FORAGING STRATEGIES IN GREY SEALS (HALICHOERUS GRYPUS) : FORAGING EFFORT AND PREY SELECTION

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“I think that animal testing is a terrible idea, they get all nervous and give the wrong answer”

Stephen Fry
To my Dad, to my Granddad, who left too early

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Abstract

Swimming speeds and prey selection of temporally captive, wild grey seals (*Halichoerus grypus*) were investigated in relation to prey characteristics in an experimental set-up at the Sea Mammal Research Unit (St Andrews, UK). For breath-hold divers, such as seals, the cost of swimming is a key variable in the management of oxygen stores. Thus it is likely that they modulate their swim speeds in order to maximise time spent feeding at a prey patch. We observed a strong relationship between swimming speed and stroke and glide pattern. Seals decreased their swim speeds by increasing their gliding period and as a result they decreased their oxygen consumption. Results indicated that mean swim speed decreased significantly with increasing distance to the patch, consistent with optimality model predictions. In addition, seals modified their swim speeds in response to changes in the speed and density of their prey. Seals decreased their swim speed as the speed of the prey increased. On the other hand, seals increased their swim speed as the density of the prey increased. Concurrently, bottom durations significantly increased suggesting that seals’ foraging strategies allowed them to most efficiently exploit their environment. Prey selection experiments investigated dietary preferences and the factors affecting their choice to select between different types of food. In the present study, seals maximised some aspects of their energy intake but also displayed some individual prey preferences.

These findings indicate the importance of fine-scale observations of foraging behaviour and the value of experimental protocols in developing our understanding of marine mammal foraging behaviour.
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Chapter 1

General Introduction
A central concern of ecology has traditionally been foraging behaviour and its underlying predator-prey interactions. In the present study, foraging behaviour of the grey seal (*Halichoerus grypus*) was investigated in relation to prey characteristics (i.e. patch distance, prey density, prey swim speed, prey species). The expected outputs were to gain a better understanding of certain behaviours that are difficult to observe in the wild. In addition, by studying prey preference we can better quantify and predict the effects of seals’ predation on marine ecosystems.

**Foraging behaviour**

*The theory*

In their struggle for life, organisms should adopt strategies that optimise their fitness (Stearns 1992). A strategy can be defined as the choice of a particular solution among several possible options and is an adaptive response resulting from natural selection. At the evolutionary level, behavioural strategies result from trade-offs (in terms of survival, growth, reproduction) that may occur at physiological, morphological, ethological, ecological and demographic levels. The concept of optimality refers to the way an animal might maximise net benefit given the cost associated with a behaviour. Organisms should therefore maximise their efficiency in resource acquisition and allocation when faced with the interlinked but sometimes conflicting tasks of survival, growth and reproduction (Stephens & Krebs 1986, Krebs & Davies 1997). In particular, feeding plays a crucial role and animals should optimise some aspects of their intake rate when foraging. Foraging consists of locating and selecting a feeding patch according to its overall profitability (prey quality, quantity and accessibility) so that the foraging efficiency is optimised (Stephens & Krebs 1986).
Successful foraging affects an animal’s chances of surviving and reproducing because foods, or rather, particular nutrients obtained from them, are essential to running the machinery of the body. For many animal populations, food is thought to be the primary limiting factor for population growth (Altmann 1998). Therefore feeding and foraging have occupied a central role in the adaptations and evolution of animals because they contribute to differential survival and reproductive success of individuals of any given population (Altmann 1998).

Within the framework of optimal foraging theory, foraging strategies are currently studied as decision making processes: Where should an individual forage? How long should it remain in a food patch? Toward which prey type should it directs its searching? (Cezilly et al. 1991). One of the first hypotheses attempting to describe the rules used by predators in determining how much time to spend searching a patch was the marginal value theorem proposed by Charnov (1976). The theorem predicts that individuals will stay longer in a given patch if (1) it is a profitable patch, (2) as the distance between the patches increases and (3) when the environment as a whole is less profitable. In addition, Krebs et al. (1974) suggested that predators can use intervals between successive captures as a measure of capture rate. Predators should therefore leave a patch when the interval since the last prey capture exceeds some critical period. This is also known as the giving-up rule.

When determining which prey type predators should include in their diet. MacArthur and Pianka (1966) suggested that an animal seeking food should try to obtain the maximum amount of food per unit time. This idea was developed and in 1986, Stephens and Krebs described foraging as locating and selecting a feeding patch.
according to its overall profitability so that the foraging efficiency is optimised.

Therefore the tactics used by predators to capture prey and the energetic consequences of these behaviours should influence which prey types are eaten (Emlen 1966).

Models of foraging behaviour for marine mammals

In the marine environment, breath-hold divers face several challenges; firstly they must balance breathing at the surface with exploiting a food resource underwater. Secondly they have to explore and exploit a three dimensional environment where food resources are scattered in aggregated patches, sometimes at great depths. Finally, once they have been to the surface to breathe, they have to relocate the feeding patch in the subsequent dive. Traditional models of diving in breath-hold animals assume that foraging decisions, mainly the decision to terminate a dive, are entirely controlled by the rate of oxygen consumption, (Kramer 1988, Houston & Carbone 1992). In these models the optimal dive durations are predicted to be close to, and in some case beyond, the aerobic dive limit. The Aerobic Dive Limit (ADL) defines the maximum time an animal can hold its breath without an increase in blood lactate during or after a particular dive (Kooyman 1989). ADL depends on the amount of oxygen stored (mainly linked to haemoglobin and myoglobin quantity and affinity for oxygen, but also lung capacity) and how fast it is used (determined by metabolic rate).

Interestingly, physiological and behavioural measurements have shown that in the wild, marine mammals generally surface well before oxygen stores are exhausted (Fedak et al. 1988, Kooyman et al. 1989, Thompson et al. 1991, Reed et al. 1994). Such inconsistencies between theoretical and measured results suggest that the stored oxygen level is not the major determinant of dive duration. Diving foragers may alter their diving behaviour in response to their perception of patch quality whilst dive
duration is ultimately limited by oxygen stores and the rate of oxygen consumption (Thompson & Fedak 2001).

MacArthur and Pianka (1966) suggested that an animal seeking food should try to obtain the maximum amount of food per unit time. Most optimal foraging models assume that the number of prey encountered during a feeding event is a linear function of the time spent foraging. This dictates that foragers have to reduce both their transit time to the feeding area and their recovery time between two successive feeding events in order to maximise the time spent feeding in the patch of prey (e.g. Ydenberg et al. 1992). In the marine environment there is a direct correlation between the depth at which divers forage and the travel duration and associated energy costs. Consequently, the expected foraging gain (energetic value of the prey ingested less the costs of acquiring it) that follows the end of a dive decreases with increasing depth. Kramer (1988) developed a model to predict the changes in surface duration in response to variation in the depth of foraging. The Houston and Carbone model (1992), which is a modification of the optimal breathing model (Kramer 1988), described how breath-hold divers should modify their diving behaviour in order to limit the proportion of time spent at the surface and hence maximise the proportion of time foraging underwater over the complete dive cycle (i.e. dive duration plus surface duration). One prediction of the model is that breath-hold divers will reduce their time spent foraging if the associated energetic cost increases while surface duration should remain the same. Hasley et al. (2003) found that the mean surface duration of the tufted ducks, Aythya fuligula, did not differ significantly whether or not foraging cost increased in accordance with the model of Houston & Carbone (1992). They found, however, that the foraging duration of the ducks increased with increasing foraging
cost. Thus their study showed that some of the assumptions that models of diving optimality rely on might be biased. For example the cumulative oxygen uptake curve may vary between dives and in their study the tufted ducks compensated for the increase in foraging costs by increasing their rate of oxygen uptake while on the surface. This study shows that models of diving optimality can not predict all the behaviours observed in breath-hold divers but they do provide frameworks within which we can improve our understanding of the diving and foraging behaviour of wild animals.

Deciding when to leave a patch is central to the foraging theory which states that animals should leave a patch when they perceive that patch quality has dropped below a particular threshold (Krebs et al. 1974, Charnov 1976). These models assume that the decision to quit a patch is based on some aspect of prey acquisition such as net rate of energy gain. For divers, however, there are more immediate constraints such as the need to return to the surface to replenish their oxygen stores. Thompson and Fedak (2001) suggested that breath-hold divers could increase the overall rate of energy gain by giving-up early (i.e. terminate the dive before the depletion of their oxygen stores) in low-quality patches. They showed, however, that the benefit of giving-up was reduced when diving to greater depths. As travelling duration increases and becomes a larger proportion of the dive duration, the benefit of quitting a low quality patch will decrease. Therefore, deep divers are expected to perform dives close to their aerobic limits.

When submerged, breath-hold divers must balance the energetic demands of locomotion with the conservation of a limited oxygen store (Castellini et al. 1985,
Skrovan et al. (1999). As swim speed increases, the oxygen stores are depleted more rapidly following a U-shaped curve (Schmidt-Nielsen 1998). Thus in order to maximise efficiency, breath-hold divers should adjust their swim speed in relation to the characteristics of prey that they are hunting; e.g. swim speed, energy content, density of the patch and the depth at which prey are located (Thompson et al. 1993, Wilson et al. 2002, Aguilar-Soto et al. 2008). In particular, the Thompson et al. general swimming speed model (1993) investigated the relationship between transit swimming speed and patch distance for breath-hold divers. They examined the relationship between the amount of oxygen available at depth and the combined travel and recovery times. Their model relied on the assumption that seals travel to and from depth at constant speed. Their model made three predictions about swim speed during transit between the foraging depth and surface. Firstly, seals should swim as directly as possible to their feeding site. Secondly, their optimality model suggested that seals should swim at the minimum cost of transport (MCT) speed in deep dives in order to maximise the rate of oxygen available for foraging at depth. Finally, in shallower dives, seals could increase the proportion of time spent at the patch by swimming faster between the surface and the prey patch. Even though oxygen consumption per meter will increase with increasing speed, this tactic should be employed if seals are attempting to maximise their net rate of energy intake.

Thompson et al. (1993) also modelled how the optimal foraging tactics of seals may change as a function of the interactions between constraints of both physiology (costs of swimming) and prey availability (prey density and movements). They compared the foraging tactics employed by seals to search for prey with a specialised form of line transect. Therefore, in their model, the number of prey items encountered was
determined by the area searched which was related to the distance covered. In addition, the behaviour of the prey item (i.e. swim speed) also determined the likelihood of encounter. Their model was based on the assumption that on any one dive a seal searches at a constant speed. The Thompson et al. foraging tactics model (1993) thus predicted that seals should swim at the MCT (Minimum Cost of Transport) speed when foraging on stationary or very slow-moving prey. This would enable seals to search the maximum area possible and therefore increase their chance to encounter prey. Conversely, seals should slow their swimming below MCT speed when hunting on active prey in order to maximise their energetic efficiency by limiting their energy expenditure. In addition, they suggested that when prey densities are high, the cost of the dive is reduced compared with the gain per encounter and seals should swim faster for all prey swim speeds.

The present study (Chapters 4 and 5) proposed to investigate how grey seals modify their foraging behaviour in response to changes in prey characteristics by testing the predictions of the Thompson et al. (1993) theoretical models of foraging behaviour (i.e. the general swimming speed model and the foraging tactics model).
Tools to study marine mammal foraging behaviour

In the wild

The process by which mammalian predators search, stalk and subdue their prey has been the subject of considerable research efforts for terrestrial species. In contrast, less is known about the foraging behaviour of marine mammals, primarily because they are so difficult to observe in the wild. The development and use of animal-borne behavioural data recorders and video recorders has provided data on many parameters related to foraging. In terms of seal behaviour, such equipment can provide unique insights into the functionality of dive types and the detail of fine-scale foraging behaviour (LeBoeuf et al. 1989, Hindell et al. 1992, McConnell et al. 1999, Davis et al. 1999, Crocker et al. 2001, Fedak et al. 2002, Sato et al. 2003, Davis et al. 2004, Austin et al. 2006). Video recorder systems are useful for observing underwater feeding behaviour as they provide some information on the biological environment, such as prey distribution, which is essential to studying foraging in diving animals (Bowen et al. 2002, Hooker et al. 2002, Fuiman et al. 2002, Davis et al. 2003, Watanabe et al. 2003). Due to restrictions in the amount of digital memory or length of videotape, however, the data obtained cover a relatively short period of time when recording continuously (Watanabe et al. 2003). Advances in instrumentation and labelled water techniques are providing new insights into at-sea behaviour and energetics of freely diving animals (Costa 1988, Green et al. 2007, Hooker et al. 2007).

Efficient aquatic locomotion is essential for breath-hold divers that need to minimise their energy expenditure in order to increase their time available to forage underwater.
Therefore marine mammals use a variety of strategies to reduce the cost of locomotion (Kramer and McLaughlin 2001, Williams 2001). For example, swimming with discrete stroke and glide phases, has been identified as a particularly efficient strategy (Williams and Kooyman 1985, Williams et al. 2000). The deployment of video-data logging and the recent development of accelerometer tags have permitted the study of stroke and glide patterns in wild aquatic animals (Sato et al. 2003, Williams et al. 2004, Miller et al. 2004, Lovvorn et al. 2004, Watanabe et al. 2006, Wilson et al. 2006). The relationship between stroke and glide patterns and swimming speed has also been studied for a range of species in the wild (Williams et al. 2000, Yoda et al. 2001, Wilson and Liebsch 2003, Lovvorn et al. 2004, Watanabe et al. 2006, Sato et al. 2007). For example, a recent study by Sato et al. (2007) showed that stroke frequency was related to body size for breath-hold divers ranging from 0.5 kg seabirds to 30 000 kg sperm whales. In addition, another study suggested that speed and acceleration are primarily mediated via changes in stroke amplitude rather than stroke frequency (Wilson and Liebsch 2003). Buoyancy has also been reported to significantly affect the diving behaviour of seabirds and marine mammals (Lovvorn and Jones, 1991; Webb et al., 1998; Skrovan et al., 1999; Beck et al., 2000; Williams et al., 2000; Biuw et al., 2003; Watanuki et al., 2003; Sato et al., 2003; Miller et al., 2004; Sato et al., 2007). Sato et al. (2003) demonstrated that the mode of locomotion during descent in free-living Weddell seals (Leptonychotes weddellii) was related to body fatness. Prolonged gliding while descending was observed in thinner females but the fatter ones exhibited only stroke and glide swimming throughout their descent and ascent. Another study by Watanabe et al. (2006) demonstrated that Baikal seals (Pusa sibirica) adopted different stroke patterns according to their individual buoyancy. By comparing the swimming pattern of a Baikal seals with and without an attached lead
weight, they showed that when the seal was less buoyant it used longer prolonged gliding on the descent. In the present study, we assessed the relationships between stroke and glide patterns and swimming speeds, by deploying accelerometer tags on seals swimming horizontally underwater (Chapter 3).

Little is known about prey selectivity for aquatic carnivores because examining predation decisions within the context of their immediate environment is difficult. Our knowledge of this area relies heavily on indirect methods such as diet analyses by faecal and stomach content examination (Rae 1973, Prime & Hammond 1990, Bowen and Harrison 1994) and on more recent developed technologies such as fatty acid analysis of tissues (Iverson et al. 2004). While current wild diet studies can help assess existing relationships between predators and their environment, their predictive capabilities are limited. These diet studies give only minimal information about the factors that affect the diet of wild seals and therefore it is hard to predict what seals would eat in a certain environment and which aspects of the prey characteristics (species, density, size, etc.) dictate their choices. Captive studies can help assess which prey characteristics affect predators’ choices (Chapter 6).

In captivity

Despite its importance, the feeding behaviour of most marine mammals is poorly understood. Feeding usually occurs at depth and over large spatial scales. Direct observations are therefore difficult or impossible. In addition, fine-scale prey availability is difficult to measure directly for individual animals foraging in the wild. Researchers have recently used underwater still and video cameras to obtain additional information on seals’ foraging behaviour (Davis et al. 2004, Hooker et al.)
These new technologies can help identify foraging habitat, prey species and three-dimensional foraging behaviour (Bowen et al. 2002, Davis et al. 2003). They can not, however, provide accurate information on prey characteristics such as movements and swim speed. In this context, captive experimental studies can create a range of environmental conditions or physiological states while controlling for confounding variables (Kramer and McLaughlin 2001).

Few studies have investigated marine mammal foraging behaviour in an experimental set-up, mainly because of their large size (Cox et al. 1996, Boyle 1997, Cornick and Horning 2003, Sparling et al. 2007). Except the study carried out by Sparling et al. (2007), animals used in these experiments were long-term captive animals and the number of animals tested were low (three or less). Therefore the relevance of their findings to wild animals may be limited. For example, Cornick and Horning (2003) and Sparling et al. (2007) found that dive duration, foraging duration and foraging efficiency increased significantly with increasing prey encounter rate. In Cornick and Horning’s (2003) study, however, captive Steller sealions (Eumetopias jubatus) were trained to inspect feeding stations in response to visual signals whilst Sparling et al. (2007) left the choice up to the grey seals to swim and inspect the feeding station. In addition, food was always offered when Steller sealions inspected the feeding station. To the contrary, grey seals did not always find prey at the feeding station. Therefore Sparling et al. (2007) could investigate the giving-up strategies employed by foraging seals in low quality patches. Other more serious limitations to the Cornick and Horning (2003) study were the size of their tank (145 m$^2$), the non-restrictive access to the surface and the short distances seals had to swim between the feeder tube
outlets (between 6 and 13 metres). Overall, Sparling et al. (2007) managed to recreate quasi-realistic dives with distances between surface and the prey patch varying between 40 and 120 metres similar to wild diving distances. They also successfully recorded, simultaneously, the costs and benefits of seals’ chosen foraging strategies.

The present study used the SMRU facility (Sea Mammal Research Unit, St Andrews, UK) in order to test existent theoretical models and investigate prey preference in temporally captive wild grey seals.

The grey seal

Grey seals were used in the present study for three main reasons. Firstly there is a competitive interaction between seals and fisheries in UK waters which requires detailed information to help predict the diet of wild seals. Secondly, as benthic foragers they provide an appropriate model to test theoretical models of foraging behaviour. Finally, for marine mammals, their size, behaviour and ecology are adequate with the requirements of captive studies.

Seals and fisheries

The grey seal is the larger of the two British seal species (the other one being the harbour seal, *Phoca vitulina*). It is a medium sized phocid (males approx 280 kg, females approx 150 kg) found throughout the temperate waters of the North Atlantic, with three distinct populations: Western North Atlantic, Eastern North Atlantic and Baltic. The UK hosts about 45% of the world population of grey seals. Over 90% of
the British population breed in Scotland, the majority in the Hebrides and the Orkney (Duck & Thompson 2007).

Seals are important predators in the marine ecosystem and estimating their diet has been central to many studies investigating predator-prey relationships, interactions with fisheries and monitoring the environment (Harwood and Croxall 1988, Boyd 2002). The British grey seal population, a major predator of commercially fished sandeels (Prime & Hammond 1987, Prime & Hammond 1990, Hammond et al. 1994) is widespread, locally very abundant, and still increasing. There are approximately 120,000 grey seals and they are at the top of the food web in the coastal seas around the UK (Duck & Thompson 2007). Grey seals diet, based on faecal analyses, consists primarily of fish and cephalopods, including both inshore species and species with a wide distribution (Pierce et al. 1990). Additionally, grey seals feed opportunistically on demersal fish such as sandeels, whitefish and flatfish (Prime & Hammond 1987, Prime & Hammond 1990, Pierce et al. 1990, Bowen and Harrison 1994).

Observed and perceived increases in seal populations are seen by many fishermen as a serious threat to their livelihoods, especially at a time when competition amongst fishermen is also increasing (Harwood 1987, Harwood & Croxall 1988, Harwood 1992, Matthiopoulos et al. 2008). It has been calculated that a grey seal requires an average of 23150 k joules per day; equivalent to about 7 kg of cod (*Gadus morhua* L.) or 4 kg of sandeels (Hammond et al. 1994). These food requirements, combined with some individual grey seals taking or damaging salmon from fishing nets, have brought frequent demands by fishermen for grey seal numbers to be controlled. Mathematical models have been used in a number of ecosystems to synthetise
information of seal biology and ecology and to extrapolate it to predict their impact on prey species (Winship et al. 2002, Matthiopoulos et al. 2008).

There is, however, a lack of data on diet selection in pinnipeds (Boyle 1997) and how seals respond to changes in prey availability. For example, the preference of seals for certain sizes and species of prey have not been investigated experimentally, so answers to basic questions about whether seals prefer certain species when prey availability is equal, or the potential role of preferences in prey selection remain unknown (Boyle 1997). Therefore, the debate about the effects of marine mammal predation on commercially exploited fish stocks and associated fisheries will continue until their interactions and impacts are thoroughly assessed and properly managed (Mathiopoulos 2008). Towards this end, the present study investigated prey selection by combining experimental manipulation of prey availability in terms of species and number and allowing the seals to select their diet (Chapter 6).

**Grey seals’ diving behaviour**

Information is available on where and when grey seals forage. Satellite tracking in the UK revealed that grey seals can make transits between haul-out sites, which are sometimes hundred of kilometres apart (McConnell et al. 1992, McConnell et al. 1999). The majority of movements, however, remain local. Several studies have shown that seals usually repeat trips to offshore areas with characteristic sediment types, which are likely to be foraging sites (Thompson et al. 1991, McConnell et al. 1992, McConnell et al. 1999). Foraging dives have been identified because diving behaviour varies with the function of the dive. Thompson et al. (1991) found that travelling is characterised by V shaped dives whereas during foraging, grey seals
swim slower at the bottom where they spend 60% of the dive duration. Foraging dives are thus characterised by a square shape profile. There is less information, however, on seals’ diving behaviour in response to prey characteristics. As mentioned previously it is difficult to obtain fine-scale details of the seals environment whilst feeding in the wild. Although the main types of prey eaten by grey seals are known, the factors that influence foraging behaviour and diet are poorly understood.

Overview of the thesis

Scientists have been collecting information on wild marine mammals for more than 20 years on topics including population abundance, foraging behaviour and diet. In order to interpret some of these data and test existing theoretical models, the SMRU pool facility was built. This unique facility allows identification of the features of the environment which can affect the foraging behaviour of seals; such as dive depth, prey density and prey characteristics. This set-up also provides the opportunity to investigate, at a fine-scale, the swimming pattern (i.e. stroke and glide) employed by foraging grey seals. Initial experiments have shown that seals do indeed alter their behaviour in response to varying factors such as dive depth and prey density (Sparling et al. 2007).

In the present thesis I investigated swimming speed and stroke and glide pattern (Chapters 3, 4 and 5), key variables in both the management of oxygen stores and foraging strategy selection; and prey choice (Chapter 6).

The principle aims of the present study are as follows:
1. Describe the fine scale stroke and glide patterns of foraging grey seals in the absence of buoyancy effects (Chapters 3 and 4).

2. Examine the model of Thompson et al. (1993) which predicts that seals should decrease their swim speed as patch distance increases (Chapter 4).

3. Determine how seals adjust their swim speed in relation to prey swim speed and how the density of the prey affects that relationship (Chapter 5).

4. Determine if seals maximise their time spent foraging in the manner predicted by the model of Thompson et al. (1993). The predictions of the model were that seals should decrease their swim speed as the speed of the prey increases. Seals should also increase their effort in higher density patches (Chapter 5).

5. Determine whether grey seals have the capacity to exhibit prey preferences (Chapter 6).
References


Chapter 2

Overview of the experimental designs
Captive animals

Four adult and eleven juvenile grey seals were used in this study (n = 15). Table 2.1 shows the name, age classes, origin, mass and the chapters where the experiments relating to them can be found. Seals were caught from local haul-outs at Aberdare sands or the Isle of May (Figure 2.1) and taken by boat or in a van to the captive facility. Seals at Aberdare were caught using the rush and grab method or by deploying nets in the water. Rush and grab is where after a fast landing by boat right in front of the haul-out, seals are entangled in hoop nets on the sandbank. The second method was tangle nets deployed by boat adjacent to the shore. The seals get tangled in the net as they try to escape underwater. Seals from the Isle of May were caught on the shore in the breeding colony with a hoop-net. Seals were inspected upon arrival and before departure from the facility and on a monthly basis by an accredited veterinary surgeon. Due to permit condition, seals were released back into the wild after a maximum period of 13 months.

