cells, and those of Hobson et al. (1996) for hair and muscle (TEF_{mmt}). The *TP* of marine mammals was calculated using:

$$TP = 2 + (D_m - POM - TEF_{mmt})/TEF$$

In order to compare isotopic values sampled from different tissues between species of marine mammals, $\delta^{13}C$ values of marine mammals were transformed to obtain $\delta^{13}C$ of their average diet by subtracting from their $\delta^{13}C$ value, the ^{13}C TEF obtained for the particular tissue (Results section, Table 2.5).

The importance of different prey in marine mammals diet was examined using a two-source mixing model:

$$\%_x = (\delta^{15}N_c - \delta^{15}N_y) / (\delta^{15}N_x - \delta^{15}N_y)$$

where $\%_x$ = proportion of the diet derived from prey 'x', $\delta^{15}N_c$ = nitrogen isotopic signature of the consumer's tissue; and $\delta^{15}N_x$ and $\delta^{15}N_y$ = nitrogen isotopic signatures of the consumer's tissue corresponding to exclusive diets of type 'x' and 'y', respectively (Gearing 1991).

Statistical analyses

All comparisons among and within groups were made using red blood cells or muscle tissue. For each marine mammal species-location-tissue combination, the effects of year, age, and sex on $\delta^{13}C$ or $\delta^{15}N$ values (or $\delta^{13}C$ of diet or *TP*), or any interaction between these effects were tested simultaneously using a multivariate analysis of variance (MANOVA), type III sum of squares and the Hotelling's T^2 (2 groups) or Wilks' lambda (≥ 3 groups) statistics (Hair et al. 1995). When no significant interaction between effects was indicated (*i.e.* $P > 0.05$), results from the *n*-way ANOVAs were examined for each isotope and effect. Based on these results, sex/age/year groups of a given species/location identified as significantly different in their $\delta^{13}C$ or $\delta^{15}N$ values were used for the between-species comparisons of isotopic signatures. For the latter analyses, the two isotopes were examined separately (*i.e.* two *one-way* ANOVAs), since groups having significantly different $\delta^{13}C$ values were not necessarily those that had significantly different $\delta^{15}N$ values. *Post hoc* Tukey's tests (*one-way* MANOVA or ANOVA) or *t*-tests using least-squares means (*two- or three-way* MANOVA or ANOVA) were used to identify significant differences between pairs of values. Significance levels in each *post hoc* comparison were adjusted to account for the number of possible comparisons. A natural-log or square root transformation was used when non-normality or variance-covariance matrix heterogeneity was indicated. When all of the standard parametric assumptions were still not met or when residuals were not normally distributed, results from the previous analysis were validated by repeating the MANOVA or ANOVA using ranks for $\delta^{13}C$ and $\delta^{15}N$ values (Conover 1980). Although a lack of significant differences may have resulted in some cases from small sample sizes, animals from a given species/group showing no significant differences between years in either isotope were grouped for subsequent analyses.

Differences among tissues in the estimated δ^{13}C of average diet or *TP* were examined using paired *t*-tests. Harbour seals were segregated into two groups based on the date of sampling, *i.e.* 'early summer' (before July; $n = 30$) or 'late summer' (in or after July; $n = 45$) to identify potential movements outside the Lower Estuary during winter and spring from the comparison of blood cells and serum isotopic signatures. No such segregation was possible for Estuary grey seals due to the small number of captures for each sex and age class in the first period (all $n \leq 3$). Diet composition of harbour and grey seals were assumed to be consistent between years, and thus years were grouped for each species, age class and sex to increase sample sizes. Significance level for comparisons was fixed at 0.05 unless otherwise stated.

Results

Diet-tissue fractionation of ^{13}C and ^{15}N

All captive seals raised on a constant diet had hair, blood serum and red cells enriched in ^{13}C and ^{15}N relative to their diet. Isotopic signatures and diet-tissue fractionation factors were generally consistent among conspecifics and among species for a given tissue (Table 2.4). Hair, blood serum and red cells isotopic values of conspecifics held at the same facility were within 0.1, 0.6 and 0.4‰ of each other for δ^{13}C, and within 1.2, 1.2 and 0.6‰ of each other for δ^{15}N. Similarly, individuals of different species from the same facility varied in their isotopic values by less than 0.5‰ (serum) and 0.6‰ (cells) for δ^{13}C, and less than 1.2‰ (serum) and 0.6‰ (cells) for δ^{15}N. As a result, mean TEF in δ^{13}C or δ^{15}N for species from the same facility were within 0.2‰ for both blood serum and red cells. Mean TEF in δ^{13}C and δ^{15}N also remained relatively consistent among the different facilities; values generally differed by $\leq$

0.5‰ regardless of the tissue used. An exception was the mean TEF in $\delta^{13}C$ for blood cells, which varied in harbour seals from different facilities by ≤ 0.8‰.

Both $\delta^{13}C$ and $\delta^{15}N$ enrichment factors differed among tissues (Table 2.5). Trophic enrichment in ^{13}C was significantly higher in red blood cells than in blood serum (paired *t*-test: $t_{14} = 6.88$, $P < 0.0001$), but both blood components had lower TEF than hair (not tested statistically since $n_{\text{hair}} = 2$ and the specific source animal was unknown). The trophic enrichment factor for $\delta^{15}N$ was significantly higher in blood serum than in red blood cells (paired *t*-test: $t_{14} = 11.14$, $P < 0.0001$), but ^{15}N TEF was similar in blood serum and hair (not tested statistically). Enrichments in ^{13}C and in ^{15}N were generally similar in blood cells and hair (Tables 2.4, 2.5), but for blood serum, enrichment in ^{13}C was lower than in ^{15}N.

Patterns of ^{15}N and ^{13}C signatures

The geographical location of collections significantly affected isotopic signatures of community components other than marine mammals (*one-way* MANOVA on ranks, $F_{2,509} = 24.91$; $P < 0.0001$). Specifically, geographical location of collections had significant effects on $\delta^{13}C$ values (ANOVA, $F_{1,510} = 47.61$; $P < 0.0001$), but had little effect on $\delta^{15}N$ values (ANOVA, $F_{1,510} = 0.12$; $P = 0.72$). Community components collected in the Gulf were depleted in ^{13}C (± SE = -19.2% ± 0.1) relative to those from the Estuary (± SE = -18.6% ± 0.1), but $\delta^{15}N$ values were similar in the two regions (± SE = 13.8% ± 0.1 and 14.1% ± 0.1 for the Gulf and Estuary, respectively). This general pattern was also observed when examining fish species individually, particularly the American sand lance, American plaice, Arctic cod, Atlantic cod, Atlantic herring, lumpfish, the Cottidae (sculpins) and Rajidae (skates). Consequently, regions were considered separately in subsequent analyses that involved either C or both isotopes.

Isotopic signatures varied with size in several fish species and thus, length classes were analysed separately. In all cases where size had a significant effect on $\delta^{15}N$ (*i.e.* Atlantic cod, herring, tomcod and mackerel, American plaice, Arctic cod, Greenland halibut, the Cottidae, lumpfish, rainbow smelt, redfish, white hake, and smooth flounder) or $\delta^{13}C$ (*i.e.* Gulf Atlantic herring, mackerel, witch flounder, pollock, redfish and Greenland halibut, and Estuary American sandlance, Greenland halibut and rainbow smelt), fish became enriched in ^{15}N or ^{13}C as they increased in length. Fish whose isotopic signatures were affected by size were presented separately for each length class in Tables 2.6 and 2.7.

Significant variations in isotopic signatures were observed between years in all marine mammal groups sampled during more than one year except Estuary grey seals (*three-way* MANOVA, $F_{2,10} = 0.98$ for effect of year, $P = 0.41$). Stable N isotope ratios remained consistent between years in 2+ and yearlings of harbour seals and in beluga whales. However, $\delta^{13}C$ was higher in yearling and 2+ harbour seals from 1995 than from 1996 or 1997 (*post hoc* *t*-tests: $P < 0.005$ for each comparison) and in beluga whales from 1997 compared to 1988, 1989 or 1990 (*post hoc* *t*-tests, each $P \leq 0.001$). Female hooded seals had similar $\delta^{15}N$ enrichment in 1995 and 1996 (*post hoc* *t*-test, $P = 0.565$), but this was not the case for male hooded seals whose ^{15}N-enrichment was greater in 1995 than in 1996 (*post hoc* *t*-test, $P < 0.001$). Both male and female hooded seals were more ^{13}C-enriched in 1995 than in 1996 (*two-way* MANOVA, ANOVA for effect of year on $\delta^{13}C$, $F_{1,40} = 4.52$; $P = 0.040$). Male and female Gulf harp seals captured in 1995 were more enriched in ^{15}N than those captured in 1996 (*two-way* MANOVA, ANOVA for effect of year on $\delta^{13}N$, $F_{1,35} = 5.96$; $P = 0.020$), but their $\delta^{13}C$ signatures were similar during the two years ($F_{1,35} = 1.59$; $P = 0.215$).

Tissue $\delta^{13}C$ and $\delta^{15}N$ varied with age in marine mammals. This was most evident in the 1995 harbour seal samples, which included nursing and weaned pups, yearlings and 2+ animals, and in 4 of 5 individually marked harbour seals recaptured 2–3 times over periods ranging from 1–12 months. During nursing, harbour seal pups red blood cell were similar in their $\delta^{13}C$ values to other age classes, but were significantly more enriched in ^{15}N than older animals (*post hoc t*-tests significant, i.e. $P < 0.008$, for nursing pups *vs* each of 2+ animals, yearlings and weaned pups) (Figure 2.3a). $\delta^{15}N$ values decreased in pups during their first year of life and attained a minimum at about age one. In the 1995 animals, yearlings and 2+ animals were similar in their $\delta^{13}C$ and $\delta^{15}N$ values. However, in 1996 when only yearlings and 2+ animals were sampled, yearlings were significantly depleted in both ^{13}C and ^{15}N relative to older animals (*post hoc t*-tests, both $P \leq 0.001$). Similarly, muscle tissues of harp seal yearlings captured in the Estuary were significantly depleted in ^{13}C relative to those of 2+ animals (*two-way* MANOVA, ANOVA for effect of age on $\delta^{13}C$, $F_{1,14} = 25,17$; $P = 0.0002$), but their mean $\delta^{15}N$ were not significantly different from those of 2+ animals ($F_{1,14} = 0.36$; $P = 0.56$) (Figure 2.3b). This general pattern also prevailed in both blood serum and red cells in 4 of 5 harbour seals recaptured several times, although these changes were usually 2 to 3 times larger in serum than in red cells (Figure 2.4). Isotopic signatures in red blood cells of 2+ grey seals from the Estuary varied differently between years relative to yearlings, resulting in a significant interaction between year and age class. In 1995, mean $\delta^{13}C$ and $\delta^{15}N$ values were slightly lower in yearlings ($n = 4$) compared to 2+ animals ($n = 3$), but these differences were not significant statistically (*post hoc t*-tests: $P = 0.060$ and 0.048, respectively). In 1996, $\delta^{13}C$ and $\delta^{15}N$ signatures of 2+ animals ($n = 6$) were lower than in 1995, and were similar to those of yearlings from 1996 ($n = 6$) (*post hoc t*-tests: $P = 0.916$ and 0.251 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Small sample sizes may be responsible for the shifting patterns.

Sex influenced the $\delta^{15}N$ signature of 2+ animals, but not that of yearlings. Males of age 2 + were generally ^{15}N-enriched relative to 2+ females (Table 2.8). This effect was significant in beluga whales in each year (*post hoc t*-tests, $P \leq 0.003$ in each year) and in hooded and harp seals captured in the Gulf in 1995 (*post hoc t*-tests, $P = 0.004$ and 0.01, respectively), and marginally insignificant in harp (*post hoc t*-test: $P = 0.085$) and grey seals ($P = 0.072$) captured in the Gulf in 1996. Nitrogen isotope ratios were similar in both sexes of harbour seals, Estuary grey or harp seals, and in hooded seals captured in 1996. In the latter two groups, $\delta^{15}N$ values were 0.2–0.3‰ lower in males than in females.

Stable carbon isotope ratios differed between sexes only in 2+ animals, and only in two species (Table 2.8). In beluga whales, females from each of the four years of sampling were consistently depleted in ^{13}C relative to males (*two-way* MANOVA, ANOVA for effect of sex on $\delta^{13}C$, $F_{1,29} = 62.06$, $P = 0.0001$). Contradictory results were obtained from harbour seals between years, since females were significantly ^{13}C-enriched relative to males in 1995 (*post hoc t*-test: $P = 0.0005$), whereas the two sexes had similar enrichments in 1996 and 1997 (*host hoc* t-test: $P = 0.717$ and 0.888, respectively).

Trophic structure of the St Lawrence community

Carbon isotope ratios varied by up to 9‰ among organisms from a given region (Figure 2.5; Tables 2.6, 2.7). Primary producers were found at both extremes, with macroalgae being the most ^{13}C-enriched source, and POM the least ^{13}C-enriched source. Given the wide variation in δ^{13}C values among organisms from a given region and *TP*, two main C pathways appear to be important in the St Lawrence food webs (Figure 2.5). Each pathway incorporates a progressive enrichment of ~ 1.5‰ in δ^{13}C with trophic level. Assuming that the 2–3‰ depletion of Gulf POM relative to Estuary POM would translate into a similar depletion in Gulf zooplankton, ^{13}C contents increased with ascending *TP* from POM through zooplankton, fish and marine mammals in both regions. A similar increase in ^{13}C abundance with increasing *TP* was also observed from *Ascophyllum nodosum* to amphipods, urchins, molluscs, and worms to decapods and smooth flounders. Among macroalgae species, ^{13}C contents varied by nearly 4‰, with the infralittoral species *Laminaria longicruris* being enriched compared to the intertidal species *Ascophyllum nodosum.*

Nitrogen isotope ratios varied by 12‰ among organisms from a given region (Figure 2.5; Tables 2.6, 2.7). The least enriched species were primary producers with δ^{15}N values of 4.5–7.9‰. Benthic and planktonic invertebrates were enriched in ^{15}N relative to primary producers, but generally were less enriched than most fish and marine mammals. Marine mammals were the most enriched group in both the Estuary and Gulf communities, and occupied the highest *TP*, along with a few fish species such as white hakes and smooth flounders of ≥ 32 cm, sea ravens and fourline snakeblennies.

The various species, age class and sex groupings of marine mammals differed significantly in both *TP* and δ^{13}C of their average diet (ANOVA on ranks: $F_{13,236} = 21.40$ and $F_{15,234} = 48.33$, $P < 0.0001$ for both *TP* and δ^{13}C of diet) (Tables 2,8, 2.9, 2.10). Estuary harp seals and female beluga whales occupied the lowest *TP* of all marine mammals, whereas harbour and hooded seals were found at the other extreme. Gulf harp seals, grey seals and male beluga whales occupied intermediate *TPs*. When examining $\delta^{13}C$ values of the average diet, marine mammal groups segregated further. Harbour seals and beluga whales fed on the most ^{13}C-enriched diets, whereas harp seal yearlings from the Estuary, 2+ harp seals from the Gulf and grey seals captured either in the Estuary or Gulf fed on the least enriched prey. The only exception was observed in 1996-97 yearling harbour seals, whose diet was similar in $\delta^{13}C$ to that of grey seals and Gulf harp seals. Diets of Gulf hooded seals and 2+ harp seals from the Estuary were intermediately enriched in ^{13}C.

The trophic position and $\delta^{13}C$ of the average diet also varied over time in Estuary grey and harbour seals. Diets integrated in red blood cells were ^{13}C-depleted relative to those integrated in serum in all males and females of both yearling and 2+ grey seals (averages of 0.8–1.2‰; range 0.3–1.5‰; paired *t*-tests: $P < 0.001$ for each of the age classes) (Figure 2.6a). Trophic positions estimated from either tissue were similar for yearling males and females, and for 2+ males and females. In harbour seals captured in late summer, *TP* and diet integrated by the two tissues were similar (Figure 2.6b), regardless of age class or sex (all $P > 0.05$). However, for harbour seals captured in early summer (Figure 6c), yearling females ($P < 0.10$ for both *TP* and $\delta^{13}C$ of diet; $n = 3$) and 2+ females ($P < 0.05$ for both *TP* and $\delta^{13}C$ of diet; $n = 8$) had on average a lower *TP* (0.1‰ for each age class), and fed on diets depleted in $\delta^{13}C$ by 0.5 and 0.6‰ respectively, when diet was estimated from their blood serum rather than from their blood cells. Diets reflected by blood serum or red cells of 2+ and yearling males captured in early summer were similar in $\delta^{13}C$ values, but *TP* of 2+ males were, like in 2+ females, 0.1‰ higher according to blood cells than to serum ($P = 0.043$; $n = 9$). When comparing $\delta^{13}C$ of diet and *TP* integrated in blood cells to those in hair, males and females of both yearling and 2+ harbour seals occupied similar *TPs* (all $P > 0.10$), but were on average 0.8–1.1‰ depleted in $\delta^{13}C$ in their hair relative to their blood cells (range from 0.4‰ enriched to 2.1‰ depleted; all $P < 0.002$).

Discussion

Diet-tissue fractionation of ^{13}C and ^{15}N

The diet-tissue fractionations observed in captive seals lead to an enrichment in the heavier C and N isotopes. The enrichment in ^{15}N of consumers over that in their diet is a well recognised phenomenon (Table 2.1), and the magnitude of ^{15}N enrichments obtained for red blood cells and hair closely matched those reported previously for captive seals (Table 2.5). In contrast, the existence of a significant diet-tissue fractionation in ^{13}C is controversial, with conclusions varying from negative, to no change or positive enrichment of consumers relative to their diet, and from TEFs of -2.1 to +4.5‰ (Table 2.2). The failure to extract ^{13}C-depleted lipids from tissues may account for some of this variability. In studies where lipids were extracted prior to analyses, TEF were generally positive and less than + 2‰ per trophic level (Table 2.2), which is similar to the +1.5-2.3 TEF found in this study.

The constancy of TEF in $\delta^{13}C$ and $\delta^{15}N$ among the captive seals and their relatively large values compared to within-group variability make these isotopes useful tracers of both *TP* and $\delta^{13}C$ values of seals' diets. Variability observed in $\delta^{13}C$ and $\delta^{15}N$ TEF in this study are among the smallest reported for either conspecifics or different species raised on the same diet. Deviations of up to 1.8‰ for $\delta^{13}C$ and 3.2‰ for $\delta^{15}N$ have been reported among grasshopper conspecifics and between fly species, respectively (DeNiro and Epstein 1978; 1981; Hobson and Clark 1992a, b; Hilderbrand et al. 1996; Hobson et al. 1996). However, lipid contents were not accounted for in most studies and likely contributed to $\delta^{13}C$ variability. The type of diet has been shown to affect $\delta^{13}C$ and $\delta^{15}N$ TEF of some consumers, including crows and polar bears (Hobson and Clark 1992a; Hilderbrand et al. 1996). However, this variability may have resulted from differential fractionation associated with C_3 *vs* C_4 plants in these studies (Hobson and Clark 1992a) and may not represent a relevant source of variability in this study.

Marine mammals and the trophic structure of the St Lawrence food webs

Primary sources differed widely in their $\delta^{13}C$ values, with POM being, as expected, ^{13}C-depleted relative to benthic macroalgae (Fry and Sherr 1984). Benthic microalgae may represent an important C source for several benthic organisms (Deegan and Garritt 1997) but benthic microalgae were not sampled in this study. In other estuarine systems, benthic microalgae had $\delta^{13}C$ values that were relatively similar to macroalgae and $\delta^{15}N$ values that were similar to POM (Riera et al. 1996; Page 1997). Macroalgae from the infralittoral (*Laminaria longicruris*) and intertidal zones (*Ascophyllum nodosum*) differed markedly in their $\delta^{13}C$ values. This large variation (4‰) is likely attributable to lower turbulence and recycling of dissolved C in the boundary layer of infralittoral species, resulting in a progressive increase in ^{13}C concentration, as well as greater access by intertidal species to ^{13}C-depleted air CO_2 during emersion (Osmond et al. 1981; Surif and Raven 1990). Despite this variation, macroalgae still differed from POM by 5.3–9.1‰, a sufficiently large difference to distinguish between pelagic and benthic organisms, in at least those from the lower trophic levels.

Two C pathways or components were observed in the trophic food webs. One involved POM and pelagic-dependent species, while the other involved benthic micro- or macroalgae and more benthic species (Figure 2.5). However, the variation in $\delta^{13}C$ within each component suggests that some mixing between the two pathways might occur. This could result from sedimentation of phytoplankton, consumers feeding in both benthic and pelagic regions, or from resuspension of benthic algae and marsh detritus. Most fish were ^{13}C-enriched relative to POM and zooplankton, but depleted relative to benthic algae, indicating that the pelagic component of the system was where they accrued most of their food resources. Species such as *Littorina* sp, sea urchins, *Gammarus* sp, *Nereis* worms, blue mussels, decapods, smooth flounders, Atlantic tomcod and Cottidae were 1.0–5.1‰ enriched in δ^{13}C relative to pelagic-feeding species from a similar *TP* such as herring, capelin or redfish, and likely depend to a greater extent on benthic resources. Marine mammals were generally ^{13}C-enriched relative to POM and slightly depleted relative to benthic macroalgae, suggesting that none of them relied exclusively on benthic resources. However, some benthic or demersal organisms are known to be important prey for some of these species, *e.g.* Greenland halibut for hooded seals (Ross 1993), and *Nereis* worms and shrimps for beluga whales (Vladykov 1946). These likely contribute to enriching the δ^{13}C values of these marine mammals relative to those of species that depend heavily on more pelagic prey.

Factors such as distribution may also have contributed to the δ^{13}C variation observed among and within the marine mammal species studied. δ^{13}C of a C source may differ among regions (Dunton et al. 1989; this study) resulting in consumers having different δ^{13}C values despite the exploitation of the same resources. The Lower Estuary POM is generally enriched in δ^{13}C by 2–3.5‰ compared to the Upper Estuary or Gulf POM (ca -25‰). This is likely the result of a high C demand or a change in the phytoplanktonic species that dominate these areas (Tan and Strain 1979; 1983). The ^{13}C-depletion observed in Gulf harp and grey seals, relative to Estuary harbour seals and beluga whales, may result from an exploitation of ^{13}C-depleted Gulf resources by these species. The similarity of δ^{13}C values between Estuary grey seals and seals from the Gulf indicates that their tissues may still reflect the isotopic signature of resources exploited while in the Gulf. Therefore, it is likely that grey seals captured in the Lower Estuary had only recently entered the area. The comparison of grey seals' short-term (serum) and long-term (cells) diet integrators led to a similar conclusion, since their recent diet was ^{13}C-enriched relative to their diet integrated over the last few months (Figure 2.6a). These data concur with anecdotal observations that suggest that grey seals over-winter outside the Estuary and return to this region in the late spring (Lavigueur et al. 1993).

Similarly, the ^{13}C-depletion of harp seals sampled in March on the whelping patch in the Gulf indicates that few of them had visited the Estuary. However, harp seals captured in February in the Estuary were more similar to Estuary harbour seals or beluga whales than to other species from the Gulf when their lower trophic position was accounted for, *i.e.* when $\delta^{13}C$ values were corrected using a 1.3‰ ^{13}C-enrichment per trophic level (Table 2.5). The $\delta^{13}C$ value of Estuary harp seals suggests that they had been in the Estuary since at least early December, assuming a half-life of 4 wk for muscle tissue and a spread over 2–3 months in $\delta^{13}C$ changes (Tieszen et al. 1983). This coincides nicely with the seasonal timing of when the first large numbers of harp seals are sighted in the Lower Estuary (Sergeant 1991).

Gulf hooded seals had $\delta^{13}C$ values that were intermediate between Estuary and Gulf animals, suggesting that they might have visited the Estuary in the months preceding their capture. Alternatively, their higher enrichment relative to other Gulf species might have resulted from a greater dependence on benthic or demersal resources. Both hypotheses are possible. Although the proportion of hooded seals entering the Estuary each year is largely unknown, a greater number of hooded seal winter sightings were made in 1996 in the Estuary compared to other years (L.M. Measures and V. Lesage, unpubl. data). Northwest Atlantic hooded seals are also reported to ingest large quantities of demersal Greenland halibut, principally in the size range from 20–40 cm (Hammill et al. 1997). The $\delta^{13}C$ of their average diet was about -18.8‰ and was, therefore, compatible with Greenland halibut of this size class from either the Estuary (-18.6 to -19.2‰) or Gulf (-18.7 to -19.8‰) (Tables 2.6, 2.7).

Male beluga whales were significantly enriched in $\delta^{13}C$ relative to females, suggesting either a larger dependence by males on benthic species or different distributions of the two sexes. It is unlikely that the larger ^{13}C-enrichment of males is related to more intense benthic feeding since the observations from stable isotopes are opposite to what would be expected from the limited diet data available for this species in the St Lawrence Estuary (Vladykov 1946). The lower $\delta^{15}N$ values of female beluga whales suggests that females feed at lower trophic levels than males and therefore, that their ^{13}C-depletion relative to males might in part result from their lower trophic position. However, some of this variability might also result from differences between the sexes in terms of their geographic distributions. This idea is supported by recent observations that indicate a segregation of adult beluga whales during summer, with females being observed most frequently in the ^{13}C-depleted Upper Estuary, and adult males mainly in the ^{13}C-enriched Lower Estuary (Kingsley 1993; Michaud 1993).

The comparison of carbon isotope ratios in short- and longer-term integrators of diet provided little evidence for seasonal movements of harbour seals outside the Estuary. If significant excursions in the Upper Estuary or Gulf of St Lawrence had occurred during winter, $\delta^{13}C$ of short-term integrators should have been ^{13}C-enriched (Lower Estuary) relative to longer-term integrators. Although these results must be interpreted with caution given that seasonal shift in diet is possible, the data obtained in this study are in agreement with the limited harbour seal satellite telemetry data available for this area (Chapter 4), and support the widespread hypothesis that harbour seals are relatively sedentary (Boulva and McLaren 1979; Thompson 1993).

Although it appears that most of the variation observed in $\delta^{13}C$ may be explained by species' distributions, some variation among sympatric species was likely related to food preferences. The slightly higher $\delta^{13}C$ values observed in most beluga whales relative to harbour seals suggests a greater reliance by beluga whales on benthic or demersal prey. The ingestion of a larger proportion of invertebrates in beluga whales would also be consistent with their lower *TP* relative to harbour seals. Contents from 2 stomachs collected in 1989 and 1995, and diet reports from the late 1930s, indicate that invertebrates such as *Nereis* worms and shrimp-like decapods, as well as Atlantic tomcod (150–200 mm), sand lance (140–185 mm) and redfish may be important species in the St Lawrence beluga's diet, along with the more pelagic capelin (135–180 mm) (Vladykov 1946; Béland 1995; Lesage and Hammill, unpubl. data). Sand lance and capelin are commonly found in the stomach of St Lawrence harbour seals and thus, also appear to be important prey for this species (Lesage, Hammill and Kovacs, unpubl. data). However, shrimp-like decapods or other benthic invertebrates occur only occasionally in harbour seal stomachs. The higher $\delta^{13}C$ in hooded seals relative to other Gulf species may result from their preference for more ^{13}C-enriched demersal prey, *e.g.* Greenland halibut (Ross 1993; Hammill et al. 1997). According to their $\delta^{13}C$ values, Greenland halibut (26-36 cm) and Arctic cod (13-21 cm), the two most important prey of hooded seals off Newfoundland during winter (Ross 1993), would account for 71% and 29% of the seals' diet. However, $\delta^{15}N$ values of both prey (ca 15.3‰) are very close to that of hooded seals (ca 15.7‰ for all classes of hooded seals except 1995 males), which suggests that hooded seals in the Gulf also fed at lower trophic levels or they fed predominantly on smaller (< 20 cm) Greenland halibut than the 26–36 cm range reported in the literature (Table 2.7).

The St Lawrence Estuary and Gulf systems each consisted of at least five trophic levels (Figure 2.5). Killer whales, whose diet may include seals and whales, would likely add a further trophic level to the Gulf system. Most ecosystems appear to be limited to 4–6 trophic levels, with terrestrial chains generally being shorter (Briand and Cohen 1987; Schoener 1989). Factors constraining food chain length are controversial. Food chains may remain short due to the progressive depletion of energy transferred to higher trophic levels, or because long food chains may suffer population fluctuations so severe as to impair the persistence of top predators (reviewed in Pimm 1982; DeAngelis 1995; Power et al. 1996). Recent hypotheses that have not yet been fully explored involve dimensionality of habitats, *i.e.* 3-dimension habitats may support longer chains than 2-dimensions habitats (Briand and Cohen 1987; Pimm et al. 1991) and species richness, *i.e.* chains should be longer in communities supporting a larger number of species (Martinez 1991; Bengtsson 1994; Martinez and Lawton 1995).

Nitrogen isotopes appeared to fractionate similarly in Estuary and Gulf POM (Gearing and Pocklington 1990) and more consistently among different taxonomic groups than C isotopes (Tables 2.1, 2.2) and are, therefore, a better marker of *TP*. Zooplanktonic species seemed to not rely directly on phytoplankton since they occupied *TP* of 2.5–3.0. In aquatic systems in particular, predator–prey relationships are often determined largely by size (Werner and Gilliam 1984). Phytoplankton in the Lower Estuary is dominated by small-sized diatoms (< 25 μm; Levasseur et al. 1984) and zooplankton collected in this study were generally > 160 μm. Planktonic ciliated protozoa (25–75 μm), intermediate in size between phytoplankton and the sampled mesozooplankton, are regarded as an important trophic link between these two groups in the Lower Estuary (Sime-Ngando et al. 1995). Similarly, the dominant copepod in the Gulf, *Calanus finmarchicus*, may rely mainly on heterotrophic microzooplankton for egg production and net lipid synthesis (Ohman and Runge 1994). The absence of species at *TP* 2 in this study and the 1.7–4.0‰ ^{13}C-enrichment of mesozooplankton relative to POM (Table 2.6), *i.e.* nearly twice the 1.3–2.3‰ trophic enrichments reported for lipid-free tissues of marine organisms (Table 2.2), support the hypothesis that protozoa are the main primary consumers of POM in the Estuary. Nevertheless, some macrozooplankton such as *Calanus hyperboreus*, which showed relatively low *TP* and δ^{15}N, likely had mixed diets of microzoo- and phytoplankton. Larger decapods varied widely in *TP*, perhaps because of their habit of feeding on a variety of benthic invertebrates including grazers (*e.g.* sea urchins), consumers of necrotic mollusks (*e.g.* whelks) and suspension feeders (*e.g.* some bivalves). Trophic positions varied little amongst most fish, which likely preyed to a large extent on macrozooplankton. However, decapods, smaller fish or fish larvae probably became prominent in the diet of larger and more ^{15}N-enriched fish such as white hakes, sea ravens, large Atlantic cod, redfish and some Cottidae.

Harbour seals, along with other marine mammals, occupied the top positions in both webs and, according to the narrow range of their *TP*, overlapped trophically with one another. However, an overlap in *TP* does not necessarily imply an overlap in diet, since animals may feed on different species but still occupy similar *TP* if the various prey that they eat result in a similar *TP*. The extent of the trophic or diet overlap between species was difficult to ascertain in this study, because diet was not integrated over exactly the same period among the different marine mammals. Harbour seals and beluga whales that occupy the Estuary throughout the year could only be sampled during the summer, whereas harp seals and hooded seals that normally summer in the Arctic were only sampled during winter. Grey seals captured in summer in the Estuary had signatures reflecting a Gulf diet, and there is some uncertainty as to whether harp, grey and hooded seals sampled in the Gulf actually entered the Estuary prior to sampling. Nevertheless, it is unlikely that two species overlapped completely in their resource requirements (Schoener 1974). Often, potential competitors will either occupy different habitats so that they do not really coexist on a local scale, or will differ in body size, resulting in slight differences in diet composition or preferred prey size. A two fold difference in mass, or 1.25 ratio if using linear dimensions, is often considered sufficient for competition avoidance (Schoener 1974; Bowers and Brown 1982). Among the marine mammals in this study, important variations in body size occur between and within species. The 2+ animals are larger than yearlings and 2+ males are larger than 2+ females. Harp and harbour seals are relatively similar in body mass (~ 110–130 and 80–120 kg, respectively), but are considerably smaller than grey and hooded seals (~ 200–350 and 260–400 kg, respectively) (Reeves et al. 1992). Adult beluga whales are much larger than any other species with a mean mass of 700–970 kg (this study).

The similarly-sized harp and harbour seals differed most in their *TPs*, while harbour *vs* hooded seals, and grey *vs* Gulf harp seals were the species which overlapped most closely trophically. However, these species appeared to differ in their habitat requirements, which reduces the possibility of actual resource overlap. Harbour seals remain in the Estuary and probably feed, to a large extent, on pelagic species found near the coast, whereas hooded seals likely remain in the Gulf and feed mostly on offshore demersal species. Grey seals are relatively coastal (Thompson et al. 1991; J.-F.Gosselin, Fisheries and Oceans Canada, Mont-Joli, QC, unpubl. data), whereas harp seals are mainly pelagic (Sergeant 1991). Estuary harp seals and beluga whales overlapped in their *TP*, but their average diet differed significantly in $\delta^{13}C$, indicating the use of different resources. Indeed, the stomachs of harp seals sampled in this study contained mainly capelin and euphausiids, although sand lance and crustaceans were also regularly consumed (Hammill, unpubl. data). Assuming that only capelin and euphausiids were ingested, the latter would account for up to 75% of the Estuary harp seal diet. The greater reliance of beluga whales on ^{13}C-enriched benthic or demersal invertebrates and of harp seals on ^{13}C-depleted euphausiids could explain the divergence in their $\delta^{13}C$ values and their similarity in *TP*.

An overlap in food preferences may also have been possible between 2+ animals of small species and yearlings of larger species. In our study area, juvenile grey seals and adult harbour seals, two similarly-sized groups, often hauled out very close to each other. However, slight differences were observed in *TP* of adult harbour seals relative to Estuary grey seals, which consisted mainly of subadult or yearling individuals, indicating some partitioning of food resources. Tracking of adult harbour seals and subadult grey seals using satellite telemetry also indicated that subadult grey seals consistently dive to deeper depths than the harbour seals while at sea (Lesage et al. 1995), which might indicate spatial partitioning of foraging areas in a 3-dimensional sense.

Differences in body size, diving capabilities or food handling ability between age classes (Scholander et al. 1942; Kleiber 1961) may result in animals feeding on different trophic levels as they mature (life-history omnivory; Werner and Gilliam 1984; Sprules and Bowerman 1988). Many species of fish become more piscivorous with age, which would increase their trophic position relative to juvenile conspecifics. In marine mammals, lower prey capture or handling skills and diving ability in young individuals (LeBoeuf et al. 1996; Horning and

Trillmich 1997; Chapter 4) would promote feeding at lower trophic levels (*e.g.* Boulva and McLaren 1979; Lawson et al. 1995; Proust 1995) and would tend to reduce competition with older animals. Isotopic C and N provided evidence of life-history omnivory in both marine mammals and fish. In species where this phenomenon was observed, smaller individuals were ^{15}N-depleted or ^{13}C-depleted relative to larger individuals, suggesting that they fed at lower trophic levels. Life-history omnivory has been documented from stomach content examination (Werner and Gilliam 1984; Huse and Toresen 1996), and from stable isotope analysis (*e.g.* Gearing et al. 1984; Hobson and Welch 1995; France 1996b; Sierszen et al. 1996).

Very little information exists on the diet of yearlings and 2+ St Lawrence harbour seals. Capelin and sand lance were the two most common prey found in the few non-empty stomach contents taken from weaned pups ($n = 8$), with invertebrate parts also being observed occasionally (Lesage, Hammill and Kovacs, unpubl. data). These prey were also observed frequently in the diet of yearlings ($n = 5$) and older animals ($n = 3$), along with herring (both yearlings and older animals) and a few Cottidae and Pleuronectidae. The relative importance of capelin and herring in the harbour seal diet cannot be determined because of their similar C and N isotopic values. However, their contribution to the diet relative to sand lance may be calculated given the 2‰ difference between the two groups. Sand lance would have contributed up to 70% of the diet of yearlings, but less than 26% of that of older animals.

Body size dimorphism between males and females may also have led to differences in *TP*. Adult males of the dimorphic species (beluga whales, hooded and grey seals, and to a much lesser extent harp seals) were generally found at higher *TPs* than females, and may have consumed food resources inaccessible to, or too large, for females (Kooyman 1989; Boyd and Croxall 1996). Sex-related variation in *TP* was not observed in Estuary harbour seals, and may have been the result of a less pronounced physical dimorphism in this species. Differences in *TP* between sexes were also not observed in 2+ Estuary grey and harp seals, probably as a result of the relatively similar size of the two sexes in these immature animals.

The use of multiple tissues and multiple stable isotopes has provided insights into the trophic relationships of both the Estuary and Gulf of St Lawrence ecosystems, as well as providing a valuable framework or validation tool for the construction of multispecies ecosystem models. Harbour seals occupy a high trophic position within the Estuary and appear to be mainly piscivorous. Although some resource overlap appears to occur with other marine mammals, it is likely that the combination of seasonal changes in distribution and habitat would reduce resource overlap and, consequently, the potential for competition. More complete sampling is required to examine the question further. The stable isotope approach is limited in its ability to identify the contribution of individual species occupying the same trophic level. However, this approach provides a reliable picture of the contribution of invertebrates to the diet and indicates that some species (harp seals and beluga whales) may derive a considerable amount of their energy from invertebrate food resources.

