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Annual Cycles of Diving Behavior and Ecology of the Weddell Seal

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and Gerald L. Kooyman

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INTRODUCTION

Annual diving patterns in pinnipeds are difficult to study because most seals and sea lions are at sea and inaccessible for a large portion of the year. Consequently, until recently, most studies of pinniped biology were concerned with the onshore behavior of species that breed in accessible sites. Only a few species have a behavioral cycle that allows studies of their habits at sea. Of these, the most detailed behavioral data have been collected for female sea lions and fur seals that make repeated foraging trips to sea and return to shore at regular intervals to suckle their pups (Gentry and Kooyman [eds] 1986). For the true seals (Phocidae), there is much less information on annual variation in behavior patterns. For example, although abundant data are available for the on-shore behavior of elephant seals *Mirounga angustirostris* (Le Boeuf and Kaza 1981), only recently have scientists started to gather data on the diving behavior of these seals (Le Boeuf et al. 1986, 1988, 1989; DeLong and Stewart 1989; DeLong et al. 1989).

Other seasonal studies are now in progress on several species of pinnipeds: Ross (*Ommatophoca rossi*) and crabeater seals (*Lobodon carcinophagus*) (Hill unpub. obs.; Bengston, pers. comm.), harbor seals (*Phoca vitulina*) (Stewart et al. 1989), grey seals (*Halichoerus grypus*) (Thompson unpub. obs.), southern elephant seals (*Mirounga leonina*) (Hindell unpub. obs.), northern fur seals (*Callorhinus ursinus*) (Croxall and Gentry 1987), Hookers' sea lions (*Phocarctos hookeri*) (Gentry unpub. obs.), Australian sea lions (*Neophoca cinerea*) (Costa, pers. comm.), Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al. 1991) and California sea lions (*Zalophus californianus*) (Feldkamp et al. 1989).

Of all the species studied, however, the Weddell seal (*Leptonychotes weddellii*) presents a remarkable exception to the generally incomplete view of the natural history of marine mammals. The south polar, fast ice environment of Weddell seals provides an unparalleled opportunity for diving studies. Because Weddell seals regularly haul out onto the sea ice surface, investigators can approach the seals whenever sea ice is present. As a result, it is possible to study adult males, females, and sub-adults at different times in their life cycles and examine their breeding success and population movements (Testa and Siniff 1987, Testa et al. 1990). Most information on Weddell seals comes from studies conducted in the Ross Sea area. This region has two large year-round scientific facilities (McMurdo Station and Scott Base). Scientists have excellent logistical support from the United States and New Zealand Antarctic Research Programs. A satellite-based seasonal study of diving pattern in female Weddell seals in this area is currently in progress (Testa, pers. comm.).

We present information collected during six field seasons, including a full year study in 1981. The goal of this project was to examine how behavioral responses to diving in the Weddell seal vary with season and location. In order to correlate diving

behavior with seasonal or geographical variations, it is necessary to discuss the seals' environment. This includes not only the physical environment above and below the sea surface, but also how the seals may navigate and hunt under those conditions and what prey would be available. The following sections describe the study sites and examine the navigation abilities and feeding habits of the seals. By reviewing this information first, the reader will have a better understanding of some of the factors that may influence the diving patterns that are reported later.

HABITAT AND STUDY SITES

HABITAT

The principal habitat of Weddell seals is the sea ice surrounding the Antarctic continent. Although the largest concentrations of Weddell seals occur in areas of annual ice, they have also been observed along perennial cracks in glacier ice and permanent ice shelves. Fast ice is annual sea ice that is attached to the shore, usually where it formed, varies in thickness from several centimeters to about 3 m, and may extend up to 400 km from the coast. Sea ice 1.5-2.0 m thick with 4 cm of snow cover has a typical under-ice irradiance of less than 1% of the surface light level (Palmisano et al. 1987). Water clarity during the winter months is great, with visibility over 180 m (Kooyman 1981). During summer, however, phytoplankton blooms can reduce visibility in the upper 20 m to less than 3 m (pers. obs.). At White Island, the water remains clear year round because the thick shelf ice prevents phytoplankton growth except near tidal cracks.

Sea temperature in the Antarctic is very stable on a seasonal basis (Littlepage and Pearse 1962) and almost uniform with depth. The ambient water temperature in the ice covered regions of the Antarctic is about -1.9°C (Lewis and Weeks 1971).

Summer and winter temperatures in Antarctica differ by 30° to 40°C, but the average daily temperature during a particular season remains fairly constant. The coldest days along the coast are usually windless and clear, and may not occur during the peak winter months. In 1981, the coldest temperature at White Island occurred in the fall, a day in May when the temperature dropped to -60°C, about 20°-30°C colder than the average for that time of year. A concise overview of climatic variables for the Ross Sea area is given by Keys (1984). Solar radiation (insolation) is primarily seasonal during the summer and winter, but more diurnal during the spring and autumn when there are equal periods of daylight and darkness. At McMurdo Sound (77°S), the sun remains above the horizon from October 21 until February 23, and continually below the horizon for four months from about April 23 to August 24. During the summer months (December-February) when the sun is at its highest point above the horizon, the insolation per minute in this area is about one half that in equatorial regions. During the austral winter (April to August), the full moon can provide sufficient light on a clear night to allow mountains 60 km away to be seen.

Annual distribution patterns of the seals are influenced by biological demands in addition to the ice and climatic conditions discussed above. At traditional pupping areas in the southern Ross Sea, adult female Weddell seals begin to appear on the fast ice in early October. At the same time, adult males establish underwater territories, and there is considerable vocalizing and underwater fighting. Outside of these areas, animals of various ages gather in small nonbreeding groups at ice leads or along the ice edge. At the pupping sites, the female remains on the ice with the newborn pup until weaning at about 7-8 weeks. The pup grows from about 25 kg at birth to almost 100 kg, while the female decreases in weight from 450 kg to about 350 kg (Hill et al. 1986, Tedman and Green 1987). As the time for weaning approaches, the female introduces the pup to its

underwater environment by taking it on short dives. After about 7 weeks, the female abandons the pup and breeds with the male seal that has established a territory near her area of the colony. In December through February the seals molt while hauled out on the ice, and finally, with the breakup of the fast ice, they disperse for the season. An important exception to this pattern is found south of McMurdo Sound at nearby White Island where a group of Weddell seals (about 30) have established a small colony. This island is separated from the open water and fast ice regions of McMurdo Sound by an unbroken ice shelf that is from 10 to 100 m thick. Here, the females give birth to their pups about 1 month later than at McMurdo. Only 3-5 pups are born per season (pers. obs.) and the seals cannot disperse after breeding. Ongoing projects at White Island are studying the population parameters of this group of seals (Testa, pers. comm.).

STUDY SITES

McMurdo Sound (77°30'S, 165°E), is a deep southern extension of the Ross Sea (Figures 1a, 1b, 2). The maximum depth of the sound is about 800 m. The bottom descends steeply along the coast of Ross Island reaching the 300 m isobath within 2-5 km of shore. Fast ice covers much of the 5000 km² of McMurdo Sound from April to January, although the date of the annual breakout and refreezing varies. The northern part of the sound along the west coast of Ross Island begins to break out in October or November, but will often remain covered with pack ice until December depending on the prevailing wind direction. Fast ice or multi-year ice extending 10-15 km from shore can persist, however, in certain regions around Ross Island until January or February. The water immediately south of McMurdo Station remains covered with fast ice until mid-February and during peak haul-out times 200-300 Weddell seals may be concentrated there.

Although McMurdo Sound is covered by fast ice for much of the year, Weddell seals are able to range throughout the sound by following cracks formed by tidal movements and wind. In addition, perennial cracks occur in consistent locations throughout the area. These cracks may extend over 10 km from shore and provide breathing holes for seals foraging in deep water. Weddell seals cannot penetrate very thick ice, but they can easily break through several centimeters of ice to reach the surface to breathe. They prevent holes from refreezing by reaming the edges with their robust upper canines and incisors.

Terra Nova Bay is a fast ice embayment north of McMurdo Sound between Cape Washington and Campbell Glacier Tongue (Figures 1b, 3). Like McMurdo Sound, this area (34 km long by 16 km wide) is one of several along the western Ross Sea coastline where fast ice persists well into summer. In October and November, Weddell seals distribute themselves along perennial cracks within the bay and as the summer progresses, they also begin hauling out along tidal cracks that form along the shoreline. Usually by mid-January the entire bay is ice free. Water depth at the ice edge 5 km west of the tip of Cape Washington is about 300 m.

The triangular White Island, 25 km south of Ross Island, 30 km long and 15 km wide is surrounded by permanent shelf ice (Figure 2). The northern and western shoreline descends steeply and water depths of 600 m occur within 5 km of the island. Except for a narrow strip along the tidal crack and in a rift zone at the northern tip of the island, the ice cover is more than 10 m thick and completely blocks the penetration of light from the surface. The south and east coasts of White Island are bounded by the Ross Ice Shelf, while to the west is the McMurdo Ice Shelf, an extension of the Ross Ice Shelf.

The westward movement of the McMurdo Ice Shelf is greatest at the north end of the island and the rapid movement of ice away from the northwest coast keeps a tidal crack open year round. In this area there is a resident population of Weddell seals (about 30) that has existed there for at least 25-30 years (Harrington 1959). The animals do not move away from the area because the distance under the shelf to McMurdo Sound is too great to swim across. Seals are usually seen along this tidal crack north of the winter camp site (Site "X," Figure 2) and a few haul out to the south. The water directly beneath the tidal crack that runs along the shore on the north end of the island ranges in depth from 10-70 m. The island slopes steeply, thus the depth increases rapidly away from the tidal crack area: the water depth at the campsite (75 m offshore) was 280 m.

DIET AND PREY

The purpose of this section of the project was to test whether seals living at different locations and diving at different times of the year exhibited any dietary variation. The recovery of otoliths, cephalopod, and invertebrate remains from feces was used to determine what prey items were being consumed by the seals.

PREY DETECTION AND NAVIGATION

The senses used by Weddell seals when capturing prey and navigating are not well understood but the most likely modes of sensory perception are vision and hearing.

The minimum light level under which Weddell seals can see is unknown, but tests with spotted seals (*Phoca largha*) and harbor seals (*Phoca vitulina*) indicate that their vision is sensitive enough to see a moving object on a moonlit night at a depth of 160 m in clear oceanic water (Wartzok pers. comm.), which is equivalent to a depth of at least 500 m under clear skies at noon (Clarke and Wertheim 1956). The maximum depth for visual perception will depend on many environmental variables (the angle of the sun, ice thickness, snow cover, the presence of under-ice algae, and water clarity). If we assume (1) a visual sensitivity similar to that for spotted seals and harbor seals, (2) a 10^3 reduction in the surface light that penetrates the fast ice (Palmisano et al. 1987), and (3) a ten-fold reduction in light for every 60 m of depth in clear oceanic water (Clark and Wertheim 1956), then Weddell seals should be able to see an object at a depth of at least 320 m under average fast ice at mid-day. Vision would also be important for detecting bioluminescence emitted by the prey or when other bioluminescent organisms are disturbed by the prey. There are no data for the Antarctic on the vertical or horizontal distribution of luminescent animals or the quantity, quality, or periodicity of the light produced. However, in the sea, where only blue-green light is transmitted efficiently, nearly all bioluminescence has a peak wavelength of 470-510 nm (Nealson 1981). This corresponds to the wavelength of maximum light absorption by the visual pigments of many marine animals, including Weddell seals (Lythgoe and Dartnell 1970).

What environmental features can be used for under-ice navigation while the seals are hunting? The most obvious visual aid would be ice holes and cracks that can probably be seen from great depths. During deep dives the seal need only orient toward the surface in order to relocate the bright hole or tidal crack above. Shallow dives hundreds of meters away from an ice hole are more challenging. Previous observations made from an underwater viewing chamber have shown that seals depart and return along the same track from an isolated ice hole (Kooyman 1968, 1975). This would enable the seal to see the features of the under-ice surface and use them as landmarks on its return.

Sound may also be important for under-ice navigation, especially under low-light

conditions. The hearing ability of Weddell seals has not been tested, but other phocids are more sensitive to underwater sounds than to airborne sounds, and they display good spatial resolution of sounds (Schusterman 1981).

Weddell seals are very vocal underwater; at least 34 call types have been described for the seals in McMurdo Sound (Thomas and Kuechle 1982). Some of these calls appear to be used for social interactions but the function of most is unknown (Thomas et al. 1983). Although there is circumstantial evidence for echo-ranging in polar phocids, they generally neither emit the type of sound nor have the underwater hearing ability to echolocate (Schusterman 1981). Kooyman (1981) has speculated that some of the low frequency sound emitted by Weddell seals may be used to determine their approximate location in the water column. This would mean that the seals use the echo from the vocalization to determine distance above the bottom or depth below the ice cover.

