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THE DIVING AND RANGING BEHAVIOUR OF
SOUTHERN ELEPHANT SEAL, *MIROUNGA LEONINA*, BULLS

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The diving and ranging behaviour
of southern elephant seal,
Mirounga leonina, bulls.

by

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ABSTRACT

Geolocation-Time-depth Recorders (GLTDRs) were used to record the diving and ranging behaviour of eleven southern elephant seal, *Mirounga leonina*, adult males from sub-Antarctic Marion (n = 7) and Macquarie (n = 4) Islands during their pelagic annual cycle. A total of 39 897 dives during 894 days were recorded and were categorised into twelve dive types which were hypothesized to serve in travelling, searching for prey, exploration, resting, benthic foraging, pelagic foraging and combinations of two or more

functions, and seals dived virtually continuously (86%-92% of the time underwater) most often to depths ranging from 390 m to 920 m and dive durations from 18.6 min to 36.6 min (maximum duration = 80 min) spending only 2.4 min to 3.6 min on the surface between dives. Although the maximum measured dive depths for two males from Marion Island (1 446 m and 1 452 m) are the deepest dives measured yet for male southern elephant seals, these seals often exceeded the depth limit of the GLTDRs. The Macquarie males travelled to Antarctica mostly foraging benthically over the Antarctic continental shelf whilst the males from Marion Island stayed relatively close to the island, diving deeper and longer pursuing pelagic prey species. The results in this study suggest that different physical environmental conditions resulted in the different diving behaviours displayed by *M. leonina* males.

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Chapter 1 INTRODUCTION

The southern elephant seal, *Mirounga leonina*, breeds on islands on both sides of the Antarctic Polar Front and comprises of three stocks - these being referred to as the South Georgia, Macquarie and Kerguelen stocks (Laws 1960). The last includes not only elephant seals of the Kerguelen archipelago, but also those found at Heard, Marion and Prince Edward Islands, Iles Crozet, and Amsterdam and St. Paul Islands (Fig.1, Bester 1988).

Although *M. leonina* is the largest pinniped, relatively little was known about its diving and ranging behaviour until recently. Male southern elephant seals spend the largest part of their lives at sea submerged whilst diving (Boyd & Arnborn 1991; Campagna, Le Boeuf, Blackwell, Crocker & Quintana 1994; Slip, Hindell & Burton 1994). Adult southern elephant seals have two haul-out periods each year that are associated with breeding and moulting (Hindell & Burton 1988; Le Boeuf & Laws 1994). Adult males from Marion and Macquarie Islands come ashore for the breeding season from August to November and after a sojourn at sea (post-breeding period), they return for the moult. The moult haul-out for adult males peaks in February and March for the Marion and Macquarie males respectively, before they return to sea until the next breeding season (Condy 1979; Hindell & Burton 1988; Hindell, Burton & Slip 1991a).

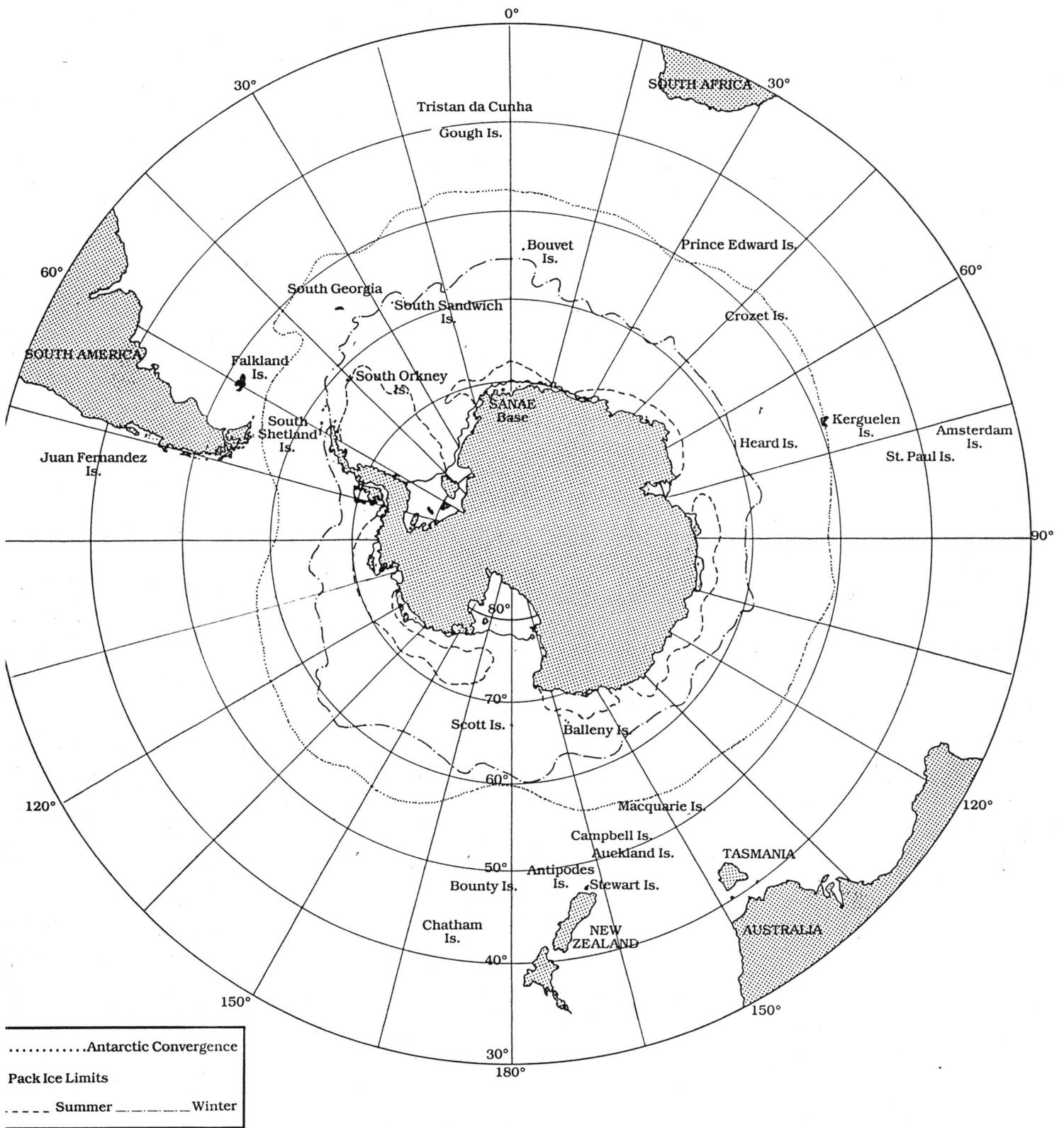


FIG 1. Map showing the most important islands in the southern ocean.

Southern elephant seals have decreased significantly in number during the last half of this century (Skinner & van Aarde 1983; McCann 1985; Burton 1986; Hindell & Burton 1987; Bester & Wilkinson 1994; Laws 1994). The percentage decline in numbers over the last 40 years for colonies in the Southern Ocean adjacent to the Antarctic Polar Front is estimated at 50% for Heard Island, 84% for Marion Island, 58% for Macquarie Island, 96% for Campbell Island, 93% for Signy Island, and up to 80% for some colonies in the Kerguelen archipelago (Laws 1994). The population of breeding females in the Kerguelen archipelago has been stable between 1984 and 1989 (Guinet *et al.* 1992) and the South Georgia colony which is the largest with more than 350 000 seals, is considered to have remained stable since the 1950's, but estimates are based on only two censuses (Laws 1960; McCann 1985).

The percentage decline for the populations of southern elephant seals from Marion and Macquarie Islands is 4,8% (Bester & Wilkinson 1994) and 2,1% (Laws 1994) per annum respectively. Southern elephant seals have been well studied during their terrestrial phases, but knowledge of their behaviour and ecology when at sea for eight to nine months each year is limited (Hindell *et al.* 1991a; Jonker & Bester 1994). To date, there is no information available concerning the diving and ranging behaviour of male southern elephant seals from Marion Island and very little from the Macquarie Island male population (Hindell, Slip & Burton 1991b). Food and feeding behaviour are fundamental factors in the definition of any organism's ecological niche. Basic data on diet, foraging behaviour and foraging grounds are important requirements for conservation and management programmes and central to understanding the recent changes in populations

of southern elephant seals (Hindell *et al.* 1991b). The causes of the reduction in numbers of southern elephant seals are unknown, but is evidently due to factors operating mainly during the pelagic phase of the annual cycle, because increases in mortality during the terrestrial phases have not occurred (Wilkinson & Bester 1988; Bester & Wilkinson 1994; Laws 1994; Hindell, Slip & Burton 1994). There is, however, a major gap in the understanding of the southern elephant seal's diet, because all the studies on the stomach and faecal contents were done during the moulting and breeding season haul-outs and give only an insight into what the animals ate some hours before they returned to the island after an eight month journey (Hindell *et al.* 1991b). From the little information available, it is known that the diet of southern elephant seals is basically composed of several cephalopod and fish species (Slip 1995).

Water temperature and light intensity are probably the most important factors affecting vertical distribution of pelagic prey (Boyd & Arnbom 1991). 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 abilities (Hindell *et al.* 1991a & b; Campagna *et al.* 1994; Jonker & Bester 1994). With the development of geolocation time-depth recorders that measure the diving and ranging abilities of elephant seals, studies on their behaviour have been made possible. Location and the pattern of diving reflects the general type of prey consumed (Campagna *et al.* 1994; Le Boeuf & Laws 1994). From information such as depth and duration of dives, surface interval between dives and timing of dives, suggestions about the type of prey exploited can be

made. Antarctic fur seals *Arctocephalus gazella* exhibit a diurnal diving pattern, this would suggest they are feeding on pelagic prey that is migrating vertically (Croxall, Everson, Kooyman, Ricketts & Davis 1985; Le Boeuf, Costa, Huntley & Feldkamp 1988). Boyd & Arnborn (1991) and DeLong & Stewart (1991) suggested that the characteristic diel diving pattern of elephant seals resulted from the pursuance of vertically migrating prey.

Elephant seals are the deepest diving pinnipeds (Le Boeuf, Costa, Huntley, Kooyman & Davis 1985; Cherfas 1987). Male elephant seals are capable of extremely deep dives, over 1 500 m in northern elephant seals, *Mirounga angustirostris*, and over 1 200 m in southern elephant seals (De Long & Stewart 1991; Hindell *et al.* 1991b). Dives of up to two hours have been recorded for southern elephant seals (Hindell *et al.* 1991b), with mean post dive surface intervals between dives ranging from two to four minutes (Hindell *et al.* 1991b; Jonker & Bester 1994). Despite the long mean dive durations (20-22 min) and short post dive surface intervals, elephant seals can dive virtually continuously. Because elephant seals spend the largest part of their life at sea, the exact physiological mechanism making such long duration diving without any extended surface intervals possible is difficult to research. It seems however as if elephant seals do not exceed their aerobic dive limit altering various physiological processes, for example: 1) Oxygen loading and carbon dioxide dumping are accomplished quickly during the respiratory period; 2) their heart rate decreases; 3) hematocrit levels in the blood increase and blood flow to the peripheral tissues is decreased to conserve the oxygen-rich blood for the more aerobic central organs, such as the brain and heart; 4) they need to reduce their metabolic rate

below their resting metabolic rate during dives (Le Boeuf, Naito, Huntley & Asaga 1989; Hindell *et al.* 1991b; Le Boeuf, Naito, Asaga, Crocker & Costa 1991; Hindell, Burton & Bryden 1992; Castellini 1994; Crocker, Le Boeuf, Naito, Asaga & Costa 1994).

The current study was aimed at investigating the diving behaviour of male southern elephant seals in the Southern Ocean ecosystem by deploying time-depth recorders on adult males from Marion Island. This was expected to provide data on the diving and ranging abilities, potential diet, foraging behaviour and movement patterns of male southern elephant seals. The main objective of the study was to examine different dive types and what these dive types and assumed foraging locations suggest about the type of prey (pelagic or benthic) male southern elephant seals might be taking. By comparing the locations and dive patterns of male elephant seals from Marion Island with those from Macquarie Island in particular, the possible influence of the different locations on diving behaviour of the male southern elephant seals was further investigated.

Chapter 2 MATERIALS & METHODS

2.1 Study areas

Male southern elephant seals from two sub-Antarctic islands, Marion Island and Macquarie Island were studied.

Marion Island ($46^{\circ} 54' S$, $37^{\circ} 45' E$) is one of two islands in the Prince Edward island group which lies 2 300 km south-east of Cape Town in the South Indian Ocean (Condy 1979) and about 2 300 km from Enderby Land in Antarctica (Fig. 1). The estimated southern elephant seal population size at Marion Island is approximately 2 000 seals and has declined most drastically of all breeding colonies, except those at Signy and Campbell Islands (Laws 1994).

Macquarie Island ($54^{\circ} 30' S$, $158^{\circ} 57' E$), which is situated in the Southern Ocean, lies approximately 1 700 km from Lenningradskaya, Antarctica. This is the most continuously studied population of elephant seals and Laws (1994) reported a total population of 77 791 elephant seals for 1990.

2.2 Subjects

Tagged adult male southern elephant seals from Marion Island, of known age and with a known history of returning to the island to breed and moult, were selected. The hexadecimal files of four males (one post moulting and three post breeding) from Macquarie Island, as generated by Time-depth recorders (see below) and studied by Hindell *et al.* (1991a & b), were obtained from Mark A. Hindell (Department of Zoology, University of Tasmania, Hobart, Tasmania 7050), and re-analysed to make valid comparisons between the Marion- and Macquarie males possible.

2.3 Deployment of recorders

The selected males from Marion Island were sedated with an intramuscular injection(s) of a mixture of ketamine hydrochloride and xylazine hydrochloride when they were about to leave the island for their main feeding periods at sea (Bester 1989). Each recorder was screwed down onto a 18 x 5-cm aluminium plate by three stainless steel hose clamps after the plate had been glued to the dorsal pelage between the shoulders of each seal. A length of cotton mesh or shade netting was stitched onto each of the aluminium plates with nylon thread through 0.2-cm holes drilled into the plate. Attachment was by quick-setting epoxy resin adhesive (Araldite AW 2101/HW 2951, Ciba-Geigy) so that the long axis of the recorders were parallel to the long axis of the seal (Bester & Pansegrouw 1992).

2.4 Recorders

Microprocessor-controlled geolocation time-depth recorders (GLTDRs, Wildlife Computers, Redmond, Washington, USA) were attached to selected adult males during 1994, 1995 and 1996 at Marion Island. Functional GLTDR models Mk3+ (256 or 768 Kbytes of memory) and Mk3e (768 Kbytes of memory) were deployed on the selected male southern elephant seals. The GLTDRs were housed in small titanium cylinders and were each equipped with a pressure transducer, quartz clock, temperature probe and light sensor mounted in a clear plastic cap (DeLong, Stewart & Hill 1992).

The instruments were programmed to collect data continuously from the moment the seals entered the water, recording hydrostatic pressure (dive depth), water temperature and the ambient light levels. Dive depth was usually recorded on two channels using a two-stage pressure transducer. The first channel sampled every 30 s and operated from 0 to 500 m with an accuracy of ± 2 m, while the second channel sampled every 60 s (from 500 to 1 500 m) with an accuracy of ± 6 m. Some of the Mk3e GLTDRs had a single (0-500 m) depth channel, and were formerly used on fur seals. Water temperature was recorded on a second or third channel every 300 s. Ambient light levels (used for geolocation) were recorded until the GLTDRs ran out of memory. Upon retrieval, the recorded binary files were loaded into a personal computer. Software from Wildlife Computers (see sections 2.5 & 2.7) was used for further analyses of the data.

The water temperature data sets of the Macquarie males were compared to water temperatures at the surface, 100 m, 200 m and 500 m depths as described in the atlas by Gordon & Molinelli (1982) in order to establish certain areas that showed similarity in water temperatures (Hindell *et al.* 1991a).

2.5 Dive analysis

With the strip chart software (Wildlife Computers; Ver. 3.0), a strip chart representation of the time-depth profile of a representative set of dives for each male was printed and used to identify dive types usually using the criteria described by Le Boeuf, *et al.* (1988); Hindell *et al.* (1991b); Slip *et al.* (1994) and Bester & Jonker (1994).

The zero offset correction (ZOC) software (Wildlife Computers; Ver. 1.22) was used to correct the surface readings for depth and transform the binary files offloaded from the GLTDRs to hexadecimal records of time and depth. These data were converted into graphical representations of each dive with the Dive Analysis software program (Wildlife Computers; Ver. 2.0). Each dive made by a seal was individually analysed and then subjectively classified as one of 12 dive types. For each dive, the nine variables that were recorded as an ASCII file for further statistical analyses were: **date of dive**; **time of dive**; **dive depth** (m) = the maximum depth of the dive; **dive duration** (min) = the duration between the time of the surface readings immediately preceding and following the dive; **bottom time** (min) = elapsed time between the end of the descent phase and the beginning of ascent phase of a dive (the position of these two points were user-selected); **average**

rate of descent (m/s) = calculated from the beginning of descent to the beginning of bottom time; **average rate of ascent** (m/s) = calculated from the end of bottom time to the end of the dive; **post dive surface interval** (min) = the total time spent at the surface since the last analysed dive; **dive type** = subjective classification as one of 12 dive types considering all the dive parameters and the appearance of the dive profile (Fig. 2).

The amount of wiggles observed was taken into consideration when classifying dives. Wiggles are defined as the rapid increase and decrease in the dive depth as the seals moved at the bottom of their dives (Slip *et al.* 1994).

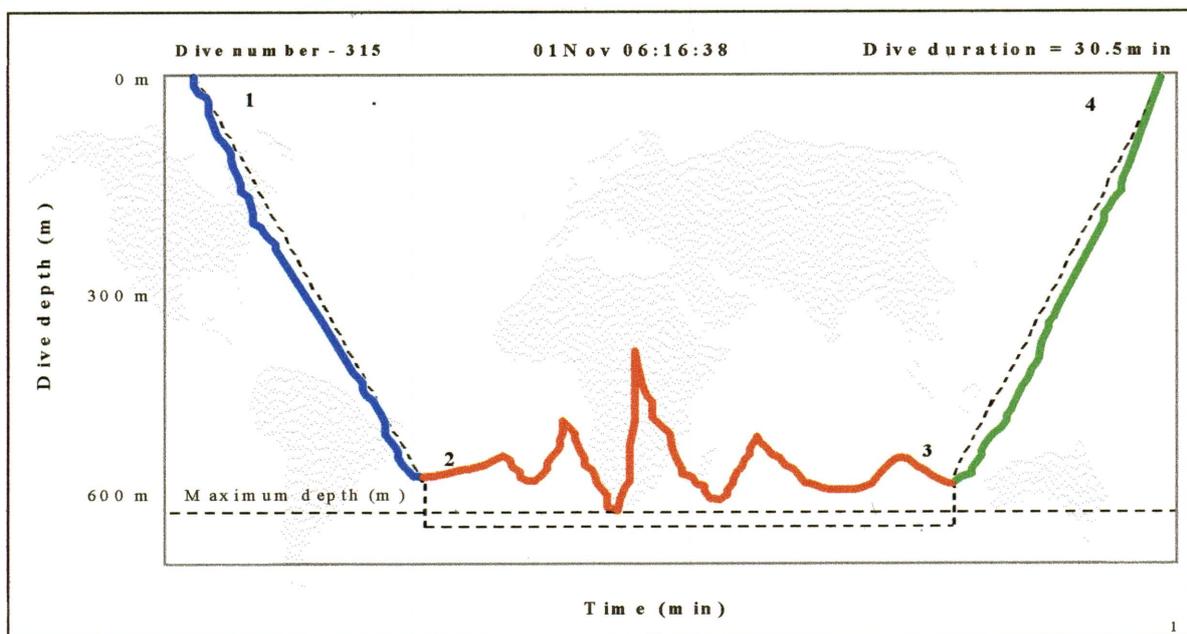


FIG 2. Example of a typical dive as presented by the dive analysis program (Wildlife Computers) showing the user selected markers 1, 2, 3 & 4 that determine the start and end points of the descent phase (1 — 2), bottom time (2 — 3) and ascent phase (3 — 4).

The most important feature used in the classification of separate dive types was the dive shape taken from graphical representations of time over depth. When using the means of the nine measured dive parameters, detail about the dive shape is lost. It is therefore either difficult or impossible to classify dives meaningfully by only using statistical procedures.

Post dive surface intervals that exceeded ten minutes were defined as extended surface intervals (ESIs) following Le Boeuf *et al.* (1988) and Jonker & Bester (1994). Also recorded was the time spent hauled out, which was the period when a recorder was dry.

2.6 Statistical analyses of data

The ASCII files that were created for each seal were used for all further analyses. The SAS statistical package (SAS Institute Inc 1994) was used to perform all statistical analyses. The Shapiro-Wilk test was used to test for normality on all dependant variables, and the homogeneousness of the data was tested using the Bartlett-test. Normal one- and two-way analysis of variance (ANOVA) was used to test for significant differences in the dive parameters between individuals, locations, dive types and day and night. In all statistical analysis “day” was defined as the time from 10:00 - 14:00 and “night” from 22:00 – 02:00 to allow for time differences resulting from the different geographical positions of the seals at sea to make comparisons possible (Le Boeuf *et al.* 1988, Jonker & Bester 1994). Differences in the non-normal distributed data, for example surface

intervals, were tested with the Kruskal-Wallis non-parametric test. Where differences between only two groups of non-normal distributed data were tested, the Wilcoxon test was used. Chi-square (χ^2) analysis was used to test for differences in ratios of frequency of occurrence of dive types. In an attempt to objectively test the validity of the classification of the dive types using statistical procedures the discriminant function analysis was employed (Schreer & Testa 1994). Maximum dive depth (m), maximum dive duration (min), average descent rate (m/s), bottom time (min) and the average ascent rate (min) were specified as the five parameters used by the discriminant function analysis. All dives in the diving record of each seal were used in all analyses and the 0.05 level of probability was accepted as indicating statistical significance.

2.7 Foraging locations

The foraging areas of the male southern elephant seals from Macquarie Island were used as published in Hindell *et al.* (1991a), who used recorded water temperature data to estimate their locations (Fig. 3) from the seawater temperature atlas of Gordon & Molinelli (1982).

For the males from Marion Island, the Geolocation Analysis software package (ver 1.0) was used to calculate their locations at sea. The light level and temperature data were extracted from the hexadecimal files (created by the GLTDRs) and displayed graphically on a day-by-day basis. The times of dawn and dusk for each day were used to calculate

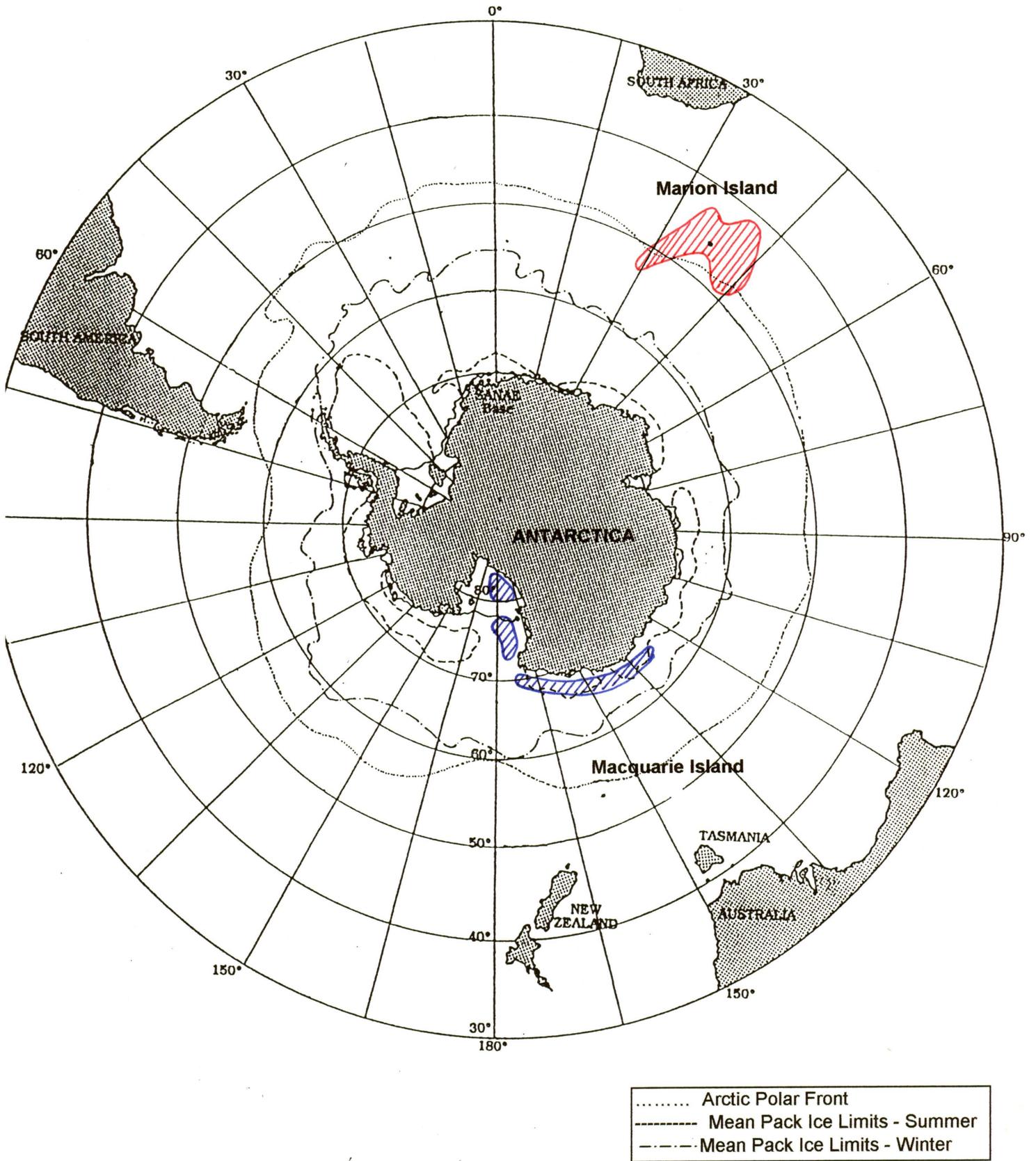


FIG. 3: Areas where males from Marion Island  and Macquarie Island  spent most of their time.

daylength and local-apparent-noon. From an algorithm using daylength, the latitudinal positions were calculated and the longitudes using local-apparent-noon (Hill 1994). The locations could be determined to a precision of about ± 60 nautical miles under good conditions (De Long *et al.* 1992; Stewart & De Long 1994).

