The Foraging Ecology of South American Sea Lions (*Otaria flavescens*) on the Patagonian Shelf

Dissertation

zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität zu Kiel

Vorgelegt von

Gabriele Müller

Kiel 2004

CONTENTS

INTRODUCTION

Pinnipeds are a diverse group of mammals with an amphibious life style, being dependent on an aquatic environment for food, and on land or ice for breeding and moulting. Even though the time that a pinniped spends at sea varies from species to species, this time is of crucial importance to its survival as it is the only time available for acquisition of energy.

The technological advances that took place since the development of the earliest time-depth-recorders in the mid 1960´s (Kooyman 1965) now allow us to study the foraging behaviour of pinnipeds at sea – hundreds of kilometres away from land and at depths of over 1300 m (Campagna *et al*. 1999; Le Boeuf *et al*. 2000). But despite the radical increase in knowledge over the last two decades on the diving and foraging behaviour of a wide range of pinniped species, few studies have been so detailed as to be able to compare males and females. The few examples are found almost entirely within the phocids (earless seals) (Le Boeuf *et al*. 1993; Thompson *et al*. 1998; Baechler *et al*. 2002; Beck *et al*. 2003). These studies suggest that the differences in foraging ecology and diving behaviour between the two sexes increase with increasing size dimorphism. As almost all otariids (eared seals: fur seals and sea lions) are highly dimorphic, with males reaching up to three times the size of females, sex segregation very likely plays an important role in this group of pinnipeds although it awaits further investigation. Size-dependent differential foraging patterns might allow the two genders to exploit different niches which might explain why otariids can occur in substantial numbers while phocids generally occur in small groups or singly.

The main purpose of this study is to elucidate the foraging ecology of South American sea lions (*Otaria flavescens*) from Patagonia. This sea lion is an example of an otariid of which only very little is known about the foraging ecology, and the existing knowledge being limited almost exclusively to lactating females (Werner & Campagna 1995; Campagna *et al*. 2001). In order to obtain an overall picture the practical investigations are focussed on male sea lions as the knowledge regarding this part of the population is extremely scarce. The information obtained is then used to compare the movements and diving behaviour of males and females and derive important information relating to space use, prey consumption and foraging strategies of South American sea lions on the Patagonian shelf.

Figure 1.1: Male, pup and female (left to right) of South American sea lion (*Otaria flavescens*) from the Punta Buenos Aires rookery, Argentina.

1.1 THE SOUTH AMERICAN SEA LION

The South American sea lion (*Otaria flavescens*) is one of only five species of sea lion that make up the subfamily Otariinae, part of the family Otariidae. Its distribution ranges from southern Brazil down to Cape Horn on the Atlantic side and up to northern Peru on the western side of South America, with the major part of the population occurring on the Patagonian coasts and southern islands. The total population size is unknown, but for the southwestern Atlantic coast it has been estimated to about 110,000 animals (Cappozzo 2002).

This species is one of the largest and most dimorphic among the otariids (Figure 1.1). Males can reach lengths of 3 m and weigh up to 350 kg, whereas the smaller females only reach lengths of 2 m and weights of 150 kg. Sexual maturity is attained ages of six and five for males and females, respectively (Cappozzo 2002). Males, however, usually do not form an effective part of the breeding population until several years later when they have attained an appropriate physical size and strength that allows them to compete with other fully grown, adult males. South American sea lions are polygynous and the size of a harem is usually less than three but can reach up to ten females (Campagna 1985; Campagna & Le Boeuf 1988). The breeding season begins in mid-December and lasts until early February. Depending on local circumstances and time of the breeding season, males are often territorial and may switch to direct defence of females as the number of both males and females increases and the available space on the breeding beaches decreases (Campagna & Le Boeuf 1988). Females give birth shortly after their arrival at the breeding sites, and make foraging trips to sea throughout the lactation period, which usually lasts between 8 and 10 months (Cappozzo 2002).

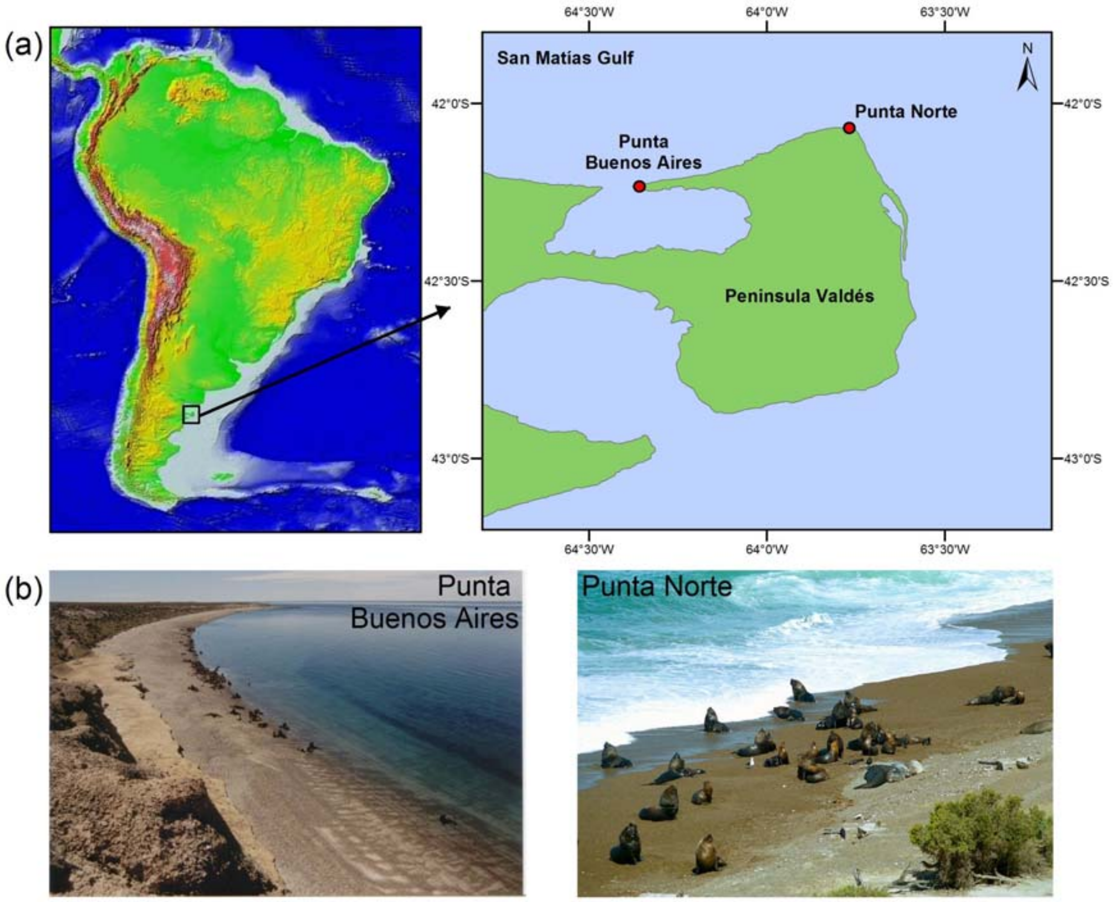


Figure 1.2: (a) Map of Peninsula Valdés, with the two study areas indicated by red circles. (b) Photos of the study areas, Punta Buenos Aires (left) and Punta Norte (right).

1.2 Study Area

Peninsula Valdés, a headland located on the coast of Patagonia in Argentina (Figure 1.2a), is a breeding site for three marine top-predators exploiting the highly productive Patagonian shelf for food: the South American sea lion (*Otaria flavescens*), the southern elephant seal (*Mirounga leonina*) and the Magellanic penguin (*Spheniscus magellanicus*) (Campagna 1985; Peters *et al.* 1998; Campagna *et al.* 1999). There are four large sea lion breeding rookeries on the peninsula of which two were chosen for field work based on their accessibility and physical characteristics (Figure 1.2b). Punta Buenos Aires (42.067°S, 63.783°W) is located on the north-western tip of the peninsula, whereas Punta Norte (42.083°S, 63.767°W) is found on the north-eastern corner. Both rookeries are about the same size with ca. 1300 pups being born each year (Campagna *et al*. 2001). In addition, both breeding beaches consist of mildly sloping pebble with up to 80 m of mudflats or sandstone being exposed at low tide. The shelf waters around Peninsula Valdés are comparatively shallow (0–200 m), and depths gradually increase towards the shelf break east of the peninsula with the shelf break being defined by the 200 m depth contour. However, depths of up to ca. 200 m are also attained inside the San Matías Gulf, providing the animals with an opportunity to dive as deep close to the colony.

1.3 ANIMAL IMMOBILISATION

Because of their large size it was necessary to anaesthetize the male sea lions in order to equip them with telemetry devices. This was done by three field veterinarians from the Field Veterinary Program of the Wildlife Conservation Society in New York and one veterinarian from Acuario de Buenos Aires y Jardín Zoológico de Buenos Aires. All veterinarians were familiar with pinniped physiology and two of them had substantial previous experience with anaesthetizing South American sea lions. A brief description of the procedure is given below.

Animals were chosen based on their behaviour and position on the beach. Individuals that were resting or sleeping, preferably away from other animals high up on the beach, were most suitable as they were least likely to show a significant reaction to the dart, with which the anaesthesia was administered. Work was only carried out during low tide because a large distance between the animal and the water line decreases the risk of the animal moving into the water after receiving the anaesthetic. Animals were anaesthetized with Telazol® given intramuscularly at a dose of 1.5 mg/kg estimated body weight by darting (Campagna *et al.* 2001). The animals were approached after five to ten minutes when the anaesthesia had taken effect. If necessary, animals were given supplemental gas anaesthesia to induce full anaesthesia. All animals were given antibiotics as they showed smaller wounds as a result of fighting with other males. During January 2003 seven males were successfully equipped with satellite tags. In November 2003 another nine males were anaesthetized. Unfortunately, one of these animals displayed a strong negative reaction to the anaesthesia and died subsequently. All remaining animals, however, recovered within one to two hours after darting and their well-being was ascertained by re-sightings or by the transmission of satellite data for up to two months after immobilisation.

1.4 LITERATURE CITED

Baechler, J., Beck, C.A. & Bowen, W.D. (2002) Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* **80**, 1569–1577.

Beck, C.A., Bowen, W.D., McMillan, J. & Iverson, S.J. (2003) Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour* **66**, 777–789.

Campagna, C. (1985) The breeding cycle of the southern sea lion, *Otaria byronia*. *Marine Mammal Science* **1**, 210–218.

Campagna, C. & Le Boeuf, B.J. (1988) Reproductive behaviour of southern sea lions. *Behaviour* **104**, 233–261.

Campagna, C., Fedak, M.A. & McConnell, B.J. (1999) Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* **80**, 1341–1352.

Campagna, C., Werner, R., Karesh, W., Marín, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology, London* **257**, 205–220.

Cappozzo, H.L. (2002) South American sea lion. *Encyclopedia of Marine Mammals* (eds W.F. Perrin, B. Würsig & J.G.M. Thewissen), pp. 1143–1146. Academic Press, San Diego, CA.

Kooyman, G.L. (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Record* **12**, 391–394.

Le Boeuf, B.J., Crocker, D.E., Blackwell, S.B., Morris, P.A. & Thorson, P.H. (1993) Sex differences in diving and foraging behaviour of northern elephant seals. *Marine Mammals: Advances in Behavioural and Population Biology* (ed I.L. Boyd), vol. 66, pp. 149–178. Symposium of the Zoological Society of London, Oxford University Press, Oxford, UK.

Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M. & Houser, D.S. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs* **70**, 353–382.

Peters, G., Wilson, R.P., Scolaro, J.A., Laurenti, S., Upton, J. & Galleli, H. (1998) The diving behavior of Magellanic penguins at Punta Norte, Peninsula Valdes. *Colonial Waterbirds* **21**, 1–10.

Thompson, P.M., Mackay, A., Tollit, D.J., Enderby, S. & Hammond, P.S. (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology* **76**, 1044–1053.

Werner, R. & Campagna, C. (1995) Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Canadian Journal of Zoology* **73**, 1975–1982.

A NEW SHOT AT A RELEASE MECHANISM FOR DEVICES ON FREE-LIVING ANIMALS

Müller *et al.*

Wildlife Society Bulletin, to be published in spring 2005

2.1 ABSTRACT

Detailed studies of the behavior and location of free-ranging animals can be considerably enhanced with the use of animal-mounted devices. A few devices, such as data loggers, have to be recovered to access the data, whereas satellite tags or radiocollars often are left on the animal after the study period. Recovery of devices, which usually necessitates animal recapture, can be problematic, especially in larger species. This paper presents a new, non-electronic release-mechanism requiring no power source on the animal, that was successfully tested on South American sea lions (*Otaria flavescens*) in Argentina during the 2003–2004 austral summer. The system has potential for many larger terrestrial or aquatic animals.

2.2 INTRODUCTION

Detailed study of the whereabouts and behavior of animals often is problematic by simple observation because animals might change their behavior when humans are in their vicinity (Elwood *et al*. in press) or because they live in an environment which makes it impossible to follow and observe them (e.g. aquatic animals). To overcome these obstacles, devices have been produced which allow remote tracking of a wide range of animals. Tracking devices range from the use of VHF tags (Van Parijs *et al*. 1997; Deutsch *et al*. 1998; Osborn & Parker 2003) to modern satellite tags (Lowry *et al*. 1998; Mate *et al*. 2000; Amstrup *et al*. 2001) or global positioning systems (GPS) (Sisak 1998; Girard *et al*. 2002). In addition to transmission technology, data loggers have been particularly useful for the study of aquatic species. This technology was first used by Kooyman (1965) who collected information on dive time and depth of Weddell seals (*Leptonychotes weddellii*) with so-called Time-Depth-Recorders (TDRs). Since then, advances in technology have made it possible to build data loggers collecting data from multiple parameters, including allowing the 3-dimensional route to be reconstructed from the collected data (Wilson 2004).

All devices must be attached to the study animal and this can be done through implantation (Amstrup *et al*. 2001), ingestion (Winger & Walsh 2001; Keefer *et al*. 2004), adhesion to the fur with glue (Green 1997; Campagna *et al*. 2001; Bradshaw *et al*. 2002), adhesion to feathers with tape (Wilson *et al*. 2001, 2002), or by using collars (Girard *et al*. 2002; Dique *et al*. 2003; Osborn & Parker 2003). The fate of the device (and also the animal that is connected to it), however, usually depends on the type of device and its value to the researcher. Data loggers must be recovered to access data, whereas the recovery of satellite tags is not essential. A high value of the device, perhaps in connection with the desire to use it on other animals, can be an incentive for recovery. However, there is an important moral responsibility to remove devices that no longer collect or transmit data because of potential long term effects (de Mendonca 1999; Hatch *et al*. 2000; Tuyttens *et al*. 2002; Demers *et al*. 2003).

In some species, device recovery can be effected by recapturing the animal and removing the logger by hand (Campagna *et al*. 2001). However, in many species recapture can be problematic, particularly where chemical immobilization is needed (Campagna *et al*. 2001). To circumvent this a few release mechanisms have been used whereby the device can be electronically released when the animal is sighted (Andrews 1998; Hammill *et al*. 1999) or where the device is released upon corrosion of a magnesium trigger (Orthmann 2000). Electronic release mechanisms increase both the size and mass of the overall package and must be recovered within a limited time because of battery drain. Failure to recover them may result, therefore, in an even more substantial impact on their carrier.

We present a new non-electronic release mechanism which eliminates these problems by using an external energy source to release the logger unit, thus providing a durable and long-term attachment method without time limits on recovery.

2.3 METHODS

2.3.1 Principle of operation

The system consists of three main parts: a housing, a metal base plate, and an obvious red resin disc. The housing, in which a logger is embedded, rests on the base plate. Extensions from the base plate, bent upwards, stabilize the housing anteriorly and along the sides. Posteriorly, the housing is connected to the base plate via a hook and eye system, which is locked in position by the insertion of the disc. To release the housing (and the logger therein) the disc is shot with an air gun pellet so that it shatters. This uncouples the housing from the base plate, so that the housing can be lifted or falls off the base plate when the animal moves.

2.3.2 The housing

The housing for the loggers (Figure 2.1) is made of resin mixed with Microbubbles (Type MS-V-2, Potters, UK) in an approximately 70:30 weight-ratio to obtain a

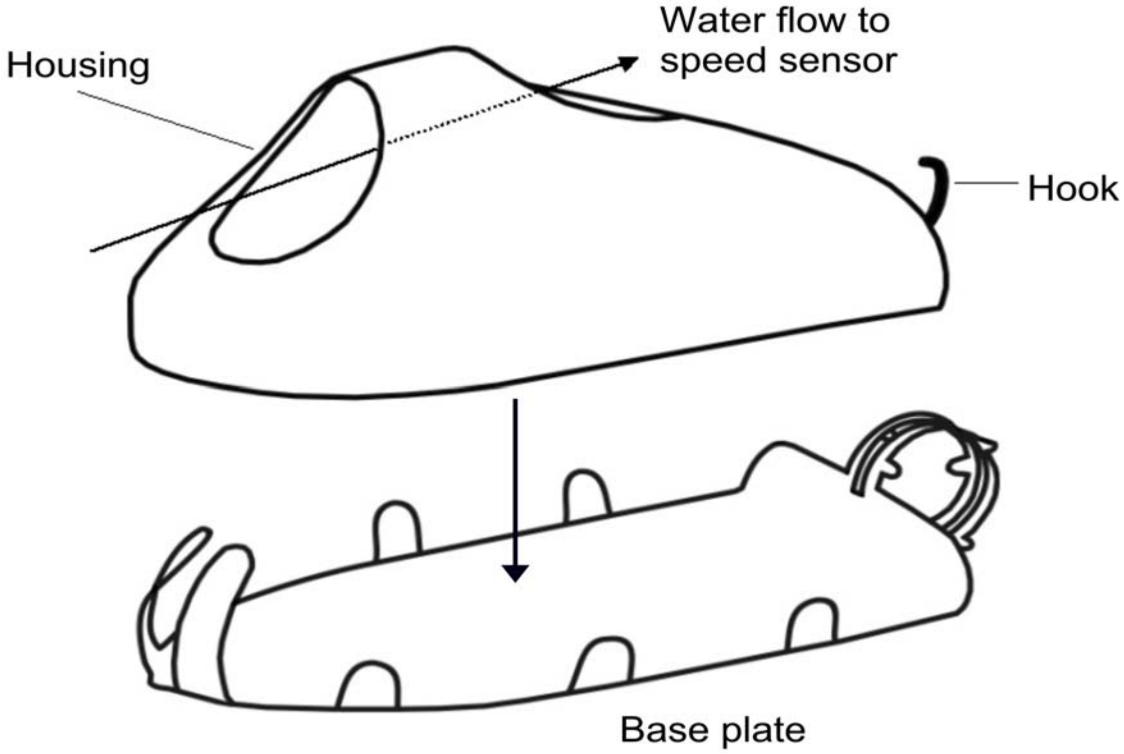


Figure 2.1: Drawing of the logger housing and its relation to the base plate with stabilizing tabs located laterally.

strong and stable matrix with low mass. Depending on the weight of the logger, the housing can be made positively buoyant by increasing the amount of Microbubbles in the mixture. The exterior shape of the housing is molded to reduce drag while the inside is molded to accommodate the shape of the 2 loggers used in our study. The maximum dimensions of the housing are 14 x 8.4 x 5.3 cm (L x W x H) with a mass of 113 g in air. A hook made of 2.0-mm V2A wire is incorporated into the rear end of the housing, adding another 3 cm to the total length of the device.

2.3.3 The base plate

The base plate (Figure 2.1) is made of 1-mm-thick V2A steel cut into the required shape with a laser. Tabs around the base of the plate are bent upwards to hold the housing in place. A steel loop is welded to the bottom of the plate at the back to increase stability (Figure 2.2). Small holes are drilled into the base plate and serve as attachment points for a mesh that is sewn to the underside of the plate to increase the adhesion between the device, the glue, and the fur of the animal.

2.3.4 The retaining disc

The retaining disc (Figure 2.2) is made of pure resin, colored bright red, and has a diameter of 2.5 cm. Dummy field trials showed the optimal thickness to be 0.9 cm at the rim reducing to 0.5 cm at its center. This ensures that the disc disintegrates with a single shot. Six notches are cut into the disc on each side from the periphery to facilitate this. Despite its susceptibility to breaking, this shape provides sufficient stability to hold the housing securely in place. A groove is made on the rim to hold the metal hook from the housing in place.

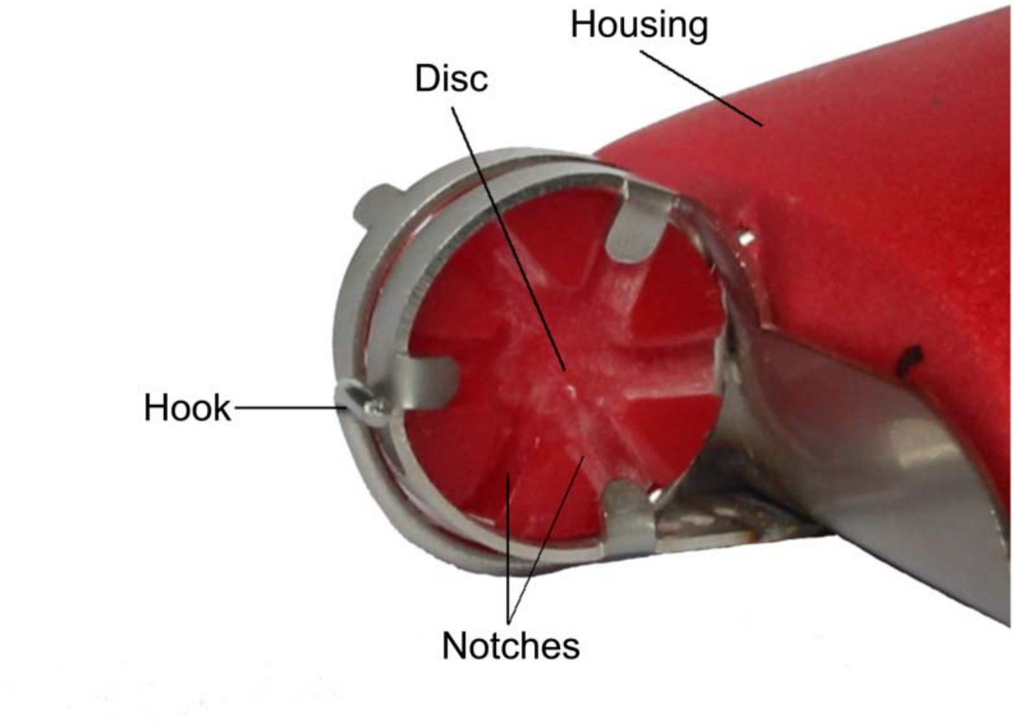


Figure 2.2: Photo of the release mechanism with the disc inside the metal frame and the tabs closed on one side. The end of the hook is bent at a 90° angle at the tip to avoid interlocking with the metal frame.

2.3.5 Air gun and pellets

A Feinwerkbau 300S air gun (caliber 4.5/177, Feinwerkbau, Westinger & Altenburger GmbH, Oberndorf/Neckar, Germany) was used to shoot at the disc with standard air gun pellets. Trials showed that pointed pellets were less effective than flat pellets in destroying the disc because they tended to break away small sections of the disc rather than shattering it, as did the flat pellets with their greater area of impact.

2.3.6 Fieldwork

During November 2003, we equipped 8 South American sea lions (*Otaria flavescens*) with the package at Punta Norte (42°05'S, 63°46'W) on Peninsula Valdés, Argentina (Figure 2.3) following necessary, appropriate ethics approval from the

Figure 2.3: Photo of a sub-adult male South American sea lion (*Otaria flavescens*) with the logger unit attached to the top of the head. The location of the disc in the release mechanism is shown with an arrow.

Dirección de Fauna de la Provincia de Chubut. Our permit allowed us to equip a maximum of 10 animals for these trials. We chemically immobilized the sea lions (Campagna *et al*. 2001) and glued the logger unit to the animals´ heads with epoxy glue (ITW Devcon®, Danvers, MA). For recovery of the devices we approached the animals carefully by crawling until we reached a distance of 4–5 meters for shooting. A second person was always present to keep watch for animals that might approach the marksman from behind. Previous trials showed that to ensure a certain (100%) hit with our air gun, the marksman needed to be within 10 m of the device.

2.4 RESULTS

Of the 8 equipped animals, 5 returned to Punta Norte where we successfully recovered all 5 devices between 4 and 9 weeks after deployment. Two animals returned without the housing, but still had the base plates on their heads although the retaining tabs had been bent flat. A third animal was seen once briefly but did not spend enough time on the beach for recovery to be attempted.

Except for 1 disc, which was completely destroyed by the first shot, the pellets only removed parts of the disc so 2 or 3 shots were necessary to completely destroy the discs. After removal of the discs, we lifted the devices off the base plates with a hook on the end of a 2.5-m pole in 3 animals and devices fell off due to the animals moving in 2 cases.

2.5 DISCUSSION

2.5.1 Reactions of the animals

The 2 youngest animals showed the greatest reactions to the recovery procedure. They lifted their heads several times and looked at the approaching person but did not move. The other animals just looked at the marksman but did not move at all. The shooting procedure itself elicited twitches, at most, as the pellets destroyed the discs. For the removal of the device from the base plate, the animals were approached further, which caused the 2 youngest animals to move toward the water. The remaining 3 animals paid more attention to the person as the distance was reduced, but the most marked reaction was for the animals to lift their heads briefly.

2.5.2 Suitability for other species

We consider that this release-mechanism worked particularly well because sub-adult male South American sea lions are tolerant to approach by humans and barely react to the shooting itself. They, thus, appear ideal for such a system. The low weight and small size makes this mechanism suitable for a wide range of species, including the smaller fur seals, depending on their allowing an approach to an appropriate distance of 10–15 meters. For terrestrial animals this could occur at water holes or other places frequented by animals, possibly aided by the use of hides.

In addition, the form of the release-mechanism can be readily modified according to the type and size of logger and could be molded according to species-specific requirements. It could even be modified to be incorporated into collars.

Furthermore, the lack of any electronic components means that no batteries need to be incorporated into the logger pack, further minimizing the size and weight of the unit.

2.5.3 Recommendations

Despite the high success rate (5 recovered devices in 5 recovery attempts) the system could be improved. Because South American sea lions often tilt their heads to one side, the disc positioned at the rear of the device (to reduce the risk of damage to it), with the metal loop attached to the bottom of the base plate, meant that the long fur of the mane of sub-adult and adult sea lions sometimes reduced the visible area of the disc. To get a clear shot, the disc should be positioned somewhat higher, but not so high that animals lying on their backs could damage the frame holding the disc.