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Table 2.1. Enrichment in ^{15}N (TEF) between diet and consumer tissues (M = muscle, W = whole animal, B = bone collagen) obtained from marine (MR) or freshwater (FW) organisms during field (F) or captivity (C) studies, or from compilation of published literature (L).

System	Tissue	Prey type and method used	Study type	TEF in $\delta^{15}N$ (‰)	Reference
MR	W	overall average	F	+3.3	Wada et al. (1987)
MR	M	fish *vs* gut contents	F	+3.4–3.8	Fry (1988)
MR	W	zooplankton *vs* presumed diet	F	ca +3	Goering et al. (1990)
MR	W	copepods *vs* POM[a]	F	+3.3–4.2	Montoya et al. (1990)
FW	W	copepods *vs* POM[a]	F	+3.2 ± 0.3	Kling et al. (1992)
FW	M	arctic grayling *vs* gut contents	F	+3.1	Peterson et al. (1993)
FW	M	presumed cannibalistic char	F	+3.7	Hobson and Welch (1995)
FW	W	zooplankton or shrimp *vs* diet	F	+3–4	Gu et al. (1996)
MR	M + W	planktonic fish *vs* presumed diet	F	+3	Jennings et al. (1997)
FW	M	broad whitefish *vs* diet	C	+3.0–3.8	Hesslein et al. (1993)
FW	M	*Chasmistes cujus vs* diet	C	+2.9–3.6	Estep and Vigg (1985)
MR + FW	W	guppys *vs* diet	C	+3.2	Minagawa and Wada (1984)
	W	brine shrimp *vs* diet	C	+4.9	
	M + W	overall average	F	+3.4 ± 1.1	
MR	B	overall average	L	+3.3	Schoeninger and DeNiro (1984)
MR	W	overall average	L	+2.6 ± 2.1	Owens (1987)
MR + FW	W	overall average	L	+3.2	Peterson and Fry (1987)

[a] POM = Particulate Organic Matter

Table 2.2. Enrichment in ^{13}C (TEF) between diet and consumer tissues (M = muscle, W = whole animal, B = blood, S = skin, P = plasma) obtained from terrestrial (T), marine (MR) or freshwater (FW) organisms during field (F) or captivity (C) studies, or from compilation of published literature (L).

Study type	Tissue	System	lipid contents	TEF in $\delta^{13}C$ (‰)	Species and method used	Reference
C	W + M	MR + T	with fat	-0.6 to +2.7	several species vs diet	DeNiro and Epstein 1978
C	W	MR	with fat	-2.1 to +0.8	polychaete vs 3 diets	Haines and Montague 1979
C	W	MR	with fat	-0.9 to -1.3	amphipod vs diet	Macko et al. 1982
C	M	T	with fat	<1	gerbil vs diet	Tieszen et al. 1983
F	W	MR	with fat	0.8–2.2	zoopl. or copepods vs POM[a]	Thayer et al. 1983
C	W	MR	with fat	ca 0	amphipods or isopods vs diet	Stephenson et al. 1986
	M			+1.1–6.0	lobsters or oysters vs diet	
C	M	FW	with fat	+2.0	broad whitefish vs diet	Hesslein et al. 1993
C	P	T	with fat	+0.4–4.5	bear vs diets of -18.5 to -25.5‰	Hilderbrand et al. 1996
C	S	MR	with fat	+4.0	manatee vs diet	Ames et al. 1996
C	W	MR	with fat	+2	POM[a] vs copepods	Checkley and Entzeroth 1985
F	M	MR	with fat	+0.73–1.38	overall average; no plankton	Rau et al. 1983
F	W	MR	with fat	-0.6 to +0.6	zoopl. vs POM[a]	Tan and Strain 1983
F	W + M	MR	with fat	+1.9	zoopl. vs POM[a]	Fry et al. 1984
				+1.7	shrimp vs gut contents	
F	M + W	MR	with fat	+1.5–1.6	fish vs gut contents or mean diet	Fry 1988
F	W	MR	with fat	+0.5–0.7	zoopl. vs phytopl.	Goering et al. 1990
F	W + M	FW	with fat	+1–2	overall average[b]	Gu et al. 1996
F	W + M	FW	with fat	ca 0	overall average	France 1996a
L	W + M	MR + T	with fat	-0.7 to +0.7	overall average	Fry and Sherr 1984
L	W + M	?	with fat	+0.4 ± 1.4	overall average	Gearing et al. 1984
L	W + M	?		+0.6 ± 1.4	overall average	
F	W	MR		≥ +0.5	zoopl. vs phytopl.	
L	W + M	MR, FW, T	with fat	+0.2	overall average	Peterson and Fry 1987
L	W	MR	with fat	+2.7	zoopl. vs POM[a] (open ocean)	del Giorgio and France 1996
				+1.8	zoopl. vs POM[a] (coastal waters)	
				+0.8	zoopl. vs POM[a] (estuaries)	
L	W + M	MR + FW	> 95% of samples with fat	+1.1	overall (open ocean)	France and Peters 1997
				+0.8	overall (coastal marine waters)	
				+0.5	overall (estuaries)	
				+0.2	overall (freshwater)	
F	W	MR	corrected	+1.5	obtained from basic physiology	McConnaughey and McRoy 1979
F	M + W	MR	fat-free	+2.0	anchovy vs gut content	Monteiro et al. 1991
				+2–3	overall average - model	
F	M	MR	fat-free	+2.1–2.3	fish vs gut content	Sholto-Douglas et al. 1991
C	B	T + MR	with fat	-0.3; +1.2	2 sp. of bird vs diet	Hobson and Clark 1992a
	M		fat-free	+0.3–1.1	3 sp. of bird vs diet	
C	M	MR	fat-free	+1.3	harp seal vs diet	Hobson et al. 1996
	B		with fat	+1.7		

[a] POM = Particulate Organic Matter

[b] Extrapolated from their Figure 1

Table 2.3. Tissues collected from males (M) and females (F) of the different marine mammals for the determination of isotope ratios of stable carbon and nitrogen.

Species	Region (period)	Age class	Year	Mean mass ± SD (kg)	Mean age ± SD (yr)	Number of samples taken								
						Total	Blood cells		Blood serum		Muscle		Hair	
							F	M	F	M	F	M	F	M
Harbour seal	Lower Estuary (Apr.–Nov.)	*Nursing pup*	1995	19.4 ± 5.9	0	21	9	12	8	12	-	-	-	-
		Weaned pup	1995	23.9 ± 4.6	0	8	5	3	5	3	-	-	-	-
			1996	22.2 ± 1.1	0	6	4	2	4	2	-	-	-	-
		Yearling	1995	36.2 ± 5.4	1	10	6	4	6	4	-	-	4	4
			1996	36.3 ± 4.1	1	13	3	10	2	9	-	-	-	-
			1997	35.8 ± 2.6	1	10	7	3	-	-	-	-	-	-
		2+ animals	1995	66.8 ± 15.8	5.5 ± 2.0	18	6	12	6	12	-	-	7	11
			1996	73.4 ± 18.7	6.9 ± 3.2	21	11	10	11	9	-	-	-	-
			1997	61.4 ± 20.6	3.6 ± 2.2	5	2	3	-	-	-	-	-	-
Beluga	Estuary (Apr.–Nov.)	*2+ animals*	1988	-	21.9 ± 3.8	9	-	-	-	-	6	3	-	-
			1989	-	22.1 ± 5.2	10	-	-	-	-	6	4	-	-
			1990	-	19.3 ± 4.3	8	-	-	-	-	4	4	-	-
			1997	-	21.9 ± 8.9	10	-	-	-	-	6	4	-	-
Grey seal	Lower Estuary (Apr.–Nov.)	*Yearling*	1995	53.6 ± 16.2	1	4	3	1	3	1	-	-	-	-
			1996	57.3 ± 14.4	1	6	5	1	5	1	-	-	-	-
		2+ animals	1995	140.8 ± 48.5	-	3	1	2	1	2	-	-	-	-
			1996	95.5 ± 13.5	-	6	3	3	3	3	-	-	-	-
	Port-Hood (N.S.) (Jan.)	*2+ animals*	1996	200.1 ± 47.6	15.5 ± 6.8	16	8	8	-	-	-	-	-	-
Hooded Seal	Magdalen Islands (Mar.)	*2+ animals*	1995	223.0 ± 49.8	17.2 ± 6.8	27	20	7	-	-	-	-	-	-
			1996	252.9 ± 37.9	11.6 ± 2.9	17	8	9	-	-	-	-	-	-
Harp Seal	Lower Estuary (Feb.)	*Yearling*	1995	33.5 ± 5.7	1	9	-	-	-	-	4	5	-	-
		2+ animals	1995	68.1 ± 12.3	3.9 ± 0.8	9	-	-	-	-	7	2	-	-
	Magdalen Islands (Mar.)	*2+ animals*	1995	110.4 ± 23.4	9.0 ± 3.9	24	18	6	-	-	-	-	-	-
			1996	129.4 ± 16.4	8.9 ± 3.9	15	8	7	-	-	-	-	-	-

Table 2.4. Mean isotopic ratios and TEF in $\delta^{13}C$ and $\delta^{15}N$ (± 1 SD, in ‰) for fat-free tissues (hair, blood serum and red blood cells) of seals raised in captivity on a constant diet of 100–300 g herring. Food isotopic signature was calculated from a mixture of 3 herring and 3 capelin for seals held at Memorial University, since the amount of each prey fed daily to the animals is unknown.

			Mean isotopic ratios (‰)									Mean trophic enrichment or TEF (‰)					
Site	Species	*n*	Serum		Cells		Hair		*n*	food		^{13}C			^{15}N		
			$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$		$\delta^{15}N$	$\delta^{13}C$	Serum	Cells	Hair	Serum	Cells	Hair
University of Guelph	Harbour seal	2	16.6	-17.9	15.3	-17.5	15.6	-17.3	7	13.4	-19.6	+ 1.7	+ 2.2	+ 2.3	+ 3.2	+ 1.9	+ 2.3
			(0.5)	(0.3)	(0.1)	(0.2)	(0.8)	(0.1)		(0.4)	(0.3)						
	Grey seal	5	16.7	-18.0	15.0	-17.6	-	-	7	13.4	-19.6	+ 1.6	+ 2.1	-	+ 3.3	+ 1.7	-
			(0.2)	(0.1)	(0.1)	(0.2)				(0.4)	(0.3)						
Quebec Aquarium	Harbour seal	3	16.0	-18.2	14.8	-18.1	-	-	4	13.3	-19.6	+ 1.3	+ 1.5	-	+ 2.7	+ 1.5	-
			(0.4)	(0.2)	(0.3)	(0.2)				(0.2)	(0.3)						
	Grey seal	2	16.2	-18.3	14.9	-17.9	-	-	4	13.3	-19.6	+ 1.3	+ 1.7	-	+ 2.9	+ 1.6	-
			(0.3)	(0.1)	(0.3)	(0.1)				(0.2)	(0.3)						
Shippagan	Harbour seal	4	15.6	-18.8	14.9	-18.6	-	-	4	12.9	-20.0	+ 1.2	+ 1.4	-	+ 2.8	+ 2.0	-
			(0.3)	(0.1)	(0.2)	(0.1)				(0.2)	(0.2)						
Memorial University	Harp seal	9	17.4	-18.0	15.7	-17.7	-	-	6	14.1	-19.7	+ 1.7	+ 1.9	-	+ 3.3	+ 1.6	-
			(0.4)	(0.8)	(0.2)	(0.1)				(0.7)	(0.3)						

Table 2.5. Trophic enrichment factors (TEF) in δ^{13}C and δ^{15}N in tissues (hair, muscle, blood serum and red cells) of harbour and grey seals held in captivity on a constant diet of herring. Shaded factors were those used in this study.

		Lipid	TEF δ^{13}C (‰)			TEF δ^{15}N (‰)		
Tissue	*n*	Contents	Mean	SD	Range	Mean	SD	Range
Cells	17	with fat	+1.4	0.3	0.9–1.9	**+1.8**	0.3	1.1–2.2
		fat-free	**+1.8**	0.4	1.2–2.4			
	14	with fat	+1.7*			+1.7*		
Serum	17	with fat	+0.7	0.3	0.3–1.2	**+3.0**	0.4	2.3–3.6
		fat-free	**+1.5**	0.3	1.1–2.1			
Hair	2	fat-free	+2.3	0.1	2.3–2.4	+2.3	0.8	1.7–2.8
	10	fat-free	**+2.8***			**+3.0***		
Muscle	2	fat-free	**+1.3***			**+2.4***		

* From Hobson et al. (1996)

Table 2.6. Stable carbon and nitrogen isotope ratios and trophic position of components of the St Lawrence Estuary community. Length classes (in mm) are presented in parentheses.

Species	*N*	Mean δ^{13}C (‰)	Mean δ^{15}N (‰)	Trophic Position
Particulate organic matter (POM)	3	-22.9 ± 1.7	4.5 ± 0.9	1.0
Benthic macroalgae				
Ascophyllum nodosum	1	-17.6	7.6	
Laminaria longicruris	1	-13.8	7.9	
Arthropoda - Crustacea				
Copepoda				
Calanus hyperboreus	1	-21.2	9.8	2.5
Euchaeta norvegica	2	-19.8 ± 0.2	10.5 ± 0.4	2.8
Microcalanus pusillus	1	-18.9	10.5	2.8
Calanus sp	1	-19.6	10.9	2.9
Metridia sp	2	-20.4 ± 0.2	12.3 ± 1.1	3.3
Malacostraca				
Mysidacea				
Mysis sp	1	-20.4	10.9	2.9
Amphipoda				
Caprella sp	1	-17.9	6.0	1.4
Gammarus sp	1	-17.8	9.1	2.4
Euphausiacea				
Thysanoessa inermis et *T. raschii*	4	-19.6 ± 1.1	10.1 ± 1.5	2.6
Meganyctiphanes norvegica	1	-19.3	11.5	3.1
Decapoda[a]				
Rock crab *Cancer irroratus* (176-256)	2	-16.5 ± 0.4	12.7 ± 1.0	3.4
Pandalus borealis	1	-17.8	13.2	3.5
Snow crab *Chionoecetes opilio* (60)	1	-17.8	13.2	3.5
Pandalus montagui	2	-17.5 ± 0.4	13.8 ± 0.0	3.7
Snow crab *Chionoecetes opilio* (910)	3	-16.7 ± 0.6	14.0 ± 0.7	3.8
Sclerocrangon boreas	2	-17.8 ± 0.6	14.2 ± 0.2	3.9
Mollusca				
Bivalvia				
Blue mussel *Mytilus edulis*	1	-19.2	7.4	1.8
Chlamys islandica	1	-16.7	11.8	3.1
Annelida - Polychaeta				
Nereis sp	1	-16.2	10.6	2.8
Echinodermata				
Echinoidea				
Green urchin *Strongylocentrotus droebachiensis*	3	-14.6 ± 0.2	7.7 ± 0.7	2.0

Table 2.6. (Continued)

Species	*N*	Mean $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)	Trophic Position
Pisces[b]				
American sand lance *Ammodites americanus* (96-102)	2	-19.9 ± 0.4	11.5 ± 0.3	3.0
American sand lance *Ammodites americanus* (115-205)	9	-18.5 ± 0.4	11.4 ± 0.3	3.0
Atlantic herring *Clupea h. harengus* (103-165)	10	-18.8 ± 1.1	13.1 ± 0.6	3.5
Greenland halibut *Reinhardtius hippoglossoides* (135-165)	5	-19.7 ± 0.4	13.1 ± 0.7	3.5
Capelin *Mallotus villosus* (95-147)	13	-19.4 ± 0.6	13.5 ± 0.5	3.6
American plaice *Hippoglossoides platessoides* (184-206)	3	-18.0 ± 0.1	13.7 ± 0.2	3.7
Pollock *Pollachius virens* (327)	1	-19.7	13.8	3.7
Redfish *Sebastes* sp (79-126)	6	-19.1 ± 0.7	13.9 ± 0.5	3.8
Redfish *Sebastes* sp (185-305)	6	-18.9 ± 0.3	14.0 ± 0.3	3.8
Atlantic herring *Clupea harengus harengus* (215-315)	14	-18.9 ± 0.7	13.9 ± 0.4	3.8
Atlantic cod *Gadus morhua* (230)	1	-18.4	14.0	3.8
Arctic cod *Boreogadus saida* (98)	1	-18.2	14.2	3.9
Greenland halibut *Reinhardtius hippoglossoides* (219-275)	8	-19.2 ± 0.3	14.3 ± 0.2	3.9
Cottidae (196-205)	2	-16.7 ± 0.9	14.4 ± 0.4	3.9
Lumpfish *Cyclopterus lumpus* (176-320)	6	-19.5 ± 0.5	14.6 ± 0.3	4.0
Skate *Raja* sp (126-330)	5	-18.0 ± 0.5	14.6 ± 0.6	4.0
Fourline snakeblenny *Eumesogrammus praecisus* (300)	2	-18.2 ± 0.0	14.7 ± 0.6	4.0
Witch flounder *Glyptocephalus cynoglossus* (190-460)	19	-17.6 ± 0.5	14.7 ± 0.5	4.0
Rainbow smelt *Osmerus mordax* (78-99)	2	-20.0 ± 0.2	14.8 ± 0.4	4.0
Arctic cod *Boreogadus saida* (140-146)	2	-18.0 ± 0.2	14.8 ± 0.2	4.0
American plaice *Hippoglossoides platessoides* (232-315)	6	-18.2 ± 0.5	14.9 ± 0.4	4.1
Snailfish *Liparis* sp (184-235)	4	-18.0 ± 0.4	14.9 ± 0.4	4.1
Lycodes sp (215-340)	3	-18.1 ± 1.0	15.0 ± 1.1	4.1
Atlantic tomcod *Microgadus tomcod* (88-107)	3	-16.2 ± 1.6	15.0 ± 0.2	4.1
Macrouridae (230)	1	-18.7	15.0	4.1
American eel *Anguilla rostrata* (715-1040)	18	-21.1 ± 2.9	15.1 ± 1.4	4.1
Greenland halibut *Reinhardtius hippoglossoides* (344-420)	6	-18.6 ± 0.3	15.3 ± 0.8	4.2
American plaice *Hippoglossoides platessoides* (335-410)	4	-18.1 ± 0.1	15.4 ± 0.2	4.2
Smooth flounder *Liopsetta putnami* (76-176)	3	-14.3 ± 0.8	15.4 ± 0.4	4.2
Atlantic cod *Gadus morhua* (330-545)	6	-18.3 ± 0.5	15.6 ± 0.7	4.3
Fourbeard rockling *Enchelyopus cimbrius* (235)	1	-18.9	15.6	4.3
Atlantic tomcod *Microgadus tomcod* (145-190)	6	-18.0 ± 1.6	15.7 ± 0.4	4.3
Black dogfish *Centroscyllium fabricii* (405-455)	3	-18.4 ± 0.1	15.7 ± 0.5	4.3
Rainbow smelt *Osmerus mordax* (152-216)	7	-19.0 ± 0.4	15.7 ± 0.4	4.3
Cottidae (280)	1	-17.4	15.8	4.3
Atlantic tomcod *Microgadus tomcod* (270-330)	4	-18.1 ± 0.2	16.4 ± 0.1	4.5
Atlantic poacher *Agonus decagonus* (205)	1	-18.4	16.2	4.5
Smooth flounder *Liopsetta putnami* (316-334)	3	-14.8 ± 0.5	16.5 ± 0.4	4.5
White hake *Urophycis tenuis* (324-520)	3	-17.8 ± 0.3	16.7 ± 0.5	4.6

[a] Length classes are based on width of 'carapace' in mm

[b] Length classes are based on fork lengths in mm

Table 2.7. Stable carbon and nitrogen isotope ratios and trophic position of components of the Gulf of St Lawrence community. Length classes (in mm) are presented in parentheses.

Species	*N*	Mean $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)	Trophic Position
Arthropoda - Crustacea				
Decapoda				
Lobster *Homarus americanus* (125-200)[a]	6	-17.5 ± 0.4	11.4 ± 0.4	3.0
Snow crab *Chionoecetes opilio* (107)[b]	1	-17.6	12.1	3.2
Eualus sp - 3 ind.	1	-18.0	12.6	3.4
Pasiphaea tarda	1	-19.3	13.0	3.5
Snow crab *Chionoecetes opilio* (55-57)[b]	2	-18.7 ± 0.1	13.3 ± 0.1	3.6
Sclerocrangon boreas - 2 ind.	1	-18.5	13.3	3.6
Pasiphaea multidentata - 3 ind.	2	-19.6 ± 0.9	13.5 ± 0.1	3.6
Pandalus montagui	5	-18.0 ± 1.1	13.5 ± 0.4	3.6
Pandalus sp	4	-18.0 ± 0.4	13.9 ± 0.5	3.8
Lebbeus groenlandicus	1	-17.5	14.0	3.8
Sclerocrangon boreas	1	-16.4	14.8	4.0
Mollusca				
Gasteropoda				
Littorina sp	2	-14.8 ± 0.1	8.6 ± 0.0	2.2
Whelk *Buccinum undatum* (48)[c]	3	-17.6 ± 0.5	11.1 ± 0.3	3.0
Bivalvia				
Blue mussel *Mytilus edulis*	1	-19.6	7.3	1.8
Cephalopoda				
Squid *Illex illecebrosus* (142-210)[d]	6	-19.2 ± 0.3	13.0 ± 0.4	3.5
Pisces[e]				
Atlantic mackerel *Scomber scombrus* (74-83)	3	-21.0 ± 0.3	11.2 ± 0.3	3.0
American sand lance *Ammodites americanus* (147-215)	8	-19.6 ± 0.3	11.9 ± 0.5	3.2
Lumpfish *Cyclopterus lumpus* (125-136)	4	-20.9 ± 0.8	12.7 ± 0.2	3.4
Greenland halibut *Reinhardtius hippoglossoides* (165-185)	2	-18.9 ± 0.1	12.8 ± 0.1	3.4
Atlantic mackerel *Scomber scombrus* (220-403)	13	-20.2 ± 0.5	12.9 ± 0.6	3.5
Winter flounder *Pseudopleuronectes americanus* (205-345)	6	-18.9 ± 0.5	13.0 ± 0.4	3.5
White baraccudina *Notolepis rissoi* (220-245)	5	-19.8 ± 0.3	13.1 ± 0.6	3.5
Atlantic herring *Clupea h. harengus* (144-180)	6	-20.7 ± 0.7	13.3 ± 0.4	3.6
Atlantic herring *Clupea h. harengus* (185-325)	30	-19.9 ± 0.3	13.4 ± 0.4	3.6
Pollock *Pollachius virens* (230-290)	4	-20.4 ± 0.1	13.6 ± 0.9	3.7
Capelin *Mallotus villosus* (105-155)	13	-20.0 ± 0.8	13.7 ± 0.7	3.7
Yellowtail flounder *Limanda ferruginea* (235-305)	4	-19.1 ± 0.8	13.7 ± 0.4	3.7
Lumpfish *Cyclopterus lumpus* (260-265)	2	-20.5 ± 0.4	13.7 ± 0.3	3.7
Longfin hake *Urophycis chesteri* (160-320)	5	-19.8 ± 0.4	14.0 ± 0.5	3.8
Arctic cod *Boreogadus saida* (121-135)	6	-19.9 ± 0.6	14.0 ± 0.2	3.8
Greenland cod *Gadus ogac* (160-235)	7	-19.3 ± 0.8	14.3 ± 0.4	3.9
Greenland halibut *Reinhardtius hippoglossoides* (230-270)	4	-19.8 ± 0.4	14.3 ± 0.3	3.9

Table 2.7. (Continued)

Species	*N*	Mean δ^{13}C (‰)	Mean δ^{15}N (‰)	Trophic Position
American plaice *Hippoglossoides platessoides* (134-195)	4	-19.6 ± 0.4	14.3 ± 0.4	3.9
Pollock *Pollachius virens* (300-310)	2	-19.6 ± 0.4	14.4 ± 0.1	3.9
American plaice *Hippoglossoides platessoides* (220-320)	8	-19.4 ± 0.5	14.5 ± 0.4	3.9
Lycodes sp (185-365)	6	-19.2 ± 0.8	14.5 ± 0.4	3.9
Atlantic cod *Gadus morhua* (145-320)	11	-19.5 ± 0.5	14.6 ± 0.8	4.0
Redfish *Sebastes* sp (120-145)	5	-20.1 ± 0.1	14.6 ± 0.4	4.0
Redfish *Sebastes* sp (152-335)	11	-19.2 ± 0.5	14.7 ± 0.7	4.0
Witch flounder *Glyptocephalus cynoglossus* (165-190)	3	-19.4 ± 0.2	14.6 ± 0.3	4.0
Haddock *Melanogrammus aeglefinus* (185)	1	-19.6	14.7	4.0
Skate *Raja* sp (240-405)	4	-18.7 ± 0.2	14.8 ± 0.3	4.0
Silver hake *Merluccius bilinearis* (365)	1	-19.6	14.8	4.0
Moustache sculpin *Triglops murrayi* (145-175)	3	-19.6 ± 0.1	15.0 ± 0.3	4.1
Macrouridae (168-300)	4	-19.1 ± 0.9	15.1 ± 0.6	4.1
Spatulate sculpin *Icelus spatula* (194)	1	-18.6	15.2	4.1
Cottidae (210-265)	3	-18.8 ± 0.5	15.2 ± 0.1	4.1
Arctic cod *Boreogadus saida* (150-220)	6	-19.4 ± 0.4	15.2 ± 0.6	4.1
White hake *Urophycis tenuis* (215-245)	3	-17.5 ± 0.3	15.2 ± 0.3	4.1
Witch flounder *Glyptocephalus cynoglossus* (285-370)	5	-17.9 ± 0.5	15.2 ± 0.6	4.1
Greenland halibut *Reinhardtius hippoglossoides* (305-430)	6	-18.7 ± 0.8	15.3 ± 0.6	4.2
White hake *Urophycis tenuis* (315-525)	4	-18.4 ± 0.5	15.7 ± 0.8	4.3
Black dogfish *Centroscyllium fabricii* (300-395)	3	-18.6 ± 0.2	15.7 ± 0.2	4.3
Arctic cod *Boreogadus saida* (240-280)	2	-19.5 ± 0.1	15.8 ± 0.3	4.3
American plaice *Hippoglossoides platessoides* (360-385)	3	-18.8 ± 0.0	15.8 ± 0.7	4.3
Atlantic cod *Gadus morhua* (330-466)	9	-19.2 ± 0.4	15.8 ± 0.7	4.3
Atlantic wolffish *Anarhichas lupus* (230-355)	4	-18.2 ± 0.6	15.9 ± 0.5	4.4
Fourbeard rockling *Enchelyopus cimbrius* (195-220)	3	-19.3 ± 0.2	16.0 ± 0.3	4.4
Cottidae (280-301)	4	-18.2 ± 0.9	16.1 ± 0.2	4.4
Sea raven *Hemitripterus americanus* (200-385)	3	-18.3 ± 0.1	16.3 ± 0.8	4.5
Redfish *Sebastes* sp (370-415)	3	-18.5 ± 0.2	16.6 ± 0.7	4.5
Fourline snakeblenny *Eumesogrammus praecisus* (145-165)	3	-18.3 ± 0.3	16.8 ± 0.1	4.6
Cottidae (320-327)	2	-18.5 ± 0.3	17.0 ± 0.0	4.7

[a] Length of cephalothorax in mm

[b] Width of carapace in mm

[c] Length of shell in mm

[d] Length of mantle in mm

[e] Fork lengths in mm

Table 2.8. Mean trophic position (TP ± SD), and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios for male and female yearling and 2+ marine mammals from the Estuary and Gulf of St Lawrence presented by species.

Species	Region	Year	Age class	Male				Female			
				n	$\delta^{13}C$	$\delta^{15}N$	TP	*n*	$\delta^{13}C$	$\delta^{15}N$	TP
Harbour seal	Estuary	1995	Yearling	4	-16.3 ± 0.4	16.0 ± 0.2	4.9 ± 0.1	6	-16.2 ± 0.4	15.8 ± 0.2	4.8 ± 0.1
			2+ animals	12	-16.4 ± 0.5	15.9 ± 0.4	4.8 ± 0.1	6	-15.7 ± 0.5	15.9 ± 0.2	4.8 ± 0.1
		1996-97	Yearling	13	-17.6 ± 0.5	15.6 ± 0.5	4.8 ± 0.2	10	-17.5 ± 0.3	15.3 ± 0.7	4.7 ± 0.2
			2+ animals	13	-16.7 ± 0.2	16.0 ± 0.5	4.8 ± 0.1	13	-16.7 ± 0.4	15.9 ± 0.6	4.8 ± 0.2
Beluga	Estuary	1988-90	2+ animals	11	-16.7 ± 0.2	15.8 ± 0.6	4.6 ± 0.2	16	-17.3 ± 0.2	15.1 ± 0.4	4.4 ± 0.1
		1997	2+ animals	4	-16.2 ± 0.3	16.3 ± 1.1	4.8 ± 0.3	6	-16.7 ± 0.2	15.3 ± 0.5	4.5 ± 0.1
Grey seal	Estuary	1995-96	Yearling	2	-18.1 ± 0.2	14.8 ± 0.2	4.5 ± 0.1	8	-17.8 ± 0.4	15.5 ± 0.5	4.7 ± 0.2
			2+ animals	5	-17.6 ± 0.6	15.6 ± 0.9	4.8 ± 0.3	4	-17.8 ± 0.5	15.2 ± 0.6	4.6 ± 0.2
	Gulf	1996	2+ animals	8	-17.4 ± 0.5	15.6 ± 0.7	4.7 ± 0.2	8	-17.7 ± 0.8	15.0 ± 0.9	4.6 ± 0.3
Harp seal	Estuary	1996	Yearling	5	-18.3 ± 0.3	13.1 ± 0.3	3.8 ± 0.1	4	-18.4 ± 0.2	13.6 ± 1.1	4.0 ± 0.3
			2+ animals	2	-17.6 ± 0.1	13.5 ± 0.2	3.9 ± 0.1	7	-17.6 ± 0.3	13.7 ± 0.7	4.0 ± 0.2
	Gulf	1995	2+ animals	6	-17.7 ± 0.4	15.5 ± 0.4	4.7 ± 0.1	18	-17.7 ± 0.4	14.9 ± 0.4	4.5 ± 0.1
		1996	2+ animals	7	-17.9 ± 0.5	15.0 ± 0.5	4.6 ± 0.1	8	-17.8 ± 0.4	14.5 ± 0.7	4.4 ± 0.2
Hooded seal	Gulf	1995	2+ animals	7	-16.9 ± 0.4	16.5 ± 0.7	5.0 ± 0.2	20	-17.0 ± 0.3	15.7 ± 0.5	4.8 ± 0.2
		1996	2+ animals	9	-17.1 ± 0.3	15.5 ± 0.6	4.7 ± 0.2	8	-17.3 ± 0.3	15.8 ± 0.5	4.8 ± 0.1

Table 2.9. Comparisons among trophic position (TP) of the different groups of marine mammals in the Estuary (E) and Gulf (G) of St Lawrence. Groups showing statistically similar TP (*post hoc* Tukey's tests using an error rate of 0.10) are linked by a solid line. '2+' = animals 2 years of age or older, 'Yrl.' = yearlings, 'f' = female, 'm' = male. Groups of marine mammals were formed based on results from within species/location analyses.

	Harp E	Beluga 88-90; 97 2+ f	Harp 1996 G 2+	Harp 1995 G 2+ f	Beluga 88-90; 97 2+ m	Grey G 2+	Grey 95-96 E	Harbour 96-97 Yrl.	Harp 1995 G 2+ m	Hooded 1996 2+ m	Hooded 95-96 2+ f	Harbour 96-97 2+	Harbour 1995	Hooded 1995 2+ m
Harp E	—	—												
Beluga 88-90; 97 2+ f	—	—	—	—										
Harp G 1996 2+		—	—	—	—	—			—					
Harp G 1995 2+ f		—	—	—	—	—			—					
Beluga 88-90; 97 2+ m			—	—	—	—	—	—	—	—	—			
Grey G 2+			—	—	—	—	—	—	—	—	—			
Grey 95-96 E					—	—	—	—	—	—	—	—		
Harbour 96-97 Yrl.					—	—	—	—	—	—	—	—	—	
Harp G 1995 2+ m			—	—	—	—	—	—	—	—	—	—	—	—
Hooded 1996 2+ m					—	—	—	—	—	—	—	—	—	—
Hooded 95-96 2+ f					—	—	—	—	—	—	—	—	—	—
Harbour 96-97 2+							—	—	—	—	—	—	—	—
Harbour 1995								—	—	—	—	—	—	—
Hooded 1995 2+ m									—	—	—	—	—	—

Table 2.10. Comparisons among $\delta^{13}C$ of average diets of the different groups of marine mammals in the Estuary (E) and Gulf (G) of St Lawrence. Groups showing statistically similar $\delta^{13}C$ of diet (*post hoc* Tukey's tests using an error rate of 0.10) are linked by a solid line. '2+' = animals 2 years of age or older, 'Yrl.' = yearlings, 'f' = female, 'm' = male. Groups of marine mammals were formed based on results from within species/location analyses.

	Harp E Yrl.	Grey 95-96 E	Harp G 2+	Harbour 96-97 Yrl.	Grey G 2+	Hooded 1996 2+	Harp E 2+	Hooded 1995 2+	Beluga 88-90 2+ f	Harbour 96-97 2+	Harbour 1995 2+ m	Harbour 1995 Yrl.	Beluga 1997 2+ f	Beluga 88-90 2+ m	Harbour 1995 2+ f	Beluga 1997 2+ m
Harp E Yrl.	—	—	—	—	—											
Grey 95-96 E	—	—	—	—	—											
Harp G 2+	—	—	—	—	—											
Harbour 96-97 Yrl.	—	—	—	—	—											
Grey G 2+	—	—	—	—	—	—	—									
Hooded 1996 2+					—	—	—	—								
Harp E 2+					—	—	—	—	—							
Hooded 1995 2+						—	—	—	—							
Beluga 88-90 2+ f							—	—	—	—	—		—			
Harbour 96-97 2+									—	—	—	—	—			
Harbour 1995 2+ m									—	—	—	—	—	—	—	—
Harbour 1995 Yrl.										—	—	—	—	—	—	—
Beluga 1997 2+ f									—	—	—	—	—	—	—	—
Beluga 88-90 2+ m											—	—	—	—	—	—
Harbour 1995 2+ f											—	—	—	—	—	—
Beluga 1997 2+ m											—	—	—	—	—	—

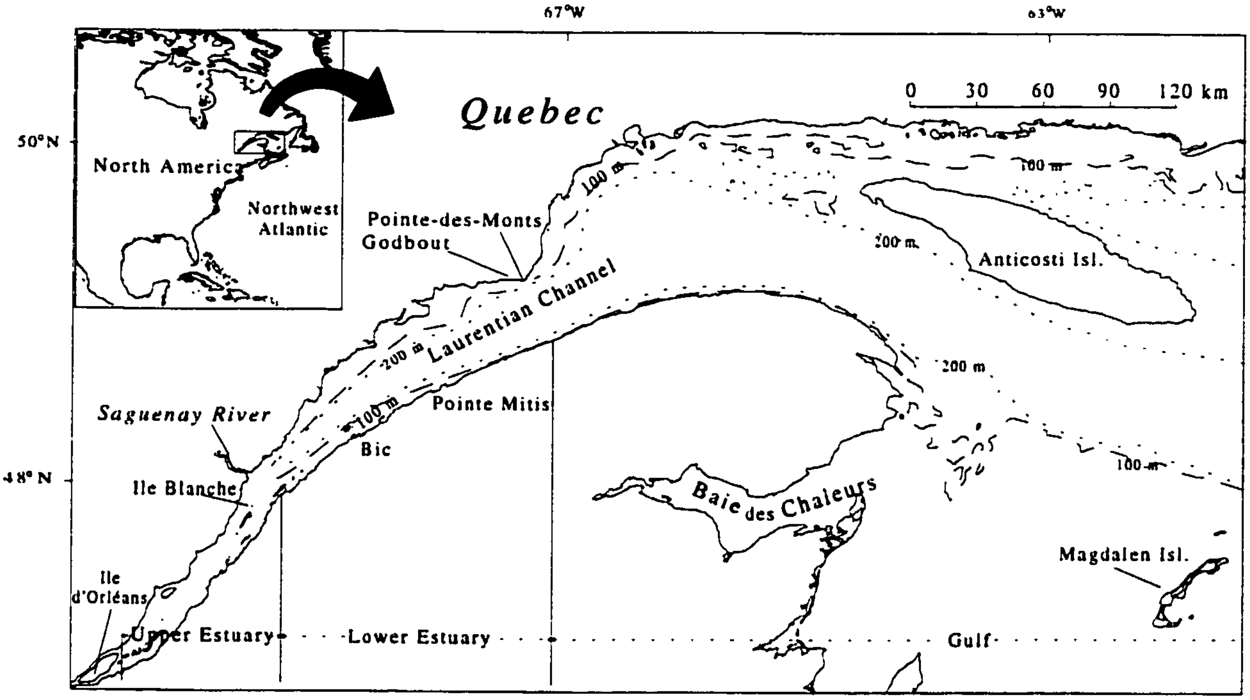

Figure 2.1. Sampling area in the Estuary and Gulf of St Lawrence, eastern Canada.

