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RANGING AND DIVING BEHAVIOUR OF ADULT FEMALE SOUTHERN ELEPHANT SEALS FORM MARION ISLAND

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Ranging and diving behaviour of adult female southern elephant seals from Marion Island

by

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ABSTRACT

The diving and ranging behaviour of thirteen adult southern elephant seal, *Mirounga leonina*, postbreeding (n = 9) and postmoulting (n = 4) females from sub-Antarctic Marion Island (46°54′S 37°45′E) were recorded during their pelagic annual cycling of 1990 - 1994, using Geolocation-Time-depth Recorders. A total of 66 807 dives were categorized into seven distinct types which were hypothesized to serve as functional transit, exploratory and foraging dives. No benthic foraging dives were recorded. Dive depth and duration were positively correlated and both unimodal and bimodal in their frequency distributions. Extended surface intervals were more common during long journeys at sea and were probably associated with successful foraging. It is postulated that the seasonal and individual variation in the diving behaviour of females are related to their geographic locations and the abundance and behaviour of their prey. Movements were categorized into outbound transit, distant foraging and inbound transit phases. The relative frequency of foraging, exploratory and transit dive types, as well as the duration and location of the different phases of movement suggest two clearly different seasonal foraging strategies used by postbreeding and postmoulting females. Bathymetrical features could possibly provide cues to females at least during part of the journey, to reach distant foraging grounds. Postbreeding and postmoulting females foraged largely within inter-frontal zones. Diel differences in the depth of hypothesized foraging dives appear to be associated with concentrated foraging on vertically migrating prey. A homogeneous temperature layer at foraging depth seems to cause shifts in the diel patterns of prey dispersal, whereas a heterogeneous temperature layer appears to promote little difference in the diel patterns of migrating prey, thereby causing differences in the diel diving depth of foraging elephant seals. Elephant seals could be using changes in water temperature to predict the presence of prey when foraging at inter-frontal zones, away from readily locatable oceanic features where primary production is known to be high.

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CHAPTER 1

INTRODUCTION

The southern elephant seal, *Mirounga leonina*, is the world's largest phocid (King 1983). The harem males are usually 4.3 - 4.6 m in length and weigh 2 500 - 3 000 kg of which up to 40% is skin and blubber (Laws 1960). The females are smaller, between 2.4 - 3.0 m long and weigh 200 - 600 kg. Adult elephant seals are pelagic and only come ashore to breed and moult although immatures of both sexes often come ashore for short periods throughout the year (McCann 1980).

Southern elephant seals breed and moult on many sub-Antarctic islands during the austral spring and summer (Condy 1978 a, b). Adult breeding elephant seals on Marion Island are ashore for four months from August to November and after a sojourn at sea, they return for the moult haulout that peaks in January and February for females and males respectively. Juveniles haul out to moult in late November and December having been absent from the beaches during the breeding season. They again are ashore for a short period during winter, a haulout for which no specific function has been ascribed (Condy 1979). Adults moult within approximately 30 days and from May to August very few elephant seals occur on the islands, and are presumably feeding at sea (Condy 1979).

Population declines in southern elephant seals

The total world population of southern elephant seals in 1990 was estimated at 664 000 (Laws 1994). Of the three main populations, the South Georgia population (islands in the South Atlantic and the Peninsula Valdés, Argentina) account for 60% of the total; the Kerguelen populations (islands within the Southern Indian Ocean) 28%, and the Macquarie population (islands in the Southern Pacific Ocean) 12%. Between 1949 and 1990 some populations of southern elephant seals have either increased (Peninsula Valdés, Argentina by 150% from 1975 to 1992 - Vergani *et al.* 1987; Campagna & Lewis 1992); have probably remained stable after rapid recovery from exploitation (South Georgia, 15% owing to post-exploitation recovery of the male population); or have decreased dramatically at annual rates varying between 2.1% and 8% at different islands and over various periods.

Total percentage decreases since 1949 were estimated at 50% for Heard Island, 84% for Marion Island, 57% for Macquarie Island, 96% for Campbell Island and 93% for Signey Island (Laws 1994).

On the Crozet Archipelago, the Possession Island population showed a reduction in numbers of females ashore since 1966, with the decline being more rapid since 1983 as the number of breeding females decreased from 1 044 to 698 between 1980 and 1988 (Jouventin & Weimerskirch 1990). At Iles Kerguelen, elephant seals declined drastically during the 1970s and early 1980s (Pascal 1981; Van Aarde 1980), however, the population of breeding females had stabilized between 1984 and 1989 (Guinet *et al.* 1992). Rand (1962) estimated that the total southern elephant seal population of Marion Island at 12 817 in 1951. The population of southern elephant seals at Marion Island subsequently declined at a rate of 4.8% per annum (Bester & Wilkinson 1994) which gave an estimated total population of 2 009 in 1990, constituting a decline of 83.7% since 1951 and 48.5% since 1976 (Laws 1994). These differing numerical trends of elephant seal populations show that factors acting on the populations must be analysed on a regional basis. Furthermore, no factors operating on land have been identified to be responsible for the decline, and it would therefore appear that factors operating during the pelagic phase of the annual cycle, of subadult and adult females in particular, hold the key to the decline process (Bester & Wilkinson 1994).

Diving and ranging behaviour

Little is known about the distribution and diving behaviour of elephant seals at sea, where most of the individual's life is spent, and where feeding takes place (Le Boeuf *et al.* 1986). Distribution of prey in space and time may have an influence on the ecology and especially the feeding behaviour of predators. Information obtained through the use of recorders on marine vertebrates in monitoring behavioural activities could possibly improve knowledge of their diving patterns and abilities, but this can ultimately only be meaningful by including interpretations of data on prey distribution and abundance (Croxall *et al.* 1985). Attempts to explain the decline in several major breeding populations of southern elephant seals (Pascal 1986; Hindell & Burton 1987; Bester 1990; Wilkinson & Bester 1990; Hindell *et al.* 1994) were also hindered by the lack of basic ecological data.

There is strong suggestions that the elephant seal's dive pattern is set up by the habits of its prey (Le Boeuf *et al.* 1988), and therefore basic data on their dive patterns, movements and interactions with their oceanic environment could be linked to hydrographic features and the distribution of potential prey within the water column (Boyd & Arnbom 1991; McConnell *et al.* 1992a; McConnell & Fedak 1996).

Until recently the ranging behaviour of southern elephant seals has been derived entirely from chance sightings of marked animals (Bester 1989; Gales & Burton 1989; Hindell *et al.* 1991a). Consequently, remote sensing or recording devices had to be employed to discover the locations of the seals during the postmoulting and postbreeding periods at sea (Hindell *et al.* 1991a).

The development and testing of a geographic location time-depth recorder (GLTDR) during 1989 in the USA, to study the pelagic movements of northern elephant seals (DeLong *et al.* 1992), permitted investigations of the pelagic ranging behaviour of southern elephant seals in the sub-Antarctic waters in the Southern Indian Ocean, including those from Marion Island (Bester & Pansegrouw 1992; present study). Northern elephant seals were the first to be reported in making two migrations during a single year, their individual movements being the greatest yet recorded for a mammal (Stewart & DeLong 1995). For high resolution spatial data with which to interpret the behavioural data, specially designed satellite-linked data loggers, compatible with the Argos Satellite System (Argos 1989), have also been used to visualize the 3-dimensional movements of elephant seals moving over distances covering 2 600 km (McConnell *et al.* 1992a).

Due to the circumpolar distribution, mobility and diving capabilities of southern elephant seals which make it possible to travel great distances and reach great depths, it gives them the potential to have a major impact over an enormous range of habitats in the Southern Ocean (McConnell *et al.* 1992a). This year-round pattern of continuous, long, deep dives with only brief surface intervals explains why elephant seals' pelagic whereabouts and migrations have long been unknown (Stewart & DeLong 1995).

Food webs and potential prey of southern elephant seals

Edwards & Heap (1981) believe it is useful to think of the living resources of the Southern Ocean in terms of three broad levels of population: (1) species in the *low trophic levels*, which form the food base for species in higher trophic levels (e.g. zooplankton, particularly krill); (2) species at *intermediate trophic levels*, which prey on low trophic levels but are themselves subject to significant predation by the top trophic level (e.g., squid and fish); and (3) species at the *top trophic level*, which prey on levels (1) and (2) but are not themselves subject to significant natural predation (e.g., whales, seals and birds).

The food webs of the Southern Ocean reflects the fact that incoming energy from the sun, nutrients, bacteria, and phyto- and microplankton is the basis of all higher life in the sea (Laws 1985). Like most of the Antarctic life forms, the most important phytoplankton species are circumpolar in distribution. High values of nutrients, chlorophyll, and primary production are recorded at oceanic fronts (Lutjeharms *et al.* 1985), owing either to vertical upwelling or horizontal transport. In the Southern Ocean ecosystem, krill plays a key role in the conversion of plant biomass to animal biomass. Krill is the dominant herbivore at the base of the food web, and thus affects growth and survival of groups such as whales, seals, birds, fish and squid (Knox 1984, 1994).

Much of the dietary studies suggest that southern elephant seals feed mainly on squid (Laws 1977 a, b; Clarke & MacLeod 1982a, b; Rodhouse *et al.* 1992; Slip 1995), contributing 75% of all food taken, and that fish is mainly taken when the seals are in inshore water. Although analysing stomach contents of seals revealed high estimates of cephalopod remains, sources of bias could arise underestimating fish prey (Bigg & Fawcett 1985). However, Green & Burton (1993) found that difficulties arise in the collection of dietary samples of southern elephant seals (Macquarie and Heard Island populations) main foraging areas. Since most of their foraging areas were far from their natal haulout sites, it complicates the study of feeding ecology of this species in comparison with other Southern Ocean species. There is therefore still a need for data on the relative proportions of fish and cephalopods in the diet of southern elephant seals whilst they are actively feeding (Rodhouse *et al.* 1992).

Based on information from trawls, prey species of elephant seals are concentrated at depths exceeding 300 m in the Southern Ocean (Rodhouse & Clarke 1985, 1986; Rodhouse 1988) and below the cold sub-surface waters. Known fish prey species of northern elephant seals such as Pacific hake (Condit & Le Boeuf 1984) school in large numbers and migrate from deep waters during the day up to 200 - 400 m at night. Similarly, a diel change in the depth at which squid occurs in the Southern Ocean exists, squid becoming more abundant at shallow depths during the night than during the day (Rodhouse & Clarke 1986; Rodhouse 1988). This change could affect the diving behaviour of potential predators. Therefore the predator-prey interactions between southern elephant seals and their potential prey species, are clearly an important component of the Southern Ocean food web system (Rodhouse *et al.* 1992).

Distribution of prey

Information about where in the water column southern elephant seals feed may provide a valuable insight into the major distribution of their prey sources and potential interactions. All cephalopods in the diet of southern elephant seals are known to be found at, and to the south of the Antarctic Polar Front (APF), and extends to the Antarctic Continent although some of the squid species are found to the north of the APF (Rodhouse *et al.* 1992).

Although it is known that several species of Antarctic squid feed on krill (Marr 1962; Dell 1965; Nemoto *et al.* 1985), there is little information available on either the production or food consumption rates of squid. In addition, although knowledge of Antarctic squid diets is extremely limited (Okutani & Clarke 1985), it is reasonable to assume that they also feed to some extent on organisms other than krill.

There is some evidence to indicate that vertical stratification in some of the hydrographic variables (eg. temperature) may influence aggregation indirectly by serving to concentrate krill at certain depths. Similarly, variable current flow in the vicinity of large aggregations may ensure some exchange of vital metabolites, thereby constraining such aggregations in both time and space (Johnson *et al.* 1984).

Little specific information is available on the influence of phytoplankton concentration and availability on krill aggregating behaviour. Correlations found between phytoplankton and swarm biomass (Weber 1984; Weber & El-Sayed 1985) may indicate a causal link between swarming and phytoplankton density. Pingree (1978) has suggested that cross-frontal eddies will be important in the development of frontal phytoplankton blooms. Concentrations of krill in frontal zones and in regions of pronounced variation has been attributed to the joint effects of current flow and velocity gradients associated with such features (Beklemishev 1960; Bogdanov 1974).

Hydrographical and bathymetrical features in the Southern Ocean marine ecosystem

Plancke (1977) has stated that increases in biomass and productivity occur at the northern edge of the Sub-Tropical Convergence area, and similar increases were found at the APF (Pomazanova 1980). Cross-frontal mixing may take the form of baroclinic eddies and has been observed to do so at upwelling fronts (Lutjeharms *et al.* 1980), at shelf-edge fronts (Pingree 1978) and across the Sub-Tropical Convergence (Lutjeharms 1981). Mixing of warm nutrient poor Sub-Tropical surface water across the Sub-Tropical Convergence may have the same stabilizing and thus, biological enhancing effect. On the basis of a preliminary study, using closely spaced stations between Africa and Antarctica, Allanson *et al.* (1981) demonstrated a correspondence between the geographical location of sea-surface fronts and high values in primary productivity. It has also been suggested that bottom topography effects may enhance productivity at certain locations in the Southern Ocean (Golubev *et al.* 1983) but these areas, if they exist, are most probably of geographically limited extent.

Studies of mineral cycling in the marine environment can be informative in regard to understanding food web dynamics and general functioning of the ecosystem. Most chemical elements show a unique distribution pattern in the water column, which reflects their biological and chemical reactivities and the rates at which they are resolubilized. In the deeper layers, there is a meridional transport of nutrients and zooplankton by the relatively warm deep water moving southward. In the pelagic zone, the relationship with water masses and fronts becomes very apparent (Holm-Hansen 1985).

Environmental changes such as during the 1982 and 1983 disturbance to the Southern Ocean was caused by an El Niño Southern Oscillation (ENSO) (Cane 1983; Fielder 1984; Barber & Chavez 1983). Such alterations to the marine environment caused by ENSO events could modify the feeding area and the distribution of elephant seal populations (Vergani & Stanganelli 1990). The ENSO is an irregularly occurring interannual oceanographic event evidenced by rises in sea level and sea-surface temperatures (Cane 1983). These increased ocean temperatures are correlated with increased salinity, decreased zooplankton (McGowan 1984), and decreased fish abundance (Barber & Chavez 1983). Most reports on the biological consequences of El Niño were restricted to the devastating affects near the heart of the El Niño in the eastern central Pacific Ocean and off the coast of South America where high mortality and even total reproductive failure of marine birds and mammals were the norm (Barber & Chavez 1983; Limberger *et al.* 1983; Simon 1983; Trillmich & Limberger 1985). Le Boeuf *et al.* (1986) also suggested that during 1983 female northern elephant seals, *M. angustirostris* travelled further to obtain prey because of the effect of an intensive and wide spread El Niño event in progress throughout much of the Eastern Pacific that caused a reduction in plankton, fish and squid. Plankton samples also revealed a dramatic drop off southern California (Fielder 1984; McGowan 1984). This decrease in the lower food chain may have yielded both immediate and longer term drops in available prey for seals.

Food availability and productivity can therefore be affected by environmental factors such as the occurrence of frontal systems, upwelling fronts, shelf-edge fronts and eddies (Lutjeharms *et al.* 1985), which in turn could affect the distribution of potential prey species. Climatic effects such as overall warming of Southern Ocean sea temperatures noted by Jacka, Christou & Cook (1984) will affect productivity and species composition (Lutjeharms *et al.* 1985), thereby influencing the biology of marine organisms. Thus, although the causative environmental factors are unknown, climatic changes may have forced or have been associated with changes in the ocean environment that could result in reduced food resources for elephant seal populations declining (Hindell *et al.* 1994). The South Georgia population may have been unaffected by such changes and remained stable because variation in environmental conditions differ from one area of the Southern Ocean to another (Sahrhage 1988).

An organism living in an environment where the temperature changes either rapidly or seasonally cannot afford such fine tuning of it's physiology, instead it must be able to cope with a range of temperatures (Clarke 1990). Although physiological studies have revealed a significant capacity for adaptive response in marine organisms, the response to climatic change is often migration, and migration is only possible when there are suitable areas to go to (Clarke 1990). There is, moreover, cases of boundaries of distribution shifting by processes including mortality of adults and differential survival of young stages.

It is therefore conceivable that an understanding of the ranging and diving behaviour of southern elephant seal females might contribute towards understanding reasons for the elephant seal population decline at Marion Island. Bester & Wilkinson (1994) suggested that elephant seal females from Marion Island mate at an early age, reproduce at the maximum rate, but are not living long enough to maintain the population. Furthermore, most of our knowledge of the behaviour of the southern elephant seal has been focused onshore (Laws 1956; Carrick *et al.* 1962; Condy 1978a, b; Condy 1979; Hindell & Burton 1988), but 70% to 80% of the elephant seals time is spent at sea (Condy 1979; Hindell *et al.* 1991a). Given current knowledge of the terrestrial component of the life cycle of elephant seals at Marion Island, factors affecting these animals during the pelagic phase of the annual cycle is still unknown. The period after weaning the pup and mating is also the ideal time to record an elephant seal female's activity at sea, due to the fact that females fast throughout lactation and lose approximately a third of their mass (Costa *et al.* 1986) and then only feed soon after departing the rookery.

Since little is known about the diving behaviour, distribution, ranging behaviour and foraging grounds of the Marion Island population of females during their annual foraging movements, it makes it important to access whether these factors may hold a key in the population decline on Marion Island during their postbreeding (summer) or postmoulting (winter) pelagic phases out at sea.

CHAPTER 2

STUDY AREA AND GENERAL METHODS

Study Area

Marion Island (46°54′S, 37°45′E) which falls within the Kerguelen population stock for southern elephant seals is situated within the Prince Edward Island group approximately 2 300 km southeast of Cape Town, South Africa (Figure 1). The island is 290 km in area, measuring 24 km from the east to the west and 17 km from the north to south, and has a circumference of approximately 90 km (Wilkinson 1992). Elephant seals breed and moult predominantly in the eastern sector of the island, from Storm Petrel Bay in the north to Kildalkey Bay in the south (Figure 2).

General Methods

Immobilization

Southern elephant seal females were given intramuscular injections of ketamine hydrochloride (Ketalar, Parke Davis Laboratories (Pty) Ltd, Isando, SA) and xylazine hydrochloride (Rompun, Bayer Pharmaceuticals (Pty) Ltd, Johannesburg, SA). Ketamine (200 mg/ml solution) and xylazine (50 mg/ml solution) were combined in the approximate ratio 5 ketamine : 1 xylazine by mass (Bester 1988a). The desired dosage for elephant seal females was 5mg/kg ketamine and 1mg/kg xylazine (Bester 1988a).

Elephant seal females could not be weighed before or during immobilization. The standard length was estimated roughly before immobilization and the approximate body mass obtained from the regression equation that relates body mass to body length in *M. leonina* females (Ling & Bryden 1981). The desired dose was calculated and administered intramuscularly in the dorsal hip area using a 10 ml hand-held syringe or a modified version of the remote injection method (tubing between needle and syringe) described by Ryding (1982). A 150 mm 14 gauge biopsy needle with the point of the needle sealed, and a lateral hole drilled

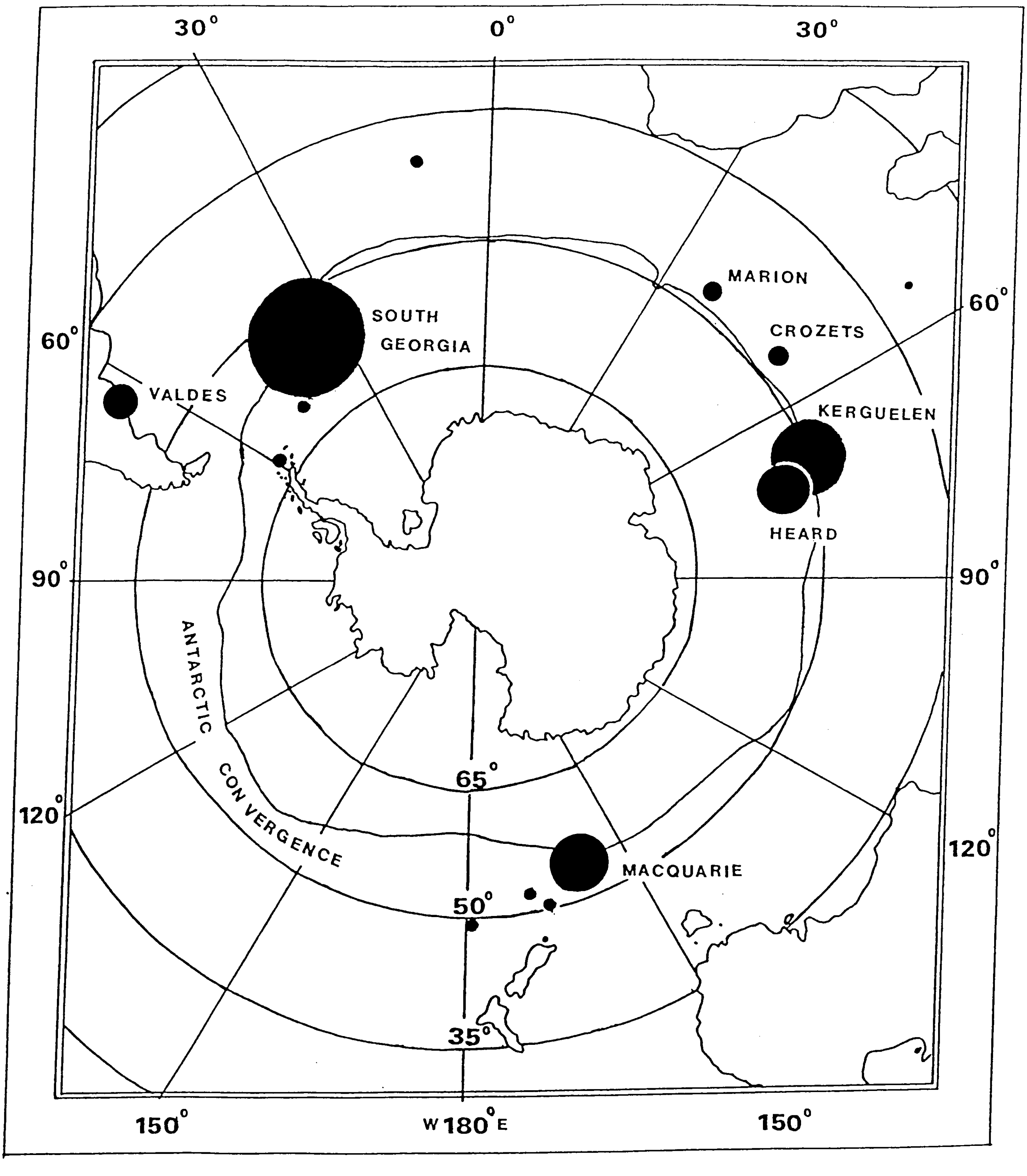


Figure 1. Breeding distribution of southern elephant seals in 1990. Closed circles indicate known breeding colonies and areas of circles are proportional to the estimated population sizes except for colonies of less than 5 000. The mean position of the Antarctic Convergence (or APF) is indicated (Modified from Laws 1994).

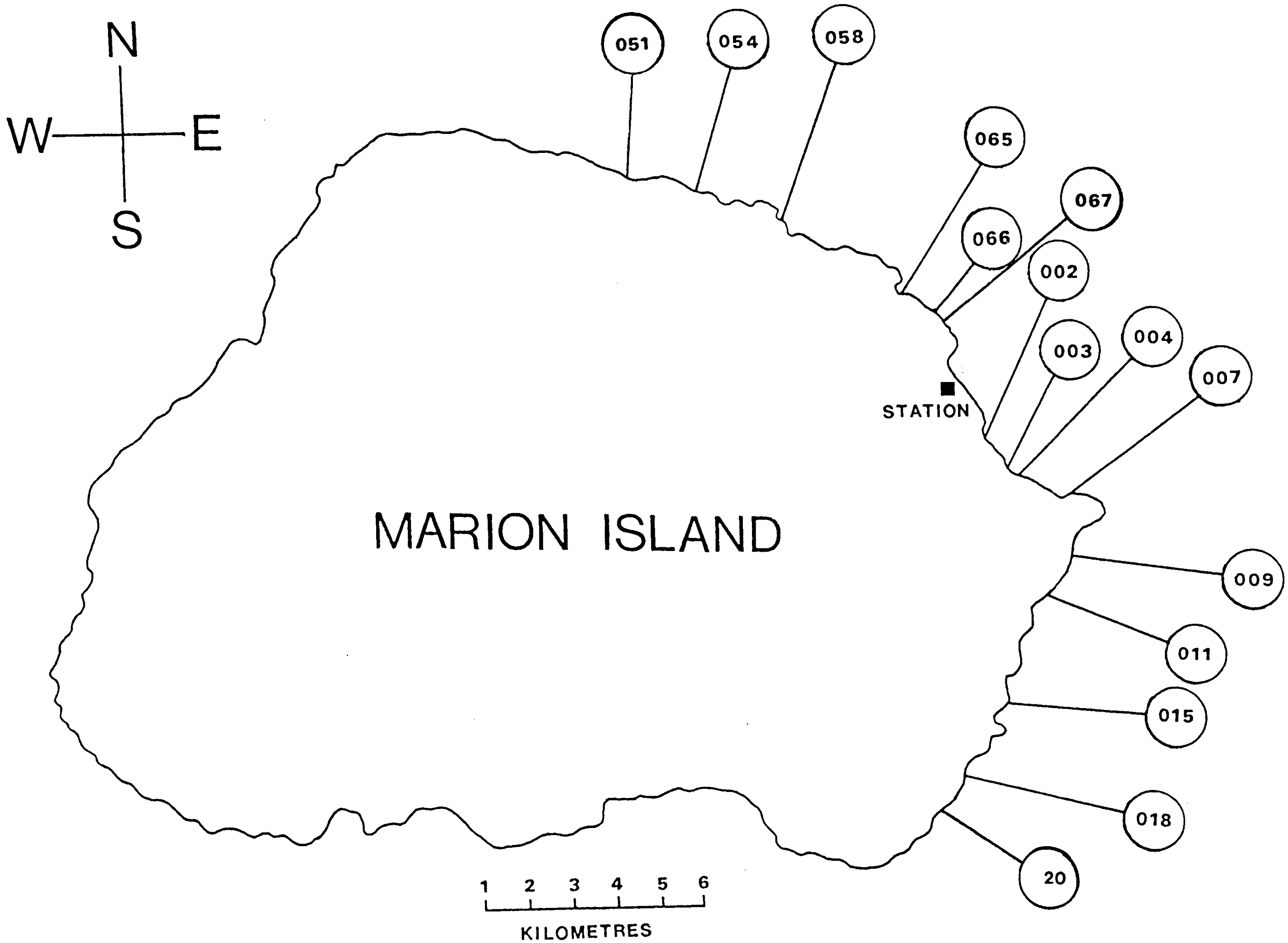


Figure 2. Marion Islands' major breeding and moulting haulout sites for southern elephant seal females. Numbers within closed circles depict beach codes and names of beaches where GLTDRs were deployed/recovered during 1990 - 1994, following Table 2.

10 mm from the tip (Parry *et al.* 1981) was initially used to deliver the dose. Subsequently 14 & 18 gauge spinal needles were used which were attached to approximately 300 cm of intravenous drip tubing following Gales and Burton (1987). The play (± 300 cm) allowed by the drip tubing provided enough latitude to allow the injection of the dose in one smooth action should the seal rear and withdraw its hind quarters after placement of the needle (Bester 1988a). Figure 3 illustrates the instrumentation used.

Deployment of Geographic Location Time-Depth Recorders (GLTDRs)

Data on individual movement and diving of elephant seal females were recorded with Geographic Location Time-Depth Recorders (GLTDRs) of Wildlife Computers (Redmond, Washington, USA) with the geolocation option. A single GLTDR consists of a tubular 15.4 × 2.9 cm titanium housing, weighs 196 g, and is fitted with a seawater temperature sensor in a clear Lexan cap at the opposite end (DeLong *et al.* 1992). The devices were programmed to record depth on two channels; the first from 0 - 500 m with an accuracy of ± 2 m, the second from 500 - 1 500 m with an accuracy of ± 6 m. Water temperature was recorded on a third channel (accuracy of 0.1 °C) and sea-surface light intensity (in the top 50 m of the water column during each ascent, and down to 10 m on the descent during dives) at 30 - 300 s intervals on a fourth channel. The highest light intensity measurement and last sea-surface temperature measurement between dives were recorded and stored with reference to an internal clock. Duty cycling (one day on, one day off) was enabled in the case of postmoulting seal 0144 to allow complete coverage of movements from the island before the memory (256 kbytes) was filled. The model of GLTDR deployed, protocol settings used, and the fundamental sampling intervals (FSI) set for each deployment are summarized in Table 1.

The recorders were deployed on tagged females which had shown fidelity to Marion Island during previous breeding and moulting haulouts (Table 2). All beaches were searched at 2 - day intervals during the breeding and moulting seasons to locate tagged females. Distances between deployment and recovery sites of GLTDRs on Marion island (Table 2) varied between 1.9 km and 23.4 km ($\bar{x}$ = 8.4 ± 7.1 km) for postbreeding females (n = 9) and between 1.2 and 8.1 km ($\bar{x}$ = 4.2 ± 3.3 km) for postmoulting females (n = 4). The degree of fidelity was

Table 1. Sampling protocol settings of southern elephant seal females (n = 13) from Marion Island, recorded during the postbreeding and postmoulting periods of 1990 - 1994.

Protocol 1

Seals	Status	FSI	Temp I (sec)	C1 < 450m (sec)	C1	C2	C3	C4	Duty cycle
Y333	pb	30	90	30	20	0	30	0	disabled
O390	pb	30	60	30	10	0	20	0	disabled
R357	pb	30	90	30	20	0	30	0	disabled
R101	pb	30	60	30	10	0	20	0	disabled
P537	pb	10	45	30	60	0	90	0	disabled
O138	pb	30	60	30	10	0	20	0	disabled
G006	pb	10	30	20	20	0	300	0	disabled
G289	pb	10	300	30	30	0	300	0	disabled
R102	pb	5	45	30	60	0	90	0	disabled
O144	pm	60	180	60	10	0	30	0	enabled
P537	pm	30	180	60	20	0	60	0	disabled
R202	pm	30	180	60	20	0	60	0	disabled
G006	pm	10	300	30	30	0	300	0	disabled

Protocol 2

Seals	Status	FSI	Temp II (sec)	C2 > 450m (sec)	C1	C2	C3	C4	Duty cycle
Y333	pb	30	90	90	0	20	30	0	disabled
O390	pb	30	60	60	0	20	20	0	disabled
R357	pb	30	90	90	0	20	30	0	disabled
R101	pb	30	60	60	0	20	20	0	disabled
P537	pb	10	45	30	0	60	90	0	disabled
O138	pb	30	60	60	0	20	20	0	disabled
G006	pb	10	30	20	0	20	30	0	disabled
G289	pb	10	300	30	0	30	30	0	disabled
R102	pb	5	45	30	0	60	90	0	disabled
O144	pm	60	180	60	0	10	20	0	enabled
P537	pm	30	180	60	0	20	60	0	disabled
R202	pm	30	180	60	0	20	60	0	disabled
G006	pm	10	300	30	0	30	30	0	disabled

FSI - Fundamental sampling interval
C1 - Depth (Channel 1)
C2 - Auxillary depth
C3 - Temperature
C4 - Light-level
Duty cycling - One day on, one day off
pb - postbreeding
pm - postmoulting

Table 2. The deployment/recovery sites, dates and distances between these sites of southern elephant seal females (n = 13) from Marion Island during the postbreeding and postmoulting periods of 1990 - 1994 (see also Figure 2).

Seals	Status	Age	Deploy Site	Deploy Date	Recovery Site	Recovery Date	Distance (km)
Y333	pb	6	007	26/10/91	054	02/01/92	15.3
O390	pb	7	002	10/10/90	066	18/12/90	3.4
R357	pb	5	007	01/11/91	011	04/01/92	4.5
R101	pb	4	002	13/10/90	015	02/01/91	11.1
P537	pb	5	007	03/11/92	003	09/01/93	1.9
O138	pb	7	065	20/10/90	007	02/01/91	8.1
G006	pb	6	007	09/10/94	009	20/12/94	2.8
G289	pb	5	058	03/11/93	018	24/01/94	23.4
R102	pb	6	004	29/10/92	066	22/01/93	5.1
						Mean	8.4
O144	pm	9	003	01/02/92	002	27/09/92	1.2
P537	pm	5	003	24/01/93	007	20/10/93	1.9
R202	pm	6	065	30/01/93	007	17/10/93	8.1
G006	pm	5	067	30/12/93	007	14/09/94	5.7
						Mean	4.2

Beach codes

020-Kildalkey Bay
018-Funk Bay
015-Landfall Beach
011-Bullard North
009-Hansens Point
007-Archway Bay and beaches
004-Macaroni Bay South
003-Macaroni Bay North
002-Trypot coastal area and moulting site
067-Van den Boogaard beaches
066-King Bird Head to Duiker's Point
065-Ship's Cove beach and moulting area
058-Pinnacle Beach
054-Goney to Log Beach/Prinsloomeer
051-Storm Petrel Bay

pb-postbreeding
pm-postmoulting

Figure 3. A close-up view of the GLTDR, attachment assemblage, remote injection equipment, anaesthetic and tranquilizer used.

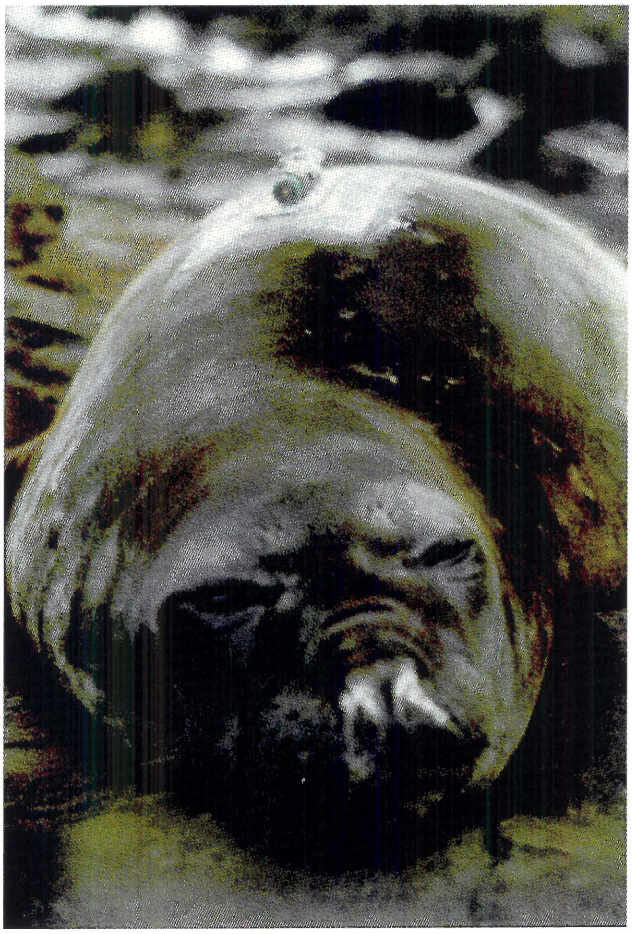


Figure 4. A GLTDR deployed on an adult southern elephant seal female from Marion Island.

determined by consulting a computer file generated by the ongoing mark-recapture programme (Wilkinson & Bester 1990) to identify suitable candidates. The GLTDR's were deployed on immobilized adult post-partum females shortly before weaning their pups, and again during the moult haulout in January once they were fully moulted and ready to depart for their winter journey at sea. The GLTDRs were attached to the females by glueing (epoxy adhesive) a length (25 x 10 cm) of nylon shade-netting, stitched to a 0.1 cm thick 18 × 5 cm aluminium plate which had 0.2 - 0.25 mm holes drilled around the edges to facilitate the stitching process using polypropylene thread, to the dorsal pelage between the shoulders (Bester & Pansegrouw 1992). Each of the three stainless steel hose clamps were looped through two slots cut 1.0 cm apart in the aluminium plate and associated mesh, evenly spaced along the length of the plate (Bester & Pansegrouw 1992) and allowed to set in epoxy adhesive (Araldite AW 2102/HW 2951, Ciba-Geigy). The GLTDRs were screwed down by the hose clamps, with its long axis parallel to the long axis of the seal, and with the light sensor facing forward (Figure 3). To retrieve the GLTDRs, the hose clamps were partially unscrewed, and the GLTDR slid out of the attachment assemblage which in turn could be recovered once it sloughed off during moulting (Bester & Pansegrouw 1992). With the breeding season arrivals of females, the GLTDRs were retrieved and broomstick handles of the same length (of the GLTDRs) were replaced in the hose clamp mountings to maintain the shape of the hose clamp mounting as GLTDRs were re-deployed on the same females after the breeding season to record the postbreeding movements. Figure 4 shows an elephant seal female with the GLTDR assemblage.

CHAPTER 3

DIVING BEHAVIOUR

Introduction

Studies on local and long-range movements of southern elephant seals from Marion Island have relied exclusively on resightings of tagged animals (Panagis 1981; Bester 1989; Wilkinson & Bester 1990). Recent developments of instrumentation have allowed studies on the diving and ranging behaviour of northern (Le Boeuf *et al.* 1986, 1988; Naito *et al.* 1989; DeLong & Stewart 1991) and southern elephant seals (Boyd & Arnbom 1991; Hindell *et al.* 1991a, b; Hindell *et al.* 1992; McConnell *et al.* 1992a; McConnell & Fedak 1996), including those at Marion Island (Bester & Pansegrouw 1992; present study). Studies such as these have described the seals diving behaviour in relation to potential prey distributions, foraging range and movement patterns. Since the distribution of prey in space and time may have an influence on especially the feeding behaviour of southern elephant seals, information obtained through the use of recorders in monitoring behavioural activities can improve knowledge of their diving patterns and proficiency. It is therefore conceivable that knowledge of the diving and ranging behaviour of southern elephant seals, and by inference, their diet, might contribute towards understanding why the elephant seal population is declining at Marion Island.

This chapter presents an overview of the current knowledge of the diving behaviour of the southern elephant seal at Marion Island by using the classification and characterization of dives performed by females that seasonally disperse to forage (see **Chapter 4**), as the basis of the study of the temporal and spatial variation of the behaviour of individuals at sea, and their relationship with potential prey distributions (see **Chapter 5**).

Methods

(a) Study animals

The diving behaviour of postbreeding (n = 9) and postmoulting (n = 4) southern elephant seal females were studied using MK3+ (with 256 Kbytes of memory) and MK3e (with 512 Kbytes of memory) microprocessor controlled, GLTDRs (Wildlife Computers 16150 NE 85th Street # 226, Redmond, WA 98052, USA) deployed at Marion Island (46°54'S, 37°45'E) during the breeding (September - November) and moulting seasons (December - February) of 1990 - 1994. Females were sedated intramuscularly before attachment and recovery of instruments using a combination of ketamine and xylazine hydrochloride (see **Chapter 2**).

Twenty nine recorders were deployed on tagged, adult females between four and eleven years of age, which had shown fidelity to Marion Island during previous breeding/moulting haulouts. Twenty two females returned to the island with their recorders in place of which nine had malfunctioned. The remaining seven recorders were lost as those females had either not returned to Marion Island, or were not located on the island during the postbreeding/postmoulting season. The pressure transducer of the GLTDR deployed on postbreeding seals R202 (1992 & 1993) were at fault which excluded these deployments in the diving analyses of Chapter 3.

(b) Diving analysis

Dives were divided into several categories following Le Boeuf *et al.* (1988, 1992) using the DIVE ANALYSIS (version 2.0) software programme of Wildlife Computers to view each dive configuration. Dives within a type were similar in appearance and dissimilar from dives in other categories. Different dive types were then compared statistically (see **Statistical analyses**). The criteria for differentiating dives were based on the following parameters for each individual dive configuration:

- dive depth (m): the maximum depth reached during a dive;
- dive duration (min): elapsed time between submergence and resurfacing;
- rate of descent (m/s): the depth at the bottom of a dive/time elapsed to reach that depth from the surface;
- rate of ascent (m/s): the depth at the bottom of a dive/time elapsed to reach the surface;
- bottom time (min): the amount of time spent at the bottom of a dive between descent and ascent;

- wiggles (prey pursuit movement): the distinct up and down movements during the bottom time of a dive.

The duration and depth of dives, and the duration of the surface intervals preceding dives, were measured by the dive analysis programme. Lack of recognition of surface intervals, which would lead to the concatenation of dives and a decline in the total number of dives recorded, was unlikely at the selected sampling frequencies (30 s intervals - *vide* Boyd 1993a; see Table 1 **Chapter 2**). Bottom time was user-selected and the mean rates of descent and ascent were calculated automatically from the beginning and the end of each dive to the beginning and end of the user-selected bottom time, respectively. Dive parameters were stored in a statistical file following categorisation. The extended surface intervals (ESIs) were defined as surface intervals longer than ten minutes (Le Boeuf *et al.* 1988). Time spent hauled out was defined as the period when the recorder was dry. Diel changes in individual dive patterns were assessed using the four hours around midday (10h00 - 14h00) and midnight (22h00 - 02h00) following Le Boeuf *et al.* (1988), during the first 40 days of the diving record for all females to eliminate the possible influence of dawn and dusk which would differ according to the season and location of the females. This was done to allow direct comparison amongst all individuals since the memory of the GLTDRs was filled for postbreeding seals R101, P537, O138, O390 and postmoulting seals O144, P537 and G006 while still at sea (Table 1, **Chapter 2**). The GEOLOCATION software package (version 2.0) was used to calculate the locations of the seals on a daily basis from light level data (see **Chapter 4**) and therefore the times of dawn and dusk, following DeLong *et al.* (1992), Bester & Pansegrouw (1992) and Hill (1994).

