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Foraging behaviour of Weddell seals, and its ecological implications

Abstract Time-depth recorder data of eight adult Weddell seals (*Leptonychotes weddellii*) provided simultaneous dive records over 8 days in the Drescher Inlet, eastern Weddell Sea coast, in February 1998. The seals primarily foraged within two depth layers, these being from the sea surface to 160 m where temperature and salinity varied considerably, and near the bottom from 340 to 450 m where temperature was lowest and salinity highest. While both pelagic and benthic diving occurred during daylight, the seals foraged almost exclusively in the upper water column at night. Trawling during daytime confirmed that *Pleuragramma antarcticum* were by far the most abundant fish both in the pelagial and close to the bottom. Pelagic night hauls at 110–170 m depth showed highly variable biomass of *P. antarcticum*. The temporal changes in the local abundance of *P. antarcticum*, particularly in the pelagial, may explain the trends in the seals' pelagic and benthic foraging activities. This study describes the jaw movements of a hunting seal, which are presumably indicative of feeding events. Trophic links from the Weddell seal to fish, zooplankton and krill, *Euphausia superba*, are discussed.

Introduction

Research projects that focus on the ecology of the Antarctic sea-ice zone require investigations on the

trophic links between top predators and their prey. The Weddell seal is adapted to exploit coastal shelf waters, which are largely covered by fast ice for most of the year. Complementary fishery and hydrographic data from locations where Weddell seals are diving and foraging are sparse. *Pleuragramma antarcticum* is the dominant pelagic fish in the Ross Sea (e.g. DeWitt 1970) and Weddell Sea (Hubold 1985) and, consequently, the main prey for Weddell seals in the Ross Sea (e.g. Castellini et al. 1984; Burns et al. 1998) and Weddell Sea (Plötz 1986). The present paper attempts to relate the diving behaviour of the Weddell seal both to the vertical distribution of its principal prey and to local hydrographic processes in a fast-ice environment that is characterised and strongly influenced by the seasonal ice break-up, particularly during late summer.

Materials and methods

During the EASIZ (II) Weddell Sea cruise of RV *Polarstern*, a joint seal-fisheries project was carried out from 26 January to 25 February 1998 at Drescher Inlet (72°52'S, 19°26'W), a 25-km-long and 1- to 2-km-wide crack in the Riiser Larsen Ice Shelf. The sea bed under the ice shelf extends over 100 km to the nearest grounding line of Dronning Maud Land (Schenke et al. 1998). According to bathymetric surveys of RV *Polarstern* (Graffe and Niederjaser 1997), the depth of the seafloor inside the inlet ranges from 430 m in the inner section to 380 m over a central 6-km-wide bank, and to 520 m at the inlet mouth. The depth outside the inlet gradually increases, reaching the 600-m isobath about 2 km distant from the inlet mouth.

Recording and processing of seal data

The seal studies were conducted from a camp on the ice shelf. Twenty-five Weddell seals were equipped with time-depth recorders (TDRs) (Driesen and Kern, Bad Bramstedt, Germany). Strong gales and sea swell induced ice break-up, which was most intensive from 13 to 16 February. Over a few days, the fast ice progressively retreated into the inlet so that the recapture of 11 instrumented seals was impossible. For this study, the data sets of eight TDRs were selected as they provided simultaneous records which allowed a direct comparison of the diving and haul-out patterns of eight seals (three males, five females) over a period of 8 days (9–17

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February). Immobilisation and deployment techniques used in this study followed Bornemann et al. (1998). The TDRs (8 bit, 130 kb) measured hydrostatic pressure (0–80 bar) at 8-s intervals, which allowed continuous data records for a maximum of 12 days. The logger housing, a titanium tube, was 12×1.8 cm. An additional reed-contact-magnet logger was deployed on 5 of the 25 seals fitted with TDRs to measure jaw action and dive depths simultaneously. The glass-encapsulated reed-contact switch and its shielded extension cable (both 2 mm in diameter) were coated with polyurethane resin for stabilisation and protection against seawater. The cable was screw-sealed where it led into the logger housing. The reed-contact and magnet (10×10×2 mm) were glued onto the hair-covered parts of the upper and lower flews, respectively. The reed-contact was disengaged (switched) by jaw movement (mouth opening), and the number of jaw action switches totalled over the 8-s measuring intervals. The synchronous link between the dive- and jaw-data information was achieved using the computer program Loglink (Jensen Software Systems, Germany). The independent DOS-application was programmed to analyse the logger-generated binary files. The minimum depth that was considered to be a dive was set at 6.25 m, i.e. twice the resolution of the pressure transducer. During analysis, each dive was subdivided into a descent, bottom and ascent phase, followed by its successive surface interval. Timing of the start and end of all phases was based on user-defined thresholds and slope values for the rate of depth changes per unit time. The median maximum dive depth (used in Figs. 2, 4, 5) was calculated from all 8-s sampling points recorded in the bottom phase of a dive. The bottom phase was user-selected and defined as the period spent at maximum depth between the end of the descent and the start of the ascent.

A Seacat SBE19 CTD profiler was deployed through cracks in the ice (Dieckmann and Thomas 1999) to measure hydrographic parameters within the water column of Drescher Inlet.

