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Marine Biology 17, 256—264 (1972)

Distribution and Ecology of the Pelagic Hydromedusae, Siphonophores and Ctenophores of the Barents Sea, Based on Perennial Plankton Collections

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Abstract

The evaluation of more than 10,000 samples of plankton, taken at standard stations from 1953 to 1960 in the Barents Sea, made it possible to supplement considerably the species list of medusae, siphonophores, and ctenophores, and to revise some ecological and biogeographical characteristics of many of them. Quantitative data, assembled over many years, on the occurrence of the above-mentioned groups, demonstrated the impossibility of using the vast majority of representatives of this fauna as biological indicators. During the very warm year of 1960, reproductively and vegetatively cold-adapted forms produced the same population increase as the thermophilic forms. The change in thermal conditions influenced these animals indirectly via a favourable biotic situation due to a prolongation of the nutrition period. The capability to vary the number of eggs, timing, rates and types of reproduction, to withstand long periods of starvation, etc., facilitates a flexible synchronization of the population dynamics of these pelagic predators with the quantity of plankton used for nutrition. The same properties stipulate the possibility of seasonal and annual meandering in regard to the boundaries of the water areas occupied.

Introduction

The population dynamics of pelagic hydromedusae, siphonophores, and ctenophores are of interest in at least two respects. We do not completely understand the role of these animals as powerful destructors of the biomass. It is not fortuitous that large aggregations of hydromedusae and the ctenophores of the genera *Bolinopsis* and *Pleurobrachia* are observed in both possible situations: when Copepoda, Cladocera and Pteropoda are abundant, or when the planktonic population is devastated as a result of the activity of these exceptionally carnivorous animals (Zelickman, 1969; Zelickman *et al.*, 1969). In evaluating the structure of the community, it is necessary to foresee similar situations.

Hydromedusae, siphonophores and ctenophores are readily used as biological indicators for distinguishing the water masses, and the data on them are employed to supplement the thermal characteristics of a particular year. However, such usage of this data is seriously hindered by the existence of a great number of divergent opinions on the biogeography and the nature of occurrence of each species of these faunistic groups. The source of this controversy is easily understood: initial characteristics are usually formuated on the basis of scanty material of episodical earlier collections, without any reference to the abundance of the animals.

The origin of the differences in the biogeographical characteristics of some individual species are, to a large degree, caused by the mere fact that the boundaries of the ranges of these species were determined on different occasions on the basis of rare and occasional findings of different expeditions during different climatological status in the Arctic Ocean. It should be taken into account that the variation in the boundaries of the area of the individual plankton form with seasonal, long-periodic and non-periodic changes of environment, obviates the use of plankters as biological indicators.

The fragmentary information on the range of distribution area and quantity of hydromedusae and ctenophores in the epicontinental Barents Sea (Zelickman, 1965, 1970) can be greatly complemented if the data are co-ordinated for a period covering successive years.

Material

A total of 10,000 samples were obtained in 1953 to 1960 in the region between the Kola Meridian, Novaya Zemlya and the Kara Strait (longitude 32°30′ to 58°00′ E), with latitude 76° N as the northern boundary; and also in the Motovsky Bay and in the small bights of East Murman, Orlovka, Teriberka, Dalnezelenetskaya, Jarnyshnaya, Dvorovaya, and Iokanga. Supplementary material (526 samples) was collected from the bights of Jarnyshnaya and Dalnezelenetskaya in 1967 to 1970, and from coastal waters of the island Novaya Zemlya in 1967 (latitude 75°23′ to 76°01′ N; longitude 57°02′ to 59°24′ E). Perennial strata-oriented collections were made at 224 standard stations throughout the year; they provided the basis for: (1) the list of species presented in this paper; (2) some revision of ecological and biogeographical "identification cards" for the fauna studies and for the specifying of the degree of adequacy of the use of some species as biological indicators of the water masses.

General Descriptions of the Fauna of Coelenterata and Ctenophora

An analysis of the perennial data is given in Table 1. Taxonomy and nomenclature are according to Naumov (1960, 1961).

