DIVING DEPTHS OF FOUR ALCIDS

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ABSTRACT.—Incidental catches of 12,243 Common Murres (*Uria aalge*), 875 Atlantic Puffins (*Fratercula arctica*), 36 Black Guillemots (*Cepphus grylle*), and 9 Razorbills (*Alca torda*) were recorded off Newfoundland during the summers of 1980–1982 (26,445 net-days of fishing effort). Most catch occurred in stationary gill nets set on the sea floor at depths of up to 180 m and revealed that murres, Razorbills, puffins, and guillemots can dive to depths of at least 180, 120, 60, and 50 m, respectively. Diving ability appeared to be directly correlated with body size. *Received 5 March 1984, accepted 2 June 1984.*

LITTLE is known about the depths to which alcids and other aquatic birds are capable of diving (Kooyman 1975). Using depth recorders, Kooyman (1975) and Kooyman et al. (1982) established that Emperor (*Aptenodytes forsteri*) and King (*A. patagonica*) penguins can dive to depths in excess of 240 m. Although penguins are probably the best underwater swimmers among the ten families of diving birds, Kooyman (1975) suggested that "If most other birds can descend and ascend at similar rates (e.g. 2 m/s) then a 180 m 'bounce' dive is probably within the range of most diving birds . . ." properly adapted for the extreme conditions found at those depths.

As Northern Hemisphere ecological counterparts to penguins, alcids are morphologically similar. They exploit similar prey, such as euphausiids, squid, and small schooling fishes (Bédard 1969, Kooyman 1975). All pursue prey underwater using partly folded wings to propel themselves (Bédard 1969), and numerous adaptations for underwater "flight" and feeding have evolved in the Alcidae (Storer 1952, Stettenheim 1959, Bédard 1969, Spring 1971). Studies of diets (Tuck and Squires 1955, Belopol'skii 1957) and a few records of catches in fishing gear (Tuck 1961) imply that alcids sometimes forage near the ocean bottom at considerable depths, but there are no detailed accounts of diving ability or estimates of maximum diving depths.

In Newfoundland, thousands of alcids, particularly Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*), drown each year in surface-set salmon (*Salmo salar*) and bottom-set cod (*Gadus morhua*) gill nets as they forage for capelin (*Mallotus villosus*) in waters intensively fished by man (Piatt et al. 1984). Net-mortality is acute during the one-month period that capelin form large, dense spawning schools inshore.

We have accumulated detailed data on 912 incidents involving 13,163 alcids caught in gill nets. These data suggest that the diving abilities of different alcid species differ markedly and that the maximum diving depths attainable by alcids have been considerably underestimated (e.g. Stettenheim 1959, Pearson 1968, Kooyman 1975).

STUDY AREA AND METHODS

During the summers of 1980–1982, 39 inshore fishermen from communities adjacent to 7 major seabird colonies in Newfoundland (Wadham, Penguin, Cabot, Funk, and Baccalieu islands, Witless Bay, and Cape St. Mary's) recorded daily seabird catches with details on the depths and locations of net entrapment (Piatt et al. 1984). Cod gill nets were positioned on the sea floor at varying depths up to 180 m. The bulk of inshore fishing effort occurs at depths of less than 60 m, and only 5% of fishing effort observed in our study occurred at greater depths. On about 30 occasions John F. Piatt accompanied fishermen at sea and observed fishing techniques and removal of seabirds caught in nets retrieved from depths of up to 180 m. In addition, several thousand net-drowned alcids brought in to fishing wharves were examined, and over one thousand were autopsied to determine sex, age, and stomach contents.

RESULTS

Incidental catch of alcids in nets.—Inferences about diving abilities based on gill net catch

TABLE 1. Fishing effort and Common Murre and Atlantic Puffin catch observed in gill nets in Newfoundland, 1980-1982.

