Foraging strategies and habitat use of sea ducks breeding in northeast Russia

Alexander V. Kondratyev

Institute of Biological Problems of the North, Far Eastern Branch of Russian Academy of Sciences, 685010, Magadan, K. Marx str. 24, Russia

Abstract

Twelve species of sea ducks occur in northeast Asia. This paper examines habitat relationships and foraging strategies used by both diving and sea duck species. Greater Scaup *Aythya marila* are seen in a greater number of habitats than Tufted Ducks *A. fuligula*; however, the foraging strategies and diet of these two diving ducks are similar when they are found in the same habitat. King *Somateria spectabilis* and Spectacled *S. fischeri* eiders share similar diet and habitats; however, King Eiders tend to be more restricted to coastal areas. King and Spectacled eiders and Harlequin Ducks *Histrionicus histrionicus* use more foraging techniques than other sea ducks, to take advantage of food sources in shallow water. White-winged Scoters *Melanitta fusca* tend to have a restricted distribution, whereas Black Scoters *M. nigra* are spread out widely across their range. Both have similar feeding habits, consuming highly concentrated prey items. Oldsquaw *Clangula hyemalis*, Common Goldeneye *Bucephala clangula*, Smew *Mergellus albellus*, and mergansers (Common *Mergus merganser* and Red-breasted *M. serrator*) all capture prey in the water column. Species that are more active hunters (mergansers) spend more time searching for their prey. Overall, the distribution of sea ducks seems to be closely tied to their specific foraging abilities.

Résumé

On compte douze espèces de canards de mer dans le nord-est de l'Asie. Le présent document étudie les relations entre les habitats et les stratégies alimentaires appliquées par les canards plongeurs et les canards de mer. Les Fuligules milouinans (*Aythya marila*) sont observés dans un plus grand nombre d'habitats que les Fuligules morillons (*A. fuligula*); toutefois, les stratégies alimentaires et le régime alimentaire de ces deux canards plongeurs sont semblables quand ils occupent le même habitat. L'Eider à tête grise (*Somateria spectabilis*) et l'Eider à lunettes (*S. fischeri*) partagent un régime alimentaire et des habitats semblables. Toutefois, l'Eider à tête grise a tendance à rester davantage dans les zones côtières. L'Eider à tête grise, l'Eider à lunettes et l'Arlequin plongeur (*Histrionicus histrionicus*) ont recours à plus de techniques d'alimentation que les autres canards de mer afin de profiter des sources d'aliments des eaux peu profondes. Les Macreuses à ailes blanches (*Melanitta fusca*) ont tendance à avoir une répartition limitée, tandis que les Macreuses noires (*M. nigra*) se répartissent largement sur l'étendue de leur territoire. Les deux présentent des habitudes alimentaires semblables, consommant des proies se trouvant réunies dans de grandes concentrations. L'Harelde kakawi (*Clangula hyemalis*), le Garrot à œil d'or (*Bucephala clangula*), le Harle piette (*Mergellus albellus*) et les harles (Grand Harle [*Mergus merganser*] et le Harle huppé [*M. serrator*]) capturent tous leurs proies dans la tranche d'eau. Les espèces qui chassent plus activement (harles) passent davantage de temps à chercher des proies. Dans l'ensemble, la distribution des canards de mer semble plus étroitement liée à leurs habiletés alimentaires spécifiques.

1.0 Introduction

Of the 29 species of Anseriformes breeding north of 60° latitude in northeast Asia, 12 are sea ducks (Dement'ev and Gladkov 1952). Of these 12 species, distributed among eight genera, up to nine can occur in any given local fauna (Kistchinski 1973) (potentially 40–45% of all Anseriformes). This species richness is the highest for sea ducks in the Palearctic, but lower than that for sea ducks in North America (Palmer 1976).

Sea ducks (Mergini) are distributed unevenly in northeast Asia. In eoarctic tundra landscapes (coastal plains), only two species — King Eider *Somateria spectabilis* and Oldsquaw *Clangula hyemalis* — are typical residents. The coastal Common Eider *S. mollissima* and riverine-coastal Spectacled Eider *S. fischeri* are found only along the coast and in estuaries of large rivers. Steller's Eiders *Polysticta stelleri* are also known to breed on large river deltas; otherwise, they are very rare or accidental in other parts of eoarctic tundra landscapes. Hypoarctic landscapes (non-coastal plains) have even less species diversity, sea ducks being represented only by Oldsquaw (hemiarctic species) and Black Scoter *Melanitta nigra americana*. The latter is a typical hypoarctic species in distribution (Kistchinski 1988). The White-winged Scoter *M. fusca* is also hypoarctic in its geographical range (Kistchinski 1988). However, it is distributed in a more complicated way, with no clear connection with low-bush tundra; rather, it is associated with certain types of lakes within this zone (Kistchinski 1980; Krechmar et al. 1991).

The highest species diversity occurs within forested riparian habitats. Common Goldeneye *Bucephala clangula*

and Smew *Mergellus albellus* are associated with boreal lakes, whereas Common Mergansers *Mergus merganser* exploit riverine habitats in the forest zone. All three species are obligate cavity nesters. This distinguishes them from the other riverine specialists, Harlequin Ducks *Histrionicus histrionicus* and Red-breasted Mergansers *Mergus serrator*, which occur mainly in treeless mountain landscapes with turbulent rivers, common along the Bering Sea and Okhotsk Sea coasts. Harlequin Ducks and Red-breasted Mergansers may be considered true riverine species (Kistchinski 1988).

