

Distribution of pelagic larvae of bottom invertebrates of the Norwegian and Barents Seas

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Abstract

The distribution of pelagic larvae, juvenile and epitoquous stages of shallow shelf bottom invertebrates, in the plankton of the Norwegian and Barents Seas is largely determined by the distribution of the respective parental forms. The various currents influence the distribution only secondarily and to a rather limited extent. Most larvae remain in the water masses above the zones inhabited by their parents. Thus their large scale distribution in the plankton is determined primarily by the ecological and zoogeographical patterns of distribution of the parental life cycle stages. Such dependence of larval distributions on the distribution of adults in the benthos is assumed to represent a general pattern in all shallow regions of the world oceans.

Introduction

This paper is a hitherto unpublished part of the dissertation of the author (MILEIKOVSKY, 1965). The distribution of pelagic larvae, juvenile and epitoquous stages of bottom invertebrates, was studied in the plankton of the Norwegian and Barents (southern part) Seas, including Faroe-Shetland and Bear Island-Spitsbergen regions. 3781 quantitative plankton samples (collected 1958 through 1961 during all seasons) were obtained at 1459 stations and carefully examined. About 120 different forms—almost 90% of them larvae and other juvenile and epitoquous stages—were present in the samples. About 70 of these forms were identified to species, nearly 10 others to genera (mainly larvae and juveniles of polychaetes and gastropods). The remaining forms were counted on the basis of their belonging to higher systematic groups—families, orders, classes, phylums.

General distribution patterns in the whole area of the Norwegian and Barents Seas

In the Norwegian Sea most of the surface waters of its southern part belong to the Norwegian current system. The main current enters the Sea from the Faroe-Shetland Channel and crosses its southern part from west to northeast continuing further along the Norwegian shore near the shallow shelf, and in some places above its outer border. From this main stream three strong branches originate directed northward into the open sea; the western branch flows northwesterly toward Jan Mayen, the central branch northwardly into the open sea, and the Spitsbergen branch northeasterly beyond the western border of submerged shallow shelf on which the northeastern part of the Norwegian Sea and the whole Barents Sea are located, and to the west from the Bear Island-

Spitsbergen region above the border zone between the shallow shelf of this region and the abyssal basin of the Norwegian and Greenland Seas. On its further way along the mainland, the main stream enters the Barents Sea as a strong Northcape current which divides into two main (Nearshore and Northern) and some secondary branches.

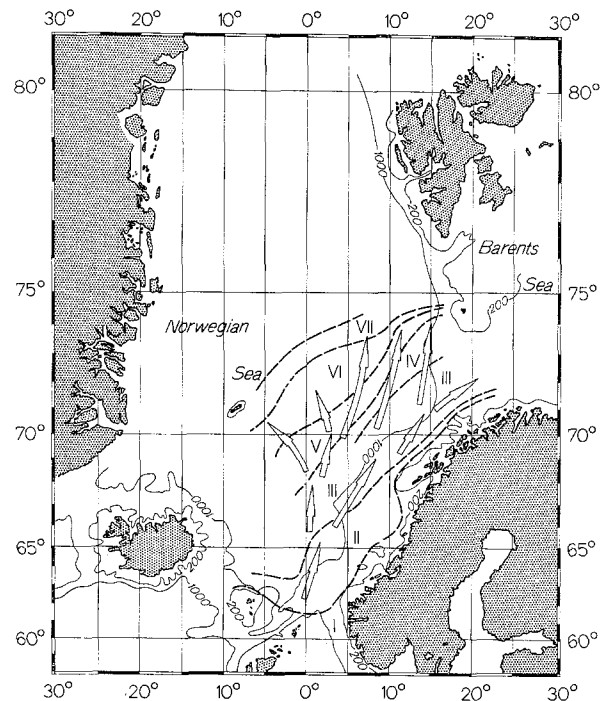


Fig. 1. Norwegian current system. Roman numbers correspond to numbers of zones with a different composition in the drifting larval fauna (Table 1). Arrows indicate directions of the branches of Norwegian current. Thin solid lines: 200 and 1000 m isobaths; heavy broken lines: borders between the zones

It was shown by us (MILEIKOVSKY, 1960, 1961, 1965, 1966) that the waters of these northwardly directed branches of the Norwegian current system transport many larvae and juveniles of the shallow shelf bottom invertebrates from the shallow shelf areas into the open sea over distances of 50 to 200 or 500 miles, sometimes even up to 600 or 720 miles (Figs. 1 and 2, Table 1).

