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## *Diving Birds of North America: 2 Comparative Distributions and Structural Adaptations*

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## 2. Comparative Distributions and Structural Adaptations

### Distributions

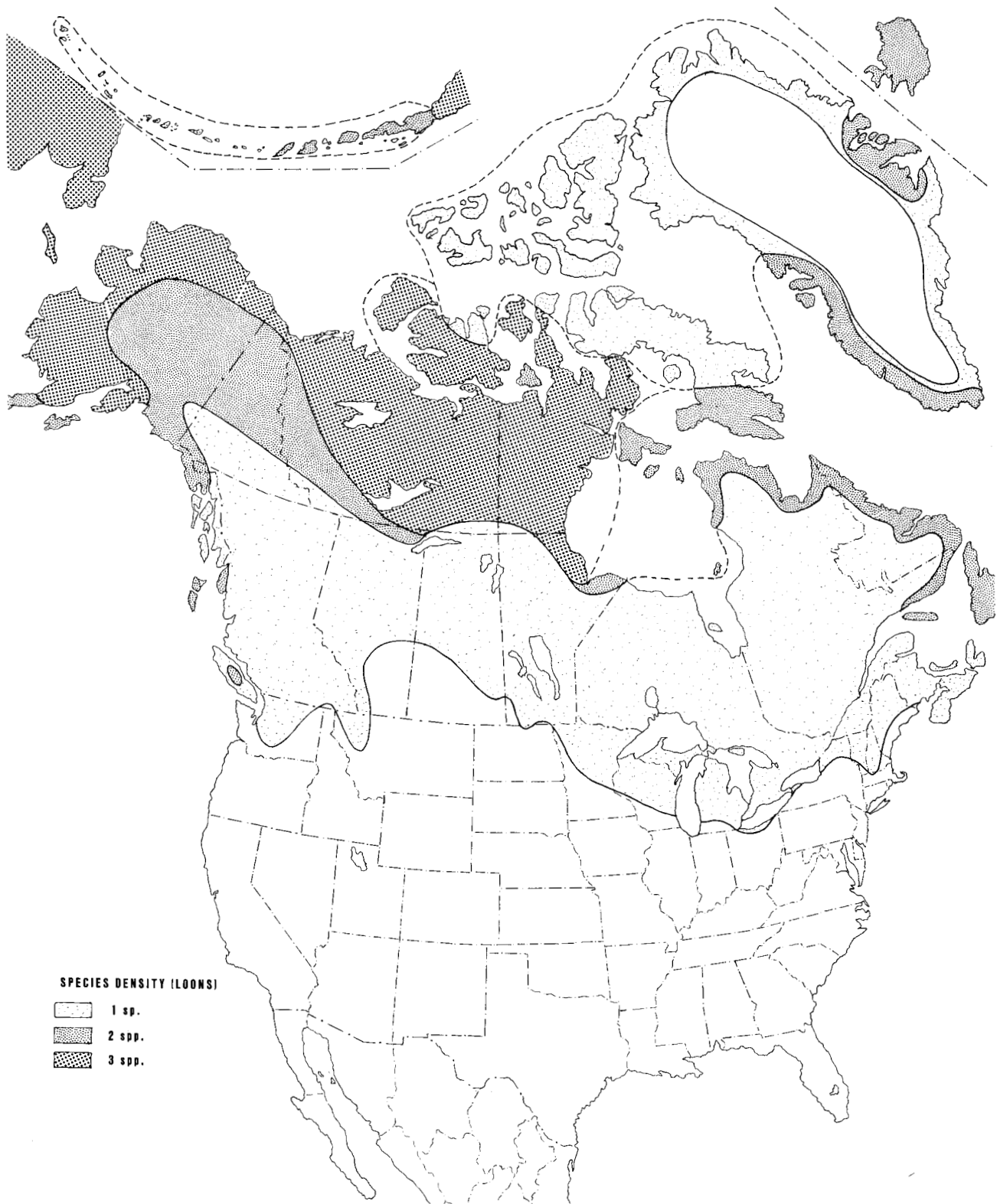
The geographic distributions of the loons, auks, and grebes are primarily reflections of the evolutionary histories of each of the groups, past climatic and geologic phenomena, and present-day climatic and ecological conditions. Thus all the loons and auks are Northern Hemisphere birds, which presumably have never been able to bridge the tropical barrier into the Southern Hemisphere, where seemingly suitable breeding habitat might exist in, for example, southern South America and Tierra del Fuego. Indeed, the breeding distribution of the Northern American loons is distinctly arctic oriented (fig. 2), with the greatest species density north of the boundaries of arctic tundra in Canada and Alaska and no breeding occurring south of the limits of continental glaciation (see fig. 4).

On the other hand, the breeding distributions of the grebes are distinctly more southerly; indeed, more than half the species of grebes are equatorial or Southern Hemisphere in occurrence. In North America the breeding distributions of grebes (fig. 3) are more closely related to topography and ecology than to climate, with the greatest species density occurring in the grasslands of southern Canada and the adjacent northern United States, in a general east-west band more or less approximating the distribution of the "prairie pothole region" (fig. 4) of Pleistocene glacial till that until recently was primarily grassland covered, but with abundant potholes and marshes. In such areas all but one of the North American grebes can sometimes be found breeding in a single marsh, which suggests that there may be substantial selective pressures for ecological segregation of foraging niches and other aspects of niche adaptation as well. Some of these questions of niche segregation will be dealt with in chapter 4.