The highest diversity of sea ducks occurs in areas of forested mountain rivers interspersed with coastal maritime tundra and hypoarctic low-bush tundra. This habitat is common along the north coast of the Okhotsk Sea, where nine species of sea ducks occur. The lowest species diversity is in areas of low-arctic tundra, such as northern Kolyma, where Oldsquaw and King, Spectacled, and occasionally Steller's eiders breed (Krechmar et al. 1991). Low diversity is also observed in areas of hypoarctic high-bush tundra and boreal lakes, where only Common Goldeneye, Smew, and Black Scoter breed regularly. These landscapes are present on the vast plains in Middle Kolyma and along the north coast of the Okhotsk Sea (Krechmar et al. 1978). Overall, in terms of generic diversity, on average three and at most seven genera occur together.

Within the sea duck tribe, three genera are represented by more than one species. *Somateria* are generally distributed along arctic coastal habitats, *Melanitta* species are found in hypoarctic areas, and *Mergus* are riverine in their distribution. The range overlap of congeners quite often takes place in areas of low overall species diversity of sea ducks. For example, in areas of sympatry of eiders and mergansers, the overall diversity is rather low (four species). Areas of sympatry between congeneric species include most of their breeding range. Patterns of life history strategies in areas of sympatry may show us the mechanisms that influence the patterns of geographical distribution of species within, and among, genera.

The foraging behaviour of guilds of ducks may be inspected from different perspectives. In contrast to the variable foraging strategies and feeding behaviour of dabbling ducks (Pöysä 1983, 1987; Dubowy 1988; Monda and Ratti 1988), the single main foraging technique of diving ducks is diving. In this paper, I analyze resource distribution and utilization patterns in areas of sympatry between congeneric diving ducks (*Aythya* spp.) to investigate niche overlap (Sugden 1973; Siegfried 1976).

Knowledge of the diet of sea ducks ranges from poor (e.g., Steller's Eider and Black Scoter) to very good (Common Eider and Common Goldeneye) (Eriksson 1978, 1979; Bustnes and Erikstad 1988). The overall picture is not yet known (Eriksson 1976; Pehrsson 1976), and I do not feel that diet can be used effectively to evaluate habitat use overlap.

It is necessary to analyze and compare foraging behaviour more precisely, and the approach presented here is based on the assumption that resource utilization patterns reflect the foraging strategies in some species-specific way. Further, I supplement the data with direct observations of foraging techniques used by the adults and ducklings of a variety of species. Thus, the data collected and described in recent papers (Kondratyev 1989; Kondratyev and Zadorina 1992) have been reexamined with the purpose of selecting specific features of prey abundance and distribution that are important in determining habitat selection of diving and sea ducks.

2.0 Methods

Comparative analyses were undertaken from 1983 to 1995 in different areas of northeast Asia, where sympatric pairs of congeneric species were common enough to ensure adequate sample sizes. Data to analyze the relationship of King and Spectacled eiders were collected at Chaun Bay. The hypoarctic forest-tundra landscape of Middle Anadyr was used to compare Tufted Duck *Aythya fuligula* and Greater Scaup *A. marila* as well as Black and White-winged scoters. Data were collected in many riverine landscapes to compare Red-breasted and Common mergansers, as well as monogeneric Oldsquaw, Harlequin Duck, Common Goldeneye (monogeneric in the Palearctic), and Smew.

I collected data on 1) length of feeding bouts, 2) diving duration, 3) diving intensity, and 4) swimming speed during feeding for a number of species at a variety of sites. Simultaneous diving is a feature that might be considered in an analysis of group foraging, but I have not included it here. To ascertain prey species taken by ducks, I used the analysis of invertebrate fauna in selected habitats and some esophageal contents taken occasionally from ducks in the lakes with known fauna, in addition to what is known from the literature.

3.0 Results

3.1 Description and timing of events in the study area

The foraging habits of all diving duck species in freshwater habitat of tundra and forest-tundra lacustrine landscapes share a number of common features connected with their feeding on invertebrates. The most numerous invertebrates in spring (May–June, i.e., pre-laying to incubation stage) are chironomids and Trichoptera larvae. The former are abundant everywhere, whereas the latter are numerous only in some places. The mass emergence of adult chironomids usually takes place by the end of June. After that, when ducklings hatch and broods appear, crustaceans become more abundant and an important food source for ducks. The most common crustaceans in tundra landscapes are from the following families: Notostraca, Cladocera, Conchostraca, Phyllopoda, Isopoda, and Amphipoda. As a result, these groups are the most common prey types consumed by ducks in July–August. Some of them are more numerous in July and rare in August (fairy shrimps), whereas others (i.e., *Lepidurus*) reach their highest biomass by August or later. Insects and molluscs are not as important in this summer period, with some particular exceptions, such as water boatmen (Corixidae), which are common in riparian habitats by the end of summer, trichopteran larvae and molluscs, which are heavily used by *Aythya* in riparian habitats, and simuliid larvae, which are consumed by Harlequin Ducks in riverine habitats (Bengtson 1972). These prey items have different patterns in distribution between and within the lakes, leading to specific patterns of distribution of sea ducks.

Specific behavioural and morphological adaptations are needed to specialize to these different prey types, so we

may expect that different species of sea ducks select habitats and prey types according to some specific features of their foraging behaviour. In this case, it is not important whether summer or winter feeding conditions had led to the development of their species-specific foraging strategies.

3.2 Comparisons among species

3.2.1 Greater Scaup and Tufted Duck

In the breeding season, these two species forage in freshwater lakes. The Greater Scaup's range extends farther north and east than that of the Tufted Duck; if both are present in an area, scaup are more abundant and are seen in a greater variety of habitats (Fig. 1). The distribution of Tufted Ducks is restricted primarily to lakes of later succession stages in riparian habitats. Foraging techniques and diving parameters are very similar (Table 1), and large differences in diet were not apparent when both species were compared in riparian habitats (Fig. 1).

