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# VIE ET MILIEU

## *Life and Environment*

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# LIFE-HISTORY STRATEGIES IN CONTRASTING POPULATIONS OF THE COASTAL GASTROPOD *HYDROBIA* III. LAGOONAL VERSUS INTERTIDAL-MARINE *H. NEGLECTA*

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GASTROPODS  
COASTAL LAGOONS  
INTERTIDAL ZONE  
LIFE HISTORY  
POPULATION DYNAMICS

**ABSTRACT** – The expected lifetime investments in reproduction (ELIR) of two populations of the directly-developing coastal mudsnail *Hydrobia neglecta*, one in its typical lagoonal habitat (in Suffolk, U.K.) and the other the only known intertidal marine population (in Finistère, France), are compared with each other and with previous data on equivalent populations of the larviparous *H. ulvae*. In lagoonal *H. neglecta*, there are two annual periods of egg production each year, and each of the two cohorts resulting can breed in both periods – the spring one both before and after their first winter, and the late summer one only after overwintering but then twice in the same calendar year. Adult mortality rates, however, are such that individuals of each cohort have an average expectation of surviving through only a single breeding period, although their differing densities ensure that the small percentage of spring cohort individuals that do survive to breed twice contribute half the eggs of the following spring. The strategy of a cohort that breeds before overwintering, not previously recorded in *H. neglecta*, has a marked pay-off in terms of increased survival through to adulthood, but at the cost of a reduced production of eggs per individual adult, relative to the typical summer cohort. The intertidal marine population displays a single short annual period of egg laying contributed solely by overwintered pre-reproductive mudsnails that do not survive through the next winter. In marked contrast to the position in *H. ulvae* although still conforming to the predicted relationship between breeding strategy and expectation of reproductive life, the intertidal and lagoonal cohorts of *H. neglecta* that overwinter before breeding had an identical ELIR, corresponding to their effectively identical expectations of adult survival. In contrast to the finding of Lassen (1979) that the annual reproductive effort of *H. neglecta* was more than twice that of *H. ulvae*, here the ELIR of *H. neglecta* was less than that of *H. ulvae*: only 16-89 % of the investment of *H. ulvae* when both are lagoonal and 71 % of it when intertidal. The large eggs/direct development strategy of *H. neglecta* appears markedly to reduce juvenile mortality, in both lagoonal and intertidal marine habitats, in comparison to that experienced by the larviparous *H. ulvae*.

GASTÉROPODES  
LAGUNES CÔTIÈRES  
ZONE INTERTIDALE  
CYCLE VITAL  
DYNAMIQUE DE POPULATIONS

**RÉSUMÉ** – L'effort de reproduction probable (ERP) durant le cycle de vie de deux populations du Mollusque de fonds vaseux côtiers, *Hydrobia neglecta*, dont le développement est direct, est comparé à la fois entre les deux populations et aux données relatives à des populations équivalentes de *H. ulvae*, dont le développement passe par des larves. Il existe deux périodes de ponte par an pour *H. neglecta* en lagune, et chacune des deux cohortes peut se reproduire pendant deux saisons – au premier printemps qui précède ou qui suit le premier hiver et une seule fois en fin d'été seulement après avoir passé un hiver, soit deux fois dans la même année dans ce dernier cas. Le taux de mortalité des adultes est tel que les individus de chaque cohorte présentent une probabilité moyenne de survie pendant une seule période de reproduction, bien que leurs densités différentes assurent le faible pourcentage des individus de la cohorte printanière qui survivent et se reproduisent une seconde fois et fournissent la moitié des œufs produits au printemps suivant. La stratégie d'une cohorte qui se reproduit avant l'hiver, non encore observée chez *H. neglecta*, présente un grand bénéfice notable en tant que survie augmentée à l'âge adulte, mais au prix d'une production d'œufs réduite par individu adulte par rapport à la cohorte estivale typique. La population marine intertidale montre une seule courte période de ponte assurée seulement par les



animaux en pré-reproduction qui ont passé l'hiver et qui ne survivent pas au-delà de l'hiver suivant. Contrastant avec la situation de *H. ulvae* qui apparait conforme à la relation attendue entre la stratégie de reproduction et le cycle reproducteur attendu, les cohortes intertidale et lagunaire de *H. neglecta* qui passent un hiver avant la reproduction offrent un ERP identique, ce qui correspond à leur probabilité de survie adulte qui est effectivement identique. Contrairement aux résultats de Lassen (1979) montrant que l'effort annuel de reproduction de *H. neglecta* est deux fois plus élevé que celui de *H. ulvae*, il ressort de la présente étude que l'ERP de *H. neglecta* est moindre que celui de *H. ulvae* : 16 à 89 % seulement dans le cas de *H. ulvae* pour les populations lagunaires des deux espèces et 71 % dans le cas de populations intertidales. La stratégie impliquant des œufs de grande taille et un développement direct de *H. neglecta* semble réduire nettement la mortalité juvénile à la fois pour les populations lagunaires et les habitats marins intertidaux, comparativement à celle de *H. ulvae* qui présente des stades larvaires.

## INTRODUCTION

In earlier papers on reproduction in intertidal marine versus lagoonal populations of the prosobranch mudsnail *Hydrobia* (Barnes, 1988 a; 1990), it was shown that in *H. ulvae* (Pennant) the contrasting patterns of numbers of eggs produced per unit time in the two environments were consonant with the different expectations of adult survival, although egg size, number of eggs per capsule and larval characteristics remained the same. The intertidal females with a low probability of adult survival produced in their 2.75 months of expected reproductive life more eggs than did the longer-lived lagoonal females in their entire first year of breeding. Some 15 % of lagoonal adults, however, live through 5 breeding seasons (equivalent to 2.5 years) (Barnes, 1990, updated by more recent data), whereas only 10 % of intertidal adults survive even for one year after reaching maturity. These data must be somewhere near maximum values because many cohorts in both the studied habitats failed to survive through to adulthood.

Two related species, *H. ventrosa* (Montagu) and *H. neglecta* Muus, differ from *H. ulvae* in several important life-history characteristics. They lack a free-living larval stage, for example, and each deposited capsule usually contains but a single large egg (Lassen & Clark, 1979; Fish & Fish, 1981); they are also generally supposed to live through a single breeding season and to achieve a maximum size of only some 4 mm (shell height) (Lassen, 1979; Lassen & Clark, 1979; Siegismund, 1982). Like *H. ulvae*, however, the habitat range of *H. ventrosa* includes both lagoonal and (very much less commonly) intertidal localities (Cherrill & James, 1985; Heide, 1960 under the name *H. stagnorum*), although until recently *H. neglecta* has solely been recorded permanently submerged in coastal lagoons or equivalent shallow, protected, brackish, non-tidal localities (Muus, 1967; Bishop, 1976; Cherrill & James, 1985; Hylleberg, 1986; and personal observations). The discovery

in 1989 of an intertidal marine population in northwestern Finistère, France (Barnes, 1991 a), means that, like the two other *Hydrobia* spp., *H. neglecta* is now known to occur in both lagoonal and intertidal sites, inviting comparison between the directly developing *Hydrobia* species and the larviparous *H. ulvae* in terms of the effect of the different mortality patterns associated with the two differing habitat types on their life-history patterns. This paper refers solely to *H. neglecta*; the smallest of the northwest European *Hydrobia*, the most restricted in its food and habitat requirements (Hylleberg, 1976, 1986), and the most local, with a recorded range only from Galway Bay (Eire) to the Kattegat and Belt Sea (Denmark) and from Orkney (Scotland) to Finistère (France).

## MATERIALS AND METHODS

The lagoonal populations of *H. neglecta* studied were those in the Reedland Marshes lagoon system, Dunwich, Suffolk, U.K. (the 150 m<sup>2</sup> lagoon at TM 484722), with supplementary sampling from the nearby Shingle Street/Bawdsey lagoon complex, Suffolk ("Lagoon 6 - South", TM 373437) which was used as a check on cohort heights. Both these lagoons are currently separated from the sea only by some 70 m of porous shingle and their salinity is that of the local sea water (34.5 ‰), with minor variation caused by the prevailing evaporation/precipitation ratio. In each of the lagoons sampled, *H. neglecta* was the only hydrobiid present although *H. ventrosa* occurs in other lagoons within each of the two lagoonal complexes. The intertidal marine population was in an isolated 20 m<sup>2</sup> patch of *Zostera noltii* Hornem, in the Anse Lostrouc'h, at Lilia, near Plouguerneau, Finistère, France, where it occurs together with a few (c. 500.m<sup>-2</sup>) *H. ulvae* - an otherwise very uncommon sympatric combination (Barnes, 1988 b, 1991 a). Barnes (1987, 1989,



1991 a) provides further details of these study sites.

In the earlier studies of *H. ulvae* (Barnes, 1988 a; 1990) it was possible to select the lagoonal and marine study sites so as to be geographically extremely close to each other, to minimise any influence of latitude/temperature on the breeding system. Such was not possible in respect of *H. neglecta*. Even though the Suffolk lagoonal systems selected are the nearest ones, latitudinally, to Finistère that support flourishing populations of *H. neglecta*, they are still 600 km away to the northeast: mean sea surface temperatures are not likely to differ between the two sites in summer, but those in winter are liable to be some 5°C warmer in Finistère (Lee & Ramster, 1981; Gohin & Langlois, 1991).

[The only locality of this species nearer to Lostrouc'h than the Suffolk sites is the Vale Pond lagoon, Guernsey (Barrett, 1976; Anon, 1977); although no living individuals could be found there in 1976 (Stiva, 1983) nor in 1992 (Barnes, unpubl.) when the lagoon contained only *H. ventrosa*]. Because of the geographical distance between the intertidal population of *H. neglecta* and Cambridge, material from it for analysis of reproductive output also had to be maintained in the laboratory, rather than being replenished at frequent intervals (the same procedure was adopted for the lagoonal *H. neglecta*), and neither it was possible so frequently to monitor its dynamics. Present procedures therefore differed in these respects from those used earlier (Barnes, 1988 a, 1990), with the result that whereas the data on *H. ulvae* were based on average reproductive output over time, those on *H. neglecta* were derived by following the same cohorts of individuals through the breeding seasons.

Insofar as was previously known, breeding in *H. neglecta* begins in April and may last through the summer (Lassen, 1979); stocks for analysis of output of eggs per female were therefore obtained in late February 1991 (to guard against possible earlier breeding, especially in the French population), 10°C being both the temperature threshold for reproduction (Lassen, 1979) and the minimum temperature for 90% embryo survival (Fish & Fish, 1981). Some 80 pre-reproductive mudsnails (i.e. from the overwintering juvenile age class) from each of the Dunwich and Lostrouc'h sites were then maintained in the laboratory under the same conditions as described earlier for *H. ulvae* (Barnes, 1990); significant numbers of overwintering post-reproductive adults were present at Dunwich (but not in the Anse Lostrouc'h) in February and approx. 80 of these were also kept under the same regime. Similar laboratory populations of Dunwich and Lostrouc'h mudsnails were set up in July (Dunwich) and August (Lostrouc'h) 1991

containing members of the pre-reproductive cohort that entered the populations in that summer. The numbers of eggs laid by members of the different cohorts were thereafter assessed at intervals of 14 days until egg laying stopped (in December); empty egg capsules being scored as hatched eggs. The number of female mudsnails in the captive Dunwich populations was assumed to be 50% of the total individuals since surveys indicated a 1 ♂ : 1 ♀ sex ratio ( $\chi^2 = 0.05$ ;  $p > 0.7$ ); the sex ratio at Lostrouc'h, however, departed significantly from equality ( $\chi^2 = 13.7$ ;  $p < 0.001$ ), with more than twice as many females as males, and the number of females in the captive population was determined directly. After each assessment, egg capsules were removed from the dishes, as were any dead mudsnails which were replaced by individuals from reserve stocks maintained under the same experimental conditions (this was only necessary for the overwintered Dunwich adults). The animals were kept in glass dishes, containing natural alga-rich sediment from near Wells, Norfolk, and laboratory sea water both of which were changed after every assessment; the dishes were positioned under a 12 hours on/off 'growlux' tube to encourage the growth of algal food supplies, including added pieces of *Enteromorpha*. All other procedures and conditions were as described previously (Barnes, 1988 a, 1990), including the one constant-temperature regime under which both sets of mudsnails were maintained in an attempt to achieve comparability of performance, and the absence of any reason to believe that the quantity and quality of food available to the various test mudsnails were not identical throughout the experimental period (McKillup & Butler, 1979; Fletcher, 1984). Samples of 25 newly laid eggs of the Dunwich and Lostrouc'h mudsnails were measured, yielding mean egg diameters of 200 and 185 µm (somewhat larger than those recorded by Lassen, 1979 and Fish & Fish, 1981); equivalent to egg volumes of 0.0042 and 0.0033 mm<sup>3</sup>, respectively. The ash-free dry weight (AFDW) of one egg plus secreted capsular material was therefore assumed to approximate 15 µg (Dunwich) and 13 µg (Lostrouc'h) on the basis of their size relative to that of *H. ulvae* (Barnes, 1988 a; 1990) and of other small gastropods.

The population density and size structure of the Suffolk mudsnails were assessed at 4-weekly intervals from February 1991 until September 1992, and those of the French population were assessed on 10 occasions between February 1991 and August 1992; procedures were those described previously (Barnes, 1990) except as follows. (i) Because both the Dunwich and Lostrouc'h populations inhabited coarse sediments [Dunwich 86% medium sand and coarser particles by weight; Lostrouc'h 84% gravel and coarse sand], a 710 µm mesh sieve had to be used to extract the mud-



snails. (ii) Adult AFDW was estimated from measured shell heights using the regression equation of Siegismund (1982) [that yields weight in mg, not  $\mu\text{g}$  as stated by that author]. (iii) The density of an age class was calculated as the product of total density and the proportion of the given age class in the population, the estimates of the latter, together with mean heights of the various age classes, being checked where appropriate by the computer programme distinguishing overlapping normal distributions contained in Press *et al.* (1989 : 521-528).

**RESULTS**

The same intraspecific difference in behaviour between intertidal and permanently submerged populations noted by Barnes (1988 a) in respect of *H. ulvae*, namely that the intertidal marine mudsnails crawled above the water level in dishes whereas the lagoonal ones did not, was observed in the two laboratory stocks of *H. neglecta*, and as also noted in *H. ulvae* shell morphology differed in the two habitat types (Fig. 1). In contrast to the findings of Fish & Fish (1981), however, that *H. neglecta* never deposited its egg capsules on the shells of conspecific individuals, early and very late in the breeding season in the laboratory a small proportion of the Suffolk capsules (< 10 %) and up to 50 % of those of the Finistère mudsnails were so deposited, and capsules were also frequently observed on mudsnails in the field.

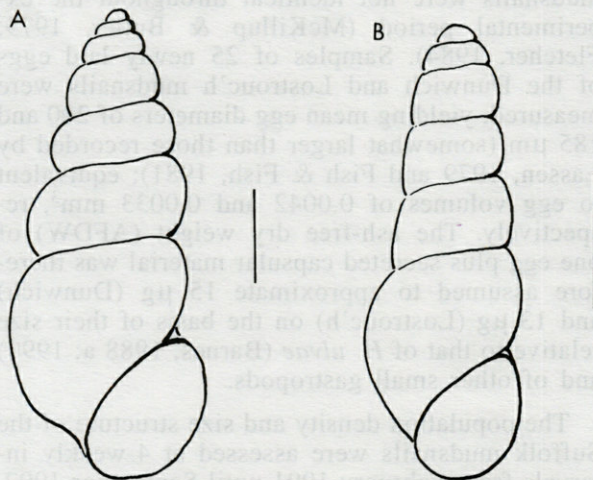


Fig. 1. - Shell morphology (camera lucida drawings) in lagoonal (A) and intertidal-marine (B) populations of *H. neglecta*: scale lines 1 mm. Note the less swollen whorls of the marine mudsnail, just as in the same comparison within *H. ulvae* (Barnes, 1988).

