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Do crabeater seals forage cooperatively?

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Abstract

Crabeater seals are abundant pack-ice predators that feed almost exclusively on krill. They have a circumpolar distribution and are generally sighted hauled out on ice floes alone or in pairs. Here we report our observations of a sighting of 150–200 crabeater seals, which were synchronised in their diving and surfacing behaviour, along with a summary of similar observations from western Antarctica of large groups of crabeater seals in synchronous dive cycles. We report on the low frequency of sightings of such groups during Antarctic pack-ice seal surveys in eastern (Greater) Antarctica. We examine plausible hypotheses to explain these observations, and suggest this behaviour is likely to represent some form of cooperative foraging behaviour, whereby a net advantage in individual energy intake rates is conferred to each seal. Current research on crabeater seal foraging using satellite-linked dive recorders is unlikely to provide sufficiently fine-scale data to examine this hypothesis. Nor will this approach indicate if a seal is foraging with conspecifics. The use of remote or animal-borne camera systems is more likely to provide an insight into fine-scale foraging tactics, as well as the possible, occasional use of cooperative foraging strategies.

1. Introduction

Batch feeders are predators that consume a large number of prey, such as krill, in a single feeding event (Heithaus and Dill, 2002). Obligate batch feeders like the mysticetes have evolved anatomical (e.g., baleen plates, throat pleats) and behavioural (e.g., lunge feeding, skim feeding) features to optimise their foraging efficiency through filtering large volumes of water and prey (Croll and Tershy, 2002). Non-whale predators of krill (e.g., seals, penguins, sea birds, fish) have evolved other strategies that generally require the individual predator to move through the prey patch consuming individual or small numbers of prey at a time. The density and behaviour of the prey (particularly predator avoidance) is highly influential on foraging performance. Cooperative, group foraging is one mechanism that could optimise the net energy intake rate of individual predators.

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Crabeater seals, *Lobodon carcinophagus*, are abundant inhabitants of the Antarctic pack-ice zone (Erickson et al., 1973; Kooyman, 1981; Laws, 1984). Their biomass is perhaps greater than any other seal (Erickson and Hanson, 1990), and their specialised foraging behaviour means they are important consumers of krill (Øritsland, 1977; Laws, 1984). Indeed, Hewitt and Lipsky (2002) estimated that crabeater seals consume more krill in the southern ocean than do whales. Many aspects of the foraging ecology of crabeater seals remain to be elucidated, primarily as a result of the inaccessibility of their habitat.

The dentition of crabeater seals is among the most specialised of any mammal. The post-canine teeth of the upper and lower jaw have elaborate cusps that interdigitate when the mouth is closed which, together with other aspects of their cranial anatomy, form an effective sieve to retain captured prey (King, 1961; Kooyman, 1981). Direct observation of crabeater seal feeding behaviour is understandably limited. Racovitza (1900) described apparent filter feeding in crabeater seals with his observation of individual seals swimming, with mouths open, through krill aggregations. Kooyman (1981) cited G.S. Wilson (personal communication) as observing crabeater seals feeding on invertebrates that were attracted to a light on a pier. The seals were capturing their prey one at a time. A different prey capture method has been observed in a few captive seals, which were observed to suck food items into their mouths from distances up to 50 cm (Ross et al., 1976; Klages and Cockroft, 1990). These authors suggested that such a strategy would enable crabeater seals to capture Antarctic krill *Euphausia superba* among the rough habitat on the bottom of ice floes.