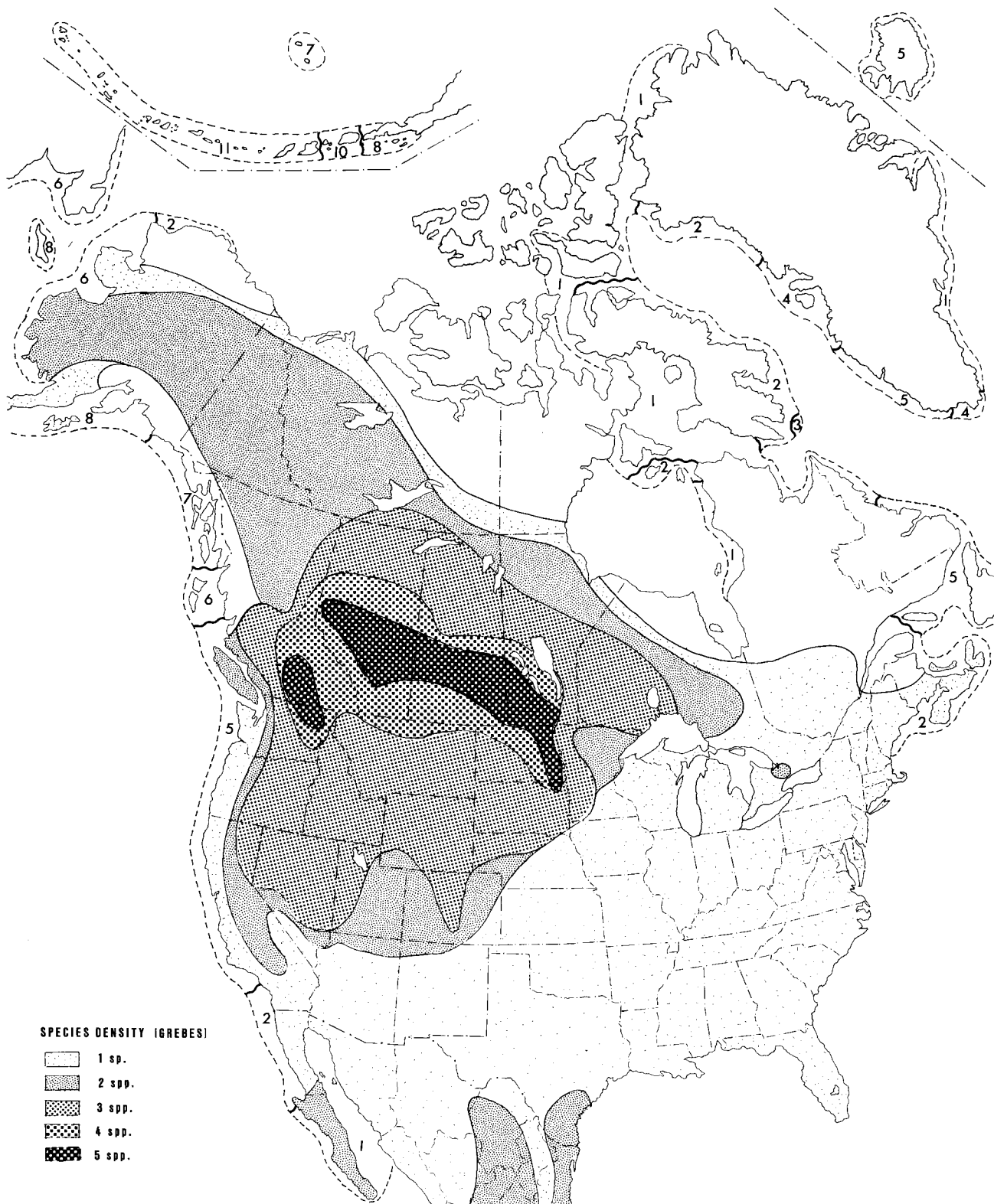
Finally, the breeding distributions of the North

American auks are, like those of the loons, distinctly arctic in orientation (fig. 3). Species densities reach a maximum in the Aleutian Islands, where as many as twelve to fourteen species might be found breeding. This is substantially greater than on the eastern coast of North America, where there is a maximum density of five sympatric breeding species. Udvardy (1979) analyzed the distribution of the Pacific alcids in considerable detail; he correlated the present-day distribution of these species with dispersal waves extending back to mid-Eocene times and reflecting a Pacific basin origin of the family centering on the Bering Sea. Udvardy imagined a series of five dispersal waves between the Pacific and Atlantic areas, reflecting the five interglacial periods when the Bering Strait was open. During at least the latest glacial period the Sea of Okhotsk was perhaps the most important and also the northernmost refuge, and many of the Pacific Ocean alcids still are essentially limited to glacial refuge areas. The present-day subtropical ranges of various southern endemics such as *Craveri* and *Xantus murrelets* were considered to be a result of their being Tertiary relicts, whose ranges and populations farther north were eliminated by climatic changes.

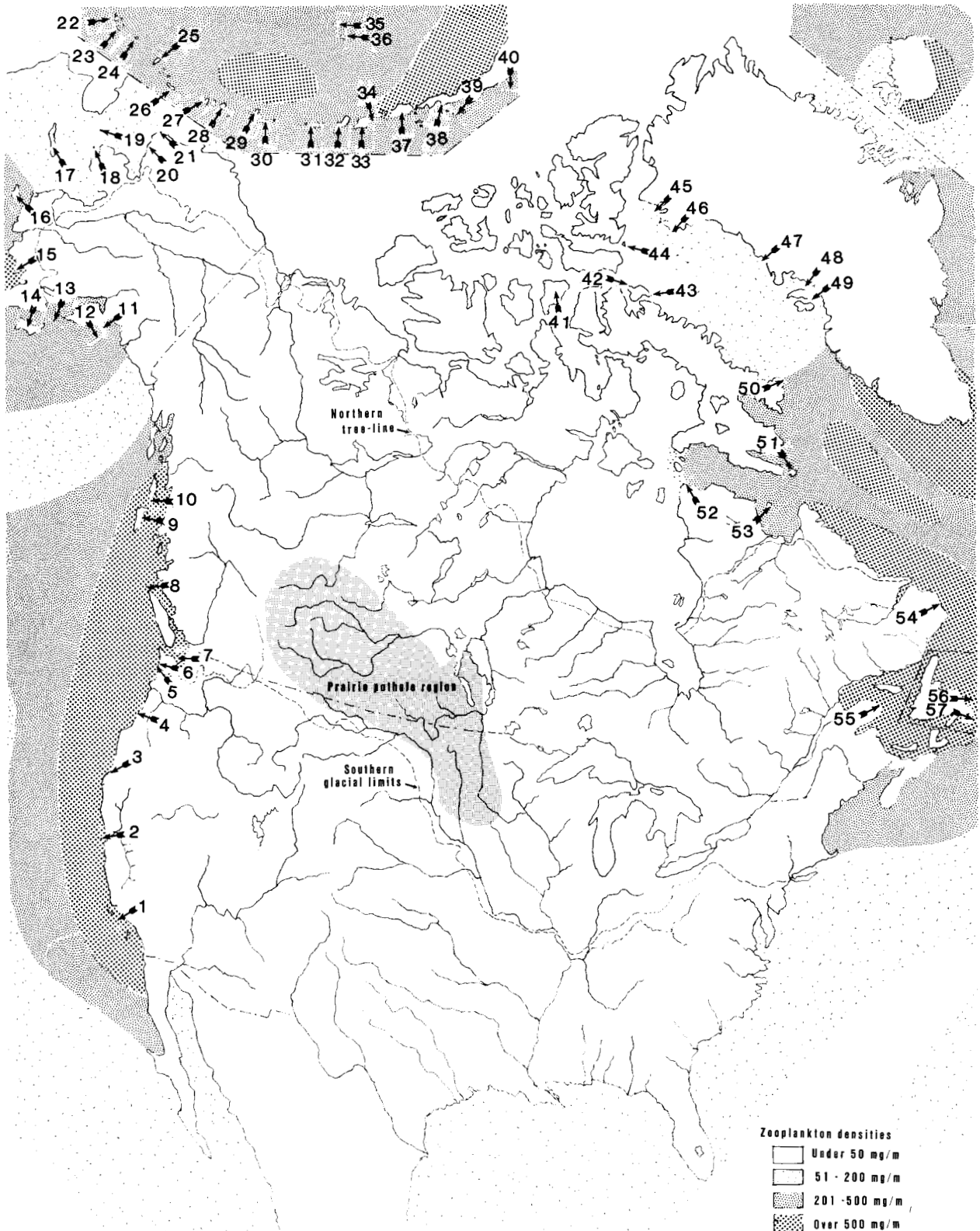
Beyond these historical effects, the current distribution of the alcids is also strongly affected by the present-day availability of marine food resources, ranging in size from planktonic invertebrates to small fish. To illustrate this relationship, the densities of zooplankton surrounding North America are illustrated in figure 4 (based on the *Atlas of the Living Resources of the Sea*, 1981, published by the Food and Agriculture Organization of the United Nations). Here it may be seen that the largest of the North American alcid colonies are all associated with adjacent ocean areas that are relatively rich in planktonic life, and doubtless also with other associated food resources of higher trophic levels.