Fish trawling

Trawling was done from RV *Polarstern*. For the pelagic trawls, a benthopelagic net (25×16 m opening, cod-end mesh size 10 mm) was used; hauls were carried out for ~40 min (38–50 min) at depth, controlled by a Scanmar net sensor system. Demersal trawling was done with a 140-ft standard otter trawl (cod-end inlet mesh size 20 mm). The haul duration was ~15 min (10–17 min) on the ground due to the voluminous by-catch, mainly sponges. Prior to and after trawling, the hydrographic profile of the water column was recorded by CTD. Previous studies on Weddell seals in the Drescher Inlet indicated that pelagic foraging was most common

around 150 m (Plötz et al. 1997). Pelagic trawling (this study) was carried out in this depth layer to identify potential food items of seals. In total, 12 hauls were taken in the inlet. These were six pelagic tows (110–170 m) during two consecutive nights (26–28 Jan.), two pelagic (30–70 m, 150–250 m) and three bottom hauls (~400 m) during daytime (3 and 22 Feb.), and one bottom haul (~400 m) at night (25 Feb.). To measure the vertical distribution pattern of fish during daytime, 3 of the total of 12 trawls were done around noon (1000, 1200, 1400 hours local time) at different depths (close to surface, 30–70 m; pycnocline, 150–250 m; and on the bottom, ~400 m depth). The same depth-stratified sampling procedure was planned for the night-time but due to a broken net this sampling could not be conducted. Fish were identified to species level and individual total length (TL) and wet weight (WW) measured. Numbers and biomass were standardised to 1 h trawling time. Fish guts were examined for prey items. In addition, fish specimens vomited by a seal onto the ice (11 Feb.) were collected and analysed in conjunction with the trawl catches.

Results

Diurnal activity and haul-out

All individual haul-out and diving records for the eight seals, measured over 8 days, were pooled to illustrate the proportion of time the seals spent on the ice and at sea (Fig. 1). At 1200 hours local time, for example, 58% and 42% of seals were hauled-out on ice and at sea, respectively. Of the total of 1,536 h recorded, time spent on the ice was 31% compared to 69% spent at sea. Overall, Fig. 1 shows the seals' preference for hauling-out during daylight and being at sea during darkness. Nocturnal periods at sea generally extended to the early morning hours, and from 0700 hours onwards the seals apparently had a tendency to haul-out onto the ice, with a distinct peak at 1300–1500 hours local time. Nevertheless, even during that peak haul-out not all the seals were on the ice every day nor were they always active during the night, and it was not uncommon to observe a few animals, including instrumented ones, resting on the ice at night-time.

Fig. 1 Diurnal activity and haul-out patterns for Weddell seals ($n=8$) combined for the period 9–17 Feb. 1998. Indented ends of the *black bar* indicate the increase in the duration of night time during the 8-day period

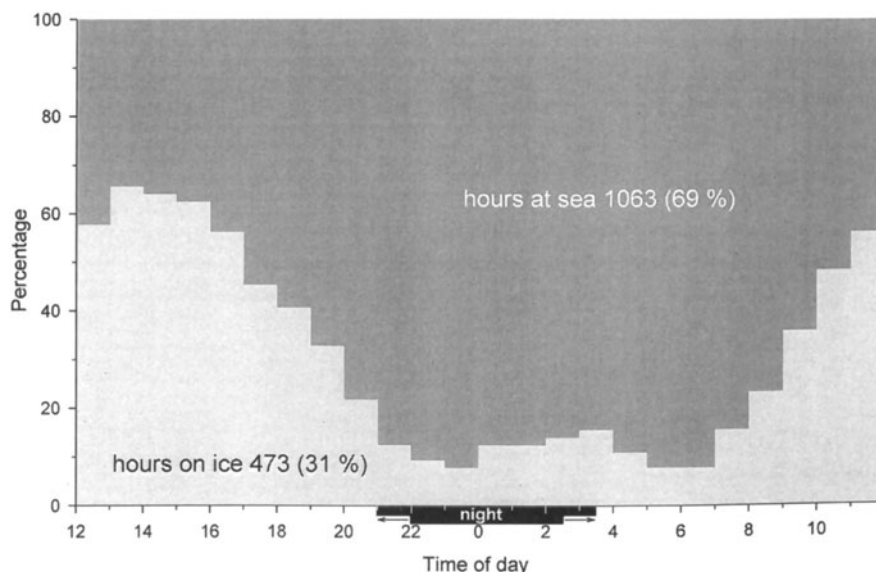
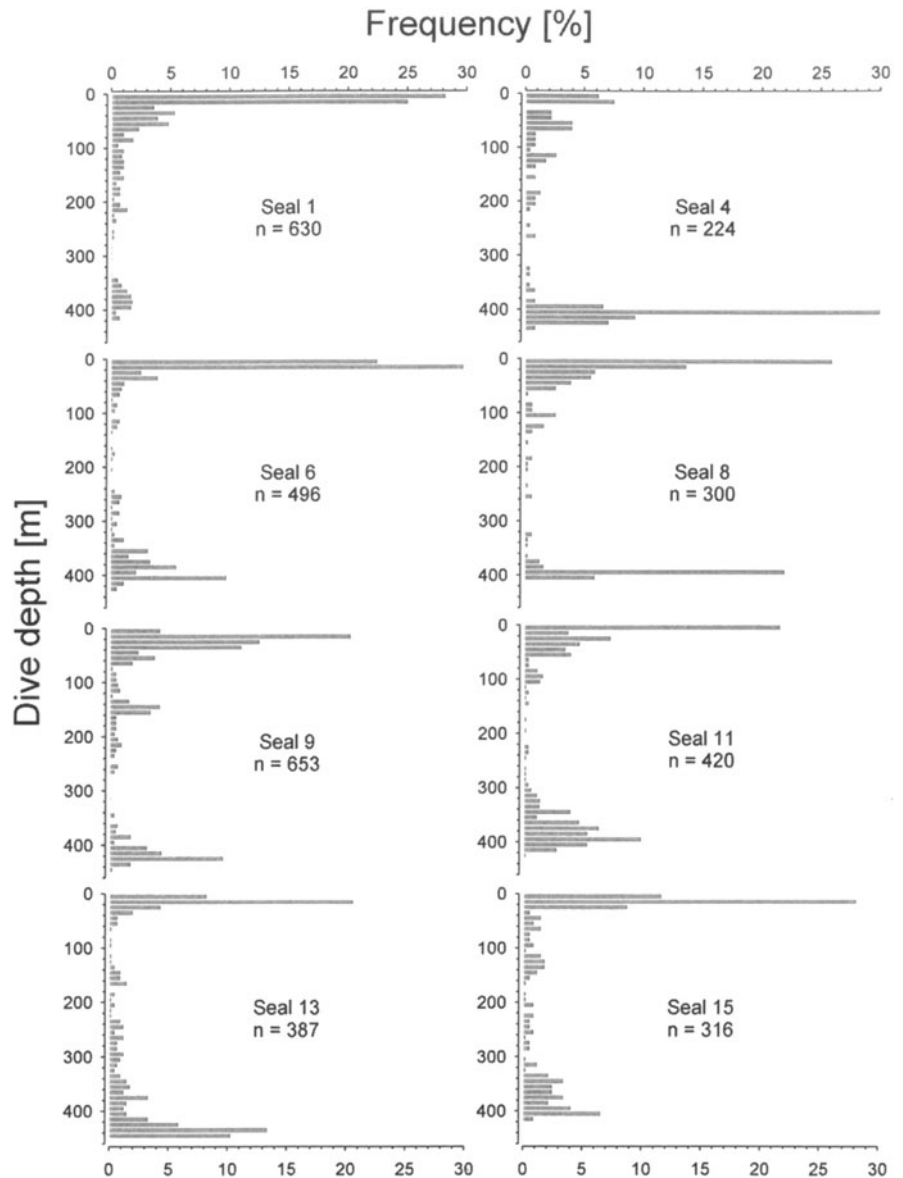


