

BEHAVIOR OF SOUTHERN RIGHT WHALES, *EUBALAENA AUSTRALIS*, FEEDING ON THE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA*

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ABSTRACT

Southern right whales, *Eubalaena australis*, were observed in 3 successive years on the western side of the Antarctic Peninsula. These whales do not appear to be from the well-documented Valdes, Argentina population. The whales we observed were feeding on Antarctic krill, *Euphausia superba*. When krill were at the surface right whales surface-skimmed at high speed, with upper jaw lifted above the water surface. In heavy weather one right whale "tail-sailed" at slow speed, with head submerged and apparently feeding. When krill were organized in subsurface schools, right whales engaged in subsurface feeding, diving repeatedly in place, apparently working a given school. One whale swam directionally to the only known large school of krill in the area and fed intensively, rested on the surface, then began a second feeding bout. Whales hyperventilated, false fluked, and fluked prior to feeding dives. These are the first detailed observations of feeding behavior of right whales in Antarctic waters and suggest that coastal Antarctica may have been (and may become again) a regular part of the summer feeding range of the species.

Right whales are among the rarest of the great whales, having been hunted almost to extinction a century ago. The southern right whale, *Eubalaena australis*, has been studied only recently and only during the austral winter when the whales aggregate inshore to bear calves and to mate (Clarke 1965; Payne 1976, 1986; Best 1981; Aguayo and Torres 1986). Because right whales were commercially extinct by the mid-1850's, very little has been learned about their ecology from the 20th century whaling industry. Information on feeding, migration, stock structure, and reproductive biology was collected for most other Antarctic mysticete whales during the heyday of whaling in this century (e.g., Mackintosh 1965; International Whaling Commission reports 1964-present). The small number of surviving right whales (ca. 2% of historic levels in the Southern Hemisphere, Breiwick and Braham 1984) has made it difficult for researchers to study this species. Our current understanding of its feeding and calving ecology in the Southern Hemisphere comes from observations made primarily off Peninsula Valdes, Argentina (Payne 1986).

In Antarctic waters south of lat. 60°S, more than 30 sightings of right whales have been reported previously (Berzin and Vladimirov 1981; Goodall and Galeazzi 1986; Ohsumi and Kasa-

matsu 1986). Most were in the vicinity of the South Orkney Islands, 9 were near the Antarctic Peninsula, 6 were in the Pacific sector of the Antarctic, and 2 were south of Africa. We have observed southern right whales during 3 consecutive austral summers near the western shore of the Antarctic Peninsula, and the sightings reported herein and in Stone and Hamner (in press) are the most southerly as well as the most detailed observations.

We sighted one individual during the 1983–84 austral summer (also recorded by Captain P. Lenie in the log of the RV *Hero*; Goodall and Galeazzi 1986), two individuals in 1984–85, and eight in 1985–86, four of which we individually identified. In 1986 a fortunate combination of fair weather and available ship time permitted us to make the first extended uninterrupted observations on the behavior of right whales feeding on the Antarctic krill, *Euphausia superba*.

METHODS

Right whales are distinguished by the absence of a dorsal fin and regions of cornified skin (callosities) on the head, jaws, and chin. Individual whales were identified by standard methods, using video tapes and telephotographs of head callosities and scarring patterns on the head and back (Payne et al. 1983; Kraus et al. 1986). When possible, we dropped large disks of plywood of

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known diameter next to the whale and included it in the photograph to measure whale size.

Behavioral patterns were observed from the ship's bridge and recorded on a portable computer as they occurred, using a program which timed entries of encoded behaviors or comments to the nearest second. Krill schools were recorded on a Simrad echosounder and the identity of the organisms causing the echograms was verified by net samples taken with an Isaacs-Kidd midwater trawl and by divers' visual confirmation of krill schools near the surface.

RESULTS

7 January 1984: At 0500 hour, north of Cape Murray near Two Hummock Island, one right whale was feeding at the surface with its upper jaw lifted above the water, swimming at high speed (estimated at 8–9 knots by the ship's captain) in feeding runs of 15–20 seconds, which we recorded on video. Three humpback whales nearby were diving in one specific location. The right whale repeatedly changed direction between surface runs so that its horizontal directional feeding excursions did not take it far from the vicinity of the vertically diving humpbacks. During these powerful filter-feeding runs enormous amounts of water were displaced, cascading beside and behind the right whale and producing a large wake.

