Invertebrates
Gastropods
Larval life
Biogeography

Invertébrés
Gastropodes
Vie larvaire
Biogéographie

Relationship between larval type and geographic range in marine species: complementary observations on gastropods

Michel R. BHAUD

Observatoire océanologique de Banyuls, Université Pierre et Marie Curie, Laboratoire Arago, 66650 Banyuls-sur-Mer, France.

Received 3/07/92, in revised form 2/03/93, accepted 8/03/93.

ABSTRACT

From a faunal list of 216 of the most common species of prosobranch gastropods at Beaufort, North Carolina, a group of 87 species was selected on the basis of known life cycles and geographic distributions. The larval types were categorized as teleplanic, actaeplanic, or nonplanktonic. The presence of these species in eight approximately equivalent latitudinal zones along the western shore of the Atlantic Ocean was then recorded (Scheltema, 1989). This list has been used, in the present paper, in three different ways: to identify homogeneity or heterogeneity of spatial distribution of the three biological groups; to record the presence of species in geographic sectors defined on the basis of average annual sea surface temperature; and to compare, at the two extremes of the region studied, the areas occupied by species having a particular type of development in common. It was found that: 1) the dominant type of development within a latitudinal zone depends on the geographic position of this zone; 2) the extent of the area of distribution of species with a given type of reproduction varies with latitude; 3) in terms of sea surface temperature limits, teleplanic and nonplanktonic species have similar patterns of distribution; 4) the distributions observed, whether along the coastline or transoceanic, are not fully accounted for by the inherent dispersal capacities related to larval type.

Oceanologica Acta, 1993. **16**, 2, 191-198.

RÉSUMÉ

Relations entre les modalités de développement larvaire d'espèces marines et leur aire de distribution : observations complémentaires chez les gastropodes

Une liste de 87 espèces de gastropodes prosobranches a été extraite d'un ensemble constitué des 216 espèces les plus communes de la région de Beaufort, Caroline du Nord, sur la base des connaissances de leur cycle de vie et de leur distribution géographique. Les larves ont été classées dans l'une des catégories suivantes : téléplaniques, actéplaniques et non planctoniques. La présence des espèces a été enregistrée dans huit secteurs d'égale dimension le long de la côte occidentale de l'Océan Atlantique (Scheltema, 1989). Dans le présent travail la même liste a été utilisée en privilégiant les trois éléments suivants : la distribution spatiale des trois groupes biologiques pour connaître leur représentation respective dans différentes parties de l'aire d'étude ; la distribution des espèces lorsque la limite des secteurs est basée sur les isothermes annuels ; l'influence du point d'observation en comparant, aux deux extrémités de l'aire d'étude, le nombre de secteurs occupés par des espèces partageant le même mode de développement.

Les résultats portent sur les points suivants : 1) le mode de développement larvaire dominant dans un secteur dépend de la position géographique de ce secteur ; 2) l'extension de l'aire des espèces partageant un mode précis de développement varie avec la latitude ; 3) par référence aux limites déduites des températures moyennes de surface, les distributions des espèces à larves téléplaniques d'une part et non planctoniques d'autre part, sont très voisines ; 4) les distributions observées, autant le long de la ligne de côte qu'en direction transversale, ne sont pas entièrement expliquées par la capacité de dispersion des différents types larvaires.

Oceanologica Acta, 1993. **16**, 2, 191-198.

INTRODUCTION

It is generally accepted that the benthic invertebrates whose life history includes planktonic larvae, *i. e.*, a life stage characterized by drifting in the open water, occupy a wider geographic range than those without such a stage. Furthermore, species with a long planktonic larval development would intuitively be expected to occupy a larger geographic area than species that spend only a short part of their life in the plankton (Crisp, 1977; Jablonski and Lutz, 1983 among others). The main assumption underlying this pattern is that passive dispersal is directly responsible for the geographic distribution of marine invertebrates, or, further, that there is a direct relation between the duration of a species' larval development and its geographic range. Such assumptions are very important in so far as major biological problems are involved, *e. g.* geological time length of species survival, colonization of oceanic islands, genetic structure of populations...; for this reason they ought to be re-examined.

Central to the problem is the question whether geographic range is really related to planktonic larval dispersal. In an attempt to answer this question, Scheltema (1989) divided the East coast of America between Canada and Brazil into eight zones of approximately equal latitudinal range. From a large faunal list of the most common mollusc species at Beaufort, North Carolina, 87 were selected on the basis of their life cycle and geographic distribution. For each of these species the number of zones occupied was then recorded. Species were first placed in two groups: those without planktonic larvae, and those with a veliger stage in their life cycle. About 90 % of species in the first group occupied only two or three zones; 65 % of those in the second group occupied four or five zones. It was concluded that on average there was a significant direct relation between the mode of development and the geographic range occupied by these prosobranchs. Of course the separation was not complete and there was an overlap between the two types of development; that is, some species of both types can occupy the same number of zones. Accordingly, 90 % of species without planktonic larvae and 25 % of species with a planktonic veliger stage occupy 2/3 of the zones.

