April 1987

Diving Birds of North America: 4 Comparative Diets and Foraging Ecologies

Paul A. Johnsgard
University of Nebraska-Lincoln, pajohnsgard@gmail.com

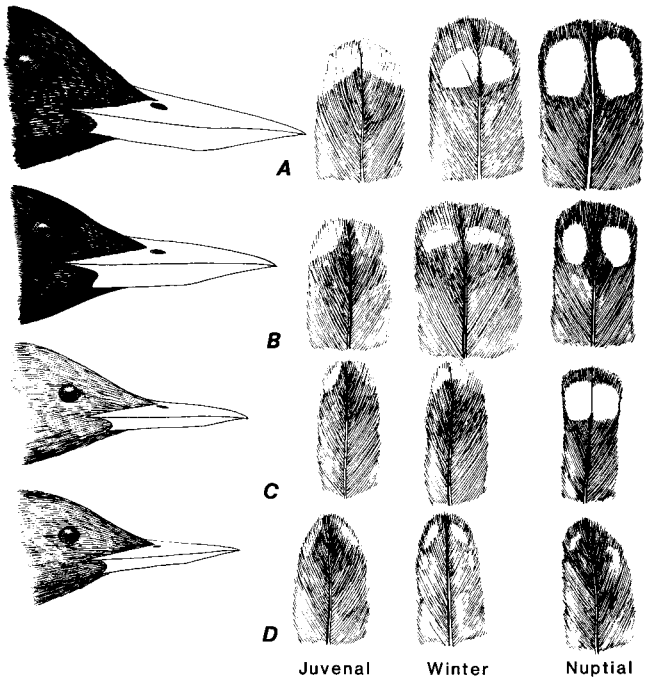
4. Comparative Diets and Foraging Ecologies

Diets

Auks, loons, and grebes are birds whose anatomies and behaviors have been sharply influenced by their foraging niche adaptations. In each species these have evolved through natural selection over extended periods of geologic time as a reflection of available food resources, the presence of competing species, and the limitations on innate variations in anatomy, physiology, and behavior imposed by available genetic mutations and recombinations. To a very considerable degree the auks, loons, and grebes seem to have adjusted to the effects of interspecific competition by evolving differences in bill shape and body size that sometimes open specific new foraging niche opportunities to them and thus reduce direct competition with other species of their group. In the loons, for example, all four species of which overlap rather extensively in at least their wintering and sometimes also their breeding distributions, there is a rather marked stepwise gradation of body size and bill length but no major changes in basic bill shape throughout the series (fig. 18). Within each species, males tend to be slightly larger than females, and there is some evidence that, at least in the common loon, males tend to take more large prey than do females (Barr 1973).

All four species of loons are evidently almost exclusively piscivorous in both breeding and wintering areas. However, so far no studies have directly addressed possible interspecific differences in the diets of loons. A tabular summary (table 13) of prey reported from the digestive tracts of the four loon species suggests that certain families of fish (clupeids, salmonids, gadids, gasterosteids, cottids, ammodytids, and gobiids) are probably important prey items for most if not all species. Data for the common loon suggest that freshwater fish of such families as the sucker and catfish groups may be more important in this species than in the other more generally arctic-nesting forms. So far too few specimens of the yellow-billed loon have been examined to make any firm statements about its preferred diet, but it seems reasonably clear that the red-throated and arctic loons are very similar to one another in their general dietary intakes.

Other than fish, the diets of loons include varying amounts of crustaceans, mollusks, aquatic insects, and



18. Comparative bill shapes and plumage traits in loons: A, yellow-billed; B, common; C, arctic; D, red-throated. Adapted from Bauer and Glutz 1966.

Table 13: Reported Prey of the North American Loons

Food Type	Red-throated	Arctic	Common	Yellow-billed
Fish				
Clupeidae (herrings)				
Brevoortia (menhaden)	—	—	X	—
Clupea (herring)	XX	XX	X	—
Dorosoma (gizzard shad)	—	—	X	—
Sardinops (sardine)	—	—	X	—
Sprattus (sprat)	XX	XX	X	—
Anguillidae (eels)				
Anguilla (eel)	—	—	X	—
Esocidae (pikes)				
Esox (pike)	—	—	X	—
Salmonidae (salmonids)				
Coregonus (whitefish)	XX	—	—	—
Leucichthyes (cisco)	—	—	X	—
Salmo (trout)	X	X	—	—
Salvelinus (char)	X	X	—	—
Thymallus (grayling)	X	X		
Osmeridae (smelts)				
Mallotus (capelin)	X	—	X	—
Osmerus (smelt)	—	—	X	—
Cyprinidae (cyprinids)				
Alburnoides (bleak)	X	—	—	—
Alburnus (bleak)	X	X	—	—
Cyprinus (carp)	—	X	—	—
Leuciscus (dace)	X	X	X	—
Phoxinus (minnow)				
Catostomidae (suckers)	—	—	XX	—
Ictaluridae (catfish)	—	—	XX	—
Gadidae (cods)				
Boreogadus (polar cod)	X	—	—	—
Gadus (cod)	XX	XX	—	X
Melanogrammus (haddock)	—	X	X	—
Merlangus (whiting)	—	X	X	—
Microgadus (tomcod)	X	—	—	X
Zoarcidae (eelpouts)	X	X	X	—
Cyprinodontidae (toothcarps)				
Fundulus (killifish)	X	X	X	—

Table 13: (*Continued*)

Food Type	Red-throated	Arctic	Common	Yellow-billed
Fish (*continued*)				
Atherinidae (silversides)				
Atherina (sand smelt)	—	XX	—	—
Syngamidae (pipefish)	—	—	X	—
Gasterosteidae (sticklebacks)	XX	XX	X	—
Cottidae (sculpins)	XX	X	X	XX
Percichthyidae (temperate bass)				
Morone (bass)	—	—	X	—
Centrarchidae (sunfish)				
Lepomis (sunfish)	—	—	X	—
Micropterus (black bass)	—	—	X	—
Poxomis (crappie)	—	—	X	—
Percidae (perches)				
Perca (perch)	X	X	XX	—
Stizostedion (pike perch)	—	—	X	—
Embiotocidae (surfperches)				
Cymatogaster (shiner perch)	XX	X	X	—
Stichaeidae (pricklebacks)				
Lumpenis (eelblenny)	X	—	—	—
Pholididae (gunnels)				
Pholis (butterfish)	X	—	—	—
Ammodytidae (sand eels)				
Ammodytes (launce)	XX	XX	X	—
Gobiidae (gobies)	XX	X	X	—
Pleuronectidae (righteye flounders)				
Amphibians (newts and frogs)	X	X	X	—
Cephalopod mollusks (squid)	X	XX	—	—
Other mollusks	X	X	X	X
Insecta	X	X	X	—
Crustacea	X	X	X	X
Annelida (polychaetes, leeches)	—	X	X	X

SOURCE: Summarized from available literature, especially Ainley and Sanger 1979.