15 January 1985: A cow and a calf were swimming slowly at the surface some 500 m from the eastern shore of Anvers Island. On approach by the ship the whales swam slowly into shallow water where we could not follow. It was near dusk and we could not get photographs for future identification.

7 January 1986: We encountered one southern right whale and six humpbacks at 1830 hour at lat. 63°46'S, long. 61°13'W, between Trinity and Hoseason Islands. We photographed the head and body of the right whale for subsequent identification. We followed the whale for approximately 2 hours, recording diving times, surface intervals, and breathing rates. The whale frequently changed directions underwater and consequently we often failed to see the whale immediately when it resurfaced, so breathing rate data for this behavioral sequence are incomplete. The whale appeared to have captured krill on at least one dive because when the whale surfaced it repeatedly and briefly opened and closed its mouth, with baleen visible, a behavior presumably associated

with separation of krill and water prior to swallowing the prey (Watkins and Shevill 1976). About 50 cape petrels, *Daption capensis*, alighted on the water and fed at the surface around the whale. When the whale's jaw movements ceased, the birds soon stopped feeding, but they remained on the water and did not follow the whale when it swam away at the surface.

2 March 1986: We observed one right whale at the northern end of the Neumayer Channel, where a large iceberg was grounded on a 93-fathom rise 2 miles east of Iceberg Point. The wind was blowing from the north at 20–24 knots and a strong surface current was flowing south, producing a bow wave on the grounded iceberg. The right whale repeatedly swam NE of the berg, raised its tail high out of the water at 90° to the wind, submerged its head, and "sailed" downwind past the iceberg, a behavior previously noted for right whales in Argentina (Payne 1976). Soon after we first saw the whale, it stopped tail-sailing and began diving, still along the N-S transect near the iceberg where it had been sailing. The presence of the ship did not cause the whale to alter its back-and-forth swimming rhythm or direction. We waited until the whale began one of its N-S transects past the iceberg and followed about 100 m behind it with the ship. A large school of krill was present on the east side of the iceberg. We recorded no other schools in the vicinity. The whale was accompanied by three female fur seals. The seals constantly darted about the head of the whale when it surfaced after long dives and appeared to annoy the whale, because several times the whale repeatedly slashed its head sideways when the seals swam too close.

3 March 1986: At 1030 hour, we spotted a single southern right whale near the mouth of Andvord Bay on the Antarctic Peninsula. The whale was swimming SSW at about 3 knots, making short dives that lasted about 19 seconds ($N = 12$, $SD = 9.0$ seconds), with brief surface intervals that averaged 6.1 seconds ($N = 12$, $SD = 2.6$ seconds) (Fig. 1). The whale then stopped diving but continued to swim SSW toward the NE tip of Lemaire Island, swimming mostly at the surface for approximately 90 minutes. During this period the whale appeared unconcerned with the ship, which remained 50–100 m behind it, but when the whale neared an iceberg that was hard aground near Lemaire Island, it turned suddenly at a right angle to its prior course and swam between the iceberg and the rocks. The ship was nonetheless able to follow the whale through the

