Ecology, 73(1), 1992, pp. 344–356

FORAGING BEHAVIOR AND PHYSIOLOGICAL ADAPTATION FOR DIVING IN THICK-BILLED MURRES[1]

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Abstract. Foraging behavior and physiological adaptations for diving were studied in Thick-billed Murres, *Uria lomvia,* in the field and laboratory. Electronic, light-emitting diode, and capillary recording devices were used to measure foraging behavior. Individual dives were a flattened U shape in profile, and occurred in bouts lasting ≈15 min. Dive patterns were nocturnal; most dives occurred between 2000 and 0400. Murres probably concentrate their foraging effort at times when prey is most available as it migrates closer to the surface in the evening as part of the deep scattering layer. Although dives averaged 18 m in depth and 55 s in duration, most time-at-depth was spent between 21 and 40 m. Thus, murres made a large number of shallow, short-duration dives. Maximum dive depth was 210 m, while maximum dive duration was 224 s. Descent and ascent rates averaged 0.94 and 0.85 m/s, respectively. Hematocrit, hemoglobin, blood volume, and pectoralis myoglobin levels were measured in the laboratory as 52.8%, 18.0 g/100 mL, 12.3% body mass, and 1.9 g/100 g, respectively. Total useable oxygen store was calculated as 44.8 mL/kg, giving an estimated aerobic dive limit (ADL) of 47 s. Murres exceeded the calculated ADL in 48% of their dives. Long-duration diving is probably a more efficient foraging strategy for murres given their relatively small size and limited oxygen storage capabilities. The observed dive depths raised questions of potential problems with decompression sickness (bends) and lung collapse.

Key words: alcid; Arctic; diving; feeding; foraging; physiology; seabird; Thick-billed Murre; Uria lomvia.

INTRODUCTION

It is a good swimmer and an expert diver.
–Arthur Cleveland Bent 1913

Until recently, the behavior of seabirds below the water surface was largely unknown. The large size of recorders developed for pinniped research precluded their use on most seabird species. However, several methods have been devised to gather information on the diving depths of seabirds: incidental entanglement in fishing nets (e.g., Conroy and Twelves 1972, Piatt and Nettleship 1985); maximum depth measurement using capillary recorders (Burger and Wilson 1988), photographic or x-ray gauges, which provide average time-at-depth integrated over the sampling period (Wilson and Bain 1984, Wilson et al. 1989); and microelectronic recorders, which provide a dive histogram record (Kooyman et al. 1982). Dive durations have been recorded through direct observation close to shore (e.g., Dewar 1924, Kooyman et al. 1971) or through the interpretation of radio transmitter signals received from foraging birds (Trivelpiece et al. 1986, Wanless et al. 1988).

These methods have yielded a number of remarkable results. For example, Emperor (*Aptenodytes forsteri*) and King Penguins (*A. patonicus*) can dive in excess of 240 m with Emperors diving for durations >18 min (Kooyman et al. 1971, 1982). Common Murres (*Uria aalge*) are capable of diving to 180 m (Piatt and Nettleship 1985), while Gentoo (*Pygoscelis papua*) and Macaroni (*Eudyptes chrysolophus*) Penguin diving depths have been shown to track closely the distribution of krill or juvenile *Notothenia,* respectively (Croxall et al. 1985). Dive records of seabirds that provide detailed dive profiles similar to those gathered for pinnipeds promise to yield a more complete understanding of the physiological capabilities of seabirds and the manner in which these animals utilize their marine habitat.

[1] Manuscript received 15 June 1990; revised 4 April 1991; accepted 19 April 1991.

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The seabird family Alcidae has been compared to penguins ecologically, morphologically, and physiologically. As wing-propelled divers, they have been viewed as northern counterparts to penguins, probably playing a similar role in northern ecosystems. However, compared to penguins, there have been few studies of the pelagic behavior of alcids. Their ability to fly greatly enhances their foraging range, but imposes a severe size restraint on the types of dive recorders that may be attached. Alcids, murres in particular, have the highest wing loading of any bird (Greenwalt 1962), limiting the mass of recorders. We have recently developed a small microprocessor-controlled electronic dive recorder that gathers profiles for individual dives in seabirds. We report here information on dive profiles, depths, durations, and swimming velocities for one species of alcid, the Thick-billed Murre (*Uria lomvia*), on Coats Island, Northwest Territories, Canada. We use these data in conjunction with parameters measured in the laboratory to report on the diving behavior, physiology, and foraging ecology of Thick-billed Murres.

Materials and Methods

Diving behavior

Study site.—We obtained dive profiles from eight murres (four in 1988, four in 1989) breeding at Cape Pembroke, Coats Island, Northwest Territories, Canada (62°57′ N, 82°00′ W) during July and August. This colony is made up of two subcolonies and numbers ≈24 000 pairs (Gaston et al. 1987). All birds selected for recorder deployment were adults that were brooding chicks, and making daily trips to sea.

Electronic dive recorders.—The recorders measured 6 cm long × 2.5 cm wide × 1.5 cm high and weighed 35 g. Depth was sensed using a 3.5 MPa pressure transducer. Amplified pressure transducer output was converted to a digital signal using an 8 bit analog-to-digital converter giving a depth resolution of 1.3 m. The recorders were potted in electrical resin and tapered at the ends to reduce hydrodynamic drag. The dive threshold value was programmable, and for this study it was set at 3 m; thus, dives shallower than 3 m were not recorded. Depths were sampled every 4 s, and stored in an 8K EEPROM (Electrically Erasable Programmable Read Only Memory). When the recorders were recovered in the field, data were downloaded via a RS232 serial port to a portable IBM-compatible laptop computer. Recorders were calibrated before deployment and rechecked after the field season. No difference was found between pre- and postseasonal recorder calibration curves.

Brooding murres were captured on their nests by means of nooses. Upon capture, each bird was weighed to the nearest 10 g. Recorders were attached to the birds along the middle of the back in the region of the scapular feathers using 5-min epoxy. To reduce profile drag, we attempted to work the recorder well into the feathers. The birds were held in a box for ≈15 min, to allow the epoxy to cure, before being released. Upon release, the birds usually flew to the water and preened, but returned to their nests within 1 h of release. Within 4 h of returning from foraging trips, the birds were recaptured, the recorders were removed by carefully trimming the epoxy-coated feathers from the bird, and the birds were reweighed. Data were transferred to a portable computer for analysis. Descent and ascent rates were calculated using the difference in depth over the time differential for each 4-s interval. Only nonzero rates were used for analysis.

Statistical analyses were performed on IBM personal computers using LOTUS and SYSTAT database and analysis programs.

LED recorders.—We obtained time-at-depth records from 16 Thick-billed Murres using LED (light-emitting diode) depth recorders (2 in 1987 and 14 in 1988). Details of the construction of the recorders and analysis of the records are described in Wilson et al. (1989). Briefly, the device employed photographic film to record the depth-dependent position of a light-emitting diode. Each unit was calibrated prior to deployment. Information on the depth and duration of dives was cumulatively recorded on the film, and the exposed film was analyzed using a densitometer. The optical density was converted to an estimate of time while the positions of the images on the film were converted to depths using a computer program provided by C. Nöldehe and R. P. Wilson of Universität Kiel.

