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BENTHIC AMPHIPOD FAUNA (CRUSTACEA) OF THE PORTUGUESE COAST: BIOGEOGRAPHICAL CONSIDERATIONS

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ABSTRACT: Biogeographic affinities of the Amphipod fauna from the Portuguese Coast were analysed. The Portuguese Coast appeared as a transition zone where faunas from the Mediterranean and of northern affinities become mixed. The biogeographic affinities between the Portuguese Coast and the Mauritanian and Senegalese regions still remained difficult to interpret. The comparison of the life cycles between several populations of *Echinogammarus marinus* (Leach), under different environmental constraints, showed that Gammarids can have large intraspecific variations in their reproductive patterns, which might have an important role in marine amphipods speciation.

Introduction

Amphipods are peracaridean crustaceans that inhabit most of permanent waters of the world, as well as particular terrestrial habitats. In marine habitats they can be found from tropics to polar regions and from the tidal to the abyssal zone. These animals can have very different trophic patterns (*e. g.* herbivores, carnivores, scavengers, deposit, detritus or filter feeders) and they serve as principal secondary and tertiary producers in marine ecosystems, representing an extremely important link in their energy cycles. Amphipods carry out the transformation of organic food material to a form suitable as food for fishes and ultimately man (Bousfield, 1978; 1981). Their importance in macrobenthic communities, both qualitative and quantitative, and the fact of being ecologically very sensitive organisms, cause many Amphipods species to be good indicators of natural or disturbed environmental conditions.

Despite of their importance Amphipods were, up to recently, very poorly studied along the Portuguese Coast. It was mainly in the last decade that benthic surveys were carried out more systematically, allowing to increase subtantially the knowledge on the amphipod fauna.

The present inventory of the Portuguese Coast includes 256 species of Gammaridea and Caprellidea, found from 0 to 670m deep (Marques, 1989). The major concentration of sampling efforts in the higher levels (0 to 30m) introduced an important bias into the available information, which is, nevertheless, a consistent contribution to the knowledge of the amphipod fauna of the North-eastern Atlantic, from the taxonomic, ecologic, and biogeographic points of view.

Biogeography can constitute an interesting approach to interpret the origin and radiation of Amphipods in marine environments. Amphipods dispersal capability is not comparable to the ones of Molluscs, Decapods or Fishes. In fact, they have direct development and a reduced swimming capacity. Moreover, migrations, both nictemeral and horizontal, cannot compensate this features. Thus, Amphipods have a limited dispersal capability, which determines a clear endemic tendency, and reduces the probability of global faunas mixtures.

Material and Methods

Biogeographic affinities of the amphipod fauna of the Portuguese Coast were analysed from data concerning a general inventory of species (Marques, 1989), and also from data exclusively on the genus *Ampelisca.* In addition, recent works about the biology of *Echinogammarus marinus* (Leach) (Gammaridae) in the Mondego estuary (Portugal) (Marques, 1989; Marques & Nogueira, *in press)* allowed to bring forward some