Zoogeographical notes are supplemented by material presented by Russell (1953) and Kramp (1959, 1961, 1968). Species lacking in our collections are not discussed, as after the first indication they were never again recorded in the Barents Sea.

Perigonimus yoldiaarcticae

This is a circumpolar arctic form, widespread in all Siberian seas (Yashnov, 1939, 1946). Yashnov considered the penetration of *Perigonimus yoldiaarcticae*

Table 1. *List of species of pelagic medusae, siphonophores, and ctenophores of the Barents Sea. +: rare species; + +: single, fairly frequently met, specimens; + + + widely distributed species, several specimens encountered at a station; + + + +: abundant species*

No. Species	Occurrence in the southern part of the Barents Sea
1. *Perigonimus yoldiaarcticae* Birula, 1897[a]	+ +
2. *Perigonimus vesicarius* (Agassiz, 1862)[a]	+ +
3. *Perigonimus abyssi* G. O. Sars, 1874	+
4. *Perigonimus breviconis* (Murbach et Shearer, 1903)[a]	+
5. *Calycopsis birulai* (Linko, 1913)[a b]	+
6. *Rathkea octopunctata* (M. Sars, 1835)[a]	+ + + +
7. *Bougainvillia superciliaris* (Agassiz, 1849)[a]	+ + +
8. *Bougainvillia principis* (Steenstrup, 1850)[a]	+ +
9. *Corymorpha aurata* (Forbes, 1848)[a b]	+ +
10. *Corymorpha tentaculata* (Linko, 1904)[a]	+
11. *Corymorpha flammea* Linko, 1904[a]	+ +
12. *Tubularia prolifer* (Agassiz, 1862)[a]	+ +
13. *Plotocnide borealis* Wagner, 1885[a b]	+ + +
14. *Coryne tubulosa* (M. Sars, 1835)[a]	+ + + +
15. *Coryne princeps* (Haeckel, 1879)[a]	+ +
16. *Sarsia gemmifera* Forbes, 1848[a]	+
17. *Gemmaria costata* (Gegenbaur, 1856)[a b]	+
18. *Campanularia johnsoni* (Alder, 1856)[a b]	+ +
19. *Obelia longissima* (Pallas, 1766)[a]	+ + + +
20. *Obelia geniculata* (L., 1758)[a]	+ + + +
21. *Ptychogena lactea* Agassiz, 1865	+
22. *Cuspidella mertensii* (Brandt, 1835)[a]	+ + +
23. *Cuspidella polydiademata* (Romanes, 1876)[a]	+
24. *Mitrocomella cruciata* (Agassiz, 1865)	
25. *Tiaropsis multicirrata* (M. Sars, 1835)[a]	+ + + +
26. *Halopsis ocellata* Agassiz, 1863[a]	+ +
27. *Melicertum campanula* (Fabricius, 1780)[a]	+
28. *Halicreas minimum* Fewkes, 1882[a b]	+
29. *Aglantha digitale* (O. F. Muller, 1776)[a]	+ + + +
30. *Pantachogon haeckeli* Mass, 1893	+
31. *Homoeonema platygonon* Maas, 1893	+
32. *Ptychogastria polaris* Allman, 1878	+
33. *Aeginopsis laurentii* Brandt, 1835[a]	+ + + +
34. *Solmaris corona* (Keferstein et Ehlers, 1861)[a b]	+
35. *Cyanea capillata* (L., 1758)[a]	+ + + +
36. *Aurelia aurita* (L., 1758)[a]	+
37. *Physophora hydrostatica* Forskål, 1775[a]	+ +
38. *Marrus orthocanna* (Kramp, 1942)[a]	+
39. *Dimophyes arctica* (Chun, 1897)[a]	+ + +
40. *Pleurobrachia pileus* (O. F. Muller, 1776)[a]	+ + +
41. *Mertensia ovum* Fabricius, 1780	+
42. *Bolinopsis infundibulum* (O. F. Muller, 1776)[a]	+ + + +
43. *Beroe cucumis* (Fabricius, 1780)[a]	+ + + +

[a] Collections made in the present study.