The LED gauges used were cylindrical, 9 cm long and 1.5 cm in diameter, weighing 11 g. Time-at-depth was measured for each 1-m interval below 2 m. Depth errors were <5% (A. E. Burger, *personal observation*), while errors in time estimates were usually <10% (Wilson et al. 1989). Birds were weighed at the time of recorder deployment and again at recapture.

Capillary recorders.—We obtained maximum dive depths from 40 murres using capillary-tube depth gauges as first described by Kooyman et al. (1971). Depth gauges were made from lengths of flexible plastic Tygon tubing 650 mm long, 1.6 mm inside diameter. Basic design of the gauges is described in Burger and Wilson (1988). Two knots were tied at one end of the tubing, which was coated on the inside with a water-soluble dye. The capillary tubes were attached to the legs of the birds by an electrical cable tie around the stainless steel identification band and clamping between the two knots. Birds returned to their nests when released and paid little attention to the recorder. The tubing trailed behind the bird when flying and diving.

Physiological parameters

Laboratory animals.—Twenty Thick-billed Murres were captured as chicks on Coats Island in 1988 and shipped to Sea World, San Diego, to be used in laboratory work. The birds were maintained in a specially

designed 365 m² enclosure, which contained a 15 × 6 × 2 m deep filtered seawater tank. Air and water temperature were maintained at 14°C. The birds were held for 1 yr prior to measurement of parameters. They were fed a diet of smelt, herring, and krill supplemented by vitamins daily. The birds spent most of their time in the water, diving frequently.

Blood oxygen stores.—Approximately 5-mL blood samples were taken from six murres from a vein near the joint of the tibiotarsus and tarsometatarsus using a butterfly 25 guage (0.03 mm outside diameter) setscalp vein needle with a 10-mL syringe and transferred into a heparinized Vacutainer test tube.

1. *Hematocrit and hemoglobin.*—Hematocrits were measured in duplicate, with heparinized microhematocrit tubes spun for 10 min using a Damon/IEC Micro Hematocrit model MB centrifuge.

Hemoglobin concentration was measured using Sigma diagnostics total hemoglobin procedure number 525, which utilizes the the cyanmethemoglobin method of Drabkin and Austin (1935). Standards for calibration were prepared from lyophilized human hemoglobin (Sigma Hemoglobin Standard number 525-18).

2. *Blood volume.*—Plasma volumes were measured by plasma dilution of Evan's blue dye using the methodology of Linden and Mary (1983). Evan's blue dye (0.2 mL of a 0.0025 g/mL solution) was injected into a leg vein, and blood samples were taken from the opposite leg. Sequential samples taken at 3-min intervals in one bird indicated that the dye had equilibrated within the bird by 10 min. Blood samples were taken after 15 min in the remaining six birds. Samples in heparinized vacutainers were kept chilled until centrifuged to separate the plasma. Absorbance of plasma samples was measured at 624 nm, and compared with a calibration curve made from known dilutions of the dye in Thick-billed Murre plasma to give the concentration of dye in the samples. We calculated total blood volumes by averaging plasma volume and hematocrit values for the birds and using the resulting means to calculate blood volume.

Muscle oxygen stores.—Muscle oxygen stores were estimated for five Thick-billed Murres collected by subsistence hunters off of Newfoundland during the winter of 1988/1989. Band returns have shown that Coats Island murres winter in this area (Richard Elliot, Canadian Wildlife Service, *personal communication*). The birds were wrapped in plastic and placed on dry ice soon after collection and held at −70°C until analysis.

1. *Myoglobin.*—Samples of the pectoralis and sartorius muscles were analyzed using the methods of Reynafarje (1963). Briefly, we homogenized ≈60 mg of muscle in a 19.53:1 dilution in a low ionic strength phosphate buffer in a tissue grinder. The homogenate was centrifuged at 98 000 m/s² for 1 h at 5°C. The supernatant was transferred to a test tube through which carbon monoxide was bubbled for 8 min. Excess sodium hydrosulfite was added and carbon monoxide bubbled for an additional 2 min to assure complete reduction. The supernatant was then placed in a cuvette and absorption was read at 538 and 568 nm. Concentration was calculated according to Beer's Law (absorbance = extinction coefficient × concentration × length [1 cm]) using extinction coefficients (e_{538} = 14 700, e_{568} = 11 800) and dilution. A myoglobin standard was prepared using horse muscle myoglobin extract (Sigma) for comparison with samples.

2. *Muscle mass.*—The major muscles of the breast (pectoralis and supracoracoideus) and leg (sartorius and gastrocnemius) were dissected and weighed to the nearest 1 g for each of the five birds.

Pulmonary oxygen stores.—

1. *Lung and air sac volume.*—The total respiratory system volume was calculated using the allometric equation of Lasiewski and Calder (1971): respiratory system volume (in millilitres) = $160.8W^{91}$, where W is the mass of the bird in kilograms. This equation was chosen because it predicts a respiratory system value similar to that measured for the Tufted Duck *Aythya fuligula,* a diving duck weighing 0.540 kg (91.8 mL predicted, 97.2 mL measured) (Keijer and Butler 1982).

Results

Diving behavior

Mass loss.—Six of the eight birds lost an average of 23 ± 11 g ($\bar{X}$ ± 1 SD; 2% of predeployment mass) while they were carrying the electronic dive recorders for ≈1 d (average = 20 h), giving a mass loss rate of 1.2 g/h. One of the two remaining birds maintained its body mass, while the other gained 20 g. Seven of the nine birds with LED gauges lost mass; the average mass loss was 53 ± 47 g (5% of predeployment mass) during the 3–4 d of recorder deployment. Mass loss rate averaged 0.6 g/h.

Dive profiles.—A typical Thick-billed Murre dive profile is presented in Fig. 1. Generally, the murres dived in short bouts lasting ≈15–30 min, rarely lasting for >1 h. The period between bouts was more variable, but also lasted ≈15–30 min. Diving effort showed a distinct circadian pattern; 65–68% of all dives occurred between 2000 and 0400 (Fig. 2). There was also a circadian pattern in dive depth. Diving depths between 2000 and 0400 were generally <20 m, whereas dives made between 0800–1200 and 1800–2000 averaged >40 m depth (Fig. 3).

