

Mesochaetopterus sagittarius: an example of a biogeography discrepancy between larval and adult boundaries: implication for recruitment studies

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A geographic discrepancy between the distribution boundaries for larvae and adults of the chaetopterid *Mesochaetopterus sagittarius* was recorded. The most northerly position where benthic individuals, probably not reproductive, have been collected in the Atlantic corresponds to the latitude of Aveiro (Portugal). The most northerly position for larvae corresponds to that of Arcachon (France). The larvae found off Arcachon constitute an influx of subtropical origin. They rarely succeed in passing the fixation stage, and when they do, the benthic stage is not capable of reproduction. The occupation of a very large zone by planktonic larvae spread over 4° of latitude (500 km), eventually resulting in sterile benthic populations, confirms that environmental constraints are less severe on larvae than on adults. This work emphasizes, through the integration of different oceanographic disciplines, the importance of knowing the structure of the spatial distribution of adults when seeking to achieve a better understanding of local recruitment.

INTRODUCTION

This work is an attempt to establish links between the distribution of benthic adults and planktonic larvae, and the hydrodynamic conditions at the northernmost boundary for the species *Mesochaetopterus sagittarius*. There are three reasons for studying species' distribution boundaries: (i) to show how ecological constraints on the species are in balance with the environmental characteristics; (ii) to take advantage of processes that are more clear-cut at the boundaries than in the centre of the distribution; and (iii) to understand time-related changes of a distribution, in order to build up palaeogeographic interpretations. The first two points are directly related to the objectives of the present study. Temperature range and the physiological boundaries differ for the different stages of development: the larvae, the juveniles, the vegetative adults and the sexually mature adults. These differences are particularly clear when the climate varies over a limited horizontal distance, giving rise to a front. These numerous factors and constraints which refer to seasonal temperatures, hydrodynamics, nature of substratum, check each stage of development. This is why the spatial distribution of a species is subdivided into zones that account for each stage of an entire life cycle, to a greater or lesser extent (Bhaud, 1998).

MATERIALS AND METHODS

The area of investigation spreads from Aveiro (Portugal) to the south coast of Brittany (Figure 1 & Table 1). The target species *Mesochaetopterus sagittarius* (Polychaeta: Chaetopteridae) (syn. *M. minutus*) is well known both in adult and larval stages. The planktonic

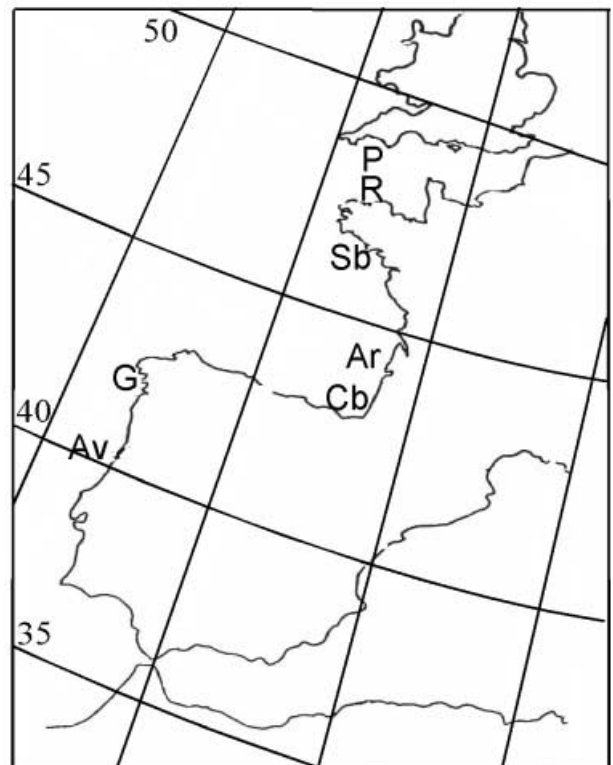


Figure 1. Map of the different locations identified in the study. For the Atlantic Ocean, the northernmost report of larvae appears to be off Arcachon (45°N). The northernmost report of adults appears to be off Aveiro (40°N). Accordingly larval drift extends at least over 5° with no corresponding representatives in the benthic fauna. Locations and references used to substantiate larval or adult presence of *Mesochaetopterus sagittarius* are given in Table 1.

Table 1. Meaning of abbreviations of locations given in Figure 1, and references used for control of larval or adult presence of *Mesochaetopterus sagittarius*.