In order to analyze in greater detail the relation between the length of the planktonic stage and the geographic range of the species, two categories of planktonic larvae were defined (Scheltema, 1989): actaeplanic (or coastal) larvae, with a planktonic stage lasting less than six weeks; and teleplanic (or sea-going) larvae, with a development time ranging from two months to one year. The zonal distribution of the actaeplanic species ranged from two to seven zones and completely overlapped with those of the species without planktonic larvae (two to three zones) or with teleplanic larvae (two to five zones). On the other hand, the distributions of these two latter categories hardly overlapped at all (Fig. 3 *in* Scheltema, 1989).

Considering the Atlantic as a geographic barrier, it then appeared that the amphi-Atlantic species were predominantly teleplanic: 18 (82 %) of the 22 species with teleplanic larvae, 7 (20 %) of the 35 species with actaeplanic larvae, and 3 (14 %) of the 29 species with nonplanktonic larvae were amphi-Atlantic. Thus there was a particularly clear relation between an amphi-Atlantic distribution and the presence of a teleplanic larval stage.

However, one specification should be made with regard to these results. The effect of the developmental type on the extent of species distribution is considered positive only if each species is facing the same environmental conditions. Scientific rigour indeed requires that the variables are tested "all other things being equal". In this paper the author poses the question whether developmental type of a species is the sole factor determining the number of latitudinal zones it occupies. It is with this question in mind that the known data are treated again, using different criteria.

MATERIALS AND METHODS

In this study, the same data were used as in Scheltema (1989), but the new analysis differed in several respects:

1) The locations of the zones occupied were taken into account, as the various zones I to VIII are probably not equally receptive to the various types of development.

2) A given type of development was compared at the two geographic extremes of the region studied; if the length of larval development regulates species spatial distribution, the number of zones occupied should be similar regardless of the point of observation.

3) The ecological criterion limited to the sea surface temperature was taken into account in two ways: a) by defining latitudinal zones that do not necessarily span the same geographic range but do span the same annual temperature range; and b) by considering that in their benthic phase, species at the limits of their area of distribution face crucial

boundary values of environmental parameters which are at the origin of this boundary.

For the present study new zones were defined on the basis of temperature (average annual sea surface temperature). Zones I, II, III, and IV are unchanged from those defined by Scheltema (1989) while the previous zones V, VI, VII, and VIII constitute a derived zone V'. These zones were constructed from a map of annual isotherms (Tchernia, 1978; Bé and Hamlin, 1967). Each is defined by the average annual temperature at its northern and southern boundaries (Fig. 1) and by the average temperature range between these boundaries (Fig. 2). The following limits, based on the annual isotherms (in °C), were used: zone I, isotherms below 3; zone II, 3 to 10; zone III, 10 to 18; zone IV, 18 to 25; and zone V', 25 to 27. Although these elements are not wholly relevant to the specific larval periods, which span only part of the year, they are nevertheless useful for characterizing the area occupied by the species, since adults also experience these temperatures (Cabioch *et al.*,1977; Brattström and Johanssen, 1983).

Introduction of average sea surface temperature creates an inconsistency in the establishment of divisions I to VIII: in the northern part, zones are based on a geographic division which overlaps with an ecologic gradient, while in the southern part they are based on a geographic distance within a homogeneous ecological pattern.

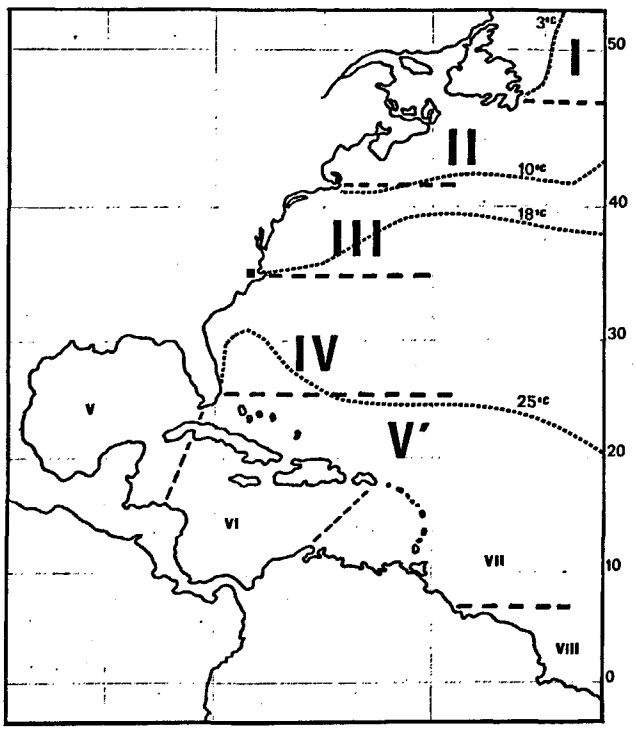

Figure 1

Western Atlantic Ocean, showing the zonal boundaries used in determining indexes of range. I-VIII, demarcated by straight broken lines (from Scheltema, 1989): successive geographical zones covering roughly equal distances. I-IV, V', demarcated by curving broken lines (present study): successive zones spanning roughly the equal ranges of annual isotherms. Divergence between the geographic and thermal patterns of division is obvious starting from geographic zone V. Black square: location of the reference faunal list.