In a general sense, the utility of the release mechanism depends critically on the abilities of the marksman and the quality of the weapon. The damage done by air guns of the type used in our study on South American sea lions, even if a pellet struck the animal, is minimal unless a highly sensitive area, such as an eye, were hit. That this will never occur can be ascertained during shooting trials coupled with appropriate device emplacement. However, we recommend that potential damage caused by stray air gun pellets to the animal concerned be assessed on a case by case basis. For example, there is no intrinsic mechanical reason why a release mechanism such as this should not be used on birds but the potential damage by a misplaced pellet may preclude its use. Note, however, that both these factors should be weighed against the detriment incurred by an animal forced to wear its device for overly extended periods or possibly forever.

Although material used to make discs proved excellent during trials in Germany, extensive exposure to sun and salt water in Patagonia made them porous. As a result 2, and sometimes 3, shots were required to destroy them. In these cases, every shot hit the disc, but only broke away a part of it. Therefore, the use of a material insensitive to sun and salt water is recommended.

Two units were not recovered due to the devices having been lost while the sea lions were wearing them. Their loss was apparently due to the retaining steel tabs bending down, possibly while animals were fighting. This clearly shows that we underestimated the power of these creatures. The problem should be easily resolved by using stronger steel or by strengthening the tabs with appropriate welding.

We suggest that logger removal would be facilitated if a metal spring were incorporated into the release-mechanism. We avoided this due to a very sensitive compass in our loggers. However, removal of the logger unit from the base plate with a long stick with a hook at the end also proved unproblematic in our study animals. If there is a perceived risk that equipped animals might enter the water before the logger unit is recovered, the amount of Microbubbles in the housing could be increased so that the housing floated and, thus, could be retrieved.

2.6 CONCLUSION

Although guns are classically used in hunting procedures, their high manufacturing standards mean that they also may be used in conservation. Actually, the method presented here results in only a minimal risk of actually hurting the animal. Our study animals had the devices on top of their heads, the most easily damaged area of their bodies, but all pellets hit the disc within the metal frame. Scatter in shooting performance can be easily assessed in trials so that deviations to the extent that an animal might be hit in the eye can be avoided. Because this release mechanism is free from any time constraints due to battery drain, there is no reason to rush recovery. Researchers can simply wait until conditions are ideal although the vagaries of animal movement and the likelihood that they might permanently move out of the recapture area must be factored into any decisions. Ultimately, the utility of the mechanism must be considered on a case by case basis.

We conclude that this release mechanism is suitable for a wide range of species, primarily because of its ability to be modified and adapted to the specific needs of each species. Furthermore, the lack of any time constraints means that recovery can be assured even after the animal has been away for long periods of time. Because of the low weight and small size, this mechanism also could be used as a backup, in case the main release mechanism fails.

2.7 ACKNOWLEDGEMENTS

This study was funded by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1). Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut and was performed in a humane manner. We are grateful to M. Kierspel, J. Blasey, S. Wulff, and W. Makoben for their help during the different phases of design and development. Special thanks go to C. Campagna and F. Quintana of the Centro Nacional Patagonico for help during animal equipment, and M. Uhart, B. Raphael, and P. Calle from the Wildlife Conservation Society as well as D.A. Albareda from Acuario de Buenos Aires y Jardín Zoológico de Buenos Aires, Argentina, for help with the anesthesia. Help from V. Ramos and P. Ledesma in recovering the devices is gratefully acknowledged.

2.8 LITERATURE CITED

Amstrup, S.C., Durner, G.M., McDonald, T.L., Mulcahy, D.M. & Garner, G.W. (2001) Comparing movement patterns of satellite-tagged male and female polar bears. *Canadian Journal of Zoology* **79**, 2147–2158.

Andrews, R.D. (1998) Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. *Marine Ecology Progress Series* **175**, 289–294.

Bradshaw, C.J.A., Hindell, M.A., Michael, K.J. & Sumner, M.D. (2002) The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures. *Ices Journal of Marine Science* **59**, 770–781.

Campagna, C., Werner, R., Karesh, W., Marin, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology* **255**, 205–220.

de Mendoca, P.G. (1999) Impact of radio-collars on Yellow-necked Mice, *Apodemus flavicollis* (Mammalia, Rodentia). *Mammal Review* **29**, 127–132.

Demers, F., Giroux, J.F., Gauthier, G. & Bety, J. (2003) Effects of collar-attached transmitters on behaviour, pair bond and breeding success of snow geese *Anser caerulescens atlanticus*. *Wildlife Biology* **9**, 161–170.

Deutsch, C.J., Bonde, R.K. & Reid, J.P. (1998) Radio-tracking manatees from land and space: Tag design, implementation, and lessons learned from long-term study. *Marine Technology Society Journal* **32**, 18–29.

Dique, D.S., Thompson, J., Preece, H.J., de Villiers, D.L. & Carrick, F.N. (2003) Dispersal patterns in a regional koala population in south-east Queensland. *Wildlife Research* **30**, 281–290.

Elwood, S., Wilson, R.P. & Addison, L. (In Press) Do gadgets help? *Hot topics in conservation biology* (eds D. MacDonald & K. Service). Blackwells, Oxford, UK.

Girard, I., Ouellet, J.P., Courtois, R., Dussault, C. & Breton, L. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management* **66**, 1290–1300.

Green, K. (1997) Diving behaviour of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. *Marine mammal research in the Southern hemisphere, status, ecology and medicine, Volume 1* (eds M. Hindell & C. Kemper), pp. 97–104. Surrey Beatty & Sons, Chipping Norton, Australia.

Hammill, M.O., Lesage, V., Lobb, G. & Carter, P. (1999) A remote release mechanism to recover time-depth recorders from marine mammals. *Marine Mammal Science* **15**, 584–588.

Hatch, S.A., Meyers, P.M., Mulcahy, D.M. & Douglas, D.C. (2000) Performance of implantable satellite transmitters in diving seabirds. *Waterbirds* **23**, 84–94.

Keefer, M.L., Peery, C.A., Ringe, R.R. & Bjornn, I.C. (2004) Regurgitation rates of intragastric radio transmitters by adult Chinook salmon and steelhead during upstream migration in the Columbia and Snake Rivers. *North American Journal of Fisheries Management* **24**, 47–54.

Kooyman, G.L. (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Record* **12**, 391–394.

Lowry, L.F., Frost, K.J., Davis, R., Demaster, D.P. & Suydam, R.S. (1998) Movements and behavior of satellite-tagged spotted seals (*Phoca largha*) in the Bering and Chukchi Seas. *Polar Biology* **19**, 221–230.

Mate, B.R., Krutzikowsky, G.K. & Winsor, M.H. (2000) Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. *Canadian Journal of Zoology* **78**, 1168–1181.

Orthmann, T. (2000) Telemetrische Untersuchungen zur Verbreitung, zum Tauchverhalten und zur Tauchphysiologie von Seehunden (*Phoca vitulina vitulina*) des Schleswig-Holsteinischen Wattenmeeres. Dissertation, University of Kiel, Kiel, Germany.

Osborn, F.V. & Parker, G.E. (2003) Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology* **41**, 68–74.

Sisak, M.M. (1998) Animal-borne GPS and the deployment of a GPS based archiving datalogger on Hawaiian monk seal (*Monachus schauinslandi*). *Marine Technology Society Journal* **32**, 30–36.

Tuyttens, F.A.M., Macdonald, D.W. & Roddam, A.W. (2002) Effects of radio-collars on European badgers (*Meles meles*). *Journal of Zoology* **257**, 37–42.

Van Parijs, S.M., Thompson, P.M., Tollit, D.J. & Mackay, A. (1997) Distribution and activity of male harbour seals during the mating season. *Animal Behaviour* **54**, 35–43.

Wilson, R.P. (2004) Reconstructing the past using futuristic developments: trends and perspectives in logger technology for penguins. *Memoirs of National Institute of Polar Research*, Special Issue **58**, 34–49.

Wilson, R.P., Locca, R., Scolaro, J.A., Laurenti, S., Upton, J., Gallelli, H., Frere, E. & Gandini, P. (2001) Magellanic penguins *Spheniscus magellanicus* commuting through San Julian Bay; do current trends induce tidal tactics? *Journal of Avian Biology* **32**, 83–89.

Wilson, R.P., Gremillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schafer-Neth, C., Scolaro, J.A., Bost, C.A., Plotz, J. & Nel, D. (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241–261.

Winger, P.D. & Walsh, S.J. (2001) Tagging of Atlantic cod (*Gadus morhua*) with intragastric transmitters: effects of forced insertion and voluntary ingestion on retention, food consumption and survival. *Journal of Applied Ichthyology* **17**, 234–239.

LUNCH OFF THE SHELF: FORAGING BEHAVIOUR OF MALE SOUTH AMERICAN SEA LIONS (*OTARIA FLAVESCENS*)

Müller *et al.*

Marine Ecology Progress Series, submitted

3.1 ABSTRACT

Movements at sea were determined for 6 sub-adult male South American sea lions (*Otaria flavescens*) from Peninsula Valdés, Argentina, using satellite tracking and dead-reckoning technology to elucidate foraging areas and overall space use over the Patagonian shelf. Animals exhibited regular foraging trips with a mean duration of 8.4 days (SD = 2.4), resting a mean of 3.9 days (SD = 1.0) at haul-out sites between successive trips. During the central part of the foraging trips, mean travelling speed was significantly lower than during the outward and inward leg in 3 of 4 animals for which travelling speed was determined. 83% of the individuals reached distances between 240 and 365 km from land. All animals showed a high degree of fidelity in both travel direction and distance from land, returning to the same general areas on successive trips. Although 6 of 7 sea lions travelled eastwards towards the shelf break, where putative foraging grounds were located, individual differences in foraging strategies were evident. The derived locations of

foraging grounds on the shelf coincide with areas of increased productivity, that also attract commercial fisheries.

3.2 INTRODUCTION

Marine mammals are considered to play a major role in shaping marine ecosystems, in places taking up to 41% of the prey biomass, considerably more than the world´s fishing fleets (Croll & Tershy 1998). Recently, Kaschner *et al.* (2001) suggested that competition between commercial fisheries and marine mammals is, however, not as intense as suspected due to spatial segregation in the areas exploited. This would not appear to be the case for South American sea lions *Otaria flavescens* over the Patagonian Shelf. Here, demersal fishing fleets take such quantities of fish and squids that stocks of southern blue whiting (*Micromesistius australis*), Argentine Hake (*Merluccius hubbsi*), and Argentine shortfin squid (*Illex argentinus*) are now considered fully to overexploited (FAO 1997). South American sea lions are also considered to feed primarily on such demersal prey (Koen Alonso *et al.* 1999). Studies on females in Argentina indicate that they forage inshore over the Patagonian shelf at depths of ca. 45 m (median depth 19 – 62 m; Werner & Campagna 1995) but the massive sex-related dimorphism in this species would indicate that the males might utilize other areas (Houston & Shine 1993; Ruckstuhl & Neuhaus 2002; Focardi *et al.* 2003). To date, however, space use has only been determined in two males (Campagna *et al.* 2001).

The aim of this study was to determine the foraging areas used by male South American sea lions breeding in Argentina so as to (1) expand the information available regarding the use by the species of the Patagonian Large Marine Ecosystem, (2) examine whether particular oceanographic features might be related to choice of the foraging location of animals and (3) identify the extent to which these animals might spatially overlap with the commercial fisheries operating over the Patagonian Shelf.

3.3 METHODS

3.3.1 Study sites and subjects

Sub-adult male South American sea lions (*Otaria flavescens*) were equipped at two rookeries, Punta Buenos Aires (42.067°S, 63.783°W) and Punta Norte (42.083°S, 63.767°W), along the coast of Peninsula Valdés, Argentina. Sub-adults were identified based on their physical appearance, being somewhat smaller and having less developed secondary sexual characteristics such as the mane and neck, than adult males. Animals that were to be equipped, were resting quietly or sleeping, preferably at the edge of a group or alone so as to minimize disturbance during the immobilization procedure (details of the rather complicated anaesthesia will be published elsewhere). The age of the animals was estimated between seven and eight years, with body weights estimated to be between 300 and 350 kg.

3.3.2 Device deployment

During January 2003, six sub-adult males from Punta Buenos Aires were equipped with SPOT2 satellite tags (Wildlife Computers, Redmond, Washington), which were glued to the top of their heads using epoxy glue (ITW Devcon®, Danvers, MA). The tags (110 x 32 x 15 mm, weighing 82.5 g in air) were programmed to transmit 16 hours per day, pausing every third hour. Satellite locations were provided by Service Argos (Service Argos, Inc., Toulouse, France). During November 2003 further eight males from Punta Norte were equipped with dead reckoners (Driesen & Kern GmbH, Bad Bramstedt, Germany) powered by 2 x 3.6V Lithium cells (SAFT, Bagnolet, France) and held in a protective housing (described in Müller *et al.* in press (chapter 2)).

3.3.3 Data analysis

All locations obtained from satellite tags were filtered manually by excluding locations requiring a swim speed of more than 3 m/s (Bonadonna *et al.* 2000; Crocker *et al.* 2001). Information on light levels collected by the dead reckoners were used to calculate animal position via geolocation (cf. Wilson *et al.* 2002 and references therein). The existing location data on two pre-breeding adult male South American sea lions from Campagna *et al.* (2001) are included here to enhance our data set. These data are referenced whenever they are used in figures.

Only data on complete foraging trips are included in the statistics. For the kernel analysis we only used locations obtained during trips with a reduced speed (less than 1.2 m/s) to identify potential foraging grounds (cf. McConnell & Fedak 1996). The satellite image of primary productivity correspond to an average image of all SeaWiffs images available for February 2003 and has been provided by courtesy of Antonio Gagliardi and Ana Dogliotti from the Instituto de Astronomia y Fisica del Espacio (IAFE-CONICET).

3.4 *RESULTS*

Five tags (one tag failed after four days and was excluded from analysis) yielded a total of 2087 unfiltered locations, of which 1151 (55.2%) locations were retained after filtering for speed. After filtering the percentage of locations in each Argos location class (see White & Sjöberg 2002) increased for classes 1 to 3 (class 3: +3.2%, class 2: +4.6%, class 3: +2.7%) and decreased for classes 0, A, and B (class 0: -5.3%, class A: -0.1%, class B: -5.1%). Locations obtained during the

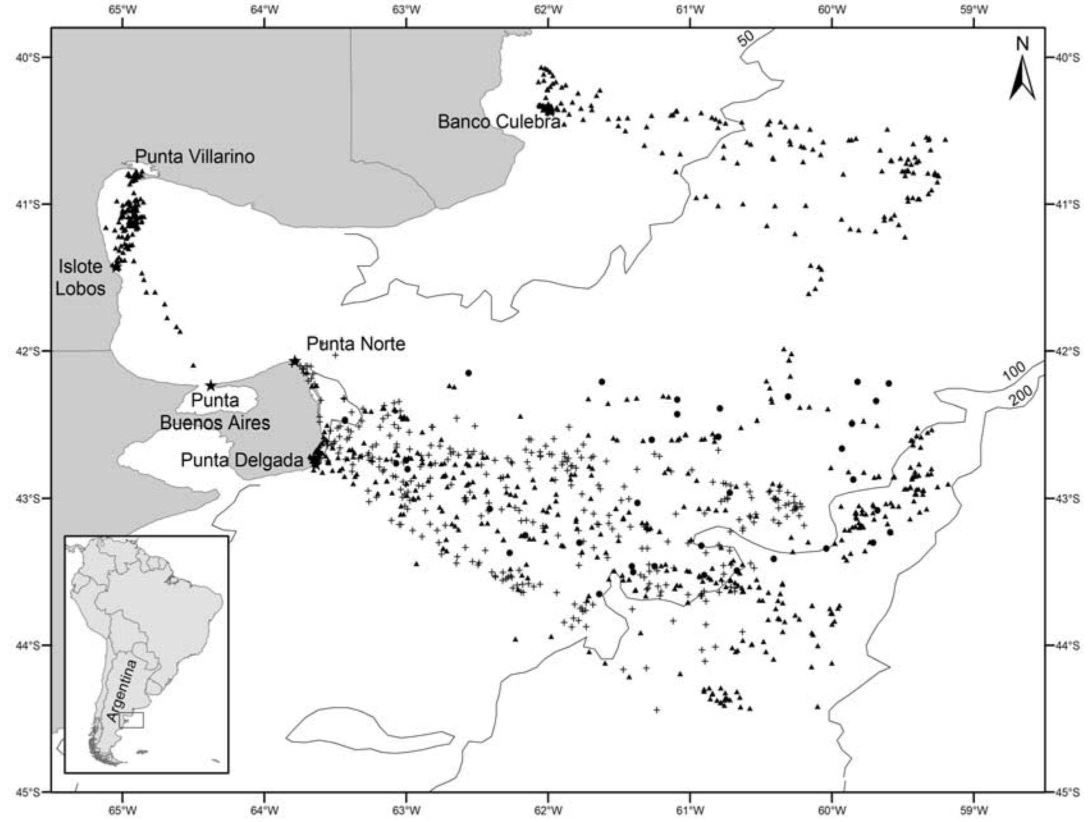


Figure 3.1: Locations obtained from South American sea lions (*Otaria flavescens*) equipped with satellite tags (triangles) and dead reckoners (circles). Crosses show location data obtained from two adult males from Campagna *et al*. (2001). Inset: General study area.

breeding season showed that sub-adult male South American sea lions (*Otaria flavescens*) undertake short trips to nearby rookeries (details of these movements will be presented elsewhere). Exclusion of locations obtained during the breeding season left 847 locations (38.7%) associated with movements at sea. Due to battery failure, only two dead reckoners collected data, providing information on 29 days at sea for two animals, from which two daily locations were calculated via geolocation. The locations calculated for one of these animals (`Sha´) showed locations that indicated that the animal was foraging over water between 100 and 200 m deep even though the dive data allude to water shallower than 100 m. This means that the errors in location for this animal could have been up to 286 km. This degree of accuracy, which was likely caused by inappropriate baseline calibrations in light thresholds corresponding to dawn and dusk (cf. Wilson *et al.* 2002), is inappropriate for the analysis conducted here, so the locational data from `Sha´ are not further presented. All remaining locations were defined within the area defined by 59° and 65.5°W and 40° and 44.5°S (Figure 3.1).

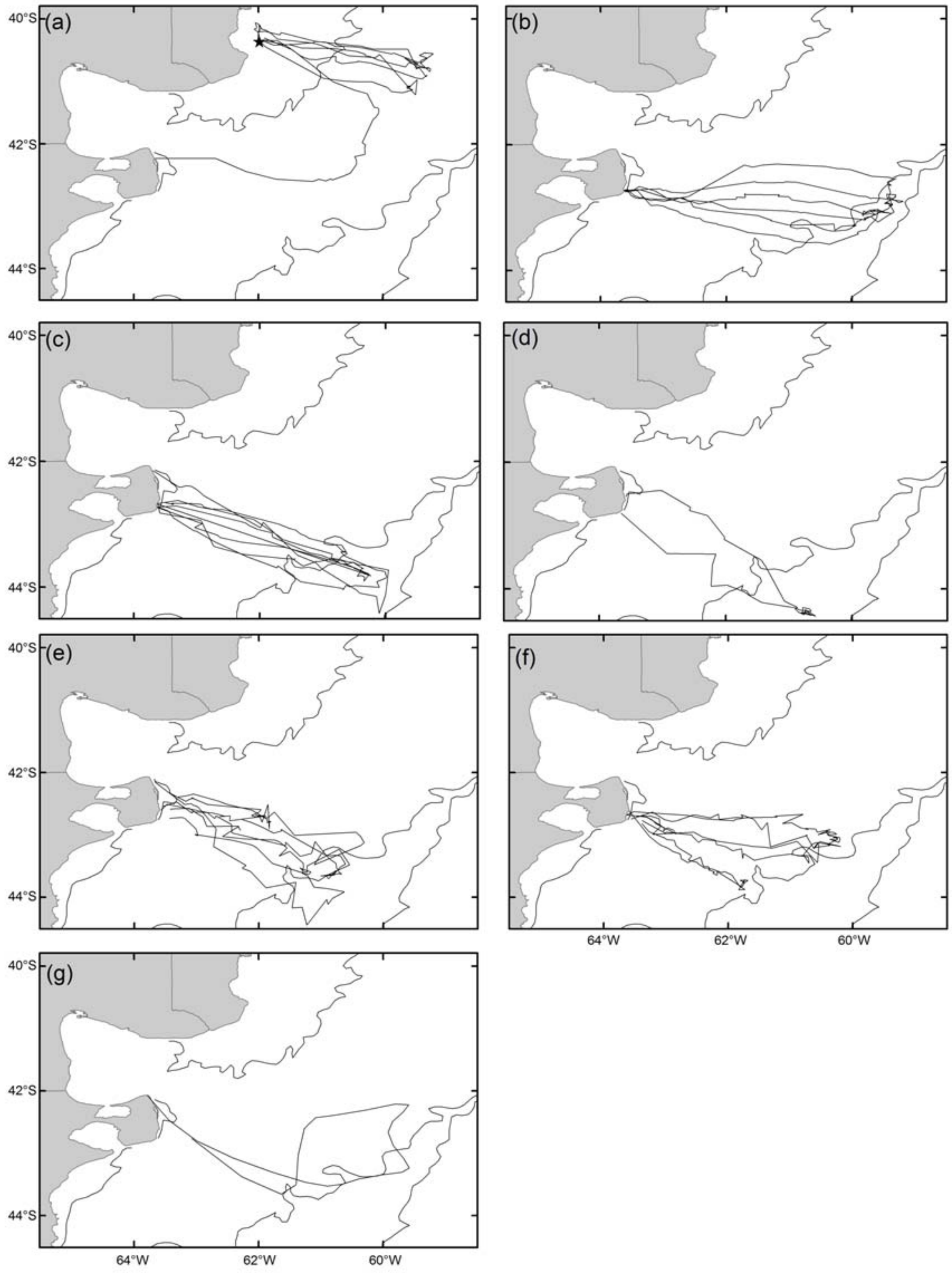


Figure 3.2: Details of the individual foraging trips made by sea lions using the offshore part of the Patagonian shelf. (a) `Sea´, (b) `Rap´, (c) `Ug´, (d) `Leo´, (e) and (f) show data from the two adult males from Campagna *et al*. (2001), and (g) `Aire´ for whom locations were calculated via geolocation.

Table 3.1: Summary information of foraging trips made by sub-adult male South American sea lions (*Otaria flavescens*). Only complete trips are included

Sea lion	Days to last location	Foraging trip characteristics						
		No. of trips	Mean duration of trips (days ± SD)	Longest trip (days)	Mean time between trips (days ± SD)	Mean travel distance (km ± SD)	Max. travel distance (km ± SD)	Max. distance from colony (km)
Ug	59	4	8.5 ± 2.1	10	3.2 ± 1.3	724 ± 88	840	342
Rap	54	3	8.5 ± 0.5	9	5.0 ± 0.0	876 ± 11	888	364
Leo	32	1	7.5	7.5	-	-	816	311
Sea	59	4	6.8 ± 0.5	7.5	4.0 ± 0.5	615 ± 31	652	291
Aire	(geolocation)	1	15.0	15.0	4.0	-	1058	365
Total	-	13	8.4 ± 2.4	-	3.9 ± 1.0	758 ± 144	-	-

3.4.1 Foraging trips

The movements of the sea lions generally consisted of distinct eastwards trips with a mean duration of 8.4 days (SD = 2.4 of 13 trips from 5 animals) and the longest trip lasting 15 days (Table 3.1). Travel distances ranged from 576.7 to 1058.2 km per trip showing a significant correlation with trip duration (Time = 44.8720 * distance + 382.1502, F = 14.8258, $P < 0.05$; where time is measured in days and distance in km). Maximum distances from land on foraging trips were between 291 and 365 km. All animals with multiple trips showed high fidelity in both distance and direction of successive trips, and also generally returned to the same haul-out place on subsequent trips, these locations being Punta Delgada (42.767°S, 63.633°W) for \`Rap´ and \`Ug´ and Banco Culebra (40.366°S, 61.983°W) for \`Sea´ (Figure 3.2). One animal (\`Blu´) stayed inside the San Matías Gulf, commuting inshore between Punta Villarino (40.814°S, 64.903°W) and Islote Lobos (41.426°S, 65.043°W; Figure 3.3).

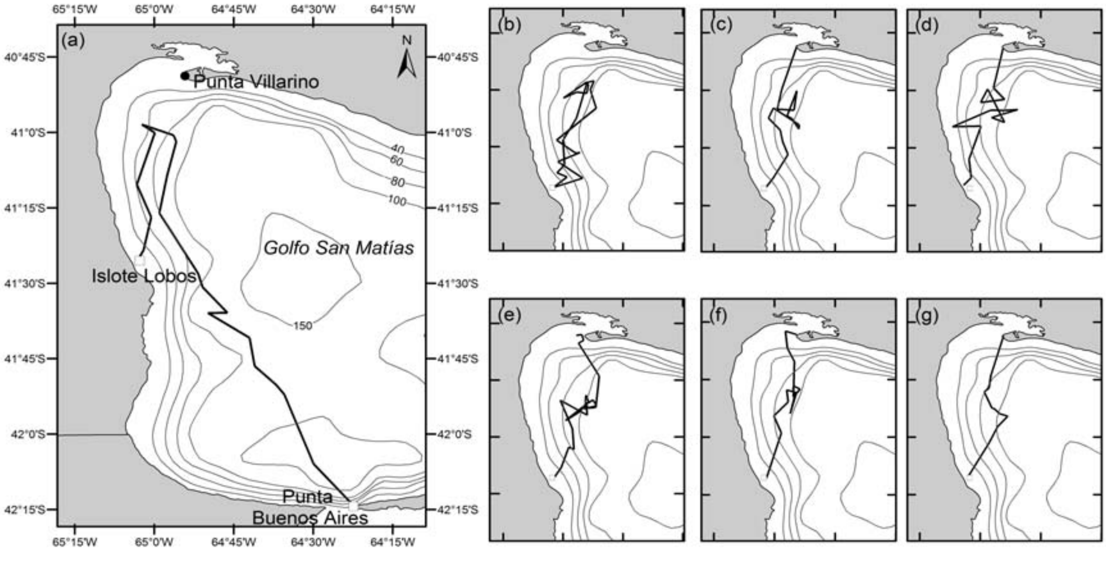


Figure 3.3: Movements of \`Blu´ inside the San Matías Gulf. (a) The first trip started directly from Punta Buenos Aires and ended on Islote Lobos. (b) – (g) Subsequent movements between Islote Lobos and Punta Villarino.

Based on differences in mean speed, the trips obtained from satellite data could be divided into three distinct phases: an outward leg, a middle part (90% of maximum distance from land), and an inward leg. The middle part of trips had a significantly slower mean speed than the other two phases (Figure 3.4) – except for data from one animal (`Leo´) (Kruskal-Wallis-Test, all P´s < 0.05). In addition, `Rap´ also showed a significant difference in mean speed between the outward and inward leg being undertaken at a greater speed (P < 0.05).