2. Species density map of breeding loon distributions in North America.



3. Species density map of breeding grebe (*shading*) and auk (*numerals*) distributions in North America.



4. Distribution of major auk colonies in North America in relation to zooplankton densities of adjoining oceans. See appendix 3 for identification of colonies. Limits of arctic tree line, south-

ern continental glaciation boundaries, and "prairie pothole" region are also indicated.

Although not shown on this map, the nonbreeding distributions of high-latitude auks and loons are strongly affected by patterns of sea-ice development during winter, which impose migrations of varied lengths and magnitudes on these forms. Winter distributions of these species are still very poorly known, since few efforts have been made to establish the distribution and abundance patterns of marine birds in

North America. However, efforts to that end have begun in Alaska (Gould, Forsell, and Lensink 1982; Forsell and Gould 1981), and similar studies have been under way in eastern Canada for some time (Brown et al. 1975; Gaston 1980). Important information on the winter distributions of loons and grebes in the southeastern states and Gulf of Mexico has been provided by Clapp et al. (1982). Unfortunately there is as yet no corresponding

Table 5: Seasonal and Ecological Distribution of Loons in the Gulf of Alaska and Eastern Bering Sea, Based on Shipboard Surveys

Species	Gulf of Alaska				Eastern Bering Sea		
	Bay	Shelf	Shelfbreak	Oceanic	Bay and Shelf	Shelfbreak	Oceanic
Common							
Spring	5.8	+	+	+	0	+	0
Summer	0	+	0	0	0	0	0
Fall	+	0	+	0	+	0	0
Winter	1.8	0	0	0	-	-	-
Yellow-billed							
Spring	+	+	0	0	0	0	0
Summer	0	0	0	0	+	0	0
Fall	+	+	0	0	0	0	0
Winter	0	0	0	0	-	-	-
Arctic							
Spring	2.9	+	+	+	+	0	0
Summer	0	+	0	0	+	0	0
Fall	+	+	+	+	8.14	0	0
Winter	0	0	0	0	-	-	-
Red-throated							
Spring	0	0	0	0	0	0	0
Summer	+	0	0	0	+	0	0
Fall	+	0	0	0	+	0	0
Winter	0	0	0	0	-	-	-
Loon (sp.?)							
Spring	17.4	15.8	5.7	0	+	0	0
Summer	+	+	+	0	+	0	0
Fall	3.56	+	+	+	8.14	0	0
Winter	3.6	1.37	0	0	-	-	-

NOTE: Calculated number of birds/100 km<sup>2</sup>, based on data of Gould, Forsell, and Lensink 1982.  
 + = small number present. 0 = not observed. - = not surveyed.

Table 6: Seasonal and Ecological Distribution of Auks in the Gulf of Alaska and Eastern Bering Sea, Based on Shipboard Surveys

Species	Gulf of Alaska				Eastern Bering Sea		
	Bay	Shelf	Shelfbreak	Oceanic	Bay and Shelf	Shelfbreak	Oceanic
<b>Common murre</b>							
Spring	93.4	79.1	34.3	+	94.2	10.8	4.1
Summer	85.0	93.9	50.2	+	380.9	6.8	4.2
Fall	466.4	143.8	8.9	2.0	16.3	+	0
Winter	373.1	30.1	19.8	0.3	-	-	-
<b>Thick-billed murre</b>							
Spring	8.7	15.8	+	9.8	134.6	43.4	2.7
Summer	+	+	+	0	105.8	20.3	12.5
Fall	+	+	2.2	0.7	132.6	+	1.5
Winter	7.3	4.1	2.2	0	-	-	-
<b>Murre (sp.?)</b>							
Spring	21.2	743.5	127.3	21.9	1,460	130.1	29.7
Summer	124.7	415.7	228.8	1.5	1,206	81.2	22.2
Fall	192.2	239.6	98.5	3.4	407	120.5	5.9
Winter	414.9	412.4	695.2	4.9	-	-	-
<b>Pigeon guillemot</b>							
Spring	69.6	15.8	+	0	13.5	0	0
Summer	102.1	13.4	0	0	+	+	0
Fall	18.8	+	+	0	+	0	0
Winter	0	0	0	0	-	-	-
<b>Marbled murrelet</b>							
Spring	46.4	15.8	5.7	0	0	0	0
Summer	73.7	13.4	5.6	0	0	0	0
Fall	14.2	+	0	0	+	0	0
Winter	54.6	0	0	0	-	-	-
<b>Kittlitz murrelet</b>							
Spring	2.9	+	+	0	+	0	0
Summer	5.7	+	0	0	+	0	0
Fall	+	+	+	0	0	0	0
Winter	0	0	0	0	-	-	-
<b>Murrelet (sp.?)</b>							
Spring	2.9	15.8	5.7	0	0	0	0
Summer	232.5	40.2	0	0	0	0	0
Fall	39.2	+	0	0	+	0	0
Winter	0	0	0	0	-	-	-

(continued)