Species	Depth range (m)	Fishing effort (net-days)	Number of catch incidents	Number of incidents/net-day	Birds caught		Number of birds caught/incident		
					n	%	$\bar{x}$	SD	Range
Common Murre	>0-10	6,895	261	0.037	2,873	23.5	14.9	28.9	1-130
	>10-20	6,397	113	0.018	2,869	23.4	27.2	110.0	1-950
	>20-30	2,992	112	0.037	2,990	24.4	26.7	69.1	1-425
	>30-40	4,896	88	0.018	998	8.1	11.3	17.9	1-84
	>40-50	2,076	26	0.013	104	0.8	4.0	4.8	1-25
	>50-60	1,783	36	0.020	587	4.8	16.3	67.4	1-407
	>60-70	6	1	0.167	1	<0.1	1.0	—	—
	>70-80	126	9	0.071	1,046	8.5	116.2	95.8	2-245
	>80-90	54	1	0.019	2	<0.1	2.0	—	—
	>90-100	541	23	0.043	184	1.5	8.0	11.0	1-47
	>100-110	15	1	0.067	36	0.3	36.0	—	—
	>110-120	33	2	0.061	17	0.1	8.5	—	2-15
	>120-130	30	2	0.067	2	<0.1	1.0	—	—
	>130-140	54	3	0.057	27	0.2	9.0	—	6-14
	>140-150	0	0	—	—	—	—	—	—
	>150-160	36	1	0.028	6	<0.1	6.0	—	—
	>160-170	42	3	0.071	42	0.3	14.0	—	5-21
	>170-180	468	16	0.034	459	3.7	28.6	32.4	1-126
Total/mean		26,445	698	0.049	12,243	100.0	19.5	—	—
Atlantic Puffin	>0-10	6,895	114	0.0170	482	55.1	4.2	11.3	1-40
	>10-20	6,397	15	0.0023	94	10.8	6.3	5.7	1-18
	>20-30	2,991	25	0.0084	233	26.6	9.4	13.5	1-48
	>30-40	4,896	14	0.0029	55	6.3	3.9	6.2	1-25
	>40-50	2,076	3	0.0014	9	1.0	3.0	—	1-5
	>50-60	1,783	2	0.0011	2	0.2	1.0	—	—
	>60-180	1,407	0	—	—	—	—	—	—
Total/mean		26,445	171	0.0055	875	100.0	5.1	—	—

may be suspect because of the possibility that birds are entangled as nets sink to the bottom or during net-retrieval (Kooyman 1975). While that definitely occurred on occasion, we concluded that the vast majority of birds were trapped in stationary gill nets placed on the sea floor. Fishermen involved in the surveys agreed. Several lines of evidence led us to this conclusion. (1) Typical 100-m cod gill nets used in Newfoundland weigh 40-50 kg and sink at rates of about 18 m/min (Ennis pers. comm.). Thus, hundreds of birds would have to be entangled within minutes of placing a gill net in water to account for many incidental-catch records (Table 1). That is extremely unlikely (and was never observed) because (2) alcids are quickly dispersed by approaching fishing boats, leaving few if any birds under the rapidly sinking net. For the same reason, few alcids are caught by rising gill nets. (3) Based on the observations of fishermen who checked or moved their nets several times a day, it appears that most alcids are caught in nets at dawn or in the early morning hours as they feed on capelin spawning in dense schools on the ocean floor (Templeman 1948, Jangaard 1974, Piatt et al. 1984). Murres ($n = 789$) and puffins ($n = 272$) removed from gill nets and autopsied contained almost entirely capelin in their stomachs (greater than 95% by occurrence or weight). Capelin spawning activity usually ends abruptly after sunrise (Templeman 1948, Jangaard 1974) and schools disperse and rise towards the surface. Fishing activity, on the other hand, peaks during midmorning and early afternoon. Most net-drowned alcids examined were saturated with water, indicating that several hours had passed between the time of net entrapment and net retrieval. (4) Finally, if alcids were being caught only in descending or ascending fishing gear, one would expect catch depth records to be similar for all species, or one would expect to occasionally encounter shallow-diving species in deep nets. This was not the case.

