

DIVING BEHAVIOR OF EMPEROR PENGUINS NURTURING CHICKS AT COULMAN ISLAND, ANTARCTICA¹

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Abstract. At the largest known Emperor Penguin colony, we determined general features of Emperor Penguin foraging commutes. The time selected for the study was one month before fledging, when maximum growth of the chicks occurs. Time/depth recorders were attached and retrieved from five adults as they departed from and returned to the colony. Nearly 16,000 dives were logged, of which 7,562 were estimated to be for foraging. Duration of the commutes averaged 14.9 days during which the birds averaged a total of 3,188 dives or 213 dives per day. Dives <200 m occurred at any time through the 24 hr cycle, and dives >400 m were restricted to 05:00 to 19:00 hr. The deepest dive was 534 m and the longest was 15.8 min to a depth <50 m. The modal depth of foraging dives was between 21 to 40 m, and the modal duration was between 4 and 5 min. Descent and ascent depth change rates were influenced by the maximum depth of the dive, but usually for dives >100 m the rates fell between 1.0 to 2.0 m sec⁻¹. The rates never exceeded 2.5 m sec⁻¹. Bottom time fraction was 0.22 to 0.28 of total dive time, for dives >100 m. Although few in number, occurrence of dives >450 m appeared consistently during the commute of every bird and suggests some important but unknown function. Because dives >400 m occurred only during high sun periods, it is proposed that such dives may not occur during the austral winter night. From behavioral data it appears that the aerobic dive limit (ADL) of about 8 min is nearly twice the calculated ADL. If this is so, then <5% of all dives exceed the ADL. Diving efficiency derived from diving and surface time in relation to bottom time declines by 50% between 100 m and 300 m dives.

Key words: *Aptenodytes forsteri*; King Penguin; Ross Sea; time/depth recorder; foraging.

INTRODUCTION

The Emperor Penguin, *Aptenodytes forsteri*, is the largest of the 17 penguin species, and also the most unusual in its breeding behavior. The Emperor Penguin lays and incubates a single egg through most of the Antarctic winter. The large body mass of the bird, more than twice that of its congener, the King Penguin, *A. patagonicus*, is an adaptation to the severe winter conditions on the sea ice. The body fat reserves of the male enable it to fast through much of the winter as it incubates the egg while the smaller female leaves to feed at sea. Even the long and dense feathers and large body mass in this species are enhanced by huddling during extremes of weather (Le Maho et al. 1976, Le Maho 1977). The huddles effectively reduce surface area and heat loss in the face of temperatures below -30°C and chilling winds. Large body mass may also be important for successful mid-winter to early-summer feeding.

The birds breed in the winter next to the Antarctic Coast. At this time, food resources may be depleted, dispersed and under sea ice. This may require greater diving capacities than for any other sea bird, and this ability is related to body mass. Simply expressed, the body O₂ store (VO₂) is directly related to body mass (M_b) and oxygen consumption is related to M_b^{0.75}. Therefore, diving duration (min) ≈ M_b^{0.25}. Based only on this relationship, one expects that Emperor Penguins would consistently dive longer and deeper than any other sea bird.

The possibility that Emperor Penguins have the greatest diving capacities of extant avian divers is well supported. From 1971 until 1992, they held the deepest reported dive for a bird (Kooyman et al. 1971). That record was eclipsed two years ago by a report of a King Penguin diving to a depth of 300 m (Kooyman et al. 1992). King Penguins held the published record only briefly, because soon after that Ancel et al. (1992) reported an Emperor Penguin diving depth of 483 m.

There are other interesting comparisons between King and Emperor Penguins. The King

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Penguin hunts at lower, ice-free latitudes where there are daily light and dark cycles; in contrast, the high latitude habitat of the Emperor Penguin remains dark or light for weeks at a time in mid-winter and summer. Both species feed on fish. The prey of King Penguins are various species of lanternfish, which tend to have a diel vertical migration pattern (Zasel'sliy et al. 1985, Perissinotto and McQuaid 1992). The most common prey of the Emperor Penguin is the Antarctic silverfish (*Pleuragramma antarcticum*). Because of the intense and long periods of light and dark occurring in mid-winter and summer, this fish may not consistently migrate vertically.

Our purpose was to determine some foraging characteristics of birds from one Emperor Penguin colony in the Ross Sea. For this initial analysis we selected Coulman Island, in 1993 the second largest known Emperor Penguin colony, because colony size may indicate the degree of resource abundance, and a greater diversity of individuals is available in a large colony. We measured: (1) duration of foraging cycles in November when chicks grow most rapidly, (2) general diving patterns, (3) variability in diving duration and depth, (4) patterns of diving depths in relation to time of day, (5) descent and ascent rates, and (6) bottom times. We used this information in comparing similar findings in the King Penguin as well as other avian and mammalian divers.

METHODS

Foraging trips of Emperor Penguins were studied at Coulman Island, Ross Sea, Antarctica during November, 1993. Birds were captured about 0.5 km seaward of the colony perimeter. Birds were randomly selected from a departure path that we estimated to be used by 90% of breeding adults. A bird was detained with a shepherd's crook and placed in a large, holding, vinyl bag. The penguin was then weighed to the nearest 100 g with a Chatillon suspension dial scale.

After weighing, the bird was passed into a tent where it was held while the time/depth recorder and radio were attached. Warmed 5-min epoxy adhesive was applied in a 3×10 cm strip to the dorsal feathers on the lower third of the back, and a 2×5 cm strip just behind the shoulders. The radio and recorder were placed on the upper and lower glue strip, respectively. Both instruments were fixed firmly in place with 0.5×15 cm nylon ties tightened with an applicator that

applied a force of 300 N before cutting the tie flush with the locking hub. While the glue was drying, identification numbers were brushed on both sides of the white chest with Nyanzol dye. The whole procedure took about 30 min from capture to release. After release, the bird usually continued to the ice edge.

The radios and receiver used were the same as those described previously (Kooyman et al. 1992). In brief, radio transmitters were potted into the shape of a half spindle, weighed 35 to 40 g, and transmitted on frequencies between 150 to 152 MHz. About every 4 hr, all frequencies of deployed transmitters were scanned with a Telonics scanner/receiver connected to an 8 m high omnidirectional antenna. If a signal was received, then a search was begun using a Yagi directional antenna coupled to a Telonics TR4 receiver. The return of a bird was detected from the pulsed VHF signal. The bird was located immediately and the transmitter and TDR were removed, and the bird was weighed if it had not fed its chick.