Table 6: (Continued)

Species	Gulf of Alaska				Eastern Bering Sea		
	Bay	Shelf	Shelfbreak	Oceanic	Bay and Shelf	Shelfbreak	Oceanic
Ancient murrelet							
Spring	2.9	47.5	+	0	356.7	173.4	68.8
Summer	17.0	53.6	39.1	1.5	126.9	74.5	0
Fall	0	+	+	-	16.3	+	0
Winter	5.5	0	0	0.3	-	-	-
Cassin auklet							
Spring	+	15.8	+	+	6.7	0	0
Summer	17.0	80.5	5.6	+	+	+	0
Fall	53.4	30.0	29.1	4.0	+	0	0
Winter	9.1	0	0	0.3	-	-	-
Parakeet auklet							
Spring	0	+	+	0	40.4	243.9	0
Summer	+	13.4	5.6	+	+	6.8	1.4
Fall	0	35.9	38.1	4.7	56.9	+	0
Winter	0	0	0	0	-	-	-
Crested auklet							
Spring	0	+	0	0	114.4	422.8	6.8
Summer	0	+	+	0	84.6	60.9	83.4
Fall	14.2	137.8	0	1.3	154.7	24.1	5.9
Winter	0	0	0	0	-	-	-
Least auklet							
Spring	0	+	0	0	666.3	1,067	159.3
Summer	0	+	0	0	63.5	94.8	23.6
Fall	0	0	0	0	58.8	0	1.5
Winter	0	0	0	0	-	-	-
Whiskered auklet							
Spring	0	284.7	17.2	0	652.8	5.4	0
Summer	0	+	0	0	21.2	13.5	0
Fall	0	0	0	0	+	0	0
Winter	0	0	0	0	-	-	-
Rhinoceros auklet							
Spring	0	+	+	0	0	0	0
Summer	+	+	+	5.9	0	0	+
Fall	0	5.6	0	4.7	0	0	0
Winter	0	0	0	0	-	-	-

(continued)



Table 6: (Continued)

Species	Gulf of Alaska				Eastern Bering Sea		
	Bay	Shelf	Shelfbreak	Oceanic	Bay and Shelf	Shelfbreak	Oceanic
Horned puffin							
Spring	11.7	15.8	5.7	0	6.7	5.4	0
Summer	51.0	80.5	111.6	1.5	42.3	40.6	9.7
Fall	64.1	89.8	29.1	4.0	16.3	+	0
Winter	0	16.4	6.6	15.0	–	–	–
Tufted puffin							
Spring	559.7	332.3	40	6.5	242.3	65.0	83.7
Summer	1,967	898.5	546.8	61.7	275.1	236.9	83.4
Fall	99.7	179.7	91.8	84.4	374.4	192.8	127.3
Winter	3.6	35.6	44.0	22.1	–	–	–
Alcid (sp.?)							
Spring	139.2	126.6	34.3	8.7	329.8	222.2	255.1
Summer	79.4	227.9	155.7	11.8	84.6	1,029	13.9
Fall	39.2	83.9	26.9	11.4	130.2	24.1	41.4
Winter	127.4	63.0	22.0	2.9	–	–	–

NOTE: Symbols and density estimates as in table 5.

information on the Pacific coastal wintering range from British Columbia south to southern California, which appears to provide major wintering sites for arctic and red-throated loons, western, eared, and red-necked grebes, and numerous species of auks.

To illustrate the importance of the Gulf of Alaska and the eastern Bering Sea as wintering areas for loons and auks, a tabular summary of the information provided by Gould, Forsell, and Lensink (1982) has been condensed and summarized in tables 5 and 6. This information suggests that the Bering Sea is used during spring and fall, with only very limited wintering occurring there. On the other hand, the data for auks suggest very high usage of the eastern Bering Sea by murre, auklets, and puffins for much of the year and similar year-round usage of the Gulf of Alaska for these same groups. In the vicinity of Kodiak Island alone it is probable that more than a million murre overwinter, a significant portion of the entire common murre nesting population of the Bering Sea and Gulf of Alaska (Forsell and Gould 1981). Similarly, perhaps the entire Gulf of Alaska population of crested auklets winters in a limited area of the Kodiak archipelago (not included in table 7). The high concentration of whiskered auklets

shown in table 7 was the result of finding large numbers in a few transects taken in the eastern Aleutian Islands and is thus an artifact of data gathering.

Gould, Forsell, and Lensink (1982) concluded that the major migratory point of entry and departure to and from the eastern Bering Sea is Unimak Pass and that some alcid species (thick-billed murre, parakeet auklet, least auklet, crested auklet) are usually many times more numerous in the Bering Sea than in the Gulf of Alaska, while the reverse is true for several others (rhinoceros auklet, Cassin auklet, ancient murrelet). Waters over the continental shelf typically show the greatest number of species, and in such areas the common murre reaches its greatest numbers, while tufted puffins are among the species dominating the avifaunas of bays and pigeon guillemots are especially characteristic of nearshore areas. Generally, seabirds reach their maximum numbers over continental shelf areas south of Kodiak Island and the Alaska Peninsula, both in summer and in winter, though during mild winters many birds may remain in the southern Bering Sea or the far western Gulf of Alaska. Grebes are generally limited to inland freshwater habitats and inshore marine areas of coastal Alaska, and the numbers recorded were too

Table 7: Estimated Breeding Auk Populations and Approximate Biomass Equivalents

Species	World Population <sup>a</sup>	North American Population <sup>b</sup>	World Biomass (tons) <sup>c</sup>
Dovekie	80,000,000	30,000,000	12,800
Thick-billed murre	20,000,000	11,000,000	20,000
Atlantic puffin	16,000,000	625,000	16,000
Common murre	10,000,000	6,500,000	10,400
Least auklet	10,000,000	6,000,000	9,200
Tufted puffin	8,000,000	4,035,000	6,400
Horned puffin	30,000,000	1,500,000	1,800
Crested auklet	2,500,000	2,000,000	715
Cassin auklet	1,800,000	1,800,000	306
Rhinoceros auklet	1,000,000	250,000	520
Parakeet auklet	1,000,000	800,000	285
Ancient murrelet	800,000	580,000	160
Pigeon guillemot	700,000	220,000	315
Marbled murrelet	500,000	300,000	110
Razorbill	416,000	40,000	287
Black guillemot	100,000	56,000	43
Kittlitz murrelet	100,000	50,000	22.5
Whiskered auklet	50,000	20,000	4.9
Xantus murrelet	20,000	20,000	3.2
Craveri murrelet	6,000–10,000	6,000–10,000	0.8–1.35

<sup>a</sup>After Thoreson, in press, with some revised estimates. Nettleship & Birkhead (1985) offer alternative estimates.

