

Habitat Use by Weddell Seals and Emperor Penguins Foraging in the Ross Sea, Antarctica¹

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SYNOPSIS. The only apex predators that live year-round at high latitudes of the Ross Sea are the Weddell seal and emperor penguin. The seasonal distribution, foraging depths, and diet of these two species appear to overlap. What makes it possible for emperor penguins and Weddell seals to co-exist at high latitude throughout the winter when other marine tetrapods apparently cannot? Both species have similar adaptations for exploitation of the deep-water habitat, forage on the same species, and routinely make long and deep dives. Yet, despite these similarities, there is probably little trophic overlap between the adults of both species due to geographical and seasonal differences in habitat use. For example, during the winter months while female emperor penguins are ranging widely in the pack ice, adult seals are foraging and fattening for the upcoming summer fast, literally beneath the feet of the male penguins. However, there is more extensive overlap between juvenile seals and adult penguins, and shifts in prey abundance and/or distribution would likely affect these two groups similarly. In contrast, juvenile penguins appear to avoid inter- and intra- specific competition by leaving the Ross Sea once they molt.

INTRODUCTION

The emperor penguin (*Aptenodytes forsteri*) and the Weddell seal (*Leptonychotes weddellii*) are the only two warm-blooded, air-breathing marine predators that live year-round at the high latitudes of the Ross Sea (~77°S). These are arguably the two such species best adapted to polar existence, and are the only pair of diving predators that co-exist at high polar latitudes throughout the year. That emperor penguins are exquisitely adapted to their high polar existence can be best illustrated by the fact that they brood their egg and chick throughout the Antarctic winter, when most other vertebrates have left the region (Stonehouse, 1964; Croxall, 1997). Similarly, Weddell seals are able to hunt underneath the thick ice of the Ross Sea throughout the dark and cold winter months, when all other marine mammals have left the region (Castellini *et al.*, 1992). Yet, despite a long history of study, we know surprisingly little

about the foraging ecology or habitat use of these two species outside of the summer research season.

The question of how these two species co-exist within the Ross Sea is of particular interest because the Ross Sea is home to large and overlapping distributions of both predators (Fig. 1). The Ross Sea is home to six emperor penguin colonies (at Cape Crozier, Beaufort Island, Franklin Island, Cape Washington, Coulman Island, and Cape Roget) that house approximately 180,000 birds (Ainley *et al.*, 1984; Kooyman and Mullins, 1990; Kooyman, 1993), and to an estimated 50,000 adult Weddell seals, which are dispersed across a wide area (Stirling, 1969). While the seal colonies within McMurdo Sound are well studied (Testa and Siniff, 1987; Castellini *et al.*, 1992; Burns *et al.*, 1999), little is known about the smaller colonies that exist along the western Victoria Land coast. The overlapping distribution of these two apex predators, and their year-round presence within the Ross Sea creates the potential for competition.

When considering potential competition between Weddell seals and emperor penguins, it is crucial to remember that these

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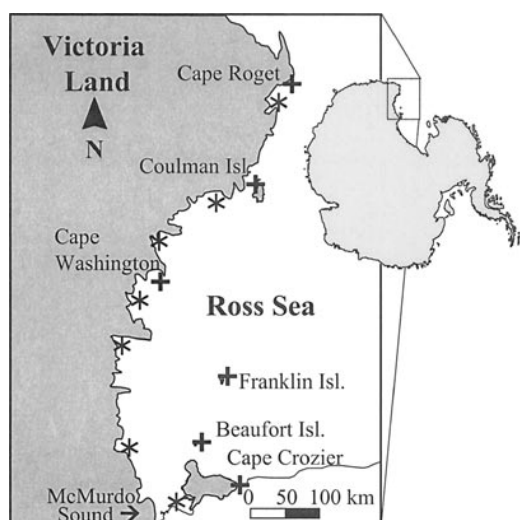


FIG. 1. Map of Ross Sea, Antarctica with the major penguin (+) and seal colonies (*) indicated. The study area is boxed on the inset map of the continent.

are both air-breathing, warm-blooded species that overlap not in their utilization of above-ice resources, but rather underwater prey. Thus, it is first essential to examine whether the two species have similar diving abilities. Over the past 30 years, many studies have shown that the ability of diving vertebrates to remain submerged depends upon the amount of oxygen that can be stored within tissues and made available during dives, and the rate at which that stored oxygen is used (Butler and Jones, 1997; Kooyman and Ponganis, 1998). The ratio of these two parameters is the aerobic dive limit (ADL), or the maximum dive duration that can be achieved by relying primarily on oxidative metabolism. Because most free-ranging divers do not rely extensively on anaerobic processes to extend dive time, the ADL can be used as an index of an animal's dive capacity (Kooyman *et al.*, 1980; Butler and Jones, 1997).