3.2.2 King and Spectacled eiders

During the pre-nesting period, both species of eiders forage on shallow lakes of coastal marshes and spring-flooded wet moss areas on tundra plains. They occupy similar habitats, have similar feeding methods, and consume similar prey species; however, the distribution of King Eiders in Chaun Bay appeared to be more restricted to the narrow coastal zone (Fig. 2). Feeding methods for eiders and Harlequin Ducks include upending and head-and-neck submerging, common among dabbling ducks; their feeding methods are thus more varied than those of other diving ducks (see also Goudie, this volume). After hatching, both eider species use similar types of habitats, although King Eiders are largely restricted to small thermokarst lakes of early succession stages. Spectacled Eiders use a wider range of habitats, whereas their feeding methods are similar (Table 1). The diet of both species was similar when they used the same habitats, but the total feeding spectrum of Spectacled Eider is wider (Fig. 3), probably because of the greater diversity of selected habitats.

3.2.3 Harlequin Duck

Harlequin Ducks are well adapted to strong turbulent waters of mountain streams and sea surf. They demonstrate a tendency to feed on localized, concentrated patches of food. My fragmented observations during different periods of their life cycle indicated that they prefer dense patches of food in areas of calm water scattered among currents (stream or surf) — similar to eiders, which also prefer benthic patches along the water edge or on shoals.

3.2.4 Black and White-winged scoters

Both species of scoters have been examined in an area of sympatry at Middle Anadyr. High-bush riparian habitats with deep lakes (formed by old river branches segregated and developed by thermokarst) were the only habitats in this area used by the White-winged Scoter. Other habitats used in northeast Asia are deep lakes in mountains and highlands (Kistchinski 1980) and boreal lakes of forest tundra in Yakutia (Krechmar et al. 1978). The scarcity of these habitats results in White-winged Scoters being rare or uncommon in the region. In contrast, Black Scoter is a rather common species everywhere in low-bush and high-bush tundra, both in riparian habitats and on plateaus (Fig. 4). The feeding methods of both species are, nevertheless, very similar (Table 1). The consumption of benthic invertebrates with high available biomass (Brown and Fredrickson 1986), concentrated in dense patches at great depth, demands little searching once the food patch is discovered, but requires long dive times at certain localities. This method is effective only where high concentrations of food are present in certain types of lakes; thus, broods aggregate at such lakes. The diet consists mainly of benthic animals (Fig. 4) and may explain the late breeding of scoters, which seems to be tied to the late appearance of high concentrations of benthic invertebrates (especially *Lepidurus*).

3.2.5 Oldsquaw

Throughout the summer, Oldsquaw use their habitat extensively, constantly moving and intensively diving (Table 1), while foraging on sparsely distributed prey from the water column (Fig. 5). The close ties of Oldsquaw to fairy shrimps (Alison 1976; Pehrsson 1976; Kondratyev 1989) may explain the early breeding of this species.

3.2.6 Common Goldeneye

The foraging strategy of Common Goldeneyes is similar to that of Oldsquaw, but some features, especially searching behaviour, are more similar to those of Smew and mergansers. The searching behaviour of goldeneye ducklings, first shown by Eriksson (1976) as an adaptation for catching the moving insects from the water column, is also exhibited by Smew and merganser ducklings. Common Goldeneyes, as well as Oldsquaw, Smew, and mergansers, may be distinguished from scaup, eiders, scoters, and Harlequin Ducks by their ability to catch prey in the water column. However, the general pattern of habitat use during feeding bouts resembles that of Oldsquaw (Table 1). Diving duration and intensity are similar to those of the Oldsquaw, as is the characteristic of low brood cohesion, as ducklings spread over the entire lake during feeding (Table 1).

3.2.7 Smew and Red-breasted and Common mergansers

The foraging strategy of Smew and mergansers is adapted to active hunting of moving prey in the water column. Their constant rapid movements along the water edge while actively searching for food (Anderson and Michael 1974; Sjöberg 1985, 1988; Wood and Hand 1985a, 1985b) distinguish them from all other species of the tribe (Table 1). Searching behaviour was least extensive in Common Goldeneyes and most extensive in Common Merganser (Table 1, Fig. 6) and was correlated with the increasing average prey size from Common Goldeneyes to mergansers.

4.0 Discussion

Foraging strategies of sea ducks can be mapped onto their phylogenetic tree (Livezey 1986) and may be considered in terms of consecutive steps. Sea duck foraging strategies are oriented to the resources they consume, the simplest pattern being shown by eiders and Harlequin Ducks, which