**Intertidal population**

The mudsnails from Lostrouc'h showed a single, very short, late spring - summer period of

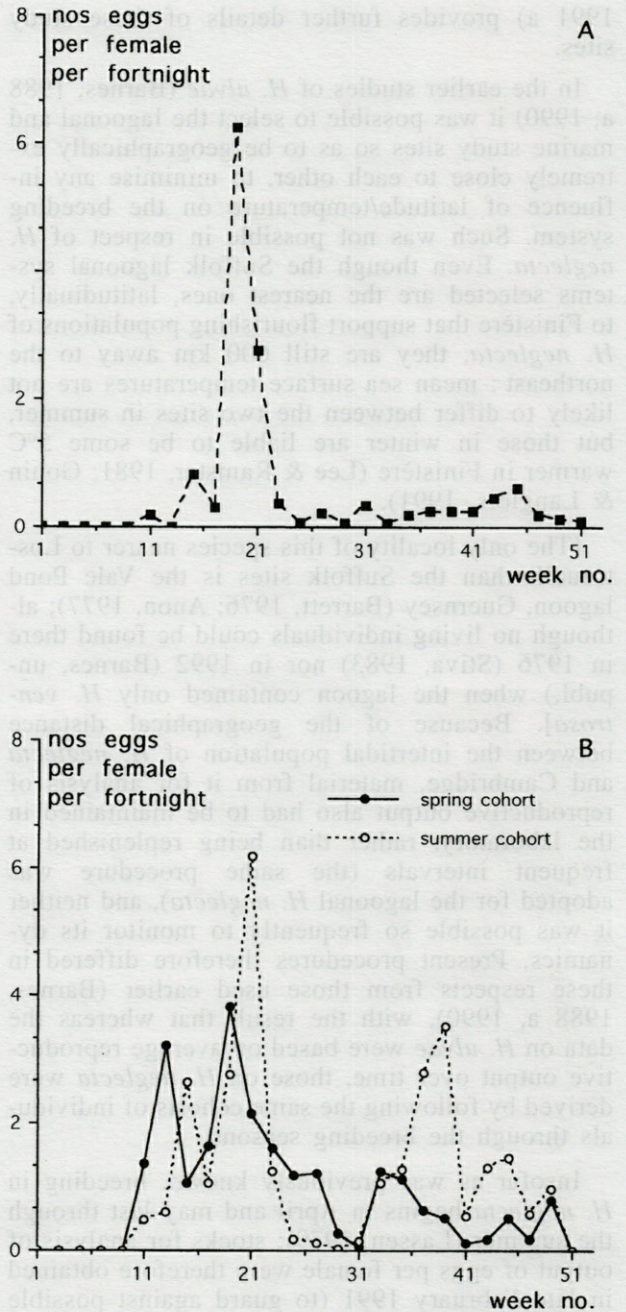


Fig. 2. - The annual pattern of egg production per female *H. neglecta* in the laboratory: A, intertidal-marine females; B, lagoonal females.

reproduction, peaking in May (Fig. 2A; 3A). All eggs were contributed by animals that first entered the censused population in the summer of the previous year but which overwintered without having bred. By December of their first calendar year, this cohort has achieved a mean height of 2 mm, increasing to 2.6 mm at the start of the breeding season and with a maximum height in the order of 4.3 mm (Fig. 4 A). Survival of these pre-and post-reproductive individuals is shown in Fig. 5 A: there was an average expectation of reproductive life of 11 weeks. Mortality between egg (as



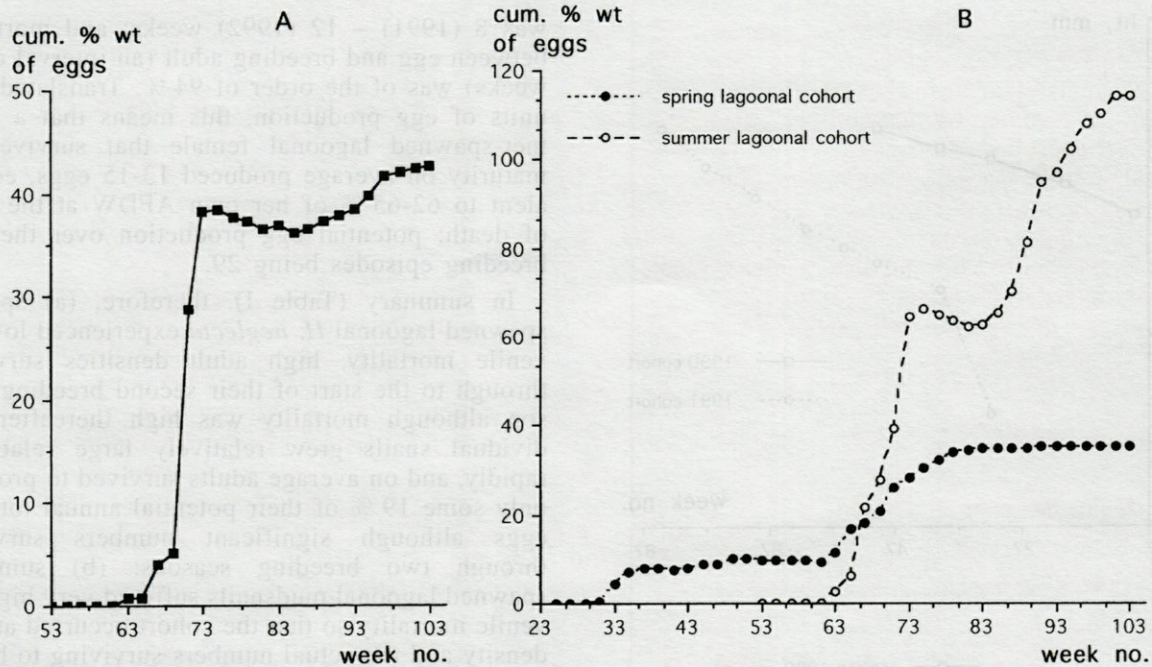


Fig. 3. - Cumulative AFDW of eggs produced per female *H. neglecta* in the laboratory from the onset of sexual maturity through the whole breeding season/s, expressed as a percentage of current female body AFDW: A, intertidal-marine females; B, lagoonal females.

estimated from Fig. 6 A) and breeding adult (an interval of 1 year) was 87 % and no adult survived through the following winter. Translated into units of egg production, this means that although capable of producing only some 14 eggs during their single breeding episode, a female that survived to maturity on average succeeded in producing 11 eggs before dying, equivalent to some 37.5 % of her own AFDW at the time of death.

#### Lagoonal population

The Suffolk lagoonal population, in contrast, displayed two peaks of reproduction during the year and consequently two annual cohorts (Fig. 2 B; 3 B). The cohort deriving from spring eggs ('spring cohort') first bred some two months later in late summer/autumn and then overwintered before breeding again in the spring. The cohort deriving from late summer/autumn eggs ('summer cohort') overwintered before breeding but then produced eggs both in the spring and again, after an interval of some 12 weeks, in the late summer/autumn. Both the annual cohorts could therefore potentially contribute to both the two peak egg-laying periods. The numbers of eggs produced per female by snails of the two cohorts were comparable during the spring laying season; during the late summer season, however, summer cohort females produced some 3-4 times as many eggs per female, as did the spring cohort females (which were then almost one and a half times the weight of the summer females). Nevertheless, in both of the survey years and during both of the

breeding periods the spring cohort mudsnails were the more numerous group and comprised the majority of the *H. neglecta* population at any one time, even in the early spring when they were the older of the two cohorts (see below). As a result, they contributed 98 % of the total summer egg production and 52 % of that in the following spring. Why survival of young mudsnails produced early in the year should be so much better than of those hatching in the autumn is not obvious, although percentage survival through to adulthood must in part be a direct reflection of the intervening length of time (17 vs 35 weeks), and differential survival over autumn/winter may be related to individual size, being better for larger snails - the spring cohort certainly invested more in individual growth up to and during their first breeding episode than did the summer cohort, and therefore achieved large size by late autumn but at the apparent cost of a lesser output of eggs (see below and Table I).

The spring cohort had achieved a mean shell height of 2.1 mm by the time of first reproduction, of 3.6 mm by the start of the second breeding episode, and a maximum one of 5.9 mm. The comparable figures for the summer cohort were 2.1 mm, c. 3.2 mm and 3.8 mm respectively (Fig. 4 B). The survival of both is shown in Fig. 5 B. In respect of the spring cohort: 14 % of adults survived to breed twice and some 8 % survived through the whole of both breeding seasons; mean expectation of reproductive life was 13 weeks; and mortality between egg (as estimated from Fig. 6B) and breeding adult (an interval of only 17 weeks)



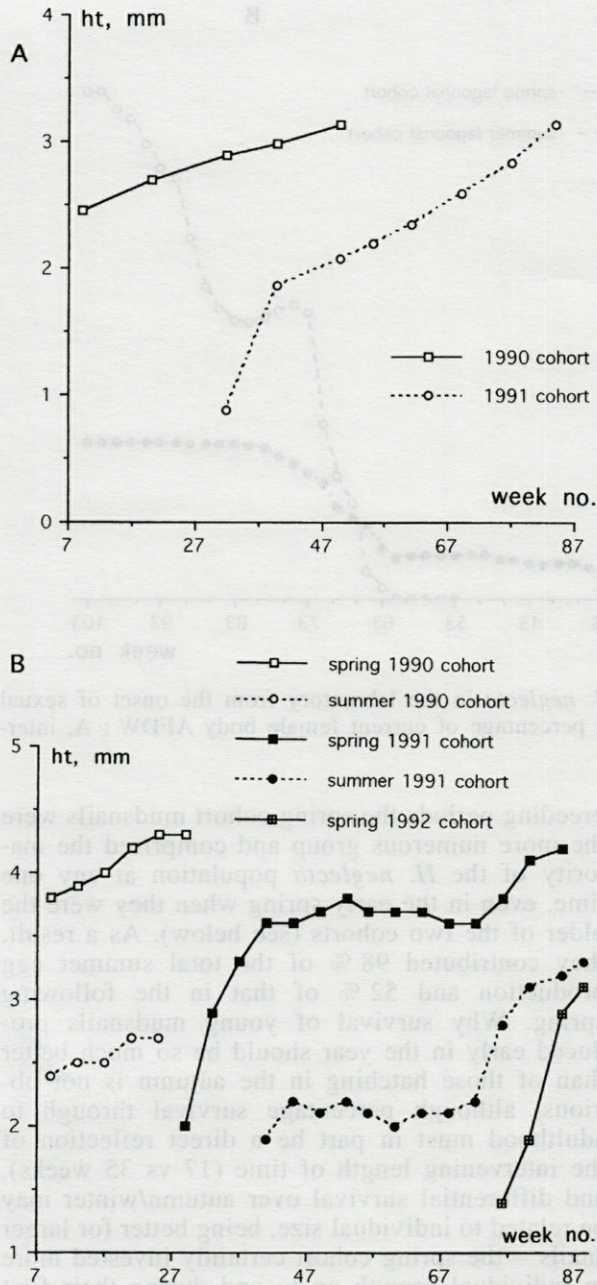


Fig. 4. - Growth curves of *H. neglecta* in the field, derived from the 1991-92 cohorts: A, intertidal-marine population; B, lagoonal population. Week 1 = 1st week of 1991; week 53 = 1st week of 1992.

was 48%. Translated into units of egg production, this means that a spring-spawned lagoonal female that survived to maturity on average only produced 4 or 5 eggs, equivalent to 9% of her own AFDW at the time of death; potential egg production over the whole of the two breeding episodes was 24. And in respect of the summer cohort: 13 (1991) - 15 (1992)% of the small number of adults present survived to breed twice, and some 9-10% survived through the whole of both breeding seasons; mean expectation of reproductive life

was 8 (1991) - 12 (1992) weeks; and mortality between egg and breeding adult (an interval of 35 weeks) was of the order of 94%. Translated into units of egg production, this means that a summer-spawned lagoonal female that survived to maturity on average produced 13-15 eggs, equivalent to 62-65% of her own AFDW at the time of death; potential egg production over the two breeding episodes being 29.

In summary (Table I), therefore, (a) spring-spawned lagoonal *H. neglecta* experienced low juvenile mortality, high adult densities survived through to the start of their second breeding season although mortality was high thereafter, individual snails grew relatively large relatively rapidly, and on average adults survived to produce only some 19% of their potential annual total of eggs although significant numbers survived through two breeding seasons; (b) summer-spawned lagoonal mudsnails suffered very high juvenile mortality so that the cohort occurred at low density and the actual numbers surviving to breed twice were negligible, the snails were individually small but fecund, adults investing heavily in reproduction and succeeding in laying some 48% of their potential 29 annual eggs; and (c) marine *H. neglecta* experienced prolonged although low-level juvenile mortality, and adults lived through a single annual breeding season in which they survived to produce 79% of their potential egg total. Juvenile and adult mortality rates were comparable in the spring lagoonal cohort and in the marine population, although those of the summer lagoonal cohort were about twice those levels.

Table I. - Summary of life-history and reproductive differences between intertidal-marine and lagoonal *H. neglecta*.

|  | Lagoonal population: spring cohort | Lagoonal population: summer cohort | Intertidal marine population |
|--|------------------------------------|------------------------------------|------------------------------|
| Mean expectation of reproductive life (wk)   | 13                                 | 10                                 | 11                           |
| Mean nos eggs produced. reproductive lifetime <sup>-1</sup>  | 4.5                                | 14                                 | 11                           |
| Potential mean annual output eggs.female <sup>-1</sup>   | 24                                 | 29                                 | 14                           |
| Mean % adult resources devoted to eggs during reproductive lifetime % [(AFDW eggs). (AFDW eggs + growth increment) <sup>-1</sup> ] | 13                                 | 70                                 | 70                           |
| Max. cumulative ratio of egg weight to female body weight % [(AFDW eggs). (AFDW body) <sup>-1</sup> ]                              | 35                                 | 114                                | 43                           |
| Max.length of adult life (attained by 5% of adults minimum) (wk)   | 50                                 | 29                                 | 45                           |
| Mortality between egg and adult (mean % wk <sup>-1</sup> )   | 3.4                                | 8.0                                | 3.9                          |
| adult mortality (mean % wk <sup>-1</sup> )   | 6.5                                | 10.0                               | 6.4                          |
| % adults surviving to breed twice  | 14                                 | 14                                 | 0                            |
| Max.adult population density (.m <sup>2</sup> )  | 12,630                             | 1,000                              | 45,400                       |
| Size (mm shell height) at first breeding   | 2.1                                | 2.1                                | 2.6                          |