In a single dive, the birds descended rapidly to a depth at which they remained for most of the dive duration (Fig. 4a, b). We observed a similar pattern in both deep and shallow dives. We defined this time-at-depth as bottom time and measured bottom time for all dives >10 m. Bottom times increased with increasing depth up to 80 m (Fig. 5). In dives >80 m, bottom times declined as a greater proportion of the dive du-

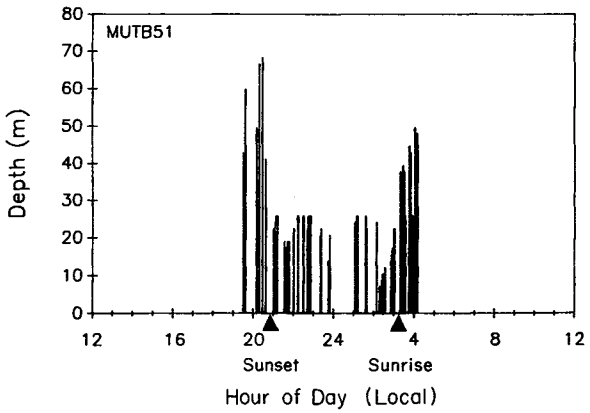

FIG. 1. Representative dive record of one foraging trip of a Thick-billed Murre on Coats Island, Northwest Territories, Canada. Times of local sunset and sunrise are indicated.

ration was spent in ascent and descent. In both years, 70% of all dives were ≤20 m (Fig. 6, Table 1).

One dive bout is particularly noteworthy due to the number of long deep dives with brief surface intervals. In 1989, MUTB72 made a series of 11 dives in a bout that lasted ≈1 h from 1015 to 1115 on 12 August. Each dive was over 3.5 min in duration, and between 60 and 90 m deep. Throughout this bout surface intervals were <2.5 min in duration (Table 2).

Dive duration, surface intervals, and depth.—Eighty percent of all dives were <80 s in duration (Fig. 7). Dive duration increased with dive depth ($r^2 = 0.90$) (Fig. 8). However, at depths >80 m, dive durations fell off (were below) the regression line. At this point dive duration remained approximately constant with increasing depths. Postdive surface intervals were significantly correlated with dive duration ($r^2 = 0.22$, $F = 18.37$, $P < .01$) (Fig. 9). The exceptional dives of MUTB72 fall well above the general regression trends.

Time-at-depth.—Most bottom time was concentrated between 21 and 40 m depth (≈46% of the dive time). Bottom times calculated from both electronic dive recorders and LED recorders (Fig. 10) show that most time was spent (≈70% of total bottom time) in water shallower than 40 m.

Maximum depths and durations.—We obtained 40 maximum dive depth measurements using capillary-tube gauges. Records were clustered between 80 and 100 m (34.5% of all records) (Fig. 11). Overall mean maximum depth was 106.6 ± 42 m ($\bar{X}$ ± 1 SD), and the maximum depth measured using these gauges was 210 m.

The deepest dive logged with the LED gauge was 135 m, while the mean maximum depth from 16 LED gauges was 65 ± 23 m (range 42–135 m).

The electronic recorder logged several remarkably deep, long-duration dives, although these were rare events. The longest duration measured 224 s, while the deepest dive measured using these recorders was 107 m. Both of these maximum values occurred in a single bird, which made exceptionally deep, long-duration dives. For most birds, the maximum depth recorded was ≈80 m (Table 1).

Descent and ascent rates.—Neither descent nor ascent rates differed between individuals or years (ANOVA, $P > .05$), so each category was pooled for comparison. Descent swimming velocity averaged 0.94 ± 0.48 m/s ($\bar{X}$ ± 1 SD, $N = 5534$), while ascent velocity averaged 0.86 ± 0.47 m/s ($N = 6029$). The maximum velocity measured was 3.5 m/s, observed in an ascending bird. Although descent rates were significantly higher ($t = 8.76$, $P < .01$) than ascent rates, these differences were small and probably a reflection of the high sample size.

Physiological parameters

Results of physiological measurements are shown in Table 3. Blood oxygen storage parameters were high (hematocrit, hemoglobin, and blood volume averaging [means ± SD] 52.8 ± 2.3% and 18.0 ± 1.8 g/100 mL, and 12.3 ± 0.9% body mass, respectively). These values are similar to those measured in penguins (Table 3). Pectoralis muscle myoglobin concentrations averaged (mean ± SD) 1.9 ± 0.2 g/100g.

TABLE 1. Diving summary statistics for Thick-billed Murres, Coats Island, Canada.

Bird	Hours deployed	Depth (m)			Duration (s)			N
		Mean	SD	Max.	Mean	SD	Max.	
				1988				
MUTB08	15	23	17	75	60	36	152	39
MUTB27	15	18	8	48	62	23	112	99
MUTB51	18	26	14	79	62	34	124	79
MUTB72	20	7	8	40	38	31	116	148
				1989				
MUTB37	24	14	17	80	38	38	176	216
MUTB38	22	16	21	80	56	44	192	184
MUTB71	20	15	16	93	44	30	152	154
MUTB72	20	33	23	107	95	51	224	133
Overall	154	18	19	107	55	42	224	1052

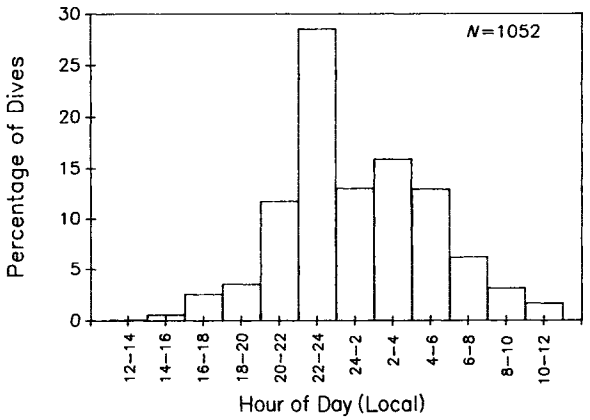

FIG. 2. Histogram of percentage of dives occurring by time of day for foraging trips of eight Thick-billed Murres, Coats Island, Northwest Territories, Canada. $N = 1052$ dives.

TABLE 2. Deep, long-duration dive bout performed by Thick-billed Murre MUTB72, Coats Island, Northwest Territories, Canada.

Dive of the series	Depth (m)	Duration (s)	Bottom time (s)	Surface interval (s)
1	83	216	112	104
2	78	212	116	136
3	74	204	116	136
4	71	212	128	136
5	68	200	112	116
6	65	208	128	124
7	65	200	120	112
8	63	204	128	120
9	62	200	124	128
10	56	204	124	...

DISCUSSION

Effect of recorder

Although essential in the study of the behavior of free-ranging marine animals, recording devices may affect their behavior. Wilson et al. (1986) addressed this problem in their study of foraging African Penguins (*Spheniscus demersus*). They found that mean foraging speeds were inversely related to the cross-sectional area of the recorder. The electronic recorders used in our study weighed <4% of the body mass and had a frontal area of 4.5 cm^2 (5% of the birds' maximum cross-sectional area). The LED recorders weighed ≈1% of the adult mass and had a frontal area of 1.8 cm^2 or 2% of the maximum cross-sectional area. Because they increased wing loading during flight and drag in both air and water, the recorders had three possible effects.