NOTE: Prey that have been reported as regular or frequent components are shown as XX; other positive records are shown as X.

other prey, especially during the breeding season. Frogs, leeches, polychaetes, and other items have also been reported, although in some cases these trace items might simply reflect food materials in the stomachs of prey species. In general, plant materials are rarely eaten, but there have been a few cases of apparent consumption of mosses (Hypnaceae) and seaweeds in considerable quantities. Seeds and fibers of some freshwater plants such as pondweeds and bulrushes have also been reported at times.

Among the grebes, there are also substantial differences in body size, ranging from species such as the western grebe, which approximates the weight of the smallest loon, to the least grebe, which approaches the size of the smallest alcids (table 14). Within this size gradient the grebes exhibit a good deal more variation in bill shape than the loons, with the larger fish-eating grebes having rather loonlike bills and the smallest grebes having bill shapes not very different from those of murrelets, for example. Among the North American

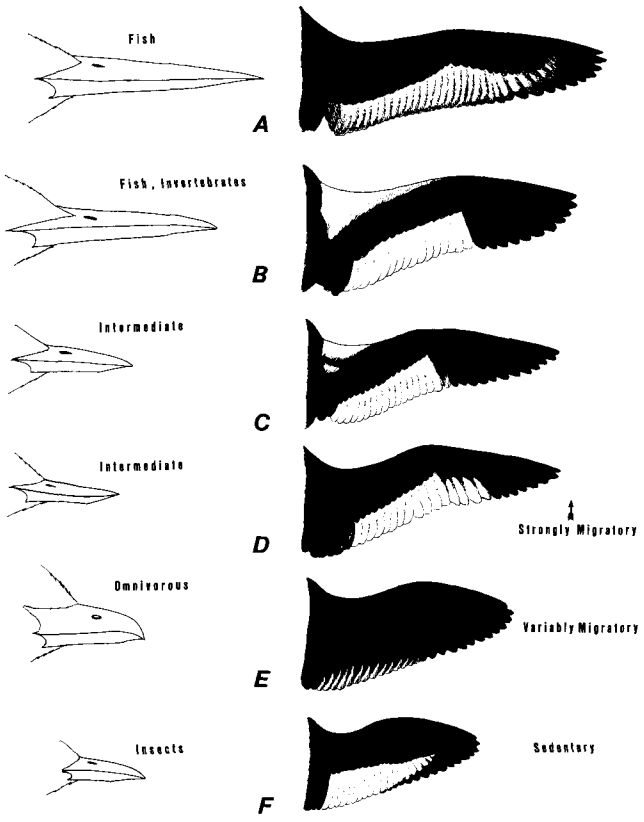
Table 14: Size Categories and Usual Diets of North American Loons, Grebes, and Auks

		Representative Species		
Weight Category	Typical Diet	Loons	Grebes	Auks
Very large (over 2,000 g)	Fish (to ca. 30 cm)	Yellow-billed Common Arctic	—	Great auk
Large (1,200–2,000 g)	Fish (to ca. 25 cm)	Red-throated	Western	—
Medium large (500–1,200 g)	Fish (to ca. 17 cm), invertebrates	—	Red-necked	Common murre Thick-billed murre Tufted puffin Razorbill Rhinoceros auklet
Medium small (250–500 g)	Fish (to ca. 15 cm), invertebrates	—	Pied-billed Horned Eared	Horned puffin Atlantic puffin Pigeon guillemot Black guillemot Crested auklet Parakeet auklet
Small (100–250 g)	Invertebrates, Fish (to ca. 10 cm)	—	Least	Marbled murrelet Kittlitz murrelet Ancient murrelet Cassin auklet Dovekie Craveri murrelet Xantus murrelet Whiskered auklet
Very small (under 100 g)	Planktonic invertebrates (to ca. 1.5 cm)	—	—	Least auklet

NOTE: Organized by descending average weights within each size category.

grebes the most divergent of all bill shapes is to be found in the pied-billed grebe, which eats a widely diversified diet, including a considerable amount of crustaceans, for the capture and crushing of which its heavy and compressed bill seems to be admirably adapted (fig. 19).

A summary of prey types reported for the North American species of grebes (table 15) indicates considerable overlap among the larger species of grebes (red-necked and western) and loons in terms of fish families utilized, specifically the clupeids, gasterosteids, and cottids among marine forms and the centrarchids and percids among the freshwater families. Certain fish families, such as the anguillids, gasterosteids, and cottids, appear to be of rather general significance to several species of grebes, and amphibians appear to be of greater importance to grebes than to loons. Among the noninsect invertebrates, amphipod and decapod crustaceans, polychaete worms, and various mollusks (mainly bivalve and univalve types) seemingly are of general food value. However, it is the insects that clearly are of special significance to grebe species other than the two largest and fish-adapted forms, with aquatic beetles, true bugs, and dragonflies being of particular importance.



19. Comparative bill shapes and wing traits in grebes: A, western; B, red-necked; C, horned; D, eared; E, pied-billed; F, least. Adapted in part from Bauer and Glutz 1966.