(c) Statistical analyses

All statistical analyses were performed using the SAS statistical package (SAS Institute Inc. 1982) and Statgraphics (version 5.0). Two-sample analysis (t-tests) was used to test differences in dive parameters of individuals between different group means. A one-way analysis of variance (ANOVA) with least-square means (Sokal & Rohlf 1981) was used to examine differences between dive parameter means of individuals (DeLong & Stewart 1991; Bengtson & Stewart 1992). A nested analysis of variance (ANOVA) was used to test differences in dive parameter means between different dive types (Hindell *et al.* 1991b). The analysis of covariance (ANCOVA) was used to test for differences in the slopes of regression lines correlating dive depth and dive duration for each female (Hindell *et al.* 1992). The Komolgorov-Smirnov two sample test (Conover 1980) was used to compare the depth, duration and surface interval distributions of females (*vide* DeLong & Stewart 1991). Chi-square (χ^2) analysis was used to test for differences in ratios of occurrence of dive types, using Yates' correction for continuity when dealing with small sample sizes (Sokal & Rohlf 1981). The 0.05 level of probability was accepted as indicating statistical significance. Sample means ($\bar{x}$) were expressed with their standard deviations (SD) as summary statistics for all dives of each seal, whereas standard errors (SE) were used when combining data for all individuals. Unless stated otherwise all dives in the diving record of each seal were used in the analysis following Le Boeuf *et al.* (1988).

Results

A total of 66 807 dives were recorded for all thirteen females of which 35 603 (53.3%) dives were executed by the postbreeding females (n = 9) and the remaining 31 204 (46.7%) dives by the postmoulting females (n = 4). All females began diving as soon as they entered the water and dived virtually continuously throughout the recording period. The total time spent at sea was between 45 and 86 days for the postbreeding females ($\bar{x}$ = 66.1 ± 13.2, n = 9) and between 239 and 269 days for the postmoulting females ($\bar{x}$ = 252.3 ± 13.8, n = 4) (Table 3).

Dive depths

On departure from the island dive depths of seals were shallow and became progressively deeper at increasing distance away from the island, and vice versa on their return to the island. The deepest dive (1 444 m) was recorded by seal Y333 (postbreeding) which was only marginally deeper than seal R202's (postmoulting) maximum depth of 1 414 m. Mean dive depths of 480 ± 74 m recorded for postbreeding females were not significantly different (ANOVA: $F_{12,57592} = 2.43$, $P > 0.05$) to that of postmoulting females which dove to 454 ± 38

Table 3. Summary statistics from the diving record of southern elephant seal females (n = 13) from Marion Island, recorded during 1990 - 1994.

Year Recorded	Seals	Status	Age	Recorded Duration (days)	Total days at sea	Total no. dives	Dives (h)	Depth (m)		Duration (min)	
								mean (sd)	Max	mean (sd)	Max
1991	Y333	pb	6	51	51	2539	2.2	562 (169)	1444	27.3 (8.5)	76
1990	*O390	pb	7	53	67	3334	2.5	531 (155)	1114	24.2 (5.5)	49
1991	R357	pb	5	45	45	2688	2.5	406 (157)	1204	23.5 (7.4)	76
1990	*R101	pb	4	58	77	3770	3.0	445 (147)	1000	20.1 (5.2)	59
1992	P537	pb	5	53	53	3621	2.5	457 (194)	1284	24.3 (8.6)	66
1990	*O138	pb	7	58	67	3419	2.5	585 (226)	1096	23.6 (5.7)	49
1994	G006	pb	6	73	73	4892	3.2	506 (221)	1194	18.8 (5.2)	56
1993	G289	pb	5	76	76	6244	3.4	355 (129)	1180	17.6 (5.4)	59
1992	R102	pb	6	86	86	5096	3.1	476 (171)	1066	19.1 (5.7)	51
		Mean		61	66	3955	2.8	480 (74)		22.1 (3.3)	
1991	**O144	pm	8	112	239	4481	1.8	487 (194)	1190	33.4 (14.6)	113
1993	*P537	pm	6	201	269	9086	2.1	425 (180)	1142	28.5 (10.5)	98
1993	*R202	pm	7	181	243	10031	2.6	488 (186)	1414	23.4 (8.4)	86
1994	*G006	pm	6	145	258	7606	2.7	419 (186)	1146	22.4 (9.9)	92
		Mean		175	252	8907	2.3	454 (38)		26.9 (5.1)	

* - Incomplete diving record for the total days at sea
** - Dive record for every second day (half the measuring period)
( ) - standard deviation
No diving records for seals: R202 (pb) 1992 & 1993
pb - postbreeding
pm - postmoulting

(a)

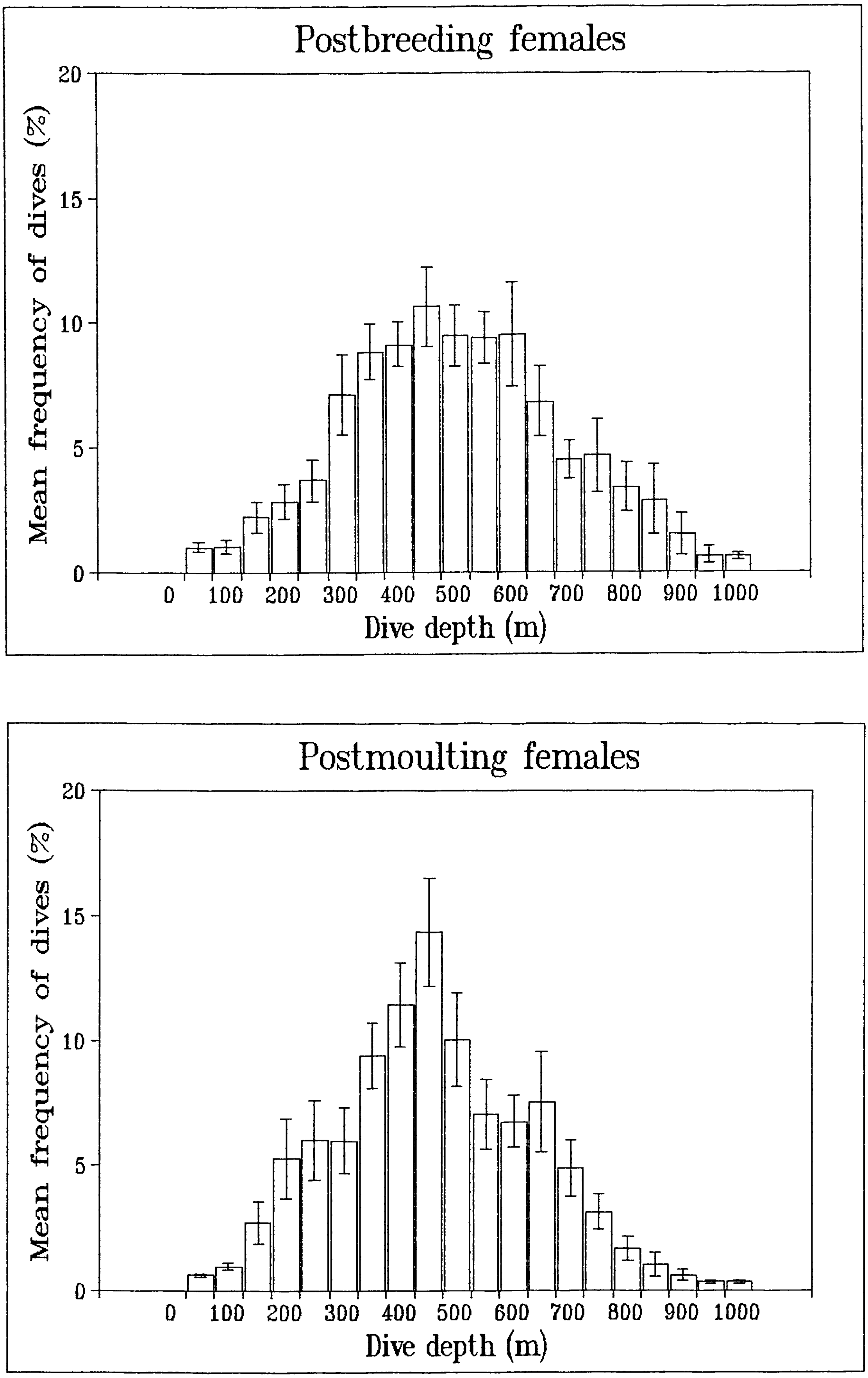
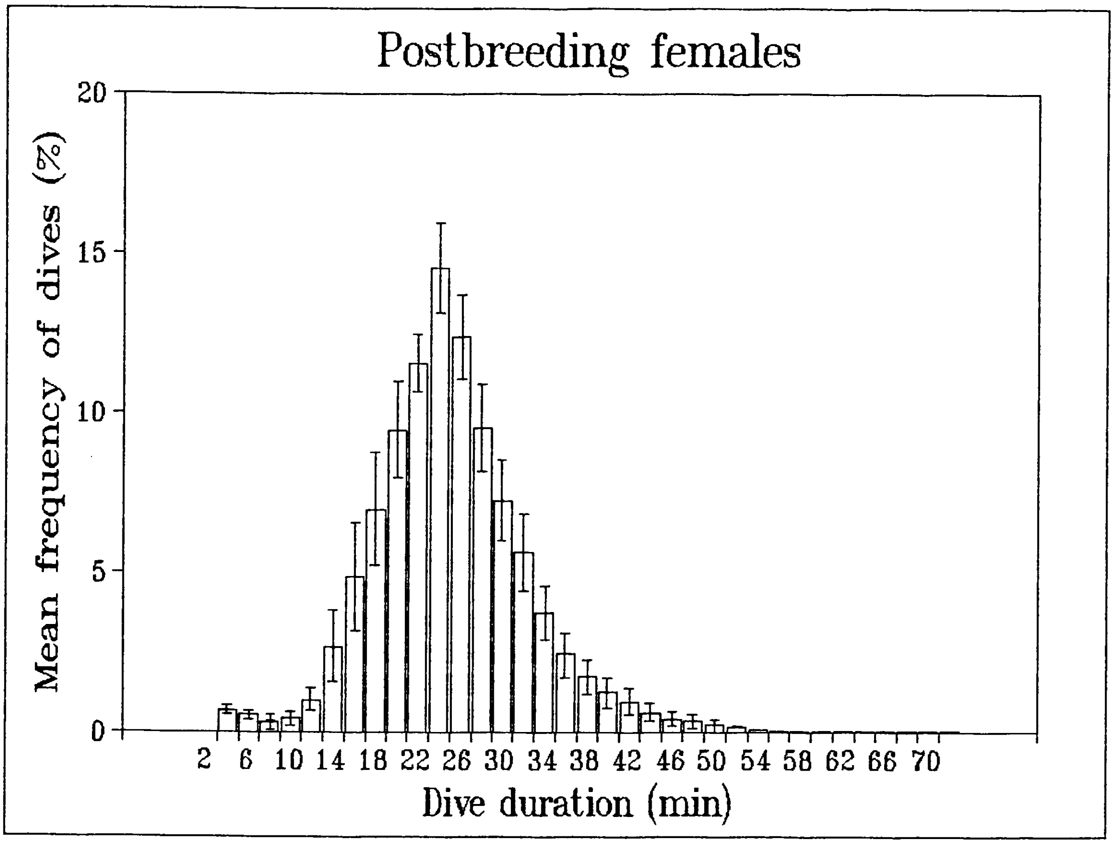


Figure 5. Frequency distributions of (a) dive depth (50 m increments), (b) dive duration (2 min increments) and (c) post-dive surface intervals of thirteen southern elephant seal females fromMarion Island (error bars are standard errors of the mean).

(b)



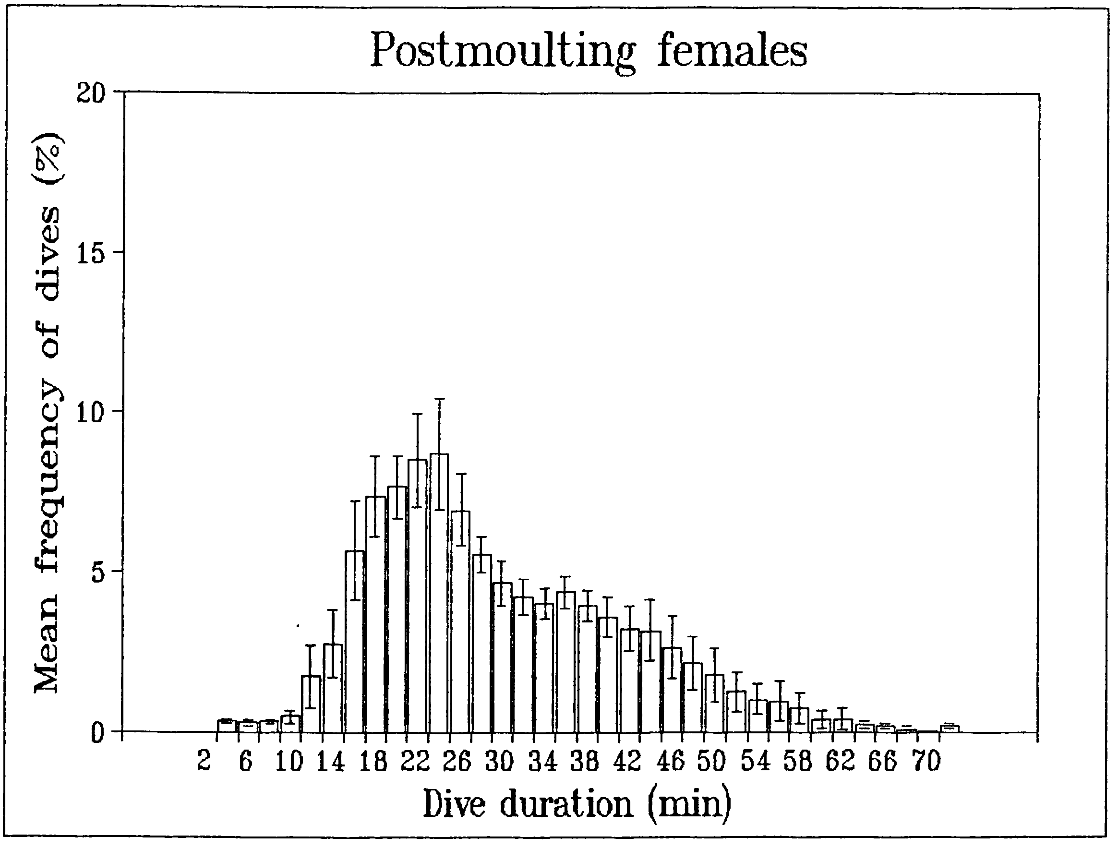


Figure 5 (Continued).

(c)

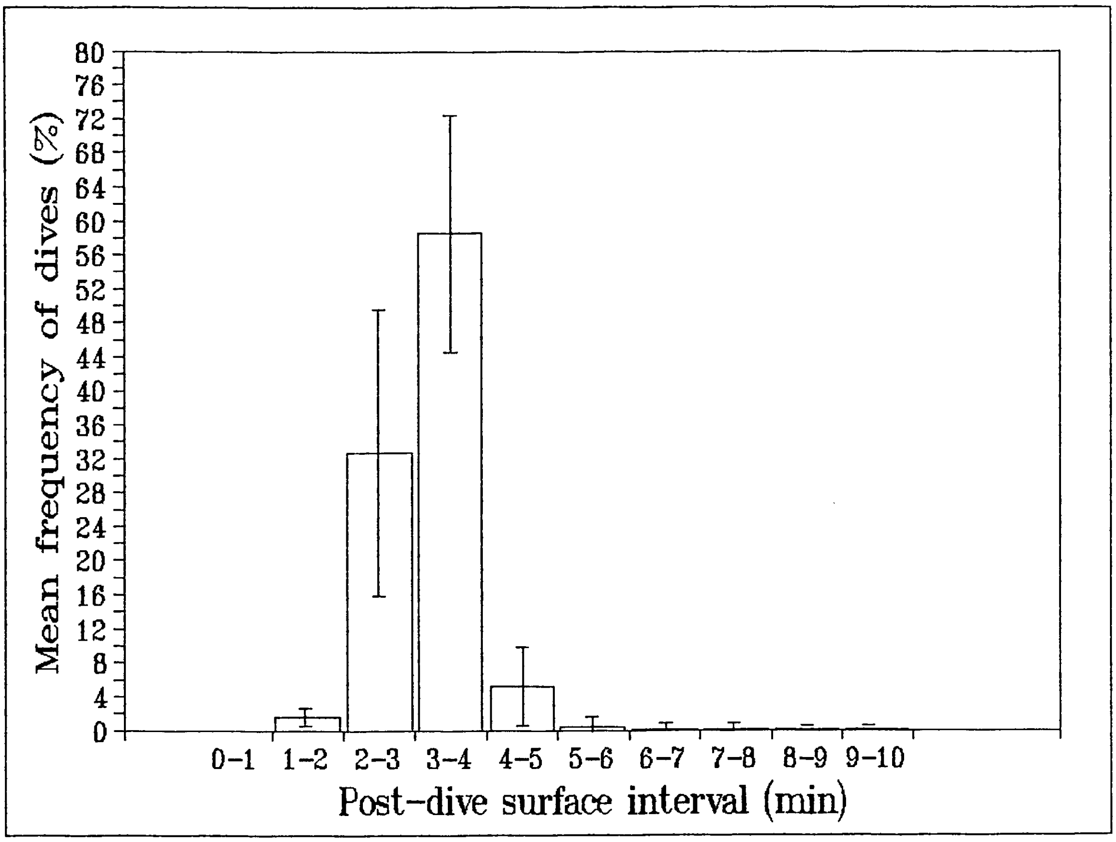


Figure 5 (Continued).

m. Mean dive depths for postbreeding females showed considerably more variation than postmoulting females (Table 3). Dives deeper than 800 m and shallower than 200 m constituted less than 10% of all dives recorded for both postbreeding and postmoulting females (Figure 5a).

Dive durations

A maximum dive duration of 113 min was recorded for postmoulting seal O144. Mean dive durations averaged 22.1 ± 3.3 min for postbreeding females, whereas postmoulting females had significantly longer (ANOVA: $F_{12,57592} = 602.42$, $P < 0.0001$) mean dive durations of 26.9 ± 5.1 min (Table 3). Dives shorter than 16 min constituted less than 10% for both postbreeding and postmoulting females, whereas 18% and 42% of dives were longer than 32 min for postbreeding and postmoulting females, respectively (Figure 5b).

Surface intervals

Females on average spent 20 hours/day submerged, and 3 hours/day at the surface. Most dives in each record were followed by surface intervals of less than 4 min. Approximately 56% of post-dive surface intervals ranged between 3 - 4 min, whereas 30% of post-dive surface intervals lasted for 2 - 3 min (Figure 5c). Surface intervals shorter than 2 min and longer than 4 min contributed to less than 14% of recorded surface intervals. The mean surface duration (of 2.9 ± 1.1 min) recorded for postbreeding females was significantly longer ($F_{12,57592} = 234.31$, $P < 0.0001$) than that of postmoulting females (2.3 ± 0.8 min).

Characterization of dive types

Seven characteristic dive types occurred throughout the diving record for all females as schematically illustrated in Figure 6. Diving characteristics between postbreeding and postmoulting females seemed to be different, and were considered separately in the diving analyses.

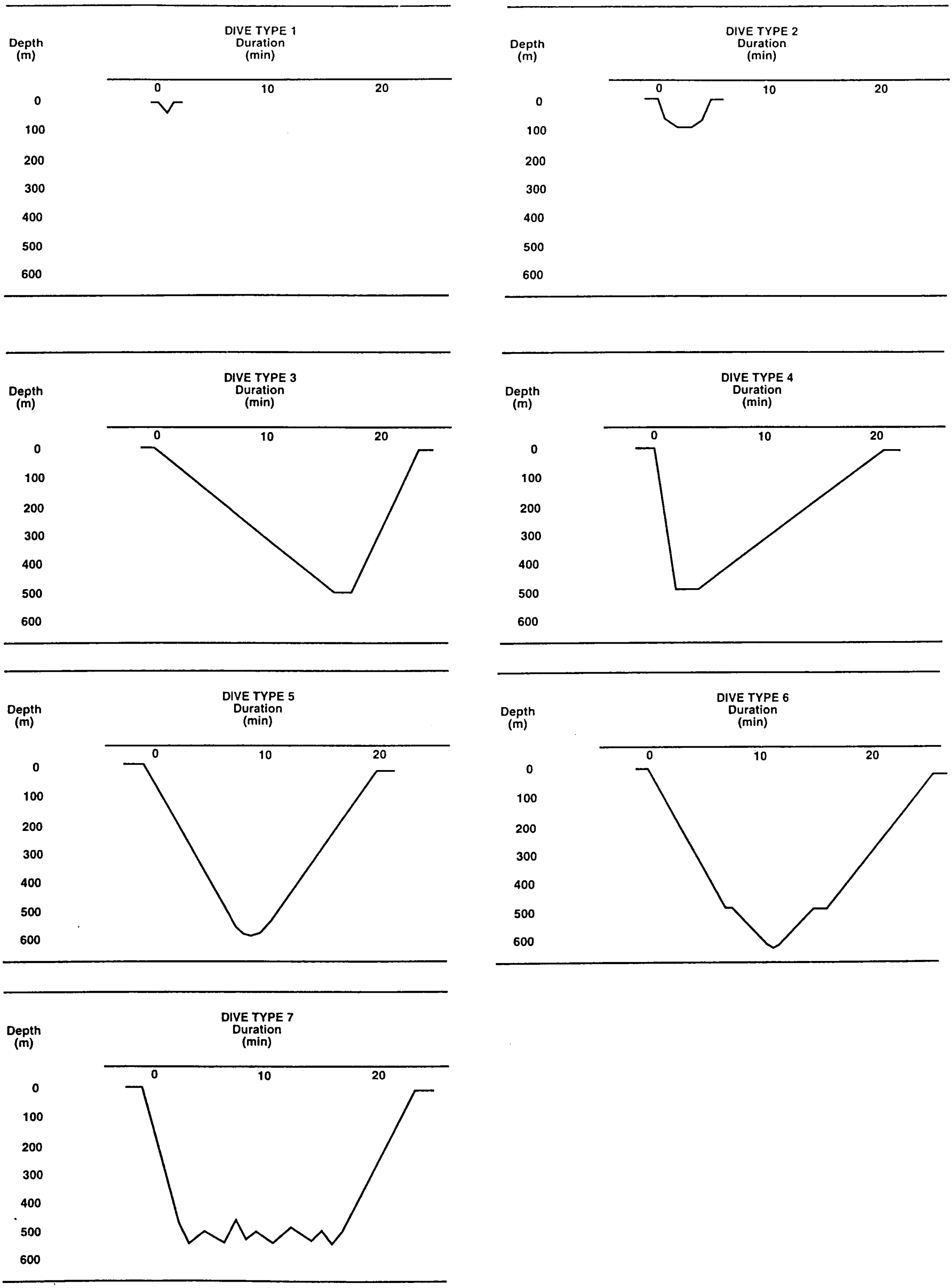


Figure 6. Schematic representation of the seven dive types that appear in the diving record of southern elephant seal females (n = 13), adjusted for depth and duration.

TYPE 1 dives

These dives were `spiked', shallow (mean depth of 46 ± 20 m) and of short duration (1.5 ± 1.2 min). The descent and ascent rates were relatively slow and virtually identical with a short mean bottom time of 0.08 min.

(a) Amongst dive types:

Depth & duration

Postbreeding and postmoulting females: Dive type 1 was significantly shallower and shorter in duration than all other dive types (Tables 4a, 4b, 4f & 4g).

Descent rates

Postbreeding females: Descent rates were significantly faster than all other dive types (Table 4c). *Postmoulting females:* Descent rates were not significantly different to type 2 and 4 dives, but significantly faster than type 3, 5 and 6 dives and significantly slower than dive type 7 (Table 4h).

Ascent rates

Postbreeding females: Ascent rates were significantly faster than all other dive types (Table 4d). *Postmoulting females:* Ascent rates were not significantly different to type 2 dives, but significantly faster than type 3, 4, 6 and 7 dives and significantly slower than type 5 dives (Table 4i).

Bottom times

Postbreeding and postmoulting females: Bottom times were significantly shorter than all other dive types (Tables 4e & 4j).

(b) Within dive types:

Type 1 dives for postmoulting females were significantly deeper (± 30 m) and longer (± 1.74 min) than postbreeding females (Tables 5a & 5b). The mean descent and ascent rates of postbreeding females were significantly faster (by 1.02 m/s) than that of postmoulting females (Tables 5c & 5d). The mean bottom time for both groups was negligible (Table 5e).

Table 4. Summary statistics (ANOVA analyses) of the relationships between dive types 1 - 7, comparing diving parameters for each individual dive namely (a) dive depth, (b) dive duration, (c) descent rates, (d) ascent rates and (e) bottom times for postbreeding females and (f) dive depth, (g) dive duration, (h) descent rates, (i) ascent rates and (j) bottom times for postmoulting females.

(a)

POSTBREEDING FEMALES
Depth

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 31.89 m 2. 156.42 m F1,641=165.99	P < 0.0001 1. 31.89 m 3. 312.69 m F1,925=143.88	P < 0.0001 1. 31.89 m 4. 309.92 m F1,167=133.07	P < 0.0001 1. 31.89 m 5. 480.48 m F1,1002=174.34	P < 0.0001 1. 31.89 m 6. 453.50 m F1,48=335.43	P < 0.0001 1. 31.89 m 7. 454.99 m F1,7041=219.66
2	P < 0.0001 1. 31.89 m 2. 156.42 m F1,641=165.99	******************** ******************** ******************** ********************	P < 0.0001 2. 156.42 m 3. 312.69 m F1,1492=637.99	P < 0.0001 2. 156.42 m 4. 309.92 m F1,734=376.71	P < 0.0001 2. 156.42 m 5. 480.48 m F1,1569=1381.39	P < 0.0001 2. 156.42 m 6. 453.50 m F1,615=275.48	P < 0.0001 2. 156.42 m 7. 454.99 m F1,7608=1724.96
3	P < 0.0001 1. 31.89 m 3. 312.69 m F1,925=143.88	P < 0.0001 2. 156.42 m 3. 312.69 m F1,1492=637.99	******************** ******************** ******************** ********************	P > 0.05 3. 312.69 m 4. 309.92 m F1,1018=0.04	P < 0.0001 3. 312.69 m 5. 480.48 m F1,1853=397.90	P < 0.0001 3. 312.69 m 6. 453.50 m F1,899=11.32	P < 0.0001 3. 312.69 m 7. 454.99 m F1,7892=535.89
4	P < 0.0001 1. 31.89 m 4. 309.92 m F1,167=133.07	P < 0.0001 2. 156.42 m 4. 309.92 m F1,734=376.71	P > 0.05 3. 312.69 m 4. 309.92 m F1,1018=0.04	******************** ******************** ******************** ********************	P < 0.0001 4. 309.92 m 5. 480.48 m F1,1095=81.50	P < 0.0015 4. 309.92 m 6. 453.50 m F1,141=10.53	P < 0.0001 4. 309.92 m 7. 454.99 m F1,7184=87.89
5	P < 0.0001 1. 31.89 m 5. 480.48 m F1,1002=174.34	P < 0.0001 2. 156.42 m 5. 480.48 m F1,1569=1381.39	P < 0.0001 3. 312.69 m 5. 480.48 m F1,1853=397.90	P < 0.0001 4. 309.92 m 5. 480.48 m F1,1095=81.50	******************** ******************** ******************** ********************	P > 0.05 5. 480.48 m 6. 453.50 m F1,976=0.20	P < 0.0001 5. 480.48 m 7. 454.99 m F1,7969=16.95
6	P < 0.0001 1. 31.89 m 6. 453.50 m F1,48=335.43	P < 0.0001 2. 156.42 m 6. 453.50 m F1,615=275.48	P < 0.0001 3. 312.69 m 6. 453.50 m F1,899=11.32	P < 0.0015 4. 309.92 m 6. 453.50 m F1,141=10.53	P > 0.05 5. 480.48 m 6. 453.50 m F1,976=0.20	******************** ******************** ******************** ********************	P > 0.05 6. 453.50 m 7. 454.99 m F1,7015=0.01
7	P < 0.0001 1. 31.89 m 7. 454.99 m F1,7041=219.66	P < 0.0001 2. 156.42 m 7. 454.99 m F1,7608=1724.96	P < 0.0001 3. 312.69 m 7. 454.99 m F1,7892=535.89	P < 0.0001 4. 309.92 m 7. 454.99 m F1,7184=87.89	P < 0.0001 5. 480.48 m 7. 454.99 m F1,7969=16.95	P > 0.05 6. 453.50 m 7. 454.99 m F1,7015=0.01	******************** ******************** ******************** ********************

Table 4 (Continued).

(b)

POSTBREEDING FEMALES
Duration

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 0.63 min 2. 11.14 min F1,641=241.02	P < 0.0001 1. 0.63 min 3. 17.09 min F1,925=378.78	P < 0.0001 1. 0.63 min 4. 15.11 min F1,167=306.08	P < 0.0001 1. 0.63 min 5. 17.22 min F1,1002=549.14	P < 0.0001 1. 0.63 min 6. 16.97 min F1,48=377.23	P < 0.0001 1. 0.63 min 7. 19.18 min F1,7041=541.61
2	P < 0.0001 1. 0.63 min 2. 11.14 min F1,641=241.02	******************** ******************** ******************** ********************	P < 0.0001 2. 11.14 min 3. 17.09 min F1,1492=545.43	P < 0.0001 2. 11.14 min 4. 15.18 min F1,734=90.21	P < 0.0001 2. 11.14 min 5. 17.22 min F1,1569=748.27	P < 0.0001 2. 11.14 min 6. 16.97 min F1,615=22.81	P < 0.0001 2. 11.14 min 7. 19.18 min F1,7608=1524.17
3	P < 0.0001 1. 0.63 min 3. 17.09 min F1,925=378.78	P < 0.0001 2. 11.14 min 3. 17.09 min F1,1492=545.43	******************** ******************** ******************** ********************	P < 0.0001 3. 17.09 min 4. 15.18 min F1,1018=16.40	P > 0.05 3. 17.09 min 5. 17.22 min F1,1853=0.31	P > 0.05 3. 17.09 min 6. 16.97 min F1,899=0.01	P < 0.0001 3. 17.09 min 7. 19.18 min F1,7892=138.27
4	P < 0.0001 1. 0.63 min 4. 15.11 min F1,167=306.08	P < 0.0001 2. 11.14 min 4. 15.18 min F1,734=90.21	P < 0.0001 3. 17.09 min 4. 15.18 min F1,1018=16.40	******************** ******************** ******************** ********************	P < 0.0001 4. 15.18 min 5. 17.22 min F1,1095=25.79	P > 0.05 4. 15.18 min 6. 16.97 min F1,141=1.46	P < 0.0001 4. 15.18 min 7. 19.18 min F1,7134=87.75
5	P < 0.0001 1. 0.63 min 5. 17.22 min F1,1002=549.14	P < 0.0001 2. 11.14 min 5. 17.22 min F1,1569=748.27	P > 0.05 3. 17.09 min 5. 17.22 min F1,1853=0.31	P < 0.0001 4. 15.18 min 5. 17.22 min F1,1095=25.79	******************** ******************** ******************** ********************	P > 0.05 5. 17.22 min 6. 16.97 min F1,976=0.04	P < 0.0001 5. 17.22 min 7. 19.18 min F1,7969=138.06
6	P < 0.0001 1. 0.63 min 6. 16.97 min F1,48=377.23	P < 0.0001 2. 11.14 min 6. 16.97 min F1,615=22.81	P > 0.05 3. 17.09 min 6. 16.97 min F1,899=0.01	P > 0.05 4. 15.18 min 6. 16.97 min F1,141=1.46	P > 0.05 5. 17.22 min 6. 16.97 min F1,976=0.04	******************** ******************** ******************** ********************	P > 0.05 6. 16.97 min 7. 19.18 min F1,7015=2.42
7	P < 0.0001 1. 0.63 min 7. 19.18 min F1,7041=541.61	P < 0.0001 2. 11.14 min 7. 19.18 min F1,7608=1524.17	P < 0.0001 3. 17.09 min 7. 19.18 min F1,7892=138.27	P < 0.0001 4. 15.18 min 7. 19.18 min F1,7134=87.75	P < 0.0001 5. 17.22 min 7. 19.18 min F1,7969=138.06	P > 0.05 6. 16.97 min 7. 19.18 min F1,7015=2.42	******************** ******************** ******************** ********************

Table 4 (Continued).

(c)

POSTBREEDING FEMALES
Descent

	Dive type 1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 2.43 m/s 2. 1.19 m/s F1,641=235.85	P < 0.0001 1. 2.43 m/s 3. 0.46 m/s F1,925=1683.11	P < 0.0001 1. 2.43 m/s 4. 1.29 m/s F1,167=75.16	P < 0.0001 1. 2.43 m/s 5. 1.01 m/s F1,1002=319.08	P < 0.0001 1. 2.43 m/s 6. 0.87 m/s F1,48=17.62	P < 0.0001 1. 2.43 m/s 7. 1.44 m/s F1,7041=264.30
2	P < 0.0001 1. 2.43 m/s 2. 1.19 m/s F1,641=235.85	******************** ******************** ******************** ********************	P < 0.0001 2. 1.19 m/s 3. 0.46 m/s F1,1492=2743.29	P < 0.014 2. 1.19 m/s 4. 1.29 m/s F1,734=6.02	P < 0.0001 2. 1.19 m/s 5. 1.01 m/s F1,1569=78.21	P < 0.0029 2. 1.19 m/s 6. 0.87 m/s F1,615=8.94	P < 0.0001 2. 1.19 m/s 7. 1.44 m/s F1,7608=243.30
3	P < 0.0001 1. 2.43 m/s 3. 0.46 m/s F1,925=1683.11	P < 0.0001 2. 1.19 m/s 3. 0.46 m/s F1,1492=2743.29	******************** ******************** ******************** ********************	P < 0.0001 3. 0.46 m/s 4. 1.29 m/s F1,1018=1871.35	P < 0.0001 3. 0.46 m/s 5. 1.01 m/s F1,1853=1355.19	P < 0.0001 3. 0.46 m/s 6. 0.87 m/s F1,899=96.52	P < 0.0001 3. 0.46 m/s 7. 1.44 m/s F1,7892=6230.97
4	P < 0.0001 1. 2.43 m/s 4. 1.29 m/s F1,167=75.16	P < 0.014 2. 1.19 m/s 4. 1.29 m/s F1,734=6.02	P < 0.0001 3. 0.46 m/s 4. 1.29 m/s F1,1018=1871.35	******************** ******************** ******************** ********************	P < 0.0001 4. 1.29 m/s 5. 1.01 m/s F1,1095=50.05	P < 0.0013 4. 1.29 m/s 6. 0.87 m/s F1,141=10.83	P < 0.0001 4. 1.29 m/s 7. 1.44 m/s F1,7134=21.36
5	P < 0.0001 1. 2.43 m/s 5. 1.01 m/s F1,1002=319.08	P < 0.0001 2. 1.19 m/s 5. 1.01 m/s F1,1569=78.21	P < 0.0001 3. 0.46 m/s 5. 1.01 m/s F1,1853=1355.19	P < 0.0001 4. 1.29 m/s 5. 1.01 m/s F1,1095=50.05	******************** ******************** ******************** ********************	P > 0.05 5. 1.01 m/s 6. 0.87 m/s F1,976=1.40	P < 0.0001 5. 1.01 m/s 7. 1.44 m/s F1,7969=1125.34
6	P < 0.0001 1. 2.43 m/s 6. 0.87 m/s F1,48=17.62	P < 0.0001 2. 1.19 m/s 6. 0.87 m/s F1,615=8.94	P < 0.0001 3. 0.46 m/s 6. 0.87 m/s F1,899=96.52	P < 0.0013 4. 1.29 m/s 6. 0.87 m/s F1,141=10.83	P > 0.05 5. 1.01 m/s 6. 0.87 m/s F1,976=1.40	******************** ******************** ******************** ********************	P < 0.0001 6. 0.87 m/s 7. 1.44 m/s F1,7015=29.55
7	P < 0.0001 1. 2.43 m/s 7. 1.44 m/s F1,7041=264.30	P < 0.0001 2. 1.19 m/s 7. 1.44 m/s F1,7608=243.30	P < 0.0001 3. 0.46 m/s 7. 1.44 m/s F1,7892=6230.97	P < 0.0001 4. 1.29 m/s 7. 1.44 m/s F1,7134=21.36	P < 0.0001 5. 1.01 m/s 7. 1.44 m/s F1,7969=1125.34	P < 0.0001 6. 0.87 m/s 7. 1.44 m/s F1,7015=29.55	******************** ******************** ******************** ********************

Table 4 (Continued).

(d)

POSTBREEDING FEMALES
Ascent

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. -2.00 m/s 2. -1.37 m/s F1,641=46.94	P < 0.0001 1. -2.00 m/s 3. -0.99 m/s F1,925=277.56	P < 0.0001 1. -2.00 m/s 4. -0.54 m/s F1,167=148.53	P < 0.0001 1. -2.00 m/s 5. -1.01 m/s F1,1002=217.25	P < 0.0136 1. -2.00 m/s 6. -1.02 m/s F1,48=6.57	P < 0.0001 1. -2.00 m/s 7. -1.31 m/s F1,7041=212.93
2	P < 0.0001 1. -2.00 m/s 2. -1.37 m/s F1,641=46.94	******************** ******************** ******************** ********************	P < 0.0001 2. -1.37 m/s 3. -0.99 m/s F1,1492=404.28	P < 0.0001 2. -1.37 m/s 4. -0.54 m/s F1,734=398.65	P < 0.0001 2. -1.37 m/s 5. -1.01 m/s F1,1469=323.45	P < 0.0090 2. -1.37 m/s 6. -1.02 m/s F1,615=6.86	P < 0.0001 2. -1.37 m/s 7. -1.31 m/s F1,7608=21.27
3	P < 0.0001 1. -2.00 m/s 3. -0.99 m/s F1,925=277.56	P < 0.0001 2. -1.37 m/s 3. -0.99 m/s F1,1492=404.28	******************** ******************** ******************** ********************	P < 0.0001 3. -0.99 m/s 4. -0.54 m/s F1,1018=360.45	P > 0.05 3. -0.99 m/s 5. -1.01 m/s F1,1853=2.17	P > 0.05 3. -0.99 m/s 6. -1.02 m/s F1,899=0.12	P < 0.0001 3. -0.99 m/s 7. -1.31 m/s F1,7892=1087.72
4	P < 0.0001 1. -2.00 m/s 4. -0.54 m/s F1,167=148.53	P < 0.0001 2. -1.37 m/s 4. -0.54 m/s F1,734=398.65	P < 0.0001 3. -0.99 m/s 4. -0.54 m/s F1,1018=360.45	******************** ******************** ******************** ********************	P < 0.0001 4. -0.54 m/s 5. -1.01 m/s F1,1095=263.35	P < 0.0001 4. -0.54 m/s 6. -1.02 m/s F1,141=51.21	P < 0.0001 4. -0.54 m/s 7. -1.31 m/s F1,7134=1026.45
5	P < 0.0001 1. -2.00 m/s 5. -1.01 m/s F1,1002=217.25	P < 0.0001 2. -1.37 m/s 5. -1.01 m/s F1,1469=323.45	P > 0.05 3. -0.99 m/s 5. -1.01 m/s F1,1853=2.17	P < 0.0001 4. -0.54 m/s 5. -1.01 m/s F1,1095=263.35	******************** ******************** ******************** ********************	P > 0.05 5. -1.01 m/s 6. -1.02 m/s F1,976=0.01	P < 0.0001 5. -1.01 m/s 7. -1.44 m/s F1,7969=1125.34
6	P < 0.0136 1. -2.00 m/s 6. -1.02 m/s F1,48=6.57	P < 0.0090 2. -1.37 m/s 6. -1.02 m/s F1,615=6.86	P > 0.05 3. -0.99 m/s 6. -1.02 m/s F1,899=0.12	P < 0.0001 4. -0.54 m/s 6. -1.02 m/s F1,141=51.21	P > 0.05 5. -1.01 m/s 6. -1.02 m/s F1,976=0.01	******************** ******************** ******************** ********************	P < 0.0002 6. -0.87 m/s 7. -1.44 m/s F1,7015=29.55
7	P < 0.0001 1. -2.00 m/s 7. 1.31 m/s F1,7041=212.93	P < 0.0001 2. -1.37 m/s 7. -1.31 m/s F1,7608=21.27	P < 0.0001 3. -0.99 m/s 7. -1.31 m/s F1,7892=1087.72	P < 0.0001 4. -0.54 m/s 7. -1.31 m/s F1,7134=1026.45	P < 0.0001 5. -1.01 m/s 7. -1.44 m/s F1,7969=1125.34	P < 0.0002 6. -0.87 m/s 7. -1.44 m/s F1,7015=29.55	******************** ******************** ******************** ********************

Table 4 (Continued).