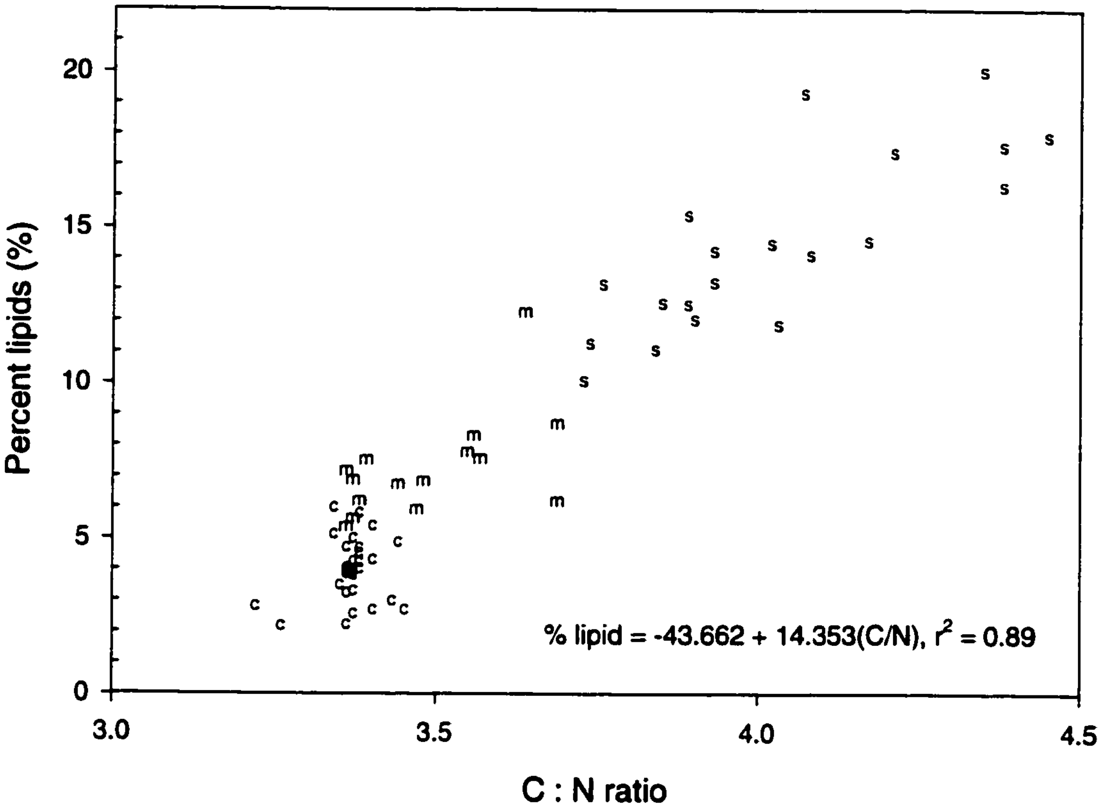

Figure 2.2. The relationship between lipid percentage and C:N ratio of tissues from 73 marine mammals (muscle = 'm', blood serum = 's' and red cells = 'c').

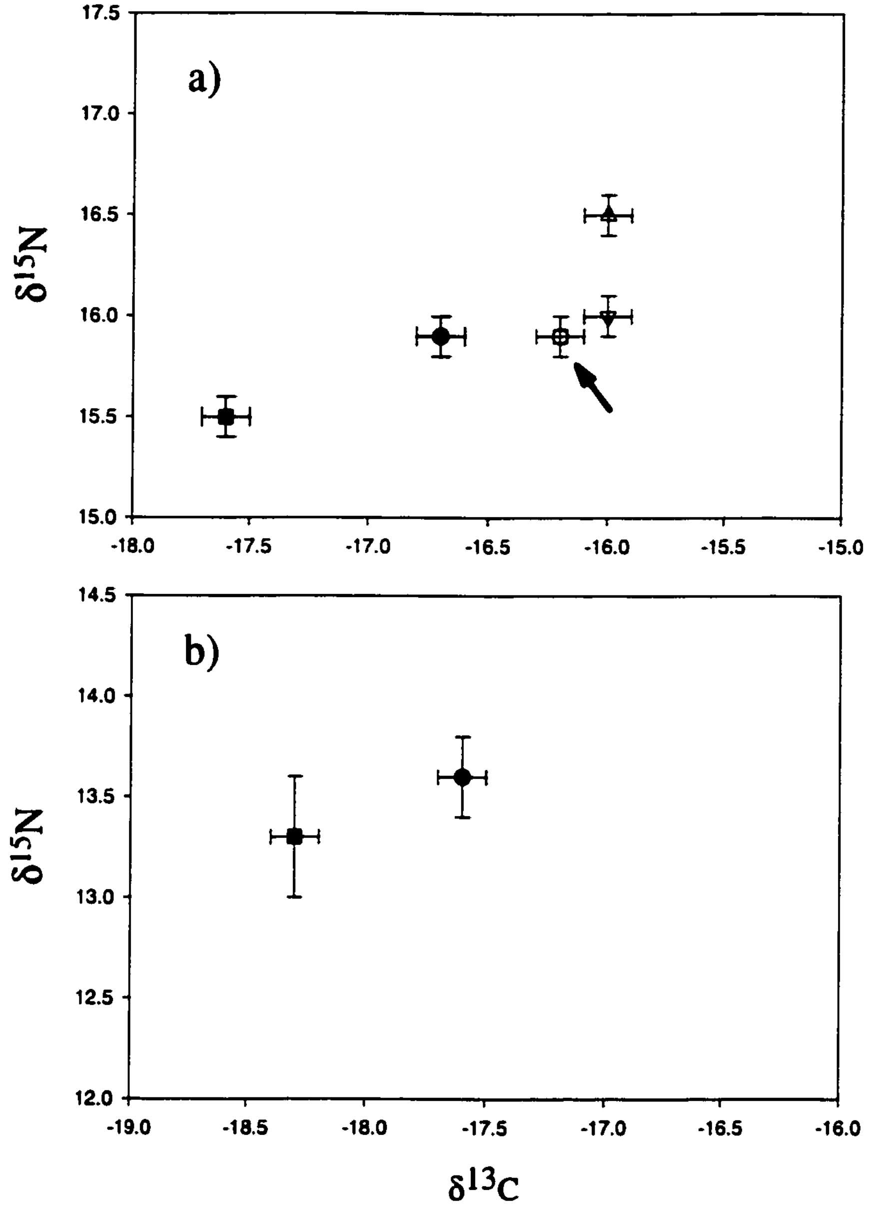

Figure 2.3. Isotopic signature (‰ ± SE) of (●) 2+ animals, (■) yearlings, (▼) weaned pups, and (▲) nursing pups of (a) red blood cells of harbour seals and (b) muscle tissues of Estuary harp seals from (open symbols) 1995 and (filled symbols) 1996. The arrow indicates superimposition of two symbols.

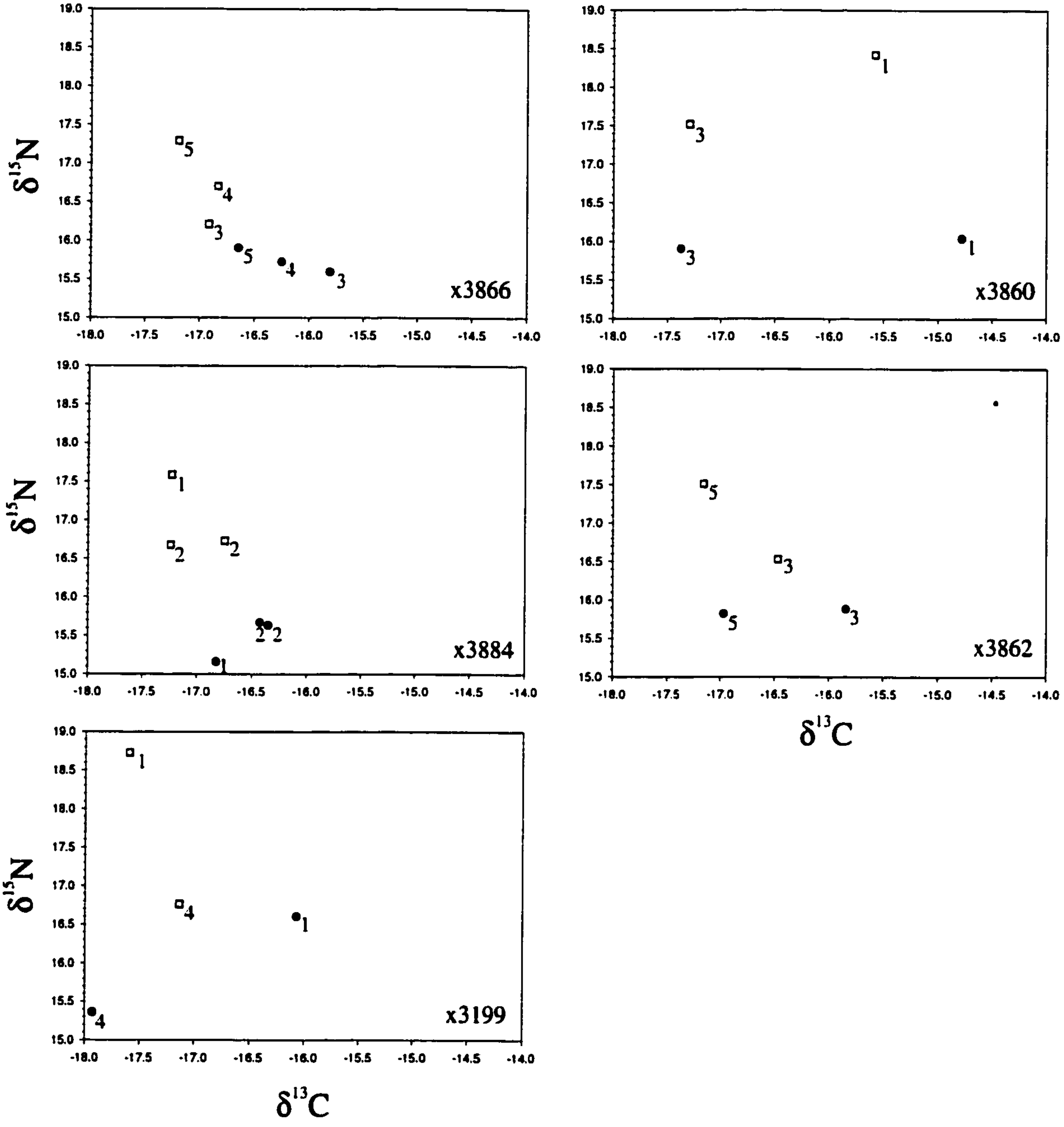

Figure 2.4. Longitudinal sampling of (□) blood serum and (●) red cell isotopic signatures (‰) of five individuals of St Lawrence harbour seals when they were (1) nursing pups, (2) weaned pups, (3) pre-moult yearlings, (4) post-moult yearlings and (5) two-yrs-old juveniles.

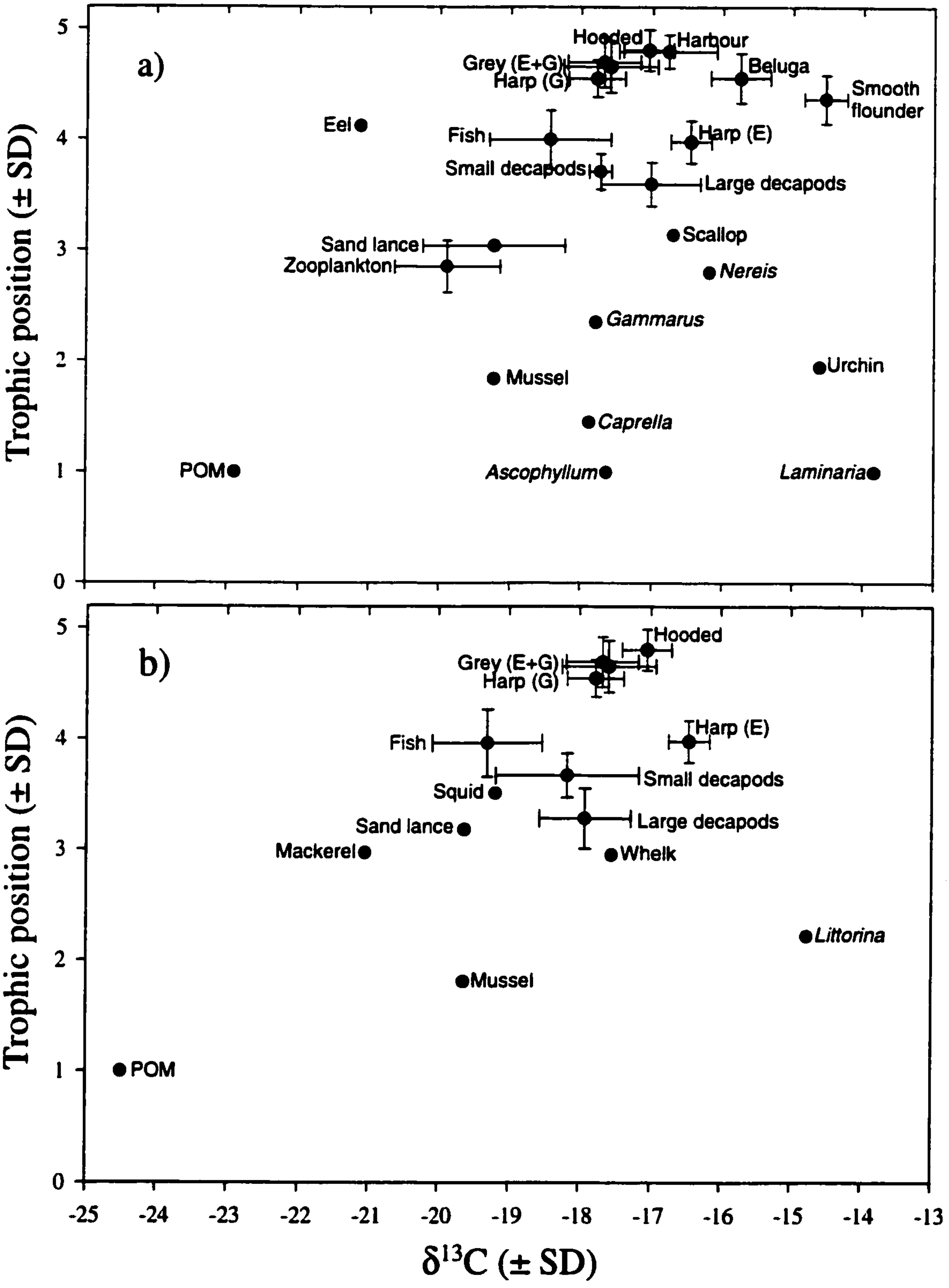

Figure 2.5. Trophic structure of the (a) Estuary and (b) Gulf of St Lawrence as determined from the trophic position and carbon isotope ratios of their different components. The $\delta^{13}C$ value for Gulf POM was obtained from Tan and Strain (1979).

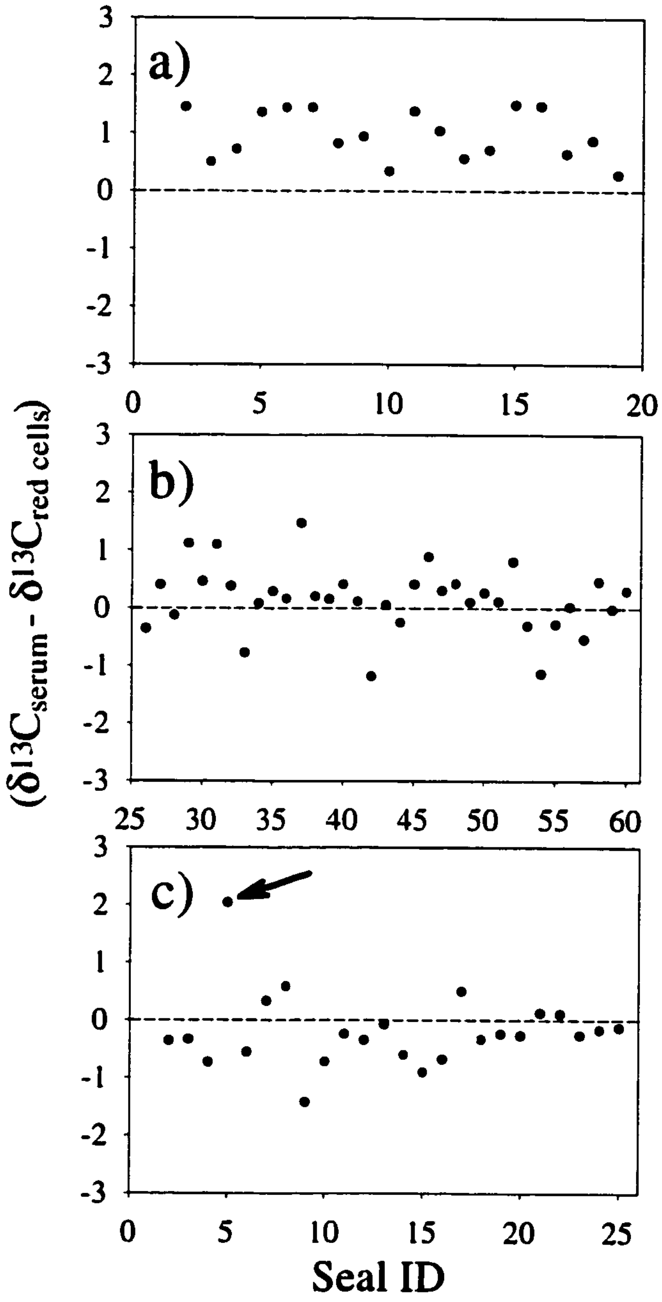

Figure 2.6. Differences in δ^{13}C values between blood serum and red cells of Estuary captured a) grey seals, b) harbour seals captured during or later than July or c) harbour seals captured before July. Values located above the zero line indicate seals that have red blood cells depleted in ^{13}C relative to blood serum. Values located well above the zero line (many animals in (a) and the individual indicated by the arrow in (c)) indicate animals that might have recently visited the Gulf of St Lawrence.

CHAPTER 3

Functional classification of harbour seal (*Phoca vitulina*) dives using depth profiles, swimming velocity and an index of foraging success

Abstract

Time-depth-speed recorders and stomach temperature sensors were deployed on 11 harbour seals in the St Lawrence Estuary to examine their diving and foraging behaviour. Fifty-four percent of dives were to depths of < 4 m. Dives that were ≥ 4 m deep were classified into five distinct types using a combination of principal components analysis and hierarchical and nonhierarchical clustering analyses. Feeding, indicated by a sharp decline in stomach temperature, occurred during dives of all five types, four of which were U-shaped, while one was V-shaped. Seals swam at speeds near the minimum cost of transport (MCT) during descents and ascents. V-shaped dives had mean depths of 5.8 m, lasted an average of 40 s, and often preceded or followed periods of shallow water activity (< 4 m). Seals invariably dove to the bottom when performing U-shaped dives. These dives were to an average depth of 20 m during daylight and occurred in shallower waters (~ 8 m) at twilight and during the night. Once on the bottom, seals (*i*) swam at MCT speeds with occasional bursts of speed (*ii*) swam at speeds near MCT but not exceeding it, or (3) remained stationary or swam slowly at about 0.15 m/s, occasionally swimming faster. It is unlikely that all dives to depths ≥ 4 m are dedicated to foraging. However, the temporal segregation of dive types suggests that all types are used during foraging, although they may represent different strategies.

Introduction

During the 1960s, the first self-contained instruments called time-depth recorders (TDRs) were developed to automatically record dive depth information (Kooyman 1965). Since then, technological advances have led to a reduction in instrument size and the incorporation of new sensors to measure light level, water temperature, swimming velocity, etc. TDRs have provided researchers with a powerful new tool to study the diving behaviour and physiology of a wide variety of marine animals (*e.g.* Thompson and Fedak 1993; Le Boeuf 1994; Boyd and Croxall 1996; Bethge et al. 1997; Boyd et al. 1997; Schreer and Kovacs 1997).

New approaches for analysing data recovered from TDRs have not evolved as rapidly as changes in the instruments themselves. Initially, records were examined manually, and dives were subjectively classified into groups using their duration and maximum depth (Kooyman 1968; Naito et al. 1989; Goebel et al. 1991; Chappell et al. 1993). This approach was later extended to include the general profile of the dive's 'shape' as an additional classification criterion (Le Boeuf et al. 1988, 1992; Hindell et al. 1991; Schreer and Testa 1995; 1996). TDRs are now capable of storing information over several weeks or months, which may represent thousands of dives. The constantly growing storage capacity, and the increase in the number of TDRs that researchers are deploying has made manual inspection and classification of dives an unreasonable task. This has lead to the exploration of new approaches, such as multivariate statistical analyses, to objectively and quickly classify dives. Hindell et al. (1991) used principal components analysis to separate dives of southern elephant seals (*Mirounga leonina*) into two groups, based on the analysis of the first two factors. These authors then further classified dives manually into more groups (see also Schreer and Testa 1995). Boyd et al. (1994) successfully used the *K*-means clustering algorithm aided by a discriminant functions analysis to classify foraging bouts of Antarctic fur seals (*Arctocephalus gazella*). Recently, Schreer and collaborators compared manual classification with various statistical algorithms and artificial neural networks, to classify dives from a variety of diving birds and mammals (Schreer and Testa 1995, 1996; Schreer 1997; Schreer et al. 1998). They demonstrated that techniques such as the *K*-means clustering method used by Boyd et al. (1994) are powerful and reliable tools for quickly and objectively classifying diving behaviour. However, this technique is sensitive to collinearity of variables and behaves poorly compared with other clustering techniques when representative starting seeds are lacking (Milligan 1980; Hair et al. 1995).

The classification methodology and assignment of function to particular dive types have relied heavily on the 'shape' of the 2-dimensional plot of depth *vs* time. For example, in many species U-shaped dives are thought to represent foraging dives. During these dives, animals swim directly, or vertically, to and from a depth where a food patch is assumed to be located (Le Boeuf et al. 1988; Hindell et al. 1991; Thompson and Fedak 1993). The relatively recent addition of sensors for measuring swimming velocity has provided an additional means of classifying dives and studying dive function. However, in the few studies in which swimming velocity has been used to separate dives into functionally significant groups, it has been used only as a second order classification criterion (*e.g.* Le Boeuf et al. 1992; Ponganis et al. 1992; Crocker et al. 1994; Wilson et al. 1996).

Associations between depth-time profiles and behaviours have been proposed, but few studies have confirmed dive type – behavior relationships, owing to the rarity of direct observations of animals diving. Bjørge et al. (1995) observed V-shaped and U-shaped dives from harbour seals (*Phoca vitulina*) fitted with acoustic transmitters that were tracked *in situ* while they were presumably travelling and foraging (see also Thompson et al. 1991; Thompson and Fedak 1993). These authors further reported that animals' stomach temperature dropped during U-shaped dives, which they interpreted as evidence of feeding. Although that study linked dive depth profiles with particular activities, it has not yet been possible to confirm that U-shaped, so-called foraging dives effectively represent the typical and exclusive way of looking for food.

Here, we classify harbour seal dives using multivariate data analysis techniques. In contrast with earlier studies, we attempt to control for multicollinearity of the variables. We use swimming velocity and depth information as primary criteria for classifying diving behaviour. Using changes in stomach temperature as a feeding index and *in situ* tracking of instrumented animals, we attempt to identify the characteristics of dives associated with different behaviours.

Materials and methods

Time-depth-velocity recorders (TDR Mk6) and stomach temperature recorders (HTR) (Wildlife Computers Inc., Redmond, WA) were deployed on 11 harbour seals from the Bic and Metis Beach regions of the St Lawrence River estuary (48°41'N, 68°02'W) between May and August of 1996 and 1997 (Table 3.1). Animals were captured in a gill net set near their haul-out sites. Seals were weighed using a 200 ± 0.5 kg Salter spring scale suspended from a portable tripod and immobilised with an intramuscular injection of Telazol® (Tiletamine and Zolazepam, Fort Dodge® Laboratories, Iowa) at a dose of 0.5 mg/kg body mass. A lower incisor was extracted for age determination by counting cementum growth layers (Bernt et al. 1996). A temperature sensor was introduced into the seal's stomach by intubation with a 3-cm (outer diameter) flexible tube. The 32-g, 2 cm x 5 cm sensor transmitted electromagnetic pulses to a 5 x 7 x 1.4 cm data logger (HTR) at intervals that varied linearly with stomach temperature. The HTR and TDR were housed on a remote-releasing instrument package (Hammill et al. 1999) that was glued mid-dorsally using a quick-setting epoxy resin. In addition, a 165-g VHF radio transmitter (LOTEK Engineering, Newmarket, Ont. Canada) was glued to the top of the animal's head. All attachments that were not released fell off during the early stage of the animals' annual moult. TDRs and HTRs were synchronised to Greenwich Mean Time (GMT) and programmed to record time and the animal's depth (±1 m), swim speed (± 0.05 m s^{-1}) and stomach temperature (± 0.2°C) every 5 s. TDR and HTR clock drifts were negligible over the deployment period (1 s every 1.3–3.4 d and 1.2–16.5 d, respectively).

The accuracy of the temperature sensors was determined in the laboratory by immersion into water baths of different temperatures (range 10.7–38.1°C). The reaction time of the sensors was also determined by introducing cold (~ 10°C) Atlantic tomcod (*Microgadus tomcod*) at regular intervals into a hermetic 1-L balloon submerged in a 38.1°C water bath. Temperatures recorded by the sensors when immersed directly in the water differed by 0.5–1.1 °C (mean ± SD = 0.7 ± 0.2°C; *n* = 10) from the temperature recorded by a glass thermometer. The initial rise in temperature was observed, on average, 6 s after immersion (SD = 1.9 s; range = 2–9 s; *n* = 10 sensors). Similar reaction times were obtained when fish were introduced into the balloon and put in contact with the sensor. Under conditions meant to simulate a large meal, the most recently 'ingested' fish did not make direct contact with the temperature sensor; this caused the reaction time to increase to 15 s. From these experiments, the time of the initial temperature drops recorded by the HTRs were corrected by subtracting one sampling interval (*i.e.* 5 s, the number of sampling intervals closest to the mean reaction time of 6 s). This correction, and negligible clock drift, allowed us to link the information from the two recorders and examine the characteristics of dives associated with feeding events.

Dive record manipulations

Data from the TDRs and HTRs were extracted using software provided by the manufacturer (Wildlife Computers Inc.). TDR files were corrected manually for changes in pressure transducer calibration over the deployment period, using the Zero Offset Correction (ZOC) program. The animal's entry into the water after a prolonged haul-out period caused a marked, negative drift of the zero depth during which its adjustment was unreliable. The duration of such drifts was examined using files from 3 TDR units for a total of 89 haul-out periods. The drift was negligible for haul-out periods of < 345 s, but when they exceeded 345 s, the pressure transducer did not stabilise for 300 s after the seals entered the water. Consequently, dives recorded during the 300 s following a haul-out period ≥ 345 s were eliminated from the analyses.

Corrected depth records were analysed using the DIVE ANALYSIS program, which produced the following descriptive parameters for each dive: dive duration and maximum depth, total long dry time since last dive (total duration of long, ≥ 3 min, periods of time spent out of the water since the last analysed dive), bottom time (time interval between the first and last depths ≥ 80% of the dive's maximum depth), average descent rate (rate of travel between the start of the dive and the beginning of bottom time), average ascent rate (rate of travel between the end-point of bottom time and the end-point of the dive) and number of vertical excursions ≥ 2 m while in the bottom phase of the dive (commonly called wiggles). Some of these parameters were manipulated to produce five additional variables, following Schreer and

Testa (1995; 1996). Bottom time was divided by (*i*) dive duration and (*ii*) maximum depth; (*iii*) maximum depth was divided by dive duration; (*iv*) average descent rate was divided by average ascent rate; and (*v*) average ascent rate was divided by average descent rate. These last two variables may be useful in detecting skewed dives. The post-dive surface interval was also calculated using purpose-built software.

Information on swimming velocity and stomach temperature was extracted separately and merged with the corrected depth records using the manufacturer's software (BINEX, 3M and MERGE, Wildlife Computers Inc.). Swimming velocity was corrected using the calibration curve developed for this particular model of TDR (*i.e.* Mk6, Wildlife Computers Inc.; Boyd et al. 1995). Using the same definition as the DIVE ANALYSIS program for the start and end of a dive, dives were split into descent, bottom and ascent phases. Five other parameters were calculated from swimming speeds: (*i*) average swimming speed at the surface (*i.e.* at depths ≤ 1 m) and during (*ii*) the descent and (*iii*) the ascent phases (*i.e.* at depths greater than 1 m, but shallower than 80% of maximum depth) and (*iv*) the median and (*v*) the maximum swimming velocity during a dive's bottom phase (*i.e.* at depths ≥ 80% of maximum depth). Angles of descent and ascent were determined as arcsin (vertical speed/true speed), where vertical and true speeds corresponded to average ascent or descent rates and swim speeds, respectively, as measured by the TDR's depth sensor and velocity meter.

A dive was defined as any excursion ≥ 2 m. However, dives < 4 m were not analysed because the combination of the criterion to determine the bottom phase (readings ≥ 80% of the maximum depth), the sampling interval (5 s) and resolution of the TDR (± 1 m) precluded accurate calculations of some of the parameters outlined above for such shallow dives. Dives to 2 and 3 m showed constant or extreme values for variables associated with dive skewness.

This tendency toward extreme values in skewness was still visible in some dives to 4 and 5 m, since approximately 20% of them were associated with the first and last 5% of the distribution of these variables. Consequently, only 80% of the dives to 4 and 5 m were included in the analyses. To examine the effect of including these data, the classification results were later compared with results obtained using only dives ≥ 6 m, where the problem associated with the skewness variables was not observed. The number of factors retained and number of clusters identified, cluster characteristics and the cross-validation misclassification rate (1.4%) were all consistent with results obtained by keeping 80% of the 4- and 5-m dives in the analyses. By completing our analysis with these shallower dives incorporated, we were able to classify an additional 6.4% of the dives.

Ten variables were used in the analyses (see Table 3.3). The mean swim speed during the descent and ascent phases was not included in the analysis because one or the other was missing in 1,800 of the 27,865 dives and the distribution of missing values was not random; values were often missing during dives to 4 and 5 m, owing to a lack of sampling at 2 and 3 m (between 20 and 80% of maximum depth). Inclusion of these variables in the analyses would have excluded a specific class of dives.

Dive classification

The 10 variables were first introduced into a principal components analysis (PCA) to reduce their number to a smaller set of uncorrelated factors (*i.e.* orthogonal or independent). The factors and their corresponding scores were then introduced into a hierarchical complete-linkage clustering procedure to determine the appropriate number of clusters and obtain a description of cluster characteristics. These characteristics were used as non-random initial seeds in a nonhierarchical, *K*-means clustering algorithm to fine-tune the results and classify the entire data base. The classification was validated using a discriminant functions analysis. All procedures were performed using SAS software (SAS Institute Inc. 1990).

None of the variables were normally distributed (assessed using a modified Kolmogorov-Smirnov test). However, PCA, like cluster analysis, is not a statistical inference technique and departure from normality may affect it only by diminishing the observed correlation (Hair et al. 1995). To maximise the clarity of the results, variables were transformed using a natural log or square-root transformation. This reduced the skew in the distributions (geometric means were within 5% of the medians), but still did not result in normalisation. All variables were standardised to a mean of 0 and a variance of 1, because both clustering methods and the PCA are highly sensitive to discordant scales (Massart and Kaufman 1989; Hair et al. 1995).

Multicollinearity must be taken into account when using cluster analysis because collinear variables are weighed more heavily in the calculation of the similarity measure (Hair et al. 1995). To eliminate collinearity, the 10 variables were introduced into a PCA (procedure FACTOR), which produced a set of uncorrelated factors that could then be used as input variables in the cluster analysis. In a PCA, variables that are collinear load on the same factor or component. These factors are therefore composite variables and have the property of being orthogonal, that is, they are uncorrelated with one another. A VARIMAX rotation was applied on the factors to simplify the interpretation and structure of the matrix. This rotation emphasises the correlation of variables with a given factor by maximising the loadings of variables correlated with it, and reduces to near zero the loadings of those that are only mildly correlated with it. The appropriate number of factors was selected using (*i*) the latent root criterion, which states that only factors with eigenvalues of 1 or above should be retained, and (*ii*) the criterion that more than 5% of the total variance be explained (Hair et al. 1995). Using the loadings of the rotated matrix, scores (one per factor) were calculated for each dive (option SCORE). These scores and uncorrelated factors replaced the original values and variables in the cluster analysis. The PCA results were validated by splitting the data base into two equal samples of 13,000 dives and re-estimating the factor models to test for consistency.

Dives were classified using a combination of hierarchical and nonhierarchical clustering procedures. Hierarchical procedures are generally quick and permit a visual inspection of the structure of the data and detection of outliers. However, they are not amenable to analysing very large samples and may be substantially distorted by outliers. Nonhierarchical clustering methods are less susceptible to outliers and the inclusion of irrelevant or inappropriate variables and less affected by the distance measure used. However, these benefits are realised only with the use of pre-determined or non-random seed points (Hair et al. 1995). To identify the appropriate number of clusters and compute representative seed points, scores and factors obtained from the PCA were introduced into a complete-linkage hierarchical cluster analysis of the dives (procedure CLUSTER). The complete linkage is an agglomerative method in which the classification criterion is based on the maximum distance between objects in two clusters. At each stage of the agglomeration, the two clusters with the smallest maximum distance between them are combined. The complete linkage is a severe clustering method, because an observation must be closely linked to all the other observations already in the group to be included. However, results from a complete-linkage cluster analysis may be heavily distorted by outliers and it is recommended that 10% of the observations (option TRIM) with low estimated probability densities (determined by the kth-nearest-neighbour method) be eliminated before this procedure is run (SAS Institute Inc. 1990). Since this hierarchical procedure cannot be used with large data sets, cluster solutions were obtained from three separate samples of 1000 randomly chosen dives and compared in order to ensure consistency of the results. To determine the appropriate number of clusters, the agglomerative coefficient (procedure TREE) was used to compute percent change in the clustering coefficient from one classification level to the next for 2–10 clusters. The agglomeration coefficient represents the squared Euclidean distance between the two clusters being combined; the joining of two very different clusters results in a large coefficient. The cluster centroids, identified by the complete-linkage method and each consisting of four scores (one per factor), were then used as initial seeds in a nonhierarchical *K*-means clustering procedure to fine-tune the classes formed (procedure FASTCLUS). Observations were assigned to the cluster with the closest centroid, based on Euclidean distances. New cluster centroids were calculated after each iteration and the process was repeated until the changes in centroids became small or zero (MAXITER option).

The classifications were validated with a discriminant functions analysis by using two nearest neighbours to develop the discriminant functions and the identification of the cluster to which they had been assigned (procedure DISCRIM). Since the same data set was used to develop the classification criterion and to validate the classification, error rates (or the percentage of misclassified dives) were calculated by cross-validation, *i.e.* the discriminant functions were calculated while excluding the observation being classified and were then applied to classify the one observation left out.

There is some controversy over the appropriateness of using factors and scores in cluster analysis. Some studies have demonstrated that variables which distinguish the underlying groups are often not well represented in factor solutions (Temple 1994; Hair et al. 1995). The effect of using factor scores as input variables into the cluster analysis was verified by comparing classification results and misclassification rates using the 10 variables directly with those obtained when using factors and their corresponding scores. Although the use of a larger number of input variables should have reduced the classification error rate (Schreer et al. 1998), the error rate using the 10 variables directly was more than four times that observed when using the 10 variables as part of 4 uncorrelated factors. This confirmed that the use of factor scores was more appropriate for this specific situation.

Dive categories and possible functions

Information from stomach temperature changes and *in situ* tracking of instrumented animals were used to tentatively relate dive characteristics to particular functions. Stomach temperature sensors generally record a feeding event as an abrupt drop, followed by an exponential rise in temperature (*e.g.* Grémillet and Plös 1994; Pütz and Bost 1994; Wilson et al. 1995). Changes in metabolic activity may also result in a decline in stomach temperature, but the amplitude of the drop is generally smaller and more progressive than that observed when food is ingested (Hill et al. 1987). The use of a minimum temperature decline of 0.2°C within 5 s as a criterion for identifying feeding events may lead to the incorrect inclusion of slow temperature variations related to an animal's metabolic activity as feeding events, whereas the use of a 0.4°C threshold may result in the rejection of true feeding events (Lesage, personal observation). To avoid these problems, we used a minimum drop of 0.2°C as a starting point. An event was then considered to be false if the minimum temperature attained (the reading preceding the one where the temperature started to rise) differed from the initial temperature (the reading preceding the one where a decline was observed) by less than 0.8°C, and the temperature remained within 0.4°C of the minimum for more than 15 min. Dives showing the initial drop in temperature were referred to as 'feeding dives'.