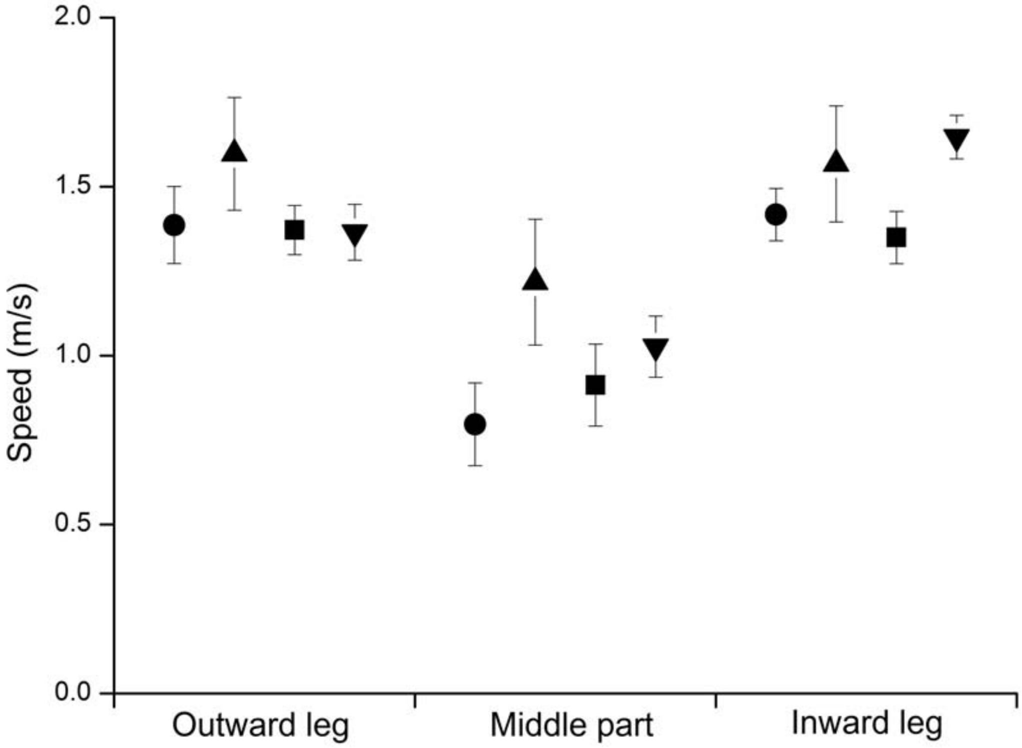


Figure 3.4: Mean speed (± SE) of the three phases of the trips for data obtained during February and March 2003 (● `Ug´, ▲ `Leo´, ■ `Sea´, ▼ `Rap´). The first trip of `Sea´ and the last trip of `Ug´ were not included because of the trip not starting from the `haul-out place´ and the lack of data for the inward leg of the trip, respectively.

3.4.2 Foraging area

The target area of most trips was along the 100 m depth contour east and southeast of Peninsula Valdés with some animals almost reaching the shelf break (indicated by the 200 m depth contour in Figure 3.1). Locations (with speeds less than 1.2 m/s, see above) obtained during February and March 2003 showed partial overlap with highly productive areas from the shelf break (Figure 3.5). Two animals (`Sea´ and `Blu´) chose different foraging areas; `Sea´ foraged northeast of Peninsula Valdés in shallower waters (between the 50 and 100 m depth contour) ca. 140 km from the shelf break and `Blu´ in coastal waters up to 100 m inside the San Matías Gulf (Figures 3.2 and 3.3).

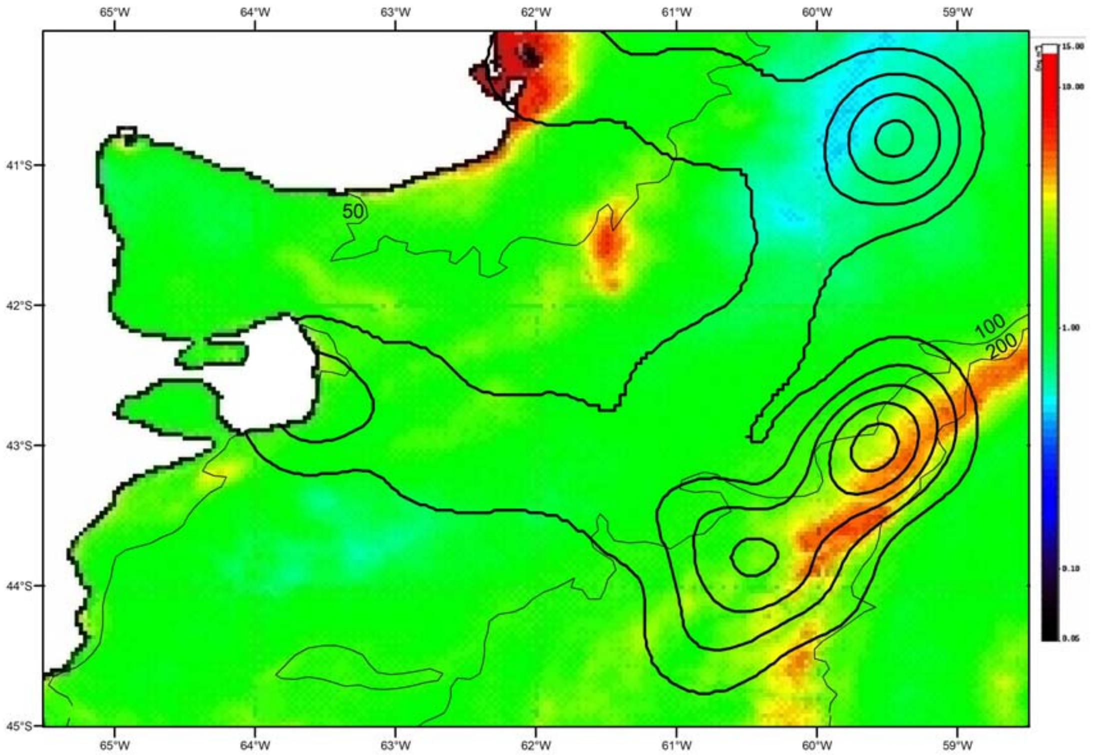


Figure 3.5: Kernel analysis (contour levels at 10 to 90% location density with 20% intervals) of locations at sea with a speed less than 1.2 m/s from the four males foraging on the outer shelf during February and March 2003. The kernel contours are superimposed on a satellite image showing the average chlorophyll production for February 2003.

3.5 DISCUSSION

3.5.1 Foraging activity

Variation in speed between successive locations at sea has been used in other species to divide foraging trips into separate phases, with the outward and inward leg showing higher speeds than the middle part (McConnell & Fedak 1996; Bonadonna *et al.* 2000). Bonadonna *et al.* (2000) showed, by means of concurrently collected dive data, that Subantarctic fur seals (*Arctocephalus tropicalis*) foraged during the middle part of the trips, whereas the other phases were used for travel between the colony and the foraging sites. South American sea lions (*Otaria flavescens*) in this study generally showed patterns of speed differences, indicating that they use off-shore areas for foraging. Except for one, all sea lions, including the two adult males equipped by Campagna *et al.* (2001), moved eastwards towards the shelf break on their foraging trips. The information on the different phases of the trips supports the assumption that South American sea lions from the Valdés area forage close to the shelf break. The directed movements during the outward and inward legs are consistent with travel to and from foraging areas.

Along the Argentine continental shelf break, the subantarctic shelf waters meet the cooler waters of the Malvinas current, producing a permanent shelf-break front, the inner boundary of which is located along the 90-100 m depth contour (Martos & Piccolo 1988; Acha *et al.* 2004). Because of its high productivity, the front gives rise to a high concentration of zooplankton, fish, squid and scallops, which are preyed upon by a variety of pelagic seabirds and marine mammals (Podestá 1989; Acha *et al.* 2004 and references therein). Available information on prey types and numbers suggest that South American sea lions are non-specialist feeders, with females preying mostly on a variety of benthic species, and males mostly on demersal-pelagic prey (George-Nascimento *et al.* 1985; Thompson *et al.* 1998; Koen Alonso *et* *al.* 1999). In Patagonia the most frequent prey types of female sea lions are red octopus (*Enteroctopus megalocyathus*), Argentine shortfin squid (*Illex argentinus*), Argentine hake (*Merluccius hubbsi*), "raneya" (*Raneya brasiliensis*), and Argentine anchovy (*Engraulis anchoita*), whereas males consume a broader spectrum of prey types dominated by Argentine hake, Patagonian squid (*Loligo gahi*), Argentine shortfin squid, "raneya", and red octopus (Koen Alonso *et al.* 1999). Diving data, however, indicate that females also spend a significant proportion of their time at depths corresponding to mesopelagic dives (Werner & Campagna 1995), indicating that females might exploit both benthic and pelagic prey and that their choice may depend on local availability of different prey types.

Foraging ranges of lactating South American sea lions are restricted to coastal areas, most likely because of the need to regularly return to their pups (Campagna *et al.* 2001). The San Matías Gulf, one of the deepest locations on the otherwise rather shallow Patagonian shelf, provides lactating females from the coast with the chance to dive as deep as the males foraging close to the shelf break. Despite this proximate access to deeper water dive data from six lactating females show that only one animal dived to 175 m and maximum dive depths of the remaining animals were 112 m or less (Werner & Campagna 1995). Allometric considerations predict that males should be able to dive considerably deeper than females (Schreer *et al.* 2001) and since all locations from males were over water shallower than 200 m, it seems unlikely that male sea lions are limited in their dive depth by their physiological diving capacities. Thus, differences in physiological diving capacities are unlikely to be the reason for the observed segregation of foraging areas between males and females. Both Steller sea lions (*Eumetopias jubatus*) and New Zealand fur seals (*Arctocephalus forsteri*) with dependent young increase their trip durations as well as their distance from the colony in winter (Merrick & Loughlin 1997; Harcourt *et al.* 2002). Additional information on movements of female sea lions outside the lactation period would therefore be necessary to identify the proximate causes of the observed segregation of the foraging areas between males and females.

One sea lion (`Blu´) employed a different strategy by leaving the rookery and heading in a northwesterly direction into the San Matías Gulf. Here, the main foraging area seemed to be the northwestern corner of the Gulf over water deeper than 80 m. Because of the movements between two different points, Islote Lobos and Punta Villarino, the time at sea could not be classified into distinctive foraging trips as has been done for the other animals. However, this animal also showed a high degree of fidelity in direction of travel on successive movements.

3.5.2 Interaction with fisheries

Fishery catches off the Patagonian shelf are dominated by mid- and deep-water demersal species such as cod and hake, with squid forming an increasing part of total fish production since the early 1980´s (FAO 1997). After maximum catches of 2.4 million tons in 1987 for the whole area 41 (ranging from southern Argentina up to northern Brazil) the production has levelled off with an increasing number of stocks being fully to overexploited (FAO 1997). A reduction in fish biomass should, however, only directly affect sea lion populations if there is a direct competition between fisheries and predators.

Along the coast of Patagonia the fishing activity is dominated by the trawling fishery, whereas longlining and jigging are only used by a minor number of fishing vessels (Crespo *et al.* 1997). The trawling fishery in northern and central Patagonia mainly targets shrimp (*Pleoticus muelleri*) and hake, with vessels taking shrimp close to the coast while the hake fishery concentrates its efforts south and southeast of Peninsula Valdés, with the areas closest to the peninsula being used during summer and those further away during winter (Crespo *et al.* 1997). The squid fishery, targeting shortfin squid and black squid (*Martialia hyadesi*), operates mainly between the 100 and 200 m depth contours from 38 down to 53°S, with the main areas being located in southern Patagonia between February and April, in central Patagonia between April and July and in northern Patagonia between July and September (Crespo *et al.* 1997). The pink cusk-eel (*Genypterus blacodes*) and hake targeted by the longline fishery are, like the trawling fishery for hake, taken in areas south and southeast of Peninsula Valdés (Crespo *et al.* 1997).

Foraging ranges of lactating females overlap with the more coastal shrimp and hake fisheries, whereas locations of males obtained in this study are found in areas in which the squid fishery concentrates its activities during autumn and winter (Crespo *et al.* 1997; Campagna *et al.* 2001). If male sea lions from more southern colonies use the same strategy of foraging close to the shelf break as our sea lions, the potential for interaction with fisheries would increase significantly, not only with respect to the timing of interaction but also with respect to the area in which interaction may occur. The large range of prey types taken by sea lions suggests, however, that they may not be immediately adversely affected by depletion of particular fish stocks by commercial enterprises. However, the number of stocks, including species that dominate the diet of sea lions, that according to FAO (FAO 1997) are fully or overexploited is increasing and long-term effects of a switch to other, perhaps less profitable, prey cannot be ruled out.

In conclusion, the foraging trips performed by male South American sea lions suggest that areas along the shelf break are used by this species for primary foraging grounds. More information on movements of sea lions throughout the year are necessary to determine the degree of spatial and temporal overlap between sea lion foraging areas and fishery activity and also to assess the potential for direct competition.

3.6 ACKNOWLEDGEMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. We are indebted to M. Uhart, B. Raphael, P. Calle (Field Veterinary Program of the Wildlife Conservation Society, New York) and D. A. Albareda (Acuario de Buenos Aires y Jardín Zoológico de Buenos Aires, Argentina) for assistance with the anaesthesia of the sea lions. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina. The help from V. Ramos and P. Ledesma in recovering the dead reckoners is gratefully acknowledged.

3.7 LITERATURE CITED

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *Journal of Marine Systems* **44**, 83–105.

Bonadonna, F., Lea, M.A. & Guinet, C. (2000) Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. *Polar Biology* **23**, 149–159.

Campagna, C., Werner, R., Karesh, W., Marìn, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology, London* **257**, 205–220.

Crespo, E.A., Pedraza, S.N., Dans, S.L., Koen Alonso, M., Reyes, L.M., García, N.A., Coscarella, M. & Schiavini, A.C.M. (1997) Direct and indirect effects of the highseas fisheries on the marine mammal populations in the northern and central Patagonian coast. *Journal of Northwest Atlantic Fishery Science* **22**, 189–207.

Crocker, D.E., Gales, N.J. & Costa, D.P. (2001) Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology, London* **254**, 267–277.

Croll, D.A. & Tershy, B.R. (1998) Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biology* **19**, 365–374.

FAO (Food and Agriculture Organization) (1997) *Review of the state of world fishery resources: marine fisheries. 6. Southwest Atlantic*. Marine Resources Service, Fishery Resources Division, Fisheries Department, FAO, Rome, Italy; available at http://www.fao.org/docrep/003/w4248e/w4248e12.htm#AREA41.

Focardi, S., Farnsworth, K., Poli, B.M., Ponzetta, M.P. & Tinelli, A. (2003) Sexual segregation in ungulates: individual behaviour and the missing link. *Population Ecology* **45**, 83–95.

George-Nascimento, M., Bustamante, R. & Oyarzun, C. (1985) Feeding ecology of the South American sea lion *Otaria flavescens*: food contents and food selectivity. *Marine Ecology Progress Series* **21**, 135–143.

Harcourt, R.G., Bradshaw, C.J.A., Dickson, K. & Davis, L.S. (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series* **227**, 11–24.

Houston, D. & Shine, R. (1993) Sexual dimorphism and niche divergence – feeding-habits of the arafura filesnake. *Journal of Animal Ecology* **62**, 737–748.

Kaschner, K., Watson, R., Christensen, W., Trites, A.W. & Pauly, D. (2001) Modeling and mapping trophic overlap between marine mammals and commercial fisheries in the North Atlantic. *Fisheries Impact on North Atlantic Ecosystems: Catch, Effort and National/Regional Data Sets* (eds D. Zeller, R. Watson & D. Pauly). Fisheries Centre Research Reports **9(3)**, 35–45.

Koen Alonso, M., Crespo, E.A., Pedraza, S.N., García, N.A. & Coscarella, M.A. (1999) Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin* **98**: 250–263.

Martos, P. & Piccolo, M.C. (1988) Hydrography of the Argentine continental shelf between 38° and 42°S. *Continental Shelf Research* **8**, 1043–1056.

McConnell, B.J. & Fedak, M. (1996) Movements of southern elephant seals. *Canadian Journal of Zoology* **74**, 1485–1496.

Merrick, R.L. & Loughlin, T.R. (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology* **75**, 776–786.

Müller, G., Liebsch, N. & Wilson, R.P. (In press) A new shot at a release mechanism for devices on free-living animals. *Wildlife Society Bulletin.*

Podestá, G.P. (1989) Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fishery Bulletin* **88**, 167–177.

Ruckstuhl, K.E. & Neuhaus, P. (2002) Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* **77**, 77–96.

Schreer, J.F., Kovacs, K.M. & O´Hara Hines, R.J. (2001) Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* **71**, 137–162.

Thompson, D., Duck, C.D., McConnell, B.J. & Garrett, J. (1998) Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *Journal of Zoology, London* **246**, 135–146.

Werner, R. & Campagna, C. (1995) Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Canadian Journal of Zoology* **73**, 1975–1982.

White, N.A. & Sjöberg, M. (2002) Accuracy of satellite positions from free-ranging grey seals using ARGOS. *Polar Biology* **25**, 629–631.

Wilson, R.P., Gremillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schafer-Neth, C., Scolaro, J.A., Bost, C.A., Plötz, J. & Nel, D. (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241–261.

THE COST OF COMMUTING: FORAGING CYCLES AND THEIR EFFECT ON ENERGY BUDGETS IN SOUTH AMERICAN SEA LIONS (*OTARIA FLAVESCENS*)

Müller *et al.*

Marine Ecology Progress Series, submitted

4.1 ABSTRACT

Pinnipeds show a wide range of different foraging strategies. Some species have foraging trips that last no more than a day, whereas others stay offshore for several months. We examined the foraging cycles (duration of foraging trips and the subsequent time spent on land) of male South American sea lions on the Patagonian shelf. The sea lions foraged from a central place and showed a regular pattern in the timing of their foraging cycles, with foraging trips lasting between 6 and 9.5 days (mean 8.3 days) and 2.5 to 5 days (mean 4.1 days) on land between consecutive trips. The time spent on land and in transit cannot be used for foraging so the energy required for the whole foraging cycle must be consumed during the time spent foraging (17.8% of the foraging cycle). In contrast to females, which are obliged to return to their colonies to provision pups after 2–5 days at sea, males are

apparently able to choose high quality foraging areas which are out of reach of females which compensates for the increased travel costs. The difference in foraging areas between males and females suggests that the impact on prey populations by male sea lions may be concentrated in highly productive areas that are also targeted by commercial fisheries. Using published data on field metabolic rates and assimilation efficiency for sea lions, we calculate that a single male from our study site would have to consume ca. 168 kg for every day spent in the foraging area. According to this scenario, the population of male South American sea lions foraging over the Patagonian shelf consumes between 24,000 and 36,000 tons/annum, with values depending on the percentage of fish or squid in the diet as well as on the actual partitioning of time adopted by the animals, these potentially varying with the distance between the colonies and the shelf break.

4.2 INTRODUCTION

The concept of central place foraging (Orians & Pearson 1979) has been critical in our understanding of how animals should divide their time and energies between a central place (the colony, nest or equivalent) and some part remote from that where energy is accrued. In particular, many predictions have been made about aspects related to food quality, quantity, load size and time that should be spent in the foraging area (e.g. Kramer & Nowell 1980; Jackson 2001; Ropert-Coudert *et al.* 2004).

Pinnipeds, dividing their time between periods on land and at sea, show a variety of species-specific strategies that appear to lead from the concept of a central place on land, with forays to sea to feed (Arnould *et al.* 1996) to species that live primarily at sea, perhaps in a central place, making forays on land to reproduce or moult

(Campagna *et al*. 1999; Le Boeuf *et al*. 2000). This latter is apparently a reversal of the classic situation but its definition, as such, may be trivial. It is clear, however, that the relative times spent at sea and on land must result in appropriate benefits for the various strategies adopted.

We examined the time and location of foraging of the South American sea lion *Otaria flavescens* in relation to periods spent on land. This was considered with respect to the periods spent travelling between the two sites during periods of the year when attendance at the colony was not dependent on breeding. We reasoned that at this time the energy gain during periods at sea must approximate the energy expenditure of the animals during both foraging, transit and on land (i.e. the energy gained during foraging is equalled by that expended over the full cycle – cf. Wilson *et al*. (in press)). Following this, we considered that the periods spent in each of the three phases (land, transit and foraging) must be related to the rates of energy gain and expenditure in each of the situations and used a simple model to determine the effects that prey density and travel time have on the animal´s energy expenditure.

4.3 METHODS

4.3.1 Foraging cycles

The deployment procedure and study site have been described in detail in Müller *et al*. (subm, chapter 3) and will therefore only be explained briefly here. During January 2003, six sub-adult male South American sea lions from the Punta Buenos Aires rookery (42.067°S, 63.783°W) on the coast of Peninsula Valdés, Argentina, were equipped with SPOT2 satellite tags (Wildlife Computers, Redmond, Washington). The tags (110 x 32 x 15 mm, weighing 82.5 g in air) were glued to the top of their heads using epoxy glue (ITW Devcon®, Danvers, MA) and programmed to transmit 16 hours per day, pausing every third hour. Satellite locations were provided by Service Argos (Service Argos, Inc., Toulouse, France). All locations obtained from satellite tags were filtered manually by excluding locations requiring a swim speed of more than 3 m/s.

These data have been previously used to elucidate the movements and foraging locations of male South American sea lions (Müller *et al.* subm, chapter 3). In this study, however, a different approach is taken by using the information obtained on duration of foraging trips and subsequent haul-out periods to calculate the duration of foraging cycles (one trip to sea and the subsequent haul-out period) as well as the amount of time spent in transit and foraging. The durations of foraging trips and periods on land were determined to the nearest half day. In cases where departure from or arrival at the haul-out site could not be determined with this accuracy, the midpoint between the last location on land and the first location at sea (or the opposite) was used as departure or arrival time, respectively.

Determination of the time spent at sea actually used for foraging compared to that spent for transit is less tractable. The maximum amount of time spent foraging is given by the total time that the animals actually spent at sea. Typically, however, the period spent foraging corresponds to some time close to the point of maximum distance from the colony (Bonadonna *et al.* 2000; Le Boeuf *et al.* 2000; Weimerskirch & Guionnet 2002). In many marine endotherms, foraging behaviour differs from travelling behaviour in a number of respects: different dive profiles (e.g. Le Boeuf *et al.* 2000; Simeone & Wilson 2003), differences in the consistency of the heading (e.g. Wilson 2004) and an overall reduction in the speed of translocation (Le Boeuf *et al.* 2000), even though the instantaneous speed of the animal in question may not change due to optimization of the cost of transport

(Culik *et al.* 1994; Schmidt-Nielsen 1997). Our PTT-derived data allowed us to assess the speed of translocation to look for points of inflection, or a step function in the values over time, that might allow us to identify foraging, rather than travelling, behaviour. Thus, we plotted a running mean of three points of the speed of translocation (the distance between two fixes (separated by a period of greater than 2 h) divided by the time between them) against the percentage of maximum distance from the colony. The step functions apparent in these graphs (see later) were then used to derive working values for the amount of time spent foraging during trips to sea. However, our model (see below) also allowed us to vary the parameters to see the effect of various travelling:foraging time ratios.

4.3.2 Model parameters

To elucidate how the energy requirements of the sea lions vary with changes in the duration of the individual phases of a foraging cycle a simple model is used. We assume the individual foraging cycles to be steady-state situations, in which the energy acquired during the foraging phase is equal to the energy expended over the entire foraging cycle (cf. Wilson *et al.* in press). The total energy expended over a foraging cycle (E_{total}) depends on how much time is spent in the different activities such as resting on land, travelling and active foraging and can be expressed as follows:

$$E_{total} = (t_{land} * E_{land}) + (t_{transit} * E_{transit}) + (t_{forage} * E_{forage}) \qquad (1)$$

where E_{land}, $E_{transit}$ and E_{forage} are the energies expended per unit time on land, in transit and during foraging, respectively, and t_{land}, $t_{transit}$ and t_{forage} are the times spent in each of these activities. We assume that the rates of energy expenditure during the transit and foraging phases are equal ($E_{sea} = E_{transit} = E_{forage}$) so that equation 1 can be reduced to:

$$E_{total} = (t_{land} * E_{land}) + E_{sea} * (t_{transit} + t_{forage}) \qquad (2)$$

The total mass of food ingested during a single foraging cycle (M) can be derived by dividing the total energy expended (E_{total}) by the energetic value of the prey (Ev_{prey}) multiplied by the assimilation efficiency (AE) of the sea lion:

$$M = E_{total} / (Ev_{prey} * AE) \qquad (3)$$

The rate at which energy has to be acquired, ΔE_{gain}, is equal to the total mass of prey ingested during the foraging cycle divided by the time spent in the foraging area:

$$\Delta E_{gain} = M / t_{forage} \qquad (4)$$

4.3.3 Bioenergetic parameters

For the estimation of the food requirements of sea lions we assume that the basal metabolic rate (BMR) increases with body weight according Kleiber´s (1975) equation:

$$\text{BMR (kJ/day)} = 292.88 * M^{0.75} \qquad (5)$$

where M is body weight (kg). Since no measurements of field metabolic rates exist for the South American sea lion, we used 6.0 times the BMR as the 'at sea' metabolic rate, which corresponds to values reported for Australian (*Neophoca cinerea*) and New Zealand (*Phocarctos hookeri*) sea lions (Costa & Gales 2000, 2003) and 2.7 times BMR as 'on shore' metabolic rate (Costa & Gales 2003). The main part of the diet of South American sea lions consists of fish and squid (George-Nascimento *et al*. 1985; Koen Alonso *et al*. 1999) so we assume an average energy density of 5 kJ/g (wet weight) for fish and 3.5 kJ/g (wet weight) for squid (Croxall & Prince 1982; Balmelli & Wickens 1994; Rosen & Trites 2000). We also used an assimilation efficiency of 0.94 for fish and 0.90 for squid (Rosen & Trites 2000).