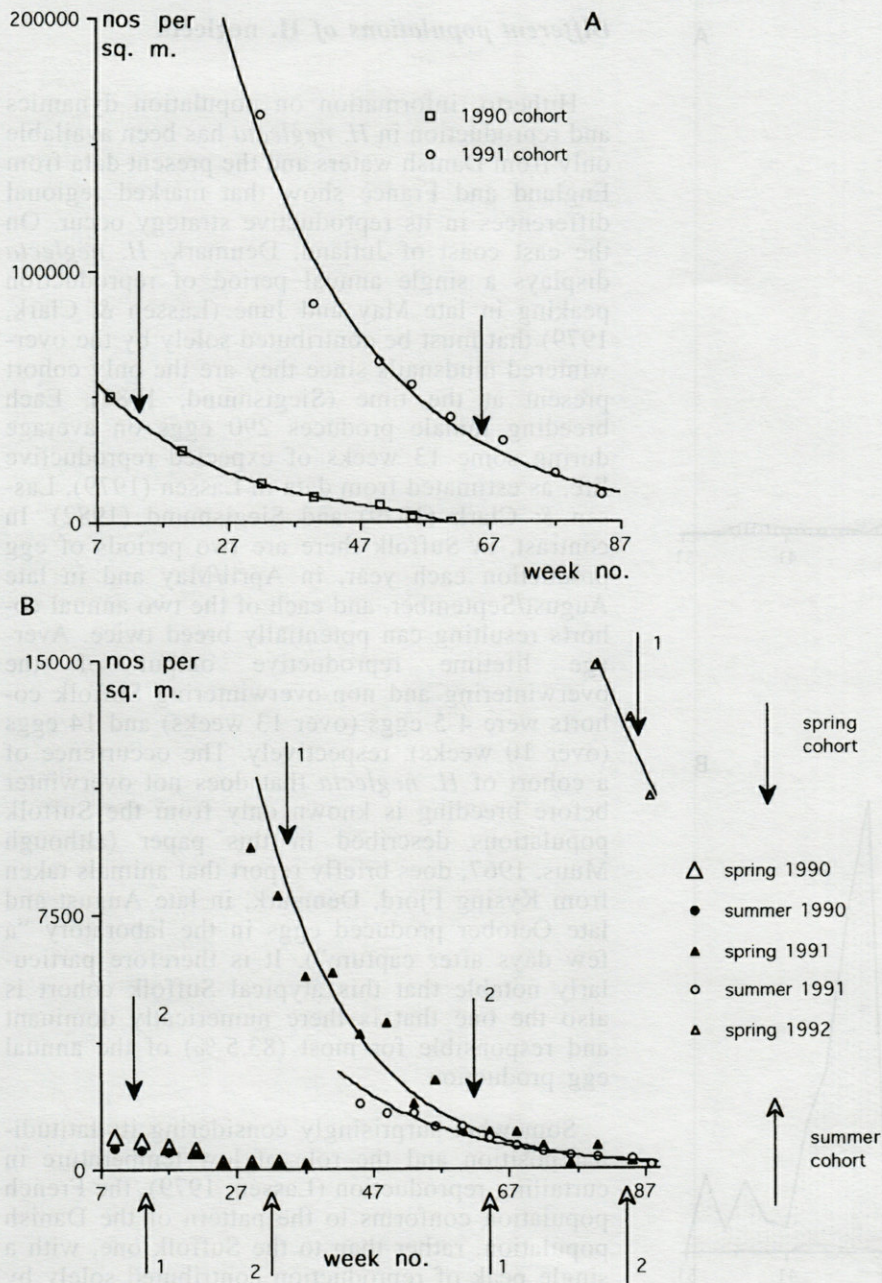


Fig. 5. - Survival of the 1991-2 cohorts of *H. neglecta* in the field: A, intertidal-marine population; B, lagoonal population. The onset of the breeding seasons is marked by arrows. Week 1 = 1st week of 1991; week 53 : 1st week of 1992.

**DISCUSSION**

As in *H. ulvae* (Barnes, 1990), considerable annual and intra-annual variation in strength and longevity of individual cohorts appears to occur in *H. neglecta* (see also the data on the 1977 and 1978 cohorts in Siegismund, 1982), and annual differences in growth rates were also evident. The extent to which the field data presented here for 1991 and 1992 are "typical" is therefore questionable, as it must be in all such short-term field studies; nevertheless useful comparisons including between habitat types are still possible.

In the laboratory, *H. neglecta* can survive for up to 3 years (Hylleberg, 1986), although in the

field survival is clearly considerably less : average life expectancy of a 2 mm mudsnail [itself some 6-10 weeks (Dunwich) or 5.2 months (Lostrouc'h) old] was only a further 11-16 weeks. Growth rates in Suffolk and Finistère are equivalent to those recorded for this and other similar small hydrobiids elsewhere : a maximum juvenile growth rate of some 0.2 mm per week (Siegismund, 1982; Mandracchia & Ruber, 1990). The Dunwich (and Shingle Street) individuals, however, may attain a larger size than has otherwise been recorded (Siegismund, 1982; Hylleberg, 1986) in part by virtue of their longer life but also because growth occurs over a longer period and, in the spring cohort, at the expense of egg production. Thus Siegismund (1982) records that in Denmark re-



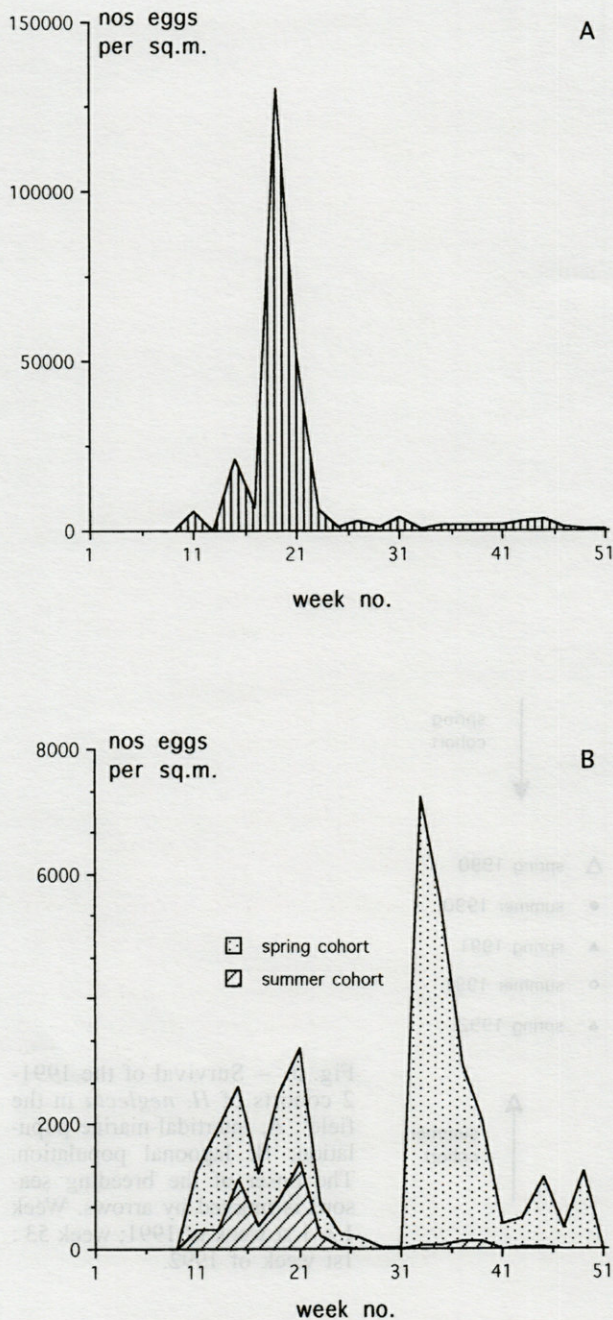


Fig. 6. Total production of *H. neglecta* eggs per m<sup>2</sup> in the field during the year, as estimated from laboratory data on numbers of eggs produced per female per fortnight and the 1991-2 field data on density of reproductively active females at intervals during the breeding periods: A, the intertidal-marine population; B, the lagoonal population.

recruitment (of 1 mm sized snails), occurs in a series of pulses between July and September and that by the following November the earlier recruited individuals had attained a mean size of 2.3 mm and the later ones 1.3 mm; the equivalent sizes for the young of the year Suffolk mudsnails in November were 3.6 and 2.2 mm.

### Different populations of *H. neglecta*

Hitherto, information on population dynamics and reproduction in *H. neglecta* has been available only from Danish waters and the present data from England and France show that marked regional differences in its reproductive strategy occur. On the east coast of Jutland, Denmark, *H. neglecta* displays a single annual period of reproduction peaking in late May and June (Lassen & Clark, 1979) that must be contributed solely by the overwintered mudsnails since they are the only cohort present at the time (Siegismund, 1982). Each breeding female produces 290 eggs on average during some 13 weeks of expected reproductive life, as estimated from data in Lassen (1979), Lassen & Clark (1979) and Siegismund (1982). In contrast, in Suffolk there are two periods of egg production each year, in April/May and in late August/September, and each of the two annual cohorts resulting can potentially breed twice. Average lifetime reproductive output of the overwintering and non-overwintering Suffolk cohorts were 4.5 eggs (over 13 weeks) and 14 eggs (over 10 weeks), respectively. The occurrence of a cohort of *H. neglecta* that does not overwinter before breeding is known only from the Suffolk populations described in this paper (although Muus, 1967, does briefly report that animals taken from Kysing Fjord, Denmark, in late August and late October produced eggs in the laboratory "a few days after capture"). It is therefore particularly notable that this atypical Suffolk cohort is also the one that is there numerically dominant and responsible for most (83.5%) of the annual egg production.

Somewhat surprisingly considering its latitudinal position and the role of low temperature in curtailing reproduction (Lassen, 1979), the French population conforms to the pattern of the Danish population, rather than to the Suffolk one, with a single peak of reproduction contributed solely by overwintered pre-reproductive mudsnails, the single annual cohort producing 11 eggs in an expected 11 weeks of reproductive life. It may be significant here that *H. neglecta* appears to be essentially a northern species (although it has a low tolerance to freezing and is frequently severely reduced or rendered locally extinct by Danish winters; Hylleberg, 1986; Hylleberg & Siegismund, 1987), and that Lassen & Clark (1979) have shown that the duration of the breeding season in Danish material decreases as temperature increases under experimental regimes; at Lostrouc'h, the species is both at the southern limit of its known range and in an atypical habitat - this may be reflected in the unusual sex ratio there. Since it is particularly sensitive to high temperatures under conditions of low salinity (Lassen & Hylleberg Kristensen, 1978), it is prob-



ably also significant that at this relatively low latitude it occurs in full strength sea water.

Comparing the corresponding cohorts (those that overwinter before breeding), the lagoonal and intertidal populations had identical reproductive investments, in marked contrast to that previously shown in *H. ulvae* (Barnes, 1990). This clearly parallels the close similarity of expected adult life span at Dunwich and Lostrouc'h. Other features of the breeding and general biology of the *H. neglecta* populations do not so easily accord with postulated relationships between reproductive investment and expectation of adult survival. The short-lived summer lagoonal cohort did produce eggs at a faster rate than the longer-lived spring cohort, for example, but the few eggs of the latter and the more plentiful eggs of the former would appear to equate more with the differential adult densities. The unusual strategy of a cohort of *H. neglecta* that breeds before overwintering clearly has a pay-off in terms of increased survival through to adulthood, but at the cost of a reduced production of eggs per individual adult, relative to the typical summer cohort. Since, however, the adult survival rates are such that individuals of each cohort have an average expectation of surviving through only a single breeding period, it follows that in practice one cohort ought solely to be the direct descendent of the previous one, and the high survival/few eggs versus poor survival/more eggs system simply alternate through the generations. In fact, however, such is the numerical dominance of the spring cohort that the small percentage of those mudsnails that do survive to breed twice nevertheless comprise significant numbers of individuals and they account for half the spring egg production. The percentage of the summer cohort adults that survive to breed twice is the same as that of the spring cohort, but numbers of individuals are very small (some 100 ♀.m<sup>-2</sup>). The explanation of these contrasting lagoonal cohorts is presumably environmental rather than evolutionary, although shortage of resources for the spring cohort under conditions of high population density would seem unlikely to be responsible for the low output of eggs since mudsnail growth rates were then high, and higher than of the low-density summer-cohort individuals that devoted their resources to egg production.

Various authors (e.g. Hylleberg, 1986) have assumed, on the basis of Lassen's (1979) estimates, that *H. neglecta* is an *r*-selected, fugitive species that can maintain its presence in an area only because of its especially high reproductive rate. The data presented here indicate that in several areas its rarity may be more a consequence of a low rate of reproduction, and its failure to persist in certain localities (Barnes, 1991 b) a consequence of recruitment problems.

### *H. neglecta* versus other *Hydrobia* species

Adult mortality in *H. neglecta* was at a much higher rate (2-6 times) than that reported earlier for *H. ulvae* (Barnes, 1990). This is not unreasonable in that *H. neglecta* has generally been considered to be a small, short-lived, semelparous species in comparison to the larger, potentially iteroparous *H. ulvae*: some 14% of lagoonal *H. neglecta* may survive through two breeding seasons but nevertheless in the laboratory mortality was very high amongst the overwintered spring-cohort Dunwich adults, then one year old, even in the absence of predators (although not of trematode parasites). The close similarity of adult mortality rates of the dominant cohort in the lagoonal habitat and that in the intertidal environment is surprising in the light of the differential mortality rates in *H. ulvae* (Barnes, 1990). It is possible that the small adult size of *H. neglecta* places it below the threshold of the relevant bird and large fish predators that are present in the coastal sea but absent from lagoons, so that its main predators may be the infaunal polychaetes and nemertines that are equally represented in both the habitat types.

Lassen (1979) estimated the annual reproductive effort of Danish *H. neglecta* to be more than twice that of local *H. ulvae*. That of *H. ulvae* is itself variable dependent on habitat (Barnes, 1990) but comparing like with like, expected reproductive effort (estimated as AFDW eggs ÷ AFDW eggs plus growth increment) of lagoonal *H. neglecta* is 16 or 89% that of lagoonal *H. ulvae* (both from East Anglia, U.K.), dependent on cohort, and of intertidal marine *H. neglecta* is 71% that of *H. ulvae* from the same habitat type (a Finistère vs East Anglia comparison). That in this study *H. neglecta* should apparently invest less in reproduction than *H. ulvae* is in part a reflection of a smaller annual output of eggs than in Denmark. Lassen (1979) estimated a mean total of 290 eggs per female per year whereas annual output was here 14 (Finistère) to 24-29 (Suffolk). The extent to which this difference requires explanation is debatable, however, in that few adult mudsnails survive throughout the breeding season to produce their potential total, except at the Finistère site where the breeding season is very short. Nevertheless, the apparent decrease in output along the Denmark

Suffolk Finistère gradient may again reflect the basic cool-water nature of *H. neglecta*.

The potential number of eggs that can be produced per annum by the Suffolk and Finistère *H. neglecta* also suggests that generally this species may be very much in the same league as the otherwise ecologically extremely similar lagoonal spe-



cies *H. ventrosa* (which can lay some 50 eggs in a year; Lassen, 1979). Hitherto, the two mudsnails have been regarded as being at opposite ends of the hydrobiid reproductive-investment spectrum (Lassen, 1979), with an investment by *H. ventrosa* of only 17 % that of *H. neglecta*. Although it is not yet possible to convert the published egg production data of *H. ventrosa* into those of lifetime reproductive investment, *H. ventrosa* and *H. neglecta*, which often occur sympatrically (Fenchel, 1975; Cherrill & James, 1985; Hylleberg, 1986), have similar lifespans, body sizes and productivity (Siegismund, 1982), similar sized eggs and development patterns (Lassen, 1979; Fish & Fish, 1981) and now similar expected reproductive lifetimes (see above) and potential annual egg production, so that a similar investment in reproduction would not be unexpected.

In fact it would not be unexpected either that the essentially lagoonal species, including *H. neglecta*, should have a lesser investment in reproduction than the mainly intertidal marine and estuarine *H. ulvae* since lagoons are likely to be more stable than the intertidal zone and in them mortality rates of large individuals are generally lower and less variable than those of the young stages, favouring small reproductive effort and the production of few (large) young, as in *Littorina* (Hughes & Roberts, 1980; Hart & Begon 1982) and within *H. ulvae* (Barnes, 1990).

