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Behavior of midwater fishes under the Antarctic ice: observations by a predator

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Abstract Few details are known of the habits of Antarctic midwater fishes, especially those living below the heavy pack ice and shore-fast ice, are known, because they are difficult to capture or observe at depth. We used video sequences with synchronized positional data recorded by Weddell seals to describe the vertical distribution, diel movements, trends in abundance, and swimming behavior of two ecologically important fish species in McMurdo Sound, Antarctica. *Pleuragramma antarcticum* occurred in loose aggregations (individuals 2–4 m apart) and migrated daily between mean depths of 252 m at night and 346 m by day (vertical transit of 94 m). Their depth during November was correlated with surface light intensity even in the absence of a daily sunset. Interannual variations in local abundance indicated that the *Pleuragramma* population did not remain stationary. Large *Dissostichus* frequently occurred at shallow depths (12–180 m) and showed a significant change in depth with time of day. *Dissostichus* encounters followed a diel cycle having a mean depth of 93 m, a nighttime minimum of 17 m, and a daytime maximum of 168 m. Their depth was not correlated with surface

light intensity. *Dissostichus* were present even when *Pleuragramma*, their principal prey, were scarce. When chased by a seal, one *Dissostichus* sustained a speed of 3.4 m s^{-1} for a period of 24 s. This use of a marine predator as a guided, high-speed sampling device for its midwater prey provided clarification and new insights into the behavior, interactions, and ecology of species that have been especially difficult to study.

Introduction

Few details are known of the habits of midwater fishes, especially those living below the heavy pack ice and shore-fast ice, because the fishes are difficult to capture or observe at depth. Inferences have been made from trawl catches in ice-free areas, individuals caught on baited hooks, their diet, and the gut contents of their predators. These indirect sources of data are difficult to interpret and may lead to erroneous conclusions about the habits of even the most common fish species. During a study of the foraging behavior and diving energetics of Weddell seals (*Leptonychotes weddellii*), we obtained direct observations of their piscine prey, Antarctic silverfish (*Pleuragramma antarcticum*) and Antarctic toothfish (*Dissostichus mawsoni*), under the ice at McMurdo Sound, Antarctica.

Trawl catches have shown that the Antarctic silverfish is the most abundant fish in most shelf areas of the Southern Ocean (DeWitt 1970; Hubold 1984, 1985). It is a food resource for so many species – fishes (Eastman 1985; Schwarzbach 1988), seals (Testa et al. 1985; Plötz et al. 1991; Castellini et al. 1992), whales (Yukhov 1970), penguins (Emison 1968; Gales et al. 1990; Kirkwood and Robertson 1997), and other seabirds (Young 1963; Arnould and Whitehead 1991) – that it is considered a keystone species in the food web of the High-Antarctic Zone, the same position occupied by krill (*Euphausia superba*) in Antarctica's Seasonal Pack-Ice Zone (Hubold 1991). Despite its apparent abundance and

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importance in the Antarctic marine food web, attempts to capture *Pleuragramma* beneath the ice have been unsuccessful and little is known about its behavioral ecology. *Pleuragramma* is reported from depths of 0–900 m (Kock et al. 1984; Gerasimchuk 1986; Ekau 1990). There is clear size segregation by depth, with the smallest, youngest individuals shallowest, and adults below 400 m (Hubold 1984; Kellermann 1986; Hubold and Ekau 1987). *Pleuragramma* is thought to form shoals (Eastman 1985), an inference that is possibly based on its abundance and resemblance to herrings.

The much larger Antarctic toothfish sometimes ranks second in abundance and first in biomass in bottom trawls (Ekau 1990). This piscivore feeds heavily upon *Pleuragramma* (Calhaem and Christoffel 1969; Eastman 1993) and is, in turn, the prey of whales (Yukhov 1971; Thomas et al. 1980) and seals (Testa et al. 1985; Calhaem and Christoffel 1969). It has been considered second in importance to *Pleuragramma* in the Antarctic pelagic food web (Testa et al. 1985; Eastman 1993). Adult *Dissostichus* are known from near-bottom waters at depths of 300–1600 m (Ekau 1990; Eastman 1993; Vacchi and Greco 1994), although juveniles 11–71 cm in length have been reported from depths of 0–300 m (Yukhov 1971).

Our direct observations were made with a video camera and synchronized multi-sensor data recorder attached to several seals as they foraged under the ice in McMurdo Sound. This new information expands the base of knowledge for two of the most important fish species in Antarctica and indicates that some existing notions about their distribution and behavior may need to be revised.