Fig. 2 Frequency distributions of dive depths of Weddell seals ($n=8$) recorded from 9 to 17 Feb. 1998. Original identification number (e.g. Seal 1) and total number of dives for each seal are indicated on the individual histograms



General diving pattern

The frequencies of maximum dive depths were summed for each seal (Fig. 2). The range of benthic dives from 380 to 450 m reflects the irregular bottom topography inside the Drescher Inlet. Dives to 410 m (Seal 8, female), 420 m (Seals 1, male and 15, female), 430 m (Seals 6, female and 11, male), 440 m (Seal 4, female) and 450 m (Seals 9, male and 13, female) were the deepest recorded.

A broad comparison amongst the dive profiles showed considerable variation in dive depths between (ANOVA on ranks: $P < 0.001$) and within individual seals (ANOVA on ranks: P -values between < 0.001 and 0.042), except seal 8 ($P = 0.124$). Series of deeper dives to the seafloor which were alternated with abrupt shifts to series of shallower dives were evident in all the seals studied. Numbers of dives recorded for each seal varied

greatly, with Seal 4 ($n = 224$) diving the least and Seal 9 ($n = 653$) being the most active diver (Fig. 2). Seal 9 performed a few very long dives ($n = 10$); the maximum duration was 67 min and the remaining 9 dives lasted 47–61 min. These dives were single events occurring within a 5-day period (11–16 Feb.), and all were consistent to 150 m (± 20 m) and most of them ($n = 7$) were night-time dives. Seal 15 showed a progressive change in depths (Fig. 3). Deepest dives were made from 0800–1000 hours in the morning (15 Feb.) and then they gradually decreased in depth. At night, foraging was most common around 50 m. After a haul-out period of 2 h on the ice, the animal continued pelagic foraging in the early morning hours, and then dived increasingly deeper. Such sporadic events of a progressive change in depths were evident in all seals but differed in appearance and duration. They commonly lasted 2, 3 or up to 7 h and dive depth over time did not necessarily show a

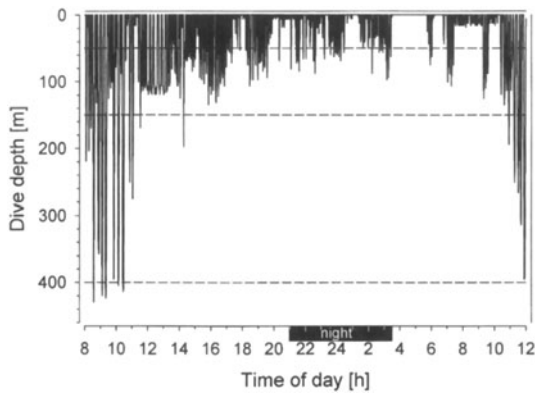
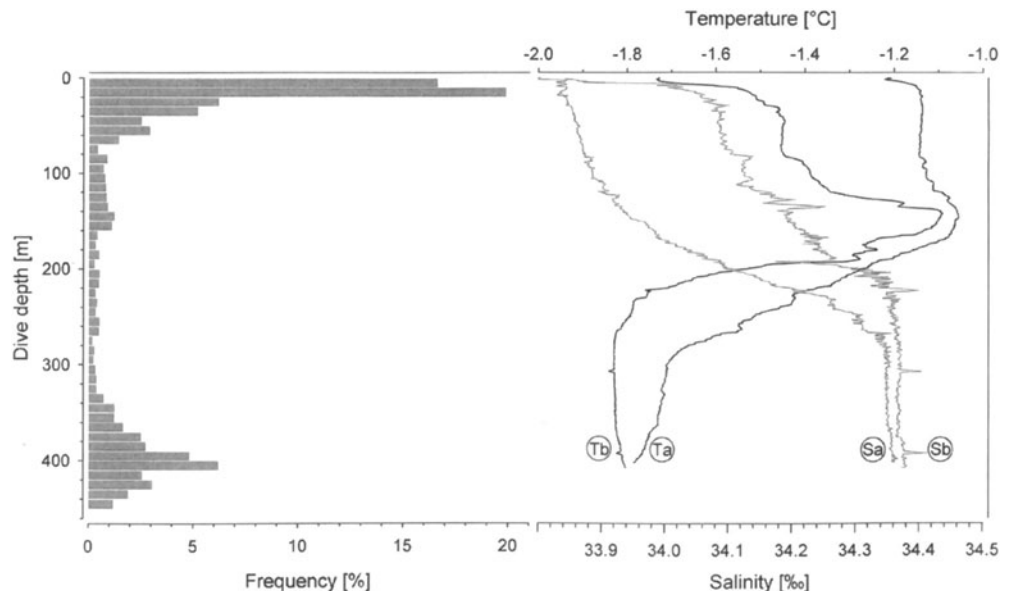