[b] Species recorded by me for first time either for Barents Sea as a whole, or for its south-eastern part.

into the Barents Sea as doubtful, but later this euryhaline neritic medusa was repeatedly caught, particularly eastward of longitude 39° E (Abramova, 1957; Zelickman, 1961, 1966). In August (1958, 1959, 1960), near the Pechora Estuary, one vertical haul in aggregations of these animals collects hundreds of individuals of all age groups.

Perigonimus vesicarius

Perigonimus vesicarius is widespread circumpolar, and subarctic in origin; it displays a propensity for the south-eastern sector of the Barents Sea, but it is more stenohaline and abyssal than *P. yoldiaarcticae* (Zelickman, 1961, 1966). Sexual reproduction occurs in August and September.

Perigonimus breviconis

This is a northamphiboreal oceanic species (Naumov, 1960). Single specimens were found by us 5 times within the Murman branch of the Northcape current. *Perigonimus breviconis* enters the Barents Sea from the west, but does not usually penetrate to the east of longitude 38° E. On one occasion, *P. breviconis* was collected by us near the Maslennikov Cape (Novaya Zemlya).

Calycopsis birulae

Calycopsis birulae is euryhaline, and endemic in the east Arctic. Four mature specimens were discovered in the Pechora Estuary (ca. 17‰ S). It is possible that *C. birulae* penetrates into the Barents Sea through the Kara Strait.

Rathkea octopunctata

Almost world-wide neritic, *Rathkea octopunctata* is, presumably, of north-boreal origin. It often populates inshore bays, which are periodically exposed to heavy salinity reductions. The existence of zones of nonsterile exiles in regions of local cyclonic rotations over banks is a characteristic pattern for *R. octopunctata*.

On the basis of investigations carried out in the North Sea and cultivation of North Sea *Rathkea octopunctata* polyps in a tank, this medusa was assigned to the reproductive/cold-adaptive forms (Werner, 1961). The critical temperature of the formation of medusae by polyps is higher in the North Sea than that recorded in the Barents Sea. Probably, in the Barents Sea, *R. octopunctata* is represented by a physiological race which differs from the North Sea species. For example, in Jarnyshnaya Fjord, medusae juveniles are born in the middle of June when warming increases. In the Barents Sea, medusae bud-off from the polyps in July, and sexual proliferation occurs in August, the warmest season of the year. From July through September, in the region from the Motovski Bay to the Kara Strait, this medusa forms aggregations at scattered intervals along the shore; these aggregations cover many miles, and comprise hundreds or thousands of specimens per m^2 (Zelickman, 1961, 1969). Such phenomena were observed in the Barents Sea at a temperature no lower than 5° to 7 °C. In winter, medusae are rarely encountered. The life span of *R. octopunctata* is about 3 to 4 months.

Bougainvillia superciliaris

This is an arctic-boreal, relatively euryhaline neritic form. Single adult individuals are encountered from spring until autumn over the whole area under investigation, but they are more frequent to the east of Cape Swiatoy Nos (May/August). Sexually mature specimens were found only from August through October. While *Bougainvillia superciliaris* is reproductively cold-adapted in the North Sea (Werner, 1961), this is not the case with the Barents Sea population.

Bougainvillia principis

This boreo-arctic species, of Atlantic origin, was encountered by us twice in the nearshore branch of the Northcape Current (longitude 35° E; latitude 70° N) in 1954. *Bougainvillia principis* seems to be an immigrant from the west during the periods of increases of the Gulf Stream.

Corymorpha aurata

Corymorpha aurata is a boreo-arctic Atlantic neritic form. We encountered this species 18 times, most frequently in the period from April until June. Individuals with mature eggs were not discovered.

Corymorpha tentaculata

This is an arcto-boreal Atlantic neritic species. One specimen was found at the Kola-Fjord Meridian in December, 1957.