<sup>b</sup>Including Greenland.

<sup>c</sup>Metric tons (equals 2,204 pounds, or 1,000 kilograms).

small to warrant inclusion in tables 5 and 6. Common loons made up 56 percent of the total loons observed in the Gulf of Alaska and 24 percent of those seen in the eastern Bering Sea, while the arctic loon composed 39 percent and 59 percent respectively. Migrant loons were often observed as far as 300 kilometers from land and in water more than 100 meters deep, and during summer periods they were usually within 50 kilometers of land and in water no more than 50 meters deep.

It is still impossible to judge the numbers of North American loons and grebes, owing in part to their great breeding and wintering dispersion and to difficulties of censusing them on a continental basis. However, some efforts have been made to estimate continental populations of the alcids. Thus Nettleship (1977) provided estimates of the total numbers of alcids in eastern Canada, and Thoreson (in press) has done the same for all of North America and the world. With minor changes I

have accepted Thoreson's estimated totals for North America and the world, and they are summarized in table 7, together with a calculated world biomass based on average adult weights shown elsewhere in this text. The enormous avian biomass represented by the auks becomes evident with such calculations, and thus the role of the alcids in coastal and marine ecosystems can be more readily visualized.

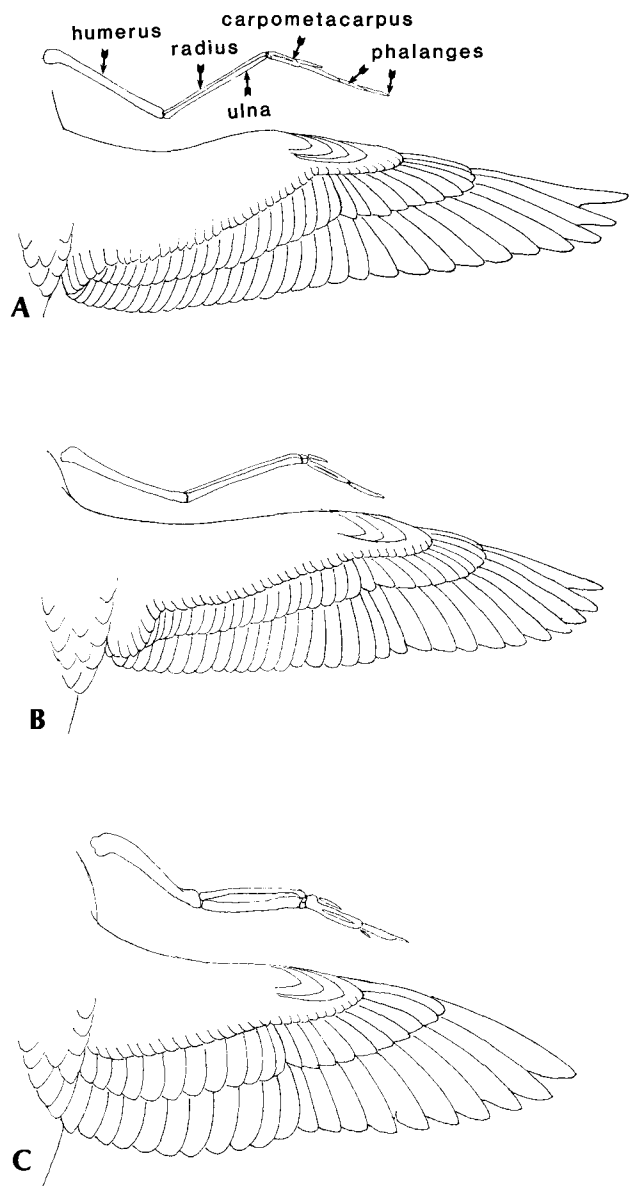
### Structural Adaptations

The specializations of the loons, grebes, and auks for swimming, diving, and flight are among the most interesting for any birds. Storer (1960) has traced the general evolutionary patterns associated with the development of both the wing-propelled diving birds (auks in the Northern Hemisphere and penguins and diving petrels in the Southern Hemisphere), and the foot-propelled

divers (loons, grebes, and the extinct hesperornithiform birds). These two groups have followed distinctly different pathways, though in some respects there are certain similarities imposed by the diving syndrome. According to Storer, the wing-propelled divers are all marine and largely pelagic forms, whereas foot-propelled divers are more associated with freshwater and littoral habitats. He judged that one possible reason for this is that the subsurface aquatic vegetation so typical of freshwater habitats might impede wing-propelled divers more than foot-propelled ones. A second disadvantage of wing-propelled diving is that there is an upper size limit on the birds, above which selection for the small wings associated with efficient diving results in flightlessness, a condition typical of all penguins, the great auk, and the extinct Lucas auks. Storer also notes that simultaneous molting of the flight feathers, as is common in aquatic birds, influences the diving efficiency of wing-propelled divers, with smaller wing areas needed for diving than for flying. Thus the smallest alcids (such as the least and whiskered auklets) molt their wing feathers gradually, since in these alcids the relatively small wing needed for flying more nearly approaches the optimal size for use underwater.

Wing shapes and wing areas of the loons, grebes, and auks thus differ substantially (fig. 5), with loons tending to have relatively long and narrow wings and in particular primaries that are relatively long and supported by a long and relatively weak carpometacarpus-phalanges component. They also have a very large number of secondaries, supported by a long and relatively weak ulna. In spite of their long wings, loons have a relatively high wing loading (table 8). This wing loading is substantially greater than that reported for any grebe, though total weight differences between loons and grebes make such comparisons questionable.

The wing shape of grebes varies from moderately long to distinctly short and elliptical (with an aspect ratio of only 2.51 in the least grebe, according to Hartman 1961). Like the loons, their primaries are supported by a relatively thin and (compared with loons) relatively short carpometacarpus-phalanges component, and their numerous secondaries are supported by a long and fairly weak ulna. In both loons and grebes the upper medial wing coverts are variably enlarged and partially cover the innermost secondaries, presumably providing additional structural support. The wing loading of grebes appears in general to be the lowest of the three groups under consideration here, though grebes are not considered either strong or rapid fliers. There is virtually no information available on the flight speeds of grebes, and also very little on wingbeat rate, which seems to be



5. Comparison of wing shapes and relative lengths of arm and hand bones: A, loons (*Gavia*); B, grebes (*Podiceps*); C, auks (*Alca*).

somewhat higher than that of loons (table 9), as might be expected from their smaller size.