4.4 RESULTS

4.4.1 Foraging cycles

Three of the animals equipped with satellite tags exhibited distinct and similar foraging trips. One animal moved back and forth between two locations on land and thus did not show the central place foraging strategy purported to be typical of this species (Campagna *et al*. 2001) and a further animal conducted a single trip where the start and end point were not identical. Finally, one tag stopped transmitting after four days and thus did not provide any data on foraging locations for this

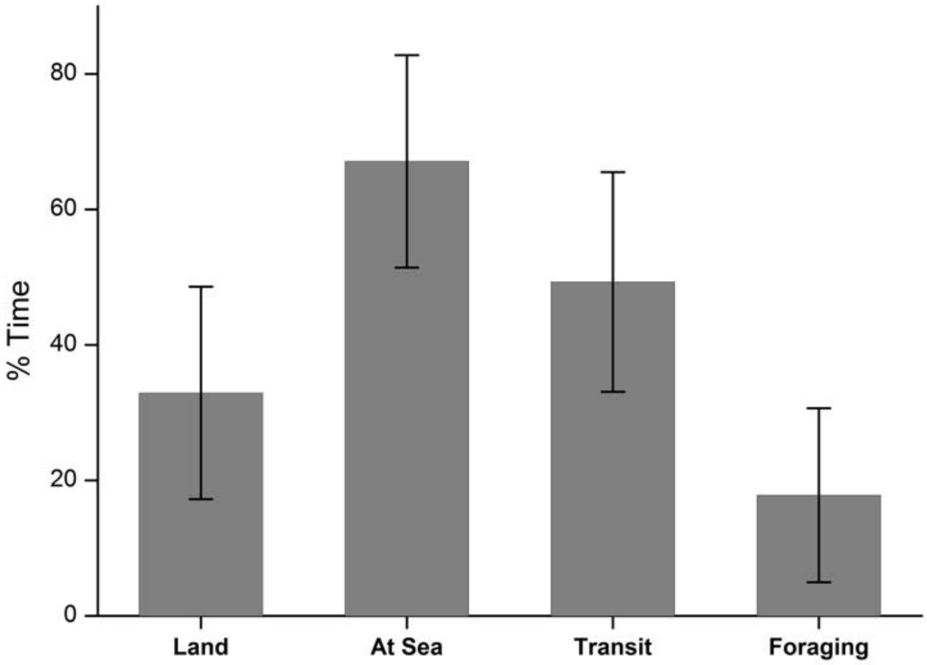


Figure 4.1: Distribution of mean time in percent (± 1 SD) spent on land, in transit and foraging during foraging cycles of male South American sea lions.

animal. Thus, data from these three latter animals were thus excluded from analysis. The remaining animals provided a total of eight complete foraging cycles for which time allocations to the various activities could be determined although one of these was excluded because the start and end points of the trip were not identical. The duration of the remaining seven foraging cycles ranged from 10.5 to 14 days with a mean of 12.4 days (Figure 4.1, Table 4.1). Mean duration of time spent on land and at sea were 4.1 (32.9%) and 8.3 (67.1%) days, respectively.

Table 4.1: Mean durations (days) of recorded foraging cycles, including times spent in the various phases the cycle (on land, at sea, in transit and foraging). Percentage of total time is given in parentheses

Cycle #	Total duration days	Time on land days (%)	Time at sea days (%)	Time in transit days (%)	Time foraging days (%)
1	14.0	5.0 (35.7)	9.0 (64.3)	7.0 (50.0)	2.0 (14.3)
2	13.5	5.0 (37.0)	8.5 (63.0)	5.5 (40.7)	3.0 (22.2)
3	11.5	3.0 (26.1)	8.5 (73.9)	6.5 (56.5)	2.0 (17.4)
4	12.0	2.5 (20.8)	9.5 (79.2)	7.5 (62.5)	2.0 (16.7)
5	14.5	5.0 (34.5)	9.5 (65.5)	6.5 (44.8)	3.0 (20.7)
6	10.5	4.5 (42.9)	6.0 (57.1)	5.0 (47.6)	1.0 (9.5)
7	10.5	3.5 (33.3)	7.0 (66.7)	4.5 (42.9)	2.5 (23.8)
Mean	12.4	4.1 (32.9)	8.3 (67.1)	6.1 (49.3)	2.2 (17.8)
SD	1.7	1.1 (15.7)	1.3 (15.7)	1.1 (16.2)	0.7 (12.8)

4.4.2 Estimates of time spent foraging

The plot of mean speed of translocation against distance from the colony shows a sharp decrease in speed when the animals had covered 80 to 95% of the maximum distance from the colony (Figure 4.2). Using the steepest part of the slope as the point of inflection to delineate the division between travelling and foraging, it would appear that foraging activity mainly takes place within 10% of the maximum distance from the colony at mean speeds less than 1.05 m/s. Approximately 40% of the total time at sea is spent at speeds below this value. If the foraging time is calculated for individual foraging trips by using locations within 10% of the maximum distance, the mean time (of total time at sea) spent in the foraging area is

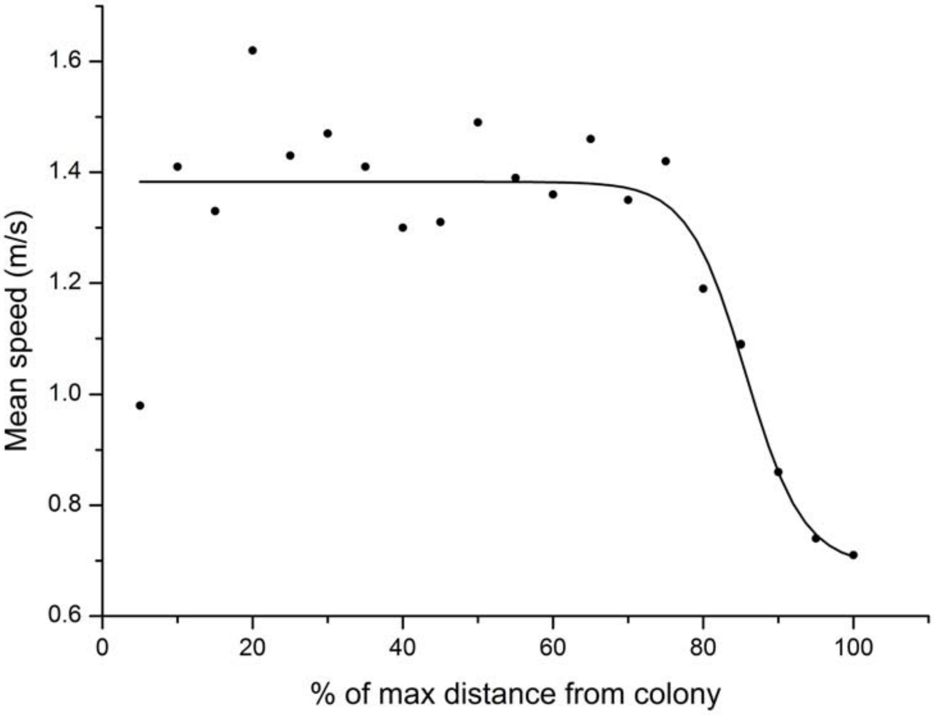


Figure 4.2: Changes in mean speed of translocation as function of percentage of maximum distance from the colony.

26.6% which corresponds to 17.8% of the foraging cycle (Table 4.1). The mean speed of translocation for the travel phase (0 – 85% of maximum distance) was 1.35 m/s compared to only 0.77 m/s within the presumed foraging area (Figure 4.2).

4.4.3 Model output - The projected standard scenario

The estimated energy expenditure during a typical foraging cycle of 12.4 days duration is 1.4 MJ. On a mixed diet (50% fish and 50% squid), sea lions adhering to this regime would have to ingest a total of 369 kg of prey to cover this expenditure. Assuming that the time spent in the foraging area is 26.6% of the time spent at sea, this amounts to 167.7 kg/day or 7.0 kg/h. If the diet consists solely of fish or squid the amount of prey changes accordingly to 307 kg of fish or 458 kg of squid. Again, assuming that animals spend 26.6% of their time in the foraging area, this amounts to about 139.5 kg/day (5.8 kg/h) for those feeding exclusively on fish and 208.2 kg/day (8.7 kg/h) for those taking exclusively squid.

4.4.4 The effect of varying travel times and variable time at sea on animals maintaining a constant rate of prey acquisition

If we assume that the rates of prey acquisition as defined by us (e.g. 167.7 kg/day for the 50:50 mixed diet) remain constant, as does the amount of time spent at the colony, but that the amount of time spent travelling may vary (according to the location of suitable foraging spots), it is apparent that animals have to adjust the amount of time that they spend in the foraging area to accord if they are to balance energy use with energy input (Figure 4.3). Sea lions spending only one day travelling only need to spend 0.8 days in the foraging area whereas animals spending 10 days travelling must forage for 3.3 days to compensate. The relationship is linear and is best described by the equation $y = 0.28*x + 0.51$.

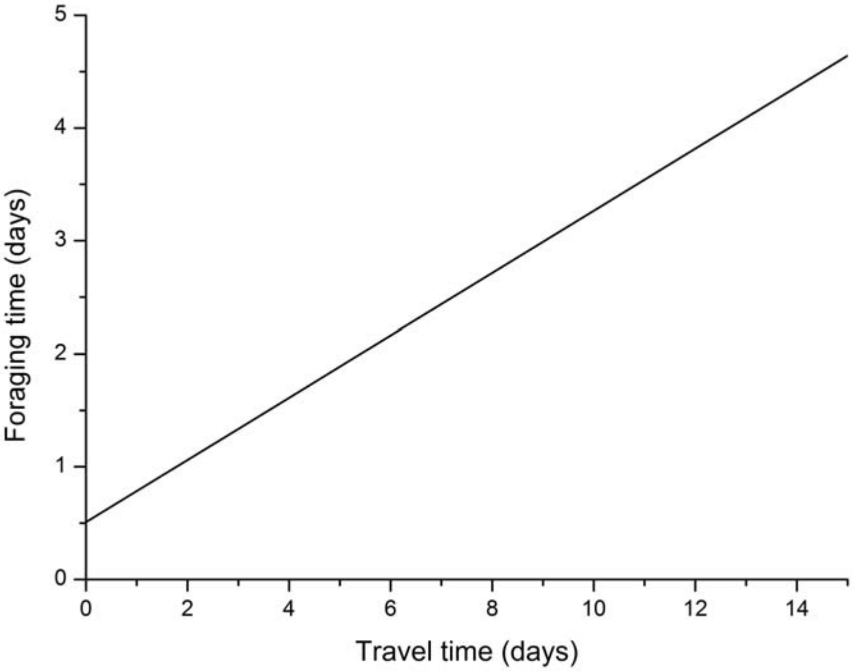


Figure 4.3: Change in foraging time as function of an increase in travel time at a constant rate of prey acquisition of 7.0 kg/h of a mixed prey diet in the foraging area.

4.4.5 The effect of varying travel times with a constant time spent at sea

When the time spent at sea and on land is held constant, variation in the time spent travelling has a radical effect on the necessary rate of prey ingestion because not only does the act of travelling increase the non-gain energetic costs but it also results in a reduction in the period spent in the area where prey can be acquired (Figure 4.4). We note that this condition becomes particularly apparent in animals on a pure squid, rather than pure fish, diet. A similar pattern is apparent if haul-out times on land change although the effect is less marked since the energy expenditure of animals on land is markedly less than those in the water. Finally, as the time spent in the foraging area increases, so the putative rate of energy gain decreases exponentially (Figure 4.5) until values are approached representing a minimum rate of energy gain that is necessary for the animal to sustain itself.

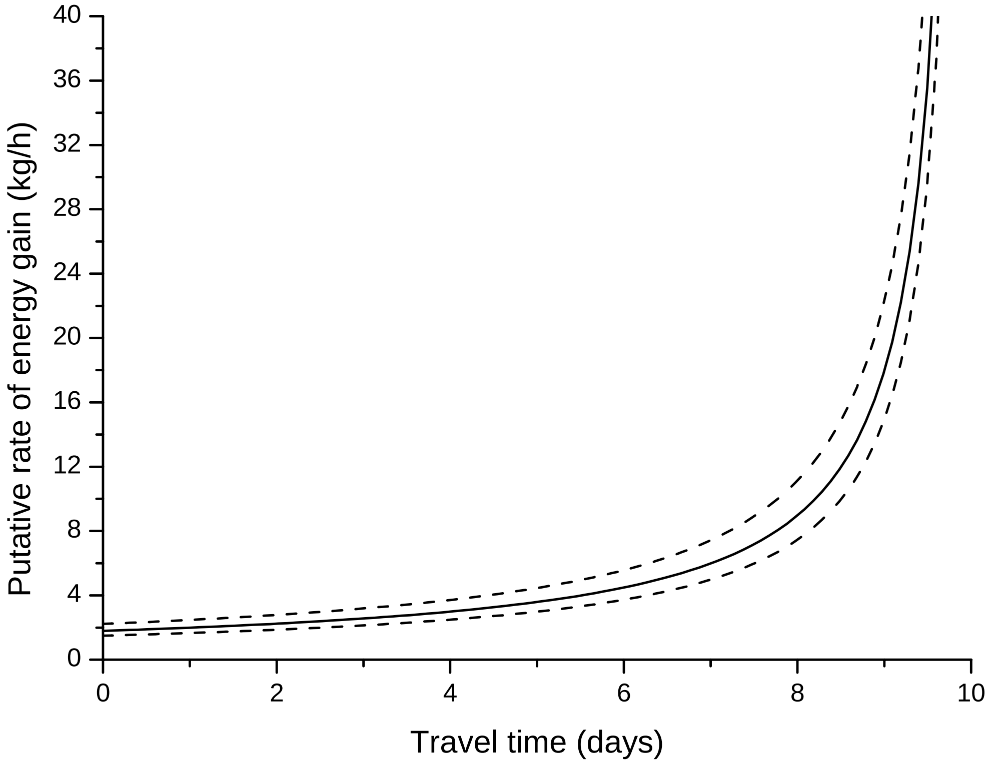


Figure 4.4: Putative rate of energy gain as function of travel time when time at sea is constant. The solid line corresponds to a diet of 50% fish and 50% squid, the upper and lower dashed lines show the putative rate of energy gain for a 100% squid and 100% fish diet, respectively.

4.5 DISCUSSION

The observation that so many pinnipeds commute regularly between foraging grounds and haul out spots (e.g. Thompson *et al.* 1991; Gales & Mattlin 1997; Merrick & Loughlin 1997; Bowen *et al.* 1999; Robinson *et al.* 2002; Thompson *et al.* 2003) intimates that there must be a large selective advantage for them to do so. The male South American sea lions in this study exhibited this pattern even though they are not constrained in their movements, as are females, by having to tend to offspring. By doing so, these animals apparently incur substantial costs associated with travelling to and from the foraging grounds, making up a total of 49.3% of the time and 60.1% of the total energy used during a typical foraging cycle. In fact, our

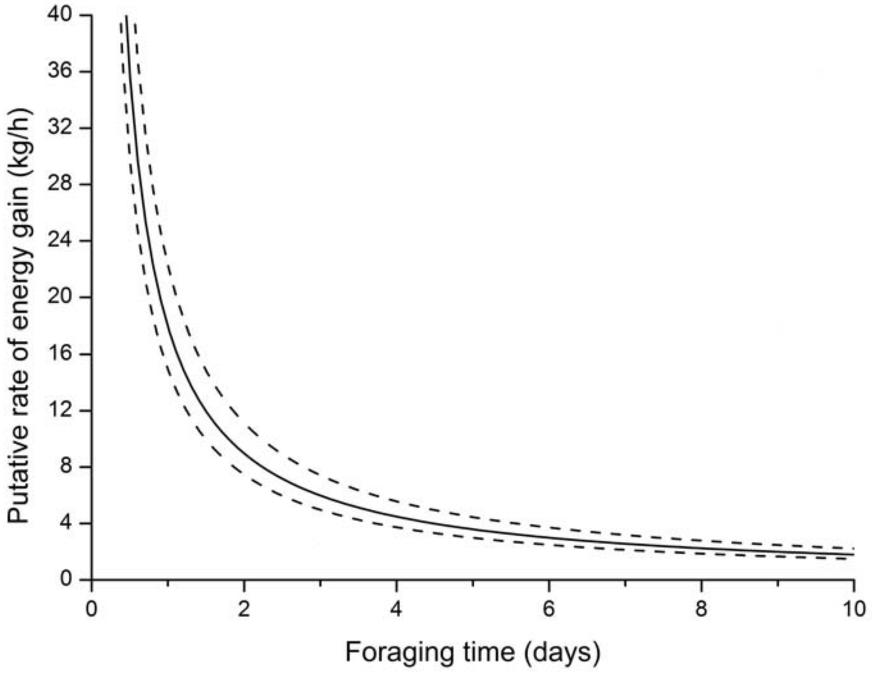


Figure 4.5: Putative rate of energy gain as function of time spent foraging when time at sea is held constant. The solid line corresponds to a diet of 50% fish and 50% squid, the upper and lower dashed lines show the putative rate of energy gain for a 100% squid and 100% fish diet, respectively.

results indicate that only a rather small part of the total time (17.8%) and energy (21.7%) is spent in the foraging area, something that is only tenable if the rate of prey acquisition in the foraging area is exceptionally high. In this respect, it has been suggested that male sea lions can take advantage of the highly productive Argentine shelf break front (Müller *et al.* subm, chapter 3) which could provide such high prey densities (Acha *et al.* 2004).

The strategy of moving rapidly to foraging areas close to the shelf break, means that male sea lions may avoid prey depleted areas close to the colonies (cf. Ashmole 1963; Birt *et al.* 1987). Interestingly, female sea lions have to provision their pups every 3-5 days (Campagna *et al.* 2001) and are therefore obliged to forage in areas close to the colonies, having to cope with the potentially meagre conditions that this would imply.

Knowing the travelling speed of South American sea lions and having derived a feeding rate, which we assume to be associated with the shelf break, we can examine what the putative foraging cycles might be for animals at different colonies down the coast of Argentina. The literature identifies 53 colonies (Figure 4.6) spaced down the Argentinian coast from Cabo Blanco at 47°S to Isla de los Estados at 55°S (Schiavini *et al.* 2004). The distances of these various colonies from the shelf break (in an east-west direction) range from less than 10 km at Isla de los Estados to ca. 800 km at 51°S. Using the mean speed of translocation derived from the data these distances transpose into total travelling times of 0.2 to 13.8 days. Assuming that the time spent on land is the same at all colonies and that rate of prey (equal parts fish and squid) acquisition is 167.7 kg/day (see earlier), this means that these animals must spend between 0.6 and 4.3 days in the foraging zone, respectively, resulting in foraging cycle durations of between 4.9 and 22.2 days. According to this scenario, the longer distances travelled to reach the shelf break result in a greater impact of the animals on their resources, primarily by virtue of the fact that a higher percentage of their total time is spent at sea. In this

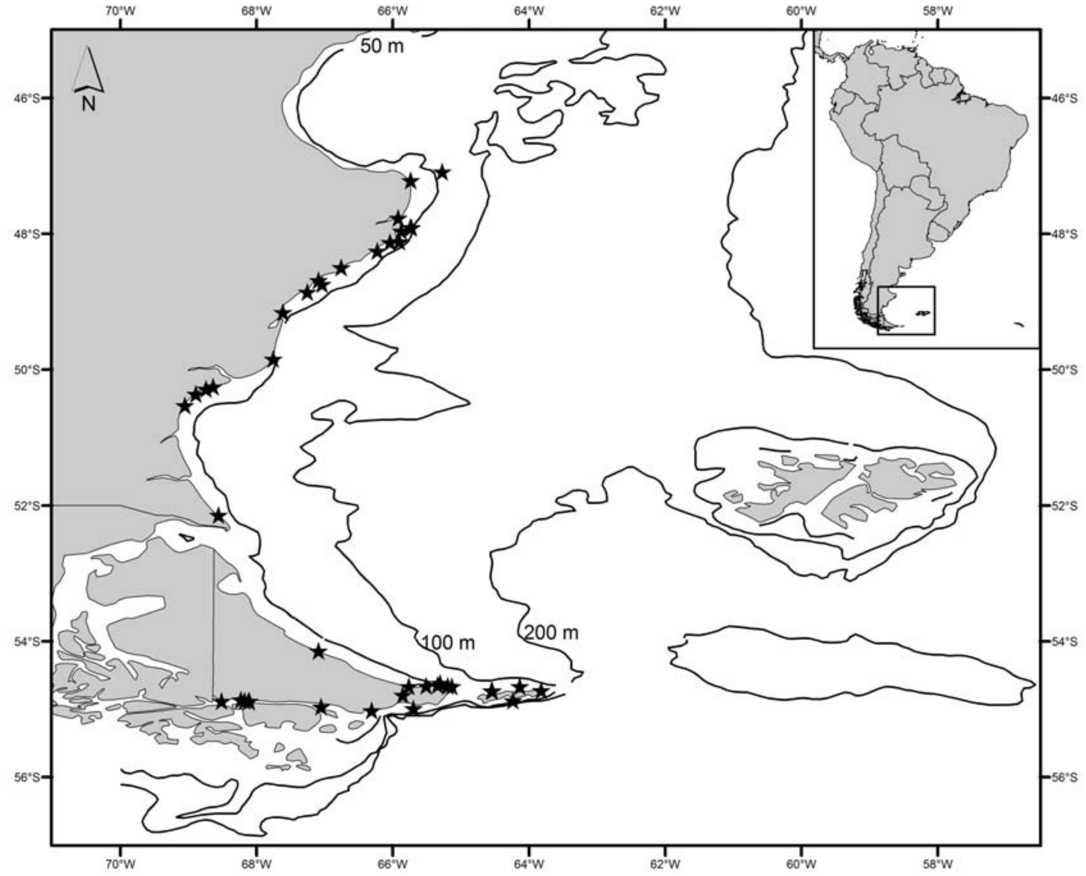


Figure 4.6: Map of South American sea lion rookeries and haul-out sites in southern Patagonia. The shelf break corresponds to the 200 m depth contour. Data taken from Schiavini *et al*. 2004.

case, the mean daily energy expenditure would increase by 60% when choosing the long-travel variant. Sea lions may, however, adjust the time they spend on land accordingly so that their relative impact stays the same, irrespective of the origin of their colonies. We note, however, that adherence to this pattern requires that the animals have the ability to fast for extended periods without overly compromising their well-being. Their substantial body size is likely to be an important factor in this.

According to our simple model, the total consumption of all sub-adult and adult South American sea lion males (with an average weight of 300 kg and comprising approximately 10% of all non-pup individuals (Reyes *et al*. 1999)) for the Patagonian shelf between the limits bounded by 40°S and 56°S and for colony sizes and locations detailed by Lewis and Ximénez (1983), Reyes *et al*. (1999) and Schiavini *et al*. (2004) is ca. 29,000 tons/year for a squid/fish mixed diet, with this value rising to ca. 36,000 tons/year if the diet were exclusively squid and dropping to ca. 24,200 tons/year for fish. As noted earlier, ca. 53% of this total energy consumption is due to the animals travelling between the site of the colony and the foraging location. If animals remained permanently at the foraging site outside the breeding season, total consumption over the shelf would be ca. 34.500 tons/year for a mixed diet, primarily because the metabolic rate of animals in water is markedly higher than for animals on land (see earlier). This means that, breeding apart, South American sea lions impact the shelf area less by returning to their colonies and spending a certain proportion of their time on land.

4.5.1 Why should South American sea lions return to their colonies?

By returning to the colony, the reduction in energy expenditure not only results in a smaller impact on the prey stocks but also reduces the time that a sea lion needs to spend foraging and/or reduces the necessary rate of energy gain in the foraging area. The latter would, however, only be an advantage if prey densities fell below a certain threshold, which may not apply to the shelf break front. In this study it was assumed that the energy expenditure of travel and foraging were equal. If, however, the cost of these two activities differed, then the total energy expenditure would depend on the relative durations of the travel and foraging phases as well as the difference in energetic costs between these. In addition, the energetic costs associated with a stay on land or at sea may differ for different groups of species such as otariids and phocids.

Another benefit of returning to land could be a decreased risk of predation, simply because less time is spent in the water. Even though some pinnipeds show diving behaviour that may also be used as a predator avoidance strategy (Le Boeuf & Crocker 1996), no quantitative information exist as to the extent to which predation may be an important factor in sea lion mortality at sea. Around colonies of highly colonial pinnipeds, however, distinct predatory strategies have been observed among sharks, and the areas in front of colonies, where animals have to pass on their way to and from the colony, may become high-risk areas (Klimley *et al.* 2001). Depending on the extent of such a predation risk, it may outweigh the disadvantage of staying at sea for a longer time, especially when considering the comparatively low chance of a predator encounter in large areas of the Patagonian shelf where sea lion density must be comparatively low.

As has been noted before, the ability to fast for extended periods may determine whether an animal can choose high quality foraging grounds further from the colony. In smaller animals the duration of travel to and from the foraging area plus the time spent on land may be beyond the animal's fasting capacity and thus simply exclude it from certain foraging grounds. This could apply particularly to juveniles or pups, or to the smaller species of fur seals.

In conclusion, despite the lack of any apparent constraints, male South American sea lions show distinct foraging cycles where the time at sea can be divided into travel and foraging activity based on the mean speed of translocation. The time spent travelling between the colony and the foraging area is an important factor in determining the time spent foraging, total energy expenditure and amount of prey consumed. In addition, the energetic costs associated with being on land, travelling and foraging as well as the energetic content of prey also significantly influence these parameters. There may, however, be important factors other than energy considerations that determine the movements of male sea lions.

4.6 ACKNOWLEDGEMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. We are indebted to M. Uhart, B. Raphael, P. Calle (Field Veterinary Program of the Wildlife Conservation Society, New York) and D.A. Albareda (Acuario de Buenos Aires y Jardín Zoológico de Buenos Aires, Argentina) for assistance with the anaesthesia of the sea lions. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina.

4.7 LITERATURE CITED

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *Journal of Marine Systems* **44**, 83–105.

Arnould, J.P.Y., Boyd, I.L. & Speakman, J.R. (1996) The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *Journal of Zoology, London* **239**, 769–782.

Ashmole, N.P. (1963) The regulation of numbers of tropical and oceanic birds. *Ibis* **103b**, 458–473.

Balmelli, M. & Wickens, P.A. (1994) Estimates of daily ration for the South African (Cape) fur seal. *South African Journal of Marine Science* **14**, 151–157.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K. & Montevecchi, W.A. (1987) Ashmole´s halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* **40**, 205–208.

Bonadonna, F., Lea, M.-A. & Guinet, C. (2000) Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. *Polar Biology* **23**, 149–159.

Bowen, W.D., Boness, D.J. & Iverson, S.J. (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology* **77**, 978–988.

Campagna, C., Fedak, M.A. & McConnell, B.J. (1999) Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* **80**, 1341–1352.

Campagna, C., Werner, R., Karesh, W., Marín, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology, London* **257**, 205–220.

Costa, D.P. & Gales, N.J. (2000) Foraging energetics and diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. *Journal of Experimental Biology* **203**, 3655–3665.

Costa, D.P. & Gales, N.J. (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs* **73**, 27–43.

Croxall, J.P. & Prince, P.A. (1982) Calorific content of squid (Mollusca: cephalopoda). *British Antarctic Survey Bulletin* **55**, 27–31.

Culik, B.M., Wilson, R.P. & Bannasch, R. (1994) Underwater swimming at low energetic cost by Pygoscelid penguins. *Journal of Experimental Biology* **197**, 65–78.

Gales, N.J. & Mattlin, R.H. (1997) Summer diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. *Canadian Journal of Zoology* **75**, 1695–1706.

George-Nascimento, M., Bustamante, R. & Oyarzun, C. (1985) Feeding ecology of the South American sea lion *Otaria flavescens*: food contents and selectivity. *Marine Ecology Progress Series* **21**, 135–143.

Jackson, T.P. (2001) Factors influencing food collection behaviour of Brants´ whistling rat (*Parotomys brantsii*): a central place forager. *Journal of Zoology, London* **255**, 15–23.

Kleiber, M. (1975) *The fire of life*. Krieger Publishing, New York, NY.

Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S. & Kelly, J.T. (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology* **138**, 617–636.

Koen Alonso, M., Crespo, E.A., Pedraza, S.N., García, N.A. & Coscarella, M.A. (1999) Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin* **98**, 250–263.