Corymorpha flammea

Widespread in arcto-boreal neritic waters, *Corymorpha flammea* was found 17 times to the west of Cape Swiatoy Nos. Its distributional area extends to latitude 75° N. In winter, the youngest individuals were caught at a depth of more than 100 m. The polyps probably bud-off in the period of most intensive heating of the bottom layer, at 2 °C.

Tubularia prolifer

This arcto-boreal neritic hydroid hydromedusae is mostly encountered in spring and summer, when it propagates in bays. Actinulae are rare. *Tubularia prolifer* was collected over the whole area under investigation, except in the Kanin-Kolguev region.

Plotocnide borealis

This arctic eurybathic species was considered a rarity in the seas of the Soviet Arctic Sector (Yashnov, 1939; Naumov, 1960). Judging from our collections, this medusa is a common species (in some cases 5 to 10 specimens per m^3 were present). *Plotocnide borealis* is present in the plankton all the year round, decreasing in numbers in November/January and reaching its maximum in April/June, when juveniles are also encountered. In the Barents Sea, this species is reproductively cold-adapted and stenohaline, although the relict habitat of *P. borealis* in the Baltic Sea is indicative of its potential euryhalinity.

Coryne tubulosa

Of arctoboreal origin, this widespread species tends to inhabit neritic waters. Every year, mainly from June through September (the time of its sexual reproduction), *Coryne tubulosa* is encountered over the whole area under investigation, as far as Cape Swiatoy Nos. In the North Sea, this species is reproductively cold-adapted.

Coryne princeps

This hydromedusae is similar to *Coryne tubulosa* in its pattern of distribution, but is more rare in occurrence.

Sarsia gemmifera

Sarsia gemmifera is a boreal Atlantic-Mediterranean species. In the warm year of 1959, we found 9 specimens at the most inshore stations of the Kola longitudinal section.

Gemmaria costata

Boreal atlantic, this species had been previously recorded only by Spassky (1929) in the Kola Fjord. We found it once at the traverse of the Kola Meridian.

Campanularia johnsoni

This is a widespread boreal oceanic species. Fourteen specimens were encountered in the streams of the less transformed Atlantic water mass, mostly near the bottom, in autumn and winter. The species extends to the Goose Bank. We repeatedly found juveniles, but sexually mature medusae were not observed.

Obelia geniculata

Obelia geniculata is widespread and of boreal origin. The medusae appear in July/August; sexual reproduction occurs in September and October.

Obelia longissima

This species is widely distributed in the northern hemisphere. Previously, the *Obelia* genus was considered to be poorly represented quantitatively in the Barents Sea (Linko, 1907; Virketis and Kiselev, 1933). This is no longer the case, at least in respect to the neritic waters proper. Both *Obelia longissima* and *Obelia geniculata* are especially abundant in the Kanin-Kolguev and Pechora shallow waters from August until September. In this period, many thousands of immature and ripe *O. longissima* can be collected with an ichthyoplankton net within 5 min. In British waters, *O. longissima* exists in the plankton all the year round, being most abundant from early spring until late autumn (Russell, 1953). In the area under study, hydroids reproduce the whole year round, but the reproduction rate varies. In winter, in cooler waters of the south-east sector of the Barents Sea, the formation of medusae in the gonothecas of polyps is suppressed.

Cuspidella mertensii

Arctoboreal epipelagic, *Cuspidella mertensii* is encountered in spring and summer. In some cases, ripe *C. mertensii* were observed in aggregations spread along the Murman shallows in bands hundreds of meters long, and dozens of medusae were within the observer's view field. Immature individuals were found at the Krestovye Islands near Novaya Zemlya in August, 1967.

Cuspidella polydiademata

Single individuals of this north-boreal species were recorded 7 times in the least modified Atlantic water mass. While revising the collections of 1910/1946, Yashnov (1970) also discovered purely arctic *Mitrocomella* (*Cuspidella*) *cruciata* (Agassiz, 1965) in the Barents Sea. However, either this species (earlier identified as *Cuspidella polydiademata*) was not represented in our samples, or at least it could not be identified.