Partie occidentale de l'Océan Atlantique montrant les différentes limites des zones utilisées pour définir un index d'occupation. Les limites I-VIII indiquées par les lignes droites discontinues (d'après Scheltema, 1989) définissent des zones consécutives couvrant chacune une distance de côte approximativement égale. Les limites I-IV puis V' indiquées par les lignes courbes discontinues définissent des zones supportant approximativement la même amplitude de température. La divergence entre la division géographique et la division basée sur la température commence à partir de la zone V. Carré noir: point d'établissement de la liste faunistique de référence.

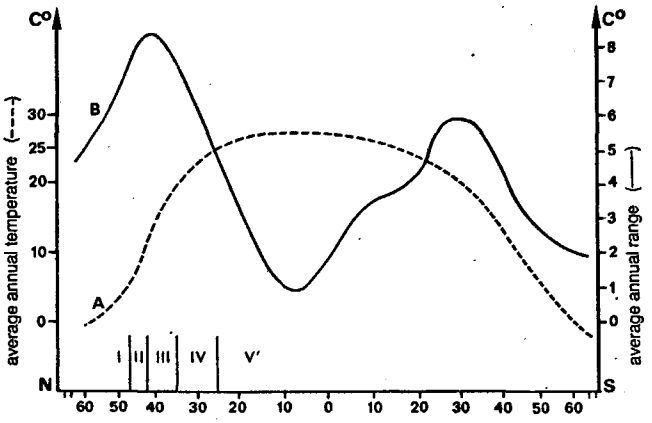

Figure 2

Temperature data for the Atlantic Ocean. Average annual: A) sea surface temperature; and B) sea surface annual range of temperature, plotted against latitude (modified from Sverdrup et al., *1946; Wüst* et al., *1954). Geographic boundaries of I-V' zones allow to deduce thermal characteristics.*

Données de température pour l'Océan Atlantique en fonction de la latitude. A : moyenne annuelle de la température de surface ; B : moyenne de l'amplitude annuelle (Sverdrup *et al.*, 1946; Wüst *et al.*, 1954, modifié). Les limites géographiques des zones I-V' permettent de déduire leurs caractéristiques thermiques.

RESULTS

Heterogeneity of the environment

The first step was to determine whether there is any spatial heterogeneity in the geographic region under study, and more specifically, whether the biological phenomena are the same throughout the study area, whether at any given location there is a constant probability of observing the same number of species for each strategy, and whether probability of dispersal of a given larval type is the same from one region to another.

Heterogeneity with regard to type of development

The zones I to VIII used to evaluate the extent of the distribution of gastropods of the western Atlantic are not homogeneous. Teleplanic species are well represented in the southern but not in the northern zones; their progression towards the northern border may be limited by various constraints related to reproductive type rather than by larval dispersal capacities. Likewise, the northern species

with direct development may not progress southward because of similar constraints. The relation found between the number of zones occupied and the dispersal capacity of the larvae would be valid if all the zones had the same capacity to accommodate representatives from all categories. Representatives of the different types of reproduction, however, do not occupy the various zones equally. It is well known that the developmental strategies used within a taxon differ between latitudes (*see* Thorson, 1950; Ockelman, 1965; Jablonski and Lutz, 1983). In the present case, most of the species with direct development were found to occupy zone I, while zone VIII was occupied by species with long-lived planktonic larval stages. Under such circumstances, the "occupation" of geographic zones by species representative of a given type of development can be evaluated, but relating such occupation to the type of development requires the assumption that a difference in the location of the observer does not affect the number of zones seen occupied.

Since the species of the three larval categories (nonplanktonic, actaeplanic and teleplanic) had different spatial distributions (nonplanktonic species were dominant in the north, while teleplanic species were dominant in the south and were not even present north of zone III), other factors than planktonic phase duration were perhaps responsible for the observed distribution. For instance, if zones I and II, from which species with teleplanic larvae were absent, have particular oceanographic features (such as currents) or climatic characteristics (such as annual temperature range or spatial gradient) preventing the survival of these species, the correlations suggested between length of larval life and geographic range would not be valid.

Heterogeneity with regard to hydrological conditions (transport and temperature)

Within the area considered, which extends from the equator to 50°N, the biogeographical boundary near Cape Hatteras (the border between zones III and IV) is particularly important. It separates two biogeographical domains (Beardsley *et al.*, 1976; Briggs, 1972; Bumpus, 1973; Tchernia, 1978). From Cape Hatteras northward the Gulf Stream leaves the American continent and runs over deep ocean. The space between the continent and the open ocean is occupied by slope water formed by the mixture of the Gulf Stream with Virginian water. This is the southernmost tip of the extension of water coming from the north. Larvae from zones V to VIII are quite likely to enter the Gulf Stream current and thence the North Atlantic drift, whereas larvae from northern zones can of course reach the south but only if they can tolerate high temperatures. On the other hand, from the equator to 20°N (southern Florida), the temperature gradient is again small. From Florida to Cape Hatteras (zone IV) the gradient is small, but beyond the cape (in zone III) it steepens considerably. Even if they are carried towards the open sea, larvae from zones II, III, and, to a lesser extent, IV must be tolerant of wide variations in temperature. But the dispersal of larvae coming from zones V, VI, VII, and VIII, and to a lesser extent from IV, is favored by stability of the surface temperature and by strong ocean currents.