Kramer, D.L. & Nowell, W. (1980) Central place foraging in the Eastern chipmunk, *Tamias striatus*. *Animal Behaviour* **28**, 772–778.

Le Boeuf, B.J. & Crocker, D.E. (1996) Diving behavior of elephant seals: Implications for predator avoidance. *Great white sharks: the biology of* Carcharodon carcharias (eds A.P. Klimley & D.G. Ainley), pp. 193–206. Academic Press, San Diego, CA.

Le Boeuf, B.J., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M. & Houser, D.S. (2000) Foraging ecology of northern elephant seals. *Ecological Monographs* **70**, 353–382.

Lewis, M.N. & Ximénez, E.I. (1983) *Dinámica de la población de* Otaria flavescens *(Shaw) en el área de Península Valdés y zonas adyacentes (Segunda parte)*. Technical Report **79**. Centro Nacional Patagónico, Puerto Madryn, Argentina.

Merrick, R.L. & Loughlin, T.R. (1997) Foraging behavior of adult females and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology* **75**, 776–786.

Müller, G., Wilson, R.P., Campagna, C. & Quintana, F. (subm) Lunch off the shelf: foraging behaviour of male South American sea lions (*Otaria flavescens*). *Marine Ecology Progress Series*.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of ecological systems* (eds D.J. Horn, R.D. Mitchell & G.R. Stairs), pp. 155–177. Ohio State University Press, Columbus, OH.

Reyes, L.M., Crespo, E.A. & Szapkievich, V. (1999) Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Argentina. *Marine Mammal Science* **15**, 478–493.

Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. & Hindell, M.A. (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research* **53**, 1071–1082.

Ropert-Coudert, Y., Wilson, R.P., Daunt, F. & Kato, A. (2004) Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behavioral Ecology* **15**, 824–830.

Rosen, D.A.S. & Trites, A.W. (2000) Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, Pollock, squid, and salmon. *Canadian Journal of Zoology* **78**, 234–239.

Schiavini, A.C.M., Crespo, E.A. & Szapkievich, V. (2004) Status of the population of South American sea lion (*Otaria flavescens* Shaw, 1800) in southern Argentina. *Mammalian Biology* **69**, 108–118.

Schmidt-Nielsen, K. (1997) *Physiologie der Tiere*. Berlin: Spektrum Akademischer Verlag GmbH, Heidelberg.

Simeone, A. & Wilson, R.P. (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology* **143**, 825–831.

Thompson, D., Hammond, P.S., Nicholas, K.S. & Fedak, M.A. (1991) Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *Journal of Zoology, London* **224**, 223–232.

Thompson, D., Moss, S.E.W. & Lovell, P. (2003) Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. *Marine Ecology Progress Series* **260**, 285–296.

Weimerskirch, H. & Guionnet, T. (2002) Comparative activity pattern during foraging of four albatross species. *Ibis* **144**, 40–50.

Wilson, R. P. (2004) Reconstructing the past using futuristic developments: trends and perspectives in logger technology for penguins. *Memoirs of National Institute of Polar Research*, Special Issue **58**, 34–49.

Wilson, R.P., Scolaro, J.A., Grémillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E., Müller, G., thor Straten, M. & Zimmer, I. (In press) Distance limits in central place foragers: How do Magellanic penguins *Spheniscus magellanicus* cope with prey variability over the species distributional range? *Ecological Monographs*.

IS BIGGER BETTER? SEXUAL DIMORPHISM AND DIVING BEHAVIOUR IN SOUTH AMERICAN SEA LIONS

Müller, *et al*.

Marine Ecology Progress Series, submitted

5.1 ABSTRACT

Body size is one of the main factors that determine diving capacity and larger animals usually have longer dive durations than smaller animals. The effect of size on general dive characteristics as well as dive efficiency (bottom time divided by total dive cycle duration) was investigated using dive data from highly dimorphic male and female South American sea lions (*Otaria flavescens*) from Patagonia to examine whether this dimorphism might result in differential efficiencies over depth which may ultimately facilitate niche separation and thus reduce intraspecific competition. The results showed that the diving capacity differs between males and females according to allometric predictions, with males showing longer dive durations than females. Dive efficiency had maximum values in different depth ranges, with males being more efficient than females at greater depths. The majority of dives of both sexes occurred at depths with high dive efficiencies. In females dive efficiency decreased continuously with increasing depth. Dive

efficiency in males showed a minimum at very shallow depths followed by an increase up to the maximum depth recorded.

5.2 INTRODUCTION

Central place foraging, where an animal divides its time between a central place (a nest or a colony) and some part remote from that where energy is acquired (Orians & Pearson 1979) is the norm for many otariids (fur seals and sea lions, which perform foraging trips lasting from a few hours to several days (Merrick & Loughlin 1997; Crocker *et al*. 2001; Harcourt *et al*. 2002; Robinson *et al*. 2002)). As otariids are often highly colonial, local consumptive intra-specific competition may lead to prey depletion around this central place (cf. Birt *et al*. 1987) and could potentially affect reproductive success (Ashmole 1963; Gaston *et al*. 1983; Hunt *et al*. 1986; Birt *et al*. 1987). Ultimately, the appropriate distance for these animals to travel from the colony in order to feed will depend on the extent of this consumptive competition as a function of distance and the time and/or effort involved in travel (for extended discussion of this see e.g. Fretwell & Lucas 1970; Guillemette & Himmelmann 1996; Diaz *et al*. 1998). Unlike analogous terrestrial animals however, colonial marine endotherms such as otariids have a third spatial dimension which can be utilised to reduce the effect of competition, that of depth. The diving capacities of marine endotherms appear to be closely related to body size, with larger animals generally diving deeper and for longer (Boyd & Croxall 1996; Schreer *et al*. 2001). This is relevant in pinnipeds since many species, particularly those that are colonial on land (notably the Otariids), are sexually dimorphic so that sex-linked differential depth exploitation might indeed help reduce intra-specific competition.

The South American sea lion (*Otaria flavescens*) is a highly dimorphic species that shows segregation of foraging areas between males and females (Campagna *et al*.

2001; Müller *et al.* subm, chapter 3). The aim of this study is to determine whether the observed size dimorphism in South American sea lions leads to differences in dive efficiency which could explain the differences observed in foraging areas.

5.3 METHODS

5.3.1 Study site and instruments

The study sites as well as capture and deployment procedures are presented elsewhere (see Werner and Campagna (1995) for females and Müller *et al.* (subm, chapter 3) for males) and will therefore only be described briefly here. A total of seven lactating female South American sea lions (*Otaria flavescens*) from Punta Norte (42.083°S, 63.767°W, Figure 5.1)), Peninsula Valdés, Argentina, were captured during the 1993, 1994 and 1995 breeding seasons and equipped with MK-4 time-depth-recorders (Wildlife Computers, Redmond, Washington) that were programmed to sample depth every five or ten seconds. The devices were attached with epoxy glue on the dorsal midline above the shoulders. All devices were recovered by re-capture of the animals. During November 2003 eight sub-adult males, also from Punta Norte, were equipped with dead reckoners (Driesen & Kern, Bad Bramstedt, Germany) by having them stuck with epoxy glue to the top of their heads. These devices recorded, among other things, depth at intervals of 3 or 10 seconds. Recovery of the devices took place via a remote release-mechanism (Müller *et al.* subm, chapter 2) which enabled the recovery of five of the eight devices although only two provided data due to battery failure in the remaining instruments.

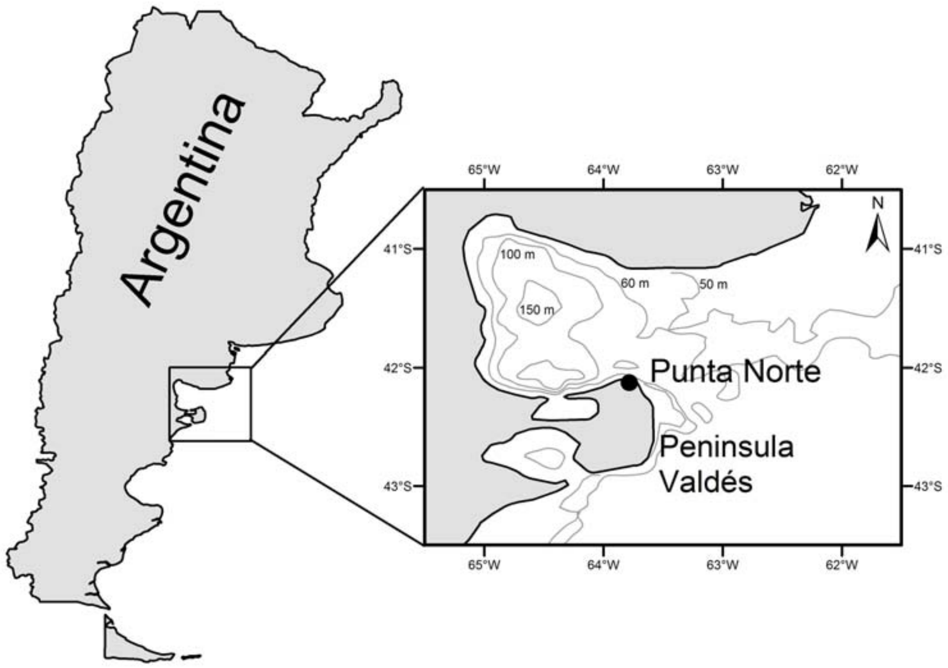


Figure 5.1: Map of the study area showing the location of the Punta Norte rookery and depth contours in the vicinity of Peninsula Valdés.

5.3.2 Data analysis

Downloaded data from both TDRs and dead reckoners were converted into ASCII files and analysed using the custom-written software MT-Dive (Jensen Systems Software, Laboe, Germany). Nominally, the programme sought out points of inflection in the dive profile (depth on the y-axis versus time on the x-axis) so as to identify the beginning and end of the descent, bottom and ascent phases. These points were highlighted by cursors which were then checked visually before being approved. In the case of the males, the determination of inflection points was aided by inspection of other parameters recorded by the dead reckoners such as dive angle. Dives less than 3 m were excluded from analysis. The results were exported as ASCII files pending further analysis. In order to avoid pseudoreplication due to differences in the number of dives made per individual, all data were reduced at random so that individuals contributing to the male or female pool of dives all had the same number of events. The dive data obtained from six of the seven females have been cursorily analysed previously (Werner & Campagna 1995), but will be investigated in more detail here together with data from a seventh animal. Results are presented as mean ± standard deviation (SD) unless otherwise stated. Dive efficiency was defined as the proportion of the dive cycle that was spent in the bottom phase and given by:

$$\text{Dive Efficiency} = \frac{\textit{Time spent in the bottom phase of the dive}}{\textit{descent duration} + \textit{bottom duration} + \textit{ascent duration} + \textit{surface duration}}$$

For the analysis of the surface interval the upper 95% confidence interval of the mean was derived and all surface intervals exceeding this value were excluded. This was done to exclude overly long surface pauses that were not related to recovery from the preceding dive, but might have served other purposes such as resting or social interaction, and thus to obtain a more exact relationship between surface interval and intense diving related to foraging activity (Kooyman *et al.* 1992).

5.4 RESULTS

The seven females made a total of 18,057 dives over 26 foraging trips with the number of dives per female ranging from 873 to 4,297. The two males performed a total of 4617 dives during one complete and two partial foraging trips (Table 5.1). Of the total time at sea, females spent a mean of 51.8% (Table 5.2) submerged,

Table 5.1: Basic dive statistics of female and male South American sea lions. Values represent mean values for the randomly reduced data ± standard deviation.

	Dive characteristics						
	# of dives	Mean dive duration (min)	Max dive duration (min)	Descent duration (min)	Bottom duration (min)	Ascent duration (min)	Mean surface interval (min)
Females	18,057	2.9 ± 1.1	7.1	0.8 ± 0.3	1.3 ± 0.8	0.9 ± 0.4	2.4 ± 9.5
Males	4617	3.8 ± 1.7	9.0	0.9 ± 0.4	1.8 ± 1.3	1.1 ± 0.5	3.3 ± 14.3

with individual values ranging from 48.4 to 65.5%. Males spent more than half the time at sea below the surface (Table 5.2) with the bottom phase taking up almost half of the total dive time. Diving at sea was not continuous but instead interrupted by irregular surface intervals of varying duration in both males and females (Figures 5.2 and 5.3).

Table 5.2: Division of time at sea into periods at and below the surface as well as division of dive time (time submerged) into the three different phases of the dive (descent, bottom and ascent phase).

	Time at sea		Time submerged		
	At surface (%)	Submerged (%)	Descent (%)	Bottom (%)	Ascent (%)
Females	48.2	51.8	24.7	46.6	28.7
Males	43.0	57.0	25.2	46.0	28.8

The maximum depth distributions of both males and females were bimodal and significantly different, with the second mode occurring at a greater depth in males (80 – 100 m) than in females (50 – 70 m) (χ^2 = 723.83, P < 0.01, df = 10 and χ^2 = 1390.84, P < 0.01, df = 10 for males and females respectively, Figure 5.4). Only one female dived deeper than 120 m, performing a significant amount of dives (23.8% of all dives conducted by this animal) between 140 and 160 m.

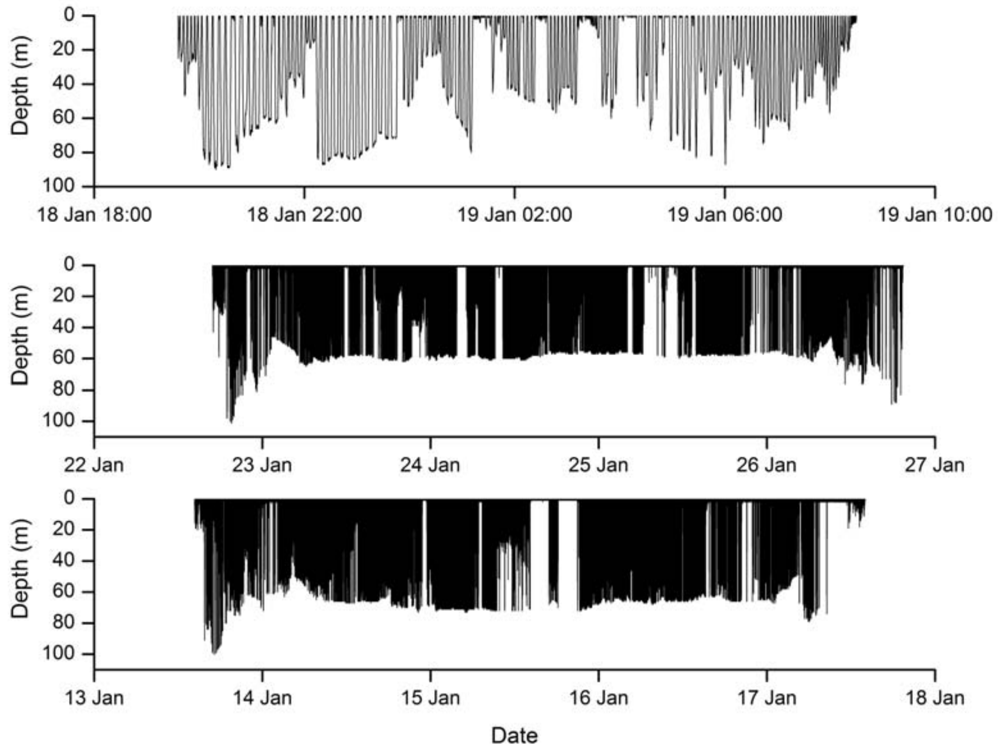


Figure 5.2: Three examples of foraging trips made by three female South American sea lions spanning from less than two to more than four days.

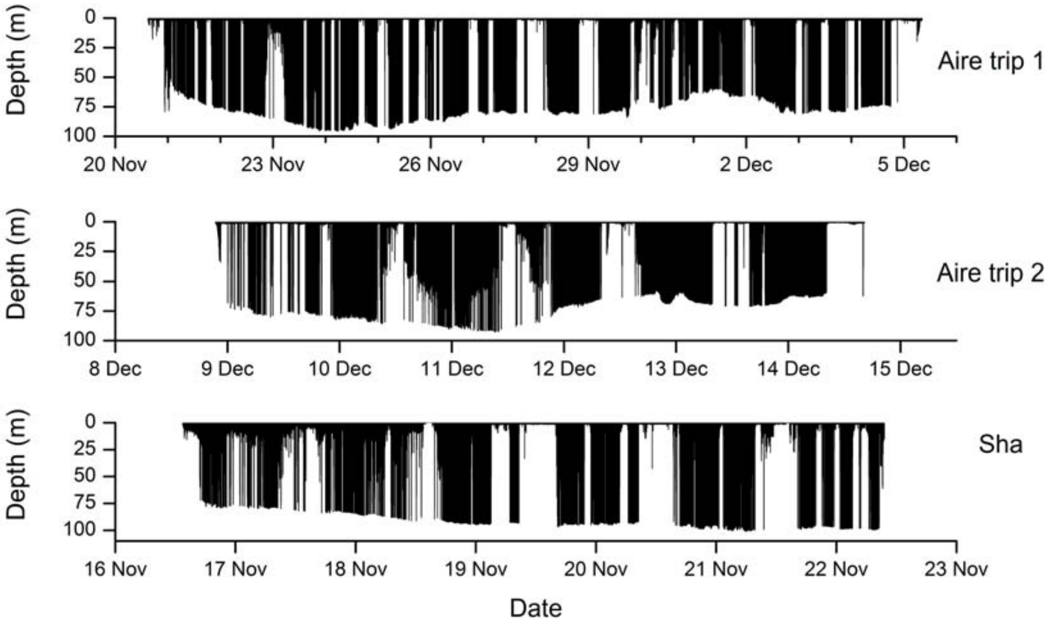


Figure 5.3: The recorded foraging trips made by two male South American sea lions. Animal and trip numbers are indicated on each graph. The lower two examples represent partial foraging trips as the devices stopped recording due to a full memory while the animal was still at sea.

Mean dive duration for all females was 2.9 ± 1.1 min (median = 3.1), with a maximum dive duration of 7.1 min (Table 5.1). For the males mean dive duration was 3.8 ± 1.7 (median = 4.0) and maximum dive duration was 9.0 min. However, dive duration was positively correlated with dive depth in both males and females (Duration = $(0.803 + 0.315 * \ln(\text{depth}))^2$, $F = 113.7$, $P < 0.05$ for males and Duration = $(0.657 + 0.283 * \ln(\text{depth}))^2$, $F = 198.1$, $P < 0.05$ for females, Figure 5.5). The relationship between dive duration and maximum depth reached during the dive is significantly different between males and females ($F = 12.92$, $P < 0.05$).

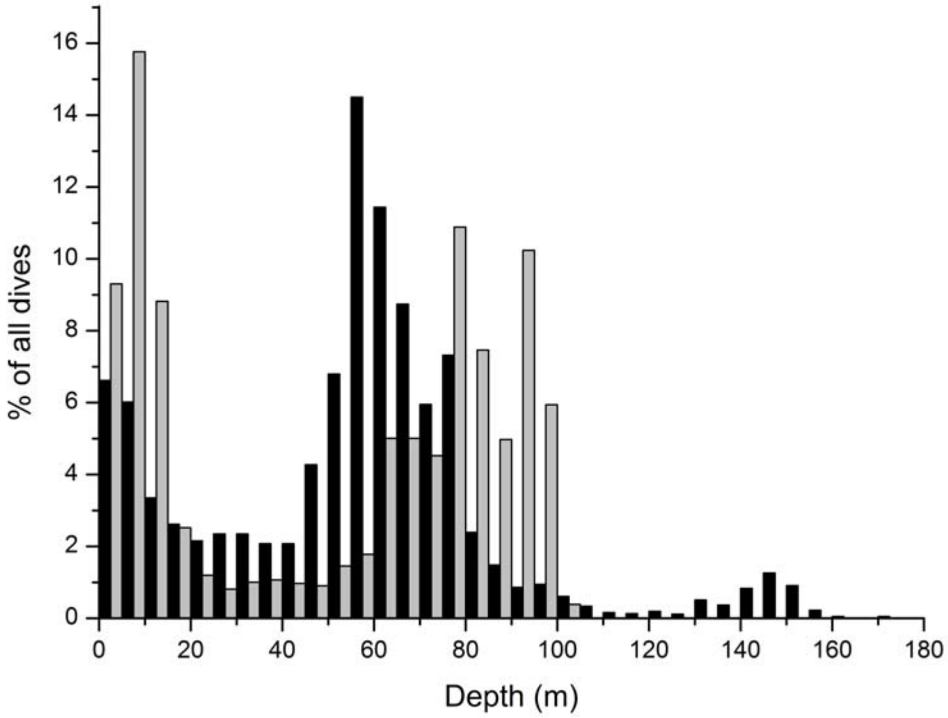


Figure 5.4: Frequency distribution (expressed as % of all dives) of dive depths from female (black bars) and male (grey bars) South American sea lions.

Females spent a mean of 2.4 ± 9.5 min (median = 1.0 min) at the surface between dives, whereas the mean surface interval of males was 3.3 ± 14.3 (median = 1.5 min) (Table 5.1). Surface intervals increased in both males and females with increased dive duration (Surface interval = 0.0062 * depth +0.6817, F = 97.76, $P < 0.05$ for females and Surface interval = 0.0144 * depth +0.6633, F = 203.15, $P < 0.05$ for males, Figure 5.6). The difference between males and females was statistically significant for both slope and intercept (F = 34.84, $P < 0.05$ and F = 46.54, $P < 0.05$, respectively).

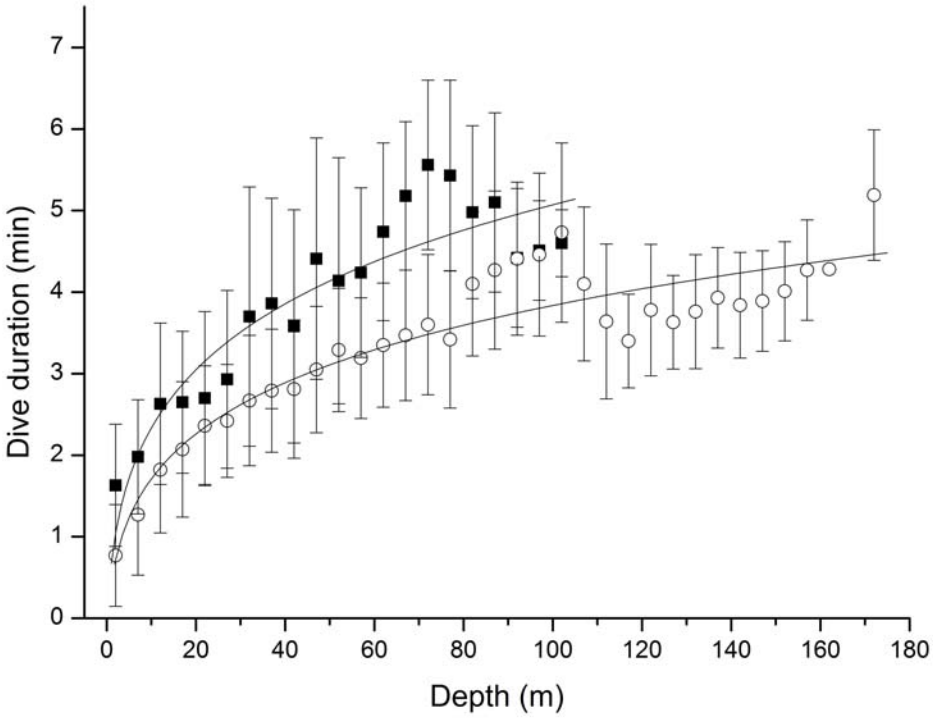


Figure 5.5: Dive duration (± SD) as function of dive depth for male (solid squares) and female (open circles) sea lions. Solid lines represent least squares regressions (see text for details).

Mean durations of the descent, bottom and ascent phase were 0.8 ± 0.3, 1.3 ± 0.8, and 0.9 ± 0.4 min, respectively, for females and 0.9 ± 0.4, 1.8 ± 1.3, and 1.1 ± 0.5 min, respectively, for males (Table 5.1). The duration of the descent and ascent phases showed significant positive correlations with dive depth in females (Descent duration = 0.007 * depth +0.3920, F = 608.28, $P < 0.05$ and Ascent duration = 0.0085 * depth + 0.4373, F = 622.93, $P < 0.05$). No significant relationship was apparent for the bottom phase (F = 0.2466, $P > 0.05$). In males the durations of all dive phases were significantly correlated with depth (Descent duration = 0.065 * depth + 0.6537, F = 59.62, $P < 0.05$, Bottom duration = 0.0202 * depth + 0.7159, F = 51.27, $P < 0.05$ and Ascent duration = 0.0054 * depth + 0.9101, F = 14.10, $P < 0.05$, Figure 5.7). The slope of the regression for the descent phase was not significantly different between males and females (F = 0.40, $P > 0.05$), the intercept, however, was (F = 68.50, $P < 0.05$). In the ascent phase the slope ascent duration against depth was significantly different between males and females (F = 7.67, $P < 0.05$) as was the intercept (F = 17.26, $P < 0.05$).

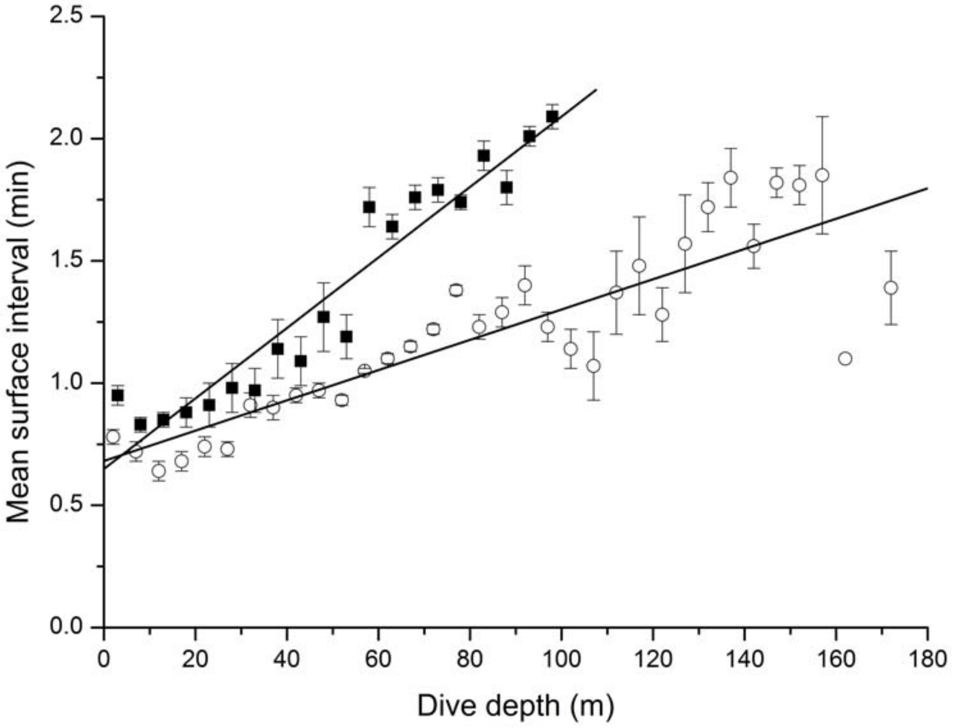


Figure 5.6: Surface intervals (± SE) as function of dive depth for male (solid squares) and female (open circles) sea lions. Solid lines represent least squares regressions (see text for details).