Sea surface temperatures (SST) recorded by the GLTDRs were converted to an ASCII file using the 3 M software program (Wildlife Computers). The highest recorded temperature for each day was used to make estimations of the position of the elephant seals in relation to Marion Island by using the seawater temperature atlas by Gordon & Molinelli (1982). The SSTs were only used to estimate the positions of those seals the GLTDRs of which malfunctioned and did not record light level data.

Chapter 3 RESULTS

3.1 Ranging behaviour

3.1.1 Recorders & Geolocation data

Of the sixteen geolocation time-depth recorders which have been deployed on male southern elephant seals at Macquarie Island after their breeding and moulting haul-outs, only four recorders were recovered, each containing temperature data that was used for estimation of the position for each seal (Table 1). From these positions of the foraging areas the ranging behaviour of the animals were estimated (Fig. 3).

At Marion Island two recorders were recovered intact after the males returned for the breeding season in September. Both recorded water temperature whilst none of them recorded light-level data. Five GLTDRs were recovered intact after the males returned to Marion Island for the annual moult. Three of the five GLTDRs successfully recorded both light level and temperature data, one recorded only light-levels and the other one only water temperature (Table 1).

3.1.2 Geolocation using light levels

Partial migratory paths could be calculated for four out of the seven seals using the light level data recorded. None of the GLTDRs recorded light-level data for the complete trip at sea (Table 1). Although movement records are incomplete, certain assumed foraging areas could be identified and general conclusions made. The information obtained from the light-level data showed that seal 360n94 foraged over the widest area and travelled the furthest away from the island (± 1134 km), first moving to the north east of Marion Island and then travelling to the south east crossing the Antarctic Polar Front (APF) where it remained in a general area for 23 days before returning to the island (Fig. 4). Post breeding, male 1183n94 immediately travelled to a very specific assumed foraging area near the APF approximately 850 km south south east of Marion Island

TABLE 1. Summary of data for male southern elephant seals the GLTDRs of which were recovered and successfully recorded information about their ranging and/or diving behaviour.

Male no.	Island	GLTDR deployed	Date		GLTDR recovered	No. of days at sea	No. of days not recorded	Dives recorded	Geolocation data recorded
			of first record at sea	of last record at sea					
1183n94	Marion	94/11/11	94/11/17	95/03/01	95/03/01	104	0	< 450 m	Light levels
1183m94	Marion	95/03/11	95/03/22	95/07/29	95/09/14	176	47	< 450 m	Temperature
335n94	Marion	94/11/02	94/11/29	95/01/22	95/02/21	84	30	yes	Temperature
335a94	Marion	94/04/05	94/04/26	94/09/09	94/09/16	143	7	yes	Temperature
031n93	Marion	93/11/05	93/11/15	94/02/23	94/02/23	100	0	yes	Light levels & Temp.
360n94	Marion	94/11/11	94/11/17	95/02/03	95/03/10	113	35	yes	Light levels & Temp.
gw410	Marion	96/11/05	96/11/12	97/01/06	97/02/08	88	33	no	Light levels & Temp.
1453	Macquarie	88/02/13	88/02/13	88/04/13	-	-	-	yes	Temperature
1475	Macquarie	88/11/18	88/11/21	89/02/06	-	-	-	yes	Temperature
1963	Macquarie	88/11/19	88/11/21	89/02/08	-	-	-	yes	Temperature
1969	Macquarie	88/11/21	88/11/27	89/02/12	-	-	-	yes	Temperature

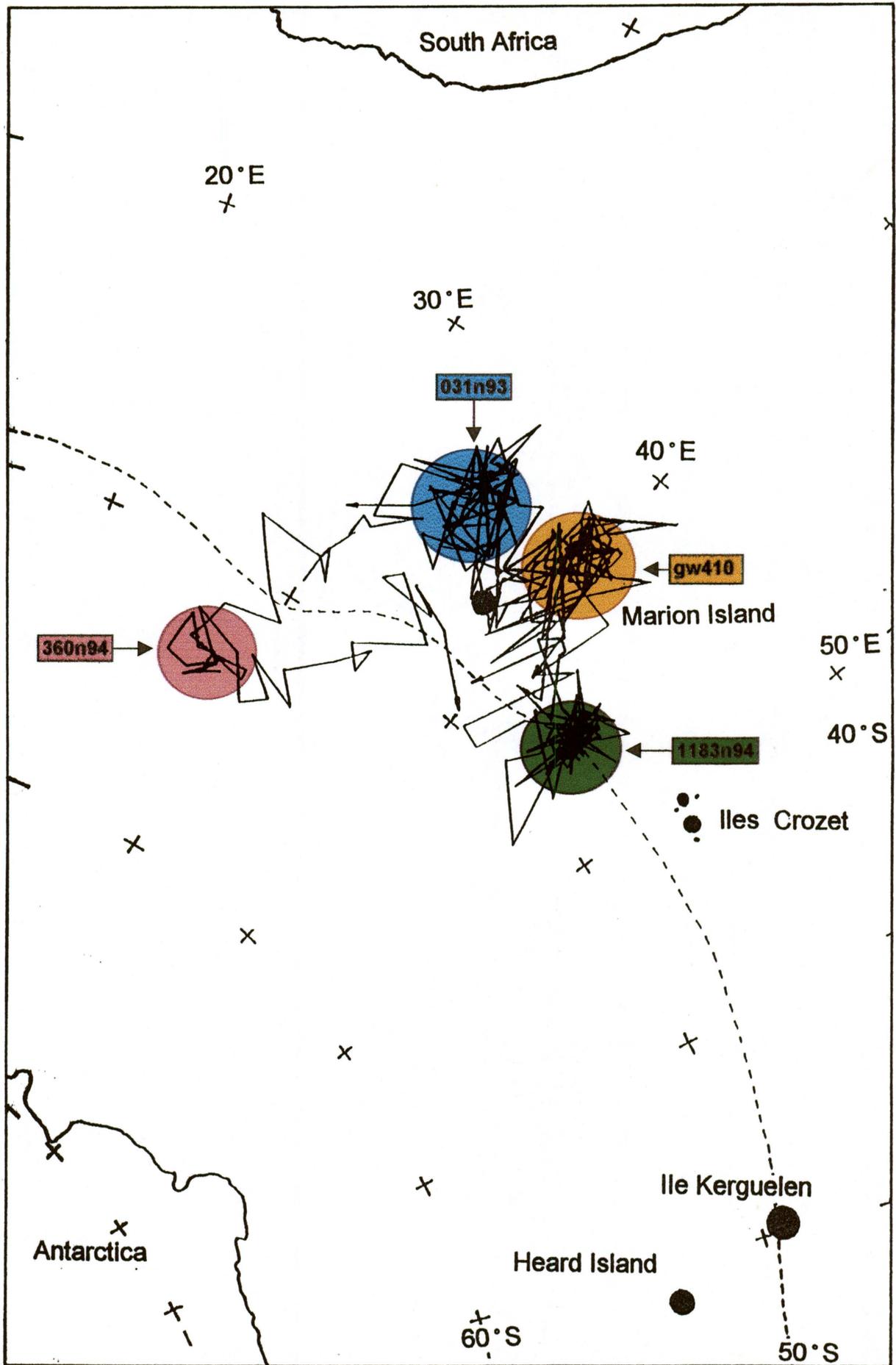


FIG. 4: The movements of four male southern elephant seals from Marion Island as estimated from the light-level data collected. The approximate position of the Antarctic Polar front is indicated by the dashed line.

where it remained for 73 days before returning to the Island (Fig. 4). Although the light level records of seals 031n93 and gw410 were incomplete, the temperature data (see section 3.1.3) showed that these two males remained relatively close (within approximately ± 505 km and ± 753 km respectively) to Marion Island (Fig. 4).

3.1.3 Location using sea surface water temperatures

Hindell *et al.* (1991a) found that the four males from Macquarie Island immediately headed south as soon as they left the Island. As they headed south, the mean SST declined steadily from 6 °C to around -1 °C where it stayed relatively constant and all the males moved into waters south of the Antarctic Circle. The males appeared to have been utilising two different regions, one in which the surface waters were warmer than the deeper water and the other where surface waters were colder than the deeper waters, and all the males moved to within the 1000 m depth contour off the Antarctic coast.

Male 360n94 moved the furthest south with the SST, at departure from Marion Island, ranging from 6 - 9 °C and decreasing to as low as 0 - 2 °C during migration across the APF (Fig. 5). Males gw410 and 031n93 experienced SSTs that varied little (6.4 °C – 10.2 °C) during the entire recording period, which indicated that they remained relatively close to the Island. The SSTs for males 335n94 and 335a94 (malfunctioned light sensors) suggested that they stayed in an area to the north of Marion Island with SSTs above 6.1 °C (Fig. 5). The SSTs encountered by male 1183m94, suggest that it travelled to the south of Marion Island where the SSTs dropped from 5.6 °C to as low as 3.0 °C (Fig. 5).

Although the recorded SSTs of male 1183m94 indicated that it moved south which correlated with its post-breeding journey (figure 4), it never crossed the APF (SST > 3.0 °C) during the post moulting period (Fig. 5). The SST data set for seal 335 showed a similar temperature pattern for both the post breeding and post moulting periods and this may indicate that it utilised the same feeding grounds (Fig. 5).

3.2 Haul-out patterns

The recorded temperatures encountered by the three post-breeding males from Macquarie Island showed large increases of up to 22.7 °C (Fig. 6), attributable to haul-outs in the middle of the recording period at regular intervals.

None of the Marion Island males showed any regular haul-out patterns. Only seal 335a94 had one prolonged haul-out of nine days when the maximum recorded temperatures reached a high of 22.7 °C, 50 days before the recorder was recovered (Fig. 5). The seal went back into the water and dived for short periods of time within the overall haul-out period. It is likely that this haul-out took place on the nearby Prince Edward Island, since this male was not spotted on Marion Island during that specific period. As far as the records show, all the other instrumented males from Marion Island remained at sea constantly until the recorders ran out of memory or failed.

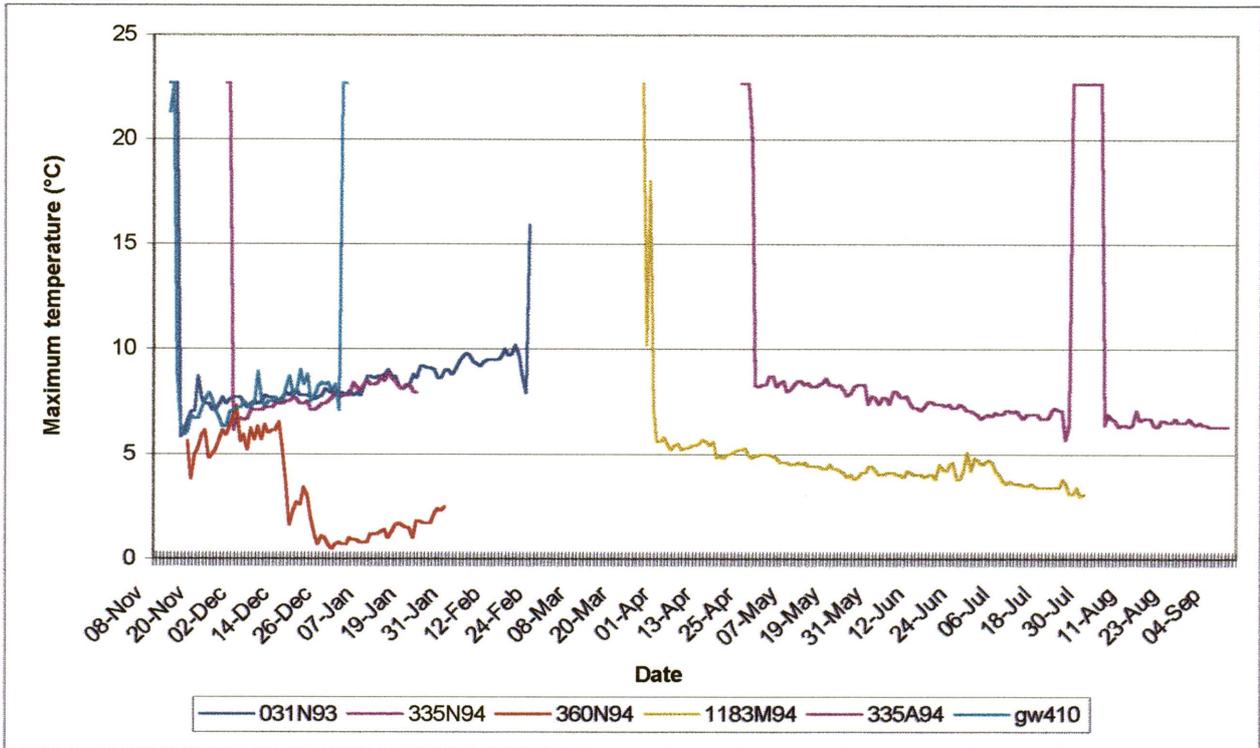


FIG. 5. Maximum recorded sea surface temperatures (SST) for each day for six male southern elephant seals from Marion Island.

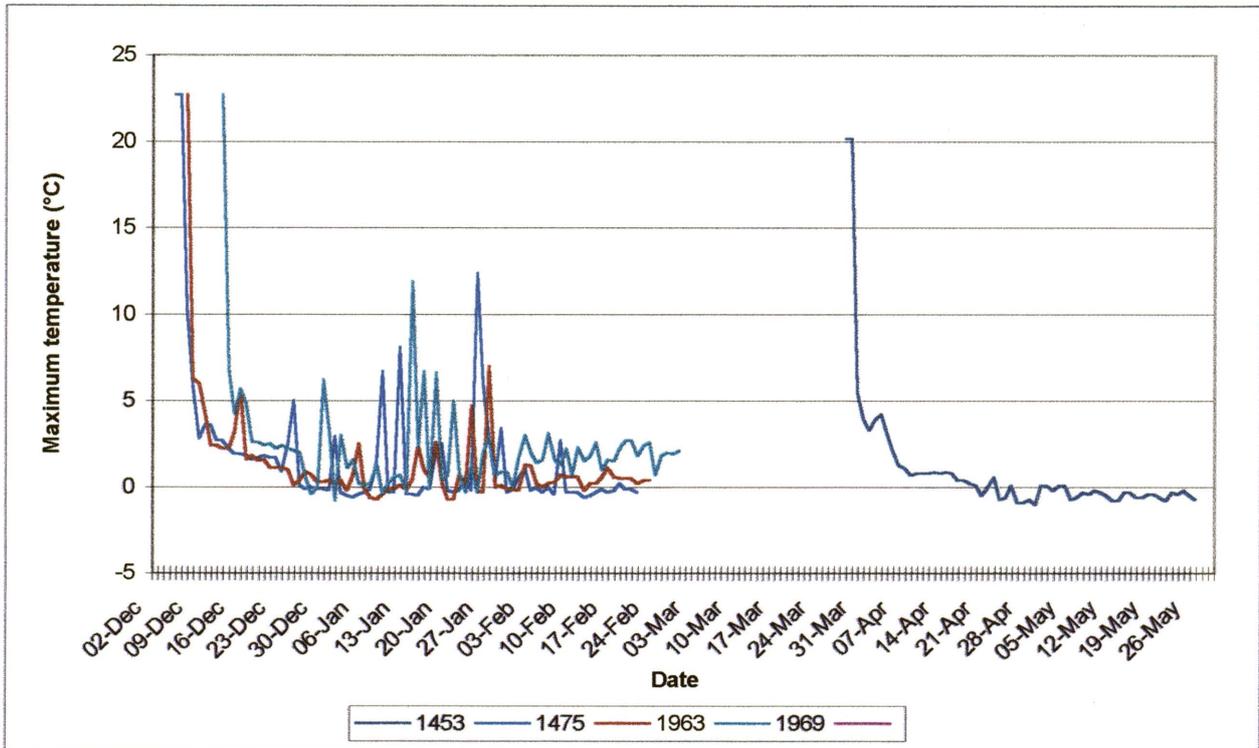


FIG. 6. Maximum recorded sea surface temperatures (SST) for each day for four male southern elephant seals from Macquarie Island.

3.3 Diving behaviour

3.3.1 Summary of dive statistics

The recorded dives of the Macquarie Island males did not exceed the depth limits of the recorders (Table 1). Two of the seven recorders (1183n94 and 1183m94) recovered at Marion Island (fur seal GLTDRs) could record depth to a maximum of 450 m, and were used to determine dive duration, dive tempo and surface interval. One GLTDR (gw410) recorded only geolocation data (Table 1). The remaining four recorders recorded all nine dive parameters successfully until its memory capabilities were exhausted. An average of 97 days was recorded for males from Marion Island and 75 days for those from Macquarie Island (Table 2).

TABLE 2. Summary of data of trips for seven male southern elephant seals from Marion Island and four males from Macquarie Island.

Male no.	Island	Status	No. of days recorded	No. of dives recorded	No. of dives/h	% time diving
1183n94	Marion	PB	104	6030	2.7	86.0
1183m94	Marion	PM	129	4632	1.5	92.4
335n94	Marion	PB	54	2317	1.8	90.6
335a94	Marion	PM	136	5339	1.7	86.7
031n93	Marion	PB	100	3490	1.4	90.1
360n94	Marion	PB	78	3945	2.1	89.0
gw410	Marion	PB	55	-	-	-
1453	Macquarie	PM	60	2547	1.9	91.8
1475	Macquarie	PB	77	3765	2.1	87.2
1963	Macquarie	PB	79	4276	2.3	85.9
1969	Macquarie	PB	77	3556	1.9	90.7

PB - post breeding, PM - post moulting

All males began diving immediately after leaving the Islands and dived virtually continuously for the entire time at sea (Table 2). The frequency of diving ranged from 1.4 to 2.7 dives per hour with seals spending 86% - 92 % of their time submerged (Fig. 7, Table 2). A total of 39 897 dives during 894 days were recorded with the longest and deepest recorded dives being 80 min and 1 446 m respectively (Table 3). The mean dive depths of all seals ranged from 390 m to 920 m and the mean dive duration from 18.6 min to 36.6 min (Table 3). Post dive surface intervals were short with the mean ranging between 2.4 min and 3.6 min (Table 3).

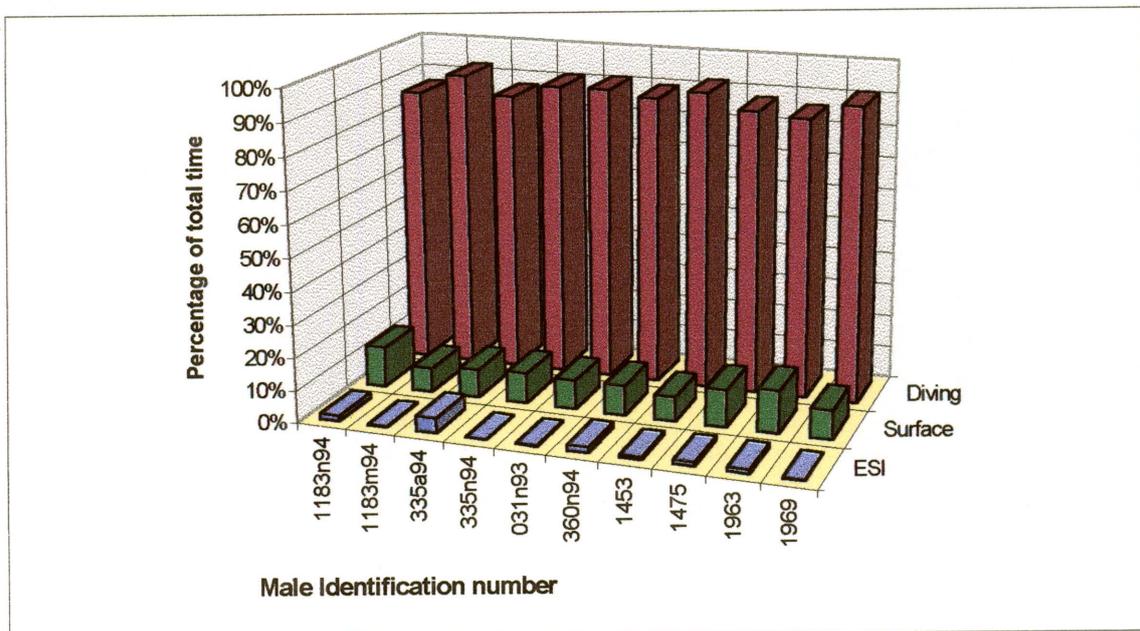


FIG 7. Percentage of time spent diving, at the surface and on extended surface intervals (ESI) for ($n = 10$) male southern elephant seals while at sea.

TABLE 3. Summary of dive statistics of dives $\geq 10\text{m}$ for the six male southern elephant seals from Marion Island and the four males from Macquarie Island.

Male no.	Dive depth		Dive duration		Bottom time		Suface interval	Extended surface intervals		
	(m)		(min)		(min)		< 10 min	> 10 min		
	Mean \pm SD	Max.	Mean \pm SD	Max.	Mean \pm SD	Max.	Mean \pm SD	<i>n</i>	Mean \pm SD	Max.
<u>Marion Island</u>										
1183n94	-	-	18.6 \pm 5.2	38	-	-	2.7 \pm 0.9	48	42.0 \pm 34.8	129
1183m94	-	-	35.3 \pm 9.8	69	-	-	2.9 \pm 0.9	16	22.1 \pm 17.1	80
335n94	767 \pm 263	1444	29.9 \pm 7.3	62	10.3 \pm 7.1	34	3.1 \pm 0.8	2	16.6 \pm 4.2	20
335a94	809 \pm 313	1446	30.5 \pm 6.7	70	9.4 \pm 6.7	43	3.1 \pm 0.9	18	480.2 \pm 784.9	2477
031n93	923 \pm 444	1452	36.6 \pm 7.3	64	10.9 \pm 7.0	36	3.6 \pm 1.1	7	53.6 \pm 71.3	211
360n94	411 \pm 203	1258	24.9 \pm 8.6	65	11.3 \pm 7.6	41	2.6 \pm 1.1	67	29.2 \pm 33.0	232
<u>Macquarie Island</u>										
1453	394 \pm 152	1078	29.1 \pm 10.1	80	13.4 \pm 8.3	65	2.4 \pm 1.4	21	28.8 \pm 18.5	75
1475	450 \pm 127	1148	25.0 \pm 5.7	62	10.9 \pm 6.2	54	3.4 \pm 0.9	42	33.3 \pm 44.4	268
1963	443 \pm 134	800	21.7 \pm 5.1	47	8.9 \pm 5.3	28	3.3 \pm 0.9	45	27.0 \pm 30.4	158
1969	421 \pm 74	864	27.6 \pm 5.3	62	15.0 \pm 5.7	51	2.7 \pm 0.8	9	32.9 \pm 32.4	114

n - number of extended surface intervals

3.3.2 Classification of dive types

Twelve dive types were recognised and these are schematically represented in Figure 8 and summary statistics given in Table 4. In this study dives were subjectively classified into 12 dive types and thereafter the validity of the classifications was tested with objective statistical procedures. There was great variation in the dive parameters for each dive type among individuals, different areas and for different hours of the day. Although the P-values indicated differences in depths and durations between the dive types, the variation (r-values) was too large to confirm significant differences.