However, from the plankton of the shallow shelf areas these current branches remove and transport only a rather small portion of the larval population

which was born in the shelf waters — much less than 10% of its total quantity as summarized for all seasons

of the year. During all seasons the main mass of the larval population was concentrated in the plankton of the narrow zone above the shallow shelf bordering the shores of the Scandinavian peninsula, Faroe and Shetland Islands, and above the shallow shelf of the Faroe-Shetland Ridge. Such pattern of distribution is typical for the larvae of all systematic groups; in Figs. 3 and 4 it is exemplified by data obtained on polychaete and lamellibranch larvae.

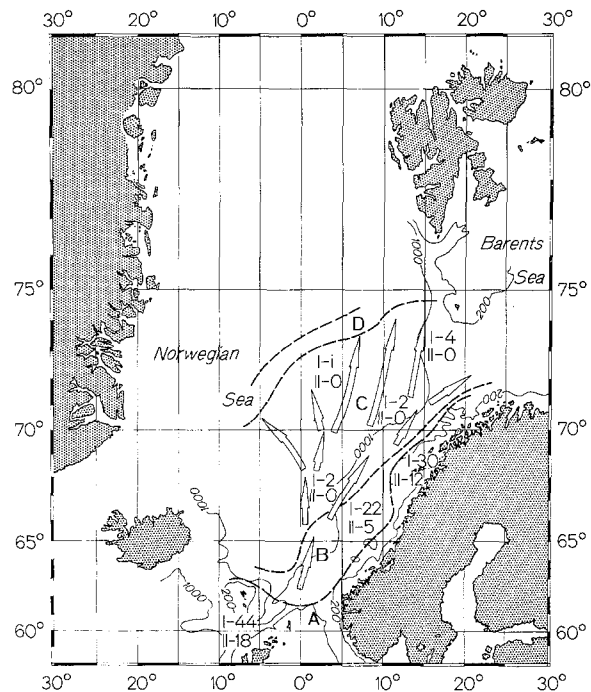


Fig. 2. Quantities of forms (identified species and genera) of polychaete and prosobranch gastropod larvae present in the northerly directed branches of the Norwegian current at different distances from the shores of Faroe-Shetlands and the mainland. Arrows: Directions of current branches; I: polychaete larvae; II: prosobranch gastropod larvae; arabic numbers: quantities of forms; A: zone of shallow shelf waters, B: 50 to 200 miles, C: 250 to 500 miles, D: 600 to 720 miles from shallow shelf. Thin solid lines: 200 and 1000 m isobaths, heavy broken lines: borders between zones A, B, C and D

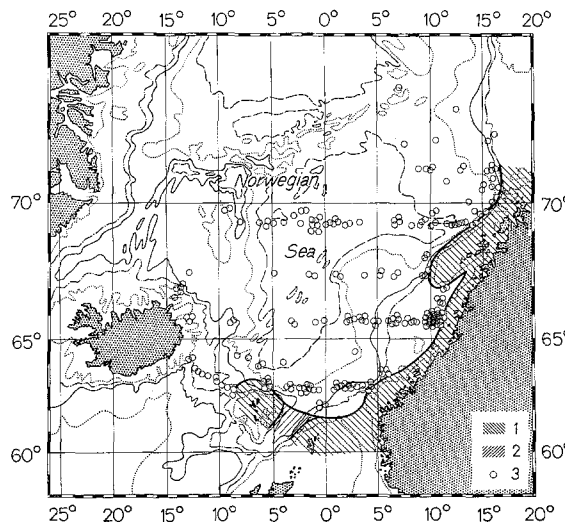


Fig. 3. Distribution of polychaete larvae in the Norwegian Sea. 1: zone of maximum abundance of larvae in the water above the shallow shelf; 2: zone of common abundance of larvae drifted from the shallow shelf above the Faroe-Shetland Channel; 3: drifted larvae found in the open sea. All data refer to the water column surface to 50 m depths and have been averaged for all seasons (see also Fig. 4)