Weddell seals and emperor penguins are both champion divers, with similar modifications to both oxygen stores and use rates. Both species have increased oxygen stores 3–4 fold over typical terrestrial values (87 ml $O_2 \cdot kg^{-1}$ in Weddell seals, 62 ml $O_2 \cdot kg^{-1}$ in penguins, *vs.* ~ 20 ml $O_2 \cdot kg^{-1}$ in humans; Ponganis *et al.*, 1993; Kooyman *et al.*, 1999). In addition, both species have shift-

ed the bulk of their oxygen stores from the lungs to their muscle and blood. This reduces problems inherent in breath-hold diving with large, freely exchanging gas volumes (Kooyman and Ponganis, 1998). Penguins and seals also use several techniques to reduce oxygen consumption. For example, both significantly reduce heart rates during long dives, and reduce transport costs by utilizing burst-and-glide swimming patterns (Hill *et al.*, 1987; Kooyman *et al.*, 1992; Davis *et al.*, 1999; T. Williams, personal communication). Therefore, it appears that emperor penguins and Weddell seals possess similar adaptations to exploit the underwater prey resources available to them within the Ross Sea. In addition, studies of diving behavior have indicated that both use their underwater habitat in similar ways (Fig. 2; Testa, 1994; Kooyman and Kooyman, 1995).

Thus, prior studies have demonstrated that Weddell seals and emperor penguins live in the same area, have similar diving capacities and can use the same foraging depths. These results suggest that the potential for foraging competition between these two species is high, should resources become limiting. Furthermore, studies linking Weddell seal foraging patterns and reproductive success to environmental conditions suggest that food availability does have the potential to impact predator population dynamics (Burns and Schreer, 2000; Testa *et al.*, 1991). Unfortunately, there is no equivalent data available for emperor penguins. Even if resources are not always limiting, when top predators co-exist within a stable environment, they generally do so through niche separation. Since the Antarctic environment is relatively stable within the long lifetimes of seals and penguins, these results demonstrate the potential for foraging competition between the two species. It is this potential for trophic overlap between emperor penguins and Weddell seals within the Ross Sea that we propose to address here.

DISCUSSION

Given the extant data, it is possible to evaluate three main strategies that emperor penguins and Weddell seals might use to

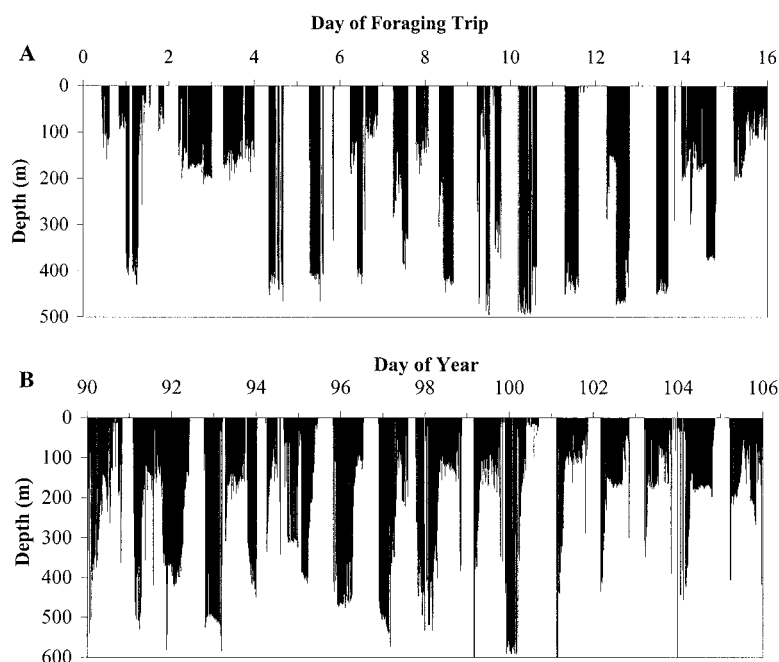


FIG. 2. Diving patterns of (A) an adult emperor penguin during the course of a 16 day chick provisioning trip; and (B) of an adult female Weddell seal approximately one month after completing the molt.

maximize niche separation and so reduce the potential for interspecific competition. These strategies include differential prey selection, utilization of different foraging depths, and seasonal or geographic separation of habitat use. Each of these hypotheses will be considered in turn.