Materials and methods

We attached a video camera and data recorder to Weddell seals to study foraging behavior and diving energetics of seals and to observe fishes directly, in situ, under the sea ice of McMurdo Sound, Antarctica. In October 1997, 1998, and 1999, we cut a rectangular depression (2.5 m × 1.5 m × 1 m deep) in the 3-m-thick sea ice and drilled a hole (1.3 m diameter) through one end. The work was done where there were no other holes or cracks for the seals to breathe through within a 2-km radius. We positioned a portable hut over the hole to serve as a laboratory. Holes were located approximately 10 km west of Cape Armitage, Ross Island, adjacent to the McMurdo Ice Shelf, where the sound is 570 m deep (1997: 77° 51' 52.9"S, 166° 14' 21.9" E; 1998: 77° 51' 51.7" S, 166° 14' 26.0" E; 1999: 77° 51' 43.3" S, 166° 14' 3.4" E). The field season continued through early December each year.

The video system and data recorder and their deployment were described in detail by Davis et al. (1999). Briefly, the miniature, low-light-sensitive, black-and-white video camera (6 cm long × 6 cm diameter; minimum illumination 0.05 lux; angle of view 80° horizontal, 60° vertical) was encircled by an array of near-infrared light-emitting diodes (LEDs). These LEDs enabled the camera to record images underwater in complete darkness to a distance of about 1 m. When additional ambient light was available, objects were visible at much greater distances. Because seals have a maximum visual sensitivity under low-light conditions in the spectral region of 496 nm, the near-infrared LED light source ($\lambda_{\text{max}} = 850$ nm) was believed to be invisible to them and their prey (Lythgoe and Dartnell 1970; Lavigne et al. 1977; Nelson 1981).

This prevented alterations in the normal behavior of the seals and their prey due to artificial light from the instrument. For most dives, the camera was mounted on top of the seal's head so that the seal's eyes and muzzle were visible in the lower part of the field of view.

The torpedo-shaped main housing (35 cm long × 13 cm diameter) contained an 8-mm video tape recorder (VTR), rechargeable lithium-ion batteries, and a microprocessor that controlled the VTR and data acquisition. The microprocessor received data from the following onboard instruments and stored them on a PCMCIA card once per second: clock, pressure transducer (calibrated for depth), flowmeter (calibrated during postprocessing for water speed using the method of Blackwell et al. 1999), and gimballed flux-gate compass (calibrated locally using the sun's position). A time signal was encoded on one audio track of the video tape once per minute to synchronize the video and data. The flux-gate compass was in a separate housing (17 cm long × 5.5 cm diameter) positioned behind the main housing. Sound was recorded on one audio channel of the VTR with a hydrophone which had a frequency response of 50 Hz to 16 kHz. Flipper stroke frequency obtained from an accelerometer (6 cm × 3 cm × 2 cm) mounted near the base of the tail was recorded as an audible signal on the second audio channel of the video tape. The main housing rested in a non-compressible foam cradle positioned middorsally, just behind the seal's shoulder. The cradle provided enough buoyancy to make the entire video system and data recorder neutrally buoyant. Instruments were activated by an external switch. The data record was limited by the video tape to 6 h.

We worked with 15 adult or subadult Weddell seals, 1 at a time and 5 each year. There were 10 males and 5 females, having a mean standard length of 2.4 m (± 0.8 SD) and mean body mass of 406 kg (± 60 SD). After the equipment was attached to a seal, the animal was allowed 18 h to recover from anesthesia before being released into the breathing hole. Each instrumented seal was used for 4 to 5 days, after which time the equipment was removed and the seal was returned to the place it was captured. Within 24 h of release into the breathing hole, the seals began performing voluntary dives similar in depth and duration to those reported for free-ranging seals (Castellini et al. 1992). The rectangular depression around the hole allowed seals to rest horizontally at the surface. Every 6–12 h, while a seal rested, the main housing of the video system was removed from the seal and the data were transferred to a computer database. The batteries and videotape were replaced and the main housing was reattached to the seal. Each 8-mm videotape was duplicated in VHS format immediately after recovery, when a time code was superimposed on the video display to facilitate subsequent analysis. Video tapes were screened for encounters with prey which were recorded in the database. Many fishes and invertebrates were seen on the videotapes, but only fishes that could be confidently identified are reported here.