Sounds emitted by prey or sounds produced by their activity, such as swimming, could be used by seals during foraging. Although nothing is known about the sounds produced by the prey of Weddell seals, many species of fishes produce sounds (Myrberg 1981), as well as many species of crustaceans and some squids (Hawkins and Myrberg 1983).

FEEDING HABITS

Prior data on Weddell seal feeding habits were obtained almost exclusively during the austral summer. The earliest observations were anecdotal and mentioned fish as the major prey species (Wilson 1907). However, cephalopod beaks and crustacean remains were also noted in fecal samples. During the winter months at McMurdo Sound, Wilson reported that the Weddell seals consumed fish species of the genera *Trematomus*, *Notothenia*, and *Gymnodraco* with an occasional take of “cuttlefish.” During the 1930s, Lindsey (1937) was able to study Weddell seals in the Bay of Whales area (ca. 78°34' S, 163°56' W), but wrote only a single sentence about their food habits: he reported a large pregnant female hauled out during a warm mid-winter night whose stomach was full of *Pleuragramma antarcticum*, a small smelt-like nototheniid fish commonly known as “Antarctic silverfish” (DeWitt and Hopkins 1977).

In 1940, Bertram reported on observations taken during the British Graham Land expedition. In this project, he cited both nototheniid fish and cephalopods as equal food sources for the seals. He felt, however, that the seals were probably opportunistic and would take “whichever is the more convenient or abundant.” Bertram footnotes his estimates by remarking that this information was gathered during the molting period (December and January) and may not be representative of the year-round cycle.

The first comprehensive study on Weddell seal feeding patterns was done in the McMurdo Sound area during the summers of 1958 to 1961 (Dearborn 1965). The

stomach contents of 44 seals taken during these years were examined and of these, 8 were empty. Using frequency of occurrence analysis, Dearborn showed that fish were the most common prey species (found in 35/36 stomachs) while cephalopod remains were found in only 6/36 stomachs. Dearborn felt, as did Bertram, that the seals probably fed opportunistically on whatever was available and that they would occasionally take the large fish *Dissostichus mawsoni* (Murphy 1962).

Testa et al. (1985) were able to collect Weddell seal stomach samples (n=36) and scat samples (n=49) near McMurdo in November through January 1982-1983. Based on frequency of occurrence of prey items, they showed that Weddell seals seem to feed mostly on smaller nototheniid fish (*P. antarcticum*, *Trematomus* sp.), decapods, amphipods, crustaceans, and cephalopods. *P. antarcticum* remains were found in 35 of 49 fecal samples while other fishes were found in only 5 samples. Cephalopod remains were contained in only 3 of 49 samples. Of the 35 stomach samples, 26 contained *P. antarcticum*, 4 contained other unknown fish remains and 5 had evidence of cephalopods.

Recently, Green and Burton (1987) collected fecal and stomach samples from Weddell seals in both the McMurdo region and at Davis Station in the Indian Ocean sector of the Antarctic continent. Samples from Davis were collected through the entire year of 1984, and the McMurdo samples were taken in January 1984. They found that fish, prawns (*Chorismus antarcticus*, *Notocrangon antarcticus*), and cephalopods constituted 77%, 21% and 2% respectively of the mass of 16 stomach content samples at Davis. At McMurdo, fish remains accounted for over 99% of the mass of 20 stomach samples. Seasonal analysis of fecal samples showed little variation in the frequency of occurrence of fish or cephalopod remains, but prawn remains occurred more often during the summer. *P. antarcticum* constituted 93% by frequency of the fish remains in the McMurdo samples and 70% of the samples from Davis. At McMurdo, the standard length of *P. antarcticum* collected from seal stomachs was 14.9 ± 2.3 cm (n=330; \pm SD) and at Davis it was 15.0 ± 1.7 cm (n=169). The authors noted that the calculated lengths of *P. antarcticum* based on otolith size in fecal remains were slightly smaller (3%) than values obtained from whole fish samples taken from stomachs and that erosion of otoliths would cause underestimation of fish size.

PREY DISTRIBUTION

To understand how prey preference might influence seal diving behavior, it is important to examine what is known about the life history, distribution, and abundance of prey species.

P. antarcticum appears to be the most common fish species, representing over 90% in both number and mass of the midwater fish in the Ross Sea region and in the Antarctic peninsula area (DeWitt 1970, Hubold 1984, 1985). These small fish school and may be differentially distributed in the water column by size (Hubold and Eka 1985).

Not as much is known about *Pagothenia borchgrevinki*, except that this fish inhabits the sub-ice platelet zone (DeWitt 1971, DeVries and Eastman 1981). This species has been observed to form sub-ice swarms and will hide up against the bottom of the ice surface

when alarmed (Andriashev 1970). We have taken them on hook and line from as deep as 150 m and have observed them swimming as schools as deep as 50 m (Castellini, pers. observation from a sub-ice viewing chamber). Estimates of their distribution and abundance have not been attempted.

Most of the bottom fish species in the Ross Sea belong to the genus *Trematomus*, which is benthic, although some species have life stages that are pelagic (DeVries and Eastman 1981, Eastman 1985). Individuals of this genus are small and slow growing (Wohlschlag 1964, Everson 1984). Various species live at different depths (DeVries and Eastman 1981) but their abundance is unknown.

The abundance and distribution of the large (up to 65 kg) *D. mawsoni* ("Antarctic cod") during the austral summer is widely known because of an extensive study by DeVries and others (Eastman and DeVries 1981). This fish is usually caught below 300 m and within 50-100 m of the bottom, although there is evidence that it may feed at any level (Eastman 1985). Based on catch data, *D. mawsoni* appears to be most common in McMurdo Sound from mid-October to early December (Testa et al. 1985), although its relative abundance is unknown.

Prior to the winter study at White Island, evidence of fish life under the Ross Ice Shelf was very limited. In December 1976, a single *P. borchgrevinki* was caught about 80 km from the ice edge (Bruchhausen et al. 1979) and several unidentified fish were observed by divers at White Island (Oliver et al. 1976). At the J-9 Ross Ice Shelf project site (about 600 km from the open water), a bottom fish was photographed, but not captured (Bruchhausen et al. 1979). During our year-long study at White Island, seven species of fishes were captured with baited cages or dip nets and several dozen *Pleuragramma antarcticum* remains were retrieved from seal haul-out areas (Castellini et al. 1984). In addition, during the austral summer of 1983-1984, we found the remains of a *D. mawsoni* in a seal regurgitation sample. We also photographed a variety of *Trematomus* sp. and chaenichthyid species under the ice shelf near Heald Island, approximately 30 km from the open water of McMurdo Sound.

Little information is available on the distribution, diversity, and abundance of pelagic invertebrates in the McMurdo region, because ice cover prohibits the use of standard trawling techniques. The most common "krill" species in this area is *Euphausia crystallorophias* (Keys 1984), rather than *E. superba*, which is the dominant antarctic species and the subject of most studies on krill. *E. crystallorophias* has never been identified in Weddell seal stomach or scat samples from the McMurdo region. In other areas, "krill" constitute less than 1% of the remains in Weddell seal stomachs (Laws 1984). Another pelagic invertebrate group that seals prey on is squid. During this study, a seal that was feeding under the ice in McMurdo Sound brought a live specimen of *Pyschroteuthis glacialis* to the surface. This squid specimen was collected late at "night" in October when the seal was diving next to the McMurdo Ice Shelf (about 100 m away). The sea ice at this site was unusually thick with about 4 m of solid ice and another 4 m of platelet ice. This suggests that this species of squid may prefer low light levels in ice covered areas as it is usually found between 200-700 m (Roper et al. 1985).

METHODS

At White Island, fecal samples were collected from every haul-out site and after all the initial samples were removed from the ice, each site was checked weekly throughout the year for fresh fecal remains. By contrast, because of the large number of seals in McMurdo Sound and because the sound is ice free for several months, fecal samples were collected opportunistically from haul-out areas whenever ice conditions allowed travel. Fecal samples were not collected from Terra Nova Bay. Whole fecal samples were placed in plastic bags and brought back to the laboratory, where they were kept frozen until analyzed. The fecal samples were dissolved under running water and sifted through progressive sieves. Otoliths, chitinous material, and other remains were then removed from the screens for identification.

Frequency of occurrence of prey remains in fecal samples have been used in order to compare the present data with those in all previous studies of Weddell seal feeding habits. Given the relatively few prey species that are available to Weddell seals in the McMurdo Sound region (see below), this methodology should provide a broad perspective of dietary habits.

RESULTS

Frequency of prey items

The frequency of prey items found in the fecal samples is presented for the McMurdo Sound and White Island region in Table 1. Fish remains were found in 89% of the McMurdo samples and 49% contained invertebrate remains other than cephalopod beaks which were found in 5% of the samples. The monthly patterns show that fish remains were found in at least 80% of the fecal samples regardless of season at McMurdo, and invertebrate remains occurred in more samples during the dark winter months (26/37 for July and August) than in the summer months (15/45 for November-January). This difference was significant (Chi-squared statistic = 9.6; $p \leq 0.005$). When compared to White Island, the McMurdo samples were similar in frequency of occurrence of fish and invertebrate remains, but more cephalopod remains were found in the White Island samples (Chi-square statistic for: cephalopods (15.6; $p \leq 0.005$); fish (0.52); invertebrates (0.05).

Otolith analysis

Sagittal otoliths recovered from fecal samples were identified by comparison with otoliths recovered from known fish species captured in McMurdo Sound or at White Island. The maximum length of each otolith was measured to the nearest 0.02 mm under a binocular microscope. Of the 3,137 otoliths recovered, 2,991 were identified as *Pleuragramma antarcticum* and the remainder came from the genus *Trematomus* (Table 2).

Otoliths from *P. antarcticum* ranged from 0.5 - 2.8 mm in length (Figure 4). Based on the allometric relationship of otolith size to the standard length and mass of the fish (Hubold 1985), this corresponds to fish with a standard length (SL) of 3.6 -

22.7 cm and a fresh weight of 0.2 - 103 g. The four most abundant otolith sizes (1.0-1.3 mm) represented 62% of all recovered otoliths and corresponded to SL 7.8-10.3 cm fish. These size and mass estimates would be minimum values given corrections for otolith digestion; the actual values could be up to 3% higher (Green and Burton 1987). Because only 6% of the recovered otoliths were collected at White Island, no statistical comparisons were made between White Island and McMurdo except that the size range of otoliths recovered at both locations were similar (0.5-2.8 mm).

Cephalopod beak analysis

Cephalopod beaks were found in 16 fecal samples. Many more beaks were found at White Island than the McMurdo region (Table 3). All of the squid beaks appeared to belong to the family Mastigoteuthidae. Following a beak-size to mantle length and weight relationship described by Clarke (1986), the average mass of the squid was calculated to be 126 ± 41 gm with a mean mantle length of 12.7 ± 1.6 cm. All of the beaks at White Island were recovered in November and 23 of the 34 beaks from McMurdo were found in August and September.

DISCUSSION

The primary conclusions of these studies are:

- 1) Fish remains occurred more often than any other prey remains in Weddell seal fecal samples regardless of season or location.
- 2) *P. antarcticum* remains accounted for more than 95% of all recovered otoliths.
- 3) Invertebrate remains were more common in the McMurdo fecal samples during winter compared to summer.
- 4) In 1981 squid were captured by seals at White Island during the summer and at McMurdo during the winter.

These data suggest that seals at White Island and McMurdo were consuming approximately the same diet. Therefore, when analyzing diving patterns, it is important to realize that the seals were not hunting for different prey types or sizes.

There are many limitations to fecal analysis, including the observations that differential digestion of otoliths can create errors in estimating prey size or mass ingested (Murie and Lavigne 1985, Green and Burton 1987, Silva and Neilson 1985). The most serious error would be in estimating total mass ingested because adventitious collection of fecal samples yields no information on the total fecal production per time by the seal or the mass of the seal for comparison. Therefore, no estimates of total mass ingested were made in the present analysis. It is also possible that fecal remains can be from prey eaten far from the collection sites, for example, as with whales that can travel great distances between feeding grounds (Clarke 1980). This is not a problem with Weddell seals in McMurdo Sound because the seals in this area are site specific and fecal samples probably represent remains of prey captured within 2-4 km of the collection site.

DIVING BEHAVIOR AND PATTERNS

The goals of this section of the study are to: (1) compare diving behavior in three separate seal populations in which environmental conditions differ, (2) determine the variation of free ranging diving behavior through an entire annual cycle, and (3) compare the diving behavior of seals restricted to sea ice laboratories with the behavior of free ranging seals.

SELECTION OF STUDY SITES

In 1978, we began deploying dive recorders on free ranging seals in the McMurdo region (from Scott Base in the south to Cape Evans in the north) from early August through February. The seals were recaptured after several days or weeks and the dive recorders recovered. Seals were also studied from a sea ice laboratory in October through mid-December of 1977, 1987, and 1988.