	Meaning of abbreviations given on the map Figure 1 and latitudinal position	Presence (+) or absence (-) for larvae (L) and adults (A)	References
P	Plymouth 50°25'	L - A -	Lebour, 1917 Nelson-Smith et al., 1990
R	Roscoff 48°45'	L - A -	Bodo, 1965 Cabioch et al., 1968
Sb	Southern Brittany 47°40'	L ? A -	Glémarec, 1973
Ar	Arcachon 44°40'	L + A -	Bhaud et al., 1990 Bachelet, 1987
Cb	Cap Breton 43°30'	L + A -	Sorbe, 1990 Amoureux, 1987
G	Galicia 42°30'	L ? A -	Lopez-Jamar, 1982
Av	Aveiro 40°40'	L + A +	Personal observations (G.M.) Ravara, 1997

?, no work in the literature.

larvae are large enough to attract attention when a sample is sorted *in vivo*. A young larva with one ciliated ring may be 600 μm long, while an older one with two ciliated rings and close to metamorphosis may be 2500 μm long.

Metamorphosis has been observed in larvae from the Mediterranean Sea and from the Indian Ocean (M.R.B., unpublished data). The adult distribution of *M. sagittarius* is limited to the upper levels of intertropical and

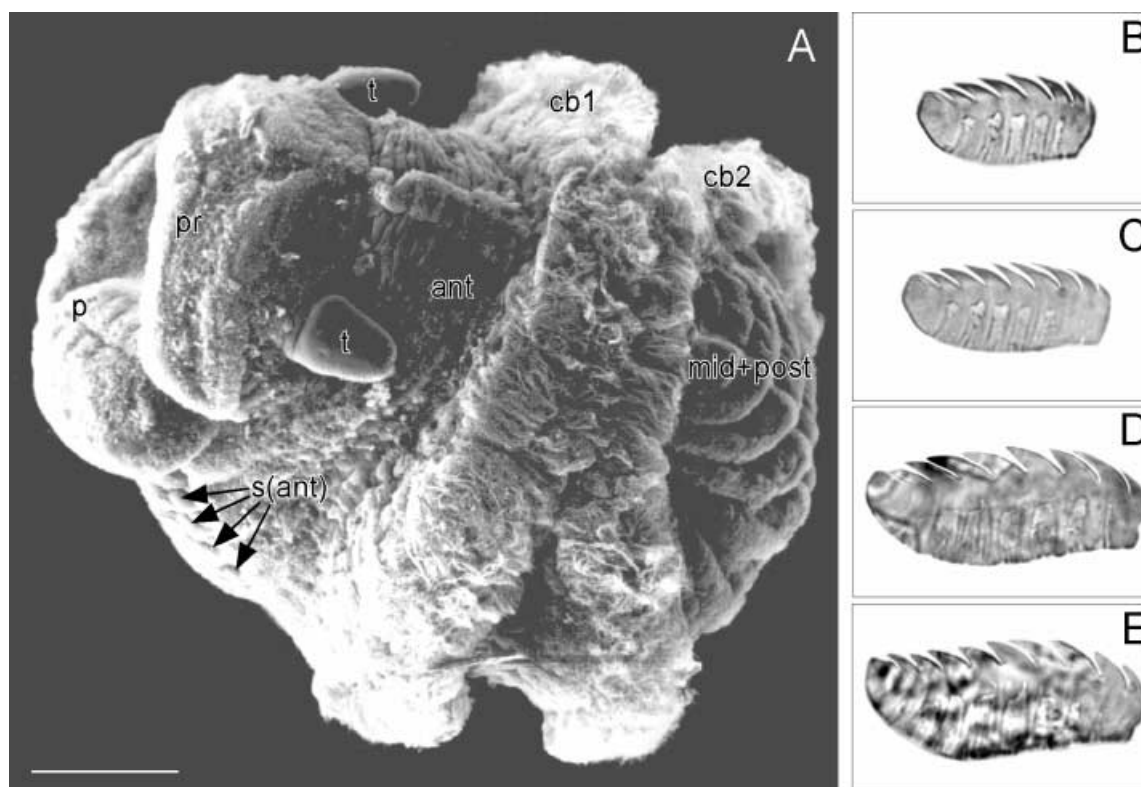


Figure 2. The target species *Mesochaetopterus sagittarius*. (A) Scanning electron microscope (SEM) image of a larval specimen collected off Cap Breton, French coast of the Atlantic Ocean. Metamorphosis is a progressive process in the development of parapodia with an increase in their components; it is not destructive, except for ciliary belts. Setae and uncini are already observable on larvae; p, prostomium; pr, peristomium; t, tentacle; cb, ciliated belt; s(ant), segments of anterior region; mid+post, middle and posterior region. Scale bar: 245 μm . (B&C) Uncinal plates of larvae collected in Arcachon area (length: 25 and 30 μm , respectively). (D&E) Uncinal plates of benthic specimens collected in Aveiro area; length for both: 40 μm . In B to E, anterior part is on the left. Notice that tooth root is vertical in all *Mesochaetopterus* sp. and oblique in all *Chaetopterus* sp.