Prey selection

There have been numerous studies of Weddell seal and emperor penguin diets, both within and outside of the Ross Sea (Plötz, 1986; Green and Burton, 1987; Castellini *et al.*, 1992; Putz, 1995; Kirkwood and Robertson, 1997a; Burns *et al.*, 1998; Cherel and Kooyman, 1998). In almost all studies, fish make up the bulk of the diet, with cephalopods and crustaceans generally accounting for less than one-third of the prey consumed. Within the Ross Sea, Cherel and Kooyman (1998) showed that fish made up 89–95% (by mass) of the emperor penguin's diet, and Green and Burton (1987) demonstrated that Weddell seals were even more specialized fish consumers (99.3% diet by mass). In addition *Pleurogramma antarcticum*, the Antarctic silver-

fish, is the primary fish prey for both predators (88.6% by numbers for penguins, 95.3% for seals; Castellini *et al.*, 1992; Cherel and Kooyman, 1998). This is not surprising, given that *P. antarcticum* is probably a large component of the fish biomass throughout the Ross Sea (>90% of the biomass in McMurdo Sound; Eastman, 1985; Everson, 1985).

More remarkably, despite differences in body and mouth size, seals and penguins do not appear to be selecting different size classes of *P. antarcticum* (Fig. 3). Although seals eat slightly larger fish than do penguins, individuals of each species consume fish of many size classes. Juvenile fish (those <100 mm SL) dominate the diet of both predators (Castellini *et al.*, 1992; Burns *et al.*, 1998; Cherel and Kooyman, 1998). Differences in the mean size of ingested prey are likely due to the different locations, seasons, and years at which prey samples were collected (seal scats were collected throughout 1981 from Erebus Bay and White Island; penguin stomach samples were collected periodically at Coulman Island, Cape Washington, and Cape Roget

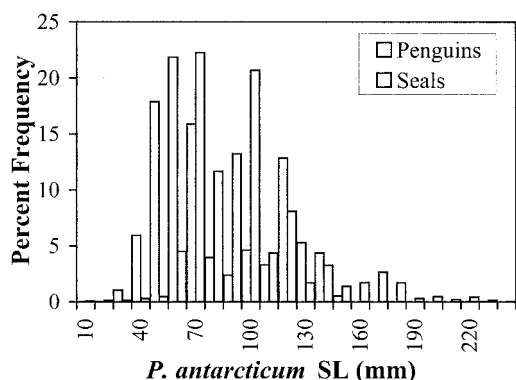


FIG. 3. Frequency distribution of size classes of *P. antarcticum* selected by adult emperor penguins and Weddell seals of all age classes. Fish standard lengths (SL) were estimated from measurements of mandible lengths (for penguins; Cherel and Kooyman, 1998) or otolith diameters (for seals; Castellini *et al.*, 1992). Seal age classes could not be separated due to collection methods.

between October and December, 1986–1993). While approximately 10% of the fish selected by seals were larger than any selected by penguins in the Ross Sea, the absence of large (>140 mm) *P. antarcticum* in the penguin diet may be due to the fact that diet samples were collected only during the chick rearing period. If adult birds return to the colonies with smaller fish for their chicks, but take larger fishes for themselves early in each foraging trip, then diet samples would be biased toward smaller fish sizes. Observed changes in penguin dive patterns towards the end of foraging trips support this hypothesis (Kooyman and Kooyman, 1995; Cherel and Kooyman, 1998). In addition, emperor penguins foraging along the Mawson coast eat slightly larger fish during the winter than when rearing chicks in the summer (Kirkwood and Robertson, 1997a, b). This pattern may hold in the Ross Sea as well. Thus, it seems that seals and penguins forage predominantly on the same species and take fish of similar sizes. Trophic separation, if present, must arise through other mechanisms.

Diving behavior

While early studies of diving behavior demonstrated that both penguins and seals were capable of reaching similar depths

(Kooyman *et al.*, 1971; Castellini *et al.*, 1992; Ancel *et al.*, 1992; Testa, 1994; Kooyman and Kooyman, 1995; Fig. 2), they did not reveal whether seals and penguins preferentially foraged at similar depths. While predators must forage at depths where prey are abundant, to maximize prey intake, they must also increase the proportion of the dive cycle (dive time + surface recovery time) spent at depth. Therefore, preferred foraging depths (*i.e.*, the maximum depth of foraging dives) generally integrate both predator diving capacity and prey behavior (Kooyman *et al.*, 1980; Butler and Jones, 1997; Kooyman and Ponganis, 1998).