Seals were fed daily on a variety of fish species over the years; herring (*Clupea harrengus*), sprat (*Sprattus spratus*), whiting (*Gadus merlangus*), mackerel (*Scomber scombrus*), haddock (*Melanogrammus aeglefinus*) and sandeel (*Ammodytes marinus*). Adults were given 4 - 6 kg per day and juvenile 0.5 – 3 kg per day. Food was supplemented daily with two multivitamin tablets (Aquavits, International Zoo Veterinary Group, West Yorkshire) and one iron supplement (ferrous glucanate, 300 mg, IZVG). All capture and handling procedures conformed to the Animals (Scientific Procedures) Act 1986, under Home Office project licence 60/2589 and 60/3303 from 2005.
Table 2.1. Details of the seals used in this study.

<table>
<thead>
<tr>
<th>Name</th>
<th>Age</th>
<th>Origin</th>
<th>Capture date</th>
<th>Mass at capture (kg)</th>
<th>Release date</th>
<th>Mass at release (kg)</th>
<th>Chapter</th>
</tr>
</thead>
<tbody>
<tr>
<td>L*</td>
<td>Adult</td>
<td>Isle of May</td>
<td>12/12/01</td>
<td>168</td>
<td>25/10/02</td>
<td>172</td>
<td>4</td>
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<tr>
<td>K*</td>
<td>&lt; 1 year</td>
<td>Isle of May</td>
<td>12/12/01</td>
<td>31.6</td>
<td>15/11/02</td>
<td>35</td>
<td>4</td>
</tr>
<tr>
<td>N*</td>
<td>&lt; 1 year</td>
<td>Isle of May</td>
<td>12/12/01</td>
<td>27</td>
<td>15/11/02</td>
<td>36</td>
<td>4</td>
</tr>
<tr>
<td>R*</td>
<td>&lt; 1 year</td>
<td>Abertay</td>
<td>06/02/03</td>
<td>31.5</td>
<td>04/10/03</td>
<td>59</td>
<td>4</td>
</tr>
<tr>
<td>Q*</td>
<td>Adult</td>
<td>Abertay</td>
<td>06/02/03</td>
<td>119</td>
<td>20/10/03</td>
<td>179</td>
<td>4</td>
</tr>
<tr>
<td>W*</td>
<td>&lt; 1 year</td>
<td>Abertay</td>
<td>15/01/04</td>
<td>26</td>
<td>14/10/04</td>
<td>41.4</td>
<td>4</td>
</tr>
<tr>
<td>X*</td>
<td>&lt; 1 year</td>
<td>Abertay</td>
<td>13/02/04</td>
<td>22</td>
<td>14/10/04</td>
<td>36.6</td>
<td>4</td>
</tr>
<tr>
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<td>&lt; 1 year</td>
<td>Abertay</td>
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<td>34.6</td>
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<td>45</td>
<td>6</td>
</tr>
<tr>
<td>P6</td>
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<td>14/10/05</td>
<td>37</td>
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<td>Abertay</td>
<td>17/01/06</td>
<td>132</td>
<td>02/10/06</td>
<td>163.8</td>
<td>3 &amp; 5</td>
</tr>
<tr>
<td>A2</td>
<td>Adult</td>
<td>Abertay</td>
<td>17/01/06</td>
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<td>02/10/06</td>
<td>177.6</td>
<td>6</td>
</tr>
<tr>
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<td>Isle of May</td>
<td>15/02/06</td>
<td>29.6</td>
<td>03/11/07</td>
<td>48</td>
<td>3, 5 &amp; 6</td>
</tr>
<tr>
<td>P2 **</td>
<td>&lt; 1 year</td>
<td>Isle of May</td>
<td>15/02/06</td>
<td>25.8</td>
<td>10/11/07</td>
<td>51.4</td>
<td>3, 5 &amp; 6</td>
</tr>
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<td>Isle of May</td>
<td>22/12/06</td>
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<td>36.6</td>
<td>3 &amp; 5</td>
</tr>
<tr>
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<td>&lt; 1 year</td>
<td>Isle of May</td>
<td>22/12/06</td>
<td>40</td>
<td>19/10/07</td>
<td>48</td>
<td>3 &amp; 5</td>
</tr>
</tbody>
</table>

* indicates that the data were recorded before I started my PhD by Dr J-Y. Georges and Dr C. E. Sparling but they were analysed by me during my PhD.

** indicates that the seal was a male.
Figure 2.1. A) Map of Great Britain indicating the area (Fife, Scotland) where grey seals were caught. B) Details of the area with the numbers 1, 2 and 3 indicating The Isle of May, SMRU (St Andrews) and Abertay Sands respectively.
Experimental foraging design

The study was conducted at the Sea Mammal Research Unit in St Andrews, Scotland. The SMRU’s experimental facility (Figure 2.2) comprises a large pool (42 x 6 x 2.5 m) that can be totally covered by aluminium meshed panels that were placed 50 cm below the surface of the water, so that animals can only surface to breathe in a small respirometry chamber linked to a respirometry system. The pool can be longitudinally partitioned into “lanes” using nets so that distance between the surface and the feeding station could be manipulated (Figure 2.3).

The feeding station consisted of a purpose built device that delivers fish semi-automatically at a controlled rate on a conveyor belt to a feeding window 2 metre below the surface. The frame was 3 m tall x 1.5 m wide and sited on the bottom of the pool. Within the frame was a conveyor belt holding 80 consecutive slots in which fish could be fitted by hand from an open access point at the top of the feeder. The conveyor belt was driven by an electric motor powered by a 12 V DC battery. The speed of the belt could be held constant or could be programmed to vary in response to the behaviour of the seal at the feeder (see Chapter 5 for more details). As the belt was turning, fish became available to seals within a 1 m x 0.3 m wide opening situated at the bottom of the frame. A force plate could be added to the feeder (Figure 2.4) in order to record the force exerted by the seals while feeding and manipulate the speed of the belt (see Chapter 5 for more details). An underwater video camera linked to a time/date generator and a monitor/VCR was placed on the feeding station to record time (± 1 s) of arrival and departure from the feeder, and seals’ behaviour in front of the opening.
All experiments were carried out with fasting animals to ensure a similar state of hunger between experiments. Experiments where carried out in the morning when seals had not been fed since the previous evening i.e. usually unfed for the last 15 hours. The seal was placed under the panels one hour before the feeding experiment started and it stayed within the set-up for another hour after completion of the feeding experiment. Feeding experiments were completed once the seal had eaten its daily ration. A small amount of food was kept for training purpose and moving animals between pools at the end of an experiment.

Oxygen consumption was measured using an open circuit respirometer (Fedak et al., 1981). The breathing box had an inlet which opened to the outside and an outlet which was connected to a pump inside the laboratory by a 6 m long and 1.5 inch diameter flexible hose. Atmospheric air was drawn through the box, at a rate of 200-400 L.min\(^{-1}\), sufficient to obtain a change in oxygen concentration during breathing around 1 %. Flow was maintained and monitored using Sable Systems Flow Kit 500H (Sable Systems International). A 500 mL.min\(^{-1}\) sub-sample was pumped at positive pressure through a drying column, a CO\(_2\) absorber and another drying column before entering a Servomex paramagnetic oxygen analyser (model OA570, Sybron Taylor, Taylor instrument Analytics Ltd, UK), which measured the oxygen concentration in the sample gas. The oxygen analyser was connected to a laptop computer using a PCMIA16-bit analogue to digital converter (PC-CARD DAS16/16, Amplicon Liveline) (Figure 2.5). The oxygen analyser output was sampled 10 times per second using a program written for this application. Every second the program calculated and stored a moving average of the fractional oxygen concentration (Sparling and Fedak, 2004). The output from the oxygen analyser was monitored continuously in a
laboratory inside the building so that seals were not aware of any human presence throughout experiment trials.

At the end of each daily experiment, the system was calibrated by bleeding nitrogen into the system at a known flow rate for a fixed amount of time. The flow meter used for the nitrogen was calibrated weekly. For each dive, oxygen consumption of the seal was calculated using the following equation from Fedak et al. (1981):

$$VO_2 = \frac{0.2094 V_{N_2}}{0.8} \left( \frac{\Delta C}{\Delta C^*} \right)$$

Where $\Delta C$ and $\Delta C^*$ refer to the deflection of the analyser during measurement and calibration respectively and $V_{N_2}$ is the volume of nitrogen used in the calibration. The volume of oxygen consumed was then divided by the duration of the dive cycle (dive + post-dive surface interval), to give an average Diving Metabolic Rate (DMR) over each dive.
Figure 2.2. View of the SMRU experimental facility. It comprises a large pool (42 × 6 × 2.5 m) where the experiments are held. The pool can be covered to ensure that the study animal can only breathe in the respirometry chamber.

Figure 2.3. Schema of the experimental set up to study the behaviour of grey seals in relation to patch quality (patch distance and prey density). The seal can only breathe in the respirometry chamber (R), and the feeder (F) can be placed at any distance from the surface access of the pool to simulate different distances from the surface to the patch.
Figure 2.4. Detail of the feeding station equipped with a force plate (See text for full explanation).

Figure 2.5. Schematic diagram of the open-flow respirometry system used at the SMRU’s experimental facility in order to measure the oxygen consumption of captive grey seals. The arrows show the direction of the air-flow through the system.
Design for the prey choice experiments

The SMRU experimental facility also comprises two small circular pools (3 and 5 meters diameter).

An underwater feeding apparatus was designed and constructed to present and deliver fish to seals in the feeding experiment. A paired presentation design was chosen to provide a sensitive measure of preference (Boyle 1997). Fish were inserted manually into two clear plastic tubes (50 cm long, 18 cm diameter) and presented to the seal. This design presented a pair of stimuli (fish) and the apparatus provided differential reinforcement (fish delivery) following the operant choosing one tube or the other. The choice was made by the seal touching one of the tubes with its nose.

The apparatus was fixed to the side of the 5 m diameter pool, inside a shed (Figure 2.6). It was constructed in clear plastic with a one-way mirror to hide the experimenter from the seal’s view during fish presentation but allowing the seal’s behaviour to be observed at the same time (Figure 2.7). This set-up was used in chapter 6.
Figure 2.6. The feeding apparatus used for the prey choice experiments is fixed to the side of one of the small pools (5 m diameter), inside a shed.

Figure 2.7. Details of the prey choice apparatus, a) view from the pool and b) view from inside the shed.
Constraints

Because of the nature of the work there were inherent constraints associated with the experiments. Equipment failure also had to be taken into account as this is common to field experiments. Other constraints, however, were more specific to captive studies. For example, fish used during the experiments were dependent on supplier’s capacity. There were some size limits and time of year constraints on fish exploited commercially. Therefore some species were not available on a year round basis and others were not available every year. These constraints limited the range of fish we could use during experiments. In addition, it is not allowed to use live prey to feed captive animals for scientific purpose under UK legislation so only dead fish could be used. Therefore we could not directly measure the cost of pursuing and acquiring different fish as seals face in the wild.

Working with short-term captive animals was a challenge and required a lot of effort and time to get the animals settled to the experimental set-ups. Several months was needed before experiments could start with any individual seal and no more than four animals could be kept at the same time. Because of concurrent studies on the energetic of diving seals during the first two years, time available for the present study was reduced. In addition, unplanned building work in and around the pool dramatically reduced the timeframe when experiments could be carried out and reduced the number of tested animals as adult seals did not settle well in the noisy environment of a building site.
References


Chapter 3

Stroke and glide patterns in foraging grey seals
Summary

For breath-hold divers such as seals, the cost of swimming is a key variable in the management of oxygen stores. Swimming with discrete stroke and glide phases has been identified as a particularly efficient way of travelling. In addition buoyancy directly affects stroking pattern. For example, free ranging seals show different glide durations in ascent and descent swimming in line with their buoyancy.

Here we describe fine scale stroke and glide pattern of grey seals during foraging dives in a purpose built swimming tank in which seals had to swim 80 m horizontally underwater from a breathing box to a submerged automatic feeding station. The fact that seals swam horizontally allows us to investigate the relationship between swimming speed and stroking pattern in the absence of vertical buoyancy effects. We measured swim speed and stroking patterns using a 3D accelerometer data logger (W1000L-3MPD3GT, Little Leonardo Co., Tokyo) during simulated foraging dives of 5 captive grey seals.

Interestingly, all seals swam faster on their way to the feeding station compared to the return to the breathing box. Stroking patterns were different between transits to and from the feeding station. On the return phase of the dive, the percentage time gliding increased whilst total number of strokes decreased. However dominant stroke cycle frequencies, calculated by power spectral density, were higher during the return phase. Lower swim speeds were therefore characterized by longer periods gliding, less total strokes but had a higher dominant stroke cycle frequency. In addition, both the initial and final speeds of individual glide phases were higher on the way to the feeding station compare to the return journey. The results showed significant
relationships between swimming speeds and stroking pattern and demonstrate that the energy expended during a dive was best explained by stroking characteristics.
Introduction

Breath-hold divers must divide their time between breathing at the surface and foraging underwater (Dunstone and O’Connor 1979). It is assumed that the number of prey encountered is a linear function of time spent searching. Thus foraging breath-hold divers are expected to maximise their time spent underwater (Kramer 1988, Houston & Carbone 1992, Carbone & Houston 1996). In addition, there is a close relationship between oxygen depletion and swimming speed (Davis et al. 1985, Feldkamp 1987, Williams et al. 1993, Sparling & Fedak 2004). Foraging duration is ultimately limited by the oxygen stores of the animals thus breath-hold divers are expected to modulate their swimming activity in order to minimize the cost of transport (Ponganis et al. 1990, Ponganis et al. 1992, Fish 1993, Thompson et al. 1993, Williams et al. 1993, Ropert-Coudert et al. 2002). Swimming speeds and patterns are therefore key variables in the management of oxygen stores for breath-hold divers (Feldkamp 1987, Skrovan et al. 1999, Williams et al. 2004). For example high level of activity will presumably lead to the termination of a dive earlier as oxygen stores are quickly depleted. As a result, energetically efficient modes of locomotion provide an advantage while diving by increasing the time available for locating and catching prey (Skrovan et al. 1999, Sato et al. 2003).

Marine mammals can use a variety of strategies to reduce the cost of locomotion. For example intermittent locomotion including porpoising, wave-riding and gliding mode can increase the efficiency of aquatic locomotion (Kramer and McLaughlin 2001, Williams 2001). Swimming with discrete stroke and glide phases, as seals do, has been identified as a particularly efficient way of travelling. Williams and Kooymant (1985) demonstrated that body drag is lower during gliding phases compared to
stroking movements because of drag increase as a result of stroking. Another study by Williams et al. (2000) showed that prolonged gliding in Weddell seals (Leptonychotes weddellii) provided an energetic advantage by reducing their oxygen consumption. By combining measurements of stroke and glide characteristics with post-dive oxygen consumption, they found that interrupted swimming (i.e. gliding) during a dive resulted in a 9.2 – 59.6 % energetic saving for Weddell seals. Their study was based on a comparison between two groups of dives by Weddell seals covering equal distances but varying in swimming pattern and depth. Effectively, during vertical movements, aquatic animals can take advantage of their positive or negative buoyancy to allow unpowered downward or upward locomotion for a longer period (Kramer and McLaughlin 2001).

Buoyancy is one of the primary external forces acting on breath-hold divers and has been reported to significantly affect the diving behaviour of seabirds and marine mammals (Lovvorn and Jones, 1991; Webb et al., 1998; Skrovan et al., 1999; Beck et al., 2000; Williams et al., 2000; Biuw et al., 2003; Watanuki et al., 2003; Sato et al., 2003; Miller et al., 2004; Sato et al., 2007). Buoyant forces act in a vertical direction in the water column and result from the mass, volume and compressibility of the tissues and air space of the animal body (Heine 1995). Animals that are positively or negatively buoyant must expend extra energy when they move in the direction opposite to buoyant forces, whilst they may save energy when moving in the same direction (Lovvorn and Jones, 1991). It is not clear, however, if any energy saved in one direction balanced the increase energy spent in the other direction. A recent study by Davis and Weihs (2007) on elephant seals (Mirounga angustirostris) was inconclusive in this respect. In diving, air-breathing animals that do not trap air in thick fur or feathers, or that regularly dive below the depth at which lung collapse
occurs, net buoyancy is largely determined by the relative amounts of low-density lipid and high-density lean tissues in the body. The deployment of video-data logging and the recent development of the accelerometer tag have permitted the study of stroke and glide pattern in wild aquatic animals (Sato et al. 2003, Williams et al. 2004, Miller et al. 2004, Lovvorn et al. 2004, Watanabe et al. 2006, Wilson et al. 2006). For example, Watanabe et al. (2006) demonstrated that Baikal seals (Pusa sibirica) adopted different stroke patterns according to their individual buoyancy. By comparing the swimming pattern of a Baikal seal with and without an attached lead weight, they showed that when the seal was less buoyant it used longer prolonged gliding on the descent.

Grey seals are thunniform animals that swim with oscillatory movements of a paired hind flipper (Webb 1988). Thrust is the major component acting against drag to move forward (review in Webb 1988) and propulsive efficiency for phocid is high at approximately 0.85 (Fish et al. 1988). This high efficiency is common to all marine mammals compared to semi-aquatic mammals with a propulsive efficiency as low as 0.2 (Fish 1993). The high efficiency for seals is due to the maintenance of nearly continuous thrust production over the stroke cycle and a hydrofoil morphology which enhances high thrust with reduced drag (Fish 1994). In this study, we describe fine scale stroke and glide pattern of grey seals during foraging dives in the absence of vertical buoyancy effect. Seals had to swim 80 m horizontally underwater from a breathing box to a submerged automatic feeding station in a purpose built swimming tank. 3-D accelerometers were deployed on the animals to detect fine-scale oscillatory movements of their paired hind flipper. The aims of the study were to:

a) Compare the stroke and glide patterns employed by animals swimming to and from the feeding station.
b) Determine if there was a relationship between swimming speed and stroking patterns.

c) Examine the relationship between locomotory cost and swimming characteristics
Material and methods

Study animals

Five grey seals *Halichoerus grypus* (one adult female A1 and four pups P1-P4) were used in this study. All seals were caught in the wild at Abertay Sands (Fife, UK) and kept in outdoor seawater pools in the captive facility at the Sea Mammal Research Unit (SMRU, St Andrews, UK). Seals were fed daily on various combination of herring (*Clupea harraengus*, 2005 and 2006), sprat (*Sprattus spratus*, 2005 and 2006), whiting (*Gadus merlangus*, 2005), mackerel (*Scomber scombrus*, 2006) and haddock (*Melanograminus aeglefinus*, 2006 only for the adult seal). Seals were regularly weighed on a platform to an accuracy of ± 0.1 kg. Seals were released into the wild after a maximum of 13 months in captivity (see Chapter 2 for more details). All capture and handling maintenance procedures conformed to the Animals (Scientific Procedures) Act 1986 under project licence number 60/3303.

Experimental design

The SMRU experimental facility comprises a large seawater pool (42 × 6 × 2.5 m) that can be totally covered by aluminium meshed panels so seals can only surface in a breathing box linked to an open-flow respirometry system (see Chapter 2 for more details). The pool was longitudinally partitioned with a net into lanes so that the distance between the breathing box and the feeding station was 80 m (Figure 3.1). Hereafter, travel distance from the breathing box (equivalent to the surface) to the feeding patch (equivalent to the depth of the feeding patch) will be referred to as the “descent” and the return journey the “ascent”. The foraging patch consisted of a
purpose built device that delivered fish on a conveyor belt to a feeding window 2 m below the surface. An important aspect of the set-up was that seals were free to dive at will and select their own foraging behaviour.

![Plan of the experimental pool](image.jpg)

Figure 3.1. Plan of the experimental pool (42 x 6 x 2.5 m). Seals surface to breathe at the respirometry chamber (RC). The feeding station (F) was placed 80 m away from the RC.

Experiments

Foraging trials were conducted with the feeding station positioned 80 m away from the breathing box to simulate patch depth. A trial comprised a series of dives to the feeding station from the breathing box. The start and end time of each dive and times of arrival at and departure from the feeding station were recorded from direct observation at the breathing box and an underwater video system at the feeding station. These recorded observations represent the visual data. Swim speed was estimated as distance between breathing box and feeding station (i.e. 80 metres) divided by time between observed departure and arrival. All seals were equipped with an accelerometer (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan) attached on their lower back during experiments which recorded swim speed every second and
3-D accelerations 32 times per second, to provide an independent measure of swimming speed and stroking pattern. Accelerometers were deployed on the animals for 5 or 7 consecutive days and were replaced if experiments lasted longer. Side to side flipper movements could be detected as fluctuations in acceleration along the transverse axis (x axis, hereafter referred to as swaying acceleration).

**Acceleration data analyses**

Data downloaded from the accelerometer were analysed (Matlab software, version 7.0.1) to obtain high resolution graphs showing the lateral swaying accelerations during a particular dive (Figure 3.2). Raw sensor data were initially filtered to eliminate any low frequency variations that resulted from various turning and rolling movements. The remaining peaks and troughs with absolute amplitudes greater than a set threshold were considered to be strokes and used in analyses (Sato et al. 2003). Thresholds were determined for each individual using survival curves showing the number of strokes detected versus a range of thresholds. The threshold for which the curve started to flatten was selected for each seal (Figure 3.3). Peak-trough duration or trough-peak duration corresponded to a single flipper stroke; left to right or right to left. The overall flipper stroke frequencies (Hz) during “descent” and “ascent” phases were calculated from the total number of strokes divided by the duration of each phase for each dive.
Figure 3.2. x-axis data from a 3D accelerations recorder (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan) for a juvenile seal showing changes in lateral acceleration over a dive.

Figure 3.3. Typical example of lateral acceleration of a grey seal swimming back to the respirometry chamber (a). Example of a survival graph used to select a threshold to detect strokes in the analyses (b).
The within burst stroking rate (hereafter referred as dominant stroke cycle frequency) represents the frequency at which seals move their paired-hind flippers to produce thrust during swimming. It differs from the overall stroke frequency by not taking into account gliding period where there was no movement of the paired-hind flippers. The dominant stroke cycle frequency represents the frequency at which seals oscillate their paired-hind flippers during stroking period. Therefore the dominant stroke cycle frequency was higher than the overall stroke frequency. The dominant stroke cycle frequency was determined using Fast Fourier Transformation. This technique can be applied to signals with periodic properties as swaying accelerations. Power spectral density (PSD) was calculated dive by dive on the “descent” and “ascent” for each seal to determine the dominant stroke cycle frequency using a Fast Fourier Transformation (Figure 3.4). Peaks were apparent on PSD graph and represented the dominant stroke cycle frequency used by seals on the “descent” or the “ascent” of a particular dive.

![Graph](image)

Figure 3.4. Typical example of lateral acceleration of a grey seal swimming to the feeding station (a). Example of power spectral density calculated from lateral accelerations of grey seals swimming to and from the feeding station (b).

We measured the percentage of time each seal was actively stroking with its tail during “descent” and “ascent” of dives using the methodology of Miller et al. (2004).
Briefly, we used acceleration values in the accelerometer’s $x$-axis (i.e. lateral axis) to quantify when seals were stroking versus gliding. Filtered acceleration values were squared and smoothed over the period of a typical stroke (0.63 s, see Figure 3.5). For each seal a threshold of three times the maximum acceleration value during long glides was used as a threshold to identify gliding periods in the dive records. Acceleration values superior to that threshold were designed as stroking and values below as gliding.
Figure 3.5. Example of measurements of data from accelerometer tag (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan) during the “descent” (Ai – Ci) and “ascent” (Aii – Cii) of a pup swimming to and from the feeding station. (A) shows the swaying acceleration. (B) and (C) show the calculation step necessary to estimate the percentage of time seals were actively stroking during transit swimming to and from the feeding station. The dotted line represents the threshold value. Under the threshold the seal was gliding and above the threshold the seal was actively stroking (see text for more details).