In January 1981, a winter camp was constructed at White Island and a hole melted through the shelf ice with a steam-drill (Love et al. 1982). A hut was placed over the hole and a custom pre-fabricated aluminum tube was reconstructed and lowered into the hole to maintain a clear water pathway through the ice into the water below. This hole provided year-round access to the water for biological, oceanographic, and acoustic measurements (Davis et al. 1982). From the base at White Island, dive recorders could be deployed and retrieved from seals year round, a situation not available anywhere else on the continent.

In 1986 a camp was established by one of us (GLK) at Terra Nova Bay from October to January. The area within Terra Nova Bay is similar to McMurdo in terms of ice conditions and the deployment and recovery of dive recorders on Weddell seals followed the general procedures used in McMurdo.

INSTRUMENTATION

The data in this report were collected from two types of dive recorders. The first was an opto-mechanical time-depth recorder (TDR) and the second an electronic depth-histogram recorder (DHR). Engineering details for both have been described elsewhere (Kooyman et al. 1983a). The TDR was placed in a watertight pressure housing attached to the seal by an anklet strap or glued to the fur with epoxy. The instrument weighed about 500 gm, was 20 cm long and 5.3 cm in diameter. When the TDR was recovered, the film containing the latent pressure and timing trace was removed and developed for analysis. The DHR was smaller (95 gm; 9.5 cm long and 2.8 cm diameter) and was attached by an anklet. After the instrument was recovered, the data were transferred to a microprocessor analyzer that constructed a histogram of the total number of dives and the number within each depth range. DHR data do not indicate diving duration, only depth.

Both male and female adult seals were chosen for the project. Diving behavior studies on juvenile seals have been conducted previously and the results discussed elsewhere (Kooyman et al. 1983b).

RESULTS

A total of 24,199 dives were recorded from 69 seals during the course of this project. Total record time was over 9,100 hours of instrument deployment. The Appendix contains the data summaries for each of the 69 seals broken down by geographic and seasonal distribution. Some records contain only depth or time data because of instrument design or failure. Partial diving records for some individual seals have been published previously (Kooyman et al. 1980, Kooyman 1981, Kooyman 1989).

Geographic comparisons of average diving depth and duration

To test for geographical or seasonal differences in diving depth or duration, diving data were analyzed using nonparametric Kruskal-Wallis single factor analysis of variance by ranks (Zar 1984). In all cases, the null hypothesis was that the means of diving depth and duration were similar among the tested groups and significance was set to $p \leq 0.05$. The Kruskal-Wallis statistic and the p value using Chi-square approximations were computed using STATISTIX software from NH Analytical Software, Roseville, MN.

A comparison of diving data by location showed that apparent range of average diving duration (10.1 to 13.0 min) was not significantly different among the study sites (Table 4). By contrast, average diving depth at White Island was significantly less (about one half) the diving depth at the other sites (Table 4). Despite the overall shallower dives at White Island, average diving duration was not different.

Seasonal comparisons of average diving depth and duration

Data from free ranging seals in the McMurdo area show that there was no seasonal shift in average diving depth or duration for August through January (Table 5). Similar analysis of the diving data for White Island also indicated no seasonal variation in average diving depth or duration (Table 6). However, in the one instance where the same site was sampled over two seasons (McMurdo, January 1979 and January 1981) there was a statistical difference with the average depth in 1979 being about half the average depth in 1981 (see below and Figure 5). This suggests that year to year variations in average diving depth can be greater than variations within a single season. A considerable amount of information is lost by averaging data. Further analysis using diving depth and duration frequency histograms revealed patterns that were masked by the analysis of average values.

Frequency distributions of diving depth and duration

Histogram analysis (Kolmogorov-Smirnov) demonstrates that the diving depth pattern varies throughout the year such that all locations and seasons were significantly different from one another ($p < 0.001$; Figure 5). The diving depths from the hut experiments (October-December, 1977, Panel 1) never exceeded 350 m but had a mode (15%) in the 300-350 m depth range. By contrast, the diving depth distribution of free ranging seals in McMurdo Sound in August and September (Panels 2,3) showed a smooth decline in diving depth frequency down to >600 m. As in the hut experiments,

diving depth frequencies in October through December at McMurdo Sound (Panel 4) had a secondary modal point at 350-450 m. The late summer (January) dives in 1979 and 1981 at McMurdo (Panels 5,6), all dives at White Island (Panels 7,8), and the December dives at Terra Nova Bay (Panel 9) showed a pattern of increasing dive frequency to about 150 m with only few dives beyond 200 m. In fact, Terra Nova Bay showed a greater distribution of dives in the 150-200 m depth range (31%) than any other location or season. In most instances however (except for January 1981 near McMurdo [Panel 6] and Terra Nova Bay [Panel 9]), 45% or more of the dives were less than 100 m. Therefore, while a broad inspection of the histograms may reveal general patterns that appear similar (for example, August and September at McMurdo [Panels 2, 3]), statistical analysis demonstrates that diving-depth frequencies changed on a month to month basis in these study areas. These patterns may also change on an annual basis: the depth frequencies at McMurdo in 1979 and 1981 were statistically different with the seals showing a deeper diving pattern in 1981.

As with the above data on distribution of diving depths, there were geographical and seasonal patterns in diving duration that were masked by the variability among individuals, seasons, and study site. The frequency distribution of diving duration for the same 9 locations and seasons (Figure 6) were also analyzed using the Kolmogorov-Smirnov technique and, as with the depth histograms, the patterns were all significantly different from each other ($p \leq 0.001$) except for the January 1979 and January 1981 at McMurdo (panels 5,6) which were not statistically different ($p = 0.48$).

While the majority (about 60%) of dives from the hut in 1977 were longer than 5 min, the most frequently observed dive times were in the 0-5 min block (Figure 6, Panel 1). The frequency of dives over 5 min declined at an exponential rate ($y = 0.64e^{-0.13x}$ [$r^2=0.98$]). During the late winter at McMurdo (August), dives in excess of 30 min were nearly non-existent and there was an even distribution of dives of up to 20 min (Panel 2). By September, the majority of dives (54%) were less than 10 min (Panel 3) with an exponential decline in diving duration frequency beyond 10 min ($y = 1.37 e^{-0.14x}$ [$r^2 = 0.97$]). During the summer (October through December) at McMurdo, the diving durations showed two modes, at less than 5 min (41%) and between 15-20 min (22%; Panel 4). There was an increasing tendency for more dives to be less than 5 min and fewer dives greater than 10 min from August through December. By January however, the pattern shifted to a modal diving duration of 10-15 min (>40%; Panel 5) and this pattern was found in both January 1979 and January 1981 (Panel 6). The January data from White Island (Panel 7) also showed a modal diving duration of between 10-15 min, which was not statistically different from the patterns seen in McMurdo during January. During the winter at White Island (Panel 8), the modal duration was still at 10-15 min but the frequency of this mode declined to 23% from the summer value of 45%. At Terra Nova Bay (Panel 9), there was a steady increase in diving-duration frequency up to about 29% in the 15-20 min block.

Histogram analysis of depth and duration frequencies demonstrate that diving patterns changed significantly through the seasons both at McMurdo and White Island.

However, the January patterns at White Island were similar to those in January in McMurdo Sound and both differed from the late December results from Terra Nova Bay. These data indicate that there was not a “typical” diving depth or duration consistent with region or season. The seals could dive to midwater depths or they could dive to the bottom; they usually dived for less than 20 min but could stay underwater for over 50 min under natural free ranging conditions and up to 82 min when diving from the huts.

Time patterns in diving frequency

The diving plots in Figures 7 and 8 show that Weddell seals dive in patterns of bouts, although the lengths vary. The patterns were analyzed by constructing histograms of dive frequency by hour of the day (Figure 9). To test for nonuniform diving patterns the observed frequency of diving was compared with an expected frequency assuming a completely equal distribution of dives throughout the day. That is, in a uniform distribution 4.16% of all dives would occur in any given hour (100%/24). The observed and expected patterns were compared using Chi-square analysis following the techniques of Zar (1984). For all seasons and locations, except the two instances discussed below, the pattern of diving was not uniform (Table 7). The two exceptional cases occurred during the month of January 1979 at McMurdo and during the entire winter sampling period at White Island (Figure 9, Panels 5,8). The uniform diving pattern observed in January appeared to be an isolated instance in light of all the other McMurdo data. However, the winter data from White Island suggest that diving behavior occurred uniformly throughout a 24 hour period. Because summer dives at White Island occurred in a nonuniform pattern (Panel 7), the results indicate that there was a summer-winter difference in diving behavior at White Island.

Maximum depth and duration limits

Of the 24,199 dives recorded, average diving depth ranged from 59 m at White Island to 150 m during the hut experiments in McMurdo Sound. Of the 69 seals studied, 22 dived deeper than 400 m, 6 made 110 dives (0.45%) greater than 500 m and only 1 seal made 4 dives greater than 600 m. Several of the maximum diving efforts by individual seals are now presented to provide some perspective of the seal's capabilities and limits. The following results are not necessarily the maximum physiological capacities, but the scarcity of long and deep dives shows that they are a rare event. The maximum depth recorded during our study was 626 m, and the profile of this dive shows several points of interest (Figure 10). The duration of the dive was 17.7 min. The descent was at an average rate of 120 meters/min, a very rapid rate for Weddell seals (Kooyman 1968) and was followed by 3.5 min of bottom time at depths between 620 to 625 m. However, in the last 2 min of descent, the seal accelerated to 150 meters/min, which is extremely fast and indicates a 90 degree descent angle since this speed is close to the highest swim velocity we have measured to date (unpub. obs). Ascent was at an average rate of 61.5 meters/min. This dive was the eighth in one of the most remarkable series of deep dives ever recorded for a Weddell seal (Figure 11): twelve dives were made in a 4.5 hour period in which the average depth was 580 m. The shortest dive was 12.8 min, the

longest was 28.3 min, and the average surface time was 5.5 ± 3.3 min ($n=11$; \pm SD). All dives were characterized by rapid descents with a few minutes near maximum depth before returning to the surface. Ascent to the surface was usually direct but less rapid than descent.

The average diving duration for seals ranged from 10.3 to 11.8 min. A total of 41 dives (0.17%) exceeded 40 min and 16 dives were in excess of 50 min but 13 of these were recorded from 6 seals during the hut experiments. Only three free ranging dives in excess of 50 min were recorded (2 seals; 50.9, 51.0, 53.0 min). The longest dive recorded was 82 min measured during the hut experiments.

DISCUSSION

Diving depth

There are many factors that can influence the pattern of diving depth for seals. When a seal is hunting, diving depth would probably indicate the depth distribution of its prey and it is easy to understand how the behavior of prey species such as *Pleuragramma antarcticum* or *Dissostichus mawsoni* could influence the diving behavior of a Weddell seal. If a school of *P. antarcticum* concentrated at 275 m and the nearby seals were foraging, then the seals would probably dive to about 275 m. If the prey moved throughout the water column, then the seal would presumably follow. Correlations between diving and prey depth have been found in the Antarctic fur seal *Arctocephalus gazella* (Croxall et al. 1985) a species that feeds almost exclusively on krill. It is unknown if the consistent diving depths seen in some bouts of Weddell seals were results of swimming to the bottom or preying upon a school of fish at a midwater depth. In some cases, the appearance of a deep dive in the middle of an otherwise shallow series of dives would suggest that most of the dives were well above the bottom.

Little is known of the daily movements of Weddell seal prey species in the Ross Sea area; therefore correlation of average diving depth or frequency of diving to prey distribution was not possible. In fact, the shallow dives during January at McMurdo seemed counterintuitive because there was little sea ice and 24 hours of light should have influenced the prey to move to greater depths. Perhaps the sea ice and intense summer phytoplankton blooms alter patterns of diurnal vertical migration of fish and invertebrates in these regions and consequently there were no obvious diurnal shifts in seal hunting patterns. In contrast, the relatively shallow dives at all seasons at White Island may have been influenced by a tendency of prey to remain in shallow water throughout the year in response to the much lower light levels under the thick shelf ice.

Another factor that could influence diving depth would be whether the dive was an exploratory dive from one location to another. Kooyman (1968) has described Weddell seal exploratory dives as lengthy and shallow; foraging dives appear deep relative to the duration. However, the actual average depth of foraging dives is unknown and could not be defined in this study because many of the short duration, shallow dives may have involved activities other than foraging. For example, in the course of coming to or

leaving a breathing hole, two or more seals may meet and remain near the hole to display to each other. This may be especially true from September to December, which is the breeding season for the seals. The depth and duration histograms show a large number of dives less than 50 m deep and shorter than 5 min (Figures 5 and 6). This type of diving was not seen in the other months, especially in January when McMurdo Sound is ice free and there are no holes to defend. If social behavior could be factored out, then many of the very short and shallow dives might be distinguished from foraging dives.