Table 1. Larvae and juvenile forms of bottom invertebrates found in the Norwegian Sea (western, central and Spitsbergen branches of Norwegian current) at different distances from the shores of mainland and Faroe-Shetland region. (After MILĚIKOVSKY, 1966)

Groups of larvae	Shallow shelf waters	Distance from shores (in miles)					
		50—200	250—320	350—400	500	600	660—720
Number of zone in Fig. 1	i	ii	iii	iv	v	vi	vii
Polychaeta	+++	+++	++	++	++	+1/	—
Gastropoda Prosobranchia	+++	+	—	—	—	—	—
Gastropoda Opisthobranchia (Nudibranchia)	+++	+++	+++	+++	+++	—	—
Nemertini	+++	—	—	—	—	—	—
Archannelides (Polygordius)	+++	—	—	—	—	—	—
Cirripedia (<i>Balanus</i> spp.)	+++	++	+	+	—	—	—
Decapoda	+++	+	+	+	—	—	—
Lamellibranchia	+++	+++	+++	+++	+++	+++	++
Bryozoa	+++	++	+ ?/	++	—	—	—
Phoronida (<i>Phoronis mülleri</i>)	++	—	—	—	—	—	—
Asteroidea	+++	—	—	—	—	—	—
Ophiuroidea	+++	+++	++	+	+	—	—
Echinoidea	+++	++	+	—	—	—	—
Holothuroidea	++	—	—	—	—	—	—
Enteropneusta	++	—	—	—	—	—	—
Ascidia	++	—	—	—	—	—	—

Symbols: + few specimens, ++ common in one season, +++ present at many stations in one season or common in different seasons, — absent. 1/ Rostraria-larvae of *Euphrosyne borealis*. ?/ Evidently insufficient dates; these forms must be more common in this zone.

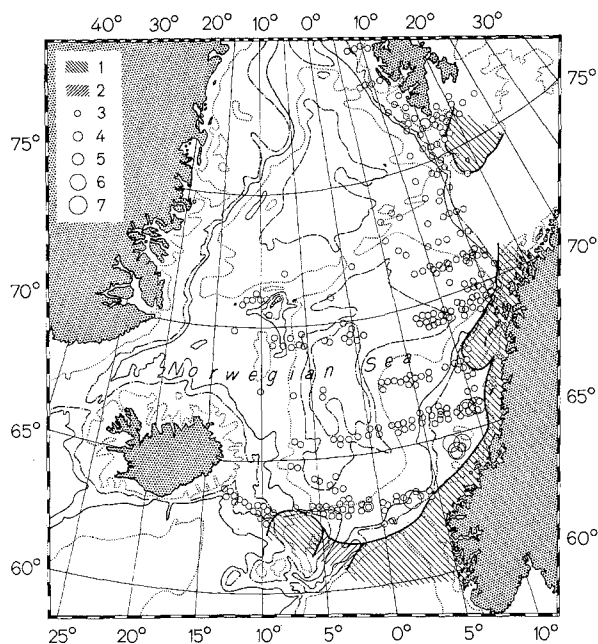


Fig. 4. Distribution of lamellibranch larvae in the Norwegian Sea. 1, 2: as in text to Fig. 3; 3 to 7: drifted larvae found in the open sea (3: 1 to 10; 4: 11 to 25; 5: 26 to 50; 6: 51 to 100; 7: 101 to 200 specimens per m^3). All data refer to the water column surface to 50 m depths and have been averaged for all seasons

Similarly, in the Bear Island-Spitsbergen region larvae were present mainly above the shallow shelf between these islands and in the narrow zone above the shallow shelf bordering the west coasts of Bear Island and Spitsbergen. Above the abyssal depths of the Norwegian and Greenland Seas only few larvae of shallow shelf bottom invertebrates, originating from shelf plankton, were present immediately to the west of this region, mainly in the Spitsbergen branch of the Norwegian current. Such pattern of distribution is typical for larvae of all systematic groups; this is exemplified in Fig. 4.

