Amphi-Atlantic distribution of marine Mollusca based on the results of the BIOFAR investigations

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Abstract

The BIOFAR investigations showed that 394 marine mollusc species live in Faroese waters. Some of them have a northern distribution into the Norwegian Sea and the Arctic, some are distributed more locally and some have a distribution along the whole European continent and also the Atlantic. Of these widespread species 15 have a main southern distribution area or an amphi-atlantic distribution in the southern part of their distribution. Three more have a northern amphi-atlantic distribution. The Bay of Biscay is central in the distribution of the southern species and the Bay of Biscay could thus be a very central place for the evolution and spreading of deep-sea mollusc species into the North Atlantic. It has been suggested that larvae spend their planktonic life in considerably more shallow water than after settlement as adults, and species living in the Bay of Biscay will spread their larvae both northward and westward as indicated by the distribution of the mollusc species discussed here.

Introduction

Recent studies of marine prosobranch molluscs (see for ex. Bouchet and Warén, 1985; 1986; 1993; Sneli, 1992; Sneli *et al.*, 2005) based on older and recent expedition material have revealed many species with amphi-atlantic distribution.

During the "BIOFAR programme" 1987 to 1990, 344 species of marine molluscs were sampled in the Faroese Exclusive Economic Zone (Faroese EEZ). Only 50 species known from before at the Faroes were not recorded, and they mainly live in the littoral zone and in shallow water. Before the start of the BIOFAR, 276 marine mollusc species were recorded alive in the area. During BIOFAR 118 species new to the area were found, giving a total of 394 species recorded alive at the Faroe Islands (Sneli *et al.*, 2005).

Of the recorded BIOFAR species 25 % did expand their so far known distribution area. One example is the bivalve species *Pandora pinna* (Montagu, 1803) that before BIOFAR was found on the south and west side of Great Britain north to the Scottish east coast. As many of the BIOFAR samples were taken in deep water, down to more than 1000 m depth, recorded species also confirmed records done 150 years ago by the "Lightning" and "Porcupine" expeditions in the Shetland-Faroe Channel.

In the BIOFAR mollusc material some of the species expanded their distribution area considerably as they earlier were not

known to be distributed north of the Bay of Biscay. In 1990 a programme similar to BIOFAR called BIOICE began in Iceland. In addition Icelandic amateur mollusc collectors sampled rare mollusc species from commercial trawl samples. Some of this material is published by Warén (1989; 1991; 1993; 1996). The data from Iceland will support the results of the BIOFAR investigations concerning species expanding their geographical range considerably. This article will look into how transportation of larvae will influence spreading of a species far away from its main distribution area.

Results

In the BIOFAR 1 material five species have their distribution from the Bay of Biscay along the continental slopes and the bathyal part of the East Atlantic north to the Faroes or even further west:

Buccinum oblitum Sykes,1911: S Iceland – the Faroes (also western Norway, Gibraltar), seamounts at SW Portugal (200-1,100 m)
Granigyra arenosa Warén, 1993: SW Faroes and SW Portugal (900-2,000 m)
Haloceras aff. *laxus* (Jeffreys, 1885): N Faroes – W Spain (700-2,175 m) (larvae present in the Faroese specimens)
Iphinopsis alba Bouchet and Warén, 1985: W Iceland – the Faroes – Rockall Trough – Bay of Biscay (1,000-3,000 m)
Tjaernoeia boucheti Warén, 1991: E Greenland – N Iceland – the Faroes – Rockall Trough – Bay of Biscay (550-2,091 m)

Four species are distributed from the Faroes south to the Bay of Biscay and then further south and west towards the Azores:

Bathycrinicola micrapex Bouchet and Warén, 1986: S Faroes – SW Portugal – Azores (1,083-2,360 m)
Boreotrophon dabneyi Dautzenberg, 1889: SW Faroes – Bay of Biscay – Cap Verde – Azores (1,125-2,670 m)
Boreotrophon echinatus (Kiener, 1840): the Faroes – Rockall Trough – Bay of Biscay – Azores (1,000-3,000 m) (also Mediterranean)
Krachia cossmanni (Dautzenberg and Fischer, 1896: SW Iceland – the Faroes – Azores (150-1,600 m)

Six species have an amphi-atlantic distribution from the Faroes south to the Bay of Biscay and then south and west across the Atlantic to the east American coasts:

Benthonella tenella (Jeffreys, 1869): S Iceland – the Faroes – south Atlantic – E American coast south to the Caribbean (500-4,000 m)
Cardiomya curta (Jeffreys, 1876): the Faroes – Atlantic Ocean – S to Iberian Peninsula – Azores – off Bermuda (35-2,078 m)
Placiphorella atlantica (Verrill and Smith, 1882): S Iceland – the Faroes – W Africa – Azores – E America (500-2,000 m)
Pleurotomella packardi Verrill, 1872): Iceland – the Faroes – south to Madeira – New England (200-4,425 m)
Thyasira subovata (Jeffreys, 1881): Iceland – the Faroes – Hebrides – W Ireland – south to Cape Verde – Angola – Argentina (216-3,917 m) (also Mediterranean)
Thyasira succisa (Jeffreys, 1876): Iceland – the Faroes – Portugal – New England to Florida (73-2,813 m) (also Mediterranean)