Beyond these food types, grebes also have the unusual behavior trait of swallowing varying amounts of feathers. The function of such activity is still unproved, but it has generally been believed that feather swallowing may be related to fish consumption, and that feathers may enmesh swallowed fish bones that might be a potential danger to the bird. Feathers not only are swallowed by the older birds, mainly during self-preening, but they are often also fed to the young, sometimes within a day of hatching. These feathers soon decompose into a feltlike, amorphous mass, often forming a ball. Apparently all grebes except the two species of *Poliocephalus* swallow feathers, and in general the species of grebes that have diets rich in fish are more prone to feather eating. However, the two species of *Poliocephalus* are known to eat fish under some conditions, and so the apparent absence of feather eating in these forms is difficult to explain (Fjeldså 1983a).

The diets of the alcids are much more diverse than those of the loons and grebes, partly reflecting the considerably greater number of species involved, which exhibit a size range from larger than the largest loon to smaller than the smallest grebe (table 14). Throughout this range the larger species (guillemots and larger) eat mostly fish, while the smaller auklets and murrelets eat varying quantities of invertebrates, including those of planktonic size.

The diets of the North American alcids have not been well documented in some cases, especially those of several murrelets, but tables 16 and 17 give summaries of fifteen of the twenty-one North American species. It is clear from this summary that murres and puffins overlap with loons and the larger grebes in at least some aspects of their diets, showing an apparent dependence on such fish as clupeids, osmerids, gadids, scorpaenids, cottids, and ammodytids. The pigeon guillemot seems to have a considerably more diverse diet than these other fish eaters, and it specializes on bottom-dwelling fish that are associated with the intertidal and inshore coastal zones.

The bill shape, upper palate, and tongue characteristics of the alcids provide excellent clues to their diets (fig. 20), as has been amply demonstrated by Bedard (1969d). Bedard classified the alcids into plankton feeders (*Aethia, Alle,* and *Ptycoramphus*), fish feeders (*Uria, Alca,* and *Cepphus*), fish and plankton feeders (*Fratercula* and Cerorhinca), and a remaining group of little-studied and unclassified types (*Synthliboramphus* and *Brachyramphus*) that apparently feed on a diverse array of small fish and marine invertebrates. He

Table 15: Reported Prey of the North American Grebes

Food Type	Least	Pied-billed	Horned	Red-necked	Eared	Western
Fish						
Clupeidae (herrings)	—	—	X	XX	—	XX
Anguillidae (eels)	—	X	X	X	X	X
Engraulidae (anchovies)	—	—	X	—	—	—
Osmeridae (smelts)	—	—	—	—	—	X
Cyprinidae (cyprinids)	—	XX	X	—	—	—
Catostomidae (suckers)	—	X	—	—	—	—
Ictaluridae (catfish)	—	X	—	—	—	—
Atherinidae (silversides)	—	—	—	—	—	X
Gadidae (cods)	—	—	—	—	—	X
Cyprinodontidae (toothcarps)	—	X	—	X	—	—
Poeciliidae (live-bearers)	X	X	—	—	—	—
Gasterosteidae (sticklebacks)	—	X	XX	XX	—	—
Scorpaenidae (rockfish)	—	—	X	—	—	—
Cottidae (sculpins)	—	XX	X	XX	X	XX
Percidae (perches)	—	X	—	—	—	XX
Embiotocidae (surfperch)	—	—	X	—	—	XX
Stichaeidae (pricklebacks)	—	—	—	—	—	X
Gobiidae (gobies)	—	—	—	—	X	—
Amphibians	X	X	—	X	X	X
Crustaceans						
Euphausiacea	—	—	X	—	—	—
Mysidae	—	—	X	—	XX	—
Amphipoda	—	X	XX	X	XX	—
Decapoda	X	XX	X	X	—	X
Annelida						
Polychaeta	—	—	X	X	X	X
Hirudinea	—	XX	—	—	—	—
Mollusca	—	X	X	X	X	X
Insecta						
Coleoptera	XX	XX	XX	X	XX	X
Hemiptera	XX	XX	XX	X	X	X
Odonata	XX	X	X	X	XX	X
Other orders	X	X	X	X	X	X

NOTE: Symbols as in table 13.

Table 16: Reported Prey of Primarily Fish-Eating Species of North American Alcids

Food Type	Murres		Pigeon Guillemot	Rhinoceros Auklet	Puffins		
	Common	Thick-billed			Tufted	Horned	Atlantic
Fish							
Petromyzontidae (lampreys)	—	—	X	X	—	—	—
Chimaeridae (chimaeras)	—	—	X	—	X	—	—
Clupeidae (herrings)							
Clupea (herring)	XX	—	—	XX	XX	—	XX
Sardinops (sardine)	—	—	—	—	—	—	XX
Sprattus (sprat)	—	—	—	—	—	—	XX
Engraulidae (anchovies)	XX	—	—	XX	—	—	—
Salmonidae (salmonids)							
Salmo (trout)	X	—	—	—	—	—	—
Onchorhynchus (salmon)	—	—	—	X	—	—	—
Osmeridae (smelts)							
Allosmerus (smelt)	—	—	—	X	—	—	—
Hypomesus (smelt)	XX	—	X	XX	XX	—	—
Mallotus (capelin)	XX	X	—	XX	XX	X	X
Spirinchus (smelt)	—	—	—	XX	—	—	—
Thaleichthya (eulachon)	X	—	—	—	—	—	—
Bathylagidae (deep-sea smelt)							
Nansenia (argentines)	—	—	—	XX	—	—	—
Myctophidae (lanternfish)	X	X	—	X	—	—	—
Paralepididae (barracudinas)	—	—	—	X	—	—	—
Gadidae (cods)							
Boreogadus (polar cod)	XX	XX	X	—	XX	XX	—
Ciliata (rockling)	—	—	—	—	—	—	X
Eleginus (saffron cod)	—	—	—	—	XX	—	—
Gadus (cod)	—	—	—	—	—	—	XX
Gaidropsarus (rockling)	—	—	—	—	—	—	X
Melanogrammus (haddock)	X	X	—	—	—	—	—
Merlangus (whiting)	—	—	—	—	—	—	X
Microgadus (tomcod)	X	—	—	—	XX	—	—
Pollachius (pollack)	X	—	—	—	—	—	X
Theragra (walleye pollack)	XX	XX	—	X	XX	XX	—
Ophidae (cusk eels)	—	—	—	X	—	—	—
Zoarchidae (eelpouts)							
Gymnelis (ocean pout)	—	X	—	—	—	—	—
Lycodes (eelpout)	—	X	—	—	—	—	—
Scomberesocidae (sauries)							
Cololabris (saury)	—	—	—	XX	—	—	—