There remains the question of whether the contrasting breeding strategies of *H. neglecta* and *H. ulvae* influence juvenile mortality, as the equivalent ones do, for example, in the polychaete *Streblospio benedicti* Webster (Levin & Huggett, 1990). *H. neglecta* produces large young (hatching at some 300 µm; Fish & Fish, 1981) that develop directly, whereas *H. ulvae* is larviparous and its planktonic young hatch at some 150 µm (Fish & Fish 1977; Barnes 1988 a). Here any variation in juvenile mortality between the two mudsnails must relate solely to the difference between "egg mortality" (*H. neglecta*) and "egg + larval mortality" (*H. ulvae*), since in both species the young snails begin to lead an independent benthic existence at exactly the same size (Fish & Fish, 1981; Bachelet & Yacine-Kassab, 1987). Egg mortality in *H. neglecta* was not specifically assessed in this study, but whereas Barnes (1990) estimated minimum mortality between egg and adult in *H. ulvae* to be 99.85 % (lagoonally) and 97 % (intertidally), the comparable figures for *H. neglecta* were here 48.24 % (lagoonally) and 87.2 % (intertidally). This does at least indicate greater juvenile survival in *H. neglecta*, although the time intervals involved are not the same. The percentage mortalities stated for *H. ulvae* were over periods of some 39 weeks whereas those for *H. neglecta* were of 17 or 35 (dependent on cohort) and 52 weeks respectively, so that when the data are expressed as

average mortality per week (the data being consistent with exponential declines), the figures for *H. ulvae* are 15.7 % (lagoonally) and 8.8 % (intertidally), and for *H. neglecta* are 3.4%/8.0 % (lagoonally) and 3.9 % (intertidally). Hence rates of juvenile mortality of the directly-developing *H. neglecta* are only half – at most – those seen in *H. ulvae*, and indeed, in contrast to *H. ulvae*, juvenile mortality rates are less than those of the adult *H. neglecta* in both habitats and in both lagoonal cohorts.

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# DISTRIBUTION SPATIALE D'UNE ESPÈCE BENTHIQUE ÉPITOQUE EN ZONE INTERTIDALE : RÔLE DE L'HYDRODYNAMISME ?

*Spatial distribution of an epitokous estuarine species in a tidal flat : the role of hydrodynamic processes ?*

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DISTRIBUTION SPATIALE  
LARVE  
HYDRODYNAMISME  
NEREIS VIRENS  
INTERTIDAL

**RÉSUMÉ** – Sur la base des travaux réalisés sur le site de l'Anse-à-l'Original, estuaire maritime du Saint-Laurent (Québec, Canada), nous avons évalué l'importance des sollicitations hydrodynamiques sur la distribution spatiale des individus d'une population intertidale de la Polychète *Nereis virens* Sars (Polychaeta : Nereidae). La répartition spatiale de cet Annélide repose sur une ségrégation édaphique des individus matures et immatures qui est corrélée à la texture du substrat, à sa teneur en matière organique et, en ce qui concerne les Vers de plus grandes tailles, à l'épaisseur de la couche colonisable des sédiments. Dans la partie supérieure de la zone intertidale, les densités maximales de larves sont observées dans les secteurs où les courants de marée sont les plus faibles entraînant le dépôt de fines particules sédimentaires. Par contre, les plus fortes concentrations d'adultes sont observées dans les zones du niveau inférieur qui correspondent au panache de diffusion des eaux de vidange de la baie. La comparaison des données physiques avec la répartition spatiale des individus suggère que les larves, transportées dans la colonne d'eau durant leur brève vie pélagique, sédimentent et se fixent dans les zones de faible énergie due aux courants de marée. Au terme de 3 à 4 années de croissance, les individus matures et immatures (250 à 1000 mg) entreprennent une migration vers le bas de la zone intertidale. Malgré la capacité nataoire de ces individus, les résultats de l'étude laissent croire que cette migration aurait un caractère passif et serait principalement orientée par les processus hydrodynamiques.

SPATIAL DISTRIBUTION  
LARVAE  
HYDRODYNAMIC  
NEREIS VIRENS  
TIDAL FLAT

**ABSTRACT** – From observations made in the partially protected intertidal flat (« Anse-à-l'Original », Lower St. Lawrence estuary, Québec, Canada), we argue the influence of hydrodynamic processes on the spatial distribution of *Nereis virens* Sars population (Polychaeta : Nereidae). Data obtained during this study revealed an edaphic segregation between sexually mature and immature individuals. This observation is correlated with the sediment texture, the organic matter content of the substratum and, for large worms, with the thickness of the colonizable sediment layer. Highest densities of the polychaete larvae occurred at uppermost part of the intertidal flat in which we observed a weak tidal currents and fine particle deposits. In lower part of tidal zone, the higher adult densities were found in the diffusion areas of waters ebbing. Comparison between hydrodynamic data and spatial distribution suggest that larvae will be transported in the water mass during their brief pelagic life and settled in calm areas. After a growth period of 3 to 4 years, sexually mature and immature worms (250 to 1000 mg) begin migration toward the lowermost part of the intertidal flat. Despite their swimming ability, it seems that migration is rather passive and mainly directed by hydrodynamic processes.



## INTRODUCTION

L'hydrodynamisme du domaine intertidal est fonction essentiellement des effets combinés des houles dues aux vents et des courants générés par les marées. Les processus hydrodynamiques influencent plusieurs facteurs responsables de la répartition spatiale des espèces et des individus des populations benthiques (Bhaud *et al.*, 1981; Keough & Downes, 1982; Eckman, 1983; Hannan, 1984; Banse, 1986; Butman, 1987). En outre, l'hydrodynamisme contrôle la distribution spatiale des particules sédimentaires (Wieser, 1959; Leeder, 1984; Pethick, 1984). En règle générale, les courants de flot possèdent une capacité de transport plus grande que ceux du jusant ce qui se traduit par une accumulation de particules dans le haut de plage (Leeder, 1984; Reise, 1985). Dans un environnement semi-protégé comme le site de la présente étude, on observe ainsi un envasement dans les zones abritées (fond de baie) et des dépôts sableux dans les parties ouvertes aux houles du large (bas de la zone intertidale). De cette façon, les processus hydrodynamiques vont agir sur la répartition spatiale des organismes benthiques en limitant l'accès à certains types de sédiments (Bellan, 1977). L'hydrodynamisme contribue bien évidemment au transport de larves chez les espèces benthiques à développement larvaire pélagique. Dans ce cas, l'influence des processus hydrodynamiques dépendra principalement de la durée de la phase larvaire pélagique et de la capacité des larves au déplacement.

Dans la région choisie pour cette étude, la communauté boréo-atlantique à *Macoma balthica* (L.) domine la zone intertidale où les processus hydrodynamiques sont importants (Desrosiers *et al.*, 1980; Desrosiers & Brêthes, 1984). Cette communauté comporte un faible nombre d'espèces, dont un Annelide Polychète, *Nereis virens*. Cette Polychète préfère habituellement les sédiments sablo-vaseux, les moulières et les réseaux de racines des marais salés, où l'hydrodynamisme est relativement faible (Pettibone, 1963; Bellan, 1977). *N. virens* peuple également les fonds de baie et serait l'espèce caractéristique du groupement annélien lagunaire eurytherme et euryhalin (Bellan, 1978). Pour apprécier les effets de l'hydrodynamisme sur la distribution spatiale de cette espèce, nous devons connaître assez bien son cycle de vie. D'abord, cette Polychète présente un développement indirect avec une brève phase pélagique au stade larvaire (Bass, 1970; Bass & Brafield, 1972; Desrosiers *et al.*, 1991b). Les premières larves trochophores deviennent planctoniques à la fin du 6<sup>ème</sup> jour de leur développement pour une période de 12 à 15 h (Bass & Brafield, 1972). Par la suite, les larves benthiques (Bhaud et Cazaux, 1982) se retrouvent sur les sédiments de la partie supérieure de la zone intertidale où

elles subissent certaines transformations morphologiques (Desrosiers, *et al.*, 1991b). Au moment de cette sédentarisation larvaire, les individus possèdent 3 segments sétigères. Les post-larves demeurent à la surface des sédiments jusqu'à 6 segments. Les individus s'enfouissent par la suite diminuant leur exposition aux contraintes hydrodynamiques.

Au terme de leur première année de croissance segmentaire, les juvéniles atteignent plus de 40 segments sétigères (Desrosiers *et al.*, 1991b). Les juvéniles demeurent dans la partie supérieure du domaine intertidal pendant 2 à 4 années (Miron & Desrosiers, 1990). Après quoi, ceux-ci atteignent leur maturité sexuelle et migreraient vers le bas de plage afin de poursuivre leur croissance essentiellement pondérale jusqu'à la reproduction (Miron & Desrosiers, 1990). Au terme du cycle de développement, les adultes de la Polychète *N. virens* pèsent plus de 10 g (Miron & Desrosiers, 1990; Caron, 1991) et on estime leur âge entre 6 et 8 ans (Desrosiers, non-publié).

Pendant le cycle de vie de cette Polychète, il semble évident que les processus hydrodynamiques influencent la répartition spatiale des individus de taille variée. Malheureusement, nous ne possédions pas, à l'époque, de modèle hydrodynamique de la baie afin d'expliquer la répartition spatiale des individus. A partir de nouvelles données physiques (Côté, 1991), le présent travail a pour principal objectif de confronter les données écologiques aux données physiques afin d'extraire l'importance de l'hydrodynamisme chez une espèce épitoque colonisant la zone intertidale. La Polychète *N. virens*, constituant un cas particulier dans cette étude, a été choisie puisque nous connaissons très bien son cycle de développement et sa distribution spatiale en zone intertidale (Desrosiers *et al.*, 1991a; 1991b; Caron *et al.*, sous presse). A cet effet, ce choix nous permet de mieux apprécier les effets des processus hydrodynamiques.

## MATÉRIEL ET MÉTHODE

### *Caractéristiques du site d'étude*

L'Anse-à-l'Original se localise à une vingtaine de km à l'ouest de Rimouski, Québec, Canada (Long. : 68° 33' W; Lat. : 48° 20' N). Elle s'oriente vers le nord et est abritée des vents dominants (sud et sud-ouest) et des courants résiduels de surface (El-Sabh, 1988). Cette baie possède une zone intertidale d'une superficie supérieure à 2 km<sup>2</sup> avec une faible pente de 0,40 % (Miron & Desrosiers, 1990; Caron, 1991; Caron *et al.*, sous presse). Les caractéristiques granulométriques, la



teneur en matière organique du substrat ainsi que l'épaisseur de la couche colonisable des sédiments varient significativement selon le niveau hypsométrique (Miron & Desrosiers, 1990; Caron, 1991). Dans la partie supérieure de la zone intertidale de l'Anse-à-l'Original (Fig. 1), nous observons un sédiment hétérogène de sables graveleux vaseux et riche en matière organique (7 à 15 %). Au niveau inférieur, les sédiments plus homogènes possèdent une faible teneur en matière organique (1 à 2 %) et sont constitués principalement de sables. Le centre de la plage présente des caractéristiques granulométriques intermédiaires dont la variabilité spatiale à petite échelle (de l'ordre du 100 m) est importante. L'épaisseur de la couche colonisable des sédiments diminue du bas vers le haut de plage en relation avec la présence d'une argile indurée. Cette argile correspond aux dépôts d'une ancienne mer glaciaire, la Mer de Goldthwait (14 000 ans AA), que l'on observe à une profondeur inférieure à 10 cm dans le haut de l'estran (Dionne, 1978).

#### Description sommaire du modèle hydrodynamique

Le modèle numérique utilisé pour la simulation des courants de marée dans la baie est décrit par Bauer et Stroud (1978). C'est un modèle à couches tridimensionnelles qui résout les équations de continuité et de mouvement selon un schéma aux différences finies. A l'origine, ce modèle a été conçu spécialement pour l'étude des processus hydrodynamiques côtiers. A cet effet, il inclut les termes non-linéaires des équations du mouvement ainsi qu'un terme de friction quadratique, permettant une meilleure estimation des courants en zone peu profonde. De plus, il permet de simuler le découvrage/recouvrement périodique de l'estran par la marée selon un processus de fermeture de cellules sèches. Cette caractéristique est particulièrement intéressante dans le cas de l'Anse-à-l'Original, une partie importante de sa surface se découvrant périodiquement. Dans le cadre de cette étude, une seule couche fut imposée pour l'étude de la baie. En fait, on a posé ici l'hypothèse que le mélange dans le secteur est suffisamment important pour que la colonne d'eau soit homogène. Le modèle n'a donc été utilisé que dans sa configuration bidimensionnelle. Finalement, il a été calibré à l'aide de mesures de courants et de niveaux d'eau recueillies au cours de l'été 1988 (Côté, 1991).

#### Échantillonnage

L'échantillonnage a été planifié dans le but de confronter la distribution spatiale de différentes classes de taille des individus de la Polychète *N. virens* avec les résultats simulés à partir du modèle

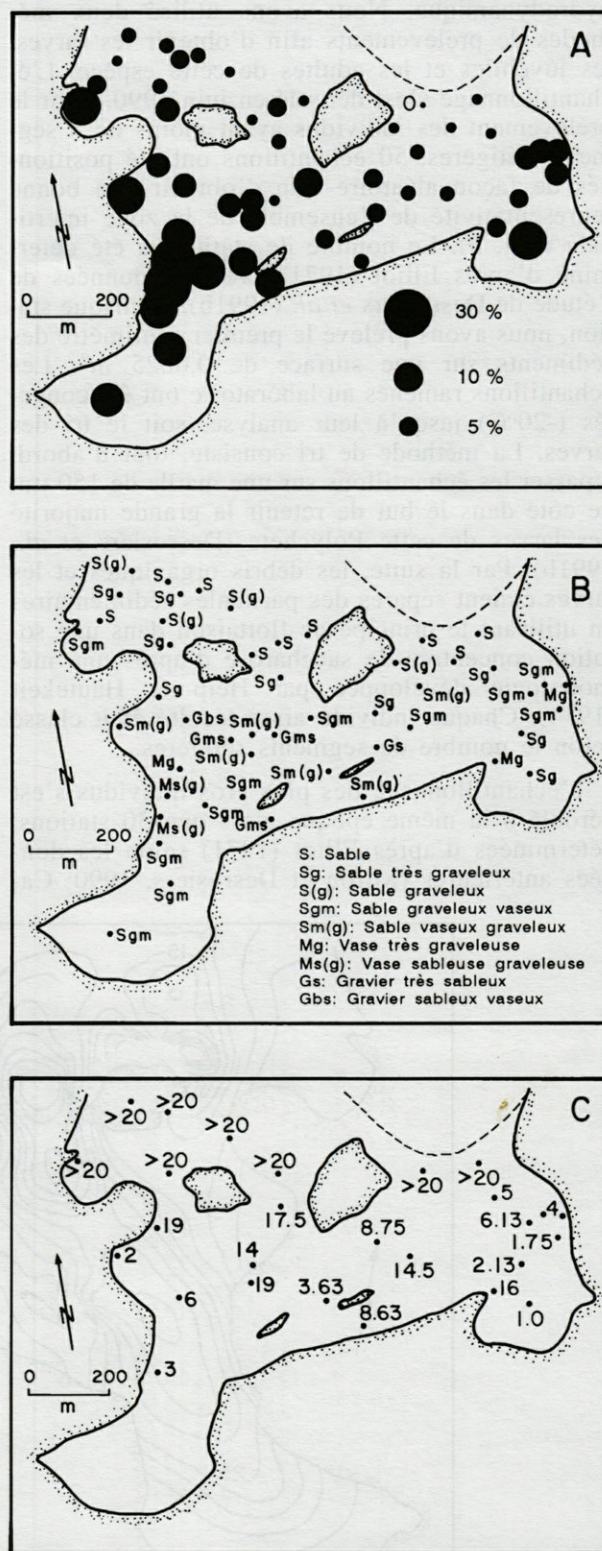


Fig. 1. — Teneur (%) en matière organique (A), granulométrie (B) et épaisseur (cm) de la couche colonisable des sédiments (C) observées à l'Anse-à-l'Original.