Fig. 3 Diurnal dive pattern of a Weddell seal (Seal 15) during 15/16 Feb. 1998

regular dome-shaped distribution, such as over the maximum record of 28 h presented here (Fig. 3). Most of such dive sequences included a diurnal component, with progressively shallower dives during dusk and progressively deeper dives towards dawn.

The frequency distribution of maximum dive depths for all seals combined is shown in Fig. 4. Highest frequencies were recorded to 70 m (55% of dives). A moderate increase of pelagic diving appeared from 80 to 160 m (9% of dives). The slight increase in this 80- to 160-m depth range is more or less pronounced in all individuals as indicated by additional peaks at these particular depths (Fig. 2). The mid-water layer from 170 to 330 m (6% of dives) was mainly used by the seals to commute so as to reach the seabed, where there was an activity peak at around 400 m. Overall, the seals primarily foraged within two depth layers, these being from the sea surface to 160 m (64% of dives) and from 340 to 450 m (30% of dives).

Fig. 4 Frequency distribution of the depths of all dives ($n=3426$) for Weddell seals ($n=8$) during 9–17 Feb. 1998 combined with temperature and salinity profiles recorded on the day before (T_b and S_b) and 3 days after (T_a and S_a) an intensive ice break-up from 13 to 16 Feb. 1998



The distribution pattern of dive depths is related to CTD profiles (Fig. 4), which show the variation in the water temperature and salinity regime of the Drescher Inlet before and after an intensive ice break-up. A characteristic hydrographic feature is the stable thermo(pycno)cline between 130 and 230 m corresponding to the temperature maximum of -1.05°C at around 150 m. The fast ice was up to 2 m and the underlying platelet-ice layer up to 5 m thick. Before ice break-up, the surface layer was cooled to a depth of about 40 m, forming a weak thermocline in between, while a remnant of warmer water was still trapped between 50 and 150 m. After ice break-up, the upper water column was mixed down to the stable pycnocline, resulting in a warming up of the entire water body above 150 m, and consequent melting of masses of brash and platelet ice, as is reflected by a distinct temperature increase (T_a) and decrease in salinity (S_a). The 150-m depth range of large variation in temperature (T_b and T_a) and salinity (S_b and S_a) coincides with the seals' most intensive pelagic foraging activity, as identified from the frequency of dives to these depths. This situation changed in the mid-water layer between 170 and 330 m where the decrease in foraging activity is consistent with the gradual temperature decrease. A further distinct increase in foraging activity occurred from 340 m depth down to the seafloor where temperature was lowest (T_b and T_a) and salinity highest (S_b and S_a) with little variation.

Figure 5 shows that both dive frequency and dive depth varied with time of day. Of the total of 3,426 dives recorded, 34.9% occurred during the short (max. 6.5 h) night period. According to the seals' diurnal activity (see Fig. 1), dive frequency began to increase at least 2 h before dusk and remained high for about 4 h into the morning crepuscular period. The diurnal pattern in dive depth indicates a preference for foraging deeper during daylight and shallower during darkness (Mann-Whitney

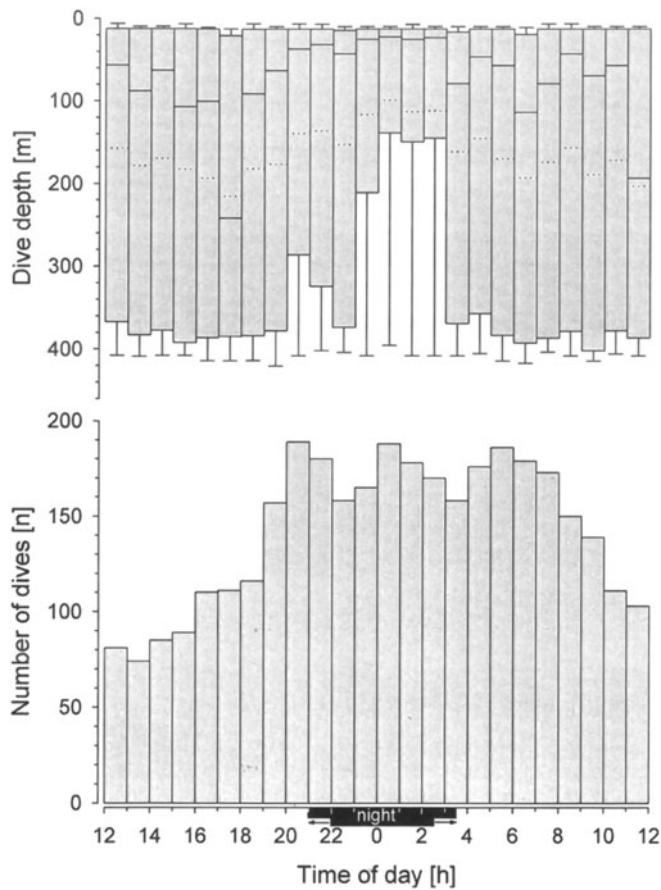


Fig. 5 Box plot (above) and frequency diagram of the diurnal variation in depth and number of all dives ($n=3426$) made by Weddell seals ($n=8$) during 9–17 Feb. 1998. The whisker caps define the 5th and 95th percentiles. Median solid lines, mean stippled lines