(continued)

Table 16: (*Continued*)

Food Type	Murres		Pigeon Guillemot	Rhinoceros Auklet	Puffins		
	Common	Thick-billed			Tufted	Horned	Atlantic
Fish (*continued*)							
Gasterosteidae (sticklebacks)	—	—	X	X	—	—	—
Scorpaenidae (rockfish)	XX	X	XX	XX	XX	—	—
Anoplopomatidae (sablefish)	—	—	—	XX	—	—	—
Hexagrammidae (greenlings)							
Hexagrammas (greenling)	—	—	—	XX	—	—	—
Pleurogrammus (Atka mackerel)	—	—	—	X	XX	XX	—
Cottidae (sculpins)							
Gymnocanthus (sculpin)	—	X	—	—	—	—	—
Hemilepidotus (lordfish)	—	—	XX	—	X	—	—
Icelus (sculpin)	—	X	X	—	—	—	—
Myoxocephalus (sculpin)	X	X	XX	—	—	—	—
Triglops (sculpin)	X	XX	XX	—	—	X	—
Seven additional genera	—	—	X	X	—	—	—
Agonidae (poachers)	—	—	X	—	X	—	—
Liparidae (snailfish)	—	X	X	—	—	—	—
Embiotocidae (surfperch)							
Cymatogaster (shiner perch)	X	—	X	—	—	—	—
Kyphosidae (sea chubs)	—	—	—	X	—	—	—
Trichodontidae (sandfish)	—	—	—	—	—	X	—
Bathymasteridae (ronquils)	—	—	X	—	—	—	—
Clinidae (clinids)	—	—	X	—	—	—	—
Stichaeidae (pricklebacks)							
Cebidichthys (monkeyface eel)	—	—	X	—	—	—	—
Chirolophus (blenny)	X	X	—	—	—	—	—
Lumpenus (blenny)	—	XX	XX	—	—	—	—
Xiphister (blenny)	—	—	X	—	—	—	—
Pholidae (gunnels)	X	—	X	—	—	—	—
Cryptacanthodidae (wrymouths)	—	—	X	—	—	—	—
Zaproridae (prowfish)	—	—	—	—	X	—	—
Ammodytidae (sand eels)	XX	XX	XX	XX	X	XX	XX
Centrolophidae (medusafish)	—	—	—	X	—	—	—
Stromateidae (butterfish)	—	—	—	X	—	—	—
Bothidae (lefteye flounders)	—	—	X	X	—	—	—
Pleuronectidae (righteye flounders)							
Hoppoglossoides (sole)	—	—	—	X	—	—	—
Lipidosetta (sole)	—	—	X	—	—	—	—
Reinhartius (halibut)	—	X	—	—	—	—	—

(*continued*)

Table 16: (*Continued*)

Food Type	Murres		Pigeon Guillemot	Rhinoceros Auklet	Puffins		
	Common	Thick-billed			Tufted	Horned	Atlantic
Crustaceans							
Copepods	—	X	—	—	—	—	—
Euphausiacea	XX	XX	—	X	X	—	—
Amphipods	X	XX	X	—	X	XX	—
Isopods	X	—	X	—	—	—	—
Decapods	X	X	X	—	—	—	—
Polychaete annelids	X	XX	—	—	XX	X	XX
Cephalopod mollusks	X	XX	X	XX	XX	X	X

NOTE: Symbols as in table 13.

observed that the ratio of bill width to gape length provides a useful index to the species' diet, with plankton feeders having ratios of 0.3 or more, fish feeders ratios of less than 0.2, and intermediate types ratios of between 0.2 and 0.3. He also observed that the species that eat considerable amounts of plankton have a large number of cornaceous papillae (denticles) in the anterior palate region, while in fish feeders the number of denticles is greatly reduced and the individual papillae are more sharply pointed. The tongues of such fish eaters as murres are long and slender, with a rigid horny shield at the tip, apparently adapted to "locking" prey against the palatal denticles. In the plankton eaters the tongue is much less cornified and tends to be short and wide. In the puffins the tongue is of an intermediate type, with a cornified tip but a generally fleshy upper surface. This adaptation may help in holding several prey items simultaneously and also may be related to an increased proportion of invertebrates in the diet.

Bedard made the important point that in the alcids the bill not only serves as a food-getting device but also is important as a visual releaser in social interactions, which probably also influences the degree of interspecific variability in bill shape and appearance. He also stated that the fish-feeding alcids have evolved toward an optimum size that appears to approach the upper threshold of body weight compatible with both aerial and underwater flight. The smallest of the fish feeders, the murrelets, are so small that it is doubtful they rely entirely on fish, and it also is questionable whether they can effectively carry fish back to their nestlings. The plankton feeders of about the same general size have evolved gular pouches for carrying food back to their young, but the murrelets seem to have dealt with this problem by reducing the nestling period. Thus in the marbled and Kittlitz murrelets the nestling period is probably less than a month, while in the genus *Synthliboramphus* the nestling period has been reduced to only a few days, during which the young are apparently not fed. These two murrelets have seemingly modified this important aspect of their reproductive biology as a result of dietary considerations.

Similarly, the plankton feeders have evolved body sizes that presumably cannot exceed the upper limits that are probably set by their prey size, while lower size limits are presumably set by physiological factors such as surface/volume ratios, in Bedard's view. Although Storer (1945) considered the *"Endomychura"* (marbled and Kittlitz) murrelets relatively primitive, Bedard concluded that they are actually specialists, particularly insofar as their modified nesting biology is concerned.