Type 1

These were the shallowest dives ($\bar{x} = 21 \pm 22$ m) with short mean durations (less than two minutes) and accounted for only 0.95 % of all dive records. The bottom times were very short ($\bar{x} = 0.3 \pm 1.2$ min) with the descent and ascent rates almost identical.

Type 2

Type 2 dives were relatively shallow ($\bar{x} = 207 \pm 84$ m) with the mean dive duration being 18.3 ± 8.0 min. These dives have a smooth profile with a rapid descent to a rounded inflection point, maintaining constant depth at the bottom of the dive, followed by another rounded inflection point with a direct ascent to the surface. The descent and ascent rates were almost the same with a long bottom time accounting for 50.82 % of the total dive duration. This dive type occurred in bouts of several dives, especially at the beginning and end of the seal's journey at sea.

Dive types

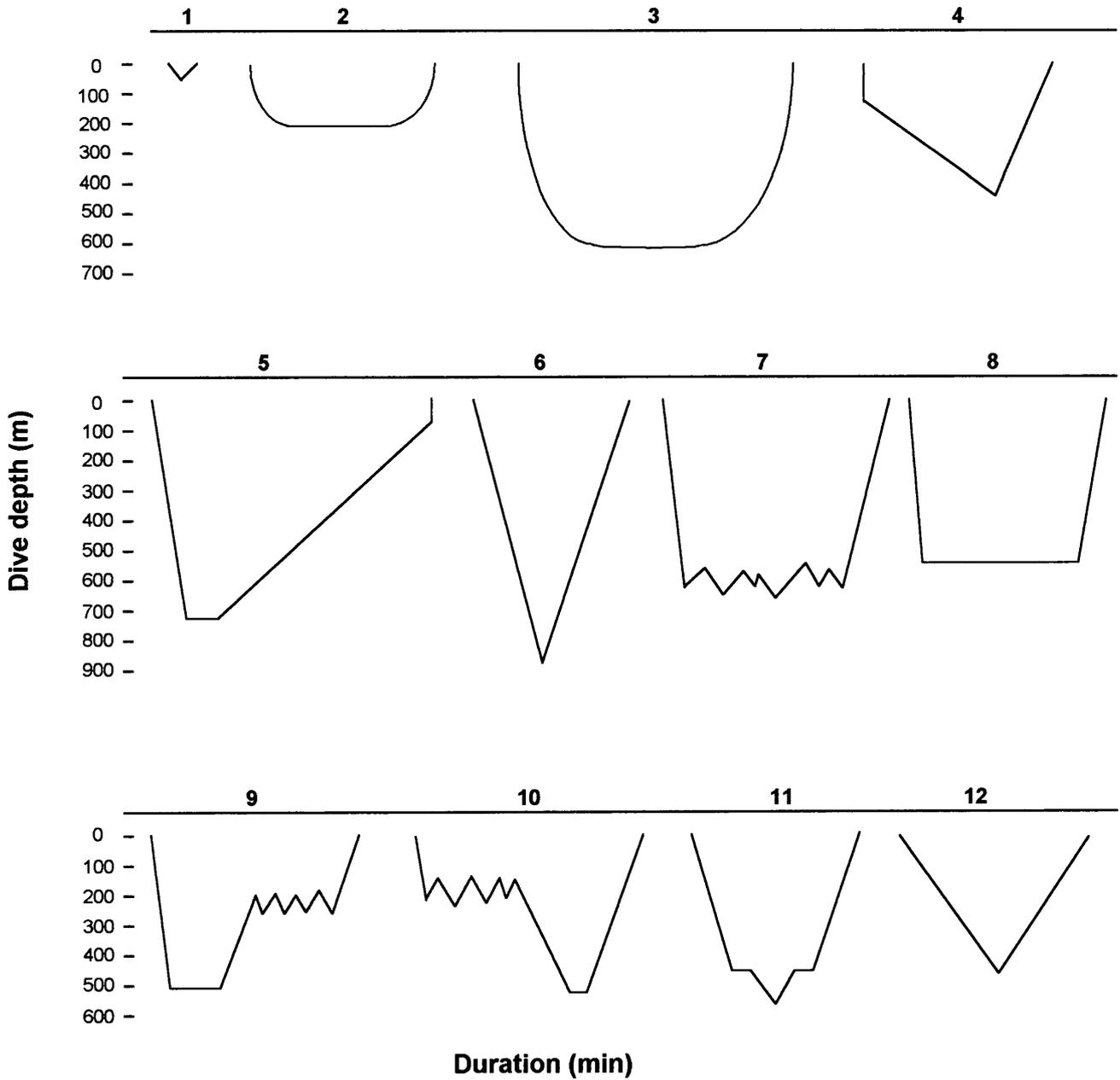


FIG 8. Graphical presentation of the profiles of the twelve dive types identified after analysis of the diving records of eight male southern elephant seals.

TABLE 4. Summary of statistics for the 12 dive types identified.

Dive type	No. of dives	Dive depth (m)		Dive duration (min)		Descent rate (m/s)		Bottom time (min)		Ascent rate (m/s)	
		Mean \pm SD	Max.	Mean \pm SD	Max.	Mean \pm SD	Max.	Mean \pm SD	Max.	Mean \pm SD	Max.
1	278	21 \pm 22	318	1.9 \pm 2.4	29	0.68 \pm 0.41	2.3	0.3 \pm 1.2	11	-0.65 \pm 0.38	-2.0
2	1781	207 \pm 84	580	18.3 \pm 8.0	62	0.73 \pm 0.29	2.3	9.3 \pm 6.4	21	-0.72 \pm 0.22	-1.6
3	6151	662 \pm 314	1452	29.7 \pm 6.9	65	1.38 \pm 0.66	3.0	11.7 \pm 5.7	54	-1.03 \pm 0.32	-2.2
4	3202	460 \pm 148	1312	26.1 \pm 6.8	61	0.47 \pm 0.13	2.0	0.9 \pm 1.5	19	-0.90 \pm 0.19	-1.7
5	552	704 \pm 357	1450	31.65 \pm 8.6	70	1.39 \pm 0.60	2.9	2.4 \pm 3.1	20	-0.56 \pm 0.22	-0.2
6	272	873 \pm 392	1444	25.3 \pm 7.6	44	1.28 \pm 0.57	2.9	0.7 \pm 0.7	4	-1.06 \pm 0.26	-1.8
7	8077	675 \pm 336	1450	30.4 \pm 7.8	80	1.50 \pm 0.53	3.0	14.6 \pm 5.6	66	-1.19 \pm 0.28	-2.2
8	7823	571 \pm 289	1450	27.9 \pm 6.9	57	1.72 \pm 0.39	2.8	14.3 \pm 4.8	39	-1.12 \pm 0.24	-1.9
9	256	526 \pm 297	1450	30.1 \pm 10.5	66	1.21 \pm 0.46	2.4	5.1 \pm 5.1	22	-0.53 \pm 0.19	-0.2
10	245	537 \pm 241	1366	27.8 \pm 8.9	55	0.54 \pm 0.20	1.2	3.1 \pm 3.4	19	-1.03 \pm 0.27	-1.7
11	140	564 \pm 318	1272	26.2 \pm 7.9	50	0.77 \pm 0.41	2.2	1.5 \pm 1.5	7	-0.69 \pm 0.25	-1.2
12	488	494 \pm 144	1230	28.7 \pm 7.1	52	0.57 \pm 0.14	1.2	0.5 \pm 0.6	5	-0.62 \pm 0.14	-1.3

Type 3

The commonly occurring parabolic Type 3 dives accounted for 21.02 % of all dives and were similar to the Type 2 dives but on average 455 m deeper and with faster descent and ascent rates. Mean bottom times were only 2.4 min longer than that of Type 2 dives but only accounted for 39.39 % of the total dive duration. Within Type 3 dives, there were large variations in dive depth, dive duration and the dive shape. Many Type 3 dives were quite similar to Type 7 dives, but if wiggles occurred whilst at the bottom of the dive, they were very small (subjective observation).

Type 4

Type 4 dives were characterised by a very fast first descent phase to a certain depth, at which a sharp inflection point occurred, and the descent rate decreased dramatically during the second descent phase until the bottom of the dive was reached. Less than 3.5 % of the total duration of the dive was spent at the bottom of the dive which was followed by a fast and direct ascent ($\bar{x} = 0.90 \pm 0.19$ m/s) to the surface (Fig. 8, Table 4). These dives accounted for 10.94 % of all dives recorded and usually occurred in bouts preceding and following Type 7 and Type 8 dives (subjective observation).

Type 5

The shape of these dives were practically mirror images of Type 4 dives, but were on average 244 m deeper and 5.55 min longer with the bottom time accounting for 7.58 % of

the total dive duration. Type 5 dives occurred infrequently (1.88 %) and was dispersed throughout the diving records.

Type 6

Although these dives accounted for only 0.93 % of all dives, they were easily identifiable amongst other dives. The dives had a spiked shape with a fast and direct descent to the bottom of the dive followed immediately by a similar fast and direct ascent to the surface. Type 6 dives were dispersed as single dives throughout the recording period.

Type 7

After a fast descent to a specific depth, 48.03 % of the dive time was spent on the bottom of the dive followed by a fast ascent. The bottom time of the dives showed discrete movements (wiggles) as the descending and ascending rates changed whilst at the bottom of the dive. As the most common dive type (27.60 %), these dives were easily identified by their extended bottom times and large wiggles. These dives occurred in long series and showed a diel pattern, dives being deeper during the day than during the night.

Type 8

Similar to Type 7 dives, these dives were characterised by the fast descent and ascent rates but had extended “flat” bottom times. These dives were dominant during the middle period of the male’s journey at sea and accounted for 26.73 % of all dives. The bottom time accounted for 47.04 % of the total dive duration. No diel variation in the depth of Type 8 dives was evident.

Type 9

Type 9 dives, identified by its very characteristic ascent phase, had a fast descent phase and a bottom time that accounted for 16.94 % of the dive duration. The ascent phase started rapidly, but then suddenly stopped at depth with a couple of wiggles, before the seal finally resumed the ascent and returned to the surface. This slowed the mean ascent rate down to -0.53 m/s.

Type 10

The shape of Type 10 dives was similar to that of Type 9 dives, but with the interruption occurring during the descent phase. Type 9 and 10 dives were rare and both accounted for less than 0.9 % of all dives.

Type 11

These dives were characterised by the two “shoulders” formed during the descent and ascent phases at equal depths. The “shoulders” occurred at no specific depth and did not have a constant duration. Type 11 dives were the rarest of all (0.48 %) and differed markedly from the profiles of the other dive types.

Type 12

Graphing depth over time type 12 dives had a simple shape showing direct and similar descent and ascent phases (0.57 ± 0.14 m/s and $- 0.62 \pm 0.14$ m/s) with almost no bottom time and accounted for 1.67 % of all dives.

3.3.3 Validity of the classification of dive types

Table 5 shows the percentage of dives correctly classified into the 12 types when employing the discriminant function analysis.

TABLE 5. Percentage of dives reclassified into the 12 dive types by using an objective statistical procedure (discriminant function analysis) to test the validity of the subjective classification of the dives.

Dive Type	Percentage of dives correctly classified (%)											
	1	2	3	4	5	6	7	8	9	10	11	12
1	97	2	-	-	-	-	-	-	-	-	-	-
2	2	86	2	-	-	-	3	1	1	2	1	-
3	-	14	28	1	1	2	18	23	3	6	3	1
4	-	-	-	76	-	2	-	-	-	8	1	12
5	-	1	1	-	61	8	1	1	11	-	11	6
6	-	4	1	5	1	68	-	1	-	3	8	8
7	-	12	17	-	-	-	39	27	2	3	1	-
8	-	2	5	-	-	-	10	79	2	2	-	-
9	-	6	4	-	28	3	-	-	36	-	16	6
10	-	4	1	36	-	6	1	-	-	40	6	6
11	-	2	2	6	3	18	-	-	3	2	36	29
12	-	-	-	3	-	2	-	-	-	-	7	86

Using the parameters specified (see methods), the results acquired by the discriminant function analysis were not clear because the dive shapes were not taken into account when testing the validity of the dive types. It seems that dive types 1, 2, 4, 6, 8, & 12 were largely correctly classified because a high percentage of dives were reclassified by the

discriminant function analysis into the same dive types, than what they were assigned to subjectively.

Possible reasons why the discriminant function analysis misclassified some dives, are as follow:

Type 3 dives were misclassified as Types 2, 7 and 8 dives because of the similar descent and ascent rates and bottom times. Type 5 dives were incorrectly classified as Types 9 and 11 as they have similar maximum dive depths, dive durations, bottom times and slow ascents. Type 9 showed a slow ascent because the interruption in the ascent phase led to a slower mean ascent time. The parameters of Type 11 dives had means similar to those of Type 5 dives, except for the ascent phase. The most important feature of Type 7 dives is the large wiggles occurring during the bottom time. When only the means of each dive parameter are used to distinguish between dive types, wiggles are not accounted for and Type 7 dives can then be confused with Types 2, 3 and 8 dives. As was the case for Type 5 dives, Type 9 dives with a slow mean ascent rate were classified as dive Types 5 and 11. Type 10 dives bear a strong resemblance to Type 4 dives because only the mean descent rate was used and the unique characteristic of an interruption in the descent phases of Type 10 dives was lost with the creation of the statistical file. Type 11 dives also showed two “shoulders” during the descent and ascent phases that resulted in lower descent and ascent rates. As a result of the loss of these special characteristics when averaging descent and ascent rates, these dives were incorrectly classified as Type 12 dives.

3.4 Individual differences amongst males

A summary of the dive types each male used is given in Table 6. Male 360n94 had a unimodal distribution for dive depth with a significant ($F = 5\ 787$, $P < 0.0001$) lowest mean dive depth of 411 ± 203 m for males from Marion Island (Fig 9, Table 3).

TABLE 6. The percentage frequency of occurrence of the 12 dive types for eight male southern elephant seals.

Male no.	Dive Type											
	1	2	3	4	5	6	7	8	9	10	11	12
335a94	0.4	1.0	30.3	16.6	3.7	2.1	41.2	0.9	0.7	0.6	0.4	2.1
335n94	0.7	0.6	32.8	16.6	1.9	1.2	42.0	0.3	0.8	0.9	0.4	1.8
031n93	0.3	5.1	19.9	16.0	1.2	0.7	33.5	20.0	0.4	0.8	0.3	1.9
360n94	1.8	9.3	12.3	7.7	0.4	2.6	58.3	0.2	2.0	2.4	1.9	1.0
1453	4.2	12.2	17.9	1.7	4.9	0.0	10.1	43.7	2.0	0.7	0.3	2.2
1475	0.4	3.2	23.7	13.9	1.0	0.0	14.4	41.2	0.5	0.5	0.2	0.8
1963	0.8	14.0	13.5	8.9	1.2	0.0	6.7	52.2	0.6	0.2	0.1	1.7
1969	0.2	3.8	18.7	3.4	0.3	0.0	9.7	60.7	0.4	0.6	0.2	2.1

This male had the highest frequency of occurrence of Type 2 and 7 dives and the lowest frequency of occurrence of Type 3 dives of all studied males (Table 6). The frequency distributions of the dive depth for male 335 were unimodal during the post moulting as well as the post breeding season and it dived on average only 42 m deeper ($F = 5787$, $P < 0.0001$) and 0.6 min longer ($F = 2790$, $P < 0.0001$) after the moult. The percentage occurrence of the 12 dive types for the post-moulting season approximated that of the post-breeding season for this seal (Fig. 6). Seal 031n93 dived the deepest and longest of

all males with a mean dive depth of 923 ± 444 m and a mean dive duration of 36.6 ± 7.3 min (Table 3). This seal regularly dived beyond the measurable depth of the GLTDR and the mean and maximum dive depths are even deeper than that recorded. It was also the only seal that showed a bimodal distribution for dive depth (Fig. 9). Males 1963 and 1969 never dived deeper than 900 m and showed the highest preference for Type 8 dives of all males (Tables 3 and 6). Distinct peaks in the frequency distributions of the dive depth were evident for males 1453 (500 - 550 m) and 1475 (450 - 500 m) (Fig. 9). The frequency distributions of dive durations were unimodal for all males and the males from Macquarie Island showed a unimodal distribution for their dive depths (Fig. 10).

3.5. Marion versus Macquarie males

3.5.1 Dive depth-duration ratio

Dive depth and dive duration for both Marion and Macquarie males were positively correlated (Fig. 11). A quadratic relationship ($r^2 = 0.8787$, $\text{dive depth} = -115.65 + 33 \times \text{dive duration} - 0.16 \times (\text{dive duration})^2$) existed between the dive depth and dive duration, when the dive duration was less than 60 min, for the Marion males. Macquarie males showed a linear relationship ($r^2 = 0.9534$, $\text{dive depth} = -9.62 + 18.36 \times \text{dive duration}$) between dive depth and dive duration for dives with a duration of less than 30 min. Dives that exceeded these limits did not show any correlation between dive depth and dive duration.

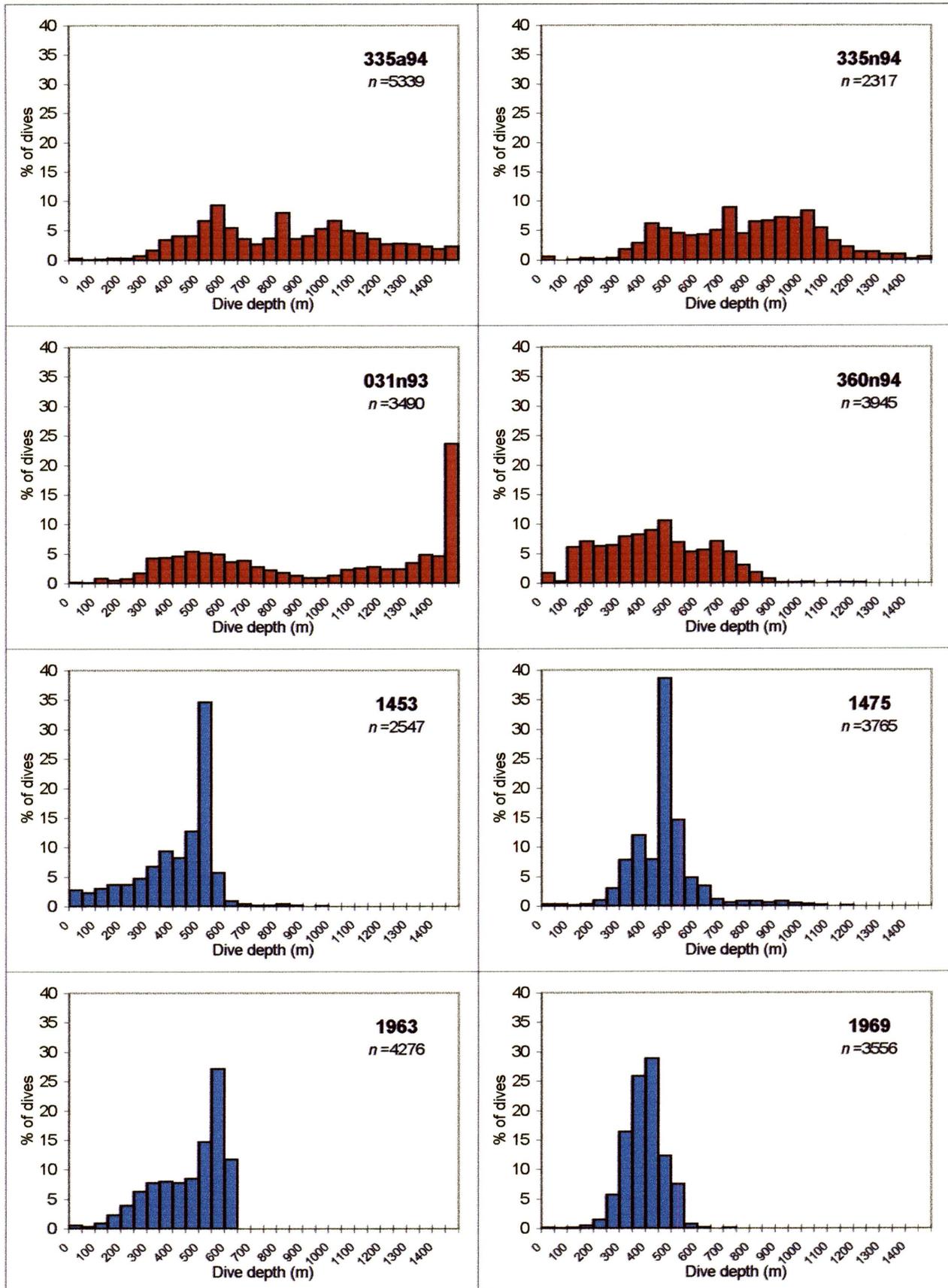


FIG 9. Frequency distributions of the depth of dives for male southern elephant seals from Marion and Macquarie Islands (n = number of dives).