The wing shape of auks is relatively similar in all the flying species and may be characterized as relatively short, paddlelike, and with a short, stout forearm (Kozlova 1961). The bones supporting the primaries are broad and strong, making up approximately a third of the total wing skeleton. The ulna is short and robust; probably it and the radius are responsible for withstand-

Table 8: Estimates of Wing Loading and Foot Loading in Loons, Grebes, and Auks

Species	Weight (g)	Wing Area (cm <sup>2</sup> )	Foot Area (cm <sup>2</sup> ) <sup>a</sup>	Foot/Wing Ratio (%)	Wing Loading (g/cm <sup>2</sup> )	Foot Loading (g/cm <sup>2</sup> )	References
Loons							
Common	2,425	1,358	130.4	9.6	1.78	18.6	Pool 1938
Grebes							
Least	—	—	—	—	0.67	—	Hartman 1961
Pied-billed	343.5	291	—	—	1.18	—	Pool 1938
Pied-billed (average of 4)	372	301	30.2	9.4	1.23	13.2	Various sources
Giant pied-billed	414	804.5	—	—	1.9	—	Bowes 1965
Horned	369.5	350	30.9	8.8	1.05	12.2	Pool 1938
Auks							
Dovekie	96	146	—	—	0.66	—	Pool 1938
Murres	982–1,069	ca. 400 <sup>b</sup>	34.9	8.7	2.5–2.6	ca. 29	Kartashev 1960
Razorbill	774	ca. 340 <sup>b</sup>	30.0	8.8	2.3	25.8	Kartashev 1960
Great auk	ca. 5,000	—	—	—	over 4.0	—	Kartashev 1960
Black guillemot	421	ca. 300 <sup>b</sup>	—	—	1.4	—	Kartashev 1960
Pigeon guillemot	539	157	—	—	1.63	—	Lehnhausen 1980
Marbled murrelet	234	146	—	—	1.60	—	Stettenheim 1959
Parakeet auklet	247	149.6	—	—	0.83	—	Lehnhausen 1980
Least auklet	92	132.9	—	—	0.69	—	Sealy 1968
Tufted puffin	872	219.6	—	—	1.99	—	Lehnhausen 1980
Atlantic puffin	552	ca. 290 <sup>b</sup>	25.5	8.8	1.9	21.6	Kartashev 1960

<sup>a</sup>Personal estimates.    <sup>b</sup>Estimated from graphic data of author cited.

ing much of the stress associated with wing-propelled diving. The total wing area of auks is relatively small, resulting in a high wing loading (1.9 g/cm<sup>2</sup> in the Atlantic puffin, compared with 1.05 in the comparably sized horned grebe), and the auks typically have a very rapid wingbeat in flight, especially in the smaller species.

A substantial difference between auks and the foot-propelled loons and grebes is to be expected in the relative development of their feet. In general, auks should exhibit relatively small foot surfaces in conjunction with their limited roles during diving (being used mainly for steering and to a limited extent for in-place paddling while bottom foraging). Major differences in foot shape and leg skeletal structure are indicated in figure 6, but comparisons are easier in table 8, where the estimated surface areas of the two feet (toes maximally

expanded) are shown for six species. There is no apparent difference in the foot-to-wing surface area data for the available species; in all cases the ratio of foot area to wing area ranges from about 9 to 10 percent, in spite of the differing roles of the feet in these three groups. On the other hand, the ratio between foot area and total body weight does suggest that auks have substantially smaller foot areas relative to body weight than do loons or grebes, and that grebes perhaps have the most efficient surface area to body weight ratios for paddling and diving when using the feet alone.

Differences in the hind limbs of these birds may also be found in the skeletal elements of their legs. Shufeldt (1904) described the anatomy of the hind limbs of loons and grebes in some detail. He stated that the pelvic limb of a grebe is "altogether one of the most beautiful

Table 9: Speeds and Wingbeat Rates during Flight and Diving in Loons, Grebes, and Auks

Species	Speed (km/hr)	Wingbeat Rate (beats/min)	References
<b>Loons</b>			
Arctic (flight)	71 ± 6.8 (air)	—	Davis 1971
Arctic (diving)	2.5–5 <sup>a</sup>	—	Lehtonen 1970
Red-throated	75–78 (air)	—	Davis 1971
Yellow-billed	64 (ground)	—	Davis 1971
Common	—	256–62	Meinertzhagen 1955
Common	74.9 (air)	—	Kerlinger 1982
<b>Grebes</b>			
Great crested (flight)	—	360–400	Meinertzhagen 1955
Great crested (diving)	4.3	—	Bolam 1921
<b>Auks (flight)</b>			
Common murre	129–42 (ground)	270–348	Meinertzhagen 1955
Razorbill	127–40 (ground)	—	Meinertzhagen 1955
Black guillemot	—	324–482	Meinertzhagen 1955
Atlantic puffin	62–132 (ground)	320–400	Meinertzhagen 1955
Dovekie	—	720–1080	Rüppell 1969
<b>Auks (diving)<sup>b</sup></b>			
Common murre	3.2–6.1	—	Stettenheim 1959
Common murre	Avg. 4.07 ( <i>n</i> = 12)	109	Kenneth Fink and author
Pigeon guillemot	—	104	Kenneth Fink and author
Rhinoceros auklet	Avg. 3.96 ( <i>n</i> = 4)	82	Kenneth Fink and author
Tufted puffin	Avg. 3.84 ( <i>n</i> = 14)	92	Kenneth Fink and author
Horned puffin	Avg. 4.07 ( <i>n</i> = 19)	—	Kenneth Fink (pers. comm.)
Atlantic puffin	Avg. 3.60 ( <i>n</i> = 2)	—	Kenneth Fink (pers. comm.)