(e)

POSTBREEDING FEMALES
Bottom time

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 0.00 min 2. 7.39 min F1,641=152.41	P < 0.0001 1. 0.00 min 3. 1.11 min F1,925=33.23	P < 0.0001 1. 0.00 min 4. 1.59 min F1,167=64.43	P < 0.0001 1. 0.00 min 5. 1.79 min F1,1002=68.42	P < 0.0001 1. 0.00 min 6. 0.67 min F1,48=30.84	P < 0.0001 1. 0.00 min 7. 9.60 min F1,7041=375.37
2	P < 0.0001 1. 0.00 min 2. 7.39 min F1,641=152.41	******************** ******************** ******************** ********************	P < 0.0001 2. 7.39 min 3. 1.11 min F1,1492=2261.30	P < 0.0001 2. 7.39 min 4. 1.59 min F1,734=318.22	P < 0.0001 2. 7.39 min 5. 1.79 min F1,1569=1847.02	P < 0.0001 2. 7.39 min 6. 0.67 min F1,615=39.99	P < 0.0001 2. 7.39 min 7. 9.60 min F1,7608=284.05
3	P < 0.0001 1. 0.00 min 3. 1.11 min F1,925=33.23	P < 0.0001 2. 7.39 min 3. 1.11 min F1,1492=2261.30	******************** ******************** ******************** ********************	P < 0.0001 3. 1.11 min 4. 1.59 min F1,1018=19.33	P < 0.0001 3. 1.11 min 5. 1.79 min F1,1853=141.88	P > 0.05 3. 1.11 min 6. 0.67 min F1,889=6.79	P < 0.0001 3. 1.11 min 7. 9.60 min F1,7892=6774.92
4	P < 0.0001 1. 0.00 min 4. 1.59 min F1,167=64.43	P < 0.0001 2. 7.39 min 4. 1.59 min F1,734=318.22	P < 0.0001 3. 1.11 min 4. 1.59 min F1,1018=19.33	******************** ******************** ******************** ********************	P > 0.05 4. 1.59 min 5. 1.79 min F1,1095=3.01	P < 0.010 4. 1.59 min 6. 0.67 min F1,141=6.79	P < 0.0001 4. 1.59 min 7. 9.60 min F1,7134=902.30
5	P < 0.0001 1. 0.00 min 5. 1.79 min F1,1002=68.42	P < 0.0001 2. 7.39 min 5. 1.79 min F1,1569=1847.02	P < 0.0001 3. 1.11 min 5. 1.79 min F1,1853=141.88	P > 0.05 4. 1.59 min 5. 1.79 min F1,1095=3.01	******************** ******************** ******************** ********************	P < 0.0033 5. 1.79 min 6. 0.67 min F1,976=8.69	P < 0.0001 5. 1.79 min 7. 9.60 min F1,7969=6163.98
6	P < 0.0001 1. 0.00 min 6. 0.67 min F1,48=30.84	P < 0.0001 2. 7.39 min 6. 0.67 min F1,615=39.99	P > 0.05 3. 1.11 min 6. 0.67 min F1,889=6.79	P < 0.010 4. 1.59 min 6. 0.67 min F1,141=6.79	P < 0.0033 5. 1.79 min 6. 0.67 min F1,976=8.69	******************** ******************** ******************** ********************	P < 0.0001 6. 0.67 min 7. 9.60 min F1,7015=103.00
7	P < 0.0001 1. 0.00 min 7. 9.60 min F1,7041=375.37	P < 0.0001 2. 7.39 min 7. 9.60 min F1,7608=284.05	P < 0.0001 3. 1.11 min 7. 9.60 min F1,7892=6774.92	P < 0.0001 4. 1.59 min 7. 9.60 min F1,7134=902.30	P < 0.0001 5. 1.79 min 7. 9.60 min F1,7969=6163.98	P < 0.0001 6. 0.67 min 7. 9.60 min F1,7015=103.00	******************** ******************** ******************** ********************

Table 4 (Continued).

(f)

POSTMOULTING FEMALES
Depth

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 60.85 m 2. 174.84 m F1,1830=481.89	P < 0.0001 1. 60.85 m 3. 456.98 m F1,1565=593.26	P < 0.0001 1. 60.85 m 4. 413.95 m F1,463=3388.52	P < 0.0001 1. 60.85 m 5. 573.95 m F1,2219=738.27	P < 0.0001 1. 60.85 m 6. 571.64 m F1,149=604.38	P < 0.0001 1. 60.85 m 7. 459.69 m F1,19462=628.92
2	P < 0.0001 1. 60.85 m 2. 174.84 m F1,1830=481.89	******************** ******************** ******************** ********************	P < 0.0001 2. 174.84 m 3. 456.98 m F1,3195=4637.81	P < 0.0001 2. 174.84 m 4. 413.95 m F1,2093=2226.74	P < 0.0001 2. 174.84 m 5. 573.95 m F1,3849=7239.48	P < 0.0001 2. 174.84 m 6. 571.64 m F1,1779=2072.82	P < 0.0001 2. 174.84 m 7. 459.69 m F1,21092=5449.57
3	P < 0.0001 1. 60.85 m 3. 456.98 m F1,1565=593.26	P < 0.0001 2. 174.84 m 3. 456.98 m F1,3195=4637.81	******************** ******************** ******************** ********************	P < 0.0001 3. 456.98 m 4. 413.95 m F1,1828=19.52	P < 0.0001 3. 456.98 m 5. 573.95 m F1,3584=369.20	P < 0.0001 3. 456.98 m 6. 571.64 m F1,1514=23.49	P > 0.05 3. 456.98 m 7. 459.69 m F1,20828=0.39
4	P < 0.0001 1. 60.85 m 4. 413.95 m F1,463=3388.52	P < 0.0001 2. 174.84 m 4. 413.95 m F1,2093=2226.74	P < 0.0001 3. 456.98 m 4. 413.95 m F1,1828=19.52	******************** ******************** ******************** ********************	P < 0.0001 4. 413.95 m 5. 573.95 m F1,2482=224.97	P < 0.0001 4. 413.95 m 6. 571.64 m F1,412=33.10	P < 0.0001 4.413.95 m 7. 459.69 m F1,19725=29.14
5	P < 0.0001 1. 60.85 m 5. 573.95 m F1,2219=738.27	P < 0.0001 2. 174.84 m 5. 573.95 m F1,3849=7239.48	P < 0.0001 3. 456.98 m 5. 573.95 m F1,3584=369.20	P < 0.0001 4. 413.95 m 5. 573.95 m F1,2482=224.97	******************** ******************** ******************** ********************	P > 0.05 5. 573.95 m 6. 571.64 m F1,2168=0.01	P < 0.0001 5. 573.95 m 7. 459.69 m F1,21481=939.08
6	P < 0.0001 1. 60.85 m 6. 571.64 m F1,149=604.38	P < 0.0001 2. 174.84 m 6. 571.64 m F1,1779=2072.87	P < 0.0001 3. 456.98 m 6. 571.64 m F1,1514=23.49	P < 0.0001 4. 413.95 m 6. 571.64 m F1,412=33.10	P > 0.05 5. 573.95 m 6. 571.64 m F1,2168=0.01	******************** ******************** ******************** ********************	P < 0.0001 6. 571.64 m 7. 459.69 m F1,19411=24.44
7	P < 0.0001 1. 60.85 m 7. 459.69 m F1,19462=628.92	P < 0.0001 2. 174.84 m 7. 459.69 m F1,21092=5449.57	P > 0.05 3. 456.98 m 7. 459.69 m F1,20828=0.39	P < 0.0001 4.413.95 m 7. 459.69 m F1,19725=29.14	P < 0.0001 5. 573.95 m 7. 459.69 m F1,21481=939.08	P < 0.0001 6. 571.64 m 7. 459.69 m F1,19411=24.44	******************** ******************** ******************** ********************

Table 4 (Continued).

(g) .

POSTMOULTING FEMALES
Duration

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 2.37 min 2. 14.68 min F1,1830=559.59	P < 0.0001 1. 2.37 min 3. 30.32 min F1,1565=540.96	P < 0.0001 1. 2.37 min 4. 22.80 min F1,463=365.73	P < 0.0001 1. 2.37 min 5. 20.35 min F1,2219=520.82	P < 0.0001 1. 2.37 min 6. 25.52 min F1,149=712.20	P < 0.0001 1. 2.37 min 7. 26.00 min F1,19462=646.33
2	P < 0.0001 1. 2.37 min 2. 14.68 min F1,1830=559.59	******************** ******************** ******************** ********************	P < 0.0001 2. 14.68 min 3. 30.32 min F1,3195=2385.34	P < 0.0001 2. 14.68 min 4. 22.80 min F1,2093=469.81	P < 0.0001 2. 14.68 min 5. 20.35 min F1,3849=656.82	P < 0.0001 2. 14.68 min 6. 25.51 min F1,1797=201.48	P < 0.0001 2. 14.68 min 7. 26.00 min F1,21092=2474.68
3	P < 0.0001 1. 2.37 min 3. 30.32 min F1,1565=540.96	P < 0.0001 2. 14.68 min 3. 30.32 min F1,3195=2385.34	******************** ******************** ******************** ********************	P < 0.0001 3. 30.32 min 4. 22.80 min F1,1828=118.45	P < 0.0001 3. 30.32 min 5. 20.35 min F1,3584=894.56	P < 0.0052 3. 30.32 min 6. 25.51 min F1,1514=7.83	P < 0.0001 3. 30.32 min 7. 26.00 min F1,20828=278.45
4	P < 0.0001 1. 2.37 min 4. 22.80 min F1,463=365.73	P < 0.0001 2. 14.68 min 4. 22.80 min F1,2093=469.81	P < 0.0001 3. 30.32 min 4. 22.80 min F1,1828=118.45	******************** ******************** ******************** ********************	P < 0.0001 4. 22.80 min 5. 20.35 min F1,2482=26.72	P > 0.05 4. 22.80 min 6. 22.51 min F1,412=2.97	P < 0.0001 4. 22.80 min 7. 26.00 min F1,19725=41.76
5	P < 0.0001 1. 2.37 min 5. 20.35 min F1,2219=520.82	P < 0.0001 2. 14.68 min 5. 20.35 min F1,3849=656.82	P < 0.0001 3. 30.32 min 5. 20.35 min F1,3584=894.56	P < 0.0001 4. 22.80 min 5. 20.35 min F1,2482=26.72	******************** ******************** ******************** ********************	P < 0.0001 5. 20.35 min 6. 25.51 min F1,2168=20.79	P < 0.0001 5. 20.35 min 7. 26.00 min F1,21481=720.87
6	P < 0.0001 1. 2.37 min 6. 25.52 min F1,149=712.20	P < 0.0001 2. 14.68 min 6. 25.51 min F1,1797=201.48	P < 0.0052 3. 30.32 min 6. 25.51 min F1,1514=7.83	P > 0.05 4. 22.80 min 6. 22.51 min F1,412=2.97	P < 0.0001 5. 20.35 min 6. 25.51 min F1,2168=20.79	******************** ******************** ******************** ********************	P > 0.05 6. 25.51 min 7. 26.00 min F1,19411=0.14
7	P < 0.0001 1. 2.37 min 7. 26.00 min F1,19462=646.33	P < 0.0001 2. 14.68 min 7. 26.00 min F1,21092=2474.68	P < 0.0001 3. 30.32 min 7. 26.00 min F1,20828=278.45	P < 0.0001 4. 22.80 min 7. 26.00 min F1,19725=41.76	P < 0.0001 5. 20.35 min 7. 26.00 min F1,21481=720.87	P > 0.05 6. 25.51 min 7. 26.00 min F1,19411=0.14	******************** ******************** ******************** ********************

(h)

Table 4 (Continued).

POSTMOULTING FEMALES
Descent

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P > 0.05 1. 1.19 m/s 2. 1.14 m/s F1,1830=1.18	P < 0.0001 1. 1.19 m/s 3. 0.40 m/s F1,1565=1020.77	P > 0.05 1. 1.19 m/s 4. 1.23 m/s F1,483=0.35	P < 0.0009 1. 1.19 m/s 5. 1.07 m/s F1,2219=11.03	P < 0.0001 1. 1.19 m/s 6. 0.77 m/s F1,149=17.74	P < 0.0004 1. 1.19 m/s 7. 1.33 m/s F1,19462=12.71
2	P > 0.05 1. 1.19 m/s 2. 1.14 m/s F1,1830=1.18	******************** ******************** ******************** ********************	P < 0.0001 2. 1.14 m/s 3. 0.40 m/s F1,3195=3675.85	P < 0.0009 2. 1.14 m/s 4. 1.23 m/s F1,2093=11.05	P < 0.0001 2. 1.14 m/s 5. 1.07 m/s F1,3849=33.59	P < 0.0001 2. 1.14 m/s 6. 0.77 m/s F1,1799=36.57	P < 0.0001 2. 1.14 m/s 7. 1.33 m/s F1,21092=377.49
3	P < 0.0001 1. 1.19 m/s 3. 0.40 m/s F1,1565=1020.77	P < 0.0001 2. 1.14 m/s 3. 0.40 m/s F1,3195=3675.85	******************** ******************** ******************** ********************	P < 0.0001 3. 0.40 m/s 4. 1.23 m/s F1,1828=3246.16	P < 0.0001 3. 0.40 m/s 5. 1.07 m/s F1,3584=4710.30	P < 0.0001 3. 0.40 m/s 6. 0.77 m/s F1,412=53.40	P < 0.0001 3. 0.40 m/s 7. 1.33 m/s F1,20828=9022.86
4	P > 0.05 1. 1.19 m/s 4. 1.23 m/s F1,483=0.35	P < 0.0009 2. 1.14 m/s 4. 1.23 m/s F1,2093=11.05	P < 0.0001 3. 0.40 m/s 4. 1.23 m/s F1,1828=3246.16	******************** ******************** ******************** ********************	P < 0.0001 4. 1.23 m/s 5. 1.07 m/s F1,2482=59.81	P < 0.0001 4. 1.23 m/s 6. 0.77 m/s F1,412=53.40	P < 0.0001 4. 1.23 m/s 7. 1.33 m/s F1,19725=25.38
5	P < 0.0009 1. 1.19 m/s 5. 1.07 m/s F1,2219=11.03	P < 0.0001 2. 1.14 m/s 5. 1.07 m/s F1,3849=33.59	P < 0.0001 3. 0.40 m/s 5. 1.07 m/s F1,3584=4710.30	P < 0.0001 4. 1.23 m/s 5. 1.07 m/s F1,2482=59.81	******************** ******************** ******************** ********************	P < 0.0001 5. 1.07 m/s 6. 0.77 m/s F1,2168=38.84	P < 0.0001 5. 1.07 m/s 7. 1.33 m/s F1,21481=411.74
6	P < 0.0001 1. 1.19 m/s 6. 0.77 m/s F1,149=17.74	P < 0.0001 2. 1.14 m/s 6. 0.77 m/s F1,1799=36.57	P < 0.0001 3. 0.40 m/s 6. 0.77 m/s F1,412=53.40	P < 0.0001 4. 1.23 m/s 6. 0.77 m/s F1,412=53.40	P < 0.0001 5. 1.07 m/s 6. 0.77 m/s F1,2168=38.84	******************** ******************** ******************** ********************	P < 0.0001 6. 0.77 m/s 7. 1.33 m/s F1,19411=115.61
7	P < 0.0004 1. 1.19 m/s 7. 1.33 m/s F1,19462=12.71	P < 0.0001 2. 1.14 m/s 7. 1.33 m/s F1,21092=377.49	P < 0.0001 3. 0.40 m/s 7. 1.33 m/s F1,20828=9022.86	P < 0.0001 4. 1.23 m/s 7. 1.33 m/s F1,19725=25.38	P < 0.0001 5. 1.07 m/s 7. 1.33 m/s F1,21481=411.74	P < 0.0001 6. 0.77 m/s 7. 1.33 m/s F1,19411=115.61	******************** ******************** ******************** ********************

Table 4 (Continued).

(i)

POSTMOULTING FEMALES
Ascent

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P > 0.05 1. -1.20 m/s 2. -1.22 m/s F1,1830=0.11	P < 0.0008 1. -1.20 m/s 3. -1.06 m/s F1,1505=11.18	P < 0.0001 1. -1.20 m/s 4. -0.49 m/s F1,463=260.60	P < 0.05 1. -1.20 m/s 5. -1.13 m/s F1,2219=4.03	P < 0.0002 1. -1.20 m/s 6. -0.79 m/s F1,149=14.70	P < 0.05 1. -1.20 m/s 7. -1.27 m/s F1,19462=5.28
2	P > 0.05 1. -1.20 m/s 2. -1.22 m/s F1,1830=0.11	******************** ******************** ******************** ********************	P < 0.0001 2. -1.22 m/s 3. -1.06 m/s F1,3195=104.26	P < 0.0001 2. -1.22 m/s 4. -0.50 m/s F1,2093=765.29	P < 0.0001 2. -1.22 m/s 5. -1.13 m/s F1,3849=46.51	P < 0.0001 2. -1.22 m/s 6. -0.79 m/s F1,1779=37.98	P < 0.05 2. -1.22 m/s 7. -1.27 m/s F1,21092=4.95
3	P < 0.0008 1. -1.20 m/s 3. -1.06 m/s F1,1505=11.18	P < 0.0001 2. -1.22 m/s 3. -1.06 m/s F1,3195=104.26	******************** ******************** ******************** ********************	P < 0.0001 3. -1.06 m/s 4. -0.50 m/s F1,1828=697.82	P < 0.0001 3. -1.06 m/s 5. -1.13 m/s F1,3584=34.42	P < 0.0001 3. -1.06 m/s 6. -0.79 m/s F1,1514=22.77	P < 0.0001 3. -1.06 m/s 7. -1.27 m/s F1,20828=632.31
4	P < 0.0001 1. -1.20 m/s 4. -0.49 m/s F1,463=260.60	P < 0.0001 2. -1.22 m/s 4. -0.50 m/s F1,2093=765.29	P < 0.0001 3. -1.06 m/s 4. -0.50 m/s F1,1828=697.82	******************** ******************** ******************** ********************	P < 0.0001 4. -0.49 m/s 5. -1.13 m/s F1,2482=1230.26	P < 0.0001 4. -0.49 m/s 6. -0.79 m/s F1,412=81.00	P < 0.0001 4. -0.49 m/s 7. -1.27 m/s F1,19725=2227.54
5	P < 0.05 1. -1.20 m/s 5. -1.13 m/s F1,2219=4.03	P < 0.0001 2. -1.22 m/s 5. -1.13 m/s F1,3849=46.51	P < 0.0001 3. -1.06 m/s 5. -1.13 m/s F1,3584=34.42	P < 0.0001 4. -0.49 m/s 5. -1.13 m/s F1,2482=1230.26	******************** ******************** ******************** ********************	P < 0.0001 5. -1.13 m/s 6. -0.79 m/s F1,2168=50.69	P < 0.0001 5. -1.13 m/s 7. -1.27 m/s F1,21481=411.74
6	P < 0.0002 1. -1.20 m/s 6. -0.79 m/s F1,149=14.70	P < 0.0001 2. -1.22 m/s 6. -0.79 m/s F1,1779=37.98	P < 0.0001 3. -1.06 m/s 6. -0.79 m/s F1,1514=22.77	P < 0.0001 4. -0.49 m/s 6. -0.79 m/s F1,412=81.00	P < 0.0001 5. -1.13 m/s 6. -0.79 m/s F1,2168=50.69	******************** ******************** ******************** ********************	P < 0.0001 6. -0.79 m/s 7. -1.27 m/s F1,19411=118.91
7	P < 0.05 1. -1.20 m/s 7. -1.27 m/s F1,19462=5.28	P < 0.05 2. -1.22 m/s 7. -1.27 m/s F1,21092=4.95	P < 0.0001 3. -1.06 m/s 7. -1.27 m/s F1,20828=632.31	P < 0.0001 4. -0.49 m/s 7. -1.27 m/s F1,19725=2227.5	P < 0.0001 5. -1.13 m/s 7. -1.27 m/s F1,21481=411.74	P < 0.0001 6. -0.79 m/s 7. -1.27 m/s F1,19411=118.91	******************** ******************** ******************** ********************

Table 4 (Continued).

(j)

POSTMOULTING FEMALES
Bottom time

	Dive type						
	1	2	3	4	5	6	7
1	******************** ******************** ******************** ********************	P < 0.0001 1. 0.16 min 2. 9.87 min F1,1830=399.15	P < 0.0001 1. 0.16 min 3. 1.94 min F1,1565=69.39	P < 0.0001 1. 0.16 min 4. 2.42 min F1,463=103.09	P < 0.0001 1. 0.16 min 5. 2.43 min F1,2219=166.28	P < 0.0001 1. 0.16 min 6. 0.99 min F1,149=44.97	P < 0.0001 1. 0.16 min 7. 15.35 min F1,19462=376.25
2	P < 0.0001 1. 0.16 min 2. 9.87 min F1,1830=399.15	******************** ******************** ******************** ********************	P < 0.0001 2. 9.87 min 3. 1.94 min F1,3195=3195.16	P < 0.0001 2. 9.87 min 4. 2.42 min F1,2093=790.03	P < 0.0001 2. 9.87 min 5. 2.43 min F1,3849=4098.75	P < 0.0001 2. 9.87 min 6. 0.99 min F1,1779=160.88	P < 0.0001 2. 9.87 min 7. 15.35 min F1,21092=796.21
3	P < 0.0001 1. 0.16 min 3. 1.94 min F1,1565=69.39	P < 0.0001 2. 9.87 min 3. 1.94 min F1,3195=3195.16	******************** ******************** ******************** ********************	P < 0.0001 3. 1.94 min 4. 2.42 min F1,1828=12.60	P < 0.0001 3. 1.94 min 5. 2.43 min F1,3584=49.36	P < 0.0037 3. 1.94 min 6. 0.99 min F1,1514=8.46	P < 0.0001 3. 1.94 min 7. 15.35 min F1,20828=4164.27
4	P < 0.0001 1. 0.16 min 4. 2.42 min F1,463=103.09	P < 0.0001 2. 9.87 min 4. 2.42 min F1,2093=790.03	P < 0.0001 3. 1.94 min 4. 2.42 min F1,1828=12.60	******************** ******************** ******************** ********************	P > 0.05 4. 2.42 min 5. 2.43 min F1,2482=0.01	P < 0.0001 4. 2.42 min 6. 0.99 min F1,412=17.54	P < 0.0001 4. 2.42 min 7. 15.35 min F1,19725=965.98
5	P < 0.0001 1. 0.16 min 5. 2.43 min F1,2219=166.28	P < 0.0001 2. 9.87 min 5. 2.43 min F1,3849=4098.75	P < 0.0001 3. 1.94 min 5. 2.43 min F1,3584=49.36	P > 0.05 4. 2.42 min 5. 2.43 min F1,2482=0.01	******************** ******************** ******************** ********************	P < 0.0001 5. 2.43 min 6. 0.99 min F1,2168=29.43	P < 0.0001 5. 2.43 min 7. 15.35 min F1,21481=5593.01
6	P < 0.0001 1. 0.16 min 6. 0.99 min F1,149=44.97	P < 0.0001 2. 9.87 min 6. 0.99 min F1,1779=160.88	P < 0.0037 3. 1.94 min 6. 0.99 min F1,1514=8.46	P < 0.0001 4. 2.42 min 6. 0.99 min F1,412=17.54	P < 0.0001 5. 2.43 min 6. 0.99 min F1,2168=29.43	******************** ******************** ******************** ********************	P < 0.0001 6. 0.99 min 7. 15.35 min F1,19411=163.83
7	P < 0.0001 1. 0.16 min 7. 15.35 min F1,19462=376.25	P < 0.0001 2. 9.87 min 7. 15.35 min F1,21092=796.21	P < 0.0001 3. 1.94 min 7. 15.35 min F1,20828=4164.27	P < 0.0001 4. 2.42 min 7. 15.35 min F1,19725=965.98	P < 0.0001 5. 2.43 min 7. 15.35 min F1,21481=5593.01	P < 0.0001 6. 0.99 min 7. 15.35 min F1,19411=163.83	******************** ******************** ******************** ********************

Table 5. Statistical relationships (ANOVA analyses) between postbreeding and postmoulting females for (a) dive depth, (b) dive duration, (c) descent rates, (d) ascent rates and (e) bottom times of dive types 1 - 7. (pb - postbreeding; pm - postmoulting).

(a) Dive Depth

Dive type	Mean dive depth (m)		P-value	F-value
	pb	pm		
1	31.89	60.85	P < 0.0001	F1,137=18.23
2	156.42	174.84	P < 0.0001	F1,2334=53.15
3	312.69	456.98	P < 0.0001	F1,2353=472.26
4	309.23	413.95	P < 0.0001	F1,493=35.61
5	480.48	573.95	P < 0.0001	F1,3084=151.02
6	453.50	571.64	P > 0.05	F1,60=3.67
7	454.99	459.69	P < 0.05	F1,26366=4.20

(b) Dive Duration

Dive type	Mean dive duration (min)		P-value	F-value
	pb	pm		
1	0.63	2.37	P < 0.0001	F1,137=30.76
2	11.14	14.68	P < 0.0001	F1,2334=228.15
3	17.09	30.32	P < 0.0001	F1,2353=958.40
4	15.12	22.80	P < 0.0001	F1,493=62.62
5	17.22	20.35	P < 0.0001	F1,3084=132.57
6	16.97	25.51	P < 0.0012	F1,60=11.49
7	19.18	26.00	P < 0.0001	F1,26366=3400.16

pb - postbreeding
pm - postmoulting

Table 5 (Continued).

(c)

Descent rates

Dive type	Mean descent rates (m/s)		P-value	F-value
	pb	pm		
1	2.43	1.19	$P < 0.0001$	F1,137=53.21
2	1.19	1.14	$P < 0.0095$	F1,2334=6.73
3	0.46	0.40	$P < 0.0001$	F1,2353=79.49
4	1.29	1.23	$P > 0.05$	F1,493=1.85
5	1.01	1.07	$P < 0.0001$	F1,3084=17.93
6	0.87	0.77	$P > 0.05$	F1,60=1.44
7	1.44	1.33	$P < 0.0001$	F1,2636=467.61

(d)

Ascent rates

Dive type	Mean ascent rates (m/s)		P-value	F-value
	pb	pm		
1	-2.00	-1.19	$P < 0.0001$	F1,137=20.76
2	-1.37	-1.22	$P < 0.0001$	F1,2334=46.34
3	-0.99	-1.05	$P < 0.0001$	F1,2353=18.40
4	-0.54	-0.49	$P > 0.05$	F1,493=3.45
5	-1.01	-1.13	$P < 0.0001$	F1,3084=79.56
6	-1.02	-0.79	$P < 0.0052$	F1,60=8.43
7	-1.31	-1.27	$P < 0.0001$	F1,26366=97.34

pb - postbreeding
pm - postmoulting

Table 5 (Continued).

(e) Bottom times

Dive type	Mean bottom times (min)		P-value	F-value
	pb	pm		
1	0.16	0.00	P > 0.05	F1,137=0.31
2	7.39	9.87	P < 0.0001	F1,2334=128.16
3	1.11	1.94	P < 0.0001	F1,2353=101.29
4	1.59	2.42	P < 0.0001	F1,493=14.88
5	1.79	2.43	P < 0.0001	F1,3084=88.98
6	0.67	0.99	P > 0.05	F1,60=0.58
7	9.60	15.35	P < 0.0001	F1,26366=3484.11

pb - postbreeding
pm - postmoulting

TYPE 2 dives

At a mean depth of 165 m and mean dive durations of 12.9 min, these dives were on average 119 m deeper and 11.4 min longer than that of type 1 dives. The descent and ascent rates were virtually identical, but slower than type 1 dives by 0.5 m/s. There was a significant increase in mean bottom times by 8.6 min over type 1 dives (Figure 4e).

(a) Amongst dive types:

Dive depth and duration

Postbreeding and postmoulting females: Mean depth and duration of type 2 dives were significantly increased over type 1 dives, but significantly shallower and shorter than all other dive types (Tables 4a, 4b, 4f & 4g).

Descent rates

Postbreeding females: Mean descent rates were significantly slower than dive types 1, 4 and 7 dives, and significantly faster than dive types 3, 5 and 6 (Table 4c). *Postmoulting females:* As for postbreeding females, except that mean descent rates were not significantly different to dive type 1 (Table 4h).

Ascent rates

Postbreeding females: Mean ascent rates were significantly slower than dive types 1, and significantly faster than all other dive types (Table 4d). *Postmoulting females:* Mean ascent rates were significantly slower than dive types 7, significantly faster than dive types 3 - 6, but not significantly different to type 1 dives (Table 4i).

Bottom times

Postbreeding and postmoulting females: Bottom times were significantly longer than dive types 1 - 6, but significantly shorter than dive type 7 (Tables 4e & 4j).

(b) Within dive types:

Type 2 dives were significantly deeper (by 18.42 m) and longer (by 3.54 min) in postmoulting females (Tables 5a & 5b), as were the mean bottom times (Table 5e). Rates of descent and ascent were significantly faster in postbreeding females (Tables 5c & 5d).

TYPE 3 dives

At a mean depth of 388 m and mean dive duration of 27.3 min, these dives were on average deeper (by 233 - 343 m) and longer (by 10.7 - 22.2 min) than dive types 2 and 1, respectively. Mean ascent rates were significantly ($P < 0.0001$) faster than the descents by 0.59 m/s, whereas mean bottom times were relatively short (at 1.5 min) (Figure 7).

(a) Amongst dive types:

Dive depth

Postbreeding females: Type 3 dives were significantly deeper than dive types 1 and 2, significantly shallower than dive types 5 - 7, but not significantly different to type 4 dives (Table 4a). *Postmoulting females:* Type 3 dives were significantly deeper than dive types 1, 2 and 4, significantly shallower than dive types 5 and 6, but similar to type 7 dives (Table 4f).

Dive duration

Postbreeding females: Mean dive durations were significantly longer than dive types 1 - 3, significantly shorter than dive type 7, and similar to type 5 and 6 dives (Table 4b). *Postmoulting females:* Mean dive durations were significantly longer than in all other dive types (Table 4g).

Descent rates

Postbreeding and postmoulting females: Mean descent rates were significantly slower than all other dive types (Tables 4c & 4h).

Ascent rates

Postbreeding females: Mean ascent rates were significantly slower than dive types 1, 2 and 7, significantly faster than dive type 4, and similar to type 5 and 6 dives (Table 4d). *Postmoulting females:* Mean ascent rates were significantly slower than dive types 1, 2, 5 and 7, but significantly faster than dive types 4 and 6 (Table 4i).

Bottom times

Postbreeding females: Mean bottom times of type 3 dives were significantly longer than dive type 1, shorter than dive types 2, 4, 5 and 7, but similar to dive type 6 (Tables 4e). *Postmoulting females:* Mean bottom times were significantly longer than dive types 1 and 6 and significantly shorter than dive types 2, 4, 5 and 7 (Table 4j).

(b) Within dive types:

Mean depths recorded for postmoulting females were significantly greater and longer ($P < 0.0001$) than that of postbreeding females (Tables 5a & 5b). The descent rates were significantly slower than the ascent rates (Tables 5c & 5d). Bottom times of postmoulting females were significantly longer (by 2.48 min) than postbreeding females (Table 5e).

TYPE 4 dives

Mean dive depths (361 ± 74 m) were virtually similar to type 3 dives, but of shorter duration by 8 min (mean dive duration 18.9 ± 5.4 min). Mean descent rates were significantly ($P < 0.0001$) faster than the ascents by 0.75 m/s, whereas mean bottom times were relatively short (at 2 min) (Figure 7).

(a) Amongst dive types:

Dive depth

Postbreeding females: Type 4 dives were significantly deeper than dive types 1 and 2, significantly shallower than dive types 5 - 7, but similar to type 3 dives (Table 4a). *Postmoulting females:* Similar to postbreeding females, but also significantly shallower than dive type 3 (Table 4b).

Dive duration

Postbreeding females: Dives were significantly longer than dive types 1 and 2, significantly shorter than dive types 3, 5 and 7, but similar to type 6 dives (Table 4b). *Postmoulting females:* These dives were significantly longer than dive types 1, 2 and 5, significantly shorter than dive types 3 and 7, but similar to type 6 dives (Table 4g).

Descent rates

Postbreeding females: Descent rates were significantly faster than dive types 2, 3, 5 and 6, but significantly slower than dive types 1 and 7 (Table 4c). *Postmoulting females:* Rates were significantly faster than dive types 2, 3, 5 and 6, significantly slower than dive type 7, but similar to type 1 dives (Table 4h).

Ascent rates

Postbreeding and postmoulting females: Mean ascent rates were significantly slower than all other dive types (Table 4d).

Bottom times

Postbreeding and postmoulting females: Bottom times were significantly shorter than dive types 2 and 7, significantly longer than dive types 1, 3 and 6, but similar to type 5 dives (Table 4e).

(b) Within dive types:

Dives of postmoulting females were significantly deeper and longer than those of postbreeding females (Tables 5a & 5b). The descent and ascent rates were not significantly different between the two groups (Tables 5c & 5d), whereas postmoulting females had significantly longer bottom times than postbreeding females (Table 5e).

TYPE 5 dives

Mean depth was 527 ± 66 m and mean duration was 18.8 ± 2.2 min, which was very similar to type 4 dives. Rates of descent and ascent were virtually identical (at 1.05 m/s) and similar to the ascent rates of type 3 dives, with mean bottom times relatively short at 1.1 ± 0.1 min (Figure 7).

(a) Amongst dive types:

Dive depth

Postbreeding and postmoulting females: Dives were significantly deeper than dive types 1 - 4 and 7, but similar to type 6 dives (Tables 4a & 4f).

Dive duration

Postbreeding females: These dives were significantly longer than dive types 1, 2 and 4, significantly shorter than dive type 7, but similar to type 3 and 6 dives (Table 4b). *Postmoulting females:* Dives were significantly longer than dive types 1 and 2, but significantly shorter than dive types 3, 4, 6 and 7 (Table 4g).

Descent rates

Postbreeding females: Descent rates were significantly slower than dive types 1, 2, 4 and 7, significantly faster than dive type 3, but similar to type 6 dives (Table 4c). *Postmoulting females:* Rates were significantly faster than dives types 3 and 6, but significantly slower than dive types 1, 2, 5 and 7 (Table 4h).

Ascent rates

Postbreeding females: Ascent rates were significantly slower than dive types 1, 2 and 7, significantly faster than dive types 4, but similar to type 3 and 6 dives (Table 4d). *Postmoulting females:* Rates were significantly faster than dive types 3, 4 and 6, significantly slower than dive types 2 and 7, but similar to type 1 dives (Table 4i).

Bottom times

Postbreeding females and postmoulting females: Bottom times were significantly longer than dive types 1, 3 and 6, significantly shorter than dive types 2 and 7, but similar to type 4 dives (Tables 4e & 4j).

(b) Within dive types:

Dives of postmoulting females were significantly deeper (by 93.47 m) and longer (by 3.13 min) than postbreeding females (Tables 5a & 5b respectively). The mean descent and ascent rates of postbreeding females were significantly slower than that of postmoulting females (Tables 5c & 5d), whereas mean bottom times of postmoulting females were significantly longer by 0.64 min (Table 5e).

TYPE 6 dives

These dives had profiles similar to type 5 dives, with mean dive depths of 512 ± 83 m and mean dive durations of 21.2 ± 6.0 min, but with shorter mean bottom times (by 1.3 min). At a depth of approximately 400 m the rates of descent and ascent slowed down considerably. The mean descent and ascent rates (of 0.89 m/s) were virtually identical with the bottom of the dive spiked, owing to a short bottom time and an increase in the rates of descent and ascent before and after reaching the bottom of the dive (Figure 7).

(a) Amongst dive types:

Dive depth

Postbreeding females: Dives were significantly deeper than dive types 1 - 4, but similar to type 5 and 7 dives (Table 4a). *Postmoulting females:* Dive depths were significantly deeper than dive types 1 - 4 and 7, but similar to type 5 dives (Table 4f).

Dive duration

Postbreeding females: Dives were significantly longer than dive types 1 and 2 dives, but similar to dive types 3 - 5 and 7 dives (Table 4b). *Postmoulting females:* Type 6 dives were similar to dive types 4 and 7, but significantly longer than dive types 1 - 3 and 5 (Table 4g).

Descent rates

Postbreeding females: Rates of descent were significantly slower than dive types 1 - 4 and 7, but similar to type 5 dives (Table 4c). *Postmoulting females:* Rates were significantly slower than dive types 1, 2, 4, 5 and 7, but significantly faster than type 3 dives (Table 4h).

Ascent rates

Postbreeding females: Ascent rates were significantly slower than dive types 1, 2 and 7, significantly faster than dive types 4, but similar to dive types 3 and 5 (Table 4d). *Postmoulting females:* Rates were significantly slower than dive types 1 - 3, 5 and 7, but significantly faster than types 4 dives (Table 4i).

Bottom times

Postbreeding females: Dives were significantly longer than dive type 1, significantly shorter than dive types 2, 4, 5, and 7, but similar to type 3 dives (Table 4e). *Postmoulting females:* Bottom time were significantly longer than dive types 1, but significantly shorter than dive types 2 - 5 and 7 (Table 4j).

(b) Between dive types:

Dive depths were not significantly different between the two groups, although dive durations of postmoulting females were significantly longer than that of postbreeding females (by 8.54 min) (Table 5a & 5b). Descent rates were not significantly different ($P > 0.05$) between the groups, but ascent rates of postmoulting females were significantly slower (by 0.23 m/s) than that of postbreeding females (Table 5c & 5d). Bottom times were not significantly different (Table 5e).

TYPE 7 dives

At a mean depth of 457 ± 3.2 m and mean dive durations of 22.6 ± 4.8 min, these dives were on average shallower (by 55 m) but virtually similar in duration than that of type 6 dives. These dives were characterized by rapid mean descents (1.38 ± 0.1 m/s) and ascent (1.29 ± 0.1 m/s) rates, and well demarcated, extended bottom times (at 12.5 ± 4.1 min) which were ± 5.5 min longer than the mean recorded for all other dive types. Bottom times were distinguished from other dive types by having distinct up and down movements (wiggles).

(a) Amongst dive types:

Dive depth

Postbreeding females: Dives were significantly deeper than dive types 1 - 4, significantly shallower than dive type 5, but similar to type 6 dives (Table 4a). *Postmoulting females:* Dives were significantly deeper than dive types 1, 2 and 4, significantly shallower than dive types 5 and 6 dives, but similar to type 3 dives (Table 4f).

Dive duration

Postbreeding females: Dives were significantly longer than dive types 1 - 5, but similar to type 6 dives (Table 4b). *Postmoulting females:* These dives were significantly longer than dive types 1, 2, 4 and 5, significantly shorter than dive type 3, but similar to type 6 dives (Table 4g).

Descent rates

Postbreeding females: Rates of descent were significantly faster than dive types 2 - 6, but significantly slower than dive type 1 dives (Table 4c). *Postmoulting females:* Rates were significantly faster than all other dives types (Table 4h).

Ascent rates

Postbreeding females: These dives were significantly faster than dive types 3 - 6, but significantly slower than dive types 1 and 2 (Table 4d). *Postmoulting females:* Dives were significantly faster than dive types 3 - 6, but not significantly different to dive types 1 and 2

(Table 4i).

Bottom times

Postbreeding and postmoulting females: Bottom times were significantly longer than all other dive types (Table 4e & 4j).

(b) Within dive types:

Dive depths and durations of postmoulting females were significantly greater than that of postbreeding females (Table 5a & 5b). The rates of descent and ascent of postmoulting females were significantly faster than that of postbreeding females (Table 5c & 5d) and with significantly longer mean bottom times (by 5.75 min) (Table 5e).

Relationships between dive elements

Significant positive linear relationships existed between dive depth and dive duration for all dive types in both postbreeding and postmoulting females (Table 6a). The correlation coefficients for these two variables were highest for postbreeding females in each of the different dive types, although overall poor, especially for dive types 3 and 7 in postmoulting females. There were significant positive linear relationships between dive depth and bottom time for all but dive type 6 in postbreeding females, and types 6 and 7 for postmoulting females. Correlation coefficients were very low for all the groups (Table 6b).

In both groups of females, the linear relationship between dive duration and bottom time was significant for all but dive type 6. Dive types 2 and 7 showed high correlation coefficients between the two parameters, whereas the remainder of dive types were weak (Table 6c). Significant linear relationships existed between descent rates and bottom time for dive type 5 in postbreeding females, and dive types 2 and 7 for postmoulting females, but with negligible correlation coefficients. Linear relationships between ascent rates and bottom times were significant for dive types 2, 5 and 7 for postbreeding females, and dive types 2, 4 and 7 for postmoulting females despite very low correlation coefficients. No relationships existed between dive depths and descent and ascent rates, as well as dive durations and descent and ascent rates for any of the dive types (Tables 6d & 6e).

Table 6. Linear relationships between (a) depth/duration, (b) depth/bottom time, (c) duration/bottom times, (d) descent/bottom times and (e) ascent/ bottom times of dive types 1 - 7 for postbreeding and postmoulting females from Marion Island, recorded during 1990 - 1994.

(a)

Depth/Duration

Dive type	Status	Y=mx+c	R-Square	F-value	Pr > F
1	pb	Y=3.66x+33.15	0.69	F1,36=82.05	P < 0.0001
2	pb	Y=0.39x+10.56	0.55	F1,603=745.75	P < 0.0001
3	pb	Y=0.51x+22.81	0.69	F1,887=1969.59	P < 0.0001
4	pb	Y=2.10x+16.52	0.32	F1,129=61.75	P < 0.0001
5	pb	Y=1.18x+30.92	0.42	F1,964=683.96	P < 0.0001
6	pb	Y=5.14x+20.86	0.62	F1,10=16.49	P < 0.0023
7	pb	Y=0.31x+24.61	0.47	F1,7003=6263.53	P < 0.0001
1	pm	Y=0.01x+0.03	0.38	F1.99=61.88	P < 0.0001
2	pm	Y=0.20x+5.08	0.27	F1,1729=625.43	P < 0.0001
3	pm	Y=0.32x+5.97	0.19	F1,1464=354.47	P < 0.0001
4	pm	Y=0.73x+9.24	0.30	F1,362=158.46	P < 0.0001
5	pm	Y=0.43x+13.87	0.33	F1,2118=1064.01	P < 0.0001
6	pm	Y=2.72x+15.39	0.40	F1,48=32.13	P < 0.0001
7	pm	Y=0.12x+5.90	0.12	F1,19361=2613.42	P < 0.0001

pb - postbreeding
pm - postmoulting

(b)

Depth/Bottom time

Dive type	Status	Y=mx+c	R-Square	F-value	Pr > F
1	pb	Y=39.22x+86.00	0.12	F1,36=4.81	P < 0.05
2	pb	Y=0.50x+10.35	0.41	F1,603=425.67	P < 0.0001
3	pb	Y=4.14x+11.90	0.01	F1,887=8.27	P < 0.0041
4	pb	Y=10.22x+39.98	0.11	F1,129=15.31	P < 0.0001
5	pb	Y=4.95x+34.86	0.05	F1,964=49.55	P < 0.0001
6	pb	Y=57.63x+59.95	0.09	F1,10=1.08	P > 0.05
7	pb	Y=0.67x+12.41	0.05	F1,7003=339.56	P < 0.0001
1	pm	Y=23.58x+86.95	0.12	F1,99=13.59	P < 0.0004
2	pm	Y=0.22x+4.55	0.19	F1,1729=410.29	P < 0.0001
3	pm	Y=1.79x+19.37	0.07	F1,1464=116.84	P < 0.0001
4	pm	Y=3.78x+24.82	0.11	F1,362=43.10	P < 0.0001
5	pm	Y=2.15x+24.38	0.06	F1,2118=128.46	P < 0.0001
6	pm	Y=20.66x-4.24	0.00	F1,48=0.04	P > 0.05
7	pm	Y=0.15x-0.26	0.00	F1,19361=3.29	P > 0.05

pb - postbreeding
pm - postmoulting

Table 6 (Continued).