We used Wildlife Mk 4.5 and 5.0 time/depth recorders. These units contained 128 kilobytes RAM and weighed 50 g. The mass included an attached nose taper to reduce drag. All units sampled every 10 sec. The recorders had a depth range of 750 m in steps of 3 m. When calibrated simultaneously in a pressure vessel using a Heise 1,000 psi gauge, the recorders were within about 20 m of the pressure equivalent of 500 m.

The ice edge was located 3 to 6 km from the colony, and it took birds about one hour to toboggan from the colony to the edge. Nearly all birds tobogganed in transit. The average speed was 0.72 m sec^{-1} (± 0.78), $n = 15$. These values were measured over a 50 m course on a well used route from the ice edge to the colony.

The TDR records were hand-edited before detailed analyses were made. Editing reduced the emphasis on shallow, most likely non-foraging dives. The level of editing can be ascertained by comparing the total dives of a trip to the number of estimated foraging dives (Table 1). The most important criteria for deletion of a dive were depth, duration and occurrence within a sequence. If they were: (1) single, isolated dives, (2) a series of short (< 2 min), shallow dives (< 20 m), (3) occasional shallow dives interspersed between a series of deeper dives in which the profile near maximum depth showed frequent depth changes of several meters (ragged dives), or (4)

shallow dives of dissimilar profile that occurred within a series of very deep dives, they were deleted. Therefore, dives to a consistent depth and profile character were assumed to be for feeding. The rationale for this assumption is that if prey are stratified and once detected, the predator will persist in searches at that depth. We have no direct measure of prey capture. Nevertheless, this assumption seemed a more logical way to analyze the data than including all dives as an unedited set. The most clearcut deletions were the shallow dives <20 to 50 m scattered among a series of dives to depths deeper than 300 m. The duration of the deep dives was long enough that an extended recovery period for the birds was necessary. These shallow dives may be part of the recovery from an O₂ debt (Brooks and Fahey 1984). On the other hand, shallow, serial dives were difficult to edit because they could be traveling dives or shallow foraging dives.

RESULTS

GENERAL RESULTS

Cycle duration. Cycle durations averaged 14.9 days (Table 1). The last recapture was bird 9 on 23 November. Because of deteriorating ice, we were forced to leave Coulman Island on 26 November 1993. Some marked birds may have returned after that date, as did one bird used for another study that was being tracked by satellite. It returned on 28 November.

TABLE 1. Basic features of the diving records of Emperor Penguins used in this study.

Bird #	Mass (kg)	Cycle duration (days)	Total dives	Foraging dives	Dives/day
1	25.7	14.3	3,807	1,799	266
5	29.3	15.1	2,803	1,186	186
7	24.6	12.9	2,292	1,005	178
8	22.5	15.1	2,910	1,742	193
9	30.7	17.2	4,126	1,837	240
Aver.	26.6	14.9	3,188	1,514	213

Diving patterns. The entire records of two birds show the overall diving pattern through the course of their feeding trip (Fig. 1). Bird 9 is a more conventional record. Bird 5 was an exceptionally deep diver. Typically, birds begin their trips with a series of shallow dives (not deeper than about 200 m). By day two or three, dives over 400 m are sprinkled among the shallower dives until a day or two before returning to the colony. The last diving series or episode is usually to depths no deeper than 300 m. This episode is one of extended activity where the birds continuously dive for more than 24 hr.

Diurnal patterns. All five records were analyzed for depth distribution of each foraging dive over the 24 hr day. The majority of dives are <200 m (Fig. 2). Shallow dives of <200 m occurred throughout the 24 hr day. All dives deeper than 400 m occurred between the hours of 05:

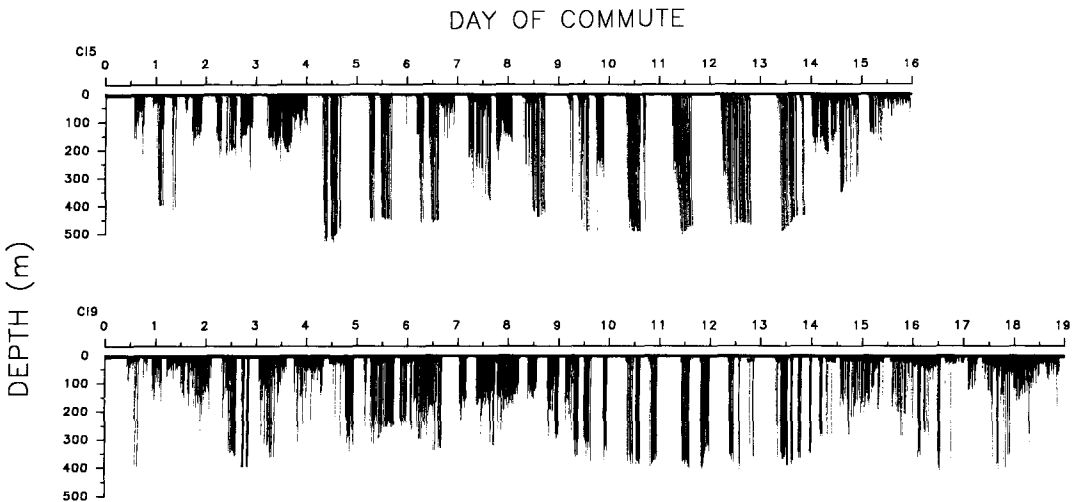


FIGURE 1. Compressed records of the entire dive cycle for two birds (CI5 and CI9). CI5 made an exceptional number of deep dives. CI9 was more conventional in its hunting effort.