Common Murre.—Incidental catch of Common Murres was highest during the second week of capelin spawning, and it was common to find several hundred murres caught in a single net (Table 1). Although most murres (80.2%) were caught at depths of less than 50 m (Fig. 1, Table 1), this appeared to reflect human fishing effort rather than murre diving ability. When catch was expressed as the number of murres caught/incident of catch or when the range in the number of murres caught/incident was examined (Table 1), no obvious trends of catch-at-depth emerged. If the limits of diving ability were being approached at the greatest depth of catch observed (180 m), one would expect fewer murres caught/incident at depths approaching 180 m because of individual variation in diving ability. There was, however, little correlation between the mean number of murres caught/incident and depth ($r = -0.088$, $t = 0.341$, df = 15, $P > 0.25$, one-tailed test). Similarly, one might expect the number of catch incidents/fishing effort to diminish with depth (Table 1), but they did not ($r = 0.19$, $t = 0.74$, df = 15, $P > 0.10$, one-tailed test). These data suggest that murres are not stressed at dives of up to 180 m and that they may dive to even greater depths.

Atlantic Puffin.—Atlantic Puffins appeared in gill nets much less frequently than murres, and the mean number or range of puffins caught/incident was markedly smaller (Table 1). Puffins were never recorded in nets set deeper than 60 m. Again, it would be expected that if 60 m was the limit of puffin diving ability, there should be fewer puffins caught/incident at depths approaching 60 m. There was some correlation, although it was not significant, possibly due to the small sample size ($r = -0.58$, $t = 1.78$, df = 4, $0.05 < P < 0.10$, one-tailed test). The correlation between the number of catch incidents/fishing effort and depth, however, was high and significant ($r = -0.75$, $t = 2.29$, df = 4, $P < 0.05$, one-tailed test). Thus, we conclude that 60 m is approximately the maximum diving depth for puffins.

Black Guillemot.—Only 34 incidents involving 36 Black Guillemots (*Cepphus grylle*) were observed, probably because guillemots are less abundant in the region. The numbers caught were: 19 at 0–10 m, 8 at 10–20 m, 6 at 20–30 m, 1 at 30–40 m, and 2 at 40–50 m. Again, regression analysis of the number of catch incidents/fishing effort at each depth suggests that 50 m is the maximum diving depth attainable by guillemots ($r = -0.75$, $t = 1.93$, df = 3, $0.05 < P < 0.10$, one-tailed test).

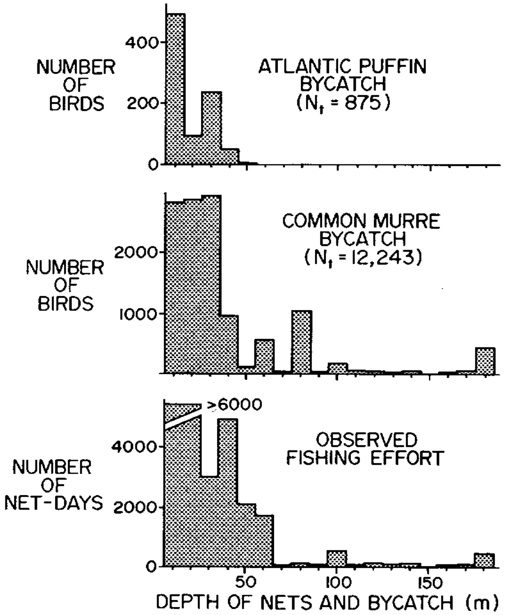

Fig. 1. Frequency distributions of Common Murre and Atlantic Puffin catch and fishing effort at 10-m depth intervals up to 180 m.

Razorbill.—Few records of Razorbill (*Alca torda*) catch were obtained because the species is relatively uncommon in the region. Of 9 catch records with depth information, 1 bird was caught at 0–10 m, 3 at 10–20 m, 2 at 20–30 m, 2 at 30–40 m, and 1 at each range of 40–50 m, 70–80 m, and 110–120 m. These data are insufficient to consider any catch-depth relationships, but we conclude that Razorbills can dive to depths of at least 120 m.