Tiaropsis multicirrata

This is a north-amphiboreal, strictly neritic species (Zelickman *et al.*, 1969). Along the east Murman Coast (Kola peninsula) it is common but not numerous. However, in the Yarnyshnaya Fjord, each year, a gigantic aggregation of medusae appears in late June at the same place. Sexual reproduction occurs in July/August. *Tiaropsis multicirrata* has not been encountered to the east of Cape Cherny. The duration of the life cycle varies from 1.5 to 3 months. This medusa can withstand prolonged (up to 3 weeks) reversible starvation; it is capable of modifying its sex-ratio and growth rate (which is generally very high) and, if food is abundant, it can reach the stage of sexual reproduction in half the time needed under normal conditions. We observed this phenomenon in 1970, when

T. multicirrata reached 24 mm (umbrella diameter) by the middle of July, and each female contained no fewer than 800 eggs. Mass laying of planulae and the death of individuals after spawning began as early as the beginning of August instead of the middle of September. In 1970, crustacean plankton in the Jarnyshnaya Fjord developed very early and quickly due to the abundance of *Calanus finmarchicus*.

The capability of *Tiaropsis multicirrata* to assimilate dissolved metabolites of algae has been demonstrated experimentally (Yerokhin, 1971). This capability seems to guarantee additional source of food for *T. multicirrata* when the quantity of zooplankton is insufficient.

Halopsis ocellata

This is a common arcto-boreal epipelagic species. Mature specimens and juveniles were found over almost the entire water area to the west of Cape Kanin Nos.

Melicertum campanula

Amphiboreal Atlantic, this species was encountered 6 times to the west of longitude 39° E.

Halicreas minimum

This amphiboreal oceanic bathypelagic species was found twice in 1959, in the main and north branches of the Northcape Current.

Aglantha digitale

Aglantha digitale is nearly cosmopolitan eurybathoceanic, and arctoboreal in origin. The southern boundaries of its area depend on the inrush of Arctic waters. *A. digitale* exemplifies incompatibility of characteristics ascribed to it by various authors. Linko (1907) considered it to be a boreal form, but later (1912), he came to the conclusion that it is an arctic species, sporadically appearing in coastal waters in winter. Manteufel (1941) subscribed to this conclusion, although previously (1939), he had attributed *A. digitale* to the fauna of the warmer west part of the Barents Sea (May/January). Virketis (1928) considered *A. digitale* to be an oceanic cold-water aboriginal Barents Sea species, which disappeared with seasonal heating of the water. A dense network of observation stations working all the year round demonstrated that *A. digitale* is one of the most common and constantly occurring medusae in the southern part of the Barents Sea. *A. digitale* is reproductively cold-adaptive, and this indicates that its Barents Sea population is of Arctic origin. The population numbers of *A. digitale* are considerable in all layers up to 200 m. Large medusae (umbrella height 20 mm and more) are frequent at depths below 50 m; juveniles remain near the surface. The eurybionity of *A. digitale* is high; e.g. in August, 1958, one of the stations recorded 1160 juvenile specimens per m^3 in the 25 to 0 m layer and 580 specimens per m^3 in the bottom to 0 m layer. This station (depth 80 m) had a bottom temperature of 1.78 °C (34.29‰ S) and a surface temperature of 8.52 °C (31.02‰ S).

Unfortunately, nobody has studied this "species" as a whole. Probably, it is composed of physiologically heterogeneous species.

Aeginopsis laurentii

This is a widespread arcto-boreal eurybathic-oceanic species. In the years of mass production, adult individuals and juveniles alike occur in the plankton all the year round, juveniles being more numerous in winter. *Aeginopsis laurentii* is generatively cold-adapted; presumably, it is physiologically heterogeneous.

Solmaris corona

Solmaris corona is boreal east-Atlantic epipelagic. In the autumn of the warm year 1959 (Zelickman, 1966), we encountered 7 specimens at the traverse of the Kola-Fjord Meridian, where the section crossed both the euneritic water mass and the coastal branch of the Northcape Current.