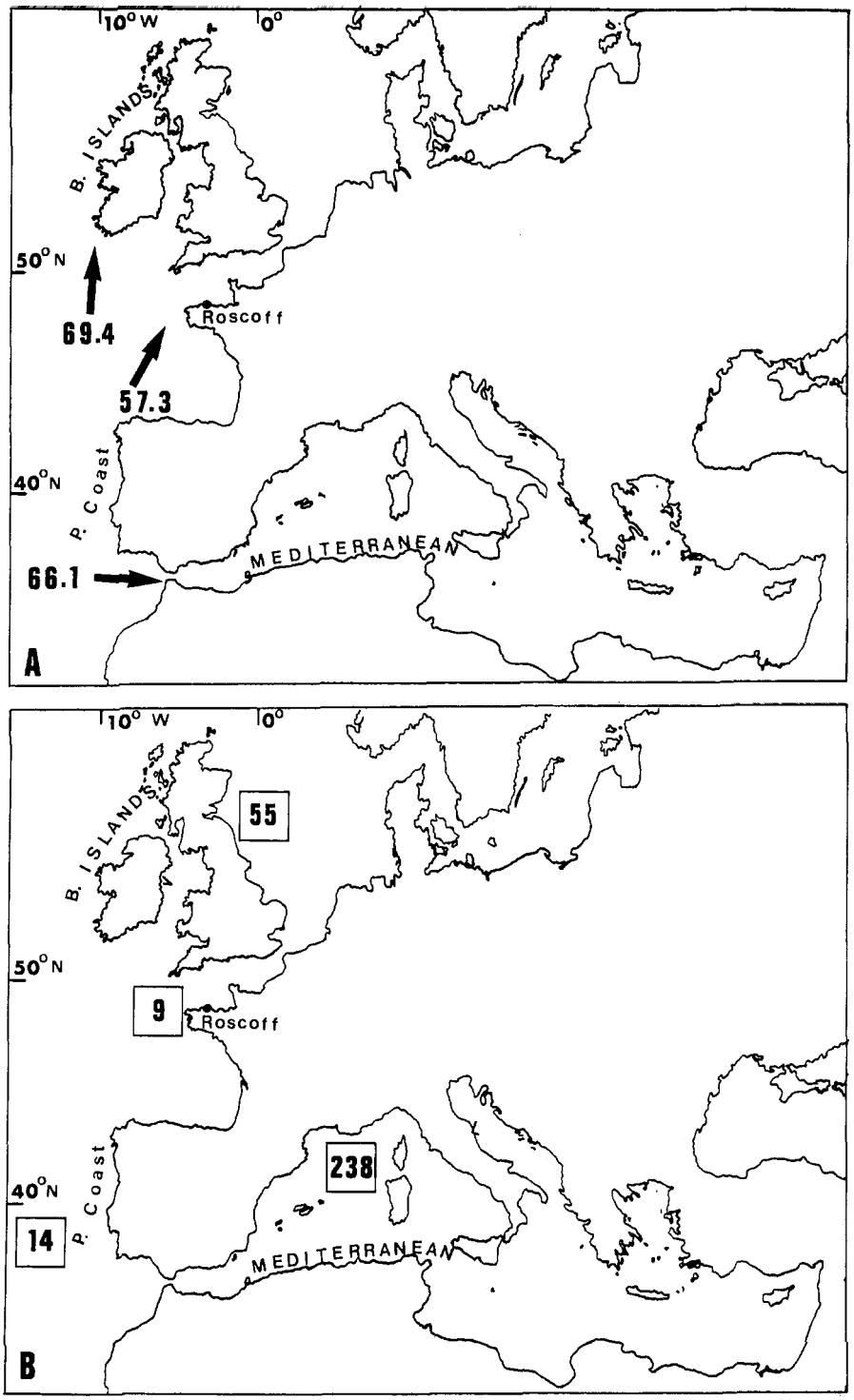

Figure 1. Comparison between the Amphipod faunas from the Portuguese Coast, the British Islands, the region of Roscoff, and the Mediterranean. A: Proportion (%) of species in common with each one of the other regions, based on the 239 Gammaridea species found along the Portuguese Coast. B: Number of species exclusively found in each region.

considerations about the latitudinal variations of the reproductive patterns within this species.

Taking into consideration the reliability of the available information, it was possible to compare the Amphipod fauna from the Portuguese Coast (256 species) with the ones from (fig. 1):

—The British Islands: Gammaridea (270 species) (Lincoln, 1979);

—The region of Roscoff (West English Channel): Gammaridea and Caprellidea (183 species) (Truchot, 1963; Toulmond & Truchot, 1964; Cabioch & Rodriguez Babio, 1975; Gentil & Bermudez, 1976; Dauvin, 1981; 1983; 1985; Dauvin & Cabioch, 1988; Dauvin & Gentil, 1979; 1980; 1983; Dauvin & Toulemont, 1988);

—The Mediterranean: Gammaridea, Caprellidea, and Ingolfiellidea (438 species) (Cavedini, 1981; Ruffo [ed] *et al.*, 1982; 1989; Krapp-Schickel & Ruffo, 1986; Bellan-Santini & Diviacco, in press; Ruffo [ed] et al., in press).

Nevertheless, one must take into consideration that there is an important bias in the available information.