Bengtson and Stewart (1992) described the autumn diving behaviour of six crabeater seals, and noted a diel pattern of diving that encompassed depths and times where the animals might encounter krill aggregations. They argued that the pattern of deep dives (100–250 m) during crepuscular periods (twilight), shallow (20–50 m), continuous dives during the night, and haul-out during the day, was responsive to prey movement in the water column, as well as maximising hunting efficiency by foraging in minimum light. Nordøy et al. (1995) reported similar foraging patterns for eight crabeater seals in the late summer, through autumn period, and concluded the behaviour was consistent with that of a specialist krill predator. More recent research efforts including the international initiative of the Antarctic Pack Ice Seal (APIS) Program, and the US Southern Ocean Global Ocean Ecosystems Dynamics Program (SO GLOBEC) (Hofmann et al., 2002; Burns et al., 2004) are providing further insights into the seasonal foraging behaviour of individual, instrumented crabeater seals. These studies are characterising large- and meso-scale spatial and temporal aspects of how crabeater seals interact with their prey, but will not provide an insight into fine-scale foraging strategies, and in particular whether or not crabeater seals forage independently, or in association with others.

The foraging behaviour of another Antarctic krill consumer, the Antarctic fur seal *Arctocephalus gazella*, has been widely reported (e.g., Boyd, 1996, 1999; Goebel et al., 2000). Analyses of many dive records have provided insights into the way this species search and move between krill patches, but it has not been until the recent innovation of using a seal-borne camera that fine-scale foraging tactics have been examined (Hooker et al., 2002). In five of six deployments of the camera, sub-surface photographs included the presence of other fur seals. Surface aggregations of fur seals in the vicinity of prey patches have been observed, but this was the first record that the aggregations were maintained, to some extent, at depth (Hooker et al., 2002).

Determining if a group of predators are actually cooperating in their foraging, as opposed to acting independently, requires at least two criteria to be satisfied (modified from Heithaus and Dill, 2002). First, in the context of a batch feeder, there must be a short-term opportunity cost to the individual by not attacking prey immediately while herding. Second, the cooperative strategy must lead to a net increase in energy intake rate compared to feeding independently. The existence of these criteria is difficult to demonstrate methodologically for marine predators, and generally our interpretation of group foraging strategies is constrained to direct observations. In this paper we report on the behaviour of a large aggregation of foraging crabeater seals that provides some evidence that this species may hunt cooperatively. Further, we examine two extensive sightings data sets to determine how often this species is seen in large groups, along with some notes on group behaviour.

2. Methods

Data are reported from three sources. The first are observations by three of us (NG, WF and DC) from the vessel ARSV *Lawrence M. Gould* (LMG), which, during July and August, was conducting one of four SO GLOBEC cruises in 2001. A broader description of the process and survey SO GLOBEC cruises, and maps can be found in Hofmann et al. (2002, 2004). A component of the planned work on the LMG was the capture and deployment of satellite-linked dive recorders on crabeater seals and daylight observations for seals was maintained from the ship's bridge.

The other sources of data are two extensive crabeater seal sightings datasets, which were examined for information on group size and activity. The first dataset (the APIS dataset) is from the Australian APIS surveys conducted off eastern Antarctica in the period of September to December in the years 1994–1997. The data are all from structured ship-based or aerial ice-seal surveys (C. Southwell, unpublished data). The second dataset (the Fraser dataset) was collected as opportunistic sightings of crabeater seals recorded during research work around Palmer Station, western Antarctica (64° 46′S, 64° 04′W) between 1990 and 2002 (W. Fraser, unpublished data). The data were collected between October and March, with most sightings during December, January and February.