Foraging Ecologies

The ecological aspects of foraging similarities and differences in the loons, grebes, and alcids are of great interest and have only recently begun to receive the attention of ornithologists. There are as yet no good studies on the comparative foraging ecologies of the rather widely sympatric red-throated and arctic loons, though some fairly extensive samples of winter foods of these two species are now available from Danish waters (table 17). Thus Madsen (1957) found that cod (*Gadus morhua*) made up over 50 percent of the total volume of foods found in 173 samples of red-throated loons and also composed about a third of the diet of arctic loons, based on an analysis of 123 samples. Cod remains were found in 71 percent of the red-throated loon samples

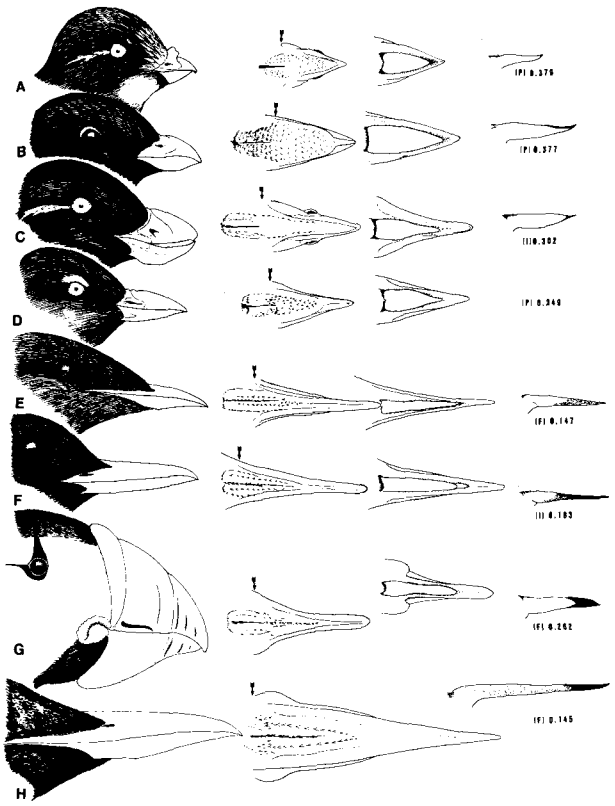
Table 17: Reported Prey of Primarily Plankton-Eating Species of North American Alcids

		Murrelets		Auklets				
Food Types	Dovekie	Ancient	Marbled	Cassin	Parakeet	Least	Whiskered	Crested
Copepoda								
Calanoidea	XX	—	—	—	XX	XX	—	XX
Malacostraca								
Euphausiacea	XX	XX	XX	XX	XX	X	—	XX
Mysidacea	XX	XX	XX	—	—	X	—	XX
Amphipoda	XX	X	—	XX	XX	XX	XX	XX
Gammaridea								
Gammaridae	—	XX	—	—	—	—	XX	—
Hyperiidae	XX	—	—	—	—	—	—	—
Decapoda								
Caridea	—	—	X	—	X	XX	X	X
Decapod larvae	X	X	—	—	—	—	—	—
Polychaetes	X	—	—	—	X	—	—	—
Cephalopod larvae	X	—	X	X	X	—	—	X
Fish								
Engraulidae (anchovies)	—	—	XX	—	—	—	—	—
Osmeridae (smelts)	—	—	X	—	—	—	—	—
Gadidae (cods)	—	—	—	—	XX	X	—	X
Scorpaenidae (rockfish)	—	X	X	—	—	—	—	—
Cottidae (sculpins)	—	—	—	—	X	—	—	—
Stichaeidae (pricklebacks)	—	—	XX	—	—	—	—	—
Ammodytidae (sand eels)	—	XX	XX	—	—	—	—	—

NOTE: Symbols as in table 13.

and were the only food present in 38 percent, while in the arctic loon a combination of cod, gobies (mainly *Pomatoschistus* and *Chaparrudo*), and sticklebacks (*Gasterosteus*) made up 90 percent of the total food and were the only fish present in 80 percent of the total sample. Gobies and sticklebacks were also frequently found in the samples from red-throated loons but collectively made up only about 25 percent of the total sample. It thus seems that, at least during winter, there are rather marked similarities in the diets of arctic and red-throated loons in Danish waters. Along the Pacific coast of North America arctic and red-throated loons have broadly overlapping winter distributions, although the red-throated loon tends to winter much more along the Atlantic coast than does the arctic loon, which may help to reduce foraging competition during that time of year.

McIntyre (1975) studied the winter feeding behavior of common and red-throated loons along the coast of Virginia and noted that typically the red-throated loons foraged in small groups in areas where the tidal currents were swift but only occasionally were seen in bays and coves. However, common loons were regularly found feeding singly in the quiet waters of bays and coves, suggesting that these two species might utilize quite different foraging strategies. She estimated that each common loon used an average of 10 to 20 acres for its foraging area, which she believed to represent typical

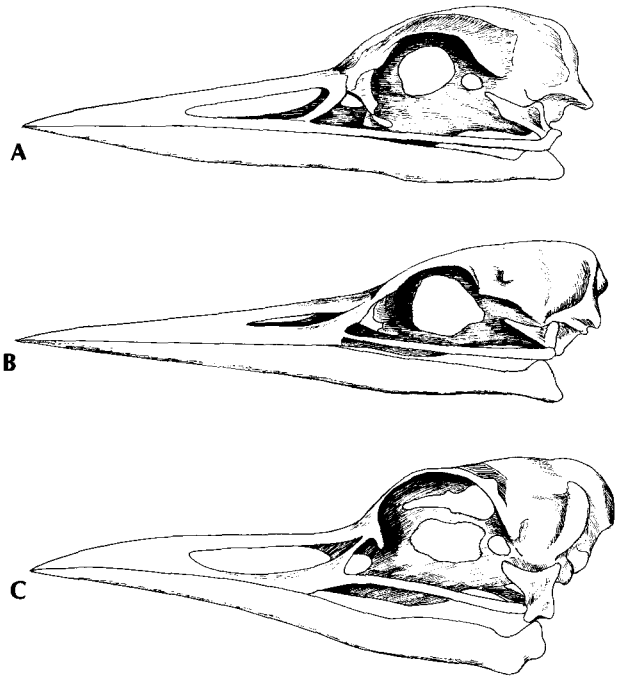


20. Comparative bill shapes and tongue traits in auks: A, least auklet; B, dovekie; C, parakeet auklet; D, Cassin auklet; E, marbled murrelet; F, pigeon guillemot; G, horned puffin; H, common murre. The palate surface, lower mandible and tongue, and tongue profile are shown, with shading of the tongue indicating relative cornification. The arrows indicate the commisural point, the numbers indicate the ratio of bill width to length, and the letters indicate primary foods (P = plankton, I = intermediate, F = fish). Adapted from Bedard 1969a.

wintering loon density in optimum habitat. The apparently greater sociability of red-throated loons in winter compared with common loons should be investigated in terms of the possible role of social rather than individual foraging tactics. Although detailed information is lacking, the arctic loon also appears to be less social in winter than the red-throated loon. The yellow-billed loon also reportedly migrates and winters singly or in small parties that may be family groupings.