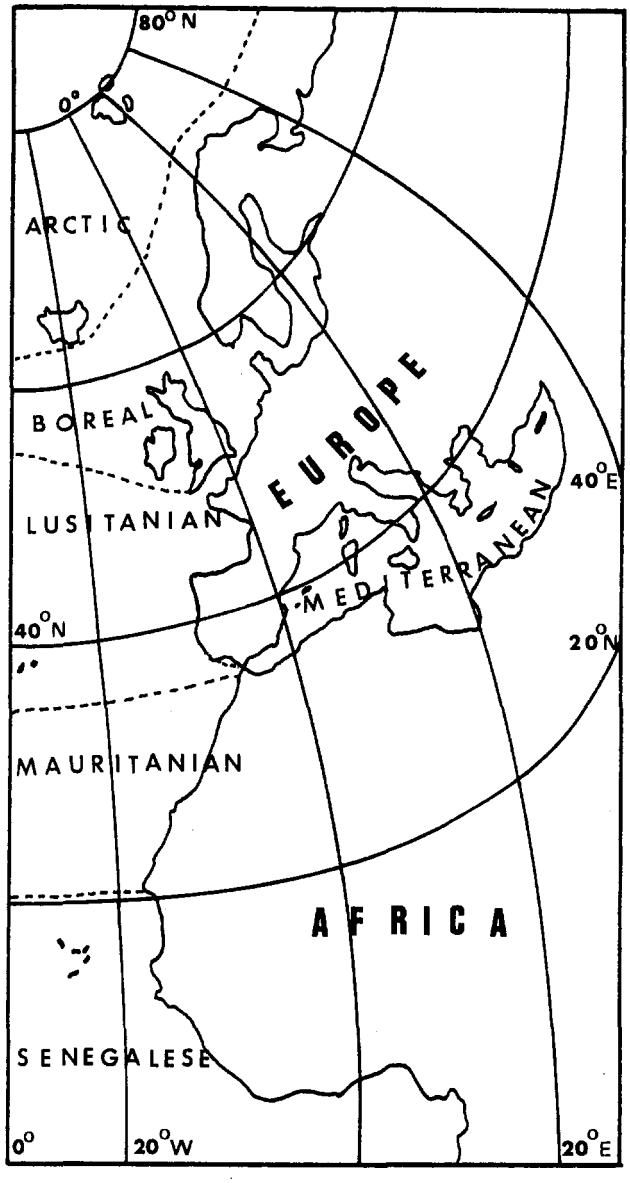

Figure 2. Biogeographical classification used in the analysis of *Ampelisca* species distribution (Fredj, 1974), to which some minor modifications were introduced (Bellan-Santini & Dauvin, 1988a; 1988b).

Actually, although the four faunas reached a total of 615 species (Gammaridea, Caprellidea, and Ingolfiellidea), for obvious reasons, the data considered as comparable between the four inventories were confined to the Gammaridea (583 species). In addition, the sampling efforts, the time of the studies, and the authors were distinct for each region.

The goal of using particularly data on *Ampelisca* was primarily to analyse the biogeographical affinities of the Portuguese Coast in the context of the North-Eastern Atlantic and Mediterranean. This genus, now well known (Bellan-Santini & Dauvin, 1988a; 1988b; 1989; Dauvin & Bellan-Santini, 1988) is taxonomically complicated but homogenous, presenting a wide world distribution, and a high rate of local endemics. Furthermore, since it is basically a littoral group (Bellan-Santini & Dauvin, 1989), the available data were less biased. Finally, of the 53 known species from the North-Eastern Atlantic and the Mediterranean (Dauvin & Bellan-Santini, 1988; Bellan-Santini & Diviacco, in press) 25 were found along the Portuguese Coast (Marques, 1989). The analysis of *Ampelisca* latitudinal distribution was based upon a biogeographic classification (Fredj, 1974), to which some minor changes were introduced (Fig. 2). For the analysis, the Portuguese Coast, although geographically included in the Lusitanian region, was considered separately, and the Mediterranean was considered as an independent biogeographic region. A Bathyal zone was also considered, independently from the horizontal regions, characterized by the four *taxa* always found at more than 200m deep.

A qualitative analysis of the available information, taking into consideration both the Gammaridea species recorded along the Portuguese Coast (239 species X 4 size matrix: Portuguese Coast, British Islands