Identification of fishes was based on a suite of characteristics that could be observed through frame-by-frame analysis of the video recordings. In most instances, encounters occurred under very dark conditions so that the fish first came into view when it was < 50 cm from the seal's muzzle and brightly illuminated by only the LED array. *Pleuragramma* was identified by its small size (about 1.5–2.0 times the width of the seal's muzzle), brightly reflective surface, pointed snout, compressed body, and lack of dark pigmentation (Fig. 1A). *Dissostichus* was identified by its large size; entire fish were only seen at a distance (Fig. 1B). More often, a small portion of a fish was observed as a seal inspected it at a distance of several centimeters (Fig. 1C). *Pagothenia borchgrevinki* was similar in size to *Pleuragramma* but was distinguished by its more robust head and body, rounded snout, and its dull, non-reflective body (Fig. 1D). Using these criteria, almost all fishes could be confidently identified.

Surface light levels were recorded at half-hour intervals approximately 2.5 m above the sea ice using a cosine quantum light sensor (Li-Cor, Inc.). Surface light intensities during fish encounters were based on the most recent measurements of light intensity.

Three-dimensional positions of fishes observed on the video record were measured as the position of the seal at that moment.

The seal's position was computed for every 1 s of a dive from the time, depth, compass bearing, and swimming speed recorded by the onboard sensors. Positions were corrected for ocean currents by calculating "set" and "drift" using standard "dead-reckoning" methods (Bowditch 1995). This technique assumes that current speed and direction are temporally and spatially uniform during each dive. Statistical analyses were performed using Systat (version 8.0, SPSS Inc.). Tests for diel vertical migration employed methods of circular statistics as described by Batschelet (1981).

Results

Pleuragramma antarcticum

The most frequently observed fish species was adult *Pleuragramma*, approximately 20–25 cm in length ($n = 336$ fish in 58 successful foraging dives by 6 seals). All *Pleuragramma* were encountered within a horizontal radius of 939 m of the breathing hole (Fig. 2A). Ten were observed under the nearby permanent ice shelf, 20–175 m beyond its edge, which was estimated to be at least 30 m thick. Nearly all (97%) *Pleuragramma* were observed at depths > 160 m and the maximum depth was 414 m. The remaining nine fish were at depths between 56 and 137 m.

Pleuragramma were observed at nearly every hour of the day, and differences in their depth at the time of encounter suggested that they might undergo diel vertical migration. Actual observations showed that *Pleura-*

gramma were shallowest between midnight and 0300 hours (mean depth $218 \text{ m} \pm 109 \text{ SD}$, $n = 7$ dives) and deepest between 1430 and 1730 hours (mean depth $348 \text{ m} \pm 22 \text{ SD}$, $n = 9$). To test for vertical migration, we examined the relationship between depth and time of day for the first *Pleuragramma* encountered in each dive ($n = 58$). In 46 of the 51 dives with multiple *Pleuragramma* encounters, the depth of the final encounter was shallower than the first encounter, indicating that the fish fled upward. The final encounter averaged 66 m shallower than the first encounter and was as much as 196 m

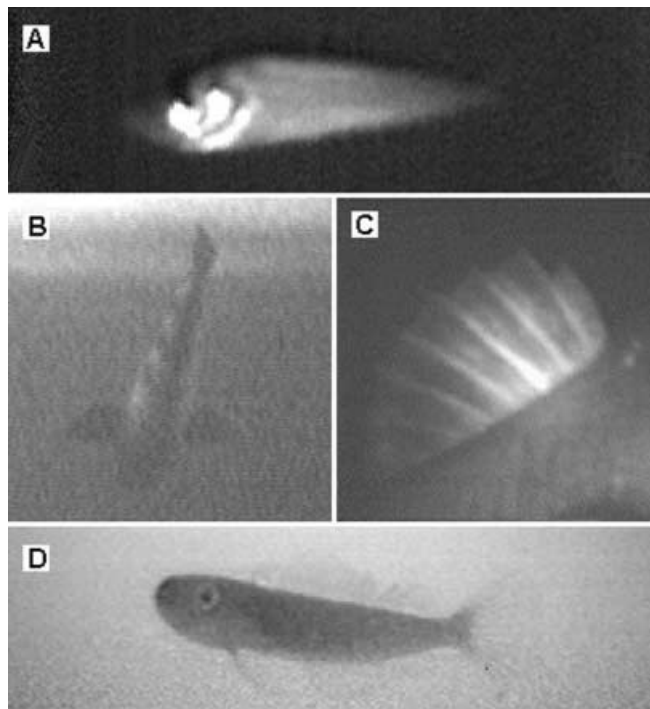


Fig. 1A–D Fishes observed through a video camera mounted on the head of Weddell seals. **A** *Pleuragramma antarcticum* at a depth of 220 m. **B** *Dissostichus mawsoni* at a depth of 12 m; note vertical bands on flank. **C** Dorsal fin of an adult *Dissostichus mawsoni* at a depth of 326 m. **D** *Pagothenia borchgrevinki* immediately below the sea ice