Diving duration

While Weddell seals are capable of long-duration dives, their normal behavior did not routinely approach these limits. For example, few dives exceeded 25 min, and most were less than 15 min. The usual upper limit is probably reflected in the deep series of dives of seal 32 (Figures 10, 11). While making these 12 dives to 600 m, the average diving duration was 16 min, and the longest was 19 min, not counting dive #6.

Aerobic dive limits (ADL) for Weddell seals have been calculated based on measured available O₂ stores and estimated diving metabolic rates (Kooyman et al. 1980; Kooyman et al. 1983b). The calculated ADL for adult seals is about 16 to 20 min. Because the average diving duration (10-13 min) for the adult seals in this study was less than the calculated ADL, either the seals had a margin for occasionally remaining underwater for longer periods without exceeding their aerobic capacity or the theoretical ADL was overestimated.

Seasonal and geographical differences in dive patterns

Because of the variability in diving depth and duration both within and between individual seals, the average values for separate seal groups were not statistically different. However, when the data were analyzed using frequency-of-distribution histograms, statistically significant differences in diving depth and duration became apparent. For example, in McMurdo Sound during September (a time of increased antagonism among seals probably related to the breeding season), the most common diving depth was less than 50 m. During January when breeding was over, the most common depth was 100-150 m. Similar geographical and seasonal differences were found in diving duration and in the number of dives per hour throughout the day. However, these differences may also reflect additional factors other than foraging requirements. The low light level, cold, and more inclement weather in September may be why the seals rest below the ice more frequently than in January. January is generally a very warm month on the ice surface. The seals haul out more often in January because of the pleasant ice surface, than in the winter months (Smith 1965 and pers. obs.). The seals are also molting during January, and they may need warm and dry skin to facilitate this process.

These above-ice distribution patterns of seals are mirrored in the diving frequency patterns. The data for diving patterns by hour of day (Figure 9, Table 7) indicate that during the winter and spring (periods of low or fluctuating light levels) the fewest dives

occurred from 2300 to 0100 hours. During the 24-hour-light period the fewest dives occurred between noon and 1500 hours. This is best demonstrated in Figure 9, panels 2 and 6, that compares dive frequency at McMurdo in August with January. The two patterns are essentially negative images with the August data showing most dives during the “day” and the January data showing most dives during the “night.” Kooyman (1975) found that when seals were diving from a hut in September, they made more dives during the daylight hours. Exactly the same results were found in free ranging seals during September in this study (Figure 9, panel 3). Whether this pattern relates to the above ice conditions, prey distribution, or social behavior is not known.

The seasonal diving patterns were also significantly different at White Island and are more difficult to explain because there never really are summer conditions under the thick ice and the water remains dark and ice covered throughout the year. Perhaps there might have been enough underwater light near the tidal crack in the summer at White Island to influence the distribution of prey and encourage the seals to dive shallower than during the winter darkness. Like the seals in McMurdo sound, the seals at White Island in January tended to dive at “night.” During the winter however, there was no hourly pattern of diving frequency (Figure 9, panels 7, 8). Unfortunately, prey distribution patterns and abundance are essentially unknown under the shelf ice at White Island making correlations to seal diving patterns almost impossible.

Diving energetics

A seal dives with a finite amount of oxygen. The rate at which it consumes that oxygen will determine the time it can remain underwater. The diving metabolic rate is therefore a major factor in determining dive time and dive efficiency. Diving metabolic rate can be influenced by many factors, including physiological and biochemical limitations, body mass and swimming speed. For example, small seals have a higher mass specific metabolic rate than larger seals, a lower ADL (Kooyman et al. 1983b) and cannot stay underwater as long. Furthermore, a lean seal will not have the thermal insulation of a fatter seal and heat loss may raise its metabolic rate. A mating seal may need to spend more time in the water than a seal that is not breeding and a pregnant female will have a different energetic demand than a nonpregnant female (for reviews of these factors in pinnipeds, see Kooyman 1989, Castellini and Kooyman 1989, and Castellini 1991). Finally, the most powerful influence of all on diving metabolic rate is swimming speed. The swimming seal’s metabolic rate is directly related to drag, which itself increases exponentially with swim speed (Williams and Kooyman 1985). All of these factors will determine the metabolic rate of diving. For example, for dives shorter than 30 min, there is a relationship between the diving depth and duration, the deeper the dive, the longer the period underwater (Figure 12). (The very long dives of over 40 min tend to be shallow, exploratory dives; Kooyman 1968). Thus, diving behavior, duration, depth, oxygen stores, and metabolic rate appear to be interrelated. If a seal is foraging during diving, then considerations must also be made for hunting behavior, prey density, and prey type in order to build a realistic model of hunting energetics.

Some broad approximations of these various parameters have been made in Weddell seals and allow a few simple calculations of foraging budgets. For example, assume that the mass specific metabolic rate for an adult diving Weddell seal (Kooyman et al. 1973 and unpub. obs.) is about 3.8 ml O₂/min-kg (or about 0.074 kJ/min-kg using the conversion of 19.7 kJ/l O₂ at a respiratory quotient of 0.7), the seal has a mass of 400 kg, the seal is hunting exclusively for *P. antarcticum* (6.5 kJ/gm fresh weight, unpub. obs.) and the dive time is 12 min of which 6 min is spent feeding. At this metabolic rate, the cost of the dive is 355 kJ ([12 min] x [0.074 kJ/min-kg] x [400 kg]). If the energy gain of the dive is to be larger than the energy cost of the dive, then >355 kJ worth of energy must be gained from *P. antarcticum* during the 6 min of feeding. At 6.5 kJ/gm of fish, approximately 54 gm of fish must be obtained during the 6 min. The fecal analysis showed that the most common size of *P. antarcticum* captured by the Weddell seals in this study was about 50 gm; therefore the seal must capture 1-2 fish per dive to stay in energy balance.

Manipulation of foraging energetics models illustrate the behavioral envelope within which the seals must operate while hunting. These models are useful in analyzing the diving patterns, and they also expose the present limits of available data. Estimates of diving metabolic rate are critical to understanding diving efficiency but they are also some of the most difficult estimates to obtain. Since the time that the data presented in this report were collected, dive recorders have been built that can measure swim velocity, stroke frequency, and several physiological parameters such as diving heart rate, body temperature and blood oxygen levels. By combining all of these measurements, future projects will hopefully come even closer to defining an accurate metabolic cost of diving.

When all of these behavioral, environmental, and physiological factors are considered, it is not surprising that diving behavior in the Weddell seal is so complex and variable. Interestingly, this lack of obvious pattern is very different from the diving behavior of female elephant seals, which exhibit distinct patterns in diving behavior at certain times of the year (Le Boeuf et al. 1989). Female elephant seals and adult Weddell seals are about the same mass, but elephant seals dive consistently deeper (modal depth between 350-600 m) and on average, longer (modal duration 25 min; Le Boeuf et al. 1986, 1988, 1989; DeLong and Stewart 1989). The elephant seal shows a strong diurnal pattern in its diving depth, whereas the Weddell seal does not. The Weddell seal dives in bouts that last about 12 hours and the elephant seals dive continuously for days without an extended surface interval. Such distinct differences could be a function of the ice habitat of the Weddell seal compared with the pelagic habitat of the elephant seal. The Weddell seal can haul out on the ice at any time, an option not available to the northern elephant seal. Perhaps when the diving habits of the southern elephant seal are better known (a species that does have access to sea ice at certain times and locations), it will help us to understand if a stable platform, such as sea ice, induces elephant seals to break their pattern of diving bouts. Another major difference is that at the time of year that northern elephant seals are studied, they are

migrating great distances to and from feeding grounds. The Weddell seals studied in this project were not migrating or traveling great distances and were almost always captured within a few kilometers of their release site.

The variable diving habits of the Weddell seal, in contrast with the more regular diving habits of some other species, demonstrate that the biology of diving is not a simple phenomenon that can be examined easily by looking at diving physiology or behavior in isolation. It requires a synthesis of environmental, physiological, and behavioral factors and interpretation of how each can influence diving patterns in pinnipeds.

CONCLUSIONS

In this monograph we have attempted to summarize the basic aspects of annual patterns in the diving behavior of the Weddell seal. The primary conclusion of this study is that diving depth, duration, and frequency vary widely both within and between individuals, by season and by location. Thus, the characteristic nature of Weddell seal diving behavior is that of variability as distinct from a uniform or repetitive depth, duration, or frequency. These differences in diving pattern are not clearly related to dietary diversity nor to easily recognized differences in physical habitat unlike some other species of pinnipeds in which dive patterns can be related to prey habit and strict diurnal rhythm. In fact, these variable diving patterns are all the more remarkable because the diet is almost monospecific from which it may be inferred that *Pleuragramma antarcticum* ranges throughout the water column and may not follow a daily vertical migration.

These conclusions should not be interpreted to mean that the diving patterns of Weddell seals are completely unpredictable. Most Weddell seal dives occur in 8-12 hr bouts, are between 10-13 min long, and are to depths of 150-200 m. It would be unusual, for example, to observe a large number of dives to depths greater than 500 m, and in this study, less than one-half of one percent of all dives were in this depth range. Similarly, it would be uncommon to observe a bout of dives longer than the calculated ADL; no such series was observed in the six seasons of work reported here. Finally, it would be unusual to record hunting dives that had extended surface intervals between dives. Most such dives occur in a series and are not characterized by long recovery times before the next dive.

There are probably many subtle patterns in the diving data presented here that have gone unnoticed. In the last few years, the amount of free ranging diving information that has been gathered from marine mammals using remote recorder and satellite linked devices has expanded greatly, but our abilities to interpret the information has not kept the pace. Some projects use analysis of frequency of certain dive types to attempt to understand diving behavior (Le Boeuf et al. 1989). Others use swimming speed patterns to interpret behavior (Ponganis et al. 1990), and others use average daily metabolic rates as the basis for comparisons (Costa 1991). As of yet, there is no consistent, widely accepted analytical technique that is broadly used to interpret diving behavior in pinnipeds. Thus, we present these data knowing that there is much more information in the records than what is discussed here and that methods may be developed in the future that will facilitate the extraction of that information.

SUMMARY

FEEDING HABITS

Fish are the most common prey items and *Pleuragramma antarcticum* accounts for nearly all fish consumed. There was no seasonal or geographical alteration in the consumption of fish by the seals.

AVERAGE DIVING DEPTH

Less than one third of the Weddell seal dives were deeper than 400 m, less than one tenth were deeper than 500 m and only one exceeded 600 m. Average diving depths were shallower at White Island than at McMurdo Sound. There were no seasonal differences in average dive depth at either White Island or McMurdo. There was an annual difference in average diving depth between January 1979 and January 1981 at McMurdo.

DIVING DEPTH FREQUENCY DISTRIBUTION

The frequency distribution of diving depths was different between all sites and seasons. In all areas, the December and January diving depth distributions showed a tendency to shallower diving than at other times.

AVERAGE DIVING DURATION

Only 16 dives exceeded 50 min duration and 13 of these were from seals diving from the experimental sea ice hut laboratory. The longest dive recorded was from the hut at slightly over 82 min. Average diving durations for all seasons and sites were similar.

DISTRIBUTION OF DIVING DURATION

Diving duration distributions differed geographically and seasonally with the exception of January 1979 and 1981 at McMurdo, which were similar.

FREQUENCY OF DIVING

Hourly patterns of diving frequency were not uniform except during the winter at White Island. During the winter darkness, most dives occurred during the "daylight" hours whereas during the summer, most dives occurred during the "night."

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APPENDIX

Summary of dive records collected from free ranging seals in McMurdo Sound (McM), White Island (WI), and Terra Nova Bay (TNB). Records were also collected from seals diving from an experimental site on the sea ice in McMurdo Sound (Hut). Mean values for depth and duration are given with \pm standard deviations.