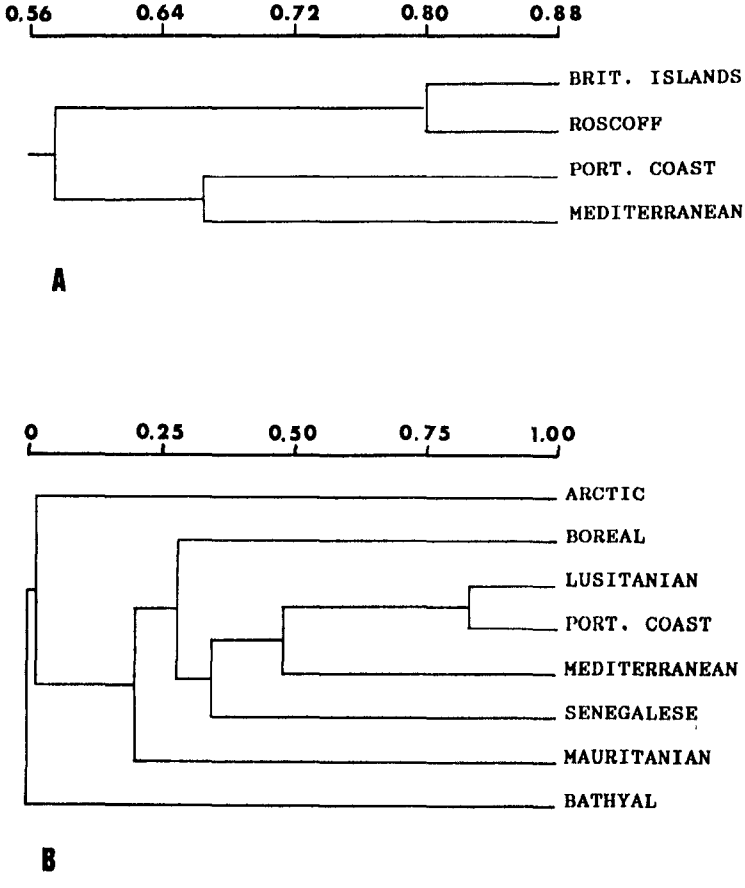

Figure 3. Biogeographic similarity (presence/absence, Q mode, Jaccard, UPGMA): A-Between the Portuguese Coast, the British Islands, the region of Roscoff, and the Mediterranean, based on 239 Gammaridea species found along the Portuguese Coast (r=0,82278); B-Of the Portuguese Coast within the North-Eastern Atlantic, based on 53 *Ampelisca* species (r=0,97420).

region of Roscoff, and the Mediterranean) and data on the genus *Ampelisca* (53 species X 8 size matrix: Arctic, Boreal and Lusitanian regions, Portuguese Coast, Mediterranean, Mauritanian and Senegalese regions, and the Bathyal zone), was accomplished using the Jaccard similarity coefficient (Q analysis) and the UPGMA clustering method (Legendre & Legendre, 1984; Sneath & Sokal, 1973). The statistical treatment was carried out with the NTSYS-PC 1.30 programs system (Rohlf, 1987).

Results and Discussion

From the analysis of the four general inventories, taking only into consideration the Gammaridea (239 species), the Portuguese Coast showed in common with the British Islands, the region of Roscoff, and the Mediterranean respectively 166 (69.4%), 137 (57. 3%) and 158 (66.1%) species (Fig. 1 A). In addition, taking into consideration the available data (Gammaridea) for each region, 55, 9, 14, and 238 species were exclusively found, respectively, in the British Islands, the region of Roscoff, the Portuguese Coast, and the Mediterranean (Fig. 1 B).

The similarity analysis (presence/absence), based upon the 239 Gammaridea species recorded along the Portuguese Coast, showed relatively stronger biogeographic affinities between this one and the Mediterranean than with the British Islands and the region of Roscoff as a whole (Fig. 3 A).

Despite of the bias above-stated, these results suggested that the Mediterranean, taking into account the large number of endemics (Fig. 1 B), constitutes an important speciation center. Moreover, the number of species in common with the Portuguese Coast showed an obvious affinity between these two regions. Therefore, the Portuguese Coast exhibited a transition fauna between the ones of Mediterranean and of northern affinities (Fig. 3 A).

The percentage of species in common between the Portuguese Coast and each one of the other faunas was roughly comparable. Nevertheless, the species composition of each group showed significant differences. Between the Portuguese Coast and the British Islands, the most important genera in number of common species, were found to be *Corophium* (eight species), *Ampelisca* (seven), *Apherusa* and *Bathyporeia* (six each), *Harpinia, Melita. Microdeutopus, Stenothoe,* and *Urothoe* (five each). Between the Portuguese Coast and the region of Roscoff the most important genera were *Ampelisca* (11 species), *Bathyporeia* (six each), *Apherusa, Microdeutopus,* and **Urothoe** (five each). Finally, between the Portuguese Coast and the Mediterranean the most important genera were *Ampelisca* (18 species), *Hyale* and *Leucothoe* (seven each), *Orchestia* (six each), *Corophium, Microdeutopus,* and *Stenothoe* (five each).