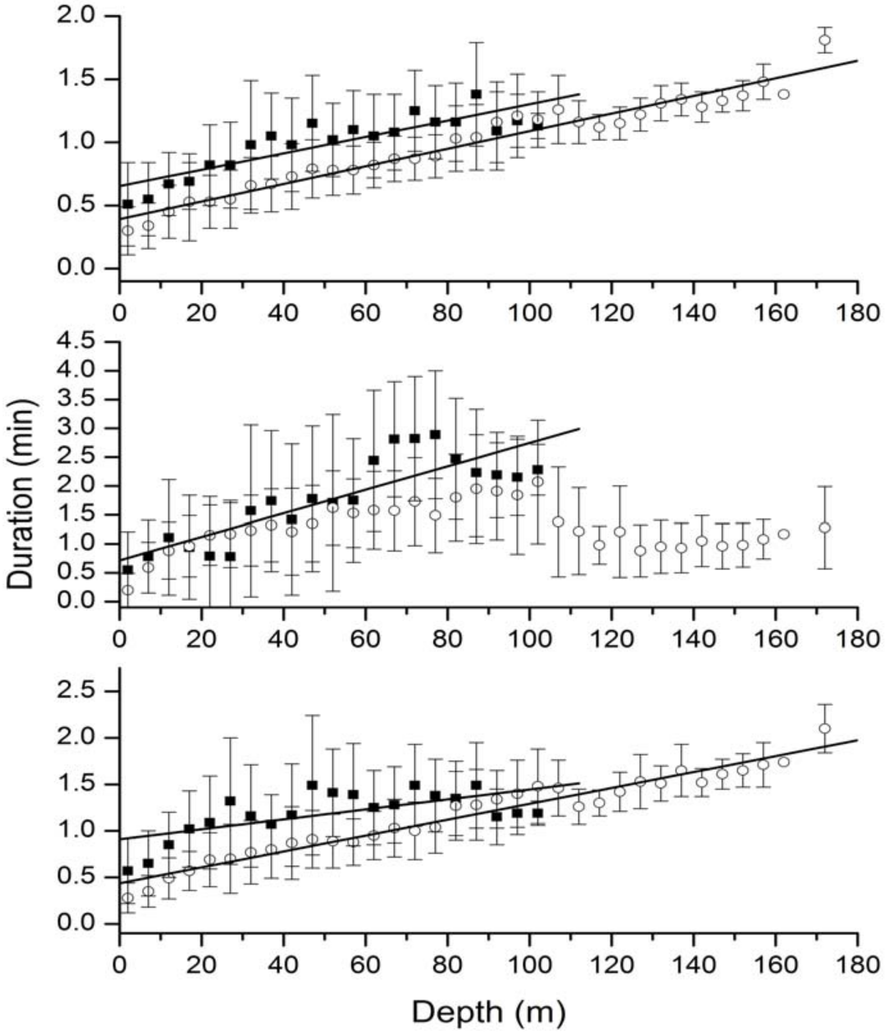


Figure 5.7: Duration (± SD) of individual dive phases (descent, bottom phase and ascent (from top to bottom)) as function of dive depth for male (solid squares) and female (open circles) sea lions. Solid lines represent least squares regressions (see text for details).

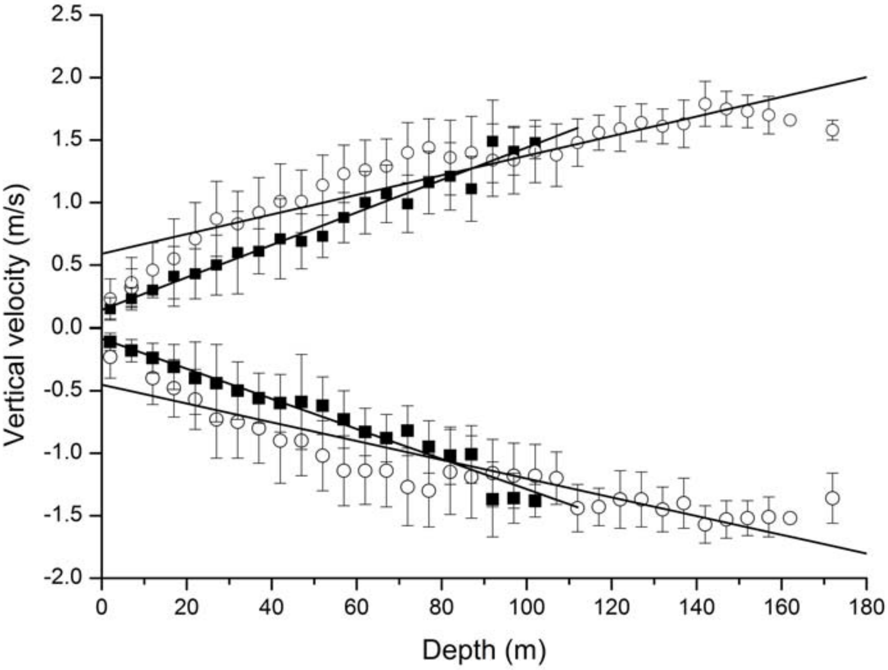


Figure 5.8: Vertical velocities (± SD) as function of dive depth for male (filled squares) and female (open circles) sea lions. Solid lines represent least squares regressions (see text for details).

Vertical velocity in females had mean values of 1.1 ± 0.5 and 1.0 ± 0.5 m/s for descent and ascent, respectively, but increased significantly with maximum dive depth (Descent velocity = 0.078 * depth +0.5907, F = 202.40, $P < 0.05$ and Ascent velocity = -0.0075 * depth - 0.4524, F = 107.01, $P < 0.05$, Figure 5.8). Mean descent and ascent rates for males (0.81 ± 0.5 and 0.70 ± 0.5 for descent and ascent, respectively) were lower than for females (t = -23.96, df = 9364, $P < 0.001$ and t = -25.52, df = 9364, $P < 0.001$ for descent and ascent rate, respectively). Males also showed significant correlations between vertical velocity and depth for both the descent (Descent velocity = 0.0130 * depth + 0.1414, F = 766.49, P <

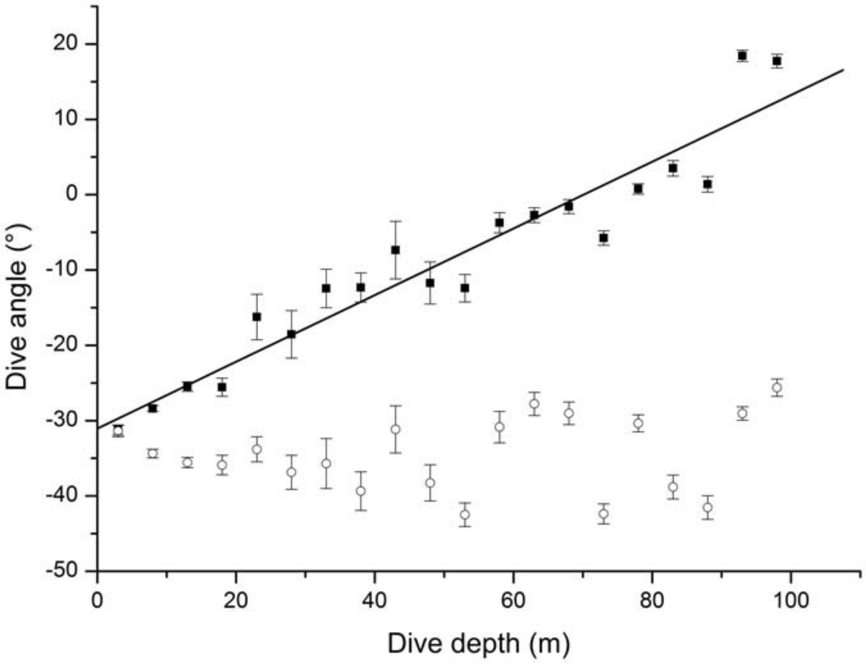


Figure 5.9: Dive angle (± SE) during descent (open squares) and ascent (solid squares) as function of dive depth in male sea lions. Solid line represents least squares regression (see text for details).

0.05) and the ascent phase (Ascent velocity = -0.0120 * depth – 0.0832, F = 500.26, P < 0.05, Figure 5.8). For the descent phase, both slope and intercept of the regressions differed significantly between males and females (F = 23.88, P < 0.05 and F = 10.26, P < 0.05, respectively). For the ascent phase the differences between the regressions of males and females were significantly for the slope (F = 10.96, P < 0.05) but not for the intercept (F = 3.61, P < 0.05). The mean rate of descent was significantly greater than the ascent rate in both females and males (t = 13.52, df = 12538, P < 0.001 and t = 8.62, df = 6190, P < 0.001 for females and males, respectively). In addition, the mean swim angle in males increased with increasing depth for the ascent phase of the dives (Dive angle = 0.4427 * depth – 31.0458, F = 192.40, P < 0.05, Figure 5.9) although no significant relationship was obtained for the descent phase (F = 0.38, P > 0.05).

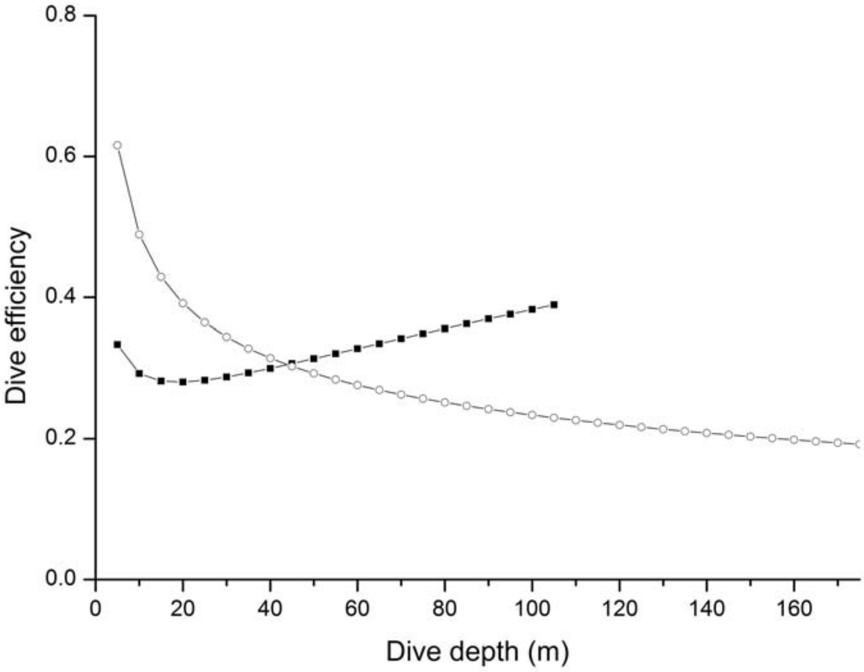


Figure 5.10: Dive efficiency of male (solid squares) and female (open circles) sea lions as function of dive depth.

Dive efficiency in females decreased over the whole range of observed depths, whereas the efficiency in males showed a minimum around 20 m and then continuously increased up to the maximum depth recorded for them (ca. 100 m) (Figure 5.10). At shallow depths females showed a higher dive efficiency than males but at approximately 45 m the curves cross so that the efficiency of males is greater at greater depths.

5.5 DISCUSSION

Our results highlight that there are differences between male and female sea lions in depth utilisation. This may primarily stem from the use of different areas as foraging sites, males tending to forage farther offshore, closer to the shelf break (Müller *et al.* subm, chapter 3), while females forage in more coastal areas close to their colonies (Campagna *et al.* 2001). Sea lions are primarily benthic feeders (George-Nascimento *et al.* 1985; Koen Alonso *et al.* 2000) so that it is the bottom topography of the selected sites that will reflect the frequency distribution of maximum depths reached during foraging trips rather than some arbitrary maximum depth of animals foraging in the water column. The areas available to the animals will be partly determined by the time the two genders have to forage. In this, females, having to provision young at this time, only have trips of the order of 3.4 days long, which, at a travelling speed of 0.75 m/s (Campagna *et al.* 2001) would allow them to range a maximum distance of 110 km from the colonies, assuming that the animals travel in a straight line, do not use any distance in vertical displacement (something which is patently untrue if our data are considered realistic cf. Figure 5.2) and do not spend any time in a defined foraging area. Males, on the other hand, have foraging trips that average 8.4 days (Müller *et al.* subm, chapter 3) and so have an equivalent theoretical maximum foraging range of 272 km when travelling at the same speed as females. Clearly, this gives males an ability to reach areas unattainable to the females so that they need not compete for food close to the colonies. However, does their body size confer a selective advantage on them with regard to diving in those areas?

Overall, both males and females in this study accord with many diving marine endotherms in that almost all prime parameters used to describe the dive: descent duration, bottom duration and ascent duration are all highly correlated with the maximum depth reached during the dive (see e.g. Le Boeuf *et al.* 1988; Kooyman *et al.* 1992; Wilson & Quintana 2004). Increases in descent and ascent duration with increasing maximum depth reached are to be expected since they reflect an increased time to cover the greater distance between surface and seabed. Increases in bottom duration with increasing depth are also often observed as animals have to do this to maintain foraging efficiency (sensu Ydenberg & Hurd 1998) by extending the prey-encounter phase of the dive to accord with the increases occurring during the other phases of the dive (e.g. Kooyman *et al*. 1992). Ultimately, however, as animals approach their maximum breath-hold capacity, increases in dive depth (and therefore transit duration) must result in decreases in bottom duration and such a pattern has, for example, been observed in tufted ducks *Aythya fuligula* (Halsey *et al*. 2003). It is theorized that such a reduction in bottom duration is only tenable if the returns in terms of prey acquisition make it viable (e.g. Wanless *et al*. 1998).

However, the case examined here is particularly interesting because it shows that there are unequivocal differences in the time-based organisation of male and female sea lions as a function of depth. Females have higher mean vertical velocities than males for both the descent and the ascent phases of the dive (Figures 5.7 and 5.8) for almost all depths, which apparently makes them more efficient because more time can be allocated to the bottom phase of the dive when prey are likely to be encountered. However, this is only true if both gender swim at their lowest cost of transport (for definition see Pinshow *et al*. 1977) because increases or decreases in absolute swim speed outside these values result in more oxygen used per metre swum which will reduce time available for prey searching. Although larger animals are theoretically able to swim faster than smaller individuals (Bonner 1965; Peters 1983), the speed at which the lowest cost of transport should occur is more complex and may be more obviously dependent on body shape and form than size. For example, Culik *et al*. (1994) note differences in speeds of lowest costs of transport in the three Pygoscelid penguin species that are not apparently body mass dependent despite the fact that all species are superficially remarkably similar. Thus, the observation that female sea lions dedicate less time to the commuting phases between the water surface and the sea bed during foraging than the males cannot be attributed to some allometric effect. It does, however, lead to them apparently being more efficient in this regard. Interestingly, both males and females increase their vertical velocity with increasing maximum dive depth (Figure 5.8). This can be brought about by steepening the descent and ascent angles (which is clearly something that occurs at least in the males (Figure 5.9)) and/or by animals having changing minimum costs of transport speeds as a function of water depth. This latter may occur because the physical characteristics of the animals are likely to change with hydrostatic pressure, as has been shown for 2 pinniped and 2 cetacean species by Williams *et al*. (2000) (see also Sato *et al*. 2002, 2003). Specifically, air in the respiratory spaces and in the pelage (which is particularly thick around the neck in male sea lions) becomes compressed with increasing water depth, reducing the upthrust accordingly so that the amount of energy that animals must invest to attain a particular speed also changes (cf. Wilson & Zimmer 2004).

Perhaps the most radical difference in time allocation to the different phases of the dive between male and female sea lions occurs in the bottom phase. Here, the gradient of the regression of bottom duration versus dive depth shows a steep increase in males, but no significant overall change in females. This difference may be attributable to the size dimorphism in this species (Boyd & Croxall 1996; Schreer *et al*. 2001). Larger animals may spend longer underwater because mass-specific metabolic rate in homeotherms scales with mass according to a negative power term (Hemmingsen 1960; Peters 1983) whereas body oxygen carrying capacity seems to be linearly related to body mass (see Parer & Metcalf 1967 and Gehr 1981 for a discussion of this). Specific data on metabolic rates of the South American sea lion are lacking but a comparison between males and females determined by doubly-labelled water (e.g. Costa & Gales 2004) or gas respirometry (Sparling & Fedak 2004) coupled with a detailed assessment of body oxygen stores (e.g. Kooyman 1989) could go a long way to helping explain the observed differences.

The final missing element in assessment of the efficiency of the two genders as a function of dive depth is the surface interval between dives. This is actually only really relevant to depth in as much as it is related to dive duration and this is related to depth (see above). An increase in surface interval with increasing depth, as observed in this study (Figure 5.6), has been noted for a number of species (e.g. Croxall *et al*. 1991; Wanless & Harris 1991) and is to be expected since although the rate of oxygen uptake is highest at lowest body oxygen levels, animals diving for long periods need extensive oxygen stores for their dives and must thus stay at the surface for extended periods loading oxygen when body partial pressure oxygen levels are not very different from those of the surrounding air (Wilson & Quintana 2004). This general condition is, however, likely to be modified according to animal size because scale effects affect respiratory gas exchange. Both tidal volume and vital capacity increase virtually directly with body mass (Guyton 1947; Adolph 1949; Stahl 1967; Peters 1983) and lung volumes also bear a nearly constant proportionality to body mass (Stahl 1962; Tenney & Remmers 1963; Weibel 1973, summarized in Peters 1983). However, respiratory frequency decreases with mass according to about $M^{-0.25}$ (Guyton 1947; Adolph 1949; Stahl 1967) resulting in a rate of air flow that scales with body size according to the standard ¾ law. Specific adaptations found in diving homeotherms such as surface tachycardia (Butler & Woakes 1979) and hyperventilation (Butler & Jones 1997) relating to increased oxygen flow to the tissue may modify this somewhat but given that it is the physics of air (and blood) flow (see e.g. Hansen 2003) coupled with diffusion chemistry that primarily modulates the process, it is not to be expected that size-related gender differences in sea lion surface intervals are exempt from this. It is thus perhaps relevant that females recover from longer dives more rapidly than males (Figure 5.6) which will tend to make them more efficient. Calculations of efficiency (Figure 5.10) show, however, that the relatively rapid recovery times shown by females (Figure 5.6) are not enough to counteract the huge increases in bottom duration that males are able to invest with increasing dive depth compared to females

(Figure 5.7) so that, at around 45 m, there is a cross-over, with males becoming more efficient. Our paucity of data highlights a difficulty in this type of study since during a total of 1600 h of diving from 7 animals, only one female dived appreciably deeper than 100 m. This is little surprizing since, if the efficiency shown by this animal is typical, there are good reasons why females should not dive to such depths although this is something which virtually precludes us from making statements about efficiencies at depths where animals cannot forage optimally. In addition, in over 600 h of diving behaviour, neither male dived deeper than just over 100 m although this may have been related to bottom topography (see later).

We conclude that scale effects leading to sex-related differential dive efficiencies have potential relevance with regard to intraspecific competition in South American sea lions. Frequent pup provisioning means that the females have limited time to forage and thus are constrained to operate close to the colony. Aside from the unusually deep water (ca. 200 m) in the Golfo San Matías, this means that animals generally forage over waters up to about 80 m deep. Although, with their longer foraging trips, males have access to the areas visited by females, they appear to be less efficient at shallow depths (Figure 5.10) and also may benefit by moving farther away where they will be less exposed to intraspecific competition. Their general movement East (Campagna *et al*. 2001; Müller *et al*. subm, chapter 3) takes them into deeper waters, albeit still over the Patagonian shelf, where their dive efficiency is markedly higher than in the shallower waters. The obvious coloniality of South American sea lions, their benthic feeding habits, their sexual dimorphism related to gender-specific variable foraging efficiency as a function of depth together with the constraints on the length of the foraging trips mean that the topographic- and prey density-conditions provided by the extensive Patagonian shelf may prove particularly important for the well-being of this species. As such, the extensive demersal fishery in the area (FAO 1997) should perhaps be considered as a conservation issue. Future work could also address the biology of the South American sea lion along the West coast of South America where water depth drops off very rapidly to depths ostensibly untenable for this species.

5.6 ACKNOWLEDGEMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. The help of M. Uhart, B. Raphael, P. Calle and D.A. Albareda with the anaesthesia of the sea lions, and of V. Ramos and P. Ledesma in recovering the devices is gratefully acknowledged. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina.

5.7 LITERATURE CITED

Adolph, E.F. (1949) Quantitative relations in the physiological constitutions of animals. *Science* **109**, 579–585.

Ashmole, N.P. (1963) The regulation of numbers of tropical and oceanic birds. *Ibis* **103b**, 458–473.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K. & Montevecchi, W.A. (1987) Ashmole´s halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* **40**, 205–208.

Bonner, J.T. (1965) *Size and cycle: an essay on the structure of biology*. Princeton University Press, Princeton, N.J.

Boyd, I.L. & Croxall, J.P. (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* **74**, 1696–1705.

Butler, P.J. & Woakes, A.J. (1979) Changes in heart rate and respiratory frequency during natural behaviour of ducks with particular reference to diving. *Journal of Experimental Biology* **79**, 283–300.

Butler, P.J. & Jones, D.R. (1997) Physiology of diving of birds and mammals. *Physiological Reviews* **77**, 837–899.

Campagna, C., Werner, R., Karesh, W., Marín, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology, London* **257**, 205–220.

Costa, D.P. & Gales, N.J. (2004) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion (*Neophoca cinerea*). *Ecological Monographs* **73**, 27-43.

Crocker, D.E., Gales, N.J. & Costa, D.P. (2001) Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology, London* **254**, 267–277.

Croxall, J.P., Naito, Y., Kato, A., Rothery, P. & Briggs, D.R. (1991) Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology, London* **225**, 177–199.

Culik, B.M., Wilson, R.P. & Bannasch, R. (1994) Underwater swimming at low energetic cost by Pygoscelid penguins. *Journal of Experimental Biology* **197**, 65–78.

Diaz, M., Illera, J.C. & Atienza, J.C. (1998) Food resource matching by foraging tits *Parus* spp. during spring-summer in a Mediterranean mixed forest; evidence for an ideal free distribution. *Ibis* **140**, 654–660.

FAO (Food and Agriculture Organization) (1997) *Review of the state of world fishery resources: marine fisheries. 6. Southwest Atlantic*. Marine Resources Service, Fishery Resources Division, Fisheries Department, FAO, Rome, Italy; available at http://www.fao.org/docrep/003/w4248e/w4248e12.htm#AREA41.

Fretwell, S.D. & Lucas Jr, H.L. (1970) On territorial behaviour and other factors influencing habitat distribution in birds I. Theoretical Development. *Acta Biotheoretica* **19**, 16–36.

Gaston, A.J., Chapdelaine, G. & Noble, D. (1983) The growth of thick-billed murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. *Canadian Journal of Zoology* **61**, 2465–2475.

Gehr, P., Mwangi, D.K., Ammann, A., Maloiy, G.M.O., Taylor, C.R. & Weibel, E.R. (1981) Design of the mammalian respiratory system. V. Scaling morphometric pulmonary diffusing capacity to body mass: wild and domestic mammals. *Respiration Physiology* **44**, 61–86.

George-Nascimento, M., Bustamante, R. & Oyarzun, C. (1985) Feeding ecology of the South American sea lion *Otaria flavescens*: food content and selectivity. *Marine Ecology Progress Series* **21**, 135–143.

Guillemette, M. & Himmelmann, J.H. (1996) Distribution of wintering common eiders over mussel beds: does the ideal free distribution apply? *Oikos* **76**, 435–442.

Guyton, A.C. (1947) Measurement of the respiratory volumes of laboratory animals. *American Journal of Physiology* **150**, 70–77.

Halsey, L., Woakes, A. & Butler, P. (2003) Testing optimal foraging models for air-breathing divers. *Animal Behaviour* **65**, 641–653.

Hansen, S. (2003) *Nostril-dependent: air-flow restrictions on breathing cycles in seals*. M.Sc. Thesis, University of Kiel, Kiel, Germany.

Harcourt, R.G., Bradshaw, C.J.A., Dickson, K & Davis, L.S. (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series* **227**, 11–24.

Hemmingsen, A.M. (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Reports of the Steno Memorial Hospital and Nordinsk Insulin Laboratorium* **9**, 6–110.

Hunt, G.L., Eppley, Z.A. & Schneider, D.C. (1986) Reproductive performance of seabirds: the importance of population and colony size. *Auk* **103**, 306–317.

Koen Alonso, M.A., Crespo, E.A., Pedraza, S.N., García, N.A. & Coscarella, M.A. (2000) Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin* **98**, 250–263.

Kooyman, G.L. (1989) *Diverse divers: physiology and behavior*. Springer-Verlag, New York, NY.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V. & Kooyman, C.A. (1992) Diving behavior and energetics during foraging cycles in King penguins. *Ecological Monographs* **62**, 143–163.

Le Boeuf, B.J., Costa, D.P., Huntley, A.C. & Feldkamp, S.D. (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology* **66**, 446–458.

Merrick, R.L. & Loughlin, T.R. (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology* **75**, 776–786.

Mitani, Y., Sato, K., Ito, S., Cameron, M.F., Siniff, D.B. & Naito, Y. (2003) A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology* **26**, 311–317.

Müller, G., Liebsch, N. & Wilson, R.P. (In press) A new shot at a release mechanism for devices on free-living animals. *Wildlife Society Bulletin.*

Müller, G., Wilson, R.P., Campagna, C. & Quintana, F. (Subm) Lunch off the shelf: Foraging behaviour of South American sea lions (*Otaria flavescens*). *Marine Ecology Progress Series*.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of ecological systems* (eds D.J. Horn, R.D. Mitchell & G.R. Stairs), pp. 155–177. Ohio State University Press, Columbus, OH.

Parer, J.R. & Metcalf, J. (1967) Respiratory studies of monotremes: 1. Blood of the platypus (*Ornithorhyncus anatinus*). *Respiratory Physiology* **3**, 359–385.

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.

Pinshow, B., Fedak, M. & Schmidt-Nielsen, K. (1977) Terrestrial locomotion in penguins: it costs more to waddle. *Science* **195**, 592–594.

Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. & Hindell, M.A. (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research* **53**, 1071–1082.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J.B.,Bost, C.A., Handrich, Y. & Le Maho, Y. (2002) Buoyancy and maximal diving depth in penguins: do they control inhaling air volume. *Journal of Experimental Biology* **205**, 1189–1197.

Sato, K, Mitani, Y., Cameron, M.F., Siniff, D.B. & Naito, Y. (2003) Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206**, 1461–1470.

Schreer, J.F., Kovacs, K.M. & O`Hara Hines, R.J. (2001) Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* **71**, 137–162.