While we know little about the under-ice movements of *P. antarcticum*, the diving capacity of both Weddell seals and emperor penguins has been well characterized, and can be compared to foraging behavior as measured by dive recorders (Fig. 4). The ADL of adult emperor penguins (<5 min, determined from post-dive lactate levels) is similar to that of Weddell seal juveniles, as is their modal dive duration (juvenile seals 5.8 min, adult penguins 5 min; Kooyman and Kooyman, 1995; Burns and Castellini, 1996; Burns, 1999). These values are considerably shorter than those of the larger adult seals (ADL <20 min, modal dive duration <13 min; Kooyman *et al.*, 1980; Burns, 1999). That a much greater proportion of free ranging dives made by juvenile seals and emperor penguins exceed their ADL suggests that both are commonly operating at close to a physiological limit (Burns, 1999).

Since greater breath-hold ability provides access to deeper depths, the fact that Weddell seal adults make a larger proportion of deep dives than either juvenile seals or adult penguins is expected (Fig. 4B; dives limited to those >50 m). However, there is considerable overlap between the foraging dive depths of all three age classes (Kooyman and Kooyman, 1995; Schreer and Testa, 1996; Burns and Schreer, 2000). This is particularly true at the shallow depths for adult penguins and juvenile seals, which suggests that the largest potential for trophic overlap exists between these two groups. Remarkably, very deep dives

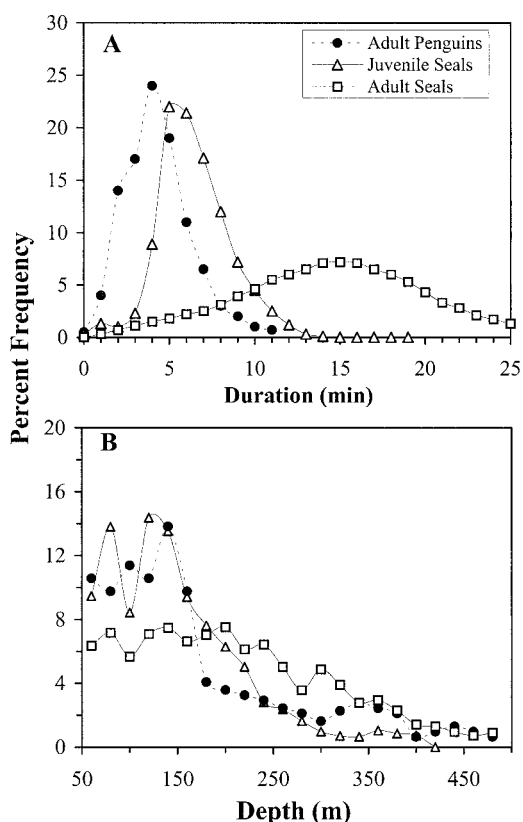


FIG. 4. Frequency histograms of dive duration (A) and depth (B) for adult penguins, and juvenile and adult Weddell seals. Dive behavior was determined from time-depth-recorders deployed on free ranging animals (penguins: Kooyman and Kooyman, 1995; juvenile seals: Burns, 1999; adult seals: Testa, 1994).

(>350 m) make up a similar proportion (<10%) of the behavioral repertoire of both adult seals and penguins. Thus, despite differences in physiological capacity, there is little indication that depth separation is the main mechanism by which the potential for foraging competition is reduced.

Seasonal patterns of habitat use

Direct competition for the same prey resources can be minimized if predators forage in different geographic areas or at different times of the year. For emperor penguins and Weddell seals, satellite telemetry and population studies have provided data on seasonal patterns of habitat use that can be used to address this hypothesis (Ancel *et al.*, 1992; Testa, 1994; Kooyman *et al.*,

1996; Burns *et al.*, 1999). However, differences in the basic life history of these species must be considered first.

The life history pattern of emperor penguins closely ties them to their colonies. In the fall, adults gather in the colonies to form pair bonds and mate. After egg laying, females forage to replenish energy reserves, but males remain in the colonies and incubate the egg until it hatches in mid-winter. Then, both sexes provision the chick throughout the spring by undertaking 1–3 wk long foraging trips. In late December, chicks fledge, and adults leave the colonies to feed and molt. Three to four months later, adults return to the breeding colonies and the cycle starts again (Stonehouse, 1964; Kooyman and Kooyman, 1995; Croxall, 1997; Kirkwood and Robertson, 1997a).