*Organic matter content (A), sediment types (B) and colonizable layer depth of substratum (C) observed at « Anse-à-l'Original ».*



hydrodynamique. Nous avons utilisé deux méthodes de prélèvements afin d'obtenir les larves, les juvéniles et les adultes de cette espèce. L'échantillonnage s'est déroulé en juin 1990. Pour le prélèvement des individus ayant moins de 8 segments sétigères, 50 échantillons ont été positionnés de façon aléatoire afin d'obtenir une bonne représentativité de l'ensemble de la zone intertidale (Fig. 3). Le nombre de stations a été déterminé d'après Elliot (1971) avec les données de l'étude de Desrosiers *et al.* (1991b). A chaque station, nous avons prélevé le premier centimètre des sédiments sur une surface de 0,0625 m<sup>2</sup>. Les échantillons ramenés au laboratoire ont été congelés (-20°C) jusqu'à leur analyse, soit le tri des larves. La méthode de tri consiste, tout d'abord, à passer les échantillons sur une maille de 150 µm de côté dans le but de retenir la grande majorité des larves de cette Polychète (Desrosiers *et al.*, 1991b). Par la suite, les débris organiques et les larves étaient séparés des particules sédimentaires en utilisant le principe de flottaison dans une solution concentrée de saccharose d'après une méthodologie développée par Heip & Hautekeit (1974). Chaque individu ainsi récolté était classé selon le nombre de segments sétigères.

L'échantillonnage des plus gros individus s'est déroulé à la même époque alors que 30 stations, déterminées d'après Elliot (1971) selon les données antérieures (Miron et Desrosiers, 1990; Ca-

ron *et al.*, sous presse), ont été aléatoirement choisies parmi les 50 sites de prélèvement que nous avons décrits auparavant. A chaque station, nous avons récolté, aléatoirement et à 3 reprises, 20 à 30 cm de sédiments sur une surface de 0,10 m<sup>2</sup>. Nous avons fixé les résidus d'un pré-tamassage sur une maille de 1 mm<sup>2</sup> d'ouverture dans une solution formolée tamponnée (4 %). Au laboratoire, tous les individus furent triés et comptés. Nous avons déterminé le poids total formolé essuyé de chacun des individus. Nous avons réparti les individus dans 3 classes de taille : 0 à 250 mg, 250 à 1 000 mg et > 1 000 mg.

## RÉSULTATS

### *Processus hydrodynamiques*

Dans l'Anse-à-l'Original, les marées sont de type semi-diurne (M<sub>2</sub>) et génèrent des courants supérieurs à 20 cm s<sup>-1</sup>. Le modèle hydrodynamique à deux dimensions couvrant-découvrant utilisé par Côté (1991) nous permet d'intégrer les énergies moyennes liées à ces courants lors d'un cycle complet de marée (Fig. 2). Les secteurs de faible énergie se localisent presque uniquement le long du rivage. Elles coïncident avec les plus fortes teneurs en matière organique et les plus grandes

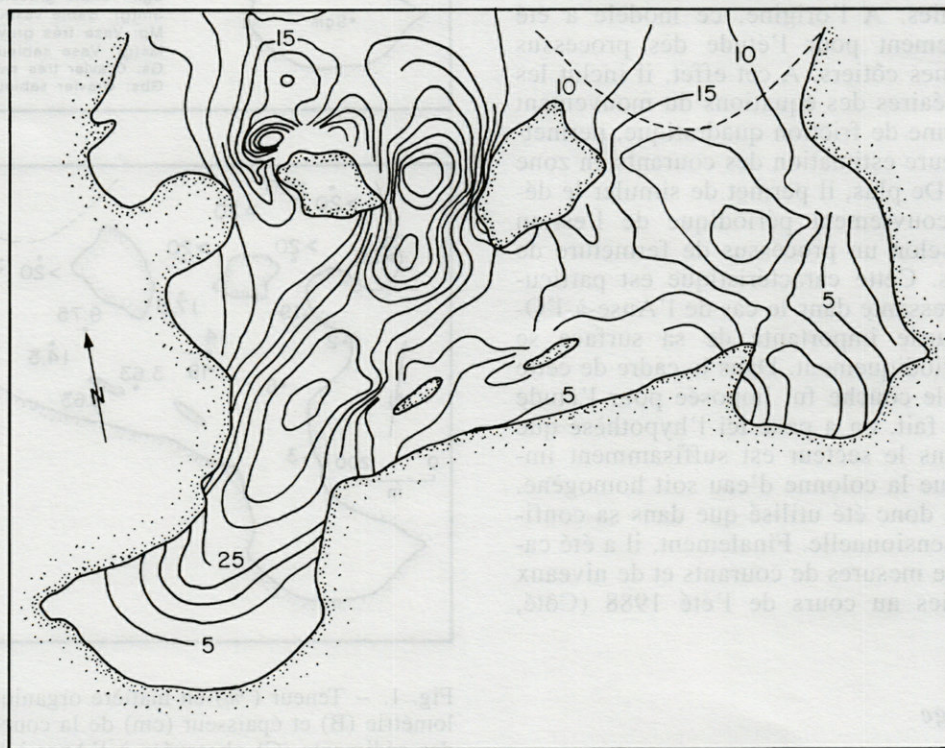


Fig. 2. - Contours d'énergie moyenne exprimée en  $m^2 s^{-2} \times 10^{-4}$  lors d'un cycle de marée M<sub>2</sub> (d'après Côté, 1991). Chaque ligne représente une augmentation ou une diminution de  $5,0 \times 10^{-4} m^2 s^{-2}$ .

*Contour lines of integration current energy ( $\times 10^{-4} m^2 s^{-2}$ ) over one tidal cycle (M<sub>2</sub>). Each contour line represents an increase or decrease of  $5.0 \times 10^{-4} m^2 s^{-2}$ .*



concentrations en particules fines (Fig. 1A et 1B). Les contours d'énergie moyenne nous indiquent également un site dont l'hydrodynamisme du aux marées est particulièrement intense et variable. Ce secteur se situe entre les deux principales îles de l'Anse-à-l'Original où les sédiments sont plus grossiers et contiennent une plus faible quantité de matière organique.

La position géographique de l'Anse-à-l'Original la rend sensible à l'influence des vagues générées par des vents du nord et du nord-est. La distance sur laquelle agissent de tels vents (« fetch ») dans l'estuaire maritime du Saint-Laurent est bien supérieure à 40 km permettant le développement de vagues d'intensité moyenne à forte. La figure 3 illustre les aires potentiellement protégées lors des conditions de tels vents. Entre les mois de mai et d'août, les vents soufflant du nord et nord-est possèdent une fréquence de 15 % alors que les vents du sud et sud-ouest dominent avec 25 %. L'estimation de ces pourcentages est basée sur un échantillonnage journalier pendant plus d'une trentaine d'années (Environnement Canada, 1984). La variabilité inter-annuelle est étonnamment faible pendant la même saison. Les vents peuvent ainsi devenir un facteur très important puisque les résultats d'un échantillonnage menés sur un cycle mortes-eaux vives-eaux au printemps 1991 montre des courants de houle pouvant atteindre  $50 \text{ cm s}^{-1}$

pour une période de 4 secondes. Cette vitesse représente 2,5 fois celle générée par les marées.

### Répartition spatiale des individus

La figure 4 montre une distribution spatiale des individus de l'espèce *N. virens* suivant une évolution selon la taille. D'abord, nous observons l'arrivée des larves trochophores à la surface des sédiments entre mai et juin (Desrosiers *et al.*, 1991b). Les larves se déposent ensuite préférentiellement dans les secteurs nord-ouest de la baie et de chaque côté du chenal passant entre les deux îles où nous avons identifié des énergies moyennes particulièrement intenses et variables. Les plus fortes densités d'individus de 3 segments sétigères sont observées à l'extrême nord-ouest de l'Anse-à-l'Original, secteur riche en matière organique. Les individus de plus forte taille, les post-larves (6 segments sétigères) et les juvéniles (0 à 250 mg) colonisent à plus faible densité une bande plus large s'étendant vers l'est. Les densités maximales d'individus ayant 6 segments sétigères s'observent dans les mêmes secteurs que les larves trochophores. Par contre, les juvéniles (0 à 250 mg) se retrouvent en forte densité dans les secteurs opposés, au nord-est de la baie, où l'on remarque un marais à Spartine (*Spartina alterniflora*).

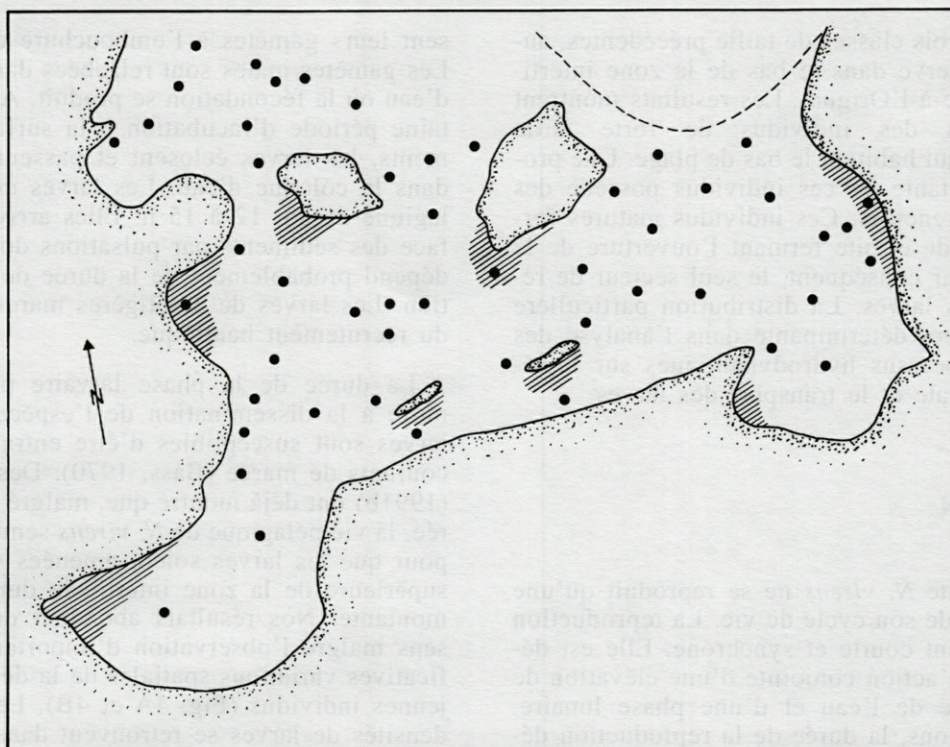


Fig. 3. – Aires potentiellement protégées (hachures) lors des conditions de tempête. Les points représentent l'emplacement des stations d'échantillonnage.

Map of potential sheltered areas (hachuring) during storm conditions. Dark circles represent sampling stations.



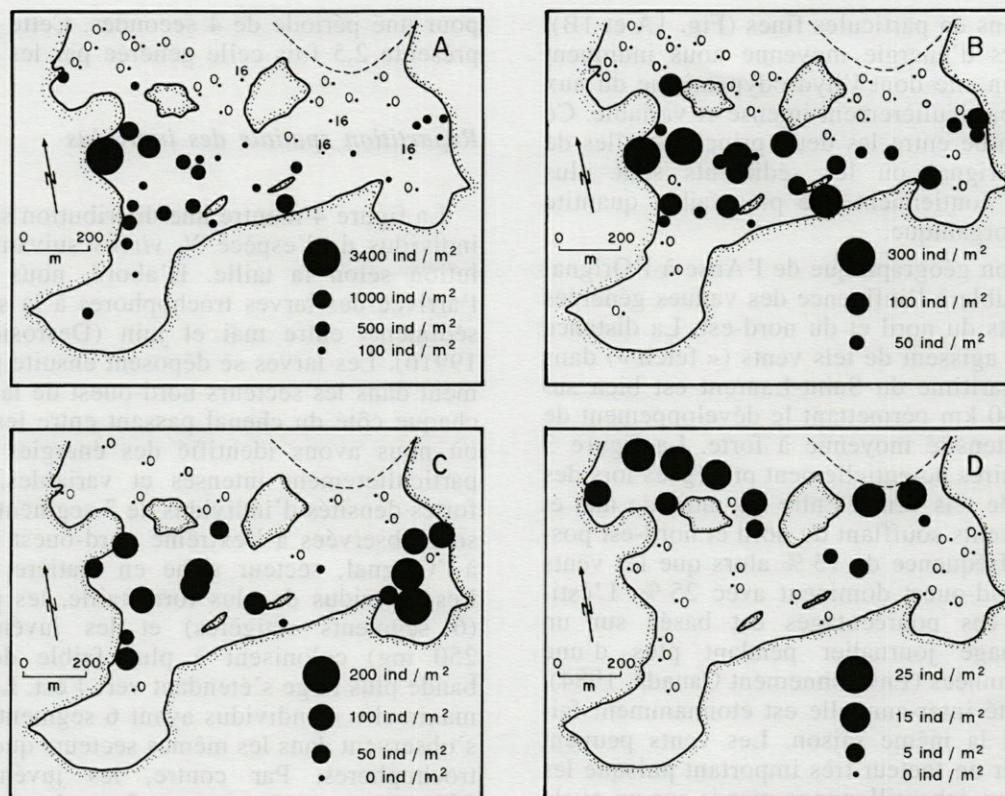


Fig. 4. – Densités (ind.  $m^{-2}$ ) des individus de l'espèce *Nereis virens* de l'Anse-à-l'Original. A, 3 segments sétigères; B, 6 segments sétigères; C, 0 à 250 mg de poids total; D, poids total > 1 000 mg.

Densities (individuals. $m^{-2}$ ) of *Nereis virens*. A, Three chaetigerous segments. B, Six chaetigerous segments. C, 0 to 250 mg total weight and D, Total weight > 1 000 mg.

Parmi les trois classes de taille précédentes, aucune ne s'observe dans le bas de la zone intertidale de l'Anse-à-l'Original. Les résultats montrent que ce sont des individus de forte taille (>1 000 mg) qui habitent le bas de plage. Une proportion importante de ces individus possède des gamètes différenciés. Ces individus matures forment une bande étroite fermant l'ouverture de la baie. C'est, par conséquent, le seul secteur de relâchement des larves. La distribution particulière des adultes sera déterminante dans l'analyse des effets des processus hydrodynamiques sur la répartition spatiale et le transport des larves.

## DISCUSSION

La Polychète *N. virens* ne se reproduit qu'une fois au cours de son cycle de vie. La reproduction est relativement courte et synchrone. Elle est déclenchée par l'action conjointe d'une élévation de la température de l'eau et d'une phase lunaire. Dans nos régions, la durée de la reproduction dépend des conditions climatiques allant d'une semaine à presque un mois. Les mâles sortent de leur terrier et nagent à la recherche d'ouvertures de terrier femelle. Les femelles de cette espèce expul-

sent leurs gamètes à l'embouchure de la galerie. Les gamètes mâles sont relâchés dans la colonne d'eau où la fécondation se produit. Après une certaine période d'incubation à la surface des sédiments, les larves éclosent et passent directement dans la colonne d'eau. Les larves demeurent pélagique durant 12 à 15 h. Elles arrivent à la surface des sédiments par pulsations dont le nombre dépend probablement de la durée de la reproduction. Les larves de 3 sétigères marquent le début du recrutement benthique.

La durée de la phase larvaire peut aider ou nuire à la dissémination de l'espèce puisque les larves sont susceptibles d'être entraînées par les courants de marée (Bass, 1970). Desrosiers *et al.* (1991b) ont déjà montré que, malgré sa courte durée, la vie pélagique de *N. virens* semble suffisante pour que les larves soient amenées vers la partie supérieure de la zone intertidale durant la marée montante. Nos résultats abondent dans le même sens malgré l'observation d'importantes et significatives variations spatiales de la densité des très jeunes individus (Fig. 4A et 4B). Les plus fortes densités de larves se retrouvent dans les secteurs où l'on observe une faible « énergie moyenne » des courants de marées, une forte concentration de particules fines et des teneurs élevées en matière organique. L'ensemble de ces facteurs in-



fluence, sans aucun doute, la distribution spatiale des larves (Pratt, 1953; Tyler & Banner, 1977; Butman, 1987; Desrosiers *et al.*, 1991b).