(c)

Duration/Bottom time

Dive type	Status	Y=mx+c	R-Square	F-value	Pr > F
1	pb	Y=0.86x+3.63	0.33	F1,36=17.91	P < 0.0002
2	pb	Y=0.02x+1.05	0.86	F1,603=3599.17	P < 0.0001
3	pb	Y=0.15x+1.29	0.08	F1,887=79.77	P < 0.0001
4	pb	Y=0.30x+2.48	0.34	F1,129=67.62	P < 0.0001
5	pb	Y=0.09x+1.13	0.12	F1,964=128.13	P < 0.0001
6	pb	Y=2.29x+0.12	0.00	F1,10=0.03	P > 0.05
7	pb	Y=0.01x+1.22	0.57	F1,7003=9380.53	P < 0.0001
1	pm	Y=1.16x+4.38	0.13	F1,99=14.36	P < 0.0003
2	pm	Y=0.01x+0.98	0.86	F1,1729=10793.84	P < 0.0001
3	pm	Y=0.13x+1.58	0.09	F1,1464=144.03	P < 0.0001
4	pm	Y=0.19x+2.75	0.36	F1,362=207.58	P < 0.0001
5	pm	Y=0.09x+1.59	0.14	F1,2118=348.08	P < 0.0001
6	pm	Y=0.85x+0.39	0.00	F1,48=0.22	P > 0.05
7	pm	Y=0.01x+1.04	0.78	F1,19361=70402.61	P < 0.0001

pb - postbreeding
pm - postmoulting

(d)

Descent/Bottom time

Dive type	Status	Y=mx+c	R-Square	F-value	Pr > F
1	pb	Y=1.95x-1.34	0.01	F1,36=0.47	P > 0.05
2	pb	Y=0.01x+0.01	0.00	F1,603=0.03	P > 0.05
3	pb	Y=0.01x-0.01	0.00	F1,887=0.50	P > 0.05
4	pb	Y=0.03x-0.05	0.02	F1,129=2.52	P > 0.05
5	pb	Y=0.01x+0.07	0.05	F1,964=46.37	P < 0.0001
6	pb	Y=0.09x+0.15	0.22	F1,10=2.76	P > 0.05
7	pb	Y=0.01x-0.01	0.00	F1,7003=0.49	P > 0.05
1	pm	Y=0.46x+0.11	0.00	F1,99=0.06	P > 0.05
2	pm	Y=0.01x+0.01	0.02	F1,1729=41.16	P < 0.0001
3	pm	Y=0.01x+0.01	0.00	F1,1464=0.89	P > 0.05
4	pm	Y=0.01x-0.01	0.01	F1,362=1.97	P > 0.05
5	pm	Y=0.01x+0.01	0.00	F1,2118=3.55	P > 0.05
6	pm	Y=0.03x+0.01	0.00	F1,48=0.05	P > 0.05
7	pm	Y=0.01x-0.01	0.08	F1,19361=1747.28	P < 0.0001

pb - postbreeding
pm - postmoulting

Table 6 (Continued).

(e)

Ascent/Bottom time

Dive type	Status	Y=mx+c	R-Square	F-value	Pr > F
1	pb	Y=2.00x+1.64	0.02	F1,36=0.67	P > 0.05
2	pb	Y=0.01x-0.04	0.12	F1,603=84.55	P < 0.0001
3	pb	Y=0.01x-0.01	0.00	F1,887=0.02	P > 0.05
4	pb	Y=0.02x-0.01	0.00	F1,129=0.01	P > 0.05
5	pb	Y=0.01x-0.03	0.01	F1,964=13.67	P < 0.0002
6	pb	Y=0.07x-0.04	0.03	F1,10=0.27	P > 0.05
7	pb	Y=0.01x-0.01	0.01	F1,7003=73.13	P < 0.0001
1	pm	Y=0.48x+0.26	0.00	F1,99=0.29	P > 0.05
2	pm	Y=0.01x-0.02	0.04	F1,1729=77.15	P < 0.0001
3	pm	Y=0.01x-0.01	0.00	F1,1464=3.62	P > 0.05
4	pm	Y=0.01x+0.01	0.02	F1,362=6.96	P < 0.0087
5	pm	Y=0.01x+0.01	0.00	F1,2118=3.88	P < 0.05
6	pm	Y=0.03x+0.01	0.00	F1,48=0.04	P > 0.05
7	pm	Y=0.01x+0.01	0.06	F1,19361=1250.27	P < 0.0001

pb - postbreeding
pm - postmoulting

Diving characteristics of postbreeding and postmoulting females

(i) Dive depths and durations

The relationship between mean dive depth and duration of dives differed significantly amongst all females when comparing the slopes of the regression lines (ANCOVA: $F_{12,57592} = 1054.7$, $P < 0.0001$). All females showed significant ($P < 0.0001$) positive linear relationships between these two parameters (see above).

Mean dive depths of postbreeding females (Figure 7a) were significantly different (ANOVA: $F_{12,57592} = 601.23$, $P < 0.0001$) from each other, although seals G006 and O138 were very similar in that more than 50% of dive depths ranged between 400 - 700 m with comparable maximum depths. The mean dive depths, however differed marginally as seal O138 dived significantly deeper ($P < 0.0001$) by 78 m. Seals P537 and R101 showed similar trends, although dive depths were significantly shallower ($P < 0.0001$) with more than 50% of the mean dive depths that ranged between 300 - 600 m. Seal P537 had significantly deeper ($P < 0.001$) mean dive depths (by 14 m), than that of seal R101. There were no significant differences ($F_{12,57592} = 601.23$, $P > 0.05$) between postmoulting seals P537 and G006 and seals R202 and O144 (Figure 7b), whereas seals G006, R202 and O144 and seals P537, R202 and O144 showed significant differences (Figure 7b). The frequency distributions of dive depths between all postbreeding females were not significantly different ($T > 0.19$, $n = 21$, $P > 0.05$), with the exception of seal G006 that differed significantly ($T > 0.43$, $n = 21$, $P < 0.05$) to that of the remaining postbreeding females. Frequency distributions of postmoulting seal O144 differed significantly ($T > 0.42$, $n = 21$, $P < 0.05$) to all other postmoulting females, whereas there were no significant differences ($T > 0.19$, $n = 21$, $P > 0.05$) between seals P537, R202 and G006. All frequency distributions of postbreeding females were not significantly different ($T > 0.19$, $n = 21$, $P > 0.05$) to that of postmoulting seal O144, whereas all postbreeding females (with the exception of seal G289) were significantly different ($T > 0.42$, $n = 21$, $P < 0.05$) to postmoulting seals P537, R202 and G006. Postbreeding seals Y333, O138 and G006 had deeper secondary modes at 800 - 900 m (Figure 7a), whereas postmoulting seals R202 and P537 had bi-modal

(a)

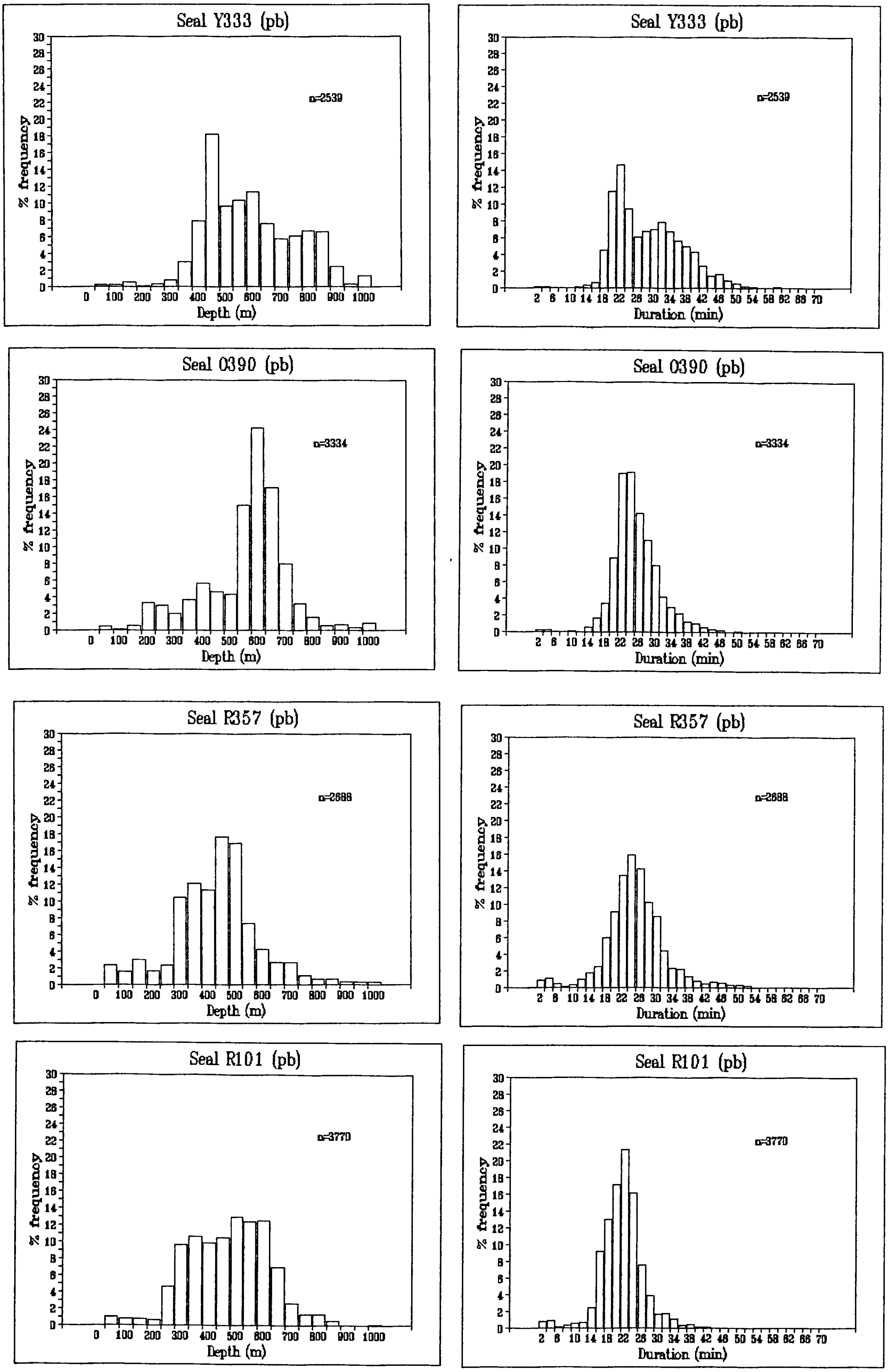


Figure 7. The frequency distributions of dive depth (50 m increments) and dive duration (2 min increments) of (a) postbreeding and (b) postmoulting southern elephant seal females from Marion Island. (pb - postbreeding; pm - postmoulting).

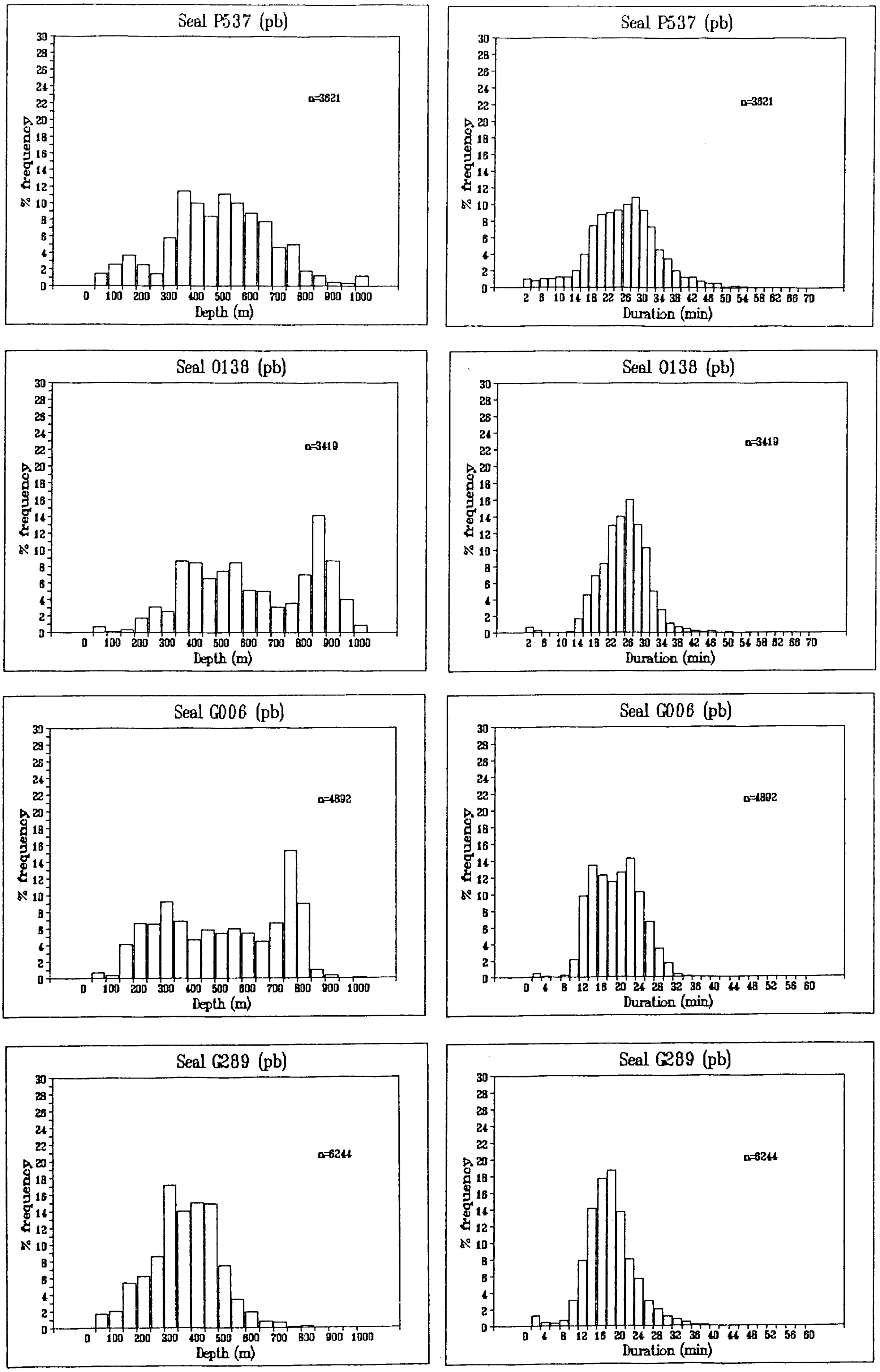


Figure 7 (Continued).

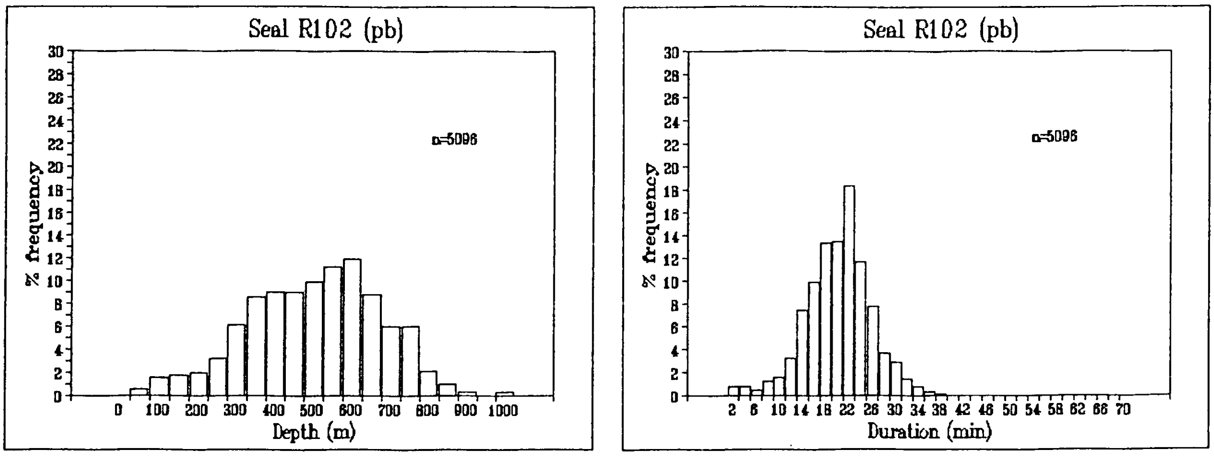
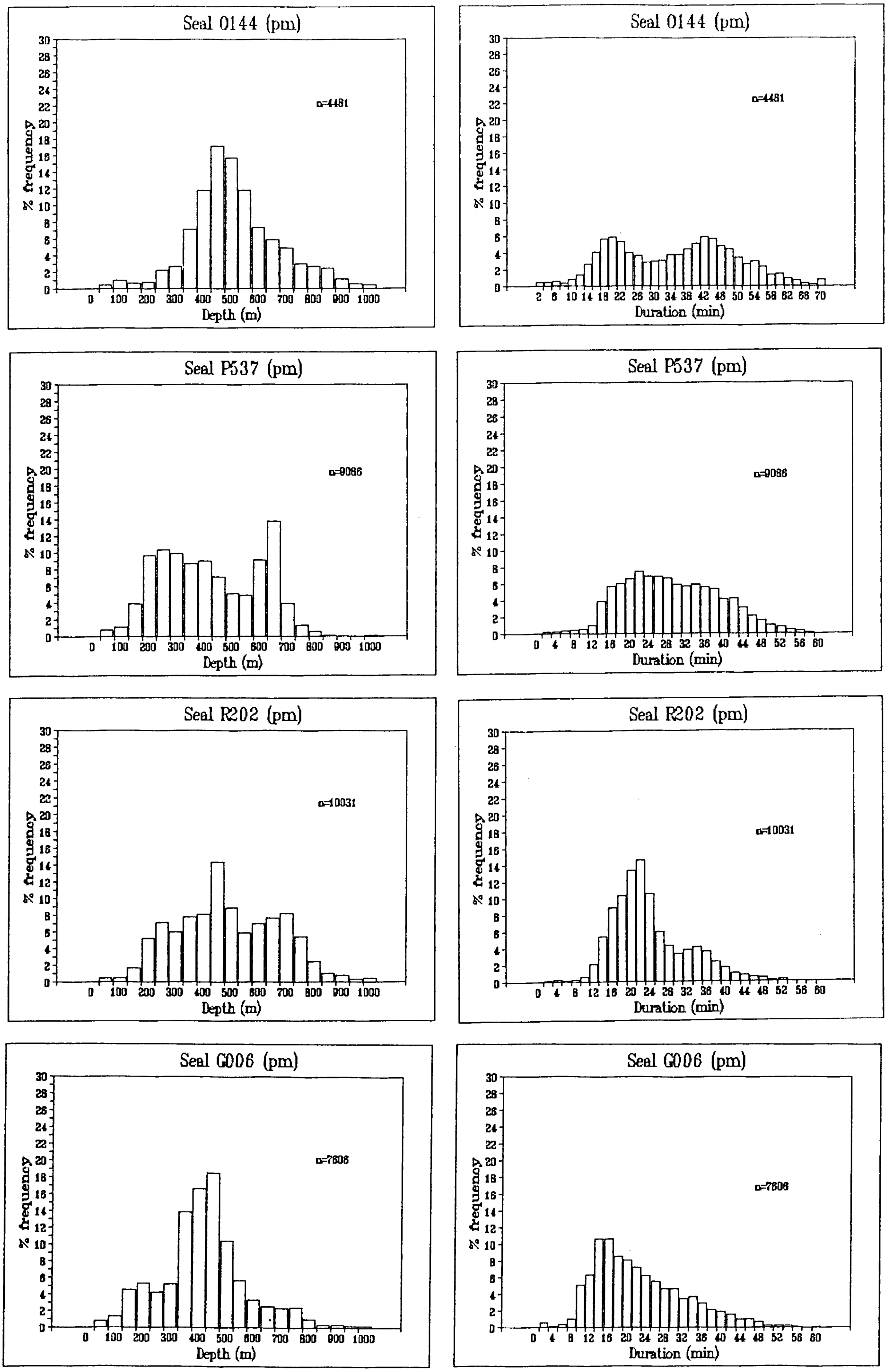


Figure 7 (Continued).

(b)


Seal 0144 (pm)

Seal 0144 (pm)

Seal P537 (pm)

Seal P537 (pm)

Seal R202 (pm)

Seal R202 (pm)

Seal G006 (pm)

Seal G006 (pm)

Figure 7 (Continued).

distributions, with secondary modes occurring at 600 - 700 m (Figure 7b).

Mean dive durations of postbreeding females (Figure 7a) differed significantly ($F_{12,57592}$ = 1227.43, P < 0.0001) between most females with exceptions for seals O138 and R357 and seals O390 and P537. There were significant differences ($F_{12,57592}$ = 1227.43, P < 0.0001) in mean dive durations between all postmoulting females (Figure 7b), with seal P537 that had more than 50% of the mean dive durations that ranged between 20 - 32 min, seal G006 between 15 - 30 min and seal O144 between 20 - 45 min. Seal R202 differed to that of the other postmoulting females, whereas mean dive durations were not significantly different ($F_{12,57592}$ P > 0.05) to that of postbreeding seals O390 and R357 with more than 50% of the dives that lasted between 20 - 25 min. The frequency distributions of dive durations for postbreeding seals Y333 and R357 were not significantly different (T > 0.25, n = 36, P > 0.05) to that of the remaining postbreeding females, whereas all the other postbreeding females showed significant differences between each other (T > 0.25, n = 36, P < 0.05). The frequency distributions of dive durations for postmoulting seal O144 were significantly different (T > 0.41, n = 36, P < 0.05) to all other postmoulting females, whereas comparisons between postmoulting seals P537, R202 and G006 were not significantly different (T > 0.16, n = 36, P > 0.05) to each other. Comparisons between postbreeding and postmoulting females showed that there were significant differences (T > 0.33, n = 36, P < 0.05) in the frequency distributions between the two groups. Postmoulting seals R202, G006 and P537 had unimodal distributions in mean dive durations that lasted between 12 - 36 min for seals R202 and G006, whereas seal P537 had a far wider range in distributions as most dives lasted between 14 - 48 min (Figure 7b). Seal O144 had a bi-modal distribution, with secondary modes occurring between 40 - 44 min. All postbreeding females had unimodal distributions in dive durations (Figure 7a).

(ii) Post-dive surface intervals

Mean post-dive surface intervals (including extended surface intervals or ESIs) for most postbreeding females differed significantly (ANOVA: $F_{8,27904}$ = 2179.30, P < 0.0001) between each other and lasted between 1.8 and 9.7 min, whereas seals R357 and O390 had surface intervals that were not significantly ($P > 0.05$) different and lasted ± 10.1 min. There were no differences (ANOVA: $F_{3,29688} = 0.78$ $P > 0.05$) in post-dive surface intervals (of ± 1.9 min) between postmoulting seals G006 and R202, and that of seals P537 and R202 that lasted ± 1.7 min.

The frequency distributions of post-dive surface intervals (excluding ESIs) were significantly different ($T > 0.42$, $n = 21$, $P < 0.05$) between most postbreeding females, with no significant differences ($T > 0.19$, $n = 21$, $P > 0.05$) between that of seals R101 and R102 and seals P537, G006 and G289. There were however, significant differences ($T > 0.47$, $n = 21$, $P < 0.05$) in the frequency distributions between all postmoulting females. Comparisons between postbreeding and postmoulting periods resulted in significant differences ($T > 0.42$, $n = 21$, $P < 0.05$) in frequency distributions between most females, with the exception of postbreeding seals P537, G006 and G289 that were not significantly different ($T > 0.19$, $n = 21$, $P > 0.05$) to that of postmoulting females.

The GLTDRs did not record dry periods during ESIs. The minimal mean number (including all recorded dives of females with incomplete diving records) of ESIs for postmoulting females ($n = 32$) were on average higher than that of postbreeding females ($n = 18$) (Table 7). Extended surface intervals (ESIs) occurred at all hours, but less frequently (20.7%) during the day than at night (79.2%) for all females combined. Postmoulting females showed a higher proportion (82.2%) of ESIs that occurred at night with a lower proportion (17.6%) during the day, than that of postbreeding females where 76.2% occurred at night and 23.8% during the day. There were significant increases (ANOVA: $F_{1,162} = 6.01$, $P < 0.02$) in the mean dive durations from 12.39 - 14.58 min for dives immediately before and after ESIs for all postbreeding females, respectively, both periods being shorter than the mean dive duration (22.1 min). Postmoulting females also showed significant increases (ANOVA: $F_{1,192} = 5.92$, $P < 0.02$) from 19.17 - 23.24 min, both periods being shorter than the mean dive duration (26.9 min), however both periods being significantly longer (ANOVA: $F_{3,351} = 23.18$, $P < 0.0001$) in duration than that of postbreeding females. Dives preceding and following ESIs were deep

Table 7. The duration of periods of continuous diving and the frequency of extended surface intervals (ESIs) that appeared in the diving record of southern elephant seal females (n = 13) from Marion Island, recorded during 1990 - 1994.

Seals	Status	Surface time (min)		Longest bout of continuous diving			ESIs				
				No. of dives	Duration (days)	%	No. of ESIs	Mean duration (h)	Max duration (h)	Total duration (h)	Max ESIs per day
		mean (sd)	Max								
Y333	pb	3.5 (0.5)	4	2539	51	100	0	0.0	0.0	0.0	0
*O390	pb	2.5 (5.6)	100	1781	30	57	6	0.5 (0.5)	1.6	2.8	1
R357	pb	4.9 (6.2)	55	1124	20	44	8	0.4 (0.3)	0.8	3.4	1
*R101	pb	2.0 (1.6)	205	1445	21	36	5	1.0 (1.5)	3.4	4.1	1
*P537	pb	4.5 (3.6)	29	1666	29	54	4	0.3 (0.1)	4.1	1.1	1
*O138	pb	2.5 (5.7)	62	1512	25	43	1	1.0 (0.0)	1.0	1.0	1
G006	pb	2.4 (5.9)	236	2981	44	60	7	1.1 (1.3)	3.9	7.5	3
G289	pb	2.1 (5.5)	337	3912	45	59	84	0.4 (0.6)	5.6	33.0	20
R102	pb	2.2 (7.5)	110	1684	22	25	26	1.1 (1.7)	8.0	27.4	5
	Mean	2.9	126	2071	32		18	0.6	3.2	8.9	4
**0144	pm	3.4 (3.5)	113	407	Unknown		>31	0.6 (0.6)	2.0	>18.6	5
*P537	pm	1.8 (6.9)	638	4376	108	54	9	1.4 (3.5)	10.6	12.6	1
*R202	pm	1.8 (1.9)	85	1421	25	14	33	0.4 (0.3)	1.4	13.6	3
*G006	pm	2.0 (2.3)	116	479	14	7	55	0.3 (0.3)	1.9	18.5	5
	Mean	2.3	238	2092	49		32	0.7	4.0	14.9	3

* - Incomplete diving record for the total days at sea
** - Dive record for every second day (half the measuring period)
( ) - standard deviation

pb - postbreeding
pm - postmoulting

(between 227 m and 403 m) for all females. Postbreeding and postmoulting females showed no significant differences (ANOVA: $F_{3,352} = 1.43$, $P > 0.05$) in mean dive depths before and after ESIs. However, mean dive depths of postmoulting females were significantly deeper (ANOVA: $F_{3,352} = 20.49$, $P < 0.0001$) before and after an ESI (by 151 m and 148 m, respectively) than that of postbreeding females.

Postbreeding females: ESIs averaged one per day for most postbreeding females, with the exception of seals G006, G289, R102 and Y333 (Table 7). Seal G289 had a maximum of 20 ESIs with mean durations of ± 24 min occurring on one single day. This female spent 76 days at sea, had the highest number of ESIs ($n = 84$), as well as the longest bout of continuous diving that lasted 59% of recorded dives without an ESI having occurred. However, only 51.8% of the ESIs occurred during the day with 48.1% at night, with no significant differences ($t = -0.9474$, $df = 94$, $P > 0.05$) in mean dive durations before and after ESIs. By comparison, seal R102 spent the most days ($n = 86$) at sea with a total of $n = 26$ ESIs (with mean durations of ± 66 min) but had the shortest bout of continuous diving (lasting 1 684 dives, or 22 days) without an ESI. 63.1% of ESIs occurred during the day with 36.9% at night, also with no significant increases ($t = -0.6368$, $df = 20$, $P > 0.05$) in mean dive durations (by 1.68 min) before and after ESIs. Maximum duration of ESIs ranged from less than 1 to 8 hours for postbreeding females (Table 7). Total duration of ESIs ranged from 1 to 33 hours (excluding seal Y333 which had no ESIs). The six-year-old seal Y333, dived continuously over the entire period of 51 days at sea without an ESI (Table 7).

Postmoulting females: ESIs averaged between 3 and 5 per day for most females, except seal P537 which averaged one per day (Table 7). Seal P537 spent the longest period at sea (201 days) and had the longest bout of continuous diving (54% of recorded dives) without an ESI. It also had the least number of recorded ESIs ($n = 9$) but mean duration of ESIs were the longest (± 84 min). In contrast seal G006 spent the shortest period at sea (145 days), and had the shortest bout of continuous diving (7% of the recorded dives) without an ESI. Mean duration of ESIs were shortest, lasting ± 18 min. Maximum duration of ESIs ranged from 2 to

10.6 hours for postmoulting females (Table 7).

(iii) Dive types

Postbreeding females: The frequency of occurrence of type 7 dives, the most frequently used dive, varied from 56% to 81% for postbreeding females (mean = 69%) whereas dive types 1 and 2 (0.1 - 11%) occurred infrequently, followed by dive types 3 - 6 (0 - 21%). The ratio of exploratory dives (type 5 and 6 combined, see **Discussion**) versus foraging dives (type 7 dives), indicated that seal Y333 had significantly more exploratory dives ($\chi^2 > 103$, df = 8, $P < 0.001$) than the other postbreeding females, as well as that of all postmoulting females ($\chi^2 > 321$, df = 4, $P < 0.0001$). This was evident in the 51% increase in the mean percentage occurrence of type 5 dives, reducing the type 7 dives by 19% below the average mean (Table 8). Comparing seal Y333 (n = 0 ESIs, 51 days at sea) with seal R102 (n = 26 ESIs, 86 days at sea), both six-year-olds with complete diving records, showed that the mean bottom time of foraging dives for seal Y333 (Table 9) was significantly longer ($F_{1,4303} = 979.57$, $P < 0.001$) as was the combined duration of the exploratory dives ($F_{1,1187} = 198.60$, $P < 0.001$).

Postmoulting females: The frequency occurrence of type 7 dives for postmoulting females varied from 71% to 83% (mean = 78%) (Table 8). Seal G006 had a high frequency of occurrence of dive type 5, but the percentage contribution of other dive types were similar to the other females . Seal O144 showed above average bottom times of type 7 dives, and the dive durations were significantly longer ($F_{12,42837} = 6065.53$, $P < 0.0001$), as was the combined durations of exploratory dives ($F_{12,6406} = 44.91$, $P < 0.0001$) than that of all the other females combined (Table 9).

Differences in the frequency occurrence of dive types between seal G006 recorded for the postbreeding and postmoulting seasons, differed significantly ($\chi^2 > 4.64$, df = 1, $P > 0.05$) between that of dive types 2, 4 and 6, whereas there were no significant differences ($\chi^2 > 0.62$, df = 1, $P > 0.05$) between dive types 1, 3, 5 and 7. Similarly, seal P537 recorded for both seasons differed significantly ($\chi^2 > 12.21$, df = 1, $P < 0.0001$) between that of dive types 3 - 6, with no significant differences ($\chi^2 > 0.67$, df = 1, $P > 0.05$) between dive types 1, 2 and 7.

Table 8. Summary of the frequency (%) contributions of dive types 1 - 7 in the diving records of southern elephant seal females (n = 13) from Marion Island, recorded during 1990 - 1994. (pb -postbreeding; pm - postmoulting).

Seals	Status	Dive types						
		1	2	3	4	5	6	7
Y333	pb	0.15	0.23	7.62	7.62	20.75	7.38	56.25
O390	pb	0.18	0.24	5.12	3.64	12.59	6.04	72.19
R357	pb	0.95	1.11	9.35	5.43	9.67	5.75	67.74
R101	pb	0.53	0.10	12.47	5.26	12.31	4.89	64.44
P537	pb	0.20	2.33	6.87	4.81	3.29	0.75	81.75
O138	pb	0.24	0.24	8.19	2.54	6.25	10.31	72.23
G006	pb	0.45	11.42	5.31	1.36	10.46	0.28	70.72
G289	pb	0.37	2.21	12.30	1.35	9.67	0.00	74.10
R102	pb	0.13	2.09	10.49	8.67	6.25	5.31	67.06
	Mean	0.35	2.22	8.64	4.52	10.14	4.52	69.61
O144	pm	0.58	2.28	4.89	2.01	3.58	2.73	83.93
P537	pm	0.37	2.77	5.23	1.72	6.44	0.24	83.22
R202	pm	0.38	9.33	6.45	0.88	7.89	0.26	74.81
G006	pm	0.70	8.71	5.65	1.87	11.50	0.06	71.51
	Mean	0.51	5.78	5.56	1.62	7.35	0.82	78.36

Table 9. Mean duration of dive types 5 and 6 ('exploratory'dives) and bottom times of type 7 dives ('foraging' dives) that appeared in the diving record of each southern elephant seal female (n = 13), recorded during 1990 - 1994 from Marion Island.

		Dive types		
		5	6	7
Seals	Status	Duration (min)	Duration (min)	Bottom time (min)
Y333	pb	23.21 (5.67)	31.56 (8.90)	13.64 (4.80)
O390	pb	22.06 (4.32)	28.80 (6.39)	11.95 (2.79)
R357	pb	22.93 (7.87)	24.98 (6.20)	12.70 (3.74)
R101	pb	19.46 (4.07)	20.42 (5.39)	11.86 (2.58)
P537	pb	25.58 (10.15)	28.90 (7.38)	13.65 (4.34)
O138	pb	22.50 (5.02)	24.59 (4.97)	12.12 (3.70)
G006	pb	17.85 (3.56)	16.97 (5.16)	9.43 (2.95)
G289	pb	16.68 (4.88)	19.73 (5.89)	9.74 (3.12)
R102	pb	18.03 (5.32)	21.84 (5.28)	9.34 (3.12)
	Mean	20.92	24.19	11.60
O144	pm	19.45 (9.69)	30.95 (15.23)	22.85 (11.58)
P537	pm	24.11 (7.66)	25.42 (9.69)	18.21 (9.09)
R202	pm	20.99 (7.10)	25.16 (7.23)	13.09 (5.68)
G006	pm	17.17 (7.50)	28.12 (8.63)	14.46 (7.65)
	Mean	20.51	27.41	17.15

( ) - standard deviation
pb - postbreeding
pm - postmoulting

Differences between postbreeding seals R101 and P537 (females that followed similar patterns in movement to foraging grounds, see **Chapter 4**), were not significantly different ($\chi^2 = 0.75$, df = 1, $P > 0.05$) between dive types 4, whereas dive types 1 - 3 and 5 - 7 were significantly different ($\chi^2 > 5.45$, df = 1, $P < 0.05$) between the two females.

(iv) Diel patterns

Depth, duration and bottom times of dive types:

Comparisons of diel differences between postbreeding and postmoulting females were made between using the four hours around midday (10h00 - 14h00) and midnight (22h00 - 02h00) over the first 40 days of the diving record (see **Diving analysis, Methods**).

There was significant diel differences (ANOVA: $F_{6,11199} = 28.60$, $P < 0.0001$) in mean dive depths, durations and bottom times of dive types 2 - 3 and 5 - 7 with the exception of dive types 1 and 4 (ANOVA: $F_{6,11199} = 1.75$, $P > 0.05$) between postbreeding and postmoulting females. Mean dive depths of type 7 dives for postmoulting females were significantly deeper (ANOVA: $F_{1,186} = 4.24$, $P < 0.05$) during midday, whereas postbreeding females showed no significant differences (ANOVA: $F_{1,180} = 0.06$, $P > 0.05$). Both the mean dive durations and bottom times of type 7 dives for postbreeding and postmoulting females were not significantly different ($P > 0.05$) between midday and midnight hours. Mean dive depths, durations and bottom times of type 5 dives for postmoulting females were significantly deeper (ANOVA: $F_{1,771} = 15.07$, $P < 0.0001$) and longer in durations ($P < 0.0001$) during midday hours, whereas postbreeding females showed no significant differences (ANOVA: $F_{1,519} = 0.53$, $P > 0.05$) in mean dive depths whereas mean dive durations and bottom times were significantly longer ($P < 0.0001$) during midday hours. Mean dive depths of type 3 dives for postbreeding females were significantly deeper (ANOVA: $F_{1,333} = 9.83$, $P < 0.01$) during midnight hours, whereas that of postmoulting females were not significantly different ($P > 0.05$) between midday and midnight hours. Mean dive durations and bottom times for postmoulting females were significantly longer in durations (ANOVA: $F_{1,204} = 6.82$, $P < 0.01$) during midday hours, whereas that of postbreeding females did not differ significantly ($P > 0.05$) during midday and midnight hours. Mean dive depths, durations and bottom times of type 2 dives for postbreeding females were significantly deeper (ANOVA: $F_{1,91} = 28.60$, $P < 0.0001$) and longer in durations ($P < 0.0001$) during midnight hours, whereas mean dive depths did not differ significantly ($P > 0.05$) between midday and midnight hours for postmoulting females. However, mean dive durations and bottom times during midnight hours were significantly longer in durations (ANOVA: $F_{1,368} = 9.06$, $P < 0.01$) for postmoulting females.

Postbreeding females: Mean dive depths, durations and bottom times of dive types 3 - 7 during midday were significantly deeper (ANOVA: $F_{6,7911} = 358.53$, $P < 0.0001$) and longer in durations (ANOVA: $F_{6,7911} = 188.08$, $P < 0.0001$) than that of midnight dives, with the exception of bottom times of type 6 dives where there were no significant differences ($P > 0.05$) in duration. Dive type 2 was significantly shallower (ANOVA: $F_{1,150} = 107.73$, $P < 0.0001$) and shorter in durations and bottom times ($P < 0.0001$) during midday when compared to midnight dives, whereas dive type 1 did not differ (ANOVA: $F_{1,28} = 2.15$, $P > 0.05$) in depths, durations and bottom times between midday and midnight hours.

Postmoulting females: Similar results were obtained for postmoulting females as mentioned above, where mean dive depths, durations and bottom times of dive types 3 - 7 during midday were significantly ($P < 0.0001$) deeper and longer in durations than that of midnight dives, whereas dive type 2 was significantly ($P < 0.0001$) shallower, and shorter in durations during midday, with no significant differences ($P > 0.05$) between midday and midnight hours for dive type 1.

Frequency occurrence of dive types:

There were significant diel differences in the ratios of occurrence of dive types between postbreeding ($\chi^2 = 64.69$, df = 6, $P < 0.0001$) and postmoulting females ($\chi^2 = 169.26$, df = 6, $P < 0.0001$) during the first 40 days of the recorded period at sea (Table 10).

Dive type 1: There were no significant ($\chi^2 = 2.19$, df = 1, $P > 0.05$) diel differences in the ratios

Table 10. Diel differences in the mean frequency contribution of dive types between postbreeding and postmoulting females for the first 40 days of the recorded period at sea.

	Postbreeding females		Postmoulting females	
	Midday	Midnight	Midday	Midnight
Dive type				
1	17	13	10	17
2	43	109	50	261
3	306	481	29	120
4	111	183	11	23
5	346	553	175	220
6	180	187	2	1
7	2544	2852	1185	1198

of type 1 dives between postbreeding and postmoulting females, however 56% of the dives occurred at midnight for postmoulting females whereas 63% occurred during midday for postbreeding females.

Dive type 2: There were significant ($\chi^2 = 9.48$, df = 1, $P < 0.01$) diel differences in the ratios of occurrence of type 2 dives within postbreeding and postmoulting females. The highest frequency of dives occurred during midnight for both groups (71% and 83% respectively). Diel differences between the two groups indicated that postmoulting females in having had overall higher frequencies of dives during midday and midnight (53% and 70% respectively), when compared to that of postbreeding females (46% and 29% respectively).

Dive type 3: There were significant ($\chi^2 = 20.56$, df = 1, $P < 0.001$) diel differences in the ratios of type 3 dives within postbreeding and postmoulting females. The highest proportion of dives occurred during midnight for both groups (60% and 80% respectively). Diel differences between the two groups indicated that postbreeding females in having had overall higher frequencies of dives during midday and midnight (91% and 80% respectively), when compared to postmoulting females (8% and 19% respectively).

Dive type 4: There were no significant ($\chi^2 = 0.38$, df = 1, $P > 0.05$) diel differences in the ratios of occurrence of type 4 dives within and between postbreeding and postmoulting females, however postbreeding females had overall higher frequencies of dives during midday and midnight (90% and 88% respectively), compared to postmoulting females (9% and 11% respectively).

Dive type 5: There were significant ($\chi^2 = 3.86$, df = 1, $P < 0.05$) diel differences in the ratios of occurrence of type 5 dives within postbreeding and postmoulting females. The highest frequency of dives occurred at night for both groups (61% and 55% respectively). Differences between the two groups indicated that postbreeding females had overall higher frequencies of dives during midday and midnight (66% and 71% respectively), compared to postmoulting females (33% and 28% respectively).