The importance of *Ampelisca* was particulaly evident within the group of common species with the Mediterranean (11.4% of the common fauna), which seems to be meaningful.

Knowledge about the distribution of *Ampelisca* species is quite complete for the Arctic and Boreal regions and for the Mediterranean (table 1). Studies in progress in the Lusitanian region are also well advanced. The available data for the Mauritanian and Senegalese regions is nevertheless older and fragmentary, and therefore less reliable.

Ampelisca eschrichtii Kröyer, which is quite rare in the Lusitanian region, appeared therefore as typical of Boreal and Arctic regions. *Ampelisca macrocephala* Liljeborg and *A. pusilla* Sars were found exclusively in the Boreal region, while *A. lusitanica* Bellan-Santini & Marques and *A. remora* Bellan-Santini & Dauvin, both uncommon to rare, were found only in the Lusitanian region.

Ten species, *A. antennata* Bellan-Santini & Kaim-Malka, *A. intermedia,* Bellan-Santini & Diviacco, *A. jaffaensis* Bellan-Santini & Kaim-Malka, *A. ledoyeri* Bellan-Santini & Kaim-Malka, *A. melitae* Dauvin & Bellan-Santini, *A. multispinosa* Bellan-Santini & Kaim-Malka, *A. planierensis* Bellan-Santini & Kaim-Malka, *A. truncata* Bellan-Santini & Kaim-Malka, *A. unidentata* Schellenberg, and *A. vervecei* Bellan-Santini & Kaim-Malka, all rare to very rare, were exclusively found in the Mediterranean.

Seven species, *A. bidentata* Schellenberg, *A. ctenopus* Schellenberg, *A. hupferi* Schellenberg, *A. monoculata* Dauvin & Bellan-Santini, *A. palmata* Barnard, *A. senegalensis* Chevreux and *A. verga* Reid, uncommon to very rare, were found only in the Senegalese region.

Four species, *A. abyssicola* Stebbing, *A. compacta* Norman, *A. odontoplax* Sars and *A. uncinata* Chevreux were considered as bathyal.

The remaining 27 species, *A. aequicornis* Bruzelius, *A. amblyops* Sars, *A. anomala* Sars, *A. anophthalma* Bellan-Santini & Kaim-Malka, *A. armoricana* Bellan-Santini & Dauvin, *A. brevicornis* s. l. (Costa), *A. calypsonis* Bellan-Santini & Kaim-Malka, *A. dalmatina* Karaman, *A. diadema* (Costa), *A. gibba* Sars, *A. heterodactyla* Schellenberg, *A. latifrons* Schellenberg, *A. massiliensis* Bellan-Santini & Kaim-Malka, *A. provincialis* Bellan-Santini & Kaim-Malka, *A. pseudosarsi* Bellan-Santini

Table 1. Biogeographical distribution of the 53 *Ampelisca* species found in the North-Eastern Atlantic and the Mediterranean. VR-very rare (found only once); R-rare (found 2 to 4 times); UC-uncommon (5 to 10 times); C-common (11 to 20 times); VC-very common (more than 20 times); ?-probable presence (Bellan-Santini & Dauvin 1988a; Dauvin & Bellan-Santini, 1988; Marques, 1989).