Further insights into dive function were gained by *in situ* tracking of the TDR/HTR animals from a 7-m Boston Whaler equipped with a 6-element Yagi antenna mounted 4 m above sea level. The tracking boat remained 300-400 m away from the seal to minimise disturbance. Information on dive and surface times was logged onto a PC interfaced with the boat's Global Positioning System and echosounder, to record GMT, boat position, water depth and surface temperature. The seals' activities were determined by direct observation as (*i*) *hauled out*, (*ii*) *foraging* if they dived repetitively for at least 30 min in the same spot at more than 500 m from a haul-out site and if either a current front was observed at the surface or prey were detected by the echosounder, (*iii*) *travelling* if they moved horizontally over more than 500 m either towards offshore waters or other haul-out sites, or (*iv*) *moving*, or (*v*) *stationary diving*, depending on whether the animal, while remaining within 500 m of a haul-out site, did or did not change location.

Several parameters were examined in order to investigate the function of the different dive types obtained from the classification. Tracking periods during which seals were visually located and their behaviour was ascertained were compiled and the frequency of occurrence of each behaviour in the different dive categories was calculated. To further specify the context in which dives in each category were performed, the cluster membership of the dive (or bout) performed prior to and after each dive (or bout) was examined. Consecutive dives formed a bout if they belonged to the same cluster. Associations between dive types were investigated using contingency tables.

This paper describes the characteristics of harbour seal dives and thus, deals only with the variability among dives. Between-individual variability in the pattern of use of the different dive types is presented elsewhere (Chapter 4).

Results

Ten of the eleven packages were recovered but only 8 provided complete records: one TDR contained no information, owing to battery failure (ID 4601), and the velocity meter failed on the second (ID 2699) (Table 3.1). Seals retained the stomach temperature sensors for 3–576 h (median = 54 h) while the TDRs recorded diving activity for 7.5–19 d (median = 15.5 d). After eliminating dives performed after long periods of haul-out, the combined records included 61,495 dives. However, 33,190 dives (54%) were to depths < 4 m and were therefore not classified further, leaving 46% of the initial data base available for developing the classification.

Dive classification

The PCA performed on the 10 variables suggested the retention of 4 factors that accounted for 88.8% of the total variance (Table 3.2). According to the latent-root criterion, only the first 4 factors had sufficient explanatory power, *i.e.* had eigenvalues of 1 or above, and should be retained. The criterion that more than 5% of the total variance be explained would have included a fifth factor, but its low eigenvalue (0.51) relative to the latent-root criterion value of 1.0 precluded its inclusion.

The VARIMAX-rotated factor matrix showed that all variables should be included in the analysis, since all loaded significantly (loading > 0.30; Hair et al. 1995) on at least one factor

(Table 3.3). The proportion of the total variance explained remained the same as it was prior to rotation, but the variance was redistributed over the 4 retained factors. Only the quotient of maximum depth/duration (X_6) loaded on more than one factor. Variables that loaded heavily on factors 1–4 were those associated with dive bottom time and duration (factor 1), dive skewness (factor 2), swimming velocity (factor 3) and maximum dive depth relative to dive duration (factor 4). Significant loading values were generally positive. Exceptions were the quotient between maximum depth and duration (X_6) on factor 1, and the index of skewness during ascent (X_{10}) on factor 2. This means that dives with both a long duration and a long, deep bottom time would have had a small quotient of max. depth / duration. Also, dives that had a slow descent rate compared with the ascent rate, and thus scored high on X_9, would have scored low on X_{10}, and vice versa. Validation of the factor analysis produced two 13,000-observation factor matrices that were similar in terms of the number of factors retained, loadings and communalities (*i.e.* amount of variance shared by an original variable with all other variables) for all 10 variables (Table 3.4).

The 4 factors and calculated scores for each observation obtained from the PCA were used as input variables and values in a complete-linkage cluster analysis. The results of this analysis suggested different cluster solutions for the 3 subsamples of 900 dives (1,000 dives minus 10%, owing to the TRIM option). The percent change in the agglomeration coefficient from one classification level to the next indicated cluster solutions of 5, 6 and 7 groups for subsamples 1, 2 and 3, respectively. The characteristics of the groups were examined after they were fine-tuned with the *K*-means cluster analysis. Five groups were consistently identified in each subsample (Figure 3.1). The sixth and seventh groups contained either few observations (< 88), or were subdivisions of one of the 5 larger groups. Furthermore, the 5-clusters solution had the tightest clusters, with a maximum distance of 2.7 between an observation and its seed, compared with 3.8 and 3.0 for the 6- and 7-clusters solution, respectively. The appropriateness of a 5-clusters solution was verified by classifying the 2,700 dives from the 3 subsamples combined, using a *K*-means cluster analysis and the 5 centroids from the fine-tuned cluster solution of subsample 1 as initial seeds. Cluster centroids were recalculated after each iteration. The characteristics of the 5 final clusters were similar to those obtained from subsample 1 (Table 3.5), and cross-validation error rates produced by discriminant functions analysis showed that 97.5% of the dives had been classified correctly.

The entire database was then classified using *K*-means cluster analysis with the cluster solution from subsample 1 (see Table 3.5) as initial seeds. The inclusion of outliers was limited by fixing a maximum Euclidean distance of 2.7 between an object and a seed. This value corresponds to the maximum distance observed between an object and its seed in subsample 1. Two percent of the 26,410 dives (*i.e.* 557 dives) were not classified because the Euclidean distance exceeded this threshold value. The classification error rate obtained by cross-validation revealed that 98.5% of the remaining dives had been correctly classified.

Four of the 5 clusters contained dives that had a U shape (Figure 3.1). The mean proportion of diving time spent in the bottom phase of these dives ranged from 64 to 72% (Table 3.6). The exception was type-2 dives, which were V-shaped, shallow and of short duration. Type-2 dives were associated with variable swimming speeds during the short bottom time. Dives in the 4 categories of U-shaped dives were similar in duration (means = 122–168 s) but differed in many other aspects. Type-1 and -3 dives, which constituted 50% of the total number of dives, had the fastest mean/median swim speeds in all 3 phases of the dives, with descent and ascent swim speeds falling into a narrow range of 1.14–1.25 m/s. Despite this consistency, they differed from one another in maximum depth, and rates and angles of ascent and descent. Type-1 dives were deeper and had steep angles and similar rates of ascent and descent, whereas type-3 dives had shallower maximum depths and less steep angles of ascent and descent, the descent angle and corresponding rate being lower than during ascent. Type-4 dives resembled type-3 dives in their relatively shallow depths and shallow angles of descent and ascent. However, they had intermediate swimming speeds during the bottom phase and differed from the other dive categories in their gradual angle and particularly slow rate of ascent. Dives classified into cluster 5 resembled the deep U-shaped and non-skewed type-1 dives, but differed from them in their slow median swim speed during the bottom phase. The two dive categories that included deep dives (type-1 and -5) had steeper angles of ascent and descent than the three shallower dive types. Descent and ascent swim speeds were similar across dive types 2, 4 and 5, varying between 0.71–0.85 m/s, and were slower than in dive types 1 and 3 (1.14–1.25 m/s).

Dives of a given type often occurred in bouts. *Chi*-square values from two-way cross-tabulation tables indicated that 20–84% of dives of a particular type were preceded or followed by a dive of the same kind. To further clarify associations between dive types, a similar table was constructed after consecutive dives of the same type were grouped in bouts (Table 3.7). Bouts of type-3 dives were often preceded by bouts of type-4 dives, and vice versa. Similarly, bouts of type-4 and type-5 dives were frequently performed in close association. Bouts of all types of dives were often associated with bouts of unclassified dives (*i.e.* < 4 m). However, the particularly large chi-square value observed for the association between type-2 dives and < 4 m dives ($\chi^2 = 658$, Table 3.7) suggests that bouts of type-2 dives often preceded or followed periods of shallow-water activities. However, type-2 dives were not strictly associated with shallow-water activities. At times, they were interspersed between peaks of, or sometimes overlapped with, all of the other dive types.

Diel variations in dive frequency were observed in 4 of the 5 dive types (Figure 3.2). Type-1 dives were abundant during the day, and most abundant during twilight hours. Type-3 dives were also most abundant during twilight hours, but their peak preceded that of type-1 dives in the morning, and followed that of type-1 dives at night, *i.e.* type-3 dives peaked in lower light conditions than the deeper type-1 dives. Type-4 and -5 dives both peaked in abundance during the night. The diel variation in the frequency of type-2 dives was weak. No diel changes were observed in maximum depth for dive types 1–4. However, the maximum depth of type-5 dives was greater during daylight hours than during the night (Figure 3.2). This pattern was maintained when individual seals were examined separately (Chapter 4).

Dive categories and possible functions

A behaviour was assigned to 818 dives. In 533 of these dives, the behaviours were observed directly from six animals that were tracked *in situ* for a total of 34 h during periods when they were located visually in the water (Table 3.8). Dives associated with the 'foraging' behaviour category all came from a single 4-h tracking session of an animal diving at depths of 14–17 m near an oceanic front 8 km from the nearest haul-out site. Dives classified as 'feeding dives' ($n = 285$) were not necessarily performed while we tracked animals, as this behavioural category was assigned based on a HTR registered drop in stomach temperature. In fact, all animals except one had lost the temperature sensor by the time they were tracked. Sixty-three percent of dives with a known behaviour could not be classified because the depths were < 4 m (Table 3.8). This left 60–65% of the dives associated with the feeding or foraging categories for the dive type – behaviour analysis, but only 12–16% of the activities documented in waters near haul-out sites (*i.e.* moving and stationary diving behaviour categories).

The 299 dives associated with a known behaviour that could be classified by cluster analysis were examined to determine how they were distributed with respect to dive type (Table 3.9). This analysis revealed that none of the behaviour categories were exclusively associated with a particular dive type. Changes in stomach temperature, indicative of feeding activity, were observed for all dive types. However, 75% of the 'feeding dives' were associated with type-1 and type-3 dives, which both had a U shape and high bottom swim speeds. During the single tracking of a foraging animal, 90% of the dives classified, including 5 dives where stomach temperature variation and thus, feeding was recorded, belonged to type 1 ('foraging'). Type-1 and -3 dives also occurred when animals travelled between distant haul-out sites, 72% of the travelling dives being of these types. The proportion of these dives that represented feeding could not be verified because the animals tracked while travelling had lost their temperature sensors. Type-3 dives were common when animals were performing stationary dives near haul-out sites. Some feeding activity was recorded during the V-shaped, shallow, short type-2 dives. This dive type was also associated with travelling and movements near haul-out sites, but was most common when animals were doing some stationary diving. Type-4 dives were infrequent during tracking and were recorded mostly during movements near haul-out sites. Similarly, type-5 dives were rarely observed during tracking and were only occasionally associated with successful foraging or with stationary diving.

Discussion

Multivariate statistical techniques provide an effective means of processing and classifying the large volume of data recovered from time-depth-velocity recorders. The addition of swimming velocity information to the primary classification criteria permitted further discrimination among dives that had similar profile characteristics, but possibly different functions. The use of stomach temperature sensors confirmed associations between particular dive characteristics and actual feeding, and indicated that successful foraging dives in harbour seals may adopt several shape and swim speed characteristics, but are most often associated with a U-shaped depth profile.

Dive classification

K-means cluster analysis is one of the best tools available for classifying multivariate observations such as dives (Schreer and Testa 1995, 1996; Schreer et al. 1998). In diving behaviour studies that have used cluster analysis, *K*-means clustering has usually been completed using random seeds, while allowing for more than one iteration, and re-computation of cluster means (Boyd et al. 1994; Schreer and Testa 1995; Schreer et al. 1998). However, the *K*-means algorithm does not perform as well as hierarchical methods when initial seeds are selected at random (Milligan 1980). By using a complete-linkage hierarchical clustering procedure prior to the *K*-means analysis, the appropriate number of clusters as well as non-random, representative initial seeds for use in the *K*-means analysis are identified. The maximum distance between an observation and its seed is also calculated, and can be used to prevent the inclusion of outliers in the later clustering. When the two methods were compared, a slight increase in the overall percentage of the variance explained by the clusters (random *vs.*

non-random: 49.5% *vs* 53.5%), and in the mean distance between the nearest clusters (random *vs.* nonrandom: 2.08 *vs* 2.15), as well as a slight decrease in the cross-validation misclassification rate (random *vs* nonrandom: 1.7% *vs* 1.5%) was achieved by using non-random seeds. Also, 11% of the dives were clustered differently by the two methods, leading to clusters with somewhat different characteristics (MANOVA, Wilks' Lambda tests; $F_{4,11008}$ = 158–2102 for dive types 1–5; all $P < 0.0001$).

In larger, more pelagic phocids, dives to depths < 5–10 m account for only a small portion of the dive record, and may be excluded with little impact on the analysis (Le Boeuf et al. 1986; Boyd and Arnbom 1991; Schreer and Testa 1995). However, the deepest dive recorded in this study was 75 m, with most dives not exceeding 25 m. These dives are quite shallow compared with those of other phocids (*e.g.* Kooyman 1981; Le Boeuf et al. 1992; Schreer and Kovacs 1997), but are consistent with observations for harbour seals in some other regions (*e.g.* Fedak et al. 1988; Boness et al. 1994; Coltman et al. 1997; Tollit et al. 1998). We defined a dive as any excursion ≥ 2 m. However, dives < 4 m deep were impossible to analyse accurately, and difficulties were encountered when classifying 4 and 5 m dives because of the relatively fast swim speed of animals compared to the 5-s sampling interval and the instrument's ±1 m resolution. Unfortunately, this means that 58% of harbour seal dives recorded during the study could not be classified. Since, on average, 35% of the feeding events (range 1–72% among individuals; Chapter 4) were associated with dives < 4 m, this represents an important component of harbour seal foraging ecology that could not be examined in greater detail.

Dive categories and possible functions

Previous studies have used dive shape, duration and depth information to describe the diving behaviour of marine species (*e.g.* Le Boeuf et al. 1988; Hindell et al. 1991; Williams et al. 1992; Schreer and Testa 1996). The addition of swim speed information to the primary classification criteria permits greater refinement of dive descriptions than was possible using depth-time characteristics alone (type-1 and -5: Table 3.7; Fig. 3.2), and may also provide insights into energy expenditure during diving (Davis et al. 1985; Hind and Gurney 1997). It also suggests that classifications based exclusively on dive shape may group dives with potentially different functions.

Based on depth-time and swim speed characteristics, harbour seal dives ≥ 4 m could be classified into 5 distinct groups, of which 4 were U-shaped and 1 was V-shaped. Such distinction between U and V shapes has often been used for distinguishing between behaviours (*e.g.* Boyd and Croxall 1992; Le Boeuf et al. 1992; Slip et al. 1994; Schreer and Testa 1996). In many species, U-shaped dives are considered to be foraging dives, during which animals spend time in a food patch, while V-shaped dives are thought to represent travelling or exploration, depending on the maximum depth attained (*e.g.* Hindell et al. 1991; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Slip et al. 1994; Schreer and Testa 1996). A further distinction between foraging on benthic and pelagic prey is made on the basis of the presence or absence of wiggles during the bottom phase of dives (*e.g.* Hindell et al. 1991; Le Boeuf et al. 1992; Schreer and Testa 1996). U-shaped dives represent an important component of the diving behaviour of several species including grey seals (*Halichoerus grypus)* and southern elephant seals, walruses (*Odobenus rosmarus*) and blue-eyed shags (*Phalacrocorax atriceps*) (Thompson et al. 1991; Slip et al. 1994; Schreer 1997). However, in some species such as

Gentoo penguins (*Pygoscelis papua*) and Antarctic fur seals, a greater proportion of the dives at certain times of the day may be V-shaped (Schreer 1997). These dives may be used by these krill-feeding species when pursuing prey, and result from the animal passing vertically through patches of food (Boyd and Croxall 1992; Williams et al. 1992).

Little feeding (11%) was associated with V-shaped, type-2 dives in this study. These dives were relatively short duration, shallow dives, that were often associated with periods of shallow-water activity or interspersed between bouts of the other 4 dive types. Type-2 dives are seen in many other seal and fish species and are suspected of having a travel function (*e.g.* Weihs 1973; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Thompson and Fedak 1993; Crocker et al. 1994; but see Schreer and Testa 1996). By diving rather than swimming at the surface when travelling, animals reduce drag (Williams and Kooyman 1985) and increase the possibility of encountering prey without markedly increasing travel distances (Thompson et al. 1991). The regular association of type-2 dives with dives of type 3, 4 and 5 in periods that appeared to represent foraging bouts suggests that type-2 dives may also be used after a food patch is located, and could represent direct descent to a known food patch.

U-shaped dives were strongly associated with foraging in this study. These dives are associated with both foraging and resting in pelagic phocids that spend long periods of time away from land (Le Boeuf et al. 1992). The latter does not appear to be the case for harbour seals, which have a very tight coastal association and haul out regularly to rest (Thompson 1993; Chapter 4). Observations obtained from tracking instrumented and non-instrumented animals, as well as information from VHF monitoring stations, indicated that harbour seals in the St Lawrence Estuary usually remained within a few kilometres of their haul-out sites (Chapter 4), and that food was readily available near these sites. Therefore, it seems likely that harbour seals would return to nearby haul-out sites to rest and that most, though probably not all, dives ≥ 4 m are dedicated to either the transit or active search components of foraging behaviour. These findings are similar to observations of grey seals in western Scotland, which indicated that animals were unlikely to spend time resting in foraging areas and returned instead to known haul-out sites to rest (Fedak and Thompson 1993).

'Typical' pelagic foraging dives with frequent depth changes during the bottom phase (wiggles) (Le Boeuf et al. 1988; Bengtson and Stewart 1992; Boyd and Croxall 1992) may be lacking in shallow-diving coastal species such as the harbour seal, and a different foraging strategy may be adopted. Prey patches near the surface are unlikely to be visible from the bottom in deep water. Thus, predators must search for food at depths where prey are most likely to be encountered. Although harbour seals are capable of diving to depths of 450–500 m (Kolb and Norris 1982; Stewart and Yochem 1994; U. Swain, unpublished in Schreer and Kovacs 1997) and of detecting moving objects at these depths on a clear moonlit night in clear water (Wartzok 1979; Renouf 1991), animals in this study generally dove to depths of only approximately 20 m during the day and 8 m at night. Animals likely dove to the bottom during much of their dives, because in our study area, waters within a few kilometres from haul-out sites are generally restricted to depths of ≤ 25–30 m. At these depths, light penetration is unlikely to limit prey detection, even at night. Therefore, the best strategy for St Lawrence estuary harbour seals may be to dive to near the bottom, where they would be able to actively search, or lie and wait for prey moving along the bottom or passing overhead. The lack of wiggles during 92% of the dives with some bottom time, the consistency of depths attained within bouts (SD = 1.00, 0.84, 0.65 and 0.82 m for dives of type 1, 3, 4 and 5 respectively), and the similarity of maximum depths in consecutive dives that involved different levels of swimming during the bottom phase (including some where no swimming was recorded) support this hypothesis.

Type-1 and type-3 dives appeared to represent active searching or pursuit of prey, but in deeper (type-1) or shallower (type-3) waters. In the depth profiles of both dive types, >67% of total dive time was spent in the bottom phase, which probably represents the depth where prey were encountered. They also involved swimming, and probably active pursuit of prey, judging from the high bottom (median = 1.00 and 1.21 m/s for type-1 and –3 dives, respectively) and maximum swim speeds (mean = 2.16 and 1.87 m/s for type-1 and –3 dives, respectively). Descent and ascent swim speeds during type-1 and -3 dives were the fastest recorded, with means of 1.14 and 1.25 m/s, respectively. The latter observations are consistent with the prediction that seals seek to maximise the time spent in a foraging area (presumed to be the dive bottom layer, where the food patch is located) and do so by maximising the amount of oxygen available for use in the food patch (Thompson et al. 1993; see also Boyd et al. 1995). Divers should therefore swim directly (vertically) to the patch at the swim speed that represents minimum cost of transport (MCT), which is estimated to be 0.85–1.4 m/s for harbour seals (Davis et al. 1985; Hind and Gurney 1997). Mean and median swim speeds observed during the transit and bottom phases, respectively, in these two types of dives fell within the MCT range. Harbour seals also maximised the time spent in the patch by continuing to swim at MCT swim speed (Thompson et al. 1993). The steep angles of ascent and descent observed during type-1 dives are consistent with predictions. However, this did not hold true for the shallower type-3 dives, which showed more oblique angles of ascent and descent. The steep descent and ascent angles in deeper dives were also obvious in the remaining 3 dive types, and had been observed previously in Antarctic fur seal and Gentoo penguin dives (Boyd et al. 1995;

Wilson et al. 1996). For an animal swimming at MCT swim speed with a certain maximum dive duration limit, greater depths can be reached without changing the dive duration by increasing the steepness of the descent and ascent phases. When the animal is diving at shallower depths, the constraints on the angle of transit to the food patch may not be as strong and may permit more oblique angles of descent and ascent.

Type-4 dives peaked in abundance during the night, were often to depths < 10 m, and involved some swimming. They had a flat bottom phase that represented 64% of the total dive duration. During this phase, median and maximum swim speeds were slower than those of type-1 and -3 dives, but were near or comparable to the estimated MCT speed. This suggests that pursuits rarely occurred during the bottom phase of dives or if they did, seals were pursuing less mobile prey. Thompson et al. (1991) have suggested that when hunting slow moving or stationary prey, seals will maximise both the area covered and number of encounters by swimming at MCT swimming speed. Alternatively, bottom time may represent a search component where an animal swam at near MCT speed while scanning the water column above. A pursuit would translate into an oblique angle of ascent (31°) and a slow ascent rate (0.2 m/s). However, the slow maximum rates of ascent and descent (mean 0.45 and 0.64 m/s, respectively) did not suggest that any consistent pursuits took place during these phases. The long ascent phase may simply have added a horizontal search component to the dive. It may also have resulted from swimming along a bottom that became progressively shallower (Schreer and Testa 1996).

Type-5 dives appeared to represent a sit-and-wait strategy. These dives were also U-shaped, but median swim speeds were particularly slow during bottom time. Dives associated with slow bottom swimming in elephant seals may represent food-processing dives because these dives, which should have been longer if they were to be more energetically economical, were similar in duration to other foraging dives, suggesting a higher metabolic rate that is likely associated with digestion (Crocker et al. 1997). Type-5 dives were, on average, 25–47 s longer than other foraging dive types that involved active swimming, and were therefore unlikely to have been associated with food processing. Twenty-five percent of these dives had maximum swim speeds exceeding 1.8 m/s during the bottom phase, suggesting that pursuits did occur. The sit-and-wait foraging strategy has also been observed in grey seals, and may be an optimal choice when hunting mobile prey, where the encounter rate is a function of the speed of both the hunter and targets (Thompson et al. 1991). This strategy is also the most economical when the benefits per unit effort are considered (Nagy et al. 1984), and could be used when longer-term energy conservation is an issue. Type-5 dives were slightly more abundant at night than during the day. By resting on the bottom, animals would be able to intercept mobile prey moving inshore at night. The diel variation in maximum depth in this dive type coincided with that observed in the general behaviour of the seals, with dives to about 8 m at night and, when performed, to 20 m during the day. The mixing, or alternating use, of type-5 dives with the other dive types suggests that harbour seals may switch between strategies within a foraging bout.

Type-3 dives were frequently associated with type-4 and -5 dives and peaked in frequency during twilight hours, just prior to or following peaks in type-1 dives. All 4 dive types may have been used by animals to search for prey along the bottom or detect prey swimming overhead. However, the abundance of type-1 and -3 dives during twilight periods, with type-1 dives being performed in brighter light conditions than the shallower type-3 dives, suggests that they forage on vertically migrating prey (*e.g.* Le Boeuf et al. 1988; Hindell et al.

1991; Bengtson and Stewart 1992; Boyd and Croxall 1992; Williams et al. 1992). Success in foraging on vertically migrating prey could be greater at dawn and dusk because prey are more densely clumped at these times than during the rest of the day or night, and their silhouette against the surface may be detectable at greater distances at twilight than at night (Muntz 1983). The greater number of successes observed in the two types of foraging dives that peaked in frequency around dawn and dusk (type-1 and -3) than those that peaked later during the night (type-4 and -5) is consistent with the hypothesis of a higher probability of success at twilight. The shallow angles of descent and ascent observed in type-3 dives would further increase the total horizontal distance travelled and the chance of encountering prey (Wilson et al. 1996). Two types of prey consumed by harbour seals that are abundant in the Bic and Metis regions are capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*) (Chapter 4). These species appear to move towards shore during twilight and darkness while undertaking their migrations towards the surface (Bailey et al. 1977; S. Bérubé, Fisheries and Oceans Canada, Mont-Joli, QC, unpublished data). During daylight, these species are found in deeper waters, where they are scattered or found in small stationary schools along the bottom (Bailey et al. 1977). The increase in frequency of type-1 dives just before sunset and during the early morning hours just after sunrise suggests that animals intensify their foraging activity as their prey ascend and continue foraging as they descend.

In conclusion, harbour seals in the St Lawrence estuary spend a considerable amount of their time at depths less than 4 m. Although it is unlikely that all dives to depths ≥ 4 m are dedicated to foraging, this behaviour appears to be a predominant goal when seals enter deeper waters. While foraging, harbour seals used a variety of strategies, switching from one dive type to another within a foraging trip. Some dive types appear to be more economical than others, and the use of the different types can be expected to vary according to prey availability, energy requirements, and other limitations. The use of multivariate statistical methods and the addition of swimming velocity have led to improvements in the classification procedure, while the monitoring of stomach temperature provides information on foraging activity. The combination of stomach temperature changes and information from the classification of dives could be used to estimate foraging effort and efficiency, by allowing calculation of the proportion of time spent performing dives associated with foraging (in water ≥ 4 m for St Lawrence estuary harbour seals) and the relative number of feeding events recorded. Although such an index would remain a coarse estimate of foraging effort and efficiency, it would provide further insight into key aspects of the foraging ecology of these animals.

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Table 3.1. Deployment period and characteristics of harbour seals instrumented with TDRs (time-depth recorders) and HTRs (stomach temperature sensors) during 1996 and 1997.

Seal No.	Region	Mass (kg)	Sex	Age (yr)	Period of deployment	Duration of record TDR (d)	Duration of record HTR (h)	No. of dives
3199	Bic	36	m	1	20 Aug. - 6 Sept. '96	15.5	73	8424
3860	Bic	39	m	1	20 - 28 Aug. '96	7.5	47	3416
4615	Bic	102.5	m	10	10 - 24 June '96	13.5	54	6344
4618	Bic	100	m	8	11 - 27 June '96	15.5	113	7530
4619	Bic	69	f	10	12 - 28 June '96	16	88	9244
4601	Metis	83	m	7	7 June - 12 July '96	0	63	-
4612	Metis	83.5	m	6	7 June '96 - (lost)	-	-	-
2699	Bic	96.5*	f	6	3 - 21 June '97	17	576	9215
2700	Bic	35.5	f	1	3 - 22 June '97	19	34	11750
3502	Metis	38	f	1	18 June - 5 July '97	16.5	52	10701
3508	Metis	38.5	m	1	8 - 17 July '97	9	34	4086

* pregnant

Table 3.2. Component factors identified using 10 dive characteristics. Underlined values indicate the appropriate number of factors to extract according to the latent root (eigenvalue) and percent of explained variance exceeding 5% criteria.

Factor	Eigenvalue	% of variance explained	Cumulative % of variance
1	3.87	38.7	38.7
2	2.28	22.8	61.5
3	1.55	15.5	77.0
4	1.18	11.8	88.8
5	0.51	5.1	93.9
6	0.36	3.6	97.5
7	0.18	1.8	99.3
8	0.05	0.5	99.8
9	0.01	0.1	99.9
10	0.01	0.1	100.0

Table 3.3. VARIMAX rotated component analysis factor matrix. Significant loadings (*i.e.* $P <$ 0.30; Hair et al. 1995) are underlined.

Variable		VARIMAX-rotated factor loadings				
		Factor 1	Factor 2	Factor 3	Factor 4	Communality
X_1	max. depth	0.279	0.042	0.103	0.931	0.96
X_2	duration	0.885	-0.079	-0.046	0.153	0.81
X_3	bottom time	0.963	-0.024	0.020	0.163	0.95
X_4	bottom time / duration	0.875	0.037	0.120	0.101	0.79
X_5	bottom time / max. depth	0.894	-0.034	0.073	-0.113	0.82
X_6	max. depth / duration	-0.665	0.108	0.089	0.672	0.91
X_7	median swim speed (bottom phase)	-0.054	0.089	0.908	0.018	0.84
X_8	max. swim speed (bottom phase)	0.148	0.063	0.856	0.217	0.81
X_9	$\bar{x}$ ascent rate / $\bar{x}$ descent rate	-0.038	0.994	0.056	-0.024	0.99
X_{10}	$\bar{x}$ descent rate / $\bar{x}$ ascent rate	0.029	-0.994	-0.063	-0.055	1.00
Sum of squares (eigenvalue)		3.82	2.01	1.61	1.44	8.88

Table 3.4. Validation of the component factor analysis by split-sample estimation with VARIMAX rotation. Values for the two subsamples are indicated as sample 1, with sample 2 in parentheses. Significant loadings are underlined.

Variable		VARIMAX-rotated factor loadings				Communality
		Factor 1	Factor 2	Factor 3	Factor 4	
X_1	max. depth	0.253 (0.286)	0.029 (0.057)	0.138 (0.081)	0.934 (0.928)	0.96 (0.95)
X_2	duration	0.883 (0.886)	-0.056 (-0.105)	-0.033 (-0.061)	0.162 (0.152)	0.81 (0.82)
X_3	bottom time	0.956 (0.964)	-0.022 (-0.030)	0.016 (-0.018)	0.195 (0.153)	0.95 (0.95)
X_4	bottom time / duration	0.867 (0.876)	-0.018 (0.056)	0.102 (0.134)	0.140 (0.100)	0.78 (0.80)
X_5	bottom time / max. depth	0.894 (0.896)	-0.031 (-0.042)	0.067 (0.079)	-0.050 (-0.134)	0.81 (0.83)
X_6	max. depth / duration	-0.730 (-0.647)	0.079 (0.142)	0.099 (0.081)	0.597 (0.691)	0.90 (0.92)
X_7	median swim speed (bottom)	-0.059 (-0.058)	0.089 (0.092)	0.903 (0.908)	0.039 (0.067)	0.83 (0.84)
X_8	max. swim speed (bottom)	0.124 (0.165)	0.075 (0.055)	0.865 (0.845)	0.183 (0.261)	0.80 (0.81)
X_9	$\bar{x}$ ascent rate / $\bar{x}$ descent rate	-0.035 (-0.045)	0.994 (0.994)	0.062 (0.054)	-0.012 (0.038)	0.99 (0.99)
X_{10}	$\bar{x}$ descent rate / $\bar{x}$ ascent rate	0.028 (0.036)	-0.994 (-0.993)	-0.065 (-0.063)	-0.038 (-0.070)	0.99 (1.00)
Sum of squares (eigenvalue)		3.86 (3.82)	2.00 (2.03)	1.62 (1.59)	1.35 (1.49)	8.83 (8.93)

Table 3.5. Results of a nonhierarchical cluster analysis with initial seed points from hierarchical results performed on subsample 1, with values for the 3 subsamples combined in parentheses. F_1– F_4 represent factors 1–4.

	Mean values				
Cluster	Type 1	Type 2	Type 3	Type 4	Type 5
max. depth (m)	15.0 (19.0)	4.7 (5.2)	6.0 (7.4)	6.7 (7.6)	9.7 (13.1)
duration (s)	122.3 (132.4)	42.3 (42.0)	107.0 (124.1)	117.7 (142.3)	163.3 (169.0)
bottom time (s)	89.1 (90.8)	4.8 (6.5)	64.9 (87.5)	69.5 (94.6)	128.7 (126.7)
bottom time / duration	0.71 (0.67)	0.14 (0.17)	0.59 (0.68)	0.57 (0.65)	0.76 (0.72)
bottom time / max. depth	6.47 (5.00)	1.01 (1.27)	11.06 (12.26)	10.61 (12.92)	14.95 (13.12)
max. depth / duration	0.14 (0.15)	0.17 (0.19)	0.06 (0.07)	0.06 (0.06)	0.07 (0.09)
median swim speed (bottom) (m/s)	1.13 (1.03)	0.50 (0.46)	0.98 (1.08)	0.70 (0.67)	0.39 (0.16)
max. swim speed (bottom) (m/s)	2.23 (2.23)	1.07 (0.94)	1.75 (1.79)	1.43 (1.34)	1.03 (0.86)
$\bar{x}$ ascent rate / $\bar{x}$ descent rate	1.13 (1.12)	1.13 (1.13)	2.35 (1.98)	0.39 (0.41)	1.03 (1.34)
$\bar{x}$ descent rate / $\bar{x}$ ascent rate	1.03 (1.02)	1.28 (1.34)	0.58 (0.69)	3.32 (3.03)	1.16 (0.96)
F_1 bottom time and dive duration	0.133 (0.094)	-1.797 (-1.734)	0.105 (0.330)	0.065 (0.387)	0.722 (0.632)
F_2 dive skewness	0.110 (0.084)	0.002 (-0.022)	1.008 (0.773)	-1.242 (-1.148)	0.112 (0.420)
F_3 swimming velocity(bottom phase)	0.749 (0.580)	-0.469 (-0.597)	0.367 (0.473)	0.050 (-0.096)	-0.750 (-1.178)
F_4 max. depth relatively to duration	0.602 (1.074)	-0.697 (-0.555)	-1.142 (-0.809)	-0.828 (-0.615)	-0.256 (0.219)

Table 3.6. Number, proportion and characteristics (mean ± 1 SD) of the dives classified in the different dive categories.

Cluster	Type-1	Type-2	Type-3	Type-4	Type-5
					
max. depth (m)	19.6 ± 5.8	5.8 ± 2.8	7.8 ± 2.7	7.9 ± 2.7	12.2 ± 7.2
duration (s)	135.7 ± 37.5	40.1 ± 29.8	122.4 ± 50.9	142.3 ± 52.9	167.9 ± 80.1
bottom time (s)	92.5 ± 34.0	5.5 ± 6.8	85.8 ± 51.0	93.0 ± 48.9	126.6 ± 83.6
bottom time / duration	0.67 ± 0.15	0.15 ± 0.17	0.67 ± 0.22	0.64 ± 0.20	0.72 ± 0.18
bottom time / max. depth	4.92 ± 1.98	0.91 ± 1.17	11.48 ± 7.11	12.42 ± 7.07	13.80 ± 12.2
max. depth / duration	0.15 ± 0.05	0.21 ± 0.15	0.07 ± 0.04	0.06 ± 0.03	0.08 ± 0.05
median swim speed (bottom) (m/s)	1.00 ± 0.47	0.47 ± 0.56	1.21 ± 0.44	0.68 ± 0.40	0.15 ± 0.25
max. swim speed (bottom) (m/s)	2.16 ± 0.62	0.88 ± 0.71	1.87 ± 0.57	1.28 ± 0.50	0.78 ± 0.65
$\bar{x}$ ascent rate / $\bar{x}$ descent rate	1.13 ± 0.46	1.25 ± 0.93	2.06 ± 1.69	0.41 ± 0.17	1.44 ± 0.89
$\bar{x}$ descent rate / $\bar{x}$ ascent rate	1.01 ± 0.40	1.34 ± 1.01	0.69 ± 0.33	3.06 ± 1.87	0.89 ± 0.42
$\bar{x}$ ascent swim speed (m/s)	1.20 ± 0.34	0.71 ± 0.46	1.14 ± 0.46	0.74 ± 0.41	0.80 ± 0.34
$\bar{x}$ descent swim speed (m/s)	1.25 ± 0.38	0.76 ± 0.47	1.20 ± 0.51	0.85 ± 0.33	0.74 ± 0.36
angle of ascent (degree)	70.0 ± 27.8	59.0 ± 33.6	48.0 ± 29.3	31.2 ± 26.8	75.9 ± 24.1
angle of descent (degree)	63.6 ± 29.8	59.8 ± 34.4	32.1 ± 28.9	64.0 ± 28.6	71.8 ± 27.4
post-dive surface interval (s)	42.6 ± 23.5	43.8 ± 60.7	40.2 ± 31.0	38.6 ± 34.8	44.8 ± 31.9
% of the dive cycle spent diving*	76.4 ± 10.0	55.1 ± 0.2	75.1 ± 12.4	78.9 ± 11.0	78.1 ± 10.8
Total number (proportion) of dives	7279 (0.282)	3310 (0.128)	5572 (0.216)	5969 (0.231)	3723 (0.144)

* Excluding dives with extended post-dive surface interval, *i.e.* > 330 s (Chapter 4)

Table 3.7. Association between the different bout categories, obtained by examining the identity of consecutive bouts. Number of observations, deviation from expected value and cell chi-square statistic are presented. Frequency of occurrence higher and lower than expected are indicated with '--' and '**', respectively.