In contrast to these two areas, in the region located completely on the submerged shallow shelf of the southern part of the Barents Sea, larvae were present practically everywhere; above the banks and shallows far from the shores they were found in quantities comparable to, or even greater than, those typical of nearshore waters (Figs. 5 to 7). But also in this area, as is evident from the larval distribution of littoral and some mainly nearshore species (MILEIKOVSKY, 1965, 1966), dispersion of some larvae occurs with the Northcape current over distances from 150 to 200, or 300 to 320 miles, in a few cases over 500 miles. Examples of such dispersions are the distribu-

tions of all larvae of Nudibranchia and of the saccoglossan species *Limapontia capitata* (Figs. 7 and 8).

These patterns of the distribution of planktonic larvae in the Norwegian and Barents Seas, taken as a whole have been summarized by MILEIKOVSKY (1965). They confirm, together with data from literature (GIESE, 1959; MARSHALL, 1954; LEMCHE, 1948; BERNARD, 1953; GORDON, 1960; MILLAR, 1959; SOKOLOVA, 1959; MILEIKOVSKY, 1961) THORSON's view (THORSON, 1946, 1950, 1952) that among bathyal and abyssal bottom invertebrates the development via pelagic larvae is a very rare feature—it has thus far been demonstrated only for the decapod family Eryonidae by BERNARD (1953) and GORDON (1960)—and that species with pelagic development are mainly inhabitants of the shallow shelf.

An analysis of data on the systematic composition of bottom communities of the Norwegian and Barents Seas (BROZKAYA and ZENKEVITCH, 1939; THORSON, 1957 and others) shows that, in accordance with THORSON's conception, bottom invertebrates with pelagic development are concentrated on the shallow shelf: in the Norwegian Sea along the mainland coastline and around the narrow nearshore zones of the islands and in its southern part; in the Barents Sea, which is completely situated on the submerged shelf, in nearly every shallow region of its southern part.

The information available at present demonstrates that the general "large scale" distribution of pelagic bottom invertebrate larvae in the plankton of the

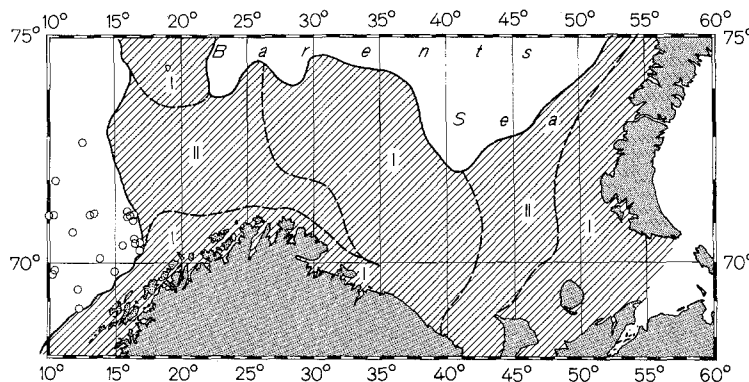


Fig. 5. Distribution of polychaete larvae in the southern part of the Barents Sea. Hatched area: zone of mass abundance above the shallow shelf; I: regions with maximum quantities of larvae; II: regions with lower total quantities and fewer species; o: a few drifted larvae found in the Spitsbergen current

whole Norwegian and Barents Seas is determined by the distributional pattern of the parental benthonic species and by the dispersion of these larvae via currents. Patterns of distribution of parental species determine the occurrence of the main mass of the larvae during all seasons above the shallow shelf; dispersion with currents determines the patterns of distribution of the lesser part of the total larval population beyond the borders of the shallow shelf.