Three more species have a northern amphi-atlantic distribution in the North Atlantic:

Calliotropis ottoi (Philippi, 1844): North Carolina – Nova Scotia – Newfoundland – SW Iceland – the Faroes – Mediterranean (85>1,000 m)
Cyclopecten pustulosus (Verrill, 1873): Massachusetts – Gulf of Maine – Iceland – the Faroes (225-850 m)
Mohnia glyptus (Verrill, 1882): Off New Jersey – W Greenland – S Iceland – the Faroes (300-1,319 m)

Discussion

None of the 18 species with the above mentioned distribution pattern are recorded in coastal waters along the western European coasts. *Cyclopecten pustulosus* may be doubtful as a species, but if it is a "good" species as assumed by Ockelmann (1958) and not a subspecies of *Cyclopecten imbrifer*, then this species is distributed from the east coast of North America to Iceland and with eight records at the Faroe Islands.

The distribution of the polyplacophoran *Placiphorella atlantica* (5 finds during BIOFAR) has been discussed earlier by Sneli (1992). Earlier records with 11 finds and a total of 14 specimens of *P. atlantica* have mainly been made in more than 1000 m depth, from the New England coast on the east American coast to West Africa (25°39'N, 15°58'W) , the Azores and the Bay of Biscay (Fig. 1). It is remarkable that although six records of this species were made during the BIOFAR programme, it has not been found during the rather extensive sampling made in the Rockall Trough since 1973 (Seaward, 1990; 1993).

If larvae evolved primarily for dispersal, then one might predict that planktonic larval development should be less common in the deep sea, where conditions tend to be more stable and habitats more continuous than in shallow water (Young, 2003). Bouchet (1976) collected deep-sea larvae among the shallow-water plankton, and Bouchet and Warén (1979) gives a very rough estimate that about 30 % of the species of the northeastern Atlantic from depths greater than 1,000 m have a larval shell indicating planktotrophic development. Using the deep sea living species *Benthonella tenella* as an example, Bouchet and Warén (1979) suggest that the larvae spend their planktonic life considerably more shallow than their parents.

During BIOFAR one find of the prosobranch *Boreotrophon dabneyi* was made south of the Faroe Islands at 1,319 m depth. Earlier records of the species have all been made south of 50° N in the bathyal parts of the East Atlantic, from the Cape Verde Islands and Azores to the northern part of the Bay of Biscay. In this area it is recorded from many stations and with many specimens (Bouchet and Warén, 1985). It is the only *Trophon* species that has a drifting larva. It is also a true bathyal species (Bouchet and Warén, 1985). In the Atlantic the distribution of *Boreotrophon dabneyi* is somewhat similar to what is known for *Placiphorella atlantica* (Fig. 1).

The species *Benthonella tenella*, *Pleurotomella packardi*, *Thyasira succisa*, and *Cardiomya curta* are together with *Placiphorella atlantica* not only distributed along the European continental slopes but also on the western side of the Atlantic (Fig. 1).

The surface circulation in the southern part of the North Atlantic starts with the North Equatorial Current driven by the Northeast trade winds (Fig. 1). This current flows to the west and is joined from the south by that part of the South Equatorial Current, which has turned across the equator into the North Atlantic. Part of this combined flow goes northwest as the Antilles Current east of the West Indies. From about Cape Hatteras it breaks away from the