Comparison within a reproductive group

Species with a given type of development were compared with regard to:1) the distribution of species as a function of number of zones occupied: the "zone-frequency distribution"; and 2) the breadth of geographical distribution of these species at the two ends of the latitudinal gradient. If in fact the duration of larval development controls the area of distribution, then species with a given type of development should occupy rather similar numbers of zones, regardless of the place where the observation is made.

a) The actaeplanic species, taken as a group, were very widely distributed, ranging from zones I to VIII (Tab. 1), the richest zones being the southern ones. So many species (indeed the majority) were observed in IV simply because the reference list was established at Beaufort, which is at the boundary between zones III and IV. The decrease in either direction is not equal, however; it is less marked in the southerly direction, no matter whether geographic (zones IV to VIII) or temperature zones (zones IV to V') are considered. This difference suggests that the two directions (north and south) are not equivalent as regards the dispersal of species with actaeplanic larvae. This observation is an additional reason for questioning the variation in spatial occupation by different species with the same larval dispersal capacity.

In addition to which zones were occupied by species of the same group, the number of zones was also considered. The zone-frequency distribution varied from 2 to 7, even though all the species had the same type of larval dispersal (Fig. 3).

Looking more specifically at the extremes of distribution (that is, at the five species occupying two zones and those five occupying six or seven zones) the five narrowly distributed species were found in zones IV and V (four species) or IV and VI (one species). In contrast, the five widely distributed species were all present at least in zones VI, VII, and VIII (*see* Tab. 1 of Scheltema, 1989). Thus, within a single larval category, the geographic location of a species does seem to affect the number of zones it occupies. This finding is shown even more clearly in Figure 4, which

Table 1

Numbers of actaeplanic prosobranch species in observation zones defined according to geographic position (I-VIII) or ecological considerations (I-V'). V' corresponds to the combined geographic zones V to VIII. The vertical line indicates the location for settling in the faunal list.

Nombre d'espèces de prosobranches à larves actéplaniques dans les différentes zones définies sur un critère géographique (I-VIII) ou sur des considérations écologiques (I-V'). V' correspond à la réunion des zones V à VIII. Le trait vertical indique le lieu d'établissement de la liste faunistique utilisée

Zone no.	I	II	III	IV	V	VI	VII	VIII
								V'
No. of species	2	9	19	36	25	24	17	19
								32

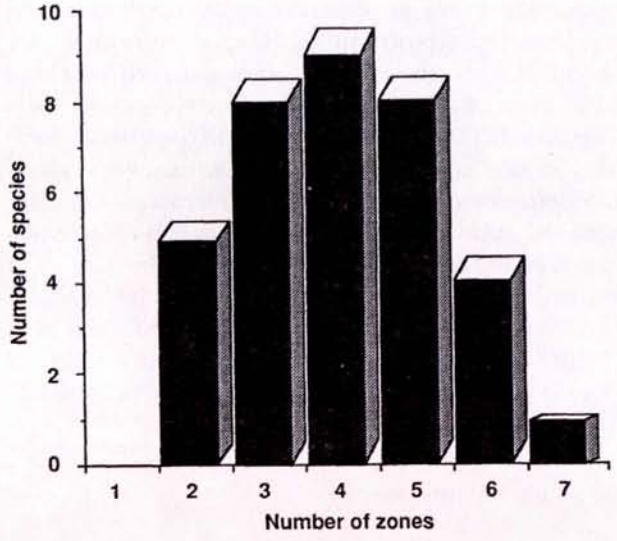

Figure 3

Zone-frequency distribution of 35 prosobranch species with actaeplanic larvae. Species in this single category occupy various numbers of zones. Two species known to have been dispersed by human action were neglected (from Scheltema, 1989).

Distribution des 35 espèces de prosobranches à larves planctoniques du type actéplanique, en fonction du nombre de zones occupées. Les espèces appartenant à un seul type de développement occupent un nombre varié de zones. Deux espèces dont la dispersion s'est faite sous l'influence humaine, ont été négligées (Scheltema, 1989).

gives zone-frequency distributions for the actaeplanic species present in zone II (Fig. 4A) and in zone VIII (Fig. 4B). Of the eight species present at the northern end of the region considered, the largest number occupied three zones, while at the southern end the largest number of species occupied five zones. The mean numbers of geographic zones occupied by northern and southern species (3.87 and 4.88, respectively) were significantly different (at 1 % level of a t-test). Again it appears that for this single type of larval dispersal there are two different patterns of zonal occupation: only a few zones for the more northern actaeplanic species, which could be called cold temperate species, and several zones for the more southern species, which could be called warm temperate.

b) Developing the same comparison among the species with nonplanktonic larvae, the mean numbers of geographic zones occupied by seven species from zone II (northerly species) and by eight species from zone VI (southerly species) were 2.4 and 3.75, respectively. These were significantly different at the 0.5 % level of a t-test. Once again, the number of zones occupied seems to be correlated not with the length of the planktonic larval mode of life but with the geographic position of the observer. This suggests that the size of the area of distribution of a given species depends less on the reproductive strategy than on a parameter related to the environment.