Seal	Location	Date	Record Length (hours)	Total Dives	Mean Depth (m)	Maximum	Mean Duration (min)	Maximum	Sex	Mass (kg)
1	McM	9/78	284	722	133	555	11.8 \pm 7.2	53	M	408
2	McM	9/78	219	544	76 \pm 70	345	11.3 \pm 7.7	43	M	358
3	McM	9/78	268	418	134 \pm 119	429	13.6 \pm 8.7	37	F	385
4	McM	9/78	226	419	83 \pm 100	457	6.9 \pm 5.7	42	F	385
5	McM	10/78	39	83	272 \pm 156	438	14.7 \pm 6.8	30	F	381
6	McM	11/78	58	159	235 \pm 208	523	10.5 \pm 6.9	32	F	385
7	McM	11/78	105	76	44 \pm 61	370	6.5 \pm 6.1	28	F	NA
8	McM	11/78	94	213	85 \pm 140	396	5.7 \pm 6.4	24	F	407
9	McM	11/78	14	88	33 \pm 77	378	4.5 \pm 3.3	22	F	422
10	McM	11/78	20	47	183 \pm 183	489	12.1 \pm 7.8	26	F	443
11	McM	11/78	45	106	222 \pm 186	415	11.6 \pm 7.9	51	F	335
12	McM	12/78	126	193	247 \pm 177	442	13.5 \pm 7.4	39	M	342
13	McM	12/78	46	190	124 \pm 147	401	6.3 \pm 5.5	23	M	481
14	McM	12/78	58	147	223 \pm 187	484	10.7 \pm 8.8	24	M	447
15	McM	12/78	18	130	76 \pm 77	247	6.5 \pm 6.4	20	M	454
16	McM	12/78	73	83	103 \pm 120	401	6.8 \pm 7.9	29	F	490
17	McM	1/79	55	112	50 \pm 44	257	9.5 \pm 6.0	29	F	458
18	McM	1/79	90	181	57 \pm 59	372	NA	NA	F	421
19	McM	1/79	134	308	64 \pm 40	400	10.7 \pm 3.6	22	F	339
20	McM	1/79	92	180	93 \pm 87	432	12.9 \pm 5.3	39	F	404
21	McM	1/81	87	188	97 \pm 48	270	9.7 \pm 3.4	22	NA	245
22	McM	1/81	180	284	142 \pm 85	523	10.7 \pm 4.0	25	NA	272
23	McM	1/81	106	236	144 \pm 62	410	12.9 \pm 4.5	27	F	445
24	McM	1/81	105	83	122 \pm 54	260	10.8 \pm 5.5	31	NA	390

(Continued On Next Page)

APPENDIX (Continued)

Seal	Location	Date	Record Length (hours)	Total Dives	Mean Depth (m)	Maximum	Mean Duration (min)	Maximum	Sex	Mass (kg)
25	McM	1/81	161	146	143 ± 84	319	14.2 ± 6.3	40	NA	NA
26	McM	1/81	141	372	121	460	NA	NA	F	NA
27	McM	1/81	72	292	108	330	NA	NA	M	367
28	McM	1/81	411	933	NA	560	NA	NA	F	278
29	McM	1/81	139	365	131	220	NA	NA	M	353
30	McM	1/81	210	543	140	350	NA	NA	M	NA
31	McM	8/81	193	440	138 ± 77	383	11.9 ± 4.8	26	F	363
32	McM	8/81	145	257	279 ± 206	560	14.0 ± 6.5	25	F	NA
33	McM	9/81	173	454	172 ± 137	626	NA	NA	F	NA
34	McM	9/81	276	700	80 ± 69	488	11.7 ± 6.6	33	F	517
35	WI	12/78	81	86	68 ± 44	155	10.8 ± 6.3	23	F	506
36	WI	12/78	239	240	64 ± 41	137	12.2 ± 6.1	25	F	451
37	WI	1/81	256	388	56 ± 29	164	12.2 ± 4.2	22	F	611
38	WI	1/81	96	128	58 ± 44	241	13.6 ± 3.9	29	F	522
39	WI	1/81	140	196	69 ± 40	149	12.0 ± 7.0	40	F	526
40	WI	1/81	160	292	69 ± 29	171	11.3 ± 4.7	38	F	317
41	WI	3/81	16	323	117 ± 38	272	15.3 ± 4.3	33	F	423
42	WI	4/81	195	401	66 ± 45	193	10.1 ± 4.8	28	F	686
43	WI	4/81	138	258	NA	260	15.4	48	F	626
44	WI	5/81	237	438	88 ± 54	311	16.7 ± 8.9	41	F	617
45	WI	2/81	216	1405	33	>218	NA	NA	F	686
46	WI	2/81	312	973	59	>218	NA	NA	F	526
47	WI	3/81	456	1352	34	>218	NA	NA	M	554
48	WI	3/81	504	2871	37	>218	NA	NA	M	426
49	WI	3/81	120	89	29	>100	NA	NA	M	268
50	WI	6/81	456	1653	31	>218	NA	NA	F	617

APPENDIX (Continued)

Seal	Location	Date	Record Length (hours)	Total Dives	Mean Depth (m)	Maximum	Mean Duration (min)	Maximum	Sex	Mass (kg)
51	TNB	12/86	57	136	72 ± 56	174	7.2 ± 5.0	20	M	247
52	TNB	12/86	84	126	152 ± 110	376	12.5 ± 7.6	26	M	450
53	TNB	12/86	65	163	168 ± 39	357	14.0 ± 4.1	22	F	266
54	TNB	12/86	107	140	134 ± 49	265	13.1 ± 4.1	21	M	227
55	HUT	10/77	23	14	202 ± 86	>300	28.7 ± 14.8	53	F	397
56	HUT	11/77	91	114	156 ± 95	>300	10.7 ± 10.3	48	M	445
57	HUT	11/77	90	277	131 ± 94	>300	8.0 ± 6.7	41	F	429
58	HUT	11/77	48	40	176 ± 102	350	16.8 ± 11.4	57	M	386
59	HUT	10/87	NA	39	NA	NA	10.8 ± 2.2	16	M	NA
60	HUT	11/87	NA	395	175 ± 60	246	6.8 ± 1.9	13	F	123
61	HUT	11/87	NA	114	NA	NA	12.9 ± 11.0	82	F	377
62	HUT	11/87	NA	62	140 ± 98	438	14.2 ± 12.2	46	M	404
63	HUT	12/87	NA	99	NA	NA	8.9 ± 7.3	38	F	328
64	HUT	12/87	NA	103	205 ± 99	337	10.5 ± 6.3	38	M	333
65	HUT	12/87	NA	79	NA	NA	8.8 ± 8.4	36	M	310
66	HUT	10/88	NA	77	NA	NA	16.5 ± 14.8	>71	F	376
67	HUT	11/88	NA	65	145 ± 101	433	8.1 ± 8.5	43	M	438
68	HUT	12/88	NA	86	NA	NA	12.0 ± 10.7	65	M	402
69	HUT	12/88	NA	129	NA	NA	12.3 ± 10.6	56	M	448

TABLE 1
Frequency of occurrence of prey remains in Weddell seal fecal samples.

Number of Samples	Date	Number of samples containing:		
		Fish	Invertebrate	Cephalopods
McMurdo Sound:				
14	July	13	13	2
23	Aug	21	13	3
19	Sept	15	10	1
36	Oct	33	16	0
39	Nov/Dec	34	13	1
6	Jan	6	2	0
Total	137	122	67	7
White Island:				
11	Jan-April	9	4	1
5	May-August	5	1	0
13	Oct/Nov	5	8	8
Total	29	19	13	9

TABLE 2

Occurrence of otoliths in fecal samples

	Number of Fecal Samples	Otoliths
<i>Pleuragramma antarcticum</i>	121	2991
<i>Pagothenia borchgrevinki</i>	10	43
<i>Trematomus bernachii</i>	3	51
<i>Trematomus centronotus</i>	1	52

TABLE 3

Occurrence of cephalopod beaks in fecal samples

	Number of fecal samples	Number of beaks:	
		octopus	squid
White Island	9	42	88
McMurdo	7	26	6

TABLE 5Seasonal averages \pm SD for diving duration and depth in McMurdo Sound seals

Date	Average Duration (min)	Average Depth (m)	Number of Seals	Number of Dives
Aug-Sept	12.5 \pm 1.3	167 \pm 83	4	1851
Sept-Oct	11.6 \pm 3.0	139 \pm 79	5	2186
Oct-Nov	8.5 \pm 3.3	200 \pm 14	6	689
Nov-Dec	8.8 \pm 3.2	154 \pm 76	5	743
Jan 79	11.0 \pm 1.7	66 \pm 57	4	781
Jan 81	11.7 \pm 1.8	128 \pm 66	10	3442
<hr/>				
Kruskal-Wallis				
<i>p</i>	0.571	0.463	-	-

Analysis of these means using the Kruskal-Wallis technique showed no significant differences for diving duration or depth in the different seasons. However, there was a significant difference in diving depth pattern ($p < 0.001$, Kolmogorov-Smirnov test) when the same site was studied in January 1979 and January 1981.

TABLE 7
Dive pattern by hour of day

Location	Number of Dives	Mode (hr)	Trough (hr)	Chi X²_p
Huts	1697	1500,1100	2000-0100	≤ 0.01
Aug-McM	1243	0800,1800	0100	≤ 0.005
Sept-McM	1697	1200	2300	≤ 0.005
Oct-Dec-McM	1835	2300	1500	≤ 0.005
Jan 79-McM	779		No significant pattern	
Jan 81-McM	935	0100	1200	≤ 0.005
Jan 81-WI	1004	0500	1300	≤ 0.005
Apr-June-WI	1422		No significant pattern	

Mode and trough value is the hour of day based on a 24 hour clock where the most or the least number of dives occurred. Significance was tested by comparing the observed pattern to a uniform pattern (equal probability of dive occurring at any hour) using Chi X² analysis

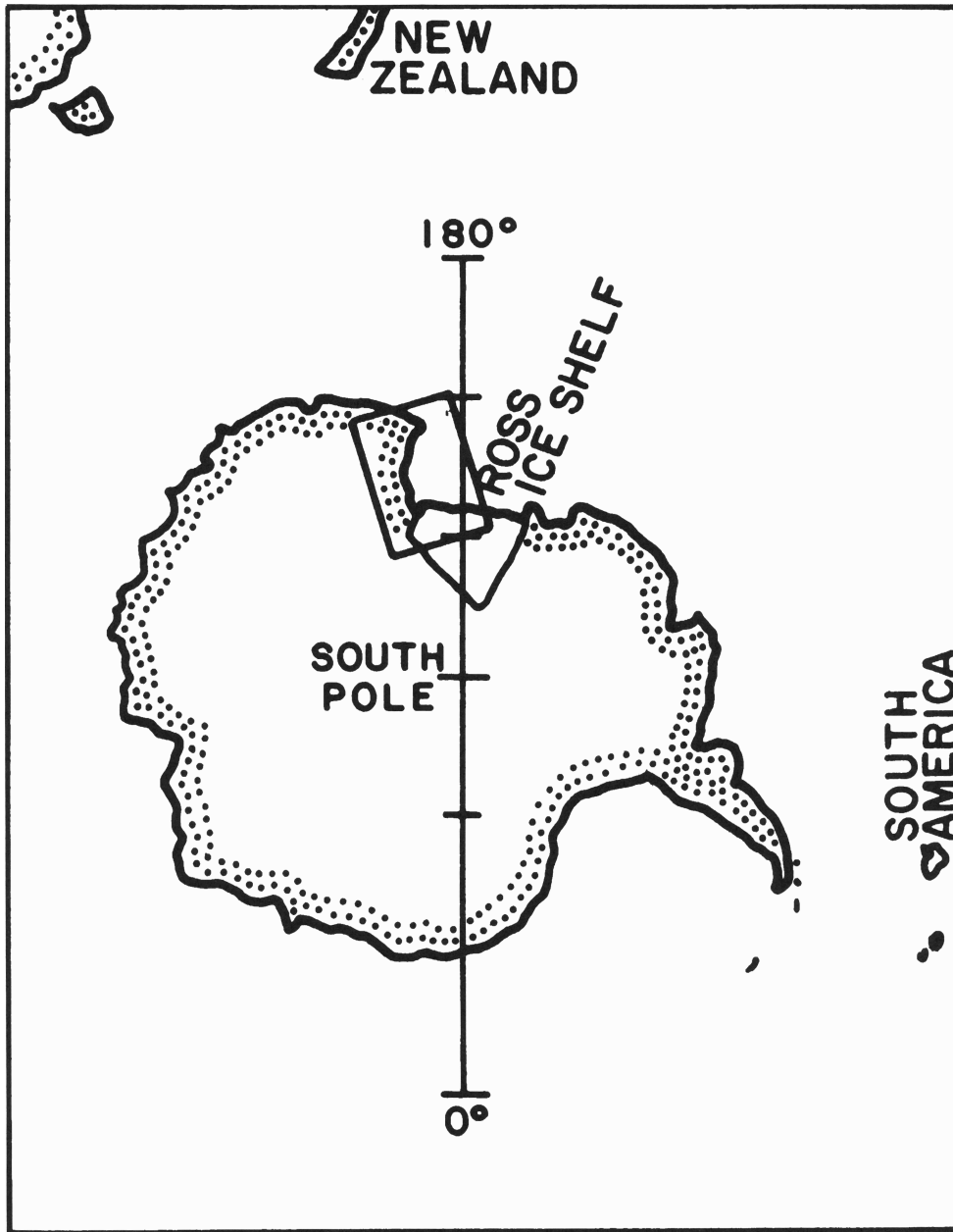


Figure 1a. Map of the Antarctic continent.