Figure 1
Diet and habitat use of Greater Scaup and Tufted Duck at Middle Anadyr

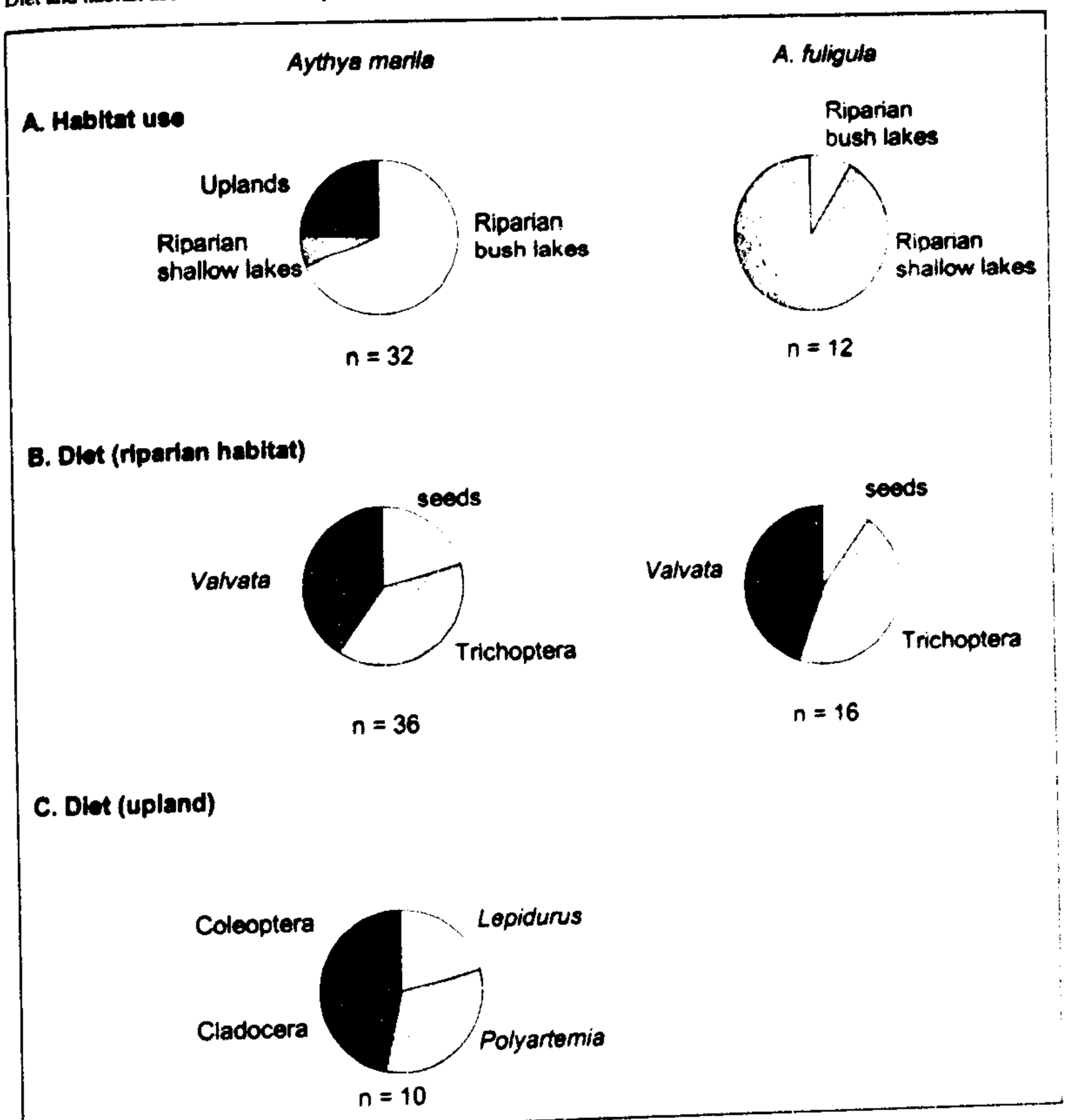
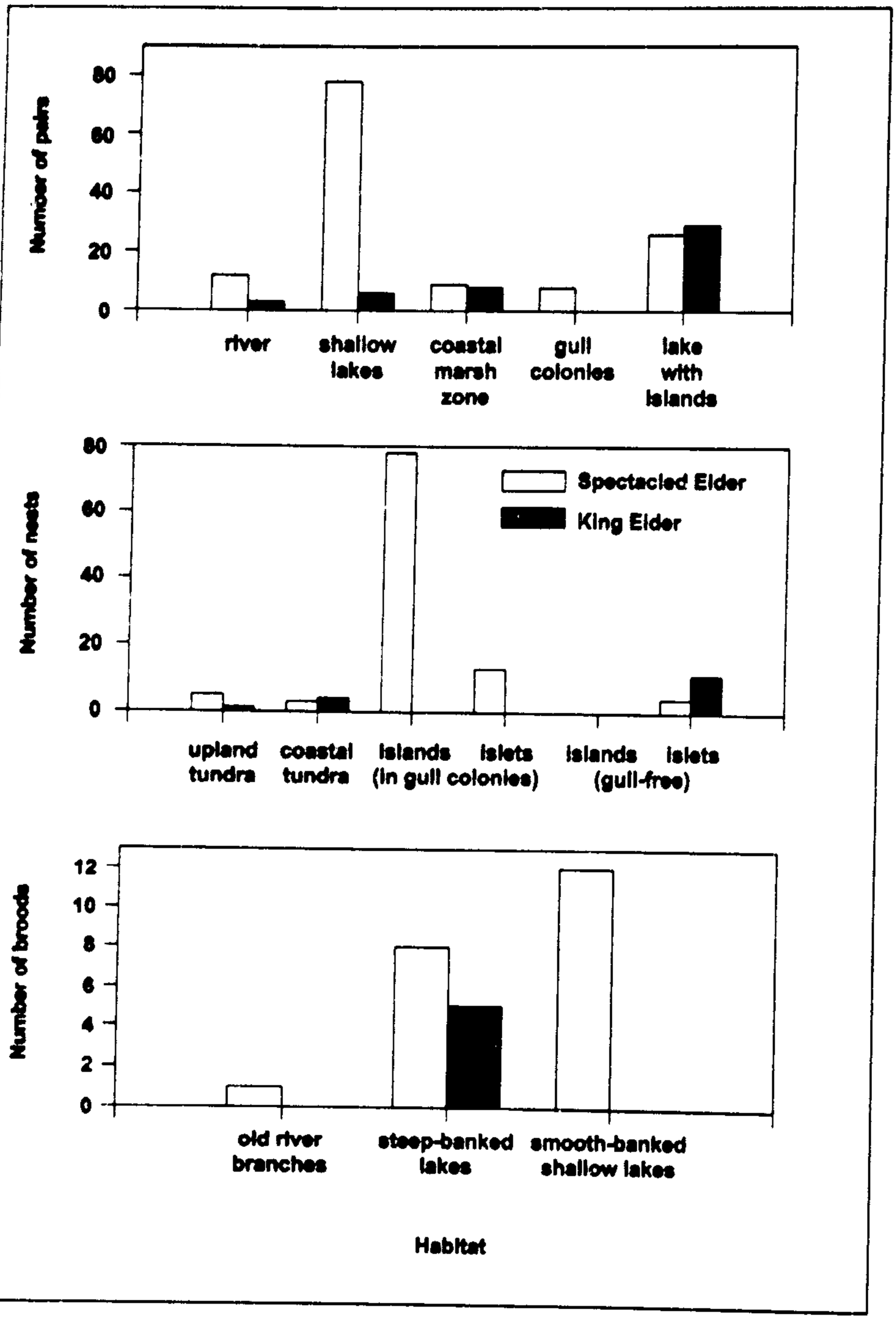