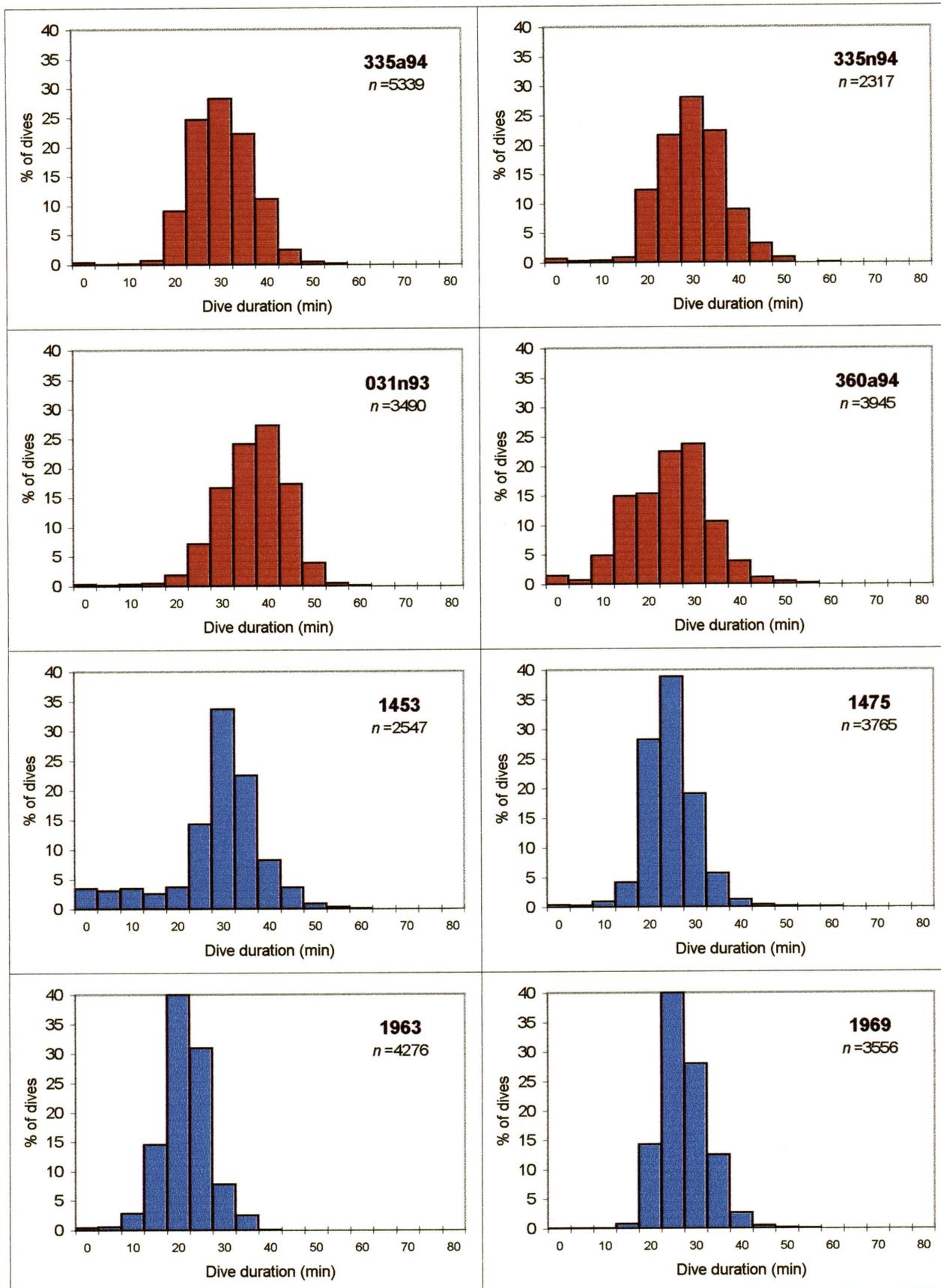


FIG 10. Frequency distributions of the dive durations for male southern elephant seals from Marion and Macquarie Islands. (n = number of dives)

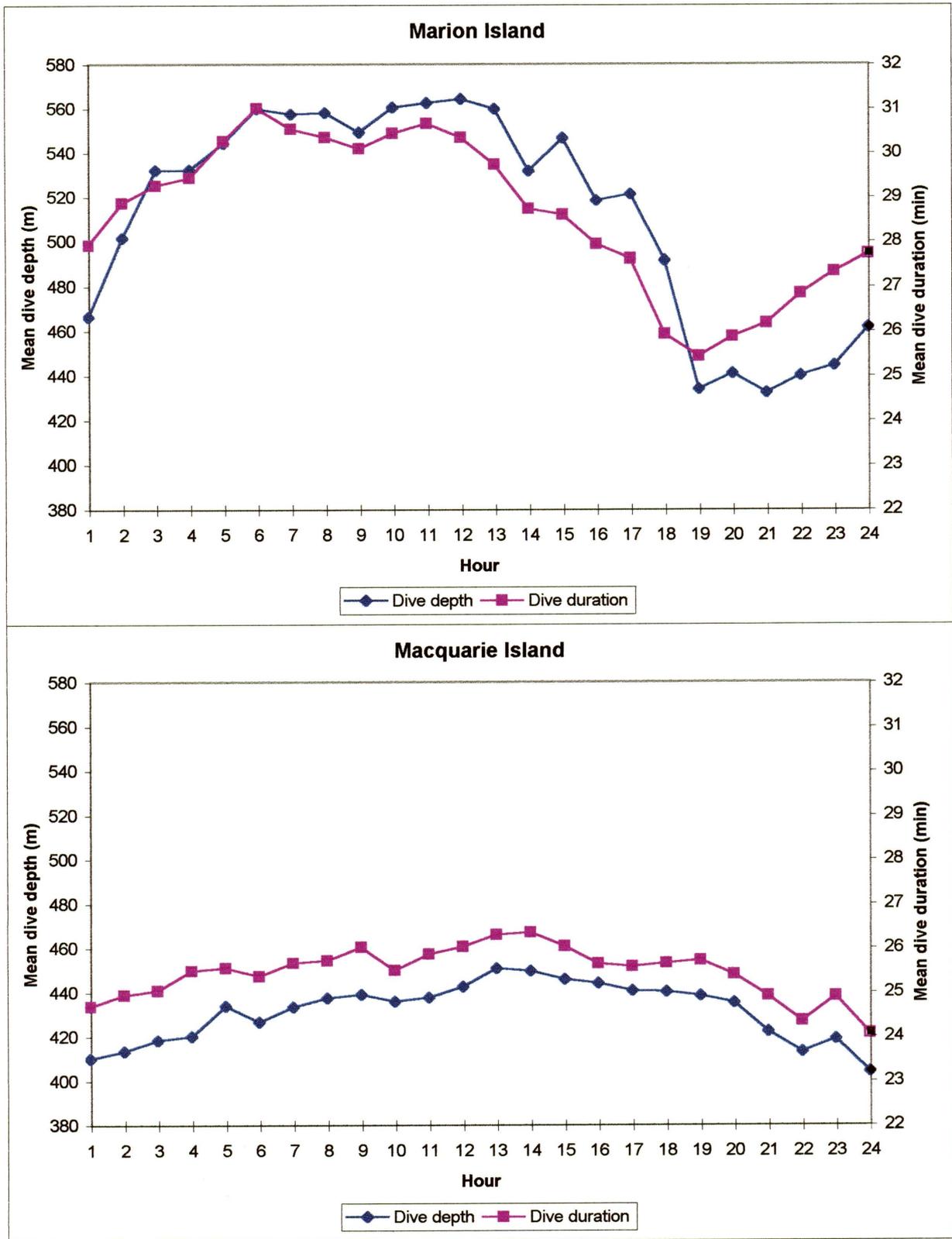


FIG 11. The diel variation in dive depth and dive duration of the four male southern elephant seals from Marion Island and four males from Macquarie Island.

Figure 12 show that Marion males dived over a larger range of dive depths than those from Macquarie Island. Marion and Macquarie males showed significant differences in the frequency distributions of their dive depths ($\chi^2 = 17\ 222$, $df = 29$, $P < 0.001$), dive durations ($\chi^2 = 3\ 544$, $df = 16$, $P < 0.001$) and surface intervals ($\chi^2 = 1\ 570$, $df = 20$, $P < 0.001$) (Fig. 11). Marion males dived significantly deeper ($F = 581$, $P < 0.0001$), longer ($F = 1\ 072$, $P < 0.0001$) and had significantly longer bottom times ($F = 301$, $P < 0.0001$) than those from Macquarie Island (Table 3). The Macquarie males dived significantly faster ($F = 436.30$, $P < 0.001$) due to the shorter dives but no differences in the post dive surface intervals (< 10 min) ($t = 0.0873$, $df = 1$, $P > 0.05$) between males from the two islands were found. (Tables 2 and 3).

3.5.2 Dives types executed

There were remarkable differences in the dive types executed by seals from the two different Islands, especially as far as Type 7 and 8 dives are concerned. There appears to be an inverse relationship in the percentage of Types 7 and 8 dives used by males from the Marion and Macquarie Islands (Fig. 13). Marion males showed significantly more Type 7 dives and Macquarie males significantly more Type 8 dives ($\chi^2 = 9\ 473$, $df = 11$, $P < 0.001$). Type 7 dives for Marion males were on average 320 m deeper ($F = 1\ 228$, $P < 0.0001$) and 3.63 min longer ($F = 263$, $P < 0.0001$) than for those from Macquarie Island. The same was true for the Type 8 dives as males from Marion Island dived deeper ($F = 99\ 999$, $P < 0.0001$) and longer ($F = 5\ 518$, $P < 0.0001$) than the Macquarie males when they executed Type 8 dives. The modal dive depth of type 8 dives for the Macquarie males

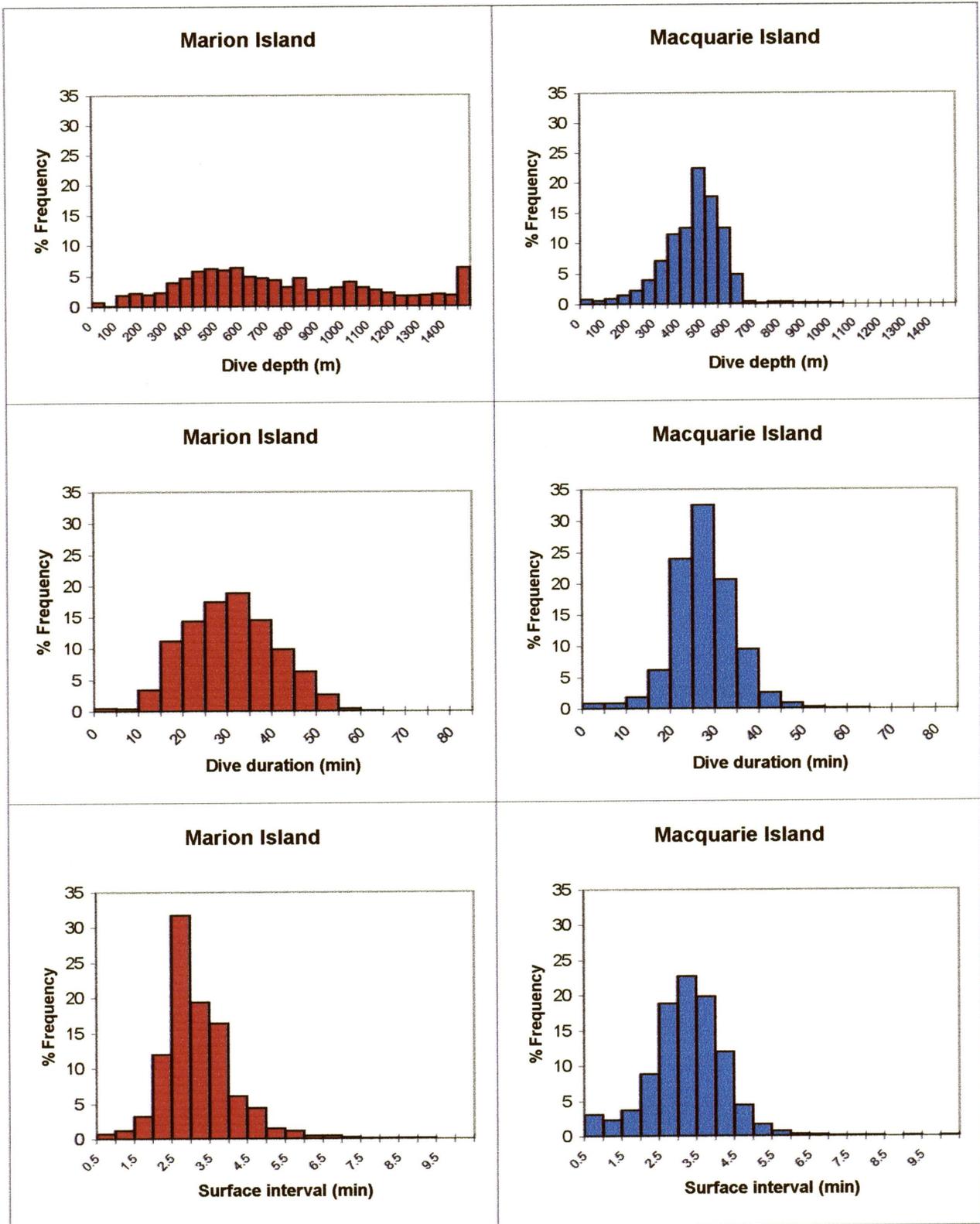


FIG 12. Frequency distributions of all dives of four male southern elephant seals from Marion Island and four males from Macquarie Island showing dive depth, dive duration and post-dive surface interval (<10 min).

was 450 m – 500 m whereas all type 8 dives for the Marion males were in excess of 1440 m (Fig. 14). Other notable differences in the diving behaviour were the Types 3 and 4 dives which were used more by the Marion males, and the Type 2 dives that occurred more in the case of Macquarie males ($\chi^2 = 9\ 473$, $df = 11$, $P < 0.001$) (Fig. 13). The Macquarie males did not execute Type 6 dives (Fig. 13).

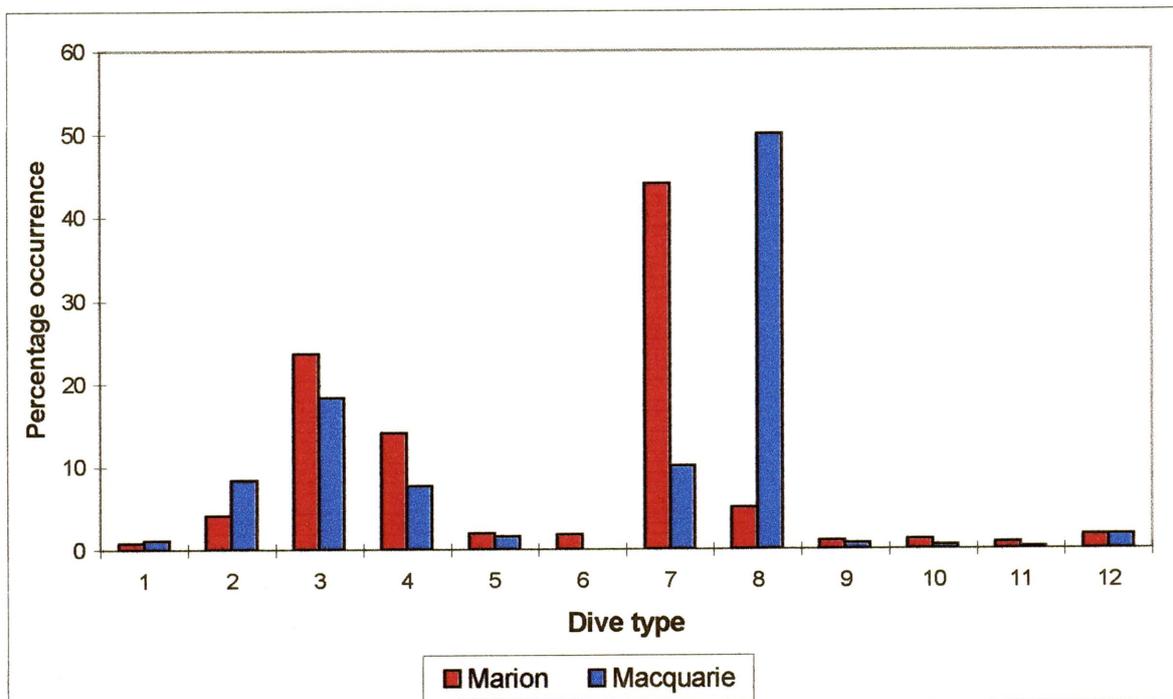


FIG 13. The percentage frequency of occurrence of the 12 dive types for male southern elephant seals from Marion and Macquarie Islands.

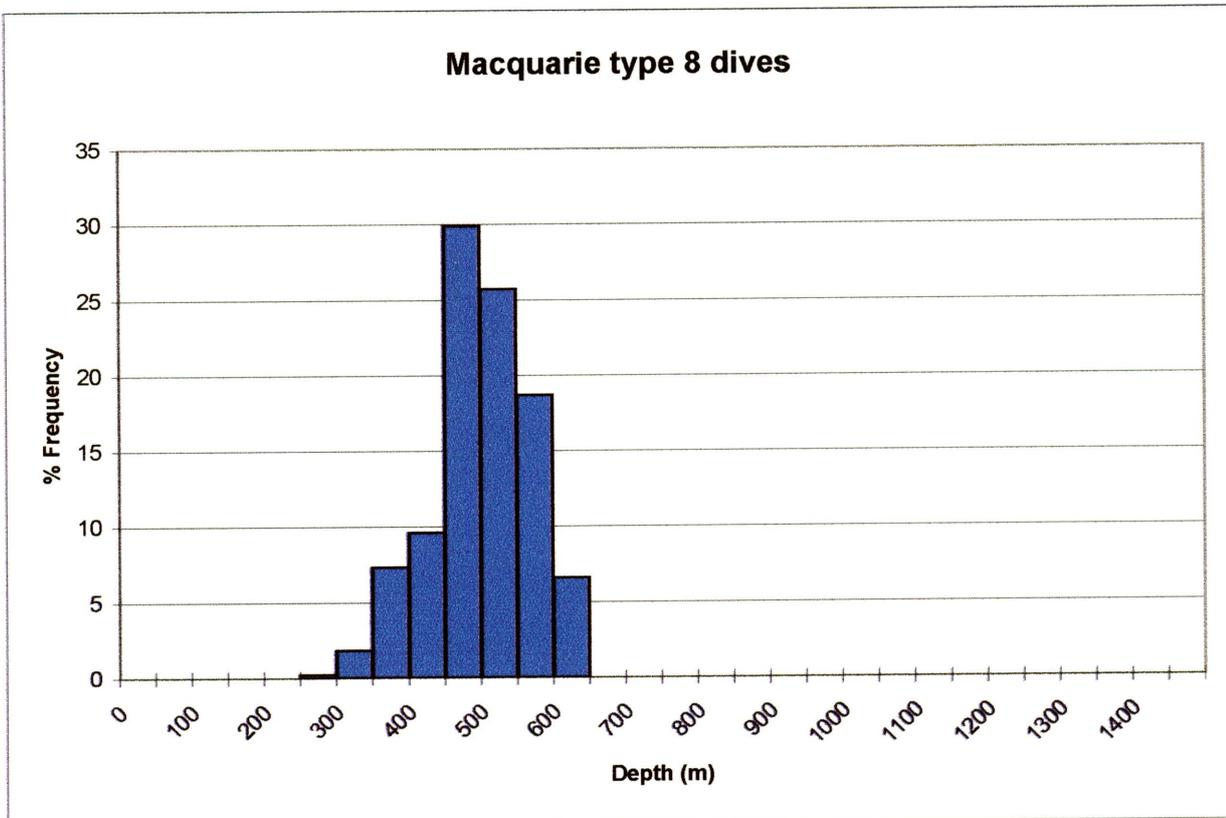
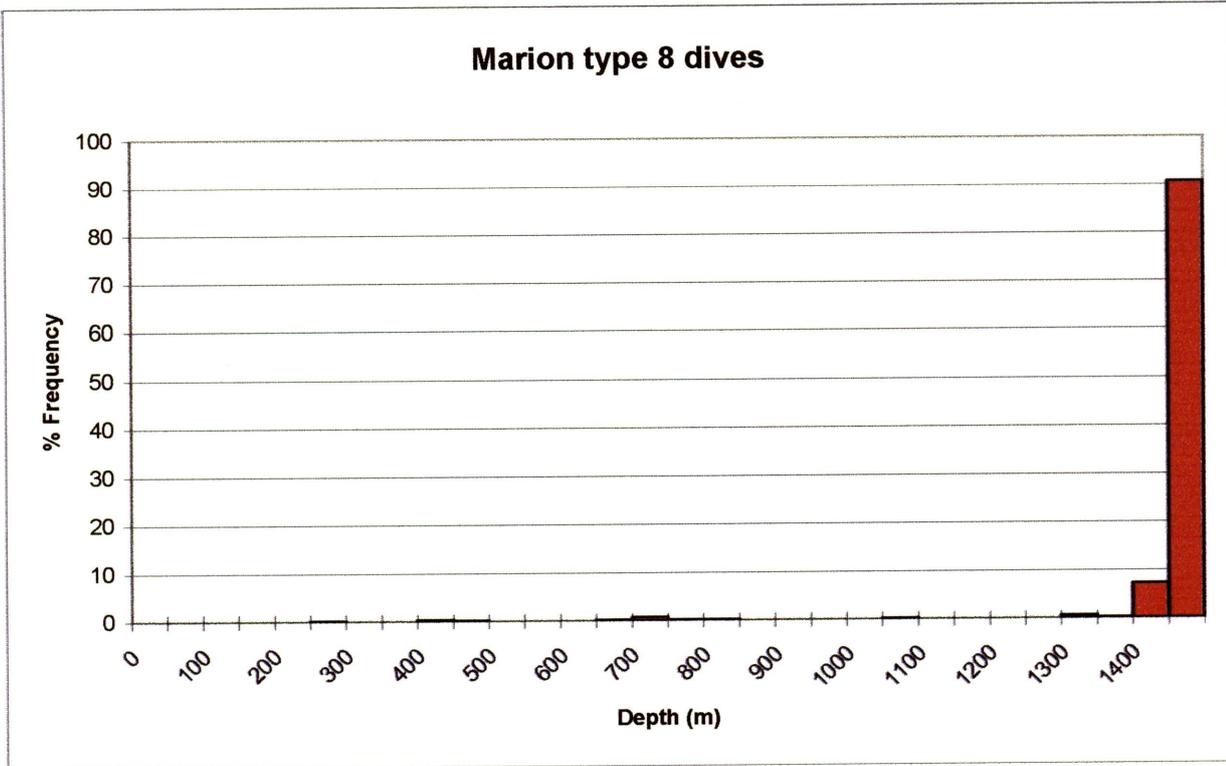
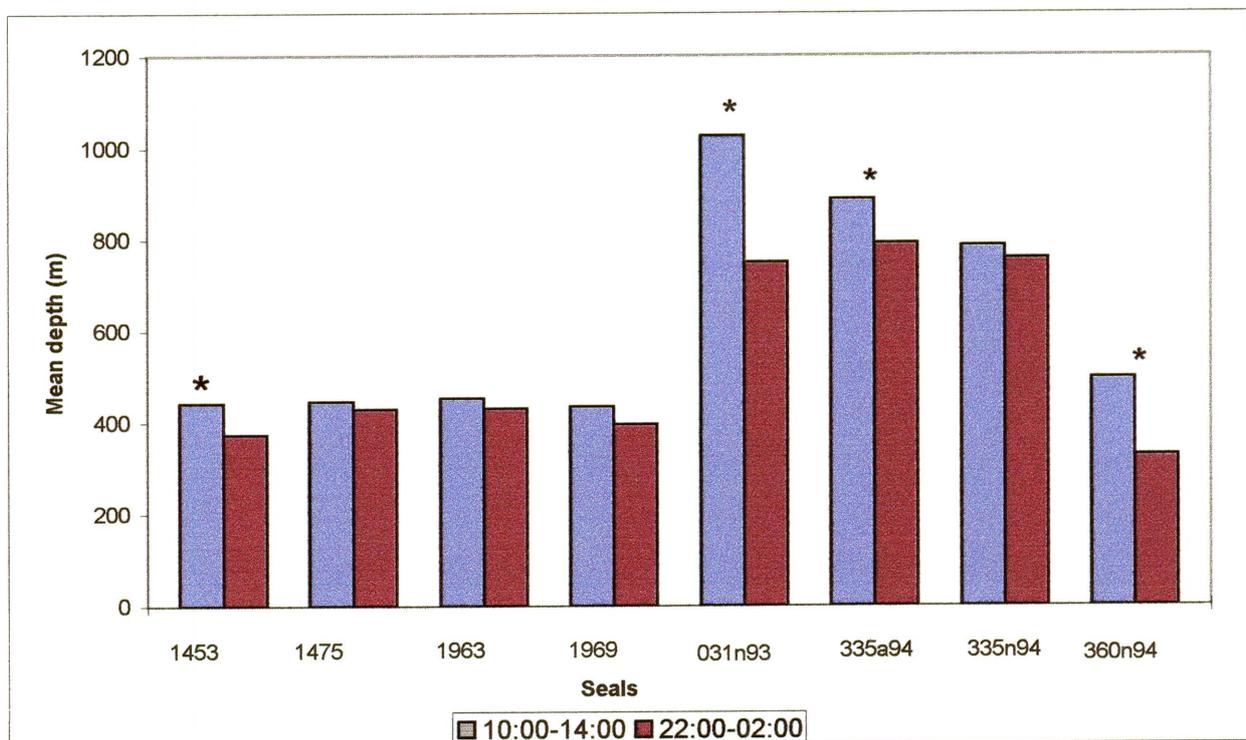


FIG 14. Frequency distributions of the dive depths of Type 8 dives for male southern elephant seals from Marion- and Macquarie Islands.

3.6 Diel patterns

3.6.1 Dive depth

Three of the four males from Marion Island showed diel variations in their dive depth with dives being significantly deeper ($P < 0.05$) during the day (10:00-14:00) than during the night (22:00-02:00) (Fig. 15).



* - Significantly differences ($p < 0.05$) in dive depth between day (10:00 - 14:00) and night (22:00 - 02:00)

FIG. 15. The mean dive depth (m) for day and night dives of each male southern elephant seal.

Male 031n93 had a dive depth-duration diel pattern with dives being deeper during the day than night but with no decline in the dive duration when the seal dived to shallower depths (Fig. 17). The males from Macquarie Island did not show marked diel variations in their dive depths after reaching their foraging grounds, excluding male 1453 which showed a significant diel variation in its dive depth ($F = 177.37, P < 0.05$) (Fig. 15).

3.6.2 Dive types

There were large differences in the percentage frequency of occurrence of the dive types during day and night. Dive Types 2, 4, and 12 occurred more frequently during the night and Types 3 and 8 more frequently during the day (Fig. 16).

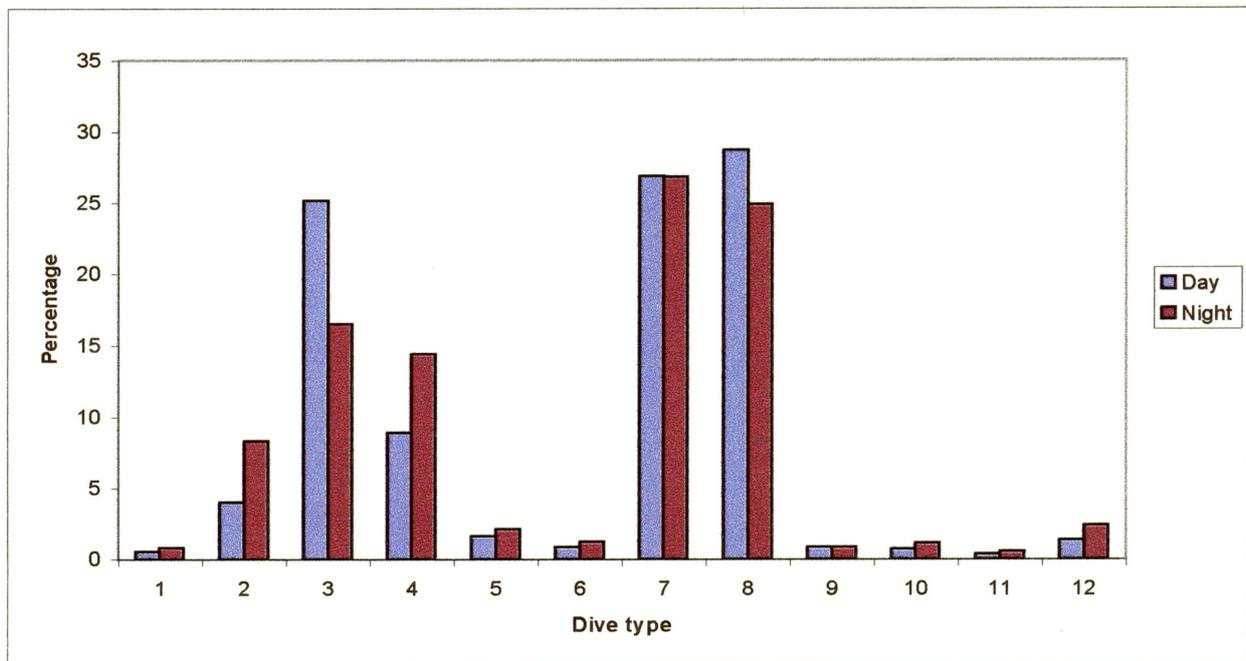


FIG 16. Comparison of the percentage occurrence of the different dive types between day and night.

