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Coregonid fishes in Arctic waters

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The Arctic ichthyofauna is represented by 460 fish species (2.0% of the world fauna), of which 123 (26.7%) are true Arctic species. The macrostructure of the Arctic ichthyofauna differs significantly from the observed ratio of taxa in the world fauna, and the core elements are salmoniforms, scorpaeniforms, and perciforms. Characteristic features of the Arctic fish fauna are a small number of monotypic genera, a low proportion of endemic genera and species, as well as polymorphism and euryphagy. Polymorphic species of coregonids are represented by forms that have various feeding regimes and different spawning seasons. Coregonids play a major role in transferring energy through trophic chains. A major constraint on the reproductive strategy of Arctic fishes is the need for suitable larval and juvenile rearing conditions during the short polar summer. Among the coregonids, mature individuals generally do not spawn annually, but as a rule spawn every one to three years.

Introduction

Accurate numbers of species in the Arctic are available for certain well-studied taxa, such as vertebrates (mammals, birds, reptiles, amphibians, fishes and Cyclostomata; Table 1). For the Arctic, Schwarts (1963) recorded 61 terrestrial mammal species. In total, including marine Arctic species, there are about 75 species or 1.7% of the world's mammal fauna. Among these 75 species, true Arctic species constitute only 20 or 26.6% of the Arctic fauna. The birds of the Arctic consist of 240 species (or 2.8% of all bird species), but this number included only 74 true Arctic species or 30.8% of the bird fauna in the Arctic. Reptiles are generally absent from the Arctic, with only a few species extending into the sub-Arctic. Amphibians are also poorly adapted to life in polar environments, but several species are abundant in the forest tundra and the southern tundras. Four frogs (genus *Rana*) and one salamander (genus *Salamandrella*) species are found in the Arctic, or more precisely, in the sub-Arctic fauna (Schwarts & Ishenko 1971).

It is very difficult to give a precise definition of an "Arctic species", because the southern border of the Arctic is very subjective. Areas of the species that are considered to be most characteristic Arctic inhabitants, are situated not only in the Arctic zone, but extend a long way to the south. The ranges of most Arctic species go out of the Polar zone in some region or sector of the Arctic. In fact, the "Arctic species" cannot be recognized solely by distributional area borders, abundance, or ecological particularities.

I have subdivided all of the fish considered in this study into five categories according to their geographical area and propose that the groups I (Arctic) and II (Arcto-Boreal) belong to true "Arctic species":

I Arctic — species that live and spawn almost solely in Arctic waters, i.e. most or all of the distributional area lies in Arctic waters (*Dallia*, *Coregonus autumnalis, C. nasus, S. leucichthys*, etc.). Most of the representatives of the Arctic freshwater faunistic complex recognized by Nikolsky (1980) fall into this category.

II Arcto-Boreal — species that are distributed in Arctic and boreal waters, but with a significant part of the distributional area occurring in Arctic waters (*C. albula, C. artedii, C. tugun, C. nigripinnis, P. coulteri* or *Thymallus acticus* and some representatives of Nikolsky's (1980) pre-mountainous freshwater faunistic complex).

III Boreal — species that live in boreal waters and have only a small part of their distributional area occurring in the Arctic *(Brachymystax lenok* and many representatives of the boreal pre-mountainous freshwater faunistic complex, in addition to *Rutilus rutilus* and other representatives of Nikolsky's (1980) boreal plain freshwater faunistic complex).

IV South-Boreal — species that are spreading into boreal waters, but sometimes the distributional area reaches Arctic waters (*Abramis brama* and other representatives of Nikolsky's (1980) pontic freshwater faunistic complex).

V Rare Visitor — species that live in boreal waters, but sometimes occur in Arctic waters. For example, *Petromyzon marinus* is an anadromous species that lives in waters of southern Europe, but sometimes occurs in Murmansk.

Those categories are similar to the freshwater faunistic complexes of Nikolsky (Nikolsky 1947, 1980, Reshetnikov 1981), but there are fundamental differences. According to Nikolsky all coregonids have an Arctic origin and belong to the Arctic freshwater faunistic complex. The Coregonidae has probably existed from the early Neogene as an independent group with all characteristic attributes and division into three modern genera (Reshetnikov 1980, 1992). The problems of origin, distribution and speciation in this group have been considered in several publications (Reshetnikov 1980, 1981, 1992, 1995, 2001). The present distribution of coregonids is mainly accounted for by the history of the Quaternary period, in particular by the development of drainage networks during the last glacial advance and retreat (10 000 to 25 000 years ago). In this communication, I have subdivided all fishes into five categories according to their modern geographical distribution only.