SPECIES	LITTORAL ZONE							BATHYAL ZONE
	ARCTIC REG.	BOREAL REG.	LUSITAN. REG.	PORTUG. COAST	MEDITER. SEA	MAURIT. REG.	SENEGAL REG.	
A. eschrichtii	VC	VC	VR					
A. macrocephala		VC						
A. pusilla		UC						
A. amblyops		R	VR					
A. anomala		R	R					
A. toulemonti		R	R					
A. aequicornis		VR	UC			R	VR	
A. brevicornis s. l.		VC	VC	VC	VC	VC	VC	
A. diadema		VC	VC	VC	VC	?	VC	
A. gibba		C	UC	R	UC	VR		
A. spinifer		R	UC	R	R	?	R	
A. spinipes		VC	VC	C	UC	VC	R	
A. spooneri		UC	UC	UC		?	R	
A. tenuicornis		VC	VC	UC	UC	VR	R	
A. typica		VC	VC	UC	C	?	UC	
A. lusitanica			UC	UC				
A. remora			R	R				
A. anophthalma			VR	VR	VR			
A. calypsonis			UC	UC	VR			
A. dalmatina			R	R	R			
A. massiliensis			VR	VR	VR			
A. provincialis			VR	VR	R			
A. pseudosarsi			R	R	VR			
A. pseudospinimana			UC	UC	R			
A. ruffoi			R	R	R			
A. armoricana			C	UC		?	C	
A. heterodactyla			R	R			UC	
A. latifrons			R	R		?	UC	
A. rubella			UC	R	C	?	R	
A. sarsi			C	C	R	?	R	
A. serraticaudata			UC	UC	UC	VR	VR	
A. spinimana			VR	UC		?	UC	
A. antennata					VR			
A. intermedia					VR			
A. jaffaensis					VR			
A. ledoyeri					R			
A. melitae					VR			
A. multispinosa					R			
A. planierensis					VR			
A. truncata					R			
A. unidentata					R			
A. vervecei					VR			
A. bidentata							VR	
A. ctenopus							UC	
A. hupferi							R	
A. monoculata							VR	
A. palmata							VR	
A. senegalensis							R	
A. verga							UC	
A. abyssicola								R
A. compacta								R
A. odontoplax								UC
A. uncinata								R

& Kaim-Malka, *A. pseudospinimana* Bellan-Santini & Kaim-Malka, *A. rubella* Costa, *A. ruffoi* Bellan-Santini & Kaim-Malka, *A. sarsi* Chevreux, *A. serraticaudata* Chevreux, *A. spinifer* Reid, *A. spinimana* Chevreux, *A. spinipes* Boeck, *A. spooneri* Dauvin & Bellan-Santini, *A. tenuicornis* Liljeborg, *A. toulemonti* Dauvin & Bellan-Santini and *A. typic* (Bate) were not confined to a single region. The extension of their horizontal distributions were, nevertheless, quite variable (Table 1).

The analysis (presence/absence) based upon the *Ampelisca* species (Fig. 3 B) showed that the Portuguese Coast, whereas included in the Lusitanian region, does not present a complete similarity relatively to it. Actually, several species present in the Lusitanian region have not been found along the coast of Portugal, which might be due to an insufficient sampling effort. The Mediterranean come next in similarity relatively to the Lusitanian region, owing primarily to the species in common with the Portuguese Coast. Affinities with the Senegalese region, although less significant, are still stronger than with the Boreal region. The low similarity relatively to the Mauritanian region, due to the bias introduced by fragmentary information, was not considered especially significant. The total dissimilarity of the Arctic and Bathyal faunas, both between each other and relatively to the others, was most obvious and do not require an explanation.

With regard to life cycles it is commonly accepted that the reproductive patterns of Gammarids evolved in relation to environmental constraints (Skadsheim, 1984; Steele & Steele, 1975; Wildish, 1982). Recent studies over the population of *Echinogammarus marinus* in the Mondego estuary (Marques & Nogueira, *in press)* allowed, up to a certain point, to test this model. Actually, in the Mondego, this species was semi-annual, with three or four generations per year (multivoltin life cycle). Other populations of this species showed very different life cycles, respectively univoltin in Denmark, in a cold-temperate to sub-polar climate (Skadsheim, 1982), and bivoltin in Normandy, in a maritime-temperate climate (Pinkster & Broodbakker, 1980).

Supposing that the observed life cycles are evolutionary stable, we must assume that Gammarids can have large intraspecific variations concerning reproductive patterns. Actually, this feature might have an important role in marine Amphipods speciation.

Conclusions

With regard to Amphipods, the Portuguese Coast appeared as a transition zone, were Amphipod faunas of Mediterranean and northern affinities become mixed. In fact, the Mediterranean influence extends beyond the straight of Gibraltar and, therefore, the Amphipod fauna of the Portuguese Coast should be considered as atlantic-mediterranean.

Biogeographical affinities between the Portuguese Coast and the Mauritanian and Senegalese regions still remained diffcult to interpret.

Finally, the comparison of life cycles between several populations of *Echinogammarus marinus,* under different environmental constraints, showed that Gammarids can have large intraspecific variations concerning their reproductive patterns, which might have an important role in marine Amphipods speciation.

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