Cyanea capillata

This is a nearly cosmopolitan scyphomedusa, presumably of northern origin. It occurs in the Barents Sea the whole year round, and undergoes considerable fluctuation in numbers. In the years of maximum reproduction, it is particulary numerous in summer and autumn.

Aurelia aurita

This nearly cosmopolitan syphomedusa occurs in summer and autumn. Mass abundances were observed twice in warm years.

Physophora hydrostatica

Physophora hydrostatica is an almost cosmopolitan siphonophore. Its appearance in the Arctic Ocean is strictly conditioned by the increasing inflow of Atlantic waters. Linko (1912) was the first to record *P. hydrostatica* near the Novaya Zemlya. Manteufel (1941) was of the opinion that live siphonophores had been penetrating the Barents Sea since 1931, when the rise in temperature of the Arctic Ocean intensified, but it is more probable that recorded occurrences became more frequent with the increase in the number of expeditions. A great immigration of *P. hydrostatica* to the shores of the East Murman occurred in 1950 (Naumov, 1951). In July and August of the warm year 1954, we collected scores of live colonies of various age groups in the Dalnezelenetskaya Bight. In some cases, live colonies reached Cape Cherny at that time. According to our data, nectophores of these physophorae are carried at least as far as latitude 73° N.

Marrus orthocanna

This is a high-arctic bathypelagic species. In 1956, we twice found gastrozooids and nectophores of this species to the north of latitude 75° N on the Persey Bank, where they must have been carried from the Polar Basin.

Dimophyes arctica

Dimophyes arctica is bipolar eurybiotic. We repeatedly collected definitive nectophores and eudoxiae with ripe gonophores (several specimens in a sample). In the southern Barents Sea, this siphonophore is common in winter and spring, and is more frequent at depths below 100 m. In high latitudes of the Barents Sea, *D. arctica* sometimes constitutes a considerable biomass in the November/February period (Abramova, 1956, 1957). Being relatively eurythermic, it is strictly stenohaline (Zelickman, 1970). Although this siphonophora was registered within a temperature range from 1.13° to 13.26 °C (Totton, 1965), it is especially abundant at 1° to 2 °C. It reproduces at temperatures not exceeding 10 °C (Stepanyants, 1967).

Pleurobrachia pileus

This nearly cosmopolitan neritic ctenophore occurs regularly in small numbers from the Motovski Bay to Cape Swiatoy Nos; it reproduces in summer and autumn. *Pleurobrachia pileus* is particularly abundant to the east of Cape Kanin Nos in August and September; it reaches as far as latitude 76° N. Being a non-selective planktophagous form, *P. pileus* competes with pelagic fishes for food (Fraser, 1970).

Bolinopsis infundibulum

This is an arctoboreal neritic species. Eggs form in the second half of May, ripe ctenophores are abundant in July and August; they disappear in September and October. The number of *Bolinopsis infundibulum* depends on the amount of food available for this non-selective predator, and on the abundance of its main enemy in the Barents Sea, the ctenophore *Beroe cucumis*, which appears to feed in that basin solely on *B. infundibulum*. *B. infundibulum* has been forced out of the Kanin-Kolguev region by *Pleurobrachia pileus*, its food competitor.

Beroe cucumis

Beroe cucumis is arctoboreal oceanic; it reproduces nearly all the year round. Throughout the year, specimens of 20 to 25 cm occur even near the surface. In summer, this species inhabits the surface layer, sinking somewhat in winter. It is very rare in south-eastern shallow waters.

The above list contains 36 medusae species; previously, only 25 species (Kramp, 1959) were registered in the Barents Sea as a province of the Arctic region. Twenty-three of these constitute a neritic complex. There are only two authentic oceanic holoplankters (*Aglantha digitale* and *Aeginopsis laurentii*) constantly inhabiting the Barents Sea. Of the species mentioned by Kramp (1959, p. 12, p. 210), the only one which we did not encounter was the boreal Atlantic *Paratiara digitalis*; this species is said to inhabit the extreme west of this water area and the Murman inshore waters. Out of 29 species of neritic hydromedusae of the Arcto-Pacific region (Kramp, 1968), 17 species are mutual to the Barents Sea.