Table 1
Foraging behavio[u]r of selected diving and sea ducks in northeast Russia

	Head/neck submerging[a]	Upending[a]	Diving of ducklings[a]	Diving of adults[a]	Searching (s)	Swimming speed (m min)	Maximu[m] brood diameter (m
Aythya marila	no	no	10	20	no	3.3	
A. fuligul[a]	no	no	7	20	no	3.3	
Somateria fischeri	5.5 (75%)	7.8 (80%)	3	13 (56%)	no	3	
S. spectabilis	5.3 (75%)	rare	no data	13 (60%)	no	3	
Histrionicus histrionicus	3.4 (40%)	rare	no data	17 (56%)	no	1	
Melanitta nigra	no	no	10 (62%)	26 (66%)	no	1.5	
M. fusca	no	no	12.5 (48%)	38 (68%)	no	2.5	
Clangula hyemalis	no	no	5.3 (64%)	28 (82%)	rare	10	
Bucephala clangula	no	no	7.5	25	2.5	3	
Mergellus albellus	no	no	5	18	3.1	12	
Mergus serrator	no	no	7	18 (65%)	3.4	15	
M. merganser	no	no	7	25 (45%)	4.8	15	

[a] Values are time(s) engaged in feeding behaviour (% of time devoted to behaviour in feeding bout).

Figure 2
Habitat use of Spectacled and King eiders at Chaun Bay



consume patchily distributed invertebrates in shallow waters, more typical of dabbling ducks and *Aythya* spp. Showing various adaptations to a range of habitats and conditions, eiders and Harlequin Ducks use upending in shallows where possible, and they usually move slowly within the food patch, diving with moderate efficiency.

Different species of scoters are adapted to different habitats but utilize resources in a similar manner — i.e., consuming concentrations of large benthic invertebrates in very dense patches by long dives, sometimes to considerable depths. Once the food patch is discovered, it is used intensively. Synchronous dives are often observed in foraging groups (Schenkeveld and Ydenberg 1985; Kondratyev 1989). This manner of intensive use of a discovered food patch is also observed in winter during the marine part of their life

Figure 3
Diet of Spectacled and King eiders at Chaun Bay

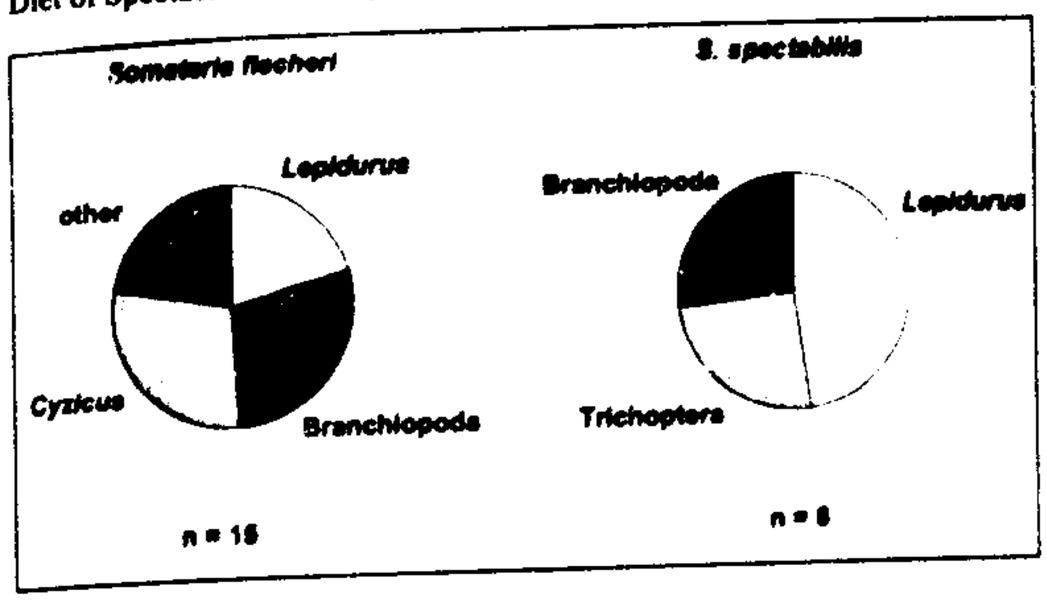
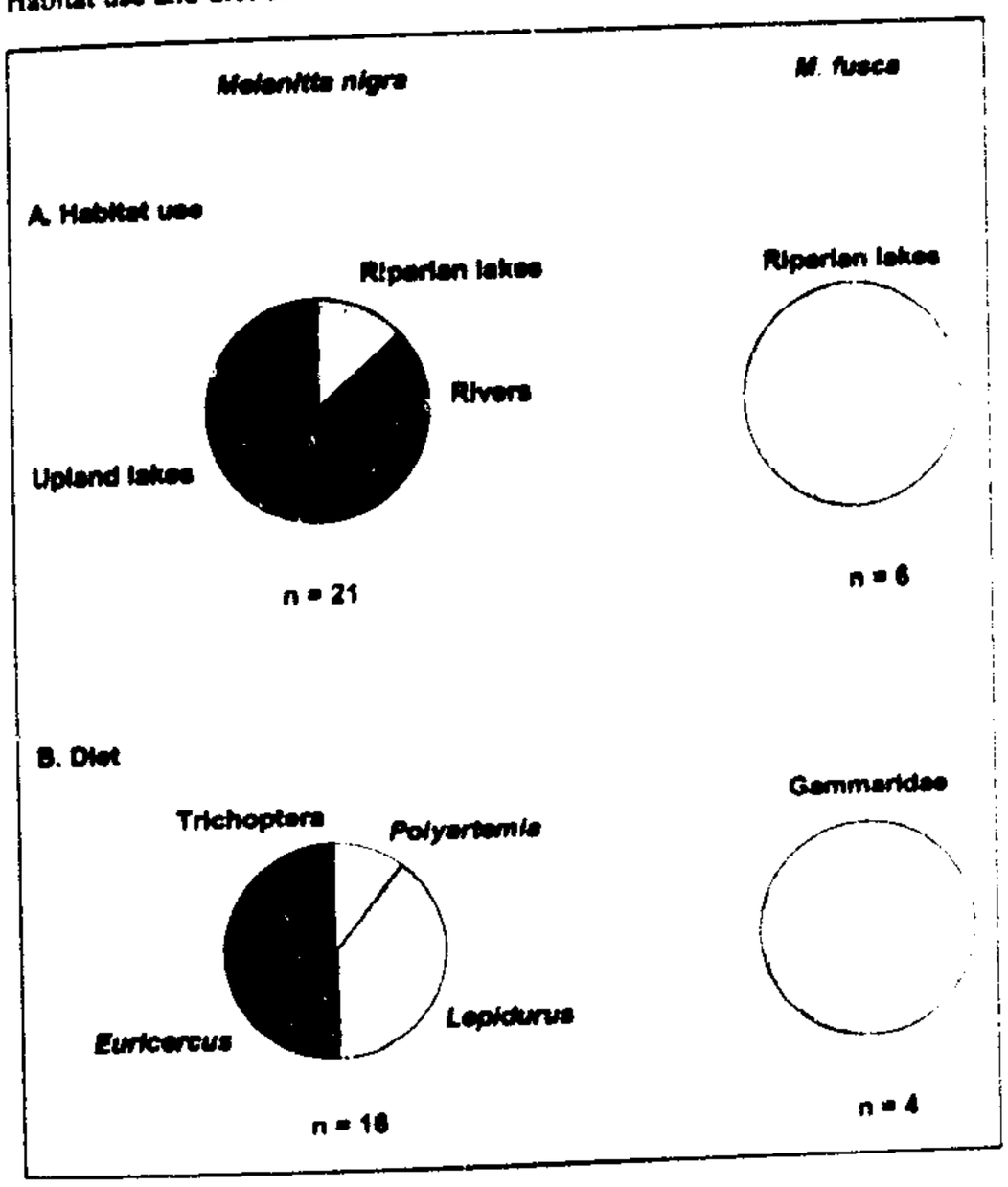