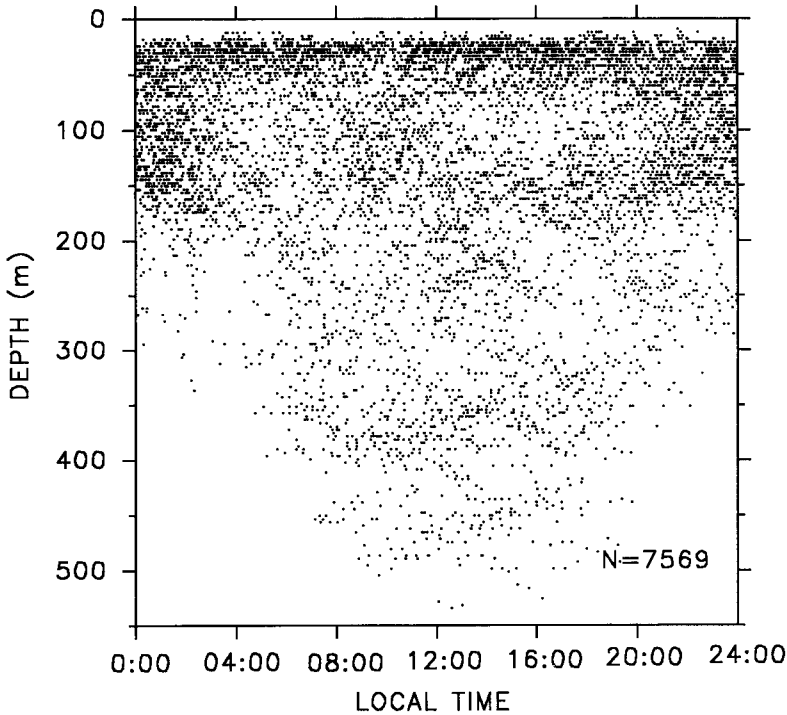


FIGURE 2. Foraging depth (as defined in Methods) in relation to time of day for all birds.

00 and 19:00. Such deep diving usually occurred daily until the last one or two days of the trip.

Frequency of depth and duration. Figure 3A displays the frequency distribution of all 15,938 diving depths recorded. The result of eliminating all dives not ascribed to hunting is shown in Figure 3B. From this total of 7,569 dives only 2.4% were <20 m compared to 43% of the unedited dives. Modal depth was 21 to 40 m in which 23% of all dives occurred; however, there is a shoulder between 61 to 180 m and then a slow decline at 320 m where a rise persists to 400 m. Seventy-six percent of all foraging dives occurred between 21 to 180 m, and 2.6% of dives were >400 m. The deepest dive was 534 m.

Duration of all dives declined about evenly to 11 min with an extended tail to 15 min (Fig. 4A). The longest dive was 15.8 min. The modal of foraging duration of dives was between 4 and 5 min in which 24.2% of all dives occurred (Fig. 4B). Eighty-five percent of all dives occurred between 2–7 min.

Although there is a strong correlation in which 79% of the diving duration is explained by depth, there are several outliers (Fig. 5A). These exceptional outliers are mostly at depths <200 m. Some

long dives show much longer diving durations than dives >300 m. For example, the longest dive of 15.8 min was <50 m (EP7). Also interesting was EP5, which had only two outliers. The time/depth correlation for this bird excluding the outliers was 0.92 (Fig. 5B).

DETAILED ANALYSIS

Descent/ascent rates and bottom time. For dives <100 m, descent and ascent rates were erratic with reversals in direction. Such ragged depth profiles made it difficult to discern what was actually the descent or ascent rates (D/A), or the bottom time (BT) of the dive. BT was probably less discrete than for deeper dives because the birds may actually have been hunting throughout the water column in this depth range. Therefore, D/A and BT were analyzed only for dives >100 m where the travel phase of the dive was consistent. For example, there was an abrupt change in the descent rate to about 0 m sec⁻¹ as the bird leveled at depth. BT ended when, again, there was an abrupt change in the profile as the bird ascended at a rapid and nearly undeviating rate toward the surface.

Average descent rate increases with depth to

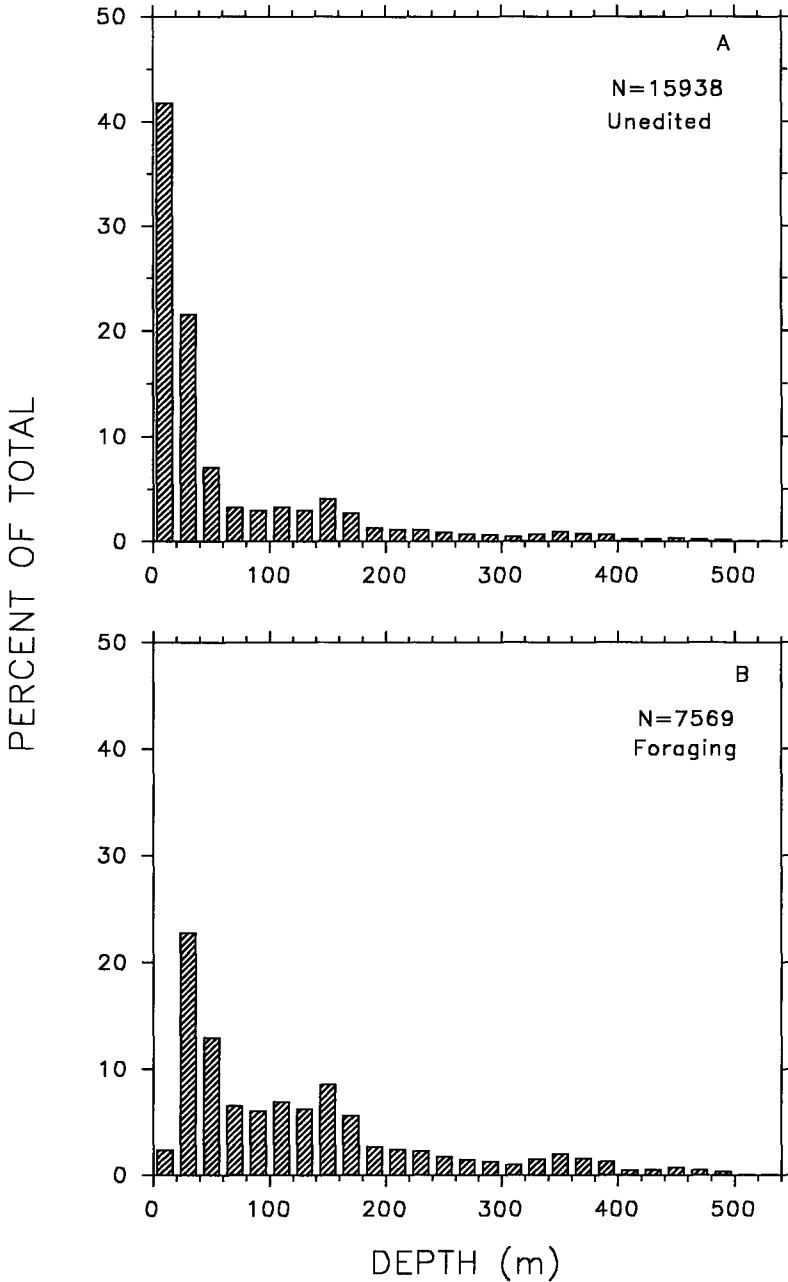


FIGURE 3. A. Frequency of occurrence of diving depths for all dives of all birds. B. Frequency of occurrence of diving depths for all foraging dives (as defined in Methods) for all birds.

about 200 m after which there was little or no influence of diving depth (Fig. 6A). The correlation coefficient for all birds was $R = 0.49$. The correlation coefficient for each bird varied between 0.32 to 0.75. The descent rate from 200 m and beyond was about 1.7 m/sec (Fig. 6A).