There are no endemics in the Barents Sea. All species mentioned, except *Calycopsis birulae*, also belong to the west Arctic fauna. The list has increased mainly due to Atlantic immigrants encountered, for the most part, in the warm years 1954, 1959, and 1960. Only a negligible number of newcomers which penetrate the Barents Sea water mass attain sexual maturity. They do not affect the subarctic character of the fauna of Hydromedusae and Ctenophora, which are generally represented by widely distributed arctoboreal and amphiboreal species. For these species, the Barents Sea shelf is one of the areas where they exist in independent populations. Regarding the overwhelming majority of Atlantic immigrants, their ephemeral penetration signifies only the meandering of boundaries of the expatriation zone.

Discussion

Perennial samples taken at standard stations in the Barents Sea and generalization of World Ocean data demonstrated that, because of the rare occurrence of stenobiotical allochthonous Medusae, Siphonophora and Ctenophora, and the nearly complete lack of endemic forms of these groups in this region, retrospective and approximate judgment on the intensity of warm-water inflow into this sea is possible on the basis of the faunistic composition of these animals. The criterium is the degree of remoteness of the places where boreal Atlantic organisms are found in a north-east direction. Occurrence and abundance indices of the species serve as an index revealing sign and scope of the positive thermal anomaly. Accordingly, the west and south-west boundaries of the area of high-Arctic immigrants serve as an index of the negative anomaly. A comprehensive analysis calls for an adequate number of standard stations operating all the year round.

The determination of the biogeographical nature of a species requires differential appraisal of the area and the state of organisms in a hydrologically isolated water area (Bogorov, 1945; Beklemishev, 1967). This fact is often neglected; it affects particularly the characteristics of widespread species. In oceanic Coelenterata and Ctenophora, it is necessary to distinguish 2 stages of area transformation: (1) periodic penetration into other seas or alien water masses; (2) occupation of a certain ecological niche during the whole life cycle. To achieve this, it is necessary to know the biology of a species, both in the "nucleus" area of its range of distribution and in the marginal zone; however, this information is not available. Inasmuch as the same species may be generatively cold-adaptive and vegetatively warm-adaptive in one water area, and as this situation may have been historically reversed in another area, the geographical characteristics (label)

Table 2. *Occurrence (%) of some common species in years with different thermal regimes. A summary of collections, at practically the same stations; for 1959, stations at Novaya Zemlya and Pechora shallow waters are added*

Species	Year and thermal regime		
	1958 (Hydrologically cold)	1959 (Hydrologically moderately warm)	1960 (Hydrologically very warm)
Plotocnide borealis	12.9	17.2	22.0
Aglantha digitale	17.4	25.1	39.4
Aeginopsis laurentii	0.0	1.7	23.4
Physophora hydrostatica	0.4	8.0	11.4
Dimophyes arctica	0.4	14.6	54.24
Total no. of stations	241	474	236

of any species should be considered most carefully. A marked tolerance to temperature and salinity, peculiar to mass species in the Barents Sea (Zelickman, 1970, pp 78—79, Fig. 1a—e), also hinders ecological labelling of the fauna. Because of the lack of knowledge on reproductive biology, the possibilities of physiological divergence into sibling species, the stability of isolates, population dynamics, etc., it must be admitted that, in the Barents Sea (essentially a shelf basin with large-scale water mixing), jelly fish, siphonophores, and ctenophores cannot, at present, be used as biological indicators of water masses.

What accounts for the differences in population dynamics and the distribution of mass forms in different years? It is supposed that giant population outbursts of species of different geographical origins (there is a tendency to trace the origin by these outbursts) depend primarily on thermal conditions during the current year. If we consider the average annual occurrence of common species usually taken to be indicators (Table 2), we obtain interesting results.