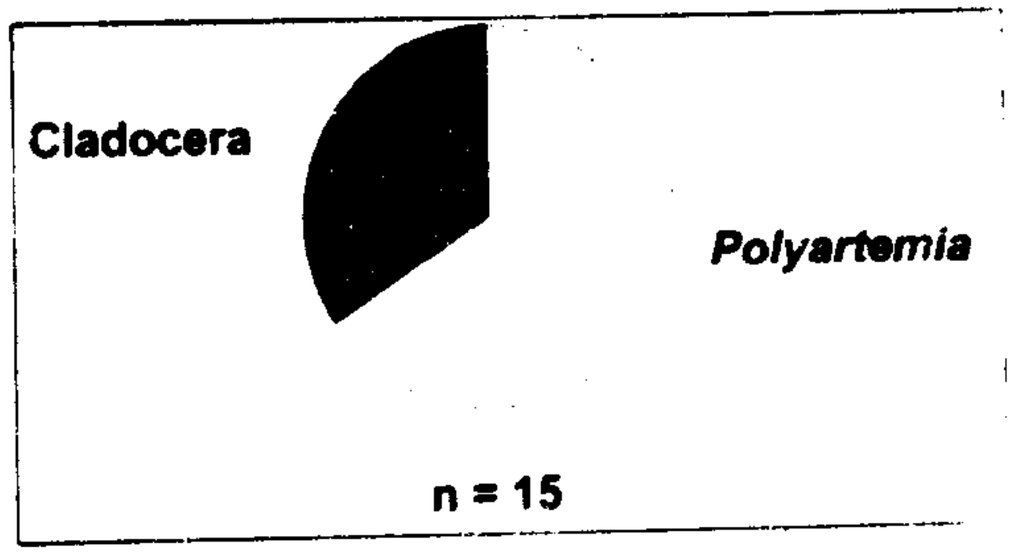
Figure 4
Habitat use and diet of Black and White-winged scoters at Middle Anadyr



cycle (Vermeer 1983; Vermeer and Bourne 1984; Goudie and Ankney 1986).

Another foraging method shown by sea ducks involves a shift from shallows and shoreline (eiders and Harlequin Ducks) and deep-water habitats (scoters) to the use of the water column. Species feeding in the water column include Oldsquaw and Common Goldeneye (Pehrsson 1974; Alison 1976; Snell 1985; Pehrsson and Nyström 1988). They can also feed effectively on benthic invertebrates, notably in winter (see Goudie and Ankney 1986), but the ability to feed on sparsely distributed prey (both on the bottom and in the water column) and to use the water surface area extensively distinguishes them sharply from eiders and scoters. This ability to forage on sparsely distributed prey has also been shown in different areas and during different periods of their life cycle (Suter 1982; Sanger and Jones 1984; Goudie and Ankney 1986). The ability to catch prey in the water column

Figure 5
Diet of Oldsquaw at Middle Anadyr (upland lakes)



is found in all sea duck species, and young eiders and scaup also feed on macroplankton invertebrates, such as *Polyartemia forcipata* and *Cyzicus* spp. The duration of this method of foraging during duckling growth varies from days to weeks. The ability to feed on swimming prey lasts longer in Oldsquaw, goldeneyes, and mergansers during the growing period, and the importance of these kinds of resources in the diet of adults is also higher. Feeding in the water column is connected with changing from "grazing" to "hunting" tactics and, finally, to a specialization to active hunting of big and fast-moving prey in the water column (Smew and mergansers). In this final group, there are specialized behavioural features, such as collective hunting (Anderson and Michael 1974; Rad 1981; Wood and Hand 1985b; Wood 1987a, 1987b).