rank sum test, $P < 0.001$). For daytime dives, the hourly variation in the medians of the depths (Fig. 5, solid lines) is significantly higher compared to those carried out at night (Mann-Whitney rank sum test, $P = 0.042$). This shows that the seals concentrated their diving activities during daylight hours over a wider depth range by foraging either in the water column above the pycnocline, or considerably deeper down to the seafloor as is also demonstrated in Fig. 4. Night-time dives between 2300 and 0300 hours, in particular, were the shallowest and almost exclusively to less than 220 m, most of them concentrated well above the pycnocline. There was an abrupt change to considerably deeper dives just after sunrise, deep dives continuing throughout the daylight hours.

Feeding dives

Two of five seals instrumented with reed-contact-magnet loggers were not recaptured. The remaining three reed-contact-magnet units provided partial records of up to 6 days, which only in one case (Seal 1) overlapped with

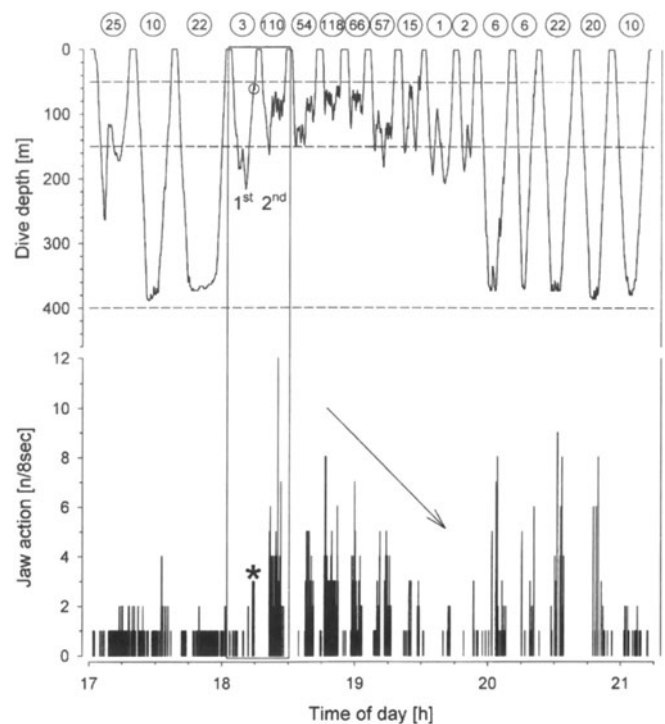


Fig. 6 Synchronous records of diving and jaw activity of a Weddell seal (Seal 1). The sequence of selected dives was measured on 9 Feb. 1998. Jaw action signals (JASs) were accumulated over 8-s intervals. A single JAS means that the seal opened its mouth once within 8 s. Therefore, 2/3/4 JASs in a single vertical stroke translates into 2/3/4 mouth openings within 8 s. Numbers (in circles) correspond to the number of JASs measured during the bottom phase of each dive. Explanation for 1st and 2nd (in frame) see text; asterisk indicates 9 JASs within 24 s coinciding with a short interruption (at 60 m, unfilled circle) in the ascent phase of the 1st dive. Arrow indicates decrease of JASs

the 8-day period of the present study. Figure 6 illustrates one of many scenarios of diving behaviour and concomitant jaw movements. This first demonstration of jaw action was also chosen as it constitutes a representative sample of diving characteristics observed in virtually all individuals studied. Dive duration in this sequence of 17 dives ranged from 9.6 to 22.0 min for the 7 benthic dives and 7.3 to 15.8 min for the 10 pelagic dives. The post-dive intervals at the sea surface were consistently brief (range 1.7–2.9 min). All dives showed a similar rapid descent, followed by a sustained activity period of 0.9–12.4 min bottom time before a rapid ascent. The movements from or to the sea surface sometimes coincided with a short interruption (spike) at various depths. During the bottom time, the seal exhibited up and down movements. This vertical zigzag pattern was most intensive in the bout of nine pelagic dives between 1800 and 2000 hours, with the shallowest two dives being made in mid-period.

During the first three dives, the last two of which reached the seafloor, the seal opened its mouth mostly once per 8-s measuring interval. A significant increase in jaw action signals (JASs) occurred when the seal

switched from benthic to pelagic dives. These signals were most intensive within the 50–150 m depth layer, where a remnant of warmer water was trapped before the ice break-up (Fig. 4). The slight increase in signals (9 JASs within 24 s) in the first pelagic dive (see frame in Fig. 6) coincided with a short interruption (spike) in the ascent at a depth of 60 m. At that particular depth the seal apparently encountered prey in high density because the subsequent (second) dive showed a dramatic increase of up to 12 JASs per 8-s interval, coincident with an intensive zigzag dive pattern, also in the 4 following pelagic dives, covering a range of as much as 60 m. After the second dive, the frequency of signals declined more or less gradually, followed by a subsequent increase in jaw action which coincided with the seal's switching to a series of deep dives about 1 h before sunset.