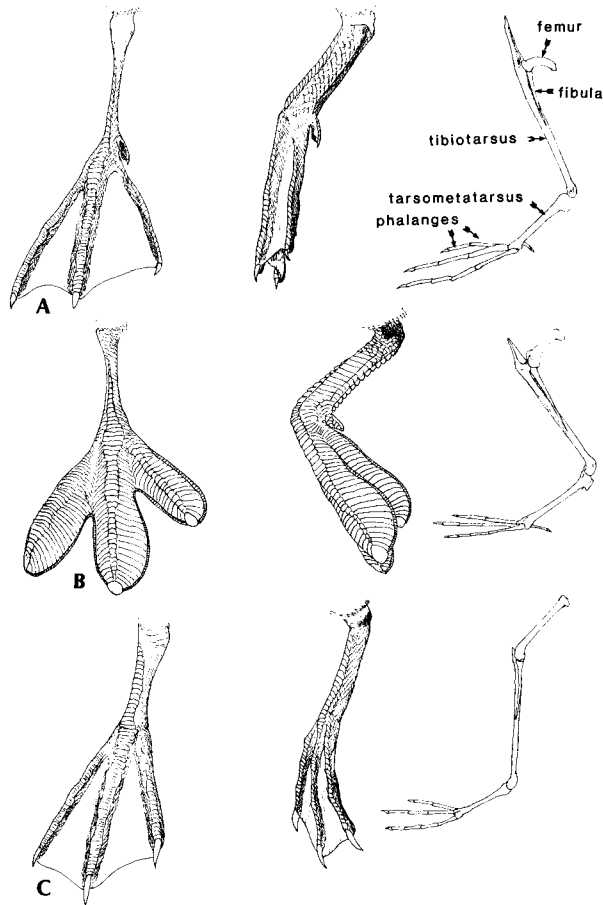
<sup>a</sup>For dives lasting 5 seconds or more.

<sup>b</sup>In confinement at Sea World, San Diego.

adapted structures," which by appropriate articulations is "an avian oar." Its tarsus is compressed to the maximum degree, so that when it and the blade-like toes are brought forward they offer minimum resistance, but during the backward stroke the articulation permits the spread and expanded toes to be turned, and to some extent also the tarsus, thus exposing the maximum surface. The femur and tarsometatarsus are of about equal length, and the head of the femur is large. The tibiotarsus has a long cnemial crest, and this is supported posteriorly by a separate patella, providing substantial mechanical advantage for muscle contraction.

In loons the femur is short and thick and lies perpendicular to the sagittal plane of the body, causing the legs to be strongly splayed and essentially preventing walking on land. It has a large and globular head and is distinctly shorter than the tarsometatarsus, which as in grebes is extremely flattened. The tibiotarsus is marked by a greatly developed cnemial process but no separate patella, the latter apparently having become fused with the cnemial process in earlier evolutionary development.

By comparison, the hind-limb structures of the alcids are relatively simple, and they have been analyzed by

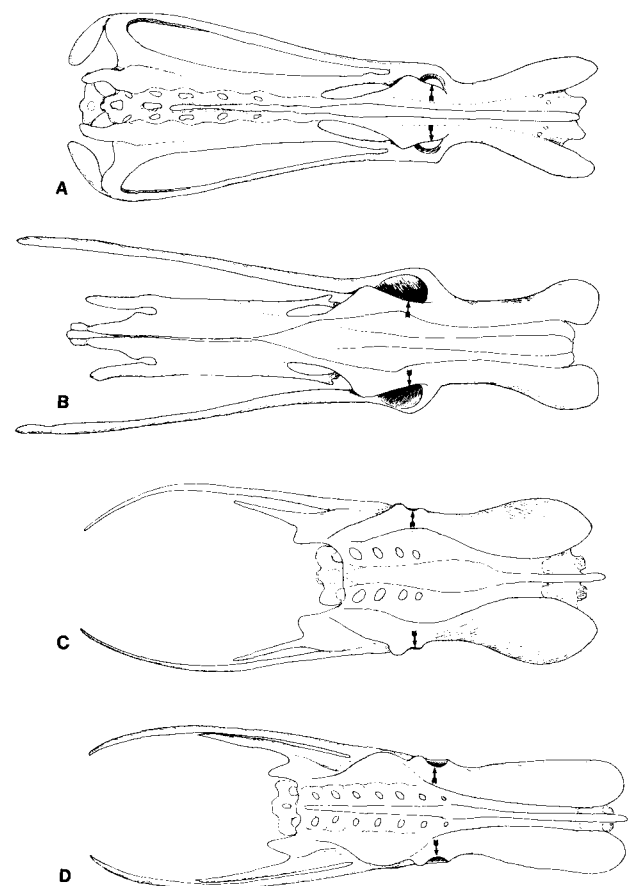


6. Comparison of foot structures and relative lengths of leg and foot bones: A, loons (*Gavia*); B, grebes (*Podiceps*); C, auks (*Uria*).

Storer (1945) and Kuroda (1954) in some detail. Storer noted that the leg length is greatest in the puffins, auklets, and *Cephus* and is intermediate in the "auks" (great auk and razorbill), murres, dovekie, and murrelets except for *Brachyramphus*, in which it is shortest. Storer noted that in the genus *Cephus* the legs are long and have heavy joints, a feature that in connection with a broad pelvis is associated with extensive walking. In puffins the long legs and heavy joints are also associated with ambulatory and fossorial adaptations; these are the only alcids that regularly stand with the tarsometatarsus raised above the ground (digitigrade posture). Fossorial adaptations of the puffins are evidenced in the thickness of the tarsometatarsus and the long, deep and curved claws, which are apparently used in burrow excavation. Auklets tend to have long legs but short pelvic bones, and the dovekie also has short, weak legs, so all these species are rather poor walkers. The murrelets fall into

two categories, the burrowing forms (*Synthliboramphus*) and the surface-nesting forms (*Brachyramphus*). The burrowing forms tend to have heavy femurs and heavy claws, but in general the murrelets have short femurs and tarsometarsi, suggestive of selection for swimming and diving rather than burrowing. However, in *Brachyramphus* the legs are usually short and the pelvis is especially broad, in conjunction with surface-nesting behavior.