The sea-surface temperature criterion

When the isotherm map is superimposed, it can be seen that the various zones exhibit different temperature gradients and ranges of temperature. The more northerly the zone, the closer together the isotherms. Within a zone the thermal gradient becomes less steep from north to south.

The frequency with which species occupy a number of ecological zones is shown in Figure 5. Of the 29 nonplanktonic species, 23 (80 %) occupied two zones and 6 (20 %) occupied three zones. Of the 37 actaeplanic species, 18 (48 %)

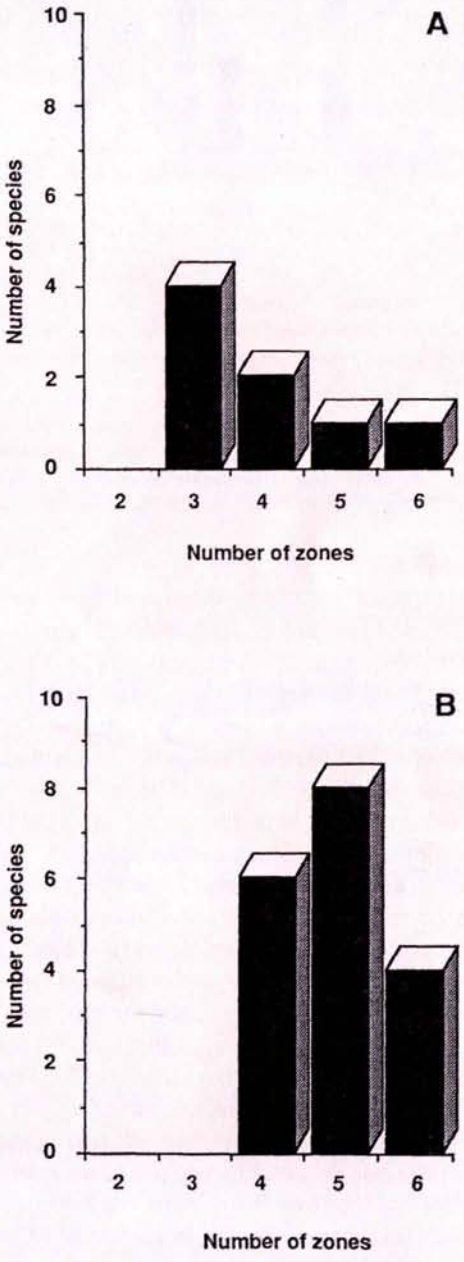

Figure 4

Zone-frequency distribution of actaeplanic larval species at the two extremes of the studied area. A: Distribution for the 8 species present in zone II (northern end); B: distribution for 18 species present in zone VIII (southern end). In the south (B) no single species occupied just three zones, whereas in the north (A) species occupying just three zones were the most numerous.

Distribution, en fonction du nombre de zones géographiques occupées, des espèces à larves actéplaniques situées aux deux extrémités de l'aire d'étude. A : distribution des 8 espèces présentes en zone II (partie septentrionale) ; B : distribution des 18 espèces présentes en zone VIII (partie méridionale). Parmi les espèces méridionales, aucune n'occupe trois zones alors que parmi les espèces septentrionales, celles occupant trois zones sont les plus nombreuses.

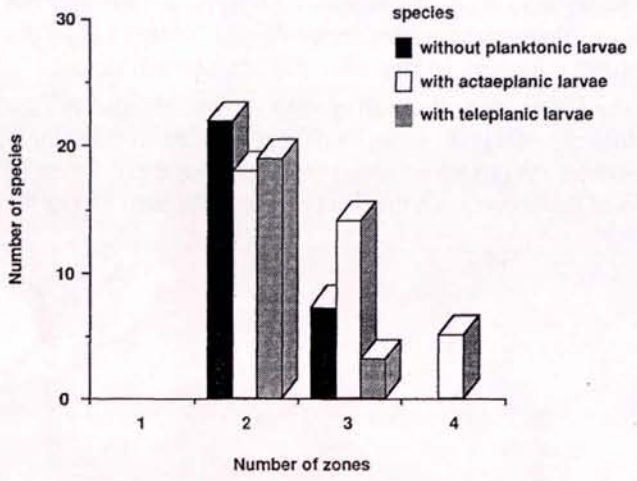

Figure 5

Zone-frequency distribution of prosobranch species according to average sea surface temperature zones. Species without planktonic larvae and species with teleplanic free-drifting planktonic development show roughly the same ecological ranges: two and three zones.