The foraging ecologies of the grebes have received substantially more attention than those of loons and offer several points of interest. The skull and bill anatomy of such fish-catching grebes as the great crested grebe is remarkably streamlined and highly adapted as a fish-getting device (fig. 21) and shows certain convergent similarities to the skulls of loons and fish-catching alcids. Of the North American grebes, only the western (including *clarkii*) appears to be almost exclusively a fish eater (table 18), but the red-necked grebe probably takes most of its foods from this type of resource, at least in the case of the North American race.

In other parts of the world, as in North America, most of the grebe species appear to have foraging ecologies that are predominantly dependent upon aquatic invertebrates (table 19), with the smallest species largely or exclusively insect eaters, and only the largest species that have bill lengths of more than 30 millimeters being essentially fish dependent. North America, South America, and Eurasia each support two fish-dependent species. South America supports an additional seven species of grebes, and North America and Eurasia have four and three more respectively, making South America the most grebe-rich area in the world. There is a rather striking similarity between the grebe fauna of North and South America, in that beyond the commonly occurring least and eared grebes (the South American population of eared grebes is considered by some to be a distinct species), the remaining four species of North American grebes have close replacement counterparts in South America, at least in terms of their



21. Comparative skull shapes in fish-eating loons, grebes, and auks: common loon (*top*); western grebe, female (*middle*); common murre (*bottom*). After museum specimens.

Table 18: Reported Percentages of Various Components in the Diets of North American Loons, Grebes, and Selected Alcids

Species	Sample Size	Fish	Crustaceans	Insects	Polychaetes	Mollusks	References
Loons							
Red-throated	173	100.0	—	—	—	—	Madsen 1957
Arctic	123	100.0	tr[a]	—	—	tr	Madsen 1957
Common	27	100.0	tr	tr	—	tr	Olson and Marshall 1952
Yellow-billed	4	100.0	tr	—	—	tr	Cottam and Knappen 1939
Grebes							
Least	6	—	—	100	—	—	Cottam and Knappen 1939
Pied-billed	174	24.2	31.1	46.3	—	tr	Wetmore 1924
Horned	122	34.6	17.9	46.0	—	tr	Wetmore 1924
Red-necked	46	55.5	20.0	21.5	—	tr	Wetmore 1924
Eared	27	9.8	tr	84.2	—	—	Wetmore 1924
Western	19	100.0	—	—	—	—	Wetmore 1924
Alcids							
Razorbill	71	90.0	10.0	—	tr	tr	Madsen 1957
Common murre	117	95.2	3.6	—	—	1.2	Hunt, Burgeson, and Sanger 1981
Thick-billed murre	233	76.0	17.1	—	0.1	5.3	Hunt, Burgeson, and Sanger 1981
Black guillemot	26	67.0	33.0	—	tr	—	Madsen 1957
Least auklet	258	0.7	92.7	—	—	—	Hunt, Burgeson, and Sanger 1981
Crested auklet	107	tr	100.0	—	—	—	Bedard 1969a
Parakeet auklet	55	26.6	48.5	—	23.5	0.4	Hunt, Burgeson, and Sanger 1981
Tufted puffin	23	79.7	3.4	—	11.9	1.7	Hunt, Burgeson, and Sanger 1981
Horned puffin	39	81.4	11.1	—	3.9	0.7	Hunt, Burgeson, and Sanger 1981
Atlantic puffin	117	83.1	11.8	—	11.8	—	Wehle 1980

NOTE: Calculated from volumetric percentages except for Atlantic puffin, which is based on frequency-of-occurrence data. For unknown reasons, data of Hunt et al. 1981 do not approach 100 percent in some cases.

[a]tr = trace.

bill shape and general head plumage characteristics (fig. 22).

By far the best discussion of the foraging ecologies of grebes is the review by Fjeldså (1983a), based on studies of nearly three thousand museum specimens and extensive fieldwork in Europe, South America, and Australia. He has noted that in all the observed cases where two closely related species overlap locally, either one or both of these species exhibit indications of divergent bill morphology, or "character displacement." In at least three of these cases there was evidence that these morphological changes were associated with dietary differences that reduced the degree of interspecific food overlap. He suggested that such ecological foraging displacement is most likely to occur in stable environments utilized by species showing K-strategy reproductive characteristics (deferred reproductive maturity, longer reproductive lives, extended parental care, etc.). In isolated areas supporting only a single species of grebe there is a tendency for that species to evolve an "all purpose" bill that permits opportunistic fish catching without loss of the ability to forage efficiently on small aquatic arthropods. Furthermore, grebes that live under relatively poor foraging conditions tend to exploit

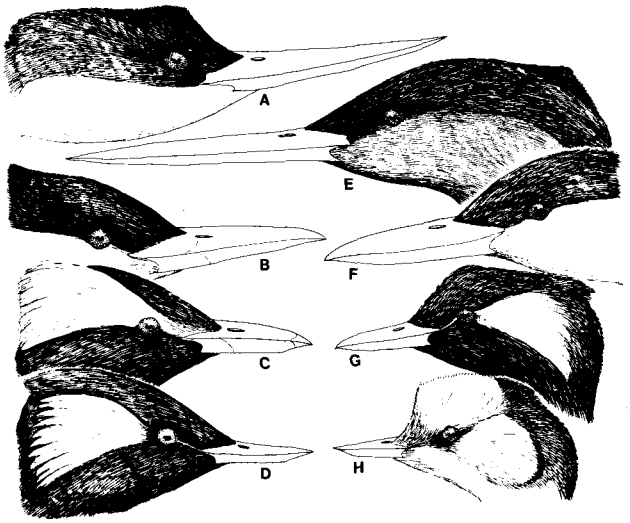
Table 19: Distribution of Grebe Species by Diet and Bill-Length Categories