Sparling, C.E. & Fedak, M.A. (2004) Metabolic rates of captive grey seals during voluntary diving. *Journal of Experimental Biology* **207**, 1615–1624.

Stahl, W.R. (1962) Similarity and dimensional methods in biology. *Science* **137**, 205–212.

Stahl, W.R. (1967) Scaling of respiratory variables in mammals. *Journal of Applied Physiology* **22**, 453–460.

Tenney, S.M. & Remmers, J.E. (1963) Comparative quantitative morphology of the mammalian lung: diffusing area. *Nature* **197**, 54–56.

Wanless, S. & Harris, M.P. (1991) Diving patterns of full-grown and juvenile Rock Shags. *Condor* **93**, 44–48.

Wanless, S., Grémillet, D. & Harris, M.P. (1998) Foraging activity and performance of Shag *Phalacrocorax atriceps* in relation to environmental characteristics. *Journal of Avian Biology* **29**, 49–54.

Weibel, E.R. (1973) Morphological basis of alveolar-capillary gas exchange. *Physiological Reviews* **53**, 419–495.

Werner, R. & Campagna, C. (1995) Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Canadian Journal of Zoology* **73**, 1975–1982.

Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.J., Horning, M., Calambokidis, J. & Croll, D.A. (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133–136.

Wilson, R.P. & Quintana, F. (2004) Surface pauses in relation to dive duration in imperial cormorants; how much time for a breather? *Journal of Experimental Biology* **207**, 1789–1796.

Wilson, R.P. & Zimmer, I. (2004) Inspiration by Magellanic penguins: reduced swimming effort when under pressure. *Marine Ecology Progress Series* **278**, 303–307.

Ydenberg, R. & Hurd, P. (1998) Simple models of feeding with time and energy constraints. *Behavioral Ecology* **9**, 49–53.

THREE-DIMENSIONAL DIVING BEHAVIOR OF A SOUTH AMERICAN SEA LION (*OTARIA FLAVESCENS*)

Müller *et al.*

Proceedings of the 22nd Wakefield Symposium, submitted

6.1 ABSTRACT

Even though the use of Time-Depth-Recorders (TDRs) has dramatically increased knowledge about pinniped diving behavior, recent studies have shown the limitations of two-dimensional plots of time and depth in interpretation of animal activity. Recently, new technologies have become available allowing collection of more dive parameters so that dives can be depicted in three dimensions. This study uses information collected by a 12-channel dead-reckoner to provide detailed information on movements in space of a male South American sea lion (*Otaria flavescens*) in Patagonia, Argentina. The information was analyzed using an Area-Interest-Index (AII) which reflects the directionality of movement. The AII was calculated for a complete foraging trip where the middle part showed the highest values, indicative of foraging activity. Activity estimations based on three-dimensional dive profiles (four dimensions with speed) showed good agreement with the calculated AII. The use of the AII is thus a promising tool for the determination of activity of marine animals over varying spatial scales.

6.2 INTRODUCTION

Determination of animal activity at sea has generally been hindered by the lack of information on animal movement in three-dimensional space so that behaviors cannot be assigned to specific areas. However, in recent years advances in technology have allowed collection of information which allows animal movements to be determined in more than the conventional two dimensions or depth over time (Harcourt *et al*. 2000; Hindell *et al*. 2002; Mitani *et al*. 2003).

Relatively little is known about the distribution at sea and diving behavior of the South American sea lion (*Otaria flavescens*), knowledge to date being almost exclusively limited to lactating females equipped with satellite tags and time-depth recorders (Werner & Campagna 1995; Campagna *et al*. 2001). This study details recent investigations on male sea lions using dead reckoners to elucidate general diving behavior. Here, the data are used to reconstruct the three-dimensional route during a foraging trip to sea. To determine the general behavior of the animal throughout the trip an activity index was created and applied to the route. Furthermore, individual three-dimensional dive profiles are provided to exemplify specific activities observed at different stages of the trip.

6.3 METHODS

A sub-adult male South American sea lion (*Otaria flavescens*) from Punta Norte, Peninsula Valdés, Argentina, was equipped with a dead-reckoner (Driesen & Kern GmbH, Bad Bramstedt, Germany) in November 2003. The device recorded time, depth, swim speed, compass heading (in 3 dimensions), and tilt angle (pitch and roll up to 70 degrees in each direction) at a sampling interval of 10 seconds. From these data the three-dimensional route was reconstructed using the custom-written software MT-Route (Jensen Software Systems, Laboe, Germany). The route was corrected for drift by correlating depth readings with depth contours as well as incorporating the known start and end point of the trip.

An Area-Interest-Index (AII) was used to describe animal activity at sea (Figure 6.1a). It relates the total distance traveled between two points (`a´ through to `e´) to the direct distance between the first and the last point (F):

$$AII = 1 - \frac{F}{a + b + c + d + e}$$

A high AII value corresponds to a convoluted track whereas low values indicate more directional movements. Because of the long duration of the trip the data were thinned out so only every tenth data point was included in the calculation of the AII, which spanned five successive points and thus was calculated over a time interval of 360 seconds (Figure 6.1b). In order to see the change in AII over time the trip was divided into intervals, each covering 5% of the total time, and an inverse polynomial curve was fitted to the means of the AII for each interval.

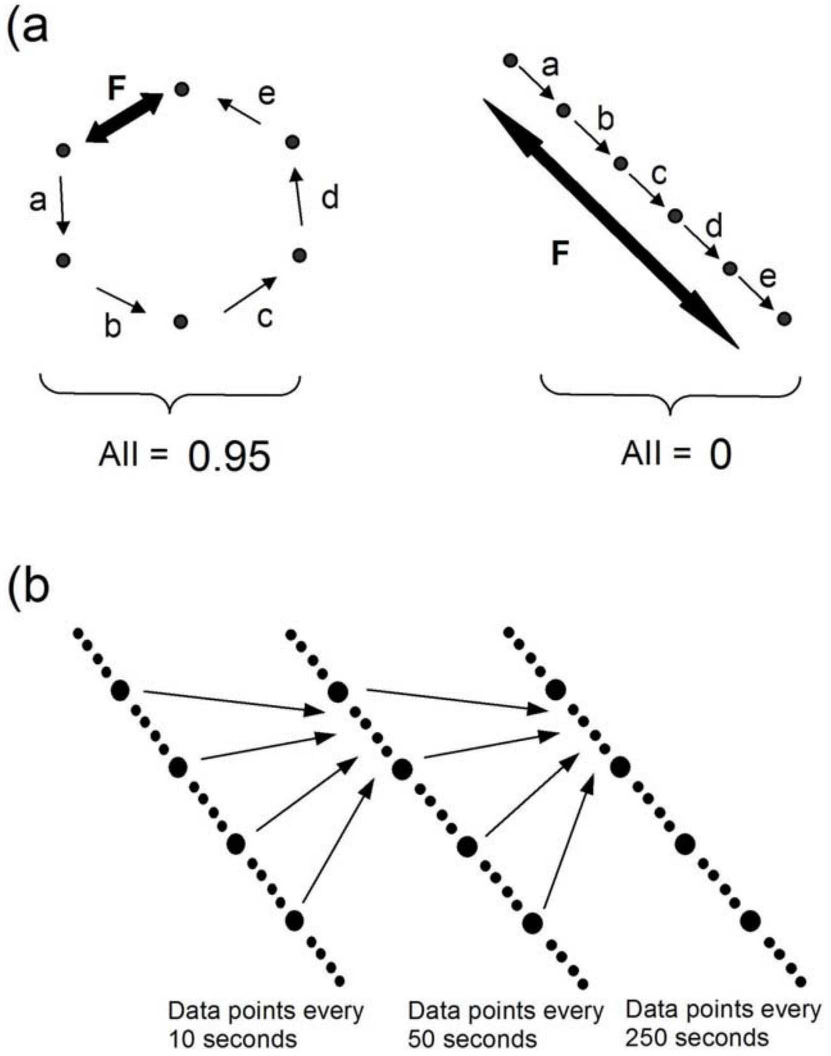


Figure 6.1: (a) Calculation of the Area-Interest-Index (AII) over six successive points illustrating concentrated movement in a small area (left) and highly directional movement (right). (b) Reduction of the number of data points allows the calculation of the AII over increasing timescales (from left to right).

6.4 RESULTS

During the 16 day foraging trip the sea lion made 2163 dives, of which the majority were square (U-shape) dives. From Punta Norte the animal headed eastward towards the shelf break, turning north just before reaching the 100 m depth contour, and finally turning south-west on return to the colony (Figure 6.2). The AII was highly variable, but an inverse polynomial curve fit through the means of each time interval showed that the index increased over time reaching a maximum at about five days into the trip and then declining again towards the end of the trip (Figure 6.3). AII values less than 0.2 were found in the first 10% and the last 25% of the trip with the middle part showing greater AII values.

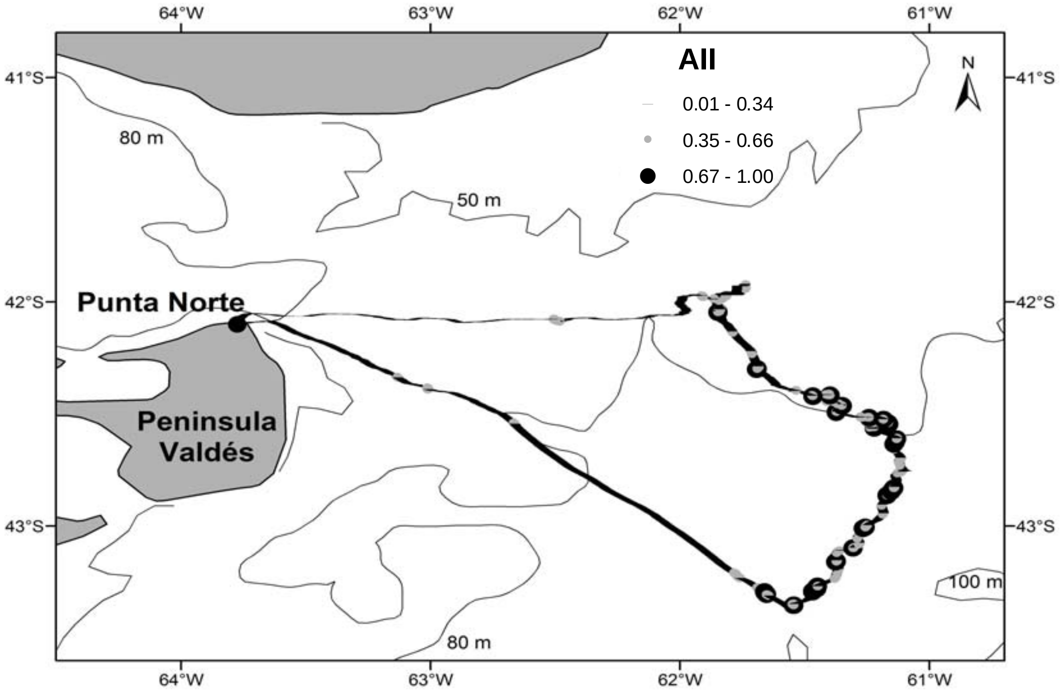


Figure 6.2: Map showing the route of the foraging trip performed by a male South American sea lion. For each dive only one AII value (corresponding to the start time of the dive) is depicted. The AII was calculated over five successive points with only every tenth data point being used in the calculation.

A selection of individual dives from three different parts of the foraging trip is shown in figures 6.4 – 6.6. All 2-d time-depth profiles are similar in being U-shaped and differing only in maximum depths attained. The time-AII profiles, on the other hand, show considerable differences between these dives. The differences become even more apparent in the three-dimensional presentations of these dives.

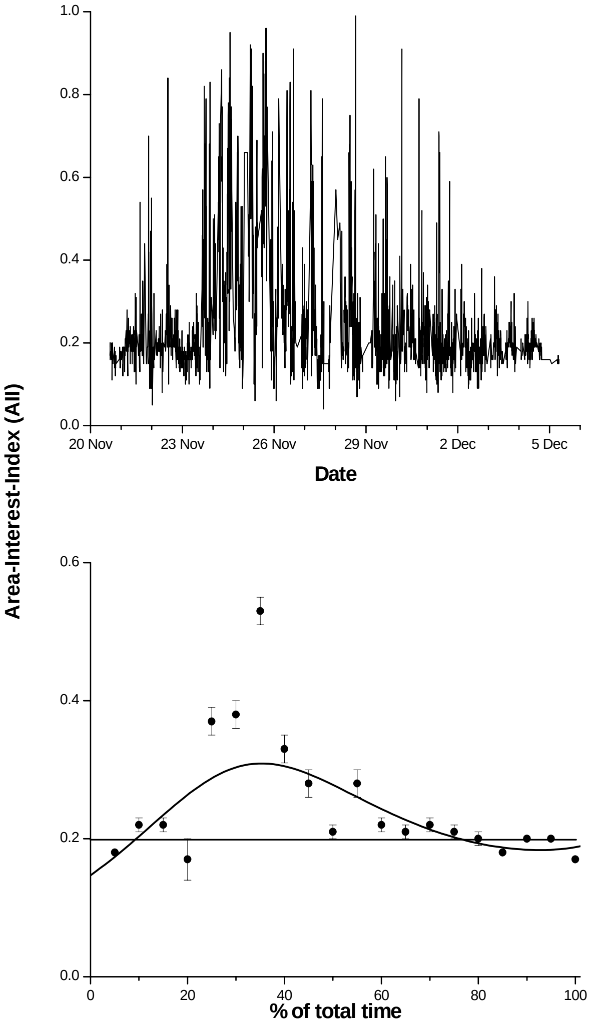


Figure 6.3: The change in Area-Interest-Index (AII) over the course of the complete foraging trip (above) and AII means for time intervals (each covering 5% of total time) with an inverse polynomial curve fit ($y = 1/(6.8017923-0.2313366*x+0.0045242*x^2-0.0000024*x^3)$, $r^2 = 0.5$, below).

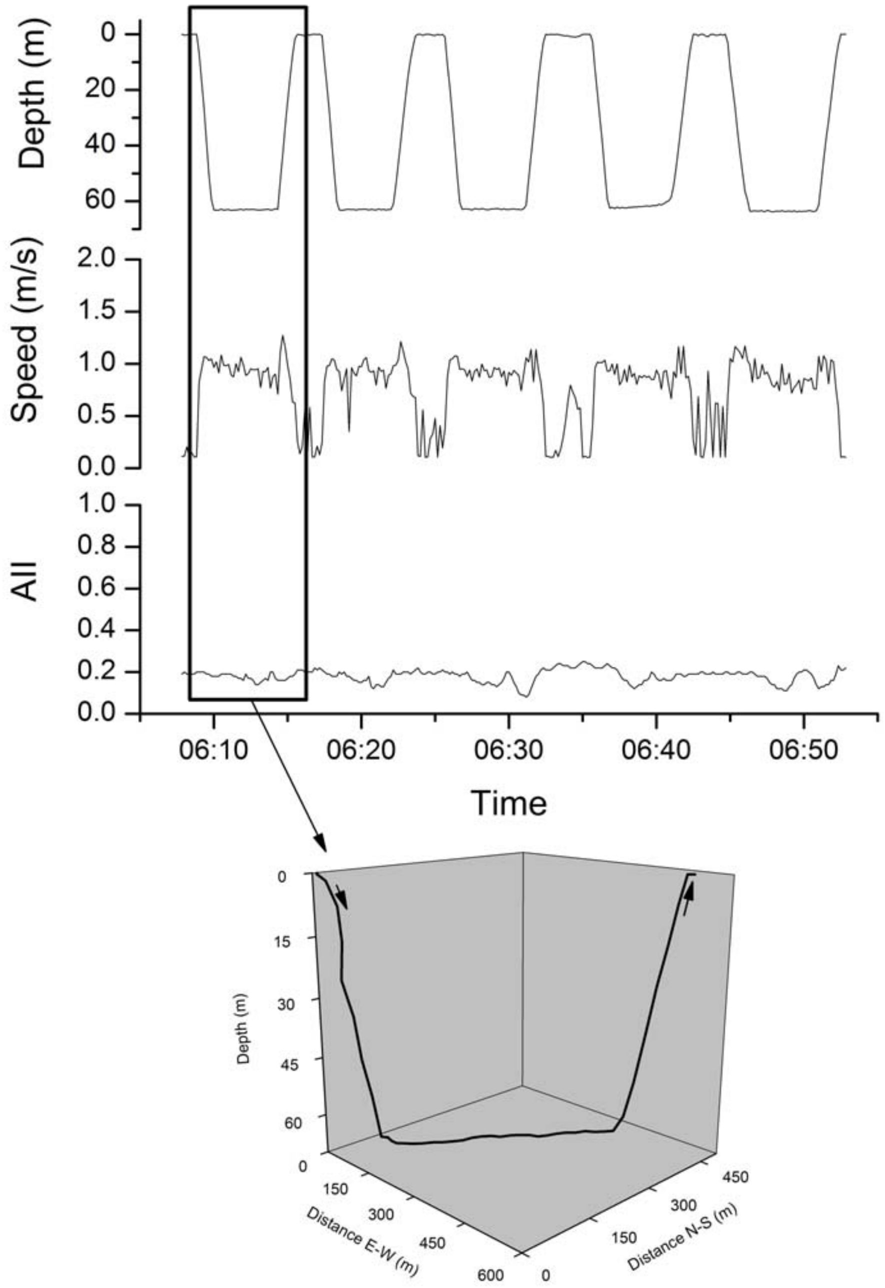


Figure 6.4: Example of dives from the beginning of the foraging trip with relatively constant speed throughout the dives and low AII values. The three-dimensional dive path of the framed dive is depicted below.

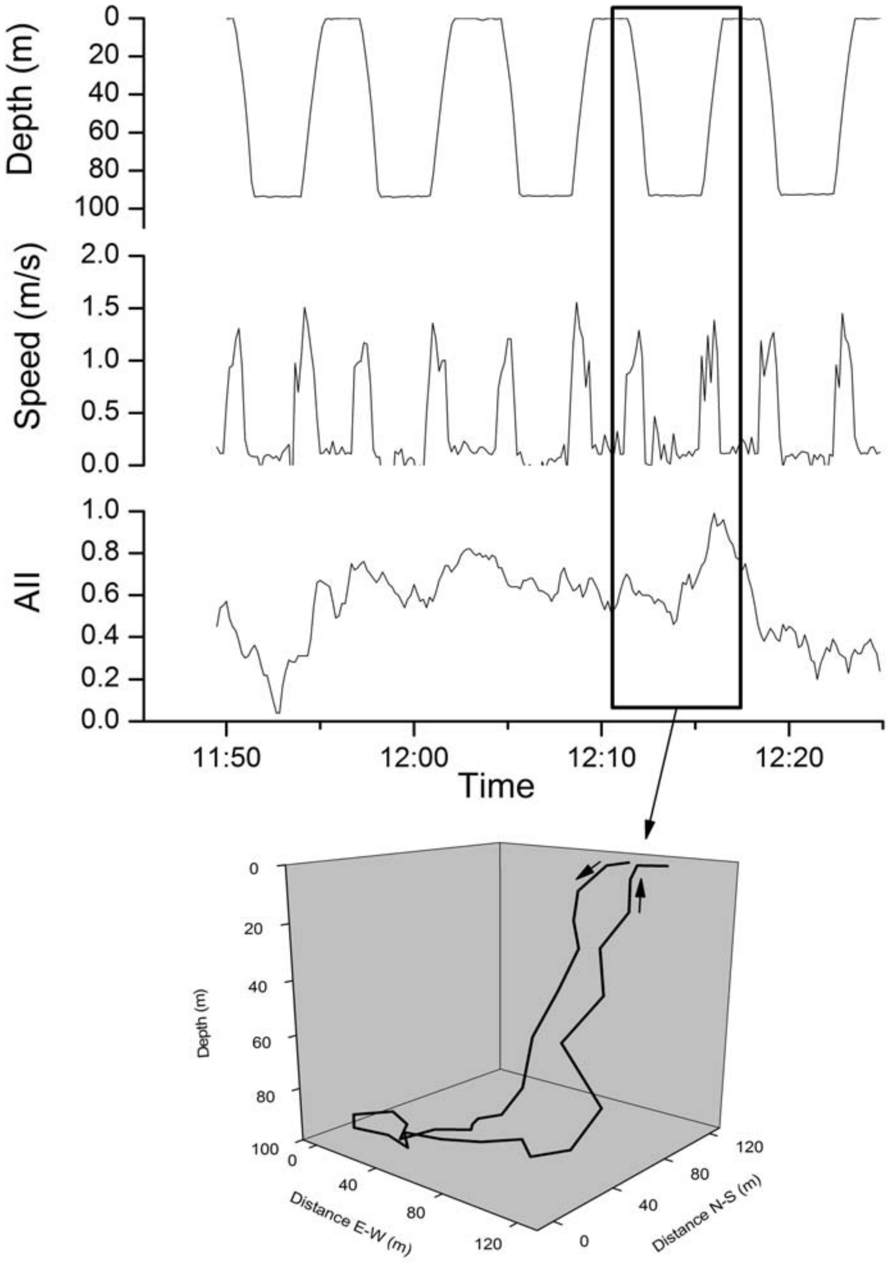


Figure 6.5: Example of dives from the middle part of the foraging trip with slow speed throughout the dives and variable AII values. The three-dimensional dive path of the framed dive is depicted below.

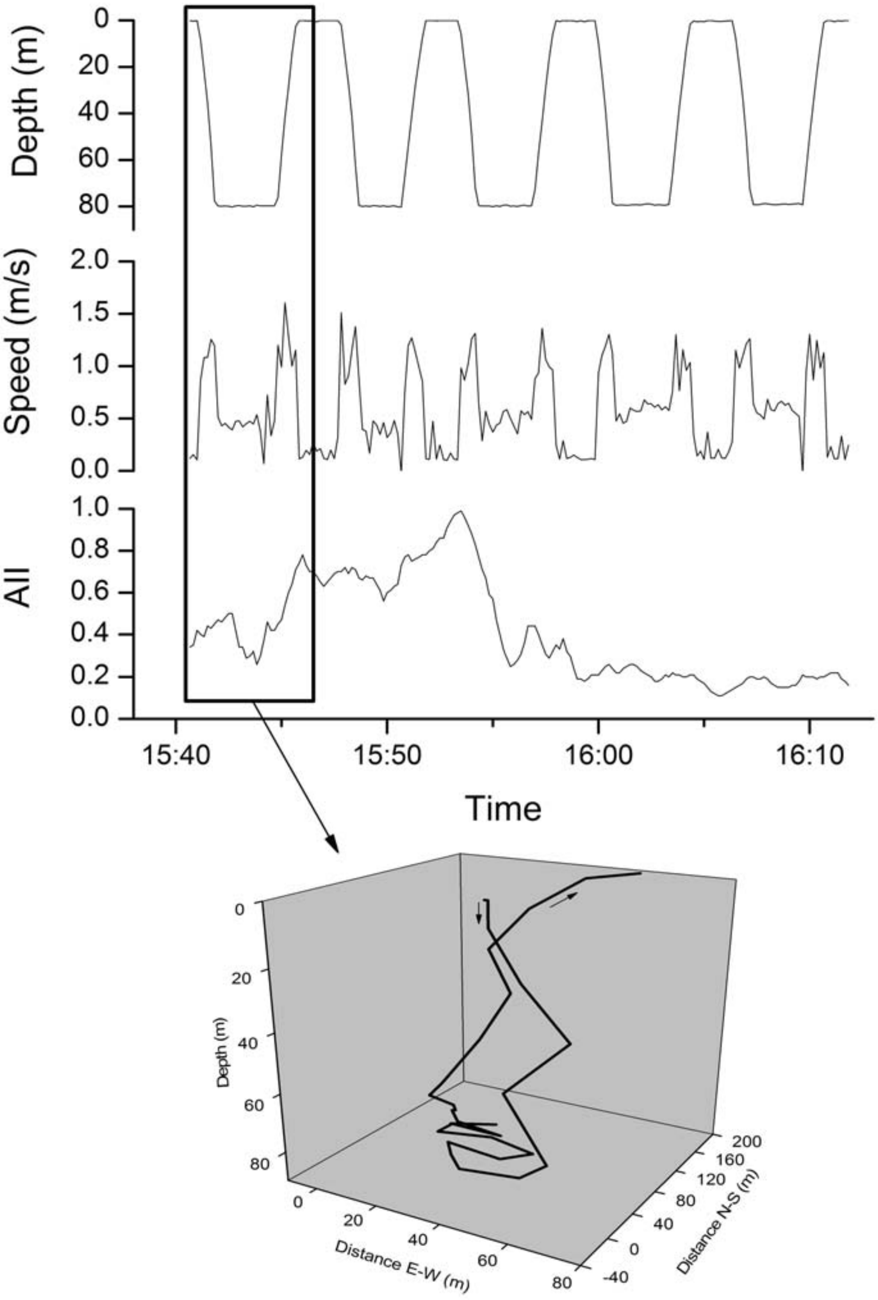


Figure 6.6: Example of dives from the middle part of the foraging trip with variable speed and AII values throughout the dives. The three-dimensional dive path of the framed dive is depicted below. Note the convoluted path in the bottom phase of the dive.

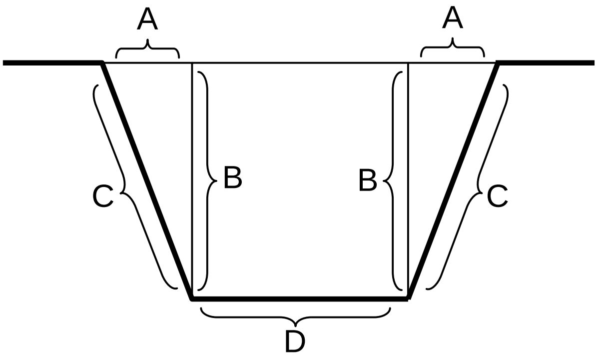
The first dive, taken from the beginning of the trip, has a low AII value of around 0.2 and shows very directional movement through all phases of the dive with a relatively constant, high speed (Figure 6.4). The two dives with higher AII values from the middle part of the trip (Figures 6.5 and 6.6) are much less directional in all phases of the dive. The last dive shows extremely convoluted movements during the bottom phase (Figure 6.6). In the latter two dives the speed during the bottom phase is much slower and more variable than in the first dive.

6.5 DISCUSSION

The results of this study highlight the advantage of incorporating information on three-dimensional behavior and movements in the determination of animal activity at sea and the association of these activities with specific areas. The sea lion in this study foraged on the Patagonian shelf, as has been shown for other males from Peninsula Valdés (Campagna *et al*. 2001; unpubl. data, chapter 3). The combination of position and Area-Interest-Index shows that only the middle part of the trip (in terms of distance covered) is characterized by consistently high AII values. Both the outward and inward legs of the trip show mainly low AII values (indicative of directional movement), but each covers approximately the same distance as the middle part, suggesting that the sea lion employs a strategy of comparatively fast and directional travel to foraging grounds in order to maximize the time available for foraging. This division of time at sea into distinct travel and foraging phases has also been noted in southern elephant seals (*Mirounga leonina*) (McConnell & Fedak 1996) and Antarctic fur seals (*Arctocephalus gazella*) (Bonadonna *et al*. 2000). The travel function of these parts of the trip is further supported by inspection of individual three-dimensional dive profiles. During these apparent travel dives the animal shows very straight movements during all phases of the dive, with only minor changes in speed during the entire dive. The reduction in speed at the surface does not necessarily reflect the actual swim speed of the animal, as the device was located on the sea lion´s head and therefore was not able to measure speed at the surface. In addition, the location of the device led to a high variability in speed measurements, as movements of the head do not necessarily reflect movements of the body. Therefore the measured speed might not always correspond to the actual swim speed although the overall changes in speed are assumed to be generally correct.