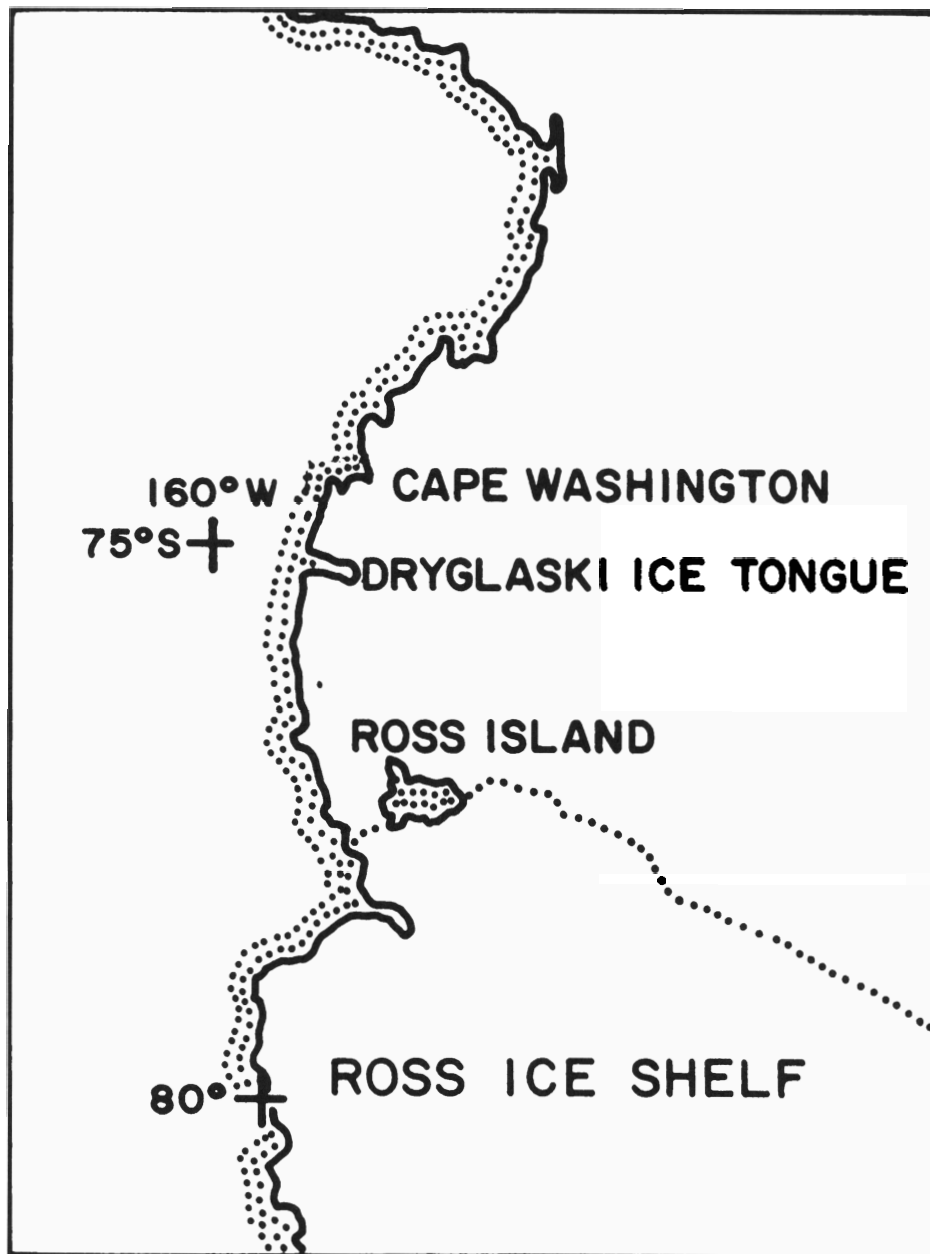


Figure 1b. Map of the Ross Sea sector showing the location of Cape Washington relative to the Ross ice shelf and Ross Island.

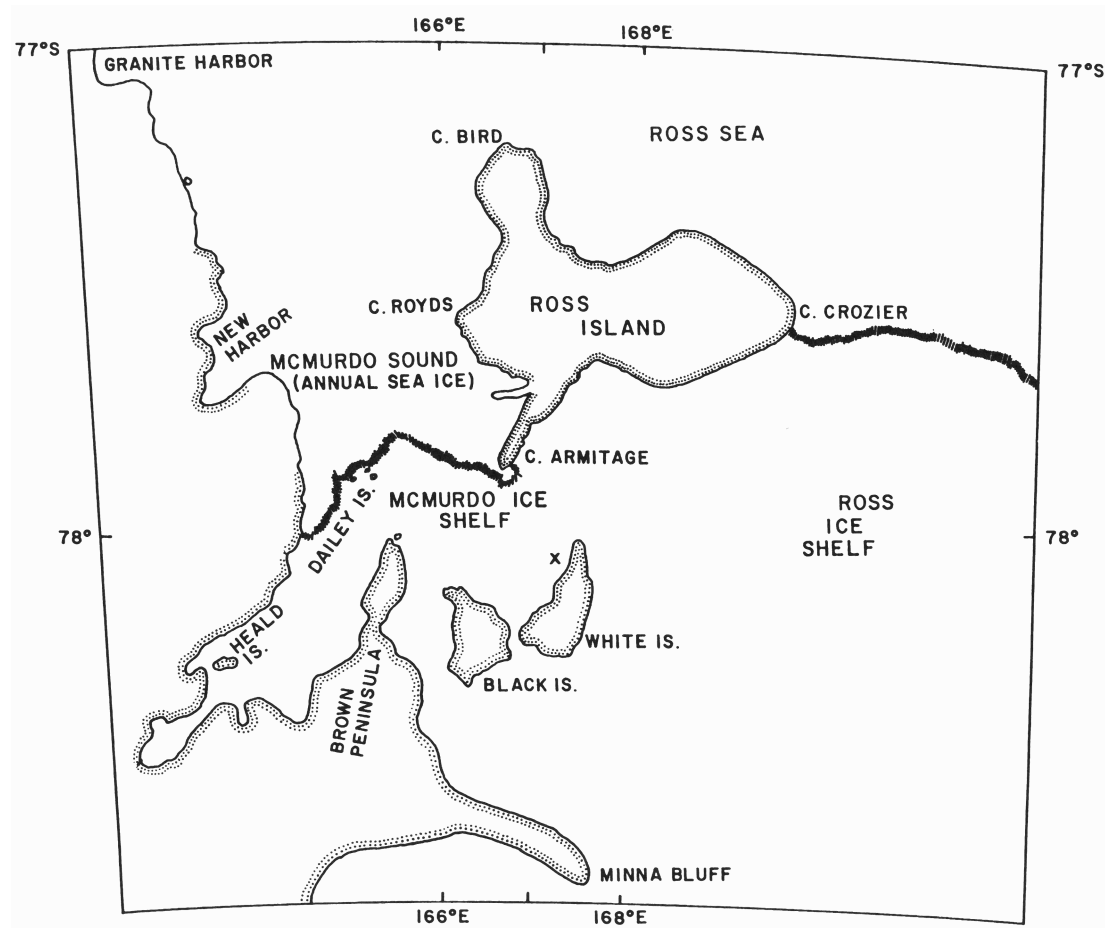


Figure 2. Map of the Ross Sea sector showing the locations of Ross Island, White Island, and the Ross and McMurdo ice shelves. The 1981 winter campsite at White Island is marked by "x."

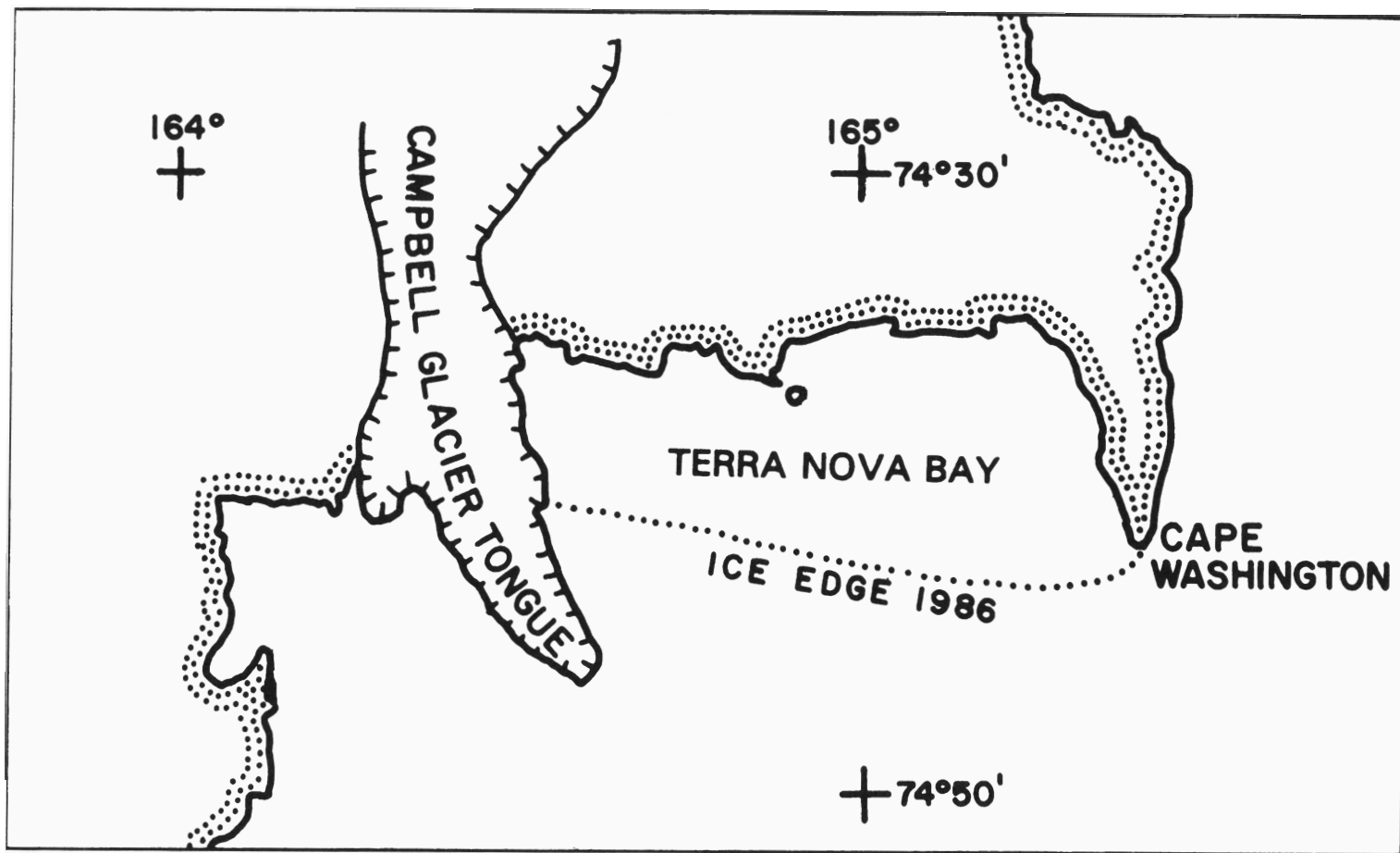


Figure 3. Detailed map of the Cape Washington, Terra Nova Bay study site.

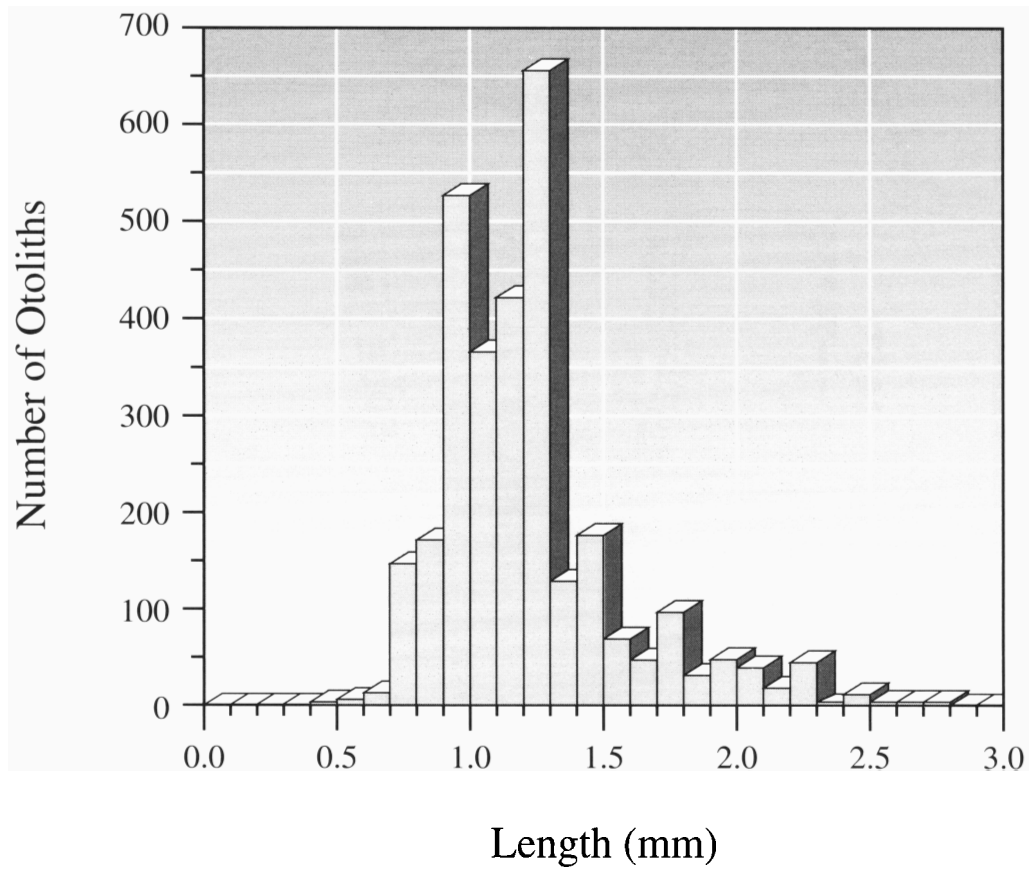


Figure 4. Size histogram of 2,991 *Pleuragramma antarcticum* otoliths recovered from seal fecal samples.