Table 2. Origins of plankton samples. (1) Samples on the slope of the south Brittany shelf; (2) collection on a transect 44°31'N at two stations: 7 (bottom at 179 m depth, 35 miles from the coast) and 3 (bottom at 91 m depth, 14 miles from the coast); (3) collection off Cap Breton; all larvae were large, always >1700 µm long; (4) collection off Aveiro.

References	Date	Bottom depth	Sample depth	Number of larvae	Position
(1) collection off south Brittany					
9038	02/03/89	109	100	0	46°50.00'N
9138	17/03/89	110	101	0	03°13.00'W
9012	02/03/89	91	85	0	46°43.77'N
9112	17/03/89	90	85	0	03°01.52'W
9104	16/03/89	82	80	0	46°31.78'N
9204	10/04/89	83	83	0	02°44.70'W
(2) collection off Arcachon Basin					
PK8	10/05/86	179	0	0	
PK8	10/05/86	179	50	44	Station 7:
PK8	10/05/86	179	100	53	44°31.00'N
PK8	10/05/86	179	150	4	02°04.50'W
PK8	10/05/86	179	174	9	
PK6	10/05/86	91	0	0	
PK6	10/05/86	91	15	8	Station 3:
PK6	10/05/86	91	29	6	44°31.00'N
PK6	10/05/86	91	52	108	01°36.00'W
PK9	12/05/86	91	88	14	
(3) collection off Cap Breton					
Pk17	07/07/88	133	30	37	43°42.80'N, 01°51.60'W
Pk25	08/07/88	620	30	25	43°37.50'N
Pk25	08/07/88	620	100	15	01°43.50'W
Pk78	14/07/88	120	0	6	
Pk78	14/07/88	120	30	21	43°32.40'N
Pk78	14/07/88	120	100	30	01°44.00'W
(4) collection off Aveiro					
17–19 July 1997; sampling each hour during 36 h; each sampling with surface and bottom tows; total number: 76 samples		bottom from 3 to 6.5 m depth in terms of the tide; two larvae caught	Pk 46 and Pk 49: these two samples at surface and during high tide		40°30.80'N 08°25.10'W