The Arctic ichthyofauna is of special interest with respect to the whole Arctic biota because fish, together with birds, insects, and spiders, belong to animal groups that are established successfully in high-latitude environments. Nikolsky (1947, 1980) describes coregonids as typical Arctic fish that belong to the Arctic freshwater faunistic complex. The family Coregonidae comprises three genera and 28 species: six species in the genus *Prosopium*; one in *Stenodus*; and 21 species in *Coregonus*. However, of the 28 species, only 16 inhabit Arctic waters. The other 12 species do not reach the Arctic zone (Reshetnikov 2001). This fact leads us to doubt whether coregonids are typical Arctic fish, and we, there-

Table 1. Species richness of the Arctic vertebrate fauna.

Taxonomic group	Total	Arctic species	Arctic species (%)	True Arctic species	
				Number	Percentage of Arctic fauna
Cyclostomata*	100	7	7.0	2	28.6
Pisces*	22500	460	2.0	123	26.7
Amphibia/Reptilia**	11850	7	0.1	0	0
Aves**	8600	240	2.8	74	30.8
Mammalia**	4500	75	1.7	20	26.6
Total	47550	789	1.6	219	27.7

Data sources: *Reshetnikov 2001, ** Chernov 1999.

fore, analysed the Arctic fish fauna to investigate the role of coregonid fishes in the Arctic.

Material and methods

The total species richness of higher taxa (excluding bacteria, viruses and protozoans) in the Arctic fauna is roughly 20 000 species, or no more than 1% of the total number of known animal species (Chernov 1988, 1995, 1999). Two check-lists of the Arctic fish fauna were published and summarized both for marine fishes (Andriashev & Chernova 1994) and freshwater fishes (Chereshnev 1996). However, these authors treat the Arctic waters in a broad sense, and hence both check-lists include many fish that may be considered as "rare visitors" in the Arctic. I summarized recent publications on the distribution of freshwater fish in Europe (Ladiges & Vogt 1979, Pethon 1985, Koli 1990), Russia (Reshetnikov 2002) and North America (McPhail & Lindsey 1970, Lee *et al*. 1980, Scott & Crossman 1973) and prepared a new check-list of Arctic fishes. The subsequent analysis and discussion are based on these many works.

Results

Taxonomic diversity of Arctic fish

The freshwater Arctic ichthyofauna (Cyclostomata and Pisces) is represented by 11 orders, 20 families, 50 genera and 116 species, but there are only 30 "true" Arctic species or 26% of the total. Our data suggest that there are a total of 420–460 species (marine and freshwater) in Arctic waters, which is about 1.8%–2.0% of the world list.

Various authors have enumerated the world fish fauna at 20 000 species to 25 000 species (Nelson 1994, Eschmeyer 1998). However, my research suggests a value of 22 500 fish species in the world. Of these, 460 inhabit Arctic waters (2.0%), but only 123 belong to true Arctic species (26.7% of Arctic fish fauna) (Reshetnikov 2001). Only the Cyclostomata are more abundant in the Arctic (seven species out of 100 in the world), but only two species are true Arctic species (28.6% of the Arctic ichthyofauna; Table 1). Therefore, many groups of vertebrates (excluding the Cyclostomata and Amphibia) that demonstrate the highest potential adaptation to the Arctic environments constitute about 1%–3% of the world fauna of each group. The fishes may be considered as one of the most progressive groups in the Arctic biota.

Taxonomic structure of the Arctic ichthyofauna

All of the Arctic ichthyofauna belong to 31 orders, 102 families, 272 genera and 460 species (Table 2). The order Salmoniformes has the most species richness among Arctic fish. In the world fauna, 63 out of 244 species (25.8%) live in the Arctic, and 45 belong to true Arctic species (36.5% of all true Arctic species). The families in the Salmoniformes (Salmonidae, Coregonidae, Osmeridae, Thymallidae, Dalliidae and Esocidae) are typical of the Arctic fish fauna. The second place belongs to order Scorpaeniformes. If the global number is assumed to be 1064 species, 100 species (9.4%) occur in Arctic waters, and 34 species (27.6%) are true Arctic ones. The scorpaeniforms are more typical of marine Arctic waters. The largest order in the world, Perciformes (6100 species), is represented in Arctic waters by 87 species (1.4%), and consists mainly of boreal and south-boreal species whose distributional areas occasionally reach the Arctic. The true Arctic species only number 24. Of the 460 Arctic species, 318 (or 69.1%) belong to five orders (Salmoniformes, Scorpaeniformes, Perciformes, Gadiformes and Cypriniformes), and 114 (or 91.1%) of the 123 true Arctic species are likewise from these five orders (Table 3).