3. Results

On 27 July 2001 at 2030 h a group of 150–200 crabeater seals was encountered by the LMG hauled out along the edge of a large ice floe (approximately 200 m × 100 m) to the west of Adelaide Island, Antarctica at 67° 30′S, 69° 30′W. Ice cover in the area was approximately 8/10th, with surrounding floes being generally smaller and more fragmented. The combination of dark conditions and light snowfall made a more accurate estimation of seal numbers impossible. With the intention of working on one or more of the seals from this group after dawn, the LMG remained close to the ice floe for the rest of the night. At about 0400 h on 28 July 2001, the Captain of the LMG, Mr. Robert Verret, reported that all the seals moved into the water over a period of about half an hour. After dawn, at about 0900 h two of us (NG and DC) went onto the ice floe the seals had been hauled out on and collected 5 fresh faecal samples. These samples consisted almost entirely of krill exoskeletons. At about 1030 h a very large group of crabeater seals was seen from the bridge of the ship in an area of water with about 7/10th ice that was to the fore and portside of the ship. Beyond about 700 m the ice cover was heavier, with no open water being in view. The animals were in the water about 500 m off the bow of the ship (which was still holding position with the starboard side of the ship alongside the floe the seals had hauled out on). The number of seals was similar to the group seen the previous night, so they were assumed to be the same animals. The most notable feature of the behaviour of this group was that their surfacing behaviour was highly synchronised. All seals in the group surfaced very close to each other between the many small floes (ranging mainly from about 2–10 m diameter), and then remained underwater for about 6 min. Subsequent surfacings occurred up to several hundred metres apart. The group was visible at the surface for a period of about 20 s. Although accurate data were not recorded for each dive, the seals were observed from the bridge to continue a highly synchronised, continuous cycle of approximately 6 min dives and 20 s surfacing periods. After about 2 h the group disappeared from view.

During the two cruises of the SO GLOBEC in 2001, satellite-linked dive recorders (SDR) were attached to 16 crabeater seals. These seals had a mean dive depth of 140 m and a mean dive duration of 7.5 min (Burns et al., 2004). The dive duration of about 6 min that we recorded from the LMG for the synchronously diving group of seals is in close accord to the data from the SDR. Similarly, the 6 min dive cycle is close to the 5.4 min mean dive time for Type III (crepuscular foraging dives) reported by Bengtson and Stewart (1992).

The APIS dataset revealed no sightings of groups comparable to the one seen from the LMG. The total number of crabeater seal sightings was 1990, of which 96% were of single or pairs of animals. The largest group recorded was 15 seals. Most sightings were of animals on ice (98%), but group sizes were not significantly different on ice or in water (*t* test; $p = 0.83$) (C. Southwell, unpublished data).

By contrast to the APIS dataset, only 54% of sightings from the Fraser dataset were of single or pairs of animals, with 23% of groups of 3–10 animals, 14% of 11–100 animals, and 9% of greater than 100 animals. The maximum group size was estimated to be at least 300 seals. Of the 18 sightings of aggregations of greater than 100 seals, three groups of an estimated 128, 155 and 299, respectively, were hauled out on ice floes. A further four groups were milling at the water surface, and 11 groups were feeding. Feeding was used as a category only when krill were seen in association with the seals. Of the feeding groups, four of the aggregations were exhibiting the synchronous diving and surfacing that we observed from the LMG.

4. Discussion

The two datasets are not readily comparable, as one was targeted and the other opportunistic, and the temporal and spatial scales are entirely different. Furthermore, as there appears to be an inverse relationship between pack-ice cover and crabeater seal density (Eklund and Atwood, 1962; Erickson et al., 1973; Bester et al., 1995) comparisons of the surveys may be further confounded. Nevertheless, the presence of substantial sightings of large aggregations of crabeater seals in the Fraser dataset is a dramatic difference. While regular sightings of large aggregations of crabeater seals are not widely reported in the literature (e.g., Kooyman, 1981; Erickson and Hanson, 1990; Bengtson, 2002), they clearly do occur, particularly around western Antarctica. Siniff et al. (1979) surveyed the region on the western Antarctic Peninsula from September through November during 1975, 1976 and 1977. They classified sightings of seals as singles, family groups, mated pairs and concentrations. The last category was generally associated with bays and fast ice, and included two sightings of more than 1000 hauled out crabeater seals. Associated with the large groups on the fast ice, they reported groups of fifty or fewer seals swimming together "surfacing periodically more or less in synchrony." Similarly, Bertram (1940) discusses the sightings of many large groups of crabeater seals by Antarctic expeditions during the early Twentieth Century, many of which were apparently travelling together in the water.