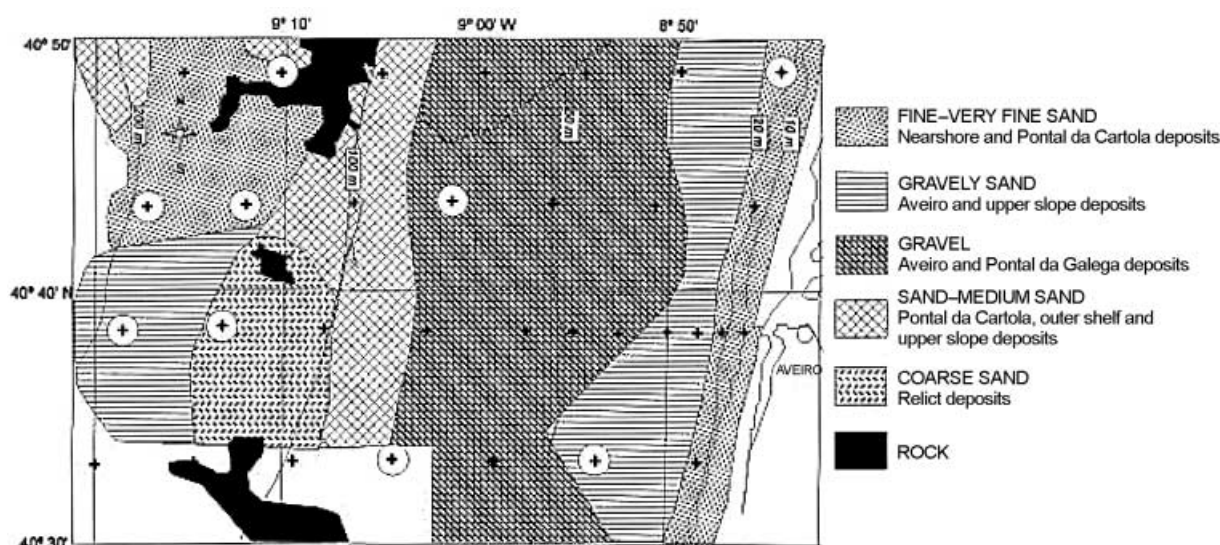


Figure 3. Map of the continental shelf off Aveiro, showing the distribution of the different sedimentary deposits (from Abrantes et al., 1994, after modifications); location of sampling stations for the study of benthic communities is indicated by a +, and positive stations for *Mesochaetopterus sagittarius* are indicated by a + within a white circle. Details are given in Table 3.

Table 3. Detailed results on the presence of benthic *Mesochaetopterus sagittarius*. This table contains the origin of benthic samples and number of specimens (Nb.S) of *M. sagittarius* for all replicates in each positive station. Stations are arranged in four transects (T) (B1 transect is south and B4 is north). On each transect (T), stations (S) are numbered from the coast to the open sea. Thirty-one stations were occupied, nine stations were positive and 25 benthic specimens of *M. sagittarius* were collected: six during the first cruise (20/07 to 03/08/1994), and 19 during the second cruise (28/07 to 05/08/1995).

T-S	Nb.S	Depth (m)	Sediment type
B1-4	5	131.8	coarse sand
B1-5	1	163.7	median sand
B2-2	1	40.7	coarse sand
B2-4	7	77.0	?
B3-4	2	71.4	coarse sand
B3-6	3	134.8	fine sand
B3-7	1	182.3	fine sand
B4-1	3	16.3	median sand
B4-6	2	124.8	?

warm-temperate regions of the Atlantic Ocean and the Mediterranean Sea. Adults are the only chaetopterids that live in a small-diameter sandy tube, in this case close to 1 mm. The duration of larval life was estimated by recording changes over time in the number and average size of successively-collected larval stocks. The extent of the planktonic stage in the larvae collected by the plankton net (200- μ m mesh) exceeds three weeks.

Four sets of planktonic samples were available (Figure 2 & Table 2). (i) The northernmost series of samples was collected on the slope of the south Armorican shelf; (ii) and (iii) in the middle part of the area, the larvae were sampled at two locations, Arcachon and Cap Breton, with the same WP2 net; (iv) in the southern part of the area of investigation, a set of 70 samples were collected in the Ria de Aveiro over a 36 h period in July 1997. Samples were taken hourly at two depths: surface and 1 m above the bottom. The plankton net was a WP2 standard model with a 200- μ m mesh. The large collection of the south Armorican shelf was sorted without success. Results of plankton sampling off Arcachon and Cap Breton were more interesting and furnished enough larvae for morphological study. Finally, in the Ria de Aveiro, only two samples collected at the surface around high tide contained *Mesochaetopterus* larvae, giving a total of two specimens.

For the benthic samples, two oceanographic surveys were carried out on the continental shelf off Aveiro: 20 July to 3 August 1994 and 28 July to 5 August 1995. Thirty-one stations were manned, spread over four parallel transects from the coast to the 200 m bathymetric level (Ravara, 1997). The material was collected with a 0.1 m² Smith-McIntyre grab, and sieved through a 1-mm mesh. The benthic samples furnished 10,353 polychaete specimens from 155 different species, including 25 specimens of *Mesochaetopterus sagittarius*, which appears in fine to coarse sands, at depths of 16 to 182 m (Figure 3 & Table 3).

In addition, the presence or absence of both planktonic larvae and benthic adults at several locations known for

their in-depth surveillance of the marine environment, was verified through scientific literature.

The following steps were involved in analysing the samples: (i) ascertain that larvae and adults belonged to the same species throughout the explored area, requiring a brief systematic review and a morphological check; (ii) identify the northernmost extensions of both larvae and adults, and deduce the drift between them; and (iii) compare this result with hydrological and thermal conditions which are susceptible to favouring planktonic larval dispersion or to creating ecological frontiers.