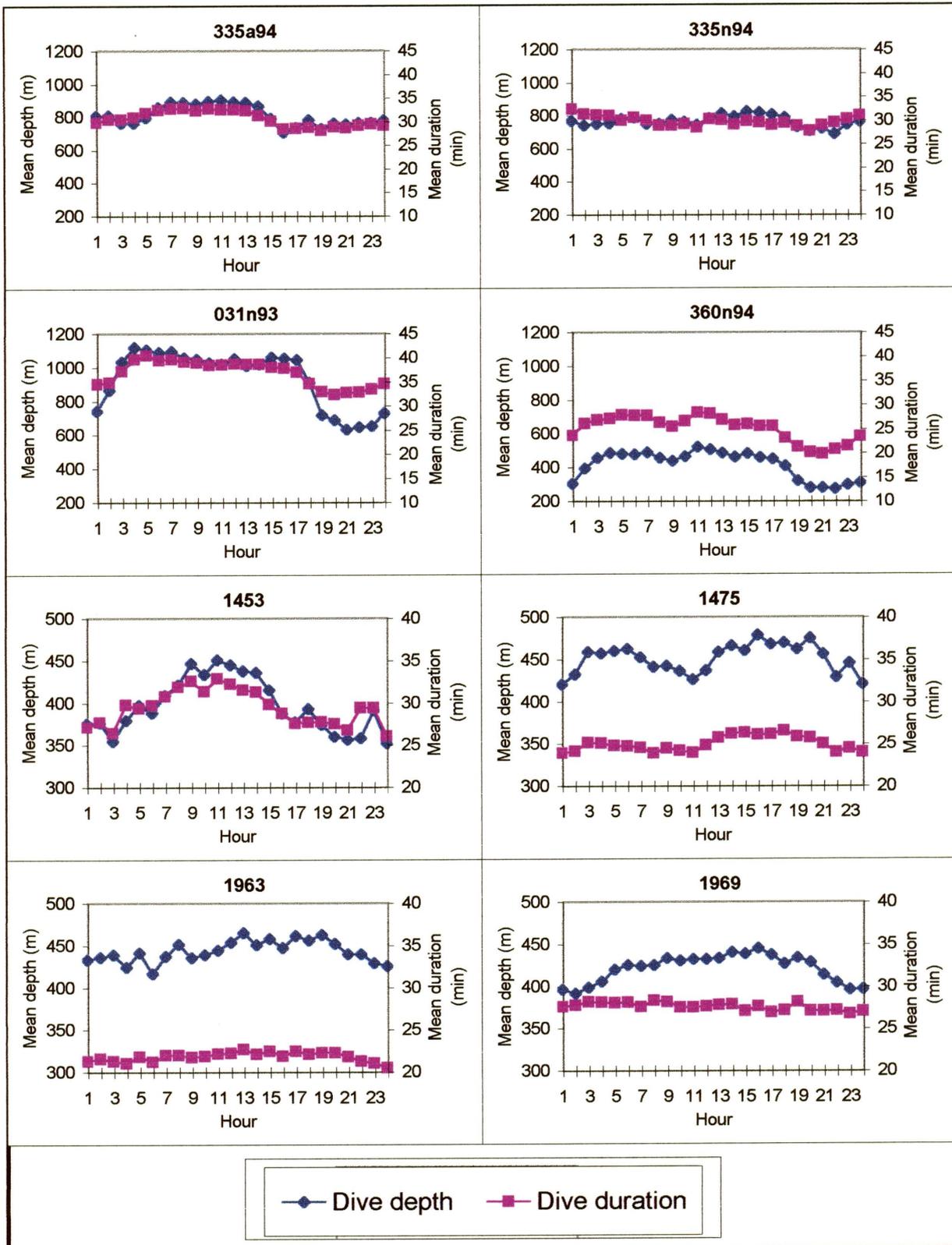


FIG 17. The diel pattern of dive depth and dive duration for eight male southern elephant seals.

All seals showed differences in the percentage frequency of occurrence and depth of their dive types when the percentages and mean dive depths were plotted against each hour of the day. Seal 335a94 showed an inverse relationship between the Types 3 and 7 dives with the Type 3 dives increasing when the Type 7 dives decreased and vice versa (Fig. 18). Type 7 dives were significantly deeper ($F = 83.12$, $P < 0.001$) during the day than during the night (Fig. 19). The depth of Type 7 dives was correlated with the percentage occurrence of Type 7 dives, dives being the deepest during the hours when the percentage frequency of occurrence was the lowest (07:00 - 14:00). Seal 335n94 also showed an inverse relationship in the occurrence of Types 3 and 7 dives (Fig. 20). Type 3 dives occurred more frequently during the day than the night, but there was no diel pattern ($F = 1.58$, $P > 0.05$) in dive depth (Fig. 21). The most pronounced feature was the large increase from 5.88 % to 35.92 % of Type 4 dives between 17:00 - 24:00 (Fig. 20). This increase in the percentage frequency of occurrence coincided with a drop in the mean dive depth which resulted in Type 4 dives being significantly shallower ($F = 26.57$, $P < 0.001$) during the night than the day (Fig 21).

A complex relationship existed between the dive types of seal 031n93. Type 7 dives reached two peaks in frequency of occurrence between 02:00 and 04:00, and around 18:00, respectively (Fig. 22). After 18:00 the percentage frequency of occurrence of Type 7 dives dropped from 49.36 % to a low of 12.27 % at 22:00. Type 8 dives showed a pattern in percentage frequency of occurrence similar to Type 7 dives. The period of decrease (18:00 - 24:00) in Type 7 and 8 dives was correlated with the rapid increase in Type 4 dives. Here Type 4 dives showed an inverse relationship with the Types 7 and 8

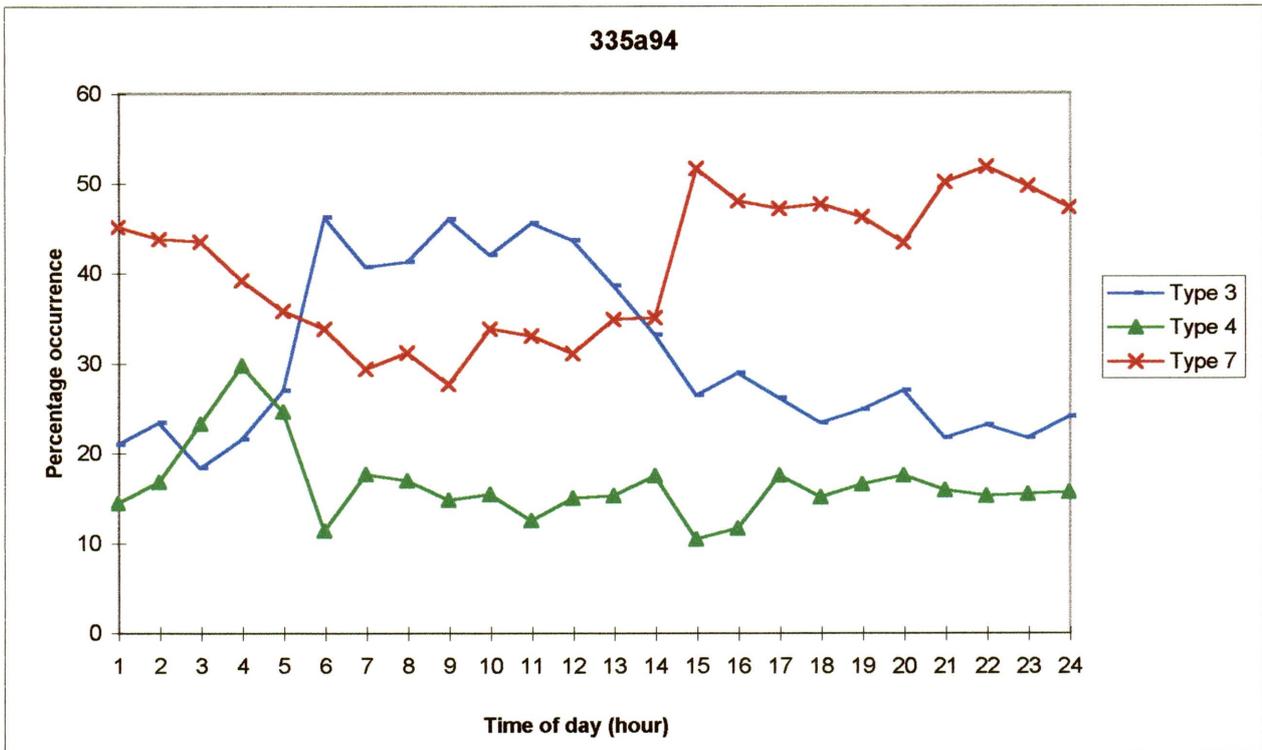


FIG 18. The relationship between Types 3, 4, and 7 dives for each hour of day for male 335a94.

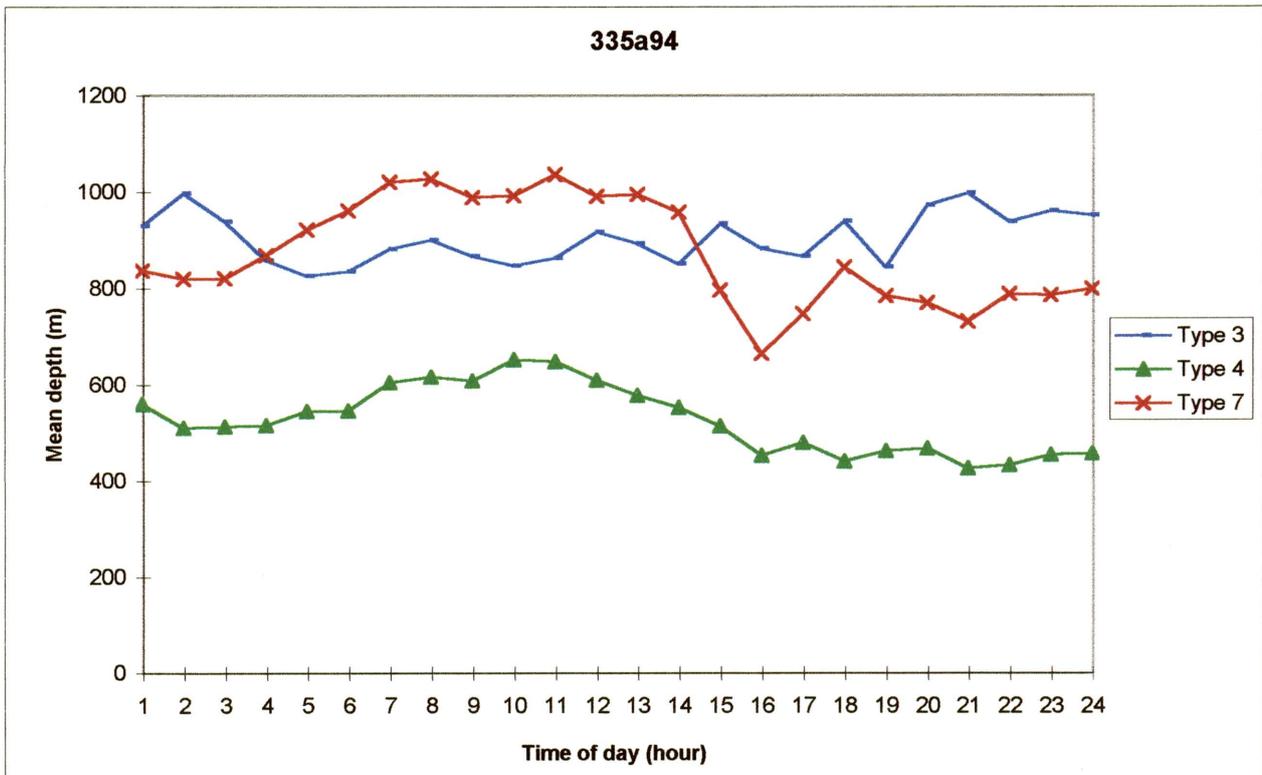


FIG 19. Mean dive depth of Types 3, 4 and 7 dives for each hour of day for male 335a94.

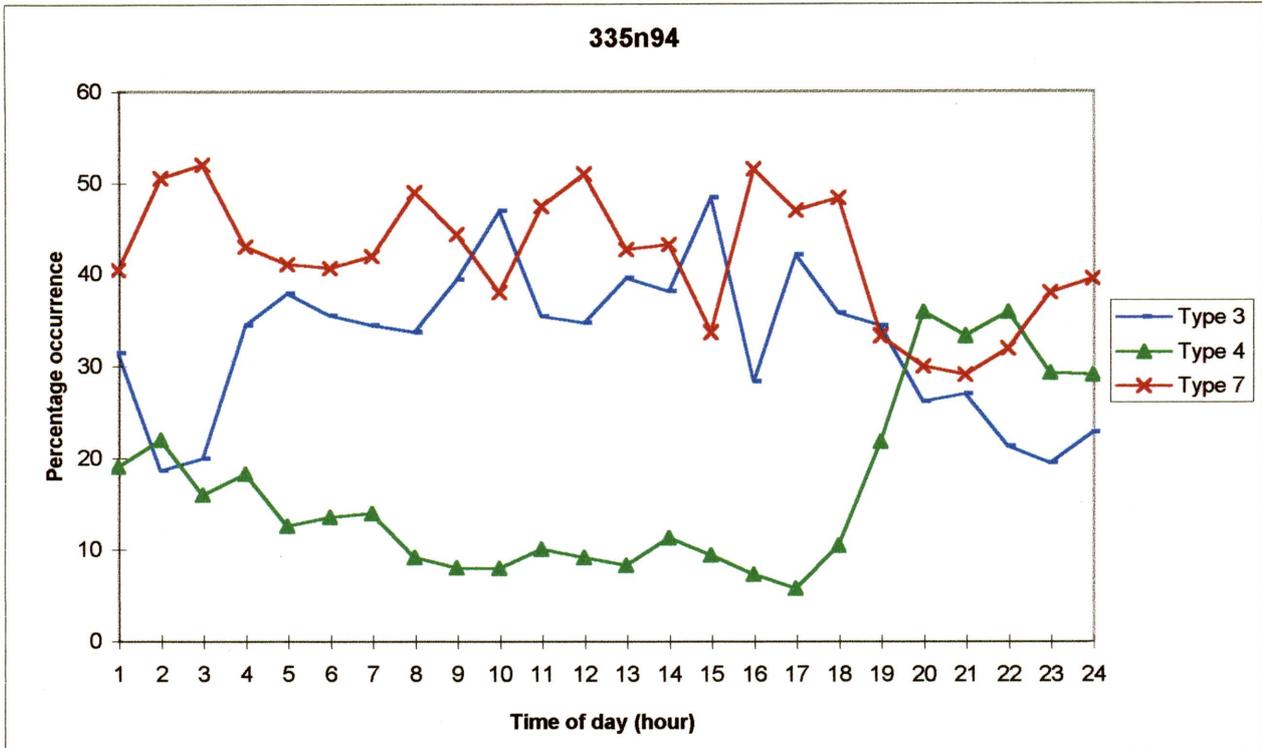


FIG 20. The relationship between Types 3, 4 and 7 dives for each hour of day for male 335n94.

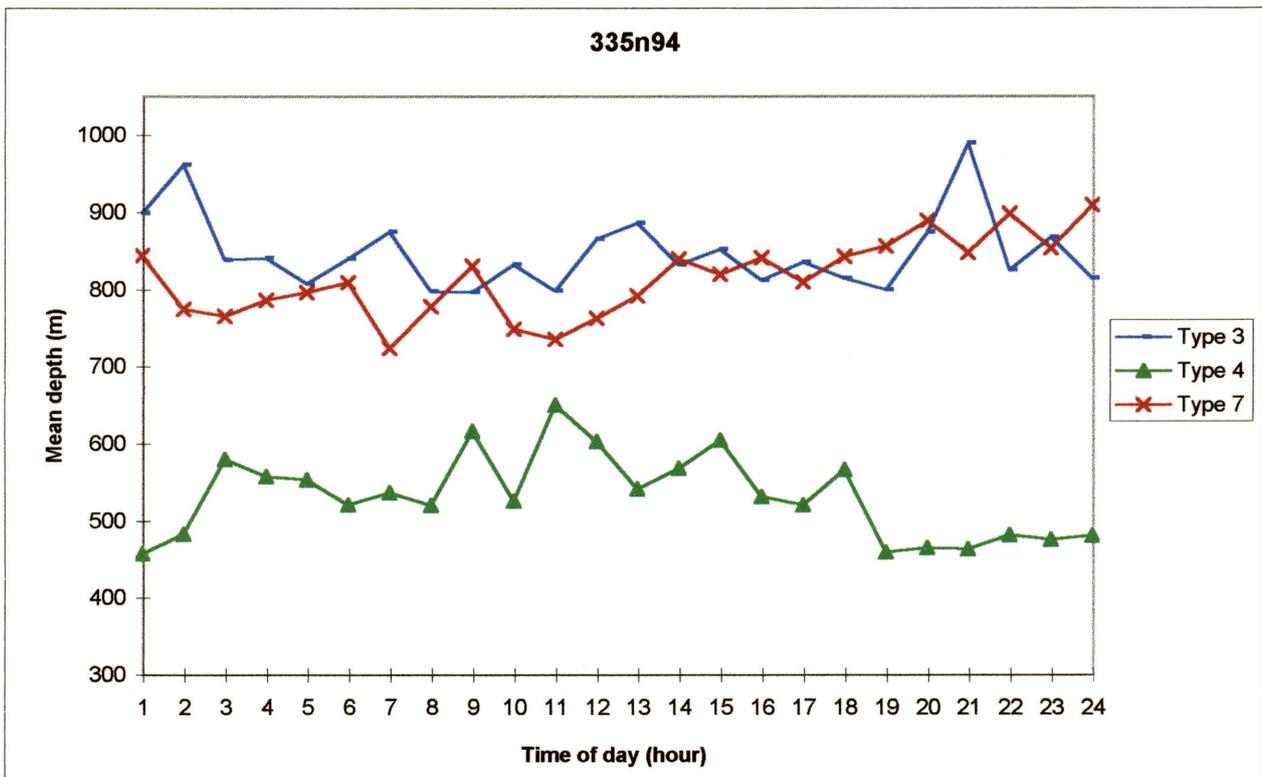


FIG 21. Mean dive depth of Types 3, 4 and 7 dives for each hour of day for male 335n94.

dives (Fig. 21). Both Type 4 ($F = 257.47$, $P < 0.001$) and Type 7 ($F = 39.94$, $P < 0.001$) dives were significantly deeper during the day than night (Fig. 23).

The Type 7 dives of seal 360n94 peaked in percentage frequency of occurrence at 19:00 (75.41 %) and then decreased reaching a low of 40.98 % at 24:00. This decrease in the percentage frequency of occurrence was correlated with an increase in Type 4 dives from 1.09 % at 19:00 to a high of 27.32 % at 24:00 (Fig. 24). A strong diel pattern was evident for Type 7 dives with dives being on average 263 m deeper ($F = 691.83$, $P < 0.001$) during the day than the night (Fig. 25).

Seal 1453 showed a diurnal pattern in the percentage frequency of occurrence of Types 2, 5, 7 and 8 dives (Fig. 26). Types 7 and 8 were more abundant during the day than the night and Types 2 and 5 dives occurred more often during the night than the day. In male 1453 it was only the Type 3 dives that showed a significant difference in dive depth ($F = 14.93$, $P < 0.001$) with dives being the deepest during the day (Fig. 27).

Type 7 dives of seal 1963 showed significant diel differences in dive depth ($F = 8.33$, $P < 0.05$) with deeper dives occurring during the day (Fig. 29). The frequency of occurrence of Type 3 dives executed by seal 1475 increased during the day whereas both Types 7 and 8 dives occurred more often during the night (Fig. 30). Seal 1969 had a higher percentage frequency of occurrence of Type 8 dives during the day than the night (Fig. 32), while Types 3 and 7 dives were deeper ($P < 0.05$) during the day (Fig. 33).

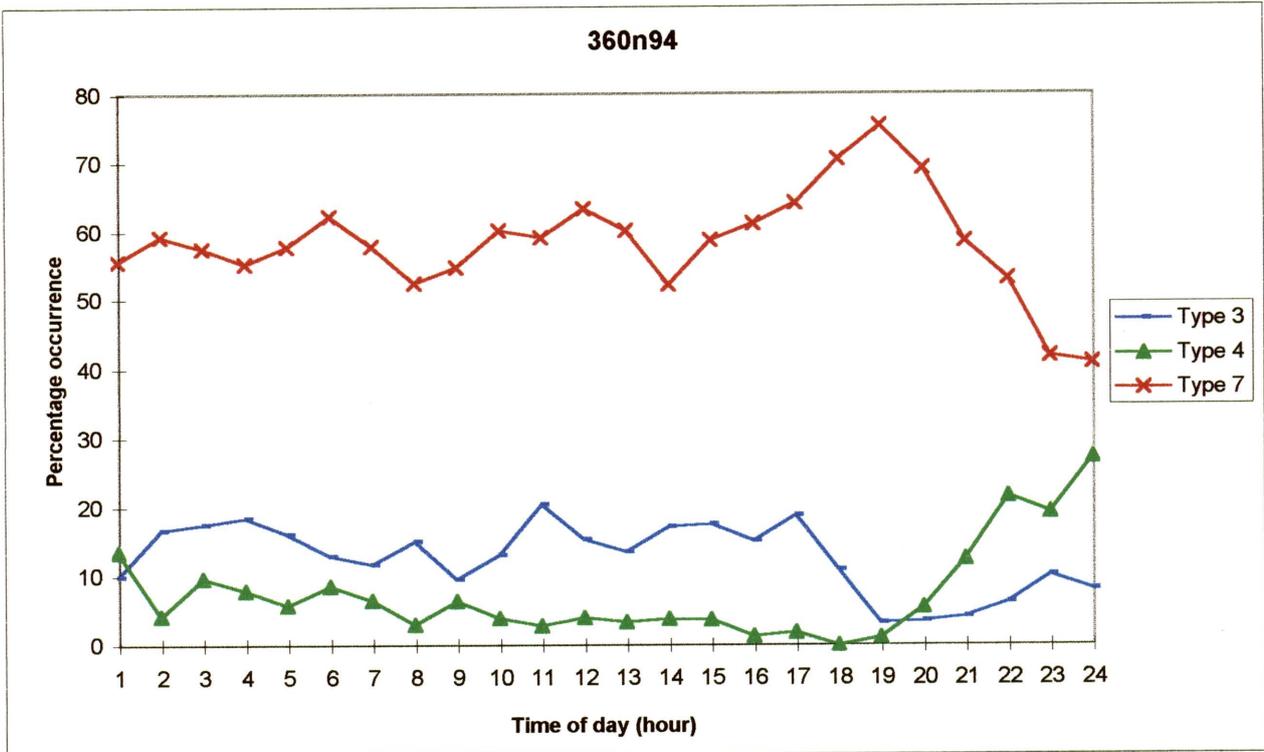


FIG 22. The relationship between Types 3, 4, 7 and 8 dives for each hour of day for male 031n93.