Swimming speed was calculated using the calculation for the rotation (rev.s\(^{-1}\)) of an external turbine. The rotation value was converted to actual swimming speed (m.s\(^{-1}\)).
using a calibration line that was estimated for the adult and the pups. The calibration line was obtained by recording the times taken to swim fixed distances along lanes in the pool. The speeds at which gliding started and stopped were assessed using accelerometry data for each seal on the “descent” and the “ascent”. The minimum speeds reached when seals turned around the net at 40 m were not included (Figure 3.6). Few swim speed data were obtained from the accelerometer tags because the turbine was regularly obstructed by seals hair and algae. The turbine was either working properly or not working at all with a majority of recorded velocities equal to zero. We visually selected swim speed profiles for dives that presented a realistic pattern. A selected swim speed profile was characterised by consistent swimming at realistic speed with acceleration and deceleration phases throughout the “descent” and “ascent” (Figure 3.2). If the swim speed profile was unrealistic for any given period of time, the entire day of experiments was taken out of the data set. An unrealistic profile was often characterised by low swim speeds and periods where the speed indicated 0 during “descent” and “ascent” phases. The selected swim speed profiles were then compared to the swim speed data obtained visually.
Figure 3.6. Turbine swim speed data for seal A\(_1\) showing changes in velocity over a dive.

*Locomotor costs*

Oxygen uptake during bouts of voluntary diving was measured by open-flow respirometry (see Chapter 2 for more details). Briefly, as stated before seals could only surface to breathe in the respirometry chamber (Figure 3.1). Air was drawn from the respirometry chamber into the laboratory where oxygen concentration of a subsample of this air stream was determined. The respirometry system was calibrated daily at the end of each experiment using the nitrogen dilution technique described by Fedak *et al.* (1981). For each dive, oxygen uptake of the seal was calculated using the following equation from Fedak *et al.* (1981):

\[
VO_2 = \frac{0.2094V_{N_2}}{0.8} \left( \frac{\Delta C}{\Delta C^*} \right)
\]

Where \(\Delta C\) and \(\Delta C^*\) refer to the deflection of the analyser during measurement and calibration respectively and \(V_{N_2}\) was the flow rate of nitrogen used in the calibration.
Locomotor costs during a dive were determined from the difference between total oxygen uptake over the dive and maintenance costs using the following equation from Williams et al. (2004):

\[
\text{Locomotor cost} = V_{O_2,\text{div}} - (BMRt)
\]

Where locomotor cost and \( V_{O_2,\text{div}} \) (total oxygen consumption for the dive) were in mL O\(_2\) kg\(^{-1}\), BMR was the basal metabolic rate in mL O\(_2\) kg\(^{-1}\) min\(^{-1}\) (according to Kleiber 1975) and \( t \) was dive duration in minutes. This equation assumes that the basal metabolic rate was a reasonable approximation of the maintenance costs for a diving seal (see Williams et al. 2004 for more details).

We then calculated the total travel costs during a dive by subtracting the maintenance cost of the time seals spent at the feeding station. Total travel costs were determined using the following equation:

\[
\text{Total travel cost} = V_{O_2,\text{div}} - (BMRt_{BD})
\]

Where \( t_{BD} \) is bottom duration (i.e. time spent at the feeder) in minute.

We selected dives where seals showed no activity at the feeding station by examining data obtained from accelerometer tags. Accelerometer tags could detect any movements of the tail of the seals during transit and foraging phases of dives. Dives used in the present chapter corresponded either to short dives where seals did not stay at the feeder or dives where seals stayed motionless in front of the feeder. Therefore, in the selected dive, locomotion costs as defined previously resulted exclusively from transit swimming.

**Statistical analyses**

\( t \)-test, paired \( t \)-test, Kolmogorov-Smirnov test for normality and Spearman’s correlation statistics (performed using R v2.60) were used in the analyses. The
relationship between swimming speed and stroke and glide pattern was investigated using linear mixed effect model. For the model, swim speed data obtained visually were used as there was insufficient velocity data obtained from the accelerometer tags. The significance of a parameter was tested by removing each parameter from the full model and looking at the effect of the deletion on the fit of the model using likelihood ratio tests.

Results

A total of 876 dives obtained from visual data and 624 dives obtained from accelerometer tag were analysed for 5 grey seals (1 adult: A₁, and 4 pups: P₁, P₂, P₃ and P₄). After visual inspection and selection, 224 dives from the accelerometer tags had usable recorded velocity for four animals (A₁, P₁, P₂ and P₄). There was no swim speed data from the accelerometer tags for P₃. There was a strong positive correlation between the visual and accelerometer swim speed data (Correlation=0.863, Z = 33.36, p<0.001), but the speed estimates obtained from visual data were on average 1.03 times higher than those from accelerometer records which was significant (Paired t-test, T=5.70, p<0.001) (Figure 3.7). In the calculation, however, visual swim speed was obtained by dividing transit durations by the distance swum. By swimming diagonally seals could reduce the swimming distance by a few metres (78.4 metres instead of 80 metres) which resulted in a distance 1.02 times lower than the one used in the calculation. When using this new distance (78.4 metres), swim speeds estimates obtained visually and from the accelerometer were not significantly different (Paired t-test, T=-1.61, p = 107). The variance in the relationship was probably due to measurement error in recording the
start and end of active swimming and seals slowing or stopping when out of view during transit to and from the surface. While this will reduce the statistical power of any comparisons and increase the probability of type II error, it ensured that any observed relationships were likely to be real, i.e. there was little chance of type I error.

Figure 3.7. Swim speeds (in m.s$^{-1}$) obtained from accelerometer tag and from visual observations. Each point represents the mean swim speed for the “descent” or “ascent” of a particular dive. The solid line gives the 1:1 linear relationship.

_Differences between “descent” and “ascent”_

Differences between “descent” and “ascent” stroke and glide patterns were investigated by analysing 624 dives obtained from accelerometer tag. Differences in mean swim speeds between “descent” and “ascent” were examined using 876 dives obtained from visual data. A summary of the swimming characteristics is shown in Table 3.1. There were no minimum and maximum speeds for P3 because there was no swim speed data recorded with the accelerometer tags for that seal.
Table 3.1. Summary of swim speed and swim pattern characteristics obtained from visual data and accelerometer tag for each seal on the “descent” and “ascent” of dives.

Values are means ± s.d. and numbers of dives are in brackets

<table>
<thead>
<tr>
<th>Transit phase</th>
<th>Seals</th>
<th>Swim speed (m.s(^{-1}))</th>
<th>% time gliding</th>
<th>Stroke frequency (Hz)</th>
<th>Dominant stroke cycle frequency (Hz)</th>
<th>Maximum speed before gliding (m.s(^{-1}))</th>
<th>Minimum speed when stopped gliding (m.s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>“Descent”</td>
<td>A(_1)</td>
<td>1.12 ± 0.17 (98)</td>
<td>45.56 ± 6.80 (72)</td>
<td>1.20 ± 0.20 (72)</td>
<td>2.73 ± 0.21 (72)</td>
<td>1.32 ± 0.15 (66)</td>
<td>0.86 ± 0.18 (66)</td>
</tr>
<tr>
<td></td>
<td>P(_1)</td>
<td>1.50 ± 0.12 (162)</td>
<td>14.81 ± 3.61 (104)</td>
<td>1.49 ± 0.10 (104)</td>
<td>1.63 ± 0.15 (104)</td>
<td>2.32 ± 0.27 (104)</td>
<td>1.34 ± 0.23 (104)</td>
</tr>
<tr>
<td></td>
<td>P(_2)</td>
<td>1.61 ± 0.20 (95)</td>
<td>8.39 ± 4.64 (54)</td>
<td>1.36 ± 0.20 (54)</td>
<td>1.70 ± 0.17 (54)</td>
<td>2.33 ± 0.38 (33)</td>
<td>1.52 ± 0.35 (33)</td>
</tr>
<tr>
<td></td>
<td>P(_3)</td>
<td>1.74 ± 0.25 (239)</td>
<td>10.55 ± 5.66 (141)</td>
<td>1.53 ± 0.20 (141)</td>
<td>1.70 ± 0.13 (141)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P(_4)</td>
<td>1.75 ± 0.13 (282)</td>
<td>13.51 ± 7.24 (263)</td>
<td>1.47 ± 0.19 (263)</td>
<td>1.89 ± 0.15 (263)</td>
<td>2.34 ± 0.07 (29)</td>
<td>1.77 ± 0.11 (29)</td>
</tr>
</tbody>
</table>

| “Ascent”      | A\(_1\) | 1.02 ± 0.14 (97) | 56.42 ± 5.07 (72) | 0.94 ± 0.15 (72) | 2.64 ± 0.17 (72) | 1.19 ± 0.14 (66) | 0.70 ± 0.15 (66) |
|               | P\(_1\)  | 1.34 ± 0.22 (162) | 32.41 ± 8.02 (104) | 1.24 ± 0.16 (104) | 2.20 ± 0.54 (104) | 2.12 ± 0.35 (104) | 1.05 ± 0.25 (104) |
|               | P\(_2\)  | 1.41 ± 0.11 (95) | 32.50 ± 8.67 (54) | 0.91 ± 0.14 (54) | 1.97 ± 0.21 (54) | 2.07 ± 0.37 (33) | 1.13 ± 0.48 (33) |
|               | P\(_3\)  | 1.51 ± 0.14 (239) | 19.29 ± 6.23 (141) | 1.35 ± 0.14 (141) | 1.84 ± 0.12 (141) |                               |                               |
|               | P\(_4\)  | 1.51 ± 0.12 (282) | 27.74 ± 8.66 (263) | 1.15 ± 0.16 (263) | 1.99 ± 0.15 (263) | 2.24 ± 0.07 (30) | 1.53 ± 0.13 (30) |

Mean “descent” speed varied between 1.12 m.s\(^{-1}\) and 1.75 m.s\(^{-1}\) while mean “ascent” speed varied between 1.02 m.s\(^{-1}\) and 1.51 m.s\(^{-1}\). The adult, A\(_1\), swam significantly slower than the pups on both “descent” and “ascent” (t-tests, T\(_{\text{Descent speed}}\) = -23.17, p<0.0001; T\(_{\text{Ascent speed}}\) = -28.97, p<0.0001). “Descent” phases were characterised by higher swim speeds and overall stroke frequencies whilst percentage time gliding was
lower than on the “ascent”. “Ascent” phases were characterised by short burst consisting of a few strokes and longer periods gliding between bursts compared with the “descent”. In addition, dominant stroke cycle frequencies, calculated by power spectral density, were lower on the “descent” for all seals except for A1. Both the initial and final speeds of individual glide phases were higher on the way to the feeding station compare to the return journey. Figure 3.8 (A-F) shows that all differences between “descent” and “ascent” stroking patterns were significant (paired t-test, p< 0.0001 for all).
Figure 3.8. Boxplots of the differences in swimming characteristics between the “descent” and the “ascent” of dives to 80 m for each seal. * indicates that the difference between the “descent” and “ascent” is significant (Paired t-tests, p<0.05). (A) shows the difference in swim speeds between “descent” and “ascent”. (B) shows the difference in percentage time gliding between “ascent” and “descent”. (C) shows the difference in stroke frequency between “descent” and “ascent”. (D) shows the difference in the dominant stroke cycle frequency between “ascent” and “descent”. (E) shows the difference in the maximum speed reached before gliding between
“descent” and “ascent”. (F) shows the difference in the minimum speed reached at the end of the gliding period between “descent” and “ascent”. The bottom and top of each box marks the 25th and 75th percentile respectively. The black and grey lines within the box represent the median and mean respectively. Whiskers above and below the box indicate the 90th and 10th percentiles.

**Relationship between swimming speeds and stroking patterns**

Mass had a significant effect on stroking pattern. Swimming speeds appeared to decrease as mass increased ($y = 1.71 - 0.004x$) ($n = 1271$, $R^2 = 0.38$, $F = 757.33$, $p < 0.0001$) and percentage gliding increased with increasing mass ($y = 7.74 + 0.299x$) ($n = 1271$, $R^2 = 0.51$, $F = 1302.87$, $p < 0.0001$) (Figure 3.9). When data from the adult seal were removed, the relationships held true but were less strong with little R-squared ($n = 1127$, $R^2 = 0.04$, $F = 44.11$, $p < 0.0001$ and $n = 1127$, $R^2 = 0.07$, $F = 82.13$, $p = 0.011$ for swimming speed in relation to mass and percentage gliding in relation to mass respectively). In addition, the analyses showed a strong negative correlation between stroke frequency and percentage gliding (Correlation = -0.870, $Z = -37.2$, $p < 0.0001$) (Figure 3.10). This correlation was due to the fact that overall stroke frequency was a result of the combined effects of percentage gliding and the dominant stroke cycle frequency used by seals during a particular dive. Therefore the relationship was not expected to be linear.
Figure 3.9. Graph showing the relationship between mass (kg) and a) swim speed (m.s\(^{-1}\)) and b) percentage gliding during transit swim speed. The solid lines give linear least-squares fit.
Chapter 3

Figure 3.10. Graph showing the relationship between percentage gliding and stroke frequency (Hz) during transit swim speeds. See text for more details.

Visual swim speeds and stroke and glide data obtained from the accelerometers were used to create linear mixed effect models to investigate the relationship between swimming speed and stroking pattern. A summary of the parameters obtained is presented in Table 3.2. Seal ID and mass were included as random effects; percentage gliding and dominant stroke cycle frequency and the interaction between percentage gliding and the dominant stroke cycle frequency as fixed effects; swim speed was the response variable. Overall stroke frequency was not included into the model as it was strongly correlated to percentage gliding. Results are summarised in Table 3.2. The model indicated that only percentage gliding had a significant effect on transit swim speeds. For all seals, swim speeds significantly decreased with increasing percentage gliding (See Figure 3.11 a). The results show, however, that there was no consistent relationship between dominant stroke cycle frequencies and swim speed.
(see Figure 3.11, b) and no interaction between percentage gliding and dominant stroke cycle frequency.

When separating data between juveniles and the adult, we found a strong positive relationship ($n = 136$, $y = -0.64 + 0.67x$) between swim speeds and dominant stroke cycle frequency for the adult ($R^2 = 0.59$, $F = 190.32$, $p < 0.0001$). On the contrary, we found a negative relationship ($n = 1126$, $y = 1.78 – 0.12x$) between swim speeds and dominant stroke cycle frequency for juvenile seals ($R^2 = 0.04$, $F = 39.46$, $p < 0.0001$). This relationship was weak ($R^2 = 0.04$) because of large variations within individuals and because of one juvenile for which the relationship seems to be positive (see Figure 3.11 b).

### Table 3.2. Results of linear mixed-effects models describing the relationship between seal’s mean swim speed during transits to and from the feeding station and stroking patterns. Seal ID and mass were included as random effects; percentage gliding, dominant stroke cycle frequency and the interaction between percentage gliding and the dominant stroke cycle frequency as fixed effects; swim speed was the response variable. The slope values ± s.e.m. are given for significant terms (in bold type).

<table>
<thead>
<tr>
<th>Term removed:</th>
<th>AIC</th>
<th>L-Ratio</th>
<th>Slope</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swim speed full model</td>
<td>-1455.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage gliding</td>
<td><strong>-1094.88</strong></td>
<td><strong>364.18</strong></td>
<td>-0.006 ± 0.002</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td>Dominant stroke cycle frequency</td>
<td>-1453.64</td>
<td>5.42</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Interaction between percentage gliding and stroke frequency</td>
<td>-1456.27</td>
<td>0.79</td>
<td>0.37</td>
<td></td>
</tr>
</tbody>
</table>

AIC, Akaike information criterium
Figure 3.11. Swim speeds in relation to stroking parameters for each animal (A₁, P₁, P₂, P₃ and P₄). Each point represents the mean swim speed during transit to and from the feeding station during a particular dive. The solid lines give linear least-square fit. a) shows the relationship between swim speeds (m.s⁻¹) and percentage gliding and b) shows the relationship between swim speeds (m.s⁻¹) and dominant stroke cycle frequency (Hz).
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Locomotor costs

Data obtained for three individuals (n = 6, 5 and 12 for A₁, P₁ and P₄ respectively) were used to examine the relationship between oxygen consumption and swimming characteristics. Only a few data were available because seals were active at the feeding station during most of the dives.

There was no significant relationship between swimming speeds and locomotor costs (Figure 3.12Ai) (p = 0.63, 0.92 and 0.77 for A₁, P₁ and P₄ respectively). For two seals, locomotor costs increased linearly with stroke frequency (Figure 3.12Bi) (R² = 0.94 and 0.47, p = 0.01 and 0.014 for A₁ and P₄ respectively) and decreased significantly with increasing gliding (Figure 3.12Ci) (R² = 0.77 and 0.46, p = 0.049 and 0.016 for A₁ and P₄ respectively). The relationships between locomotor costs and the two variables (i.e. stroke frequency and percentage gliding) were not significant for P₁ (p = 0.204 and 0.985 for stroke frequency and percentage gliding respectively).

There were no relationships between total travel costs and the different variables except for seal P₄. Total travel costs increased linearly with increasing stroke frequency and decreased with gliding for P₄ (Figures 3.12 Bii and Cii) (R² = 0.46 and 0.50, p = 0.015 and 0.010 for stroke frequency and gliding respectively).
Figure 3.12. Locomotor costs (i) and total travel costs (ii) of three diving grey seals in relation to swim speed (A), stroke frequency (B) and percentage gliding (C). Points represent individual dives. Solid lines are the least squares linear regressions through the data point for each individual where the relationship is significant.
Discussion

All seals swam faster to the feeding station compared to the return phase. This behavioural strategy that has been discussed by Gallon et al. (2007) permitted the examination of the relationship between swimming speed and stroke and glide pattern. Seals used burst and glide swimming during both “descent” and “ascent”, which has been identified as a particularly efficient way of travelling for aquatic vertebrates (Lovvorn et al. 1999, Williams et al. 2000, Lovvorn et al. 2001).

Intermittent locomotion as burst and glide swimming is usually assumed to increase energy expenditure because acceleration and deceleration add costs to the energetic demands of movements (Kramer and McLaughlin 2001). Intermittent locomotion, however, can also reduce energy costs when forward movement continues during the pauses or when muscles function more efficiently (Weihs 1974, Videler and Weihs 1982). For example, Videler and Weihs (1982) developed a model to show how fish can choose the most efficient burst and glide cycle for a given average speed. Their model was based on the observation that for a variety of fish, stroke and glide swimming was used at both slow and fast speeds and continuous stroking at intermediate speeds. They related these optimal swimming modes in relation to swim speeds with muscles characteristics (i.e. red muscles which are powered aerobically and white muscles which are powered anaerobically). In addition, prolonged gliding allows diving vertebrates to avoid active drag. High-amplitude movements are a departure from the streamlined shape of the swimmer and theoretically result in higher level of drag (Fish 1988). Videler and Weihs (1982) estimated the drag while gliding with a straight body to be only one third of the drag while swimming for fish, reducing energy expenditure by as much as 50%.
Effect of mass

The present study suggests that mass had a significant effect on the stroke and glide pattern of swimming seals. Swimming speed seemed to decrease with increasing mass. The apparent effect of mass was reinforced by the adult seal swimming much slower than the pups. Experiments with the adult were held just before the breeding season (August – September 2006) and it has been noted that pregnant female seals decrease their swim speed throughout the period before they breed in comparison to similar size non-pregnant female seals (Gallon et al. 2007). This behaviour is consistent with the hypothesis that female grey seals prepare for the breeding season by reducing their energy expenditure (Sparling et al. 2006).

Mass appeared to also have an effect on gliding durations. Gliding duration increased for heavier animals. The relationship between mass and percentage time gliding could be attributed to the effect of momentum. For a given speed, heavier swimmers will glide longer than lighter ones when they stop stroking. Momentum increases linearly with body mass and drag opposing the glide depends on surface area, which declines relative to body volume as mass increase (i.e. linear effect versus non-linear effect because surface area scales to \( Mass^{0.67} \)). Therefore fatter animals will decelerate more slowly. Clark and Bemis (1979) also found that for a range of penguin species, swimming horizontally, the duration of gliding increases with increasing body mass (1-30 kg).

Relationship between swimming speed and stroking pattern

Seals swimming to and from the feeding station in our study and seals swimming in the wild are either actively stroking or gliding. This is why there was a direct
correlation between the overall stroke frequencies (i.e. number of strokes divided by duration of “descent” or “ascent”) and percentage time gliding. Prolonged gliding allows diving animals to avoid active drag (i.e. drag resulting from the body not being in a streamline shape), however, it places a limit on maintaining propulsion. Therefore swimmers generally rely on a stroke and glide mode of swimming to maintain forward speed (Weihs 1974, Videler and Weihs 1982), at least during horizontal swimming.

The present study demonstrates a strong relationship between swimming speed and stroke and glide patterns. Swimming speed increased with increasing stroke frequency and decreased with increasing percentage gliding. Previous studies have suggested that aquatic vertebrates regulate their swim speed by varying the duration of gliding between strokes (Skrovan et al. 1999, Williams et al. 2000, Watanuki et al. 2003). Lovvorn et al. (1999) found that Brunnich’s guillemots varied glide duration to modulate speed while maintaining constant stroke duration, presumably allowing for efficient muscle contraction. On the contrary, Davis et al. (2001) found that the average swimming speed of northern elephant seals varied little with swimming mode and was not a good indicator of propulsive effort. In the wild, however, deep divers face the effect of changes in buoyant forces as depth varies and can take advantage of it. As air spaces compress with increasing depth, the volume of the diver decreases without an accompanying reduction in mass and the animal becomes less buoyant. For example, whales and seals can stop stroking and continue to glide downward with little change in swimming speed for long periods during the deeper descending portion of dives over 80 metres (Williams et al. 2000). Seals in the present study
could not take advantage of changes in buoyant forces and therefore swimming speeds decreased during gliding periods.

The speed at which seals started gliding in this study was variable. It seems that there is no particular speed for which seals should stop stroking and use momentum for gliding. The speeds at which seals started and stopped gliding were higher on the “descent” compared to the “ascent” showing that seals were working harder on the “descent” to go faster. Videler and Weihs (1982) calculated the energy saving that is possible if fish choose the right initial and final speed during stroking cycle. Their model shows how fish can choose the most efficient stroke and glide cycle for a given average speed. They found that animals have to balance between lower initial and final speeds during stroking which enhance the efficiency but increase the duration of the cycle which reduce efficiency. To which extent this work is relevant to other swimmers is unknown but further investigations into the efficiency of various stroking pattern resulting in similar average speed is needed for marine mammals.

*Variation in dominant stroke cycle frequency*

Muscle is presumed to have a maximum efficiency when contracting within a narrow range of speeds and loads (Goldspink 1977). Previous studies have suggested that alternating stroking with gliding of variable durations while maintaining a constant contraction speed is the most cost-efficient method of locomotion (Lovvorn *et al.* 1999, Lovvorn 2001). Sato *et al.* (2007) demonstrated that the dominant stroke cycle frequency for aquatic vertebrates is related to body size confirming that muscle characteristics might constrain their contraction rate.
It is not clear yet which one of the dominant stroke cycle frequency and stroke amplitude regulate swim speed. A few studies found a strong relationship between the frequency of the propulsive cycle and increasing velocity whilst amplitude remained constant (Webb 1992, Fish 1993). For example, Webb (1992) showed that bluegill sunfish (*Lepomis macrochirus*) tail-beat frequencies increased significantly with swimming speed while tail-beat amplitude increased only slightly with swimming speed with a slope not significantly different from zero. Other studies, however, suggest that speed and acceleration are primarily mediated via changes in stroke amplitude rather than stroke frequency (Wilson and Liebsch 2003). These studies were carried out on sea turtles, sea lions and penguins which all use lateral appendices for propulsion (i.e. wings and fore-flippers). The relationships between stroke frequency, stroke amplitude and swim speed might thus be related to the characteristics of the appendage used for propulsion and the style of swimming.

In the present study, the relationship between the dominant stroke cycle frequency and swim speed varied between individuals. The adult seal increased its stroke frequency with increasing velocity in accordance with previous studies on thunniform swimmers (Webb 1992, Fish 1993). Juvenile seals did not show the same pattern; three of the four reduced their dominant stroke cycle frequency as velocity increased. These results show that the adult behaved as expected whilst the large variation within the dataset of juvenile individuals suggests that they may still have been learning. In the wild, pups leave the beach as completely naïve foragers. Although they have innate diving and navigational abilities, they have no knowledge of how and where to find suitable food. Therefore, they need time to learn how to most efficiently exploit their environment. The speed at which juveniles seals learn to find their food may affect
their survival rate which is low with only around half of the female pups surviving to recruit into the breeding population (Hall et al. 2001, Hall et al. 2002).