Type of the preceding bout	Type of the current bout						Total
	< 4 m	1	2	3	4	5	
< 4 m	-	1075	1505	1111	1242	492	5428
		450	719	220	324	-66	
		323.7**	658.3**	54.5**	114.3**	7.9	
1	1076	-	230	393	110	227	2036
	457		-65	59	-234	18	
	337.7**		14.2	10.4	159.5--	1.5	
2	1514	239	-	312	318	222	2605
	722	-61		-115	-123	-46	
	658.6**	12.4		31.2	34.1	7.9	
3	1236	347	333	-	770	248	2934
	344	9	-92		274	-54	
	132.8**	0.2	19.8		151.0**	9.6	
4	1074	157	295	818	-	643	2987
	166	-187	-137	328		336	
	30.4	101.7--	43.7	219.3**		366.8**	
5	510	233	215	288	572	-	1818
	-43	24	-48	-10	265		
	3.3	2.7	8.8	0.4	227.5**		
Total	5413	2051	2578	2922	3012	1832	17808

Table 3.8. Distribution of dives to which a behaviour was assigned, and the proportion classified. Changes in stomach temperature were used to identify 'feeding' dives. Dives were assigned to the other categories on the basis of direct observations of their behaviour during VHF tracking.

Behaviour assigned	Total	Classified dives		Unclassified dives (< 4 m)	
	no. of dives	*N*	%	*N*	%
Feeding	285	171	60	114	40
Foraging	81	53	65	28	35
Travelling	82	25	30	57	70
Moving	118	19	16	99	84
Stationary diving	252	31	12	221	88
One of the above five types	818	299	37	519	63

Table 3.9. Distribution of dives associated with the different behavioural categories among the five dive types.

Associated behaviour	N (and %) of dives classified into cluster					Total
	1	2	3	4	5	
Feeding	65 (38)	19 (11)	63 (37)	7 (4)	17 (10)	171
Foraging	48 (90)	1 (2)	1 (2)	1 (2)	2 (4)	53
Travelling	9 (36)	5 (20)	9 (36)	2 (8)	- (0)	25
Moving	4 (21)	3 (16)	4 (21)	5 (26)	2 (6)	19
Stationary diving	- (0)	13 (42)	13 (42)	2 (6)	3 (10)	31

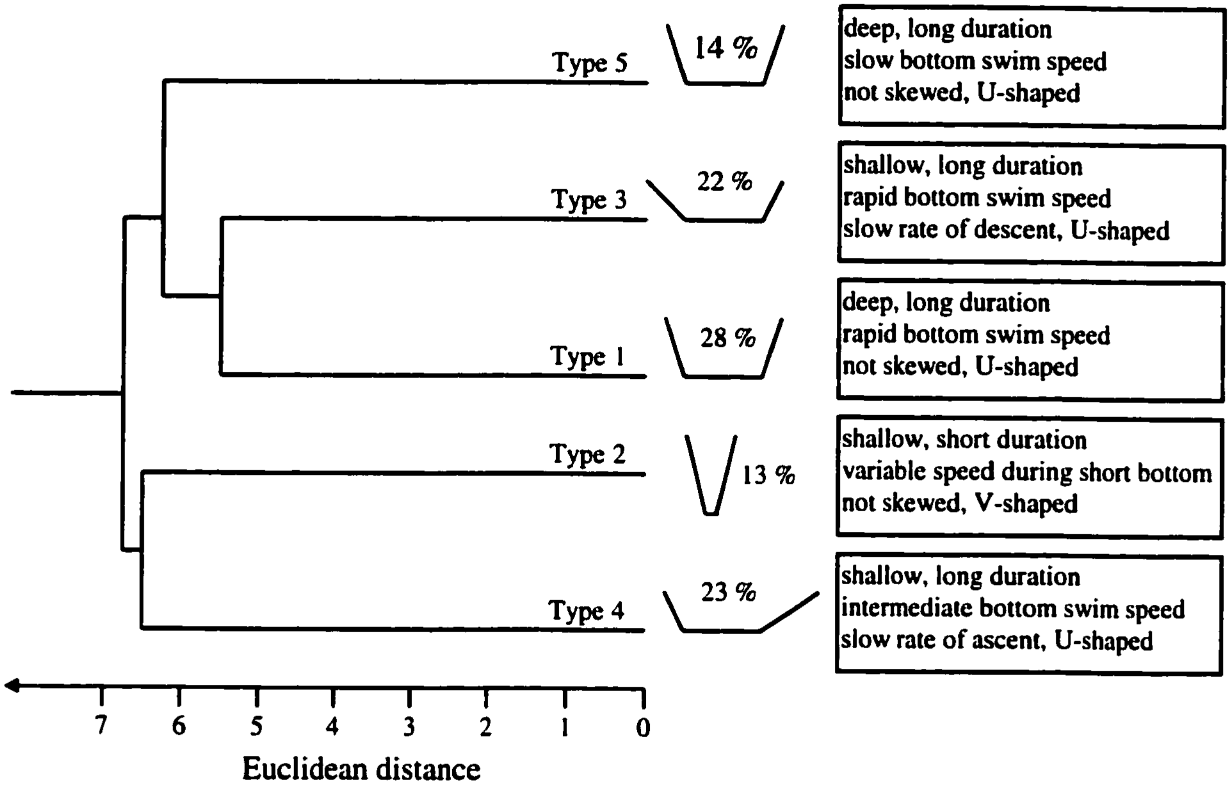

Figure 3.1. Dendrogram from the hierarchical cluster analysis using complete linkage, and the proportion of the entire database classified in each dive type.

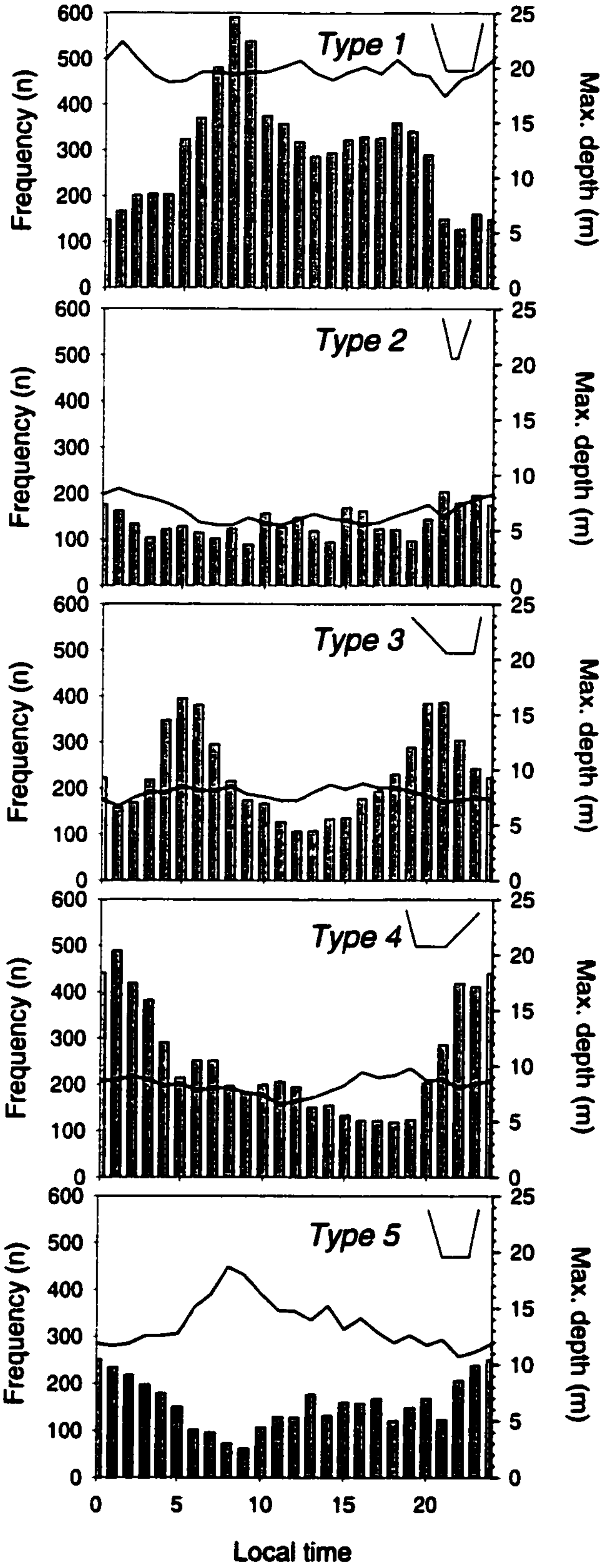

Figure 3.2. Diel variation in dive frequency and maximum depth for the five different dive types.

CHAPTER 4

Seasonal movements, diving patterns and foraging performance of harbour seals (*Phoca vitulina*) from the St Lawrence River Estuary, Canada

Abstract

Movements, diving and foraging activity of harbour seals were examined throughout the year in the St Lawrence River Estuary using a combination of satellite telemetry, time-depth-velocity recorders and stomach temperature telemetry. In late fall, when solid fast-ice formed in most bays, 4 of 7 seals moved to areas 65–520 km ($\bar{x} \pm SD = 266 \pm 202$ km) away from their summer haul-out areas to over-winter. Daily movements of 23 seals during the ice-free period were generally restricted to within 10 km from haul-out sites. However, more distant excursions of 1–6 days to regions up to 65 km away occurred regularly during this period. Harbour seals were located in coastal waters < 50 m deep on 90% of occasions when they were away from haul-out sites. Most of the locations corresponded to shallow bays or river mouths.

Most seals preferred to haul out near the daytime low tide during summer, although some seals hauled out during both low tides (particularly lactating females and a pre-breeding male) or during daytime, independent of tide height (one moulting and two post-moult juveniles). Lactating females (n =2), pre-moult juveniles ($n = 4$) and a pre-breeding male ($n = 1$) hauled out almost daily, and more frequently than breeding males ($n = 2$) or post-moult juveniles ($n = 4$). Haul-out activity decreased and diving activity intensified during winter. The seals generally spent large proportions of their time ($\bar{x} = 64\%$, range 35–95%) at depths < 4 m. Most dives (95%) performed by individuals seals were < 5–34 m in depth and < 2.7–5.0 min in duration.

Diving activity occurred during all periods of the day, but was generally most intense during twilight or at night during summer. Seals generally dove to shallower depths at night than during the day. Dives most often associated with successful foraging were U-shaped dives, with median bottom swimming speeds near the minimum cost of transport, with occasional bursts of speed. Females continued to feed during lactation, possibly on capelin spawning near shore, 1–6 km away from haul-out sites. Males also continued to feed during at least the pre-mating period. Diving activity of juveniles prior to the moult was at shallower depths (4–9 m *vs* 11–19 m) and less intensive (4.9–12.6 *vs* 9.0–12.7 h d^{-1}) than following its completion. The number of successful dives per unit diving effort at ≥ 4 m was lower in 5 of 7 juveniles than in 4 adults, with a capture every 54–241 min *vs* 24–45 min for adults.

Introduction

The annual cycles of many mammalian species display a seasonally variable pattern of energy acquisition. Many species also have a migratory phase that takes them between geographically different areas where peak periods of energy ingestion occur (*e.g.* Cameron and Whitten 1979; Lockyer 1987). In mammals, the lactation period is a time of high energy expenditure, which requires that the animals be located in a productive area where food is readily accessible (Sadleir 1969; Loudon and Racey 1987). Phocid seals have a somewhat unusual pattern of energy acquisition and balance during this period. Although these animals are dependent on the marine environment for accessing their food, they require a solid substrate for parturition, and also for mating in some species (Bartholomew 1970; Stirling 1983). Thus, during their reproductive phase, they are physically separated from their feeding habitat much, or all, of their time. They must support their metabolic needs, and fuel the costs of milk production (females) and display to mates or defense of territories/mates (males) from their stored energy reserves (*e.g.* Oftedal et al. 1987; Bowen et al. 1992; Baker et al. 1995; Boness and Bowen 1996; Lydersen and Kovacs 1996; Coltman et al. 1998). An additional period of fasting is imposed by the annual moult. During the intensive phase of the moult, that occurs for most seals some 4–6 weeks after breeding, all of the hair and, in some species, several layers of epidermis, are shed over a period of days or weeks (Ling 1970; Ashwell-Erickson et al. 1986; Fedak et al. 1994). This process occurs most efficiently if the animals are able to stay dry, *i.e.* out of the water (Boily 1995).

Not surprisingly, the periods immediately preceding and following breeding and moulting are times of high energy ingestion (Pitcher 1986; Beck et al. 1993a; Le Bœuf et al. 1993; Carlini et al. 1997). Seals must forage not only to meet daily energy requirements during these periods, but also to replenish or maximise body stores for use during periods of fasting or reduced energy intake. For example, post-lactating elephant seal females often migrate several hundreds or even thousands of kilometres to feed intensively off the continental shelf (Jonker and Bester 1998). They regain 24–54% of the mass lost during the nursing period by diving virtually continuously during the 2–2½ months preceding the annual moult. They generally spend < 3 min at the surface between dives that can last over an hour (Le Bœuf et al. 1988; 1989; Slip et al. 1994; Carlini et al. 1997; Jonker and Bester 1998). Their large body size and well developed blubber layer permit the accumulation of large amounts of stored energy reserves and hence, some separation of breeding or moulting sites from foraging areas (Bartholomew 1970; Coltman et al. 1998). Among smaller phocid species, the energy demands associated with breeding or moulting may exceed their capacity to store energy, and feeding during these crucial periods appears to be a necessity (Hammill et al. 1991; Bowen et al. 1992; Lydersen 1995; Coltman et al. 1998). The need to feed with some regularity will affect their distribution with respect to availability of both haul-out sites and food resources (Kovacs and Lavigne 1986; Boness and Bowen 1996).

The characteristics of the immediate environment play an important role in determining the range of options that are available to an animal (Stirling 1983; Wartzok 1991). One would expect more foraging to take place during the breeding and moulting seasons in regions where food abundance and proximity are higher (Boness and Bowen 1996). There is growing evidence that even relatively large phocids such as Weddell seals (*Leptonychotes weddellii*; Testa et al. 1989), harp seals (*Phoca groenlandica*; Beck et al. 1993b; Lydersen and Kovacs 1996), and grey seals (*Halichoerus grypus*; Cameron 1969; Lydersen et al. 1994; Baker et al. 1995; Goulet 1996) may take advantage of the proximity of food resources during the breeding season, despite the fact that some of these species are sufficiently large to sustain complete fasting during this period

(Boness and James 1979; Fedak and Anderson 1982; Lydersen and Kovacs 1996; Coltman et al. 1998). Coupling of feeding and nursing may be facilitated further in species with aquatically precocial pups that follow their mothers into the water soon after birth (Oftedal et al. 1987).

Foraging behaviour during moulting is impossible to discuss comprehensively in an inter-specific manner among phocids because their behaviour during this period is poorly documented. Remaining out of the water may facilitate the moulting process (Ashwell-Erickson et al. 1986; Boily 1995), and high rates of haul-out during moulting is a behaviour pattern adopted by various age and sex groups among phocid seals (Thompson et al. 1989; Worthy et al. 1992; Boyd et al. 1993; Boily 1995; Watts 1996). However, staying dry does not appear to be essential to successful completion of moulting (Boily 1995). Females of some smaller phocid species haul out little while moulting. It is thought that they are feeding intensively at this time; a behaviour interpreted as being a consequence of a higher need for the replenishment of body reserves lost during nursing than for a quick moult (Thompson et al. 1989). Nevertheless, a reduction in food consumption (Renouf and Noseworthy 1990; 1991), metabolic rate (Ashwell-Erickson et al. 1986; Markussen et al. 1992; Rosen and Renouf 1995) and activity (Worthy et al. 1992) has been observed among both captive and wild phocid seals during moulting. This suggests a shift to an energy-conservation mode, where energetic expenditures and consumption are kept to a minimum.

Sexually immature phocids do not appear to undergo long periods of fasting during the breeding season (Walker and Bowen 1993a; but see Deutsch et al. 1990). However, they are faced with relatively high energy demands throughout the year (Lavigne et al. 1986; Markussen et al. 1990; Hansen et al. 1995) because of the need to obtain enough energy to support growth, satisfy daily maintenance requirements, and to store sufficient energy to carry them through the moult (Ryder 1958) when food intake is reduced.

The harbour seal is a coastal species that hauls out regularly on exposed reefs, rocks, sand bars, etc. Owing in part to their small size (< 100 kg; Bigg 1981), harbour seals cannot sustain complete fasting during the breeding or moulting seasons (Thompson et al. 1989; Bowen et al. 1992; Boness et al. 1994; Thompson et al. 1994a; Coltman et al. 1997; 1998). This species often gives birth at sites that are only available during low tide and hence, harbour seal offspring must follow their mother into the water within a few hours following birth. This highly precocial aquatic skill exhibited by pups reduces constraints on females' aquatic behaviour and mobility. Harbour seals must have a regular access to food resources during the breeding season and thus, are generally found in productive areas. They are usually thought to undertake only limited seasonal movements (Fisher 1952; Bigg 1981; Harvey 1987; Thompson et al. 1998), although their sedentary nature may be overemphasised in the literature due to the highly seasonal nature of many studies on this species, and the limited technology available for tracking animals at sea (Thompson 1993; Lowry and Frost 1998). Although harbour seals are usually found in areas that remain ice-free throughout the year, they can also be found in regions such as Glacier Bay, Bristol Bay and the St Lawrence Estuary and Gulf, that are ice-covered to some degree during winter. Seasonal movements by this species might be expected to occur over larger scales in areas where heavy ice cover prevails during winter.

In this study, seasonal movements, diving patterns, and foraging performance of adult and juvenile harbour seals in the St Lawrence Estuary, were examined using a combination of satellite and radio telemetry, as well as time-depth recorders. In contrast with most studies of pinnipeds, where foraging activity has been inferred from changes in body mass, chylomicrons in serum, haul-out patterns, dive shape or temporal patterning, or location of diving (*e.g.* Walker and Bowen 1993a; Boness et al. 1994; Lydersen et al. 1994; Thompson et al. 1994a; Lydersen and Kovacs 1996; Coltman et al. 1997), foraging activity in this study was examined more directly by monitoring changes in stomach temperature.

Materials and methods

Harbour seals were captured in the Bic, Metis Beach and Ile Blanche regions of the St Lawrence River Estuary using a gill net deployed near haul-out sites (Figure 4.1). In these regions, harbour seal haul-out sites are located near relatively deep water, which provides animals with an easy escape from potential predators. Harbour seals in the Estuary are accustomed to dealing with gill nets and other fishing gear, and the animals often simply climbed over the float line and swam away without being entangled during capture attempts. This limited our ability to direct our capture activities to specific age or sex groups. Nevertheless, 23 animals were captured between May and October 1994–1997. The breeding status of males ≥ 70 kg was categorised, assuming a 24-d lactation period with the 25th of May used as the date of first births in the Estuary (Bowen et al. 1992; V. Lesage, M.O. Hammill, and K.M. Kovacs, unpubl. data). Based on these criteria, sexually receptive females should have become increasingly more numerous after June 21. Male harbour seals are thought to establish underwater display areas some days or weeks prior to when oestrus females start becoming available (Walker and Bowen 1993b; Temple 1994; Van Parijs et al. 1997). Thus, males captured earlier than June are referred to as *pre-breeding* males, and those captured in June and July were classified as *breeding* males. Whether females were monitored during the first or last half of the 24-day lactation period was determined using the mass of their pup; based on a birth mass of 10.6 kg (Bowen et al. 1992), and a mean daily mass gain of 0.5 kg d^{-1} in pups (Y. Dubé and M.O. Hammill, unpubl. data).

Seals were immobilised with an intramuscular injection of Telazol® (Tiletamine and Zolazepam, Fort Dodge® Laboratories, Iowa; 0.5 mg / kg), and weighed (± 0.5 kg). A lower incisor was extracted for age determination (Bernt et al. 1996). Animals were equipped with both time-depth-velocity (TDR Mk6) and stomach temperature recorders (HTR) (n = 14), a TDR only (n = 1), or a half-watt satellite-linked time-depth recorder (SLTDR; n = 8) (all instruments were built by Wildlife Computers, Redmond, WA) (Table 4.1). HTRs and TDRs were housed on a remote-release instrument package (Hammill et al. 1999) glued to the middle of the back using a quick setting epoxy resin. The 15 x 5.5 x 6 cm, 650 g SLTDRs were glued onto the back of the skull and upper-neck of the animals. A 32 g, 2 x 5 cm temperature sensor was introduced by intubation into the stomach of seals equipped with TDR/HTR packages. This pill transmitted electromagnetic pulses to the HTR, at intervals that varied linearly with stomach temperature. All instruments were synchronised to Greenwich Mean Time (GMT), and were programmed to record time, the animal's depth (± 1 or 2 m), swim speed (± 0.05 m s^{-1}) and stomach temperature (± 0.2°C) every 5 or 10 s (Table 4.1).

Seal locations

Summer movements of seals equipped with either a VHF transmitter only, or both a VHF and a TDR/HTR package were monitored directly using a 7-m Boston Whaler equipped with a 6 element Yagi antenna mounted 4 m above sea level. The tracking vessel remained 300-400 m away from each study animal to minimise disturbance. A computer, interfaced with the boat's

Global Positioning System and echosounder logged time, position of the boat, water-depth, and surface-temperature each time the animal surfaced or dove.

Seal movements during the fall, winter and spring were documented using satellite telemetry. Ice conditions during these periods were obtained from the Canadian Ice Service (Environment Canada). The ARGOS system administration provides an estimate of 'quality' for each location received for each seal. Quality classes of 0, 1, 2 or 3 have accuracies of 150 m to >1000 m, whereas class A and B locations have no accuracy estimate. Locations were validated using an iterative forward/backward averaging filter adapted from McConnell et al. (1992) to identify erroneous positions (J.-F. Gosselin, Fisheries and Oceans Canada, Mont-Joli, QC, unpubl. data). Swimming velocity was calculated for pairs of successive positions and an average velocity was calculated using velocities obtained for the two preceding and two following fixes. Locations which implied an average velocity of > 2 m s^{-1}, *i.e.* equivalent to about twice the mean speed recorded from St Lawrence harbour seals fitted with Mk6 TDRs when diving to ≥ 4 m (Chapter 2; see also Thompson and Miller 1990), were rejected. A large proportion of locations (51–70% depending on individual seals) were of poor quality (A or B). The inclusion of these poor quality positions in the calculation of mean velocity may increase mean velocity of good quality locations to values > 2 m s^{-1} and cause their rejection. If a good fix (class ≥ 0) was obtained during the preceding 24 h, then a new velocity was calculated using the good fix and the position in question. If the new velocity was ≤ 2 m s^{-1}, then the position was retained. This approach reduced the proportion of locations rejected from 43 to 30%.

Extraction and preparation of data

SLTDRs stored maximum dive depth and duration data, and the time spent at depths in 6-h-blocks (03:00-09:00, 09:00-15:00, 15:00-21:00, and 21:00-03:00, local time) corresponding to dawn, day, dusk and night, respectively. These data were transmitted in the form of frequency histograms. The resulting classes provided the number of dives with a maximum depth, or proportion of 6 h-periods spent at depths in the ranges 0–4, 4–10, 10–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–200, and > 200 m. Interval classes for dive duration frequency histograms were 0–2, 2–5, 5–10, 10–15, 15–20, 20–25, 25–30, and > 30 min. The use in 1994-95 of 0 m as the minimum depth for a dive to be logged, and the inclusion in 1997-98 of a bin with an upper limit of 2 m resulted in surface time (wet reading) being logged as dives. The duration of these 'dives' were spread over all histogram duration classes. Consequently, only dives > 4 m and duration histograms from the 1995-96 animals were analysed. Transmissions also contained the maximum depth recorded during the previous 24 h and the time spent hauled-out or in the water at depths < 2 m during the two previous 6-h blocks.

Data from the TDRs and HTRs were extracted using software provided by the manufacturer. TDR files were corrected for changes in pressure transducer calibration over the deployment period (Zero Offset Correction program). Dives recorded during the 300 s following a haul-out period that was ≥ 345 s in duration were eliminated from the analyses due to substantial zero depth drifts during these segments of the data records (Chapter 3). A dive was defined as any excursion from the surface ≥ 2 m or ≥ 4 m, depending on whether depth resolution had been set at 1 or 2 m. However, dives of < 4 m were considered to be part of the surface activity when diving behaviour was examined, because the depth resolution and sampling interval of TDRs distorted several parameters in very shallow dives. The corrected depth records

(Dive Analysis program) provided several descriptive parameters for each dive (see Chapter 3 for a detailed description), along with the duration of long (≥ 3 min) periods of haul-out. Post-dive surface interval was also calculated as the time spent ≤ 1 or 2 m (depending on depth resolution) while the salinity switch read wet, using purpose-built software. Swimming velocity and stomach temperature information were extracted separately, and merged with the corrected depth records (BINEX, 3M and MERGE, Wildlife Computers Inc., Redmond, WA). Swimming velocity was corrected using the calibration curve developed for Mk6 Wildlife Computers TDRs (Boyd et al. 1995). Using the same definition as the Dive Analysis program for the start and end of a dive, dives were split into descent, bottom and ascent phases. Average swim speeds were calculated for descent and ascent phases, and median and maximum speeds were calculated for the bottom phase.

Stomach temperature sensors generally record feeding events as an abrupt drop, followed by an exponential rise in the stomach temperature (*e.g.* Wilson et al. 1995). Possible feeding events were identified based on a minimum drop in stomach temperature of 0.2°C within 5 s. The end of an event corresponded to when the stomach temperature returned to within 0.4°C of the initial temperature, that is the reading preceding the one where a decline was observed. An event was considered to be false if the minimum temperature attained (the reading preceding that where the temperature started to rise) differed from the initial temperature by < 0.8°C, and when the temperature remained ≤ 0.4°C from the minimum for > 15 min. A 5-s correction was applied to the time of initial temperature drops in order to link HTR and TDR information (Chapter 3).

Haul-out activity

Satellite transmitters switched to a slower 'on-land' rate of transmission after 10 consecutive dry transmissions, *i.e.* after 7.5 min in all seals. The relative proportion of transmissions made at the on-land/at-sea rates was used as an index of haul-out activity.

The TDRs provided a detailed record of harbour seal haul-out activity. Factors affecting haul-out behaviour were examined by determining whether each individual seal was hauled out or not during each hour of a TDR deployment, and by correlating these *observations* to the prevailing tidal and environmental conditions available hourly either from corrected tide tables or the local weather station (Mont-Joli airport, Environment Canada 1995; 1996; 1997; 1998) using logistic regressions. The environmental parameters included time of low tide, absolute tide height and amplitude, time interval relative to the closest low tide, presence/absence of precipitation, relative humidity, wind direction and strength, air temperature in degree Celsius or relative to the daily maximum, and number of sunlight hours for the day. Other parameters that were included in the analysis were whether the closest low tide and the observation occurred during the day or night and the time elapsed since the last haul-out period of ≥ 3 min. Haul-out periods separated by < 60 min were assumed to have resulted from normal investigations of the different available haul-out sites or short-term disturbances. These short periods of haul-out activity were concatenated. The first and last day of data were not included in this part of the analyses since activity records were incomplete. Each variable was standardised (mean = 0, variance = 1). A subsample of 1000 *observations* was randomly chosen, and logistically regressed in a stepwise fashion against the binary dependent variable, *i.e.* the event of a seal being hauled out or not (Hair et al. 1995; Stokes et al. 1995). Residuals were checked for normality. The proportion of the total variance explained by the model was estimated using log likelihood values to calculate the *Pseudo* R^2 statistic (Hair et al. 1995). The analysis was repeated on three subsamples to insure consistency in the results.

Diving activity

Dive records of harbour seals were divided into bouts of near-surface and diving activity, based primarily on maximum dive depths. Bouts of diving activity were defined as a series of at least 3 consecutive dives ≥ 4 m. Post-dive surface intervals (PDSI) were used to calculate the bout-ending criterion (BEC). The cumulative probability distribution of PDSI was calculated, probit transformed and plotted against PDSI for each seal (following Boyd and Croxall 1992), using PDSI of 0–2 min at their maximum resolution (5 s), or using PDSI of 2–100 min rounded at the nearest 30 s to identify normal surface interval after single dives and the BEC, respectively. A break in the slope signifies that PDSI, rather than being normally distributed around a single mean value, cluster around two discrete mean values. Slopes for the two sections of the curve can be calculated, and their intersection defined as the BEC.

Diving activity of harbour seals was examined from the classification of their dive records following the methods and cluster solutions described in Chapter 3. Briefly, five distinguishable dive types have been described in St Lawrence harbour seal diving records, using dives ≥ 4 m obtained with 1-m resolution Mk6-TDRs and a combination of principal components and hierarchical and non-hierarchical cluster analyses (Table 4.2). Dive types 1, 3, 4 and 5 are U-shaped. Type-1 dives are relatively deep dives (~ 20 m) with median bottom swim speeds near the minimum cost of transport speed (Davis et al. 1985; Hind and Gurney 1997), and bursts of faster swimming during the bottom phase. Type-3 and -4 dives are shallower (~ 8 m) than type-1 dives, but differ from each other in their ascent/descent rates and bottom swimming speeds, as type-4 dives have slower bottom swimming speeds than type-3 dives. Type-5 dives have similar ascent and descent rates and angles, and median bottom swimming speeds near zero. However, they are more variable in terms of maximum depth than the three preceding dive types, as these dives are deeper when performed during the day (~ 20 m) than at night (~ 8 m). Finally, type-2 dives are shallow, V-shaped dives, with similar ascent and descent rates and angles.

Diving effort was estimated as the time spent diving during bouts of diving activity in TDR-equipped seals. Records collected via SLTDRs provided data on the proportion of a 6-h period that a seal spent in different depth brackets. Therefore, diving effort was estimated as the proportion of a 6-h period spent diving in any depth bracket > 4 m. The first and last day of data were discarded for the calculation of daily diving efforts since they provided an incomplete record of a seal's activities. Diel variation in diving effort was examined by dividing each day of TDR records in four periods: day (09:00–15:00), dusk (15:00–21:00), night (21:00–03:00) and dawn (03:00–09:00). Time-at-depth histograms were transmitted separately for each of these periods in SLTDRs and were used directly. Given that diving activity or dive depths were unlikely uniformly spread throughout the day (Chapter 3), the examination of seasonal variation in diving depth and effort through the analysis of daily averages of the available summary records was inappropriate. Therefore, monthly mean depth of dives and proportion of dives in the different depth classes were calculated by summing parameters over the 4 periods and the entire month and then calculating proportions. Calculations which required an estimate of parameters for each day (*e.g.* daily diving rates or efforts) or which examined diel variation in a parameter (*e.g.* in diving rates or efforts) were made by first, averaging parameters over each period and then summing up the 4 periods (daily means), or by calculating proportions directly from period averages (diel variations).

The pattern of utilisation of the different dive types was compared both between periods of the day and among seals. However, these analyses were possible only for 9 seals equipped with 1-m resolution TDRs. Additionally, records for seals whose velocity meters failed (Table 4.1) are excluded from this analysis. SLTDR records were unsuitable for this particular analysis and hence, were excluded.

A foraging success rate was calculated in TDR-equipped seals only, and was estimated as the catch per unit diving effort. This was obtained by dividing the number of successful foraging dives (*i.e.* dives associated with ≥ one feeding event) by diving effort over the corresponding period. SLTDRs summary records were often not available for all four periods each day.

Results

Seasonal movements and foraging areas

Movements of harbour seals were documented via *in situ* tracking of 16 individuals between May–August 1996-97, and from satellite monitoring of 7 seals between August–June 1994–1998. The 8th satellite transmitter deployed failed shortly after deployment. VHF-equipped seals were tracked for 246 h, spread over 41 sessions (mean = 6.0 consecutive h/tracking, range 1.5–16.5 h). Individual animals were tracked 1–8 times. The SLTDRs transmitted data for 111–295 days (mean ± SD = 245 ± 26 d). At least one position was obtained on 68–187 days in 6 of 7 seals over the deployment period. Only 12 positions spread over 7 days were received from one individual due to low battery power. The forward/backward filter of positions eliminated 13–46% of positions (mean = 31%), and reduced by 1–29% (mean = 13%) the number of days with usable positions.

Harbour seal movements during the ice-free period were quite limited. Fifteen of 16 seals tracked *in situ* were relocated at the haul-out site where they were first captured. The tracking data, which were operationally limited to daylight hours during May–August (1996–1997), suggested that most seals (83%) remained within 3 km of their haul-out sites. The few animals that moved beyond these distances remained in waters < 50 m deep. The furthest distance travelled during this summer period was 8.5 km from the capture site. Similarly, the satellite telemetry data indicated that 87.8% (SE = 3.2%; range 5.6–18.6%) of positions of quality ≥ 0 that were received from 4 satellite transmitters still functioning during May–June, were within 10 km of the summer haul-out sites. However, some more distant excursions (15–30 km) away from the haul-out sites did occur regularly during this period. Excursions were made over somewhat larger ranges during spring and fall (*i.e.* movements performed before or after winter migrations in migrating animals, or between March and October in non-migrating animals). Repeated 1–6 day trips that ranged from 15–45 km away from the summer haul-out sites were recorded in both seasons from 5 of 7 seals, along with a few 65-km long trips between Metis and Bic undertaken by 3 of the seals. During these movements the seals did not go 'off-shore'; they followed coastlines of either islands or the mainland, staying within 5 km of shore (*e.g.* Figure 4.1a).

During the winter, the Estuary is normally covered by drifting pack ice. Ice cover tends to be heavier along the south shore than along the north shore owing to prevailing north-west winds, but conditions can vary markedly over short periods of time. Open water can be replaced rapidly by heavy ice (90% coverage by small to large floes of ice up to 120 cm thick) or vice versa along the Gaspé peninsula and in most of the Lower Estuary. Near Ile Blanche, the ice is either light (coverage index 1–9+ of new ice < 10 cm) or nonexistent throughout the winter. Bays such as Metis usually freeze over by December.

Some changes in seal distribution were observed during the winter. Four adults (5–8 yr-old), captured in Metis Bay, left the Bay during November–mid December. Two of them moved 65–150 km west and over-wintered in the Bic and Ile Blanche regions, while the other two animals moved 330–520 km towards the east (Figure 4.1b). One seal over-wintered in the Cloridorme/Cap-des-Rosiers region along the Gaspé Peninsula, where ice formed between 1–8 January 1996. The other seal spent November–January in the ice-free waters of the Baie des Chaleurs near Pointe Verte (Nov), Nash Creek (Dec), and Bonaventure (Jan). This seal moved to the margin of the frozen Gaspé Bay as the ice began to form in late January, and it stayed in this location until mid-March. A fifth adult, also captured at Metis, remained near Metis throughout winter, likely occupying the marginal ice zone a few tens/hundred meters offshore. Two juveniles (2 and 3 yr-old) that were captured at Bic and Ile Blanche remained in these regions until the last transmissions from their SLTDRs in early December and February, respectively.

Three of the 4 seals that moved away from their summer haul-out sites made short trips between the wintering and summering areas before moving away from their summer site for more extended periods. Seal no. 17908, had just returned (< 12 h) from a 12-day round trip to the Cloridorme/Cap des Rosiers area, when it departed from Metis once again on 27 December to over-winter in the Cloridorme/Cap des Rosiers region. Similarly, seal no. 1854 had just returned from a 6-day trip to Bic, when it undertook its spring migration from Ile Blanche toward Bic and Metis on April 1. Seal no. 17906, marked at Metis, made several trips between Bic, Rimouski and Metis during mid-November to mid-December before establishing itself at Bic for the winter. However, once seals had moved to their over-wintering areas, movements during the winter season were limited to within a 20 km radius for 4 of 6 seals. The wintering area of seal no. 17908 was spread over 60 km of coastline. It did not make a series of short trips between the extremes of its wintering area but rather, it moved progressively through the region. Seal no. 1855, which remained near Metis all winter, made trips of 40–45 km in either direction routinely, similar to movements observed in the spring or fall.

The site fidelity observed during a given season did not necessarily hold from one year to the next. Two of 4 seals (no. 17906 and no. 17908) that were captured in the fall at Metis, and travelled to other regions to over-winter, adopted Bic rather than Metis as their haul-out region the next spring. But their last transmissions were on April 30 and May 12, so it is not known if they returned to Metis later in the spring. While Metis was the main haul-out site for the other two seals, seal no. 1854 which over-wintered near Ile Blanche, stopped at Bic for 3 weeks in April before returning to Metis.

Harbour seals movements into areas that had water deeper than 50 m were limited. VHF-equipped seals that were tracked using the boat were never observed in waters deeper than 50 m, and animals monitored using satellite telemetry were also located in waters that are < 50 m most of the time. Only 10.2% of the positions of quality ≥ 0 (range 0–26%) occurred in areas that were deeper.

Equipment recovery and overview of dive records

Fourteen of fifteen TDR or TDR/HTR packages were recovered, but only 10 provided complete diving records. The battery failed on one TDR (no. 4601), while the velocity meter failed on 3 others during part (no. 3526 and no. 3502) or the entire (no. 2699) period of deployment (Table 4.1). Useable information came from 13 seals: one *pre-breeding* male and two *breeding* males; one lactating female that had a 17-kg pup at the start of her record and one pregnant female which gave birth around 14 June, during the last half of the deployment period;

eight 1–2 yr-old juveniles, four captured before the moult and the four others after the moult. Seals retained temperature sensors in their stomachs for 3–1193 h (median = 58.5 h) whereas TDRs recorded diving activity for 7.5–19 days (median = 16.5 d). The retention period of the stomach temperature sensors corresponded to approximately the beginning of the second half of lactation (~ days 14–18) in female no. 4619, while it covered at least the first half of lactation in female no. 2699. The combined TDR records included 98,725 dives, after eliminating those performed after long periods of haul-out. Summary records of 248,105 dives from 7 seals were transmitted through the NOAA satellites.