Similar to descent rates, ascent rates tended to increase from depths of 100 to 300 m (Fig. 6B). Beyond 300 m, the rate was again about 2.0 m sec^{-1} . The correlation coefficient for all birds was 0.65. The correlation coefficient between birds varied from 0.39 to 0.84.

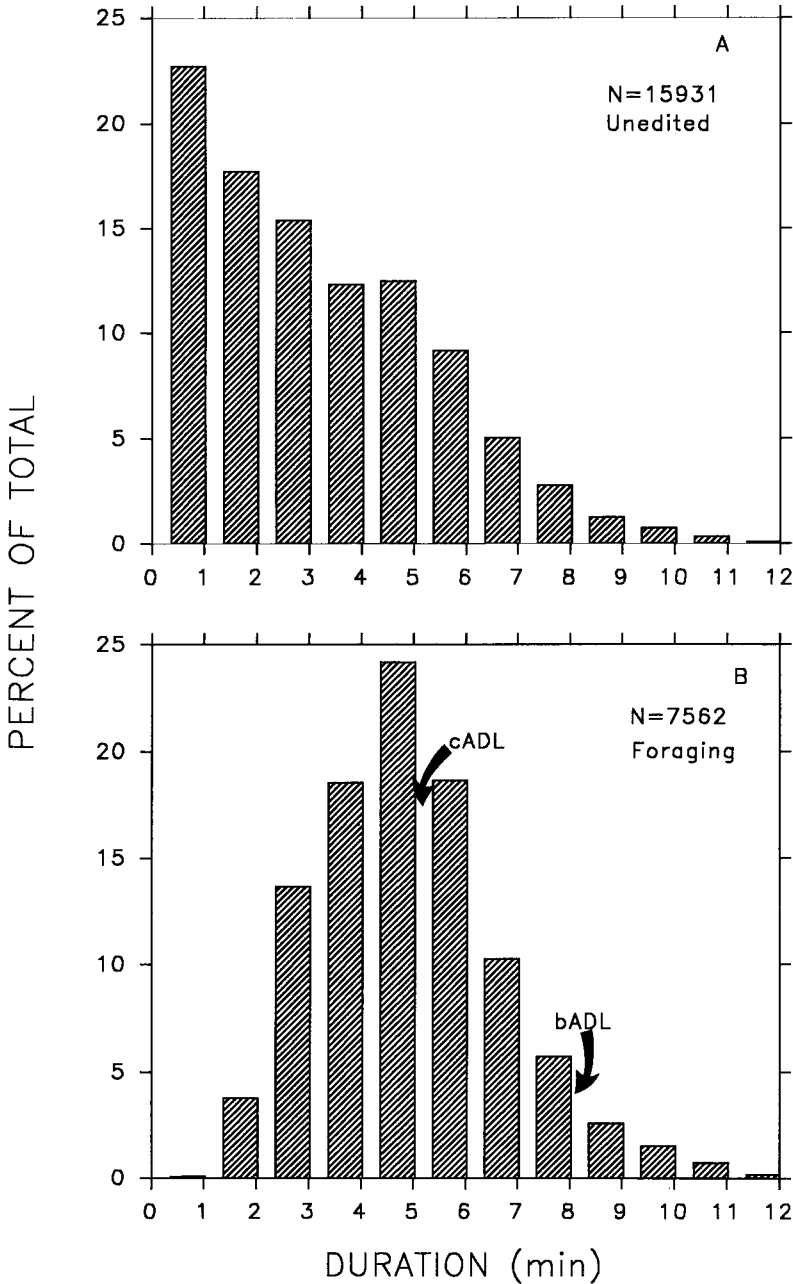


FIGURE 4. A. Frequency of occurrence of all diving durations for all birds. B. Frequency of occurrence of diving duration for all foraging dives (as defined in Methods) for all birds. The cADL is the calculated aerobic diving limit, and bADL is the behavioral estimate (see text for explanation).

Bottom time tends to increase with diving depth (Fig. 7). The difference between BT of dives between 101 to 150 m and 351 to 400 m, the last interval in which all five birds are represented, is significant (Mann-Whitney two sample

test, $P < 0.001$). All intervals are significantly different from 101 to 150 except 251 to 300 (Mann-Whitney two sample test). For dives to 101 to 150 m the bottom time is 1.36 min compared to 2.60 min for dives between 451 to 500