Dans l'Anse-à-l'Orignal, nous avons également remarqué une absence de larves et de jeunes individus dans la partie inférieure de la plage. Dans ce secteur, on retrouve des sédiments de sable grossier à faibles teneurs en matière organique. Les contours d'énergie moyenne nous suggèrent un hydrodynamisme plus important que celui du haut de plage rendant difficile le dépôt des larves. De plus, la présence d'individus adultes de cette Polychète et d'autres espèces endobenthiques tels *Mya arenaria* dans le bas de plage contribuerait à cette absence des larves par leurs actions prédatrices (Commito & Shrader, 1985; Olivier *et al.*, 1993).

A partir de l'ensemble de ces observations, nous pouvons nous demander si les larves de cette espèce possèdent la capacité de sélection active du substrat ou si, tout simplement, elles sont transportées au gré des courants. Les courants dus aux marées et aux vagues sont très puissants dans la zone de balancement des marées. De plus, les larves de 3 à 6 sétigères ne dépassent guère 500 µm et sont donc susceptibles d'être entraînées par le mouvement de la masse d'eau bien qu'elles aient une certaine capacité de déplacement. D'après les simulations de transport de particules effectuées par Côté (1991), une quantité importante de larves (considérées inertes) peut facilement atteindre la partie supérieure de la plage avec les courants de la marée montante. La sédentarisation larvaire chez cette Polychète de la zone intertidale de l'Anse-à-l'Orignal semble d'abord dépendre des grands processus hydrodynamiques influençant la répartition des particules sédimentaires. A l'échelle de la baie, nos résultats suggèrent l'incapacité des larves de 3 segments sétigères à une sélectivité active du type de sédiments. Ces observations rejoignent de nombreuses autres études qui considèrent qu'une part importante de la dispersion larvaire à grande échelle serait passive lorsque les facteurs hydrodynamiques dominent (Butman, 1987). D'ailleurs, à une échelle plus petite ( $\approx 400$  m), Desrosiers *et al.* (1991b) ont démontré l'absence de corrélation entre le type de sédiments et les densités élevées des individus de 3 à 8 sétigères. L'ensemble de ces résultats n'excluent évidemment pas la sélectivité active de l'habitat à des échelles spatiales beaucoup plus petites comme l'ont déjà montrée Butman *et al.* (1988) chez une espèce du genre *Capitella*.

La présente étude montrent également une différence importante des densités entre le stade à 3 segments et à 6 segments sétigères. Les densités sont de 3 400 ind./m<sup>2</sup> et 350 ind./m<sup>2</sup> respectivement ce qui correspond à une variation de 90 % des effectifs. La forte mortalité des individus dans

les tous premiers stades de vie représenterait une cause probable de cet écart. A cet effet, les travaux sur le recrutement larvaire de cet Annélide (Desrosiers *et al.*, 1991b) démontrent des taux de mortalité variant de 89 à 91 % entre les stades à 3 et 8 segments sétigères. Selon ces derniers auteurs, les variations de la température à la surface des sédiments et/ou la prédation par les espèces endobenthiques expliquent une part importante de la mortalité dans les tous premiers stades. D'autres auteurs arrivent aux mêmes conclusions chez *N. virens* (Commito & Shrader, 1985) et chez d'autres espèces (Mileikovsky, 1974; Woodin, 1976; Fauchald & Jumars, 1979; Hunt, 1980). Bien que la différence entre la distribution des larves à 3 et 6 sétigères puisse être expliquée par les processus hydrodynamiques, cela n'exclue nullement une mortalité différentielle des post-larves.

En revanche, la distribution spatiale des jeunes individus n'explique pas celle des adultes (Fig. 4 D). Pour ces derniers, nous remarquons une inversion de la distribution des plus hautes densités d'individus entre le haut et le bas de la zone intertidale. Les plus fortes densités d'adultes (> 1 000 mg) coïncident avec les zones de diffusion du panache des eaux de vidange de la baie. Ces observations suggèrent une migration des juvéniles du haut vers le bas de plage qui est certainement non-reliée à la reproduction. Le déclenchement de cette phase migratoire n'a pas encore été élucidé mais selon certaines observations, il serait dépendant de la densité (Miron & Desrosiers, 1990; Caron, 1991; Miron, 1991). A partir des études sur la variabilité temporelle des structures dimensionnelles de la population, la migration se produirait à la fin d'octobre ou au début de novembre juste avant la prise des glaces (Caron, 1991).

Ce type de migration a déjà été observé chez cette Polychète (Dean, 1978). De plus, Dean (1978) signale la présence des individus nageant à la surface de l'eau pendant la phase descendante de la marée mais n'observe jamais ces mêmes individus combattant le courant de marée. Une migration des jeunes a été également observée par Bass & Brafield (1972) dans le sens inverse puisque la grande majorité de la population est subtidale sur les côtes orientales d'Angleterre. Cette observation serait due principalement à la différence de température sur les zones intertidales dans ce secteur.

## CONCLUSION

Malgré la capacité natatoire des jeunes individus, l'hydrodynamisme semble jouer un rôle dans la migration des juvéniles tout comme dans la distribution des larves. Initialement, après la repro-



duction, les larves (3 segments sétigères) se retrouvent dans la colonne d'eau pendant une brève période. Incapable de combattre les courants de marées, les larves sont entraînées vers les secteurs à faible énergie en accord avec le modèle hydrodynamique couvrant-découvrant utilisé par Côté (1991). On ignore cependant si ces individus nouvellement métamorphosés sont remis en suspension dans la colonne d'eau. Par la suite, un étalement de la population vers l'est amène à la distribution des juvéniles. Ces derniers migraient vers le bas de plage mais toujours sous l'influence des processus hydrodynamiques. En effet, la répartition spatiale des adultes semble suivre les zones de diffusion du panache des eaux de vidange de la baie. L'hydrodynamisme devient probablement un des déterminants importants de la distribution spatiale de cet Annelide dans la zone intertidale. Par contre, une étude de la variabilité temporelle des distributions en fonction des processus hydrodynamiques devrait confirmer cette hypothèse.

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# ÉTHOLOGIE ALIMENTAIRE DE *CITHARUS LINGUATULA* ET *DICOLOGOGLOSSA CUNEATA* SUR LES CÔTES ATLANTIQUES DU MAROC

*Feeding ethology of Citharus linguatula and Dicologoglossa cuneata  
of the Moroccan Atlantic area*

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POISSONS *CITHARUS*  
POISSONS *LINGUATULA*  
*DICOLOGOGLOSSA CUNEATA*  
ATLANTIQUE MAROCAIN  
SPECTRE DE PROIES  
ÉTHOLOGIE ALIMENTAIRE  
COEXISTENCE

**RÉSUMÉ** – Deux espèces de Pleuronectiformes, *Citharus linguatula* (Scophthalmidae) et *Dicologoglossa cuneata* (Soleidae) ont été récoltées sur le littoral atlantique marocain. Les contenus stomacaux sont analysés en termes d'abondance, de fréquence et de taille des proies. Le régime alimentaire de *C. linguatula* est composé essentiellement de proies pélagiques et necto-benthiques (Mysidacés, Euphausiacés, Crevettes, Céphalopodes et Poissons), alors que celui de *D. cuneata* comprend des proies benthiques endogées fouisseuses ou appartenant à l'épifaune. Le comportement benthique de *D. cuneata* est à l'origine du caractère euryphage du régime alimentaire. La nature et la taille des proies sont fonction de la taille des Poissons. Contrairement à *C. linguatula*, chez *D. cuneata*, la phase d'immaturité sexuelle n'apparaît pas comme une période de forte activité trophique. *C. linguatula* manifeste en outre une faible activité alimentaire pendant la période de frai (hiver et printemps), alors que chez *D. cuneata*, les modifications saisonnières du régime alimentaire se limitent à des variations dans l'importance relative des proies. Chez cette dernière, quelle que soit la saison, les Amphipodes constituent les proies les plus abondantes. Les deux espèces qui n'utilisent pour se nourrir qu'une partie des organismes présents dans le milieu manifestent une importante divergence dans la nature des proies et les stratégies de recherche de la nourriture. Ces caractéristiques étho-écologiques en font d'excellents traceurs naturels des peuplements littoraux. Enfin, l'étude des contenus stomacaux de *C. linguatula* et *D. cuneata* se révèle précieuse dans la recherche des cycles biologiques de deux espèces de parasites : *Bothriocephalus andresi* (Cestoda) et *Acanthocephaloides propinquus* (Acanthocephala) retrouvés respectivement dans l'intestin de ces deux espèces de Poissons.

FISHES *CITHARUS*  
FISHES *LINGUATULA*  
*DICOLOGOGLOSSA CUNEATA*  
MOROCCAN ATLANTIC AREA  
PREY SPECTRUM  
FEEDING ETHOLOGY  
SPECIES COEXISTENCE

**ABSTRACT** – Two species of flatfish, *Citharus linguatula* (Scophthalmidae) and *Dicologoglossa cuneata* (Soleidae), were fished off the Moroccan Atlantic coast. Their stomach contents were analysed in terms of the abundance and size distribution of prey organisms. The diet of *C. linguatula* is composed mainly of pelagic and necto-benthic prey (mysids, euphausiids, prawns, cephalopods and fish), whereas that of *D. cuneata* includes burrowing infaunal species as well as epifaunal species. The benthic nature of *D. cuneata* accounts for this varied diet. The type and size of the prey organisms are related to the size of the fish. In contrast to *C. linguatula*, the period of sexual immaturity of *D. cuneata* would not appear to be associated with an important feeding activity. *C. linguatula* otherwise manifests a decreased feeding activity during the spawning period (winter and spring), whereas for *D. cuneata*, variations in feeding activity are limited to variations in the relative abundance of prey species. Irrespective of the season, amphipods are the most abundant prey organisms. Studies on the stomach contents appear most valuable in the researches on the life cycle of two parasite species : *Bothriocephalus andresi* (Cestoda) and *Acanthocephaloides propinquus* (Acanthocephala) respectively from *C. linguatula* and *D. cuneata*. These two species, that feed on only a limited number of prey species in their environment, demonstrate a large divergence in the nature of their diet and in their foraging strategies. They constitute excellent natural markers of littoral populations.



## INTRODUCTION

La forte productivité et la diversité des peuplements benthiques de la côte atlantique marocaine (Maurin, 1968) liées aux caractéristiques climatiques et hydrogéologiques confèrent à cette zone un caractère exceptionnel. En outre, de par sa situation géographique, le littoral atlantique marocain permet la liaison entre les mers boréales d'une part, la Méditerranée et l'Atlantique tropical d'autre part.

Cependant, à l'exception des travaux réalisés sur différentes espèces pélagiques (Belveze, 1984), les études consacrées aux peuplements ichthyiques du littoral atlantique marocain, en relation avec l'environnement sont inexistantes.

Le peuplement de Poissons Pleuronectiformes dans cette zone se caractérise par la coexistence (d'espèces tempérées chaudes et boréo-tempérées (Bianchi, 1984). Deux espèces, l'une, *Citharus linguatula* Linnaeus, 1758 (le Cithare), boreo-tempérée, l'autre tropicale, le Cétheau (*Dicologoglossus cuneata* Moreau, 1881), ont retenu notre attention dans le cadre de recherches sur les stratégies adaptatives des populations à leur environnement. La première est présente sur le littoral atlantique du Portugal à l'Angola, ainsi que sur les deux rives de la Méditerranée alors que la seconde présente en Atlantique du Cap de Bonne espérance au Golfe de Gascogne (Lagardère, 1982) ne s'observe en Méditerranée que sur le littoral africain (Sorbe, 1979)

Dans cette perspective, nous avons entrepris l'étude de l'évolution du régime alimentaire de ces deux espèces en fonction du sexe, de l'âge et des saisons, ainsi que l'incidence de la reproduction et des migrations sur la nature et l'importance relative des proies.

En outre, l'identification des proies consommées par chacune de ces deux espèces de même niveau trophique nous a paru de nature à nous éclairer sur leur comportement trophique, ainsi que sur leur coexistence.

Chez *D. cuneata*, la confrontation des espèces consommées sur le littoral atlantique marocain avec celles entrant dans le régime alimentaire du Cétheau dans d'autres aires géographiques (Forest, 1974, 1975, Lagardère, 1975 et 1982; Sorbe, 1972, 1979 et 1981) a été envisagée.

Enfin, sur le littoral atlantique marocain, *C. linguatula* et *D. cuneata* sont respectivement infestés par deux espèces de parasites intestinaux : *Bothriocephalus andresi* Porta, 1911 (Cestoda, Pseudophyllidea) et *Acanthocephaloides propinquus* Dujardin, 1845 (Palaeoacanthocephala) (Belghyti *et al.*). L'étude du régime alimentaire des deux Pleuronectes apparaît de nature à identifier les es-

pèces susceptibles d'héberger les formes larvaires des parasites.

## MATÉRIEL ET MÉTHODES

### Techniques d'études des Poissons

Un échantillonnage systématique des deux espèces a été effectué à partir des débarquements commerciaux au port de Casablanca à raison de 3 échantillons par mois.

Les techniques d'études concernant la croissance et la reproduction (longueurs totale et standard, poids plein et éviscéré, sexe, poids des gonades) sont développées dans un travail relatif à ces aspects de la biologie de ces deux espèces (Belghyti, 1990). Les Poissons ont été regroupés par classe d'âge à partir de la détermination directe de l'âge par otolithométrie et de l'établissement de courbes de croissance linéaires (Belghyti, 1990). Les équations de croissance linéaire ont été établies d'après l'équation de Von Bertalanffy (1938) :

$$L_{ST} = L_{ST}^{00} (1 - e^{-K(t-t_0)})$$

dans laquelle  $L_{ST}^{00}$  représente la longueur standard asymptotique du Poisson,  $K$  le coefficient spécifique de croissance et  $t_0 = t + 1/K L_m$ .

### Techniques d'études du régime alimentaire

Pour *C. linguatula* le régime alimentaire a été étudié à partir des contenus stomacaux. Pour *D. cuneata*, l'estomac étant mal individualisé, le tube digestif entier (estomac et intestin) a été prélevé. Les estomacs et tubes digestifs ont été conservés dans du formol à 5 % pour examens ultérieurs.

Dans ce travail, nous avons utilisé des méthodes qualitatives et quantitatives.

### Méthodes qualitatives

Les proies sont triées, dénombrées et déterminées sous loupe binoculaire à un niveau taxonomique allant de la classe à l'espèce selon leur état de conservation. Dans la plupart des cas nous avons eu recours à des spécialistes pour vérifier nos déterminations. Les individus trop digérés ont été classés dans la rubrique « Indéterminé ».

Pour certains groupes zoologiques dont le dénombrement a été rendu difficile du fait de la fragmentation, une partie caractéristique du corps a été utilisée pour leur identification (céphalothorax pour les Natantia, Euphausiacés et Mysidacés; tête ou complexe urosome-telson pour les Amphi-



podés; disques pour les Ophiurides; acron pour les Annélides).

Après détermination et comptage, les proies en bon état ont été pesées au 1/100 de gramme après dessiccation dans une étuve, à 60°C, jusqu'à stabilisation du poids (6 à 30 h). Les individus de petite taille (Mysidacés, Euphausiacés, Cumacés et Amphipodes) ont été regroupés par lots de 10 individus, afin d'estimer leur poids. Les coquilles, os et pièces cartilagineuses ou chitineuses ont été inclus dans la pesée, ces débris intervenant dans l'alimentation par la réplétion qu'ils provoquent, ainsi que par leur action mécanique sur les autres constituants du bol alimentaire.

### Méthodes quantitatives

Plusieurs indices ont été utilisés :

- La fréquence numérique (Cn) : pourcentage du nombre total d'individus d'une même espèce (ni) sur le nombre total d'individus de toutes les proies (Np).