Distribution de l'ensemble des espèces de prosobranches en fonction du nombre de zones occupées et définies par la température moyenne annuelle de surface. Les espèces sans larves planctoniques et les espèces téléplaniques supportent la même amplitude écologique : deux et trois zones.

occupied two zones; 14 (37 %) occupied three zones; and 5 (15 %) occupied four zones. And of the 22 teleplanic species, 19 (86 %) occupied two zones and 3 (14 %) occupied three zones. The distributions of species with teleplanic larvae and without planktonic larvae did not differ significantly, but differed from the distribution of species with actaeplanic larvae (t-test, $p < 0.03$ and 0.05, respectively). The nonplanktonic and teleplanic species did not differ noticeably in the number of ecological zones occupied, indicating that these two categories of species with opposite larval types have comparable ecological ranges of distribution. The mean numbers of ecological zones (I-V') occupied by the three groups of species, *i. e.* with teleplanic larvae, with actaeplanic larvae, and without planktonic larvae, were 2.13, 2.65, and 2.20, respectively. The respective variances around the means were 0.123, 0.512, and 0.170. The higher variance for species with actaeplanic larvae may be related to the wide annual temperature range at their geographic position or may be related to some unknown covariate of temperature. For the two other groups, the lower variances are probably linked to the steady annual range of temperatures they experience.

Referring in greater detail to the isothermal limits of Figure 1, the ranges which the different larval types can tolerate are as follows: the nonplanktonic species, distributed over zones II + III or III + IV or II + III + IV, occupied ranges of 15, 15, and 22°C, respectively, and were tolerant of a wider range of temperatures than the teleplanic species, which appeared to be limited to zones IV + V' (on a range of 9°C). So it appears that species with a long-lived larval stage may have limited physiological tolerance to at least one physical factor. This observation agrees with the other findings concerning the geographic centers of the species which showed teleplanic larvae concentrated in the tropical regions and hence in relatively stable conditions. The actaeplanic species are of boreo-temperate origin, are exposed to pronounced seasonal variations, and have been able to evolve the broad ecological potential characteristic of eurytherms. The teleplanic species, in contrast, are located in an intertropical zone covering a narrower range of higher temperatures than the actaeplanic species, and are warm stenotherms. It can easily be shown that the actaeplanic species in fact had a distinctly more northern center of distribution than the teleplanic ones. Of the latter, only 3 (13.6 %) of 22 reached as far north as zone III and none extended farther, while of the 37 actaeplanic species, 19 (51.3 %) were collected in zone III but 9 (24.3 %) of the 37 were still present in zone II.

The amphi-Atlantic species

Two types of comparison were made. Between-group comparison (Tab. 2) confirmed the previously observed preponderance of amphi-Atlantic species in the teleplanic group, and also indicated a strong increase of the amphi-Atlantic character from zone IV southward. Of the amphi-Atlantic species, 77 % were in zone IV or south of it and occupied a relatively narrow temperature band, spanning 9°C at most (*see* Materials and methods). The effect of geography here seems marked by the boundary noted between zones III and IV. It is no accident that the amphi-Atlantic species were found almost entirely south of this boundary (*see* "Heterogeneity of the environment").

The second comparison was limited to the group of species with actaeplanic larvae. Of these, 9 species present in zone

Table 2

Numbers of amphi-Atlantic prosobranch species in: a) geographically; and b) ecologically defined zones, according to developmental type. Note that the numbers of amphi-Atlantic teleplanic species rise sharply from zone IV and then remain steady to the south of that zone.

Nombre d'espèces de prosobranches amphi-atlantiques en fonction du type de développement larvaire, comptées dans les zones définies sur une base géographique (a), puis écologique (b). A noter que le nombre d'espèces amphi-atlantiques du groupes téléplanique augmente fortement à partir de la zone IV puis reste stable au sud de cette zone.

a) ZONES OF EQUIVALENT GEOGRAPHIC DISTANCE

	I	II	III	IV	V	VI	VII	VIII	Total
No of species									
Nonplanktonic	1	2	2	2	1	1	1	1	3
Actaeplanic	0	1	3	7	7	7	4	6	7
Teleplanic	0	0	1	18	16	18	17	16	18
Total	1	3	6	27	24	26	22	23	

b) ZONES BASED ON ISOTHERMS

	I	II	III	IV	V'	Total
No of species						
Nonplanktonic	1	2	2	2	1	3
Actaeplanic	0	1	3	7	7	7
Teleplanic	0	0	1	18	18	18
Total	1	3	6	27	26	

II had a preferentially northern distribution and 18, present in zone VIII, had a preferentially southern distribution. Of the seven amphi-Atlantic species included in these two groups, only one (1/9, or 11 %) was present in zone II and six (6/18, or 33.3 %) were present in zone VIII. Again geographic location of observation seemed to affect the amphi-Atlantic character. Thus between-group and within-group comparisons both indicated an important effect of geography on the distribution of the amphi-Atlantic character.