RESULTS

Morphological features of the larvae and taxonomic history

Among polychaete larvae, Chaetopteridae larvae have obvious and distinct characteristics. The larva is compact, barrel-shaped or globular, with the body clearly divided into three regions (Figure 2). The anterior region has a broad prostomium and peristomium, terminal mouth, one to three pairs of eyes, always two short tentacular palps, and nine setigerous segments (seven for young larvae) with notosetae that are similar to those of adults. The middle region has one, then two ciliated rings. The posterior region is tapered with segments marked by uncinigerous setae of the neuropodia and a pygidium as a terminal cylindrical appendage. Larvae are pelagic with a long planktonic life extending over several months. This family is also characterized by enlarged or modified setae, occurring on the fourth setiger of the adults. Their number and shape are distinctive characteristics for genus and species delineation. The uncini of neuropodia in the middle and posterior regions are also very useful for identifying larvae to the genus and probably also to the species level. The uncini belong to two morphological types. Type I has relatively few very prominent teeth (#10). Type II has a large number of very small teeth (#25). These differences are of value at the genus level and are applicable throughout the oceans. Other features of uncinial plates: direction, shape and number of teeth, profile of the base edge, size of tendons, are of specific value.

Among the larvae of Chaetopteridae, planktonic larvae of *Mesochaetopterus* are easily identified. They have no ventral crescent, a large buccal funnel and two ciliated rings, all of which distinguish them from *Spiochaetopterus* larvae. Both larvae and adults of *Mesochaetopterus* and *Chaetopterus* may be differentiated by their uncinial structure. The roots of the teeth may be used to differentiate between these two genera. These roots are marked by lines relative to the posterior-anterior direction of the uncinus, which are oblique in *Chaetopterus* and perpendicular in *Mesochaetopterus*. On this basis we can confirm that the larval material examined during our study belongs to the genus *Mesochaetopterus*.

To ensure that the larvae and adults examined for the study belong to the same species, it is necessary to clarify the taxonomic history of both the genus and species. Adults were first described as *Ranzania sagittaria* by Claparède (1870) and then as *Mesochaetopterus taylori* by Potts (1914). As the name *Ranzania* was already occupied, Hartman (1959) referred to *Ranzanides* Chamberlin, 1919.