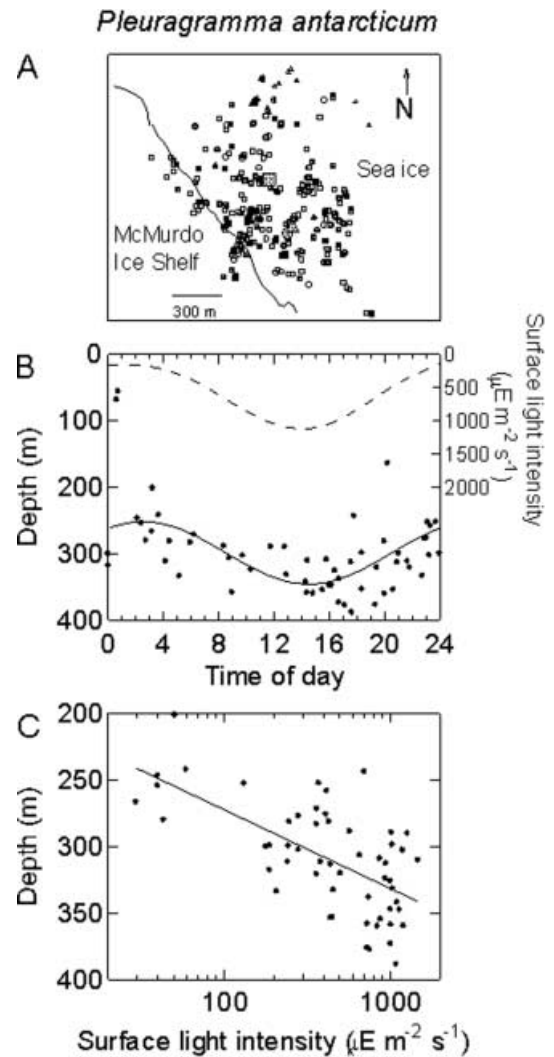


Fig. 2A–C Locations of observations of *Pleuragramma antarcticum* in McMurdo Sound, Antarctica, 1997–1999. **A** Map of the area around three study sites. Symbols denote year of observation (circles 1997; triangles 1998; squares 1999). Three larger, filled symbols mark the positions of the breathing holes through the sea ice; smaller symbols mark the positions of *Pleuragramma*. Small, filled symbols indicate the initial encounter, open symbols show "secondary" encounters. The edge of the McMurdo Ice Shelf is shown as a solid line. **B** Depth of initial encounters (solid line: $Y = 298.76 - 46.85 \times \cos(2\pi/24 \times X - 0.66)$) and surface light intensity (broken line) according to time of day. **C** Relationship between depth of initial encounters and surface light intensity. Note: ordinates in **B** and **C** represent depth downward

shallower. Using only the first encounter in a dive as an indicator of the depth of undisturbed *Pleuragramma*, there was a significant correlation between depth and time of day ($\chi^2=16.8$, $P<0.001$). Parameters of the cosine function fitted to the data (Batschelet 1981) indicated that the daily mean depth was 299 m, with an amplitude of ± 47 m (mean daily vertical transit of 94 m) and times of minimum and maximum depths were 0230 and 1430 hours, respectively. The time of minimum depth corresponded closely to the time of daily minimum light intensity on the surface of the ice (Fig. 2B). Observed maximum depths occurred somewhat later than predicted by the fitted cosine function and observed surface light intensity, suggesting asymmetry in the timing of vertical movements with respect to the solar cycle. Depth of *Pleuragramma* encounters was positively correlated with the logarithm of surface light intensity ($r=0.64$, $P<0.001$; $n=55$, excluding three unusually shallow encounters; Fig. 2C). Although this linear relationship suggests that the vertical movements of *Pleuragramma* may be mediated directly or indirectly by light intensity, the few encounters with *Pleuragramma* that took place under the permanent ice shelf were not significantly shallower than the other encounters at comparable times of day or than predicted from surface light intensity. The ice at the edge of the permanent ice shelf was estimated to be 13 m thicker than the adjacent sea ice (based on difference in elevation obtained from differential global positioning system coordinates) and transmitting about 25% as much light to the water below.