DISCUSSION AND CONCLUSIONS

The stimulus for studying geographic range as a function of developmental type, was the desire to know whether planktonic larval dispersal is really related to geographic range, and whether there is any consistent correlation between length of larval life and geographic range of a species. The underlying assumption is that the size of a species' area depends on its capacity for genetic exchange between various points within the area, and that this exchange must take place in each generation to prevent partitioning; a fraction of the individuals of the species cannot remain isolated from the whole group. Since the capacity of a species to keep the whole of its genome homogeneous stems from dispersal, a species with a planktonic larval phase has, other things being equal, a larger area of distribution than does a species with a shorter dispersal phase. This first approach considers dispersal capacity as being measured by the length of planktonic larval development. This, in combination with information about the currents, permits evaluation of the dispersal distance per generation. Many authors (Scheltema, 1981; 1988; Hansen, 1980; Jablonski and Lutz, 1983) have argued that teleplanic species have a particularly large area of distribution, an increased adaptive capacity, and, on a geological time scale, long survival. These conclusions are not universally accepted, for several reasons:

a) A rereading of Hansen (1980) seems not to confirm the pre-eminent role of larval dispersal (Bhaud, 1989; Bouchet, 1987).

b) Recognition of the role of the environment is back on the agenda to explain a poor correlation between planktotrophy and the geological duration of species. Thus Jablonski and Lutz (1983, p. 51), on the subject of gastropods of the Late Cretaceous of the Gulf and Atlantic coastal plain, noted that the "degree of environmental tolerance also played an important role in determining species durations and geographic ranges... This factor may be responsible for the lack of a simple direct relationship between planktotrophy and species durations in Late Cretaceous bivalves."

c) The fundamental idea that dispersal over the entire area of a species is required to avoid partitioning may not be realistic. Maintaining homogeneity over a large area is less important than avoiding isolation between two close points. "It seems reasonable to suggest that in a typical species gene flow may be sufficiently weak over long distances that clines and genetically distinctive clusters of populations are common, but sufficiently strong over short distances that successful speciation is rare" (Stanley, 1979, p. 51).

The geographic boundaries of species can also be considered in terms of ecological conditions, which can be simply expressed by summer and winter isothermal boundaries. These lines run roughly east-west, so that distance measured along a meridian does not have the same ecological value as that measured along a parallel, and on a given meridian a segment encompasses different ecological values depending on its location. Many attempts have been made to interpret the distribution of animals on the basis of such a scheme by integrating two dimensions (Hutchins, 1947; Bhaud, 1983) or three dimensions if the water column is included (Bhaud *et al.*, 1978). This approach may be useful in comparing the requirements of benthic stages and planktonic larvae. From this comparison emerges the concept of pseudopopulations (consisting of benthic sterile individuals) which reveal the fact that the adults usually have a narrower temperature tolerance than the larvae, so that it is the temperature tolerance of the adults that limits the species range. An example among polychaetes is shown by a detailed study of the geographic limits of *Mesochaetopterus minutus*. Adults of this species which originates in tropical latitudes, do not extend beyond 20°N (Rosenfeldt, 1982), whereas larvae are currently collected off Arcachon, France, at 45°N (Bhaud *et al.*, 1990). Among gastropods, a recent study (Bouchet and Taviani, 1992) revealed successive biological barriers encountered by larvae originating in the Atlantic when colonizing the Mediterranean. The occupation of a very large zone by sterile benthic populations regularly replenished by larvae from the Atlantic, confirms that constraints are less severe in larvae than in adults.

At the beginning of this work, the hypothesis considered was that the higher the number of zones in which a species occurs, regardless of geographic location, the greater its dispersal capacity. The number of zones deduced from adult occupation reflects not dispersal by the larval stage, but the ecological constraints on the benthic forms. This may explain why two dissimilar groups of species, those with nonplanktonic larvae and those with teleplanic larvae, undergo similar constraints (Fig. 3) and why the developmental type does not adequately discriminate species as regards spatial occupation.

In the regulation of the space occupied by species, the prime role credited to the benthic phase is consistent with the present findings:

1) The species with actaeplanic larvae are widespread from zone I to zone VIII; the number of zones occupied varies even when the type of dispersal is the same. This number depends on geography; it is indeed greater in the south.

2) On the basis of isothermal limits, the teleplanic species and the nonplanktonic species have comparable distributions with respect to the number of zones occupied. The teleplanic species experience a narrower range of temperature (9°C) than the nonplanktonic species do (at least 15°C).

3) The relation between the amphi-Atlantic character and species with teleplanic larvae holds if the zone extending from the equator to 50°N is taken as a whole. This is implied in presenting the three distributions according to zonal occupation and ignoring the geographical situation of

zones. The validity of that correlation depends on the 87 species divided into three categories being distributed equally across all latitudes. This is far from the case, and the latitudinal succession of reproductive types indicates that the sample is biased. In order to make comparisons between species with and without planktonic development in relation to their geographic range, Scheltema (1989) warned that one must avoid selecting a series of isolated examples, but must select an unbiased sample of a large number of species. It now appears that even this condition is not sufficient: the area of study must be homogeneous in terms of the reproductive strategies operating within it and must not segregate the two or three reproductive types into different zones.