- La fréquence d'occurrence des proies (Todd, 1907) établie à partir de l'indice  $F = ni / Ep$  dans lequel «ni» est le nombre d'estomacs contenant la proie «i» et «Ep» le nombre d'estomacs pleins, modifiée en remplaçant la fréquence d'occurrence F par une valeur corrigée Fc puisque  $\Sigma F > 100$  (Rosecchi et Nouaze, 1987). L'indice devient :  $Fc = 100 F/\Sigma F$

- La fréquence pondérale qui tient compte du poids des proies ingérées. Le poids sec, plus fiable et plus régulier, a été utilisé de préférence au poids humide (Windell, 1971). L'indice utilisé (Cp) est le pourcentage du poids de la proie «Pi» rapporté au poids total des diverses proies «P» ( $P = \Sigma Pi$ ).

D'autres indices ont été utilisés selon Hureau (1966) et Geistdoerfer (1975) : le coefficient de vacuité (C.V.), l'indice de réplétion (Ir), le nombre moyen de proies par estomac plein, le poids moyen des proies ingérées par Poisson et le poids moyen des proies par estomac.

Parmi les indices utilisés par Rosecchi et Nouaze (1987), nous avons retenu l'indice d'importance relative des proies (RI) qui a l'avantage de prendre en considération à la fois le nombre, le poids et l'occurrence de chaque proie (George et Hardley, 1979).

$$RI_i = 100 \frac{AI_i}{\Sigma AI_i}$$

où  $AI_i = F + Cn + Cp$

La valeur indicienne de chaque proie est exprimée en pourcentage de la somme des valeurs indicieuses de toutes les catégories de proies, ce qui permet de rapporter tous les indices à une même échelle et facilite les comparaisons inter et intraspécifiques. Une fois cette transformation effectuée, les indices sont placés par ordre de rang

décroissant. En partant de la proie 1, les indices des proies sont additionnés pour obtenir le classement suivant :

- les proies préférentielles représentent 50 % de l'indice cumulé
- les proies secondaires 25 %
- les proies complémentaires 15 %
- les proies accessoires ou accidentelles moins de 1 %.

## RÉSULTATS

### Analyse globale du régime alimentaire

#### *Citharus linguatula* (Fig. 1)

Les estomacs proviennent de 1 351 Poissons mesurant entre 30 et 260 mm de longueur totale pêchés entre février 1988 et mai 1989. La valeur annuelle relativement faible du coefficient de vacuité (26 %) traduit une forte intensité moyenne d'alimentation. Pour l'essentiel, les proies consommées appartiennent à 3 classes d'animaux : Crustacés, Poissons et Céphalopodes représentant 39 espèces réparties en 22 familles (Tabl. I). La classe des Crustacés montre une grande diversité taxonomique (16 familles et 29 espèces). Les espèces les plus représentées sont *Leptomysis gracilis*, *Processa nouveli*, *Alpheus glaber*, *Nyctiphanes couchii*, *Philocheras bispinosus*. Les autres espèces sont moins fréquentes. Les Poissons sont représentés par 5 espèces appartenant à deux familles : les Gobiidae et les Cepolidae. Les espèces *Lesueurigobius sanzoi*, *L. friesii* et *Cepola macrophthalma* sont les plus fréquentes. Les Céphalopodes sont surtout représentés par *Alloteuthis subulata* et *Todarodes sagittatus*.

Tabl. I. — Liste des proies de *Citharus linguatula* (par ordre d'importance).

List of the prey species of *Citharus linguatula*.

### CRUSTACÉS

#### MYSIDACES

##### Mysidacés

*Leptomysis gracilis* G.O. Sars, 1864  
*Schistomysis ornata* (G.O. Sars, 1864)  
*Anchialina agilis* (G.O. Sars, 1877)  
*Gastrosaccus lobatus* (Nouvel, 1950)  
*Gastrosaccus sanctus* (Nouvel, 1950)  
*Siriella norvegica* G.O. Sars, 1869  
*Mysideis parva* (Sars, 1869)  
 Indéterminés

##### Lophogastridés

*Lophogaster typicus* M. Sars, 1857

#### NATANTIA

##### Crangonidés

*Philocheras bispinosus* (Haillstone, 1835)

##### Processidés

*Processa nouveli* Adhub et Williamson, 1975



|                     |   |
|---------------------|---|
|                     | <i>Processa canaliculata</i> Leach, 1835      |
|                     | <i>Processa parva</i> Holthuis, 1951          |
|                     | <i>Processa</i> sp.                           |
| Alpheidés           | <i>Alpheus glaber</i> (Olivi, 1792)           |
|                     | <i>Athanas nithescens</i> (Leach, 1814)       |
|                     | <i>Athanas grimaldii</i>                      |
| Pandalidés          | <i>Chlorotocus crassicornis</i> (Costa, 1871) |
|                     | <i>Plesionika heterocarpus</i> (Costa, 1871)  |
| Palaemonidés        | <i>Palaemon elegans</i> Rathke, 1837          |
|                     | <i>Periclemenes scriptus</i> (Risso, 1822)    |
| Pasiphaeidés        | <i>Pasiphaea sivado</i> (Risso, 1816)         |
| Hippolytidés        | <i>Thorulus cranchii</i> (Leach, 1817)        |
| Penaeidés           | <i>Parapenaeus longirostris</i> (Lucas, 1846) |
|                     | <i>Solenocera membranacea</i> (Risso, 1816)   |
|                     | Indéterminé                                   |
| <b>EUPHAUSIACÉS</b> |   |
| Euphausiidés        | <i>Nyctiphanes couchii</i> Bell, 1853         |
| <b>STOMATOPODES</b> |   |
| Squillidés          | <i>Squilla mantis</i> (Linnaeus, 1758)        |
| <b>REPTANTIA</b>    |   |
| Homaridés           | <i>Nephrops norvegicus</i> (Linnaeus, 1758)   |
| Brachyours          | Indéterminés                                  |
| <b>AMPHIPODES</b>   |   |
| Ampeliscidés        | <i>Ampelisca brevicornis</i> (Costa, 1853)    |
| <b>ISOPODES</b>     |   |
| Cymothoidés         | <i>Cymothoe</i> sp.                           |
| <b>MOLLUSQUES</b>   |   |
| <b>CÉPHALOPODES</b> |   |
| Loliginidés         | <i>Alloteuthis subulata</i> (Lamarck, 1798)   |
|                     | <i>Loligo vulgaris</i> Lamarck, 1798          |
| Sepiidés            | <i>Sepia officinalis</i> (Linnaeus, 1758)     |
| Ommastrephidés      | <i>Todarodes sagittatus</i> (Linnaeus, 1758)  |
| Octopodidés         | <i>Octopus</i> sp.                            |
| <b>POISSONS</b>     |   |
| <b>OSTEICHTIENS</b> |   |
| Gobiidés            | <i>Lesueurigobius sanzoi</i> De Buen, 1918    |
|                     | <i>Lesueurigobius friesii</i> Malm, 1874      |
|                     | <i>Crystallogobius lineearis</i> Diiben 1845  |
|                     | <i>Aphia minuta</i> Risso, 1810               |
| Cepolidés           | <i>Cepola macrophthalma</i> (L., 1758)        |
|                     | Indéterminés                                  |

Les différentes espèces de proies totalisent 13 662 individus. Le nombre moyen de proies par estomac plein ( $N_m = 14$ ) est élevé : les proies sont en général de petite taille pour ce Poisson de taille moyenne ( $L_{Tmax} = 255$  mm) et sont ingérées souvent en grand nombre (226 Mysidacés dans l'estomac d'une femelle de 210 mm). Le poids moyen sec des proies par estomac plein est de l'ordre de 58 mg.

Les Mysidacés (RI = 55,13 %), proies préférentielles, sont les plus fréquentes (Fc = 57 %) et les

plus abondantes (Cn = 90,75 %); les Poissons (RI = 25,14 %), proies secondaires, moins fréquents (Fc = 15,32 %) et moins abondants (Cn = 1,63) que les Mysidacés sont cependant dominants d'un point de vue pondéral (Cp = 58,44 %).

Les Crevettes Natantia, les Céphalopodes et les Euphausiacés (RI = 18 %) sont des proies complémentaires. Ces proies plus fréquentes (Fc = 18 %) et plus abondantes (Cn = 5 %) que les Poissons sont moins importantes d'un point de vue pondéral (Cp = 23 %).

Le reste des proies (Stomatopodes, Amphipodes, Isopodes, Crabes et Langoustes) sont des proies accessoires ou accidentelles; leur contribution à l'alimentation de *C. linguatula* est négligeable.

#### *Dicologlossa cuneata*

La liste faunistique des proies consommées a été établie à partir de la nourriture retrouvée dans 554 tubes digestifs sur les 636 prélevés chez les Poissons pêchés entre février 1988 et mars 1989. Les Poissons étudiés mesuraient entre 110 et 275 mm.

Les proies appartiennent à 6 classes : Crustacés, Annélides, Mollusques, Echinodermes, Foraminifères et Poissons et se répartissent en 42 familles et 55 espèces (Tabl. II). La classe des Crustacés (31 familles et 38 espèces) montre une grande diversité taxonomique. Parmi les espèces les plus représentées se trouvent *Ampelisca brevicornis*, *A. diadema*, *Podocerus variegatus*, *Lembos* sp., *Phtisica marina*, *Philocheras bispinosus*, *Processa canaliculata*, *Carcinus maenas*, *Apseudes latreilli* et *Iphinoe trispinosa*. Les Amphipodes à eux seuls sont représentés par 16 espèces.

Les Annélides sont surtout représentés par des Polychètes errantes, Nereidae et Eunicidae. Du fait de leur fragilité, les déterminations n'ont pu être poussées jusqu'à l'espèce.

Les Mollusques consommés sont surtout des espèces côtières comme *Pharus legumen* et *Cylichna cylindracea*.

Sur les 636 tubes digestifs examinés, 82 étaient totalement dépourvus de nourriture, ce qui correspond à un coefficient de vacuité moyen de 12,89 %. Cette valeur annuelle assez faible est synonyme d'une forte activité alimentaire.

Au total, 6 077 proies ont été recensées, le nombre moyen de proies par estomac plein ( $N_m = 11$ ) compense leur petite taille.

Une hiérarchisation des proies en fonction de leur importance relative (RI %) pour les deux sexes, nous a permis de constater que :

Les Amphipodes (RI = 44 %) présents dans presque tous les estomacs contenant de la nourriture (F = 94,6 %) sont aussi les proies les plus



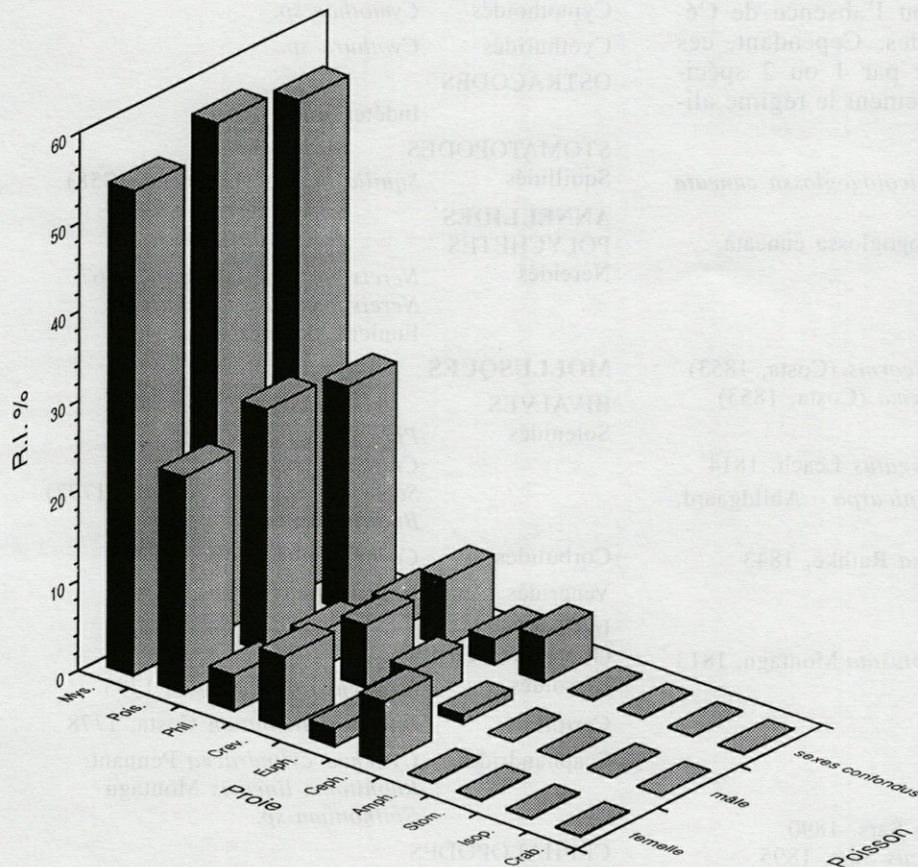


Fig. 1. — Analyse globale du régime alimentaire de *Citharus linguatula*.

Global analysis of the diet of *Citharus linguatula* from the relative importance of the prey.

Amph.: Amphipodes, Ceph.: Céphalopodes, Crab.: Crabes., Crev.: Crevettes, Euph.: Euphausiacés, Isop.: Isopodes, Mys.: Mysidacés, Phil.: *Philocheras sp.*, Pois.: Poissons, Stom.: Stomatopodes.

nombreuses (Cn = 67,9 %) et constituent des proies préférentielles pour *D. cuneata*.

Les Annélides (RI = 22,63 %) et les Crevettes Natantia (RI = 15,6) moins fréquents et moins abondants, mais généralement plus grands que les Amphipodes sont des proies secondaires.

Les Mollusques (Bivalves et Gastéropodes), Tanaïdacs, Brachyours, Cumacés, Mysidacés et Ophiurides sont des proies complémentaires, alors que les Isopodes, Poissons, Ostracodes, Mollusques Céphalopodes et Stomatopodes ne sont que des proies accessoires.

Le poids des Foraminifères, proies de très petite taille toujours associées à des sables, n'a pu être établi. Cependant, d'après leur fréquence d'occurrence, ceux-ci constituent des proies accessoires pour les deux sexes.

#### Variation du régime alimentaire en fonction du sexe

##### *C. linguatula* (Fig. 1)

Bien que les 3 classes de proies, Crustacés, Poissons et Céphalopodes se retrouvent dans le régime alimentaire des deux sexes, des différences apparaissent à un niveau taxonomique inférieur (famille ou espèce). La richesse spécifique ou plu-

tôt taxonomique du contenu stomacal est relativement plus élevée chez les femelles : 36 espèces réparties en 18 familles chez les mâles, contre 22 familles et 39 espèces chez les femelles (Tabl. I). En terme de présence-absence, on peut remarquer que les Stomatopodes, Isopodes et Reptantia (Crabes et Langoustes) sont spécifiques du régime alimentaire des femelles.

Sur le plan quantitatif, 4 767 proies ont été recensées dans les contenus stomacaux de 393 mâles contre 8 895 chez 606 femelles. Le nombre moyen de proies par estomac plein est aussi légèrement supérieur chez les femelles (Nm = 15 chez les femelles contre 13 pour les mâles).

Malgré la valeur plus élevée du coefficient de vacuité annuel moyen chez les mâles 28 % contre 24 % chez les femelles, l'intensité d'alimentation n'est pas significativement différente au seuil de 5 % ( $\chi^2_{\text{obs}} = 2,38 < \chi^2_{0,95} = 3,84$ ). Dans les deux sexes, il s'agit d'une forte intensité alimentaire.