1. *Behavior.*—The presence of the recorder may have altered the behavior of the murres. In their study of Common Murres (*Uria aalge*) Wanless et al. (1988) found that the murres' behavior was unaffected by radio transmitters weighing 0.8% of their body mass (the presence of an external aerial did, however, have a significant effect). Cairns et al. (1987) attached recording devices to Common Murres that weighed 2.5% of their body mass and had a frontal area of 7.9% of the birds' maximum cross-sectional area. Their behavioral observations found that the effect of their instruments was minimal. Immediately after deployment of the recorder, most birds flew directly to the water and preened intensively. However, all birds returned to their nests within 1 h of release and paid little attention to the device at the nest. From our experiences, and those of others, we feel the behavioral effects of the recorder were minimal.

2. *Wing loading.*—The added mass of the recorder increased wing loading and decreased flight efficiency. The Thick-billed Murre has the highest wing loading of any bird that flies (Greenwalt 1962), so this may be an important energy problem. Using a model developed by Pennycuick (1989), the electronic recorder may increase energy demand ≈5% above that of an unburdened bird, while a model developed by Caccamise and Hedin (1985) for predicting the cost of attached packages in birds predicts an increased cost of flight of 1.9%.

3. *Drag.*—The added frontal area of the device increased drag in both swimming and flight. Using the model of Caccamise and Hedin (1985), we estimate that the increased cross-sectional area (5%) increased the cost of flight by 2.7%. The combined effects of mass and drag caused an estimated increase of ≈4.6% in the cost of flight.

Thrust forces that are required for swimming at a constant velocity will be equal to the drag forces (Webb 1975). Thus, we estimate the electronic recorder required an increased thrust for swimming of ≈5%.

There is almost certainly some burden imposed on the murres either by the recorders or the procedure of attaching them. That the recorders impose an addi-

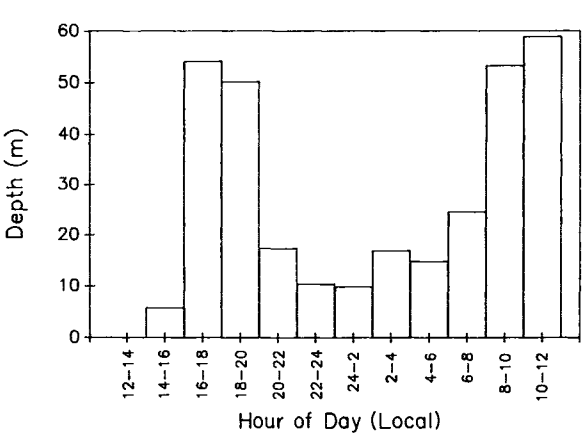

FIG. 3. Average dive depth by time of day for foraging trips of eight Thick-billed Murres, Northwest Territories, Canada. $N = 1052$ dives.

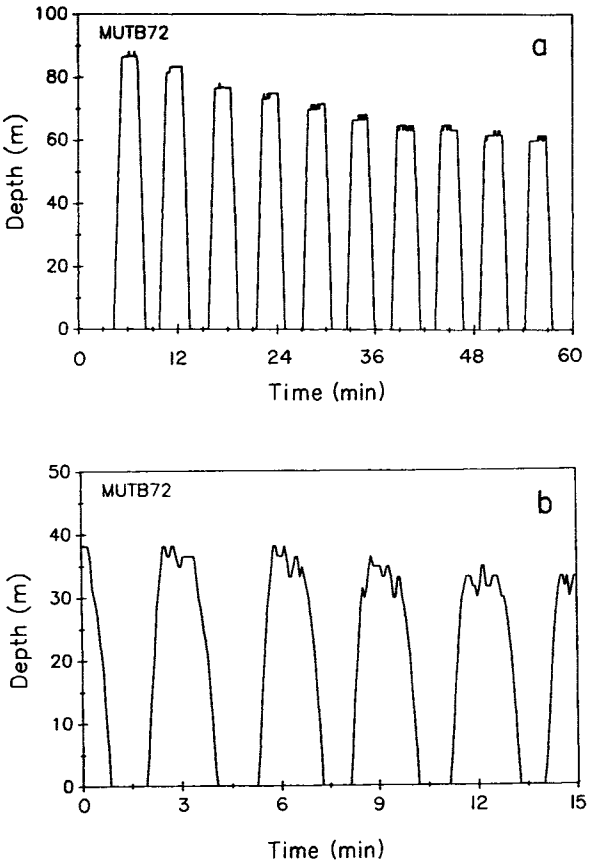

FIG. 4. Typical (a) deep-diving and (b) shallow-diving pattern of Thick-billed Murres, Coats Island, Northwest Territories, Canada.

tional burden to the birds is indicated by the mass loss of birds fitted with devices: birds with electronic devices averaged a mass loss rate of 1.2 g/h, while birds with LED recorders lost an average of 0.6 g/h. We have found that unencumbered murres on Coats Island lost an average of 32 g in 1988 and 63 g in 1989 in the early stages of chick brooding, which may be adaptive in improving flying efficiency (Croll et al. 1991). Overall, we feel that although the recorder diminished the energy efficiency of locomotion in both air and water, the birds behaved in a fairly normal manner. The LED gauges were smaller than the electronic recorders, and should have had similar, or fewer, effects on the diving behavior of the birds.

Diving behavior

Most dives had a similar pattern of a flattened U-shape (Fig. 3). The birds descended steadily to a certain depth (usually the maximum depth of the dive) and remained at that depth for much of the dive before ascending steadily to the surface. LeBoeuf et al. (1988) found that elephant seals have a similar pattern. This pattern is repeated, with each dive to a similar depth, throughout the dive bout. A possible explanation for this pattern is that the birds have located a prey patch and repeatedly dive into this patch, which remains at a constant depth. Although some shallow water is available as a thin coastal band around Coats Island, the bottom drops steeply off the island. Within 1 km the water depth is >50 m. Aerial surveys carried out on 13 August 1989 showed that the majority of murres were feeding offshore, in water >100 m deep (A. J. Gaston, *personal observation*). This indicates that the birds are feeding upon coastal or pelagic prey that congregate at discrete depths.