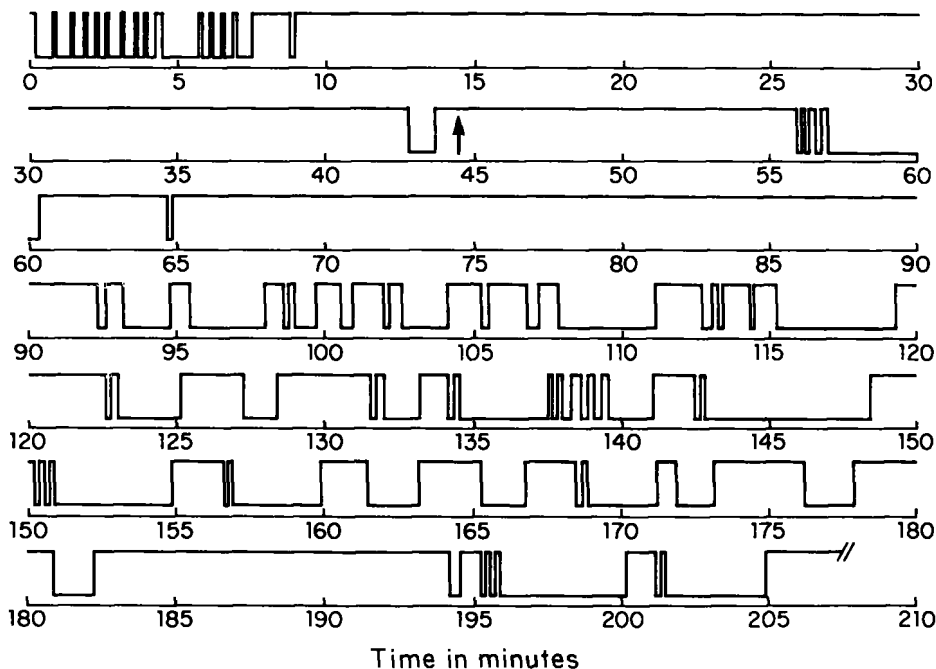


FIGURE 1.—Dive record of the right whale constantly observed for 3.5 hours on 3 March 1986. 44 minutes (arrow): The ship approached to within 10 m of the whale for i.d. photographs and size measurement. 54 minutes: The whale hyperventilated and dove in an area without krill, then swam northward. 92 minutes: The whale began diving on scattered small krill schools while still traveling N and NNW. 140 minutes: The whale stopped and began diving on one large concentration of krill. 182 minutes: The whale rested on the surface, moving its jaws. 194 minutes: The whale began a second feeding bout ca. 400 m further south.

narrow channel. Thereafter the whale ignored the ship and altered course to NNW, still swimming at the surface. The ship pulled ahead of the whale to measure its length and this may have caused the short dive noted at $t = 43$ minutes. However, the whale calmly surfaced again within 10 m of the ship and watched us while we photographed it next to the wooden disk. The whale was 11 m long. The whale then continued to swim at the surface to the NNW. During the period that the whale swam at the surface without diving the average time between breaths was 50.8 seconds ($n = 55$; $SD = 10.8$). At $t = 54$ minutes the whale began to hyperventilate, took three short dives, lifted the flukes partially clear of the water (false fluking) on the third dive, and then fully raised the flukes on the fourth dive, which lasted 210 seconds. The whale then remained at the surface for about 30 minutes while swimming northward.

This pattern of hyperventilation prior to a long dive occurred before every long dive sequence which was preceded by a surface interval of at

least 4 minutes (Fig. 2). We used this criterion to restrict our dive selection for this plot because there is some indication that there is also a brief recovery period involving hyperventilation after long dives. Of the last 19 breaths that were taken during the 90 seconds before the 5 long dives plotted in Figure 2, 18 were less than 30 seconds apart, with a mean interval of 15 seconds ($N = 19$, $SD = 7.3$). During the time preceding this 90-s hyperventilation period, the whale averaged 1 breath every 48 seconds ($N = 17$, $SD = 12.4$), not significantly different from the time of 50.8 seconds recorded between breaths during long surface intervals without dives. During hyperventilation, therefore, breathing rate increased by about $3\times$.

At $t = 92$ minutes we began to record scattered small krill schools on the echosounder and the whale began to dive erratically, with some reasonably long dives, but most quite short. Of 23 dives, 13 (56%) were shorter than 10 seconds; the time averaged for all dives was 75.3 seconds