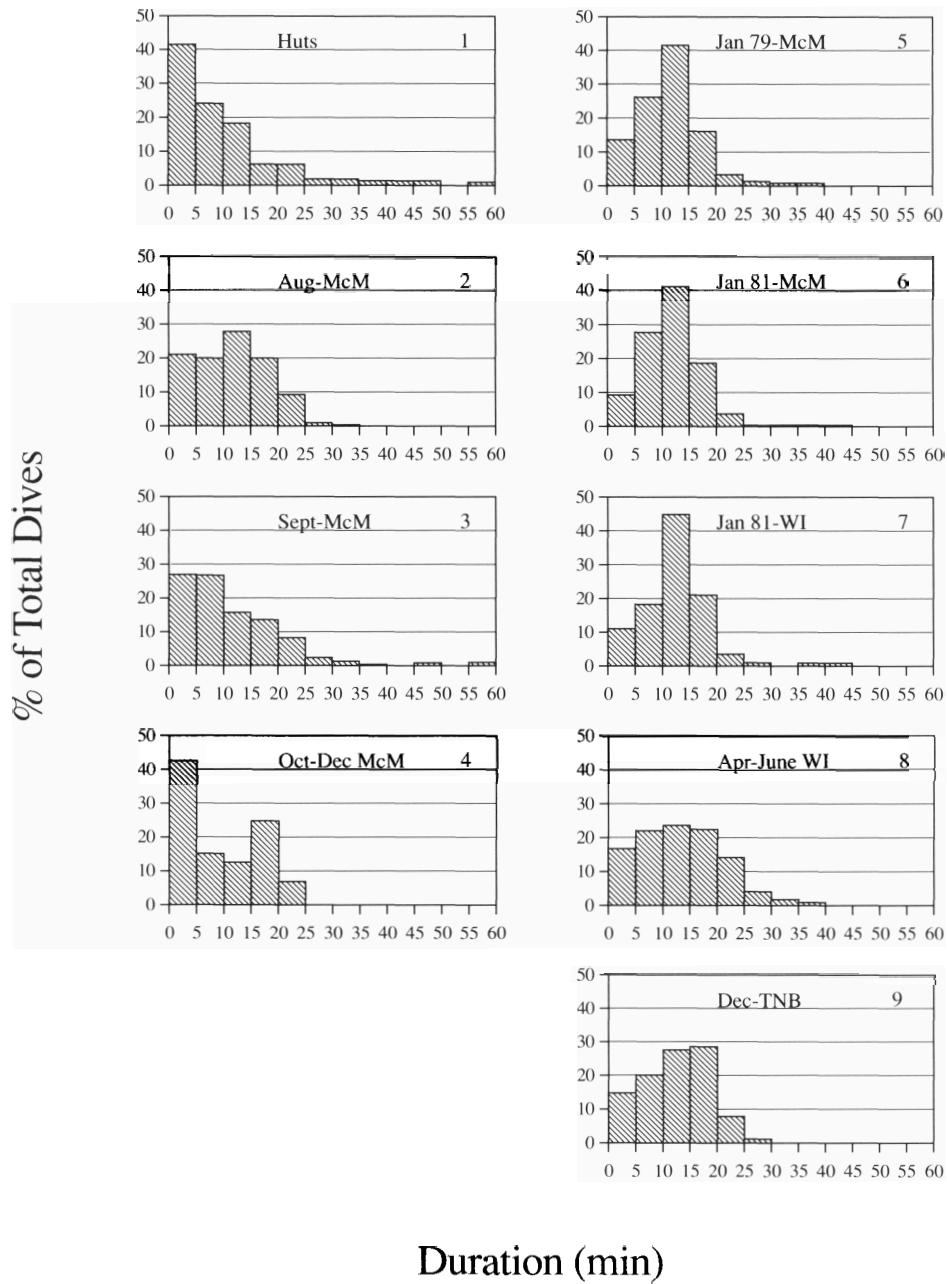


Figure 6. Histograms of diving duration frequencies. Locations and date of each study site are listed on the individual panels. Total number of dives for each panel: Panel 1: 445; Panel 2: 1,834; Panel 3: 2,099; Panel 4: 1,187; Panel 5: 779; Panel 6: 935; Panel 7: 1,004; Panel 8: 1,245; Panel 9: 563.

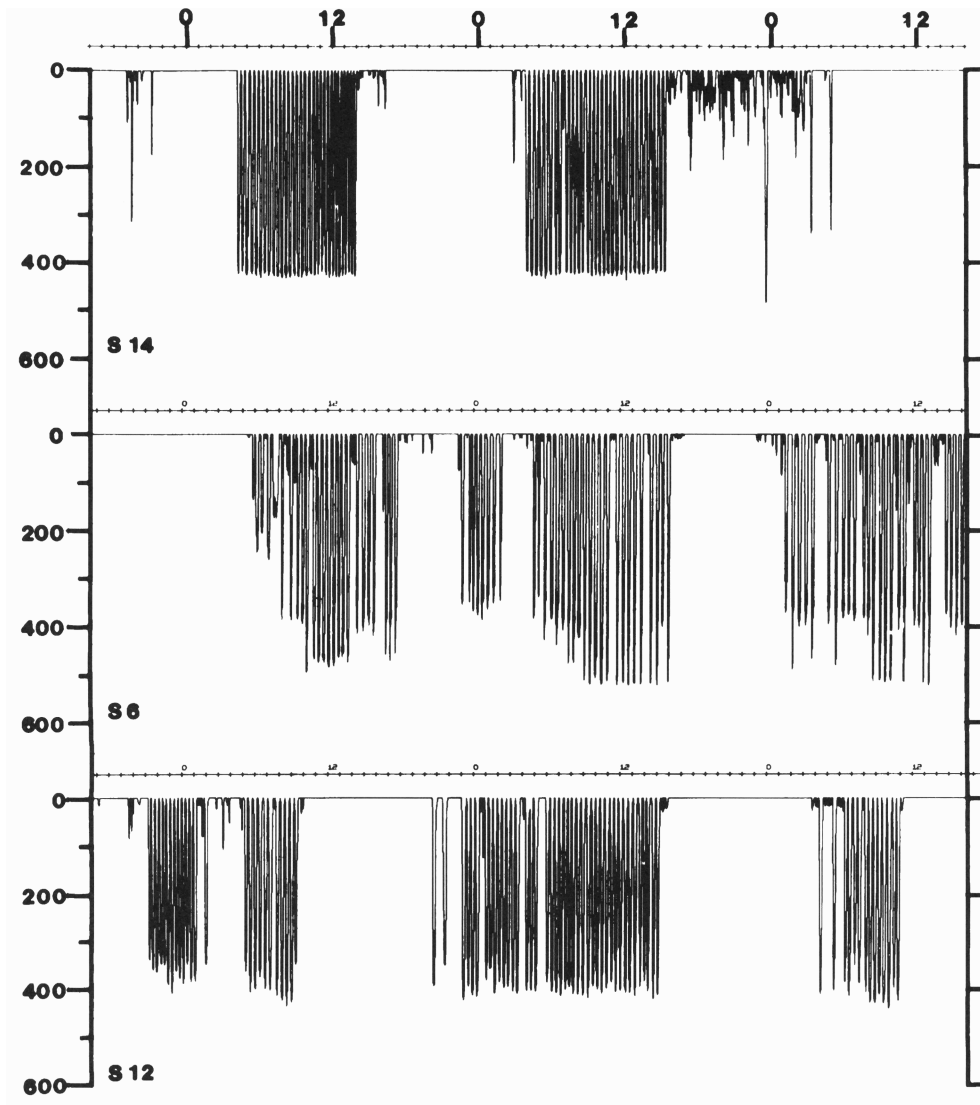


Figure 7. Time-depth profiles of a series of dives over 36 hours for three free ranging seals during November and December in the McMurdo area.

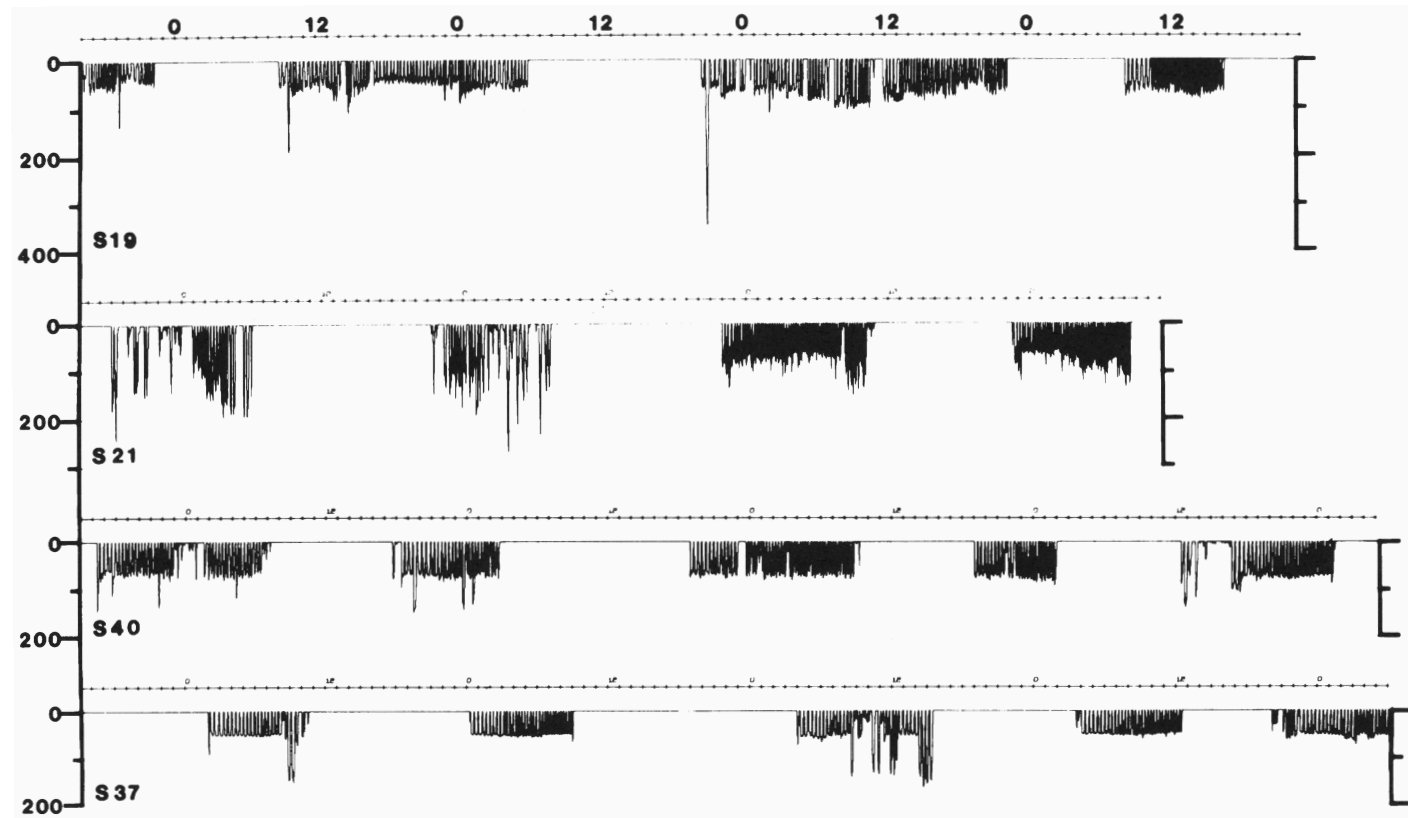


Figure 8. Time-depth profiles of a series of dives over a 4-day period for four seals during January near Scott Base.