The sighting of the crabeater seals we report from the LMG, and at least 11 of the observations in the Fraser database add to the earlier published accounts, and demonstrate that, at least in western Antarctica, crabeater seals do, on occasions, aggregate in very large numbers. While the mechanisms that lead to such aggregations are unknown, and the functions are likely to be varied (and could include predator avoidance, socialisation and foraging), the sighting of krill in the water in association with the crabeater group sightings reported in the Fraser database and the presence of krill in the seal scats we report indicate that these crabeater seal groups are often associated with aggregations of their primary prey, Antarctic krill.

Given the known patchy distribution of *E. superba* (Miller and Hampton, 1989), a finding of an associated concentration of their predators is perhaps not surprising. The focus of this paper however, is interpreting what the observations of synchrony in surface behaviour suggest.

If the rate at which each crabeater seal was able to capture krill from the patch was independent of the behaviour of the other seals, then we would expect to see no pattern in overall dive cycles within the group. While this non-synchronised pattern is commonly seen, our observations, on at least six occasions, that these large groups will surface and dive synchronously, for sustained periods, provides compelling evidence of mutually beneficial (cooperative) interactions during each dive. We are not the first to report this type of synchronised diving. Bertram (1940) described his observation of two adult crabeater seals feeding close to his ship. The seals were diving synchronously ("in almost perfect unison"), spending about 3 min submerged and 30 s at the surface. The seals dived vertically, disappearing from view in about 6 m, and resurfacing within about 20 m of where they dived.

This type of cooperative diving may function if a group of crabeater seals was able to herd the prey in order to concentrate and constrain the aggregation to enable more efficient capture rates. We have one observation made by one of us (WF), that such herding occurs. On 2nd March 1995 about 55 crabeater seals were feeding, in open water, directly off the jetty at Palmer Station. By viewing the behaviour from above, the seals were seen to be swimming relatively fast, clockwise, and in unison, around a krill aggregation about 3–5 m below the surface. This behaviour concentrated the patch in the water column and one or more seals would then feed on the patch either by "darting" out from the group into the patch, or by taking krill near the patch's perimeter while maintaining swimming formation.

It is possible that mechanisms other than herding are utilised by groups of crabeater seals. By feeding independently, but simultaneously (within the same dive cycle), a large number of predators within the same krill aggregation may sufficiently disrupt the efficiency of the prey's avoidance strategies to lead to an increase in prey capture rate. Heithaus and Dill (2002) describe such a strategy as bi-product mutualism. It is possible that other krill predators such as the Antarctic fur seal may occasionally utilise similar strategies.

Clearly, crabeater seals do not spend much of their time in large, conspecific aggregations. Indeed, the locations of the large groups of crabeater seals we discuss are limited to the shelf and near-shore waters of the western Antarctic Peninsula. This may reflect some unique physical or bio-oceanographic features of the region, or may simply reflect higher observation effort in near-shore waters. It is likely that the cooperative feeding strategy we suggest only occurs in circumstances where movements of predators and prey are such that a sufficient number of predators are feeding on a particular form (size, shape or density) of krill aggregation that triggers an advantage to such a strategy. Factors such as ice conditions or prey concentrations could lead to such circumstances. Our data suggest that at least 50–100 crabeater seals are required, but there may even be mutual advantages in synchronising the efforts of as few as two seals (Bertram, 1940). In all other circumstance we would expect crabeater seals to utilise a range of fine-scale foraging tactics that are independent of the activity of other predators.

Current research on crabeater seal foraging using satellite-linked dive recorders is unlikely to provide sufficiently fine-scale data to examine this hypothesis. Nor will this approach indicate if a seal is foraging with conspecifics. The use of remote or animal-borne camera systems (e.g., Hooker et al., 2002) is more likely to provide an insight into fine-scale foraging tactics, as well as the possible, occasional use of cooperative foraging strategies.

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