DISCUSSION

The observed diving depths of the four alcids are compatible with what is known about their diving and feeding behavior. Black Guillemots, for example, probably forage regularly near the ocean bottom as much of their prey consists of benthic fish and invertebrates

(Cairns 1981). Uspenski (1956) observed that Black Guillemots could swim underwater at speeds of 1.5–2 m/s, and we recorded a maximum dive time of 112 s for guillemots actively feeding in water 35–45 m deep. Combining these observations gives guillemots a theoretical maximum depth range of 84–112 m for what Kooyman (1975) called a "bounce dive" (down and up with little time for foraging). That is well beyond the maximum catch depth recorded in our study (50 m) and suggests that considerable time is devoted to locating food once the bottom is reached. Both Common and Thick-billed (*Uria lomvia*) murres forage to some degree on benthic prey while at their breeding colonies (Tuck and Squires 1955, Tuck 1961). Recently, dive times of up to 231 s have been observed off the Oregon coast for adult Common Murres accompanying chicks (Varoujean pers. comm.). Thus, assuming swimming speeds of 1.5–2 m/s, murres have a theoretical maximum diving range of about 170–230 m, which easily accommodates our records of murres diving to 180 m. Using a device that records maximum diving depths, A. Burger (pers. comm.) obtained 6 exact depth records for Atlantic Puffins ($\bar{x}$ depth = 46 m; range = 41–52 m) and 1 approximate record for Common Murres (65–75 m) at Witless Bay, Newfoundland, in the summer of 1984. These records further substantiate our net-mortality observations.

Stonehouse (1975) noted that "Within modern families of diving birds, flying and wing-swimming are compatible up to body weights of 1 kg; further increase in body size . . . [to facilitate sustained diving] . . . leads ultimately to loss of flight. Thus the flightless condition must have arisen in proto-penguins which were no larger than the smallest living forms." Significantly, the largest of the surviving alcids (murres) weigh just under 1 kg and the smallest penguins [Little Blue Penguin (*Eudyptula minor*)] weigh just over 1 kg (Bédard 1969, Stonehouse 1975). The implication is that the primary advantage to crossing the flight-loss threshold was the ability to dive deeper or longer than already possible. Because murres are now very close to that threshold (Spring 1971), one might predict that they should dive nearly as deeply and efficiently as the smallest penguins.

Outside of the physiological requirements for dealing with environmental extremes (e.g. pressure), diving ability is a function of two parameters: swimming speed and diving time (related to oxygen storage capacity, metabolism, etc.). Clark and Bemis (1979) found no significant differences in the maximum swimming speeds of seven penguin species ranging in size from 1.1 to 30 kg (correlation of maximum speed and size; $r = 0.02$, $t = 0.050$, df = 5, $P > 0.25$). Again, it appears that increased size evolved largely because of the advantage conferred by the resulting increase in time available for diving and foraging. If alcids, like penguins, swim at similar speeds regardless of size (which remains to be demonstrated), we expect that size would be directly related to diving ability and that the largest alcids would dive the deepest. Indeed, for the four alcids considered, weight (Bédard 1969) was directly proportional to the maximum diving depths recorded (weight and maximum diving depth for each species were: Common Murre, 931 g, 180 m; Razorbill, 738 g, 120 m; Atlantic Puffin, 510 g, 60 m; and Black Guillemot, 431 g, 50 m; $r = 0.999$, $t = 99.9$, df = 2, $P < 0.0001$, one-tailed test).

Our observations of widely varying diving abilities in four sympatric alcid species raise several questions that future studies could address, i.e. What is the role of diving ability in ecological segregation, foraging efficiency, and energy budgets? What is the pelagic distribution of alcids when in their wintering areas? And what is the impact of human fishing activities on alcid foraging behavior and success?

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