In total, the number of "true" Arctic fish includes 123 species or 27% of total fish species in the Arctic (460). Terrestrial mammals and birds have similar values (25%–30%). Therefore, it is proposed that the proportion of Arctic species among classes Mammalia, Aves and Osteichthyes is the same (25%–30%). Among freshwater Arctic fishes this value is high (50.8%).

The structure of the freshwater Arctic ichthyofauna is presented in Table 4. The families Coregonidae and Salmonidae are the most sig-

Table 2. Numbers of species in the taxonomic orders of fish in the Arctic. Species category: I = Arctic; II = Arcto-Boreal; III = Boreal; IV = South-Boreal; V = Rare Visitor.

Order	Species category					Arctic species	Percentage of total species worldwide
	I	II	III	IV	V		
Myxiniformes	–	–	–	–	1	1	4
Petromyzontiformes	–	–	–	4	2	6	15
Hexanchiformes	–	–	–	–	1	1	14.3
Lamniformes	–	–	–	2	2	4	25
Carchariniformes	–	–	–	1	2	3	1.4
Squaliformes	–	–	–	2	3	5	6.2
Rajiformes	1	–	–	5	5	11	11.3
Chimaeriformes	–	–	–	1	1	2	5.7
Acipenseriformes	–	–	2	2	1	5	19.2
Osteoglossiformes	–	–	2	–	–	2	1.7
Nothacanthiformes	–	–	–	2	–	2	8
Anguilliformes	–	–	–	2	4	6	1
Saccopharyngiformes	–	–	–	–	1	1	5
Clupeiformes	–	–	–	2	1	3	0.8
Salmoniformes	24	13	8	18	–	63	25.8
Cypriniformes	–	–	2	26	–	28	1.5
Stomiiformes	–	–	–	3	10	13	5.4
Aulopiformes	–	–	–	3	5	8	3.7
Myctophiformes	–	–	–	2	5	7	3
Percopsiformes	–	–	1	–	–	1	7.1
Gadiformes	6	2	1	10	21	40	7.6
Ophidiiformes	–	–	–	1	–	1	0.3
Lophiiformes	–	–	–	3	12	15	4.7
Beloniformes	–	–	–	1	2	3	1.5
Lampriformes	–	–	–	–	3	3	6.6
Beryciformes	–	–	–	1	3	4	2.0
Gasterosteiformes	–	–	2	2	–	4	15.6
Syngnathiformes	–	–	–	2	–	2	0.9
Scorpaeniformes	19	9	6	27	39	100	9.4
Perciformes	19	2	3	40	23	87	1.4
Pleuronectiformes	–	1	–	17	9	27	5.4
Tetraodontiformes	–	–	–	–	1	1	0.3
Total	69	27	27	180	157	460	

Table 3. Composition of the five main taxonomic orders of Arctic fishes.

Order	Arctic species	Percentage of total species worldwide	Percentage in the Arctic fauna	True Arctic species		
				Total	Percentage of total species worldwide	Percentage of true Arctic species
Salmoniformes	63	25.8	13.7	45	18.4	36.5
Scorpaeniformes	100	9.4	21.7	34	3.2	27.6
Perciformes	87	1.4	18.9	24	0.4	19.5
Gadiformes	40	7.6	8.7	9	1.7	7.3
Cypriniformes	28	1.5	6.1	2	0.1	0.2
Five main orders	318		69.1	114		91.1
Other orders	142		30.9	9		8.9
Total	460		100.0	123		100.0

nificant in the Arctic freshwater fish fauna (16 species or 27.1% for each family): the whole order Salmoniformes has 49 species or 42.2% of total Arctic fish (116), from which 39 species belong to true Arctic fish (or 66% from 59 species; Table 4). The remaining significant families in the Arctic freshwater fauna are: Cottidae (9 species and 11.8% of true Arctic fish); Petromyzontidae (6 and 6.8%, accordingly); Dalliidae (4 and 6.8%); Cyprinidae (22 and 3.3%); and Acipenseridae (5 and 3.3%).