Seals typically encountered several *Pleuragramma* on each successful foraging dive, supporting the notion that this fish species aggregates in shoals. Dives most commonly resulted in four or five *Pleuragramma* encounters, with 12–20 encounters in nine dives (Fig. 3A). The interval between successive encounters within a dive varied greatly but many observations occurred in rapid succession. Most encounters took place within 5 or 6 s of the previous encounter and half of all such “secondary” encounters occurred within 15 s (Fig. 3B). The measured distance traveled by the seal between encounters over the intervals of ≤ 5 s averaged $5.2 \text{ m} \pm 3.3 \text{ SD}$ (range: < 1 –12.4 m). This is almost certainly an overestimate of the spacing between undisturbed fish because of their flight from the seal.

During one video sequence in which the seal chased a *Pleuragramma* for several seconds, the fish’s mean tail-beat frequency was 5.5 s^{-1} (value obtained by counting video frames between nine complete tail beats during the chase). Equations relating tail-beat frequency to swimming speed for temperate species predict that a fish of 20–25 cm in length with this tail-beat frequency would be moving at 0.62 m s^{-1} (Hunter and Zweifel 1971). However, Montgomery and Macdonald (1984) measured a maximum speed of 1.1 m s^{-1} for a 22.5-cm *Pagothenia borchgrevinki* with a tail-beat frequency of 5.7 s^{-1} . We used this range of swimming speeds (0.62 – 1.1 m s^{-1}) for *Pleuragramma* to improve our estimate of the spacing between undisturbed *Pleuragramma* within a

shoal. From the actual distance between consecutive encounters when the elapsed time was ≤ 5 s, the mean distance between undisturbed fish in a shoal was approximately $3.5 \text{ m} \pm 2.2 \text{ SD}$ for fish swimming at 0.62 m s^{-1} , to $1.9 \text{ m} \pm 1.9 \text{ SD}$ for fish swimming at 1.1 m s^{-1} . These distances are equivalent to mean shoal densities of 0.15 – $0.023 \text{ individuals m}^{-3}$ or one fish per 7 – 43 m^3 .

The relative abundance of *Pleuragramma* varied greatly from year to year, as indicated by “catch per unit effort” (Fig. 4), where catch refers to encounters with fish and fishing effort is the amount of time seals spent below 160 m (the depth below which *Pleuragramma* were usually found). No *Pleuragramma* were observed in 1997, 34 were observed in 1998 (all by one seal between 27 and 29 November), and 302 in 1999 (by all five seals). The apparent absence of *Pleuragramma* in 1997 and most of 1998 was despite 234 min of fishing effort in 1997 and 494 min prior to the first capture in 1998. After the date that *Pleuragramma* first appeared in 1998 and throughout 1999, encounter rate averaged $0.44 \text{ fish min}^{-1}$ below a depth of 160 m and there were no extended periods of fishing during which *Pleuragramma* were not observed, as might be expected if shoals of fish traveled quickly through the vicinity.

Dissostichus mawsoni

In contrast to the encounters with *Pleuragramma*, in which the seal always attacked, seals attacked *Dissostichus* only occasionally, and when inspected at very close range, the fish did not flee. *Dissostichus* were observed 26 times during 14 dives (Fig. 5A). Multiple encounters within a dive were taken to be the same fish whenever the distance and elapsed time between sightings were short. All fish appeared to be adults. One individual observed at a depth of 12 m and probably about 1 m in length had a distinctive barred color pattern on its sides (Fig. 1B). All encounters were within a 253-m horizontal radius of the breathing hole (Fig. 5A). The mean depth of encounter was $132 \text{ m} \pm 87 \text{ SD}$. All *Dissostichus* were first encountered at $< 180 \text{ m}$ depth, except for one observation at a depth of 326 m (Fig. 5B). One fish was first encountered at a depth of 109 m and pursued down to 456 m, during which time the seal (and the fish) reached a speed of 3.4 m s^{-1} and sustained it for a period of 24 s before slowing to 2.5 – 3.0 m s^{-1} for more than 2 min. The fish achieved these speeds by vigorous stroking of the body and caudal fin. The undisturbed *Dissostichus* shown in Fig. 1B swam with a rigid body, using only pectoral fins for propulsion.