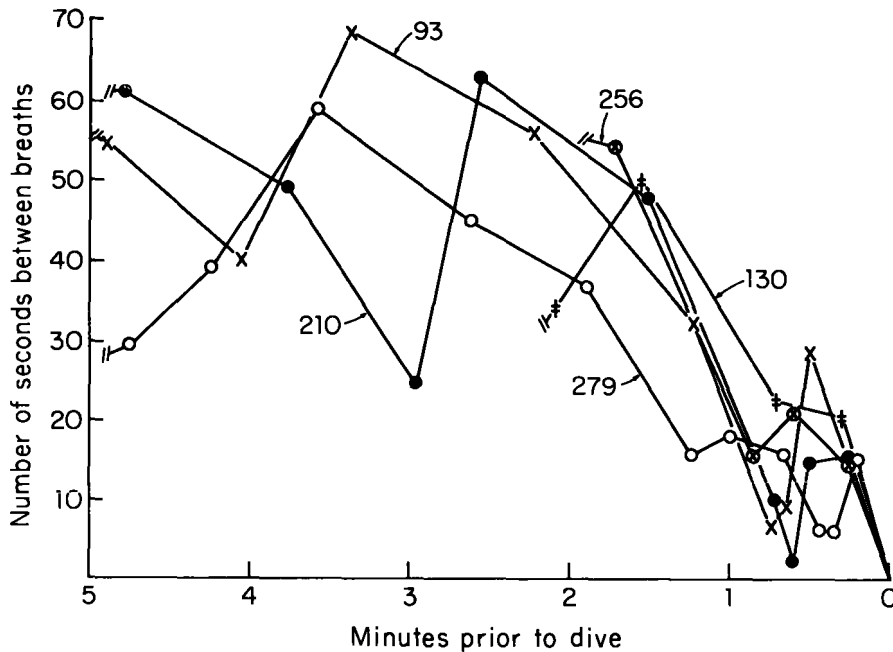


FIGURE 2.—Breath sequences prior to 5 dives lasting from 93 to 279 seconds. During the 90 seconds immediately preceding dives, the mean interbreath interval was 15 seconds. Prior to this 90-s period of hyperventilation the mean interbreath interval was 48 seconds.

($N = 20$, $SD = 74.6$). During this period of erratic diving the whale continued to swim N, then NNW. At about $t = 140$ minutes the whale stopped traveling NNW and began a series of 10 dives, the second being the longest, followed by successively shorter dives. These dives were followed by rather uniform surface intervals and all 10 lasted significantly longer ($\bar{x} = 183.5$ seconds, $N = 10$, $SD = 89.2$) than the previous mean of 75 seconds. At the end of the dive sequence, at 182 minutes, the whale stopped swimming entirely and floated motionless at the surface, occasionally moving its jaws. This inactivity lasted about 12 minutes and then the whale began a second series of dives. We called these dive sequences, which consisted of regular length surface intervals interspersed with a series of longer dives of progressively decreasing duration, “feeding bouts” because at $t = 140$ seconds the whale had reached the only major aggregation of krill in the vicinity, as verified by sonic records (Fig. 3). We saw dense schools of krill and isolated krill at the surface from the bow of the ship, and we captured krill in three successive hauls with the 1 m Isaacs-Kidd midwater trawl.

During the first feeding bout the whale slowed

from its steady 3-knot swimming speed and moved slowly at about 1 knot, but no longer in any specific direction, finally swimming some 400 m to the south before beginning the second feeding bout. The whale had fed on krill earlier also, because it defecated during the feeding sequence and the feces, as determined by later microscopic examination, were composed entirely of well-digested euphausiids.

The display of a false fluke prior to the high fluke initiating a long dive did not necessarily indicate presence or absence of krill, but when krill were present, it was a highly significant predictor of the length of the dive. In the presence of prey, when the whale showed its flukes once (i.e., did not false-fluke preceding the dive), dive duration averaged 91.2 ± 13.0 seconds ($N = 5$), whereas when both a false fluke and a high fluke preceded the dive, the dive averaged 234.7 ± 64.4 seconds ($N = 7$).

In March and April 1986 we saw a total of eight southern right whales. Of these we distinguished four as individuals on the basis of video tapes and photographs of callosities and body markings. One of these whales was the same individual that we had observed in January some 70 miles fur-