So, we may speculate that the evolution of the Mergini tribe can be expressed as a continuum from ancestral shallow feeding through deep-water diving to water column foraging and active hunting. The species' habitat use pattern might be explained as a result of selection of the proper microhabitat with certain types of prey distribution, appropriate to the species-specific feeding method.

Literature cited

Alison, R.M. 1976. Oldsquaw brood behavior. Bird Banding 47:210–213.

Anderson, B.W.; Michael, G.T. 1974. Notes on feeding behavior of the Common Merganser *Mergus merganser*. Condor 76:472–476.

Bengtson, S.-A. 1972. Breeding ecology of the Harlequin Duck *Histrionicus histrionicus* (L.) in Iceland. Ornis Scand. 3:1–19.

Brown, P.W.; Fredrickson, L.H. 1986. Food habits of breeding white-winged scoters. Can. J. Zool. 64:1652–1654.

Bustnes, J.O.; Erikstad, K.E. 1988. The diets of sympatric wintering population of Common Eider (*Somateria mollissima*) and King Eider (*S. spectabilis*) in Northern Norway. Ornis Fenn. 65:163–168.

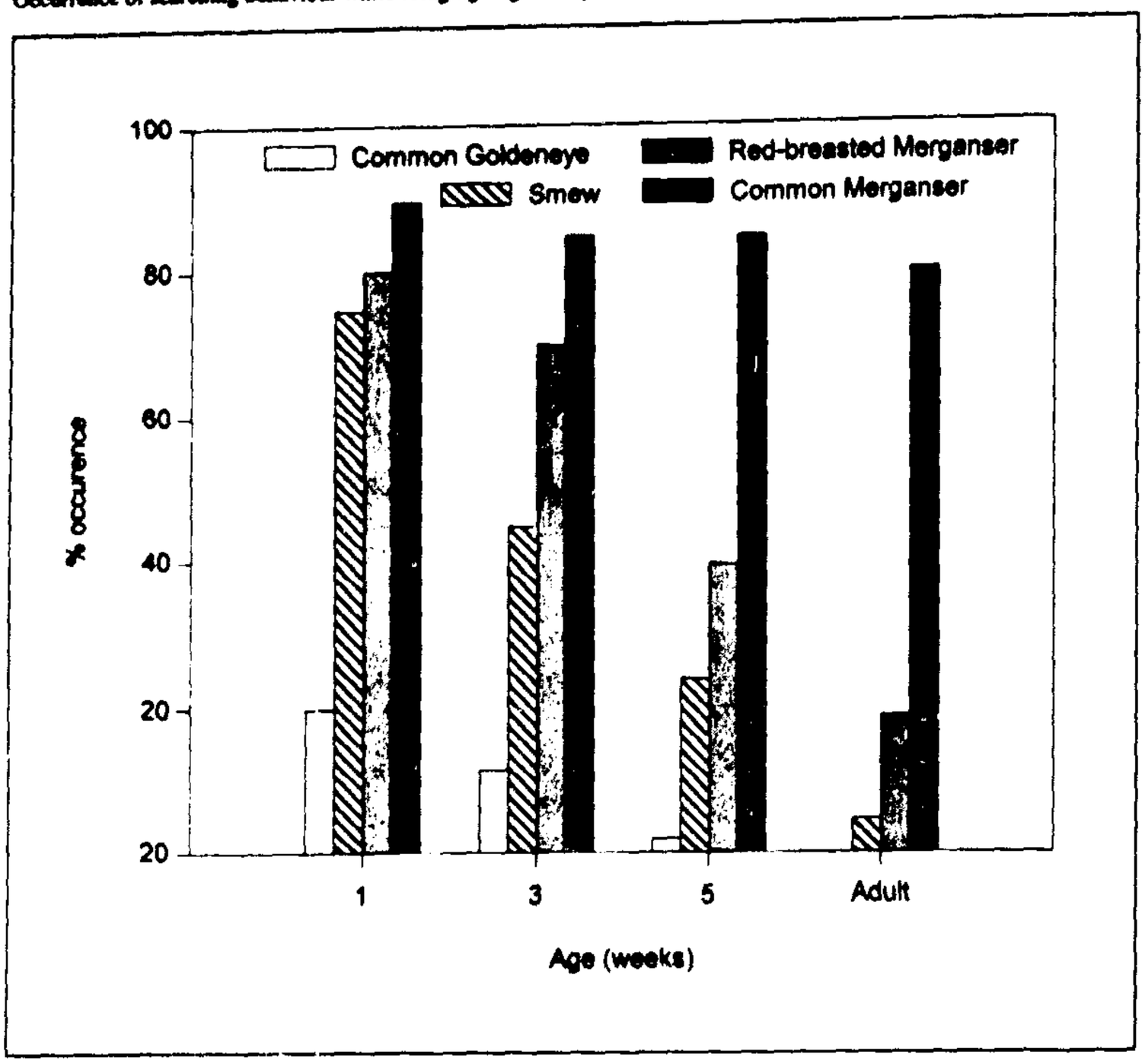
Dement'ev, G.P.; Gladkov, N.A. 1952. Birds of the Soviet Union. Vol. IV. U.S. Department of the Interior and the National Science Foundation, Washington, D.C. 683 pp.

Dubowy, P.J. 1988. Waterfowl community and seasonal environments. Temporal variability in interspecific competition. Ecology 69:1439–1453.

Eriksson, M. 1976. Food and feeding habits of downy goldeneye *Bucephala clangula* (L.) ducklings. Ornis Scand. 7:159–169.