The most characteristic feature of the Arctic fish fauna is the relatively low number of true Arctic species. Marine fish have 54 species out of a total of 355 (15.2%), and freshwater fish have 59 species out of 116 (50.8%). On the whole, for Arctic fish this value is only 26.7%. It should be noted that the proportion of true Arctic species is 30% for Aves, 21% for Insecta, 18% for vascular plants, and 6% for mosses and lichens (Chernov 1995, 1999, Chernov & Matveeva 1979). Therefore, fish is one of the most well-represented groups in the Arctic fauna and flora.

Specific features of the Arctic fauna

The low level of endemism of the Arctic fish fauna among families (5%) and genera (2%) is surprising. For example, only one family (Dalliidae) occurs solely in the Arctic. All the other families are distributed not only in the Arctic, but also a long distance from the southern Arctic boundary. In comparison, it should be noted that the Antarctic benthic ichthyofauna (more than 200 species) is richer in endemic families, genera and species than the Arctic benthic fauna (Andriashev 1986). There are many typical Antarctic families (Nototheniidae, Chaenichthyidae, Harpagiferidae, Artedidraconidae and others) and the number of the endemic taxa remains exceptionally high, reaching 88% for species and 76% for genera. Endemic fishes in Lake Baikal are more abundant than in the whole Arctic and consist of two families (Comephoridae and Abyssocottidae), eight genera and 34 species (Reshetnikov 1998, 2002, Reshetnikov *et al*. 1997).

Table 4. Numbers of species in the taxonomic families of freshwater Arctic fishes. Species category: I = Arctic; II = Arcto-Boreal; III = Boreal; IV = South-Boreal; V = Rare Visitor.

Family	Species category					Total species worldwide	Arctic species			
	I	II	III	IV	V		Total		I + II	
							n	%	*n*	%
Petromyzontidae	0	4	1	0	1	34	6	17.6	4	6.8
Acipenseridae	0	2	2	1	0	24	5	20.8	2	3.3
Hiodontidae	0	0	2	0	0	2	2	100.0	0	0
Clupeidae	0	0	0	0	1	230	1	0.4	0	0
Salmonidae	12	4	7	0	0	36	23	63.9	16	27.1
Coregonidae	10	6	0	0	0	28	16	57.1	16	27.1
Thymallidae	0	1	1	0	0	4	2	50.0	1	1.7
Osmeridae	0	2	1	0	0	14	3	21.4	2	3.3
Esocidae	0	0	1	1	0	5	1	20.0	0	0
Dalliidae	4	0	0	3	0	4	4	100.0	4	6.8
Cyprinidae	0	2	14	6	0	1280	22	1.7	2	3.3
Catostomidae	0	1	1	1	0	82	3	3.6	1	1.7
Balitoridae	0	0	0	2	0	25	2	2.0	0	0
Cobitidae	0	0	0	1	0	240	1	0.7	0	0
Percopsidae	0	1	0	0	0	3	1	33.3	1	1.7
Lotidae	1	0	0	0	0	5	1	20.0	1	1.7
Gasterosteidae	0	2	1	0	0	10	3	27.3	2	3.3
Percidae	0	0	7	3	0	160	10	5.6	0	0
Scaenidae	0	0	0	1	0	276	1	0.4	0	0
Cottidae	3	4	2	0	0	300	9	3.0	7	11.8
Total	30	29	40	18	2	2762	116		59	

This phenomenon may be a result of the relatively recent origin of the Arctic ichthyofauna, on the one hand, but might also result from an incomplete process of speciation, especially among coregonids and salmonids. Because the last invasion of coregonids and other fish into the Arctic occurred after the glacial period (about 10 000 years ago), the species structure of Arctic communities may still be in the process of formation.

Coregonid fishes in the Arctic

Among coregonids, 12 species never occur in Arctic waters, and they may be considered as boreal species (*C. alpenae*, *C. chadary*, etc.). Six species are distributed widely in both Arctic and boreal waters (*C. albula*, *C. artedi*, *C. tugun*, etc.) and may be considered as arcto-boreal species. Finally, ten species may be considered as true (typical) Arctic species that live and spawn in the polar zone and most or all of their distributional range is in the Arctic (*C. autumnalis*, *C. nasus*, *S. leucichthys* and others; Table 5). Undoubtedly, the boreal coregonid group is the result of the glacial period when coregonids migrated south during the glaciation into refuges and remained to live in some deep-water and cold lakes.