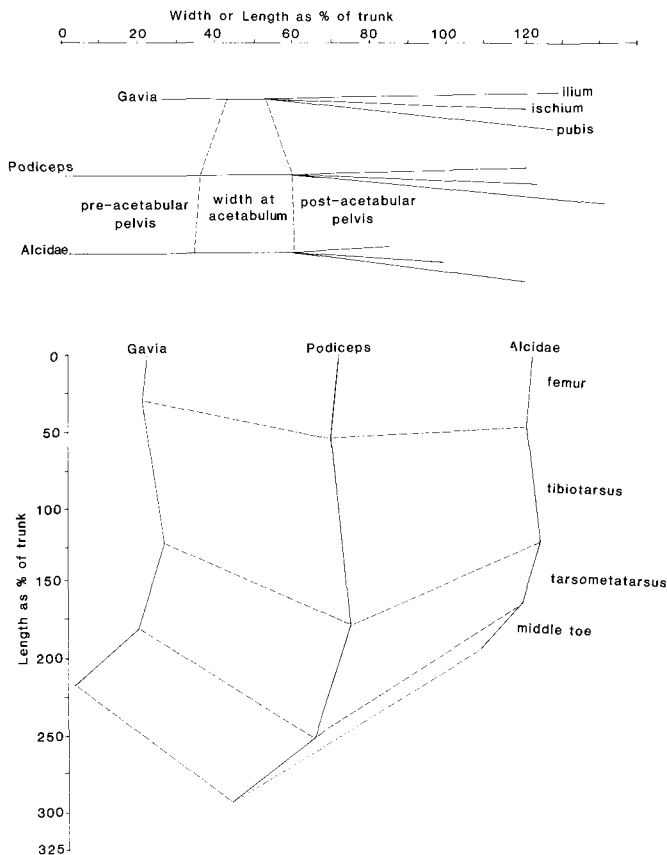
It is impossible to discuss the hind limb without reference to the pelvic structure as well as the leg structure, since the two skeletal groups are functionally coevolved. Storer (1945) states that although the pelvises of the alcids average narrower than those of gulls and typical shorebirds, significant narrowing only occurs in a few forms such as in *Uria* and *Alca*. Kuroda (1954) reported a narrow pelvis in *Synthliboramphus* as well as in *Uria* and an unusually flat and broad pelvis in *Brachyramphus*, as may be seen in figure 7. In this fig-



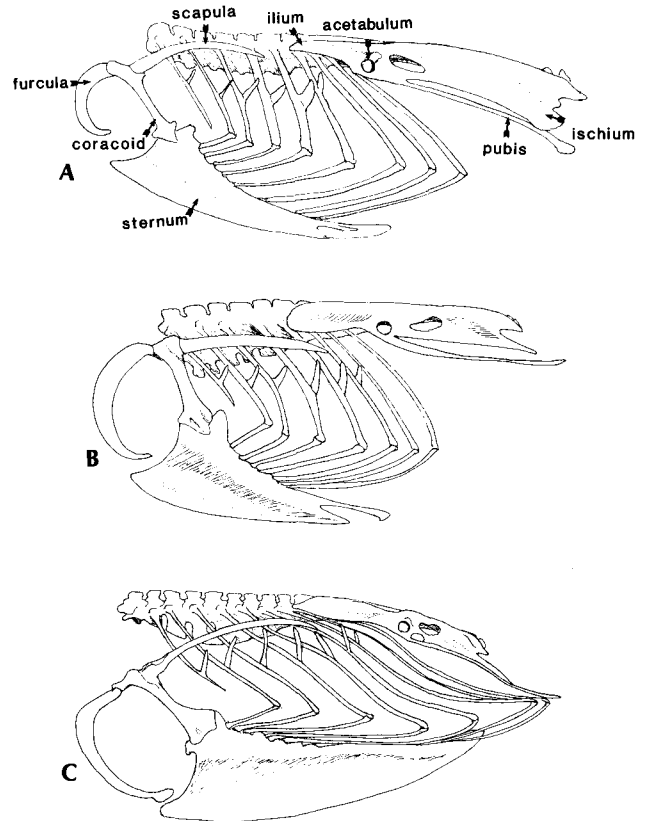
7. Comparison of the synsacrum (dorsal view): A, loons (*Gavia*); B, grebes (*Podilymbus*); C, murrelets (*Brachyramphus*); D, murres (*Uria*). In part after Cracraft 1982.

ure it is apparent that the alcids have appreciably broader pelvises than do either loons or grebes. Thus the ratio of total pelvis length to width at the acetabulum (as shown by the arrows) is 9.6 for the illustrated example of *Gavia immer*, 6.8 for *Podilymbus*, 5.9 for *Uria*, and 3.5 for *Brachyramphus*. By this measure the loon would easily be the most specialized diver and *Brachyramphus* the least.

Some similar relative proportional relationships of the pelvic girdle and leg are shown in figure 8, which utilizes numerical and graphic information presented by Storer (1945) for a representative loon (*G. stellata*) and grebe (*P. grisegena*) and calculated means for eighteen species of Alcidae. Besides having the narrowest relative pelvis, the loon also has a remarkably short preacetabular component and an extremely long postacetabular length for all three of the pelvic bone components. In *Podiceps* the postacetabular pelvic component is essentially as long as that of *Gavia*, suggesting a similarly important muscular role for the leg muscles originating on the posterior pelvis, while the preacetabular pelvic



8. Comparison of pelvis and pelvic appendage ratios in loons (*Gavia stellata*), grebes (*Podiceps grisegena*), and auks (mean of eighteen spp.), based on data provided by Storer 1945.



9. Comparison of trunk and sternal characteristics: A, loons (*Gavia*); B, grebes (*Podiceps*); C, auks (*Cepphus*). In part after Kartashev 1960.

length is substantially longer than in loons and approximately the same as that of the mean alcid length. Finally, in the alcids, the postacetabular ilium and ischium are both extremely short compared with those of the foot-propelled divers. The width of the pelvis at the acetabulum is also the greatest in the Alcidae, as indicated earlier.

Similar data summarized by Storer can be used to show the proportional relationships of the leg, foot, and toe bones (fig. 8). In this diagrammatic representation the extremely long legs and feet of loons and grebes as compared with the average alcid condition become evident. It may also be seen that in grebes the proportional lengths are greater throughout than in loons, and this is especially evident in the elongation of the tibiotarsus. Combined with the large surface area of the foot of a grebe relative to body weight, the very long feet are extremely effective propulsive mechanisms.

The relative roles of the muscles associated with the pelvic girdle as compared with those of the sternum in foot-propelled and wing-propelled divers becomes quite clear when the body skeletons of these groups are exam-

ined (fig. 9). Thus in alcids the sternum is extremely large, in association with the important wing muscles used for flight and diving, whereas in grebes and loons it is as small as or smaller than the pelvic girdle. In all three groups a substantial amount of "streamlining" is evident in the torso, the ribs are to varying degrees expanded, the coracoid is rigidly fused to the sternum, the furcula is enlarged and U-shaped, and the scapula is highly developed. In alcids the pectoralis major muscle is highly developed and constitutes 7–9 percent of the total body weight, whereas in the great crested grebe, for example, it makes up only 4 percent of the weight (Kartashev 1960). On the other hand, in grebes the muscles of the lower extremities may compose about 15–19 percent of the weight (Hartman 1961). Similarly, in the alcids the supracoracoideus muscle is unusually well developed, in conjunction with its role in underwater propulsion. Thus in alcids the weight ratio of the pectoralis major muscle to the supracoracoideus ranges from 3.04:1 to 3.65:1, while in the arctic loon it is 14.96:1 and in the eared grebe it is 7.48:1 (Kozlova 1961).