Our sparse observations of *Dissostichus* hinted at a diel vertical migration. *Dissostichus* encounters were shallowest between midnight and 0100 hours and deepest between 1700 and 1900 hours (Fig. 5B). Based on only the initial encounter during a dive, there was a significant correlation between depth and time of day ($\chi^2=23.2$, $P<0.001$). Parameters of the cosine function fitted to the data indicated that the daily mean depth was

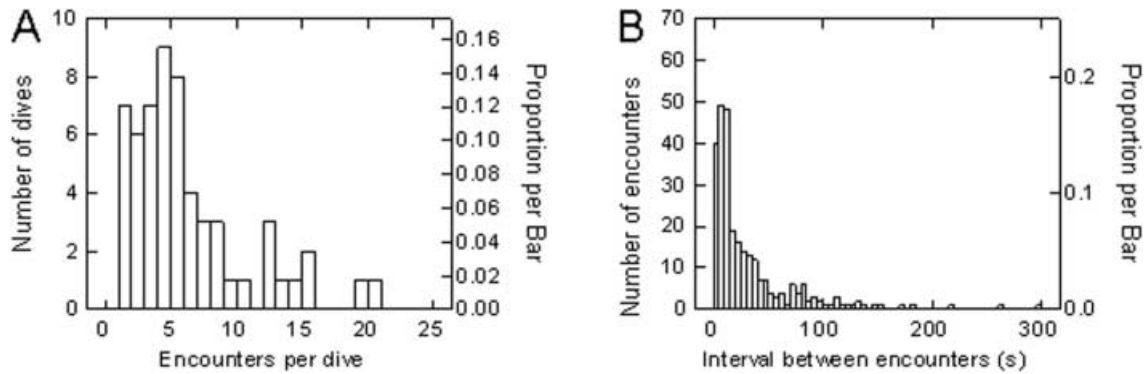
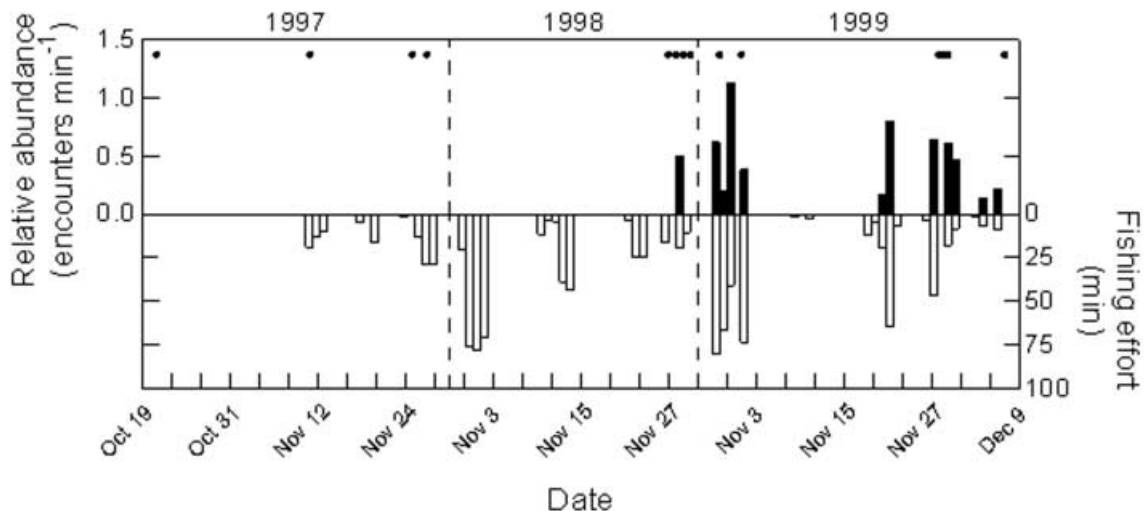


Fig. 3A, B Evidence for shoaling behavior in *Pleuragramma antarcticum* under the sea ice of McMurdo Sound, 1997–1999. **A** Frequency of encounters shows that nearly all successful foraging dives result in multiple encounters (*bar width 1*). **B** Frequency distribution for the time between consecutive encounters showing predominance of intervals less than 15 s (*bar width 5 s*)

93 m, with an amplitude of ± 76 m (mean daily vertical transit of 152 m) and times of minimum and maximum depths were 0515 and 1715 hours, respectively. These times were offset from the times of minimum and maximum surface light intensity. As a result, the regression between the logarithm of surface light intensity and depth of encounter was not significant, even after eliminating one unusually deep encounter from the analysis ($r=0.51$, $P<0.091$, $n=12$; Fig. 5C). Over the entire period of the study, *Dissostichus* were present at times when their presumed principal prey, *Pleuragramma*, were scarce or absent in 1997 (Fig. 4).