Within the constraints of this life history pattern, there are three periods when adult foraging effort is likely elevated: after egg-laying when females are replenishing energy stores, during the chick provisioning period, and after the chicks are fledged, when adults are building energy reserves for the coming molt. Satellite telemetry has revealed that habitat use patterns differ between these periods. During the chick provisioning trips adults generally remain within 200 km of the colonies and concentrate their foraging activities in the daylight hours (Ancel *et al.*, 1992; Kooyman and Kooyman, 1995; Croxall, 1997; Cherel and Kooyman, 1998; Kooyman *et al.*, 1998). Once chicks are fledged, adults travel west for approximately one month until they reach the eastern Ross Sea. There, in the drifting pack ice more than 1,200 km from their colonies, they undergo the annual molt, and shed their tracking devices (Kooyman *et al.*, 1998). In contrast, newly fledged juvenile penguins leave the colonies in January and travel north of the pack ice zone, beyond 60°S, and out of the Antarctic treaty area (Kooyman *et al.*, 1996). While adults return to their colonies roughly three months later, we do not know when juveniles return.

In contrast, Weddell seals have greater freedom of movement throughout the year. During the Antarctic spring (October–December) adults congregate in nearshore col-

onies, where females give birth to a single pup and males vie for underwater mating territories (Hill, 1987; Castellini *et al.*, 1992). During this period, breeding adults and nursing pups remain inshore, and foraging effort is low (Testa *et al.*, 1985; Hill, 1987). However, by the end of the breeding season in January, adults and newly weaned juveniles begin to disperse from the area and often do not return until the following spring. Thus, seals are tied to their fast-ice colonies for a much shorter period than are emperor penguins.

However, like penguins, satellite telemetry studies conducted within McMurdo Sound has indicated that habitat use patterns differ between adult and juvenile seals. Juveniles begin to disperse away from their natal colonies as the fast ice breaks up in early summer. They generally travel no more than 500 km north of their natal colonies and remain within 120 km of the Victoria Land coast (Burns *et al.*, 1999). In contrast, adult seals remain near the colonies throughout the summer, during which time they complete their annual molt. When adults leave McMurdo Sound, they tend to move into the central Ross Sea rather than along the coast (Testa, 1994). Consequently, adults use the deep pack ice habitat of the greater Ross Sea to a larger extent than do juveniles.