Dive type 6: There were no significant ($\chi^2 = 0.36$, df = 1, $P > 0.05$) diel differences in the ratios of occurrence of type 6 dives within and between postbreeding females, however postbreeding females had overall higher frequencies of dives during midday and midnight (98% and 99% respectively), compared to postmoulting females (1% and 0.5% respectively). *Dive type 7:* There were significant ($\chi^2 = 4.41$, df = 1, $P < 0.05$) diel differences in the ratios of occurrence of type 7 dives within postbreeding and postmoulting females. The highest frequency of dives occurred at night for both groups (52% and 51% respectively). Differences between the two groups indicated that postbreeding females had overall higher frequencies of dives during midday and midnight (68% and 70% respectively), compared to postmoulting females (31% and 29% respectively).

Discussion

Summary diving statistics

The near continuous deep ($\bar{x}$ = 480 m) and prolonged ($\bar{x}$ = 22.1 min) dives of postbreeding southern elephant seal females (n = 9) from Marion Island, with very short mean surface intervals (2.9 min) between dives, were characteristic of postbreeding females (n = 5) at Macquarie Island (439 m, 21.1 min) (Hindell *et al.* 1991b), and considerably deeper and longer than that recorded for northern elephant seal females (n = 8) (400 m, 19.2 min) at Año Nuevo (Le Boeuf *et al.* 1988).

Comparisons amongst postmoulting females indicated that the mean depth and duration of dives by southern elephant seal females (n = 4) from Marion Island (454 m, 26.9 min - present study) and South Georgia (n = 1) (391 m, 17.5 min - Boyd & Arnbom 1991) fall within the range of dives (269 - 552 m, 16.0 - 36.9 min) recorded for females (n = 14) from Macquarie Island (Hindell *et al.* 1991b; Slip *et al.* 1994) and Peninsula Valdés (431 m, 22.8 min - Campagna *et al.* 1995). The duration, but not depth of dives made by postmoulting females from Marion and Macquarie Islands was considerably greater than those from the postbreeding period. Hindell *et al.* (1991b) found no difference between the two periods in the time spent at the bottom of the dive, and suggested that the seals from the postmoulting period took longer to arrive at the maximum depth of the dive. However, unlike the females from Macquarie Island (Hindell *et al.* 1991b), the postmoulting females in the present study did not spend a similar proportion of their time on each type of dive between the two periods. They favoured foraging dives (that ranged from 71 - 83% of all dives, versus a range of 56 - 81% for that of postbreeding females) which had approximately twice the bottom time compared with the foraging dives executed by postbreeding females. Except for the first dives close to the island when the females were presumably still over the shallow Prince Edward Island shelf area, none of the dives seemed to be limited by the depth of the ocean floor. Foraging therefore appeared to be pelagic and similar to that of females from Macquarie Island (Hindell *et al.* 1991b) and Peninsula Valdés (Campagna *et al.* 1995) which seldom showed benthic dive patterns. At least one of three southern elephant seal females from South Georgia exhibited target benthic feeding when over the shallow continental shelf area (McConnell *et al.* 1992a) and the predominantly pelagic feeding northern elephant seal females (Le Boeuf *et al.* 1988) on occasion also fed benthically (Le Boeuf *et al.* 1992). It therefore seems probable that elephant seal females do not only feed pelagically in the water column, but also feed benthically when circumstances permit.

The maximum dive depth (1 444 m) by a postbreeding female in the present study exceeds that for a southern elephant seal female from Macquarie Island (1 256 m - Hindell *et al.* 1992), but falls short of the 1 567 m and 1 581 m recorded for a northern elephant seal female and male respectively (Stewart & DeLong 1990). However, overall means of maximum depths reached by postbreeding (1 175 m) and postmoulting females (1 223 m) from Marion Island were very similar to females from Macquarie Island (1 152 m and 1 256 m, respectively - Hindell *et al.* 1991b) but considerably deeper than that recorded for females from Peninsula Valdés (1 072 m - Campagna *et al.* 1995).

The maximum dive duration of 113 min recorded by the postmoulting female (present study) approximates the previous maximum for a southern elephant seal female from Macquarie Island (120 min - Hindell *et al.* 1991b) but exceeds that of northern (77 min) and southern (88.5 min) elephant seal males (DeLong & Stewart 1991; Slip *et al.* 1994). However, mean dive durations (22.1 min) of postbreeding females from Marion Island were very similar (23.4 min) to females that moved off the continental shelf into deep water from the Peninsula Valdés (Campagna *et al.* 1995). Postmoulting females from Marion and Macquarie islands undertook these very long dives during the postmoulting period, characterised by longer mean dive durations than during the postbreeding period (Hindell *et al.* 1991b; present study) without a concomitant increase in post-dive surface intervals.

Since the surface intervals between dives were short, and the dives following these and other exceptionally long dives were not significantly shorter than typical dives (DeLong & Stewart 1991), it therefore seems probable that elephant seals remained well within their aerobic dive limits (DeLong & Stewart 1991). Neither did ESIs follow or precede dives of above-average duration (Hindell *et al.* 1992; present study), or depth (Boyd & Arnbom 1991). In addition, the absence of ESIs and post-dive surface intervals longer than 4 min during a 51 day sojourn at sea (present study), and 40 days without a surface period longer than 6 min when the theoretical aerobic capacity of the animals was regularly exceeded (Hindell *et al.* 1991b & 1992), suggest other ways of dealing with by-products of anaerobic metabolism and/or limiting its production (Hindell *et al.* 1992).

Dive type classification and function

This study provides additional information on the putative function of dive types in elephant seals. Of the seven distinct dive types identified in the present study, types 1, 2 and 4 dives have not been previously described for elephant seals. Comparisons are, however, difficult as schematic drawings of dives were presented in different ways and not always backed up with all the relevant statistics.

Diving characteristics (dive depth, duration, descent rates, ascent rates and bottom times) of dive types varied within and between postbreeding and postmoulting females, which suggested that the individual and seasonal variation in the diving behaviour of southern elephant seal females are related to their geographic locations and the abundance and behaviour of their prey (present study, see **Chapter 5**).

The shallow (± 60 m), rapidly executed type 1 dive of short duration with virtually no bottom time, and the slightly deeper (± 174 m) type 2 dive of longer duration with its more distinct bottom times, both occurred predominantly during the initial departure and the final return to the island, and were hypothesized to serve as shallow `transit' dives. Type 1 dive was distinct from the Type 5 dive of Hindell *et al.* (1991b) which they discounted as possible artifacts of the recorders rather than true dives, in that type 1 dives occurred infrequently between other dive types throughout the diving record for some individuals in the present study. The infrequent occurrence of the shallow type 2 dive within a bout of deep foraging dives suggest a non-foraging function for these dive types. However, postbreeding seal G006 displayed the highest ratio (11.4%) of type 2 dives compared to that of all other females, these dives being interspersed between bouts of deep foraging dives during her diving record. Both postmoulting seals R202 and G006 showed similar trends (9.3% and 8.7% respectively) to that of postbreeding seal G006, whereas all other females had low frequencies of type 2 dives (ranging between 0.2% and 2.7%) all of which were performed close to the breeding site. Type 2 dives are therefore analogous to Type F dives of Le Boeuf *et al.* (1988), who found that northern elephant seals performed similar V-shaped dives when leaving breeding sites from Año Nuevo Island, California. However, females (present study) with higher ratios of type 2 dives displayed most of these dives away from breeding sites, and therefore were not exclusively limited by the shelf or sea bed when these dives were performed. From the diel patterns of dive types (present study, see **Diel patterns**) it was also evident that the majority of type 2 dives occurred at night, when the ratio of type 7 dives (foraging) were also the highest at shallow depths. It is therefore conceivable that these dives function as shallow, `exploratory' dives (with flat-bottomed profiles), allowing the animal to transit rapidly while frequently testing where prey could be located. In general, postmoulting females displayed a significantly higher ratio of type 2 dives (at night), although overall lower ratios of foraging dives (see **Diel patterns**), with significantly longer bottom times than that of postbreeding females.

Type 4 dives were different from type 3 dives owing to their very rapid mean descent rates and slow ascent rates despite similar mean depths (± 456 m), durations, short bottom times and low frequencies of occurrence (5 - 8% of all dives). The type 3 dive simulates the Type 3 dive of Hindell *et al.* (1991b), and the Type C dive of Le Boeuf *et al.* (1992). The slow descent, negative buoyancy of the animal and positive gravitational forces allowed covering 50% or more of the horizontal distance with a reduced swim effort in northern elephant seal females (Le Boeuf *et al.* 1992).

Similar findings in this study are consistent with the hypothesis (Le Boeuf *et al.* 1992) that type 3 dives served as `resting' function during which energy is conserved (63% of dive duration spent descending and at the bottom of the dive in the present study). The relatively fast ascent (37% of dive duration), with assumed forward movement (as implied by Le Boeuf *et al.* 1992) could function as a travelling section of the dive. Type 3 dives had similar recorded peak frequencies than that of Type C dives of northern elephant seals (Le Boeuf *et al.* 1992) which were coupled with low frequencies of foraging dives (Type D dives - Le Boeuf *et al.* 1992 and type 7 dives, present study), which therefore suggested that these two dives may have opposite functions. The mean percentage contribution of Type C dives (processing or resting dives) beyond the continental shelf for postbreeding females from the Peninsula Valdés (6.8% - Campagna *et al.* 1995) was lower than type 3 dives (8.6% - present study) for females from the Marion Island, whereas type 3 dives (present study) were higher than Type C dives of females from Año Nuevo (5.7% - Asaga *et al.* 1994) and Type 3 dives for females from Macquarie Island (4.3% - Hindell *et al.* 1991b). However, the mean percentage contribution of Type D and Type 1 dives (foraging dives) for postbreeding females from Peninsula Valdés, Año Nuevo and Macquarie Island (72.3% - Campagna *et al.* 1995; 82.9% - Asaga *et al.* 1994; 79.2% - Hindell *et al.* 1991b, respectively) was higher than type 7 dives for postbreeding females (69.6% - present study) from Marion Island.

The fast mean descent of type 4 dives which constituted only 16% of the duration of the dive, implied purposeful diving to a considerable depth (in the league of foraging dives), with a bottom time comparable to the type 6 exploratory dive (present study), and followed by the very slow ascent which constituted 69% of dive duration. Since the seals are clearly not hastened to return to the surface, and the second part of the dive (83% of total duration) was likely to involve forward movement (Le Boeuf *et al.* 1992), the type 4 dive was therefore hypothesized to serve both an `exploratory' and `transit' function.

The type 7 dive in the present study with its rapid descent and ascent to and from depth (± 500 m), long duration and extended bottom time (ranging from 50 - 59% of the total dive duration for postbreeding and postmoulting females, respectively) with so called `wiggles' at a consistent depth during a series of dives, were similar to the Type D and Type 1 dives described elsewhere (Boyd & Arnbom 1991; Hindell *et al.* 1991b; Le Boeuf *et al.* 1992). Similarly, type 7 dives maximised feeding time for seals by travelling rapidly to the depth where prey was found, remained foraging at this depth for an extended period, and then return rapidly to the surface for a short period before diving again (Le Boeuf *et al.* 1992). The distinct up and down movements (or `wiggles') during bottom time implied prey pursuit at the bottom of the dive (Bengtson & Stewart 1992), while the overall uniformity of the dive depth over a long series of dives suggested that prey patches remain at the same depth over time and are dense enough for high encounter rates (Le Boeuf *et al.* 1988). As the most frequently used dive (72% of all dives recorded), particularly during the postmoulting period (83% of all dives), with the majority of the time spent at the bottom of the dive, primarily when the seals were away from the island, the type 7 dive was hypothesized to serve as `foraging' dives.

The depths of dive types 5 and 6 exceeded that of other dive types by ± 100 m and these were hypothesized to serve as `exploratory' dives. The dive profile of the type 5 dive suggested one smooth continuous movement combining the descent, bottom time and ascent. These dives are analogous to a combination of the parabolic-shaped Type 4 and deep, spiked Type 6 dives of Hindell *et al.* (1991b), combinations of the spiked Type A and parabolic-shaped Type B dives of Le Boeuf *et al.* (1992) and spiked Type 5 and 6 dives of Boyd & Arnbom (1991).

Type 5 dives (present study) occurred throughout the diving records in the present study while Le Boeuf *et al.* (1992) and Hindell *et al.* (1991b) found the simple parabolic shaped dives predominantly in the first two weeks after the seals' departure from land and postulated these dives to have served `transit' functions. However, Hindell *et al.* (1991b) and Le Boeuf *et al.* (1988) found that the deep, spiked Type 6 and Type A dives respectively, were infrequently interspersed between foraging dives and postulated that they possibly served several functions, including exploration and predator avoidance. Similar to Type 6 dives of Hindell *et al.* (1991b) and Type A dives of Le Boeuf *et al.* (1988), type 5 dives were also infrequently found singly in amongst bouts of foraging dives (unpublished data), and therefore assumed to serve an exploratory function as they were deeper on average than the foraging dives with which they were associated. Despite the relatively long bottom times, type 5 dives (present study) did not appear to be foraging dives as bottom times had no characteristic 'wiggles' compared to that of type 7 (foraging) dives. Type 5 dives were also the most common group of non-foraging dives, accounting for 10.1% and 7.4% of the total time at sea recorded for postbreeding and postmoulting females, respectively. However, although the percentage contribution of these deep dives was only marginally higher than that recorded for southern elephant seal females from Macquarie Island (6.5% - Hindell *et al.* 1991b), Peninsula Valdés (8% - Campagna *et al.* 1995), Año Nuevo Point (7.1% - Le Boeuf *et al.* 1988) and northern elephant seal males from San Miguel Island (6.2% - DeLong & Stewart 1991), most of the deepest recorded dives were all type 5 dives (present study) and it is therefore unlikely that they could function predominantly as transit dives as suggested by Hindell *et al.* (1991b) and Le Boeuf *et al.* (1992).

The type 6 dive was assumed also to function as an exploratory dive to similar mean depths than type 5 dives, but was of a considerable longer duration, despite a shorter mean bottom time. This resulted from the temporary decline in the descent rate more than 100 m short of the bottom of the dive and a temporary decline in the ascent rate at a similar depth, which produces the two shoulders in the dive profile. These dives were similar to the Type 2 dives described by Boyd & Arnbom (1991) and appear in the graphic representation of dives classified as Type 6 dives in Hindell *et al.* (1991b). Interspersed among shallower foraging dives similar to the type 5 dives (unpublished data), the shoulder(s) of the type 6 dive appear to be produced at the same depth as the bottom of the preceding and subsequent foraging dives (present study). This may be interpreted that the type 6 dive is possibly an aborted type 7 `foraging' dive, and that the descent to greater depths in this situation suggests exploration as prey were not found at the anticipated depth. Since type 6 dives were also found in other situations not immediately preceded or succeeded by foraging dives, it may purely have an exploratory function such as the type 5 dive with which it was also associated, but showing a clear enhanced interest in a shallower depth than the maximum for the particular dive.

Characteristics of dive parameters

The positive correlation between dive depth and duration, with few exceptions within dive types (present study), followed the pattern established for other elephant seals (Le Boeuf *et al.* 1988; Boyd & Arnbom 1991; DeLong & Stewart 1991; Hindell *et al.* 1991b; Asaga *et al.* 1994). The positive relationship between these two variables was lowest for type 3 (processing or resting dives) and type 7 (foraging) dives. However, comparisons of similar dive types (Type C and Type D dives, respectively - Asaga *et al.* 1994) performed by northern elephant seal females demonstrated that the correlation between dive depth and dive duration of their Type D dives were also lowest, whereas Type C dives were the highest. Positive relationships between depth and duration of dive types 2, 3, 5 and 7 for postbreeding females were higher than that of postmoulting females , whereas relationships between duration and bottom time of dive types 2 and 7 were the highest for both postbreeding and postmoulting females. However, relationships of type 7 dives for postmoulting females were higher than that of postbreeding females, whereas relationships of type 2 dives were high and positively correlated but similar between the two groups of females.

Considerable individual variation in diving characteristics existed amongst females in the present study as evidenced by (a) the difference in the slopes of the lines regressing depth and duration of dives, (b) the difference in both diving depth and duration as well as the frequency distribution of dive durations amongst most of the individuals, and (c) the frequency distribution of surface intervals when ESIs were included. Although the distribution of dive depths and dive durations centred on 400 - 600 m and 22 - 24 min, three postbreeding females had secondary depth modes around 800 - 900 m, whereas one postmoulting female had a secondary mode around 600 - 700 m.

All postbreeding females had unimodal distributions in dive durations, whereas postmoulting seal O144 had a secondary mode around 40 - 44 min. Since females in the present study ranged widely both north and south of the Antarctic Polar Front (APF) (Bester & Pansegrouw 1992; see **Chapter 4**) such individual variation in dive parameters was likely to be related to the females' geographic locations and geographic variations in prey depth and behaviour as suggested for northern elephant seal males (DeLong & Stewart 1991) and females from Marion Island (see **Chapter 5**).

Diel patterns

The diel diving pattern of deeper dives of longer duration during the day and shallower, shorter dives during the night appeared to be the norm for elephant seals (Le Boeuf *et al.* 1988; Boyd & Arnbom 1991; Hindell *et al.* 1991b; present study) and was interpreted as the pursuance of vertically migrating prey, which is more abundant near the surface at night than during the day (Boyd & Arnbom 1991; DeLong & Stewart 1991).

Diel patterns of dive types during the four hours around midnight were contrasted with those around midday to eliminate the possible influence of dawn and dusk which would differ according to the season and location of the females. The absence of a significant difference in diel dive depths for postbreeding seal R357 in the present study was not due to benthic foraging as speculated for similarly behaving northern elephant seal males (DeLong & Stewart 1991), as the females all appeared to be foraging pelagically (present study). The frequency of `foraging' (type 7), `exploratory' (types 5 and 6) and `resting or processing' (type 3) dives were highest during midnight for postbreeding females, whereas the shallow `exploratory, transit' (type 2) dives were highest during midnight for postmoulting females.

Postbreeding females therefore utilized different foraging strategies to that of postmoulting females as the intensity of foraging, exploratory and processing or resting dives was far greater. The mean dive rate for postbreeding females (2.8 per hour) were also higher than that of postmoulting females (2.3 per hour) however, dive rates for postbreeding and postmoulting females (present study) were similar to that of northern and southern elephant seals from other populations (Le Boeuf *et al.* 1988; Hindell *et al.* 1991b). Therefore, differences in foraging strategies between postbreeding and postmoulting females could be related to seasonal differences in the type of prey, their abundance and distribution (see **Chapter 4**).

There was an inverse relationship in the daily frequency pattern of type 3 and 7 dives in all females. Type 3 dives peaked in frequency during midday whereas type 7 dives decreased concomitantly for most females. However, postbreeding seal Y333, in contrast, showed opposite trends in that type 7 dives increased during midday with type 3 dives decreasing concomitantly.

Therefore the individual variation could possibly be attributed to the interaction between prey availability and the energy requirements of individual seals as small-scale spatial and temporal variations within foraging areas may require seals to search before suitable areas are located (Hindell *et al.* 1991a). Moreover, the wide range of differences in mean dive depths between night and day (30 - 300 m), and inconsistent relationships between the relative contribution of the different dive types in the diel dive records of individuals, further strengthens the argument of response to seasonal and geographic variation in species composition and behaviour of prey (Stewart & DeLong 1990, present study - see **Chapter 5**).

Functional relationships between ESIs and time spent at sea

The postbreeding periods of absence of southern elephant seal females from Marion Island ($\bar{x}$ = 66.7 ± 12.33; range = 51 - 86 days; n = 7) were shorter on average and with a wider range than that determined for conspecific females from Macquarie Island ($\bar{x}$ = 73.7 ± 3; range = 71 - 78 days; n = 6) and northern elephant seal females from Año Nuevo Point, California ($\bar{x}$ = 72.6 ± 5.0; range = 62 - 78 days; n = 8) (Le Boeuf *et al.* 1988; Hindell *et al.* 1991b).

Postbreeding seal R102 which spent 8 to 9 days longer at sea than the other females during the postbreeding period, was otherwise similar in age (six years), displayed the longest period of continuous diving, had considerably longer extended surface intervals (ESIs) than the remaining postbreeding females and showed similarities with that of postmoulting females (which had remained at sea for ± 252 days) for number and duration of ESIs. It therefore suggests that the factors determining the presence of ESIs in the dive records of females may also affect the duration of the postbreeding period. In determining what these factors might be, it is perhaps significant that the only other six-year-old seal Y333, had been diving continuously without any ESIs (51 days, total days at sea), never spent more than 4 minutes at the sea surface, this being comparable to a six-year-old female from Peninsula Valdés which dived continuously without an ESI for 58 days (Campagna *et al.* 1995). However, seal Y333 (present study) returned the highest mean as well as maximum dive durations recorded for postbreeding females. Since seal Y333 also used significantly more `exploratory' dives (28.1%) and less `foraging' dives (56.2%) compared to all other postbreeding females (4.0 - 18.6% and 64.4 - 81.7% respectively), it possibly suggested that she was less successful in encountering prey, and consequently had to work harder at it to sustain herself and gain mass before the moult haulout. This is also supported by the fact that the bottom time of `foraging' dives of seal Y333 and presumably feeding time, as well as `exploratory' dives, were of significantly longer duration than that of seal R102, although not necessarily different from all the remaining females.

Boyd & Arnbom (1991) linked food abundance and the occurrence of ESIs predominantly at night and argued that if food abundance tended to be greater at night, then the single elephant seal females in their study may periodically have become satiated with food which could explain cessation of diving. Since ESIs also occurred more often during the night (79%) than during the day (20%), it further strengthens the relationship between the occurrence of ESIs and food abundance. The question, however, remains why seal Y333 did not simply spend a longer period at sea in order to improve her chance of obtaining food in quantity and gain weight, as a significant relationship between days at sea and percentage mass gain for females during the postbreeding period existed for northern elephant seals (Spearman Rank Correlation Coefficient $r_s = 0.71$, $P < 0.05$, $n = 7$; calculated from Table 1 in Le Boeuf *et al.* 1988).

One might then also expect that the period spent at sea would depend on the amount of resources used during lactation and time spent on land during the preceding breeding season. Northern elephant seal females that successfully reared their pups, and therefore by implication used a far greater amount of body fat reserves than those failing to rear their pups, stayed at sea significantly longer than unsuccessful females (Stewart 1989). In contrast, the length of time spent at sea by southern elephant seal females from Marion Island during the postbreeding period was negatively correlated with the duration of the breeding season haulout, but not with maternal age, size or social status, or whether a female successfully reared her pup (Wilkinson 1992).

The relatively short postbreeding period at sea of seal Y333, despite the apparent difficulty in locating prey, could therefore possibly be related to the impending onset of the moult and/or physiological state of the female. In contrast to postbreeding females, which have their available time at sea limited by the haulout for the moult (Bester 1988b) which peaks in mid-January at Marion Island (Condy 1979), the postmoulting females spent ± 252 days at sea before hauling out for the breeding season. Concentrating on foraging dives (78% of all dives) of approximately double the duration of the foraging dives of postbreeding females, postmoulting females' behaviour suggests successful foraging which could be related to high rates of ESIs (n = > 32) compared to that of postbreeding females (n = > 18). This concentrated feeding was necessary as pregnant elephant seal females need to gain condition after the moulting fast and in advance of the breeding season haulout and the rearing of a pup.

This chapter has, however, shown that the differing diel diving responses of the females, the probable role and function of the ESIs, the proportional use of the various dive types, their specific depths, durations and frequencies of distribution and lengths of postbreeding and postmoulting pelagic periods, can potentially be used as measures of the females' performances at sea. The marked individual variation in the diving behaviour of these and other females therefore needs to be scrutinized more closely as it is likely to vary seasonally and geographically in response to physical and biological environmental factors.

CHAPTER 4

SEASONAL MOVEMENTS AND FORAGING AREAS

Introduction

Southern elephant seals, *Mirounga leonina*, including the South Georgia, Macquarie and Kerguelen stocks (Laws 1994), breed and moult on islands north and south of the Antarctic Polar Front (APF). Adult southern elephant seals return to sea twice each year for approximately 2 - 8 months when they move widely in the southern hemisphere often visiting the continents abutting on the Southern Ocean, ranging as far south as the pack-ice region surrounding the Antarctic Continent (Tierney 1977; Murray 1981; King 1983; Bester 1989; Gales & Burton 1989; Laws 1994).

The movements of postbreeding and postmoulting southern elephant seal females from Macquarie Island, South Georgia and Peninsula Valdés (Boyd & Arnbom 1991; Hindell *et al.* 1991a, b; McConnell *et al.* 1992a; Campagna *et al.* 1995; McConnell & Fedak 1996) as well as congeners in the northern hemisphere from Año Nuevo Point and San Miguel Island (Le Boeuf *et al.* 1986, 1988, 1989, 1992; Naito *et al.* 1989; DeLong *et al.* 1992; Asaga *et al.* 1994; Stewart & DeLong 1994, 1995) have been described in some detail. However, the pelagic distribution and movements of postbreeding and postmoulting southern elephant seal females from Marion Island are largely unknown. Although the ranging behaviour of postbreeding females (n = 3) from Marion Island have been documented by Bester & Pansegrouw (1992), it described only a small part of their feeding range. The present knowledge of the ranging behaviour of southern elephant seals within the Kerguelen Province has been derived almost entirely from sightings of marked animals (Bester 1989; Bester & Pansegrouw 1992).

Although resightings of tagged individuals demonstrated individual movements between sub-populations within the Kerguelen Province (Bester 1988b; Bester 1989; Guinet *et al.* 1992), it is difficult to interpret resighting rates in relation to the distribution of elephant seals at sea (Bester 1989). The development and testing of a geographic-location-time-depth recorder (GLTDR) to study the pelagic movements of northern elephant seals (DeLong & Stewart

1991), permitted a preliminary investigation of the pelagic ranging and diving behaviour of southern elephant seal females (n = 3) from Marion Island (Bester & Pansegrouw 1992).

Since the location and the pattern of diving of the elephant seals at sea would reflect the general type of prey consumed (e.g. pelagic or benthic animals), the periodicity of foraging, and the effort expended (Le Boeuf *et al.* 1993; Le Boeuf & Laws 1994), the current study has relevance to possible reason(s) for the continued decline of the Marion Island population (Bester & Wilkinson 1994). This chapter describes the seasonal pelagic movements, the free-ranging diving patterns and the locations of foraging of postbreeding and postmoulting southern elephant seal females from Marion Island. The implications of the movements and foraging locations are discussed and compared with those from other breeding populations of southern elephant seals.

Methods

(a) Deployment and retrieval of instruments

The GLTDRs were glued to the dorsal pelage of postbreeding (n = 9) and postmoulting (n = 3) southern elephant seal females at Marion Island (46°54′S, 37°45′E) during the breeding (September - November) and moulting (December - February) seasons of 1990 - 1994, following Bester & Pansegrouw (1992). The recorders were deployed on tagged, adult females which had shown fidelity to Marion Island during previous breeding and/or moulting haulouts. Females were sedated with intramuscular injections of ketamine hydrochloride and xylazine hydrochloride when attaching and recovering instruments, following Bester (1988a).

The pelage of the attachment site was cleaned with acetone and quick-setting epoxy adhesive (Araldite AW 2101/HW 2951, Ciba Geigy) was placed on the dorsal midline above the shoulders (Bester & Pansegrouw 1992). The aluminium base-plate (18 x 5 cm) with fixed hose clamps, stitched onto a rectangular strip (20 x 10 cm) of nylon shade-netting, was placed on the dorsal midline of the seal parallel to the long axis of the body and embedded with the epoxy which was worked into the hair protruding through the shade-netting (Bester & Pansegrouw 1992). A GLTDR was attached to the aluminium base-plate and hose clamps, with the light sensor (Lexan cap) facing the anterior of the animal and the pressure transducer facing the rear.

To retrieve the instrumentation, the hose clamps were partially unscrewed, and the GLTDRs slid out of the attachment assemblage which in turn could be recovered once it sloughed off during moulting (Bester & Pansegrouw 1992). Instrument recoveries that took place when moulting was well advanced, involved pulling the entire attachment assemblage off using a hooked staff without sedation of the animal.

(b) Recording instruments

Geolocation Time-depth recorders (GLTDRs), models MK3+ and MK3e (Wildlife Computers, Redmond, Washington, USA) mounted with a sea-water temperature sensor in the pressure transducer bulkhead and a light sensor in a clear plastic (Lexan) cap at the opposite end (DeLong *et al.* 1992), were enclosed in cylindrical titanium housings 15.4 x 2.9 cm, which weighed 196 g. The recorders were programmed to record data as soon as the instrumented females entered the water, recording hydrostatic pressure (dive depth) every 20, 30, 60 or 90 s, ambient water temperature at 20, 30, 60, 90 or 300 s intervals. Sea-surface light intensity (SSL) and sea-surface temperature (SST) were also measured at 20 - 90 s intervals (of which maximum values were stored) each time the seal surfaced until the memory capacities (256 and 512 Kbytes for MK3+ and MK3e TDRs respectively) of the recorders were filled (see Table 1 **Chapter 2**).

Upon retrieval of the recorders, the data were transferred to a personal computer. Software packages by Wildlife Computers (Redmond, Washington, USA) were used to provide summary analyses of the diving data described in detail in **Chapter 3**. One location was estimated per day from surface light-level readings and based on the highest location quality code available (GEOLOCATION package version 2.0). The daily light-level curves were checked manually (obvious outliers were deleted), and then used to estimate time of dawn and dusk (= civil twilight) from which an algorithm calculated approximate latitudinal and longitudinal position (Hill 1994).

The predicted locations were influenced by the accuracies of civil twilight with variability in air temperature, atmospheric pressure and the durations of a seal's dive (mean dive durations of 24.4 ± 4.4 min, see **Chapter 3**) near the civil twilight (Hill 1994) which resulted in predicted error in longitude of 0.25° for each one minute of error in civil twilight (DeLong *et al.* 1992). Errors in predictions of latitude are influenced by both latitude and season as discussed by DeLong *et al.* (1992). Latitudinal locations could not be made from measurements of daylight within several weeks of the autumnal and vernal equinoxes (Hill 1994). Duty cycling (one day on, one day off) was enabled in the case of seal O144 (postmoulting period) to allow coverage of most of the movements before the memory of the recorder (256 Kbytes) was filled. Memories of GLTDRs deployed on postbreeding seals O390, R101, O138 and postmoulting seals O144, P537 and G006 were filled whilst out at sea. The sea-water temperature and light sensors of the GLTDRs deployed on postbreeding seals R102 and G289 and postmoulting seal R202 (see **Chapter 3**) were at fault which excluded these females in the analyses of **Chapters 4 & 5**.

(c) Hydrographical data

General bathymetric charts of the oceans (GEBCO, Hydrographic Office, Canada) were used to obtain information on the geographical positions of submarine topographical features in the region of Marion Island such as the Agulhas Plateau, Agulhas Basin, Southwest Indian Ridge, Mid-Atlantic Ridge, Weddell Abyssal Plain, Enderby Abyssal Plain and the Ob Bank and Lena Seamount. The tracks of females from Marion Island (present study) were plotted independently and then overlaid on an identically scaled bathymetrical chart in order to assess patterns of movements in relation to sea floor topography.

Both satellite images of the position of the northern Antarctic pack-ice edge in the sector 20°W to 40°E during the period 1990 - 1994, obtained from the Navy - NOAA Joint Ice Centre (USA) and information concerning the positioning of frontal systems within the Southern Ocean, obtained from the South African Data Centre for Oceanography (SADCO), were used within the analyses of movements of elephant seal females from Marion Island. Frontal systems defined by Lutjeharms & Valentine (1984) and inter-frontal zones, namely the Sub-Antarctic Zone (SAZ); Polar Frontal zone (PFZ); and the Antarctic Water Zone (AWZ) following Abrams

(1985) were distinguished in this data set.

(d) Classification of movements

The movements of females were divided into 3 phases based on the location of tracks and residence time in given areas, as illustrated in Figures 8a & 8b for postbreeding and postmoulting females, respectively. In general, the movements of females from Marion Island were defined as follows:

Phase 1: The period between the departure from the island in a definite one-way directional movement, to the commencement of multidirectional, seemingly haphazard, movement over several days in a defined area(s).

Phase 2: The period of multidirectional, seemingly haphazard movement in a defined area distant from the island.

Phase 3: The period between departure from the defined area of multidirectional, seemingly haphazard movement over several days, to one-way directional movement to, and arrival at, the island.

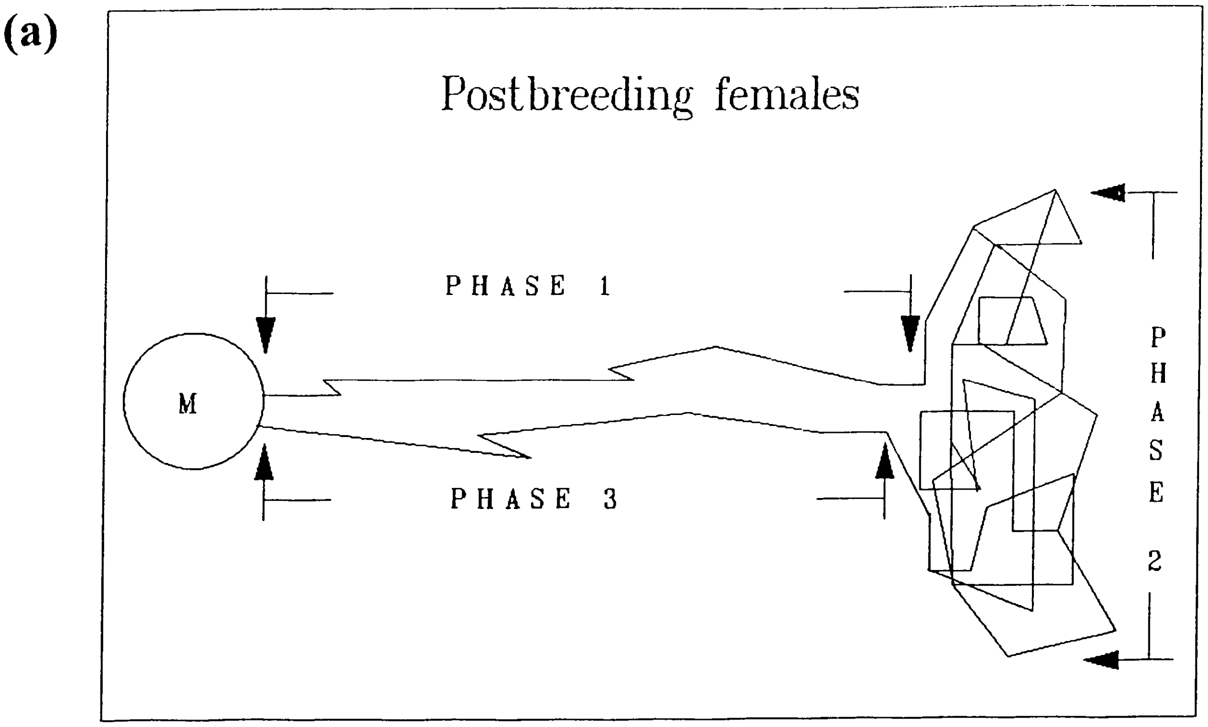
Foraging grounds (phase 2) of individuals were defined as geographical areas crisscrossed by a high number of tracks (based on daily locations). Transit areas (phases 1 and 3) were defined by single, one-way directional tracks (based on daily locations) linking the point of departure/return (Marion Island) and the defined foraging grounds.

(e) Ranging distances

The ranging distance of each female was simply calculated as the linear distance between Marion Island and the furthest geographical position reached, not including distance covered at depth of dives or the sum of differences between daily locations of movement (*vide* Le Boeuf *et al.* 1992; Stewart & DeLong 1994, 1995).

(f) Classification of dive types

Dive types were categorized (using the DIVE ANALYSIS programme, Wildlife Computers), based on dive configurations as determined by dive depths, dive durations, descent- and ascent



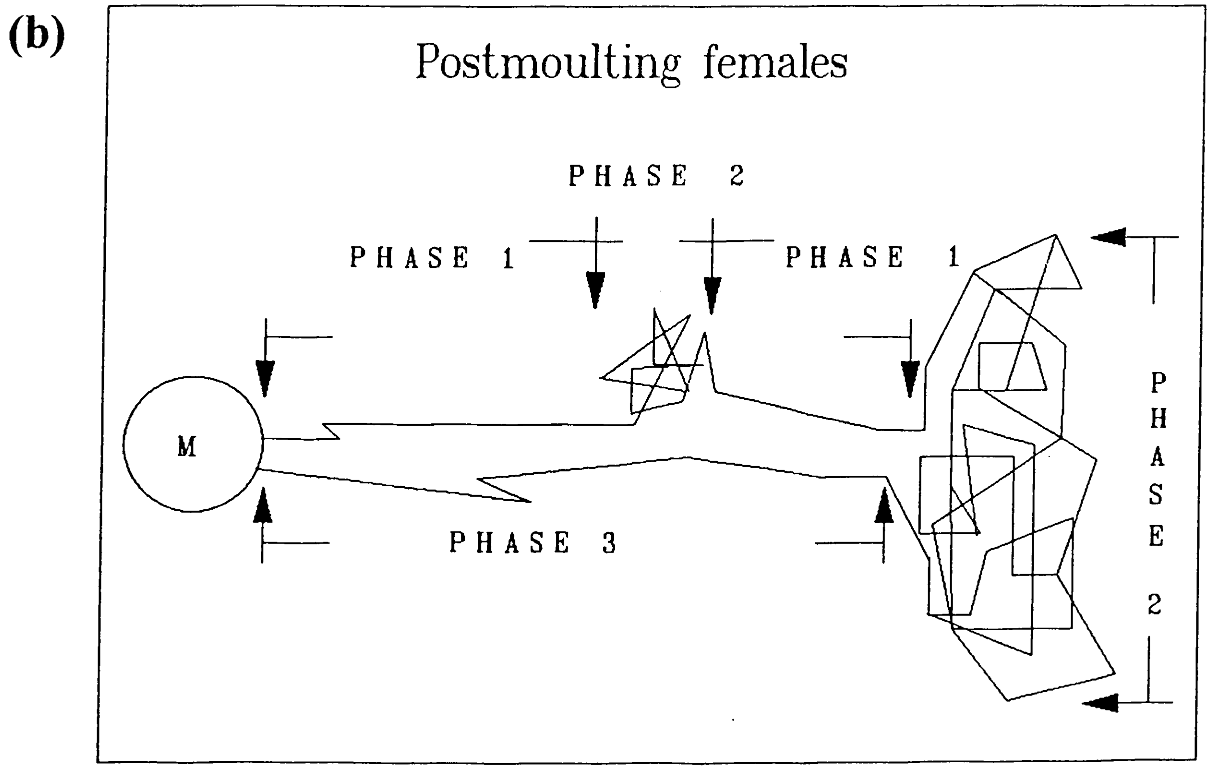


Figure 8. Schematic representation of the tracks of (a) postbreeding and (b) postmoulting females from Marion Island divided into three phases (M - Marion Island).

rates, and bottom times of dives following Le Boeuf *et al.* (1988) (see **Chapter 3**). Of the seven distinct types (see **Chapter 3**) only the major dive types, namely type 3, type 5 and type 7 dives that predominated in this data set, including the predominant type 2 shallow dive (see **Chapter 3**), were used within the analyses of movements of females (present study) during the postbreeding and postmoulting migrations from Marion Island. The frequency occurrence of these dive types was expressed as the mean percentage frequency of all dives performed over consecutive 5 day periods for the total recorded time away from Marion Island.

(g) Statistical Analysis

Chi-square (χ^2) analysis was used to test for differences in ratios of the numbers of days spent within phases 1, 2 and 3 by postbreeding and postmoulting females. Actual values were used within the analysis. The 0.05 level of probability was used to indicate statistical significance.

Results

Movements and foraging grounds

Postbreeding females: Postbreeding females (n = 9) between the ages of 4 - 8 years were tracked for 45 - 73 days from Marion Island (Table 11). Their movements are plotted in Figure 9a. The majority of the postbreeding females remained within ± 1 400 km of the island, and spent a large proportion of their time (phase 2) in defined zones. Mean linear distance reached by postbreeding females from Marion Island was 1 031 ± 302 km (Table 11). Two tracks of seals (O390 and Y333) extended in northwesterly directions and ranged between 600 - 1 300 km from Marion Island. Four tracks of seals (R202, G006 and O138) moved in northeasterly directions, ranging between 722 - 1 150 km, two of which were that of a single seal (R202) which utilized the same area (phase 2) during consecutive (1992 & 1993) postbreeding seasons.

The six tracks of postbreeding females showed long residence times in areas north of Marion Island at 40 - 45°S, centred around longitudes (a) 15°E (1 track - seal O390) over the Agulhas Basin, (b) 25°E (1 track - seal Y333) over the Agulhas Plateau, (c) 38 - 46°E (3 tracks - seals G006, R202 for 1992 & 1993) over the Southwest Indian Ridge and (d) 50°E (1 track -

Table 11. Directions of movements and the furthest geographical position recorded from Marion Island for southern elephant seal females (n = 12) ranging from Marion Island during 1990 - 1994.