A surprising result was the high dominant stroke cycle frequency found for the adult seal. It is usually assumed that the dominant stroke cycle frequency should decrease as body size increases (Bejan and Marden 2006, Sato et al. 2007). For example, Sato et al. (2007) found that the dominant stroke cycle frequency was proportional to mass\(^{-0.29}\) for animals ranging from 0.5 kg seabirds to 30 000 kg sperm whales. When looking at data within the same species it is not clear however if the relationship holds true. For example, data for Baikal seals showed large variation in dominant stroke cycle frequency between similar size individuals. Given the problems involved with working with large untrained wild animals, data for only one adult seal is presented here. Therefore, results need to be taken with caution and may be not representative and cannot be generalised. Nevertheless, data obtained from a second adult during training trials were also characterised by high dominant stroke cycle frequency during transit swimming. This animal was not kept for experiments because it refused to eat from the feeding station. These results suggest that more work is needed to properly assess the relationship between body size and the dominant stroke cycle frequency for marine mammals, at least within species.

**Oxygen consumption in relation to swimming characteristics**

Sparling et al. (2006) estimated the resting metabolic rate for grey seals to be 1.07 – 2.83 times the predicted BMR of similarly sized adult terrestrial mammals (Kleiber 1975). They found, however, that the diving metabolic rates were lower than those measured under standard conditions by 10 – 30 %, suggesting hypometabolism during
diving in grey seals. Similarly, Williams et al. (2004) calculated submerged metabolic rate of Weddell seal and found also that it was within 10% of the Kleiber (1975) prediction of BMR. If seals use hypometabolism while diving, BMR seems to be appropriate to represent the minimum basal metabolic costs of diving grey seals.

An increase in oxygen consumption with swimming speed has been demonstrated for humans (Holmer 1972) as well as seals and sea lions (Davis et al. 1985, Feldkamp 1987, Fedak et al. 1988, Williams et al. 1991). Swimming speed has therefore been assumed to directly reflect metabolic rate. In these studies, however, the animals were often placed in water flumes and required to swim continuously just below the water surface where drag is higher than a few meters below. Several studies (Weihs 1974, Videler and Weihs 1982) have shown that different swimming pattern, such as stroke and glide swimming in fish, may result in significant energy savings over continuous stroking without an apparent change in velocity. Another study by Skrovan et al. (1999) suggested that swimming speed alone was a poor indicator of locomotor cost because both gliding and active swimming (stroking) often occur at similar speeds in vertical swimming. The present study supports this observation; even when swimming horizontally, oxygen consumption during a dive seemed to be better explained by the percentage time spent gliding during transit swimming than by the mean swim speed. As the present study was based on a small sample size, more effort should be given to collect more data to confirm the present results.

In conclusion, the present study confirms that swim speeds vary in relation to stroking pattern and that the swimming mode (i.e. durations of the stroke and glide periods) adopted by the animal will affect their diving metabolic rate. In terms of locomotor
costs, the results suggest that prolonged gliding periods are economical for our study animals. It is not clear, however, if these findings hold true for wild animals that will be affected by changes of buoyancy with increasing depth.
References


Chapter 4

How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions


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Summary

The duration of breath-hold dives and the time available for foraging in submerged prey patches is ultimately constrained by oxygen balance. There is a close relationship between swim speed and oxygen utilisation so it is likely that breath-hold divers optimise their speeds to and from the feeding patch to maximize time spent feeding at depth. Optimal foraging models suggest that transit swim speed should decrease to Minimum Cost of Transport (MCT) speed in deeper and longer duration dives. Observations also suggest that descent and ascent swimming mode and speed may vary in response to changes in buoyancy. We measured the swimming behaviour during simulated foraging of 7 captive female grey seals (2 adults and 5 pups). Seals had to swim horizontally underwater from a breathing box to a submerged automatic feeder. The distance to the feeder and the rate of prey food delivery could be varied to simulate different feeding conditions.

Diving durations and distances travelled in dives recorded during these experiments were similar to those recorded in the wild. Mean swim speed decreased significantly with increasing distance to the patch, indicating that seals adjusted their speed in response to travel distance, consistent with optimality model predictions. There was however no significant relationship between the transit swim speeds and prey density at the patch. Interestingly, all seals swam 10% - 20% faster on their way to the prey patch compared to the return to the breathing box, despite the fact that any effect of buoyancy on swimming speed should be the same in both directions. These results suggest that the swimming behaviour exhibited by foraging grey seals might be a combination of having to overcome the forces of buoyancy during vertical swimming and also of behavioural choices made by the seals.
Introduction

Breath-hold divers must meet several challenges if they are to forage effectively in the marine environment. Firstly, they must balance the time spent exploiting underwater food resources with time spent unloading CO$_2$ and loading oxygen at the surface. Secondly, they have to operate in a three dimensional environment where food resources may be scattered in aggregated patches, sometimes at great depths. This means that at the end of a surface period, they have to either relocate the previously visited patch or search for another more profitable patch (Ydenberg and Clark 1989). Most optimal foraging models assume that the number of prey encountered during a feeding event is a linear function of the time spent foraging, i.e. foragers should maximise time spent feeding in the prey patch. To do this, they should reduce both their transit time to the feeding area and their recovery time between two successive feeding events (e.g. Ydenberg and Clark 1989). When marine divers feed at greater depths, the time spent travelling to depth and hence the energy cost increase. Consequently, the expected net foraging gain of a dive decreases with increasing depth, and the time-energy trade-off becomes more constrained thereby limiting the behavioural options available to the diver (Charnov 1976, Kramer 1988, Houston and Carbone 1992, Beauchamp et al. 1992).

The rate of oxygen consumption during a dive is directly proportional to the rate of energy expenditure, which is in turn a function of the swimming speed (Davis et al. 1985, Feldkamp 1987, Fedak et al. 1988, Thompson et al. 1993, Stelle et al. 2000, Rosen and Trites 2002). The swimming speeds employed during a dive will have a major impact on the rate of depletion of limited oxygen reserves (Davis et al. 1985, Williams et al. 1991, Thompson et al. 1993, Wilson et al. 2002). Effectively, in order to maximize prey ingestion while minimizing the cost of transport, breath-hold divers
are expected to modulate their swim speed, body angle and swimming pattern (Dunstone and O’Connor 1979, Sato et al. 2003). Thompson et al. (1993) modelled how the optimal foraging tactics of seals may change as a function of the interactions between physiological constraints (cost of swimming) and constraints of prey availability. Their optimality model suggested that seals should swim at the minimum cost of transport (MCT) speed in deep dives but in shallower dives, they could increase the proportion of time spent at the foraging area by swimming faster between the surface and the prey patch.

Animals swimming in the water column are affected by buoyancy, which has been reported to significantly affect the diving behaviour of seabirds and marine mammals (Lovvorn and Jones 1991, Webb et al. 1998, Skrovan et al. 1999, Beck et al. 2000, Williams et al. 2000, Biuw et al. 2003, Watanuki et al. 2003, Sato et al. 2003, Miller et al. 2004, Sato et al. 2007). In diving air-breathing animals that do not trap air in thick fur or feathers, or that regularly dive below the depth at which lung collapse occurs, the net buoyancy is largely determined by the relative amounts of low-density lipid and high-density lean tissues in the body. Individuals that are positively or negatively buoyant expend more energy to maintain a position in the water column than individuals of the same species that are neutrally buoyant (Lovvorn and Jones 1991) and net buoyancy might be expected to directly influence the speeds and swimming modes during descent and ascent swimming (e.g. Webb et al. 1998, Beck et al. 2000). However, in studies on free-diving animals, it is often difficult to distinguish between the effect of buoyancy and effects of drag and motivational state, and results from these studies are therefore often inconclusive on this point.

This paper describes the swimming behaviour of grey seals in relation to food resource availability (prey density and patch distance) in an experimental set-up that
provided us with a unique opportunity to remove the effect of buoyancy on dive
behaviour. We describe the swimming patterns employed during foraging dives. We
use observed behaviours to examine if divers decrease their swim speed as patch
distance increases, as predicted by the swimming behaviour model of Thompson et al.
(1993). As all dives are horizontal rather than vertical and therefore not affected by
buoyancy, we hypothesise that the descent and ascent swimming mode and speed will
be similar in any particular dive.

Materials and methods

Study animals
Seven female grey seals (five juveniles < 1 year of age and two adults) were used in
this study. All seals were caught in the wild at Abertay Sands and the Isle of May
(Fife, UK) and kept in outdoor seawater pools in the captive facility at the Sea
Mammal Research Unit (SMRU, St Andrews, UK). Seals were fed daily on herring
(Clupea harengus) and sandeels (Ammodytes marinus). They were regularly weighed
(+/- 0.1 kg) and body composition was determined periodically using isotopically
labelled water (Speakman, 2001; Sparling et al., 2006). Seals were released back into
the wild after a maximum of 10 months in captivity. All captures and handling
procedures occurred between 2002 and 2004 and conformed to the Animals
(Scientific Procedures) Act 1986 under project licence number 60/2589.
**Experimental design**

The SMRU experimental facility comprises a large seawater pool (40 x 6 x 2.5 m) that can be covered by aluminium mesh panels to restrict animals to surface only in a breathing box linked to an open circuit respirometry system. The pool could also be longitudinally partitioned with nets into lanes so that the distance between the breathing box and a simulated foraging patch (i.e. travel distance) could be varied between 40 and 120 m (Figure 4.1). As phocid seals have no air in their fur and routinely exhale before diving, they have few compressible spaces so that change in depth has only a small effect on buoyancy and no discernible effect on shape or drag. Net buoyancy effects due to high or low body density will approximately cancel out during the descent and ascent phases in vertical dives, so over a complete dive cycle, horizontal, underwater-swimming to and from the feeder will be energetically similar to vertical diving to an equivalent depth. Hereafter, travel distance from the breathing box (equivalent to the surface) to the feeding patch (equivalent to the bottom) will be referred as “descent” and “ascent”.

The foraging patch consisted of a purpose built device that delivered food on a conveyor belt to a feeding window 2 m below the surface (see Sparling et al. 2007). An important aspect of the design is that seals were free to dive at will and select their own foraging behaviour.

The experimenter controlled the prey encounter rate (PER) by varying the spacing of prey items on the conveyor belt. PER was held constant within a given dive, but changed randomly between dives. PER varied between 0 and 13.8 fish per minute. The upper limit of PER corresponds to the highest PER recorded in the wild with video cameras attached to freely diving harbour seals (*Phoca vitulina*) feeding on sandeel (Bowen et al. 2002).
Figure 4.1. Plan of the experimental pool (40 x 6 x 2.5 m). Animals could only surface to breathe at the respirometry chamber. The feeding patch could be placed at 40, 80 or 120 m away from the surface. This set-up allowed us to measure dive duration, “descent” speed (1), bottom time, “ascent” speed (2), oxygen consumption and quantity of prey eaten, for every dive.

**Measurement of foraging behaviour**

Foraging behaviour was investigated in relation to both prey density and the distance between the prey patch and the breathing box. Trials were conducted with the feeding station positioned 40 m, 80 m, and 120 m from the breathing box. Five of the seven seals were tested at all three distances while two of the juvenile seals were only tested at 80 m. Animals were fasted for > 15 hours before each feeding trial. The start and the end time of each dive and times of arrival at and departure from the feeder were recorded from direct observation at the breathing box and an underwater video system at the feeder. These recorded observations represent the visual data.

Swim speed was estimated as distance between breathing box and feeder divided by time between observed departure and arrival. Time-depth-recorders (Mk 8 TDR,
Wildlife Computers), attached to the seals’ heads, provided an independent measure of swimming speeds and of durations of travelling and surface periods. The MCT speed was estimated from the metabolic rate-swim speed relationship for grey seals swimming in a flume tank (Fedak et al. 1988, Thompson et al. 1993). The measured MCT speed was approximately 1.3m.s$^{-1}$ and unrelated to body mass.

**Linear mixed effect model for swim speeds**

Swimming speed in relation to patch distance and prey density was assessed using linear mixed effect models in R (v2.01). Models were constructed to predict the “descent” and “ascent” speed during the dives. We could expect a seal to alter its “ascent” speed in response to the prey encountered during a dive, but its “descent” speed could also be a response to the prey encountered on the preceding dive. Therefore we calculated an index of transit swim speeds from visual data for each dive for each animal. To make the indices easily comparable between seals we calculated an index as the sum of the:

$$
\text{Index} = (AS_n - M_{AS}) + (DS_{n+1} - M_{DS})
$$

Where $AS_n$ is the “ascent” swim speed on dive $n$ and $DS_{n+1}$ is the “descent” swim speed on the next dive. $M_{DS}$ and $M_{AS}$ are the mean “descent” and “ascent” speeds for a given seal overall distances. The index was positive when a seal swims faster to and from the feeder on a particular dive compared to the overall mean “descent” and “ascent” speeds for a given seal over all distances and vice versa.

PER and mass as continuous variables and patch distance as a factor (40, 80, 120 m) were included as fixed effects and seal $i.d.$ and PER were included as random effects.
This allows the model to fit separate slopes and intercepts for the relationship between index and PER for each seal. We used swim speed data obtained visually from 5 seals travelling to 40, 80 and 120 m to carry out this analysis. Deletion tests were used to assess the significance of each parameter in the models.

**TDR data analyses**

Swimming behaviour was investigated using Mk8 TDRs that incorporated a turbine swim speed sensor. The TDR was set to log speed every second. Each TDR speed metre was calibrated on both pups and adults by recording the times taken to swim fixed distances along lanes in the pool. Swim speed profiles were plotted and examined visually for each dive for each animal (Figure 4.2).

Swim speed profiles were characterised by a “descent” phase (active swimming from the breathing box to the feeder), a phase of foraging at the feeder and an “ascent” phase (active swimming from the feeder to the breathing box). The start and end of the dive were determined both by the wet/dry sensor of the TDR and by a sudden change in swim speed between 0 and 1.5 - 2 m.s\(^{-1}\) within 2 seconds. The foraging phase was characterised by stationary periods or relatively slow swimming in the vicinity of the feeder with occasional bursts of activity. The “ascent” phase was similar to the “descent” phase with a rapid increase in swim speed as seals left the feeder and a decrease upon arrival to the breathing box. For each dive, we calculated the mean speeds and the number of acceleration/deceleration phases (resulting from so-called ‘burst-and-glide’ swimming) during the “descent” and the “ascent” phases. Speeds are presented as means ± one standard deviation.
Figure 2. TDR data for K on the 8th of April 2002 showing changes in velocity over a dive. This was a dive to 40 m with a density of 3.2 fish.min\(^{-1}\) at the patch.

**Buoyancy calculation**

Because seals were swimming horizontally, buoyancy cannot directly explain potential differences between “descent” and “ascent” speeds in our study. However, it is possible that seals may employ a different level of swimming effort during “descent” and “ascent” as a conditioned response to their actual body condition and buoyancy. To test this hypothesis, we estimated the buoyancy for each seal through the year where body composition measures were available. For five of the experimental seals, body composition was used to calculate the seal density according to:

$$\rho_{\text{seal}} = (\rho_l \times P_l) + (\rho_p \times P_p) + (\rho_b \times P_b) + (\rho_{bw} \times P_{bw})$$
Where \( \rho \) is the density of the component and \( P \) the proportion of the component for lipid (l), protein (p), bone (b) (ash) and body water (bw) respectively. We used published values for the density of body components in humans (Moore et al. 1963) \((\rho_l=0.9007 \text{ g.cm}^{-3}, \rho_p=1.340 \text{ g.cm}^{-3}, \rho_b=2.300 \text{ g.cm}^{-3} \text{ and } \rho_{bw}=0.994 \text{ g.cm}^{-3})\).

The proportions of body water, lipid, protein and bone mineral were estimated using Reilly and Fedak’s (1990) equations for grey seals:

\[
\begin{align*}
P_{bw} &= -0.234 + 0.971 (^{3}\text{HHOspace}) \\
P_l &= 105.1 - 1.47 (P_{bw}) \\
P_p &= 0.42 (P_{bw}) - 4.75 \\
P_b &= 100 - (P_{bw} + P_l + P_p)
\end{align*}
\]

Buoyancy was then calculated using the following equation:

\[
B_T = (\rho_{\text{seawater}} - \rho_{\text{seal}}) \times V \times g
\]

Where \( B_T \) is total buoyancy (N), \( \rho_{\text{seawater}} = 1.028 \text{ g cm}^{-3}, \rho_{\text{seal}} \) is the density of the seal (g cm\(^{-3}\)), \( V \) is the volume of the seal in cm\(^3\) and \( g \) is the gravity constant. Buoyancy at the surface, at 1 m and 2 m depths was calculated by adding the density of the diving lung volume (DLV) for these different depths to the density of the seal. DLV is about 50 to 60% of total lung capacity (TLC) in phocid seals. Kooyman (1989) estimated TLC from the scaling relationship:

\[
\text{TLC} = 0.10 \text{ M}_b^{0.96}
\]

Where TLC is the volume in litres and \( M_b \) is body mass in kilograms.
Results

A total of 3220 dives obtained from visual data were analysed for 7 female grey seals (2 adults: L and Q, and 5 pups: K, N, R, W and X). Dive characteristics recorded during these experiments were similar to those recorded in the wild (see Sparling et al. 2007). A summary of the swim speed characteristics is shown in Table 4.1. Overall mean “descent” and “ascent” speeds were $1.71 \pm 0.41 \text{ m.s}^{-1}$ and $1.37 \pm 0.36 \text{ m.s}^{-1}$ respectively. Mean “descent” swim speeds were faster than the estimated MCT speed (1.3 m.s$^{-1}$, Thompson et al. 1993) for all seals except for the adult Q. Mean “ascent” swimming speeds were faster than the calculated MCT speed for all pups (range 1.53 to 2.00 m.s$^{-1}$), while for adults, ascent swimming speeds were close to or less than MCT speed (Table 4.1).

Of the 3220 dives for which swim speed was calculated from visual data, independent swim speeds were also obtained from the TDR data for 1289 dives. There was a strong positive correlation between the visual and TDR data (Correlation = 0.786, Z = 53.51, p < 0.001), but the speed estimates obtained from visual data were significantly higher than those from TDR records (Paired t-test, T = 25.17, p < 0.001) (Figure 4.3). The variance in the relationship is due to measurement error in recording the start and end of active swimming and seals slowing or stopping when out of view during transit to and from the surface. Visually recorded swim speed therefore provides a noisier index of true swim speed, while TDR derived data may be less noisy but may slightly underestimate the true swim speed. While this will reduce the statistical power of any comparisons and increase the probability of type II error it does ensure that any observed relationships are likely to be real, i.e. there is little chance of type I error.
Table 4.1. Summary of swim speed characteristics obtained visually for each seal at each patch distance. Swim speeds are in metres per second and values in brackets are standard deviations.

<table>
<thead>
<tr>
<th>ID</th>
<th>Age class*</th>
<th>(Descent-Ascent)</th>
<th>Distances (m)</th>
<th>40</th>
<th>80</th>
<th>120</th>
<th>All distances</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td></td>
<td>40</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Swim speed</td>
<td>descent</td>
<td>ascent</td>
<td>descent</td>
<td>ascent</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>40</td>
<td>1.87 (0.28)</td>
<td>1.49 (0.25)</td>
<td>1.81 (0.20)</td>
<td>1.45 (0.26)</td>
</tr>
<tr>
<td>L</td>
<td>A</td>
<td>536-530</td>
<td>80</td>
<td>1.25 (0.28)</td>
<td>0.98 (0.24)</td>
<td>1.16 (0.27)</td>
<td>0.90 (0.24)</td>
</tr>
<tr>
<td>Q</td>
<td>A</td>
<td>432-432</td>
<td>120</td>
<td>2.27 (0.28)</td>
<td>1.78 (0.26)</td>
<td>1.91 (0.25)</td>
<td>1.45 (0.21)</td>
</tr>
<tr>
<td>K</td>
<td>P</td>
<td>313-296</td>
<td></td>
<td>2.06 (0.33)</td>
<td>2.00 (0.23)</td>
<td>2.20 (0.27)</td>
<td>1.85 (0.1)</td>
</tr>
<tr>
<td>N</td>
<td>P</td>
<td>165-150</td>
<td></td>
<td>2.06 (0.33)</td>
<td>2.00 (0.23)</td>
<td>2.20 (0.27)</td>
<td>1.85 (0.1)</td>
</tr>
<tr>
<td>R</td>
<td>P</td>
<td>193-194</td>
<td></td>
<td>1.77 (0.15)</td>
<td>1.63 (0.18)</td>
<td>2.42 (0.15)</td>
<td>1.77 (0.18)</td>
</tr>
<tr>
<td>W</td>
<td>P</td>
<td>1239-1228</td>
<td></td>
<td>1.7 (0.27)</td>
<td>1.54 (0.29)</td>
<td>3.2 (0.27)</td>
<td>1.7 (0.27)</td>
</tr>
<tr>
<td>X</td>
<td>P</td>
<td>309-309</td>
<td></td>
<td>1.77 (0.15)</td>
<td>1.63 (0.18)</td>
<td>2.42 (0.15)</td>
<td>1.77 (0.18)</td>
</tr>
</tbody>
</table>

* A = adult, P = pups.
Figure 4.3. Swim speeds (m.s$^{-1}$) obtained from TDR and from visual observations. Each point represents the mean swim speed for the “descent” or “ascent” of a particular dive.

**Swimming behaviour**

A total of 1672 dives obtained from visual data for 5 female grey seals (L, Q, K, N and R) were used to create linear mixed effects models. X and W only swam to 80 m, therefore their data were not use in this analysis. A summary of the parameters obtained is presented in table 4.2. The full mixed effects model including data from all 5 seals suggested that body mass had a significant negative effect on swim speed. However, it was clear that this was being driven mainly by the mass change of one large pregnant adult female “Q” whose swim speed index decreased throughout the study (Figure 4.4). This was also apparent when comparing swim speeds to different distances. During the early pregnancy of seal Q, swim speed index to 80 m was 0.5 and in late pregnancy the index fell to –0.6 (Figure 4.5). Seal Q was therefore considered separately and removed from the overall analysis. Four seals (three pups-N, R, K and one adult-L) were therefore included in the final model. Results are summarised in table 4.2.
There was significant variation between individual seals, but the model indicated that seals did not adjust their transit swim speeds in response to changes in either PER (Figure 4.6) or body mass (Figure 4.4). However, they did appear to adjust their swim speed in response to patch distance (Table 4.2, Figure 4.7). Transit swim speeds decreased significantly with increasing patch distance. This decrease in swim speed was most pronounced between 40 and 80 m with little change between 80 and 120 m.

Figure 4.4. Index of transit swim speeds in relation to body mass (kg). There is a different symbol for the pups, the adult L and the adult Q.
Table 4.2. Summary of the parameters obtained from linear mixed-effect models in R (v2.01). Seal id., and Prey Encounter Rate (PER) were included as random effects, distance, mass and PER as fixed effects and the index was the response variable. The significance of a parameter was tested by removing each parameter from the full model and looking at the effect of the deletion on the fit of the model using likelihood ratio tests. For significant terms, the slope value and standard errors are given. Significant terms are in bold.

<table>
<thead>
<tr>
<th></th>
<th>AIC*</th>
<th>L.Ratio**</th>
<th>Value±SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>With Q</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model</td>
<td>1037.75</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Term removed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PER</td>
<td>1037.3</td>
<td>1.55</td>
<td>-0.0058±0.001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mass</td>
<td>1080.05</td>
<td>44.30</td>
<td>-0.2731±0.025</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance 80</td>
<td>1155.64</td>
<td>121.89</td>
<td>-0.2463±0.029</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance 120</td>
<td>1155.64</td>
<td>121.89</td>
<td>-0.2463±0.029</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Individual</td>
<td>0.5820±0.124</td>
<td></td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td><strong>Without Q</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model</td>
<td>642.68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Term removed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PER</td>
<td>641.57</td>
<td>0.89</td>
<td>0.3592±0.030</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mass</td>
<td>641.50</td>
<td>0.82</td>
<td>0.3830±0.032</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance 80</td>
<td>808.36</td>
<td>169.69</td>
<td>-0.3592±0.030</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Distance 120</td>
<td>808.36</td>
<td>169.69</td>
<td>-0.3592±0.030</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Individual</td>
<td>0.2539±0.033</td>
<td></td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

* AIC = Akaike Information Criterium
** L Ratio= Likelyhood Ratio Test
Figure 4.5. Transit swim speeds index in relation to distance (40, 80 and 120 m) for the adult female Q. Data for early and late experiments at 80 m are indicated on the graph.
Figure 4.6. Index of transit swim speeds in relation to PER (fish.min\(^{-1}\)) for each animal. Each point represents the index of transit swim speed during a particular dive. The solid lines give linear least-squares fit.