Species of different geographical and ecological nature occurred more frequently in the warmest of the chosen years[1]. In the warm years, peaking of the population numbers may be partly connected with the intensified budding after early establishment of a certain critical temperature, and with the supposition of the existence, in many animals, of resting eggs or other inactive stages, similar to those discovered in *Margelopsis haeckeli, Corymorpha aurata* and *C. nutans* (Berrill, 1952; Werner, 1959, 1961). This does not mean that increased temperature was the main factor which stimulated the increase in numbers of the respective species. The thermal change, in general, may have influenced Coelenterata in an indirect way in connection with the formation of a favourable biotic situation. Indeed, for many species, the period of sexual reproduction and the growth of juveniles and colonies coincides with the time of increased heating of the upper 100 m layer. At this stage, Coelenterata require intensified nutrition, and a warm year favours an early development of large Calanoida (on which oceanic medusae feed), subsequent heavy growth of small epipelagic thermophilic plankters, and survival of a mass of plankton larvae of bottom invertebrates (food of neritic medusae and ctenophores), thus prolonging the season of food abundance for Coelenterata. The elimination of juveniles decreases. This was the situation in 1960.

If mass appearance of medusae, siphonophores and ctenophores is in spatial correlation with the appearance of their food, there must be synchronization of the two phenomena. This synchronization must be especially flexible in view of an absolute predatorship of the consumer, and must be ensured by the plurality of adaptation types, e.g. by capability to withstand long periods of starvation, to alternate the type of reproduction, etc. Thus, in the Barents Sea, during fast but short heating of shallow waters, a life cycle of neritic species lasts less than 1 year; and inshore polyps are monocyclic. It may be for this reason that some species change the signs of their generative thermopathy in the Barents Sea in comparison with other parts of the area. The possibility of retardation or acceleration in development, whether it is connected with the appearance of resting stages, or with the waiting for the threshold temperature required for gonad formation, may be considered as an evolutionally-conditioned state of anticipation, a "readiness" for the flourishing of the pelagic generation. Owing to versatility of adaptation systems, the pelagic genera-

[1] In *Plotocnide borealis, Aglantha digitale and Aeginopsis laurentii*, juveniles dominated in the collections over the whole water area under investigation. This observation enables us to conclude that this phenomenon is not caused by increased transportation of individuals from the west with the waters of the intensified Northcape Current. Only more frequent findings of *Physophora hydrostatica* may be directly connected with water flow.

tion is fully prepared to respond at the beginning of population outburst of other zooplankters.

Thus, at least for the Barents Sea groups under discussion, biotic factors may control population dynamics, as previously demonstrated for the plankton as a whole (Zelickman and Kamshilov, 1960), and for the seasonal and annual changeability of the northern and southern boundaries of areas.

Summary

1. Barents Sea medusae, siphonophores and ctenophores have been collected repeatedly at standard stations over a number of years (ca. 10,000 samples). A list of the species is given, with due regard for all data in literature of the last 50 years; data on the occurrence and ecological and biogeographical characteristics of each species are included.

2. It has been shown that the vast majority of representatives of the above-mentioned groups, at least in the Barents Sea, cannot be used as biological indicators, due to the fact that their distributional boundaries undergo annual and seasonal meandering. Moreover, the extent of their water areas depends on periodical variation of the climatological status of the Arctic Ocean.

3. Powerful booms of generatively cold-adapted and generatively thermophilic species during the warm year 1960 were connected with abundant crustacean plankton observed in the same year.

4. Medusae, siphonophores and ctenophores are primitively organized predators. They are assumed to possess a versatile adaptation system, which facilitates flexible synchronization of their population booms with abundance fluctuations of plankton forms which they use for food. This synchronization includes the capability to vary the number of eggs, timing, rates and types of reproduction, to withstand long periods of starvation, to produce resting stages, and to form aggregations. These properties (many of them characteristic of ephemeral species) provide passive pelagic predators with the capability of "waiting" for a favourable biotic situation to occur.

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Date of final manuscript acceptance: August 7, 1972. Communicated by M. E. Vinogradov, Moscow