Usual Foods	Average Bill Length	Central and/or South America	North America	Eurasia	Africa	New Zealand	Australia
Fish and invertebrates	Over 30 mm	Great grebe Titicaca grebe	Western grebe Red-necked grebe	Crested grebe			
		Puna grebe[a]				New Zealand dabchick	Hoary-headed grebe Australian dabchick
Primarily invertebrates	20–30 mm	Hooded grebe	Horned grebe			*Madagascar* Aloatra grebe Madagascan dabchick	
		Eared grebe					
		White-tufted grebe Giant pied-billed[a]		Little grebe			
		Pied-billed grebe					
Insect eaters	Under 20 mm	Silvery grebe Least grebe					

[a]May be primarily fish eating.

all the available potential foods, whereas specialization on optimal foods tends to occur when foods are easy to find.

Part of Fjeldså's evidence for character displacement came from his study of the red-necked grebe, which has a relatively broad geographic distribution in Eurasia and North America. In Europe the species forages largely on arthropods, with fishes eaten only locally or temporarily. In this way it apparently attains an efficient ecological isolation from the fish-adapted great crested grebe of Eurasia. However, in eastern Siberia and North America the red-necked grebe is represented by a large and long-billed race that in some respects matches that of the great crested grebe, and fish eating appears to be a general characteristic of red-necked grebes in North America. Similarly, in northern Norway and Iceland, where the horned grebe does not encounter competition from several other grebe species (as is true farther south in Europe), the birds have larger and deeper bills and are



22. Convergent evolution in North and South American grebes: A, western; B, red-necked; C, horned; D, eared; E, great; F, Titicaca; G, white-tufted; H, silvery.

more opportunistic foragers, using a wider array of habitats and eating a more flexible diet. Fjeldså now considers this a probable case of character release in the nonsympatric populations rather than of character displacement, which was his earlier view.

The alcids offer an even greater number of closely related and sympatric species to investigate for foraging niche differences, and many such studies have been carried out over the years. Thus Hunt, Burgeson, and Sanger (1981) investigated the feeding ecologies of common and thick-billed murres, three species of auklets, and two species of puffins that breed in the eastern Bering Sea. Bedard (1969a) also compared three auklet species in the vicinity of Saint Lawrence Island. Pearson (1968) investigated the comparative foraging ecologies of nine species of seabirds of the Farne Islands, including the Atlantic puffin and the black guillemot, and Cody (1973) attempted to analyze the ecological isolating mechanisms of six alcid species found along the Pacific coast of Washington.

With regard to the comparative ecologies of the common and thick-billed murres, it is now evident from a variety of studies that these two outwardly similar species have some marked morphological differences associated with locomotion (Spring 1971). They also show marked dietary differences, with the thick-billed murre exhibiting a considerably greater reliance on invertebrate foods (Schwartz 1966; Hunt, Burgeson, and Sanger 1981).

Studies of the three widely sympatric auklets (least,

Table 20: Reported Prey Differences in Some Syntopic Alcid Species

Wild-Caught Prey (length)	Least Auklet		Crested Auklet		Parakeet Auklet		References
	Crustaceans	Fish	Crustaceans	Fish	Crustaceans	Fish	
to 7.0 mm	3,169 (3.7%)	187 (87.4%)	82 (0.4%)	0 (0%)	7 (0.1%)	0 (0%)	Bedard 1969a[a]
7.1–15.0 mm	81,986 (96.0%)	21 (9.8%)	9,698 (46.5%)	5 (8.3%)	4,566 (60.7%)	35 (15.4%)	Bedard 1969a[a]
over 15.0 mm	257 (0.3%)	6 (2.8%)	11,057 (52.1%)	55 (92.7%)	2,944 (39.2%)	192 (84.6%)	Bedard 1969a[a]

Wild-Caught Prey	Common Murre	Atlantic Puffin	References
Length (mm) of *Ammodytes*			
Length range	50–175	50–100	Pearson 1968
Commonest length	100–125	75–100	Pearson 1968
Weight (g) of all prey			
Range of weights	1–32	0–32	Pearson 1968
Average weight	8	2	Pearson 1968

Captive-Fed Birds	Common Murre	Razorbill	Atlantic Puffin	References
Weight of prey (g) (preferred/maximum)				
Clupea	14/96	4/18	4/18	Swennen and Duiven 1977
Trisopterus	16/62	6/16	6/16	Swennen and Duiven 1977
Height of prey (mm) (preferred/maximum)				
Clupea	23/44	15/26	15/26	Swennen and Duiven 1977
Trisopterus	23/41	15/23	15/23	Swennen and Duiven 1977

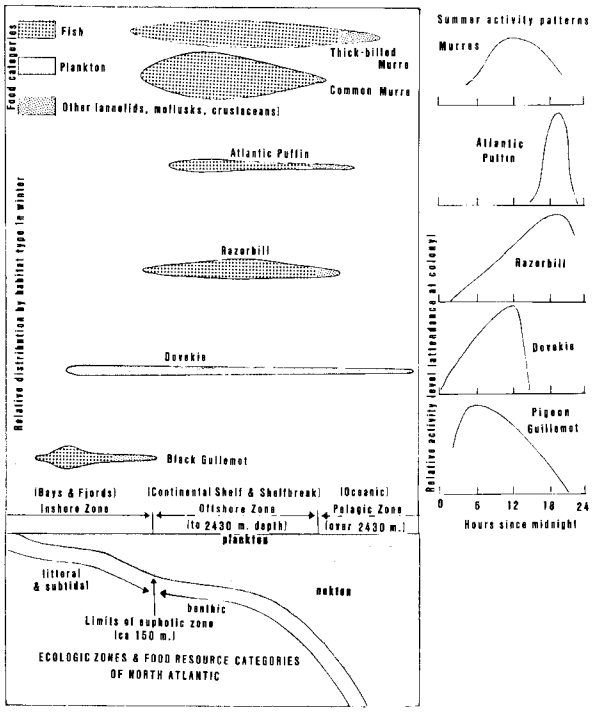
[a]Total quantities present in gullet samples during chick-rearing period as determined from table 1 of Bedard 1969a.