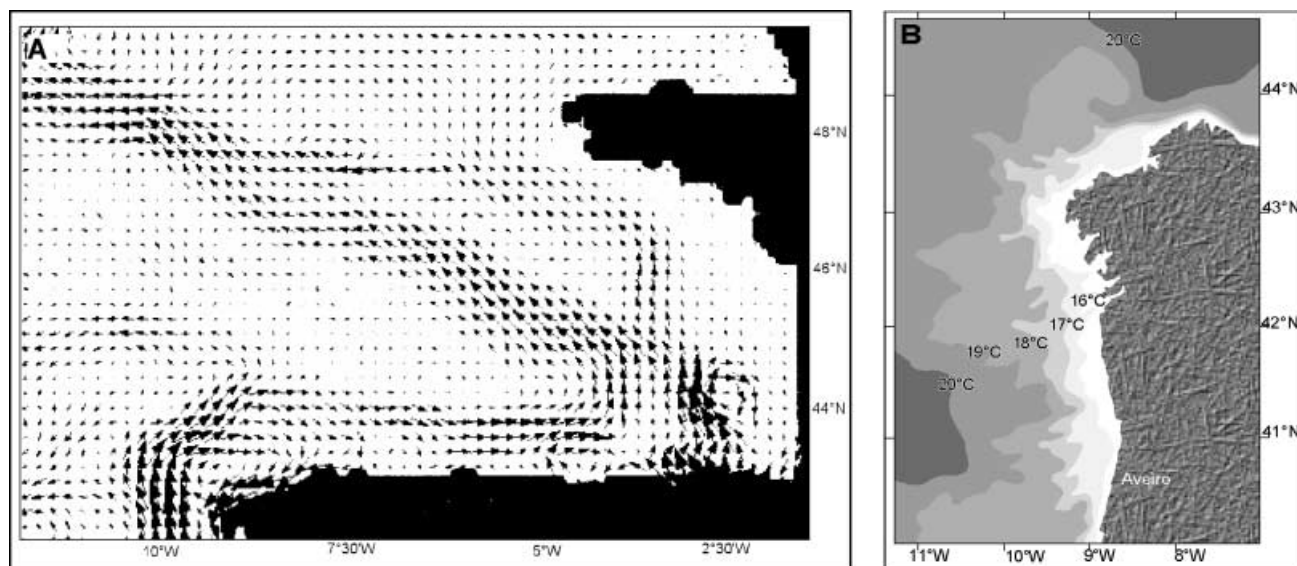


Figure 4. (A) Surface currents predicted by the OMEX three dimensional numerical model at the edge of the shelf from Galicia to southern Brittany; (B) sea surface temperature off Galicia and Portugal coasts, during summer period when the coastal up-welling is more marked.

Day (1967), Bhaud (1969), Gibbs (1972), Kudenov (1975) considered that *Mesochaetopterus* Potts, 1914 included *Ranzanides* Chamberlin, 1919. At present, the genus *Mesochaetopterus* includes chaetopterids whose bodies are composed of three distinct regions, with unilobed median notopodia which are never fused and long palps. Fauchald (1977) considers *Ranzania* Claparède, 1870 and *Ranzanides* Chamberlin, 1919 as invalid genera.

In his *Faune de France*, Fauvel (1927) used the combination of *Ranzania sagittaria* for the current '*Mesochaetopterus sagittarius*', occurring in the Mediterranean Sea and the Atlantic Ocean (Cape Verde Islands). Meanwhile, Potts in 1914 had erected the species *Mesochaetopterus minutus* for a species present in the Atlantic (Cape Verde Islands), and the Pacific (Torres Straits). Some authors, however, (Bhaud, 1969; Bailey-Brock, 1987; Nishi & Arai, 1996; Nishi, 1999) synonymized *M. sagittarius* with *M. minutus*. In light of new criteria that enables identification based on the morphology of hard structures specifically the setae and hooks, this position now seems untenable. Consequently, the denomination *Mesochaetopterus sagittarius* (Claparède, 1870) is used for species present in the Mediterranean Sea and the Atlantic Ocean. A morphological comparison shows a similitude between uncini of adult specimens from Portugal and those of larvae from Arcachon–Cap Breton. In both cases, the general shape of the uncini is asymmetric, with the lower edge describing an irregular curve, first convex in the anterior part and then concave. The posterior part of the uncinus has an oblique rectilinear border, and the height of the uncinus depends from which point it is measured. These observations confirm that we have the same species from south to north in the study area under consideration (Figure 3).

Distributions of adults and larvae off the European Atlantic coast

Off the Atlantic coast of France, no adults were collected either from the benthic communities of the continental shelf

off northern Gascony (Glémarec, 1969) or over the continental slope (Amoureux, 1987). No adults have been found in the extensive collections made in the Arcachon area (Cazaux, 1970; Bachelet, 1987) whereas planktonic samples from outside the Arcachon Basin contained many larvae (Bhaud et al., 1990). Thus, the northernmost report of larvae seems to be off Arcachon (45°N) while the northernmost report of adults seems to be from off north-west Africa at 20°N (Rosenfeldt, 1982) to 25°N (Hartmann-Schröder, 1982) and off Portugal at 40°N from the present paper. In summary, the most northerly position for larvae (i.e. Arcachon), means that they have drifted approximately 500 km north of the northernmost adults (Aveiro).

Hydrological and thermal conditions

The wind and current regime along the European continental shelf was analysed off Portugal (Crowe, 1949) and more recently in the Bay of Biscay (Pingree & Le Cann, 1989, 1990). Spatial and temporal variations in the Portuguese coastal up-welling were studied by Fiuza et al. (1982), Haynes & Barton (1990) and Silva (1992). Using a combination of satellite imagery and *in situ* hydrographic data, Frouin et al. (1990) depicted, for November 1983, a warm, salty surface current that flows towards the pole during the winter for a distance of more than 1500 km off the coasts of Portugal, Spain, and south-west France. The current is trapped geostrophically by the bathymetric discontinuity at the edge of the continental shelf. The current is 25–40 km wide, about 200 m deep and propagates with velocities of 0.2–0.3 m s⁻¹. The production of the surface current involves two parameters: the geostrophic adjustment of the large-scale oceanic flow as it impinges on the continental shelf, and the onshore Eckman transport induced by southerly winds along the Portuguese coast. Further observations from 1982 to 1988, using satellite infra-red images (Frouin et al., 1990) demonstrate the presence of warm waters propagating