Fig. 4 Variation in relative abundance of *Pleuragramma antarcticum*, fishing effort of seals, and presence of *Dissostichus mawsoni* under the sea ice of McMurdo Sound, 1997–1999. Fishing effort (*open bars*) is defined as the time (in minutes) spent by seals below 160 m depth. Relative abundance (*filled bars*) is the number of encounters per minute below 160 m and shows that *Pleuragramma* were absent throughout the 1997 field season, arrived in the area late in November 1998, and were present throughout the 1999 field season. Circles indicate the dates of encounters with *Dissostichus*



Pagothenia borchgrevinki

Pagothenia borchgrevinki is a common species that typically lives just under the ice. There were six observations of *Pagothenia borchgrevinki* at depths of 0–6 m and horizontal ranges of 162–790 m from the breathing hole. One specimen tentatively identified as *Pagothenia* was observed unusually deep (211 m), in the midst of 13 encounters with *Pleuragramma*. Janssen et al. (1992) suggested that *Pagothenia* may stray far from the under-ice surface, possibly to feed on *Pleuragramma*.

Discussion

These direct observations under the ice of McMurdo Sound make useful additions to our knowledge of two of Antarctica's common pelagic fish species. Previous trawling data found no diel trends in the vertical distribution of *Pleuragramma* (Hubold 1984), and we could find no suggestion in the literature of vertical migration for *Dissostichus*. Our data demonstrate a diel migration by *Pleuragramma* that may be directly related to ambient light intensity, even in the absence of a sunset. At the start of our field seasons in late October, daily maximum surface light intensity was about 17.5 times the daily minimum. By the end of our field seasons (early December), there was only a 5.4-fold increase in light

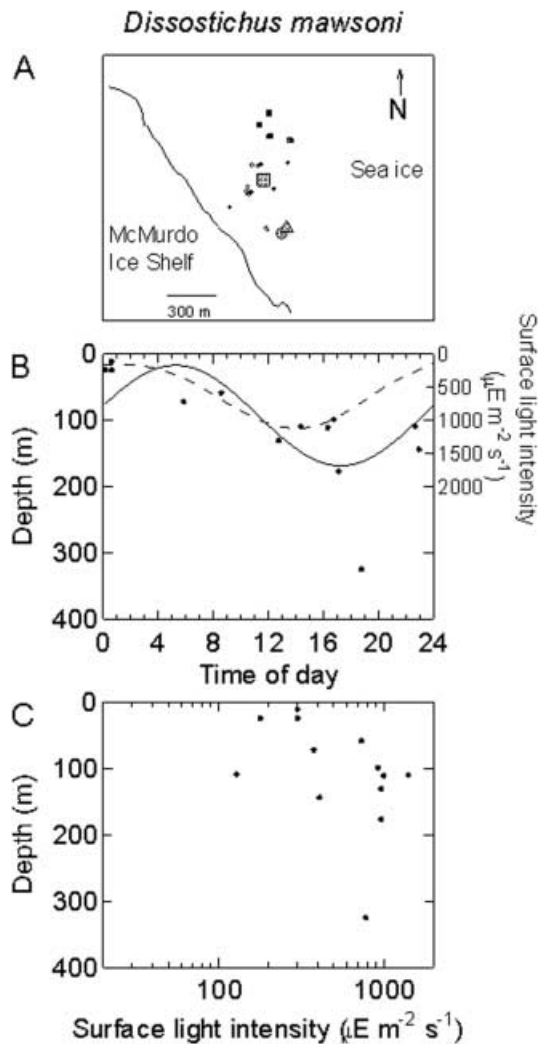


Fig. 5A–C Locations of observations of *Dissostichus mawsoni* in McMurdo Sound, Antarctica, 1997–1999. **A** Map of the area around three study sites. Symbols denote year of observation (circles 1997; triangles 1998; squares 1999). Three larger, filled symbols mark the positions of the breathing holes through the sea ice; smaller symbols mark the positions of *Dissostichus*. Small, filled symbols indicate the initial encounter, open symbols show “secondary” encounters. The edge of the McMurdo Ice Shelf is shown as a solid line. **B** Depth of initial encounters (solid line $Y = 92.82 - 75.76 \times \cos(2\pi/24 \times X - 1.38)$) and surface light intensity (broken line) according to time of day. **C** Relationship between depth of initial encounters and surface light intensity. Note: ordinates in **B** and **C** represent depth downward

intensity during the day. If ambient light intensity determines the vertical position of *Pleuragramma*, then earlier in the austral spring, when the daily range of light intensities is greater because of darker nights, shoals of *Pleuragramma* would be found shallower than 250 m within a few hours after midnight and their vertical transit would be greater than 94 m. Likewise, if the relationship between surface light intensity and depth of *Pleuragramma* (Fig. 2C) holds, the maximum depth for *Pleuragramma* at local apparent noon between May and August, when surface illumination is

negligible, could be 90 m or less. Given these observations, it is understandable that trawl data (in the absence of ice cover so that light levels would be higher) have shown that adult *Pleuragramma* are most abundant below 400 m depth (Hubold 1984; Kellermann 1986; Hubold and Ekau 1987). Nevertheless, our few observations of *Pleuragramma* under the thicker permanent ice shelf suggest that light intensity may not be the only determinant of vertical position. More observations and additional kinds of data are necessary to determine whether other factors, such as the distribution of predators or prey (which themselves may be regulated by light), determine the vertical distribution of *Pleuragramma*.