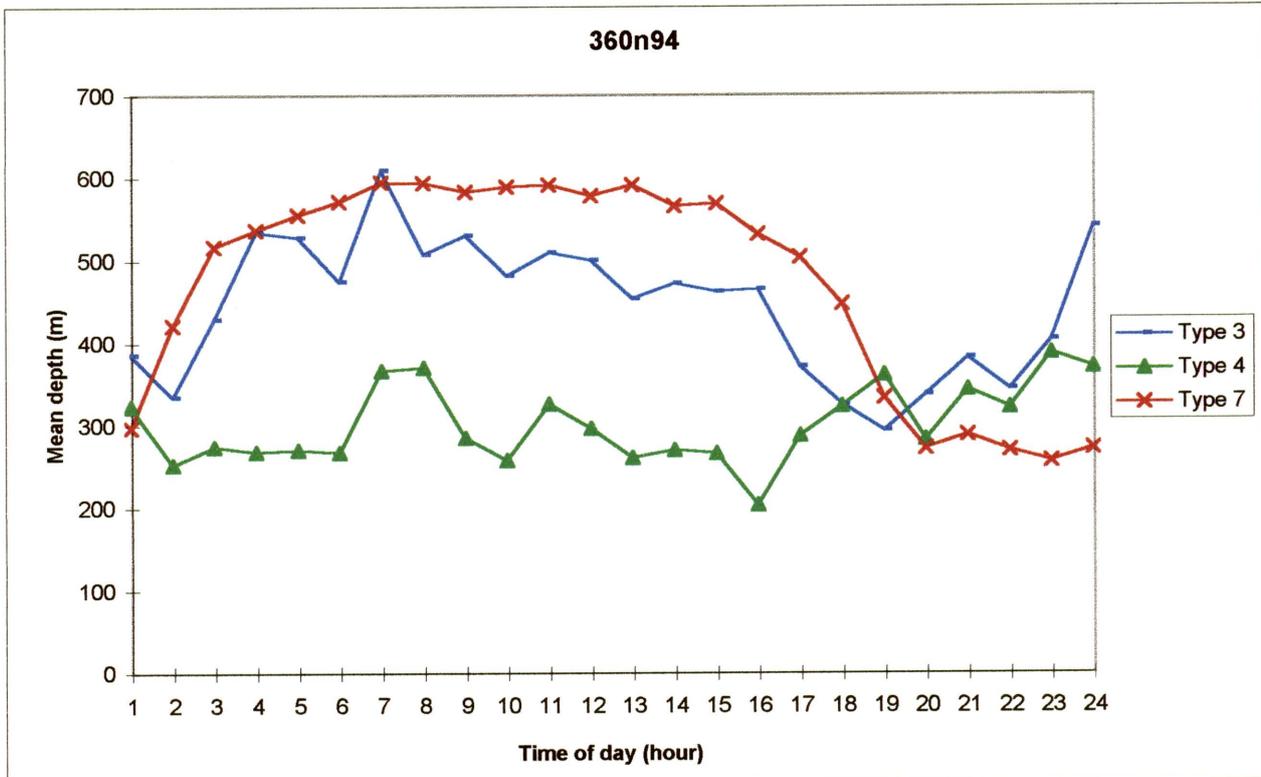


FIG 23. Mean dive depth of Types 3, 4, 7 and 8 dives for each hour of day for male 031n93.

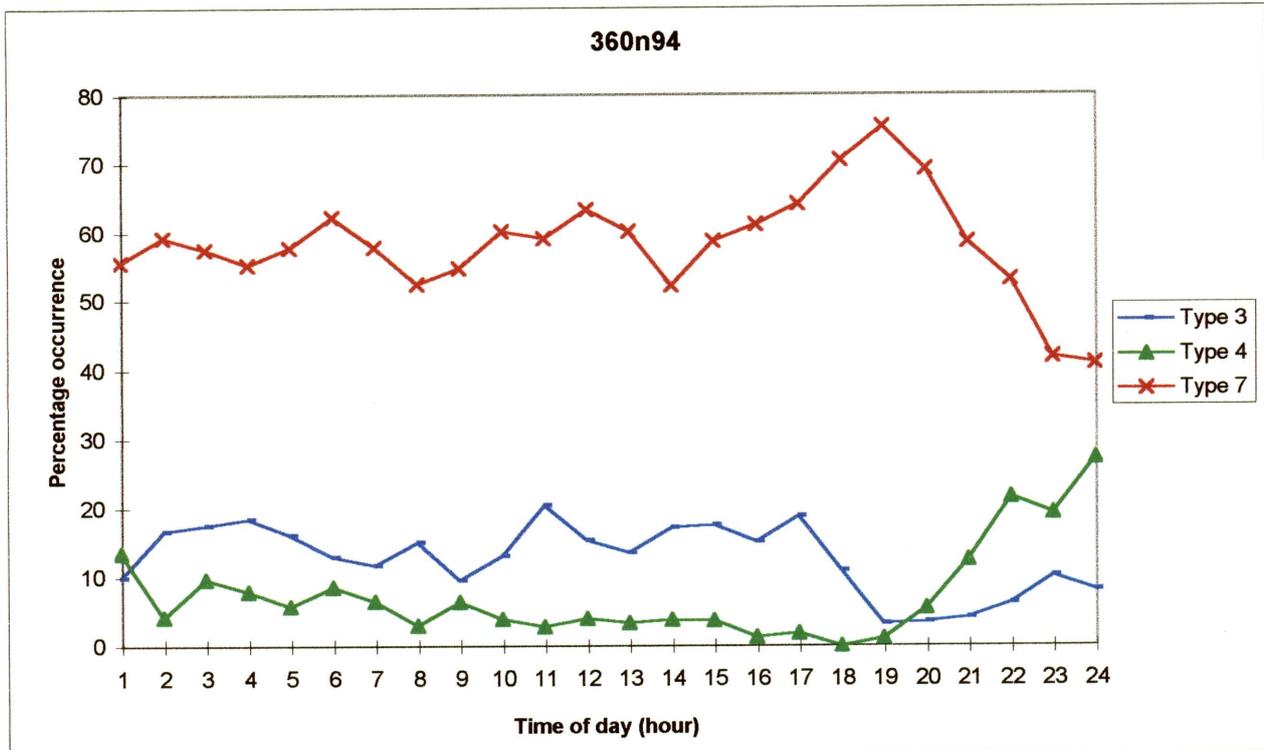


FIG 24. The relationship between Types 3, 4 and 7 dives for each hour of day for male 360n94.

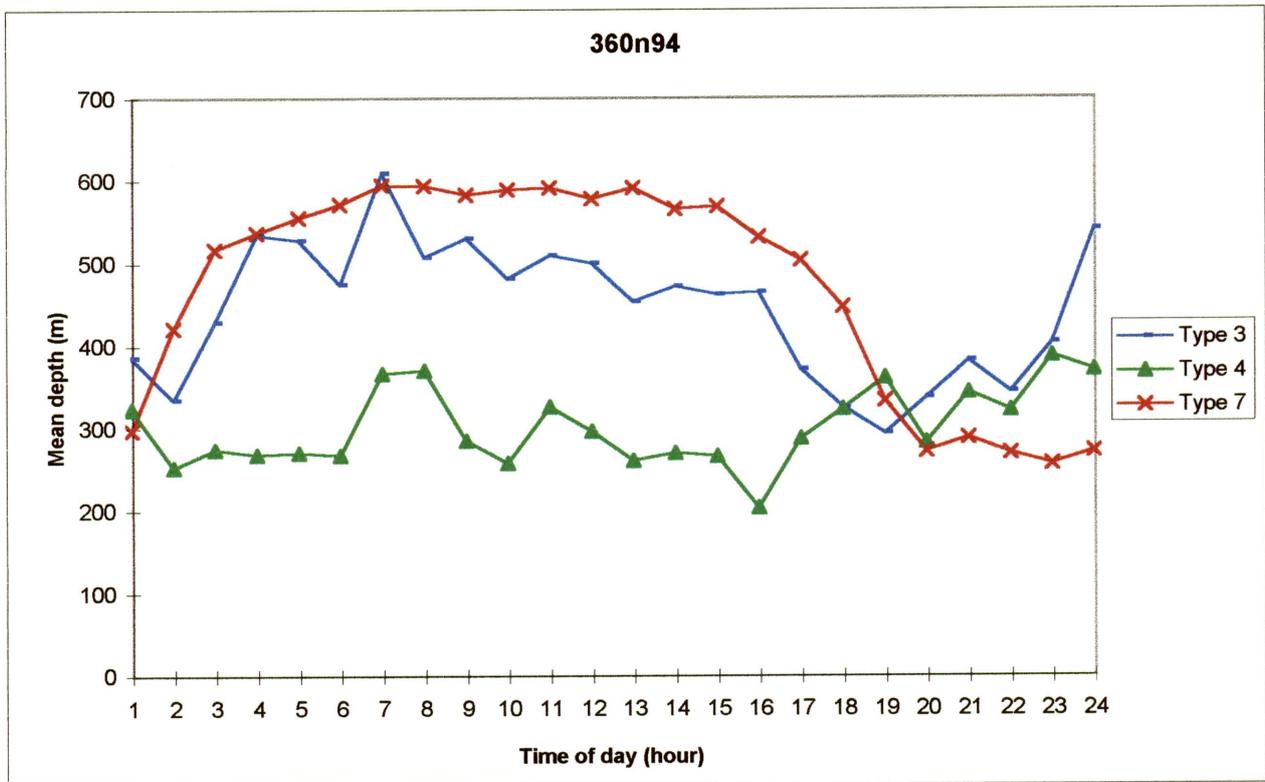


FIG 25. Mean dive depth of Types 3, 4 and 7 dives for each hour of day for male 360n94.

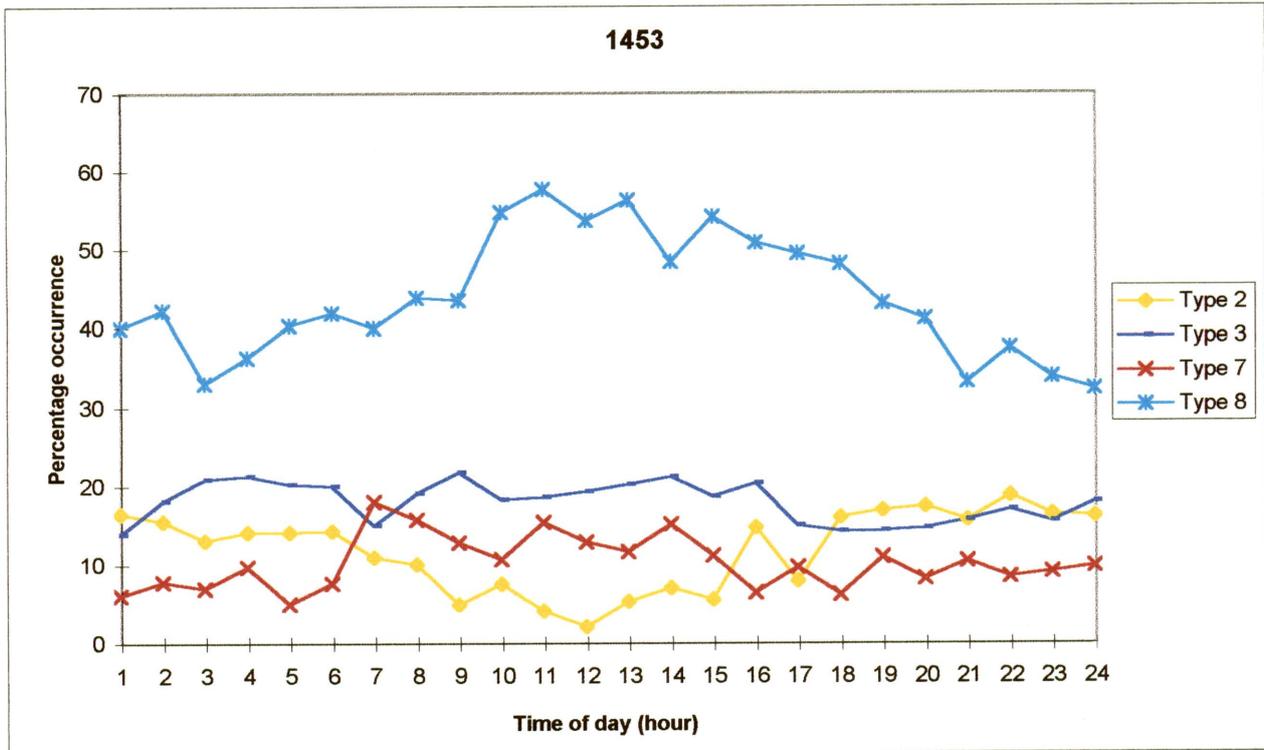


FIG 26. The relationship between Types 2, 3, 7 and 8 dives for each hour of day for male 1453.

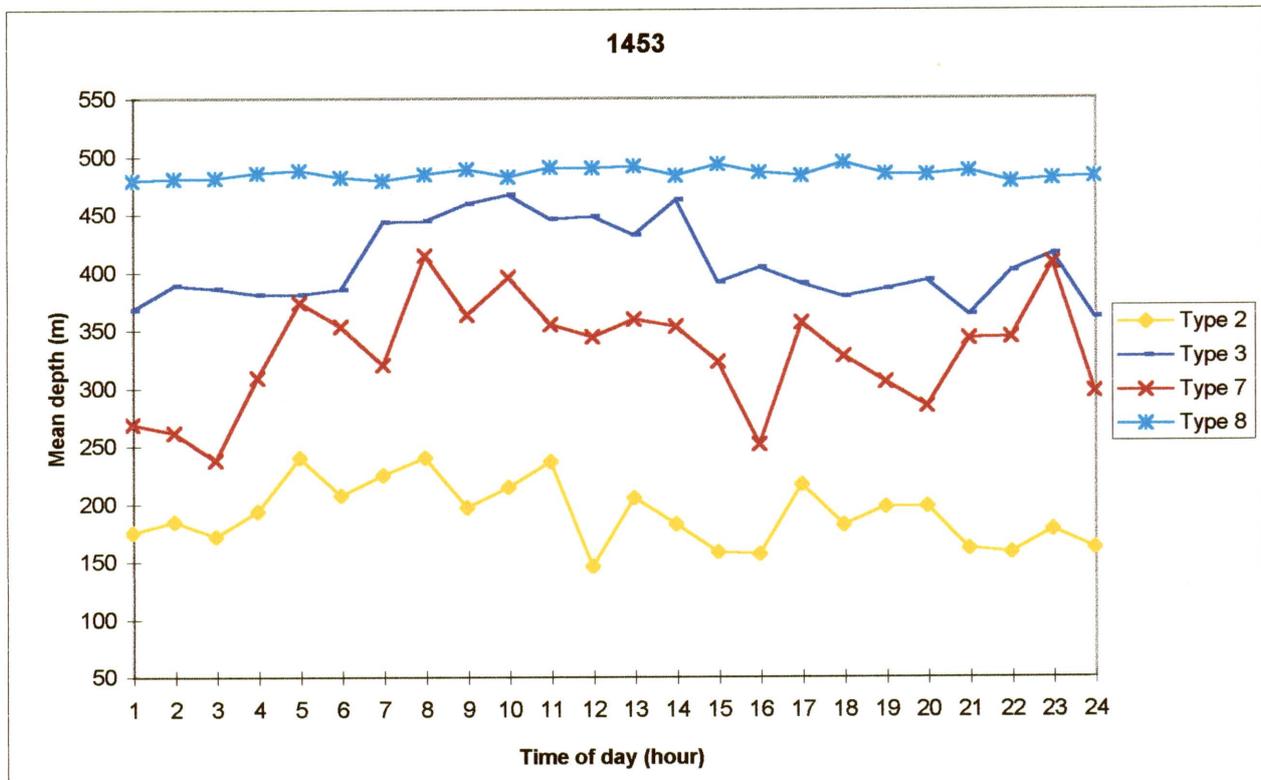


FIG 27. Mean dive depth of Types 2, 3, 7 and 8 dives for each hour of day for male 1453.

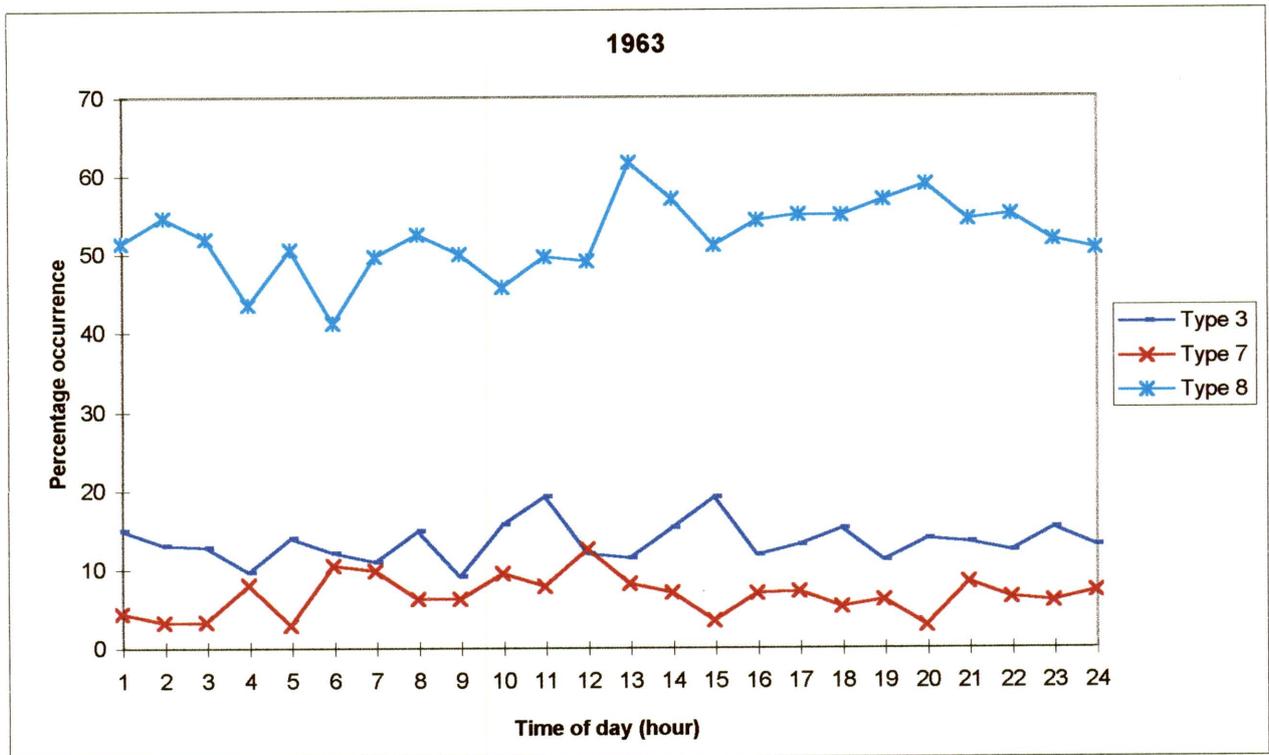


FIG 28. The relationship between Types 3, 7 and 8 dives for each hour of day for male 1963.

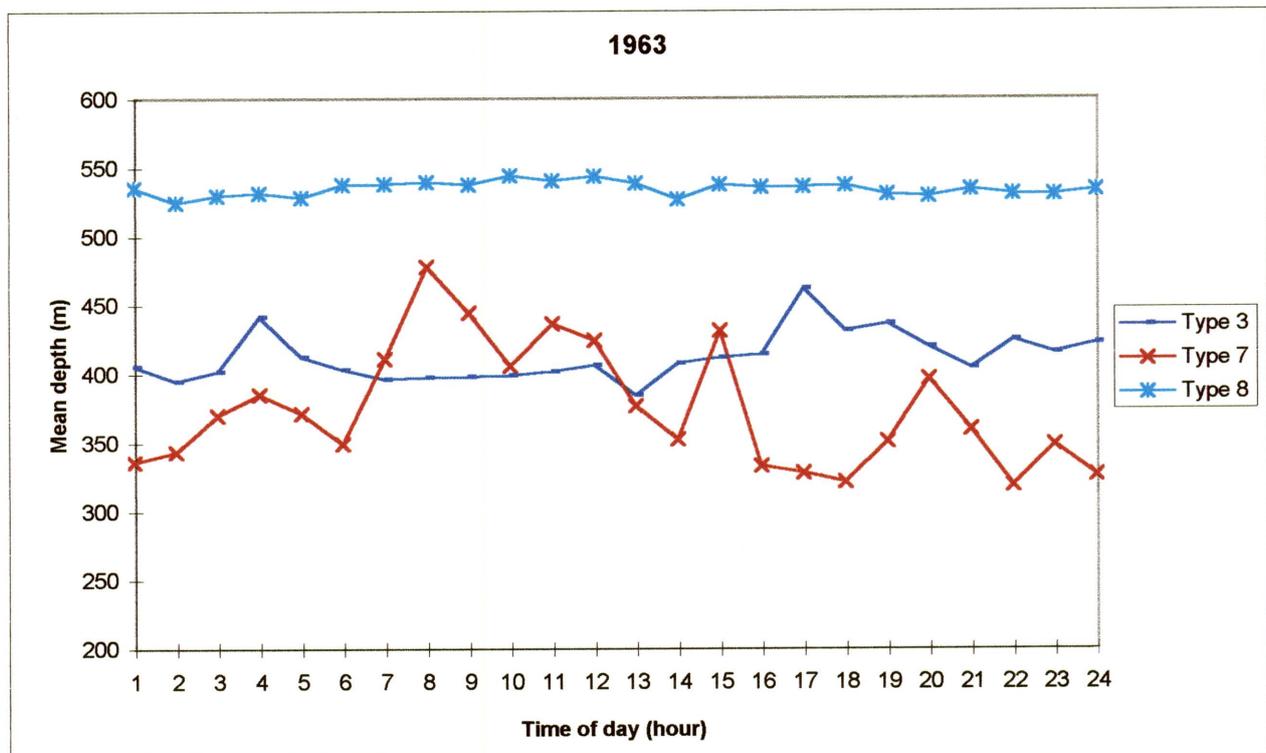


FIG 29. Mean dive depth of Types 3, 7 and 8 dives for each hour of day for male 1963.

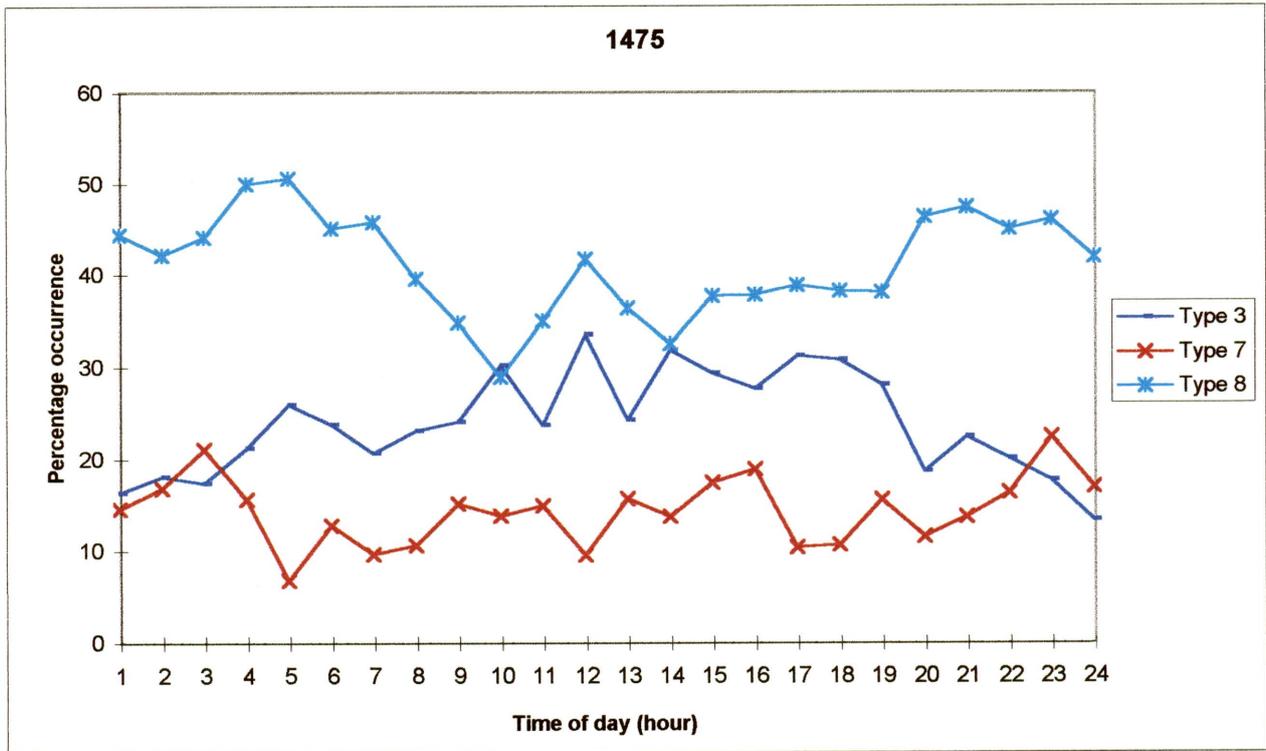


FIG 30. The relationship between Types 3, 7 and 8 dives for each hour of day for male 1475.