Acknowledgements

The author thanks three anonymous referees for endorsing the rationale underlying this paper and Rudolf S. Scheltema for his stimulating comments and suggestions.

REFERENCES

Bé A.W.H. and W.H. Hamlin (1967). Ecology of recent planktonic foraminifera. Part 3: Distribution in the North Atlantic during the summer of 1962. *Micropaleontology*, **13**, 1, 87-106.

Beardsley R.C., W.C. Boicourt and D.V. Hansen (1976). Physical oceanography of the Middle Atlantic Bight. *American Society of Limnology and Oceanography, Special Symposium*, *2*, 20-33.

Bhaud M. (1983). Les limites des distributions géographiques chez quelques invertébrés marins. *Océanis*, **9**, 4, 317-336.

Bhaud M. (1989). Rôle de la dissémination larvaire en paléobiogéographie réévalué à la lumière des données concernant l'époque actuelle. *Bull. Soc. géol. Fr.*, **5**, 3, 551-559.

Bhaud M., C. Bougnol et J.-C.Duchêne (1978). Observations sur la limite de répartition bathymétrique de la Polychète sédentaire *Terebellides stroemi* (Terebellidae) dans le Golfe du Lion. *C. r. hebd. Séanc. Acad. Sci., Paris, Sér. D*, **287**, 947-950.

Bhaud M., C. Cazaux et M.-H. Mathivat-Lallier (1990). Métamorphose retardée chez les larves de Polychètes et modèle d'acquisition de la vie benthique. *Océanis*, **16**, 3, 207-223.

Bouchet P. (1987). La protoconque des Gastéropodes: aspects biologiques, taxonomiques et évolutifs. *Thèse de Doctorat ès Sciences Naturelles, Université Pierre et Marie Curie, Paris*, 181pp.

Bouchet P. and M.Taviani (1992). The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? *Deep-Sea Res.*, **39**, 2, 169-184.

Brattström H and A. Johanssen (1983). Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia*, **68**, 289-339.

Briggs J.C. (1972). *Marine zoogeography, Chap. 8-9:The Northern Ocean.* McGraw-Hill Book Company, London, 195-298.

Bumpus D.F. (1973). A description of the circulation on the continental shelf of the east coast of the United States. *Prog. Oceanogr.*, **6**, 111-157.

Cabioch L., F. Gentil, R. Glaçon and C. Retière (1977). Le macrobenthos des fonds meubles de la Manche: distribution générale et écologie, in: *Biology of Benthic organisms, IIth European Symposium on Marine Biology*, BF. Keegan, P.O. Ceidigh and P.J.S. Boaden, editors. Pergamon Press, London, 115-128.

Crisp D.J. (1977). Genetic consequences of different reproductive strategies in marine invertebrates. in: *Marine organisms, Genetics, Ecology and Evolution*, B. Battaglia and J.A. Beardmore, editors. Plenum Press, New York, 257-274.

Hansen T. (1980). Influence of larval dispersal and geographic distribution on species longevity in neogastropoda. *Paleobiology*, **6**, 193-207.

Hutchins L.W. (1947). The basis for temperature zonation in geographical distribution. *Ecol. Monogr.*, **17**, 325-335

Jablonski D. and R.A. Lutz (1983). Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.*, **58**, 21-89.

Ockelman K.W. (1965). Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. in: *Proceedings of the First European malacological Congress*, L.R. Cox and J.F. Peake, editors. London 1962, 25-35.

Rosenfeldt P. (1982). Die Polychaeten der Fahrt 44 (1977) von F.S. *Meteor* in das Auftriebsgebiet vor Nordwest-Afrika. *Meteor Forschergebn., Reihe D, Biol.*, **35**, 43-53.

Scheltema R.S. (1981). The significance of larval dispersal to the evolution of benthic marine species. in: Genetics and reproduction of marine organisms. V.L. Kasyanov and A.I. Pudovkin, editors. *Proceedings XIVth Pacific Scientific Congress, Academy of Sciences USSR. Inst. Mar. Biol. Vladivostok*, 130-145.

Scheltema R.S. (1988). Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the east Pacific barrier. *Biol. Bull.*, **174**, 145-152.

Scheltema R.S. (1989). Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species, in: *Reproduction, genetics and distribution of marine organisms*, J.S. Ryland and P.A. Tyler, editors. Olsen and Olsen, Fredensborg, 183-188.

Stanley S.M. (1979). *Macroevolution: pattern and process.* W.H. Freeman and Company, San Francisco, USA, 332 pp.

Tchernia P. (1978). *Océanographie régionale. Description physique des océans et des mers.* ENSTA, Paris, 257 pp.

Thorson G. (1950). Reproduction and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25**, 1-45.

Sverdrup H.U., M.W. Johnson and R.H. Fleming (1946). *The Oceans: their physics, chemistry and general biology.* New York, Prentice-Hall, Inc., 1087 pp.

Wüst G., W. Brogmus and E. Noodt (1954). Die zonale Verteilung von Salzgehalt, Niederschlag, Verdünstung, Temperatur und Dichte an der Oberfläche der Ozeane. *Kieler Meeresforsch.*, **10**, 2, 137-161.