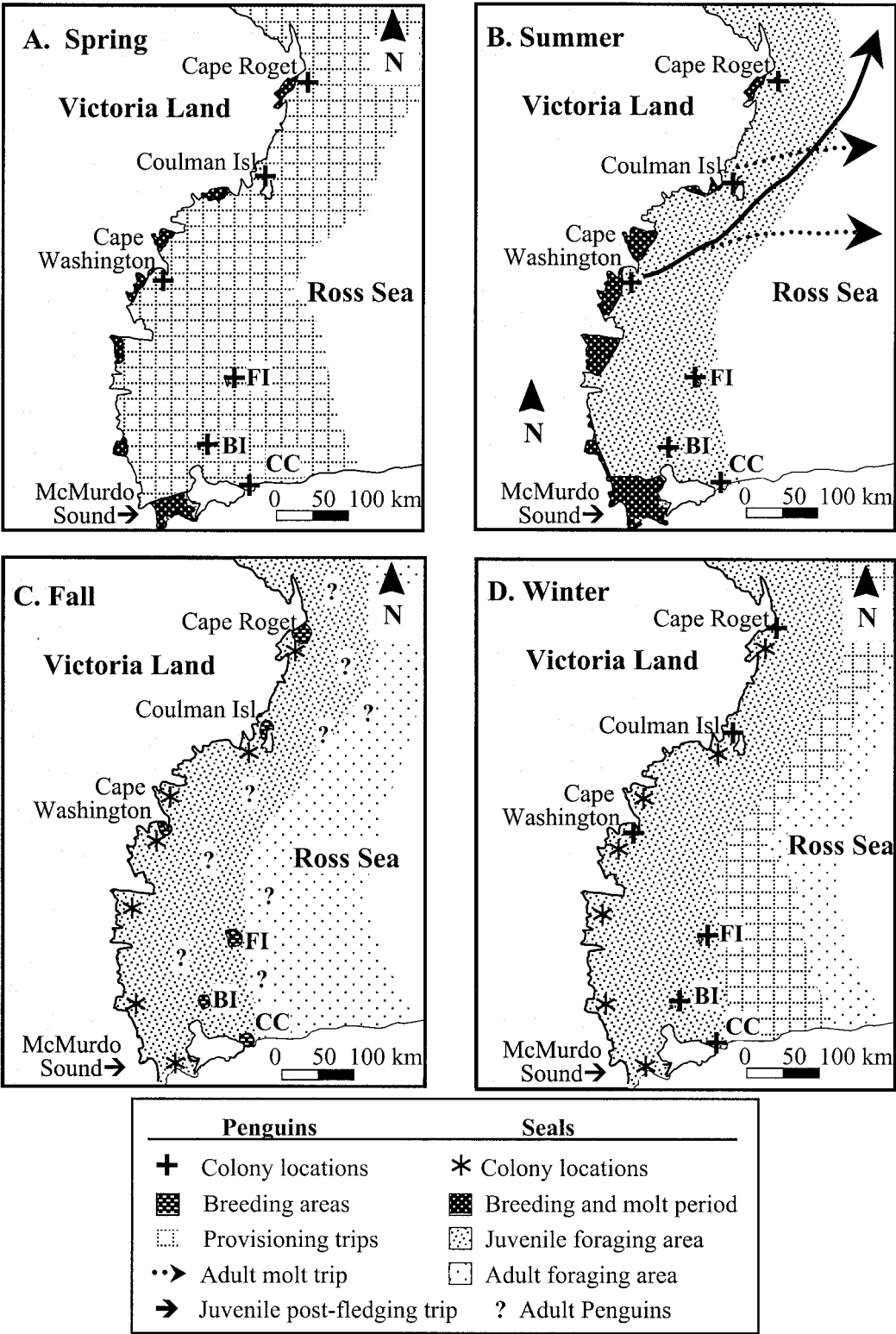
Seasonal separation

With this understanding of seasonal movements for both Weddell seals and emperor penguins, it is possible to address the question of trophic separation due to differences in foraging locations or seasonal cycles. During the spring (Fig. 5A), there is little potential for overlap because seals are in their breeding colonies and foraging little, if at all (Testa *et al.*, 1985; Hill, 1987). From the perspective of the emperor penguins, this minimizes the potential for interspecific competition during a period when adults are foraging to provision themselves and their rapidly growing chicks (Ancel *et al.*, 1992). In early summer (Fig. 5B) as juvenile seals begin to move out of the breeding colonies, both adult and juvenile penguins leave the Ross Sea (Kooyman *et al.*, 1996; Kooyman *et al.*, 1998; Burns

et al., 1999). This exodus minimizes spatial overlap between penguins and juvenile seals, which have similar dive capacities and behavior.

In the fall (April through June), habitat use patterns are effectively the reverse of the spring pattern, and there is little potential for interspecific competition (Fig. 5C). During this period, adult seals are actively foraging throughout the Ross Sea to recover mass lost during the previous breeding season, and juvenile seals are learning to forage along the coastal margins (Testa, 1994; Burns *et al.*, 1999). At the same time, emperor penguins are largely confined to their colonies to breed and incubate their eggs (Stonehouse, 1964; Croxall, 1997; Kirkwood and Robertson, 1997b). While there is little overlap between seals and penguins for most of the season, competition likely increases in June when female penguins leave the colonies to foraging after egg laying. We know little about fall movement patterns in the Ross Sea, but Kirkwood and Robertson (1997b) found that female penguins along the Mawson Coast foraged primarily within <100 km of their colony. If penguins in the Ross Sea behave similarly, then trophic overlap in the fall is likely limited to the coastal zone.

During winter months the potential for interspecific competition is high (Fig. 5D). From July through September, when adult penguins are foraging over wide areas to gather sufficient prey for themselves and their chicks, juvenile seals are foraging in the same areas, at the same depths, and likely for the same prey items. In addition, adult seals are moving back towards their inshore colonies and foraging to gain sufficient reserves to last the coming breeding season (Ancel *et al.*, 1992; Testa, 1994; Kooyman and Kooyman, 1995; Kirkwood and Robertson, 1997a; Burns *et al.*, 1999). If juvenile penguins are still far to the north at this time, it may be so they can avoid this period of high inter- and intra-specific competition. Unfortunately, data on winter foraging ecology and diving behavior of seals and penguins is scarce, so it is impossible to assess whether other factors, such as shifts in prey selection, play a larger



role in reducing potential competition at this time.