Natural regurgitation

Haul-out sites of seals often had food remnants on the ice, a grey mixture of partially digested flesh and hard-part remains of prey. On one occasion (11 Feb.; 0930 hours) we observed an apparently gorged Weddell seal which, upon leaving the water, vomited 230 specimens of *P. antarcticum* onto the ice. Their length-frequency distribution is presented in Fig. 7. With the exception of small specimens (3–11 cm) caught by net in the pycnocline, all size classes were represented in the seal's diet. The total wet weight of the regurgitated meal was 7.6 kg, which amounted to an average weight of 33 g per fish. Apart from a few tooth-marks found on only 13 specimens, all fishes were undamaged, apparently caught recently, and swallowed whole. This also shows that the canines and post-canines of the Weddell seal (if used at all) serve to catch and hold but not chew prey items up to 21 cm in length.

Pelagic and bottom trawling

Eleven fish species were caught in eight pelagic trawls (Fig. 8). *P. antarcticum* were by far the most abundant fish (87%), and predominated in biomass (~75%). *Anotopterus pharao*, a pelagic fish predator, occurred in small numbers (1%) but due to its large size (up to 95 cm TL and 490 g WW) this fish contributed about 20% of the total biomass. Abundance and biomass of all other fish species were much lower. Apart from single specimens of adult *Chionodraco myersi*, *C. hamatus*, *Dacodraco hunteri* and *Pagothenia borchgrevinki*, the catches comprised juveniles and larval stages only (Fig. 8). Pelagic trawls also contained considerable amounts of krill, *Euphausia superba*, unidentified gelatinous zooplankton and small numbers of pelagic amphipods, mainly *Themisto gaudichaudii*. The krill biomass in the first night of pelagic trawling (26/27 Jan.: 52.5 kg/h \pm 0.01 SE) was 4 times that of the second night

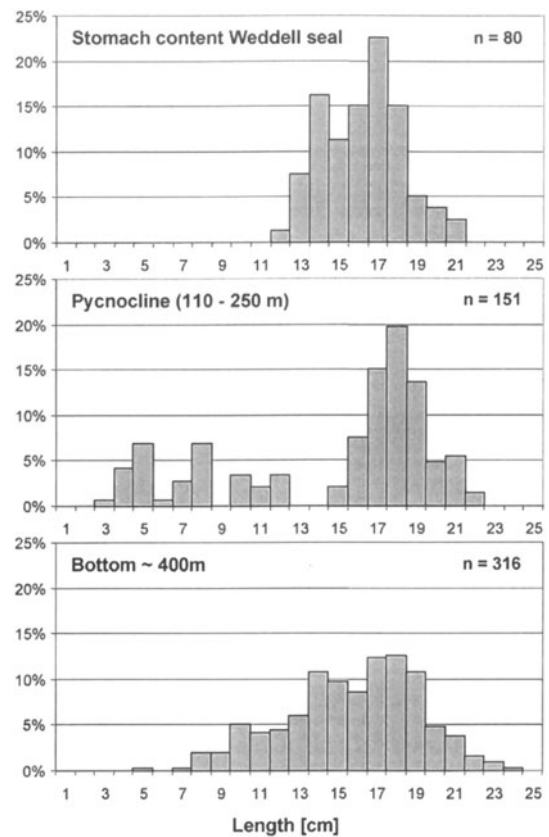


Fig. 7 Length-frequency distribution of *Pleuragramma antarcticum* caught by a Weddell seal (top) by pelagic trawling in the pycnocline (middle) and by bottom trawling (bottom)

(27/28 Jan.: 12.4 kg/h \pm 0.005 SE). The amount of gelatinous zooplankton was about 9 kg/h in both nights.

Demersal catches showed a high diversity in the composition of species (Table 1). A total of 1,179 fish specimens, belonging to 26 species and unidentified Liparididae and Zoarcidae, were caught in 4 bottom trawls. Channichthyids dominated in biomass, followed by nototheniids, which was the most abundant group.

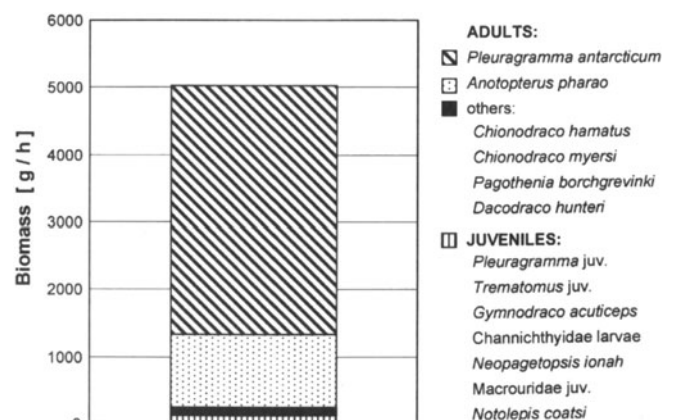


Fig. 8 Biomass and species composition of the pelagic fish community in Drescher Inlet. Average biomass (wet weight) per hour trawling summarised over all pelagic hauls ($n=7$)

Table 1 Catch composition of demersal trawls in Drescher Inlet

Species	% of total biomass	Average number/h
Channichthyidae	59.8	343
<i>Chionodraco myersi</i>	22.6	121
<i>Chionodraco hamatus</i>	15.7	70
<i>Cryodraco antarcticus</i>	19.0	96
<i>Dacodraco hunteri</i>	2.1	47
<i>Pagetopsis maculatus</i>	0.3	8
<i>Chaenodraco wilsoni</i>	<0.1	1
Nototheniidae	30.0	856
<i>Pleuragramma antarcticum</i>	14.0	553
<i>Aethotaxis mitopteryx</i>	0.9	5
<i>Trematomus scotti</i>	1.6	163
<i>Trematomus eulepidotus</i>	5.2	53
<i>Trematomus lepidorhinus</i>	3.2	49
<i>Trematomus hansonii</i>	2.7	9
<i>Trematomus loennbergii</i>	1.8	11
<i>Trematomus nicolai</i>	0.5	2
<i>Trematomus pennellii</i>	0.1	7
<i>Trematomus</i> spp. juv.	<<0.1	3
Bathydraconidae	2.9	85
<i>Gerlachea australis</i>	2.2	77
Other Bathydraconidae	0.7	7
Artedidraconidae	0.4	53
<i>Dolloidraco longedorsalis</i>	0.2	25
<i>Artedidraco loennbergii</i>	<0.1	9
Other Artedidraconidae	0.2	19
Bathyrajidae	6.6	4
<i>Bathyraya maccaiani</i>	6.6	4
Liparididae	0.1	15
Zoarcidae	<0.1	2