Figure 4.7. Index of transit swim speeds in relation to distance (m) for each animal. Each point represents the index of transit swim speed during a particular dive.
**Swimming pattern**

In order to describe the swimming patterns of our animals, swim speed profiles obtained from TDR records of 1289 dives were examined from all seven seals (L,Q,K,N at 40 and 80 m and R,W,X at 80 m). The mean “ascent” speed was always significantly slower than the mean “descent” speed for all seals, at all distances (Paired t-test, p < 0.01). All seals swam between 10 % and 20 % slower on their way back to the breathing box, despite not having to work against buoyancy in either direction (Figure 4.8). We calculated the buoyancy through the year for each seal where body composition was available. The mean body mass of the adult grey seal was 129.7 kg and 34 kg for the pups, with adipose tissue accounting for between 7.1 % and 40.8 % of body mass (Table 4.3). There was no relationship between estimated buoyancy and the relative swim speed during “descent” and “ascent”. “Ascent” swimming was always slower than “descent” swimming whereas buoyancy varied widely from +16 N to –20 N.

All seals used burst and glide swimming during both “descent” and “ascent”. Repeated acceleration (stroke) and deceleration (glide) phases were apparent in swim speed records in all dives (Figure 4.2). The number of burst and glide phases was generally significantly higher on the “ascent”, except for N and R at 80 m (Paired t-test, p < 0.05, figure 4.9).
Table 4.3. Buoyancy values at different depths for seals where body composition was available.

<table>
<thead>
<tr>
<th>ID</th>
<th>Date</th>
<th>Mass (kg)</th>
<th>TBF%*</th>
<th>DLV (L)**</th>
<th>Buoyancy with no air in lungs (N)</th>
<th>Buoyancy at the surface (N)</th>
<th>Buoyancy at 1m (N)</th>
<th>Buoyancy at 2m (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May-02</td>
<td>124</td>
<td>17.23</td>
<td>5.11</td>
<td>-61.50</td>
<td>-9.99</td>
<td>-14.68</td>
<td>-18.58</td>
</tr>
<tr>
<td></td>
<td>Jun-02</td>
<td>134</td>
<td>22.88</td>
<td>5.51</td>
<td>-50.96</td>
<td>4.53</td>
<td>-0.51</td>
<td>-4.72</td>
</tr>
<tr>
<td></td>
<td>Feb-02</td>
<td>42.5</td>
<td>40.77</td>
<td>1.6</td>
<td>0.36</td>
<td>16.48</td>
<td>15.02</td>
<td>13.80</td>
</tr>
<tr>
<td>K</td>
<td>Mar-02</td>
<td>30.4</td>
<td>21.73</td>
<td>1.4</td>
<td>-12.25</td>
<td>1.85</td>
<td>0.57</td>
<td>-0.50</td>
</tr>
<tr>
<td></td>
<td>Jun-02</td>
<td>32.5</td>
<td>12.79</td>
<td>1.45</td>
<td>-19.02</td>
<td>-4.42</td>
<td>-5.74</td>
<td>-6.85</td>
</tr>
<tr>
<td></td>
<td>Feb-02</td>
<td>34.6</td>
<td>40.32</td>
<td>1.46</td>
<td>-0.03</td>
<td>14.68</td>
<td>13.34</td>
<td>12.22</td>
</tr>
<tr>
<td>N</td>
<td>Mar-02</td>
<td>33</td>
<td>32.54</td>
<td>1.44</td>
<td>-5.75</td>
<td>8.76</td>
<td>7.44</td>
<td>6.34</td>
</tr>
<tr>
<td></td>
<td>Jun-02</td>
<td>36.4</td>
<td>31.05</td>
<td>1.57</td>
<td>-7.51</td>
<td>8.31</td>
<td>6.87</td>
<td>5.67</td>
</tr>
<tr>
<td></td>
<td>Jul-04</td>
<td>23.9</td>
<td>8.07</td>
<td>1.14</td>
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<td>-4.74</td>
<td>-5.78</td>
<td>-6.65</td>
</tr>
<tr>
<td></td>
<td>Sep-04</td>
<td>31.4</td>
<td>18.69</td>
<td>1.23</td>
<td>-14.63</td>
<td>-2.23</td>
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<td>-15.18</td>
<td>4.11</td>
<td>2.36</td>
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</table>

*TBF= Total Body Fat

**DLV= Diving Lung Volume
Figure 4.8. Boxplot of the differences in mean swim speeds (in m.s\(^{-1}\)) between the “descent” and the “ascent” of dives to 40 m and to 80 m for each seal. * indicates that the mean swim speed was significantly higher on the “descent” (Paired t-tests, p < 0.05). The bottom and top of each box marks the 25\(^{th}\) and 75\(^{th}\) percentile respectively. The black and grey lines within the box represent the median and mean respectively. Whiskers above and below the box indicate the 90\(^{th}\) and 10\(^{th}\) percentiles.
Figure 4.9. Boxplot of the differences in the number of peaks between the “ascent” and the “descent” for dives to 40 m and to 80 m for each seal. * indicates that the number of strokes is significantly higher on the “ascent”. * indicates that the number of strokes is significantly higher on the “descent”. ns stands for non significant (Paired t-tests, p < 0.05). The bottom and top of each box marks the 25th and 75th percentile respectively. The black and grey lines within the box represent the median and mean respectively. Whiskers above and below the box indicate the 90th and 10th percentiles.
Discussion

This study examines the swimming behaviour of grey seals in relation to resource availability, i.e. prey density and patch distance. The experimental set up allowed us to test theoretical models of swimming speeds in breath-hold divers. In addition, we investigated “descent” and “ascent” swimming in the absence of buoyancy effects. The study was based on a sample of seven female grey seals, a relatively large sample compared to previous captive marine mammal studies. Although the sample size restricts our ability to investigate size related effects, the behaviour of the non-pregnant adult was qualitatively similar to that of the pups throughout.

Swimming speed

The observed mean swimming speeds for both adults and pups were similar to those reported for adult grey seals foraging in UK waters (Thompson et al. 1993) but were higher than those of adult grey seals foraging around Sable Island (Beck et al. 2000). However, Beck et al. (2000) reported “descent” and “ascent” rates that are only analogous to swim speed if the seals were diving vertically to the bottom. At any other angle, such rates would underestimate swim speed.

Marine mammals and penguins should swim at or near the MCT speed when swimming to and from the surface in order to maximise the amount of oxygen available during the foraging phases of dives (Davis et al. 1985, Feldkamp 1987, Ponganis et al. 1990 1992, Fish 1993, Thompson et al. 1993, Williams et al. 1993, Ropert-Coudert et al. 2002). The MCT speed for grey seals swimming in a flume tank was approximately 1.3 m.s$^{-1}$ (Fedak et al. 1988, Thompson et al. 1993) which
was similar to those recorded for harbour seals in similar conditions (between 0.85 and 1.4 m.s\(^{-1}\); Davis et al. 1985). On average, our seals swam approximately 20\% faster than the estimated MCT speed when returning to the surface (Table 4.1), and over 40\% faster than the expected MCT speed when going to the feeder. Estimates of MCT speed based on animals swimming in flume tanks may be under-estimates.

Seals had to swim actively against the flow while breathing at the surface. Drag is greatly enhanced at or close to the surface (Herthel 1966) so seals in flume tanks would experience higher drag than during submerged swimming at similar speeds in our set-up or in the wild. At higher speeds this effect is exacerbated by seals spending proportionately longer breathing (Fedak et al. 1988). Our seals may therefore have been swimming at or close to MCT speeds during “ascent”. If so, however, they must have been swimming faster than MCT speed when travelling to the feeder.

There was no clear relationship between body mass and swimming speed in our study. Because drag scales to surface area while available power scales to body mass, larger animals should be capable of higher sustained swim speeds (Feldkamp 1987, Videler and Nolet 1990, Stelle et al. 2000). However, animals would be expected to swim at or close to their MCT speed during ascent and descent and the relationship between mass and MCT speed is not obvious. Videler and Nolet (1990) showed that MCT speed scales to \(M^{0.27}\) over a wide range of body masses. While this is apparent over the size range they investigated (0.027 - 11.5 m body length), it is not clear that such a relationship holds within the range of sizes and swim speeds observed in marine mammals, and it does not appear to fit the observed patterns of swim speeds in marine mammals (Sato et al. 2007, Hassrick et al. 2007). The broad-scale allometric relationship which was determined across swimmers from many taxa is due to the fact
that the drag coefficient \( C_D \) decreases as Reynolds number \( \text{Re} \) increases over a wide range of \( \text{Re} \) values, and \( \text{Re} \) scales linearly to body length. However, at the high \( \text{Re} (> 200000) \) which swimming pinnipeds experience, the simple relationship breaks down and \( C_D \) remains relatively constant (Vogel 1981). If we can assume that \( C_D \) is constant over the observed range of sizes and swim speeds for pinnipeds, we can approximate the metabolic costs of swimming (SMR) in terms of body mass \( (M) \) and swim speed \( (U) \), with an equation of the form,

\[
SMR = a \cdot M^{0.75} + b \cdot M^{0.67} \cdot U^3
\]

where resting or maintenance metabolic rate scales to \( M^{0.75} \) and power required to overcome drag is proportional to \( U^3 \) and surface area, which scales to \( M^{0.67} \).

Cost of transport \( (J.m^{-1}) \) is simply the metabolic rate divided by the speed:

\[
COT = \frac{a \cdot M^{0.75} + b \cdot M^{0.67} \cdot U^3}{U}
\]

By differentiating with respect to \( U \) and setting the derivative equal to zero we can see that MCT should scale to \( M^{0.027} \), i.e. MCT is almost independent of mass. Our largest animal was approximately six times heavier than our smallest so we would expect its MCT to be only around 5 % higher. This is consistent with previous studies on animals in the wild showing that swim speed is relatively constant at around 1 - 2 m.s\(^{-1}\) and not correlated to body mass over a wide range of body masses from 30 ton sperm whales to 0.5 kg seabirds (Ponganis et al. 1990, Sato et al. 2007).

**Foraging behaviour in relation to food resource availability**

Although dive duration is ultimately limited by oxygen stores, it has been suggested that seals may alter their diving behaviour in response to their perception of both the quality and depth of a prey patch (Thompson and Fedak 2001). Sparling et al. (2007) showed that grey seals do alter their dive durations in response to changes in patch
quality, by ending their dives early at low prey densities. The results presented here suggest that transit swim speeds are not simply related to prey density. This is consistent with the assumption that seals will maximise prey acquisition by maximising the rate of delivery of oxygen to the foraging patch irrespective of patch quality.

Thompson et al. (1993) showed that swim speeds in deep dives should approach but never go below MCT speed whereas in shallow dives higher swim speeds would allow animals to maximize the proportion of time spent foraging at the bottom. All seals tested in this study did alter their swimming behaviour in response to changes in patch distance; swimming faster to 40 m compared to 80 m or 120 m. Sparling et al. (2007) found that dives to 40 m were generally much shorter than the estimated aerobic dive limit (ADL- equivalent to the oxygen stores divided by the rate of oxygen consumption) but in dives to 120 m, seals were approaching ADL at the highest prey densities. Reducing swim speeds and therefore metabolic rates during transit in deep dives would allow seals to spend longer at the feeding patch without exceeding their estimated ADL. In contrast, studies on Northern fur seals, New Zealand sea lions and Brunnich’s guillemots found that swimming speed during descent increased significantly in deeper dives (Ponganis et al. 1992, Crocker et al. 2001, Lovvorn et al. 2004). Unlike phocid seals, these species store air in their lungs, fur or plumage and therefore have to work hard against buoyancy at the start of the dive. In shallow dives a higher proportion of the descent is spent working against buoyancy so that the apparent drag forces experienced by the animal will be greater in shallow compared to deep dives.
Swimming mode in absence of pressure effect

Differences between “descent” and “ascent” swim speeds are usually explained in terms of changes in buoyancy forces (Webb et al. 1998, Williams et al. 2000, Beck et al. 2000, Sato et al. 2003). However, despite the fact that all swimming between the surface and the foraging site was horizontal in our study, seals nevertheless swam slower on “ascent” than on “descent” despite not having to work against negative buoyancy (Table 4.1 and Figure 4.7). This difference between “descent” and “ascent” speeds was maintained with increasing patch distance and there was no indication that the slower “ascent” swimming was a conditioned response to perceived buoyancy. Seals were choosing to swim faster to their feeding patch. Buoyancy cannot therefore completely explain why negatively buoyant seals swim more slowly during “ascent”. Motivational state may have a direct effect on swim speeds; seals may swim faster to the feeding patch in anticipation of finding food while they might save energy for the next dive by swimming slower on their way back.

All our seals used burst and glide swimming during both “descent” and “ascent” (Figure 4.2). This is possibly an energy-efficient way of travelling for marine mammals (Lovvorn et al. 1999, Williams et al. 2000, Lovvorn et al. 2001). Data from TDRs in this study indicate that there were fewer acceleration and deceleration phases during the faster “descent” compared to the slower “ascent” (Figure 4.8). Seals might have increased the frequency and/or the amplitude of their strokes to increase their speed on the “descent”, but our TDR records were not sensitive enough to detect individual swimming strokes. Several studies have suggested that speed and acceleration are mediated via changes in stroke amplitude rather than stroke frequency (Lovvorn et al. 1999, Wilson and Liebsch 2003, Lovvorn et al. 2004). However, if we
want to determine in detail the swimming tactics used by the seals in our set-up we would have to use more precise accelerometer devices.

In summary, the results of the present study indicate that swim speeds in grey seals are closely related to resource accessibility, i.e. distance, but not to the patch quality. Seals adjusted their swim speeds in relation to dive distance allowing them to increase their time spent foraging underwater. In addition, our unexpected discovery that seals swim slower on their way back to the surface in the absence of buoyancy effects suggest that the swimming behaviour exhibited by foraging grey seals is primarily dependent on behavioural choices rather than a result of buoyancy effects during vertical swimming (Fedak and Thompson 1993, Thompson and Fedak 2001, Sparling et al. 2007).
References


Chapter 5

Foraging duration and swimming speed of grey seals in relation to prey encounter rate: letting the fish do all the work
Summary

Breath-hold divers are constrained by rigid physiological limits, within which they can vary hunting tactics to efficiently exploit their environment. While it is possible to monitor seal behaviour underwater using electronic devices, it is difficult to monitor prey distribution and prey behaviour at relevant scales.

The experimental foraging set-up at SMRU allows us to investigate aspects of foraging strategies that are difficult or impossible to observe in the wild and facilitates testing of foraging models under realistic, controlled conditions. Here we examine how grey seal foraging behaviour varies in response to changes in prey swimming speed and density. Particularly, we wanted to test the predictions from the Thompson et al. (1993) model which suggest that seals can maximise average encounter rates by sitting and waiting for fast-moving prey to come into the encounter region. This is contrary to the intuitive prediction that predators must swim faster for fast moving prey. For slow-moving prey, however, seals should swim at MCT speed to cover the longest distance most economically. In addition they suggested that in order to maximise their rate of energy gain, predators should swim faster as prey density increases.

Five grey seals (1 adult and 4 pups) equipped with accelerometers, were trained to swim 80 m horizontally underwater from a breathing box to a simulated foraging patch where food was delivered by conveyor belt to a window positioned 2 m below the surface. The feeder was activated by the seal swimming against a force plate. The density and apparent swim speed of the prey were set by the experimenter but seals
could increase the encounter rate by swimming harder against the force plate. Seals’ mean swimming speeds, when foraging, decreased significantly as prey swimming speed increased, whilst it increased significantly as prey density increased. Concurrently, foraging durations increased as prey speed and prey density increased showing that seals were increasing their energy intake by behaving as predicted in the model of Thompson et al. (1993). These findings indicate the importance of fine-scale observations of foraging behaviour and the value of experimental protocols in developing our understanding of marine mammal foraging behaviour.
Introduction

For breath-hold divers, dive duration is ultimately limited by the oxygen stores of the animal. The aerobic dive limit (ADL), defined as the maximum dive duration that is possible without any increase in blood lactic acid, is dependent on a variety of factors such as oxygen stores, swim speed and metabolic rate (Kooyman 1989). Marine mammals are thus faced with the conflicting tasks of foraging underwater and surfacing to replenish their oxygen stores. Theoretical studies of foraging behaviour by breath-hold divers have examined strategies that maximise either total time or proportion of time spent submerged because it is assumed that the number of prey encountered is a linear function of time spent searching (Kramer 1988, Houston & Carbone 1992, Carbone & Houston 1996).

When submerged, breath-hold divers are under rigid physiological limits and can vary their foraging behaviour to most efficiently exploit their environment. For example, diving foragers can alter their diving behaviour in response to their perception of patch quality (Mori et al. 2002, Hooker et al. 2002, Mori and Boyd 2004, Sparling et al. 2007). Hooker et al. (2002) showed increased bout duration with increased prey encounter rate for Antarctic fur seals (Arctocephalus gazella) feeding on krill. Divers can also modulate their swim speeds while foraging. Swimming speeds employed during a dive will have a major impact on the rate of depletion of limited oxygen reserves and thus breath-hold divers are also expected to modulate their swimming speeds and patterns as well as theirs angles of descent and ascent (Davis et al. 1985, Williams et al. 1991, Thompson et al. 1993, Wilson et al. 2002, Sato et al. 2003, Davis et al. 2007). For example, Gallon et al. (2007) found that seals adjusted their
speed in response to changes in distance to the prey patch by decreasing their swim speed as distance to the patch increased.

One of the most fundamental components of predator-prey models is prey encounter rate (PER). The rate at which a searcher encounters moving targets will be a function of the velocities of both the searcher and the target (Yapp 1956). In addition, PER will increase with increasing prey density. Based on these relationships, Thompson et al. (1993) suggested that for seals to most efficiently exploit their environment, their hunting strategies should be sensitive to prey swim speed. The Thompson et al. (1993) model does not address chasing and capture so when the prey is stationary PER is a linear function of the predator speed and when the predator is stationary PER is a linear function of the prey speed. When both the prey and the predator are moving, however, PER is a result of the combined relative speeds. Their model predicted that when hunting stationary or very slow-moving prey, seals would maximize the number of encounters in a dive by swimming at the minimum cost of transport (MCT) speed. This would enable seals to search the maximum area possible. Conversely, when hunting active prey, seals should sit and wait for prey to come into the encounter region in order to maximise their energetic efficiency. In addition, they suggested that when prey density is high, the net rate of energy gain is maximised by swimming more rapidly for all prey speeds.

The development of novel and sophisticated animal-borne equipment such as time-depth recorders (TDR) and satellite tags can provide detailed and comprehensive information on the behaviour and physiology of seals at sea (LeBoeuf et al. 1989, Hindell et al. 1992, Thompson & Fedak 1993, McConnell et al. 1999, Crocker et al.)
Researchers have recently used underwater still and video cameras to obtain additional information on seals’ foraging behaviour (Davis et al. 2004, Hooker et al. 2002, Marshall 2007, Heaslip and Hooker 2008). These new technologies can help identify foraging habitats, prey species and three-dimensional foraging behaviour (Bowen et al. 2002, Davis et al. 2003). They cannot, however, provide accurate information on prey characteristics such as movements and swim speed. As a result it is generally not possible to accurately interpret the observed dive behaviours of marine predators in relation to prey characteristics such as swim speed. Therefore, trials with short term captive wild animals are essential to test existing theoretical models and to develop our understanding of marine mammal foraging behaviour.

The SMRU pool facility offered the opportunity to study seals foraging behaviour in relation to various aspects of prey availability. This chapter describes the fine scale foraging tactics of captive wild grey seals in a experimental design that allows prey characteristics (prey swim speed and density) to be controlled. The experimental design allowed swimming effort of foraging grey seals to be recorded and alter prey encounter rate accordingly. In this study, the effects of the predator and prey movements on prey encounter rate were investigated but not the chasing and escaping behaviours. It was assumed that the prey would not take avoiding action before they have come into the encounter region and that the predator would not chase the prey. Therefore the motion of both predator and prey was assumed to be rectilinear between encounters. The objectives of the present study were to investigate how seals adjust their swim speed in relation to prey swim speed and how the density of the prey
affects that relationship. In order to test the model of Thompson et al. (1993) we tested the following hypothesis:

1. Seals should swim around MCT speed when hunting stationary or very slow moving prey.
2. Seals should reduce swimming activity when hunting active prey.
3. When prey density is high, seals should swim more rapidly for all prey swim speed.
4. Seals should adjust their swim speed in order to increase their time spent foraging at the patch.
Material and methods

Study animals

Five grey seals *Halichoerus grypus* (one adult female “A1”, three female pups “P1”, “P3”, “P4” and one male pup “P2”) were used in this study. All seals were caught in the wild at Abertay Sands and on the Isle of May (Fife, UK) and kept in outdoor seawater pools in the captive facility at the Sea Mammal Research Unit (SMRU, St Andrews, UK). Seals were maintained on a variety of fish species to allow experiments on prey choice to be carried out. For this study, however, seals were fed with the same species throughout the experiments (Herring, *Clupea harrenthus*, in 2006 for “A1”, “P1” and “P2” and sprat, *Sprattus spratus*, in 2007 for “P3” and “P4”). Seals were released into the wild after a maximum of 13 months in captivity (see Chapter 2 for more details). All capture and handling maintenance procedures conformed to the Animals (Scientific Procedures) Act 1986 under project licence number 60/3303.

Experimental design

The SMRU experimental facility comprises a large seawater pool (42 x 6 x 2.5 m) that can be completely covered by aluminium meshed panels so that seals can only surface in a breathing box linked to an open-flow respirometry system (see Chapter 2 for more details). The pool was longitudinally partitioned with a net into lanes so that the swimming distance between the breathing box and the feeding station was 80 m. For neutrally buoyant animals, descent and ascent are the exact equivalent. For negatively buoyant divers, such as phocid seals, any effects due to high body density will approximately cancel out i.e. a negatively buoyant animal may sink as depth
increases and save energy but it will have to work harder on the way back-up to the surface. As phocid seals generally exhale before diving, they have few compressible spaces so that changes in depth have little effect on buoyancy. Therefore horizontal, underwater swimming to and from the feeding station will be energetically similar to vertical swimming to an equivalent depth. Hereafter, travel distance from the breathing box (equivalent to the surface) to the feeding patch (equivalent to the bottom) will be referred as “descent” and the return journey, “ascent”. The foraging patch consisted of a purpose built device that delivered fish on a conveyor belt to a feeding window 2 m below the surface. An important aspect of the set-up was that seals were free to dive at will and select their own foraging behaviour.

Feeding station

The feeding station (Figure 5.1) was designed and built to deliver fish to seals allowing the simulation of different prey swim speed and densities. To access fish placed on the conveyor belt, seals had to put their head through a hole in a force plate. The force plate measured the force that the animal exerted on its surface through a calibrated load cell. It is important to note that seals could only exert force by swimming against the force plate. The speed of the conveyor belt was related to how hard the seal pushed on the force plate. Therefore seals could increase their prey encounter rate by swimming harder against the force plate, mimicking swimming faster and therefore covering a longer distance in the wild.

The force applied on the force plate by the seal was read from a load cell (CBES Series, Omni Instruments, Dundee, UK) by a unimeter (XQL, Autoplex International Pty Limited, South Australia, Australia). Force was logged every 0.2 s and stored in
an excel worksheet. The load cell and the unimeter were calibrated monthly against known loads when the pool was empty to insure an accurate reading from the unimeter.