Haul-out patterns

TDR-equipped harbour seals hauled out on an average of 79% of deployment days (range 31–100%; Table 4.3). However, this proportion varied between age classes, sexes and seasons. The female in her second half of lactation period hauled out almost daily (14 of 15 d); which was more often than the pregnant female, although the latter hauled out daily between 10–21 June, when it had likely given birth and was lactating. Total time spent ashore daily by the two females was similar (3.2 *vs* 3.7 h d^{-1}). The *pre-breeding* male also hauled out very regularly and usually for extended periods. In contrast, the two *breeding* males were among the animals which hauled out the least frequently (31 and 67% of days), but when they did haul out, it was generally for periods similar to those observed for other animals (2.0 and 3.4 h d^{-1}). Juveniles hauled out regularly during the pre-moult period, but not significantly more often than after the moult (means: 91% *vs* 75% of days; $n = 4$ in each; ANOVA on ranks: $P = 0.26$). Although the median value for daily haul-out time varied considerably between seals, particularly among juveniles

(1.9–8.8 h), animals that hauled out on a greater proportion of days were also those individuals that spent the longest periods ashore daily (Figure 4.2; Spearman correlation $r = 0.80$, $P = 0.001$).

Using the proportion of transmissions made at the on-land *vs* at-sea rate for animals with SLTDRs, large inter-individual variability was observed in seasonal haul-out patterns (Figure 4.3). Nevertheless, haul-out activity during the winter months appeared to be low compared to the fall or spring. Haul-out activity started to decrease at different times among individuals (Nov–Jan), the duration of the periods when seals hauled out less was variable (1–4 months), and was punctuated in some seals by haul-out activities as frequent as those observed in the fall or spring (*e.g.* January in no. 17908).

The logistical regression of tidal and environmental conditions *vs* haul-out events indicated that absolute tide height, or interval relative to low tide (two variables that were highly correlated; $r = 0.96$), represent the main conditions driving harbour seal haul-out behaviour (Table 4.4). According to the calculated odds ratios, seals sampled at high tide or long after or before low tide are 34% as likely to be hauled out than seals sampled shortly before or after low tide, or when tide height was low. Harbour seals were most likely to be hauled out when: tidal amplitude was low; during daylight hours; when wind came from the direction dominant for the season, *i.e.* westerly winds; and when the time elapsed since the last haul-out period was long. While the model fitted the data adequately (Hosmer and Lemeshow statistic: 4.13; *d.f.* = 8; $P = 0.8452$) and correctly predicted harbour seal haul-out behaviour 78% of the time, it explained only 16% of the total variance, suggesting that factors other than those included in the model influenced the haul-out behaviour of the seals. By repeating the analysis for each individual separately, it was confirmed that the haul-out schedule of all adults and 5 of 8 juveniles was dictated principally by tide height or interval since low tide. However, although several animals preferred to haul out near the daytime low tide rather than near that occurring during the night, the pregnant and lactating females and the adult male caught in May regularly hauled out during both night and daylight hours. The haul-out schedule of pre-moult juvenile no. 3508, which hauled out daily for periods of up to 10 consecutive hours, appeared unaffected by tide or weather conditions. Finally, air temperature was the most important factor influencing the haul-out behaviour of two post-moult juveniles. Juveniles sampled when air temperatures were near the daily maximum were 7 times as likely to be hauled out than juveniles sampled when air temperatures was below the daily maximum. Most of the haul-out time of these juveniles also occurred during day time (odds ratios = 2–150).

Dive depths and durations

The deepest dives recorded from seals monitored during the summer using TDRs (20–75 m) were generally shallower than those of seals followed during the fall, winter and following spring using SLTDR (72–136 m) (Table 4.5). Modal diving depths of all TDR-equipped seals were ≤ 4 m, which constituted on average 51% of seal dives, although this proportion varied from 15–93% among individuals. Most (95%) dives performed by individual seals were < 5–34 m in depth. The distribution of dives deeper than 4 m varied across individuals from a uniform utilisation of depths to 30 m, to peaks of activity at depths of about 8 m or 20 m. Only dives > 4 m were available from SLTDR-equipped seals. Similar to the TDR-equipped seals, the shallowest depths represented an important component of their diving records; a mode occurred at the shallowest depth class (4–10 m) in 6 of 7 seals, with these dives representing 32–68% of dives performed by these 7 animals. Ninety-five percent of the dives were < 40 m, the only exception being juvenile no. 17904, which performed 8% of its dives at depths > 40 m.

The longest dives recorded from individual TDR-equipped seals lasted 6.9–15.2 min, whereas 6–30 dives lasting > 30 min were recorded for the 4 SLTDR-equipped seals which had reliable dive duration histograms (Table 4.5). Nevertheless, 95% of the dives performed by individual seals were < 2.7–5.0 min in duration. TDR-equipped seals consistently had a mode at the shortest dive duration (≤ 10 s). They had a uniform dive duration distribution if their dive depth distribution was uniform or decreasing with depth, whereas they had a second peak in duration distribution at 1.9–3.0 min, when modes in depth distributions were observed at 8 or 20 m. The dive duration distribution was unimodal at durations of class 2–5 min in three SLTDR-equipped seals with reliable dive duration histograms, and of class 0–2 min in another (no. 1854). Dive duration was significantly and positively related to dive depth in all seals equipped with TDRs (Spearman correlation $r = 0.50$–0.89, all $P < 0.001$). However, this relationship was not linear since dive duration increased asymptotically with depth towards durations of ~ 3.2 min (*i.e.* 190 s, Figure 4.4). Although dive duration was not correlated with an animal's age, mass or body length, mean dive length was significantly shorter in yearlings (112–141 s; $n = 7$) than in animals of age 2 or more (138–159 s; $n = 7$) ($t_s = 4.42$, $P < 0.0008$).

The multimodal pattern observed in depth utilisation required that 4-m dives and deeper dives be analysed separately. Therefore, diving bouts are referenced to as *4-m* or *deeper*, depending on whether depths reached during a bout exceeded 4 m or not. In the case of SLTDRs, only dives > 4 m and thus '*deeper* diving' were available because of the bin settings.

Summer diving patterns - using TDRs

Plotting post-dive surface intervals (PDSI) of 0–2 min at their maximum resolution (5 s) against their probit transformed cumulative probability distribution, resulted in an inflexion point at an average of 48 s (range 42–58 s; $n = 8$). By plotting the PDSI rounded to the nearest 30 s for PDSI of 2–100 min, a second inflexion point was observed at an average of 330 s (range 295–350 s; $n = 8$). When excluding dives which had following surface intervals > 330 s, median surface intervals between dives varied between 25–45 s among seals, suggesting that the first inflexion point corresponded to the normal surface interval after single dives and the second, to the BEC. Surface intervals ≤ 330 s were significantly and positively related to the duration of the preceding dive in all seals except no. 3531, although these correlations were relatively weak (Spearman correlation $r = 0.13$–0.38, all $P < 0.001$).

Diving bouts identified using the 330 s BEC were occasionally separated by a few dives of < 4 m, resulting in sequences of brief and alternating bouts of diving and near-surface activity. These shallow dives were at first thought to be artefacts of zero depth adjustment, but validation using VHF tracking of TDR-equipped animals confirmed that these represented real underwater activity. The duration of these bouts of shallow activity, which generally numbered 1–3 dives, was calculated and those ≤ 330 s were considered to be part of the preceding diving bout.

The number of *4-m* and *deeper* diving bouts performed daily varied between seals from an average of 0.2–7.0 for *4-m* diving bouts and 1.1–7.6 for *deeper* diving bouts. However, coefficients of variation associated with these values were high (35–230% and 28–150%, respectively), indicating large day-to-day variation in diving patterns of individual seals. The *4-m* diving bouts lasted a median of 0.2 h and contained a median of 7 dives (ranges: 0.1–0.5 h and 5–23 dives among the 14 seals), whereas *deeper* diving bouts generally lasted longer (0.8 h) and consisted of a larger number of dives (24 dives, ranges: 0.4–3.5 h and 12–58 dives; $n = 14$ seals) (paired t-test: $t_s = 7.10$ and 5.85, respectively, $n = 14$ seals, both $P < 0.0001$). The proportion of time spent diving during a bout was relatively consistent across seals during *deeper* diving, (median 64.5%; range 57–77%). Although this proportion was usually smaller during *4-m* diving bouts, it was highly variable across seals (median=43%, range: 25–83%).

Daily diving effort varied a lot among individuals (Table 4.6). The pregnant and lactating females, 3 of 4 pre-moult juveniles, and the *pre-breeding* male were the animals which spent the least time diving, with median daily efforts of 1.3–6.6 h. Some *4-m* diving took place in these records, and represented medians of 2–100% of the overall diving effort in these seals. In contrast, the four post-moult juveniles, pre-moult juvenile no. 2696, and the two *breeding* males spent 9.0–15.6 h diving daily, most of which was included in *deeper* diving bouts (99–100%).

Daily diving efforts remained relatively consistent throughout the deployment period in most seals (Figure 4.5). However, the pregnant female's (no. 2699) overall diving effort gradually declined, with *deeper diving* completely disappearing about midway through the deployment period. Similarly, overall and *deeper* diving effort decreased in juvenile no. 2700 as the moulting period approached. Although these specific temporal variations were not observed in the other 3 pre-moult juveniles, their diving effort did display some seasonality. Juveniles caught early in the season (*i.e.* no. 2696) spent more time diving than those caught later (no. 3502 and no. 3508). Diving effort was variable among the adult males. The *pre-breeding* male dove for ~ 8 h d^{-1} until early June and then thereafter, its diving activity declined to ~ 3–4 h d^{-1}. The diving effort of *breeding* male no. 4615, which was caught on June 10, progressively increased until June 17 when it plateaued near 16 h d^{-1}. The other *breeding* male caught during the same period (no. 4618), maintained high diving effort (~ 16 h d^{-1}) throughout the period of the deployment (*i.e.* 12–27 June).

Overall (Figure 4.6) and *deeper* (not shown) diving effort during the different periods of the day were more variable among juveniles than among adult harbour seals. Adults either spread diving effort uniformly through dawn, day, dusk and night, or spent more time diving at night or dawn than during the day or dusk. Although similar patterns were observed in juveniles, some animals expended considerable effort diving during the day or dusk times. Effort expended in *4-m* diving bouts was uniformly spread throughout the day in most seals (not shown), but was less important during the day than at night in pre-moult juveniles no. 2700 and no. 3502, and slightly higher during the day than dawn or night in the adult females.

Mean diving depth remained relatively consistent over the deployment period, but varied between seals. The post-moult juveniles generally dove at significantly deeper depths (median: 11–19 m) than the animals caught in May–July, *i.e.* either the pre-moult juveniles (4–9 m), *pre-breeding* or *breeding* males (6–8 m) or the pregnant or lactating females (2–5 m) (*one-way* ANOVA on ranks: $F_{3,9} = 10.45$, $P < 0.003$, *post hoc* Tukey's test, all significant, $P < 0.05$) (Table 4.6). Nevertheless, diel patterns in overall and *deeper* diving depths were similar, and relatively consistent across 7 of 8 juveniles, with nightly dives being generally shallower than during the day, and either similar to, or shallower than, those performed at dawn or dusk (Figure 2.6). In contrast, the two adult females dove to deeper depths at night than during the day or at dusk, when considering diving activity as a whole. This likely resulted from the reduction in *4-m* diving effort at night, since diel variation in diving depths were insignificant when only *deeper* diving was considered. Overall and *deeper* diving occurred to deeper depths at night (7.6–8.8 m) than during the day (5.9–6.0 m) in the two *breeding* males. However, the *pre-breeding* male dove within a very narrow depth range (7.6–8.5 m), regardless of the time of day.

Variation in mean depth of diving observed between seals and periods of the day was related to the frequency of use of particular dive types (Figure 4.7). When pooling the data for all seals and day periods, mean depth of diving increased linearly and significantly with an increasing occurrence of 20-m type-1 and 10-m type-5 dives, and the decreasing occurrence of 8-m type-3 and -4 dives (stepwise linear regression of dive type occurrences, expressed as the number of dives per unit diving effort: $r^2 = 0.77$; $P = 0.0001$). The consistency in mean daily depth of diving over the deployment period was mirrored by the relative occurrence of the different dive types, which also remained consistent through time for all seals (not shown).

Dive types used during bouts of diving activity varied between seals (Figure 4.8). Type-1 dives represented the main dive type in post-moult juveniles, and these dives were used significantly more often by these animals than by any other age or 'season' group of seal (*one-way* ANOVA, *post hoc* Tukey's tests: all $P < 0.05$). Juvenile no. 3508 was an exception in this regard, since it used type-1 dives as frequently as 2 of 3 post-moult juveniles. Dive types used during bouts of diving activity were more variable among pre-moult juveniles. Juvenile no. 2700 usually dove at shallow depths using mainly type-3, but also displayed some type-2, and type-4 dives. The other two juveniles, which tended to dive at deeper depths than juvenile no. 2700, frequently used type-1 dives and, in the case of juvenile no. 3508, also type-3 dives. Type-4 dives (with some type-3 dives) dominated the behaviour of the two *breeding* males, and were used significantly more often by these individuals than by most other seals (*post hoc* Tukey's tests: all $P = 0.0001$, except for comparisons male no. 4615 or no. 4618 *vs* juvenile no. 2700, both $P = 0.20$). The lactating female rarely used type-1 dives, but used the other 4 types relatively uniformly (*post hoc* Tukey's test: $P > 0.05$). Although type-5 dives were not among the predominant dives used by seals, they did occur regularly in the records of adults and post-moult juveniles, as well as infrequently in pre-moult juveniles records.

Dives associated with successful foraging were recorded from all groups of animals including the lactating females (*e.g.* Figure 4.9) and *breeding* males. The number of successful dives recorded during sensor retention ranged from 2–194 dives (Table 4.7). Successful dives were not distributed evenly throughout the day; a higher proportion of these dives occurred at night (17–76%) compared to during the day (0–20%) in all the seals caught between May and July (Table 4.7). The reverse was observed in the 4 post-moult juveniles for which the proportion of successful dives varied between 17–50% during the day as compared to 0–16% at night. Despite these differences, a significant proportion of successful dives (17–50%) was consistently associated with dawn in all animals. The two dive types associated with bursts of faster swimming during bottom time (type-1 and type-3 dives) generally accounted for 43–92% of the successful dives that could be classified. However, type-5 dives which had near zero bottom swimming speeds were also important in the successful foraging record of juvenile no. 3526 and no. 3531 and for the *breeding* male no. 4615. Although type-4 dives were the most abundant dive type performed by the two *breeding* males, only 1–3% of the successful foraging dives of *breeding* males were of this type.

When comparing the number of successful dives to diving effort, success rate was generally better in adults than in juveniles. Success rates by adult males and females were a prey item every 44–45 min or 24–38 min of diving respectively, whereas catch per unit diving effort was lower in 5 of 7 juveniles (Table 4.6). Four juveniles caught prey every 54–59 min, while another (no. 3508) captured only 2 prey items during the 34 h pill retention period, and had a success rate of one catch every 241 min spent diving. Two juveniles (no. 2700 and no. 3502) had success rates similar to adults, with prey captures every 35–42 min. Success rate was not related to overall diving effort (Spearman correlation $r_s = 0.11$, $P > 0.05$, $n = 11$), even when juveniles no. 3502 and no. 3508 and the pregnant and lactating females were excluded from the analyses ($r_s = -0.33$, $P > 0.05$, $n = 11$).

Successful prey captures occurred during bouts of near-surface activity and thus, during dives < 4 m. The proportion of successful dives that were < 4 m varied between individuals from 1–72%; they were highest in the pregnant and lactating females and in juvenile no. 3502. Dives < 4 m represented ≤ 28% of the other juveniles' successful dives (except no. 3508: 1/2 success at < 4 m = 50%), and 22 and 46% of those recorded in the two *breeding* males.

Seasonal variation in diving activity - using SLTDRs

The distribution of dive depths varied seasonally (Figure 4.10). However, patterns appeared relatively inconsistent between seals, particularly during the fall and winter when the average dive depth ranged from 4–24 m among the seals. Dives at 4–10 m were generally the most frequent dives observed both during the fall and spring. These dives represented > 65% of daily dives during April–June, which is in agreement with the < 10 m mean depth of dives that was consistently observed during April–June (n = 6 at this time). However, 4–10 m dives generally represented a smaller proportion of daily diving records during August-November (except for no. 1855). Dives > 80 m appeared in December and disappeared in March, suggesting deeper diving habits during the winter. However, mean dive depths during these months were not the deepest observed. Nevertheless, it is clear that the proportion of 4–10 m dives declined during the winter season. The superimposition of ice conditions at seal locations onto monthly dive distributions among depth categories indicated that this decline in shallow diving often corresponded to the presence of ice.

The intensity of diving activity varied seasonally. Using either the mean daily diving rate, or the mean time spent diving > 4 m, an increase in diving effort was observed in late fall–early winter, when seals spent 45–65% of their time at depths > 4 m (Figure 4.11). This high diving activity was maintained throughout winter until February–April, when it declined rapidly for most of the seals.

The diel pattern in diving activity also changed seasonally (Figure 4.12). Diving rates and efforts were generally higher at night than during the day from August until December, when this trend changed toward a higher diving activity during the day than night. This behaviour was maintained until April when the tendency was again reversed. This pattern was observed in all seals except seal no. 17903, for which the analysis was based on only 76 transmissions spread over 8 months. However, the precise timing of reversal varied from October–December or March–May for the 7 individuals monitored.

Discussion

The number of seals that were captured during this investigation was lower than expected despite our sustained efforts to increase sample sizes. Nevertheless, this study provides new information on harbour seal distribution on an annual basis and their diving and foraging ecology. Monitoring actual incidents of food ingestion created the opportunity to examine success rates of a wild pinniped, and highlighted lower success rates in some yearlings as compared to older animals in this study. In addition, evidence of feeding during lactation in adult females and at least during the pre-mating period in *breeding* males was documented.

Harbour seals showed strong site fidelity to one haul-out area during the spring and summer months, and only occasionally undertook 1–6 day trips to areas ≤ 65 km away during this time. During August–September, harbour seals must replace energy stores that were depleted during the breeding and moulting seasons (Boulva and McLaren 1979; Drescher 1979; Pitcher 1986). Thus, it was not particularly surprising to find that their diving effort increased and haul-out activity declined during the fall and winter months (Harvey 1987; Thompson et al. 1989; Stewart and Yochem 1994; Gotthardt 1998; but see Boulva and McLaren 1979). Despite an increased need to forage, the distribution of seals remained relatively unchanged until late in the fall, and seals continued to make trips over limited distances. Very few offshore movements were documented in this study. Almost all movements away from the haul-out sites took place along the coast in waters < 50 m deep. These excursions often corresponded to animals visiting a bay or an area where a stream fed into the Estuary or Gulf. These relatively limited movements were within the range of those previously reported for this species (reviewed in Thompson 1993; see also Harvey 1987; Thompson et al. 1996; Frost et al. 1998; Suryan and Harvey 1998; Tollit et al. 1998). In the Estuary, ice normally begins to form in late November, and 5 of 7 seals left their summer haul-out areas around this time. Five of seven seals remained within the Estuary, indicating that the animals were able to forage successfully locally (Härkönen 1987). Nevertheless, 4 of 7 seals over-wintered 65–520 km away from their summer haul-out sites, including two animals that moved beyond the limits of the Estuary.

Previous work has relied heavily on VHF telemetry to monitor harbour seal movements throughout the year (*e.g.* Pitcher and McAllister 1981; Brown and Mate 1983; Thompson et al. 1989; Bjørge et al. 1995; Thompson et al. 1996; Suryan and Harvey 1998). Perhaps as a result of the limitation of such technology to detect large-scale movements (Thompson 1993), or the ice-free nature of waters in regions where most of these studies were conducted, adult harbour seals are believed to be rather sedentary, only rarely moving over 100 km (Fisher 1952; Boulva 1971; Fay 1974; Bigg 1981; Thompson et al. 1998). The largest movements reported for this species, prior to SLTDR records, were dispersal movements by immature animals rather than seasonal movements of mature individuals (Divinyi 1971; Boulva and McLaren 1979; Brown and Mate

1983; Thompson 1993; Thompson et al. 1994b; de Jong et al. 1997). Although marked changes in the seasonal distribution of harbour seals from the Bay of Fundy and Maine have been noted (Payne and Schneider 1984; Rosenfeld et al. 1988), 95% of the animals involved in the largest movements from these areas (~ 450 km to southern New England) were sexually immature (Whitman and Payne 1990). Satellite telemetry did confirm the sedentary habits of some mature harbour seals in southern California (*e.g.* Stewart et al. 1989; Stewart and Yochem 1994), but it also highlighted seasonal movement patterns of adult harbour seals in Prince William Sound (Alaska) (Frost et al. 1998), that were similar to the 65–520 km movements observed in this study. The latter investigation and the current study indicate that some adult harbour seals migrate large distances as part of their annual activity/distribution cycle.

Movements of harbour seals in the Estuary may be determined to some extent by prevailing ice conditions. Harbour seals occasionally haul out on ice, but are most often associated with ice-free waters (Mansfield 1967; Fay 1974; Calambokidis et al. 1987; Mathews and Kelly 1996; de Jong et al. 1997). During the winter, most bays in the St Lawrence Estuary are covered by solid land-fast ice and the Estuary itself is normally covered with drifting pack ice. These conditions force animals to move away from the coast. The extent and direction of their movements are likely influenced by factors such as previous experience and the spatial patterns of ice formation. The swift current in the Ile Blanche region prevents significant ice accumulation. This phenomenon might explain the lack of long-distance movements in the seal captured near Ile Blanche and the winter immigration of a seal from Metis into this region. The presence throughout winter of seals near Metis, Bic, Cap des Rosiers and the Gaspé Bay, where heavy ice conditions intermittently prevail during winter, suggests that harbour seals can tolerate heavy ice conditions for short periods of time at least, provided that ice frequently opens up, as is the case in these regions, or that some ice-free microhabitats persist within these regions (Mansfield 1967).

The presence of ice may force harbour seals to abandon some haul-out sites. However, it appears that they may also use ice as a winter haul-out platform. Although this could not be unequivocally confirmed for seals wintering in the Estuary, the distribution of several dry positions for seal no. 17905 ('on-land' rate) along the entrance of the Gaspé Bay, an area corresponding to the fast-ice margin, suggests this is the case. Ice edges are often areas of high productivity (Fraser and Ainley 1986; Smith and Nelson 1986; Stirling 1997). Hauling out at the ice margin would maximise the time and energy spent foraging by reducing time and energy expended travelling to and from foraging areas (Houston and Carbon 1992; Thompson et al. 1993).

There is very little information available concerning the diet of St Lawrence harbour seals. A recent investigation using stable isotopes ratios in seal tissues indicates that the diet of both juveniles and adults consists mainly of fish (Chapter 2). The few otoliths that were recovered from stomach lavages (*n* = 17 juveniles of 0 to 2 yrs-old and 1 adult female) belonged to a limited number of species, namely rainbow smelt (*Osmerus mordax*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), sand lance (*Ammodytes americanus*), and winter flounder (*Pseudopleuronectes americanus*). Harbour seals are opportunistic in their feeding habits, and take advantage of locally abundant prey species (*e.g.* Olesiuk 1993; Bowen and Harrison 1996; Tollit and Thompson 1996; Hall et al. 1998). During the spring (April–May), rainbow smelt move up freshwater streams to spawn (Andersen and Gagnon 1980), while capelin spawn on beaches around mid-June (Parent and Brunel 1976; Fisheries and Oceans Canada 1995). Winter flounder spawn in coastal waters during summer (Andersen and Gagnon 1980). Although herring are known to spawn only in the western parts of the study region (Munro et al. 1998), they are caught by fishermen in fixed gear deployed along the coast in the Metis–Bic region throughout summer (S. Bérubé, Fisheries and Oceans Canada, Mont-Joli, QC, unpubl. data). Schools of sand lance are regularly observed in the Metis–Bic region during summer; the sandy bottoms in these regions are important habitats for this species (Hobson 1986). During the fall, herring leave the Estuary (Andersen and Gagnon 1980), but capelin, smelt and sand lance may remain abundant. Rainbow smelt are fished through the ice in several localities, including Rimouski and the Gaspé Bay, while capelin are known to occur in abundance near the confluence of the Saguenay River and St Lawrence Estuary (Bailey et al. 1977; Andersen and Gagnon 1980) where they are preyed upon by harp seals (*Phoca groenlandica*) (Murie and Lavigne 1992; Beck et al. 1993b). Sand lance are non-migratory (Mercille and Dagenais 1987). Although they may remain buried in the sand during most of the winter (Winslade 1974), except for a short period between October and December when they are believed to spawn (Brêthes et al. 1992), seals in other regions may prey on them during winter by disturbing sediments (Tollit et al. 1998). The biology of winter flounder in the Estuary is poorly documented, but this species is available throughout the winter along the Lower Estuary's south shore (Fisheries and Oceans Canada 1995). It may move into deeper waters in the winter period than during summer (Andersen and Gagnon 1980).

The recording of successful foraging dives in all of the harbour seals monitored during this study indicates that they all spent at least some time foraging. The diel patterns in their haul-out activity and diving depth and effort suggest that most of them might have been nocturnal or twilight foragers during the ice-free months. Most seals hauled out once a day near the daytime low tide, a period when their diving effort was generally lowest, and when few successful foraging dives were recorded. Intense foraging activity at shallow depths during twilight or night hours has been reported for several other pinnipeds (*e.g.* Le Bœuf et al. 1988; Hindell et al. 1991; Bengston and Stewart 1992; Boyd and Croxall 1992). Herring and capelin, which disperse in small, stationary schools along the bottom during the day, may be more easily detected when they are clumped at dawn or dusk when they migrate from or to the surface (Woodhead 1966; Bailey et al. 1977; Muntz 1983). These species appear to cluster in inshore, shallow waters during the night in the Estuary (S. Bérubé, unpubl. data). Spawning capelin also approach beaches mainly at night (Andersen and Gagnon 1980). Feeding on these species while they are in shallow waters would be consistent with the large proportion of successful dives at < 4 m in several harbour seals that were caught in June–early July. Twilight foraging could also be directed towards smelt, as they move in and out of streams (Robitaille and Vigneault 1990), or it could be directed towards sand lance. Seals may be patrolling the bottom at twilight, and particularly at dawn when sand lance, which spend the day in tight schools near the surface, leave their night time burrows (Hobson 1986).

Nocturnal foraging habits have been reported for harbour seals from other regions (Boulva and McLaren 1979; Calambokidis et al. 1987; Thompson et al. 1989; Watts 1993; 1996; Roen and Bjørge 1995). However, some other studies suggest that harbour seals forage principally during the day (Bigg 1981; Thompson et al. 1991; Coltman et al. 1997), are ambivalent in their choice (Yochem et al. 1987; Godsell 1988; Thompson et al. 1989; Suryan and Harvey 1998) or that diel rhythms purely reflect individual preferences (Boulva and McLaren 1979; Yochem et al. 1987; Stewart and Yochem 1994; Bjørge et al. 1995). In this study, seals did not forage exclusively at night or during twilight hours, since successful foraging dives were also recorded during the day in all seals. Prey targeted during daylight hours are less clearly defined. During the day, harbour seals may target vertically migrating species while they are in small, stationary schools along the bottom (*e.g.* Thompson et al. 1991). Alternatively, daytime foraging could be oriented toward benthic prey species (see Watts 1996) such as some flounder species that are day active (Woodhead 1966). Flounders and other flatfish are difficult to detect when they are immobile because of their cryptic coloration. But, when moving they are much easier to see. Both hypotheses are consistent with the deeper depths of diving observed during the day compared to the night, and the report of an adult male harbour seal from Sable Island that was shot at midday full of freshly eaten winter flounder (Boulva and McLaren 1979). The reversal from being mainly nocturnal divers towards being daytime divers during the period from December–March in all seals may indicate a switch in diet from mainly pelagic, vertically migrating species to, possibly, more demersal species such as flounders (see Brown and Pierce 1998). Unfortunately, this possibility remains difficult to investigate given the limited data available for this season (Chapter 2).

The variability observed in this study among seasons, as well as that among individuals, in their diving schedules, dive types and other parameters is not exceptional for harbour seals (Godsell 1988; Thompson et al. 1989; Stewart and Yochem 1994; Temple 1994; Thompson et al. 1998; Tollit et al. 1998). In the Estuary, prey availability likely changes markedly through the summer. Smelt, herring and capelin all spawn in late spring–early summer, and are lean and energetically less profitable after spawning (*e.g.* Stoddard 1968). Their abundance also appears to decline in inshore areas late in the summer (S. Bérubé, unpubl. data), and seals may switch their effort to deeper depths to follow these species or to pursue others.

Juvenile harbour seals were captured both prior to and shortly after the annual moult in periods where they were expected to spend a large proportion of their time foraging to maximise or replenish their body reserves. Diving effort declined prior to the moult and then intensified in animals captured after the moult. The reduction in diving activity and increase in haul-out behaviour prior to moulting is associated with declines in thyroid hormone levels (Ashwell-Erickson et al. 1986; Renouf and Noseworthy 1991) and a general reduction in metabolic rate (Ashwell-Erickson et al. 1986; Markussen et al. 1992; Rosen and Renouf 1995). An increase in the time spent hauled out may allow skin temperature to increase, promoting cell development (Ashwell-Erickson et al. 1986; Boily 1995), while a reduction in metabolic rate reduces energy expenditure. Yearling no. 3508, which was in a very early stage of shedding when first captured, hauled out each day and spent a considerable amount of time ashore (up to 10 consecutive hours). This animal was the only individual in this study whose haul-out behaviour was independent of tide height or weather conditions. This sort of pattern is thought to be typical behaviour during the moulting period (Venables and Venables 1955; Thompson et al. 1989; Watts 1996). Although the period of stomach-temperature sensor retention was short for this seal, it was the animal from which the lowest number of successful foraging events ($n = 2$) was recorded.

The two adult females instrumented with TDRs were followed during a period when their foraging activity was, or was about to be constrained by the presence of a suckling pup. Both females hauled out daily during the period when they were presumed to be nursing their pups; a pattern also observed for lactating females at Sable Island (Godsell 1988; Boness et al. 1994) and in the Orkney Islands and in the Moray Firth (Thompson et al. 1989; 1994a). However, in contrast with lactating females from these other regions that are thought to fast during the first 10–11 d of lactation (Boness et al. 1994; Thompson et al. 1994a;), female no. 2699 did not fast during early lactation (Fig. 4.9). The continuation of feeding during lactation in the Estuary females may be related to the proximity and abundance of prey in this region. At Sable Island, foraging is presumed to occur mainly in waters > 20 m, which occur 4+ km from the Island (Coltman et al. 1997). In the Moray Firth, foraging likely occurs at water depths 10–50 m deep in areas 29–46 km from haul-out sites (Thompson et al. 1994a; Tollit et al. 1998). In the Estuary, there is evidence that foraging may occur much closer to the surface and in close proximity to haul-out sites. Adult females spend almost all of their time (87.5% and 94.6%) in water < 4 m deep, where 62 and 72% of their successful foraging dives were recorded. At Bic, mothers with very young pups (3-days old) have been observed travelling back and forth between their main haul-out site and Ha Ha! Bay (Y. Dubé and M.O. Hammill, Fisheries and Oceans Canada, Mont-Joli, QC, unpubl. data). Capelin spawn each year from mid to late June along beaches in this Bay and the Metis Bay, approximately 1–6 km from haul-out sites used by mother-pup pairs. The continuation of feeding during early lactation may result in a less dramatic re-feeding in late lactation. Adult females from Sable Island spend 66% of their time foraging during late lactation (Boness et al. 1994), whereas female no. 4619, who was also monitored during late lactation, showed no abrupt change in her diving activity (Fig. 4.5).

Two adult males were followed in this study through the mating period (≥ June 21) when a reduction in foraging might be expected (Reilly and Fedak 1991; Walker and Bowen 1993a; Coltman et al. 1997). Other studies have suggested that the breeding season in harbour seals may consist of two phases: the pre-mating period, when seals may be establishing underwater territories in anticipation of the second, mating phase, which corresponds to when oestrus females are available (Walker and Bowen 1993b; Temple 1994; Van Parijs et al. 1997). Based on body mass, diving pattern and home range size, at least periodic foraging activity is believed to be maintained during the pre-mating period, whereas foraging may cease or occur only intermittently, depending on male size and condition, when oestrus females become available (Walker and Bowen 1993a; Temple 1994; Coltman et al. 1997; Van Parijs et al. 1997). The decrease in the frequency of haul-out in the two *breeding* males in this study, relative to the *pre-breeding* male (Table 4.3), is consistent with the suggestions from these previous reports (Walker and Bowen 1993b; Temple 1994; Bjørge et al. 1995; Van Parijs et al. 1997; but see Godsell 1988). The recording of successful foraging dives in the two *breeding* males indicates that both animals did continue feeding during at least the pre-mating period. Both *breeding males* maintained a high diving activity throughout deployment, but in contrast to the lactating females, the *breeding* males spent little time in water < 4 m (35.0 and 38.3%), and most of their diving time was spent at median depths of 7–8 m (Table 4.6). These two males shared a nearly exclusive characteristic: a high usage of type-4 dives (Fig. 4.8), some shallow (~ 8 m) dives, with a slow bottom swimming velocity and ascent rate. Despite being frequently performed by *breeding* males, only 1–3% of their foraging success was associated with dives of this type. Type-4 dives in this study resemble slow, shallow 'patrolling dives' (D.J. Boness, W.D. Bowen, G. Marshall and B. Buhleier, unpubl. data, cited in Coltman et al. 1997), the U-shaped 'shallow' (20 m) dives with slow ascent and descent rates (Coltman et al. 1997), the repetitive U-shaped, 'shallow' (12–15 m) dives with near zero bottom swim speeds (Bjørge et al. 1995) or the shallow (17–18 m) dives with some wiggles during bottom time and oblique descent and ascent angles (Temple 1994) that have been described in breeding males from other regions. Type-4 dives may be 'display' dives. These dives were most abundant at night (Fig. 4.7), when lactating females were presumably foraging (Fig. 4.6), and therefore when males might be expected to encounter and advertise to females (Thompson et al. 1989; Walker and Bowen 1993b; Temple 1994; Coltman et al. 1997; Van Parijs et al. 1997).

The harbour seal is generally regarded as a species that hauls out regularly to 'bask in the sun' (King 1983). In fact, little information exists on the time individual seals spend out of the water. The longest haul-out bout reported for a harbour seal is 39 h (Yochem et al. 1987). However, mean figures range from 2.4–21.8 h d^{-1}, with most being < 5 h d^{-1} (Harvey 1987; Yochem et al. 1987; Thompson et al. 1989; Thompson and Miller 1990; Temple 1994). In the Estuary, the longest haul-out bout was ~10 h; 77% of the harbour seals hauled out for < 5 h d^{-1}, and 21% of the seals had daily haul-out periods of ≤ 2.5 h d^{-1}. Hauling out for extended periods of time may be possible in regions where tides have little effect on the availability of haul-out sites (Thompson 1989), but tidal amplitude in the Estuary may reach 5 m during spring tides. Consequently, haul-out sites exposed throughout the tidal cycle are perhaps rare in the Estuary, and seals might spend some time resting in waters near their haul-out sites. It was actually not uncommon during the *in situ* tracking to observe individual seals remaining motionless at the surface with their snout pointing vertically, or diving repeatedly for 7–8 min in an area 2–3 m deep, a few meters from their haul-out sites. The high frequency of disturbance by recreational boating and seal-watching observed in the Metis and Bic region during summer (V. Lesage. M.O. Hammill, and K.M. Kovacs, unpubl. data) might also reduce daily haul-out bout durations.

Harbour seals can dive to depths > 450 m (Stewart and Yochem 1994; see also Schreer and Kovacs 1997), but they are relatively shallow divers in most parts of their range, with dives rarely exceeding 100–150 m (*e.g.* Boness et al. 1994; Coltman et al. 1997; Gotthard 1998; Suryan and Harvey 1998; Tollit et al. 1998). These shallow diving habits are taken to an extreme in St Lawrence harbour seals, with some individual animals having their diving and foraging activity concentrated within the first few meters of the water column.

Such extremely shallow foraging activity is quite rare among phocids, and has complicated the description of harbour seals foraging activity in this study. In other phocids, foraging generally occurs at deeper depths or further away from haul-out sites. Thus, foraging activity is more easily definable and separated from social interactions or sleep activity near haul-out sites in these species than in Estuary harbour seals. In most species, foraging activity is often identified by the repetitive performance of dives with a particular depth profile at particular depths or locations and thus, can be measured (*e.g.* Le Bœuf et al. 1992; Schreer and Testa 1996; Bengston and Stewart 1997). In St Lawrence harbour seals, successful foraging dives occurred at all depths and during all periods of the day. Thus, the characteristics of foraging dives and measurement of foraging effort were difficult to obtain. Nevertheless, the predominance of U-shaped dives in all seals indicates that animals may be diving to the bottom during most of their dives. The large proportion of success associated with type-1 and -3 dives suggests that dives of these types may be important components of harbour seal foraging behaviour in the St Lawrence Estuary. During these dives, seals may be patrolling the bottom at minimal cost of transport speed (Davis et al. 1985), with occasional bursts that may reflect pursuit of prey (Chapter 3). A predominance of the shallow dive types (type-2, -3 and -4 dives) in several individuals caught from May–July suggests that they might be feeding on clustered prey in shallow waters. The predominance of the deeper type-1 dives in the diving records of seals caught later in the summer (post-moult juveniles) and a few yearlings caught in June could reflect bottom patrolling for cryptic or buried prey in deeper waters.