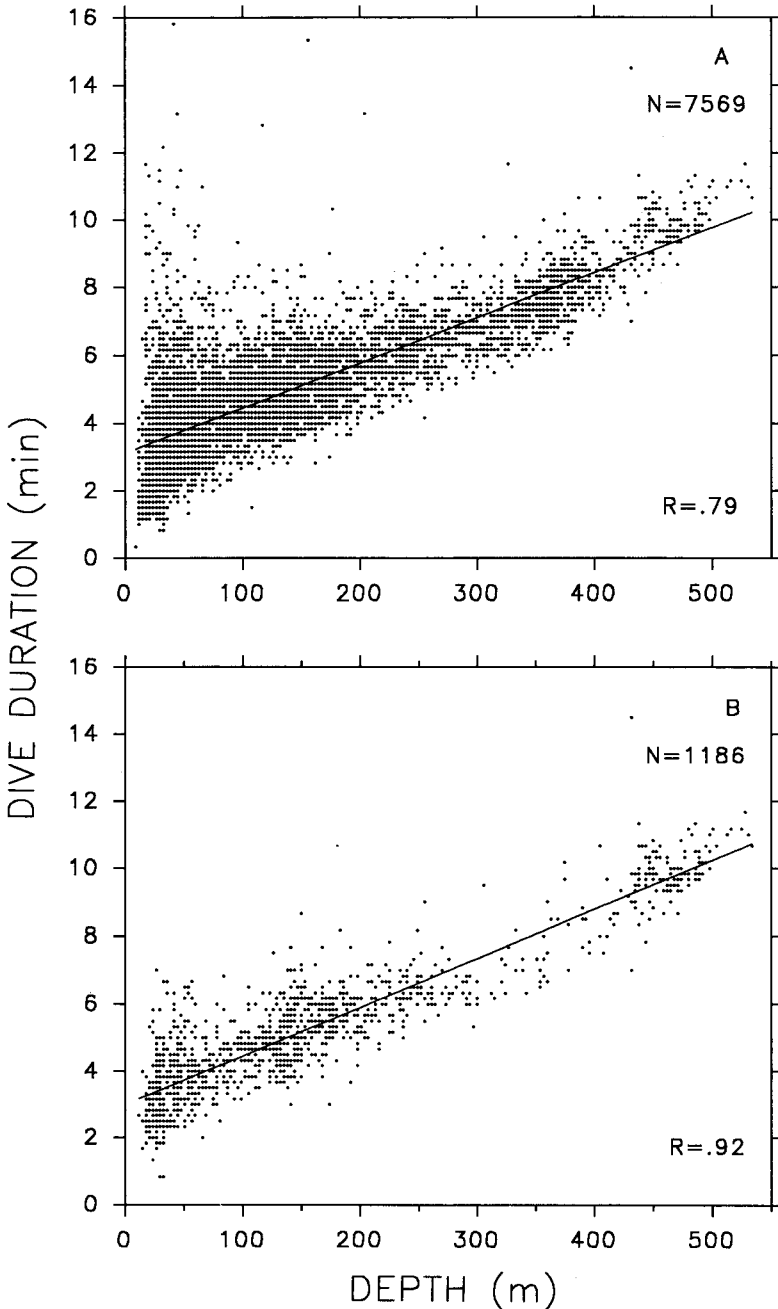


FIGURE 5. A. Diving duration in relation to diving depth for all foraging dives (as defined in Methods) for all birds. Regression equation is: $y = 0.01x + 3.12$. B. Diving duration in relation to foraging depth for CI5, an exceptionally deep diver with only a few outliers. Regression equation is: $y = 0.01x + 3.01$.

m. When BT is expressed as a fraction of total diving duration, any tendency for longer BTs at greater depth disappears and, if anything, there is a trend reversal, so that proportionately more time is spent near the maximum depth in the

shallower dives. The difference is significant (Mann-Whitney two sample test, $P < 0.001$) and between BT intervals of 101 to 150 m and 301 to 350 m. BT is about 0.22 to 0.27 of the diving duration in the intervals analyzed (Fig. 7).

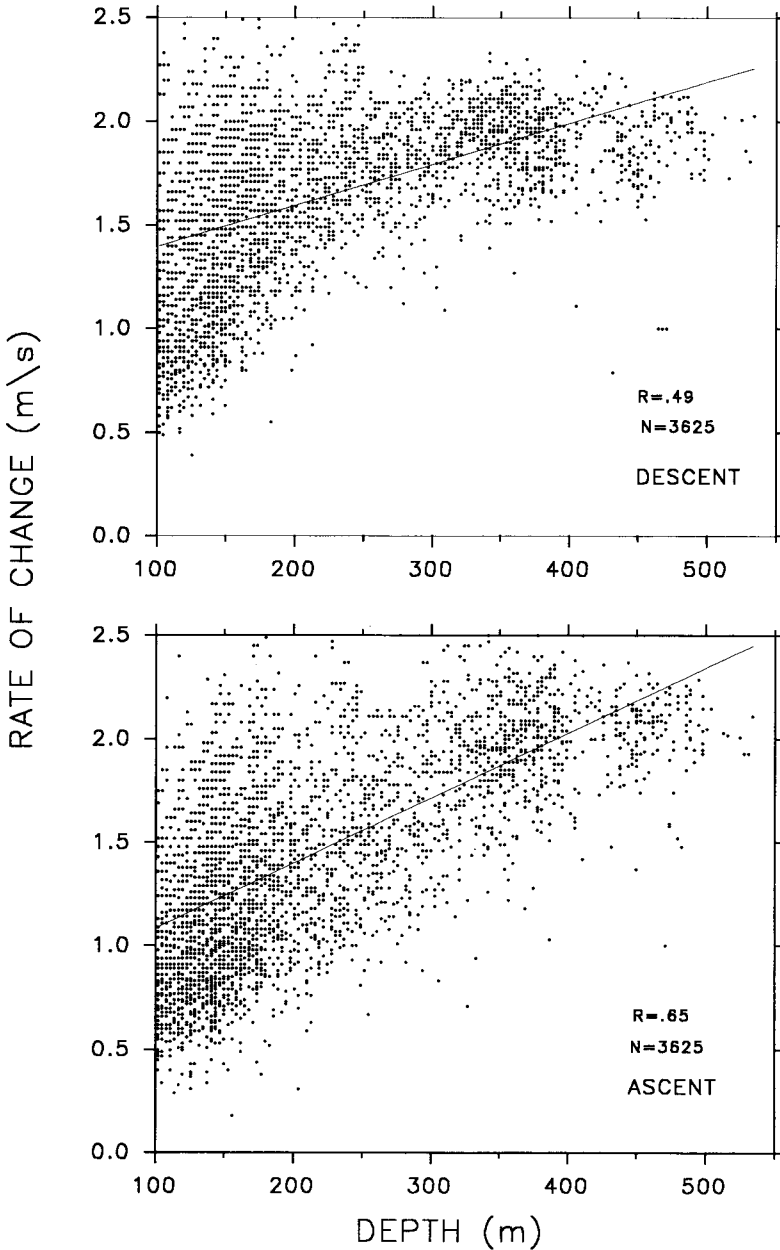


FIGURE 6. A. Average descent rates in relation to maximum depth for foraging dives between 100 to 534 m for all birds. Regression equation is: $y = 0.002x + 1.2$. B. Average ascent rates in relation to maximum depth for foraging dives between 100 to 534 m for all birds. Regression equation is: $y = 0.003x + 0.77$.

DISCUSSION

GENERAL RESULTS

The King and Emperor Penguin stand apart from other penguins in their propensity for diving to depths in excess of 100 m, and the extended duration of their foraging cycles of one to three

weeks. For those reasons, many of the comparisons to follow will be between the two species.