Among channichthyid species, the most common fish caught were *C. myersi*. The nototheniid *P. antarcticum*, however, was by far the most abundant fish in both the demersal and pelagic catches.

Vertical distribution of *Pleuragramma antarcticum*

During daytime, the biomass of *P. antarcticum* was highest above the pycnocline (30–70 m), lowest in the pycnocline (150–250 m), and high at the bottom (~400 m) (Fig. 9). A comparable picture of the vertical distribution of *P. antarcticum* cannot be shown for the night-time due to the damaged gear. Nevertheless, the results of 6 pelagic trawls (110–170 m) on 2 consecutive nights indicated that the biomass of *P. antarcticum* was highly variable in this particular depth layer (Fig. 10). During the first night (26/27 Jan.), the highest value in biomass occurred at around midnight and then gradually decreased towards dawn. This finding indicates nightly vertical migration of *P. antarcticum* into this layer of warmer water which corresponds to the temperature maximum of -1.05°C at around 150 m depth (see Fig. 4). The following night (27/28 Jan.), only single specimens of *P. antarcticum* were caught in the same depth layer, and no trend of vertical migration was detectable. The length-frequency distribution of *P. antarcticum* caught between 110 and 250 m depth was bimodal (3–12 cm and 15–22 cm TL). At the bottom,

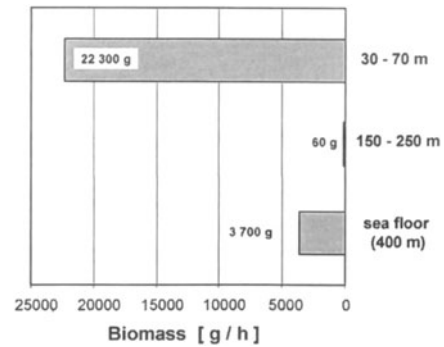


Fig. 9 Vertical distribution of *Pleuragramma antarcticum* in Drescher Inlet during daytime (between 1000 and 1400 hours). Biomass expressed as wet weight per hour trawling

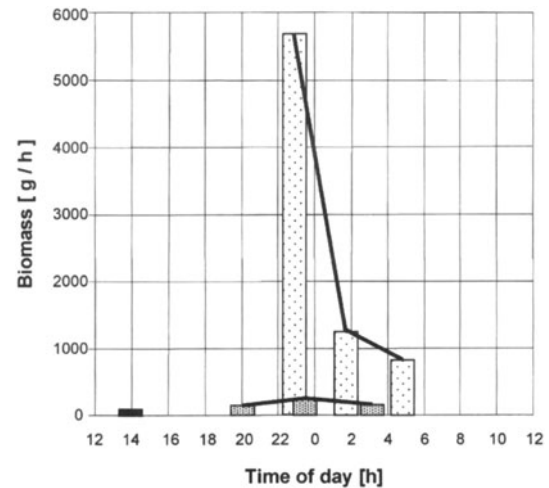


Fig. 10 Pelagic biomass of *Pleuragramma antarcticum* in the pycnocline of Drescher Inlet. Data derived from 6 hauls (110–170 m) over 2 consecutive nights (26 and 27 Jan. stippled bars) and 1 haul (150–250 m) during daytime (22 Feb. black bar). The depth of the trawls was adjusted according to the position of the pycnocline as determined by CTD profiles

sizes of *P. antarcticum* ranged between 5 and 24 cm TL with an emphasis on larger (14–21 cm) adult individuals (Fig. 7).

Discussion

Seals that use the same area on the same days conceivably are feeding under similar conditions. They should, furthermore, behave in a comparable manner with respect to their pattern of diving to certain water depths where hunting may be most efficient. The present study shows that during a period of 8 days, all eight Weddell seals confined their foraging activities within the Drescher Inlet, as evidenced by their benthic dives. The diving behaviour within and amongst individuals was, however, highly variable, as has been documented for yearlings (Burns et al. 1997) and adults studied in McMurdo Sound (Kooyman 1967; Castellini et al. 1991;

Testa 1994; Schreer and Testa 1996). Burns et al. (1997) concluded that average diving behaviour is not sufficient for comparing or understanding foraging strategies of Weddell seals, a statement with which we fully agree. Although the Weddell seal is one of the best-studied pinnipeds, the large variations in diving patterns make interpretation difficult.

Correlation of CTD profiles with the distribution pattern in dive depths of the seals (Fig. 4) indicates a close relationship between diving behaviour and the hydrography of the Drescher Inlet. In general, pelagic foraging was most intensive within the layer of warmer water above the pycnocline. By contrast, the 160-m mid-water layer between 170 and 330 m, where the temperature gradually decreased (Fig. 4), appears to be prey-deficient, as the seals mostly did not forage there but commuted through this zone in order to forage near the bottom. The abrupt shift from a series of benthic to pelagic dives observed in all Weddell seals studied is of particular interest. We believe that in many such cases the seals located pelagic prey (see Fig. 6), which also demonstrates that a hunting seal descending from the surface would not switch to benthic foraging as long as prey is readily available in the upper water column.