Some foraging activity was associated with all five dive types. However, it is unlikely that all dives at depths ≥ 4 m were dedicated exclusively to foraging. In addition, successful foraging dives occurred repeatedly in waters < 4 m in this study, and a great deal of foraging activity likely occurred in near-surface waters in some individuals. Diving efforts presented in this study most certainly incorporated dives dedicated to other behaviours (*cf.* type-4 dives in ***breeding*** males), and did not properly account for a portion of the foraging effort at depths < 4 m that was likely variable among individuals. For these reasons, success rates may reflect foraging effort more closely in some individuals than in others. Thus, it must be interpreted with caution. In addition, although the TDR/HTR packages represented < 1–3% of an animal's mass, the packages had a poor hydrodynamic shape and a large cross-sectional area relative to the seals (Hammill et al. 1999). They may have had a greater effect on the smaller juveniles than on the larger adults.

Nevertheless, evidence from other aspects of the diving behaviour and diet of juvenile harbour seals in the Estuary indicate that these young seals may have had lower success rates than adults when foraging and may feed on different species or in different size ranges of prey. Harbour seal yearlings in the Estuary occupy a slightly lower trophic position (Chapter 2) and have fatty acid signatures in their blubber that are different than those found in older seals (V. Lesage , S.J. Iverson, and M.O. Hammill, unpubl. data). Although relatively similar foraging tactics were observed among individuals (*i.e.* U-shaped dives with most success associated with type-1 and -3 dives), yearlings had shorter dives and thus possibly, lower diving capabilities than older animals. Lower foraging success among juveniles forces them to rely on more easily catchable, and possibly less energetically-profitable prey, compared to those sought by adults (Bowen and Harrison 1996; Le Bœuf et al. 1996; Trillmich and Horning 1997; but also see Muelbert and Bowen 1993). Predation by yearlings on different prey than adults has been reported in a few instances (*e.g.* Iverson et al. 1998). In waters surrounding Nova Scotia (Canada), herring eaten by yearlings and adults are similar in size (Bowen and Harrison 1996), but yearlings eat both pelagic and demersal prey and are therefore intermediate between the mainly pelagic-feeding pups and demersal-feeding juveniles and adults (>1 yr-old) (Bowen and Harrison 1996). In the Estuary, fish such as smelt, sand lance, capelin and herring were consumed by yearlings (see results). However, winter flounder has only been found in the stomach of the only adult specimen examined that had some food contents (a female caught in July). This energy-rich species may be more difficult to hunt than pelagic prey (Bowen and Harrison 1996). The lower success rate of post-moult juveniles may result from their deeper foraging habits, as the time and effort spent getting to and from a foraging area (*i.e.* the bottom in this case) likely increases with depth (Schreer and Kovacs 1997) as does dive duration (this study). Seals may compensate for these trends by feeding on larger prey with a higher energy density or by capturing more prey per dive.

In summary, it appears that harbour seals during the summer find both the necessary food resources and haul-out substrates within a limited geographic area in the St Lawrence Estuary. This reduces the separation between specific haul-out sites for moulting and breeding and high density foraging areas. During winter, increased movements are observed, but these may result from reduced access to preferred haul-out sites due to ice formation, from changes in prey distribution or both. At the same time, ice formation may allow access to new foraging areas by providing a stable platform for hauling out. The use of time-depth recorders with a better depth resolution to describe shallow diving behaviour in more detail, combined with modifications to the stomach temperature sensors to prolong their retention (Wilson et al. 1998) would increase our understanding of foraging activity in this small phocid.

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Table 4.1. Deployment period and characteristics of St Lawrence Estuary harbour seals instrumented with time-depth recorders (TDR), stomach temperature data loggers (HTR) or satellite-linked time-depth recorders (SLTDR) during 1994–98. Seals were captured at Metis (ME), Bic (BI) or Ile Blanche (IB).

Seal No.	Region	Mass (kg)	Sex	Age (yr)	Package deployed	Period of deployment	Duty cycle (on/off)	(SL)TDR resolution (m)	Sampling interval (s)	record duration (SL)TDR (d)	record duration Stomach T° (hr)	No. of dives
17905	ME	78	m	5	SLTDR	9 Sept. '94 - 1 July '95	1/1	2	10	295	-	14943[c]
17906	ME	73	m	5	SLTDR	9 Sept. '94 - 30 Apr. '95	1/1	2	10	233	-	24296[c]
17904	BI	49.5	m	3	SLTDR	20 Aug. - 9 Dec. '95	1/1	2	10	111	-	26767
1851	ME	83	m	6	SLTDR	27 Oct. '95 (failed)	1/1	2	10	0	-	0
1854	ME	82	m	6	SLTDR	25 Sept. '95 - 23 May '96	1/1	2	10	241	-	53723
17908	ME	80.5	m	8	SLTDR	18 Sept. '95 - 12 May '96	1/1	2	10	237	-	52438
17903	IB	47	m	2	SLTDR	28 Sept. '97 - 31 May '98	1/2	2	10	245	-	12387
1855	ME	76	f	6	SLTDR	16 Sept. '95 - 28 May '96	1/1	2	10	255	-	63551
3197	BI	75.5	m	5	TDR	13 May - 15 June '95	-	2	10	33	-	8320
3199	BI	36	m	1	TDR/HTR	20 Aug. - 6 Sept. '96	-	1	5	15.5	73	8424
3860	BI	39	m	1	TDR/HTR	20 - 28 Aug. '96	-	1	5	7.5	47	3416
4615	BI	102.5	m	10	TDR/HTR	10 - 24 June '96	-	1	5	13.5	54	6344
4618	BI	100	m	8	TDR/HTR	11 - 27 June '96	-	1	5	15.5	113	7530
4619	BI	69	f	10	TDR/HTR	12 - 28 June '96	-	1	5	16	88	9244
4601	ME	83	m	7	TDR/HTR	7 June - 12 July '96	-	1	5	0	63	0
4612	ME	83.5	m	6	TDR/HTR	7 June - ... '96 (lost)	-	1	5	-	-	-
2696	BI	38.5	f	1	TDR/HTR	29 May - 15 June '97	-	2	5	16.5	0	8280
2699	BI	96.5[a]	f	6	TDR/HTR	3 - 21 June '97	-	1	5	17[b]	576	9215
2700	BI	35.5	f	1	TDR/HTR	3 - 22 June '97	-	1	5	19	34	11750
3502	ME	38	f	1	TDR/HTR	18 June - 5 July '97	-	1	5	16.5[b]	52	10701
3508	ME	38.5	m	1	TDR/HTR	8 - 17 July '97	-	1	5	9	34	4086
3526	BI	33.5	f	1	TDR/HTR	9 - 26 Sept. '97	-	1	5	16.5[b]	49	7250
3531	IB	59.5	m	2	TDR/HTR	24 Sept. - 11 Oct. '97	-	2	5	17	1193	4165

[a] pregnant

[b] velocity meter failed on 18 September (ID 3526), on 28 June (ID 3502), or during the entire deployment period (ID 2699)

[c] total n of dives in the 1994 seals were calculed using only depth histograms and only dives > 4 m, and are therefore underestimations

Table 4.2. Characteristics (mean ± 1 SD) of St Lawrence harbour seal dives classified into five distinct groups using multivariate data analyses (adapted from Chapter 3).

Characteristics	Mean values				
	Type-1	Type-2	Type-3	Type-4	Type-5
					
max. depth (m)	19.6 ± 5.8	5.8 ± 2.8	7.8 ± 2.7	7.9 ± 2.7	12.2 ± 7.2
duration (s)	135.7 ± 37.5	40.1 ± 29.8	122.4 ± 50.9	142.3 ± 52.9	167.9 ± 80.1
bottom time (s)	92.5 ± 34.0	5.5 ± 6.8	85.8 ± 51.0	93.0 ± 48.9	126.6 ± 83.6
bottom time / duration	0.67 ± 0.15	0.15 ± 0.17	0.67 ± 0.22	0.64 ± 0.20	0.72 ± 0.18
bottom time / max. depth	4.92 ± 1.98	0.91 ± 1.17	11.48 ± 7.11	12.42 ± 7.07	13.80 ± 12.2
max. depth / duration	0.15 ± 0.05	0.21 ± 0.15	0.07 ± 0.04	0.06 ± 0.03	0.08 ± 0.05
median swim speed (bottom) (m/s)	1.00 ± 0.47	0.47 ± 0.56	1.21 ± 0.44	0.68 ± 0.40	0.15 ± 0.25
max. swim speed (bottom) (m/s)	2.16 ± 0.62	0.88 ± 0.71	1.87 ± 0.57	1.28 ± 0.50	0.78 ± 0.65
x ascent rate / x descent rate	1.13 ± 0.46	1.25 ± 0.93	2.06 ± 1.69	0.41 ± 0.17	1.44 ± 0.89
x descent rate / x ascent rate	1.01 ± 0.40	1.34 ± 1.01	0.69 ± 0.33	3.06 ± 1.87	0.89 ± 0.42
x ascent swim speed (m/s)	1.20 ± 0.34	0.71 ± 0.46	1.14 ± 0.46	0.74 ± 0.41	0.80 ± 0.34
x descent swim speed (m/s)	1.25 ± 0.38	0.76 ± 0.47	1.20 ± 0.51	0.85 ± 0.33	0.74 ± 0.36
angle of ascent (degree)	70.0 ± 27.8	59.0 ± 33.6	48.0 ± 29.3	31.2 ± 26.8	75.9 ± 24.1
angle of descent (degree)	63.6 ± 29.8	59.8 ± 34.4	32.1 ± 28.9	64.0 ± 28.6	71.8 ± 27.4

Table 4.3. Haul-out activity of St Lawrence harbour seals equipped with time-depth-recorders.

			Haul-out activity				
Description	Seal No.	*N* of deployment days*	*N* of days	*N* of days in %	Daily median duration (h)	Mean *n* of bouts/day	Bout median duration (h)
Juvenile (pre-moult)	2696	16	12	75	1.9	1.2	1.6
	3502	16	14	88	2.5	1.6	1.4
	2700	18	18	100	5.1	1.4	3.3
	3508	8	8	100	7.6	1.4	4.2
Juvenile (post-moult)	3526	16	10	63	1.9	1.6	0.7
	3199	16	9	56	2.3	1.6	1.0
	3531	16	13	81	3.6	1.4	1.4
	3860	7	7	100	8.8	1.6	3.4
Adult male (pre-breeding)	3197	32	29	91	6.3	1.8	1.9
Adult male (breeding)	4615	13	4	31	2.0	2.0	0.6
	4618	15	10	67	3.4	1.9	2.3
Adult female (lactating)	4619	15	14	93	3.2	1.8	1.9
Adult female (pregnant)	2699	17	14	82	3.7	2.6	0.8

* Excluding the first and last day of deployment

Table 4.4. Logistic regression analysis of tidal and environmental conditions *vs* haul-out behaviour of St Lawrence harbour seals (*n* obs. with seals hauled out / not hauled out = 183 / 817). The odds ratio compares the probability of an event occurring with the probability of it not occurring. For example, an odds ratio of 0.34 for tide height means that seals sampled at high tide, or long after or before low tide are 34% as likely to be hauled out than seals sampled shortly before or after low tide, or when tide height was low. The estimated coefficients (β_0, β_1, ..., β_n) are positive when the predicted probability of an event increases, and negative when the probability decreases.

Factor	ß	Odds ratio	*P*	Pseudo R^2
Intercept	-2.0262	-	-	-
Tide height	-1.0838	0.34	< 0.001	0.11
Tide amplitude	-0.5113	0.60	< 0.001	0.12
Haul-out during night (0) *vs* day (1) hours	0.5153	1.67	< 0.001	0.14
Wind direction (0–4 : dominant through opposite direction)	-0.3120	0.73	< 0.001	0.15
Time elapsed since last haul-out period	0.1866	1.21	< 0.05	0.16

Table 4.5. Descriptive statistics of St Lawrence harbour seals dive depth and duration, obtained directly from time-depth-recorder data or from summary records transmitted through the NOAA satellites.

Group	Season	Seal No.	% of dives ≤ 4 m[a]	Dive depth (m)		Dive duration (min)	
				Maximum	Percentile 95[b]	Maximum	Percentile 95[b]
Adult female	Pregnancy + lactation	2699	93	20	5	14.4	3.1
	Lactation	4619	86	23	7	11.3	3.4
	Post-moult + winter	1855	-	100	20–40	> 30	2–5
Juvenile	Pre-moult	3502	80	44	26	9.6	3.3
		3508	69	51	24	8.3	3.1
		2700	75	23	13	6.9	2.7
		2696	33	48	20	13.1	4.3
	Post-moult	3199	36	41	21	15.2	2.8
		3526	18	62	23	13.3	2.9
		3531	15	34	24	9.8	4.2
		3860	41	75	31	7.8	3.3
	Post-moult + winter	17904	-	72	40–60	> 30	2–5
	Post-moult + winter	17903	-	124	20–40	-[c]	-[c]
Adult male	Pre-breeding	3197	46	46	18	14.7	3.7
	Breeding	4615	42	31	12	10.3	4.4
		4618	27	22	14	13.7	4.1
	Post-moult + winter	17905	-	120	20–40	-[c]	-[c]
		17906	-	108	20–40	-[c]	-[c]
		17908	-	136	20–40	> 30	2–5
		1854	-	136	20–40	> 30	2–5

[a] depending on TDR resolution, dives ≤ 4 m comprise dives at 2 m, 3 m and 4 m (1-m resolution), or only dives at 4 m (2-m resolution); values are therefore, underestimation in animals with 2-m resolution TDRs

[b] *i.e.* 95% of dives were ≤ to this value

[c] not calculated since dive duration histograms included surface time

Table 4.6. St Lawrence harbour seals median diving depth and daily diving effort in hours (and % of overall diving effort) calculated excluding incomplete days, *i.e.* the first and last day of deployment. Catch per unit diving effort (C.P.U.E.) is calculated over the period of stomach temperature sensor retention.

Group	Seal	Daily diving effort in hrs (in %)			Diving	C.P.U.E.
	No.	Overall	Shallow	Deep	depth (m)	(n of min/capture)
Adult female (pregnant)	2699	1.3	1.3 (100)	0.0 (0)	2	37.5
Adult female (lactating)	4619	3.0	0.8 (27)	2.2 (73)	5	24.4
Juvenile (pre-moult)	3502	5.0	0.4 (8)	4.6 (92)	6	42.4
	3508	4.9	0.3 (6)	4.6 (94)	9	240.8
	2700	5.2	1.4 (27)	3.8 (73)	4	34.5
	2696	12.6	0.0 (0)	12.6 (100)	8	-
Juvenile (post-moult)	3199	12.7	0.1 (1)	12.6 (99)	16	54.6
	3526	12.5	0.0 (0)	12.5 (100)	19	59.4
	3531	9.0	0.0 (0)	9.0 (100)	16	53.7
	3860	9.6	0.0 (0)	9.6 (100)	11	57.4
Adult male (pre-breeding)	3197	6.6	0.1 (2)	6.5 (98)	6	-
Adult male (breeding)	4615	14.8	0.2 (1)	14.6 (99)	8	45.1
	4618	15.6	0.0 (0)	15.6 (100)	7	43.7

Table 4.7. Distribution of harbour seals successful foraging dives as identified from stomach temperature variation among the different periods of the day and dive types.

Group	Seal No.	*N* of dives	Distribution of successful foraging dives (% of total *n*)									
			Period				Type*					
			Dawn	Day	Dusk	Night	< 4 m	1	2	3	4	5
Adult female (pregnant)	2699	189	23	11	14	52	72	-	-	-	-	-
Adult female (lactating)	4619	58	19	5	0	76	62	2	2	16	5	3
Juvenile (pre-moult)	3502	25	24	20	12	44	60	0	20	8	0	12
	3508	2	50	0	0	50	50	0	50	0	0	0
	2700	30	30	0	53	17	20	10	0	53	3	3
	2696	-	-	-	-	-	-	-	-	-	-	-
Juvenile (post-moult)	3199	22	18	45	36	0	28	55	0	5	0	5
	3526	24	17	50	33	0	21	29	12	13	13	13
	3531	194	27	17	40	16	1	36	14	10	4	35
	3860	30	37	47	17	0	3	60	3	20	3	7
Adult male (pre-breeding)	3197	-	-	-	-	-	-	-	-	-	-	-
Adult male (breeding)	4615	30	20	7	40	33	46	7	3	13	3	20
	4618	91	34	19	19	29	22	34	11	29	1	2

* The sum of the different categories may not be 100% since dives ≥ 4 m that couldn't be classified are not presented

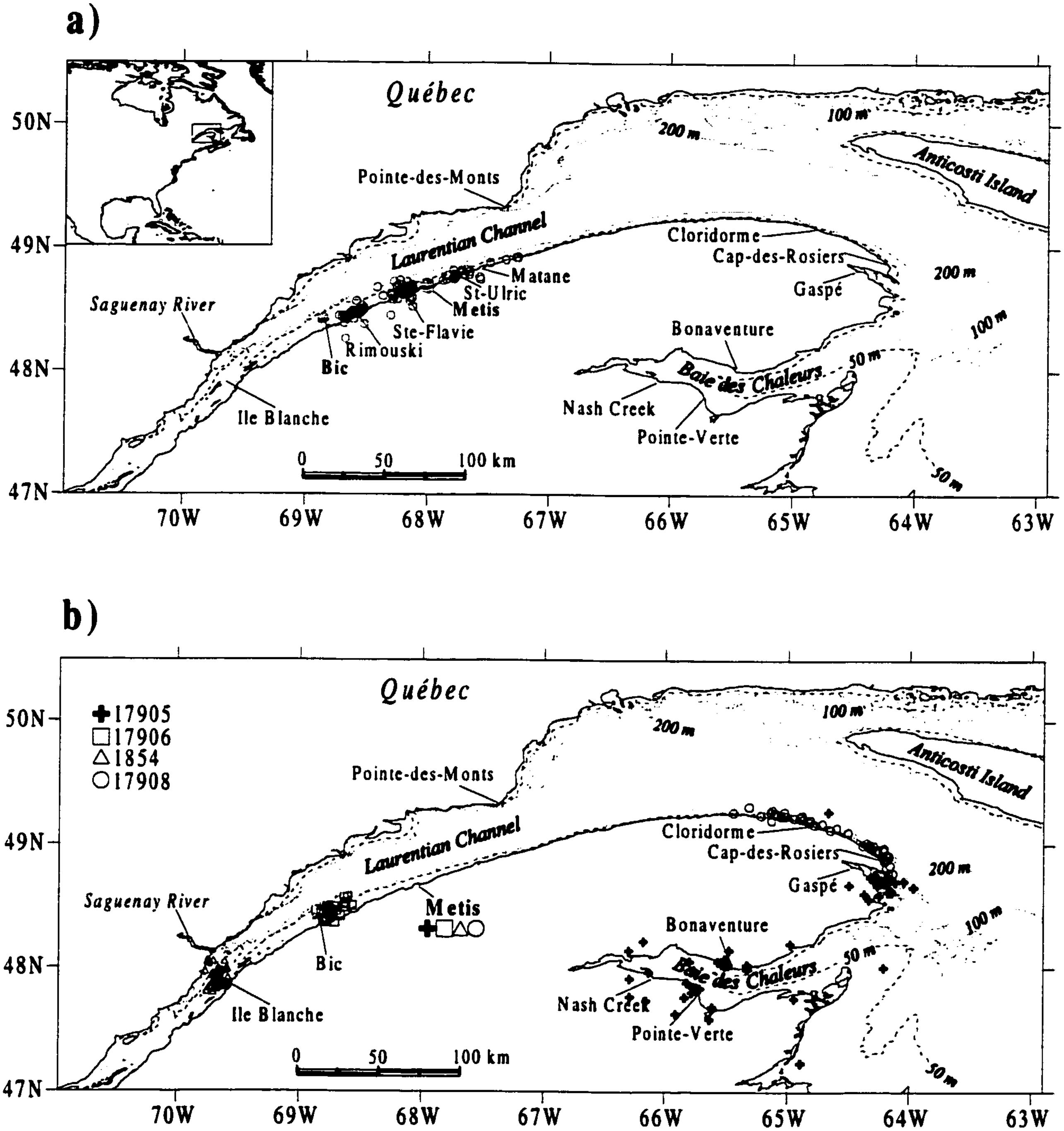

Figure 4.1. Movements of St Lawrence harbour seals documented using satellite telemetry. 1a) Capture sites (shaded circles) and regions regularly visited (hallow circles) by harbour seals during summer haul-out. The latter correspond to positions of quality 0-3 obtained from 4 individual seals. 1b) Wintering areas used by 4 adult seals captured near Metis.

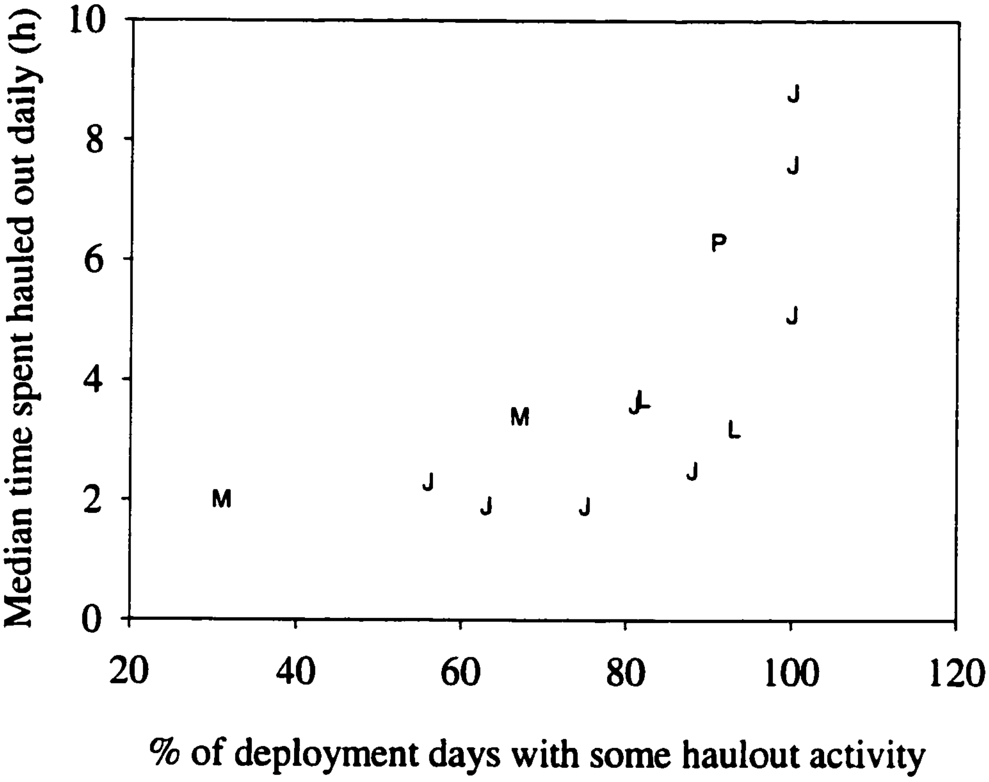

Figure 4.2. Relationships between the median time spent hauled out daily and the proportion of deployment days with some haul-out activity in St Lawrence harbour seals. Spearman's rank correlation $r_s = 0.80$; P = 0.001. Symbols represent (M) breeding males, (P) pre-breeding males, (L) lactating or pregnant females, and (J) juveniles.

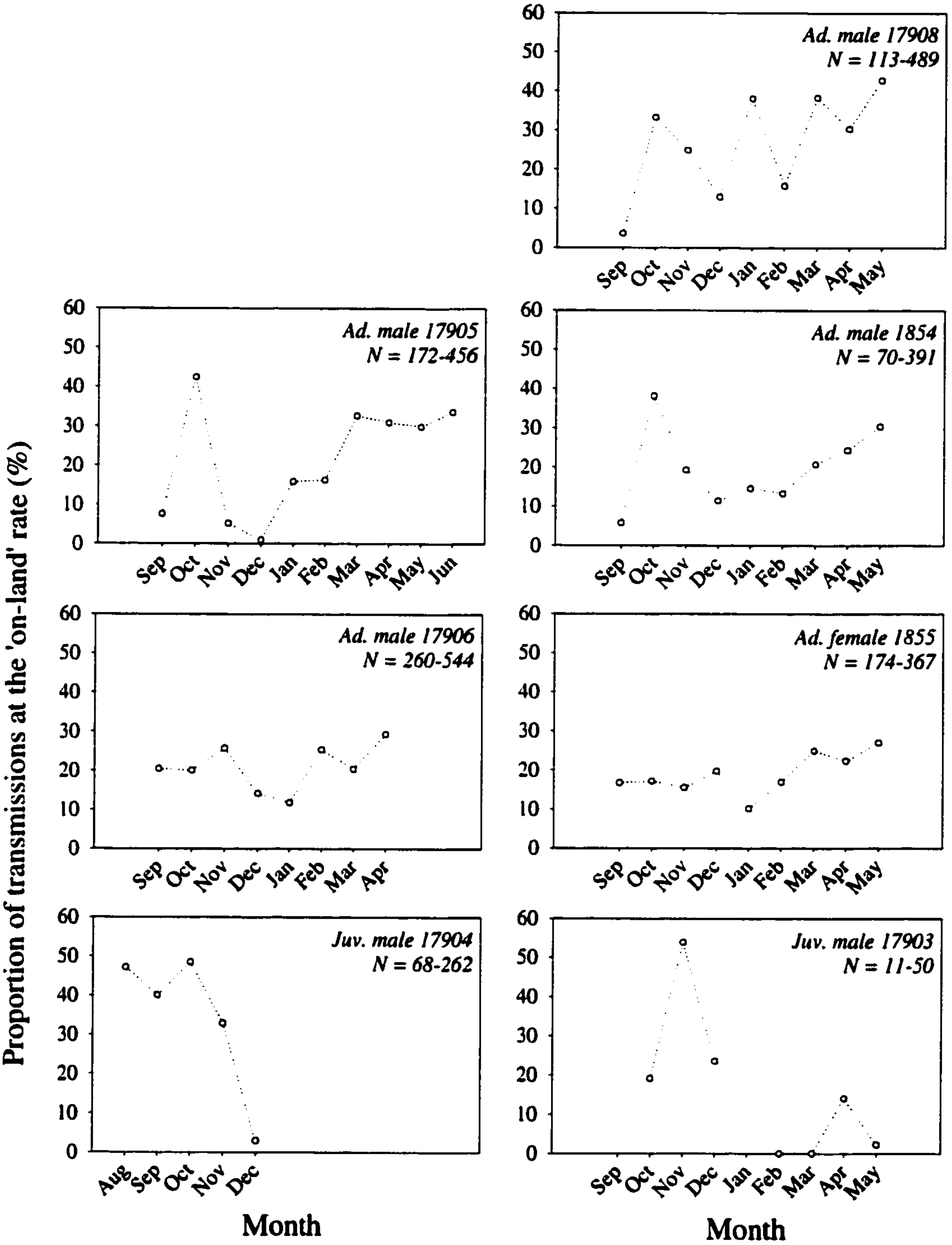

Figure 4.3. Seasonal variation in the St Lawrence harbour seal haul-out activity, as described by the monthly proportion of transmissions made at the 'on-land' rate. Months associated with < 10 transmissions were eliminated. The ranges for the number of transmissions received each month are indicated on each plot.

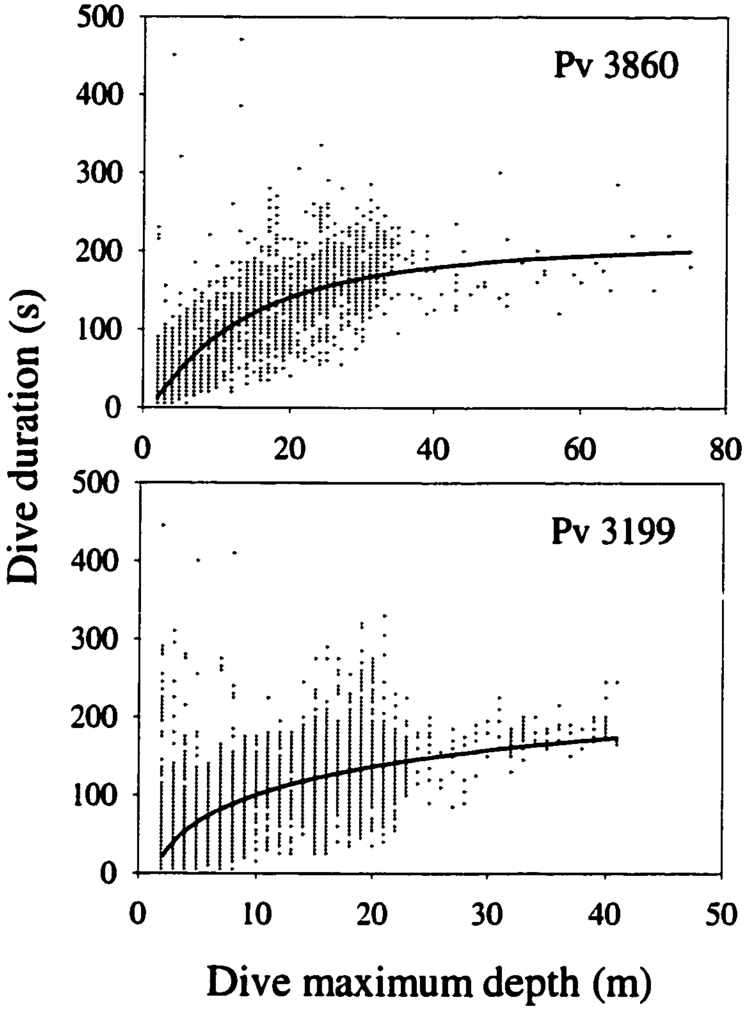

Figure 4.4. Relationships between dive's maximum depth and duration in two harbour seals from the St Lawrence Estuary.

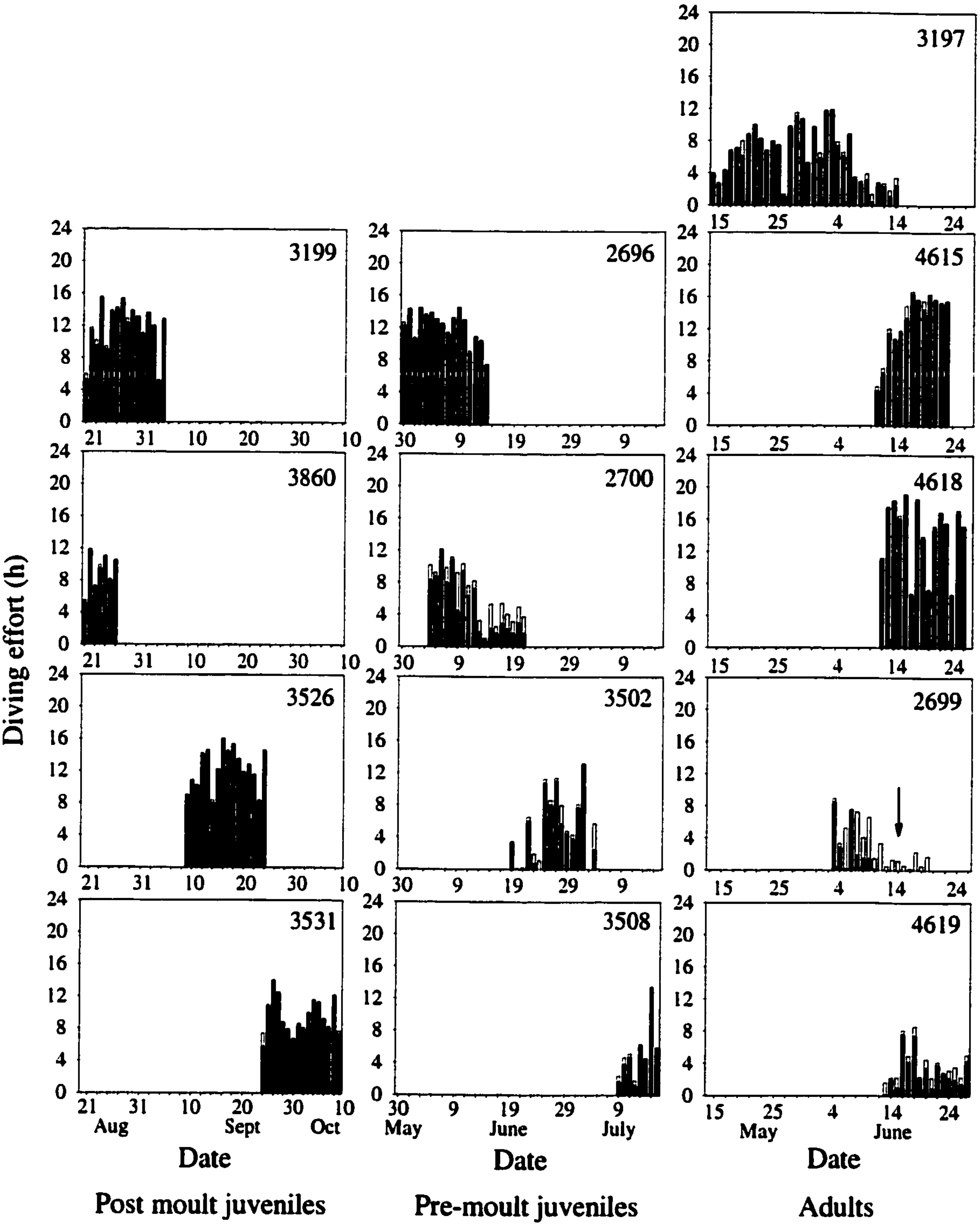

Figure 4.5. Variation in *deeper* (dark bars) and *4-m* (clear bars) diving effort through TDR deployment period. An arrow indicates the approximate date of birth of female no. 2699's pup.

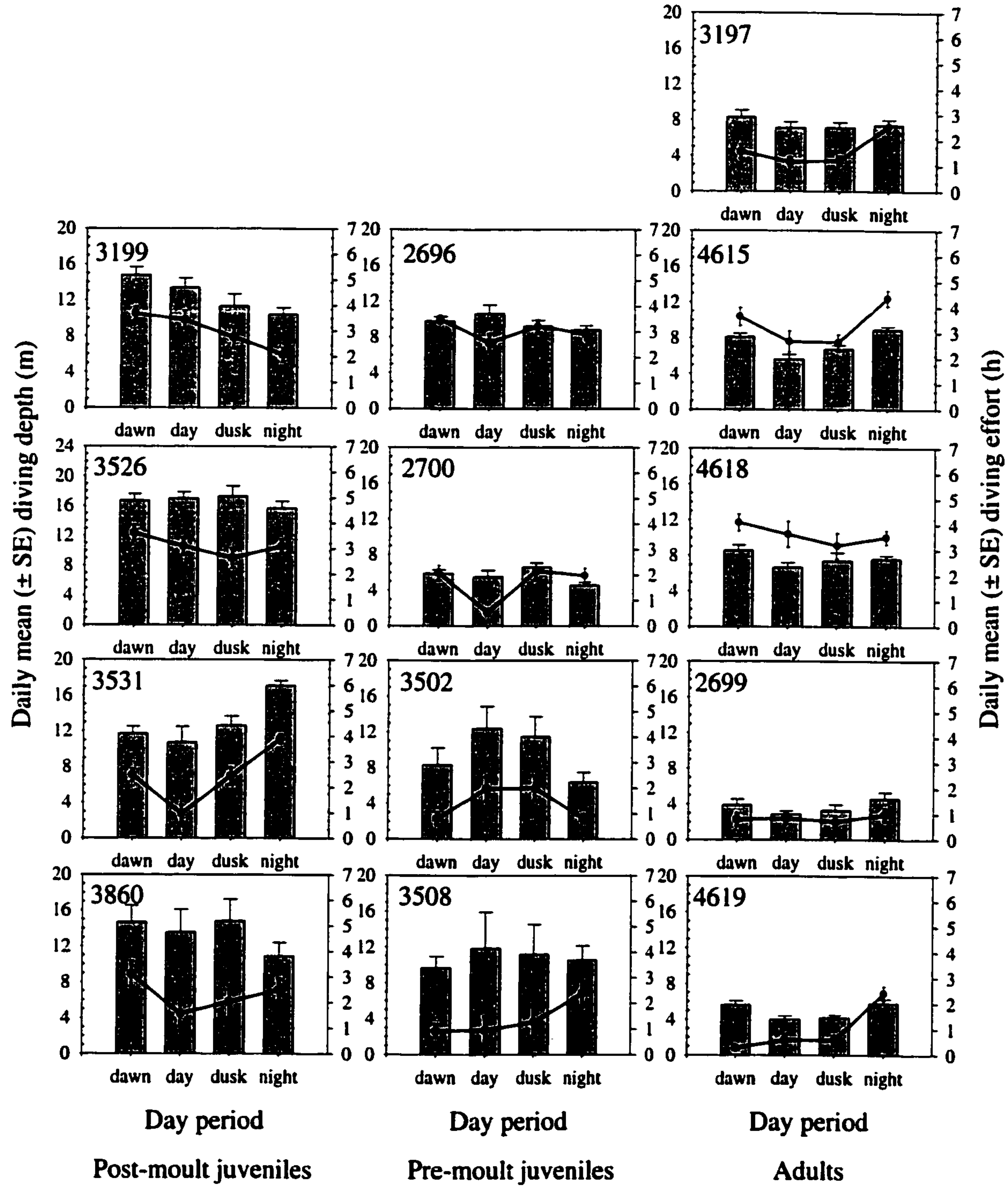

Figure 4.6. Diel variation in mean diving depth (bars) and effort (curve) in St Lawrence harbour seals equipped with time-depth-recorders.