Seals	Status	Age	Direction away from Marion Island	Furthest position away from Marion Island	Range (km) from Marion Island	Year recorded	Duration of record (days)	Total days at sea	% of the movements recorded
Y333	pb	6	NW	41.5°S 35.5°E	607	1991	51	51	100
O390	pb	7	NW	41.2°S 24.2°E	1224	1990	53	67	79.1
R357	pb	5	SW	53.5°S 33.5°E	766	1991	45	45	100
R101	pb	4	SW	57.5°S 27.4°E	1393	1990	58	77	75.3
P537	pb	5	SW	56.5°S 23.7°E	1460	1992	51	53	96.2
O138	pb	7	NE	40.9°S 49.2°E	1150	1990	58	67	86.6
R202	pb	6	NE	37.5°S 41.1°E	1068	1992	71	73	97.3
R202	pb	7	NE	40.8°S 40.8°E	722	1993	69	81	85.2
G006	pb	6	NE	40.8°S 41.6°E	894	1994	73	73	100
				Mean	1031 ± 302.5			65 ± 12.6	
O144*	pm	8	SW	53.0°S 6.2°E	2379	1991	224	239	93.7
P537	pm	6	SW	71.6°S 18.9°W	3133	1993	201	269	80.1
G006	pm	6	SW	64.7°S 25.4°E	2122	1994	145	258	52.8
				Mean	2544 ± 525.5			255 ± 15.2	

pb - postbreeding
pm - postmoulting
* - duty cycle

NW - Northwest
NE - Northeast
SW - Southwest

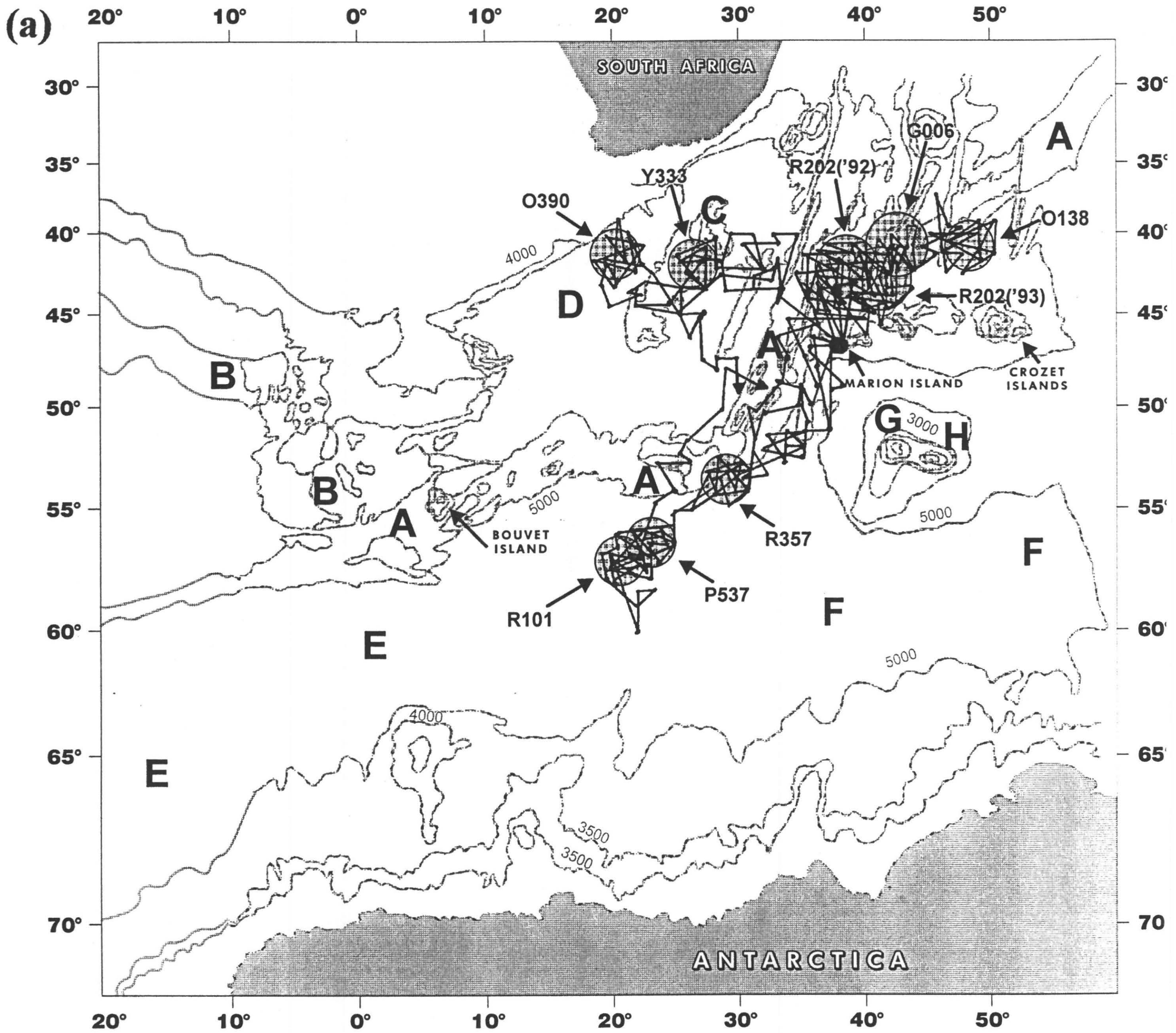
seal O138) over and/or adjacent to the Southwest Indian Ridge. All recorded transit phases (phases 1 and 3) of northerly movements of postbreeding seals were tracked over and/or adjacent to the Southwest Indian Ridge (Figure 9a).

Three recorded tracks of seals (R101, P537 and R357) moved southwest from Marion Island and ranged between 766 - 1 500 km. The phases 2 (long residence time) occurred between 50 - 55°S, centred around (a) 21 - 24°E (2 tracks - seals R101 and P537) adjacent to the Southwest Indian Ridge and extended over the Weddell Abyssal Plain and (b) 30°E (1 track - seal R357) occurring over the Southwest Indian Ridge (Figure 9a). The recorded transit phases (phases 1 and 3) of these southerly movements extended over and/or adjacent to the Southwest Indian Ridge (Figure 9a).

The northwesterly tracks of seals O390 and Y333 and the northeasterly track of seal G006 (all at 40 - 45°S) during phase 2, occurred within sea surface temperatures (SSTs) ranging between 11.5°C and 14.1°C, whereas seals R202 (recorded during 1992 & 1993) and O138 encountered colder SSTs ranging between 5.2°C and 8.8°C in their northeasterly tracks during phase 2. Seals R101, P537 and R357 (all at 55 - 60°S) encountered cold SSTs ranging between 0.8°C and -1.7°C (see **Chapter 5**) during phase 2.

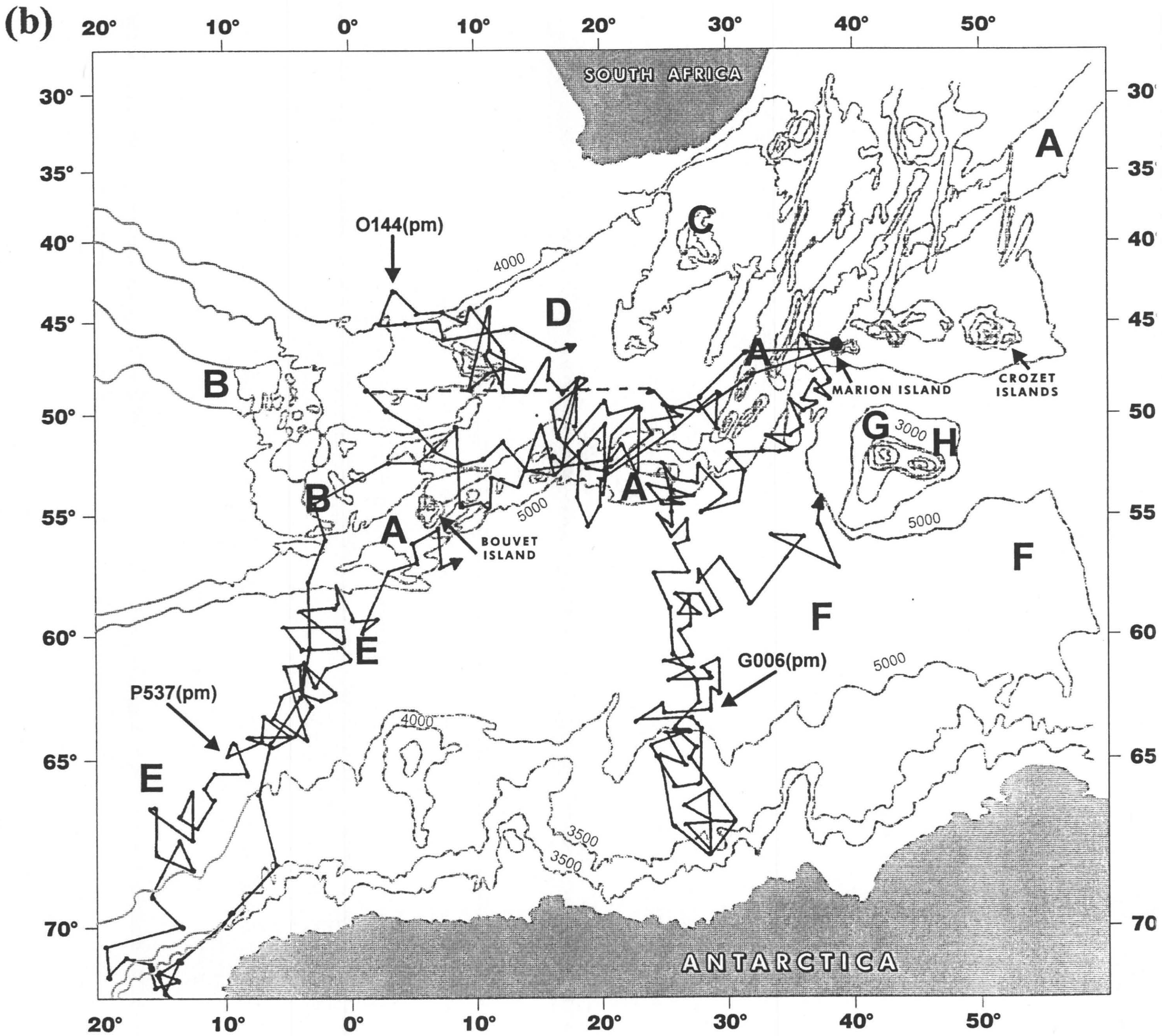
Postmoulting females: Postmoulting females (n = 3) of 6 and 8 years of age were tracked for 112 - 201 days (Table 11). Their movements are plotted in Figure 9b. All females moved in southwesterly directions from Marion Island. Mean linear distance reached by postmoulting females from Marion Island was 2 544 ± 525 km (Table 11). Tracks of seal P537 reached a maximum distance of 3 133 km from Marion Island, and was distinguished by a recorded dry time of ± 10.4 hours, which indicated a single haulout west of Kapp Norvegia on the Princess Martha Coast, Antarctica in the eastern Weddell Sea.

Two phases 2 were plotted for seal P537, on of which occurred at (a) 70 - 72°S centred, around 18°W extending over the Antarctic Continental Shelf, and the other at (b) 60 - 68°S, centred around 18°W - 0° longitude over the Weddell Abyssal Plain. The phase 2 recorded for seal G006 occurred at (c) 60 - 68°S, centred around 22 - 30°E which extended over the Weddell Abyssal Plain. Both phase 2 tracks of seals P537 and G006 projected within the outer-edge of the Antarctic pack-ice, positioned at 60 - 65°S during the recording periods



A - Southwest Indian Ridge
B - Mid-Atlantic Ridge
C - Agulhas Plateau
D - Agulhas Basin
E - Weddell Abyssal Plain
F - Enderby Abyssal Plain
G - Ob Bank
H - Lena Seamount

Figure 9. Movements (dark solid lines) of (a) postbreeding (n = 9) and (b) postmoulting (n = 3) females tracked by GLTDRs during 1990 - 1994, which were plotted independently from the bathymetry chart and then overlaid on the bathymetry chart (light solid lines) of the sea floor topography in relation to Marion Island. Contours at 500 m intervals between 2 000 - 5 000 m are shown. Broken line connects the known positions of females before and after the vernal and autumnal equinoxes when latitude could not be established.



A - Southwest Indian Ridge
B - Mid-Atlantic Ridge
C - Agulhas Plateau
D - Agulhas Basin
E - Weddell Abyssal Plain
F - Enderby Abyssal Plain
G - Ob Bank
H - Lena Seamount

Figure 9 (Continued).

of 1993 and 1994 respectively. Phase 2 of seal O144 occurred at (d) 50 - 55°S, centred around 12 - 30°E longitude over the Southwest Indian Ridge, and extended over the Mid-Atlantic Ridge. The recorded transit phases (phases 1 and 3) of the postmoulting seals occurred over and/or adjacent to the Southwest Indian Ridge (Figure 9b).

Seals P537 and G006 (at 72 - 65°S) encountered cold surface waters ranging between -2°C and -0.5°C (see **Chapter 5**) during phase 2, whereas the track of seal O144 (at 45 - 50°S) ranged within warmer surface temperatures of between 2.2°C and 4°C.

Dive types/phase relationship

The mean percentage time (days) spent by postbreeding females (n = 9) at sea within phases 1, 2 and 3 (15.0 ± 8.3%, 70.8 ± 16.9% and 14.2 ± 8.7% respectively) differed markedly ($\chi^2 = 216.97$, df = 8, $P < 0.0001$) from that of postmoulting females (n = 3), which spent less time in phase 2 (48.9 ± 3.2%) with unequal outbound (phase 1) and inbound (phase 3) transit phases (18.2 ± 12.9%) and 32.9 ± 15.3%, respectively) (Table 12). The mean proportional contribution of dive types within recorded phases of movement for postbreeding and postmoulting females showed that the type 7 dives accounted for the majority of dives followed by type 5, type 3 and type 2 dives (Table 12). During both the postbreeding and postmoulting movements of females, the mean proportional contribution of type 5 dives decreased from phase 1 to phase 2, whereas type 7 dives increased. During phase 3 (n = 3 females), the frequency occurrence of type 7 dives decreased again whereas type 5 dives increased. The mean proportional contribution of type 5 dives in postmoulting females occurred at lower levels, whereas type 7 dives occurred at proportionally higher levels, than that of postbreeding females (Table 12). At the individual level, differences in the frequency contributions of dive types 2, 3, 5 and 7 were evident within postbreeding and postmoulting females diving behaviour (Table 12).

Discussion

Foraging grounds

The utilization of six different foraging areas (four to the north and two to the south) by nine

Table 12. The proportional days (%) spent in phases 1, 2 and 3 and the frequency contributions (%) of dive types 1 - 7 (defined in Chapter 3) that occurred during the movements of postbreeding and postmoulting females from Marion Island, recorded during 1990 - 1994.

Seals	Status	Direction away from Marion	Proportion days spent within phases (%)			Mean proportion of dive types within phases (%)											
						Phase 1				Phase 2				Phase 3			
			Phase 1	Phase 2	Phase 3	Type 2	Type 3	Type 5	Type 7	Type 2	Type 3	Type 5	Type 7	Type 2	Type 3	Type 5	Type 7
Y333**	pb	NW	17.6	64.7	17.6	0	10.0	62.5	20.0	0	9.2	22.9	51.9	0	5.1	12.2	62.4
O390	pb	NW	11.9	76.1	11.9	1.0	4.0	19.7	64.0	0.1	5.4	9.7	75.8	-	-	-	-
R357**	pb	SW	14.9	74.5	10.6	6.1	10.8	12.1	62.7	0.3	8.6	6.3	73.2	1.8	9.7	18.5	54.2
R101	pb	SW	18.2	63.6	18.2	3.3	12.2	32.1	39.5	0.2	11.9	8.1	71.5	-	-	-	-
P537	pb	SW	30.2	39.6	30.2	3.7	8.3	2.3	79.3	2.1	5.0	4.6	83.3	-	-	-	-
O138	pb	NE	6.0	88.1	6.0	0.3	2.9	4.8	72.8	0.1	8.0	6.7	74.0	-	-	-	-
G006**	pb	NE	6.3	88.9	4.8	9.7	1.5	26.9	61.4	11.2	6.2	9.4	71.7	32.9	0.7	3.5	51.0
R202(92)*	pb	NE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R202(93)*	pb	NE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Mean	15.0 ± 8.3	70.8 ± 16.9	14.2 ± 8.7	3.4 ± 3.5	7.1 ± 4.2	22.9 ± 20.6	57.1 ± 20.5	2.0 ± 4.1	7.8 ± 2.4	9.7 ± 6.1	71.6 ± 9.6				
O144	pm	SW	30.5	49.4	20.1	3.1	10.0	5.6	75.0	0.2	0.2	0.7	95.4	-	-	-	-
P537	pm	SW	19.5	51.8	28.7	7.1	2.7	7.8	81.6	0.5	6.8	5.6	84.6	-	-	-	-
G006	pm	SW	4.7	45.5	49.8	10.0	5.5	12.4	70.1	6.8	5.5	9.5	75.4	-	-	-	-
		Mean	18.2 ± 12.9	48.9 ± 3.2	32.9 ± 15.3	6.7 ± 3.5	6.1 ± 3.7	8.6 ± 3.5	75.6 ± 5.8	2.5 ± 3.7	4.2 ± 3.5	5.3 ± 4.4	85.1 ± 10.0				

* - no diving record	NW - Northwest
** - complete data set	NE - Northeast
pb - postbreeding	SW - Southwest
pm - postmoulting	
(92) - 1992	
(93) - 1993	

postbreeding elephant seal females from Marion Island seems to indicate no particular pattern in the choice of foraging grounds. However, four out of the six foraging areas (or seven out of the nine tracks) of postbreeding females were positioned along a northeast/southwest line from Marion Island, at an angle parallel to that of the Southwest Indian Ridge (Figure 9a). Not one of the females (n = 9) ventured to the east of the SW-NE axis of the Southwest Indian Ridge. Furthermore, the return of a single seal (R202) to the same foraging area during consecutive postbreeding seasons (present study) was similar to movements of three (out of twenty one) northern elephant seal females during the postbreeding migrations of 1991 & 1992 (Stewart & DeLong 1995). Similarly, three seals which were tracked from South Georgia over more than one season, repeated their outward direction of travel in subsequent years (McConnell & Fedak 1996). In addition, three movements of seals from Marion Island used the same northerly routes and foraging areas, and two used similar southerly foraging areas (present study). This suggests that, in at least some instances, certain areas are preferred by individuals and that submarine ridges may have cued them during the transit phases.

The mechanisms that seals use to navigate accurately is yet unknown, however, there has been some speculation that seals could possibly be utilizing bathymetrical and topographical features as navigational cues during movements (Tierney 1977; Burton 1985; Bester 1988b; Gales & Burton 1989; Thompson *et al.* 1991; Wilkinson & Bester 1990), whereas McConnell & Fedak (1996) could find no obvious topographical features that characterized foraging areas. Although the females from Marion Island did not feed benthically (see **Chapter 3**) and the submarine ridges were considerably deeper than the deepest recorded dive, these ridges could possibly be detected through the narrow core of countercurrents deflected off the crest of a ridge causing an upward jetlike nature of flow to the surface, parallel to the ridge (Callahan 1971). These females performed deep assumed `exploratory' dives (type 5 dives) at all hours of the day (see **Chapter 3**), implying that seals probably do not need daytime vision for navigation or orientation. All the females in the present study did not use the Enderby Abyssal Plain to the southeast of the island, where no readily locatable oceanographic features occur, excluding the Ob Bank and Lena Seamount (± 880 - 1 000 km distant at depths of 247 - 3 000 m) where elephant seals from an unknown source were seen from Russian trawlers (Bester

1989).

Postbreeding females (present study) that moved to northerly foraging grounds encountered warm surface water consistent with the mean position of the STC at 41°40′S which is recognizable at the sea surface by a mean decrease in temperature from 17.9 - 10.6°C (Lutjeharms & Valentine 1984), while other northerly foraging areas (n = 2) were characterized by surface temperatures consistent with the SAF, which has a mean surface temperature expression of 7°C (Lutjeharms & Valentine 1984). However, close scrutiny of the temperature profile of the water column and daily sea-surface temperatures (SSTs) recorded during female dives (see **Chapter 5**), showed that they foraged in the inter-frontal zones rather than at the STC and SAF as suggested by Bester & Pansegrouw (1992). Similarly, tracks of postbreeding females (n = 4) from the Patagonia population, which ranged east of Peninsula Valdés (45°W), remained in the temperate waters of the South Atlantic Ocean (in the latitude range 39 - 50°S), did not seek out frontal systems, and did not venture into colder southern waters near the APF (Campagna *et al.* 1995).

Postbreeding females (n = 3) from Marion Island, in addition, also foraged in cold waters well south of the APF (found at a mean position of 50°18′S, which is recognizable at the sea surface by a mean decrease in temperature from 4.1 - 2.5°C, Lutjeharms & Valentine 1984), while postbreeding females from Macquarie Island foraged around the APF (n = 3) and in Antarctic waters along the continental shelf (n = 5) (Hindell *et al.* 1991a). One postbreeding female from South Georgia was tracked to the APF (McConnell & Fedak 1996) and three were tracked to the continental shelf-area of the Antarctic Peninsula and to Elephant Island (covering distances ≥ 1 420 km)(McConnell *et al.* 1992a), one of which moulted there (Fedak *et al.* 1994). Therefore, although the postbreeding females from Marion Island (n = 9) used the same open ocean foraging strategy as the Patagonian females, they were foraging within inter-frontal zones (i.e. the STZ and the AWZ) south of the APF, in contrast with the postbreeding females from Macquarie Island (Hindell *et al.* 1991a) and South Georgia (McConnell *et al.* 1992a; McConnell & Fedak 1996) that went to locatable oceanographic and bathymetrical features such as the APF and Antarctic Continental Shelf.

The feeding range of postbreeding females (present study) did not exceed ± 1 400 km from Marion Island for the relatively short postbreeding period at sea. It is perhaps significant that frequency occurrences of the predominant assumed foraging dives (type 7 dives) of postbreeding females were the highest at the edge of their feeding range within phase 2 (present study). This might suggests that as soon as suitable levels of prey availability are encountered, they remain in the general area to feed as hypothesized by McConnell & Fedak (1996) for South Georgia females. Furthermore, the range of 45 - 77 days at sea between the postbreeding departure and the obligate moult haulout (see Table 11), apparently constrained the extent to which the postbreeding females of Marion Island could range. There are no known distant moulting sites, e.g. at islands other than the proximate Prince Edward Island and Iles Crozet or on the Antarctic Continent (Enderby Land being the closest point at > 2 200 km distant) from Marion Island (see Gales & Burton 1989). The movements of postbreeding females from Marion Island (this study) therefore lend support to the hypothesis of Bester (1989), that the foraging range of elephant seals links with the Iles Crozet population (± 1 140 km away), but excludes the distant Iles Kerguelen (2 640 km) and Heard Island (2 740 km) populations which lie to the southeast, an area (the Enderby Abyssal Plain) which was not visited by postbreeding females in this study.

By contrast, the foraging grounds of postmoulting females (present study) exceeded ≥ 2 122 km from Marion Island to considerably more distant foraging areas which occurred (a) along the Antarctic Continental Shelf near the Princess Martha Coast, in the eastern Weddell Sea, (b) in the inter-frontal zone south of the APF within the AWZ, and (c) around the APF during the postmoulting period of 239 - 258 days at sea. Similarly, foraging areas around the APF and over the continental shelf were also sought by postmoulting females from Macquarie Island and South Georgia (Hindell *et al.* 1991a; McConnell & Fedak 1996) and well as inter-frontal zones north and south of the APF by females (n = 5) from South Georgia (McConnell & Fedak 1996).

Since foraging locations of postmoulting females from Marion Island in the present study were widely, and more distantly, distributed than that of postbreeding females, it suggests high degrees of pelagic meandering during the postmoulting period, also evidenced by differences in the duration of outbound and inbound transit phases in the latter period. The more constrained foraging excursions undertaken by postbreeding females from Marion Island, by contrast, displayed relatively short in- and outbound transit phases of similar duration with most time spent within foraging grounds. Similarly, the tracks of females from South Georgia were also generalized into three phases consisting of rapid directed movements away from the island, followed by slower, often meandering travels interspersed with slow or stationary periods, and a rapid directed return to South Georgia (McConnell & Fedak 1996).

Dive types/phase relationship

Phases 1 and 3 of the present study were consistent with transit phases to feeding grounds as dive types 1 and 2, hypothesized to serve as shallow transit dives (see **Chapter 3**) increased in the frequency occurrences during these phases. Dive types 3 and 4 were hypothesized to serve as functional 'resting/exploratory/transit' dives, whereas type 5 dives were assumed to serve as deep 'exploratory' dives (see **Chapter 3**). Type 7 dives contributed 75% or more of the dive types in each of the dive records in this study, a percentage contribution similar to assumed foraging dive types reported for females in earlier studies (Le Boeuf *et al.* 1986, 1992; Hindell *et al.* 1991b; Asaga *et al.* 1994; Campagna *et al.* 1995). The predominance of type 7 dives (present study), and its particular characteristics (see **Chapter 3**), suggests that it serves foraging (Le Boeuf *et al.* 1988, 1992; Hindell *et al.* 1991b; Campagna *et al.* 1995; see **Chapter 3**).

Since foraging grounds of postbreeding females were located within inter-frontal zones (see **Chapter 5**), their foraging grounds were therefore not reliably associated with readily locatable oceanographic features such as the STC, SAF and the APF where primary productivity is high (Plancke 1977; Pomazanova 1980; Allanson *et al.* 1981). The frequency of assumed foraging dives within postbreeding foraging grounds were generally lower (interspersed with increased frequencies of assumed transit and exploratory dives) than within the foraging grounds of postmoulting females which were situated at readily locatable oceanographic features. This possibly suggests more opportunistic feeding by postmoulting females *en route* to an area of assumed intense foraging/prey pursuit during phase 2, evident by a concomitant increase in type 7 dives during long residence time of females in a specific area.

Similarly, opportunistic feeding in grey seals also seemed to be an explanation for continuous foraging dive bouts during transit phases (McConnell *et al.* 1992b). Moreover, Hindell *et al.* (1991b) found foraging dives in southern elephant seals to occur the least in the days immediately after departure from the island and periods of reduced travel (phase 2) was hypothesized to occur in areas of increased prey availability (McConnell & Fedak 1996).

It is therefore concluded that there are two seasonal foraging strategies for adult females from Marion Island (a) short, directed outbound journeys to/from circumscribed foraging areas within the inter-frontal zones where prey distribution is likely to be unpredictable (El-Sayed 1988; Fedak *et al.* 1994; McConnell & Fedak 1996) but which may attract the same or different individuals during the relatively short postbreeding period, or (b) wide ranging meandering during the relatively long postmoulting period, interspersed with high frequencies of assumed foraging behaviour at separated distant locations which may be readily locatable. Despite the hypothesized two seasonal foraging strategies, foraging strategy may also be dependent on the diving behaviour of females, e.g. the frequency distributions of foraging dive depths, durations of dives which were on average longer during the postmoulting period than during the postbreeding period (Hindell *et al.* 1991b; see **Chapter 3**), bottom times during diel dive patterns, and the occurrences of Extended Surface Intervals (ESIs) (see **Chapter 3**). All these factors could be related to seasonal differences in the type of prey available, as hypothesized by McCann (1985), which may lead to variations in foraging range, location and diving behaviour. Furthermore, these individual differences in diving behaviour and foraging movements not only lies in the interaction between prey availability and the annual energy requirements of populations (Boyd *et al.* 1994) and individual seals, but could possibly be closely correlated with the hydrography and physical characteristics of the water column (Boyd & Arnbom 1991; Hindell *et al.* 1991a; McConnell & Fedak 1996; see **Chapter 5**).

CHAPTER 5

SPATIAL AND TEMPORAL PATTERNING IN DIVING BEHAVIOUR

Introduction

Southern elephant seals breed and moult on Marion Island during austral spring and summer (Condy 1978) and are major predators of pelagic squid and fish in the sub-Antarctic marine ecosystem (Laws 1977a). Breeding elephant seals are ashore from August to November and after a few months at sea during the postbreeding period, they return for the moult haulout that peaks in January for females. From May to August elephant seals are presumable feeding at sea during the postmoulting period (Condy 1979; see **Chapter 3**). However, relatively little is known about southern elephant seals' foraging areas (Hindell *et al.* 1991a; Bester & Pansegrouw 1992; McConnell *et al.* 1992a; McConnell & Fedak 1996; see **Chapter 4**) and the distribution of their potential prey species within the Southern Ocean (McConnell *et al.* 1992a; Rodhouse *et al.* 1992).

Boyd & Arnbom (1991) concluded that the diving behaviour of seals could be closely correlated with the hydrography of the ocean, but that seals could be using other physical characteristics of their environment to help locate suitable feeding areas. Variation in the degree of overlap in the foraging areas of seals could probably be most closely related to prey abundance and availability (Antonelis *et al.* 1990). Foraging locations and amount of overlap could possibly shift with seasonal and annual variations in prey availability (MacCall 1986), perhaps manifested in the individual variation of elephant seals (Hindell *et al.* 1991b; McConnell *et al.* 1992a; Boyd 1993b; McConnell & Fedak 1996; see **Chapter 4**). The feeding requirements of prey and their supply of food relative to its geographic distribution (both horizontal and vertical) must also be considered (Holm-Hansen & Huntley 1984). Rodhouse & Clarke (1985) speculated that the discontinuity in water density at the boundary between the minimum temperature layer (Priddle *et al.* 1986) and the warmer deep water was a point of accumulation for sinking organic matter. This may result in increased biological activity at the bottom of the minimum temperature layer, suggesting that elephant seals could be exploiting a rich food source at these depths (Boyd & Arnbom 1991).

Foraging areas of southern elephant seals have been estimated using sea-surface temperatures (Hindell *et al.* 1991a) and changes in ambient water temperature during the course of movements by northern (Hakoyama *et al.* 1994) and southern (Boyd & Arnbom 1991) elephant seals. Relating data on hydrographical and bathymetrical features of water columns in which a seal feed would, furthermore, be important in understanding the behaviour of seals to locate suitable feeding areas (Boyd & Arnbom 1991). Elephant seals being deep-diving pinnipeds, also provide an additional locational cue of temperature/depth profiles that are unavailable from shallow-diving species such as Antarctic fur seals (Kooyman *et al.* 1986).

This chapter addresses changes in ambient water temperature experienced by southern elephant seal females travelling to/from Marion Island. The specific aims are to (a) describe changes in sea surface temperatures (SSTs) and water temperature at depth during the movements of postbreeding and postmoulting females, and (b) examine changes in diving behaviour of females in relation to changes in ambient water temperature at depth. The implications are discussed and compared with those from other breeding populations of southern elephant seals.

Methods

(a) Recording instruments

GLTDRs were deployed on postbreeding (n = 9) and postmoulting (n = 3) adult southern elephant seal females from Marion Island during 1990 - 1994 following Bester & Pansegrouw (1992) (see **Chapter 2**). GLTDRs equipped with a temperature channel which measured sea temperature using a thermistor composite mounted in a transducer end cap, also periodically collected light-level readings which provided estimates of position (Hill 1994; DeLong *et al.* 1992; see **Chapter 4**). The light-level and sea water temperature readings were stored and displayed graphically on computer. The sea water temperature data was compared to the diving profiles and daily movements of females using the DIVE ANALYSIS and GEOLOCATION option software packages (Wildlife Computers, Redmond, Washington, USA) mentioned in **Chapter 2**. The 3M software package (Wildlife Computers) was used to extract daily minimum and maximum sea water temperatures recorded by females.

The GLTDRs were programmed to record water temperature every 45, 60, 90, 180 or 300 s for the respective females during the postbreeding and postmoulting periods at sea (see Table 1, **Chapter 2**). The protocol settings for postmoulting seal O144 was set on duty-cycle to save on memory as the postmoulting excursions occurred over longer time periods at sea, but this function was abandoned when GLTDRs were obtained with greater memory loading capacities. Data for the entire period at sea was obtained for postbreeding seals G006, Y333, R357 and R202 (a repeat during 1992 & 1993), whereas approximately 75 - 97% of the time at sea was sampled for the majority of the remaining females, with the exception of postmoulting seal G006 that was sampled for 52% of its time at sea (see Table 11, **Chapter 4**).

The estimated movements of females during the postbreeding and postmoulting periods are depicted in **Chapter 4**. The tracks of postbreeding and postmoulting females were categorized into 3 phases, of which phases 1 and 3 were outbound and inbound transits to Marion Island, respectively, and phase 2 as the foraging ground (see **Chapter 4**).

(b) Temperature data

Digitized SST data was obtained from SADCO (South African Data Centre for Oceanography, SA) and from VOS (Voluntary Observing Ships) for 1990 - 1994 within the areas 30 - 60°S, 15 - 60°E. These measurements consisted of closely spaced surface and expendable bathythermograph readings (Fukase 1962; Taylor *et al.* 1978). This data was used to confirm the localities of frontal zones namely the Sub-Tropical Convergence (STC); Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) following Lutjeharms & Valentine (1984). Inter-frontal zones, namely the Sub-Tropical Zone (STZ); Sub-Antarctic Zone (SAZ); Polar Frontal Zone (PFZ); Antarctic Water Zone (AWZ); Continental Water Boundary (CWB); and the Continental Water Zone (CWZ) were distinguished following Abrams (1985) for the period when the females were at sea. SST was defined as the mean water temperature that extended from 0 - 4 m. Mean daily SSTs were calculated throughout the recorded movements of all females.

Seal G006, which was recorded during both the postbreeding and postmoulting periods, was the only female used throughout the analyses of the diving depth/sea temperature relationships. Corrupted recordings of sea temperatures at depth for the remaining females resulted in all females not being used within these detailed analyses. Only the three major dive types (namely dive type 2, type 5 and type 7 dives - see **Chapter 3**) performed by seal G006 during the postbreeding and postmoulting periods, were used within this analyses which were assumed to serve as transit, exploratory and foraging dives respectively (see **Chapter 3**).

Diel differences in maximum depths of foraging dives were determined for the midday (10h00 - 14h00) and midnight (22h00 - 02h00) periods, following Le Boeuf *et al.* (1988), to eliminate the possible influence of dawn and dusk which would differ according to the season and location of the females (see **Methods**, **Chapter 3**). The vertical distribution of water temperature was presented as the mean daily water temperature at 25 m depth intervals. Mean daily water temperatures encountered at depth by seal G006 during the postbreeding and postmoulting periods were used to categorize their sojourn at sea into different stages based on patterns in the vertical distribution of sea temperatures within the water column (see **Results**).

(c) Statistical analysis

Frequency distributions of mean maximum dive depth and mean temperature at depth were examined to determine the relationship between dive depths and the temperature profile of the water column. Chi-square (χ^2) analysis was used to test the differences in ratios of the frequency of occurrence of dive types 1 - 7 (defined in **Chapter 3**) using actual values. Two sample (t-tests) were used to test differences between mean maximum depths (at midday and midnight) of diel foraging dives. A one-way analysis of variance (ANOVA) with least square means (Sokal & Rohlf 1981) was used to examine differences between dive parameter means of individuals (DeLong & Stewart 1991; Bengtson & Stewart 1992). All statistical analyses were performed using SAS statistical package (SAS Institute Inc. 1982). The 0.05 level of probability was used to indicate statistical significance.

Results

Sea Surface Temperatures (SSTs)

SSTs after departure from Marion Island ranged from ± 5°C to 14°C for females that moved north, and decreased to -2°C for females that moved south during the postbreeding and postmoulting periods. Of the postbreeders (n = 9), six moved north and remained in warmer waters with mean SSTs between 5.9°C and 9.2°C, the other three moved south through steadily decreasing SSTs to reach waters between 0.12°C and 3.11°C (Figures 10a - 10c). All three postmoulting females moved south to waters where mean SSTs ranged between -0.7°C and 3.2°C (Figure 11).

Northwesterly movements: Two postbreeding seals (O390 and Y333) set out within the Sub-Antarctic Front (SAF) from Marion Island during the outbound transit phase (phase 1). Both females progressed in northwesterly directions moving through the SAF for ± 3 - 4 days to the Sub-Antarctic Zone (SAZ). During phase 2 seal O390 spent 19.5% of her time in the STC, whereas 80.5% was spent in the SAZ. Seal Y333 spent 100% of the time in the SAZ during phase 2 where SSTs ranged between 6 - 10°C. Both females returned into the SAF during the inbound transit phase (phase 3) to Marion Island (Figure 10a).

Northeasterly movements: Four tracks of postbreeding seals O138, G006 & R202 moved within the SAF for ± 2 days during phase 1, and moved northeasterly to the SAZ. During phase 2, seal G006 spent 3.7% of her time in the STC, 3.7% in the SAF, and 92.6% in the SAZ. Seals O138 and R202 (both deployments) spent ± 100% of their time in the SAZ. Seals G006 and R202 (both deployments) returned into the SAF during the last few recorded days in December and January, respectively, during the inbound phase 3 to Marion Island, whereas the memory of the GLTDR deployed on seal O138 was filled during phase 2 (Figure 10b).

Southwesterly movements: (a) Movements of three postbreeding seals R101, R357 and P537 commenced within the SAF. Seal R357 spent ± 2 days transiting through the Polar Frontal Zone (PFZ) to the APF during outbound phase 1. During phase 2, seal R357 spent 31.5% of her time in the APF, 68.5% in the AWZ, and returned to the SAF during the last few recorded days in December and January during inbound phase 3 (Figure 10c).

(a)

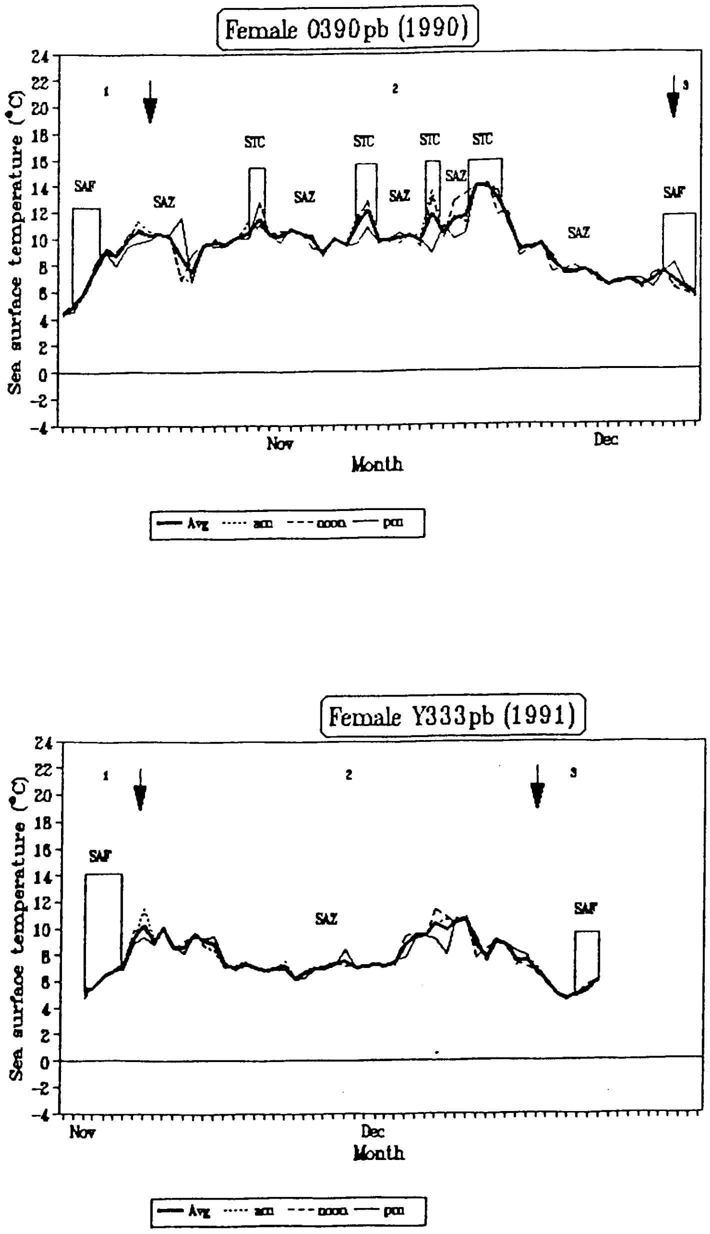


Figure 10. Sea surface temperatures (SSTs) recorded during 1990 - 1994 of post-breeding females that moved in (a) northwesterly, (b) northeasterly and (c) southwesterly directions from Marion Island. SAF - Sub-Antarctic Front; SAZ - Sub-Antarctic Zone; STC - Sub-Tropical Convergence; APF - Antarctic Polar Front; AWZ - Antarctic Water Zone (from Abrams 1985). Numbers depict the stage of movement, namely phases 1, 2 and 3. (pb - postbreeding).