northwards off Portugal and north-west Spain during all the winters between 1982–1983 and 1987–1988 (Figure 4A). The temperatures near the coast are lower than offshore and this difference, in an east–west direction, is frequently more pronounced in summer (Fiuza et al., 1982) (Figure 4B). Along the whole of the Portuguese coast, from the mouth of the Minho River to Cap San Vicente, the $T_{\text{coast}} - T_{30^{\circ}\text{W}}$ anomaly has a band of very well defined maxima with values greater than -2.5°C in July, August and September. These observations point to the occurrence of a pronounced seasonal up-welling regime along the west coast of Portugal from July through September. Thermal fronts often form parallel to these currents, sometimes taking on the role of ecological barriers. As part of a study of sardine spawning in relation to hydrography, Garcia-Soto et al. (1991) published satellite images of sea surface temperature off the Galician coast of Spain in April–May 1991. At this time of the year the summer up-welling situation was becoming established, with a lessening of the winter circulation pattern, and a dominance of a northward warm water flow off the west coast of Portugal and Spain. Maps showing this very clearly are available from the OMEX Program (Ocean Margin Exchange Project) whose web address is given in the acknowledgements. Finally, conditions are assimilated for both spreading planktonic larvae and checking settlement with surviving benthic stages.

DISCUSSION AND CONCLUSIONS

The biological and oceanographic data gathered from investigating the distribution of benthic adults and planktonic larvae of *Mesochaetopterus sagittarius* in the study area beg the answers to two questions. The first of which relates to geographic discrepancy while the second relates to population recruitment.

1. The observed geographic discrepancy between area of reproducing adults and larval area, may have a functional basis or not. In other words it may represent the consequence of a biological mechanism or it could be caused by insufficient research efforts addressed to the benthic compartment. However, two arguments seem to indicate that this discrepancy is real.
 - a. First, the geographic drift between the area of reproducing adults and that of the planktonic larvae is a general phenomenon. The geographic distribution of the reproductive adult forms does not coincide with that of either the youngest benthic stages or the oldest planktonic larvae. The reproductive adult area is smaller than that of the non-reproductive benthic individuals, and then, the difference between both areas harbours sterile populations. Although rare, examples of pseudo-populations or sterile populations have been identified in annelids (Mileikovsky, 1961; Bhaud et al., 1978), echinoderms (Gage & Tyler, 1981), and molluscs (Wells & Gray, 1960; Yamada, 1977). The area of distribution of a given species, defined as the envelope of places where the complete life cycle is achieved, is therefore not necessarily identical to the area populated by any given dispersal stage; accordingly, the observed situation is not at all exceptional.
 - b. Second, *M. sagittarius* has a very patched distribution and, thus, unrepresentative sampling might be thought to explain the observed discrepancy. In fact, benthic research often involves collecting discreet individuals (cf. for instance Bachelet, 1987). The true absence of this species is obvious as a result of a large number of studies in the different rias of Galicia (Anadon, 1977; Lopez-Jamar, 1982; Mora, 1982; Mora et al., 1982; Rey & Mora, 1984), on the Cantabrian coast (Lastra et al., 1991), and in the continuous programme of benthic observation in the sea around La Coruña (Instituto Español de Oceanografía), Bilbao (University of País Vasco) and San Sebastian (AZTI). Finally, in the area of Cap Breton and Arcachon, the situation is quite clear: despite the presence of larvae in the vicinity, benthic specimens have never been collected either inside or outside the Arcachon Basin (Cazaux, 1970; Bachelet, 1987). Given the presence of sandy bottoms in this zone, favourable a priori to the species under study, the absence of benthic individuals in the samples constitutes a particularly strong argument in favour of larval dissemination unaccompanied by any benthic part of the life cycle. Thus, individual patchiness seems not to be an explanation of the adult/larval discrepancies in distribution. Even with a reduced surface area, sandy substrates capable of receiving benthic specimens are present between Aveiro and the French coasts (Lopez-Jamar & Gonzalez, 1987). Thus, the possibility of future reports of benthic specimens in the area shall not be discarded, and shall be expected with interest due to its consequences for the distribution pattern of the species.
2. Benthic *M. sagittarius* were collected in Aveiro during both years' cruises. The low number of specimens sampled, the difference in number from one year to the other, the absence of sexual maturity, all these facts suggest repeated successful settlements of newly arrived larvae originating at various distances from the settling area, and do not suggest an auto-recruitment. Settled larvae do not give rise to another generation. The exceptional larvae collected in the Ria de Aveiro are also the consequence of a drift from a more or less distant source. However, the small size ($700\ \mu\text{m}$) of these larvae could suggest a nearby source, but a thorough description (complete development of the morphological organization with nine thoracic segments and two ciliated rings) leads to the conclusion that these larvae are well advanced in their life; in addition, the empty stomach is the symptom of mediocre developmental conditions. Thus there are no proofs of a complete, permanent life cycle on the shelf off Aveiro and benthic individuals probably do not reproduce.