The decrease in the number of species in Arctic communities is often compensated for by an increase in population density and biomass. Coregonid fish take first place by biomass, appearing as the dominant or superdominant species in many fish communities of the Arctic and the sub-Arctic. Most coregonids are valuable commercial species with a mean annual catch of 42–60 thousand metric tons.

Another interesting phenomenon of the Arctic fish fauna is a diversity of ecological forms. As a compensation for low taxonomic and ecological diversity, an increase in morphological and ecological heterogeneity within species often takes place. Adaptive radiation at the level of species and intraspecific forms is more frequent among coregonids and salmonids. These fishes include polymorphic species with a circumpolar distribution (*C. lavaretus*, *C. autumnalis*, *S. alpinus* and others), and they may be considered as superspecies or species-complexes (McPhail & Lindsey 1970, Nikolsky & Reshtnikov 1970, Reshetnikov 1980, 1986, 1995, Savvaitova 1989). Taxonomic classification becomes highly complicated when intraspecific forms of such a complex species as the European whitefish, *C. lavaretus* (L.), are considered. In comparison, a similar species-complex is recognized among birds and insects (Chernov 1995, 1999). More than 200 intraspecific forms of European whitefish have been formally described in Europe (Reshetnikov 1980, 1995), and at present some of them considered as independent species (Kottelat 1997).

Table 5. Occurrence of Coregonid fishes (*Coregonus*, *Prosopium* and *Stenodus*) in Arctic waters.

True Arctic species	
1. *C. autumnalis* (Pallas, 1776)	6. *C. nasus* (Pallas, 1776)
2. *C. clupeaformis* (Mitchill, 1818)	7. *C. peled* (Gmelin, 1789)
3. *C. lavaretus* (Linnaeus, 1758)	8. *C. sardinella* Val., 1848
4. *C. laurettae* Bean, 1882	9. *P. cylindraceum* (Pal., 1784)
5. *C. muksun* (Pallas, 1814)	10. *S. leucichthys* (Güld., 1772)
Arcto-boreal species	
1. *C. albula* (Linnaeus, 1758)	4. *C. tugun* (Pallas, 1814)
2. *C. artedi* Lesueur, 1818	5. *C. zenithicus* (Jor. & Ever., 1909)
3. *C. nigripinnis* (Gill, 1872)	6. *P. coulteri* (Eig. & Eig., 1892)
Species not living in Arctic waters	
1. *C. alpenae* (Koelz, 1924)	7. *C. reighardi* (Koelz, 1924)
2. *C. chadary* Dybowski, 1862	8. *C. ussuriensis* Berg, 1906
3. *C. canadensis* Scott, 1967	9. *P. abyssicola* (Snyder, 1919)
4. *C. hoyi* (Gill, 1872)	10. *P. gemmiferum* (Snyder, 1919)
5. *C. johannae* (Wagner, 1910)	11. *P. spilonotus* (Snyder, 1919)
6. *C. kiyi* (Koelz, 1921)	12. *P. williamsoni* (Girard, 1856)

Among closely related forms of *C. lavaretus* and *C. clupeaformis*, sympatric populations are frequently encountered that differ in the number of gill rakers, range of diet, and mode of life. Some sympatric populations occur in large lakes: Lake Imandra has five forms, lake Inari has five, Lake Ladoga has seven, and Lake Onega has nine forms (Reshetnikov 1992, 1994, 1995). The broad whitefish (*C. nasus*) has two forms in the lower Mackenzie River (Tallman *et al*. 2002).

It is known that stability and complexity of ecosystems depend on the number of species composing the community and on the complexity of functional associations. Polymorphism and euryphagy are the most typical features of Arctic fishes, especially coregonids and salmonids. The complexity of Arctic ecosystems is based on the diversity of intraspecific fish forms that are the energetic equivalent of separate species. I consider the great variability of coregonids and salmonids a consequence of their evolution in northern ecosystems along the path of increasing internal association and stability (Reshetnikov 1963, 1979, 1980, 1994, 2001).