(b)

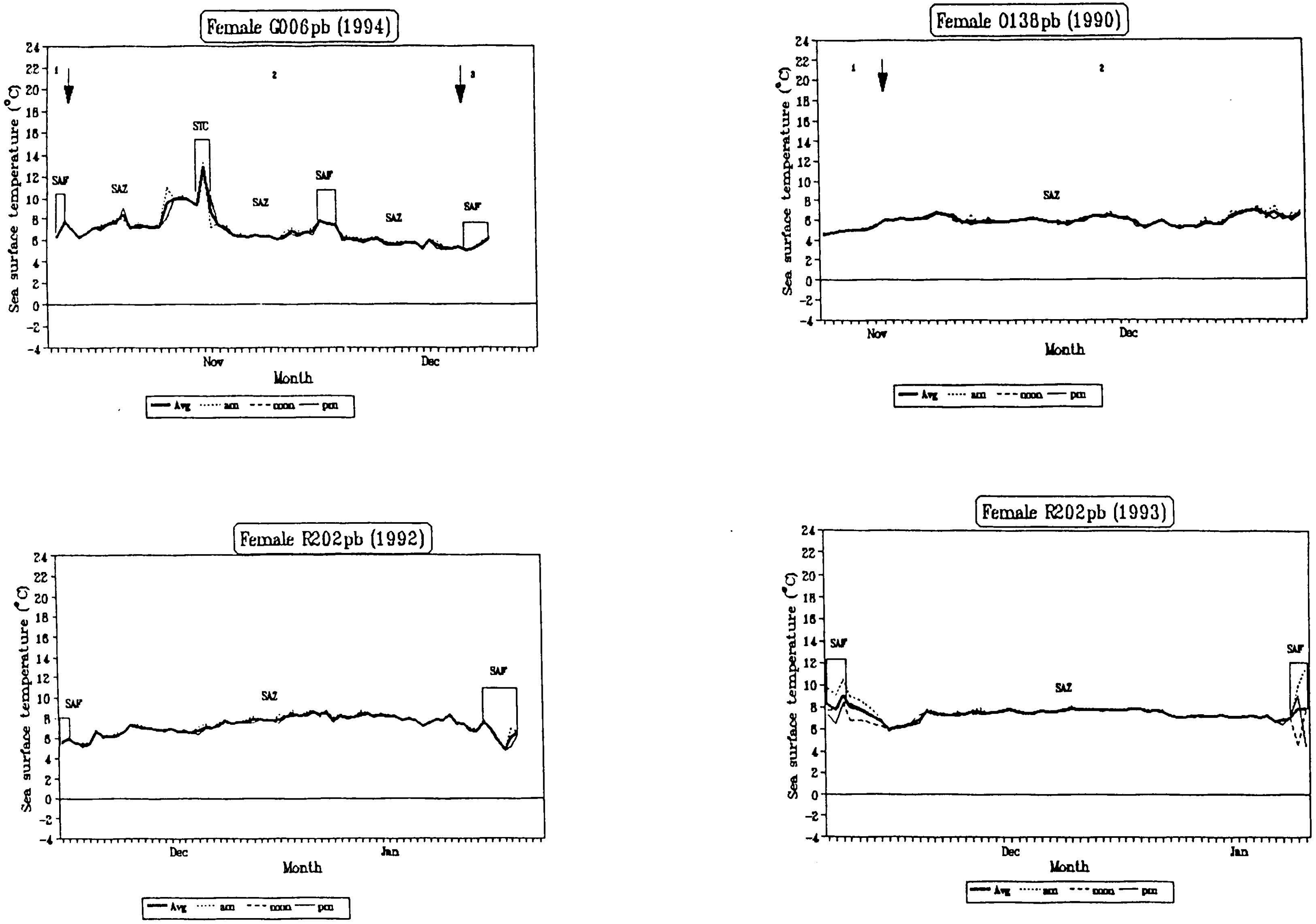
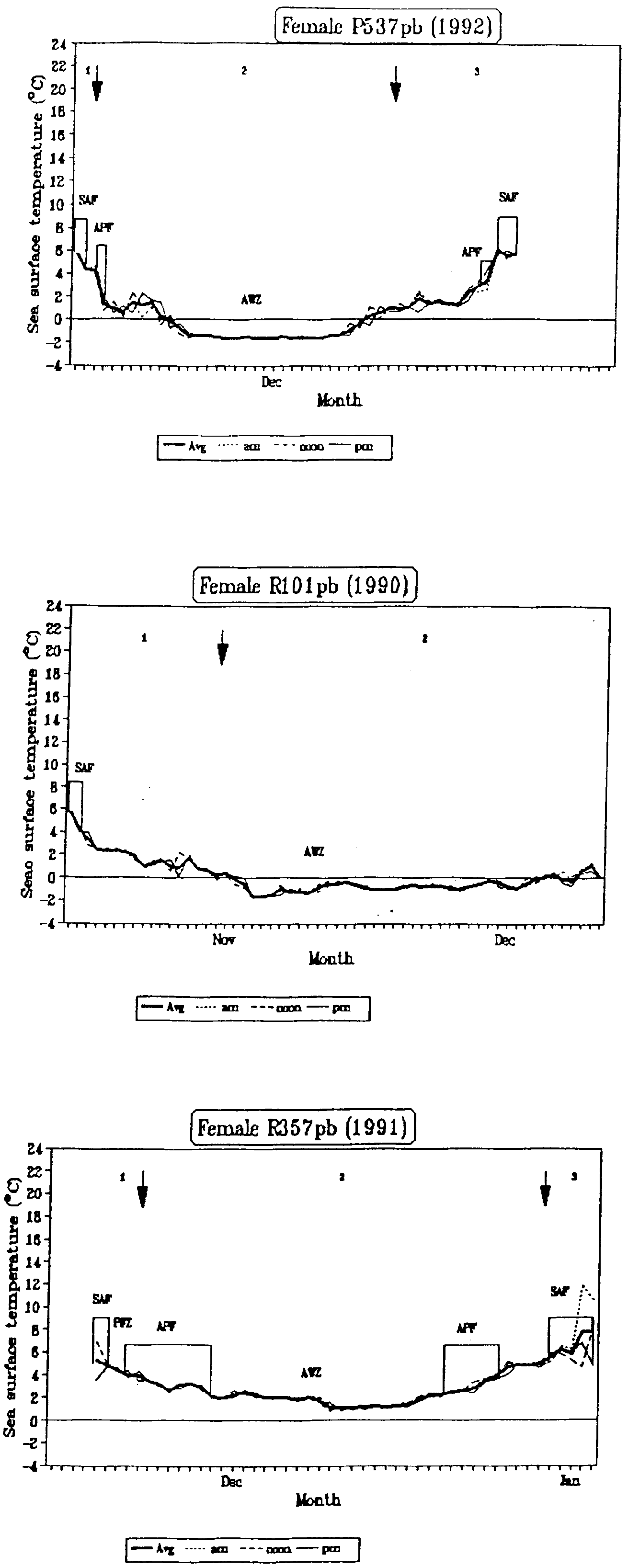


Figure 10 (Continued).

(c)



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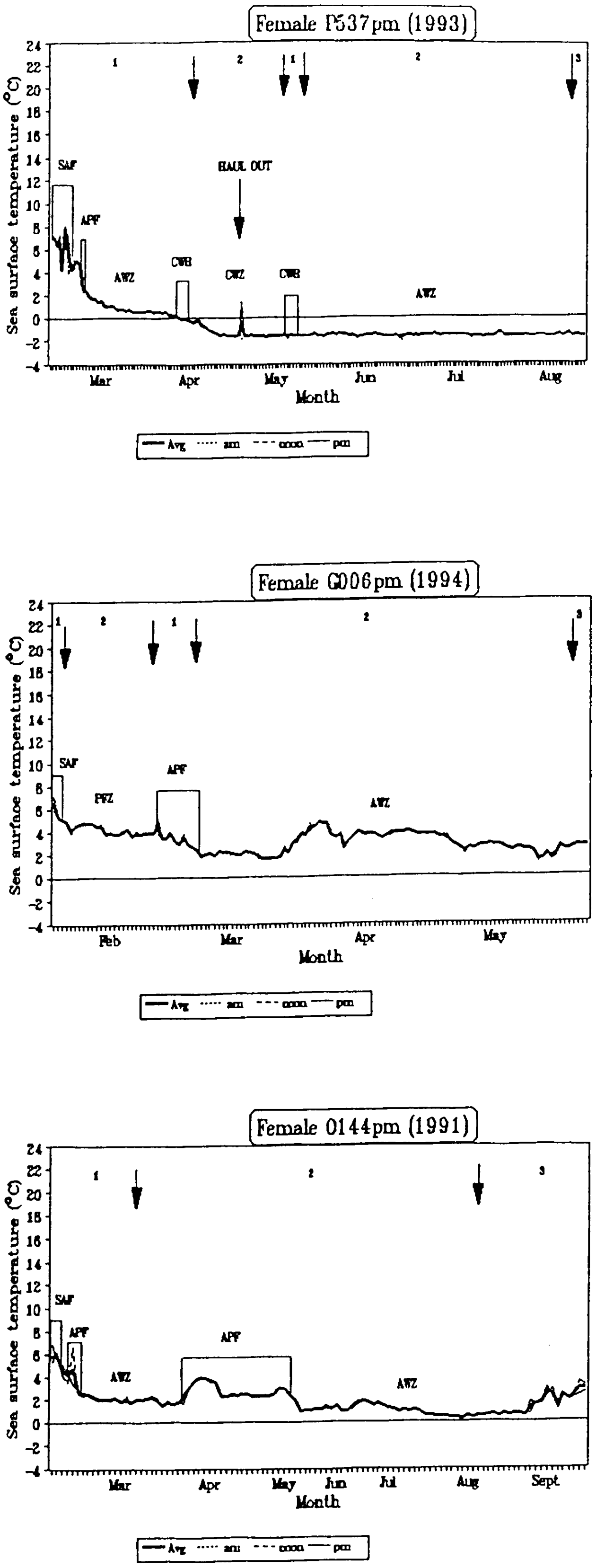


Figure 11. Sea surface temperatures (SSTs) recorded during 1991, 1993 and 1994 of postmoulting females that moved in southwesterly directions from Marion Island. SAF - Sub-Antarctic Front; SAZ - Sub-Antarctic Zone; STC - Sub-Tropical Convergence; APF - Antarctic Polar Front; AWZ - Antarctic Water Zone (from Abrams 1985). Numbers depict the stage of movement, namely phases 1, 2 and 3. (pm - postmoulting).

Seals R101 and P537 spent ± 1 - 2 days in the APF during phase 1 before moving further south to the AWZ. During phase 2 both seals spent between ± 96.8 - 100% of their time in the AWZ with seal P537 lingering for 3.2% of her time at the APF. Seal P537 spent ± 8 days within the AWZ during the inbound phase 3 to the APF where she remained for ± 2 days and reached the SAF within 2 days when the memory of the GLTDR was filled.

(b) Postmoulting seals O144, P537 and G006 ranged further south than postbreeding females, seal O144 reaching the PFZ after 3 days during the outbound phase 1, remaining within the PFZ for ± 4 days before moving south to the AWZ (Figure 11). During phase 2, seal O144 spent 30.7% of her time at the APF and 69.3% in the AWZ, and started to return from the beginning of August during the inbound phase 3 when the memory of the GLTDR was filled (Figure 11).

Seal P537, which moved the furthest distance (to the Antarctic Continent, see **Chapter 4**) reached the AWZ after ± 13 days during the outbound phase 1 and crossed over the CWB (where SSTs dropped to sub-zero) to the CWZ during the first days of April. During the first phase 2, seal P537 spent 100% of her time in the CWZ where SSTs ranged between -2°C and -0.5°C. After ± 16 days within the CWZ, she hauled out for ± 10.5 hours, and remained within the CWZ for another 12 days thereafter, before moving north over the CWB to the AWZ. During a second phase 2, seal P537 spent 100% of her time in the AWZ for ± 2½ months (from mid-May to the beginning of August) where SSTs remained at ± -2°C. The memory of the GLTDR was filled during the start of phase 3 (Figure 11).

Seal G006 reached the PFZ after ± 3 days from the SAF during phase 1. During a first phase 2, seal G006 spent 100% of her time in the PFZ, moving further south to the APF during the continuation of the outbound phase 1, spending ± 10 days transiting through the APF. During a second phase 2, seal G006 spent 100% of her time in the AWZ where SSTs ranged between 1.8°C and 5°C. The GLTDRs memory was filled during the start of the inbound phase 3 (within the AWZ) to Marion Island (Figure 11).

Vertical distribution of sea water temperature

Diving depth and temperature profiles of postbreeding seal G006 which moved north from

Marion Island showed that water temperatures remained relatively constant and warm to about 300 m, below which the temperatures slowly declined, so that water temperature decreased with an increase in depth (Figure 12a). Postmoulting seal G006 that moved south of the APF, experienced SSTs that averaged between 3 - 7 °C with a concomitant decline in temperatures to ± 300 - 400 m, below which temperatures levelled out (Figure 12b).

Figures 13a & 13b schematically represent the average daily water temperature profile in the water column (at depths ranging from ± 0 - 900 m) encountered by the female during dives. Superimposed are the diel differences in the daily mean depths of foraging dives, illustrated as line graphs during midday (10h00 - 14h00) and midnight (22h00 - 02h00) hours for the northerly postbreeding and southerly postmoulting movements of seal G006. Tables 13a and 13b depicts the water temperatures encountered at depths during the different stages (see below) of the journey during the postbreeding and postmoulting periods, respectively.

Postbreeding period: The movement of seal G006 recorded between October - December 1994 was categorized into 4 stages designated A - D (Figure 21a). The return journey of seal G006 from the furthest location from Marion Island (see **Chapter 4**), commenced on 12 November during stage C (Figure 13a).

Stage A: The frequency occurrence of foraging dives (71.44%) was high, followed by exploratory dives (15.16%), with transit dives (7.39%) used at low frequencies (Table 14). Both day and night foraging dives extended from 300 - 800 m within the 5 - 3 °C thermal layers. Night foraging dives extended within the 5 - 4 °C thermal layers at depths from ± 300 - 625 m, whereas day foraging dives remained within the 3 °C thermal layer at depths from ± 675 - 800 m (Figure 13a). The mean difference between day and night foraging dives varied between ± 50 and 500 m (Figure 14a).

Stage B: The frequency occurrence of foraging dives (84.25%) was the highest of all stages, transit dives (0.83%) the lowest, whereas exploratory dives (11.88%) was similar to the high frequency recorded for stage A (Table 14). Day and night foraging dives extended from ± 575 - 750 m within the 5 - 4 °C thermal layers. Night foraging dives remained within the 5 °C thermal layer at depths of ± 575 - 650 m, these dives being ± 275 - 300 m deeper than the night dives

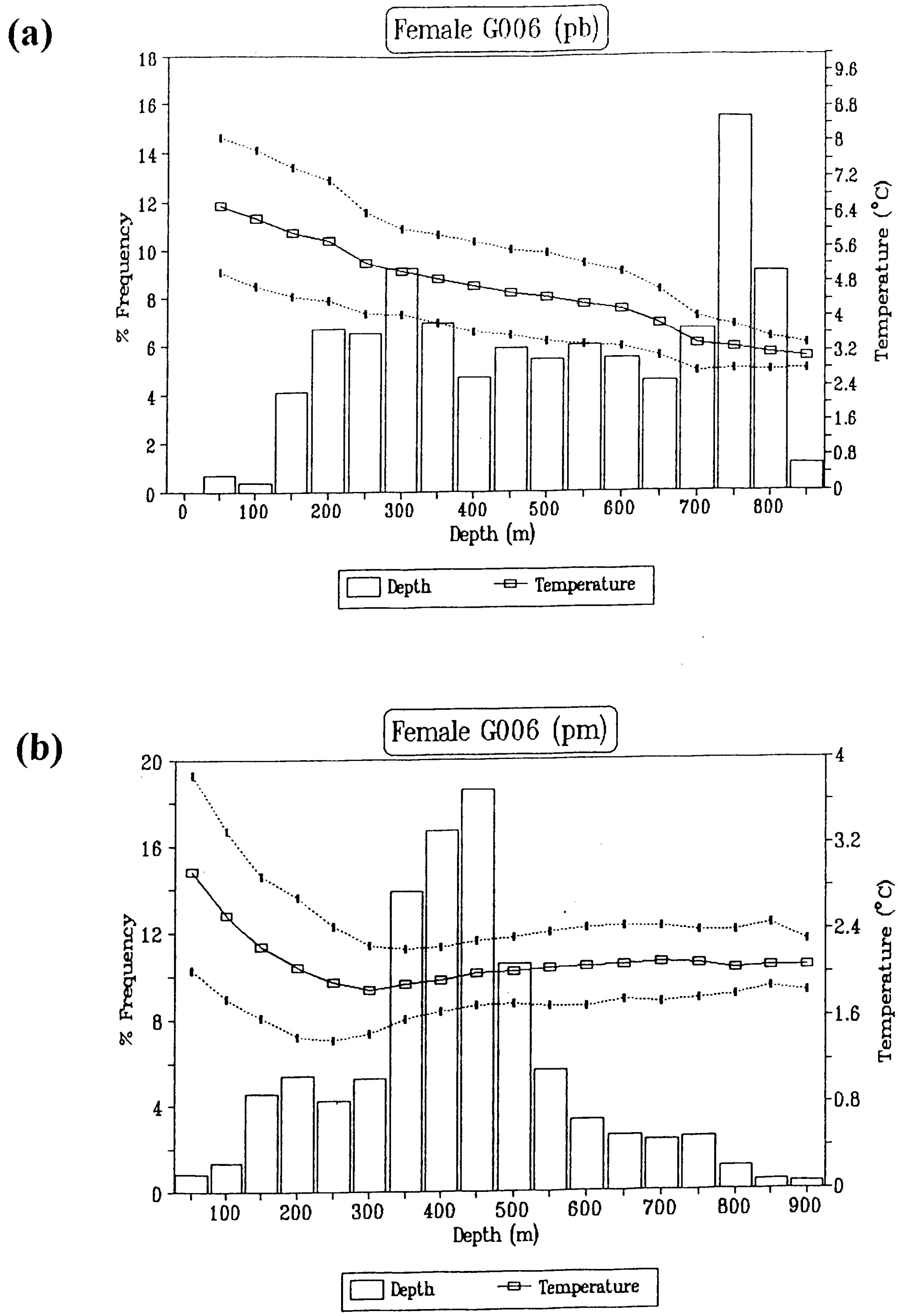


Figure 12. The frequency (%) of dive depth and temperature profiles of seal G006 during the (a) postbreeding and (b) postmoulting periods of the journeys from Marion Island. (pb - postbreeding; pm - postmoulting).

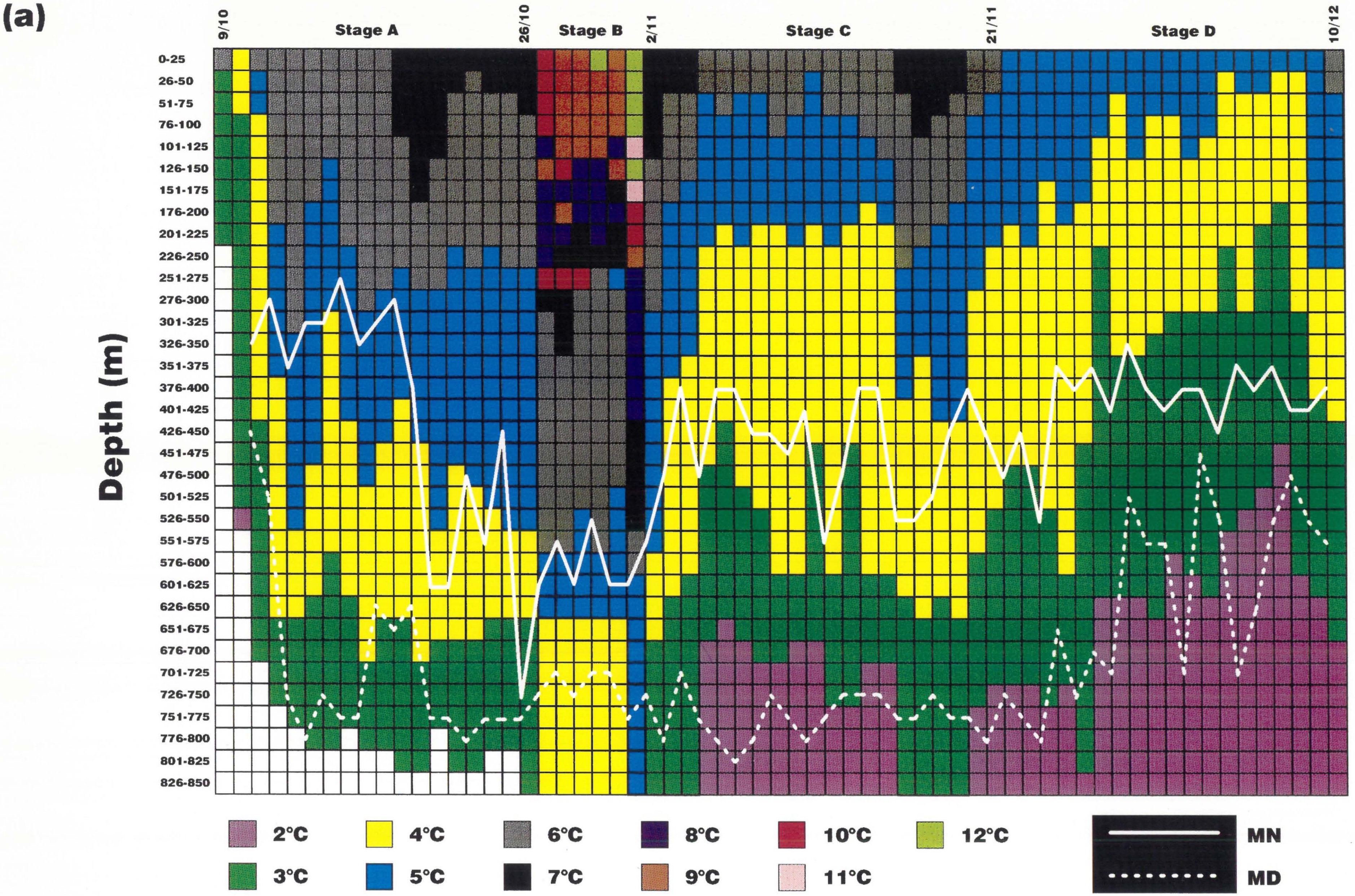


Figure 13. A schematic representation of the average daily water temperature profile of the water column encountered by seal G006 during the (a) postbreeding and (b) postmoulting movements, categorized into different stages designated A-D and A'-E' (with starting day and month), respectively. Superimposed are the diel differences in the daily mean depths of type 7 dives ('foraging' dives), illustrated as line graphs. (MD-midday; MN-midnight).

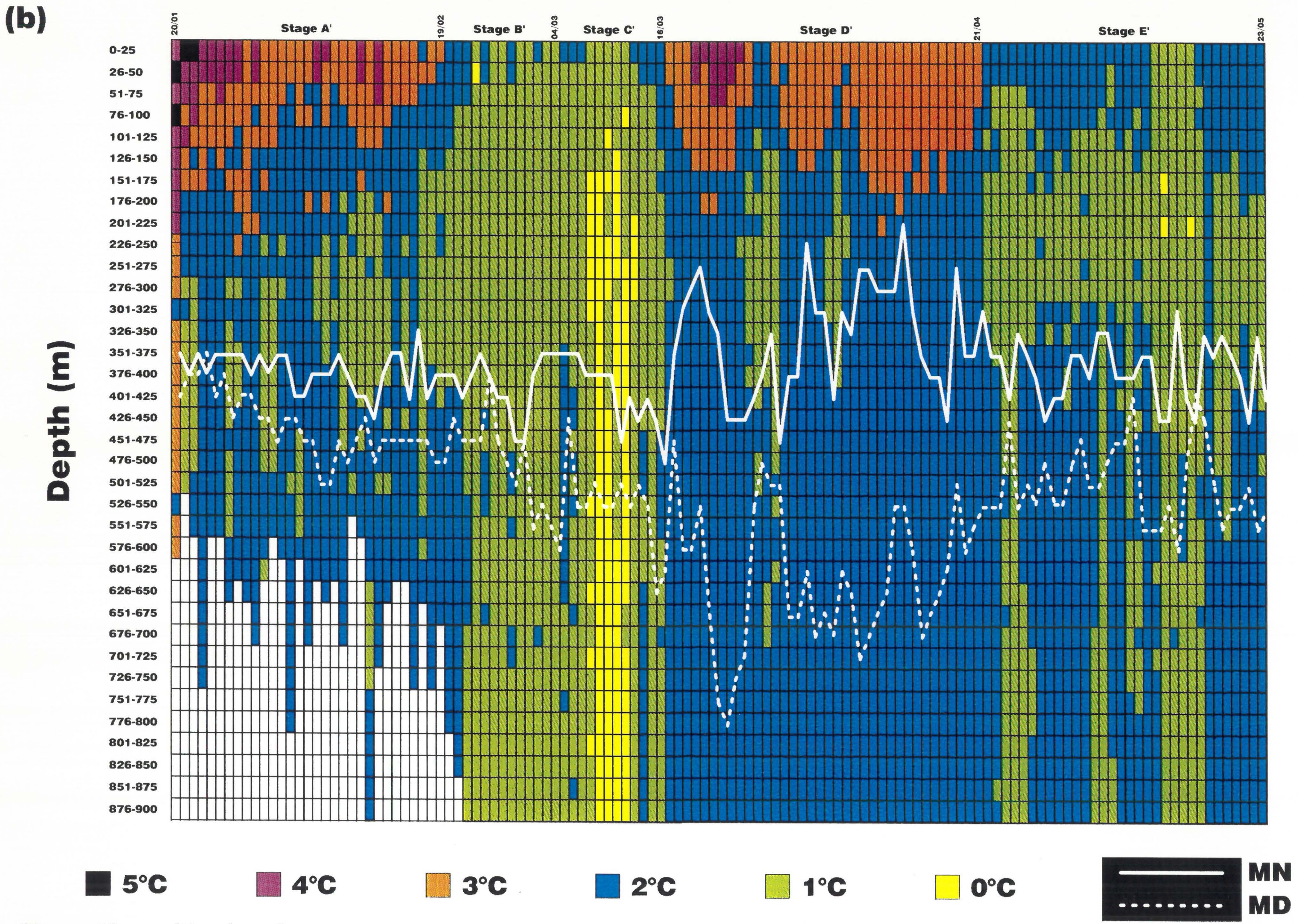


Figure 13. (Continued)

Table 13. **Water temperature layers encountered at depth within the different stages of the journey (A - D and A′ - E′) during the (a) postbreeding and (b) postmoulting periods respectively of seal G006.**

(a)

Temperature	Mean depth (m) within stages			
(°C)	A	B	C	D
12		0-75		
11		125-175		
10		0-100		
9		0-200		
8		126-400		
7	0-175	175-350	0-125	
6	0-250	300-575	0-250	
5	200-550	576-775	75-600	0-250
4	475-675	675-850	225-660	75-425
3	650-825		475-750	325-625
2			700-850	525-850

(b)

Temperature	Mean depth (m) within stages				
(°C)	A'	B'	C'	D'	E'
5	0-50				
4	0-75			0-75	
3	0-250			0-175	
2	75-800	0-50	0-25	0-900	0-900
1	200-575	0-900	0-900	150-550	0-900
0		0-50	100-900		175-225

Table 14. The frequency (%) occurrence of dive types 1 -7 (defined in Chapter 3) within the different stages of the journey (A - D and A′ - E′) during the postbreeding and postmoulting periods of seal G006 respectively.

Deployment	Stages	Date	Total amount of days	% frequency of dive types						
				1	2	3	4	5	6	7
Seal G006 (pb)	A	09/10-26/10	18	0.31	7.39	4.69	0.85	15.16	0.15	71.44
	B	27/10-01/11	6	0	0.83	2.76	0.28	11.88	0	84.25
	C	02/11-21/11	20	0.08	19.47	7.39	4.61	7.55	0.45	63.92
	D	22/11-10/12	19	0.32	10.14	4.47	2.08	7.91	0.24	74.84
Seal G006 (pm)	A'	20/01-19/02	31	0.76	12.86	5.01	0.64	15.36	0	65.38
	B'	20/02-04/03	13	0.75	2.88	2.88	1.7	7.03	0	84.77
	C'	05/03-16/03	13	0.43	0.86	3.23	0.43	3.44	0.22	91.4
	D'	17/03-21/04	36	0.29	11.86	4.03	3.39	13.85	0.06	66.51
	E'	22/04-23/05	32	0.17	1.01	3.7	2.61	3.78	0.08	88.64

pb - postbeeding
pm - postmoulting

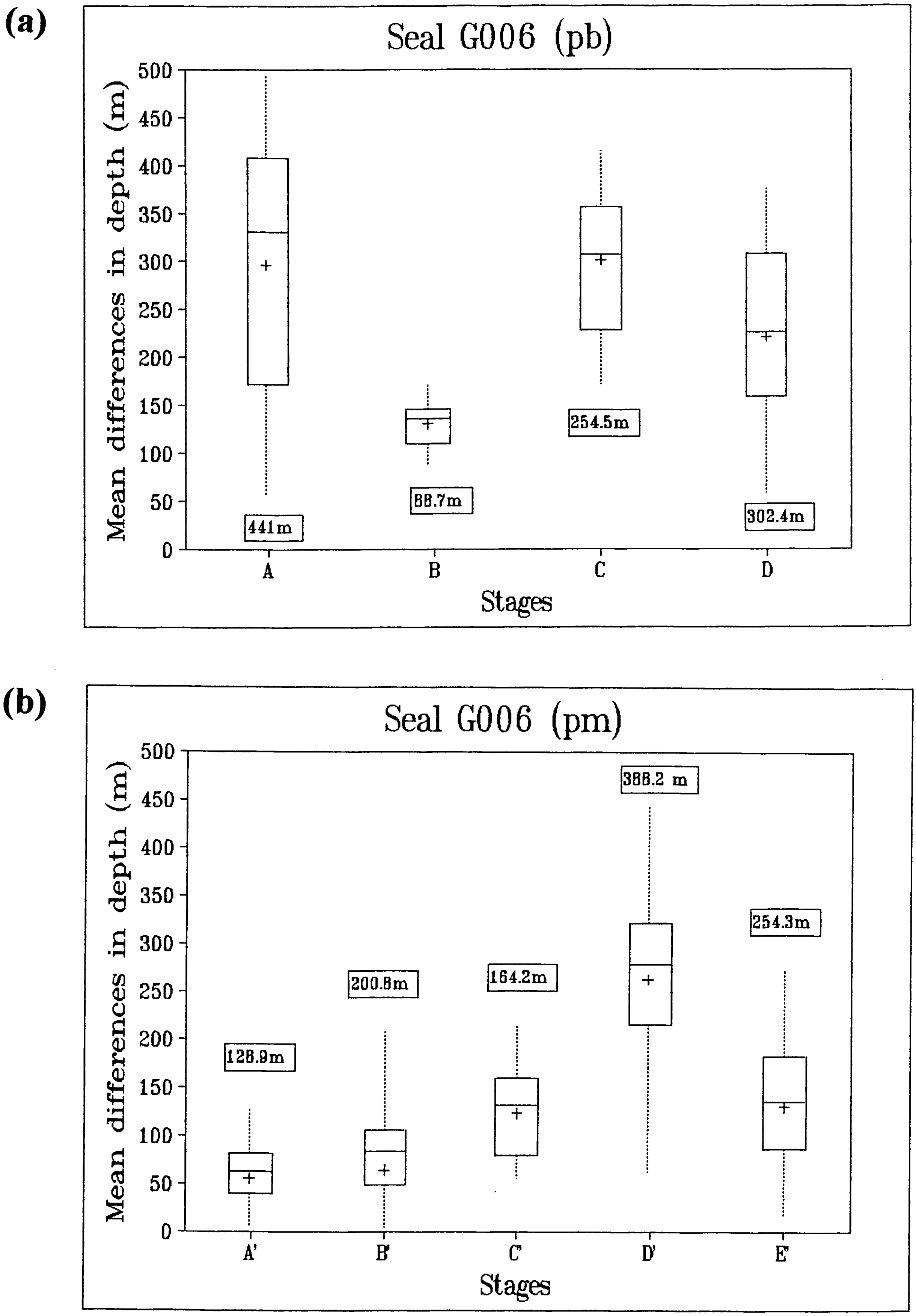


Figure 14. The mean differences in dive depth between day and night type 7 'foraging' dives within different stages of the movements of seal G006 during the (a) postbreeding and (b) postmoulting periods of the journeys from Marion Island. Depth values within boxes depict the maximum differences in depth encountered between day and night foraging dives. (pb - postbreeding; pm - postmoulting).

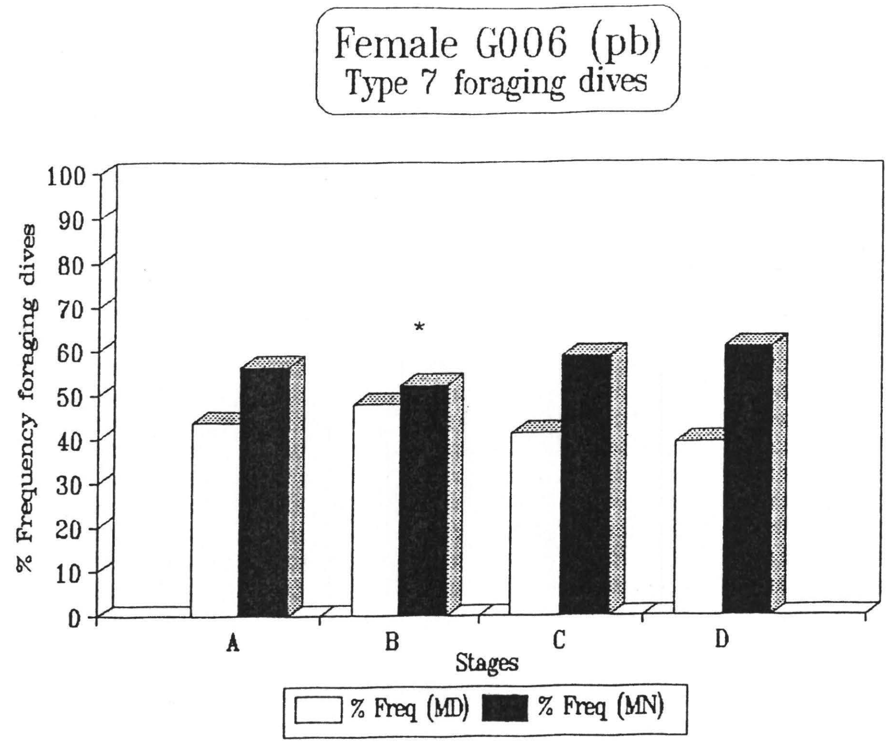
during stage A. Day foraging dives extended to the 4 °C thermal layer at a depth of ± 750 m, which was similar to the average depths of the day foraging dives during stage A, which extended to the 3 °C thermal layer (Figure 13a). The mean difference of ± 100 m between day and night foraging dives was significantly ($t < -2.36$, $df = 23$, $P < 0.01$) less than all other stages (Figure 14a). The frequency occurrence of foraging dives in stage B was significantly different ($\chi^2 = 28.23$, $df = 3$, $P < 0.01$) to all other stages with little difference between day and night dives compared to distinctly higher frequencies during midnight for all other stages (Figure 15a).

Stage C: Within dive types, the frequency occurrence of foraging dives (63.92%) and exploratory dives (7.55%) was the lowest of all stages, with transit dives (19.47%) the highest (Table 14). Day and night foraging dives of ± 400 - 800 m extended to the 4 - 2 °C thermal layers. Night foraging dives of ± 400 - 550 m remained within the 4 °C thermal layer, whereas day dives extended to the 2 °C thermal layer at depths from ± 750 - 800 m (Figure 13a). The mean difference of ± 250 - 400 m between day and night foraging dives, was not significantly ($t = -0.18$, $df = 34$, $P > 0.05$) different to stage A, but significantly ($t = -5.78$, $df = 24$, $P < 0.0001$) greater than stage B (Figure 14a).

Stage D: The frequency occurrence of type 7 foraging dives (74.84%) and transit dives (10.14%) was high, whereas exploratory dives (7.91%) occurred at low frequencies (Table 14). Day and night foraging dives extended to the 4 °C - 2 °C thermal layers at depths from ± 375 - 750 m. Night foraging dives remained within the 4 °C and 3 °C thermal layers at average depths from ± 375 - 425 m, whereas day foraging dives remained within the 3 °C and 2 °C thermal layers at depths from ± 500 - 750 m (Figure 13a). Mean differences of ± 75 - 375 m between day and night foraging dives was not significantly ($t = 1.90$, $df = 33$, $P > 0.05$) different to stage A, but significantly ($t = -2.36$, $df = 23$, $P < 0.01$; $t = 3.07$, $df = 37$, $P < 0.0001$) greater than stages B and C, respectively (Figure 14a).

Postmoulting period: The movement of seal G006 recorded between January-May 1993 was categorized into 5 stages, designated A′ - E′ (Figure 13b). The turning point for the commencement of the inbound phase 3 of seal G006 was 11 April during stage D′ (Figure 13b).

(a)



(b)

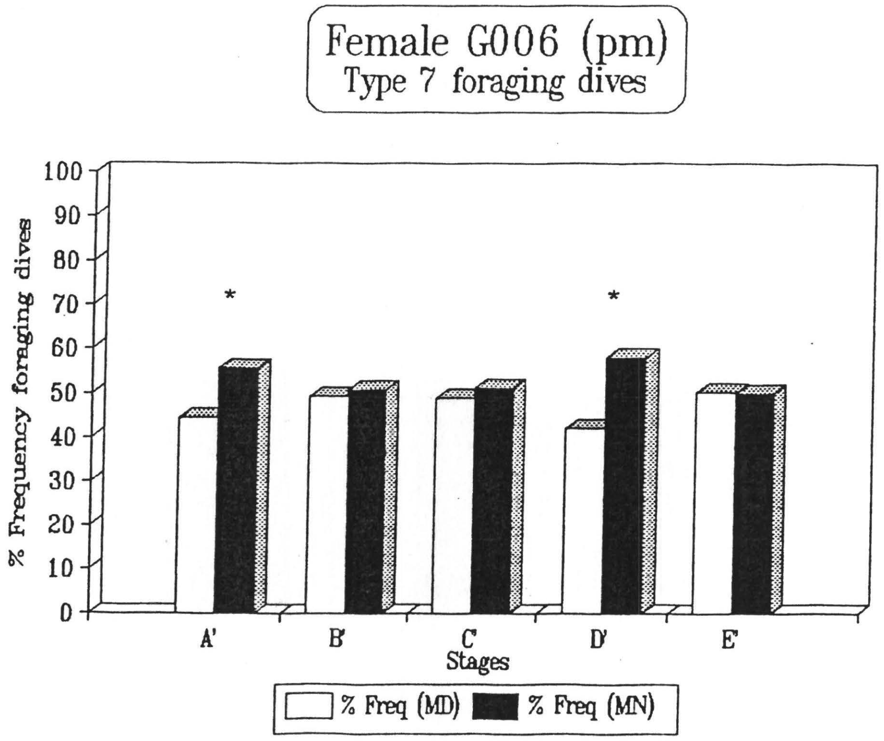


Figure 15. Diel differences in the frequency (%) type 7 'foraging' dives within different stages of movements of seal G006 during the (a) postbreeding and (b) postmoulting periods of the journeys from Marion Island. (pb - postbreeding; pm - postmoulting; MD - midday; MN - midnight; * depict significant differences).

Stage A′: The frequency occurrence of foraging dives (65.38%), comparable to the 66.51% of stage D′, was lower than all other stages, whereas shallow transit dives (12.86%) and exploratory dives (15.36%) were the highest (Table 14). Day and night foraging dives remained within the patchy 2 °C and 1 °C thermal layers at ± 375 - 525 m. The difference in the average depth of foraging dives during the day (± 375 - 450 m) and night dives (± 400 - 525 m) (Figure 13b) varied from ± 0 - 150 m (Figure 14b).

Stage B′: The frequency occurrence of foraging dives (84.77%) was high, whereas the shallow transit (2.88%) and exploratory dives (7.03%) occurred at low frequencies (Table 14). Average depths of foraging dives during the day (± 400 - 575 m) and night (± 375 - 475 m) extended within the 1 °C thermal layers (Figure 13b). The mean difference (± 0 - 200 m) between day and night foraging dives, was not significantly ($t = -1.23$, $df = 41$, $P > 0.05$) different to the mean difference between day and night foraging dives of stage A′ (Figure 14b).

Stage C′: The frequency occurrence of type 7 foraging dives (91.40%) was the highest of all stages, whereas the shallow transit and exploratory dives occurred at low frequencies (Table 14). The majority of day and night foraging dives remained within the 1 °C thermal layer at depths of ± 400 - 625 m, a few dives ending within the 0 °C thermal layer at depths of ± 400 - 550 m. Average depth of night dives extended from ± 400 - 475 m, whereas day dives extended from ± 525 - 625 m (Figure 13b). The mean difference (± 50 - 225 m) between day and night foraging dives, was significantly ($t = -4.86$, $df = 40$, $P < 0.0001$) greater than the mean difference of stage A′, but significantly ($t = -4.18$, $df = 17$, $P < 0.001$) less than the mean difference of stage B′ (Figure 14b).

Stage D′: The frequency occurrence of foraging dives (66.41%), low compared to other stages, was similar to that of stage A′. Concomitantly, shallow transit (11.86%) and exploratory dives (13.85%) occurred at high frequencies (Table 14). Average depths of foraging dives during the day (± 475 - 700 m) and night (± 275 - 475 m) extended within the 2 °C thermal layer during most of stage D′ (Figure 13b). The mean difference between day and night foraging dives (± 50 - 425 m) was significantly ($t > -11.43$, $df = 64$, $P < 0.0001$) greater than the mean differences between day and night dives of all other stages, as night dives were ± 100 m shallower and day dives ± 100 m deeper than that of all other stages (Figure 14b). Ratios in the frequency occurrence of foraging dives between day and night in stages B′, C′, and E′ were similar, but significantly different ($\chi^2 = 96.78$, df = 4, $P < 0.01$) to stages A′ and D′ that had higher frequencies of foraging dives around midnight (Figure 15b).

Stage E′: The frequency occurrence of foraging dives (88.64%) was high, and shallow transit and exploratory dives occurred at low frequencies (Table 14). Average depths of foraging dives during the day (± 475 - 575 m) and night (± 350 - 425 m) extended within the 2°C and 1°C thermal layers (Figure 13b). The mean difference (of ± 50 - 225 m) between day and night foraging dives, was significantly ($t = -5.82$, df = 60, $P < 0.0001$; $t = -4.21$, df = 40, $P < 0.0001$) greater than the mean differences of stage A′ and B′, respectively, but not significantly ($t = -0.39$, df = 42, $P > 0.05$) different to that of stage C′ (Figure 14b).

Diel foraging patterns

Differences in mean dive depths between day and night foraging dives of postbreeding and postmoulting females (Y333, R357, P537 and G006) with complete recordings of diving behaviour and movements at sea were not significantly different (ANOVA: $F_{5,209} = 1.65$, $P > 0.05$) for the majority of females during phases 1 and 3 (transit phases), whereas depths differed significantly (ANOVA: $F_{5,209} = 164.30$, $P < 0.0001$) during phase 2 (foraging grounds) by 150 - 300 m. Diel dive depths of postbreeding seal R357 were not significantly different ($P > 0.05$) during phases 1, 2 and 3, remaining relatively constant at 30 - 90 m throughout the transit and foraging phases. Diel changes in the mean dive durations and bottom times of foraging dives of postbreeding females were not significantly different (ANOVA: $F_{5,209} = 1.17$, $P > 0.05$) and remained relatively constant at 20 - 30 min and 10 - 20 min, respectively, throughout phases 1, 2 and 3 (Figures 16a - 16c).