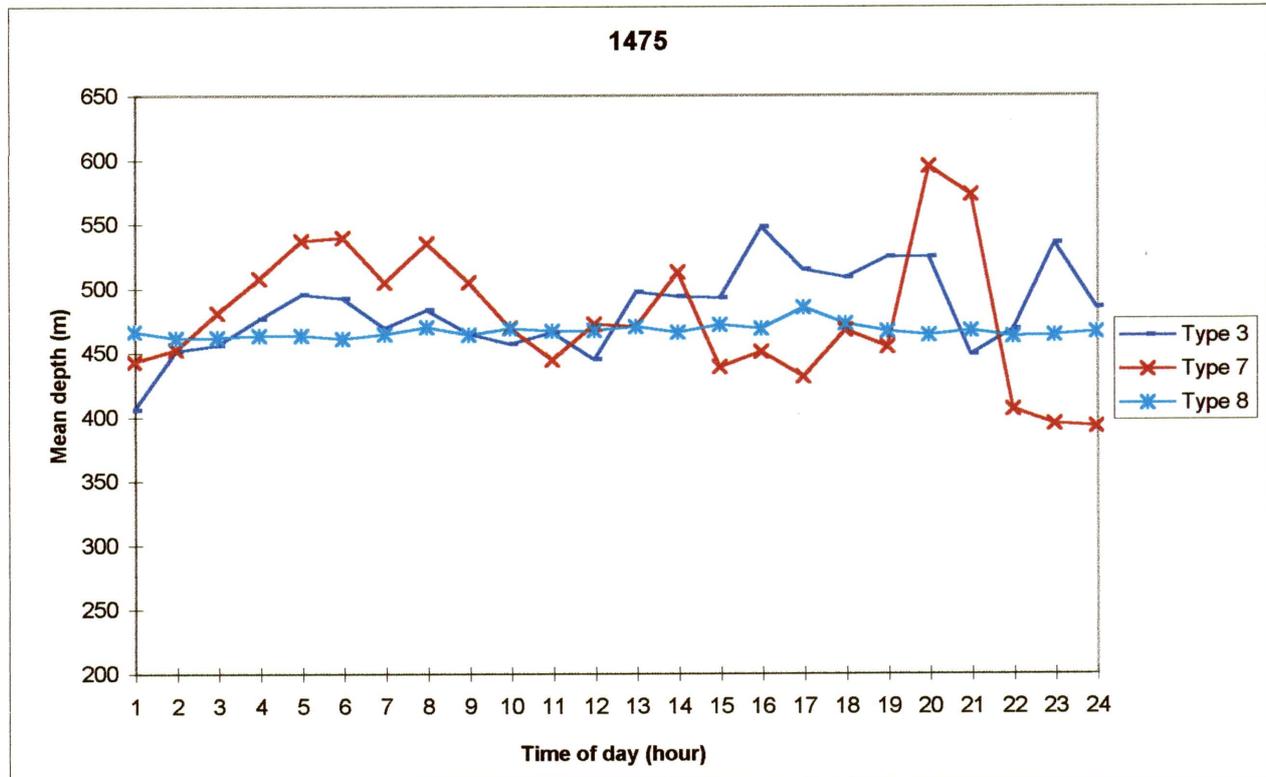


FIG 31. Mean dive depth of Types 3, 7 and 8 dives for each hour of day for male 1475.

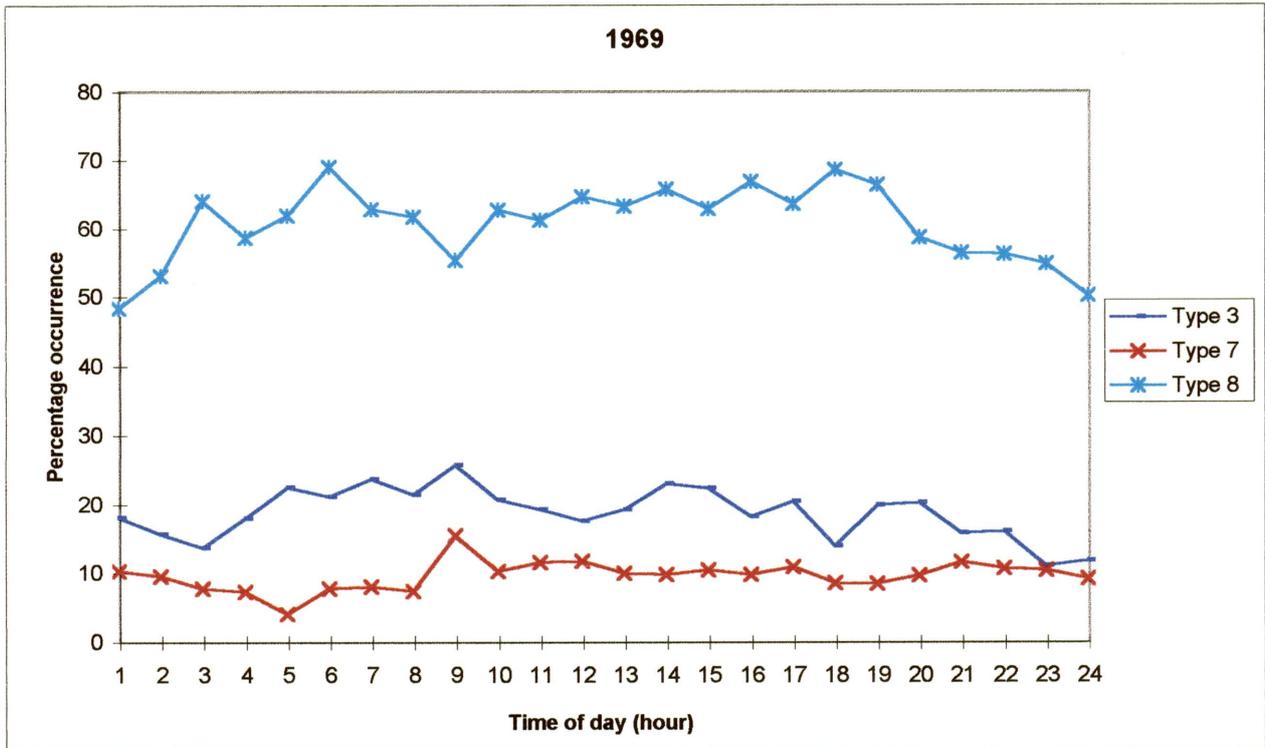


FIG 32. The relationship between Types 3, 7 and 8 dives for each hour of day for male 1969.

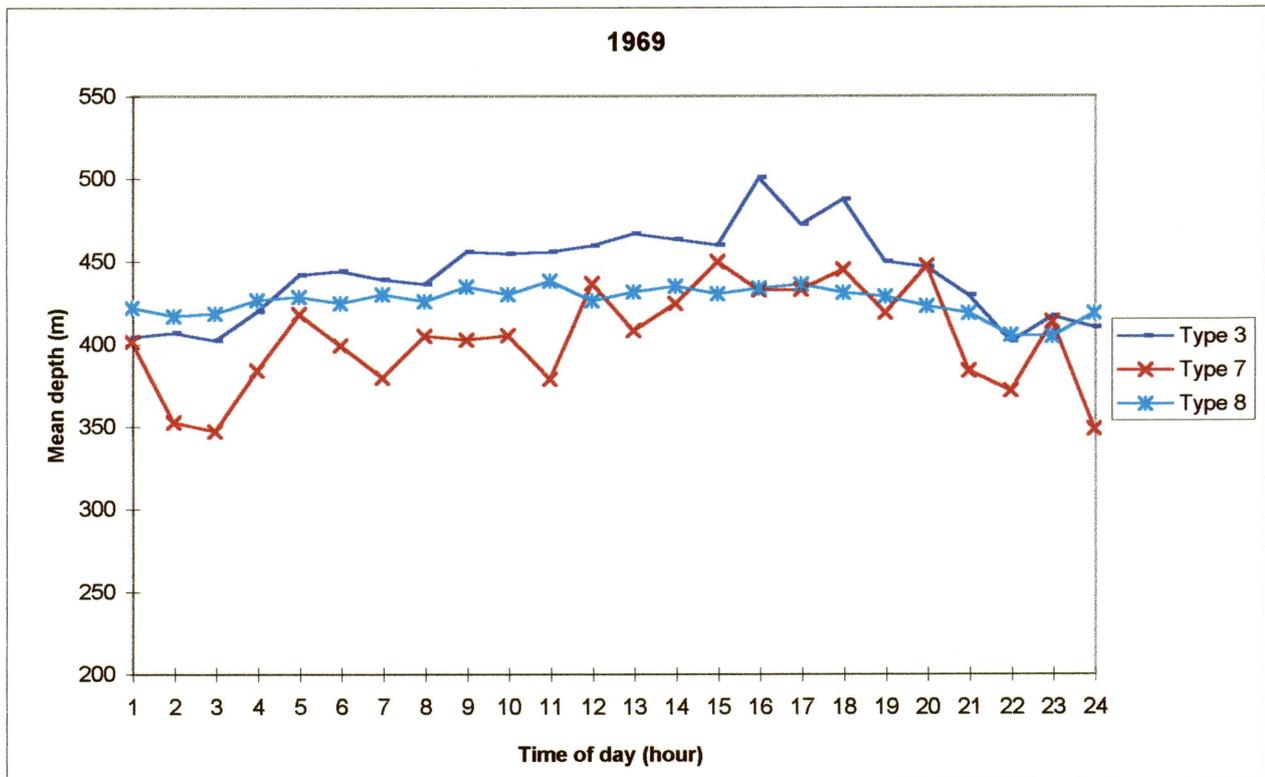


FIG 33. Mean dive depth of Types 3, 7 and 8 dives for each hour of day for male 1969.

The Macquarie males exhibited no relationship amongst any dives when graphing percentage frequency of occurrence of dive types over time of day and all dive types were to uniform depths throughout day and night (Fig. 34 & 35). There was a strong inverse relationship between the type 4 and type 7 dive types of the Marion males. After type 7 dives reached a peak in its percentage frequency of occurrence at 18:00, type 4 dives rapidly increased in percentage frequency of occurrence until 24:00 while the percentage frequency of occurrence of type 7 dives decreased accordingly (Fig. 36). The type 3 dive reached its peak in percentage frequency of occurrence during the day.

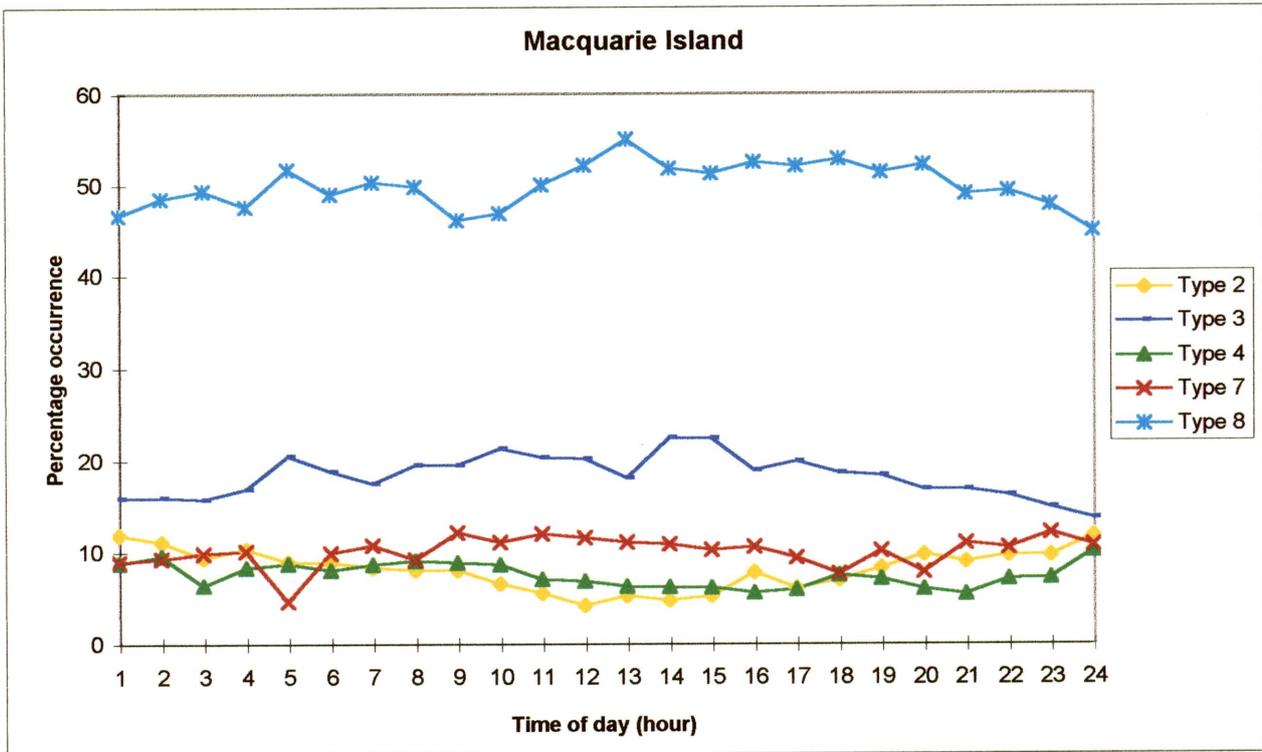


FIG 34. Percentage occurrence of Types 2, 3, 4, 7 and 8 dives for four male southern elephant seals, for each hour of day, from Macquarie Island.

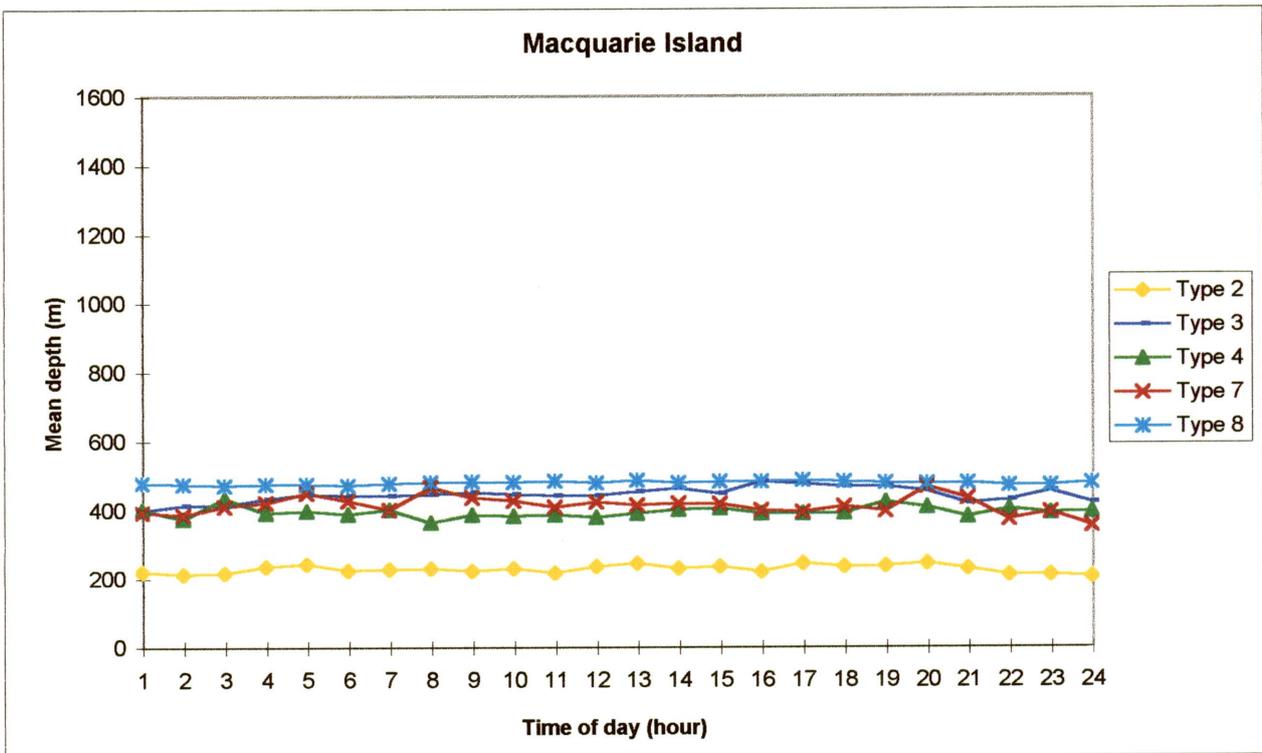


FIG 35. Mean dive depth of Types 2, 3, 4, 7 and 8 for four male southern elephant seals, for each hour of day, from Macquarie Island.

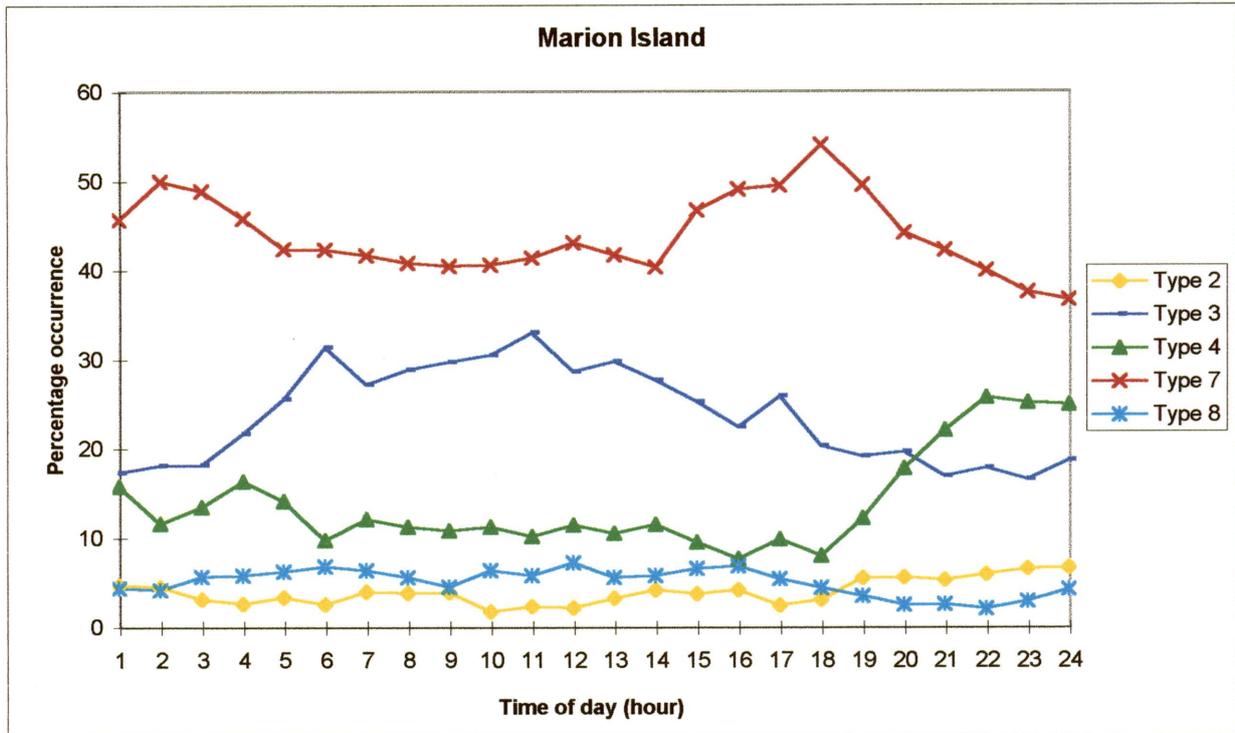


FIG 36. Percentage occurrence of Types 2, 3, 4, 7 and 8 dives for four male southern elephant seals, for each hour of day, from Marion Island.

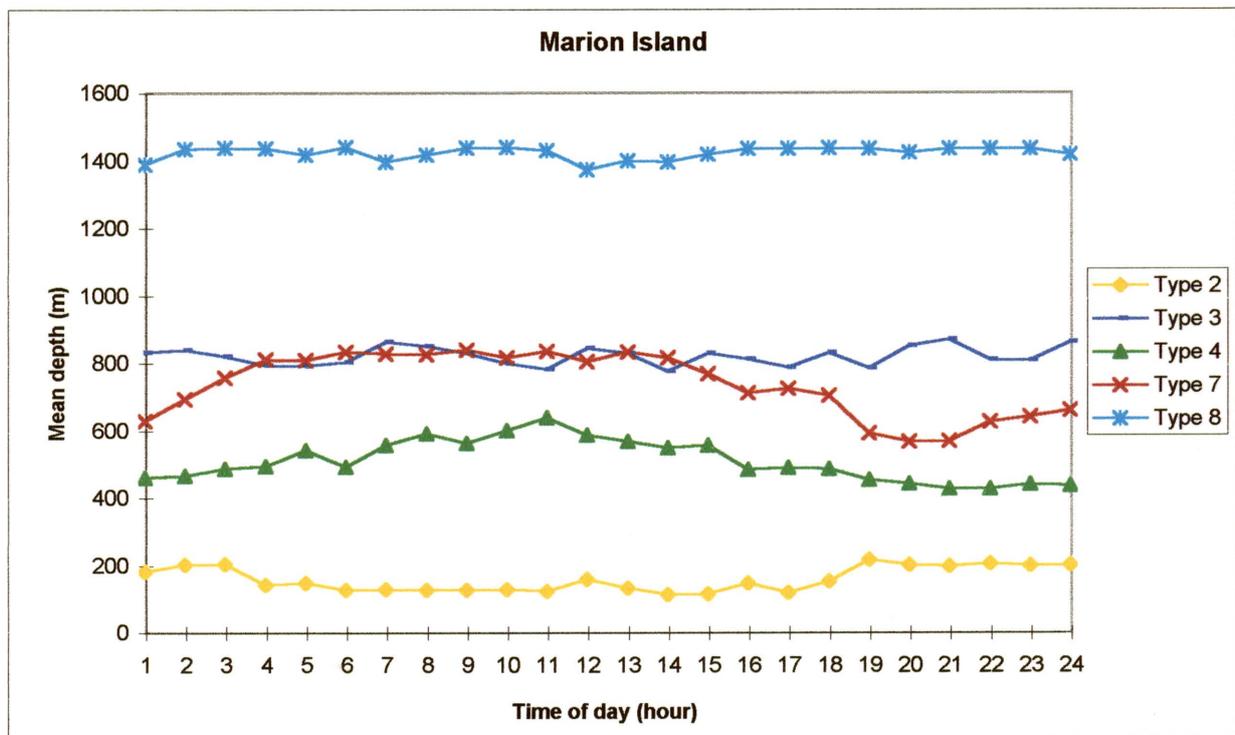


FIG 37. Mean dive depth of Types 2, 3, 4, 7 and 8 dives for four male southern elephant seals, for each hour of day, from Marion Island.

Chapter 4 DISCUSSION

4.1 Ranging behaviour

Male southern elephant seals from Marion & Macquarie Islands utilised different foraging grounds (Fig. 3), and males from a particular Island also foraged in areas with different physical characteristics. These physical differences in characteristics (bathymetry, water temperature etc.) influenced the types of dives performed by the seals. It is argued below that the diving behaviour of each male depended on the habitat the dive was executed in.

Macquarie Island's males experienced the greatest decline in temperature during the first 14-16 days as they moved south at approximately 100-130 km per day to Antarctica (Hindell *et al.* 1991a). While possibly following the Macquarie Ridge, they travelled between 1 500-1 900 km to reach their closest feeding grounds (south of 62 °S) near Antarctica (Fig. 6; Gales & Burton 1989; Hindell *et al.* 1991a). After reaching the 1 000 m depth contour off the Antarctic shelf they remained over the continental shelf break or over the shelf itself until they started their return journey (Hindell *et al.* 1991a). Another colony of southern elephant seals that is known to cover approximately 2 000 km presumably to forage in Antarctic waters is the Iles Kerguelen population (Burton 1985). Unlike the males from Macquarie Island, results for the Marion males suggest that the majority of males remained in relative close proximity to the island (Fig 3 and 4) as hypothesized by Bester (1989) based on a marking / resighting program of the Marion Island elephant seal population.

Male 360n94 foraged over the widest area and range of temperatures of all the Marion males, crossing the APF at approximately 55 °S (Fig. 4 and 5), yet remained within about 1200 km from the Island, which was similar to the 1400 km recorded for postbreeding females (Jonker & Bester 1998). McConnell & Fedak (1996) also found that male southern elephant seals from the South Georgia breeding population also remained in relatively close proximity (\pm 820 km) to the island and even used the island as a base for short trips.

The tracks estimated from light level readings, showed that each of the four males from Marion Island concentrated on a different presumed foraging area (Fig. 4) where these tracks showed slow or stationary phases for some time. McConnell & Fedak (1996) and Jonker & Bester (1998) hypothesised that these periods of reduced travel occur in areas where prey is found.