The hydrological situation of the studied area shows that for part of the year, particularly in winter, the currents are favourable to a larval transportation in a northerly direction. But, either at the same time or during a different period of the year, thermal discontinuities occur. Consequently, with northerly larval migration, the reproductive period of the adults becomes restricted, because larvae arrive in a northern zone during a time

window incompatible with the conditions required for reproduction. The variation in suitable reproduction season, from one latitude to another, with restriction of this period when latitude increases, is undeniably one of the factors responsible for the formation of sterile planktonic or benthic populations. Thus spatial continuity in larval presence in the water masses does not necessarily imply continuity in the adult benthic distribution of the species. In agreement, Mileikovsky (1968) showed that the area of larval dispersal for benthic invertebrates in the north-east Atlantic was much greater than that occupied by adults. The impact of currents in this region on the extension of two holoplanktonic copepods was also shown. The boundary circulation along the European continental slope is a transport vehicle for *Calanus helgolandicus* and *C. carinatus* in the Bay of Biscay. Thus the copepod fauna south-west of the British Isles includes a number of species which have their centre of distribution in the subtropical or tropical Atlantic (John et al., 1998).

In conclusion, two facts indicate that the 500 km zone, the estimated geographic difference between the northern boundaries of planktonic larvae and benthic individuals, is probably a minimum value: the northward warm water flow does not stop at the latitude of Arcachon, and the permanence of populations at the northern latitude of Aveiro is still unproven.

The integration of different oceanographic disciplines emerges as the only way to enable the living conditions of one particular species to be explained. Sedimentology allowed us to define the living conditions of the benthic adults (habitat, trophic activity, tube building...); currentology led to a definition of the conditions of dissemination of the planktonic phase; hydrology controlled the following steps of development at the end of the spreading period; detailed morphological observations guaranteed the homogeneity of the biological material throughout the geographical study area. It has been pointed out that a spatial continuity of larval presence in the water masses does not necessarily lead to the species continuing through the adult benthic part of the life cycle. The *M. sagittarius* larvae observed off Arcachon represent a subtropical influx; they do not manage to get through the fixation stage, or when benthic fixation does occur, their development stops at the juvenile phase. Local conditions ensure that the adult stage, capable of reproduction, is never reached. The fact that sterile benthic populations, regularly replenished by larvae, occupy a very large zone confirms that environmental constraints are less severe on larvae than on adults.

Northwards or southwards transport seem to account for the discrepancy between larval and adult boundaries more than for an effective boundary displacement. This discrepancy also illustrates the difficulty in understanding local recruitment in the absence of knowledge about the species' spatial limits (Bhaud, 2000). Inside the specific area where the complete cycle takes place, the currents function as efficient larval transport agents. Outside, the currents transport larvae that may successfully recruit but do not manage to complete the whole cycle: i.e. they are not efficient recruiters. Thus, the significance of the number of benthic individuals found in a given sampling will be strictly dependent on the knowledge of the sampled area relative to the area compatible with a complete life

cycle. Unfortunately, the position of the benthic sample with respect to this area is often unknown. The same is true for the degree of maturity. It is probable that most samples reported in the literature refer to benthic individuals that would never reach the end of their life cycle; as there is insufficient evidence to assume that the whole life cycle takes place. This requires both prudence and more careful observations. The sedimentary characteristics (or more generally, the habitat characteristics) of a species must be defined from any sample including potentially reproductive adults. In parallel, both the age and the degree of maturity of the benthic organisms collected at different seasons of the year must be defined.

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