Distribution in the shallow shelf water of Norwegian and Barents Seas

Our data (MILEIKOVSKY, 1960, 1961, 1965, 1966) and data from literature (KAMSHILOV, 1958; RZHEPISHEVSKY, 1958; KANNO et al., 1961; FISH and JOHNSON, 1937; WILLIAMSON, 1956; SOUTHWARD, 1962; and others) show that within the shallow shelf zone, dis-

quantities were found in regions inhabited by small, quantitatively poor, populations of bottom invertebrates with pelagic larvae. The greatest abundance of planktonic larvae occurred in waters bordering the shores of the islands Shetland, Faroes, Bear Island, Kolguev and Novaya Zemlja; these islands are surrounded by broad shallow areas with depths of 50 to

100 m (200 m near the outer margins); maximum values were also found in the waters above some banks of the southwestern and south-central parts of the Barents Sea surrounded by circular currents preventing evidently (ORTON, 1937; MARSHALL, 1948) transportation of larvae born on these banks away from the water covering them.

The lowest numbers of larvae were found in regions with the narrowest shallow shelf areas (nearshore zones off Norway and Murman) and with the shelf submerged to depths of 400 m (Koptiovskaya Bank region on the northeastern border of the Norwegian Sea).

The distributions of different systematic groups of larvae show the following patterns; larvae of Polychaeta (Fig. 5), Decapoda (Fig. 6), Lamellibranchia and Ophiuroidea are present everywhere; larvae of Gastropoda, Prosobranchia and Opisthobranchia (Fig. 7), Cirripedia, Echinoidea, Nemertini (Pilidium-larva), Bryozoa (Cyphonautes-larva), embryos of Holothuroidea and evidently of Asteroidea, are present in most parts of the regions; larvae of Phoronida, Echiuroidea, Enteropneusta and Ascidia occur only in few regions.

The abundance of all common groups of larvae is directly related to the abundance of their parental forms in the benthos. The scarcity of rare representatives is

determined by different factors in different groups: in Phoronida, Enteropneusta, Echiuroidea, the bipinnaria-larvae of Asteroidea and auricularia larvae of Holothuroidea, in the Barents Sea, by the low abundance of parental forms with pelagic development in the local benthos; in Ascidia larvae, by insufficient catches performed during open sea cruises; in the larvae of Asteroidea and Holothuroidea, in the Norwegian Sea, by the insufficiency of the samples not covering the main season of abundance of these larvae in the plankton.

Summarizing the data obtained on the total quantities of larvae and the different systematic

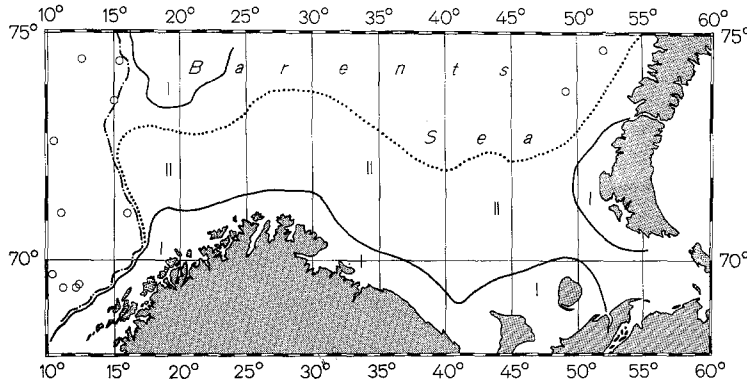


Fig. 6. Distribution of decapod crustacean larvae in the southern part of the Barents Sea. I: zones of mass abundance; II: zones of common abundance (large quantities for this group); o: zones with few larval findings; - - -: 1000 m isobath