Most dives occurred between 2000 and 0400, the period of twilight and darkness on Coats Island. These were generally <20 m deep and the majority of dive time was spent above 40 m. As the sun rose, fewer dives were made and their depth increased. This suggests that murres were following the diurnal migration of prey. Croxall et al. (1985) found that Antarctic fur seal dive depths closely tracked the diurnal migration of krill. *Parathemisto* comprised over 74% of the prey by number in birds collected by R. Elliot and D. G. Noble (*personal communication*) in 1985 off of Coats Island. The guano that covered the breeding cliffs of the Coats Island colony had a reddish coloration. This was probably due to the breakdown of pigments found in crustaceans, suggesting their importance in the diet of Coats Island murres. We feel that the murres are most likely feeding upon schools of *Parathemisto,* which become available as part of the deep scattering layer that migrates upwards in the evening. Feeding effort is concentrated during this time. With sunrise, *Parathemisto* probably becomes less available to the murres as it migrates to deeper depths. At this time the murres may switch to finding benthic fish, requiring deeper

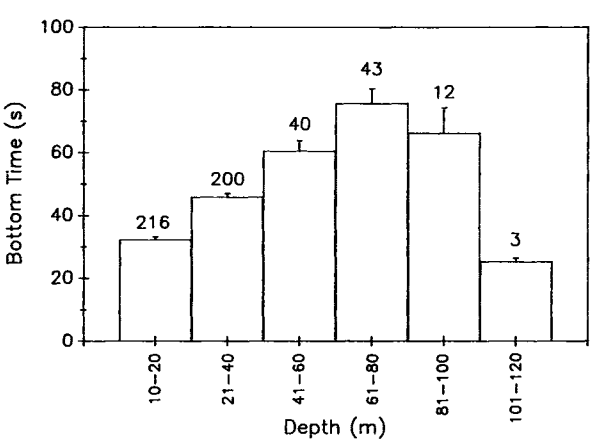

FIG. 5. Average time spent at foraging depth (bottom time) by depth for Thick-billed Murres, Northwest Territories, Canada. Record represents data from foraging trips of eight Thick-billed Murres. Numbers above bars represent number of dives. Error bars represent 1SD. Only dives deeper than 10 m were included in analysis.

TABLE 3. Blood, muscle, and respiratory variables related to O_2 capacity. Data are means (± 1 SD shown for *U. lomvia*).

Species	Hematocrit (%)	Hemoglobin (g/100 mL)	Blood volume (% mass)	Myoglobin		Source
				Pectoralis (g/100 g)	Sartorius (g/100 g)	
Uria lomvia	52.8 ± 2.3	18.0 ± 1.8	12.3 ± 0.9	1.9 ± 0.2		This study
U. aalge				1.4	0.6	Davis and Guderly 1987
Pygocelis adeliae	46.2	16.5	9.3	3.0		Kooyman 1989
P. antarctica	52.8	19.6				Milson et al. 1973
Eudyptula minor	40	18.0		2.8		Mill and Baldwin 1983

dives, such as sculpins and blennies to feed either themselves or their chicks.

Dive duration and depth were highly correlated (Fig. 8). Similar correlations have been found in a wide array of diving vertebrates (see Kramer 1988 for review). To maximize the amount of time at the foraging depth, bottom time should increase as the distance to the surface (and thus transit time) increases (Fig. 5). This requires that the bird spend more time at surface recovery when performing deeper dives. Murres appear to fit well within this model. Eventually some physiological limit must be reached due to the bird's finite ability to store oxygen. There is evidence that this limit is reached in dives exceeding 80 m, as bottom time declines in dive depths >80 m (Fig. 5). Murres rarely dive to depths exceeding this depth (Fig. 6). Given a swimming velocity of 1 m/s, it would take 160 s for a murre to make this dive, with no bottom time. If the bird remained for some time at this depth it would have to spend a substantially longer period at the surface to recover (Fig. 9).

How does diving behavior compare with estimates of oxygen stores for diving (Table 3)? Most parameters are similar to those measured for penguins. However, blood volume is particularly high; the only bird exceeding murres is the Red-throated Loon (*Gavia stellata*) (Bond and Gilbert 1958). Compared to terrestrial birds, they have a much higher oxygen store. Murres must balance the physiological demands of both prolonged diving and vigorous, sustained flight. It is interesting to compare the variables related to oxygen storage and transport with flying and diving habits to see how these habits may necessitate different adaptations in these parameters (Fig. 12). In most species, flight requires the locomotory muscles to operate aerobically, leading to high oxygen carrying capacities in the blood (high hematocrit and hemoglobin levels). Blood parameters such as hematocrit and hemoglobin may already be maximized for oxygen delivery during sustained flight, preadapting flying birds for breathold diving.

Muscle oxygen storage capacity (i.e., muscle myoglobin levels) in flying, nondiving birds are similar to those found in nonflying, nondiving birds (Pages and Planas 1983). The role of myoglobin has been thought to facilitate transport of oxygen from the capillaries to the muscle mitochondria (Wittenberg et al. 1975). However, in breathold divers myoglobin may serve the additional function of an oxygen store. By increasing myogobin concentration, breathold divers can substantially increase their oxygen stores. Thus, nonflying, diving birds have significantly higher myoglobin levels. Birds that fly and dive (i.e., murres) tend to have a myoglobin concentration intermediate between nondiving flyers and non-flying divers. The reason for this is not clear; however, Davis and Guderly (1987) proposed that the high levels of mitrochondrial enzymes needed to support flight may limit the amount of myoglobin that can be maintained in the flight muscle.

A number of assumptions must be made in order to estimate total oxygen stores. We calculated the oxygen storage capacity using similar assumptions to those used by Stephenson et al. (1989) (Appendix). The average mass of adult Thick-billed Murres on Coats Island in 1989 was 1029 g (A. J. Gaston, *personal observations*), giving and estimated respiratory system volume of 165 mL. The estimated oxygen stored for each component of the total were: arterial blood, 7.6 mL/kg; venous blood, 12.4 mL/kg; pectoralis muscle, 3.3 mL/kg; other muscle, 1.1 mL/kg; respiratory system, 28.3 mL/kg. The estimated usable oxygen storage capacity of Thick-billed Murres is 44.8 mL/kg. This is

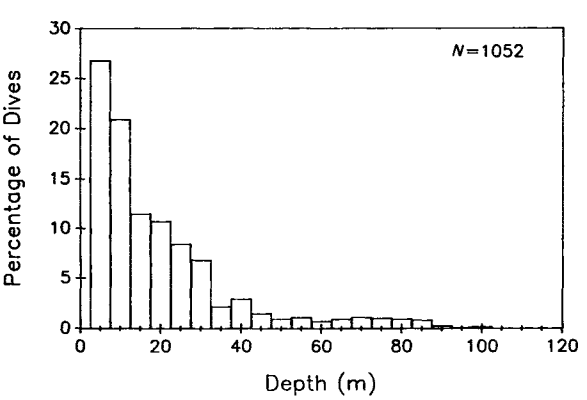

FIG. 6. Percentage of dives by depth for foraging trips of eight Thick-billed Murres, Coats Island, Northwest Territories, Canada. N = 1052 dives.