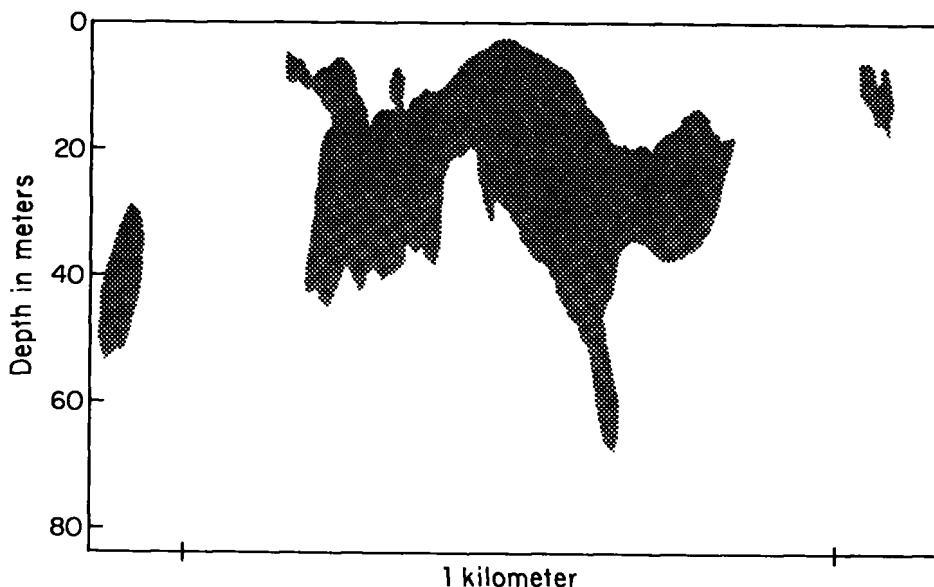


FIGURE 3.—Echogram of krill school on 3 March 1986 on which right whale stopped swimming and began feeding bout.

ther north, as confirmed by comparing video recordings of both sightings. Photographs of these four individuals were subsequently compared with the catalog of southern right whales that overwinter near Peninsula Valdes, Argentina (Payne and Rowntree 1984), but none of the Antarctic individuals were in that compendium of some 623 individuals.

DISCUSSION

Our observations of southern right whales along the Antarctic Peninsula suggest that coastal Antarctica may have been (and may well become again) a regular part of the summer feeding range of the species. These sightings indicate a more extensive distribution in the Southern Ocean than heretofore reported, an extension corroborated by the comparison of recent and historic summer distributional patterns by Ohsumi and Kasamatsu (1986). Southern right whales were hunted almost to extinction in the shallow coastal embayments where they overwinter more than 100 years before whaling began in the Southern Ocean (Harmer 1928; Townsend 1935). It is not surprising, therefore, that there are only a few scattered records of southern rights in Antarctic waters, fluke observations so to speak. During the past 50 years southern rights have

been protected, and several demes of southern right whales have increased (Best 1981; Ohsumi and Kasamatsu 1986; Whitehead et al. 1986), and a commensurate extension of the summer feeding range into areas formerly occupied by these whales may be occurring.

It is interesting that none of the 4 individual whales for which we have photographic identifications appear in the catalog of 623 individual southern rights for the Valdes, Argentina breeding population (Payne and Rowntree 1984). We believe that the right whales we encountered in Antarctic waters probably winter elsewhere, perhaps along the Chilean coast, which has been less well surveyed than has the east coast of South America (Cardenas et al. 1986).

Payne (1976) described tail-sailing among the Valdes population of southern right whales and suggested that this may be a form of play behavior. In Antarctic waters this behavior may be a method used to forage on krill. The right whale that we observed tail-sailing had three fur seals in attendance, constantly darting about its head, apparently feeding on the same prey as the whale. Furthermore, tail-sailing occurred next to a grounded iceberg at a specific location that was repeatedly transected by the whale, the only spot in the vicinity where krill were detected on the ship's sonar.

Northern right whales feed by both surface-skimming and subsurface feeding, apparently holding the jaws agape below the surface much like they do when at the surface (Watkins and Schevill 1976, 1979). Surface-skimming by northern right whales that feed on copepods and juvenile euphausiids occurs at speeds of about 3 knots with relatively little turbulence (Watkins and Schevill 1976, 1979). The one southern right whale which we observed surface-skimming, and which was also mentioned in Goodall and Galeazzi (1986), swam at about 8 knots, with an immense amount of turbulence. This whale undoubtedly was feeding on *Euphausia superba*. The extremely high speed of this whale when surface-skimming may be related to type of prey. *Euphausia superba* is a large euphausiid that swims up to 30 cm/second, and it is quite adept at avoiding scuba divers and other dark objects (Hamner et al. 1983; Hamner 1984). It may be that right whales adjust the speed of their surface feeding runs to overcome the swimming speed of the particular prey that they pursue. Fin whales also exhibit differences in breathing and diving rhythms when feeding on euphausiids and on schooled fish (Watkins et al. 1984).