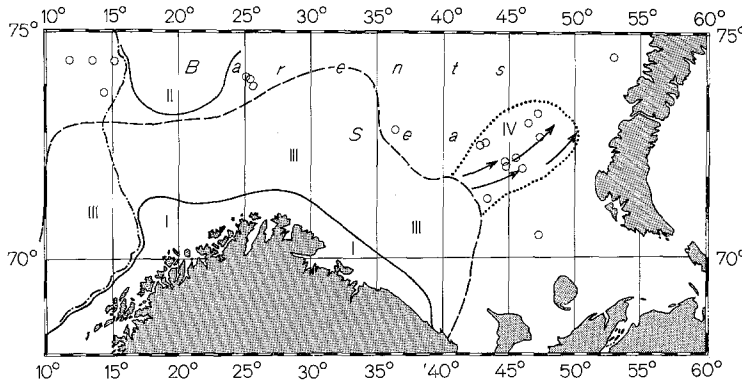


Fig. 7. Distribution of larvae of Gastropoda opisthobranchia (Order Nudibranchia) in the southern part of the Barents Sea. I: zones of mass abundance of larvae in nearshore water; II: zones of common abundance above the southern slope of the Bera Island Bank; III: zones of common abundance of drifted larvae in the waters of Northcape current; IV: zone in which larvae occurred over large distances from the places of their origin, i.e., water of the Novozemelskaya branch of the Northcape current (arrows: directions of current); o: few drifted larvae; - - -: 1000 m isobath

persion from the areas with maximum larvae abundance in nearshore surface waters toward the outer parts of the zone is not a very large scale phenomenon. Hence, the quantity of larvae in these areas is determined by the production of larvae by the local populations of bottom invertebrates with pelagic development, but not by horizontal water movements.

Within the shallow shelf zones of the Norwegian and Barents Seas, the greatest quantities of larvae were commonly present in regions characterized by the largest quantities of bottom invertebrates with pelagic development both in littoral and sublittoral inshore waters and the outer parts of the shelf; the smallest

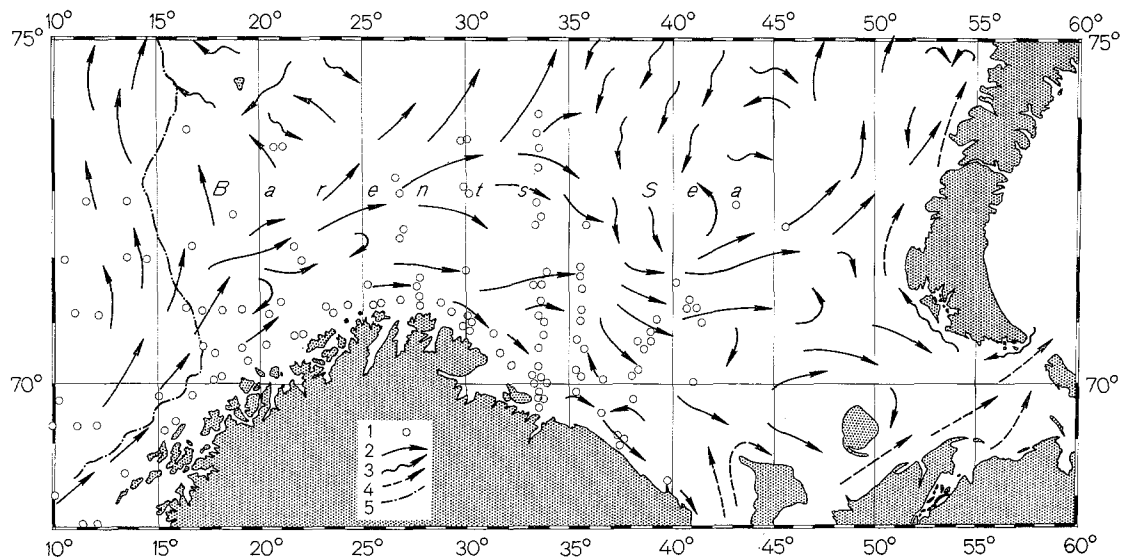


Fig. 8. Dispersion with the Northcape current of the veligers of *Limapontia capitata* (Gastropoda, Opisthobranchia, Saccoglossa) 1: presence of veligers in the samples; 2: Northcape current and its branches; 3: cold currents; 4: brackish water currents; 5: 1000 m isobath