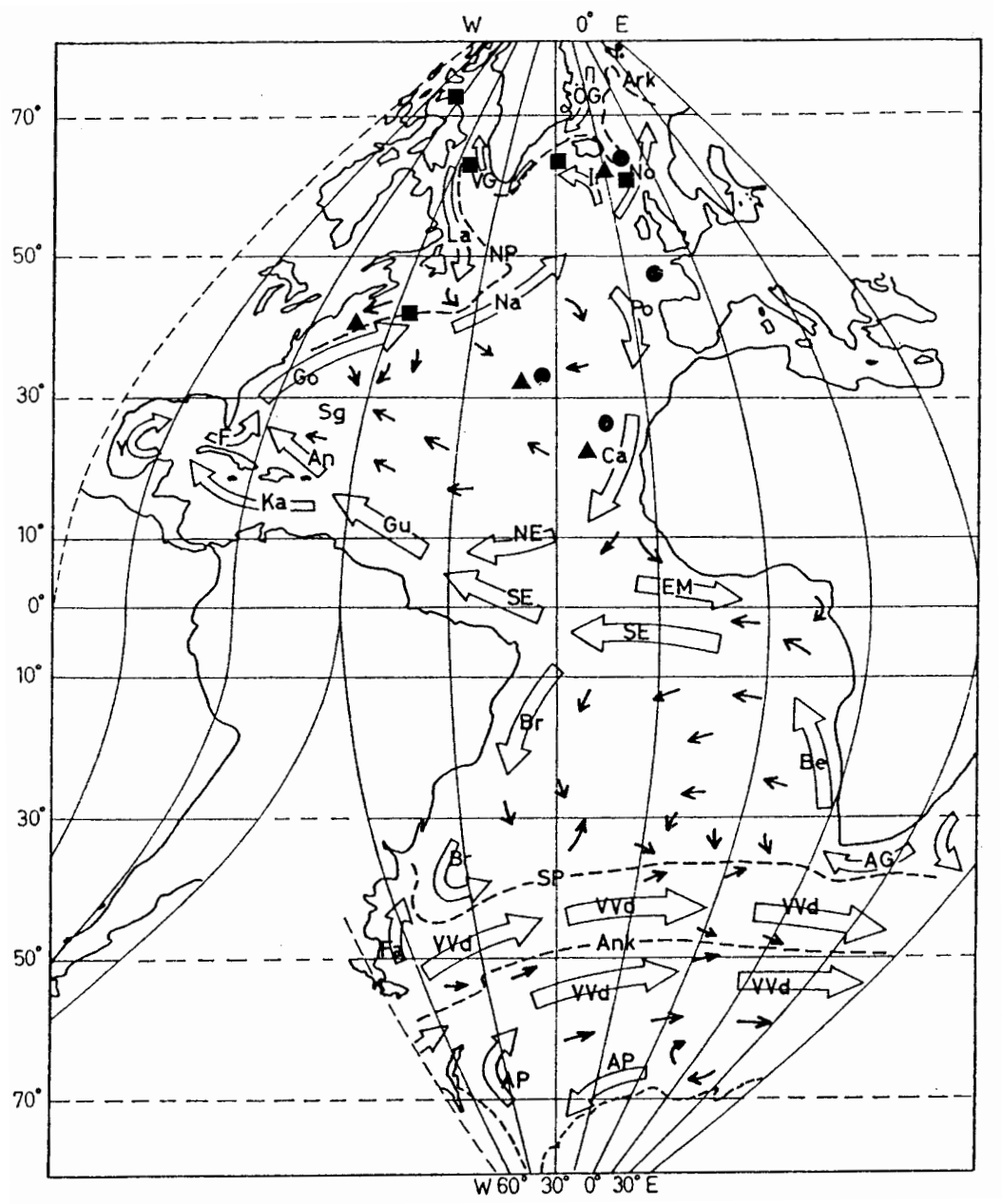

Fig. 1. *Map showing the main surface current system in the Atlantic. Na = North Atlantic Drift, Po = the Portugal Current, Ca = Canary Current, NE = the North Equatorial Current, GU = the Guianna Current, GO = the Golf Stream. Filled circles: distribution of* Boreotrophon dabneyi. *Filled triangles: distribution of* Placiphorella atlantica. *Filled squares: distribution of* Mohnia glyptus.

North American shore as the Gulf Stream. The Gulf Stream flows northeast to the Grand Banks of Newfoundland. From there, the flow that continues east and north is called the North Atlantic Drift. A part of this current turns south past Bay of Biscay, Spain and North Africa to complete the North Atlantic Gyre and to feed into the North Equatorial Current (Picard and Emery, 1990).

If planktotrophic larvae are able to make considerable vertical migrations, then the surface current patterns in the North Atlantic allow populations living in separate basins to communicate. In that way migration prevents the populations from evolving into separate species (Bouchet and Warén, 1979). Scheltema (1994) supports this idea: "It is possible that deep sea prosobranchs that use planktotrophic development, involve an ontogenetic migration to the photic zone where larvae can exploit phytoplankton as a food resource. An alternative to ontogenetic vertical migration to the surface is the hypothesis that the veliger larvae of gastropod species can remain at or near the bottom, within the nephlos or bottom boundary layer, feeding upon heterotrophic species including bacteria, flagellates and ciliates or upon particulate or dissolved organic matter".

Also the continental slopes on either side of the Atlantic which run long distances without interruption, makes it easy to spread lower-slope species a long way particularly if helped by boundary currents. A warm, north flowing current of high-salinity deep Mediterranean water, which leaves the Straits of Gibraltar with a temperature of about 13 °C passes the Bay of Biscay. By the time the warm current reaches the northern Biscay there has been a lot of mixing with colder Atlantic water but the temperature is still as high as 10 °C at 900 m depth and the 5 °C isotherm is at about 1700 m. As suitable depths and temperatures are continuous from Scotland to Greenland and Labrador it seems probable that species may occur far north (Southward, 1979). On the other hand, as a water mass having low temperature also has a low metabolic rate, a larval drift northward along the eastern American coasts into the North-Atlantic drift will transport mollusc larvae both to Greenland, Iceland and the Faroes. Not necessarily directly but stepwise, which can explain the distribution of buccinid species where the eggs hatch in a capsule and emerge as crawl away juveniles.

All the southern deep-water species recorded as far north as the Faroes during BIOFAR have their main distribution in the Bay of Biscay and its surrounding area. Having planktotrophic larvae they could easily be spread westwards by the North Atlantic Gyre and northwards by the coastal current running north. This points to the Bay of Biscay as a very central place for the evolution and spreading of deep sea mollusc species.

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