The average cycle duration for Emperor Penguins was 14.9 days in October and November of 1993 (Table 1) and exceeded by about two days that observed in previous years at Coulman Island (Kooyman, unpubl. data). It was a little

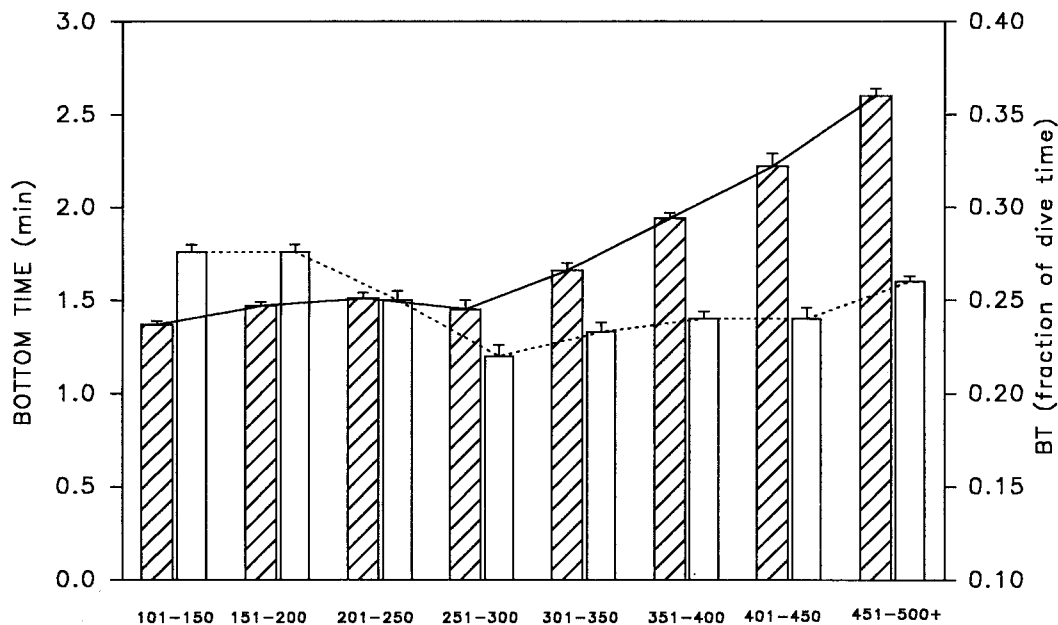


FIGURE 7. Average bottom time and bottom time as a fraction of the total diving duration for all foraging dives of all birds. Bottom time is the hatched bar and bottom time as a fraction of the dive is the clear bar. Error brackets are \pm one standard error.

more than twice the six-day cycle of King Penguins reported by Kooyman et al. (1992). The Emperor Penguin's cycle is also more than three times the 4.3 days that the Antarctic fur seal, *Arctocephalus gazella*, spends at sea while nurturing a pup (Doidge et al. 1986, Boyd and Croxall 1992). The periods at sea for these three species are long compared to most other otariids (Gentry and Kooyman 1986), and to other penguins (Chappell et al. 1993, Croxall et al. 1988). Long cycles enable these animals to range widely in their quest for food. That King and Emperor Penguins do so has been confirmed directly by location results from satellite transmitters attached to Emperor Penguins (Ancel et al. 1992), and from our more recent but unpublished data. The usual maximum distance is about 200 km. For King Penguins, the average measured foraging distances are dependent upon the time within the breeding cycle. At a state comparable in chick development and trip duration to the Emperor Penguin, the average distance was 666 km (Jouventin et al. 1994). However, the trip durations were an average 10 days compared to six days for those recorded by Kooyman et al. (1992). Since trip duration in the Jouventin et

al. (1994) study was not significantly different from birds without transmitters, this suggests to us that 1993 was a difficult year for King Penguins. If so, then the foraging range measured may be unusually great.

While traveling these long distances, the Emperor Penguin diving depths range more deeply than any of these other high-latitude commuters. Figures 1 and 3B show that foraging depths usually exceed 20 m, and dives greater than 300 m represent about 10% of all foraging dives. This shows that Emperor Penguins generally dive substantially deeper than King Penguins, for which the maximum recorded diving depth is 304 m (Kooyman et al. 1992). It is also much deeper than for Antarctic and northern fur seals, for which maximum diving depths are 181 m and 256 m, respectively (Boyd and Croxall 1992, Ponganis et al. 1992).

Some of the deepest dives of Emperor Penguins appear to extend to the bottom of the Ross Sea. This conclusion is based on the flat profile while at maximum depth, the uniform depth of a series of these dives (Fig. 1), and bathymetry in the area where some of the dives were performed (Ancel et al. 1992). In contrast, the deep-

est of the King Penguin dives, about 300 m, does not appear to be near the bottom (Kooyman et al. 1992).

The pattern of occurrence of dives also changes during the foraging commute (Figs. 1, 2). Within a day or two of departure from the colony, deep diving episodes begin and persist to the last series of dives before returning to shore. The diving pattern one to three days before returning to the colony is concentrated at mid-water depths, and is continuous until the bird reaches the colony. Assuming that these dives provide the last feeding opportunity before returning to the colony, this must be the sample collected by stomach lavage and reported by various investigators (Gales et al. 1990, Klages 1989, Offredo and Ridoux 1986). This shift in diving pattern may indicate a change in prey. If so, stomach lavages provide information on the type of prey fed to chicks as reported by Robertson et al. (1994), but such samples may not be representative of what adult Emperor Penguins feed on during most of their time at sea. This is a critically different element in the analysis of food habits of a long-cycle, long-distance commute species such as the Emperor Penguin, compared to the daily-cycle, short-distance commutes of species like the Gentoo or Macaroni Penguin (Croxall et al. 1988).

Another feature that sets Emperor Penguins apart from other divers near their body mass is the exceptional duration of some dives. These dives are the outliers of an otherwise conventional duration to depth plot (Fig. 5A). There is a strong correlation in the plot with an expected diving duration of about 10.5 min for a diving depth of about 500 m. There are only two outliers for depths > 200 m. In contrast, from about 25 to 150 m there are numerous outliers. In most of these dives, the birds were probably opting to remain submerged longer while pursuing prey. The profiles of a few dives had a long shoulder of shallow depth near their end. In the extreme, some of these dives exceeded 10 min. Such peculiar behavior may be the result of the risks involved with diving in heavy pack-ice. The level of risk is indicated by 20 outliers that exceeded 10 min, out of a total of 7,568 foraging dives (0.3%). In these dives, ascending birds may have been unable to surface because of a large plate of floe-ice blocking the surface, requiring the birds to extend their dives while searching for a breathing hole or an open lead.