groups represented, we see that in the shallow shelf waters of the Norwegian and Barents Seas, the general large scale distribution patterns of pelagic larvae of bottom invertebrates in the plankton are determined by the patterns of the distribution of their parental forms within the area of the shallow shelf.

Connection between larval distribution and ecological preferences as well as zoogeography of their parental forms

On the basis of their ecology and biogeography (HUTCHINS, 1947; HESSE et al., 1951; ZENKEVITCH, 1951; EKMAN, 1953; THORSON, 1946, 1950, 1952, 1957; MOORE, 1958; and others) the distribution of marine bottom invertebrate species can be characterized in the most general form (MILEIKOVSKY, 1965) in two ways: (1) by their zoogeographical home areas, (2) by their abundance in different ecological zones within the inhabited geographical area.

Roughly speaking the areal borders of marine bottom invertebrate species are determined by their biogeographical belonging, their ability to penetrate into neighbouring biogeographic areas and their distribution within the areas based on their preferences and tolerances of temperature, salinity, depth-range, substrate-composition, etc., and also by their connection with specific biocoenoses and bottom communities.

In order to simplify the analysis from the ecological point of view we have divided all bottom invertebrates with pelagic larvae represented in our samples into two groups: (1) inhabitants (exclusively or nearly so) of littoral and sublittoral zones; (2) inhabitants of both nearshore waters of both seas and the open part of the Barents Sea. The larvae of group (1) occur mainly near

the shores, the larvae of group (2) in the whole area of the shallow shelf waters of the two seas.

Within the seas studied is situated the borderline between boreal and arctic areas; many of the southern-boreal and boreal species of bottom invertebrates encounter here their northern distribution limits. The most hardy of them reach the region of Northcape-Ribachyi Cape along the shore of the mainland toward the east and the region of Sturfjord on the west shore of Spitsbergen toward the north. The more cold-sensitive species which prefer higher water temperatures are not met already north of the Lofoten Islands area near southern Norway. In contrast to the boreal species, the arctic-boreal species are distributed within this area very widely, to Novaya Zemlja on the east (some are met even eastward in the Kara Sea) and to the northwestern Spitsbergen (80° N and even further northward) on the north (SPÄRCK and THORSON, 1933; THORSON, 1941, 1944; EINARSSON, 1948; GAEVSKAYA, 1948; WESENBERG-LUND, 1953; NESIS, 1958, 1959; OCKELMANN, 1958; KOPYAKOVA, 1960; and others).

Our data on the larval distribution on individual species (mainly Polychaeta and Gastropoda), identified to the species or genera and adequately represented in our samples, indicate that only larvae of widely distributed arctic-boreal species or genera (represented here by several arctic-boreal and boreal species) were widely distributed over all areas of shallow shelf waters of both seas (Table 2).

The larvae of boreal (and some arctic-boreal) species with a northeastern distribution limit in the region between the Lofoten area and Northcape region (in rare cases between the Northcape region and West Murman coast) were present in the plankton along the mainland coast only to the Northcape, sometimes to

Table 2. Distribution of larvae within shallow shelf waters of the Norwegian and Barents Seas

Larvae present everywhere or nearly everywhere in all or nearly all regions and at many stations:

<i>Harmothoe imbricata</i>	<i>P. caullereyi</i>
<i>Harmothoe</i> spp. (type I)	<i>Myriochele oculata</i>
<i>Pholoe minuta</i>	<i>Pectinaria koreni</i>
<i>Euphrosyme borealis</i>	<i>Velutina velutina</i>
<i>Phyllodoce</i> spp.	<i>Limapontia capitata</i>
<i>Eteone longa</i>	Larvae <i>Nudibranchia</i> ,
<i>Castalia punctata</i>	types I and II
<i>Nephtys</i> spp.	<i>Proteolepas</i> -larvae of
<i>Glycera</i> spp.	Cirripedia
<i>Prionospio cirrifera</i>	<i>Pandalus</i> spp.
<i>Spio filicornis</i>	<i>Pagurus</i> spp.
<i>Pygospio elegans</i>	<i>Hyas</i> spp.
<i>Polydora ciliata</i>	<i>Ophiocten sericeum</i>
<i>P. flava</i>	<i>Strongylocentrotus</i>
<i>P. coeca</i>	<i>droebachiensis</i>

Not in all regions and only at a few stations were found:

<i>Harmothoe</i> spp. (type 2)	<i>Autolytus prolifer</i>
<i>Polynoidae</i> (<i>Lepidonotus</i> and	(epitoquous stages)
<i>Gattyana</i> types)	<i>A. prismaticus</i>
<i>Nereis</i> spp.	(epitoquous stages)
<i>Nerine foliosa</i>	<i>Philine</i> spp.
<i>N. cirratulus</i>	<i>Pontophilus</i> spp.
<i>Sphaerosyllis erinaceus</i>	
(epitoquous stages)	

Larvae present from Faroe-Shetland region to Northcape region; sometimes to Finmarken or Ribachyi Cape:

<i>Eunice pennata</i>	<i>Disoma multisetosum</i>
<i>Nerine tridentata</i>	<i>Aporrhais pes pelecani</i>
<i>Spiophanes bombyx</i>	<i>Trivia arctica</i>
	<i>Munida bamffica</i>

Larvae present only in the Faroe-Shetland region and along the South Norway coast to the south of the Lofoten:

<i>Pisone remota</i> ^a	<i>Alvania punctura</i> ^a
<i>Myxides</i> sp. ^a	<i>Coecum glabrum</i>
<i>Nerine</i> sp. II after HANNERZ ^a	<i>Eulima</i> sp.
<i>Microspio atlantica</i> ^a	<i>Lamellaria perspicua</i>
<i>Polydora ligni</i> ^a	<i>Philbertia linearis</i> ^a
<i>P. hermaphroditica</i>	<i>P. gracilis</i> ^a
<i>P. antennata</i>	<i>Mangelia</i> sp. ^a
<i>P. pulchra</i> ^a	<i>Odostomia</i> spp.
<i>Poecilochaetus serpens</i>	<i>Eulimella</i> spp.
<i>Magelona papillicornis</i> ^a	<i>Polygordius</i> sp.
<i>Owenia fusiformis</i>	<i>Sergestes arcticus</i> ^b
<i>Myriochele heeri</i>	<i>Galathea rugosa</i> ^a
<i>Pectinaria belgica</i>	<i>Phoronis mülleri</i>
<i>Lanice conchilega</i>	<i>Balanoglossus clavigerus</i>
<i>Helcion pellucidum</i>	

^a present only at few stations; ^b pelagic species.

the Finmarken or the Ribachyi Cape area on the West Murman coast; they were not met further eastward.

The larvae of southern-boreal and boreal species, with northern limits of distribution situated to the south of the Lofoten, were present in the plankton only in the region ranging from the Faroe-Shetland Islands to the Lofotens.

Summary

1. In the Norwegian and Barents Seas, the main large-scale patterns of distribution of pelagic larvae of bottom invertebrates in the plankton are primarily determined by the ecological and zoogeographical patterns of distribution of their parental forms.

2. The dispersion of the planktonic larvae via water currents influences their distribution only in a small portion of the total larval population without significantly affecting the general distributional pattern.

3. Data from other seas suggest, together with our information obtained in the Norwegian and Barents Seas, that such dependence of the distribution of pelagic larvae of shallow shelf bottom invertebrates on the distribution of their parents is typical for the world oceans.

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