Elephant seals may use different strategies to locate suitable foraging areas on the continental shelf and the open ocean (McConnell, Chambers & Fedak 1992; McConnell & Fedak 1996). The Macquarie males perhaps used static physical features such as the continental shelf break to locate specific foraging areas and to find high prey densities (*vide* Gales & Burton 1989, Stewart & DeLong 1994, McConnell & Fedak 1996). On the other hand, males from Marion Island that foraged around the island in deep water might have used combinations of oceanographic features, such as sea temperature, mesoscale

frontal systems and salinity gradients to find prey that are likely to be patchily distributed in both space and time (Boyd & Arnborn 1991; McConnell & Fedak 1996).

The foraging areas of male and female northern elephant seals (from California Channel Islands) and southern elephant seals (from Macquarie Island) do not overlap as males travelled the farthest to colder waters (Hindell *et al.* 1991a; Stewart & DeLong 1993; Stewart & DeLong 1994; Stewart & DeLong 1995; Stewart 1997). The opposite was found for the southern elephant seals from Marion Island and South Georgia where the males apparently stayed relatively close to the Islands and the females travelled the farthest (McConnell & Fedak 1996; Jonker & Bester 1998, this study).

Male elephant seals which can weigh up to about 3500 kg are much larger than the females (350 kg) and therefore has a much higher daily energy requirement than females (Boyd, Arnborn & Fedak 1994). Males must therefore be more effective foragers if they are to meet these high energy requirements. Both northern and southern elephant seal females do most of their foraging pursuing pelagic prey in deep waters since benthic dives are rare (Le Boeuf 1988, Jonker & Bester 1994). Because of the larger size of the males, they can take larger prey and may therefore forage on different kinds of prey species than the females (McConnell & Fedak 1996). Males from Macquarie Island forage benthically (Hindell *et al.* 1991b; present study) whilst McConnell & Fedak (1996) and Stewart & DeLong (1994) suggested that pelagic foraging males may feed on larger prey species than the females.

Various stomach samples taken from elephant seals (which only represents the last period of foraging before returning to the islands) suggest that their diet consist of several open-water prey species as well as a wide variety of species living near the sea-bed. The most important open water prey species were several epi- and mesopelagic cephalopods and fish whereas benthic species include bony fishes, cartilaginous fishes, cephalopods and jawless fishes (Condit & Le Boeuf 1984; Rodhouse, Arnborn, Fedak, Yeatman & Murray 1992; Green & Burton 1993; Antonelis, Lowry, Fiscus, Stewart & De Long 1994; Slip 1995). It is still uncertain whether male and female southern elephant seals that display pelagic foraging in deep water feed on the same prey species, however Stewart & DeLong (1994) found that male and female northern elephant seals that foraged in the same areas dived to different depths.

4.2 Diving behaviour

4.2.1 Summary data compared to other colonies

The results in the present study substantiate previous studies showing that elephant seals dive for prolonged periods to great depths spending more than 85% of their time at sea submerged (Le Boeuf *et al.* 1988; Boyd & Arnborn 1991; DeLong & Stewart 1991; Jonker & Bester 1994; Slip *et al.* 1994). The maximum depths that were recorded in this study for two male southern elephant seals of 1 446 m (male 335) and 1 452 m (male 031n93) are the deepest yet measured for male southern elephant seals. Although this falls short of the 1 581 m measured for a male northern elephant seal (Stewart & DeLong 1990), it should be noted that many dives of male 031n93 exceeded the depth limit of the

GLTDR. Measured maximum dive durations of males from Marion (74 min) and Macquarie (80 min) islands approximate the previous maximum durations (77 min) of male northern elephant seals (DeLong & Stewart 1991). The total time spent submerged for *M. leonina* (> 89 %) is slightly higher than that for *M. angustirostris* (< 86 %) (Le Boeuf 1988; Hindell *et al.* 1991b; Campagna *et al.* 1994; McConnell & Fedak 1996). The short post dive surface intervals for seals from both islands in this study indicates that the seals did not exceed their physiological diving limits (Slip *et al.* 1994). This same behaviour, where surface intervals were brief, was found in both northern and other southern elephant seals (Le Boeuf *et al.* 1988; DeLong & Stewart 1991; Hindell *et al.* 1992; Slip *et al.* 1994).

4.2.2 Possible functions of each dive type

Le Boeuf *et al.* (1988) classified the dives of female northern elephant seals into six groups. Hindell *et al.* (1991b) identified six dive types for southern elephant seals but stated that there could be more dive types. In a recent study on female southern elephant seals from Marion Island, Bester & Jonker (1994) concluded that the cows from Marion Island used seven dive types during their sojourn at sea. In this study, 12 distinct dive types were identified. Since the actions of the males were not observed while each dive type was executed it is not absolutely clear what the functions of the 12 dive types were. However, possible functions for each of the dive types can be presumed using the shape of the dive (when depth is graphed over time) and the diel variation of the dive depth.

Type 1 dives were very short and shallow and occurred throughout the diving records of all males. Hindell *et al.* (1991b) classified these dives as Type 5 dives and speculated that they could be artefacts of the recorders. However, since the GLTDRs have an accuracy of ± 2 m and the mean dive depth of Type 1 dives were over 20 m, there is sufficient justification for these dives to be classified as a distinct type. Jonker & Bester (1994) considered Type 1 dives to be travelling dives.

Type 2 dives occurred in bouts throughout the diving records, but especially at the beginning and end of the diving records as well as before the main haul-out periods. This dive type was similar to Type E and Type F dives of Le Boeuf *et al.* (1988), while Jonker & Bester (1994) also described it as type 2 dives. Considering the relatively long bottom time at a constant depth with no wiggles and the fact that these dives occurred in bouts at the beginning and end of the diving records, we classified these dives as travelling dives. This assumption is supported by the fact that Type 2 dives occurred more frequently in the diving records of the Macquarie males which travelled the furthest (Fig. 13). Although there is no certainty why these dives have such high descent and ascent rates with a mean depth of just over 200 m, Le Boeuf (1988) hypothesized that elephant seals dive deep to minimise the time spent where their predators occur.

Type 3 dives showed great variability in dive shape and were sometimes difficult to distinguish from Type 7 dives. Hindell *et al.* (1991b) and Jonker & Bester (1994) described these parabola-shaped dives as Type 4 and Type 5 dives respectively. They speculated that it could either have been used to forage, search for prey, or to travel. Because of the close association, similar depth and duration to Type 7 dives, but without

any “wiggles”, it is assumed that this dive type has a twofold function. Firstly, because Type 3 dives frequently occurred in close association with and to the same depth as Type 7 dives, one function could be to search for prey. Secondly, there is a remarkable resemblance in the shapes of Type 2 and 3 dives and it is therefore speculated that it is used to travel while searching for food.

The Type 4 dives were described by Hindell *et al.* (1991b) and Jonker & Bester (1994) as Type 3 dives and by Crocker *et al.* (1994) as Type C dives. These dives with their very distinct two-stage descent phases were usually closely associated with Type 7 and 8 dives. Characteristically, the males quickly descended to a certain depth and then seemingly stopped diving because the descent rate dramatically decreased. A possible explanation for the initial fast descent phase is to minimise the time spent at depths where predators occur. Le Boeuf *et al.* (1988) and DeLong & Stewart (1991) hypothesized that elephant seals may sleep under water. The descent phase could therefore be used to rest or even to sleep. Le Boeuf *et al.* (1991) found that although these dives had a significantly slower swim speed its durations were not significantly longer. He hypothesized that these dives may be “processing” dives, where behaviour and energy utilisation are focused on internal processes such as digestion and clearing of metabolites.

Although almost mirror images of the Type 4 dives, Type 5 dives were not so common and varied greatly in depth. Only Jonker & Bester (1994) described these dives, with its fast descent phase followed by a short bottom time and then the slow ascent phase. They suggested it to have both an exploratory and transit function. The longest dive (80 min) made by male 1453 was a Type 5 dive.

The spiked Type 6 dives were the deepest dives of all and were dispersed throughout the diving records of Marion bulls. Type 6 dives with their high descent and ascent phases with almost no bottom time, simulate the Type A dive of Le Boeuf (1988). It is suggested that these dives are used as navigational and exploratory dives in seals that forage in areas where the seabed is beyond their dive limits. As no Type 6 dives were executed by any of the Macquarie males it is evident that these dives are not necessary when following the Continental Ridge to shallow foraging areas.

Type 7 dives were described by Le Boeuf *et al.* (1988) as Type D dives, by Hindell *et al.* (1991b) as Type 1 dives and by Jonker & Bester (1994) as Type 7 dives. Because of the fast descent and ascent rates, the wiggles displayed whilst at the bottom of the dives, similar dive depths for a series of dives and the large percentage of occurrence, it is concluded that Type 7 dives were used as foraging dives (Le Boeuf *et al.* 1988; Hindell *et al.* 1991b; Jonker & Bester 1994). Crocker *et al.* (1994) classified these dives as type D dives and described the wiggles as “burst diving” with rapid decreases and increases in the swim speed, a characteristic that is consistent with foraging. More specifically these dives can be classified as pelagic foraging dives because they all showed a diurnal pattern for dive depth, with dives being deeper during the day than the night, which presumably correlates with the diel vertical migration of prey.

The Type 8 dives in the present study were also considered to be foraging dives. The dives were the most frequently executed by the males from Macquarie Island and accounted for 50 % of all their dives. Males from Macquarie dived in water within the 1000 m depth contour of the Antarctic coast and executed these dives in series with all

dives in the series being to the same depth. Type 8 dives were benthic foraging dives, showing no wiggles at the bottom of the dive. Hindell *et al.* (1991b) described these dives as Type 2 dives and Crocker *et al.* (1994) as type E dives and they also concluded that these were benthic dives associated with coastal regions, showing no diurnal patterns in its dive depth. The dives that were classified as Type 8 dives for the Marion Island males were all in excess of 1 440 meters and it seem that these dives were unlikely to be bentic foraging dives because the seals dived beyond the limits of the depth channels (1450 m) of the GLTDR and this resulted in the dives being “flat bottomed”. It is therefore assumed that the Marion Island males made no Type 8 dives.

Types 9 and 10 dives seemed to be a combination of foraging and exploratory dives. In type 9 dives, the seals apparently searched for prey at a specific depth, but only during the ascent did they appear to find prey on which they foraged. The dives that followed, usually were assumed foraging dives to the same depth at which foraging was hypothesized to occur during the preceding Type 9 dives. Type 10 dives were characterised by a foraging period followed by a deeper exploratory phase. A possible explanation for this is that the prey found in the foraging part of the dive was not energetically rewarding enough to allow further pursuit at that depth, or was no longer available.

The least common of all dives were the Type 11 dives which were previously described by Jonker & Bester (1994) as Type 6 dives. They considered these dives as exploratory dives interspersed with Type 7 foraging dives. The two “shoulders” of the dive profile (Fig. 8) was at the same depth as the preceding and following foraging dives. It seems that the

males dived to the anticipated depth of prey presence, found no rewarding prey, and then went deeper before lingering briefly at the formerly anticipated depth of prey presence during the ascent.

The distinct type 12 dive may be similar to the Type C dives of Le Boeuf *et al.* (1988). With the slow descent and ascent rates and almost no bottom time, these dives occurred in close association with the type 4 dives. It is suggested that these dives may also have a two-fold function, with the seal resting or sleeping during the descent phase and travelling during the ascent phase.

4.2.3 Comparisons of diving behaviour of southern elephant seals between different foraging areas

No two seals dived in exactly the same way. Although certain dive types were identified, there were large variations in the shapes (graphing depth over time) as well as the order and percentage occurrence of dives during each hour of the day for all seals.

Male 360n94 dived in a similar fashion than previously studied females (Jonker & Bester 1994), but different from the other males in this study. It seemed to pursue widely distributed pelagic prey species in deep water (> 3000 m) since the male used the Type 7 dives more frequently than any other seals studied and showed a strong diel variation in its dive depth. Despite the shortest mean dive duration, it spent the longest time at the

bottom of its dives which were on average > 350 m shallower than recorded for other Marion males. The strong diel variation in the depth of Type 7 dives suggests that this male foraged on vertically migrating pelagic prey. Male 360n94 had a high occurrence of ESIs ($n = 67$) and if Boyd & Arnbom's (1991) hypothesis that ESIs occur after an elephant seal becomes satiated with food, was correct, it suggests that this seal was successful in its foraging. This male seemed to have been quite successful in its feeding behaviour because Type 7 (feeding) dives constituted 58.3 % of all dives and Type 3 (search) dives only 12.3 %. The current results for male 360n94 further suggest that, although a strong relationship existed between the Type 7 (foraging) and Type 4 (resting) dives, this kind of shallow diving is not as exhaustive to the seal and therefore it did not have to rest that often (7.7 %, Type 4 dives).

Males 335a94, 335n94 and 031n93 from Marion Island, all stayed close to the island and showed similar dive patterns, diving deeper than 750 m and longer than 29.9 min on average. Although males 335a94 and 335n94 dived to similar depths, had similar mean dive durations and mean bottom times and used the same percentage frequency of occurrence of each dive type after the moult and breeding haul-outs, prey was apparently encountered at different times of the day as is evident from the percentage frequency of occurrence of Types 3, 4 and 7 dives. It is, however, also possible that different kinds of prey were encountered, because male 335a94 showed a diel variation in the dive depth for type 7 dives, but male 335n94 did not. This male (335) also rested at different times of

the day during the post breeding and post moulting periods. While 335n94 rested from 03:00-05:00, 335a94 strongly preferred to rest between 19:00 and 24:00.

The deepest diver (>1 452 m), male 031n93, might have pursued a different kind of prey species than any of the other males as evidenced by a secondary mode for dive depth starting at 1 350 m, and showed a distinctive diel variation (by 277 m) in its dive depth. Although its dive depth decreased during the night, there was no decrease in its dive duration. It therefore optimised time spent underwater and thus its feeding time pursuing vertically migrating prey, as shown by a very high percentage frequency of occurrence of feeding dives (Types 7 and 8), which peaked at 18:00, whereafter it rested (percentage frequency of occurrence of type 4 dives increased) or travelled (high percentage frequency of occurrence of type 2 dives) before the second foraging period between 02:00 and 04:00.

Males from Macquarie Island had a simpler diving pattern with unimodal distributions for dive depth with a mean that varied between 394 m and 450 m. Males 1453 and 1963 appeared to forage on the continental shelf, since the depth of their Type 3 and 7 dives rarely exceeded that of Type 8 dives. On the other hand, the depth of Type 3 and 7 dives of males 1969 and 1475 often exceeded that of Type 8 dives. Hindell *et al.* (1991a) suggested that the post moulting male 1453 made use of another foraging ground. Seal 1453 foraged more during the day (high percentage of Type 8 dives) and preferred to

travel (Type 2 dives) at night. Both males 1963 and 1969 used the Type 8 foraging dives the most and Type 7 dives the least. Their Type 7 dives were also deeper during the day than the night. Different from the others, it seems as if male 1475 found less food on the seabed between 10:00 and 20:00 and had to execute more Type 3 and 7 dives associated with pelagic foraging during these hours. The mean dive depths of Type 7 dives almost reached that of Type 8 dives, and so the seal might have pursued benthic-pelagic prey that live near the seabed.

Although southern elephant seals are capable of travelling extreme round trip distances, Fedak *et al.* (1996) hypothesised that distant foraging is only efficient when the destination is highly productive and the benefits of foraging outweigh the costs of travel. That is, a long swim in the long term may be more productive than pelagic meandering in the open reaches of the ocean where the prey are widely distributed both temporally and spatially and are therefore, unpredictable (McConnell *et al.* 1992). The results from this study suggest that it is more profitable for the males from Macquarie Island to travel to the distant Antarctic waters to feed on the continental shelf where prey is probably more abundant than closer to the Island. Marion Island is approximately 600 km further from Antarctica than Macquarie Island, and although one female southern elephant seal from Marion Island (Jonker & Bester 1998) travelled all the way to Antarctica, it does not seem to be advantageous for males to do so.

The results from this study suggest that different physical environmental conditions resulted in different types of prey being available which required different foraging strategies. In this study the most obvious differences in the physical environment between

the feeding grounds of the males from the different islands (Marion and Macquarie Islands) were the bathymetry and water temperatures. Macquarie males mainly used Type 8 dives to forage in the benthic zone on bottom dwelling prey species that occur on the Antarctic shelf. The Marion males on the other hand pursued vertically migrating prey in the pelagic zone using mainly Type 7 dives. The frequency distributions of dive depths showed benthically foraging males from Macquarie Island preferred a narrow range of dive depths in contrast to the Marion males where dives were evenly distributed throughout the water column and on average more than 350 m deeper than for males from Macquarie Island. Because the Macquarie males mainly foraged benthically on the Antarctic continental shelf and the seabed restricted their dive depth, a linear relationship between dive depth and dive duration only existed for dives with a duration of less than 30 min. The pelagic foraging Marion males by contrast showed a complex quadratic dive depth-duration ratio with dives being shallower when the dive duration exceeded 45 minutes. To extend their dive durations they had to dive to shallower depths perhaps to restrict energy-loss, which is higher when swimming to greater depths (Le Boeuf 1988).

An apparent disadvantage of the deeper dives of the Marion males was that less time could be spent at the bottom of their dives. Since there was no significant differences in the surface intervals of males from the two Islands, it can be assumed that the Marion males did not get more exhausted than the Macquarie males despite their deeper and longer dives. However, Marion males made more use of Type 4 (resting) dives, which suggest that the deeper, longer dives required more resting periods. These dives (Type 4)

increased dramatically in frequency of occurrence between 18:00 and 22:00 after the main feeding period, while Type 7 dives reached its peak frequency of occurrence at 18:00. As expected, the Marion males had a higher percentage frequency of occurrence of Type 3 dives, which suggests that they had to search more for their presumably widely distributed prey.

Haul-out patterns were completely different between the Marion and Macquarie males. From the regular haul-outs of up to six hours (probable on ice floes or land) made by the males from Macquarie Island (Hindell *et al.* 1991a, this study), it can be assumed that southern elephant seals do prefer to sometimes haul-out when it is possible (Slip *et al.* 1994). Although male 335a94 had one extended haul-out for nine days, none of the males from Marion Island showed regular haul-outs. This may be explained by the fact that there is no readily available hauling out sites such as ice floes occurring in the region of Marion Island.

Chapter 5 Conclusions

From the results it is evident that the southern elephant seals in this study used twelve distinct dive types while at sea to find and travel to their destination, locate and pursue their prey and to rest. There was great variability in the diving behaviour of all seals and none of the seals in this study dived exactly the same as another. The differences in their diving behaviour can be explained by the fact that their prey was differently distributed in space and time at the various foraging locations. The results of this study suggest that it is energetically more advantageous for southern elephant seals from Marion Island to stay relatively close to the island foraging in deep water pursuing spatially distributed pelagic prey species. Because they dived deeper than the Macquarie males less time could be spent at the bottom of their dives. In spite of the fact that their surface intervals did not differ significantly from the Macquarie males and no regular haul-outs was evident, they had more resting dives which suggest that they got more exhausted than the Macquarie males. The Macquarie male's behaviour on the other hand suggest it was more profitable for them to travel all the way to Antarctica foraging mostly benthically on the Antarctic shelf where their prey was more concentrated. Here they dived on average more than 350 m shallower than the Marion males, which resulted, that they could stay longer at the bottom of their dives. These males could make regular haul-outs on ice floes or land to rest in-between dives. Although this study give insight into the differences in the diving and ranging behaviour of male southern elephant seals from Marion and Macquarie Islands, only data for the males that returned to the Islands could be retrieved. It is

suggested that satellite telemetry should be used in future studies because data can be obtained on a regular basis throughout the seals sojourn at sea.

SUMMARY

The aim of the current study was to determine the free-ranging diving pattern and foraging locations of southern elephant seal males from Marion and Macquarie Islands by using geolocation time-depth recorders and time-depth-temperature recorders respectively. By comparing these two colonies of male southern elephant seals the influences of the different locations on the diving behaviour could be determined.

Twelve dive types were identified and were hypothesized to serve in travelling, search for prey, exploratory, resting, benthic foraging, pelagic foraging or combinations of two or more functions. Seals dived virtually continuous for prolonged periods (86% - 92% of the time underwater) to great depths, most often ranging from 390 m to 920 m (maximum = 1 452 m) and stayed on average from 18.6 min to 36.6 min (maximum duration = 80 min) underwater, spending on average only 2.4 min to 3.6 min on the surface between dives. Although the maximum measured dive depths for two seals of 1 446 m and 1 452 m from Marion Island are the deepest measured yet for male southern elephant seals these seals often exceeded the depth limit of the GLTDRs.

Although the diving behaviour of all the male southern elephant seals in this study differed from each other, seals from the two different colonies showed distinct diving patterns according to the foraging ground that they were in. The males from Marion Island did not travel to Antarctica, 2 300 km away, but stayed relatively close to the Island (maximum measured distance from Island was $\pm 1\ 134$ km) pursuing pelagic prey species in very deep water (> 3 000 m). Although it is energetically advantageous for them not to travel great

distances, they had to dive deeper (> 350 m), longer, had more resting dives and had to search more for their spatially distributed pelagic prey species than the benthically foraging Macquarie males. On the other hand it seemed as if it was more productive for the Macquarie males to travel all the way to Antarctica (between 1 500 km and 1 900 km) to forage mostly on benthic dwelling prey species concentrated over the Antarctic continental shelf. As they dived on average less than 450 m deep they could spend more time at the bottom of their dives improving their chances of being successful in its feeding. These males also rested on the readily available ice-floes or land associated with their location.

The results from this study suggest that different physical environmental conditions resulted in the availability of different types of prey available that required different foraging strategies. Southern elephant seal males have to choose the foraging grounds that will be energetically most valuable for them so they can survive.

SAMEVATTING

Die doel van hierdie studie was om die duik- en swerfgedrag van suidelike olifantrobbe vanaf Marion- en Macquarie Eilande te ondersoek. Deur hierdie twee kolonies van suidelike olifant robbe met mekaar te vergelyk kon die invloed van die verskillende voedingsgebiede op die duikgedrag vasgestel word.

Daar was twaalf duiktipes geïdentifiseer wat skynbaar as reis-, soek-, verkennings-, rus-, bentiese voedings- en pelagiese voedingsduike of as kombinasies van duike, gebruik is. Alle suidelike olifantrobbe in hierdie studie het byna onophoudelik vir lang tydperke

diep (\bar{x} = 390 tot 920 m) geduik. Al was die maksimum gemete duikdieptes (1 446 m en 1 452 m), van twee robbe, tot dusvêr nog die diepste gemeet vir suidelike olifantrobbe, het hierdie twee robbe die geolokasie- tyd- dieptemeter se dieptelimiet vele kere oorskry. Die gemiddelde duiktye het gewissel vanaf 18.6 min to 36.6 min met 'n maksimum duiktyd van 80 min. Ten spyte van die lang duiktye het die robbe slegs 2.4 min tot 3.6 min op die oppervlak tussen duike spandeer.

Alhoewel daar baie variasie in die duikgedrag van alle individuele bulle in hierdie studie was, het die onderskeie robbe vanaf Marion- en Macquarie Eilande duikgedragte getoon wat uniek vir elke eiland was. Die rede hiervoor was dat elke eiland se bulle van 'n spesifieke tipe voedingsgebied gebruik gemaak het. Die bulle vanaf Marion Eiland het nie die 2300 km na Antarktika gereis nie maar het inderedelik naby (maksimum afstand vanaf eiland was \pm 1 134 km) die eiland gebly waar hulle in water dieper as 3 000 m waarskynlik op pelagiese prooi spesies gevoed het. Alhoewel hulle baie energie gespaar het deur nie na Antarktika te reis nie moes hulle van dieper en langer duike gebruik maak, om na hul pelagiese prooi te soek en het meer 'rusduike' as die bulle vanaf Macquarie Eiland uitgevoer. Die Macquarie bulle het hierteenoor 1500 km tot 1900 km na Antarktika geswem om daar op bentiese prooi spesies oor die Antarktiese plat te voed. As gevolg van die vlakker duike (\bar{x} < 450 m) kon hulle meer tyd op die bodem van hulle duike spandeer wat die kans om suksesvol te voed vergroot het. Hierdie robbe het ook plekke (drywende ys of land) tot hul beskikking gehad waar hulle gereëld uitgeklim het.

Uit die resultate van hierdie studie blyk dit asof verskillende fisiese omgewingstoestande beskikbaarheid van verskillende prooi tot gevolg het wat veroorsaak dat die

voedingsgedrag van robbe van een voedingsgebied na 'n ander verskil. Dit is nodig vir suidelike olifantrobbe om te besluit watter voedingsgebiede vir hulle die mees produktiefste sal wees, indien faktore soos tipe prooi en afstand na voedingsgebied in ag geneem word, sodat hulle kan oorleef.

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