crested, and parakeet) likewise indicate some important foraging niche differences among them. Bedard (1969a) initially reported that the least auklet consumes the smallest prey items, especially small crustaceans, the crested auklet eats prey of intermediate size, again primarily crustaceans, and the parakeet auklet takes the largest prey (table 20). Additionally, the least and crested auklets are essentially zooplankton specialists, foraging in middle and surface depths, while the parakeet auklet takes a much wider variety of invertebrates and fishes, at least some in near-bottom (demersal or epibenthic) zones. Hunt, Burgeson, and Sanger (1981) confirmed these differences and pointed out that these dietary differences may have important implications in determining local distribution patterns, with crested and least auklets largely restricted to islands having large shelf-edge zooplankton populations while the parakeet auklet occurs more widely in coastal waters supporting diverse demersal and epibenthic prey. Further, these food preference patterns appeared to be stable over several years of study, though they varied most obviously in the more generalized parakeet auklet, which is the most opportunistic of the three auklet species.

Studies by Pearson (1968) of seabirds breeding on the Farne Islands indicated a substantial overlap in the size and species of fish taken by each of the nine species of seabirds breeding there, though the birds differed considerably in the average distance flown in search of food and the depth at which food was obtained. Of the two alcid species, common murre and Atlantic puffin, the larger common murre tended to select longer prey fish (*Ammodytes*) and heavier prey than did the Atlantic puffin, though the degree of overlap was substantial. Later studies with captive birds by Swennen and Duiven (1977) have confirmed these differences between the common murre and Atlantic puffin (table 20). The razorbill, also included in this study, took foods of essentially the same weight and height as did the Atlantic puffin. These authors concluded that the maximum size of prey fish in these three species of alcids is determined not by length but rather by diameter, and that the preferred prey size is approximately half of the maximum that the bird can swallow. This prey-size selection is evidently made visually.

In an extensive review of foraging relationships of seventy seabird species breeding in the Bering Sea and northeastern Pacific Ocean, Ainley and Sanger (1979) concluded that fewer than 7 percent feed on a single type of prey, about 60 percent feed on two or three types, and the rest feed on four or more prey types. Where dietary overlap exists, foraging partition is done by different feeding methods, selection of different-sized prey, and zonation of foraging habitats. Some of these interrelationships are evident in figure 23, which attempts to summarize some aspects of prey choice and horizontal foraging zonation tendencies (during winter), based largely on a similar diagram by Tuck (1960) for Newfoundland. Also shown are varied patterns of diurnal activity for these or related species, based on Sealy's (1972) summary, which suggests there may be significant differences in diurnal foraging intensities, at least during the summer breeding period.

Cody (1973) emphasized the possible significance of differential foraging zones in the six species of alcids that he studied off the coast of Washington, suggesting that these six species all have similar diets and breed at the same time of year and that differences in bill shape, foraging depths, and other possible differences are less important than the zonation of foraging areas in reducing interspecific competition. Bedard (1976) has strongly criticized these conclusions and in particular has illustrated how foraging zonation patterns can be locally affected by such factors as coastline and slope configuration, water circulation patterns, and oceanographic conditions. Bedard emphasized that both data from Cody's study and other data from the Atlantic Ocean tend to show considerable overlap in foraging



23. Comparative foraging ecologies of North Atlantic auks. Adapted in part from Tuck 1960.

Table 21: Major Foraging Habitats and Foods of Loons, Grebes, and Fish-Adapted Alcids

Habitats and Prey Types	Loons	Small Grebes	Large Grebes	Razorbill	Murres	Guillemots	Puffins
Saltwater areas							
Surface-dwelling fish	x	—	x	x	—	—	x
Ammodytidae (juveniles)							
Atherinidae							
Blenniidae (juveniles)							
Clupeidae (juveniles)							
Gadidae (juveniles)							
Mid-depth fish	X	x	X	X	X	x	X
Clupeidae							
Engraulidae							
Gadidae (some)							
Osmeridae							
Salmonidae							
Benthic and littoral forms	x	x	x	x	x	X	x
Fish							
Agonidae							
Ammodytidae							
Bathymasteridae							
Blenniidae							
Bothidae							
Clinidae							
Cottidae							
Cryptacanthodidae							
Embiotocidae							
Gadidae (some)							
Hexagrammidae							
Liparidae							
Pholidae							
Pleuronectidae							
Stichaeidae							
Scorpaenidae							
Trichodontidae							
Zoarchidae							
Invertebrates							
Crustaceans	x	X	X	X	X	X	X
Annelids	—	—	x	—	—	—	X
Brackish and fresh waters							
Fish	X	x	X	—	—	—	—
Anguillidae							
Catostomidae							
Centrarchidae							
Cyprinidae							
Cyprinodontidae							
Esocidae							
Gasterosteidae							
Ictaluridae							
Percidae							
Petromyzontidae							
Invertebrates	x	X	x	—	—	—	—

[a]Organized in part after Pearson 1968; X indicates major food sources; x denotes an apparently minor food source from indicated habitats of prey types.

zonation rather than spatial segregation among the species.

By way of summary, table 21 lists major prey types of loons, grebes, and the fish-adapted alcids of North America, organized by habitat and water depth. All three groups of birds tend to forage on mid-depth fishes, with more limited use of surface-dwelling and bottom-inhabiting forms, and all except loons also eat crustaceans to a considerable degree. Freshwater fish are important prey items of loons and the larger grebes, while freshwater invertebrates are major food sources for the smaller grebes. Annelids appear to be of minor importance in all groups except puffins, which sometimes eat polychaetes in substantial numbers.