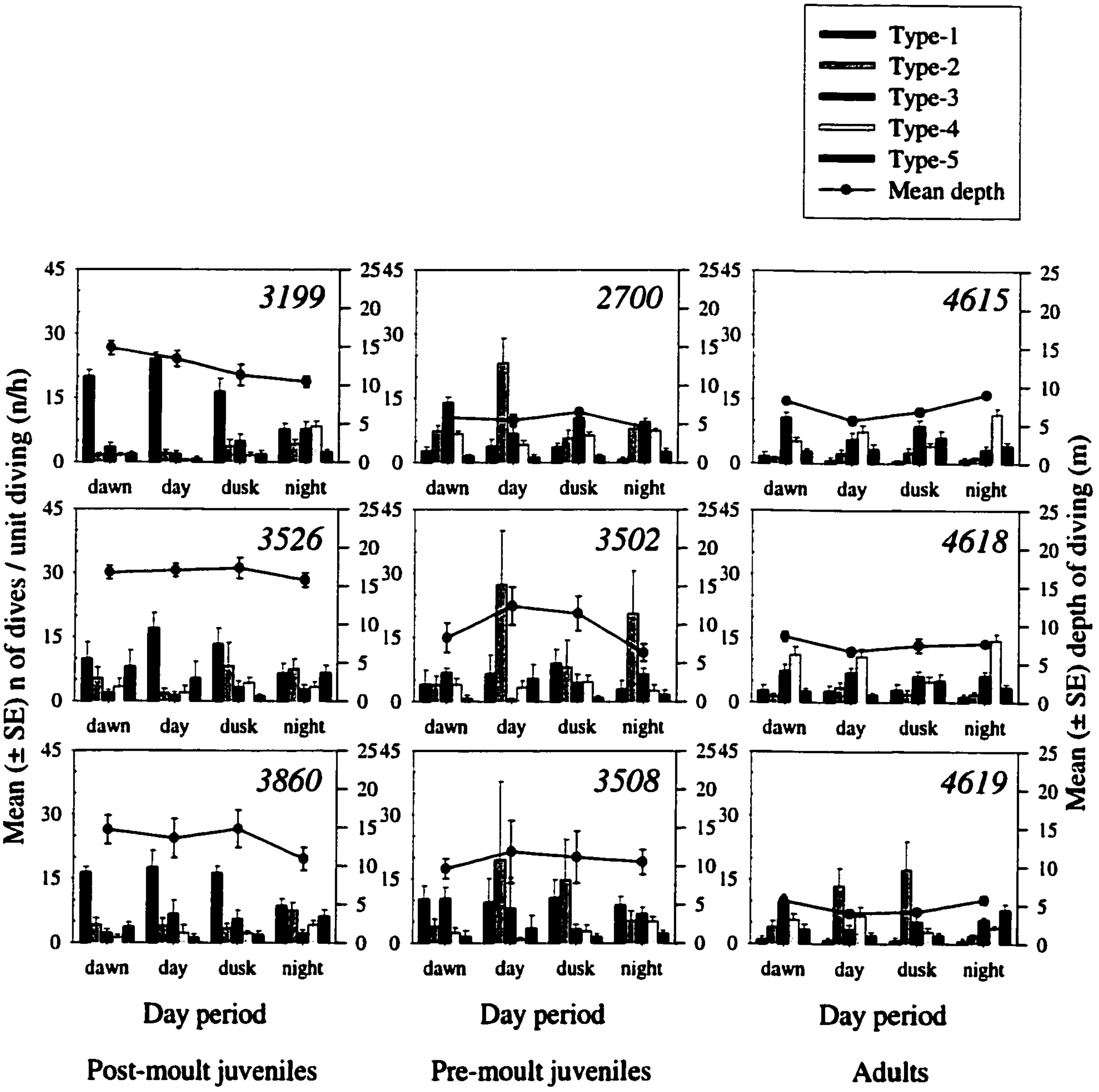

Figure 4.7. Diel variation in the mean occurrence of different dive types (bars) and mean depth of diving (curve) in St Lawrence harbour seals equipped with time-depth-recorders.

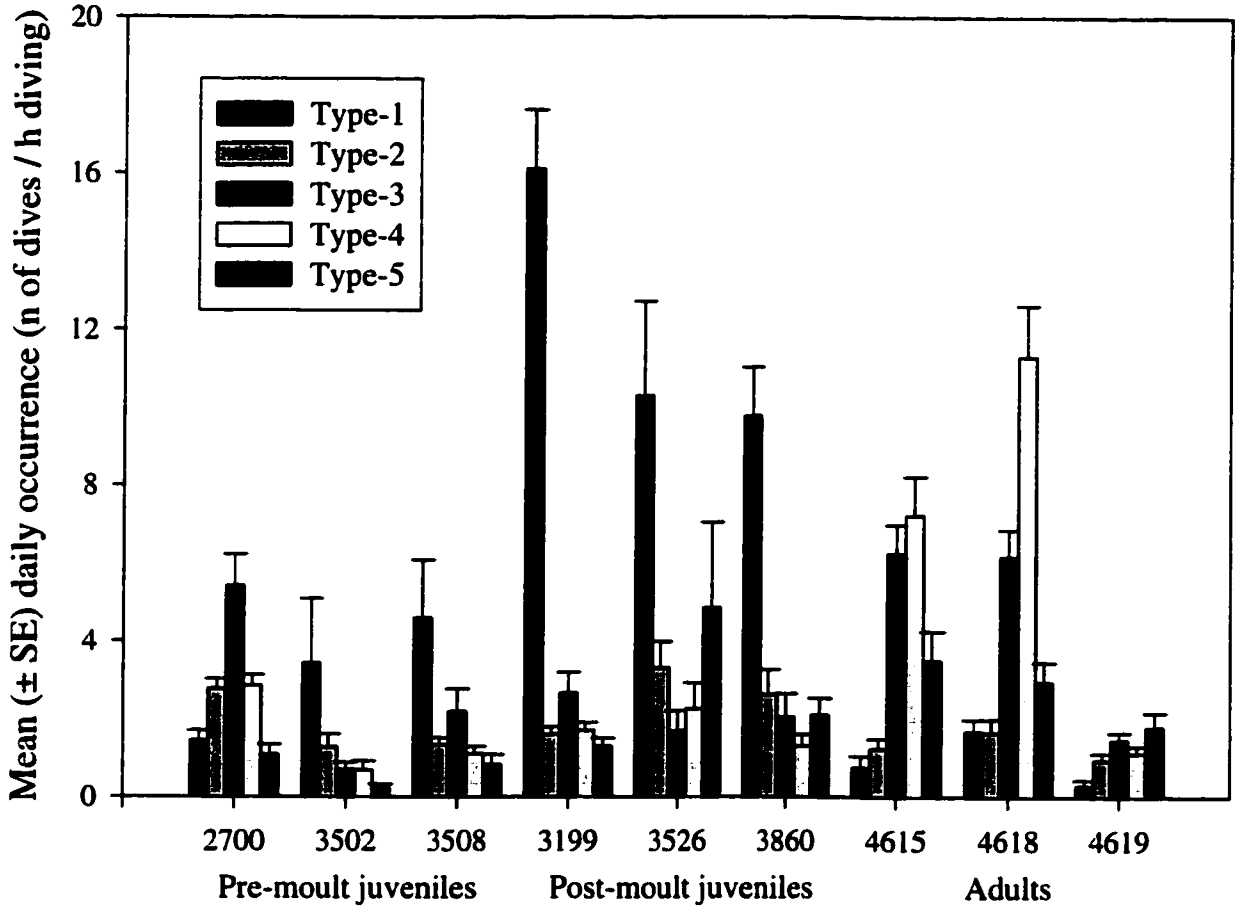

Figure 4.8. Mean occurrence of different dive types among St Lawrence harbour seals (*n* = 9).

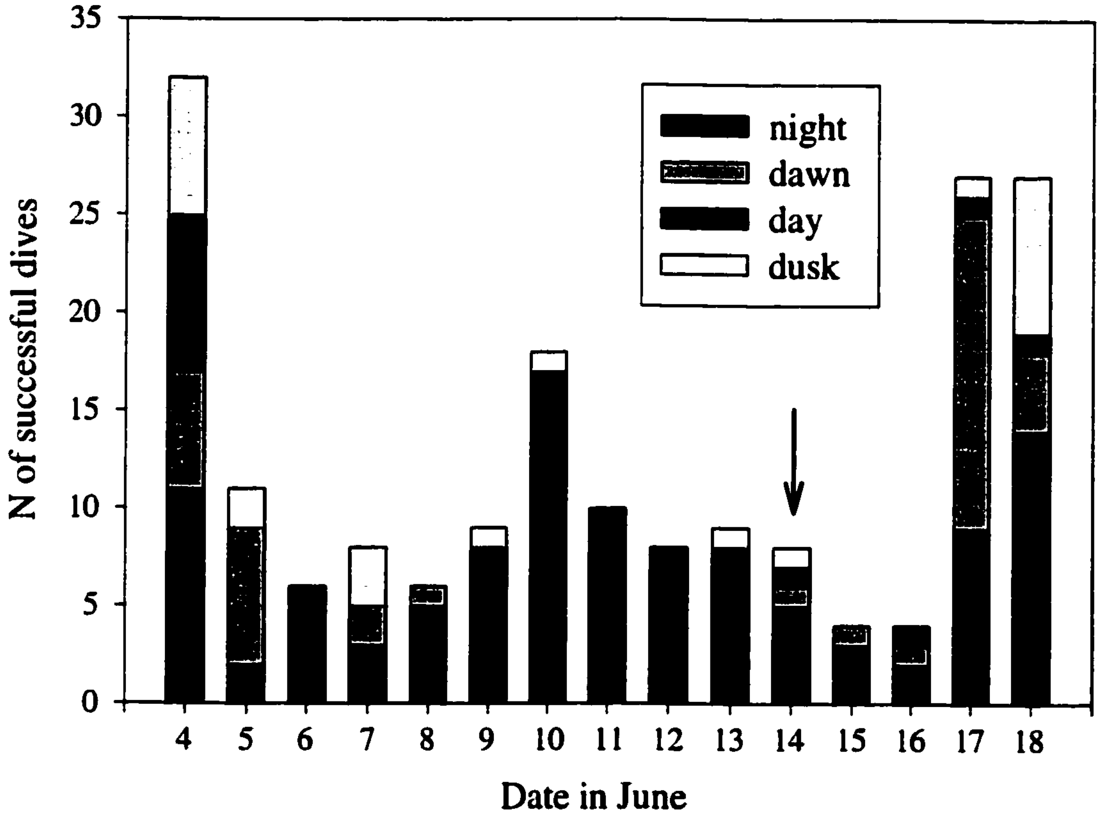

Figure 4.9. Daily number of dives associated with foraging success that were recorded from a pregnant female (no. 2699) which gave birth during the deployment period. An arrow indicates approximate date of birth.

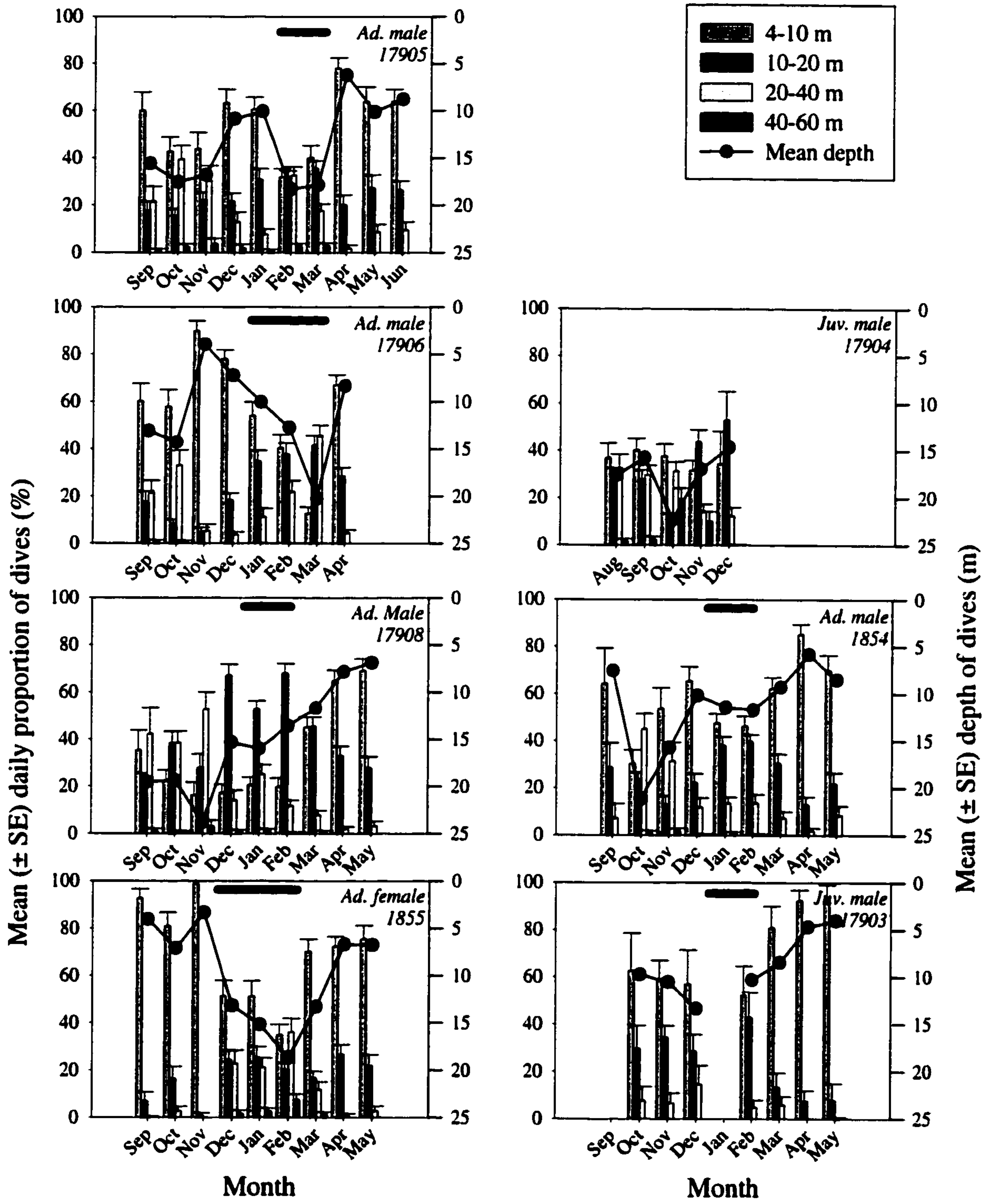

Figure 4.10. Seasonal variation in the mean depth of dives and in the relative occurrence of dives at different depths in St Lawrence harbour seals. The horizontal bar in the upper plots indicates the presence of ice at the seal's location. Depths > 60 m contained only a tiny proportion of dives, and are not presented.

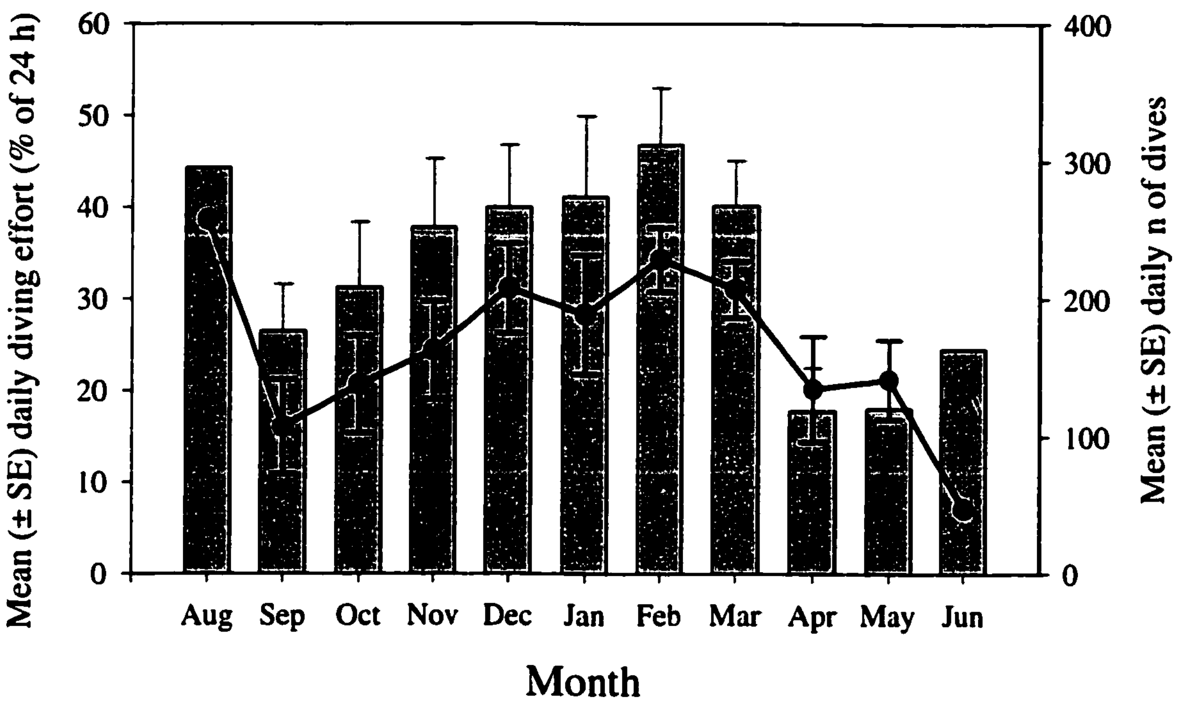

Figure 4.11. Seasonal variation in St Lawrence harbour seals mean daily diving activity, as described from the daily mean proportion of time spent diving (bars) and number of dives (curve).

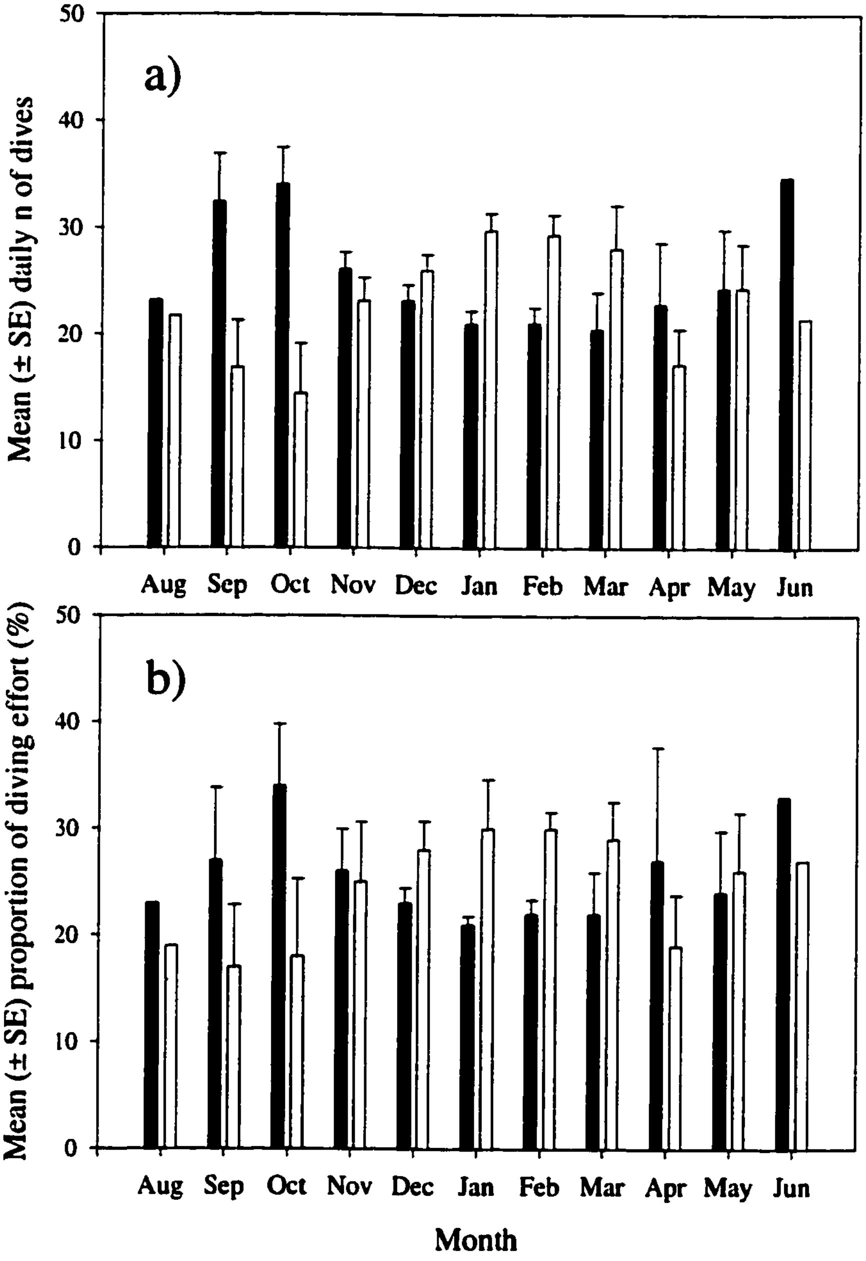

Figure 4.12. Seasonal variation in the distribution of St Lawrence harbour seals daily a) diving rate and b) diving time between the night (dark bars) and day periods (clear bars).

CHAPTER 5

General Conclusions

In this thesis, the foraging ecology of the harbour seals was investigated in order to gain some insights into their use of the St Lawrence River Estuary and evaluate the potential for overlap in resource utilisation with some other marine mammals found in the same area. The trophic position of harbour seals was examined relative to that of other marine mammal species and other components of the Estuary and Gulf communities. The diving behaviour of harbour seals was analysed and classified into different types of activity and the characteristics of foraging dives were described. The spatial dimensions of harbour seal habitat, including preferred foraging areas, were characterised and seasonal variation in their distribution was documented. Finally, variation in their diving and foraging activity patterns relative to season, age class and sex were examined.

The comparison of $\delta^{13}C$ signatures in short-term *vs* longer-term integrators of diets in harbour seals caught in late spring (Chapter 2) and the examination of seasonal movements using satellite telemetry (Chapter 4) provided little evidence for substantial movements of harbour seals outside the limits of the Lower Estuary during winter. These observations support earlier suggestions that this species is relatively sedentary (Fisher 1952; Boulva 1971; Fay 1974; Bigg 1981; Thompson et al. 1998). However, migration distances of 65–520 km were observed for some seals in this study (4 of 7 seals). These distances are at the upper limit of those previously reported for adults of this species (reviewed in Thompson 1993; Frost et al. 1998) and indicate a certain capacity among adult harbour seals for migrating over relatively large distances. However, unlike most other areas where harbour seals have been studied, ice cover in the study area may be extensive. The presence of a heavy cover of broken ice in the Estuary and solid fast-ice in bays during winter may contribute to some extent to the amplitude of the movements in this region (Chapter 4).

The use of multiple tissues and multiple stable isotopes demonstrated that harbour seals and several other marine mammal species occupy top trophic positions in the Estuary ecosystem and that these species are largely piscivorous (Chapter 2), a finding that was not totally unexpected (*e.g.* Laws 1985; Bowen 1997; Hobson et al. 1997; Tollit et al. 1997; Burns et al. 1998). Although most age or sex groups of marine mammals were at the top of the food web, some variation was observed in trophic positions both between species, with harbour seals and hooded seals occupying the highest trophic positions, and within species according to body size.

Two groups of marine mammals were identified as potentially overlapping with harbour seals in their food resource utilisation (Chapter 2). Hooded seals occupy trophic positions very similar to those of harbour seals. However, potential competition between these two species is likely minimised by local differences in their distribution and specific feeding habitats (Chapter 2). Hooded seals move into the Estuary only during winter and tend to remain in offshore areas and likely feed at deeper depths. Juvenile grey seals are found in the same areas as harbour seals and are very similar to harbour seals with respect to body size. However, juvenile grey seals and adult harbour seals were shown to differ in their trophic positions. In addition, food partitioning among these groups was confirmed from satellite telemetry where juvenile grey seals dove consistently to deeper depths than adult harbour seals while inhabiting the same area (Lesage et al. 1995).

Stable nitrogen isotope analyses showed that males of several species of marine mammals occupied higher trophic positions than females and that the difference between sexes increases with age (Chapter 2). Such variation between sexes is often thought to result from differences in diving capabilities that are linked to their different body sizes (*e.g.* Schreer and Kovacs 1997). No differences were apparent between male and female harbour seals, possibly because of the limited degree of body size dimorphism in this species.

A certain degree of life-history omnivory was observed in harbour seals and harp seals, with yearlings eating proportionally more invertebrate prey or smaller fish than older animals (Chapter 2). This may result from less developed diving and foraging skills (*e.g.* Boulva and McLaren 1979; Bowen and Harrison 1996; Burns et al. 1998). Harbour seals were, to a large extent, piscivorous by the age of one year and fed on capelin, sand lance, herring and rainbow smelts (Chapter 2 and 4). However, it was shown in Chapter 4 that some yearlings captured less prey per diving hour than adults. Dives performed by yearling harbour seals were also on average, shorter than those of animals of age 2 + (Chapter 4), indicating that their diving capabilities were probably lower than those of older animals (Kooyman 1989; Boyd and Croxall 1996). Yearlings may target fish prey from different species, or from similar species but of smaller size than those eaten by older seals (Bowen and Harrison 1996; Burns et al. 1998). However, a comparison of prey types and sizes between these groups was not possible within the framework of this study, given the small sample sizes for adult animals.

Further insight into harbour seal foraging behaviour and possible diet was gained from classifying their diving records using multivariate statistical analyses, namely principal components, hierarchical and non-hierarchical cluster analyses (Chapter 3). This method proved to be quite effective in classifying dives into distinct groups based on their depth and swim speed characteristics. Combined analyses were slightly more effective than when a non-hierarchical K-means cluster analysis was used alone (Schreer and Testa 1995; 1996; Schreer et al. 1998). The use of swim speeds in addition to dive depth profiles permitted the identification of an additional dive type that would have gone undetected if only depth data had been used (Schreer 1997). The sequence of multivariate statistical analyses classified harbour seals diving behaviour at depths ≥ 4 m into 5 types, of which 4 were U-shaped and one was V-shaped. The presence of some dives associated with drops in stomach temperature in each of these dive types indicated that all five types were associated, to some extent, with foraging (Chapter 3).

Harbour seals routinely dive to depths > 75–100 m in other regions (*i.e.* Bjørge et al. 1995; Gotthardt 1998). However, they were shown to be quite shallow divers in the Estuary, with 95% of their dives occurring at depths less than 35 m (Chapter 3 and 4). The most common form of foraging in the Estuary appears to consist of diving to the bottom and then searching ahead and above for potential prey. This conclusion is based on: the shallow depths of their dives; the U-shaped form of most dives; the similarity of depths attained among successive dives; and the large proportion of success associated with dives where swim speeds during bottom time were near the minimum cost of transport speed (Davis et al. 1985), with bursts of faster swimming (Chapter 3).

Satellite telemetry and *in situ* tracking of individuals permitted the identification of some areas, presumed to be foraging areas, that were preferentially used by harbour seals while they were away from their haul-out sites (Chapter 4). As expected from their shallow diving habits and the fish species found in their stomachs (Chapter 3 and 4), these areas were usually coastal and often corresponded to shallow bays or river mouths. These areas usually had waters < 50 m deep and were in relatively close proximity to haul-out sites (< 45 km).

Diving activity was more intensive and occurred at shallower depths at night (~ 8 m) than during the day (~ 20 m) in most seals (Chapter 3 and 4). This behaviour may be related to their foraging on vertically migrating prey (*e.g.* Le Bœuf et al. 1988; Hindell et al. 1991; Bengston and Stewart 1992). Capelin spawning on beaches in June (Fisheries and Oceans Canada 1995), capelin and herring clustering in shallow, near-shore areas (S. Bérubé, Fisheries and Oceans Canada, Mont-Joli, QC, unpubl. data) and rainbow smelt clustering near river mouths (Andersen and Gagnon 1980) are among the prey identified from stomach contents (Chapter 3 and 4) which harbour seals may be seeking during twilight and night.

Age and reproductive status were shown to affect diving activity patterns of harbour seals (Chapter 4). Satellite telemetry indicated that diving activities increased and haul-out activity decreased outside the breeding and moulting periods. Among juveniles, diving activity progressively declined as the onset of moulting approached and hair shedding began, and increased following the moult to levels higher than those preceding the moult (Pitcher 1986; Thompson et al. 1989; Watts 1996). After moulting, juveniles dove to deeper depths than animals caught earlier in the year. This might have resulted from changes in the availability of prey or a need for more energetically rewarding prey (Chapter 4). Diving activity of adult females decreased with the onset of lactation, which was not unexpected (Boness et al. 1994; Thompson et al. 1994). However, lactating females somewhat unexpectedly (Boness et al. 1994; Thompson et al. 1994) continued feeding during early lactation (Chapter 4). Foraging occurred mainly at night, in very shallow water (< 5–6 m) and may have been focussed on spawning capelin in bays 1–6 km away from haul-out sites. Finally, adult males, whose diving activities were spread uniformly throughout the day before the breeding season, became more active nocturnally during the breeding season. As expected, breeding males continued feeding during the pre-mating period (Reilly and Fedak 1991; Walker and Bowen 1993a; Temple 1994; Coltman et al. 1997), *i.e.* when underwater display areas are being established and oestrus females are still not available (Thompson et al. 1989; Walker and Bowen 1993b; Temple 1994;

Coltman et al. 1997; Van Parijs et al. 1997). Adult males maintained a high rate of diving activity during the mating season. A large proportion of their dives were shallow dives with slow bottom swimming speeds and ascent rates (type-4 dives). These dives were suspected to be dedicated at advertising to females (Chapter 4).

Harbour seals in the Estuary, as in several other regions where tidal amplitudes are relatively large, showed a clear preference for hauling out during the daytime low tide (*e.g.* Pauli and Terhune 1987; Thompson et al. 1989; Roen and Bjørge 1995; Watts 1996). Breeding males and most post-moult and pre-moult juveniles hauled out according to this schedule (Chapter 4). However, adult females that were nursing pups and pre-breeding adult males hauled out both during the night and day low tides. As expected, haul-out frequency was high in lactating females which usually hauled out several times a day (Godsell 1988; Thompson et al. 1989; 1994). Haul-out frequency declined during the breeding season in adult males (Walker and Bowen 1993b; Temple 1994; Bjørge et al. 1995; Van Parijs et al. 1997) and increased during the moult in juveniles (Thompson et al. 1989; Watts 1996). A juvenile that was shedding its fur hauled out for extended periods during daytime (up to 10 consecutive h), independently of the tide cycle.

One unusual finding relative to harbour seal haul-out behaviour in the Estuary was the very short duration of their bouts of haul-out activity (around 2–4 h, max. 10 h) as compared to harbour seals from other regions, where haul-out bouts of up to 39 h have been reported (Harvey 1987; Yochem et al. 1987; Thompson et al. 1989; Thompson and Miller 1990; Temple 1994). In regions where the tide greatly influences haul-out site availability, as is the case in the Estuary, moulting harbour seals are known to choose sites exposed for longer periods to remain out of the water for longer periods of time (Thompson 1987; 1989). The short duration of haul-out bouts in the St Lawrence Estuary seals might be related to limited availability of such sites and disturbance by recreational boating and seal-watching activities in the Metis and Bic regions during summer (Chapter 4).

This study has shown that, unlike several other phocid species (Le Bœuf et al. 1992; Schreer and Testa 1996; Bengston and Stewart 1997), and some other colonies of harbour seals (Suryan and Harvey 1998; Tollit et al. 1998), very shallow diving is important for foraging in St Lawrence harbour seals, particularly during May–July (Chapter 4). Dives < 4 m represented > 50% of all dives and 40% of dives associated with foraging success (Chapter 4). These shallow depths are often discarded from analyses because of a possible distortion of their characteristics due to low depth resolution or drift in zero depth of instruments (*e.g.* Schreer 1997; Bengston and Stewart 1997). In addition, dives to these depths in harbour seal studies are often assumed to contain no significant foraging activities and to correspond mainly to activities such as social interactions, investigation of available haul-out sites or sleeping near haul-out sites (*e.g.* Boness et al. 1994; Thompson et al. 1996; Tollit et al. 1998). Although these activities do undoubtedly occur at these shallow depths, foraging activity also takes place, at least among St Lawrence harbour seals, and it is also likely in other regions (*e.g.* Osborn 1985; Temple 1994; Ries et al. 1997). The refinement of the depth resolution of instruments and a more thorough description of shallow dives (< 4 m), using the classification methods described in Chapter 2, would improve our understanding of the types of activities that occur in shallow water.

The short retention periods for the stomach temperature sensors used in this study limited the possibilities for longitudinal comparisons of the intensity of foraging activity (also see Gales and Renouf 1993; Hedd et al. 1996; Bekkby and Bjørge 1998; Wilson et al. 1998; Andrews 1998). The shape, size and mass of the temperature sensor likely determine the duration of their retention and future efforts should be directed toward optimising these parameters for maximum periods of retention.

Our understanding of seal foraging behaviour would be greatly improved if meal size could be assessed. This would allow the construction of detailed activity–energy budgets and a more comprehensive examination of energy expenditures *vs* rewards in wild foraging animals. For example, post-moult juveniles, which foraged at deeper depths than the animals caught earlier in the summer, had the lowest success rates. It was suggested in Chapter 4 that post-moult juveniles may compensate for their higher effort while diving to deeper depths by preying on larger species or by catching more prey per trip from the surface (Kramer 1988; Houston and Carbone 1992; Thompson et al. 1993). The verification of such hypotheses is possible if meal size could be determined. However, sensor-response validation, under controlled laboratory conditions, would be required to establish the time-response of the sensors relative to meal size and intervals between meals and the effect of the prey temperature on this measure (Bekkby and Bjørge 1998). The temperature of poïkilotherm prey can be determined from the ambient water temperature at the depth where the prey is taken. Most time-depth-recorders currently available on the market can be programmed to gather information on water temperature. So, at least part of the technology required is available.

Satellite telemetry and *in situ* tracking identified areas repeatedly visited while seals were away from their haul-out sites. However, *in situ* tracking of individual seals is extremely time-consuming and the accuracy of positions obtained from satellite telemetry is often insufficient to allow a thorough examination of diving behaviour *vs* location (*e.g.* Goulet et al. 1999). Further insights into the foraging behaviour and preferred foraging areas of harbour seals could be gained from using the Global Positioning System concomitantly with TDR/HTR packages. This technology is now available for tracking phocids at sea (*e.g.* Sisak 1998) and it provides positions with accuracies of a few tens or hundred of meters. However, miniaturisation of these instruments is still necessary before they can be applied to small pinnipeds such as harbour seals. An additional limitation to this technology is the need to recover the instruments in order to access the data. Their use as part of remote releasing packages, similar to that developed during this study (Hammill et al. 1999), may help overcome this difficulty.

This thesis has improved our understanding of harbour seal activity and seasonally preferred habitats in the St Lawrence River Estuary. It indicates that they find both their necessary food resources and haul-out substrates within relatively restricted ranges throughout the year, although some seals exhibit marked seasonal movements outside the limits of the Lower Estuary. Harbour seals occupy top positions in the Estuary food web. They are opportunistic in their prey choice and feed on different prey types according to their age and, probably, on a seasonal basis. Coastal habitats, particularly shallow bays and river mouths, are important to harbour seals both as foraging and haul-out areas. During the summer months, access to haul-out sites appears essential, as seals haul-out daily at certain phases of their annual cycle, such as during the whelping or moult seasons. Food resources appear to be abundant in the Estuary in close proximity to haul-out sites throughout the year and species such as capelin, herring, sand lance, rainbow smelt and winter flounder enter the harbour seal diet at least seasonally.

Based on this information, some suggestions can be made regarding factors that might have negative effects on harbour seals in the Estuary. Owing to their high trophic position, harbour seals are susceptible to bioaccumulation of toxic compounds, which in turn might have an effect on immune system function and reproduction (Bernt 1998). Their high trophic position also places them at risk during prey shortages (Parsons 1992; Merrick 1997), although the opportunistic nature of their prey choice may reduce the impact of such stochastic phenomenon (Merrick et al. 1997). The presence of several other marine mammal species in the Estuary may result in some resource competition, but subtle variation among species in trophic position, diving behaviour and distribution may limit the degree of direct resource overlap. Finally, the reliance of harbour seals on coastal areas throughout the year makes them vulnerable to any habitat changes (*e.g.* disturbance from recreational boating or urban development along shores, damming of rivers, etc.), that affect availability of food resources, or access to or disturbance of haul-out sites.

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