CONCLUSIONS

Initial studies on the depth, foraging location, and diet of emperor penguins and Weddell seals suggested that there was a high potential for competition for prey resources. Closer examination of the extant data indicate that despite similarities in foraging depths and prey selection, trophic overlap is largely minimized by temporal and geographic differences in habitat use. Yet, while temporal shifts in breeding and molt schedules minimize the trophic overlap between adult penguins and seals, during winter months both juvenile seals and adult penguins forage in the coastal margins of the Ross Sea. Their similar size, aerobic dive capacity, and modal foraging depths further enhance the potential for competition between these two groups. While in most years the consequences to such overlap are probably small, during periods of food shortage juvenile seal survival will likely be reduced. This is because juvenile seals are already working at the edge of their physiological capabilities, and can neither increase dive effort and exploit deeper foraging areas, as can adult seals, nor reduce their intake requirements by abandoning chicks, as can adult penguins. In summary, trophic separation among these year-round residents of the Ross Sea is maintained largely by geographic and seasonal differences in habitat use, but is not complete. Consequently, competition in times of food shortage has the potential to differentially affect juveniles and adults. These findings emphasize the need to incorporate the year-round behaviors of all age classes when considering species interactions.

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REFERENCES

- Ainley, D. G., E. F. O'Connor, and R. J. Boekeheide. 1984. The marine ecology of birds in the Ross Sea, Antarctica. Ornith. Monog. 32:1-97.
- Ancel, A., G. L. Kooyman, P. J. Ponganis, J. P. Gendner, J. Lignon, X. Mestre, N. Huin, P. H. Thorson, P. Robisson, and Y. Le Maho. 1992. Foraging behavior of emperor penguins as a resource detector in winter and summer. *Nature* 360:336-338.
- Burns, J. M. 1999. The development of diving behavior in juvenile Weddell seals: Pushing physiological limits in order to survive. *Can. J. Zool.* 77: 773-783.
- Burns, J. M. and M. A. Castellini. 1996. Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddellii*) pups. *J. Comp. Physiol.* 166:473-483.
- Burns, J. M., M. A. Castellini, and J. W. Testa. 1999. Movements and diving behaviour of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biol.* 21:23-36.
- Burns, J. M. and J. F. Schreer. 2000. Changes in the behavioral repertoire of Weddell seal pups diving in McMurdo Sound, Antarctica. *In* W. Davison,

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FIG. 5. Location and foraging areas of emperor penguins and Weddell seals during spring (A), summer (B), fall (C), and winter (D). Penguin colonies are indicated with +; seal colonies with * FI = Franklin Island; BI = Beaufort Island, CC = Cape Crozier. See text for how foraging areas were identified.