COMPARISON OF DIVING DURATIONS AND PUTATIVE AEROBIC DIVING LIMIT

By almost any conventional calculation of O_2 stores and oxygen consumption rates, King and Emperor Penguins commonly exceed their calculated aerobic diving limit (cADL) (Kooyman 1989, Kooyman and Ponganis 1990, Kooyman et al. 1992). For Emperor Penguins the cADL is about 5 min (Kooyman 1989, Kooyman and Ponganis 1990). This means that 39.7% of all foraging dives exceed the cADL (Fig. 4B). This is similar to that calculated for King Penguins (Kooyman et al. 1992). Further, when an Emperor Penguin makes a dive of 500 m, it exceeds its cADL by more than two times. When Weddell seals, the only diver for which the ADL has been determined directly by post-dive blood lactate concentration, exceed their ADL by two times, the post-dive blood lactate peak is about 6 mmol (Kooyman et al. 1980). Such a lactate level would require about a 40 min recovery before blood lactate returned to normal levels. This may help to explain the frequent long intervals between deep dives in Emperor Penguins (Fig. 8). The pattern is also similar to that which is seen in King Penguins, where deep dives were separated by periods of 5 to 10 min in which only shallow dives occurred (Kooyman et al. 1992). These observations are in striking contrast to other diving vertebrates. All otariids (Gentry and Kooyman 1986) and Weddell seals (Kooyman et al. 1980) remain within a conventionally calculated cADL for about 95% of their dives. However, Adelic Penguins consistently exceeded their cADL based on metabolic rates (MR) obtained from doubly labeled water (DLW) estimates (Chappell et al. 1993), and from MR measurements of birds swimming in a flume (Culik and Wilson 1991). Nevertheless, the post-dive surface interval, usually about 0.5 of the diving duration, changes little with increasing diving duration. Chappell et al. (1993) made estimates of the cADL based on a diving MR of $6 \times$ basal metabolic rate (BMR) (their measurements with DLW), $4 \times$ BMR (VO_2 in a flume; Culik and Wilson 1991) and $2.9 \times$ BMR. Only the $2.9 \times$ BMR gives a comparable result to seals and sea lions. At $4 \times$ BMR, over 50% of the foraging dives exceeds the cADL.

After the most exceptional dives of Emperor Penguins, there is an extended post-dive interval (PDI) characterized by no dives or those of only

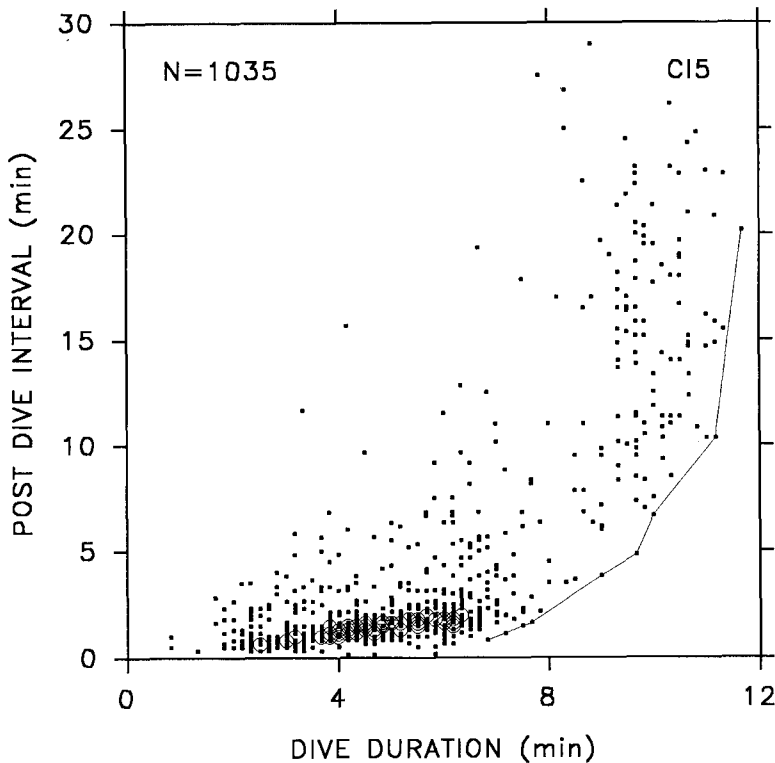


FIGURE 8. Post-dive interval in relation to diving duration in CI5. This example was selected because of the large sample size, and it was the most consistent diver. The large circles = 10 to 20 overlapping points. The dots connected by a solid line are the minimum PDIs measured.

short and shallow duration (Fig. 8). This was not seen in the Adelie Penguins. Perhaps this provides a clue to what the true ADL is if we accept the premise of Kooyman et al. (1980) and expanded upon by Chappell et al. (1993) that a long recovery is necessary from a dive in which there was a large anaerobic contribution to the total energy requirement and a post-dive increase in blood lactate concentration.

For Emperor Penguins, if we assume the only dives that exceed the ADL are those with an extended PDI, then we may detect a behavioral ADL (bADL) from an analysis of the PDI. When the PDI is plotted against diving duration (Fig. 8), an inflection of the scattergram occurs at a diving duration of about 8 min. It is more apparent if the "noise" of shorter diving durations is ignored and the minimum values of the curve are noted. It is not surprising there would be a few long PDIs after short dives because of the large sample size, and occasionally during a series of foraging dives a bird may have an ex-

tended PDI when one is not physiologically necessary. Therefore, the lower part of the curve and the minimum PDIs are the most relevant physiologically. This bottom contour plot of the data is similar to blood lactate concentration plotted against PDI for Weddell seals (Kooyman et al. 1980). We propose that the contour of the minimum PDI values of the Emperor Penguin are a result of increased blood lactate similar to the lactate PDI curve of the Weddell seal. Therefore, the rise in PDI noted in Figure 8 is at the true ADL. We conclude that the incipient rise in blood lactate in Emperor Penguins will occur at 8 min rather than the calculated 5 min. If so, then about 4% of foraging dives exceed the ADL (Fig. 4B) and most of these will be to depths > 300 m.