Eriksson, M. 1978. Lake selection by goldeneye ducklings in relation to abundance of food. Wildfowl 29:81–85.

Figure 6
Occurrence of searching behaviour while foraging in goldeneye, Smew, and merganser ducklings in relation to age



Eriksson, M. 1979. Aspects of the breeding biology of the goldeneye *Bucephala clangula*. Holarct. Ecol. 2:186–194.

Goudie, R.I.; Ankney, C.D. 1986. Body size, activity budgets and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

Kistchinski, A.A. 1973. Waterfowl in north-east Asia. Wildfowl 24:88–102.

Kistchinski, A.A. 1980. Birds of the Koryak highland. Nauka, Moscow. 335 pp. (in Russian).

Kistchinski, A.A. 1988. Avifauna of North-East Asia, history and modern state. Nauka, Moscow. 288 pp. (in Russian).

Kondratyev, A.V. 1989. A comparative ecology of *Melanitta nigra*, *M. deglandi*, and *Clangula hyemalis* in the Anadyr River middle stream basin. Zool. Zh. 68:93–103 (in Russian).

Kondratyev, A.V.; Zadorina, L.V. 1992. Comparative ecology of the King Eider (*Somateria spectabilis*) and the Spectacled Eider (*S. fischeri*) on the Chaun tundra. Zool. Zh. 71:99–108 (in Russian).

Krechmar, A.V.; Andreev, A.V.; Kondratyev, A.Y. 1978. Ecology and distribution of birds in the USSR North-East. Nauka, Moscow. 193 pp. (in Russian).

Krechmar, A.V.; Andreev, A.V.; Kondratyev, A.Y. 1991. Birds in the Northern Plains. Nauka, Leningrad. 288 pp.

Livezey, B.C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. Auk 103:737–754.

Monda, M.; Ratti, J. 1988. Niche overlap and habitat use by sympatric duck broods in eastern Washington. J. Wildl. Manage. 52:95–103.

Palmer, R.S. (ed.). 1976. Handbook of North American birds. Vol. 3. Yale University Press, New Haven, Connecticut. 560 pp.

Pehrsson, O. 1974. Nutrition of small ducklings regulating breeding area and reproductive output in the long-tailed duck (*Clangula hyemalis*). Int. Congr. Biol. 11:259–264.

Pehrsson, O. 1976. Food and feeding grounds of the goldeneye (*Bucephala clangula* (L.)) on the Swedish west coast. Ornis Scand. 7:91–112.

Pehrsson, O.; Nyström, K. 1988. Growth and movements of Oldsquaw ducklings in relation to food. J. Wildl. Manage. 52:185–191.

Pöysä, H. 1983. Resource utilization pattern and guild structure in a waterfowl community. Oikos 40:295–307.

Pöysä, H. 1987. Ecology of foraging behavior in dabbling ducks (*Anas* spp.). Univ. Joensuu Publ. Sci. No. 10.

Rød, O. 1981. Breeding distribution and habitat selection of red-breasted merganser in freshwater in western Norway. Wildfowl 31:53–56.

Sanger, G.A.; Jones, R.D. 1984. Winter feeding ecology and trophic relationships of Oldsquaws and White-winged Scoters on Kachemak Bay, Alaska. Pages 20–28 *in* D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Schenkeveld, L.E.; Ydenberg, R.C. 1985. Synchronous diving by Surf Scoter flocks. Can. J. Zool. 63:2516–2519.

Siegfried, W.R. 1976. Segregation of feeding behavior of four diving ducks in southern Manitoba. Can. J. Zool. 54:730–736.

Sjöberg, K. 1985. Foraging activity patterns in the Goosander (*Mergus merganser*) and the Red-breasted Merganser (*M. serrator*) in relation to patterns of activity in their major prey species. Oecologia 67:35–39.

Sjöberg, K. 1988. Food-selection, food-seeking patterns and hunting success of captive Goosanders *Mergus merganser* and Red-breasted Mergansers *M. serrator* in relation to the behavior of prey. Ibis 130:79–93.

Snell, R.R. 1985. Underwater flight of Long-tailed Duck (Oldsquaw) *Clangula hyemalis*. Ibis 127:267.

Sugden, L.G. 1973. Feeding ecology of pintail, gadwall, American wigeon and lesser scaup ducklings in southern Alberta. Can. Wildl. Serv. Rep. Ser. No. 24, Ottawa.

Suter, W. 1982. Feeding ecology of diving ducks (*Bucephala, Aythya*) and Coots (*Fulica atra*) wintering on the upper Rhine near Untasee (Lake of Constance). Ornithol. Beob. 79:225–254.

Vermeer, K. 1983. Diet of Harlequin Duck in the Strait of Georgia, British Columbia. Murrelet 64:54–57.

Vermeer, K.; Bourne, N. 1984. The White-winged Scoter diet in British Columbia waters: resource partitioning with other scoters. Pages 30–38 *in* D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Wood, C.C. 1987a. Predation of juvenile Pacific salmon by Common Mergansers (*Mergus merganser*) on eastern Vancouver Island. I. Predation during the seaward migration. Can. J. Fish Aquat. Sci. 44:941–949.

Wood, C.C. 1987b. Predation of juvenile Pacific salmon by Common Mergansers (*Mergus merganser*) on eastern Vancouver Island. II. Predation on stream-resident juvenile salmon by merganser broods. Can. J. Fish Aquat. Sci. 44:950–959.

Wood, C.C.; Hand, C.M. 1985a. Food-searching behavior of the Common Merganser (*Mergus merganser*) I. Functional responses to prey and predation density. Can. J. Zool. 63: 1260–1270.

Wood, C.C.; Hand, C.M. 1985b. Food-searching behavior of the Common Merganser (*Mergus merganser*) II. Choice of foraging location. Can. J. Zool. 63: 1271–1279.