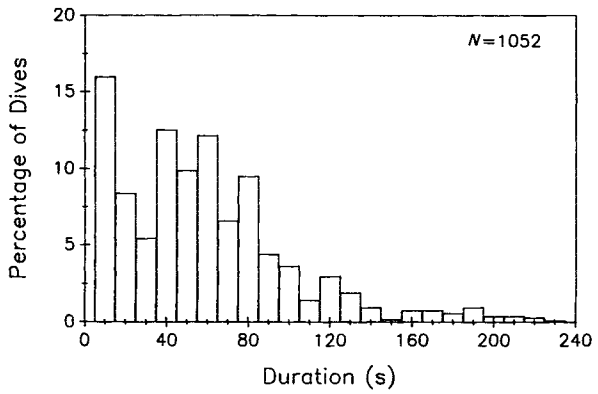

FIG. 7. Percentage of dives by duration for foraging trips of eight Thick-billed Murres, Coats Island, Northwest Territories, Canada. $N = 1052$ dives.

well within the range calculated for nonphocid diving homeotherms (35 mL/kg, *Tursiops truncatus* to 58 mL/kg, *Aptenodytes patagonicus*) (Kooyman 1989). The diving metabolic rate (O_2 consumption rate) of birds is uncertain, with different authors estimating very different rates. Butler and Woakes (1984) found that the diving metabolic rate of captive Humboldt Penguins was similar to resting rates. Woakes and Butler (1983) found that the diving metabolic rates of Tufted Ducks was 3.5 times resting rates. Baudinette and Gill (1985) measured the metabolic rate of Little Penguins swimming at 0.85 m/s as 1.3 times resting metabolic rate, while Eliassen (1960) assumed a diving metabolic rate of 2 times resting in Common Murres. The metabolic rate of Thick-billed Murres freely diving in captivity has been measured at ≈3 times the resting O_2 consumption rate of Thick-billed Murres measured by Gabrielsen (1988) (0.31 $mL \cdot s^{-1} \cdot kg^{-1}$ resting rate) (D. A. Croll and E. A. McLaren, *unpublished manuscript*). Using this diving O_2 consumption value (0.93 $mL \cdot s^{-1} \cdot kg^{-1}$), we calculate their aerobic dive limit (ADL) at 48 s. Only 52% of the measured dives made by the murres were within this limit (Fig. 7).

Butler and Stephenson (1987) have proposed that birds diving naturally use aerobic metabolism to support the activity of the locomotory muscles as well as the heart and central nervous system. Many of the dive durations we recorded exceeded this calculated ADL. This would have required the birds to utilize anaerobic metabolism for at least part of the dive, and would necessitate some physiological adjustment to conserve oxygen (peripheral vasoconstriction, bradycardia) for long-duration dives. The shorter dives (<48 s) could, presumably, be accomplished aerobically with calculated oxygen stores.

If murres exceed their calculated ADL in dives lasting >48 s, there should be a corresponding increase in the postdive surface interval as the bird replenishes oxygen stores, metabolizes lactate, and recovers normal pH levels disrupted from anaerobic activity during the dive. This does not appear to be the case. Postdive surface intervals rise steeply at ≈150 s dive durations, 3.75 times the estimated ADL. Several possibilities could explain this apparent paradox: (1) oxygen stores have been underestimated. This seems unlikely since it would require extraordinary increases in any of the parameters to make up the oxygen debt. (2) Diving metabolic rate has been overestimated. Murres are swimming vigorously when diving to propel themselves forward, requiring a metabolic rate above resting, therefore this also does not seem likely. (3) Murres are able to metabolize the lactate, recover from other physiological perturbations generated during the dive due to anaerobic metabolism, and replenish oxygen stores during the surface intervals following dive durations between 50 and 150 s. This seems unlikely because surface intervals after 50 to 150 s dives are from 50 to 100 s. Eliassen (1960) measured recovery lactate levels in forcibly submerged Common Murres and found that 260 s after a 60-s submersion muscle lactate levels were still above presubmersion levels. However, Kooyman (1985) has shown that the lactate recovery rate in free-diving seals is more rapid than that for restrained individuals. (4) Murres continue to dive with a lactate load. This would require that the bird must eventually stop diving and metabolize this lactate. If murres are feeding upon a patchily distributed, ephemeral prey resource, this may be the most likely explanation. Once a prey patch is located, the bird should dive repeatedly to the patch to maximize its gain from the patch, even it this means an eventual long surface recovery period. This is especially true if the patch lasts the same amount of time or less than the maximum dive bout capability of the murre. Ydenberg and Clark (1989) have offered a similar model to explain diving in Western Grebes. Some lactate will

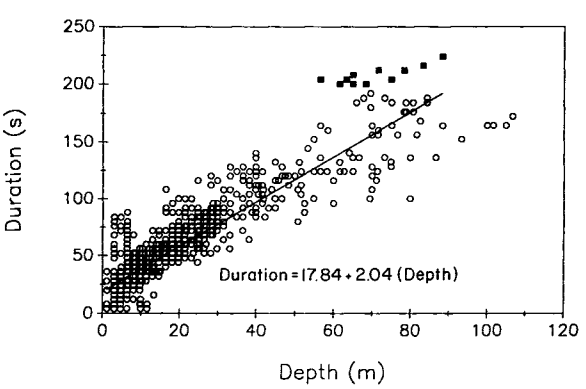

FIG. 8. Relationship of dive depth and duration of Thick-billed Murres, Coats Island, Northwest Territories, Canada. Data from foraging trips of eight murres, $N = 1052$ dives. ■ represent unique dive bout of MUTB72 (see *Results: Diving behavior: Dive profiles* for explanation).

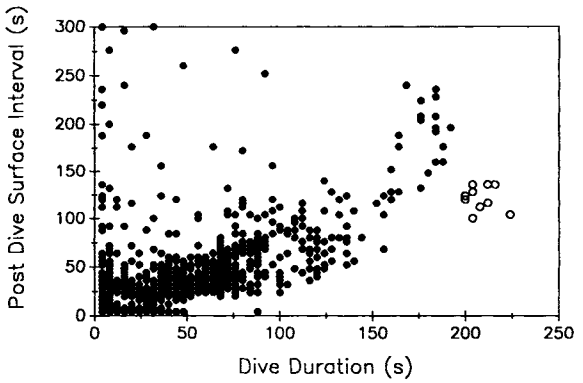

FIG. 9. Relationship of dive depth and post-dive surface interval of Thick-billed Murres, Coats Island, Northwest Territories, Canada. Data from foraging trips of eight murres, N = 1052 dives. O represent unique dive bout of individual MUTB72 (see *Results: Diving behavior: Dive profiles* for explanation).

be metabolized during both the surface interval and the aerobic portion of each dive as it may be used preferentially as a substrate. This would serve to prolong the length of both individual dives and the length of the bout. Kooyman (1989) has proposed that this mechanism is used in long-duration, continuous diving in Northern Elephant Seals. The resolution of this question will require lactate sampling in freely diving birds.

It is interesting to consider the observed diving behavior of murres as it relates to foraging efficiency. Kooyman and Davis (1987) defined foraging efficiency as time spent diving over total time: (Tf + Tt)/(Tf + Tt + Tr), where Tf is foraging time, Tt is transit time, and Tr is recovery time. Ydenberg and Clark's (1989) measure of Tf/(Tf + Tt + Tr) is a more appropriate measure of foraging efficiency since food is presumably not obtained during the transit portion of the dive. For Thick-billed Murres, we define Tf as bottom time, presuming that the murres dive directly down to a prey resource that is found at a particular depth.