High AII values are a reflection of localized movements and thus depict areas that are of particular interest to the animal. For the South American sea lion, these areas are most likely foraging spots. Again, the three-dimensional dive profiles support this as the observed movements, especially during the bottom phase, can be highly convoluted. This suggests that the animal dives down to the bottom (at approximately the same speed as during travel dives) and then slows down in order to search for prey. The slow speed supports earlier studies which showed that South American sea lions mainly feed on benthic-demersal prey (George-Nascimiento *et al*. 1985; Koen Alonso *et al*. 1999). However, as the sampling interval increases the probability of recording short events such as speed bursts during pursuit of fast-moving prey will decrease (see Ropert-Coudert & Wilson 2004 for a discussion of the errors involved in this). Thus, data logging devices sampling at high frequencies would be beneficial for a detailed study of the pursuit and capture of prey.

The time-depth profiles in combination with the AII imply that the sea lion at least partially performs square dives while traveling. Because the movement during a dive can be divided into a horizontal and a vertical component, the most efficient strategy for travel dives in which the horizontal component is to be maximized would be to make shallow parabolic dives as observed in e.g. penguins (Wilson 1995). For a constant dive duration the horizontal distance traveled will decrease



$$\text{Horizontal travel efficiency} = \frac{(2 \times A) + D}{(2 \times C) + D}$$

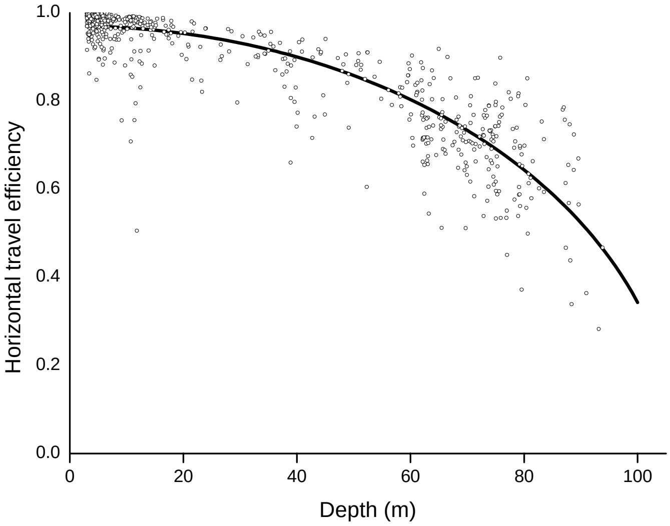


Figure 6.7: Calculation of the horizontal travel efficiency of a dive (above) where C and D are the actual distances traveled (including the vertical component), A is the horizontal distance covered during the descent and ascent phases, and B is the depth of the dive. Actual data from the trip made by the sea lion are given below.

with increasing depth, as a greater proportion of the dive is allocated to the vertical component of the movement. This can be illustrated by calculating the horizontal travel efficiency, which is the horizontal distance actually traveled divided by the total distance traveled, including the vertical component (Figure 6.7). As the vertical component increases with depth, the horizontal efficiency decreases because the horizontal movement along the bottom becomes a smaller fraction of the total movement. Such a reduction in efficiency not only leads to a loss of time for the animal but also to an apparently unnecessary expenditure of energy. However, swimming along the bottom may confer advantages that cannot be easily measured. It may allow the animal to feed on an opportunistic basis if prey is encountered which could be of particular importance after long periods of fasting on land when the foraging grounds are far from land. In addition, if a sea lion is close to the seabed it may reduce the risk of being detected by predators such as sharks, as these often approach and attack their prey from below and behind (Tricas & McCosker 1984). Ultimately, however, the possible advantages of swimming along the bottom will be eventually limited by the animals´ diving capacity and the bathymetry.

In conclusion, the analysis of a sea lion foraging trip using an index of activity showed, that in terms of distance covered, the major part of the trip was spent traveling. However, more than half the time was spent performing more localized movements at lower speed, suggesting foraging activity. This is supported by the three-dimensional dive profiles which reveal substantial differences in movements during travel and foraging dives. The obtained results emphasize that incorporation of three-dimensional data on movements is particularly useful for determining activity of animals at sea as well as inferring the function of different dive types.

6.6 *ACKNOWLEDGEMENTS*

This study was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. The help of M. Uhart, B. Raphael, P. Calle and D. A. Albareda with the anesthesia of the sea lions, and of V. Ramos and P. Ledesma in recovering the dead-reckoners is gratefully acknowledged. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina.

6.7 *REFERENCES*

Bonadonna, F., Lea, M.-A. & Guinet, C. (2000) Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. *Polar Biology* **23**, 149-159.

Campagna, C., Werner, R., Karesh, W., Marín, M.R., Koontz, F., Cook, R. & Koontz, C. (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *Journal of Zoology, London* **257**, 205-220.

George-Nascimento, M., Bustamante, R. & Oyarzun, C. (1985) Feeding ecology of the South American sea lion *Otaria flavescens*: food content and selectivity. *Marine Ecology Progress Series* **21**, 135-143.

Harcourt, R.G., Hindell, M.A., Bell, D.G. & Waas, J.R. (2000) Three-dimensional dive profiles of free-ranging Weddell seals. *Polar Biology* **23**, 479-487.

Hindell, M.A., Harcourt, R., Waas, J.R. & Thompson, D. (2002) Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* **242**, 275-284.

Koen Alonso, M., Crespo, E.A., Pedraza, S.N., García, N.A. & Coscarella, M.A. (1999) Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin* **98**, 250-263.

McConnell, B.J. & Fedak, M. (1996) Movements of southern elephant seals. *Canadian Journal of Zoology* **74**, 1485-1496.

Mitani, Y., Sato, K., Ito, S., Cameron, M.F., Siniff, D.B. & Naito, Y. (2003) A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology* **26**, 311-317.

Ropert-Coudert, Y. & Wilson, R.P. (2004) Subjectivity in bio-logging science: do logged data mislead? *Memoirs of National Institute of Polar Research*, Special Issue **58**, 23-33.

Tricas, T.C. & McCosker, J.E. (1984) Predatory behavior of the white shark, *Charcharodon carcharias*, with notes on its biology. *Proceedings of the California Academy of Sciences* **14**, 221-238.

Werner, R. & Campagna, C. (1995) Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Canadian Journal of Zoology* **73**, 1975-1982.

Wilson, R.P. (1995) The foraging ecology of penguins. *Penguins* (ed T. Williams), pp. 81-106. University Press, Oxford, UK.

CONCLUSIONS

The present study succeeded in elucidating several aspects of the foraging ecology of South American sea lions from Patagonia by using different telemetry devices. Despite the comparatively low number of animals equipped it revealed an immense amount of information on particularly male sea lions. Information that not only confirmed previous assumptions about sex segregation, but also shed light on the extensive spatial use of the Patagonian shelf by male sea lions. Importantly, it provided the first diving information from any male sea lion.

The information on sea lion movements in conjunction with available diving data and information on local bathymetry revealed that both male and female sea lions predominantly use a benthic foraging strategy while at sea. However, the foraging locations differed substantially, with males moving up to several hundred kilometres toward the shelf break and females being restricted to forage in coastal areas – at least during early lactation. The ultimate reasons for this segregation, however, still remain to be revealed.

The strong site fidelity of male sea lions outside the breeding season provided an excellent opportunity for animal "re-capture" and thus permitted the use of data loggers. The very detailed information recorded by these devices not only showed differential dive efficiencies in males and females but also elucidated important aspects on three-dimensional diving and foraging behaviour. Unfortunately, the memory of these devices was limited and thus only a restricted amount of data could be recorded. However, within the last few months a new generation of dead reckoners have become available with a memory four times as large. Not only would these devices increase the time over which data could be recorded, but the recording could also occur at higher sampling frequencies, thereby increasing the amount of detail that can be extracted from the data.

As is usually is the case when work is done on a species which has not been under investigation before, common methodologies cannot simply be transferred but need to be specifically adapted to the new study animal. This was also the case with the male sea lions in the present study. Because of their size they could not be captured by hand like females, and in order to avoid a second both risky and expensive chemical immobilisation of these animals when recovering the devices, new methodologies had to be invented and tested. Unfortunately, these tests can often only be carried out in the wild, with the risk of losing both instruments and time before proper data can be collected. The new release-mechanism that was developed in this study worked very well, and, with minor modifications, will become an effective means of recovering telemetry devices, not only for South American sea lions.

To conclude, this study provided a framework on the foraging ecology of South American sea lions from Peninsula Valdés and revealed some substantial differences between male and female sea lions as well as interesting patterns of space use on the Patagonian shelf. The information obtained did answer many questions, but at the same time it gave rise to even more new questions that now need to be addressed. One aspect that deserves particular attention is the change of foraging ranges with season (as increased age and independence of pups and juveniles are very likely to change the restrictions on movements imposed on females). This would not only provide additional information on potential competition with fisheries, as target areas move throughout the year, but also shed (more) light on the ultimate reasons of the observed segregation of foraging areas between males and females. Measurement of jaw angle, and thus feeding activity, in combination with detailed information on diving behaviour is a new methodology that can substantially increase the existing knowledge on foraging and hunting behaviour.

SUMMARY

Most studies on the foraging ecology of otariids have been done on females, as these are much smaller than males and thus easier to handle, but also because they are easy to relocate after instrument deployment as they invariably return to their pups on shore. Males, on the other hand, are generally much larger and not restricted in their movements outside the breeding season. This makes working with them very difficult but they are important study subjects as the large dimorphism in otariids suggests substantial differences in both behaviour and ecology of males and females.

The aim of this study was to elucidate the foraging ecology of South American sea lions (*Otaria flavescens*) from Patagonia. Special attention was given to male sea lions as almost nothing was known about their behaviour at sea. Field work was conducted at two sites, Punta Buenos Aires and Punta Norte, both located on Peninsula Valdés, Argentina.

The first part of the study was aimed at determining the movements at sea of sub-adult males after the breeding season. This was done using satellite tags glued to the top of the sea lions´ heads. The information obtained revealed that the majority of the males moved eastwards on their foraging trips, suggesting that foraging grounds may be associated with the shelf break and the associated, highly productive front. In addition, the data revealed a strong site fidelity in males as they consistently returned to the same colony once foraging activity commenced. Foraging trips had a mean duration of 8.4 days of which about two days could be

assigned to foraging based on a reduction in mean speed of translocation from 1.35 m/s during the travel phase to 0.77 m/s when foraging.

The obtained results on foraging cycles were used to model the energy budgets of male sea lions from all Patagonia. Energy budgets were highly sensitive to changes in time spent at sea, which, of course, is related to the location of suitable foraging grounds. Because of significant differences in basal metabolic rate on land and at sea, sea lions incur substantial increases in energy expenditure when distances to foraging grounds - and thus total time at sea – increase. Such an increase can be counteracted by either increasing the time spent in the foraging area or by increasing the putative rate of energy acquisition in the foraging area, which was estimated to be 7.0 kg/h for a typical foraging cycle. The total prey consumption for all sub-adult and adult males from Patagonia was estimated to be in the range 24,000 to 36,000 tons/annum, with values being highly dependent on energetic content of the chosen prey type.

In order to obtain information on the diving behaviour by using data loggers, a new non-electronic release mechanism was developed, thus providing the obligatory method for instrument recovery. The mechanism consisted of a metal base plate onto which a housing – including the data logger – is attached and held in place via a small resin disc. To release the housing, an air gun was used to shoot at the disc so that it shattered. Then the housing could simply be lifted off the base plate. This method turned out to be extremely well suited for South American sea lions, as they allowed an approach to within a few meters and the most marked reaction to the shooting was to lift the head.

The information obtained on the diving behaviour of male sea lions was compared to existing dive data from females from the same rookery to determine whether differential dive efficiencies (time spent in the bottom phase of a dive divided by the total duration of the dive cycle) of the two sexes could explain the observed segregation of foraging areas. Almost all dive parameters, such as depth distribution, duration of dives and individual dive phases, surface intervals, and vertical velocities, differed significantly between males and females as would be expected based on allometric relationships. The resulting dive efficiency showed that females were more efficient at shallow depths and males at greater depths, with the division point occurring at approximately 45 m. Even though no specific maximum efficiency could be determined for the observed range of depths, the observed distribution of dive depths is in accord with the observed difference in depth utilization between males and females.

Data from the dead reckoners were also used to reconstruct the three-dimensional route of a foraging trip and derive an area-interest-index which reflects the directionality of movement. Based on this index the foraging trip could be divided into three clearly separate phases: an outward leg during which the animal travels in a highly directional manner to the foraging ground, a middle part during which the animal performs more localized movements corresponding with foraging, and an inward leg also characterized by highly directional movement towards the haul-out site. The majority of all dives of this trip were u-shaped dives, which are generally believed to be foraging dives. The three-dimensional dive paths and corresponding information on swim speed, however, clearly showed that the u-shaped dives performed by this sea lion serve more than just one (foraging) function. Apparent travel dives showed a highly directional movement and almost constant swim speed throughout the entire dive cycle. This contrasts with dives where the animal descends and ascends at comparatively high speeds but performs very convoluted movements at low speeds during the bottom phase. The latter dive type is suggested to represent searching behaviour in the foraging area. The results provide clear evidence that u-shaped dives are not necessarily just limited to foraging activity, but that they also may be used for other purposes such as travelling.

This study provides a wide range of information regarding the foraging ecology of South American sea lions, but it also highlights many areas in which further work is not only desirable but also essential in terms of conservation of the species, exploitation of marine resources, and potential interaction with fisheries.

ZUSAMMENFASSUNG

Die meisten Untersuchungen zur Ernährungsökologie von Otariiden wurden an weiblichen Tieren durchgeführt, da diese deutlich kleiner und damit leichter zu handhaben sind. Durch die stetige Rückkehr zu ihren Jungtieren an Land sind sie auch wesentlich leichter wiederzufinden, was die Rückgewinnung von Geräten sehr erleichtert. Die Männchen sind generell viel größer und besitzen eine uneingeschränkte Bewegungsfreiheit außerhalb der Paarungszeit. Dieser Aspekt macht sie zu äußerst schwierigen, aber auch sehr wichtigen Forschungsobjekten, da der große geschlechtsspezifische Dimorphismus bei den Otariiden beträchtliche Unterschiede im Verhalten sowie in der Ökologie von Männchen und Weibchen vermuten läßt.

Das Ziel dieses Forschungsvorhabens war die Untersuchung der Ernährungsökologie von Südamerikanischen Seelöwen (*Otaria flavescens*) in Patagonien. Besondere Aufmerksamkeit wurde den Männchen gewidmet, da ihr Verhalten auf See fast gänzlich unbekannt war. Die Freilandarbeiten wurden an zwei Orten, Punta Buenos Aires und Punta Norte, beide auf der Halbinsel Valdés in Argentinien, durchgeführt.

Der erste Teil der Untersuchung diente der Bestimmung von Positionen und Bewegungen von sub-adulten Männchen auf See nach der Paarungszeit. Zu diesem Zweck wurden Satellitensender auf die Köpfe der Seelöwen geklebt. Die erhaltenen Informationen zeigen, daß die meisten Männchen auf ihren Beutezügen nach Osten schwammen, was vermuten läßt, daß die Nahrungsgründe der männlichen Seelöwen mit der Schelfkante und der dazugehörigen, äußerst

produktiven Front in Zusammenhang stehen. Darüber hinaus enthüllten die Daten eine ausgeprägte Ortstreue, bei der die Männchen konsequent zu ihren ausgewählten Ruheplätzen zurückkehrten. Die durchschnittliche Dauer von Beutezügen beträgt 8.4 Tage. Zwei von diesen Tagen weisen eine Reduktion in der Reisegeschwindigkeit von 1.35 m/s auf 0.77 m/s auf und werden daher als Aufenthalt im Freßgebiet angesehen.

Die Satellitendaten, in Verbindung mit bioenergetischen Parametern von anderen Seelöwenarten, wurden zudem angewandt, um die Energiebalance männlicher Seelöwen in Patagonien zu modellieren. Die Analyse ergab, daß die Energiebalance äußerst sensibel gegenüber Änderungen in der auf See verbrachten Zeit ist, welche natürlich direkt in Relation zu der Entfernung von geeigneten Nahrungsgründen steht. Da die Stoffwechselrate auf See wesentlich höher ist als an Land, führt dies zu einem beträchtlichen Anstieg im Energieverbrauch mit zunehmender Distanz zu den Nahrungsgründen und damit der insgesamt auf See verbrachten Zeit. Dieser erhöhte Energieverbrauch kann durch einen Anstieg der in dem Freßgebiet verbrachten Zeit oder durch eine Erhöhung der mutmaßlichen Freßrate (7.0 kg/h für einen durchschnittlichen Nahrungszyklus (die Zeit eines Beutezuges sowie die danach an Land verbrachte Zeit)) kompensiert werden. Die benötigte Gesamtmenge von Beutetieren für alle sub-adulten und adulten männlichen Seelöwen in Patagonien wurde auf 24,000 bis 36,000 Tonnen pro Jahr geschätzt. Dieser Wert war jedoch stark abhängig von dem jeweiligen Energiewert der gewählten Beutetiere.

Um Informationen zu dem Tauchverhalten mittels Datenspeicher zu erlangen wurde ein neuartiger nicht-elektronischer Auslöse-Mechanismus entwickelt um die Datenspeicher zurückzugewinnen. Der Mechanismus bestand aus einer Basisplatte aus Metall und einem Gehäuse in dem sich der Datenspeicher befand. Diese beiden Teile wurden von einer kleinen Scheibe aus Kunstharz zusammengehalten. Um das Gehäuse von der Basisplatte zu lösen wurde die Scheibe mit einem Luftgewehr zerschossen. Danach konnte das Gehäuse problemlos mit einem an einer langen Stange befestigten Haken von der Basisplatte abgehoben werden oder es fiel von selbst runter wenn die Tiere sich bewegten. Die Methode erwies sich als äußerst geeignet für Südamerikanische Seelöwen, da man sich ihnen bis auf wenige Meter nähern kann und sie auf die Schüsse höchstens mit dem Heben des Kopfes reagierten.

Die gesammelten Informationen zu dem Tauchverhalten der männlichen Seelöwen wurde mit bereits vorhandenen Daten weiblicher Seelöwen von der gleichen Kolonie verglichen, um herauszufinden ob die Taucheffizienz (die in der Bodenphase verbrachte Zeit geteilt durch die Gesamtdauer des Tauchzyklus (Zeit unter Wasser während eines Tauchganges sowie die darauf folgende Zeit an der Oberfläche)) geschlechtsspezifische Unterschiede aufweist und somit eine Erklärung für die vorhandene räumliche Trennung der Nahrungsgründe sein kann. Fast alle Tauchparameter wie Frequenzverteilung der Tiefe, Gesamttauchdauer sowie Dauer der einzelnen Tauchphasen, Oberflächenintervall und Vertikalgeschwindigkeit wiesen signifikante Unterschiede zwischen den beiden Geschlechtern auf. Diese Unterschiede waren aufgrund der Größenunterschiede zwischen Männchen und Weibchen zu erwarten. Die aus den Tauchparametern resultierende Taucheffizienz zeigte, daß die Weibchen in Tiefen bis zu ca. 45 m effizienter waren als die Männchen, die in Tiefen über ca. 45 m eine höhere Effizienz aufwiesen. Obwohl für die erfaßten Tiefenbereiche keine Maximal-Effizienz bestimmt werden konnte, stimmte die aufgezeichnete Tiefenverteilung mit den geschlechtspezifischen Unterschieden in der Taucheffizienz überein.

Die von den Fahrtenschreibern gewonnenen Daten wurden zudem benutzt, um die drei-dimensionale Route eines Beutezuges zu rekonstruieren, und daraus einen „Area-Interest-Index“ abzuleiten der die Direktionalität der Bewegungen wiederspiegelt. Basierend auf diesem Index konnte der gesamte Beutezug in drei klar getrennte Phasen geteilt werden: einen auswärtsgerichteten Teil, in dem der Seelöwe auf direktem Wege zu den Nahrungsgründen schwamm, einen mittleren Teil, in dem das Tier mehr lokale Bewegungen ausführte, welche mit dem Tauchverhalten während der Nahrungssuche übereinstimmten, und einen letzten Teil, in dem der Seelöwe wieder eine sehr gerichtete Bewegung zurück zum Ausgangspunkt zeigte. Die meisten Tauchgänge waren U-förmige Tauchgänge. Diese werden generell mit der Nahrungssuche assoziiert. Die drei-dimensionalen Tauchpfade und die aufgezeichneten Schwimmgeschwindigkeiten zeigen aber sehr deutlich, daß die U-förmigen Tauchgänge der Seelöwen nicht nur der Nahrungssuche sondern auch anderen Verhaltensweisen zugeordnet werden konnten. So konnten zum Beispiel Reisetauchgänge identifiziert werden, die sehr direktionale Bewegungen und fast konstante Schwimmgeschwindigkeiten über den gesamten Tauchgang hinweg aufzeigten. Im Gegensatz hierzu standen andere Tauchgänge, in denen der Seelöwe mit relativ hoher Geschwindigkeit ab- und auftauchte, aber in der Bodenphase sehr gewundene Bewegungen bei langsamer Geschwindigkeit durchführte.

Diese Studie lieferte eine Menge an verschiedenen neuen Informationen zu der Ernährungsökologie von Südamerikanischen Seelöwen, aber sie enthüllte auch viele Bereiche, in denen weitere Untersuchungen nicht nur wünschenswert, sondern auch unbedingt erforderlich sind, wenn es um den Schutz der Art, die Nutzung von marinen Ressourcen sowie potentielle Interaktionen mit der Fischerei geht.

ACKNOWLEDGEMENTS

For the past two years in which I have worked on this dissertation, I collected a wide range of experiences. Many of them were good, some of them were sad, and a few of them I definitely could have lived without. But nonetheless, all these experiences were part of my life and without them I would not have become the person that I am today. The many people I met through my work all taught me something, sometimes through explanations and discussions, and sometimes just through their behaviour and attitude, and I am grateful to all of them.

A very special and big “Thank you” goes to my supervisor Rory Wilson for making this project possible, for his advice and guidance and for always being willing to discuss and exchange ideas. But more importantly, he showed me by example how to make the best of a situation, especially when things do not go as planned (which usually is the case in this field), and also what great things can be achieved with a little creativity. Thank you!

I have to admit that I never before experienced such a team spirit and team work as in the working group at the Institut für Meereskunde, now the Leibniz….. (you know what I mean!). I would like to thank Niko, who was always willing to help with the preparation of devices, to explain the - at times obscure - behaviour of loggers and software, and to discuss and develop ideas. Mandy, thank you for the great companionship and all the help and assistance over the past two years. I am also grateful to the rest of the working group for all the interesting discussions and lots of chocolate: Sandra H., Antonia, Ilka, Sandra S., Jan, Marion and D. Adelung.

Special thanks also go to Prof. Spindler for being willing to take on all the formalities belonging to this dissertation.

The study would not have been possible without the development and construction of the devices carried out by Jens-Uwe Voigt, as well as the inventiveness of G. Dorn in turning an idea into a finished product. Jörg Blasey provided invaluable and instant assistance and support whenever computer problems came up.

This project was greatly supported by the Wildlife Conservation Society who `sponsored´ both veterinarians and equipment for the anaesthesia of the sea lions. Special thanks to Marcy, Bonnie, Paul, and Diego, who all did a great job under sometimes adverse conditions. The help of the Guardafaunas from Peninsula Valdés is gratefully acknowledged. Special thanks go to Pato and Valeria for their help in recovering my devices, and to Valeria also for the great company during my stay in Punta Norte.

PUBLIKATIONEN

Teile der vorliegenden Arbeit wurden mit Genehmigung des Dekans der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel bereits zur Veröffentlichung eingereicht:

Müller, G., Liebsch, N. & Wilson, R.P. (In press) A new shot a release-mechanism for devices on free-living animals. *Wildlife Society Bulletin.*

Müller, G., Wilson, R.P., Campagna, C. & Quintana, F. (subm) Lunch off the shelf: Foraging behaviour of South American sea lions (*Otaria flavescens*). *Marine Ecology Progress Series.*

Müller, G., Wilson, R.P., Quintana, F. & Campagna, C. (subm) The cost of commuting: Foraging cycles and their effect on energy budgets of South American sea lions. *Marine Ecology Progress Series.*

Müller, G., Wilson, R.P., Quintana, F. & Campagna, C. (subm) Three-dimensional diving behavior of a South American sea lion (*Otaria flavescens*). *Proceedings of the 22nd Wakefield Symposium.*

Müller, G., Wilson, R.P., Quintana, F., Werner, R. & Campagna, C. (subm) Is bigger better? Sexual dimorphism and diving behaviour in South American sea lions. *Marine Ecology Progress Series.*

GABRIELE MÜLLER

Geboren am: 29. März 1975 in Rendsburg
Staatsangehörigkeit: deutsch
Familienstand: ledig

1981 – 1989	Grund- und Realschule „Ejderskolen“ in Rendsburg
1989 – 1991	Realschule „Hjort-Lorenzen-Skolen“ in Schleswig, Realschulabschluss
1991 – 1994	Gymnasium „Duborg Skolen“ in Flensburg, Abitur
1994 – 1997	Grundstudium Biologie an der „Århus Universitet“ in Århus, Dänemark
1997 – 2000	Hauptstudium Biologie an der „Århus Universitet“ in Århus, Dänemark,
Dezember 2000	Diplom, Thema der Arbeit: „Effects of osmolality on oxygen binding properties of red blood cells and component Hbs from *Myxine glutinosa*: Water activity regulates oxygen binding”
2001: März – Aug.	Forschungsassistentin an der „Lighthouse Field Station“, University of Aberdeen, Cromarty, Schottland
Sept. 2001 – Aug. 2002	Vorbereitung und Planung der Dissertation, Angestellt bei Aqua-Nautic, Kiel
seit Sept. 2002	Arbeit an der Dissertation am Leibniz-Institut für Meereswissenschaften (ehemals Institut für Meereskunde) im Rahmen des DFG Projektes WI 1023/10-1 und -2

Erklärung

Hiermit erkläre ich, daß die vorliegende Dissertation nach Inhalt und Form – abgesehen von der Beratung durch meine wissenschaftlichen Lehrer – meine eigene Arbeit ist. Es wurden keine anderen als die angegebenen Hilfsmittel verwendet.

Die Arbeit hat weder ganz noch zum Teil zuvor einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegen.

Kiel, den 30. Oktober 2004