- C. Howard-Williams, and P. Broady (eds.), *Antarctic ecosystems: Models for wider ecological understanding*, pp. 85–95. New Zealand Natural Sciences, New Zealand.
- Burns, J. M., S. J. Trumble, M. A. Castellini, and J. W. Testa. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biol.* 19:272–282.
- Butler, P. J. and D. R. Jones. 1997. Physiology of diving of birds and mammals. *Physiol. Rev.* 77:837–899.
- Castellini, M. A., R. W. Davis, and G. L. Kooyman. 1992. Annual cycles of diving behavior and ecology of the Weddell seal. *Bull. Scripps. Inst. Oceanogr.* 28:1–54.
- Cherel, Y. and G. L. Kooyman. 1998. Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Mar. Biol.* 130:335–344.
- Croxall, J. P. 1997. Emperor ecology in the Antarctic winter. *TREE* 12:333–334.
- Davis, R. W., L. A. Fuiman, T. M. Williams, S. O. Collier, W. P. Hagey, S. Kanatous, S. Kohin, and M. Horning. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Sci.* 283: 993–996.
- Eastman, J. T. 1985. *Pleurogramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biol.* 4:155–160.
- Everson, I. 1985. Fish biology. In R. M. Laws (ed.), *Antarctic ecology*, pp. 491–532. Academic Press, London.
- Green, K. and H. R. Burton. 1987. Seasonal and geographical variation in the food of the Weddell seals, *Leptonychotes weddellii*, in Antarctica. *Aust. Wildl. Res.* 14:475–489.
- Hill, R. D., R. C. Schneider, G. C. Liggins, A. H. Schuette, R. L. Elliot, M. Guppy, P. W. Hochachka, J. Qvist, K. J. Falke, and W. M. Zapol. 1987. Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol.* 253:R344–R351.
- Hill, S. E. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ph.D. Diss., University of Minnesota, Minneapolis, MN.
- Kirkwood, R. and G. Robertson. 1997a. Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. *Mar. Ecol. Prog. Ser.* 156:205–223.
- Kirkwood, R. and G. Robertson. 1997b. The foraging ecology of female emperor penguins in winter. *Ecol. Monog.* 67:155–176.
- Kooyman, G. L. 1993. Breeding habitats of emperor penguins in the Western Ross Sea. *Antarct. Sci.* 5:143–148.
- Kooyman, G. L., S. F. Ackley, E. C. Hunke, R. Van Dam, and G. Robertson. 1998. Emperor penguin moult cycle: Travel, location, and habitat selection. *N.Z. Nat. Sci.* 23:97.
- Kooyman, G. L., C. M. Drabek, R. W. Elsner, and W. B. Campbell. 1971. Diving behavior of the emperor penguin, *Aptenodytes forsteri*. *Auk* 88:775–795.
- Kooyman, G. L. and T. G. Kooyman. 1995. Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor* 97:536–549.
- Kooyman, G. L., T. G. Kooyman, M. Horning, and C. A. Kooyman. 1996. Penguin dispersal after fledging. *Nature* 383:397–397.
- Kooyman, G. L. and J. L. Mullins. 1990. Ross Sea emperor penguin breeding populations estimated by aerial photography. In K. R. Kerry and G. Hempel (eds.), *Antarctic ecosystems. ecological change and conservation*, pp. 169–176. Springer-Verlag, Berlin.
- Kooyman, G. L. and P. J. Ponganis. 1998. The physiological basis of diving to depth: Birds and mammals. *Ann. Rev. Physiol.* 60:19–32.
- Kooyman, G. L., P. J. Ponganis, M. A. Castellini, E. P. Ponganis, K. V. Ponganis, P. H. Thorson, S. A. Eckert, and Y. Le Maho. 1992. Heart rates and swim speeds of emperor penguins diving under sea ice. *J. Exp. Biol.* 165:161–180.
- Kooyman, G. L., P. J. Ponganis, and R. Howard. 1999. Diving animals. In C. E. G. Lundgren and J. N. Miller (eds.), *The lung at depth*, pp. 587–620. Marcel Dekker, Inc., New York.
- Kooyman, G. L., E. A. Wahrenbrock, M. A. Castellini, R. W. Davis, and E. E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* 138:335–346.
- Plötz, J. 1986. Summer diet of Weddell seals (*Leptonychotes weddellii*) in the Eastern and Southern Weddell Sea, Antarctica. *Polar Biol.* 6:97–102.
- Ponganis, P. J., G. L. Kooyman, and M. A. Castellini. 1993. Determinants of the aerobic dive limit of Weddell seals: Analysis of diving metabolic rates, postdive end tidal PO₂'s, and blood and muscle oxygen stores. *Physiol. Zool.* 66:732–749.
- Putz, K. 1995. The post-moult diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica. *Polar Biol.* 15:457–463.
- Schreer, J. F. and J. W. Testa. 1996. Classification of Weddell seal diving behavior. *Mar. Mamm. Sci.* 12:227–250.
- Stirling, I. 1969. Distribution and abundance of the Weddell seal in the Western Ross Sea, Antarctica. *N.Z.J. Mar. Fresh. Res.* 3:191–200.
- Stonehouse, B. 1964. Emperor penguins at Cape Crozier. *Nature* 203:849–851.
- Testa, J. W. 1994. Over-winter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the southwestern Ross Sea, Antarctica. *Can. J. Zool.* 72:1700–1710.
- Testa, J. W. and D. B. Siniff. 1987. Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Ecol. Monog.* 57: 149–165.
- Testa, J. W., D. B. Siniff, M. J. Ross, and J. D. Winter. 1985. Weddell seal—Antarctic cod interactions in McMurdo Sound, Antarctica. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic Nutrient Cycles and Food Webs*, pp. 561–565. Springer-Verlag, Berlin Heidelberg.
- Testa, J. W., G. Oehlert, D. G. Ainley, J. L. Bengston, D. B. Siniff, R. M. Laws, and D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: Periodic fluctuations in the phocid seals. *Can. J. Fish. Aquat. Sci.* 48:631–639.