With this criterion, there may be situations where foraging efficiency may be maximized by long-duration dives that exceed the calculated ADL, rather than short-duration dives within the calculated ADL. Ydenberg and Clark (1989) proposed that this strategy may be favorable when prey is aggregated and temporally ephemeral (i.e., when the probability of encountering prey is higher if prey was encountered on the previous dive). This should apply to Thick-billed Murres feeding upon schooling prey such as *Parathemisto*. We further propose that long-duration dives in excess of the calculated ADL may be favorable when the prey is located at considerable depth. For example, if we assume prey is located at 20 m, the birds swim at 1 m/s, and recovery time is an isometric linear function for short-duration dives within the calculated ADL (as demonstrated by a regression of dive duration vs. surface interval for murre dives <50 s in duration; Fig. 9) and an exponential function of Total Dive Time$^{1.05}$ for long-duration dives (calculated by fitting the curve of dive duration vs. surface interval for murre dives >50 s in duration; Fig. 9), we can estimate the foraging efficiency of a murre. Performing a 45-s dive within the calculated ADL, bottom time would be 5 s, transit time 40 s, and recovery time 45 s; foraging efficiency would be 0.06. If the bird instead performed a 60-s dive that exceeded its calculated ADL, bottom time would be 20 s, transit time would be 40 s, and recovery time would be 73 s; foraging efficiency would be 0.15. Thus, in this case a long-duration dive may be more efficient than a short-duration dive. This problem may not arise in large diving vertebrates such as phocid seals, which, due to their relatively larger oxygen stores, may be able to reach prey that is located much deeper than that of the smaller diving vertebrates while diving within their calculated ADL.

Viewed as a strictly physiological problem this model poses an apparent paradox. It would appear that the most efficient strategy for the murre, if it "chooses" to make an anaerobic dive, should be to dive for the maximum duration possible. However, Ydenberg and Clark's (1989) model demonstrates that the longer surface recovery times these long anaerobic dives would require would lead to a reduced prey capture rate on the subsequent dive as chances of relocating the prey school decline with longer surface time. Thus, the observed diving behavior of Thick-billed Murres (with a high proportion of dives exceeding the ADL) appears to fit Ydenberg and Clark's (1989) model: they must balance the benefit of longer bottom time during a dive against the cost of increased surface recovery time that will lead to a reduction in the prey encounter rate in the subsequent dive. Murres may adjust their dive duration and surface recovery times based upon both their physiological status and the probability of suc-

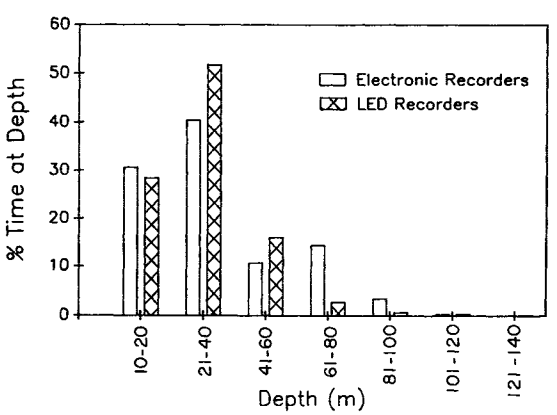

FIG. 10. Percent time at depth as a function of depth of dive for Thick-billed Murres, Coats Island, Northwest Territories, Canada. (See *Materials and methods: Diving behavior* for explanation of types of recorders.)

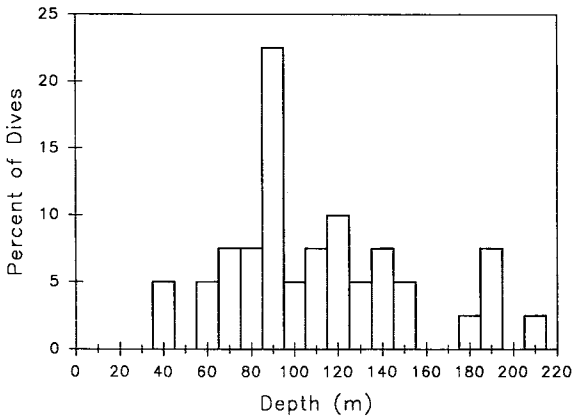

FIG. 11. Maximum dive depths of Thick-billed Murres on Coats Island, Northwest Territories, Canada. Data from capillary recorders attached to 40 birds.

cessfully encountering prey on the subsequent dive. This model would also lend some support to the hypothesis that murres continue to dive during a bout with a lactate load, and may accumulate lactate during a series of dives made when a prey school has been located. Lactate may be metabolized once the bout is terminated due to either a physiological limitation imposed by the lactate accumulation or due to the loss of the school.

Other physiological problems are raised by the observed diving depths and durations. The unique structure of the avian parabronchial respiratory system is dependent upon a constant volume of the lung during respiration for its function (Dunker 1972). The bird lung is rather rigid and attached along its dorsal surface to the ribs and vertebrae, while the associated air sac system is compliant. The gas–blood barrier in the bird lung is much thinner than that found in the lungs of other vertebrates (Fedde 1986). This thin barrier is only possible because of the rigid blood–air capillary network found in bird lungs. Thus, the bird lung should not be collapsible. As the birds dives, however, the compliant air sacs of the bird must be compressed. Jones and Furilla (1987) demonstrated that the anatomy of diving birds probably allows for the collapse of the air sacs. Dunker (1972) and Scheid et al. (1974) used different methods to estimate that the lung accounts for ≈10–15% of the total respiratory system volume. As the respiratory system is compressed according to Boyle's Law, (pressure × volume = constant), the air sacs must collapse and the air contained within move into the more rigid lung. However, at some depth, the lung should also begin to collapse. If the lung comprises 15% of the total respiratory system volume, that point will be reached when the air sacs have fully collapsed and the volume of air in the respiratory system is 15% of what it was at the surface. This pressure is 0.77 MPa or 67 m. Thick-billed Murres in this study were found to dive as deeply as 200 m. Three possible hypotheses may explain the ability of these birds to dive deeply without any apparent injury to their respiratory system. (1) The lungs of murres (and other deep divers such as Emperor Penguins) may be resistant to compression at depth. This seems unlikely, since the tissue would have to resist a compression of 16.21 Pa at 200 m. (2) The lungs of deep-diving birds are collapsible, perhaps having a different blood–air capillary network that allows collapse. This may also require different lung surfactants than have previously been described in birds. (3) The lungs of deep-diving birds may comprise a smaller proportion of the respiratory system. The answer to this question awaits further work.