In contrast, diel changes in the mean dive durations and bottom times of foraging dives of postmoulting females (G006, P537 and 0144) were significantly (ANOVA: $F_{4,417} = 254.32$, $P < 0.0001$) longer during phase 2 (at ± 30 - 60 min and 20 - 40 min, respectively) than phase 1 (at ± 10 - 15 min and 10 - 20 min, respectively), whereas similar decreases occurred during phase 3 (incomplete data sets) compared to that of phase 1 (Figure 17).

Postmoulting seal P537 exhibited reversed diel depths of foraging dives from the

(a)

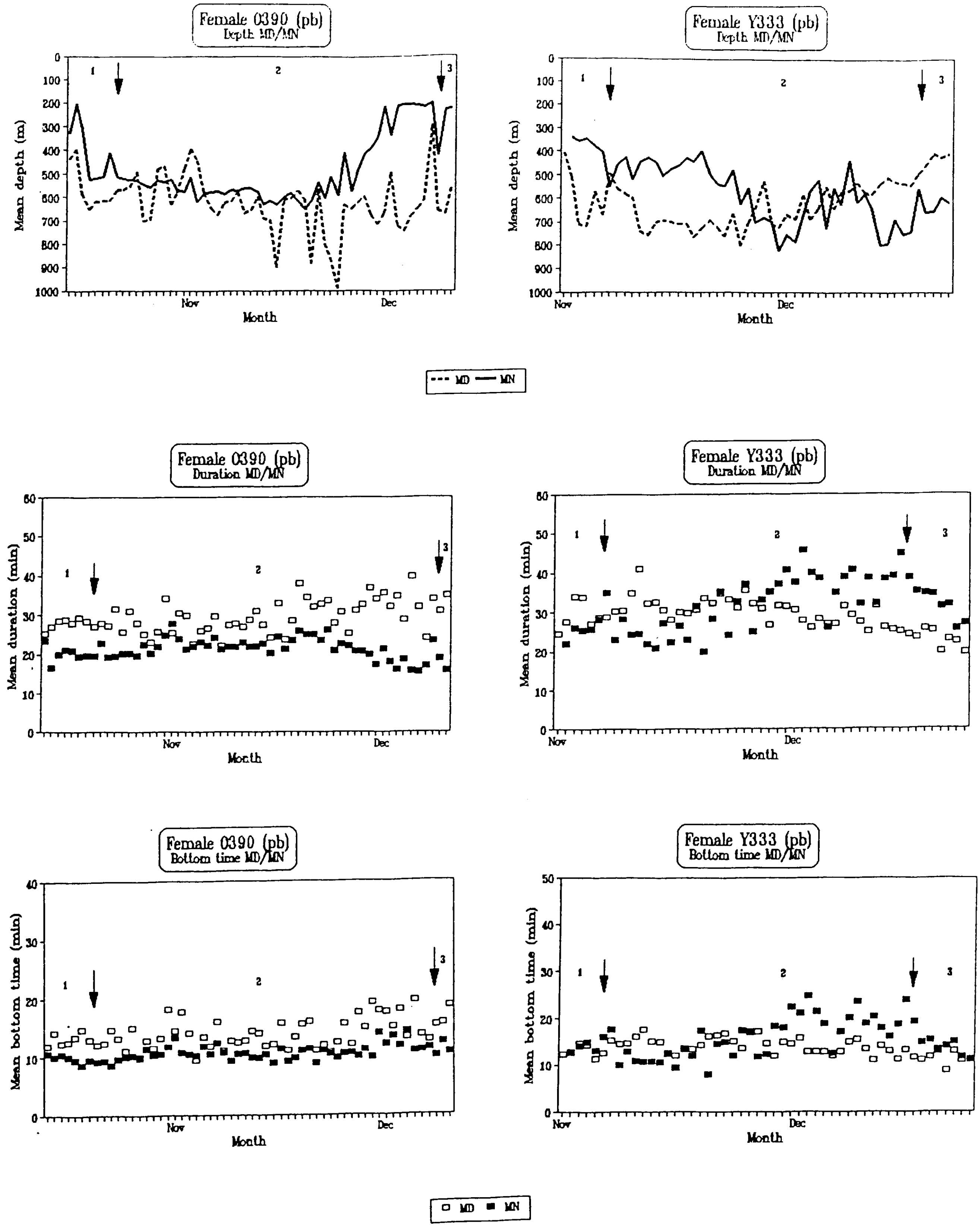


Figure 16. **Diel changes in the mean dive depths, durations and bottom times of type 7 'foraging' dives of postbreeding females that moved in (a) northwesterly, (b) northeasterly and (c) southwesterly directions from Marion Island. (pb - postbreeding; MD - midday; MN - midnight).**

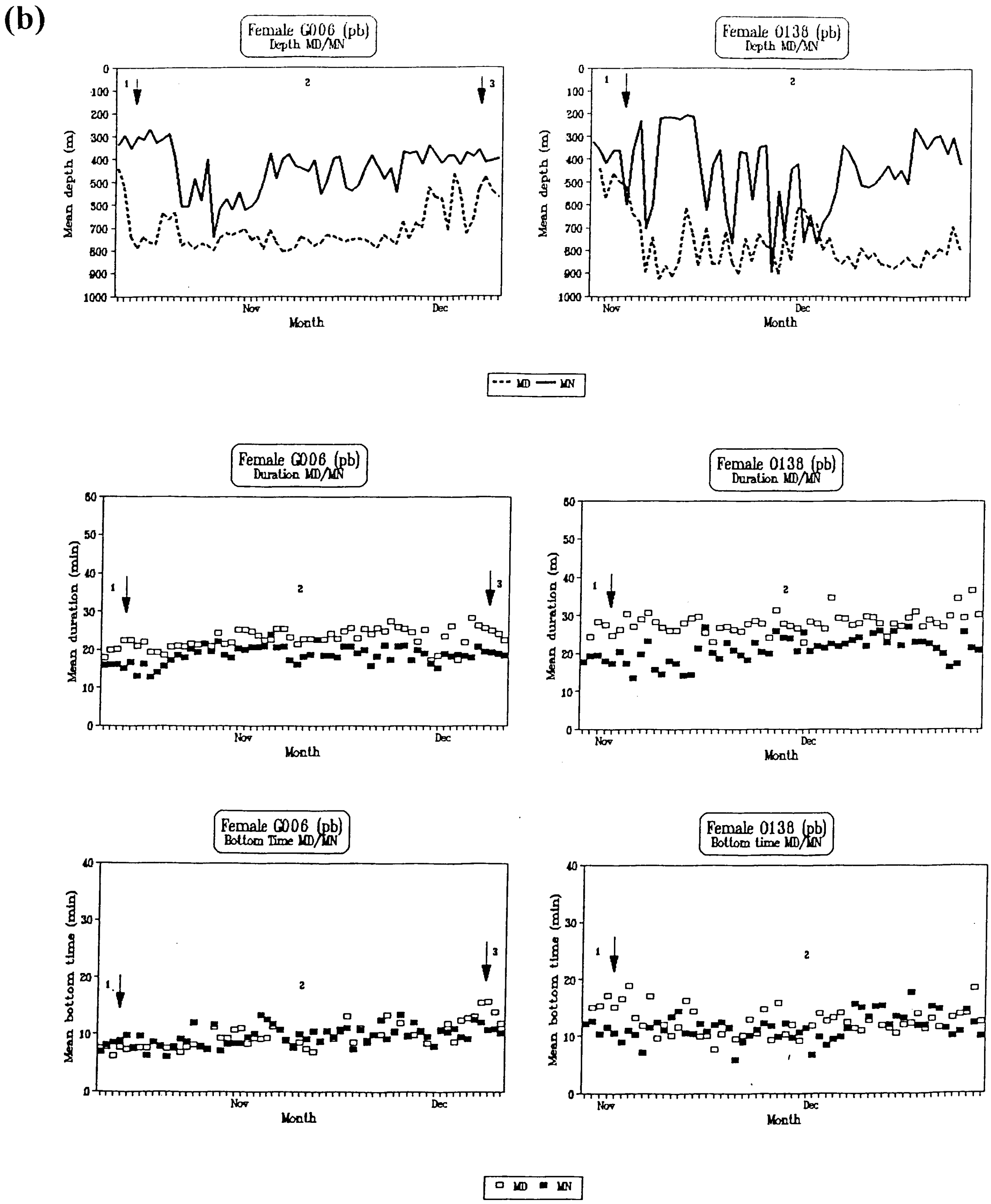


Figure 16 (Continued).

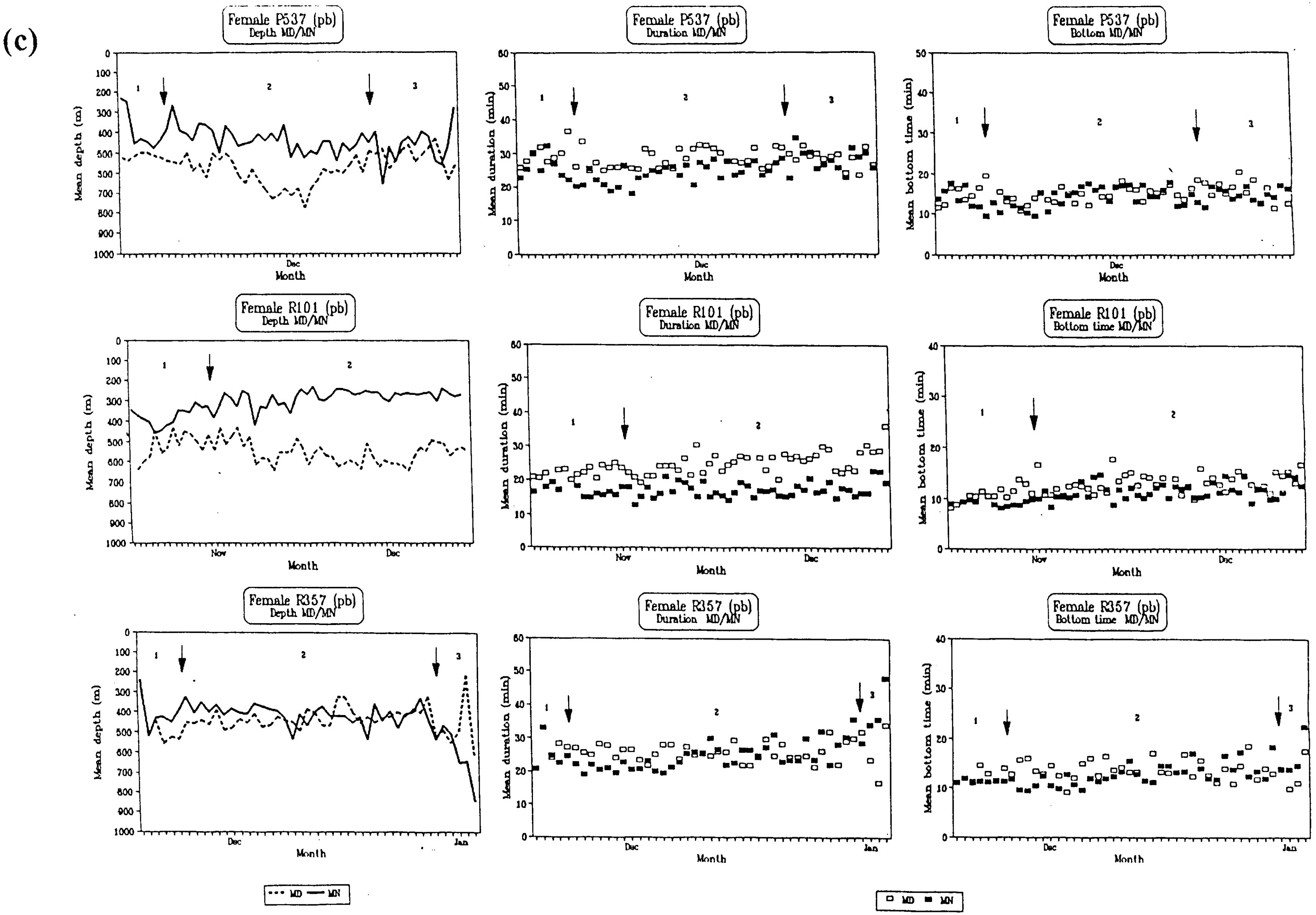


Figure 16 (Continued).

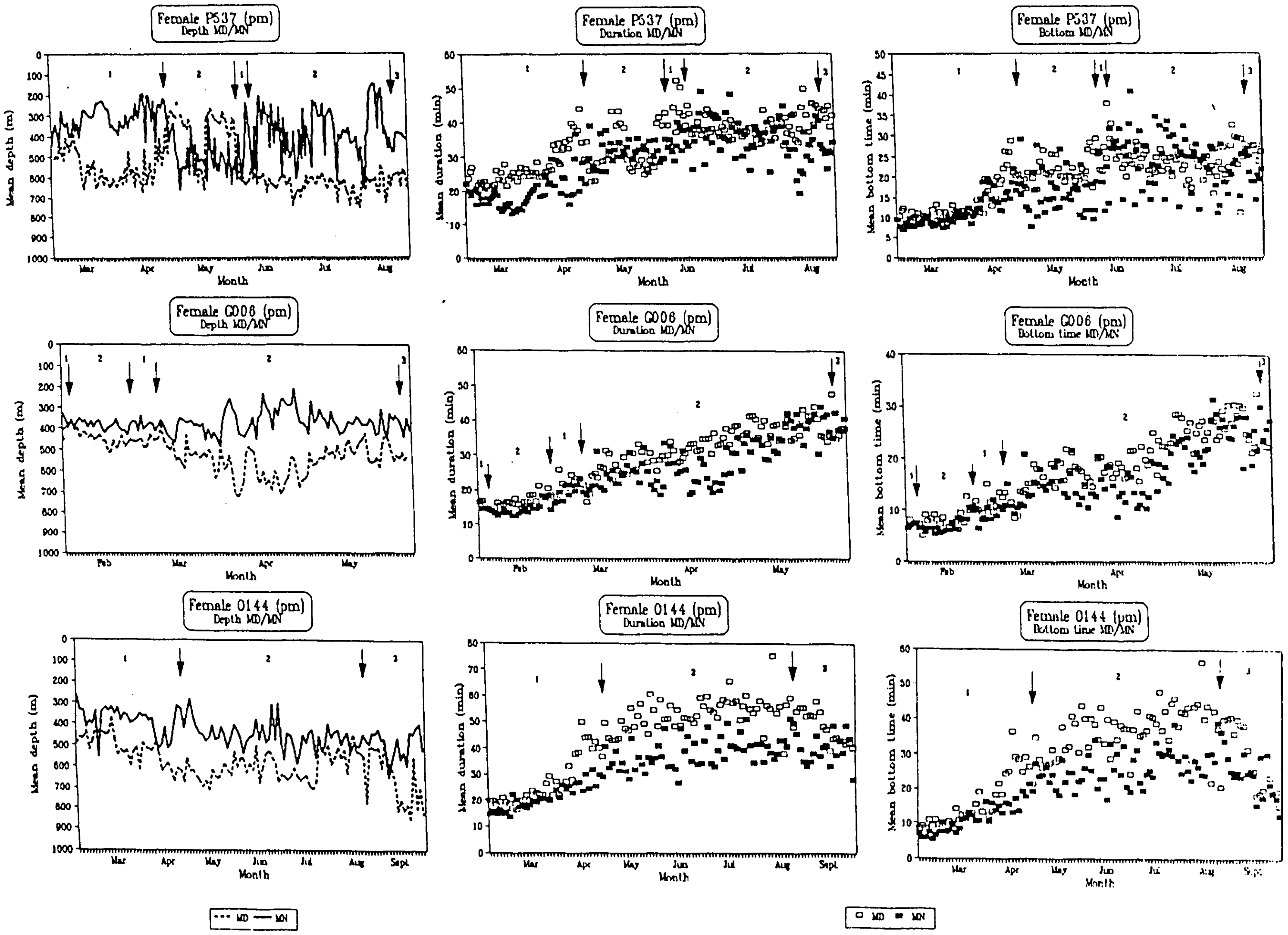


Figure 17. Diel changes in the mean dive depths, durations and bottom times of type 7 'foraging' dives of postmoulting females that moved in south-westerly directions from Marion Island. (pm - postmoulting; MD - midday; MN - midnight; * depict a haulout for seal P537 during midday hours).

beginning of April to end of May as compared to all other females (Figure 17). Midday foraging dives were significantly shallower ($t = 4.23$, $df = 59$, $P < 0.001$) than midnight dives (difference of ± 300 m) with a greater variation in dive depths than during midnight hours. This reversed diel diving pattern was only evident in the first phase 2 within the CWZ (Figure 17).

Discussion

SSTs and foraging grounds

Based on the daily SSTs encountered by elephant seal females from Marion Island, thermal frontal and inter-frontal zones were identified (present study) as for elephant seals from Macquarie Island (Hindell *et al.* 1991a) and pelagic seabirds (Abrams 1985), respectively. These frontal zones were characterized by steep thermohaline gradients and high relative abundance of nutrients, plankton, squid and fish (El-Sayed 1970; Holm-Hansen *et al.* 1977; Iverson 1977; Tranter 1982). However, in spite of the presence of these locatable areas of high productivity, most of the time spent (80 - 100%) within the foraging grounds (phase 2) of postbreeding elephant seal females that moved north occurred within the SAZ, whereas a very low proportion of time (4 - 20%) was spent foraging within the frontal zones (STC & SAF) north of Marion Island. Furthermore, most of the time spent (69 - 100%) within foraging grounds of females that moved south was within the AWZ and a similarly low proportion of time spent (3 - 32%) foraging within the APF. Postmoulting females spent most of the time (69 - 100%) at foraging grounds within the AWZ, while a low proportion of time (2 - 31%) was spent foraging within the APF. Only within the first phase 2 of seals P537 and G006, where most of the time (100%) was spent foraging within the CWZ and the PFZ, respectively, did their movements concur with the observation that the physical and chemical conditions around the Antarctic Continental Shelf area, ice edges and the frontal zones consistently produce areas of high productivity which attract many top predators (Ainley & DeMaster 1990).

It would therefore seem that southern elephant seals in the current study spent more time foraging in the open reaches of the Southern Ocean where concentrations of prey are both spatially and temporally very variable and may be associated with unpredictable hydrographical conditions (El-Sayed 1988). However, local topography may reinforce atmospheric effects in enhancing local concentrations of the food supply of prey (Miller & Hampton 1985), and adult prey species may seek and maintain themselves in favourable habitats by actively countering dispersal mechanisms. Everson (1976 & 1977), Lubimova *et al.* (1982) and Amos (1984) suggested that such habitats may arise from enhanced primary production in regions of vertical upwelling which are likely to occur at zones of divergence as well as other areas, including frontal systems, the centres of gyres, along the ice-edge of the Antarctic Continent and in the proximity of uneven bottom topography (Mackintosh 1972; Pingree 1978; Lutjeharms *et al.* 1980; Pomazanova 1980; Allanson *et al.* 1981; El-Sayed & Taguchi 1981; Lutjeharms 1981; Lubimova *et al.* 1982; Amos 1984).

Temperature/diving depth profiles

SSTs and daily water temperature/depth profiles typical of waters north and south of the APF (Gorden & Molinelli 1982) confirmed that the majority of females foraged on either side of the APF during the postbreeding and postmoulting periods. Temperature/depth profiles of females moving north from Marion Island were consistent with Type I profiles of females from Macquarie Island that frequented sub-Antarctic waters (Hindell *et al.* 1991a) where water temperatures remained relatively constant and warm to about 300 m, below which the temperatures slowly declined (Gorden & Molinelli 1982). Females from Marion Island that moved south of the APF to the AWZ showed temperature/depth profiles consistent with Type II profiles of females from Macquarie Island (Hindell *et al.* 1991a) that frequented Antarctic waters. Here SSTs averaged from ± 3 - 7°C with rapidly declining temperatures to about 300 - 400 m, below which temperatures levelled out, increasing slightly to remain relatively constant below 400 m (Gorden & Molinelli 1982). The dive depth patterns of the females in the current study were, as a result, not closely linked to steep thermal gradients in water temperature as postulated by Boyd & Arnbom (1991), but similar to the findings for northern elephant seals from Año Nuevo (Hakoyama *et al.* 1994) and southern elephant seals from Macquarie Island (Hindell *et al.* 1991a).

The diel differences in dive depth being higher in the foraging phase than the outbound and inbound transit phases for both postbreeding and postmoulting females, including the diel differences in duration of assumed foraging dives and bottom times for postmoulters only, presumably suggest active, concentrated (but not necessarily optimal) foraging (present study) in well circumscribed foraging localities (Bester & Pansegrouw 1992; see **Chapter 4**). This would be of particular importance to postmoulting females which concentrated on foraging dives (78% versus 69%) of considerable longer durations and bottom times than the foraging dives of postbreeding females (26 min and 15 min versus 19 min and 9 min, respectively - see **Chapter 3**) to regain condition after the moulting fast in advance of the breeding season haulout and the rearing of a pup (see **Chapter 3**).

On an individual level, the highest frequencies of foraging dives for postbreeding seal G006, which occurred during stage B within the STC, indicated assumed persistent foraging/prey pursuit at depth, presumably characterized by the insignificant diel differences in depths of assumed foraging dives, an increase in `exploratory' dives with decreases in `shallow transit' dives. By contrast, the lowest frequencies of assumed foraging dives occurred during stage C within the SAZ, concomitant with a significant decrease in diel differences in foraging dive depths. This presumably indicated intermittent foraging, also since the frequency of assumed shallow transit dives was highest of all stages with a concomitant decrease in assumed exploratory dives. Stages A and D were similar in the frequency occurrence of `foraging' dives, however, stage D had a higher frequency occurrence of `shallow' transit dives, indicative of the inbound transit phase. It would therefore seem that postbreeding seal G006 exhibited diel foraging patterns which were apparently directly associated with the distributional behaviour of prey, which in turn was likely to be influenced by the presence of the STC and changes of temperature within the water-column of the SAZ. Since changes in temperature can influence the physiology of marine organisms on a variety of time scales ranging from short-term fluctuations (tidal, vertical migration) to long-term climatic changes (Clarke 1990), it is conceivable that prey would remain in preferred temperature layers within the water-column and would migrate within these temperature layers as the temperature alters due to diel changes or the presence of thermal fronts.

Such presumed influences of the temperature mediated vertical distribution of prey on the diel foraging pattern of the seal at depth was particularly evident for postmoulting seal G006. The highest frequency occurrence of `foraging' dives occurred during stage C′, compared to stage D′ (different water-column temperature layers) where the frequency of `foraging' dives was considerably less and interspersed with increased `shallow transit' and `deep exploratory' dives. The mean diel difference in depths of foraging dives as considerably less within the 0 - 2°C thermal layers during stage C′, whereas mean diel differences in `foraging' dives were much greater within the practically homogeneous 2°C thermal layer that ranged between depths of ± 150 - 900 m. This suggests that the potential prey of seal G006 showed increased vertical migration during stage D′, within the broad homogeneous water-column temperature (2°C) layer, which translated into the day and night foraging patterns of seal G006 to be distinctly different in depth. On the other hand, prey migrated vertically much less due to a patchy (heterogeneous) distribution of the temperature layers in the water-column during stages A′, B′, C′ and E′ which was reflected in a less pronounced diel foraging depth pattern. Furthermore in stage D′, a less pronounced diel foraging pattern of seal G006 ensued on the only occasion where the 1°C thermal layer interspersed with the 2°C layer for several days at depths of 150 - 700 m, lending support to this hypothesis.

Factors such as phases of movements at sea (with characteristic percentage contributions of `transit', `exploratory' and `foraging' dives), distance from Marion Island (see **Chapter 4**), combined with changes in the distribution of temperature layers and the distribution and abundance of prey within the water column (this study) is likely to have marked influences on the foraging behaviour of elephant seals.

Diel foraging patterns

Foraging behaviour of females from Marion Island seem to be directly associated with the distributional behaviour of their prey, which in turn is apparently influenced by the vertical distribution of water-column temperature layers within the Southern Ocean.

A case in point is the extension of postmoulting seal P537s' foraging range as far south as the Antarctic ice-shelf where water temperatures reached -2°C, spending a considerable amount of time within the CWZ before moving north again to foraging grounds within the

AWZ. Within the ice-shelf waters the Antarctic silverfish, *Pleuragramma antarcticum*, is the only true pelagic species among notothenioid fish (Andriashev 1965), and is taken by predators, especially the large Weddell seal (Hubold 1985; Testa 1994), and conceivably by southern elephant seals too (see below). Adult *P. antarcticum*, the most abundant pelagic fish in high-Antarctic waters, occur at high concentrations within the ice-shelf waters of the Southern Weddell Sea where water temperature ranges between -1.4 to < -2.0°C (Hubold 1985), preying exclusively on krill (Takahashi 1982). When adult *P. antarcticum* feed on vertically migrating krill their day and nighttime foraging dive patterns would change according to the dispersal of their prey species. Similarly, dive patterns in which depth of dives changes with time of day have been observed in several krill predators including Antarctic fur seals (Croxall *et al.* 1985; Fraser *et al.* 1988) and crabeater seals (Bengtson & Stewart 1992).

Postulated evidence that postmoulting seal P537 (present study) fed on *P. antarcticum* (although other midwater prey species such as squid cannot be ruled out) within the ice-shelf waters, lies in it reversing its diel foraging pattern exclusively within the ice-shelf water, as night foraging dives were deeper and of longer duration than day dives. As seal P537 moved north again reaching the AWZ, the diel dive pattern reverted back to shallow foraging dives of shorter duration during the night with deeper, longer dives during the day, as was evident for all other elephant seal females from Marion Island (see **Chapter 3**) and other seals from northern (Le Boeuf *et al.* 1986, 1988, 1989, 1993; Stewart & DeLong 1990) and southern (Boyd & Arnbom 1991; Hindell *et al.* 1991a, b) elephant seal populations. This suggests that seal P537 possibly reverted back to feeding on pelagic cephalopod and other fish species once it departed the cold ice-shelf waters of the Antarctic Continent, and therefore access to *P. antarcticum*.

CHAPTER 6

CONCLUSIONS

Seven distinct dive types were categorized and hypothesized to serve as `transit', `resting', `exploratory' and `foraging' dives. No benthic foraging dives were recorded during the pelagic phase of postbreeding and postmoulting females from Marion Island. Due to individual variation in the diving behaviour of females in the present study, approximately 56 - 83% of all dive types were that of type 7 dives, hypothesized to serve as foraging dives. Mean dive depths of all types of dives combined were not significantly different between postbreeding and postmoulting periods in the present study, whereas mean dive durations of type 7 dives (assumed to serve foraging) for the postmoulting period were significantly longer than for the postbreeding period. Dive depths and durations of postbreeding females from Marion Island were characteristic of postbreeding females from Macquarie Island, whereas depths and durations of postmoulting females from Marion Island were similar to that of females from South Georgia, Macquarie Island and Peninsula Valdés. Dive depths and durations of females from Marion Island were positively correlated and mostly unimodal in their frequency distributions, although some had secondary modes in their frequency distribution.

Post-dive surface intervals were of short duration (2 - 4 min) and were unrelated to dive depths and durations of previous dives, as were the ESIs which were more frequent at night than during the day. ESIs were also more common during long journeys at sea and were possibly associated with successful foraging in the present study. The frequency occurrences and the bottom times of assumed foraging dives varied seasonally, the highest frequencies and longest bottom times recorded during the postmoulting period. The diel diving pattern of deeper dives of longer duration during the day and shallower, shorter dives during the night appeared to be the norm for both postbreeding and postmoulting elephant seal females from Marion Island, as was recorded for females from other elephant seal populations. However, mean dive rates for postbreeding females in the present study were considerably greater for postmoulting females. It is postulated that the seasonal and individual variation in the diving behaviour of southern elephant seal females in the present study were related to their geographical locations and the abundance and behaviour of their prey.

Movement of females from Marion Island were generally classified into three phases, namely the outbound transit phase (phase 1), distant foraging phase (phase 2), and inbound transit phase (phase 3). This study provides additional information on the putative function of dive types during the movement phases of elephant seal females from Marion Island. The longest residence time that postbreeding females spent during their foraging migrations was in areas at the outer edge of their feeding range (phase 2) at ≤ 1 460 km both to the north and the south of the island, largely within inter-frontal zones south of the APF and between the STC and the SAF. The frequency occurrences of the predominant assumed foraging dives (type 7 dives) of postbreeding females were the highest within these areas during phase 2, whereas in contrast, postmoulting females travelled further afield (2 122 - 3 133 km) to the APF, to inter-frontal zones south of the APF (within the pack-ice outer edge), as well as to the Antarctic Continental Shelf, with type 7 dives having occurred at proportionally higher levels during their phases 2 at more widely, separated feeding ranges.

The relative frequency occurrences of assumed foraging, exploratory and transit dives during phases of movement, the duration of time spent within phases between the breeding and moulting periods, differences in the frequency distributions of foraging dive depths, durations and bottom times during diel dive patterns and the occurrences of ESIs suggest two seasonal foraging strategies for postbreeding and postmoulting females of the present study. These are (a) short, directed outbound and inbound journeys to/from circumscribed foraging areas where prey distribution is likely to be unpredictable, but which may attract the same or different individuals during relatively short postbreeding periods, or (b) wide ranging meandering during the relatively long postmoulting period, interspersed with high frequencies of assumed foraging behaviour at separated distant locations which may be readily locatable. The current study also hypothesizes that prominent bathymetrical ridges north and south of Marion Island could possibly cue the transit phases of both postbreeding and postmoulting females from Marion Island at least during part of the journey, to reach foraging grounds and to return to the island.

Variations in the diel distribution and abundance of prey resources probably have a profound effect on movement patterns of postbreeding and postmoulting females from Marion

Island. This could account for the major differences in the nature of seasonal movements in different southern elephant seal populations (Slip *et al.* 1994; Boyd 1993a; McConnell & Fedak 1996; this study). Southern elephant seal females from Marion Island uses an open ocean foraging strategy, largely away from readily locatable frontal zones where biological productivity is reported to be high. The relatively localized and overlapping postbreeding foraging areas suggest a period of greatest prey abundance, at least seasonally, as suggested for pinnipeds in general (Antonelis & Fiscus 1980). Conversely, the wide ranging meandering during the postmoulting period with little overlap suggests a high degree of segregation, concomitant with a period of least abundance of prey (*vide* Antonelis & Fiscus 1980).

Significant diel differences in the depth of 'foraging' dives appear to be associated with concentrated foraging/prey pursuit on vertically migrating prey as it is evident within delineated foraging areas. This could be particularly true for postmoulting females in the present study, where significant diel differences in foraging dive duration and bottom times also occur. However, a more homogeneous temperature layer within the water-column at foraging depth also seems to cause shifts in the diel patterns of prey dispersal, directly influencing the diving behaviour of elephant seals in promoting widely different diel foraging depths.

In view of the decline of the Marion Island population, apparently driven by the low survivorship of breeding females (Bester & Wilkinson 1994), their ability to find, catch and consume prey is critical to their survival. Available evidence from the diel foraging patterns suggests that feeding is closely linked to the temperature of the water column (this study), possibly because seals use the changes in water temperature to predict the presence of prey (*vide* Boyd & Arnbom 1991) but does not, however, allow predictions on the actual foraging success of females (this study). The very low weaning mass of southern elephant seal pups at Marion Island might show that nutritional conditions for females are poor (Burton *et al.* 1997), and if correct, could be related to their foraging at inter-frontal zones due to a redistribution of their prey consequent upon environmental and climatic changes (*vide* Folland *et al.* 1984; Arntz *et al.* 1991; McMahon *et al.* submitted). By the very nature of the present study, only successful females, i e females that had either moulted or had weaned their pups, and which subsequently returned to the island, after a period at sea, to breed or to moult (enabling the retrieval of the recorders), were included in the investigation.

SUMMARY

The diving patterns of thirteen adult southern elephant seal, *Mirounga leonina*, females (nine postbreeding and four postmoulting) from sub-Antarctic Marion Island were recorded during the pelagic phase of their annual cycle, using Geolocation Time-depth Recorders attached to the seals. A total of 66 807 dives were categorized into seven distinct dive types representing transit, exploratory and foraging dives. No benthic foraging dives were recorded. Mean dive depths of 480 ± 74 m recorded for postbreeding females were not significantly different to that of postmoulting females which dove to 454 ± 38 m. Mean dive durations averaged 22.1 ± 3.3 min for postbreeding females, whereas postmoulting females had significantly longer mean dive durations of 26.9 ± 5.1 min. The deepest and longest dives recorded were 1 444 m and 113 min respectively. Dive depth and duration were positively correlated and mostly unimodal in their frequency distributions, whereas some females had secondary modes at 800 to 900 m and 40 to 44 min respectively. Post-dive surface intervals ranged from 2.03 ± 1.64 min to 4.99 ± 53.34 min between individuals and were unrelated to dive depths and durations of previous dives, as were extended surface intervals (> 10 min) which were more frequent at night than during the day. Extended surface intervals were also more common during long journeys at sea and were probably associated with successful foraging. The frequency of occurrence and the bottom times of foraging dives varied with the season, the highest frequency of occurrence and longest bottom times being recorded during the postmoulting period. It is postulated that the seasonal and individual variation in the diving behaviour of the southern elephant seal females are related to their geographic locations and the abundance and behaviour of their prey.

Movements of females were categorized into outbound transit, distant foraging, and inbound transit phases. Foraging grounds of postbreeding females occurred in six general areas within the Southern Ocean, of which four areas were north and two were south of the island, within ± 1 400 km from the island. The foraging grounds of postmoulting females were further afield and occurred (a) along the Antarctic Continental Shelf near the Princess Martha Coast, Antarctica in the eastern Weddell Sea, (b) in the inter-frontal zones south of the APF within the AWZ, and (c) around the APF. Close scrutiny of the temperature profile of the water column during female dives, showed that they foraged in the inter-frontal zones (STZ and AWZ) north and south of the APF, respectively. Despite overlap in the same geographical areas at sea in some instances, postbreeding and postmoulting females largely displayed different foraging strategies.

Postbreeding females made short (mean distance of 1031 ± 302 km), directed outbound and inbound transits to/from well circumscribed foraging grounds which promoted extended foraging time and therefore were constrained in total time available (the short postbreeding period of 45 - 73 days) and choice of alternative moulting haulout sites which could have extended the range of movement. Postmoulting females displayed opportunistic, patchy foraging, meandering between different foraging grounds, ranging further afield owing to an extended period between moulting and breeding (the long postmoulting period of 112 - 201 days). The current study also suggests that prominent bathymetrical ridges north and south of Marion Island, namely the Southwest Indian Ridge and the Mid-Atlantic Ridge were possibly used as navigational cues by postbreeding and postmoulting females from Marion Island at least during the transit phases to feeding grounds. All the females in the present study did not move over the Enderby Abyssal Plain to the southeast of the island, where no readily locatable oceanographic features occur.

Seasonal movements, foraging areas and diel differences in diving behaviour of females from Marion Island were also studied in relation to water temperature. Females foraged largely within inter-frontal zones during both the postbreeding and postmoulting periods. Localized and overlapping postbreeding foraging areas suggest a period of greatest prey abundance whereas meandering during the postmoulting period suggests segregation, concomitant with a period of least prey abundance. Diel differences in the depth of foraging dives appear to be associated with assumed concentrated foraging/prey pursuit on vertically migrating prey. A homogeneous, broad temperature layer within the water-column at foraging depth apparently promoted large diel differences in diel diving depth consequent on shifts in the diel patterns of prey dispersal. Conversely, patchy (heterogeneous) temperature layers at foraging depth appear to promote little difference in diel diving depth. Feeding appears to be closely linked to the temperature of the water-column possibly because elephant seals use the changes in water temperature to predict the presence of prey. The diel diving behaviour does not allow predictions on the actual foraging success of females but indicates foraging at inter-frontal zones away from readily locatable areas of high primary productivity, perhaps due to a redistribution of their prey consequent upon environmental and climatic changes.

OPSOMMING

Die duikgedrag van dertien volwasse (nege ná-teling en vier ná-verharing) suidelike olifantrobwyfies, *Mirounga leonina*, van subantarktiese Marioneiland is gedurende die pelagiese fase van hul jaarlikse siklus aangeteken deur die gebruik van Geolokasie-Tyddieptemeters wat aan robbe vasgeheg is. ń Totaal van 66 807 duike is in sewe duiktipes onderverdeel, wat deurtog-, verkennings- en voedingsduike verteenwoordig. Geen bodemvoedingsduike is aangeteken nie. Die gemiddelde duikdiepte van 480 ± 74 m aangeteken vir ná-telingwyfies het nie betekenisvol verskil met dié van die ná-verharingwyfies wat ń gemiddelde duikdiepte van 454 ± 38 m geduik het nie. Gemiddelde duurte van duike was 22.1 ± 3.3 min vir die ná-telingwyfies wat betekenisvol verskil het met duike van 26.9 ± 5.1 min vir die na-verharingwyfies. Die diepste en langste duike was onderskeidelik 1 444 m en 113 min. Daar was ń positiewe verband tussen duikdiepte en duikduurte en die frekwensieverdelings was meestal enkel-modus, terwyl van die wyfies sekondêre modusse by onderskeidelik 800 tot 900 m en 40 to 44 min gehad het. Verposings aan die oppervlak na duike het van 2.03 ± 1.64 min to 4.99 ± 53.34 min tussen individue gewissel en het nie verband gehou met duiktipes en duikduurtes van voorafgaande duike nie, soos ook in die geval van lang verposings (> 10 min) aan die oppervlakte wat meer in die nag as in die dag voorgekom het. Verlengde verposings aan die oppervlakte het ook meer gedurende lang seereise voorgekom en was waarskynlik met suksesvolle voeding geassosieer. Die frekwensie van voorkoms en die bodemtye van voedingsduike het met die seisoene verander, en die hoogste frekwensie van voorkoms en langste bodemtye is gedurende die ná-verharingstydperk aangeteken. Daar word bespiegel dat die seisoenale en individuele veranderlikheid in die duikgedrag van die suidelike olifantrobwyfies verband hou met hul geografiese verspreiding en die volopheid en gedrag van hul prooi.

Bewegings van wyfies was in deurgang na vertrek, voeding op ń afstand van die eiland, en terugkeer-deurgang fases verdeel. Voedingsgronde van ná-telingwyfies het in ses algemene areas binne die Suidelike Oseaan voorgekom, waarvan vier areas noord en twee suid van die eiland binne die bestek van 1 400 km gelê het. Die voedingsgronde van ná-verharingwyfies het verder weg (a) langs die Antarktiese Kontinentale Plaat naby die Prinses Martha Kuslyn, Antarktika in die oostelike Weddell See, (b) in die inter-frontale zones suid van die APF binne die AWZ, en (c) om die APF voorgekom. Noukeurige ondersoek van die temperatuurprofiel van die

waterkolom gedurend duike, het gewys dat hulle in die inter-frontale zones (STZ en AWZ) noord en suid van die APF, respektiewelik gevoed het. Ten spyte van die oorvleueling in dieselfde geografiese areas ter see in sommige gevalle, het ná-telingwyfies en ná-verharingwyfies meestal verskillende voedingstrategië getoon. Ná-telingwyfies het korter (gemiddelde afstand van 1031 ± 302 km), direkte vertrek en terugkeer deurgange na/van goed afgebakende voedingsgronde uitgevoer wat verlengde voedingstyd bevorder het en hul meer in tyd (die kort ná-telings periode van 45 - 73 dae) en keuse van alternatiewe verharings-aankomsgebiede beperk het wat die afstand van beweging ingekort het. Ná-verharingwyfies het opportunistiese, kol-kol voeding getoon, en tussen verskillende voedingsgronde rondgedwaal, met die gevolg dat hulle oor groter afstande kon beweeg as gevolg van ń verlengde tydperk tussen verharing en teling (die lang ná-verharingstydperk van 112 - 201 dae). Hierdie studie stel verder voor dat die prominente onderseese riwwe noord en suid van Marioneiland, naamlik die Suidwestelike Indiese Rif en die Mid-Atlantiese Rif as navigasiebakens deur ná-telingwyfies en ná-verharingwyfies gebruik was, ten minste gedurende die deurgangsfases vanaf Marioneiland na voedingsgronde. Geeneen van die wyfies in hierdie studie het die Enderby Afgrondvlak suidoos van die eiland opgesoek, waar geen geredelike opspoorbare plaaslike oseaanografiese strukture voorkom nie.

Seisoenale bewegings, voedingsareas en diel verskille in die duikgedrag van wyfies vanaf Marioneiland was ook met betrekking tot watertemperatuur ondersoek. Olifantrobwyfies het meestal binne inter-frontale zones gedurende beide die ná-telingperiode en ná-verharingperiode gevoed. Oorvleueling van gelokaliseerde ná-telingvoedingsareas stel ń periode van aansienlike prooioorvloed voor, terwyl gekronkelde bewegings gedurende die ná-verharingperiode afsondering, tesame met ń periode van lae prooibeskikbaarheid, voorstel. Diel verskille in die diepte van voedingsduike is klaarblyklik geassosieerd met moontlike gekonsentreerde voedings-prooi-najaging op vertikaal migrerende prooi. ń Homogeen, breë temperatuurlaag binne die waterkolom op voedingsdiepte blyk ń moontlike verskuiwing te veroorsaak in die diel patrone van prooiverspreiding. Daarteenoor lyk dit of heterogene temperatuurlae by voedingsdiepte klein verskille in die diel duikdiepte in die hand werk. Voeding is klaarblyklik gekoppel aan die temperatuur van die waterkolom, moontlik omdat olifantrobbe die verandering in die watertemperatuur gebruik om die teenwoordigheid van die prooi te voorspel. Die diel duikgedrag bewillig nie voorspelling van die werklike voedingsukses van wyfies nie, maar kan in verband staan met hul voeding in inter-frontale zones weg van geredelike opspoorbare gebiede van hoë primêre produksie, miskien as gevolg van ń herverspreiding van hulle prooi wat verband hou met omgewingsgebeure en klimatologiese veranderinge.

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