The southern right for which we have a 3.5-h record in 1986 fed exclusively below the surface. It swam for about an hour at the surface almost directly NNW toward the only patch of krill that we had located previously via the echo sounder during repeated transects across the mouth of Andvord Bay. It is not understood how baleen whales locate prey. They might echolocate, they might listen for krill noises, or they might remember where they had prior success and return to the general vicinity and then begin to hunt randomly. Although our data do not allow us to choose among these possibilities, it appears that this particular southern right whale did navigate directly to patches of prey, as suggested by Watkins and Schevill (1979) for northern right whales. However, some subsurface searching probably occurs as well. The whale that we followed for the longest period of time made a reasonably long dive of 210 seconds in the middle of its surface swim toward the krill patch. It apparently did not find anything to eat (nor did the sonar indicate the presence of krill), and it made no more significant dives for about 30 minutes.

When the whale reached an area with small scattered krill schools, its dives were generally short, and the temporal spacing and duration of dives and surface intervals were erratic. When

the whale reached a large school of krill it stopped swimming between dives, dives lasted longer, surface intervals between dives became more regular, and successive dives were progressively shorter. After 10 of these dives the whale floated without any swimming movements at the surface for about 12 minutes while occasionally rattling its baleen and slightly lifting its upper jaw.

The whale clearly anticipated its dives. It hyperventilated for about 90 seconds prior to all of the long dives. Hyperventilation is a common precursor to diving in air-breathing vertebrates (Kooyman et al. 1981), but this respiratory pattern apparently has not been reported previously for a baleen whale.

The data that we present in support of this feeding pattern are admittedly modest, consisting of only one continuous 3.5-h data sequence for one individual. Nonetheless, this data set is truly unique and it includes a series of statistically significant changes of behavior at the surface and at depth which are correlated with prey distribution. Since the changes of behavior are real, they merit interpretation. One hypothesis to account for the increase and then the decrease in dive length after encountering prey is that the whale dove to its full capacity in order to maximally exploit an opportunity to feed. With repeated dives its dive capacity may have diminished, producing first long, then shorter and shorter dives (Fig. 1). In contrast, this breathing pattern has not been observed in grey whales, which exhibit a sustained capacity for repetitive, nearly monotonic diving while feeding (Obst et al. in prep.). It is possible that right whales, being more specialized for surface-skimming, become exhausted more readily during sustained diving.

An alternative hypothesis to account for this pattern of behavior is that the whale captured krill with such ease on the first long dive of 348 seconds that a "digestive bottleneck" (Kenward and Sibly 1977) developed; subsequent dives would be progressively shorter because the stomach (or some storage chamber) filled more rapidly than the food could be processed. The long surface interval of immobility followed by a second feeding bout might then represent the time taken to clear such a chamber (e.g., the first of the three stomach pouches) in preparation for the next bout of feeding. If this hypothesis is correct, it implies that once a right whale has found a particularly favorable school of krill, it fills up very rapidly. This interpretation contrasts markedly with a popular impression of great whales as continuous

feeders that harvest prey while swimming lazily through diffuse planktonic resources. Herwig et al. (1984) presented preliminary evidence that microbial fermentation of ingesta may occur in the forestomach of baleen whales, a process which may be expected to limit the throughput rate of food in accordance with continuous-flow, stirred tank reactor kinetics (Penry and Jumars 1987). It is tempting to speculate that the feeding behavior of right whales, among the largest endotherms on earth, may be constrained by a digestive bottle-neck analogous to that described for hummingbirds (Karasov et al. 1986), the smallest of endotherms. These hypotheses warrant subsequent testing through more extensive time-budget analyses of right whales and other balaenopterans on their feeding grounds, such as described here and in Watkins et al. (1984).

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