Trawling in the Drescher Inlet suggested that fish, primarily *P. antarcticum*, apparently moved into the upper water column at night and, consequently, night-time dives of Weddell seals were the shallowest. Based on this we assume that the warmer water layer above the pycnocline attracts and aggregates prey, enabling effective hunting on *Pleuragramma* at night. Foraging in the pelagial also occurred during daylight hours, but over a wider depth range, in addition to a high frequency of deeper benthic dives. Correspondingly, trawling during daytime confirmed large numbers of fingerlings and adults of *P. antarcticum* in the pelagial, and of adults near the bottom. This leads us to conclude that the seals' considerable variations in pelagic and benthic foraging activities corresponded with dives to feed primarily on *Pleuragramma*, in order to optimise food intake during the day and particularly during the short (6 h) night period.

Testa (1994) proposed a continued reliance on *P. antarcticum* as the principal prey of Weddell seals in the Ross Sea region, though other fish (and cephalopods) cannot be excluded, as observed in the present study (Table 1), despite the fact that *P. antarcticum* was the most abundant species in the trawl catches, and the exclusive prey item in the regurgitated meal of a Weddell seal (Fig. 7). The predominantly intact appearance of the 230 specimens in our sample is surprising because the flesh of *P. antarcticum* is very soft. From this it appears that most fishes (of up to 21 cm in length) were sucked in by the Weddell seal in one gulp, as reported for a captive crabeater seal sucking in small fish over distances of up to 50 cm (Klages and Cockcroft 1990).

The frequency in jaw movements (see Fig. 6) cannot provide the number of prey items actually ingested by the seal, although we expect that the majority of JASs

have to do with feeding events or at least with prey-catch attempts. We surmise that a high frequency of jaw movements of a hunting seal principally indicates high prey density. The 4-h sequence of 17 consecutive dives, characterised by rapid descents and ascents from/to the surface, implies that the seal foraged at a particular site. The bout of nine pelagic dives lasted nearly 2 h during which the abrupt increase in JASs (second dive in Fig. 6) gradually decreased and phased out in the last two pelagic dives. As each of these two dives, as well as the first dive (see frame in Fig. 6), showed a single, pronounced up and down excursion during the bottom time that coincided with a few JASs only, we suggest that such dives are more typical for searching rather than for pursuing and catching prey. Within the same pelagic diving bout, however, there are five dives that showed an intensive vertical zigzag pattern during the relatively long bottom time, coincident with a high frequency of JASs. Moreover, the intensive zigzags occurred exactly within the 50–150 m depth layer where a remnant of warmer water was trapped before the ice break-up. Since zigzag dive patterns have been referred to as prey-pursuit movements (PPMs) in crabeater seals and in a Ross seal (Bengtson and Stewart 1992, 1997), our findings suggest that PPMs indeed reflect hunting behaviour during foraging dives also in Weddell seals.

The progressive change in dive depths was observed in all seals, as illustrated in Figs. 3 and 6. Although sporadic, such distinct patterns were exhibited most in crepuscular- and night-dives, suggesting that the Weddell seals' foraging behaviour is finely tuned to vertically migrating prey. Similar patterns were observed in the diving behaviour of crabeater seals (Bengtson and Stewart 1992), where the distinct diel pattern of dive timing and depth were related to prey-capture strategy of the seals, and also to possible predator avoidance behaviour by their principal prey, Antarctic krill *E. superba*. Virtually nothing is known about the vertical migratory behaviour of *P. antarcticum*, although this pelagic schooling fish appears to pursue the swarms of krill on which it feeds. For example, *Pleuragramma* have been reported as by-catch in hauls of Antarctic krill (Rembizewski et al. 1978). Juveniles feed on small zooplankton such as calanoid copepods and euphausiid larvae (Hubold and Hagen 1997), while adult *Pleuragramma* additionally ingest a higher proportion of larger euphausiids 10–40 mm long (Wöhrmann et al. 1997). Moreover, a video system-equipped vehicle observed *E. superba* patchily distributed and most plentiful underneath vast ice sheets, while vertical net catches confirmed that krill were scarce in the underlying water column (Marschall 1988). Laboratory observations (Stretch et al. 1988) additionally showed that melting ice releases algae into the water column, which induces area-intensive foraging behaviour in krill. Night trawls in the upper water column of the Drescher Inlet revealed considerable amounts of *E. superba*. At midnight all the trawled fish samples had food in their guts. Most abundant prey items were copepods and *E. superba*

(Olaso 1999). It seems, therefore, that *Pleuragramma* are more active at night and that their movements in shallower depths are linked to pelagic feeding. It is, moreover, not surprising that the guts of the many specimens of *Pleuragramma* vomited by a Weddell seal onto the ice primarily contained Antarctic krill.

Conclusions

The fish fauna of the Drescher Inlet was dominated by *P. antarcticum*, which was by far the most abundant fish both in the upper water layer and near the bottom during day and night. It is reasonable to assume that the abundance of *Pleuragramma* in the upper water layer had been caused by ice break-up in that late summer season, which was reflected in a distinct salinity decrease and temperature increase above the pycnocline. Melting brash and platelet ice released masses of algae and other organic particles into the surface layers where intermediate and upper level trophic interactions would have been maximal at that time. The continuous replenishment of biomass, formerly bound to the fast and platelet ice, constituted locally attractive feeding spots which may have induced intensive foraging behaviour in zooplankton, krill and fish aggregating underneath melting sea ice. This, in turn, may have affected the foraging behaviour of Weddell seals, which responded to changes in the vertical patchy distribution and abundance of their principal prey, *P. antarcticum*.

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