Northern water bodies are relatively low in biomass and variable in food supply, therefore euryphagy may be considered as adaptive reaction to the Arctic environments. There are few species with a narrow food specialization among coregonids, as well as among all freshwater Arctic fishes. All freshwater Arctic fish may be divided into groups based on their feeding preferences (Table 6). Among coregonids, no species feed on detritus, phytoplankton or aquatic vegetation. Zooplankton feeders include European vendace (*C. albula*) and some species of American ciscoes. Broad whitefish (*C. nasus*), *C. clupeaformis* and many species of the genus *Prosopium* feed mainly on benthos. Peled (*C. peled*), *C. sardinella, C. zenithicus* and *C. tugun* feed on both benthos and zooplankton. The European whitefish (*C. lavaretus*), *C. muksun, C. laurettae,* C. *autumnalis* are typical euryphages. The inconnu (*S. leucichthys*), *C. autumnalis* (to some extent), and large-sized forms of *C. albula* from lakes Ladoga and Onega (*ripus* and *kiletz*, respectively) are carnivorous.

If sympatric populations are encountered in a species complex (for example, *C. lavaretus* or *C. clupeaformis)* they generally differ first of all in the number of gill rakers and in their feeding preferences. For example, in waters of Finland, Norway, and Karelia, Murmansk and Leningrad regions, the European whitefish, *C. lavaretus*, is represented by two or three forms: few-rakered = *C. lavaretus pidschian*; medium-rakered = *C. lavaretus lavaretus*; and multi-rakered = *C. lavaretus pallasi*. As a rule, few-rakered whitefish feed on benthos, and the multi-rakered form feeds on zooplankton.

The basic strategy of reproduction of fishes in the Arctic is directed so that newly-hatched fry can find forage and have time to grow during the short polar summer. The best conditions are created at the end of spring and in the beginning of summer when there is a bloom of small-sized forms of zooplankton. Therefore, fishes should spawn in the early spring or at the end of winter (example: spring-spawning whitefish from Lake Baunt or winter-spawning vendace from Finland), so that fry emergence will coincide with the first wave of increasing zooplankton biomass. Alternatively, the time of spawning is postponed to autumn or winter and the period of incubation is consequently very long, covering all winter (all other coregonids and salmonids). As a rule, the fry emergence of many coregonid species is dated to ice break up. The larvae have a yolk sac reserve, and thus the transition to exogenous food is not as critical as in some other fishes.

As a rule, coregonid fishes do not spawn annually in the Arctic, and the interval between spawning is one to three years. Usually, 60%–80% of the stock takes part in spawning the first time. Reproductive strategies of the Arctic fishes are evolving respective to specificity of the food supply (Reshetnikov 1979, 1980, 2001).

Table 6. Percentage composition of feed type in Arctic fishes.

Fish group	Phytophages	Zooplankton	Benthophages	Euryphages	Detritophages	Predators
All	0	14	44	28	5	9
Coregonids	0	15	45	30	0	10

Conclusions

1. The Arctic ichthyofauna is represented by 460 species of Cyclostomata and fishes (2.0% of the world fauna), of which 123 (26.7%) are true Arctic species. This proportion is close to that observed in mammals, birds, and Diptera. The proportion of Arctic species among freshwater fishes (51%) is higher than among marine fishes (15%).
2. Macrostructure of the Arctic ichthyofauna differs significantly from the observed ratio of taxa in the world fauna. The core elements of the Arctic ichthyofauna are salmoniforms, scorpaeniforms, and perciforms. The ecological niches of cyprinids are occupied by salmonids and coregonids.
3. Characteristic features of the Arctic fish fauna are a small number of monotypic genera and a low proportion of endemic genera and species. Species with a complex intraspecific structure and species having circumpolar ranges are well-represented. Polymorphism and euryphagy are also typical features of the ichthyofauna of the North. Polymorphic species of coregonids are represented by forms having various feeding preferences and different spawning seasons. Coregonids play a major role in transferring of energy across trophic chains.
4. In the Arctic, there are few highly specialized fishes with respect to feeding type. Benthophages (44%) and euryphages (28%) are predominant, while zooplanktophages (14%), predatory ichthyophages (9%) and detritophages (5%) are relatively rare. Phytyophages are virtually absent.
5. A major constraint on the reproductive strategy of Arctic fishes is the need for suitable larval and juvenile rearing conditions during the short polar summer. The majority of freshwater Arctic fish spawn on the bottom, have nests, or defend eggs. Pelagophylic or viviparous species are absent among Arctic freshwater fish and occur exclusively among marine species. Among coregonids, most species do not spawn annually, and the interval between consecutive spawning is one to three years.

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