Our data support the prior suggestion that *Pleuragramma* live in shoals, and indicate that individuals within these loose aggregations may be spaced 2–4 m apart. The highly variable fishing success of the seals in essentially the same location and the same time period in three consecutive years suggests that the shoals of *Pleuragramma* wander slowly into and out of particular locations. It is interesting to note that they did not vacate the area of our camp in 1999 in response to the presence of predatory seals. A combination of shoaling and wandering would result in a patchy spatial distribution at any point in time.

Our methods did not permit observations of undisturbed *Pleuragramma*, but we were able to estimate their swimming speed when chased by a predator. The higher of our two estimates, 1.1 m s^{-1} , is about 4.9 body-lengths s^{-1} , which seems relatively low compared to the typical maximum burst speed of many temperate fishes (~ 10 body-lengths s^{-1} ; Beamish 1978). This agrees with the low maximum speeds ($4.3\text{--}4.9$ body-lengths s^{-1}) measured for two other Antarctic fishes of similar size, *Pagothenia borchgrevinki* and *Notothenia neglecta* (Montgomery and Macdonald 1984; Archer and Johnston 1989). The physiological constraints on maximum swimming performance in Antarctic fishes need further investigation.

Adult *Dissostichus* now are shown to be present throughout the water column and perhaps even more common at depths less than 200 m than previously thought. Published accounts describe adults as living at depths of 300–500 m (Eastman and DeVries 1982; Testa et al. 1985; Eastman 1990, 1993) and near the bottom (Fischer and Hureau 1985; Vacchi and Greco 1994). Dr. A.L. DeVries (personal communication) reports that *Dissostichus* have been caught on baited hooks at depths ranging from 70 to 315 m, but that fishing was more efficient between 400 and 500 m depth. This knowledge of *Dissostichus* in shallow water has not, to our knowledge, been published. The eyes of *Dissostichus* are the most specialized for low-light sensitivity of all notothenioids studied (Eastman 1988). They have a high density of rod photoreceptors (relative to cone photoreceptors) and a high degree of convergence of rods onto ganglion cells. These characteristics make eyes more sensitive to light, but at the expense of visual acuity. Perhaps the

greater angling success below 300 m is due to the poorer acuity in a dark-adapted retina. In this way, *Dissostichus* may see the bait in deep waters but lack the visual acuity to identify it as a normal prey item and therefore resort to olfactory cues for identification. In shallow waters they would be able to use vision to discern details and reject the bait more often.

Dissostichus also appear to undergo diel vertical movements, but more data are necessary to strengthen this tentative result. The substantial lag between the timing of extremes in vertical position and light intensity and the non-significant correlation between these variables suggest that if *Dissostichus* migrate periodically, they do so in response to some other cue, perhaps the presence of *Pleuragramma*. It is interesting, however, that the individuals we observed were shallower than the *Pleuragramma* at a given time of day. In addition, *Dissostichus* were present during periods when *Pleuragramma* were apparently absent. Perhaps they were feeding on *Pagothenia* near the under-ice surface or smaller, shallower *Pleuragramma* that the seals may have ignored. Until our arrival, the locations of our camps would have been excellent refuges for fishes from predation by seals.

All fish sampling devices have biases that limit interpretation of the data. Trawls fish selectively according to their mesh size, towing speed, and position in the water column. The reduced angling success for *Dissostichus* at depths less than 300 m may reflect the bias of baited hooks. Predators, such as Weddell seals, do not sample the environment randomly and the intensity of their fishing effort varies continuously in response to immediate experience and physiological constraints. While data from a foraging predator present certain limitations, they provide some entirely new information and greater resolution for other types of data. The use of a marine predator as a guided, high-speed sampling device for its midwater prey provided clarification and new insights into the behavior, interactions, and ecology of important species that, to date, have been especially difficult to study. The same approach could be used to study other pelagic and deep-water fishes and invertebrates that are otherwise impossible to observe in their natural environment.

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