DEEP DIVING

Though deep dives are uncommon, their daily occurrence throughout the foraging cycle (Figs. 1, 2) testifies to their importance. Such deep diving distinguishes Emperor Penguins from other

diving birds (Chappell et al. 1993, Croll et al. 1992, Prince and Jones 1992, Croxall et al. 1988, Croxall et al. 1991), as well as from many pinnipeds (Gentry and Kooyman 1986, Boyd and Croxall 1992). So far, of what we know about antarctic pinnipeds, only Weddell and elephant seals forage at equal or greater depths (Kooyman 1968, Castellini et al. 1992, Hindell et al. 1991). The function of these dives for the Emperor Penguin can only be surmised with present information. Because of the consistent depth and flat bottom profiles, many dives may be benthic. Chicks are fed stones and perhaps one function of these dives is to replace the gastric stones fed to chicks. Finally, dives >300 m occur while the sun is high (Fig. 2). These records were obtained in late spring at latitudes where the sun is always above the horizon. During the winter months of low sun or darkness, do the female breeders that are absent from the colony, as well as the non-breeding birds, dive to depths >300 m? If not, this may be an important restriction in their foraging habitat and one further positive trait for breeding in the winter.

Both King and Emperor Penguins dive deeply, mainly when the sun is high (Fig. 2). King Penguins appear to track their prey (Kooyman et al. 1992), which migrate to the surface at night and to depth during the day. Emperor Penguins may dive to almost any of a broad range of depths <300 m throughout a 24 hr cycle. Also, instead of diving nearly continuously through the foraging cycle, Emperor Penguins have extended rests on floe ice. This is an option the lower latitude King Penguin does not have.

DIVING EFFICIENCY

Whatever the reason for the deep dives, they must incur a substantial metabolic cost. The extended surface interval translates into a decline of diving efficiency if we assume that whatever the purpose of the dive, the task is accomplished during the bottom time. Current technology does not allow us to determine whether all of these dives are for foraging; therefore, we propose a slight modification of Ydenberg and Clark's (1989) equation where diving is substituted for foraging. This equation is:

$$\text{D.E.} = t_b / (t_d + t_s)$$

where D.E. is diving efficiency expressed as a non-dimensional fraction, t_b is bottom time in

min, t_d is total dive time, and t_s is post-dive surface interval. To use this equation, we averaged diving times and surface intervals from clusters of dives ranging from depths of 100 to 500 m. We only used clusters in which the standard deviation of depth was $SD = <0.3$ of the average depth. The results are plotted as D.E. against depth (Fig. 9). The correlation coefficient for a declining D.E. from about 0.20 at 100 m to <0.10 below 350 m was 0.79. D.E.s were not calculated for <100 m because of the large variability in the depth of a group of dives. Similar calculations for King Penguins result in a D.E. of 0.15 for deep dives, which is not so different from results obtained for Emperor Penguins (Kooyman et al. 1992). In absolute terms, all Adelie Penguin dives are shallow and the D.E. ranges from about 0.40 for 20 m dives to about 0.20 for 60 m dives (Chappell et al. 1993). In conclusion, the D.E. loss for Emperor Penguins as well as for King Penguins and Adelie Penguins is substantial when they make deep dives. A lower D.E. for deep dives highlights the probable importance of such dives.

DIVING LIMITS

There were nearly 16,000 dives measured from five birds in this study. Birds ranged widely in depth as well as distance from the colony. For this time of year, the limits of how deep, how long and how fast the birds will dive may have been defined. The measured maximum diving duration in this study of 15.8 min, is close to the record of 18 min (Kooyman et al. 1971). It is noteworthy that the longest dives were often shallow dives. There were so few dives >500 m that the 534 m dive may be close to the depth the birds are willing to dive, since water depth in the area where the birds were foraging was often much deeper. Birds seldom exceed a depth change rate $>2.5 \text{ m sec}^{-1}$ on either descent or ascent (Fig. 6). Also, the minimum rate of depth change varies with depth of the dive. The slowest rates of D/A dives were about 0.5 m sec^{-1} for dives of <100 m. The variability lessens with depth, and the minimum rate of descent was about 1.5 m sec^{-1} for a 500 m dive, and the minimum ascent rate was 1.8 m sec^{-1} . If we assume that the maximum duration of a deep dive is 10.5 min and that the birds can descend and ascend at a rate of 2.5 m sec^{-1} (Fig. 6A), they are conceivably capable of making dives to

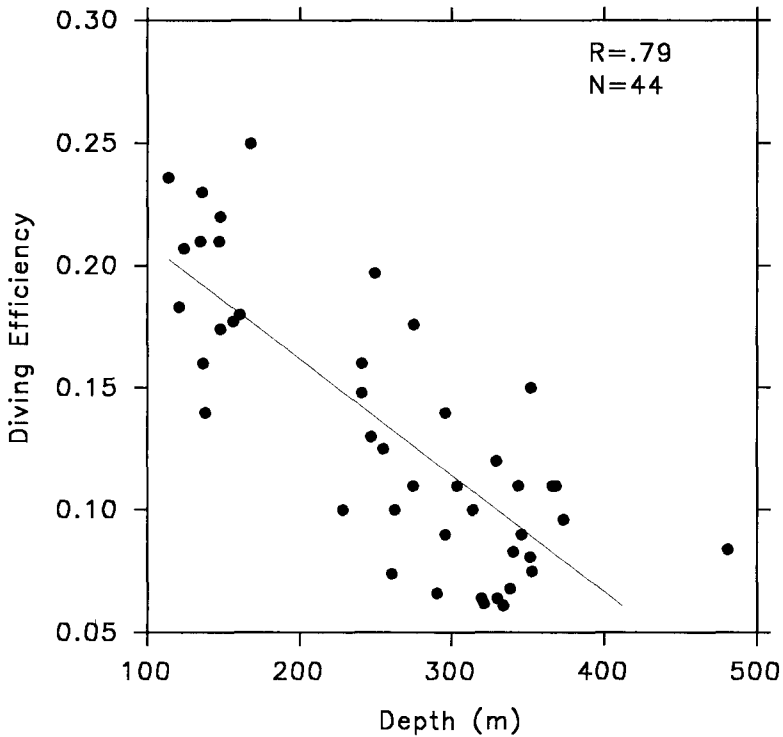


FIGURE 9. Diving efficiency in relation to foraging depth (as defined in Methods). D.E. was calculated from the average duration, PDI, and BT for each bout. There were 44 diving sequences used in which there were no fewer than 10 dives in series and the standard deviation of the average diving depth was $< \pm 0.30$ of the depth. See text for the equation and definition of terms.

nearly 800 m. Apparently some limit is set because of behavior, (e.g., suitable prey is not available) or a physical or a physiological constraint (e.g., hydrostatic pressure is too great, or it is too dark to detect prey, or no bottom time is available).

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