Kooyman et al. (1973) first recognized the potential problem of the absorption of nitrogen during deep dives in birds, given their noncollapsible lung. They found that gas exchange occurs during compression to 30 and 68 m in Adelie and Gentoo Penguins, but speculated that single, short deep dives may not pose a threat of

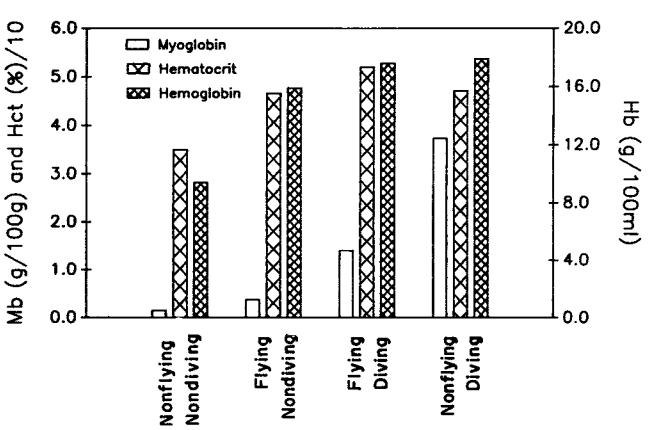

FIG. 12. Average myoglobin (Mb), hematocrit (Hct), and hemoglobin (Hb) levels in birds with various locomotion strategies. Data summarized from Kooyman (1989), Davis and Guderly (1987), Sturkie (1986), Mill and Baldwin (1983), and Bond and Gilbert (1958).

TABLE 4. Estimated nitrogen tensions developed during dive bout performed by a Thick-billed Murre weighing 0.95 kg at Coats Island, Northwest Territories, Canada.

Dive	N_2 content (mL)	N_2 tension (MPa)* N_2 equilibration pool: Blood	Blood + 20% body water	Total body water	Whole animal
1	11.7	0.75	0.34	0.13	0.05
2	13.3	0.86	0.39	0.14	0.06
3	10.9	0.70	0.32	0.12	0.05
4	11.4	0.73	0.33	0.12	0.05
5	10.0	0.64	0.29	0.11	0.04
6	11.3	0.73	0.33	0.12	0.05
7	10.7	0.69	0.31	0.11	0.05
8	11.3	0.73	0.33	0.12	0.05
9	10.4	0.67	0.30	0.11	0.04
10	9.3	0.60	0.27	0.10	0.04

* The following assumptions were used in estimating nitrogen tensions: nitrogen solubility in blood 14 $mL \cdot L \cdot MPa^{-1}$, in fat 70 $mL \cdot L^{-1} \cdot MPa^{-1}$, in water 14 $mL \cdot L^{-1} \cdot MPa^{-1}$; diving cardiac output 0.098 mL/s, resting cardiac output 0.378 mL/s, surface cardiac output 0.756 mL/s (Jones et al. 1979); fat content 21% (Gaston et al. 1985); venous nitrogen tension (absolute) 0.08 MPa, diving lung volume 0.15 L, blood volume 0.11 L, total body water 0.67 L; absorption and washout rates are assumed to be linear.

nitrogen narcosis or decompression sickness. However, they also recognized that repetitive dives even to shallow depths may become a problem in diving birds. We have found that murres dive to considerable depth repeatedly during a dive bout. Examination of the exceptional bout of MUTB72 shows that most of each dive was spent in bottom time (Table 2). We have calculated the potential nitrogen levels in this type of dive bout (Table 4). Harvey et al. (1944) found that gas bubble formation occurs in cats when the N_2 tension exceeds ambient pressure by 0.25 MPa, or 0.35 MPa at sea level. From our estimates we can see that there may be some adjustment necessary in murres to prevent decompression sickness, or bends. The N_2 tensions that may develop if the N_2 absorbed at depth is diluted into various pools has been calculated (Table 4). If there is a reduction in blood flow to the muscles and peripheral organs, as would be necessary for murres to perform dives of these durations, then N_2 tension differences would be close to those that may cause bubble formation. However, the murres may reduce this problem by allowing some blood to circulate to the muscle and peripheral organs during the dive. Thus, by regulating blood flow, murres could avoid decompression sickness.

The diving capabilities of these arctic seabirds are impressive, especially given their size. However, their capability to perform long-duration dives is probably limited by this small size constraint. It appears that murres have attempted to maximize their oxygen storage capacity. However, the ability to store oxygen is an isometric function scaling as body mass^1, while metabolic rates scale as body mass$^{0.75}$. Given this argument, smaller divers such as murres have a relatively decreased ability to remain submerged for long periods while functioning aerobically relative to pinnipeds and penguins. Thus, murres must adjust their diving behavior in order to capture prey at depth in an efficient manner, resulting in a much higher proportion of dives that exceed their predicted ADL. They appear to take advantage of cycles in the vertical migration of their prey, concentrating their diving effort at those times when prey is closest to the surface and may be captured with shallower dives.

ACKNOWLEDGMENTS

We would like to thank the many individuals that have joined us in our field work on Coats Island: Karel Allard, Leah Deforest, John Gael, Grant Gilchrist, Sue Johnson, Elizabeth McLaren, Dave Noble, Richard and Kate Elliot, and Christoph Rohner. We thank D. Garnier, K. Nelson, C. Nöldehe, and R. P. Wilson for help in the construction and analysis of LED gauges. We are indebted to Dr. Paul Ponganis, Dr. G. L. Kooyman, and Dr. Michael A. Castelini for their critical review of earlier manuscripts. We received invaluable support from the Polar Continental Shelf Project of Energy, Mines and Resources Canada, and from the Iqaluit Laboratory, Frobisher Bay. We thank Andy Theriault of Indian Affairs and Northern Development, Northwest Territories, and Bob Longworth and Paul Irngaut of the Science Institute of Northwest Territories for logistical support. Funding for this research came from the Canadian Wildlife Service, Sigma Xi, the American Museum of Natural History, and the Asociacion de Biologos Ambulantes. D. A. Croll was supported by USPHS NIH HL 17731 to Dr. G. L. Kooyman. A. E. Burger was funded by NSERC Canada and Bamfield Marine Station.

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APPENDIX

The following assumptions were used in estimating the oxygen stores of Thick-billed Murres:

1) The oxygen binding capacity of murre blood is similar to that measured in the Black-headed Gull, *Larus ridibundus*: 1.2 mL/g pigment (Viscor et al. 1984).

2) Blood volume is 70% venous, 30% arterial.

3) Arterial blood is 95% saturated and venous blood is 70% saturated prior to diving.

4) Ninety-six percent of the oxygen in the blood is used during the dive (Hudson and Jones 1986).

5) The oxygen binding capacity of avian myoglobin is 1.24 mL/g pigment (Stephenson et al. 1989).

6) Murres hyperventilate before diving and dive on inspiration (D. A. Croll, *personal observation* of murres diving in captivity). The fractional oxygen concentration of the anterior air sacs is 16%, while the concentration in the posterior air sacs is 19.5%, similar to the hyperventilating starling (Torre-Bueno 1978).

7) The posterior air sacs are assumed to constitute 45% of the total respiratory volume (Scheid et al. 1974).

8) Using assumptions 6 and 7, the mean concentration of oxygen in the respiratory system prior to diving is 17.6%.

9) A maximum of 75% of the oxygen in the respiratory system is usable (Hudson and Jones 1986).