To obtain an estimated swim speed derived from the force seals applied on the force plate, we made two assumptions. We first assumed that during any recorded effort point, seals were at equilibrium with regard to their speed in order to equate the force exerted on the force plate to drag. We then used the obtained drag to calculate an estimated swim speed. This implicitly assumes that seals accelerated to the speed equivalent to their swimming effort more or less instantaneously. The force applied by seals swimming against the force plate was recorded five times per second and these five measurements were used to give a mean exerted force per second. We believe that this process improved the estimation of the speed. For example, a force ‘x’ generated for 0.2 s would not be sufficient to accelerate a seal to the speed equivalent to force ‘x’ in that time. By taking the average force per second, any anomalously large estimations of swim speed were smoothed out. We thus rearranged the drag equation to calculate an estimated “foraging” swim speed:

$$U = \sqrt{\frac{F}{\left(\frac{1}{2} \rho x \text{Cd} x S\right)}}$$

(5.1)

where $U$ is the estimated “foraging swim speed” (m.s$^{-1}$), $F$ is the mean force (N) exerted by the seal on the force plate over a second, $\rho$ is the density of sea water (1020 g.L$^{-1}$), Cd is the drag coefficient of a grey seal (approximately 0.01, Williams & Kooyman, 1985) and $S$ is the wetted surface of the seal (0.07 x $M^{0.67}$ where $M$ is mass in kg, Irving et al., 1935).

For a given prey density, prey encounter rate is a function of the speeds of both the predator and the prey (Yapp 1956). For example, when prey is stationary, they are
encountered at a rate set by their density \((d)\) and the area searched. This is a linear function of the speed of the predator. Prey encounter rate \((\text{PER})\) is therefore given by:

\[
\text{PER} \propto d\,U_{\text{predator}} \quad (5.2)
\]

If the predator is stationary (i.e. seals not swimming against the force plate), \(\text{PER}\) is a linear function of the speed of the prey:

\[
\text{PER} \propto d\,U_{\text{prey}} \quad (5.3)
\]

When both the prey and the predator are moving, however, \(\text{PER}\) is a function of both speeds:

\[
\text{PER} \propto d\,\sqrt{(U_{\text{prey}}^2 + U_{\text{predator}}^2)} \quad (5.4)
\]

The speed of the belt represented the combined speed of the predator and the prey. Prey swim speed and prey density were set by the experimenter, whereas seal swim speed was empirically determined by the force exerted on the force plate. \(\text{PER}\) was thus a combination of set values for the density and the speed of the prey and the action of the seal (i.e. swimming against the force plate).

The computer receiving information from the load cell was linked to a 12 V DC motor controlling the speed of the conveyor belt. The program transformed the force applied by the seal into a speed (Equation 5.1) and the speed of the belt represented the combined speed of the predator and the prey (i.e. the belt speed representing \(\text{PER}\), Equation 5.4). The belt speed was calibrated against voltage to ensure the appropriate relation was used in the calculations.

In nature seals often use stroke and glide swimming (Chapter 3); to account for this it was necessary to add a deceleration speed to the belt. When seals stopped pushing, the
belt decelerated in relation to their last push on the force plate. We used the following equation based on drag to estimate their natural deceleration:

$$U_2 = U_1 + \frac{F_2 - (U_1^2 \cdot (\frac{1}{2} \rho \cdot Cd \cdot S))}{M}$$ (5.5)

where $U_2$ is the speed after the last push (m.s$^{-1}$), $U_1$ is the previous speed calculated (m.s$^{-1}$), $F_2$ is the last push exerted on the force plate (N).
Figure 5.1. Schematic diagram of the feeding station (See text for more details).
Experiments

Seals swimming speed and time spent foraging at the patch, were investigated in relation to both prey density and prey swim speed. Foraging trials were conducted with the feeding station positioned 80 m away from the breathing box to simulate patch depth. Animals were fasted for >15 h before each trial. A trial comprised a series of dives to the feeding station from the breathing box. Each trial lasted between 50 and 120 min, the duration was determined by how long it took the seal to consume a set ration. The amount fed to each seal depended on its age and size but was constant for each animal. The amount of food offered during trials was always less than the full daily ration so seals would not reach satiation. The food that was left over was used for training and moving the seal after the trials.

The experimenter controlled the density of prey by varying the spacing of prey items on the conveyor belt. During any one dive, the prey items were equally spaced on the belt and the time between encounters was a function of how hard the seal swam against the force plate. The experimenter added a fixed value for prey speed in order to simulate the effect of prey movement on encounter rate. This was entered into equation (5.4) to alter the estimated combined speed. The prey speed was held constant on a particular day of experiment, but changed randomly between days. By varying only one factor between dives on a particular day of experiment, the effects of prey density and prey swim speed on seals behaviour were not confounded.

The start and end time of each dive and times of arrival at and departure from the feeding station were recorded from direct observation at the breathing box and an underwater video system at the feeder. The time spent at the feeding station will be
referred hereafter as foraging duration. Seals were equipped with an accelerometer (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan) which recorded swim speed every second and 3-D accelerations at 32 Hz. 3-D accelerations data were used to test our experimental set-up and see if seals were actually swimming against the force plate by comparing them with the swimming pattern during transit and foraging phases of the dives. Side to side flipper movements could be detected as fluctuations in acceleration along the transverse axis (X axis, hereafter referred to as swaying acceleration).

Analyses
Data downloaded from the accelerometer were analysed to obtain high resolution graphs showing the lateral swaying accelerations during each dive. Raw sensor data were initially filtered to eliminate low frequency variations that resulted from various turning and rolling movements (see Chapter 3 for more details). Linear mixed effect models were used to investigate two relationships. Firstly, the relationships between the estimated mean predator swim speed at the feeder and both prey density and prey swimming speed. Secondly, they were used to investigate the relationships between foraging duration and both prey density and prey swimming speed. Prey density and prey swimming speed were included as fixed effects and seal ID as a random effect. The significance of a parameter was tested by removing each parameter from the full model and looking at the effect of the deletion on the fit of the model using likelihood ratio tests.
Results

A total of 901 dives were obtained from visual data for five grey seals (one adult: A1, and four pups: P1 – P4). Concurrently, for 878 dives, “foraging” swim speeds were estimated from the force plate data. Dive behaviour characteristics recorded during these experiments were similar to those recorded in the wild. For example, seals spent around 82 % of the time submerged, mean dive duration was $3.35 \pm 1.55$ min (see Table 5.1). The maximum dive duration recorded during these experiments was 10.07 min by the adult A1. Mean foraging duration varied between $1.11 \pm 0.58$ min for a pup and $3.56 \pm 1.73$ min for the adult (see Table 5.1). Seals mean swim speeds travelling to and from the feeder were comprised between 1.01 and 1.75 m.s$^{-1}$ respectively (See Chapter 3 for more details). A summary of the foraging swimming speeds is shown in Table 5.1. Overall mean “foraging” swimming speed was $1.08 \pm 0.49$ m.s$^{-1}$. Individual mean “foraging” swimming speeds were close to or less than the estimated MCT speed (1.3 m.s$^{-1}$) (Thompson et al. 1993). The adult seal A1 swam significantly slower than any of the pups (t-tests, $T_{\text{Feeding speed}}=-32.09$, $p<0.0001$).
Table 5.1. Summary of foraging diving characteristics obtained from visual data and from the force plate for each seals

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Mass (kg)</th>
<th>Foraging duration (min)</th>
<th>Dive duration (min)</th>
<th>Foraging swim speed (m.s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>All seals</td>
<td>1.95±1.43 (875)</td>
<td>3.75±1.55 (899)</td>
<td>1.08±0.49 (878)</td>
<td></td>
</tr>
<tr>
<td>A1</td>
<td>150</td>
<td>3.56±1.73 (97)</td>
<td>5.72±1.79 (116)</td>
<td>0.41±0.17 (98)</td>
</tr>
<tr>
<td>P1</td>
<td>48</td>
<td>2.51±1.47 (163)</td>
<td>4.42±1.42 (161)</td>
<td>0.97±0.51 (163)</td>
</tr>
<tr>
<td>P2</td>
<td>51</td>
<td>2.59±1.13 (95)</td>
<td>4.35±1.07 (97)</td>
<td>1.17±0.48 (93)</td>
</tr>
<tr>
<td>P3</td>
<td>32</td>
<td>1.11±0.58 (238)</td>
<td>2.77±0.56 (242)</td>
<td>1.24±0.5 (241)</td>
</tr>
<tr>
<td>P4</td>
<td>35</td>
<td>1.55±1.18 (282)</td>
<td>3.21±1.18 (283)</td>
<td>1.2±0.3 (283)</td>
</tr>
</tbody>
</table>

A, adult; P, pup.

Values are means ± s.d. (number of dives).

Swimming pattern during a dive

In order to determine the swimming patterns of our animals while foraging at the feeding station we examined the swaying acceleration profiles obtained from the accelerometer records. Dives were split into three phases and we examined the swaying acceleration profiles in the different phases: 1) A “descent” phase (active swimming from the breathing box to the feeding station), 2) A foraging phase (seal swimming against a force plate) and 3) An “ascent” phase (active swimming from the feeding station to the breathing box) (Figure 5.2, A). Seals used continuous burst and glide swimming during both transit and feeding phases of dives. Acceleration and deceleration phases were apparent in the estimated swim speed profiles (Figure 5.2,
B). These phases corresponded to the stroke and glide phases in the accelerometer X-axis (Figure 5.2, A).

Figure 5.2. A) X-axis data from a 3D accelerations recorder (W1000L-3MPD3GT, Little Leonardo Co., Tokyo, Japan) for a seal pup showing changes in lateral acceleration over a dive. B) Estimated swim speed of the seal foraging at the feeder. This was a dive to 80 m with a density of 8 fish per belt and a prey speed of 1.4 m.s$^{-1}$ at the feeding station.
Swimming speed and foraging duration

Visual data from a total of 901 dives for 5 grey seals (A1, P1, P2, P3, P4) were analysed. A summary of the swim speed characteristics when seals were foraging in relation to prey speeds is presented in Table 5.2. When the prey speed was zero the estimated swim speeds of seals at the feeder were close to the estimated MCT speed (1.3 m.$\text{s}^{-1}$) (Thompson et al. 1993) except for the adult A1 that swam slower than expected. All seals appeared to swim slower when prey speed was 2.72 m.$\text{s}^{-1}$ compared to when the prey was stationary.

Results for the linear mixed-effect models are summarised in Table 5.3. The full mixed effect model suggested that both prey speed and prey density had a significant effect on the estimated swim speed at the feeding station. There was a significant negative relationship between the estimated swim speed of the seal at the feeding station and prey speed (Table 5.3 and Figure 5.3). Additionally there was a significant positive relationship between the estimated swim speed of the seal at the feeding station and prey density (Table 5.3 and Figure 5.4). There was, however, no linear interaction between prey speed and prey density.

The relationships of prey speed and density to foraging duration were investigated using linear mixed-effects models. Seals appeared to significantly increase their foraging duration as both prey speed and prey density increased (Table 5.3, Figure 5.5 and 5.6).
Table 5.2. Summary of swim speed characteristics when foraging obtained for each seals for different prey speed

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Mean swim speed (m.s$^{-1}$) at feeding station at different prey speed (m.s$^{-1}$):</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>A1</td>
<td>0.52 (±0.13)</td>
</tr>
<tr>
<td>P1</td>
<td>1.40 (±0.29)</td>
</tr>
<tr>
<td>P2</td>
<td>1.43 (±0.48)</td>
</tr>
<tr>
<td>P3</td>
<td>1.35 (±0.21)</td>
</tr>
<tr>
<td>P4</td>
<td>1.33 (±0.48)</td>
</tr>
</tbody>
</table>

A, adult; P, pup. Values are means ± s.d.

Table 5.3. Results of linear mixed-effects models describing seals’ mean estimated swim speeds and foraging durations. The slope values ± s.e.m. are given for significant terms (in bold type)

<table>
<thead>
<tr>
<th>AIC</th>
<th>L.Ratio</th>
<th>Slope</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean estimated swim speed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model</td>
<td>601.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Term removed:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey speed</td>
<td>660.14</td>
<td>61.07</td>
<td>-0.082 ± 0.01</td>
</tr>
<tr>
<td>Prey density</td>
<td>910.71</td>
<td>311.64</td>
<td>0.039 ± 0.002</td>
</tr>
<tr>
<td>Interaction between prey speed and prey density</td>
<td>602.11</td>
<td>0.96</td>
<td>0.3274</td>
</tr>
</tbody>
</table>

Foraging duration

<table>
<thead>
<tr>
<th>AIC</th>
<th>L.Ratio</th>
<th>Slope</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full model</td>
<td>2373.71</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Term removed:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey speed</td>
<td>2403.76</td>
<td>32.04</td>
<td>0.162 ± 0.03</td>
</tr>
<tr>
<td>Prey density</td>
<td>2807.23</td>
<td>435.51</td>
<td>0.131 ± 0.01</td>
</tr>
</tbody>
</table>

AIC, Akaike information criterium.
Figure 5.3. Estimated swim speed at the feeding station in relation to prey speed (m.s\(^{-1}\)) for each animal (P3, P4, A1, P1, P2). Each data point represents the mean estimated swim speed at the feeding station during a particular dive. The solid lines give linear least-squares fit.
Figure 5.4. Estimated swim speed at the feeding station in relation to prey density (fish per belt) for each animal (P3, P4, A1, P1, P2). Each data point represents the mean estimated swim speed at the feeding station during a particular dive. The solid lines give the linear least-squares fit.
Figure 5.5. Foraging duration (min) in relation to prey speed (m.s\(^{-1}\)) for each animal (P3, P4, A1, P1, P2). Each data point represents the foraging duration during a particular dive. The solid lines give the linear least-squares fit.
Figure 5.6. Foraging duration (min) in relation to prey density (fish per belt) for each animal (P3, P4, A1, P1, P2). Each data point represents the foraging duration during a particular dive. The solid lines give the linear least-squares fit.
Chapter 5

Discussion

This study is the first fine scale examination of seals’ swimming speed and foraging durations during quasi-realistic dives and its relation to prey swim speeds and prey densities. By combining experimental manipulation of prey characteristics in an appropriately sized diving tank, where seals were allowed to dive and forage at will, we tested the predictions of the model of Thompson et al. (1993).

The range of behaviours displayed by the animals in this study, in terms of dive duration, swim speed and distance travelled was similar to that recorded in wild grey seals using satellite telemetry (McConnell et al. 1992, McConnell et al. 1999). For example our results show that seals swam between 1 and 1.75 m.s\(^{-1}\) when travelling to and from the feeder and decreased their activity while foraging at the prey patch in accordance with previous studies on wild grey seals (Thompson et al. 1991, Fedak & Thompson 1993). In addition, seals used continuous burst and glide cycles during transit swimming and also when foraging at the feeding station by swimming against the force plate. This confirms that our experimental set-up was appropriate to test the model of Thompson et al. (1993). Therefore even though there are some differences between our experimental design and the natural environment, we are confident that the foraging behaviour displayed by our seals is relevant to wild animals.

Swimming speeds in relation to slow-moving prey

While foraging at the feeder, four of the five seals swam at approximately the MCT speed when prey velocity was zero in accordance with the model of Thompson et al. (1993). The MCT speed for grey seals swimming in a flume tank is approximately 1.3
m.s\(^{-1}\) (Fedak et al. 1988, Thompson et al. 1993) and is unrelated to body mass (Gallon et al. 2007). For breath-hold divers there is a close relationship between swim speed and oxygen consumption (Davis et al. 1985, Feldkamp 1987, Williams et al. 1993, Sparling & Fedak 2004) so animals are expected to modulate their swim speeds in order to maximise the amount of time available for foraging (Ponganis et al. 1990, 1992, Fish 1993, Thompson et al. 1993, Williams et al. 1993, Ropert-Coudert et al. 2002). In addition, swim speed during foraging directly affects prey encounter rate (PER) (Yapp 1956). Breath-hold divers thus face a trade-off between increasing the PER by swimming faster or increasing foraging duration by swimming slower. By swimming around MCT speed, seals in our study could maximise their number of encounters with slow moving prey in a dive, consistent with optimality model predictions (Thompson et al. 1993). The adult seal, however, swam much slower than the MCT speed. This behaviour has been previously attributed as part of an overall energy saving strategy (i.e. lower diving metabolic rate, lower swim speeds) before the breeding season (Sparling et al. 2006, Gallon et al. 2007).

**Swimming speeds in relation to fast-moving prey**

All seals in our study significantly decreased their swim speed as prey speed increased. Pyke (1981) applied optimality theory to the speeds with which animals forage. He found that when net energy intake rate is maximised, the optimal travel speed for a foraging animal should be greater than the MCT speed, unless it is constrained to be less by other factors. The prediction relies on the assumption that energy gain increases as a linear function of search speed. For breath-hold divers, it is known that swimming costs per metre increase rapidly as swim speed falls below MCT but increase only slowly as swim speed increases above MCT. Nevertheless,
Thompson *et al.* (1993) found that seals could increase their net rate of energy gain by swimming slower than the MCT speed. They suggested that in order for seals to increase their time spent foraging underwater they should reduce their swimming activity when hunting active prey, which accords with the behaviour observed during this study. The model of Thompson *et al.* (1993) and the present study rely on the assumption that seals were not chasing prey. This is in accordance with the foraging behaviour of wild grey seals that reduce activity whilst foraging (Thompson *et al.* 1991). Some breath-hold divers, however, might use other tactics when foraging (Wilson *et al.* 2002, Aguilar-Soto *et al.* 2008). Aguilar-Soto *et al.* (2008) deployed D-tags on 23 short-finned pilot whales (*Globicephala macrorhynchus*) and found that they regularly sprint for their prey. The authors suggested that pilot whales may be balancing their high energy investment by selecting a few high-calorific prey items.

*Swimming speeds in relation to prey density*

The optimal speed of movement in relation to energy intake and prey density was first considered by Ware (1975) in a study of planktivorous fish. Ware found that while the rate of gross calorific intake and the energetic cost of movement both increased with speed of movement, the net rate of calorific intake reaches a maximum at a speed which depends on the food density. Thompson *et al.* (1993) were the first to introduce prey density as a factor affecting swim speeds of foraging divers. Their model predicted that when prey density is high, seals should swim more rapidly for all prey swim speeds in order to maximise their net rate of energy gain. In this study, all pups swam faster at high prey density compared to low density in accordance with the model of Thompson *et al.* (1993) but this was not true for the adult seal. Pups may have increased their rate of energy gain in our experimental design by behaving as
predicted in the model. On the other hand, the adult seal did not seem to increase its foraging speed as the density increased. Pregnant seals might display behaviours that reduce their energy expenditure prior to a high-cost reproduction as a capital breeder (Sparling et al. 2006). Therefore, instead of working harder to increase its net energy gain at high prey density, the pregnant seal may have chosen to work less in order to minimise its expenditure. PER increased with prey density and fish appeared more often with increasing prey density. Thus the pregnant seal, unable and/or unwilling to maintain high effort, may have chosen to sit and wait for the prey to come into the encounter region at high prey density.

Our study found that there was no interaction between prey swim speeds and prey density. This was not in accordance with the model of Thompson et al. (1993) which predicts that prey density has an effect on the relationship between seals swim speeds and prey swim speeds. More precisely this model predicts that at low density, prey swim speeds would have a strong effect on swim speed whilst the effect would be reduced at high prey density. The discrepancy between the model predictions and the results of our experiments may be explained by a curvilinear interaction that our linear model could not have identified. Another explanation could be the prey densities we used during our experiments because the density range was set by the capacity of the system (e.g. speed of the belt, number of slots to insert fish on the belt). Therefore there is the possibility that all the densities used in the present study were below the densities for which Thompson et al. (1993) found a change in the relationship between seals’ swim speeds and prey swim speeds. Thus there would be no reason to find any such interaction in our model.
Foraging duration

Foraging durations increased as prey speed and prey density increased showing that seals were increasing their energy intake by behaving as predicted in the model of Thompson et al. (1993). Previous theoretical, experimental and field studies have shown that breath-hold divers modified their behaviour in response to perceived changes in prey density (Thompson & Fedak 2001, Hooker et al. 2002, Mori et al. 2002, Cornick & Horning 2003, Mori et al. 2005, Sparling et al. 2007) and to patch distance (Thompson et al. 1993, Gallon et al. 2007). Foraging models usually assume that a predator will attempt to maximise some aspect of their energy intake at depth. In the present study, seals were maximising their rate of energy gain by spending more time at the patch when both prey swim speed and density were elevated and they were limiting their energy expenditure by swimming slower when prey speed increased.

The present study has proven the utility of experimental studies in order to test theoretical models which can not be easily tested in the wild with current technology. All seals responded to changes in prey swim speeds and densities, however, we found individual differences suggesting that seals may not always maximise their rate of energy intake. Physiological constraints, such as being pregnant, might favour strategies that minimise energy expenditure. In the future it would be interesting to develop the model of Thompson et al. (1993) using ‘energy minimisation’ as the currency and compare the output with the results of the present study.
References


Chapter 6

Prey selection in grey seals: what dictates their choices?
Summary

Operant conditioning techniques and an underwater feeding apparatus were used to test the prey preferences of five captive, wild grey seals (*Halichoerus grypus*). When offered the choice between paired presentation of the same species, seals selected a tube containing the highest number of prey items for sprat and herring. The preferences of seals between two different types of prey were investigated using binomial, linear mixed-effect models and chi-squared tests. The first model showed that seals were maximising the weight of fish in 67.9% of the trials. However, seals maximised the perceived weight gain (PWG) in 84.9% of the trials when the model incorporated handling behaviour data that was available for three seals. Overall, seals showed some prey preference but these differed between individuals. These results showed the ability of the seals to maximise their energy intake in our experimental setup; they were actively choosing the most rewarding food for them. Another interesting result was the switching behaviour displayed by the seals. This behaviour could be attributed to the evolution of either the search image or of the nutrient requirements of the seals during the study.

The results suggest that prey selection by seals may be influenced by factors other than prey availability. It is therefore important to first examine what seals are maximising when foraging before investigating prey preference.
Introduction

Dietary preferences and prey selection for terrestrial carnivores have been widely investigated as they play a key role in shaping mammalian communities (Sih et al. 1985, Cooper et al. 2007). Several hypotheses have been proposed to explain prey selection by predators. These hypotheses are based on ultimate causal factors such as energetic benefits and costs involved (MacArthur & Pianka 1966, Stephens & Krebs 1986), as well as proximate mechanisms of selection such as search image or prey vulnerability (Tinbergen 1960, Temple 1987). MacArthur and Pianka (1966) suggested that an animal seeking food should try to obtain the maximum amount of food per unit time. The idea was developed and in 1986, Stephens and Krebs described foraging as locating and selecting a feeding patch according to its overall profitability so that the foraging efficiency is optimised.

Prey selectivity has been experimentally tested, but almost exclusively on small organisms that are easier to handle (Sih et al. 1985, Magnhagen 1985, Walton et al. 1992, Woolnough and Carthew 1996). Several studies showed that larger prey are preferred over smaller prey. For example, Magnhagen (1985) found that three species of marine fish showed preference for large prey, but that size preference was influenced by prey abundance. On the contrary, Woolnough and Carthew (1996) found that small prey items represented the most energy-efficient prey option as the southern ningaui (Ningaui yvonneae, a small marsupial carnivore) can more efficiently capture, subdue and consume them than it can larger prey. For larger carnivores, non-experimental field studies have been carried out to advance our understanding of prey selection (reviewed by Karanth and Sunquist 1995). These field
studies have provided the most pertinent evidence for non-random prey selection (Curio 1976, Scheel 1993, Karanth and Sunquist 1995, Pole et al. 2004, Bodendorfer et al. 2006). Prey selection occurred at several levels, for example selectivity for prey species, prey size and age or sex classes, and selectivity towards physically substandard individuals (Karanth and Sunquist 1995, Woolnough and Carthew 1996, Pole et al. 2004, Cooper et al. 2007).

Little is known, however, about aquatic carnivores as examining predation decisions within the context of their immediate environment is difficult. With few exceptions (sea otters, manatees and northern right whale), direct observations of feeding is not possible (reviewed by Bowen et al. 2002). Our knowledge relies heavily on indirect methods such as diet analyses (faecal and stomach analyses, Rae 1973, Prime & Hammond 1990, Grellier and Hammond 2005) and on more recent developed technologies (tissue fatty acid analysis, Iverson et al. 2004). These methods allow the study of marine mammal diet and have recently been used to develop complex models of competition between marine mammals and fisheries (Matthiopoulos et al. 2008).

While current diet studies can help assess existing relationships between predators and their environment, their predictive capabilities are limited. These diet studies give little information on the factors that affect the diet of wild seals and therefore it is hard to predict what seals would eat in a certain environment and which aspects of the prey characteristics (i.e. species, density, size) dictates their choice.