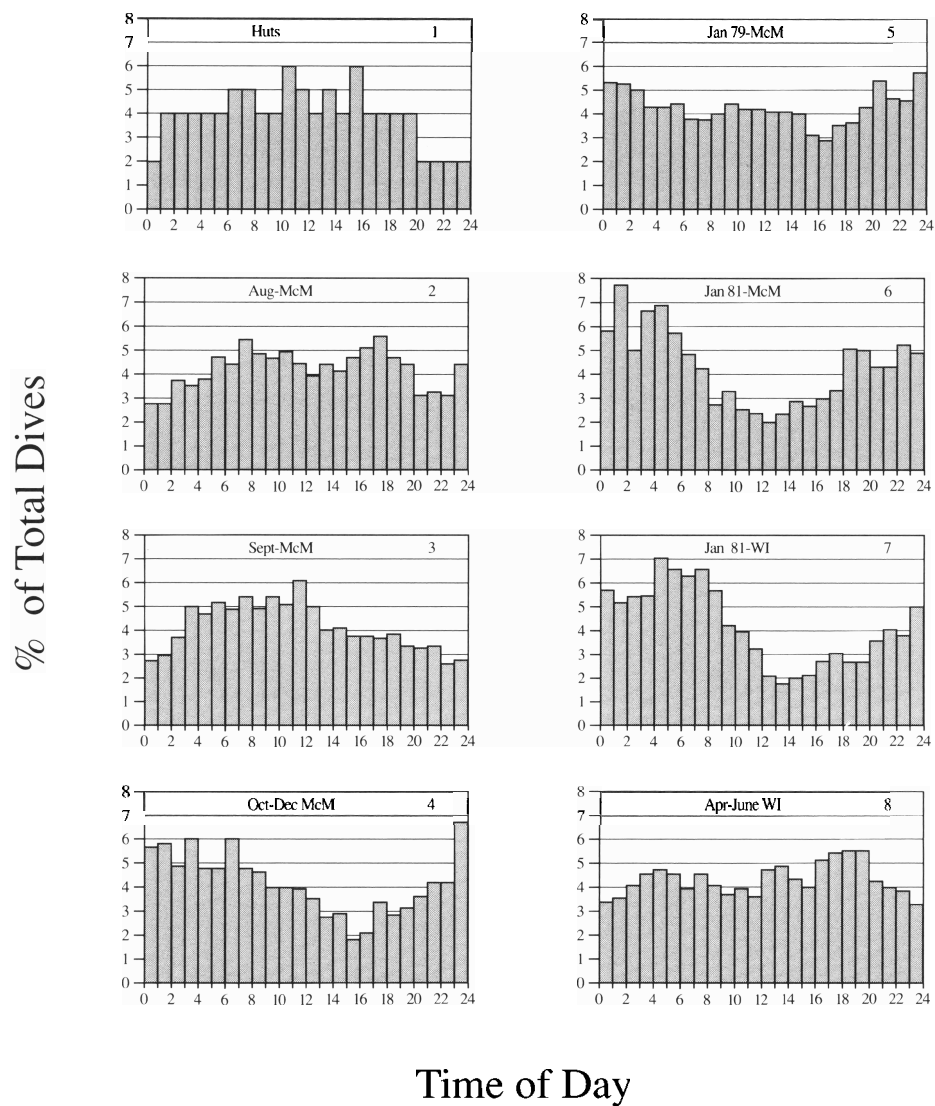


Figure 9. Histograms of dive frequency at a given hour during the day. Locations and date of each study site are listed on the individual panels. Total number of dives for each panel: Panel 1: 445; Panel 2: 1,834; Panel 3: 2,099; Panel 4: 1,187; Panel 5: 779; Panel 6: 935; Panel 7: 1,004; Panel 8: 1,245. Hourly distribution of dives were not collected at Terra Nova Bay.

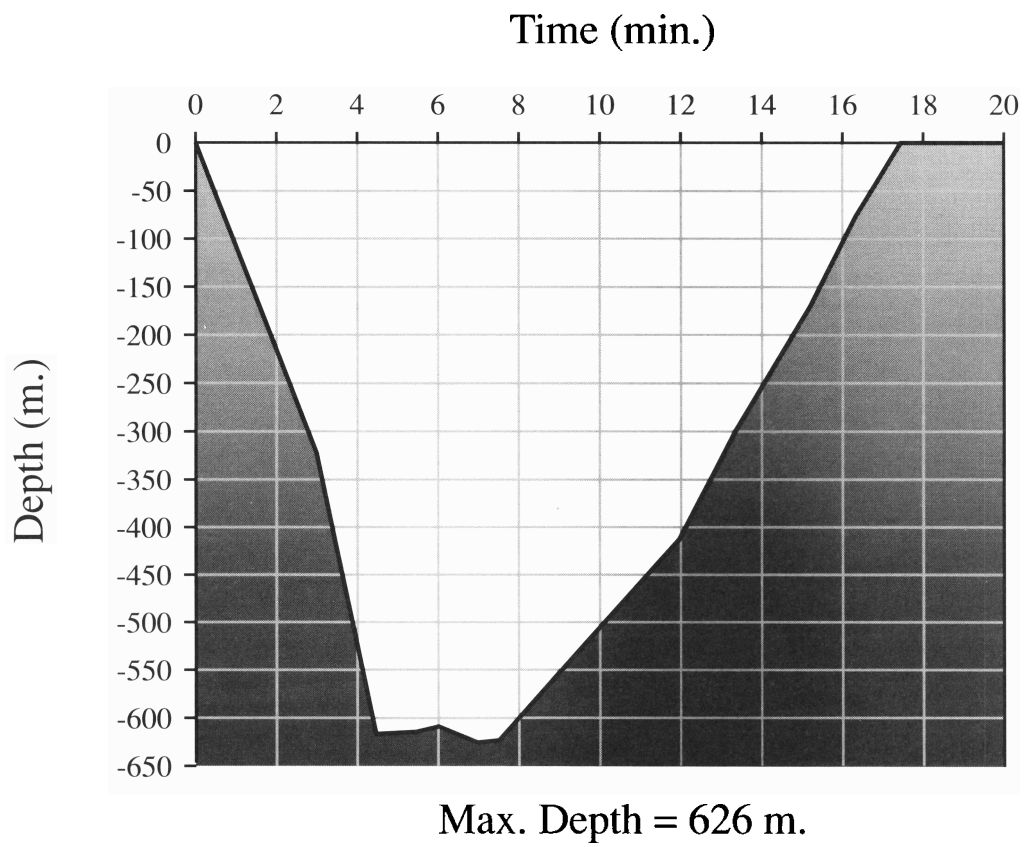
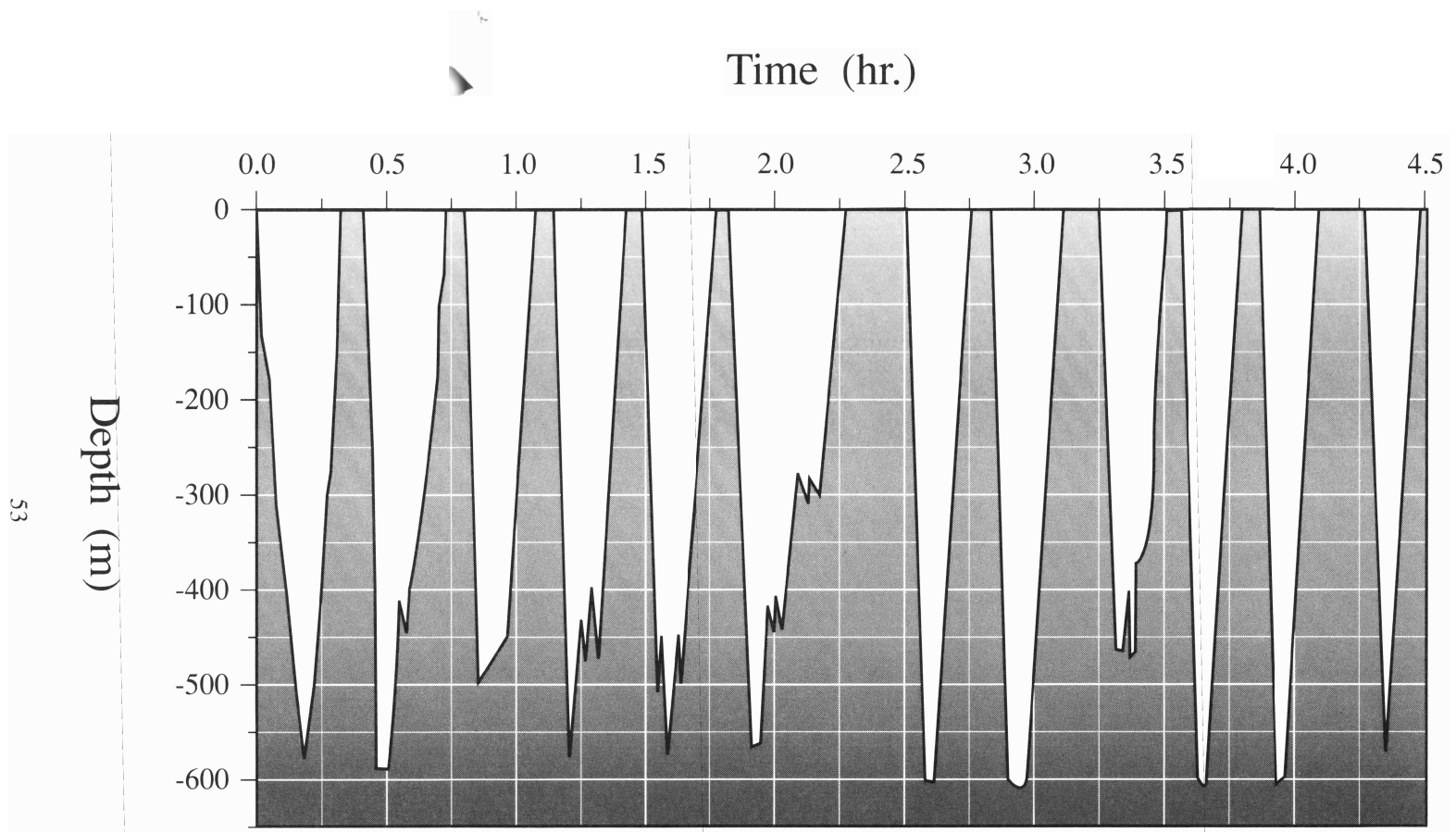


Figure 10. Time-depth profile of a 626 m dive for seal #32 in the McMurdo region during September 1978.



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Figure 11. Time-depth profiles of a bout of dives for seal #32.

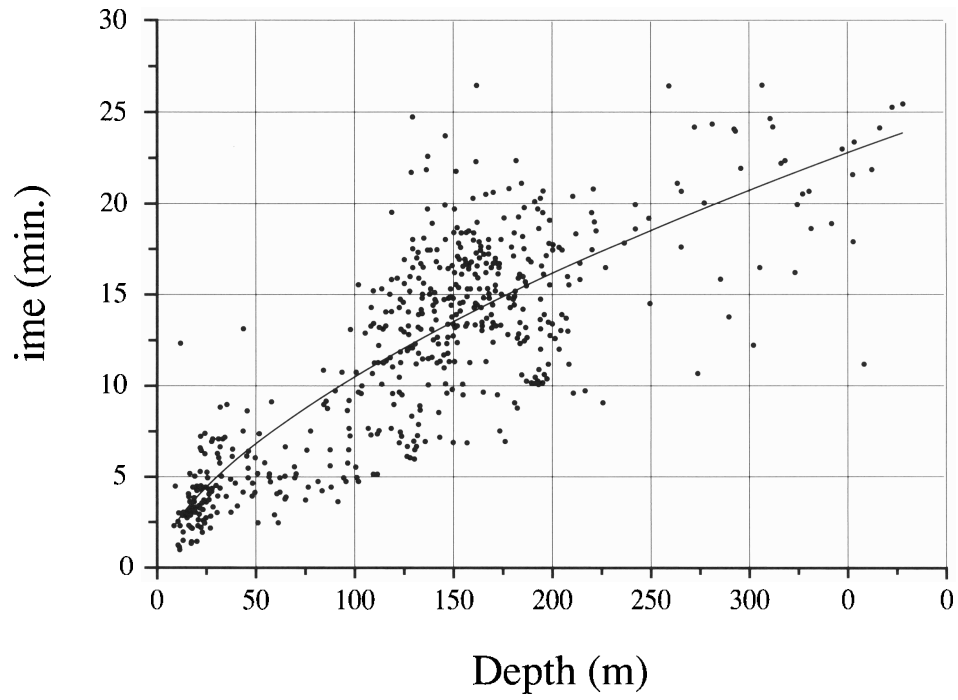


Figure 12. Relationship of diving duration to diving depth for free ranging seals at Terra Nova Bay. Data for 563 dives. The equation describing this relationship is: $\text{Time} = 0.48 * \text{depth}^{0.69}$; $r^2 = 0.85$.