Seals are important predators in marine ecosystems and estimating their diet has been central to many studies investigating predator-prey relationships, interactions with fisheries and monitoring of the marine environment (Harwood & Croxall 1988, Boyd
Grey seals are known to be generalist predators feeding mainly on benthic and demersal fish species (Hammond and Prime 1990, Hammond et al. 1994) but they will also eat pelagic schooling fish, like herring (Clupea harengus) and capelin (Mallotus villosus) (Murie & Lavigne 1992, Hammond et al. 1994). Grey seals are therefore known to be opportunistic predators which may prefer to target the most temporally abundant species within its geographical range (Bowen & Harrison 1994). However, prey selection may not be purely a function of prey availability and the factors influencing prey selection by seals are poorly understood (Pierce et al., 1990; Markussen and Oritsland 1991; Boyle 1997; Tollit et al., 1997). For example, the preference of seals for certain sizes and species of prey have not been investigated experimentally, so answers to basic questions about whether seals prefer certain prey when prey availability is equal or the potential role of preferences in prey selection, remain unknown (Boyle 1997).

In the present chapter, prey selection by temporally captive wild grey seals was examined in a design that allowed us to investigate dietary preferences between fish species and between different amounts of the same fish species. The aim was to determine the factors affecting prey selections in foraging grey seals and investigate any prey preference. Optimal foraging theory assumed that a predator will maximise some aspects of its intake (i.e. also referred as currency) whilst foraging, generally it is the net rate of energy gain (Stephens and Krebs 1986). In order to calculate this rate, we need to know the costs associated with acquiring a particular prey as well as the associated gain. It is clear that in the present set-up we could not realistically measure capture costs, so we used handling time as a proxy for cost. The following hypotheses were generated to examine the factors that seals use to select prey:
(1) When offered two amounts of the same fish species, seals should select the most numerous amounts of prey items.

(2) When offered the choice between two fish species, seals should maximise some aspects of prey intake (e.g. weight, energy density).

(3) The costs associated with a particular fish species (e.g. handling time) will affect their choice between two fish species.
Material and methods

Study animals

Five grey seals were used in this study, one adult female (hereafter A2), three female pups (hereafter P1, P5 and P6) and one male pup (hereafter P2). All seals were caught in the wild at Abertay Sands and on the Isle of May (Fife, UK) and kept in outdoor seawater pools in the captive facility at the Sea Mammal Research Unit (SMRU, St Andrews, UK). Seals were fed daily on various combinations of available species: herring (*Clupea harrengus*, 2005 and 2006), sprat (*Sprattus spratus*, 2005 and 2006), whiting (*Gadus merlangus*, 2005) and mackerel (*Scomber scombrus*, 2006). Haddock (*Melanograminus aeglefinus*) was available from June 2006 onward and was only used in the experiments with the adult. Throughout the 8 weeks prior to experiments (during conditioning sessions and regular meals) and during the experiments, seals were fed with fish from the same batch and of the same range and species as used in experiments. Seals were released into the wild after a maximum of 13 months in captivity (see Chapter 2, for more details). All capture and handling maintenance procedures conformed to the Animals (Scientific Procedures) Act 1986 under project licence number 60/3303.

Prey choice apparatus

An underwater feeding apparatus was built to present fish to seals. A paired presentation design was chosen to provide a measure of preference. Fish were inserted manually into two clear plastic tubes (50 cm long, 18 cm diameter) and presented to the seal. This design presents a pair of stimuli (fish) and the apparatus provides
differential reinforcement (fish delivery) following the seal choosing one tube or the other. The choice was made by the seal touching one of the tubes with its nose.

The apparatus was fixed inside a shed on a side of a 5 metres diameter pool. It was constructed in Perspex with a one-way mirror to hide the experimenter from the seal’s view during fish presentation but allowing the seal’s behaviour to be observed (Figure 6.1 and see Chapter 2 for more details).
Figure 6.1. Diagram of the prey choice apparatus (A) and plan of the experimental pool (B) showing the prey choice apparatus position and the stationing area (See text for more details).
Conditioning of seals

We used operant conditioning techniques on the seals. Touching one of the tubes to have fish was the desired operant and was shaped by selective food reinforcement of successive approximations to the required behaviour. Using the shaping and conditioning procedures, seals were initially trained to station away from the apparatus between presentations of fish and to perform an operant response upon presentation of fish on either side of the apparatus.

The desired sequence of events during a trial was:

1- The seal stations on its target in the dry area in front of the trainer without moving, while fish were inserted into the tubes according to a datasheet.
2- When the trainer gave the “go” signal, the seal dived into the pool and then had to choose between the two tubes.
3- When the seal touched one of the 2 tubes, the experimenter released the fish.
   The other tube was taken away.
4- Back to 1.

Experiments

Seals were fasted from the previous evening to ensure an empty stomach and a similar state of hunger within and among animals at the beginning of all sessions. Seals received the rest of their daily food intake after the experiments.

The experimenter went inside the shed 5 to 10 min before the session started. The session began when the seal positioned itself in front of the trainer with its nose on a target. The trainer waited for a “ready” signal from the experimenter to send the seal.

In 2006, the duration of the session and handling time, as the time taken to eat the prey, were also recorded. The stopwatch was started when the experimenter opened
the chosen tubes and stopped when the seal had eaten all the prey or when it came to
the surface and moved away from the feeder.

During a session, the seals had to choose between two different numbers of items of
the same prey or between two species of prey with the same or different number of
items (Table 6.1). For a given dive their choice was exclusive, i.e. they were not able
to eat prey from both tubes. The size, order, and side of presentation of fish were
randomised within each session. The two prey species used during experiments were
the same for a given week, while the fish used during training and feeding could vary.
The proportion of each species offered during a session varied between 10 and 90 %
over the week (For example 20% herring – 80% sprat on day 1 and 75% herring –
25% sprat on day 2).

Table 6.1. Summary of the experiments carried out for each seal in 2005 and 2006.

<table>
<thead>
<tr>
<th>Seals *</th>
<th>Within a species</th>
<th>Between species</th>
</tr>
</thead>
<tbody>
<tr>
<td>P5 and P6</td>
<td>Sprat</td>
<td>Sprat/Herring</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>Sprat/Whiting</td>
</tr>
<tr>
<td>P1, P2 and A2</td>
<td>Sprat</td>
<td>Sprat/Herring</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
<td>Herring/Mackerel</td>
</tr>
<tr>
<td></td>
<td>Mackerel</td>
<td></td>
</tr>
<tr>
<td>A2</td>
<td></td>
<td>Herring/Haddock</td>
</tr>
</tbody>
</table>

* P stands for pup and A for adult

Fish characteristics

Samples of ten large fish (herring, whiting, mackerel and haddock) and twenty small
fish (sprat) were taken daily. Each fish was weighed (± 0.01g) and measured (nose -
tail length ± 1mm). In addition, samples of fish (three of each species) were taken
weekly in order to measure their energy content and these were frozen.
Each weekly sample of fish was homogenized in a food mixer before taking duplicate sub samples of 2-3 g for fat and protein and 2-30 g for water analyses.

Water content was determined by placing the sample of fish in a pre-weighed aluminium foil tray for drying in an electric oven at 80 °C until constant weight was achieved.

Fat content was estimated by lipid extraction using a modified Folch method (Folch et al. 1957). Chloroform was replaced by dichloromethane in the protocol.

Nitrogen (N) was determined with an elemental Analyser (Model ECS 4010, Costech Instruments) and expressed as crude protein by assuming that 100g crude protein contained 16 gN (Robbins 1993). Carbohydrate was assumed to be negligible in comparison with lipid, crude protein and water (Sidwell et al. 1974). Energy content of the fish samples was therefore estimated from fat and protein content with calorific values for fat (39.3 kJ.g⁻¹) and protein (24 kJ.g⁻¹) (Blaxter 1989). The values obtained for the different fish species in these analyses were used to calculate the following currencies that seals could choose to maximise during the experiments:

(1) the total energy gain (TEG) contained in each tube for experiments with all five seals:

\[
\text{TEG (kJ)} = W_a \times E_a
\]

where \(W_a\) is the weight (g) of fish \(a\) and \(E_a\) is the mean energy density of fish \(a\) (kJ.g⁻¹).

(2) the perceived weight gain (PWG) offered in each tube for experiments with seals in 2006 where handling time data were available:

\[
\text{PWG} = W_a \times MW_a
\]

where \(W_a\) is the weight of fish \(a\) and \(MW_a\) is the mean rate of weight gain for a particular fish species when taking into account the handling time.
(3) the perceived energy profitability (PEP) offered in each tube for experiments with seals in 2006 where handling time data were available:

$$\text{PEP} = W_a \times ME_a$$

where $W_a$ is the weight of fish $a$ and $ME_a$ is the mean rate of energy gain calculated by multiplying the mean energy density ($E_a$) with the mean rate of weight gain ($MW_a$) for each fish species.

In the present study, handling time associated with each species of fish for each seal was used as a proxy for cost whilst the energy density and the weight associated with each species of fish were used as a proxy for benefit. By combining the cost and benefit we calculated a mean rate of weight gain and a mean rate of energy gain associated with different prey species for each seal. By multiplying the mean rates of weight and energy gain with the mass of a particular fish we were able to determine a perceived weight gain and a perceived energy profitability. Therefore TEG, PWG and PEP were different forms of currency that seals could choose to maximise.

**Analyses**

When seals had to select between different numbers of the same prey species, a trial was deemed successful when they chose the tube containing the highest number of prey items. The preferences of seals between two different species of prey were tested on the basis of number, weight (in g) and energy (kJ). During these trials seals could have maximise different currencies; the number of fish, the overall weight, the total energy gain (TEG), the perceived weight gain (PWG) or the perceived energy profitability (PEP). For each currency, a trial was deemed successful when seals selected the tube offering the highest value.
Binomial proportion tests (R software program, version 2.60) were used to test for selectivity for number of prey items during trials comparing different amounts of the same species. To see if there was a relationship between the probabilities of success (i.e. choosing the tube with the highest number of prey items) and the Ratio of Weight Offered (RWO, which is the ratio of weight of fish between the two tubes), a generalised linear model (GLM) was used for trials with sprats. This analysis could not be carried out for herring and mackerel because the range of RWO was too small for trials with these species. The binomial GLM model was fitted to the sprat data and tested against the null model for significance using likelihood ratio tests. For experiments with choices between different species, the probability of success in relation to the different currencies (weight of fish, number of fish, TEG, PEP and PWG) was assessed using binomial linear mixed-effect models. For each session, the number of trials deemed successful and unsuccessful were calculated for each currency (e.g. number of trials when seals chose the tube with the highest number of prey items versus number of trials when seals didn’t choose the tube containing the highest number of prey items). A model with data from 2005 and 2006 was fitted with seal ID and session as random effects and currency (weight of fish, number of fish items and TEG) as fixed effect. A separate analysis was performed on the data from 2006 including PEP and PWG as possible currencies. The final models were tested against the null model for significance using likelihood ratio tests. The model estimate of percentage correct for each currency was calculated using the following equation:

\[
\%Correct = \frac{\exp(I + S)}{1 + \exp(I + S)}
\]
where \( I \) is the value of the intercept for the model and \( S \) the value of the slope for each currency.

The parameter estimates obtained from the model were then used to select which of the currencies seals were maximising. The different currencies were tested for significance against each other to see if the currency maximised was significantly better than the other. The currency maximised by the seals was then used to analyse prey selection.

Grey seals prey selectivity was analysed using a chi-squared goodness of fit test. The null hypothesis was that seals selected their prey in accordance to that predicted using the currency significantly maximised in the models. The alternative hypothesis was that the observed choice was different from the expected one showing a positive selection for that particular prey species. The chi-square based on the weight of fish was calculated for all seals, while the chi-square based on the PWG was calculated for seals from 2006. Analyses were carried out with 95% certainty level; the null hypothesis was rejected if the calculated value of the test statistic was greater than the critical value. In 2006, the analyses could not be carried out for all the experiments as in some cases the expected value was zero.
Chapter 6

Results

A total of 3286 trials were obtained between 2005 and 2006 for 5 grey seals. Sessions lasted between 5 and 50 minutes with 5 to 32 trials per session depending on the amount of food given and according to the performance of the seal.

Three seals showed no lateral preference during the experiments (Binomial proportions test, $X^2_{2P6} = 0$, $p=0.90$; $X^2_{2P5} = 0.01$, $p=1$ and $X^2_{2P2} = 2.9$, $p=0.09$). Two seals showed a slight but significant preference for the right tube, selecting it in 53% and 54% of the trials ($X^2_{2A2} = 6.98$, $p=0.01$ and $X^2_{2P1} = 6.93$, $p=0.01$).

Fish characteristics

The characteristics of the fish used in this study are shown in Table 6.2. The herring in 2005 was separated in two groups. Group A was significantly smaller and had a lower percentage of lipids than group B (Student t-test, $T_{weight} = -8.46$, $p = 0.003$ and $T_{lipid} = -3.45$, $p = 0.04$). Trials using group B were removed from the final set of data because seals refused to eat them during the trials and also rejected them during training and feeding sessions. Herring in 2006 were significantly smaller than in 2005 and had a higher percentage of lipids than group A from 2005 but lower than group B from 2005 (Student t-test, $T_{weightA} = 3.16$, $p = 0.003$; $T_{weightB} = 4.94$, $p < 0.001$; $T_{lipidA} = -9.94$, $p < 0.001$ and $T_{lipidB} = 4.38$, $p = 0.022$). Sprats were the smallest fish offered in 2005 and 2006 (~14 g). Whiting had a lower percentage of lipid and was significantly bigger than the herring (Student t-test, $T_{lipid} = 4.47$, $p<0.001$ and $T_{weight} = -4.65$, $p = 0.001$). Haddock was the biggest fish offered in 2006 (~321 g) but had the lowest lipid density (3.25 % of lipid). The percentage of lipid was not significantly
different between the mackerel and the herring in 2006 (Student t-test, $T_{lipid} = 0.65$, $p = 0.527$).

Table 6.2. Summary of the fish characteristics obtained for the 5 species of fish used in 2005 and 2006.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Energy density (kJ.g$^{-1}$)</th>
<th>Weight (g)</th>
<th>Length (mm)</th>
<th>% water</th>
<th>% Lipid</th>
<th>% Protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprat 2005</td>
<td>9.26</td>
<td>14.4</td>
<td>104.4</td>
<td>63.78</td>
<td>16.09</td>
<td>15.88</td>
</tr>
<tr>
<td>Sprat 2006</td>
<td>8.30</td>
<td>14.7</td>
<td>106.6</td>
<td>67.63</td>
<td>13.86</td>
<td>14.07</td>
</tr>
<tr>
<td>Mackerel</td>
<td>7.29</td>
<td>136.9</td>
<td>246</td>
<td>68.06</td>
<td>11.51</td>
<td>16.46</td>
</tr>
<tr>
<td>Haddock</td>
<td>3.40</td>
<td>321</td>
<td>298</td>
<td>78.10</td>
<td>3.25</td>
<td>14.93</td>
</tr>
<tr>
<td>Whiting</td>
<td>4.74</td>
<td>165.2</td>
<td>246.4</td>
<td>75.52</td>
<td>4.43</td>
<td>16.19</td>
</tr>
<tr>
<td>Herring 2005A</td>
<td>6.58</td>
<td>115.3</td>
<td>201.5</td>
<td>72.56</td>
<td>5.73</td>
<td>16.20</td>
</tr>
<tr>
<td>Herring 2005B</td>
<td>10.30</td>
<td>143</td>
<td>219</td>
<td>62.67</td>
<td>18.50</td>
<td>14.18</td>
</tr>
<tr>
<td>Herring 2006</td>
<td>7.57</td>
<td>87.6</td>
<td>189.5</td>
<td>68.10</td>
<td>12.16</td>
<td>15.54</td>
</tr>
</tbody>
</table>

Handling behaviour

A2 and P1 ate individual sprat faster than herring and mackerel. P2 ate herring as fast as sprat but ate mackerel more slowly. A2 took longer to eat haddock compared to the other species (Table 6.3). Taking handling time into account, sprat appeared to be offering the smallest rate of energy gain and weight gain for all three seals. For example, it would take P2 6 times longer to obtain the same amount of energy when eating sprat compared to herring. For P1 and A2 the highest energy gain per minute was obtained with mackerel while it was with herring for P2. The highest perceived weight gain was obtained with haddock for A2, with herring for P2 and with mackerel for P1. A2 showed a similar rate of energy gain for haddock and herring suggesting that the low energy content of haddock was compensated by its large size and short handling time.
Table 6.3. Results of the mean time taken to eat different prey species and their associated gain in kilo joule per minute and in gram per minute for each seals in 2006. Values in brackets are standard deviations.

<table>
<thead>
<tr>
<th>Seal</th>
<th>Species of fish</th>
<th>Mean weight of the fish (g)</th>
<th>Mean time to eat 1 fish (min)</th>
<th>Mean rate of energy gain (kJ.min⁻¹)</th>
<th>Mean rate of weight gain (g.min⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A2</td>
<td>Herring</td>
<td>87.6</td>
<td>0.17 (±0.41)</td>
<td>3984</td>
<td>515</td>
</tr>
<tr>
<td></td>
<td>Haddock</td>
<td>321</td>
<td>0.32 (±0.21)</td>
<td>3400</td>
<td>1003</td>
</tr>
<tr>
<td></td>
<td>Mackerel</td>
<td>136.9</td>
<td>0.19 (±0.07)</td>
<td>5207</td>
<td>721</td>
</tr>
<tr>
<td></td>
<td>Sprat</td>
<td>14.7</td>
<td>0.07 (±0.07)</td>
<td>1729</td>
<td>210</td>
</tr>
<tr>
<td>P1</td>
<td>Herring</td>
<td>87.6</td>
<td>0.35 (±0.74)</td>
<td>1893</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>Mackerel</td>
<td>136.9</td>
<td>0.44 (±0.42)</td>
<td>2278</td>
<td>311</td>
</tr>
<tr>
<td></td>
<td>Sprat</td>
<td>14.7</td>
<td>0.21 (±0.24)</td>
<td>580</td>
<td>70</td>
</tr>
<tr>
<td>P2</td>
<td>Herring</td>
<td>87.6</td>
<td>0.18 (±0.21)</td>
<td>3605</td>
<td>487</td>
</tr>
<tr>
<td></td>
<td>Mackerel</td>
<td>136.9</td>
<td>0.33 (±0.31)</td>
<td>3038</td>
<td>415</td>
</tr>
<tr>
<td></td>
<td>Sprat</td>
<td>14.7</td>
<td>0.21 (±0.32)</td>
<td>580</td>
<td>70</td>
</tr>
</tbody>
</table>

Selectivity for prey numbers

During trials with sprat and herring, seals generally selected the tube with the highest number of prey items, except P5 for trials with herring (Table 6.4). When using sprat, seals chose the most numerous items in 63 % to 83 % of the trials. This percentage decreased to between 54 % and 72 % when using herring. There was, however, no apparent selection during trials with mackerel. Seals appeared not to preferentially select tubes with higher numbers of mackerel and randomly fed from one or the other tube.
Table 6.4. Results of the binomial proportion tests showing selectivity for number of prey items. Numbers in bold are statistically significant.

<table>
<thead>
<tr>
<th>Fish species</th>
<th>Seal</th>
<th>Number of trials</th>
<th>P value</th>
<th>success in %</th>
<th>failure in %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprat</td>
<td>P5</td>
<td>126</td>
<td>&lt; 0.001</td>
<td>83</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>P6</td>
<td>95</td>
<td>&lt; 0.001</td>
<td>77</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>P1</td>
<td>116</td>
<td>&lt; 0.001</td>
<td>63</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>P2</td>
<td>147</td>
<td>&lt; 0.001</td>
<td>65</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>140</td>
<td>&lt; 0.001</td>
<td>66</td>
<td>34</td>
</tr>
<tr>
<td>Herring</td>
<td>P5</td>
<td>35</td>
<td>0.633</td>
<td>54</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>P6</td>
<td>24</td>
<td>0.009</td>
<td>71</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>P1</td>
<td>126</td>
<td>0.001</td>
<td>67</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>P2</td>
<td>116</td>
<td>&lt; 0.001</td>
<td>72</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>265</td>
<td>&lt; 0.001</td>
<td>59</td>
<td>41</td>
</tr>
<tr>
<td>Mackerel</td>
<td>P1</td>
<td>34</td>
<td>0.225</td>
<td>59</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>P2</td>
<td>29</td>
<td>0.599</td>
<td>55</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>A2</td>
<td>19</td>
<td>0.052</td>
<td>68</td>
<td>32</td>
</tr>
</tbody>
</table>

A GLM carried out on sprat data showed that the probability of success increased with the ratio of weight offered (RWO) for two of the five seals (Table 6.5). Figure 6.2 shows that A2 was choosing the tubes with the highest number of sprat in 80% of the trials when the RWO offered reached 6, whereas P5 was with a RWO of 2.5. The three other seals generally chose the most numerous prey items but the proportions of successful trials did not increase with RWO.
Figure 6.2. Probability of success in relation to the ratio of weight of sprat offered for a) A2 and b) P5. The solid lines give the binomial logistic regression.

Table 6.5. Results for the GLM carried out on sprat data. The final model was tested against the null model for significance. Numbers in bold are statistically significant.

<table>
<thead>
<tr>
<th>Seal</th>
<th>Deviance</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>A2</td>
<td>11.811</td>
<td><strong>0.005</strong></td>
</tr>
<tr>
<td>P5</td>
<td>6.384</td>
<td><strong>0.036</strong></td>
</tr>
<tr>
<td>P1</td>
<td>0.111</td>
<td>0.741</td>
</tr>
<tr>
<td>P2</td>
<td>1.395</td>
<td>0.265</td>
</tr>
<tr>
<td>P6</td>
<td>1.286</td>
<td>0.275</td>
</tr>
</tbody>
</table>

Selectivity for prey profitability

The full binomial mixed effect model including data from all five seals (model 1) suggested that seals were maximising the weight of fish (67.9 %) compared to TEG or number of fish (see Table 6.6). However, the model based on 2006 data (model 2) showed that the percentage of success by maximising the PWG was not significantly different from the percentage of success by maximising PEP (p = 0.442, Table 6.6)
but they were both significantly higher from the other currencies (p < 0.001 for all, Table 6.6). Choices seemed unrelated to the number of fish contained in the tubes (17.8 % for model 1 and 19.2 % for model 2).

Table 6.6. Summary of the parameters obtained from binomial linear mixed-effect models in R (v2.60) with all 5 animals (Model 1) and with 2006 data (Model 2) included. The significance of a parameter was tested by adding each parameter to the null model and examining the effect on the fit of the model using a likelihood ratio test. The slope (± s.e.m.) is given for each selection index and the significance of each when compared to the intercept is presented. The model estimate of percentage correct is given to indicate in which proportion seals were maximising each of the currencies.

<table>
<thead>
<tr>
<th></th>
<th>AIC</th>
<th>L.Ratio</th>
<th>Slope</th>
<th>%Correct</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model 1 (5 animals)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null model</td>
<td>1967</td>
<td>681.16</td>
<td></td>
<td></td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Final model</td>
<td>1290</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight of fish (intercept)</td>
<td>0.759 (±0.118)</td>
<td>67.9</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TEG</td>
<td>-0.190(±0.080)</td>
<td>63.6</td>
<td>0.0175</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of fish item</td>
<td>-2.276(±0.101)</td>
<td>17.8</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Model 2 (3 animals)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null model</td>
<td>2538</td>
<td>913.1</td>
<td></td>
<td></td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Final model</td>
<td>1633</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PWG (intercept)</td>
<td>1.729(±0.141)</td>
<td>84.9</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PEP</td>
<td>-0.088(±0.114)</td>
<td>83.7</td>
<td>0.442</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight of fish</td>
<td>-1.172(±0.108)</td>
<td>63.6</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TEG</td>
<td>-1.258(±0.107)</td>
<td>61.5</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of fish item</td>
<td>-3.177(±0.132)</td>
<td>19.2</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

AIC = Akaike Information Criteria. L.ratio = likelihood ratio test
Selectivity for prey species

Chi-square tests based on weight showed that seals selectively avoided sprat when offered during experiments except during trials with whiting (Table 6.7). Herring was again the preferred species over mackerel and haddock for A2. On the other hand, P1 and P2, showed no preference between herring and mackerel but they appeared to select their food in order to maximise their weight gain on a trial basis.

Chi-squared tests based on PWG showed that, when taking handling time into account, results differed for one of the seals (Table 6.7). P1 preferred sprat instead of herring and preferred herring compared to mackerel suggesting that it was not always maximising its PWG. For the two other seals results did not change compared to the Chi-squared tests based on weight, the adult still appeared to prefer herring while P2 showed no preference between herring and mackerel.
Table 6.7. Grey seals’ feeding selectivity (Chi-squared test) calculated for all five fish species in the different experiments. Chi-squared was calculated based on the weight of fish offered for all seals and on the perceived weight gain for seals in 2006. The critical value calculated for a 95% certainty level was 3.84. Selective predation occurs if the calculated chi-squared was higher than the critical value. When the calculated chi-squared was less than the critical value then seals selected their food in accordance with what was expected. Bold numbers are significantly higher than the critical value. X indicates that the analyses could not be carried out.

<table>
<thead>
<tr>
<th>Seal Experiments</th>
<th>Number of trials</th>
<th>$\chi^2$ Weight preference</th>
<th>$\chi^2$ Perceived weight gain</th>
<th>Prey preference</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1 Herring-Sprat</td>
<td>112</td>
<td>52.72</td>
<td>57.36</td>
<td>Sprat</td>
</tr>
<tr>
<td>Herring-Mackerel</td>
<td>61</td>
<td>1.8</td>
<td>28.6</td>
<td>Herring</td>
</tr>
<tr>
<td>P2 Herring-Sprat</td>
<td>141</td>
<td>36.55</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Herring-Mackerel</td>
<td>66</td>
<td>0</td>
<td>0.9</td>
<td>No preference</td>
</tr>
<tr>
<td>P5 Herring-Sprat</td>
<td>279</td>
<td>52.3</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Whiting-Sprat</td>
<td>49</td>
<td>1.02</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>P6 Herring-Sprat</td>
<td>193</td>
<td>125.3</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Whiting-Sprat</td>
<td>70</td>
<td>2.4</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>A2 Herring-Sprat</td>
<td>360</td>
<td>251.08</td>
<td>8.64</td>
<td>Herring</td>
</tr>
<tr>
<td>Herring-Mackerel</td>
<td>82</td>
<td>12.7</td>
<td>180.6</td>
<td>Herring</td>
</tr>
<tr>
<td>Herring-Haddock</td>
<td>138</td>
<td>266.8</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>

Prey switching

An interesting result was the change of behaviour during experiments for the adult A2. In the first week of experiments between herring and haddock, A2 almost completely ignored the haddock and chose only the herring (Figure 6.3). Later, when
the second (two weeks later) and the third week (four weeks later) of experiments between herring and haddock were carried out, the percentage of haddock eaten in relation to the percentage of fish offered was above 80% in all trials. Table 6.8 shows that results, varied considerably when the data were divided into two blocks: week 1 and week 2&3 confirming that A2 switched from herring to haddock which was also equivalent to switching to a higher PWG.

Figure 6.3. Relationship between the percentage of fish offered and the percentage of fish eaten for the adult seal during experiments with herring and haddock. Each symbol represents a trial. H stands for herring and HA for haddock. A) represents data obtained during the first week of experiments and B) data obtained during the second and third week of experiments. H stands for herring and HA for haddock.
Table 6.8. Grey seals feeding selectivity (Chi-squared tests) calculated for A2 during experiments using herring and haddock (See Table 6.5 for more details). In this case, sessions have been separated in two blocks (1 and 2&3). Bold numbers are significantly higher than the critical value.

<table>
<thead>
<tr>
<th>Seal Experiments</th>
<th>Number of trials</th>
<th>$\chi^2$</th>
<th>Prey preference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring-Haddock 1 A2</td>
<td>32</td>
<td>752.5</td>
<td>Herring</td>
</tr>
<tr>
<td>Herring-Haddock 2&amp;3</td>
<td>106</td>
<td>0</td>
<td>No preference</td>
</tr>
</tbody>
</table>
Discussion

The present study shows that our seals were making active foraging choices based on the number and species of available prey; thus maximising their rate of energy gain (in terms of weight gain or energy profitability). Our results clearly show that seals preferred certain prey when prey availability, in terms of number and mass, was equal. By combining experimental manipulation of prey availability, in terms of species and number and allowing our seals to select their diet, we were able to investigate prey selection and examine some of the possible proximal and causal factors. Direct observations of foraging behaviour for underwater predators are difficult and sometimes impossible in the wild. Our experimental design was therefore designed to restrict the foraging choices offered to the seals in order to test simple optimal diet hypotheses. Although two out of the five seals showed a lateral preference for the right-hand tube, this percentage was close to neutral and we are confident that all seals were making selections on the basis of the characteristics of the prey presented.

*What are seals maximising while foraging*

Grey seals are generalist predators so we would expect that they should select a prey type in order to maximise the energy gain per unit of time, as predicted in optimal diet theory (Stephens & Krebs 1986). When presented with different number of items of the same species, seals generally selected the larger number in accordance with optimal foraging theory (i.e. maximising the net rate of energy gain), except for trials with mackerel. For two seals the probability of successfully choosing the tube with the highest number of individual sprat increased with the magnitude of the ratio
between the amounts offered. For the other three seals their success rate was not related to the magnitude of the ratio between the amounts offered. This is surprising as we would expect seals to improve their success as the ratio increased and to preferentially choose the highest number of prey items. These three seals might have been better at selecting the highest number of individual sprat at a low ratio compared to the other two seals. Interestingly, seals regularly ignored the tube containing the highest number of prey items and selected the tube with fewer ones. In addition, as the size of the prey increased, the percentage of success decreased to become non significant for mackerel. Seals were trained to eat all the fish in the selected tube and therefore they reduced their time spent foraging by selecting the smaller amount. It is unclear why they would choose to reduce their energy intake and/or their time spent feeding on a trial basis. An explanation is that, as captive animals, seals were fed on a daily basis and therefore they may have not always chosen to optimise their energy intake. This behaviour seemed to be reinforced with bigger fish. In this case, seals may randomly choose one or the other once the prey offered reaches a certain threshold of energy gain.

When offered a choice of two different species, grey seals selected their food in relation to the offered weight gain, perceived weight gain (PWG) and perceived energy profitability (PEP) in accordance with optimal diet theory (i.e. predators should maximise some aspect of their prey intake). If handling time data were available for 2005 we could expect seals to have been also maximising the PWG and PEP more than weight gain in 2005. Seals from both years, however, appeared not to be maximising their total energy gain or the number of prey items. Within our set-up seals would generally maximise their prey intake rate by choosing bigger fish because
“capture” time was constant for all prey and differences in handling time were restricted to the time taken to eat a range of dead fish species. For the same mass of fish, seals were generally faster at eating one big fish compared to several little fish. Several studies have shown that animals do not always select the largest available prey in preference tests (Swennen and Duiven 1991, Woolnough and Carthewew 1996) but large carnivores usually show a preference for large prey (Karanth and Sunquist 1995, Biswas and Sankar 2002; Paltridge 2002). In the wild, individual seals may specialise on different prey and the energetic profitability of feeding on a particular prey type may be a function of individual capture techniques (Pierce et al. 1990). It seems likely that wild seals would take larger fish when available, unless the energetic costs of search, capture and handling were disproportionately greater than for small prey. For example, sandeels (*Ammodytes marinus*), a major prey species in grey seals’ diet (Hammond and Prime 1990, Hammond et al. 1994), live motionless near the seabed and therefore may be a more profitable prey than other larger active prey.

*Prey preference*

The present study has demonstrated that seals were maximising some aspects of their prey intake (i.e. total weight gain, perceived weight gain and perceived energy profitability) when selecting fish in our experimental set-up. Interestingly, seals displayed some preferences over and above what they were maximising. That could be because we were not measuring what they were maximising or because they also had individual preferences. While they generally selected the fish offered in order to maximise their weight gain in 2005, or their PWG and PEG in 2006; some seals seemed to have individual preferences. This was the case for a pup in 2006 who preferred sprat compare to herring and the adult seal which preferred herring
compared to haddock. This variability between individuals is expected in order for foraging strategies to be designed through natural selection (Cezilly et al. 1991).

Although age and size can contribute to variation, systematic individual variation often remains (Estes et al. 2003).

The present study also highlights the importance of first determining what seals are maximising (i.e. the currency) before interpreting prey preference experiments. Several studies have discussed the issues with selecting the appropriate currency when testing a model (McNamara and Houston 1997, Bergman et al. 2001, Nolet 2002) and pointed out that effects other than energetic constraint can cause deviations from rate maximisation (i.e. predation risk). Prey preference differed in this study when using different currencies. For example, when using weight gain, one of the juvenile seals seemed to prefer herring compared to sprat but when using PWG, it then appeared to prefer sprat compared to herring. Therefore, wild studies based on the availability of fish in order to determine prey preference might be biased (Tollit et al. 1997, Lindstrom et al. 1998, Lindstrom and Haug 2001). These studies can only describe what is in their diet compared to what was available in the environment but we should be cautious in attributing any prey preference to predators from these data.

Switching behaviour

The observed timescale is an important aspect when studying prey selection because the foraging behaviour that maximises the amount of energy obtained by an animal over a week or a month might be different from foraging behaviour that maximises the amount obtained in one day or one hour (Katz 1974). The present study has demonstrated how the feeding behaviour of grey seals could vary over time. The most
interesting observation was the refusal from all seals to eat herring during a few days. Later analyses of these fish showed that this particular batch of herring was richer in lipid compared to the other batches. Digestive efficiencies in pinnipeds eating fish range from 83 % to 95 % (Lawson et al. 1997; Rosen and Trites 2000) with higher efficiencies for prey rich in lipids (Fisher et al. 1992; Keiver et al. 1984; Rosen and Trites 2000). Trumble et al. (2003), however, found that lipid and protein from herring might be more difficult to digest than those from lower calorific fish species. They suggested that the high concentrations of structural proteins as well as the effect of lipid were rendering dietary protein less accessible to proteolytic secretions. Therefore seals in the present study might have refused to eat herring because the high percentage of lipids (> 18 %) made it difficult for them to digest. In addition, Hilton et al. (2000) found a cost associated with switching from energy-dense fish diet to an energy-dilute diet in seabirds. Low lipid fish prey might, however, be preferred because high lipid diets require emulsification, involving higher bile input and higher gastric pH compared to protein digestion. If proteins were an important nutrient for the seals in this study, choosing the low lipid fish prey could be advantageous for them.

Choices exhibited by the seals during the trials could have been influenced by learning. For example, in trials examining the choice between haddock and herring, the adult female showed a clear change in preference over time. Initially she avoided haddock, exclusively choosing herring in the first week of trials. By the second week of trials the adult seal started selecting haddock over herring and was therefore maximising its rate of weight gain. The original preference was not due to a lack of familiarity as the seal had been trained to accept haddock as part of a mixed diet over
the preceding three weeks. This may suggest that as haddock became more familiar
the seal may have become reconditioned and concentrated its choices
disproportionately upon the new prey type. It seems that it took some time for the
adult to associate the new prey species that was offered with the one it was fed during
training sessions. The adult was used to select herring compared to sprat or mackerel
and may have needed time to accept haddock as a new alternative during experiments.
The adult seal thus exhibited a flexible search image influenced by learning.
Effectively, early experiences of particular foods might influence subsequent food
choices (Healy 2006). Tinbergen (1960) discovered that although suitable prey
usually appears in the environment gradually, they are often not accepted as food by
the birds for several days but are then accepted abruptly. The delayed acceptance led
Tinbergen to suggest that the birds do not accept a prey until they have acquired the
appropriate “specific search image”. This hypothesis could explain the seal’s
behaviour in this study; the delayed selection of haddock being a result of developing
the appropriate “specific search image”.

In conclusion, this study has demonstrated that feeding seals selected prey that
maximised their rate of energy gain (in terms of weight gain or energy profitability).
This energy maximisation was a function of handling time (i.e. time to eat a prey) and
handling time was directly influenced by seals behaviour. Optimal diet choice models
normally assume that profitability (net energetic gain per unit time) is fixed for each
prey species. In the wild, fish calorific values may vary seasonally and with size, and
the energetic cost of capture probably depends on shoal size and also on water depth
(Pierce et al. 1990). Perhaps the most critical gap remaining in our knowledge of seal
foraging strategies is the way they hunt for specific prey, and the relative energetic
costs and benefits associated with different prey (e.g. single, small, slow moving prey of high calorific value or large shoals of big, fast moving energy-low prey).

Additional data are therefore needed before the mechanisms of prey selectivity can be fully understood for foraging seals. This type of data will require additional captive studies where the cost of acquiring particular prey can be manipulated.
References


Chapter 7

General Discussion
The overall aim of the present study was to test current foraging models for breath-hold divers and to determine whether grey seals exhibit prey preferences. In addition, stroke and glide pattern of foraging grey seals were examined at a fine-scale in relation to swim speed. This thesis has proved the utility of experiments with temporally captive wild seals to develop our understanding of marine mammal foraging behaviour.

The foraging experimental design was built to create quasi-realistic dives to allow seals to behave as naturally as possible during these studies. For example, seals were free to dive at will in the tank and they were left undisturbed during experiments. Prey characteristics were also similar to those that seals experience in the wild. For example, prey swimming speeds used during these experiments were realistic. Sprat and herring swim around 1.7 m.s\(^{-1}\) (Swennen and Duiven 1991) and haddock around 0.9 m.s\(^{-1}\) (Breen et al. 2004) in the wild. Prey density corresponded to PER recorded with remote video camera deployed on freely diving harbour seals feeding on sandeels (Bowen et al. 2002) and distances between the surface and prey patch were equivalent to that experienced by grey seals in UK waters (Thompson and Fedak 1993). Despite our efforts, there were unavoidable differences between the experimental design and what seals might experience in the wild. One difference was that seals were given dead fish and did not have to pursue and catch their prey. This issue, in an experimental design, could only be addressed by experimentally manipulating the cost of acquiring different fish. For example, in Chapter 3 and 5, seals were not at rest when feeding at the prey patch. Seals were actively swimming against a force plate to access fish on the feeder. In Chapter 6, handling time was used as a proxy for the cost of acquiring different species. Another difference was that seals
had to swim horizontally underwater and did not face changes in pressure associated with depth. Phocid seals regularly exhale before diving and therefore we assume they have little air space that can be compressed as pressure increases with depth. Thus, for phocid seals, there may be little difference in the total energetic cost of swimming equivalent distances horizontally or vertically. For example, for a negatively buoyant seal, any energy saved on the descent by prolonged gliding may be cancelled out on the ascent by having to stroke more frequently.

The difficulties involved with working with large, untrained wild animals (discussed in Chapter 3) mean that the sample sizes are relatively small (between 5 and 7 seals for each chapter). This is compounded due to logistical constraints which mean that each animal can only be experimented with on a small number of occasions at different times of year. In addition, concurrent scientific studies and building work in and around the experimental facility dramatically reduced the timeframe when experiments could be carried out. Nevertheless, the sample size of animals tested in the present thesis is a relatively large compared to previous captive marine mammal studies (e.g. Cox 1996, Boyle 1997, Cornick and Horning 2003).

Within the framework of optimal foraging theory (OFT), foraging strategies in the present thesis were studied as decision making processes such as; which food types seals should eat and which speeds should seals move at between and within patches of prey. This information can then be used to better understand predator-prey interactions at a time when pressure on the marine ecosystem is increasing and more information is needed to better manage marine resources (Boyd et al. 2006,
Matthiopoulos et al. 2008). The findings of this thesis will be discussed in turn, along with suggested avenues for further research.

**Swimming characteristics**

Chapter 3 investigated the relationship between swimming speed and stroke and glide pattern in foraging grey seals during transit swimming. The results showed that swimming speed varied in relation to the swimming gait employed by the animals: swimming speed decreased as the percentage gliding increased. There were, however, variations between individuals and further work in this area is required to address the differences found between juveniles and adult seals. A recent study (Sato et al. 2007) found a strong relationship between the dominant stroke cycle frequency (i.e. the dominant stroke frequency within a stroking period) used during transit swimming by divers and body size but this finding did not hold true in the present study. Whilst Sato et al. (2007) study found that the dominant stroke cycle frequency is expected to decrease as body size increases, the adult seal in the present study had a higher dominant stroke cycle frequency compared with the juvenile seals. Future work to clarify this issue would involve more experiments with adult seals to determine if it was a behavioural decision on the adult part to use a high dominant stroke cycle frequency. If additional adult seals show the same pattern (i.e. a high dominant stroke cycle frequency) then it would be interesting to manipulate the buoyancy of seals and examine their stroke and glide patterns in response to these changes. By adding floating gear or weights to the seals it is possible to increase or decrease the buoyancy of the animals. This would enable us to determine if the dominant stroke cycle frequency is related to their body mass and/or their buoyancy.
Chapter 3 showed that travel duration and mean swim speeds were not good indicators of energy expenditure compared to stroke and glide patterns. On the contrary, an increase in oxygen consumption with swimming speed has been demonstrated for seals and sea lions in the past (Davis et al. 1985, Feldkamp 1987, Fedak et al. 1988, Williams et al. 1991). There are a few explanations for why this relationship did not hold true in the present study. First the present study differs from those involving seals swimming in flumes in that any swimming is voluntary and occurs as part of a dive. Secondly, average swim speeds in the present study rarely reached the higher speed recorded in the other studies. Finally seals in a flume are forced to swim just below the surface where drag is much higher than a few meters below. Thus the present study suggests that, within a narrow range of swim speeds, stroke and glide patterns may be better indicators of energy expenditure.

Interpretation of these results was affected by a limited number of data points and more effort should be allocated in the future to expand on these. Nevertheless, the results are in accordance with previous studies suggesting that swimming speed alone is a poor indicator of locomotor costs (Skrovan et al. 1999, Williams et al. 2000, Davis et al. 2001).

The present study has shown that for seals swimming horizontally underwater locomotor costs and swimming speeds decrease with increasing gliding duration. In addition, heavier animals appeared to glide longer because of increasing momentum forces. It is unclear, however, if stroke and glide swimming is an energy saving strategy for wild seals as suggested by several studies (Williams and Kooyman 1985, Williams et al. 2000, Kramer and McLaughlin 2001). For wild negatively buoyant
seals, one would expect that any energy saved by prolonged gliding during the
descent would cancel out during the ascent as it would have to work harder (Davis et al. 2007). Therefore it is unclear why the majority of studies (Williams and Kooymen 1985, Williams et al. 2000, Kramer and McLaughlin 2001) refer to stroke and glide swimming as an energy efficient strategy if it is the logical result of the combined effects of the physical properties of the diver (i.e. mass and buoyancy) and the changes of pressure with depth at a given speed. For example, wild, negatively buoyant seals may use prolonged gliding on the descent because they can use their mass to sink without losing their speed. The same may be true for positively buoyant animals that stop stroking as they come near the surface on the ascent as they do not need to stroke to move upward. Further work is required to elucidate the complex relationship between swimming speed, buoyancy and stroke and glide pattern and how it is affected by changes with depth.

Foraging behaviour

Chapter 4 and 5 investigated how predators’ swimming speeds vary in relation to patch characteristics (i.e. depth, density, swimming speed of the prey). There is growing evidence that breath-hold divers respond to changes in prey characteristics by altering their foraging behaviour in ways that are consistent with predictions from optimal foraging theory. Sparling et al. (2007) examined how long seals stayed in different quality prey patches and found that seals responded to prey density, leaving low quality patches earlier as predicted by the model of Thompson and Fedak (2001). The results of the present study indicate that swim speeds in grey seals are closely related to resource characteristics (i.e. distance, density, movement) as predicted by
the models of Thompson *et al.* (1993). All seals tested in this study altered their transit swimming speed in response to changes in patch distance. They also changed their foraging swimming speed in response to prey swimming speed and prey density. In addition, foraging durations increased as prey speed and prey density increased showing that seals were increasing their energy intake by behaving as predicted in the model of Thompson *et al.* (1993). Other work to further investigate these relationships might explore whether Thompson *et al.* (1993) models’ predictions hold true for similar sized phocid seals such as harbour seals. In addition, our unexpected discovery that seals swim slower on their way back to the surface in the absence of buoyancy effects suggest that the swimming behaviour exhibited by foraging grey seals is primarily dependent on behavioural choices. These results concur with the hypothesis that for shallow-divers, diving behaviour is mainly dictated by behavioural choices rather than physiological constraints that deep-divers face. Future work would involve the testing of these models with larger phocids such as Weddel seals and elephant seals. With a majority of long, deep dives (i.e. over 15 minutes and more than 150 metre deep) these species remains challenging to study in a captive facility and the testing of existing theoretical models with these species would require additional animal-borne instruments that can record the behaviour, three-dimensional movements and locomotry performance of free-ranging animals.

Both of these chapters were based on the assumption that seals attempted to maximise their rate of energy gain but it seems that not all seals may choose to maximise that currency. Pregnant seals decreased their swimming speed throughout the study (see Chapters 3, 4 and 5) and resulted in swim speeds lower than the estimated MCT speed. In addition, Chapter 5 showed that the pregnant female did not work harder at
high prey density but instead reduced its activity to sit and wait for the prey to come into the encounter region. These behavioural adjustments may be related to energy saving strategies in preparation for the breeding season (Sparling et al. 2006). Therefore, pregnant females may minimise their energy expenditure rather than maximise their rate of energy intake before the breeding season. As Katz noted in 1974, the observed timescale is important when studying foraging behaviour. Depending on time of year and of physiological constraint such as being pregnant, seals might adopt different strategies. It would be interesting to investigate changes in diving behaviour of wild pregnant grey seals as they approach the breeding season.

Prey selection

Chapter 5 explored the prey preference of foraging grey seals. The demonstration of distinct preferences of grey seals based on fish characteristics (i.e. weight, number, species, handling time, energy content) challenges the idea that wild seals are purely opportunistic predators. The potential importance of prey preference has been suggested in recent studies of prey selectivity in wild seals in which prey were not always eaten in direct proportion to their absolute or relative abundance (Tollit et al. 1997, Lawson et al. 1997, Lindstrom et al. 1998). The relevance of these kinds of analyses, however, relies on accurate and meaningful estimates of prey availability relative to the movements of seals in time and space (see Harwood and Croxall 1988).

This study has highlighted the problems associated with the assumptions that prey selectivity analyses rely on. For example, results in the present study varied depending on which currencies were tested. It is therefore important to first determine
what seals are maximising before interpreting prey preference experiments.

Traditionally, prey preference has been investigating by comparing the proportion of a species $\alpha$ in a diet given the choice between species $\alpha$ and $\beta$. This method ignores any biological aspects of prey preference. If predators are maximising their rate of energy gain, their rate of mass gain, their rate of protein intake or any other currency, different species will not have the same biological value. Another mistake is the confusion between prey preference and currency maximisation. For example, it is not because a particular prey represents the majority of the diet that it is preferred. The abundance of that prey in the diet, however, can help assess what predators are maximising.

For wild marine mammals, direct observations and measurements of predator-prey interactions are difficult so prey preference studies rely mainly on indirect measurements of predators’ diet and prey characteristics (Tollit et al. 1997, Lindstrom et al. 1998, Lindstrom and Haug 2001). Therefore conclusions from these studies remain speculative as prey selectivity is based on an estimated availability and takes little account of prey characteristics such as energetic content, protein content or handling time. Therefore more captive studies with different phocid seals and other species of marine mammals are needed to determine accurately what currency predators are maximising while foraging in order to predict their diet in the wild.

A critical gap remaining in our knowledge of seal foraging strategies is the way in which they hunt for specific prey and the relative energetic costs and benefits associated with different prey (e.g. single, small, slow moving prey of high calorific value or large shoals of big, fast moving energy-low prey). Additional data are needed
before the mechanisms of prey selectivity in foraging grey seals can be fully understood. This type of data will require additional captive studies where the cost of acquiring particular prey can be manipulated.

Future work with prey choice experiments would also involve using the data to develop multi-species functional responses. Recently there has been a growing recognition for the need to develop multi-species functional responses and for a better understanding of the behavioural mechanisms that lead to particular response function (Mori and Boyd 2004).
References