##### *D. cuneata*

6 groupes de proies ont été recensés chez les femelles : Crustacés, Mollusques, Annélides, Echinodermes, Poissons et Foraminifères. Ces proies sont réparties en 42 familles et 55 espèces (Tabl. II) chez les femelles, contre 53 espèces appartenant à 40 familles chez les mâles. La diffé-



rence porte sur la présence ou l'absence de Céphalopodes et de Stomatopodes. Cependant, ces proies représentées seulement par 1 ou 2 spécimens ne modifient pas sensiblement le régime alimentaire des femelles.

Tabl. II. – Liste des proies de *Dicologoglossa cuneata* (par ordre d'importance).

List of the prey species of *Dicologoglossa cuneata*.

### CRUSTACÉS

#### AMPHIPODES

Gammariens

Ampeliscidés *Ampelisca brevicornis* (Costa, 1853)  
*Ampelisca diadema* (Costa, 1853)

Aoridés *Lembos* sp.

Podoceridés *Podocerus variegatus* Leach, 1814

Leucotoidés *Leucothoe spinicarpa* Abildgaard, 1781

Acanthozomidés *Iphimedia obsesa* Rathke, 1843

Lysianassidés *Lysianassa* sp.

Calliopiidés *Apherusa* sp.

Gammaridés *Abludomelita obtusata* Montagu, 1813

Oediceroidés Indéterminés

Stenothoidés *Stenothoe* sp.

Corophiidés Indéterminés

Phoxocephalidés Indéterminés

Caprellidés *Phtisica marina* Sars, 1890

*Pariambus typicus* Sars, 1895

Hyperiidés *Hyperia galba* Sars, 1895

#### NATANTIA

Alpheidés *Alpheus glaber* Olivi, 1792

*Athanas nitexens* Leach, 1814

Crangonidés *Philocheras bispinosus* Hailstone, 1835

*Philocheras trispinosus* Hailstone, 1835

*Philocheras sculptus* (Bell, 1847)

*Philocheras sculptus* (Bell, 1847)

*Pontocaris lacazei* (Gourret, 1887)

Processidés *Processa canaliculata* Leach, 1815

*Processa* sp.

Gnathophyllidés *Gnathophyllum elegans* (Risso, 1816)

Indéterminés

#### BRACHYOURES

Portunidés *Carcinus maenas* L. 1758

*Portunus corrugatus* Pennant, 1777

Megalopes

TANAIDACES *Apseudes latreilli* Edwards, 1932

*Parapseudes* sp.

#### MYSIDACES

Mysidacés *Gastrosaccus lobatus* Nouvel, 1950

*Gastrosaccus sanctus* (Beneden, 1861)

#### CUMACES

Bodotriidés *Iphinoe trispinosa* Goodsir, 1843

Diastylidés *Diastylis bradyi* Norman, 1879

*Diastylis laevis* Norman, 187

#### ISOPODES

Anthuridés Indéterminés

Cymothoidés *Cymothoe* sp.

Cyothuridés *Cyothura* sp.

#### OSTRACODES

Indéterminés

#### STOMATOPODES

Squillidés *Squilla mantis* (Linnaeus, 1758)

#### ANNELLIDES

#### POLYCHETES

Nereidés *Nereis zonata* Malmgren, 1867

*Nereis succinea* Leuckart

Eunicidés Indéterminés

#### MOLLUSQUES

#### BIVALVES

Solenidés *Pharus legumen* Linné

*Cultellus tenuis*

*Solen marginatus* (Pennant, 1777)

*Bularia striata*

Corbulidés *Corbula gibba* Olivi, 1792

Veneridés *Venus verrucosa* (L., 1758)

Indéterminés

#### GASTEROPODES

Rissoidés *Barleeia rubra* Adams, 1795

Cerithiidés *Bittium reliculatum* Costa, 1778

Scaphandridés *Cylichna cylindracea* Pennant

*Raphitoma linearis* Montagu

*Epithonium* sp.

#### CEPHALOPODES

Loliginidés *Alloteuthis subulata* (Lamarck, 1798)

#### ECHINODERMES

Ophiuridés *Amphipholis squamata* Delle Chiaye, 1828

#### FORAMINIFERES

*Quinqueloculina* sp.

#### POISSONS

Indéterminés

Chez les mâles, sur les 336 tubes digestifs examinés, 48 étaient totalement vides, ce qui correspond à un coefficient de vacuité (C.V) de 14,28 %. Dans les 288 estomacs pleins, 2 551 proies ont été recensées, soit un nombre moyen de proies par estomac de 8,85.

Chez les femelles 300 tubes digestifs ont été examinés, parmi lesquels 266 contenaient de la nourriture représentant un total de 3 526 proies. Le coefficient de vacuité est donc de 11,33 % et le nombre moyen de proies de 13,25.

Les différences observées entre les coefficients de vacuité des mâles et des femelles ne sont pas statistiquement significatives au seuil de sécurité de 5 % ( $\chi^2_{\text{obs}} = 1,21 < \chi^2_{0,95} = 3,84$ ); par contre, les différences observées entre les nombres moyens de proies par estomac plein sont significatives au seuil de 5 %. Le nombre moyen de proies par estomac est plus élevé chez les femelles.



### Variation du régime alimentaire en fonction de la taille et de l'âge

#### *C. linguatula* (Fig. 2 A)

Les Poissons dont la taille varie de 30 à 255 mm ont été regroupés par classes d'âge en fonction de la première maturité. Les groupes d'âge 0, 1 et 2 correspondent aux immatures, les groupes d'âge 3 et 4 aux jeunes matures et les groupes d'âge 5+ regroupent les adultes (Belghyti, 1990). La relation entre l'âge et la taille des individus a été établie à partir de 803 femelles et 548 mâles. Pour chaque sexe, l'équation de croissance linéaire est respectivement :

$$L_{T(t)} = 31,187 (1 - e^{-0,147(t + 1,871)})$$

$$L_{T(t)} = 32,047 (1 - e^{-0,135(t + 1,901)})$$

A mesure que le Poisson grandit, on assiste à des changements dans ses préférences alimentaires.

Le régime alimentaire des mâles des classes 0, 1 et 2 diffère de celui des classes 3 et 4, par la présence de *Natantia* et l'absence de Céphalopodes et d'Amphipodes. Le régime des individus des classes 5+ ne compte plus que des Mysidacés, Poissons, Céphalopodes et *Natantia*.

— Les Mysidacés sont des proies préférentielles pour toutes les classes d'âge. Toutefois leur importance diminue en fonction de l'âge. Leur fréquence d'occurrence (Fc %) passe respectivement de 67 à 58 et à 42 % dans les classes 0-1-2, 3-4 et 5-6-7.

— Les Poissons sont des proies secondaires pour les individus des classes 0 à 4. Cependant, contrairement aux Mysidacés, leur fréquence augmente avec l'âge : leur fréquence d'occurrence passe de 11 % à 16 % chez les individus des classes 0-1-2 et 3-4. Chez les mâles des classes 5+, les Poissons sont, à côté des Mysidacés, les proies préférentielles.

— Les Céphalopodes, absents chez les immatures des classes 0-1-2, sont de plus en plus fréquents chez les adultes des classes 3-4 (2 %) et 5-6-7 (5 %).

— Les Crevettes *Natantia* sont aussi de plus en plus représentées chez les individus adultes. Leur fréquence d'occurrence passe de 4 % à 14 % et à 16 % respectivement chez les groupes d'âge 0-1-2, 3-4 et 5-6-7.

— Les Crangonidés fréquents chez les immatures (Fc = 15 %) disparaissent progressivement du régime alimentaire. Chez les mâles des classes 3-4, les Crangonidés ne représentent que 3 % des proies.

— Les Euphausiacés, plus fréquents chez les individus des classes 3-4 que chez ceux des classes 0-1-2, sont absents chez les classes d'âge 5+.

Il faut noter que chez les mâles de *C. linguatula*, toutes ces proies (Céphalopodes, *Natantia*, Crangonidés et Euphausiacés) sont des proies complémentaires à tous les stades de la vie.

Chez les femelles, les Amphipodes et les Brachyours sont présents uniquement dans le régime des individus des classes 0 à 4. Les Stomatopodes et les Isopodes apparaissent dans le régime alimentaire des femelles dès la classe 3 alors que les Homaridés (*Nephrops norvegicus*) n'apparaissent qu'à partir de la classe 5.

Jusqu'à la classe 4, les Mysidacés sont toujours des proies préférentielles (RI = 60 % et 56 %) et les Poissons des proies secondaires. Cependant, ces derniers deviennent des proies préférentielles pour les individus des classes 5 et plus.

— Les Crevettes *Natantia*, les Céphalopodes et les Euphausiacés sont toujours des proies complémentaires, mais leur importance change avec l'âge des Poissons. Les Mollusques Céphalopodes et les *Natantia* sont de plus en plus représentés chez les femelles âgées. Alors que les Euphausiacés sont plus fréquents chez les immatures de moins de 3 ans (RI = 4,08 %).

— Les Crangonidés sont des proies complémentaires chez les femelles de moins de 5 ans. Cependant chez les individus plus âgés, ces espèces sont uniquement des proies accessoires (RI = 0,28 %).

— Les Amphipodes et les Brachyours sont des proies accessoires pour les femelles des classes 0 à 4. Enfin, les Stomatopodes, Isopodes et Langoustes sont des proies accessoires pour toutes les femelles de plus de 3 ans.

Les coefficients de vacuité ont été calculés pour toute la durée de l'étude, en distinguant les groupes d'âge 0-1-2, 3-4 et 5-6-7. Chez les mâles, le coefficient de vacuité (C.V.) est de l'ordre de 16 %, 35 % et 42 %. Selon le groupe d'âge, on constate donc que le C.V. est toujours beaucoup plus élevé chez les individus des classes d'âge supérieures à 3. Le même résultat est obtenu chez les femelles chez lesquelles le coefficient de vacuité est voisin de 16 %, 31 % et 23 % en fonction de l'âge. Cependant, l'alimentation des femelles reste intense, en particulier chez les individus des classes d'âge supérieures à 5 chez lesquels le regain de consommation semble être en relation avec l'activité de reproduction.

#### *D. cuneata* (Fig. 2 B)

Pour *D. cuneata*, les classes d'âge ont été définies de la même manière que pour *C. linguatula*. La relation entre l'âge et la taille des individus a été établie à partir de 300 femelles et 336 mâles. Les équations de croissance linéaire sont respectivement :

$$L_{T(t)} = 32,69 (1 - e^{-0,126(t + 2,85)})$$

$$L_{T(t)} = 35,48 (1 - e^{-0,101(t + 3,31)})$$



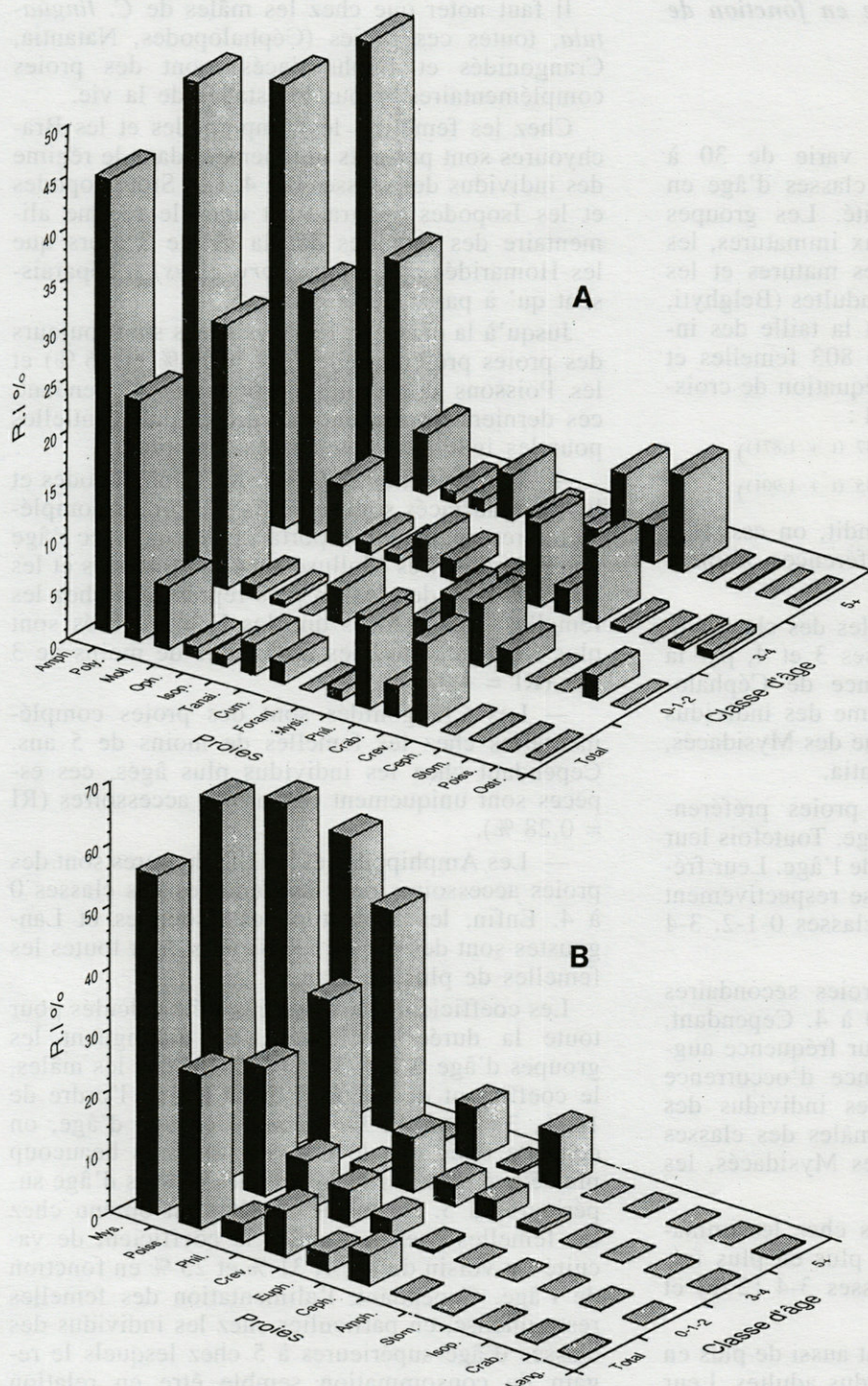


Fig. 2. - Variations du régime alimentaire en fonction de la taille et de l'âge. A : *Citharus linguatula*; B : *Dicologlossa cuneata*.

Diet changes according to the length and the age A : *Citharus linguatula*; B : *Dicologlossa cuneata*. Amph. : Amphipodes, Ceph. : Céphalopodes, Crab. : Crabes., Crev. : Crevettes, Cum. : Cumacés, Euph. : Euphausiacés, Foram. : Foraminifères, Isop. : Isopodes, Moll. : Mollusques (Bivalves et Gastéropodes), Mys. : Mysidés, Oph. : Ophiurides, Ostr. : Ostracodes, Phil. : *Philocheas sp.*, Pois. : Poissons, Poly. : Polychètes, Stom. : Stomatopodes, Tanai. : Tanaidacés.

Chez les mâles des classes d'âge 3 et 4, tous les groupes de proies sont représentés, alors que chez les classes 0,1 et 2 les Isopodes, Foraminifères, Poissons et Ostracodes font défaut. Chez les classes 5+, seuls les Poissons et des Ostracodes font défaut.

Chez les femelles des classes 0, 1 et 2, le régime alimentaire est le moins diversifié. On note l'absence d'un grand nombre de proies : Mollusques (Bivalves, Gastéropodes, Céphalopodes),

Echinodermes, Isopodes, Foraminifères, Stomatopodes et Ostracodes. Par contre, seuls les Poissons et les Stomatopodes font défaut chez les femelles des classes 3-4 et 5+.

Comme chez *C. linguatula*, les mâles et les femelles de *D. cuneata* changent de préférences alimentaires à mesure qu'ils grandissent.

Les Amphipodes sont toujours des proies préférentielles quels que soient l'âge et le sexe. Toutefois on note une baisse de leur importance chez



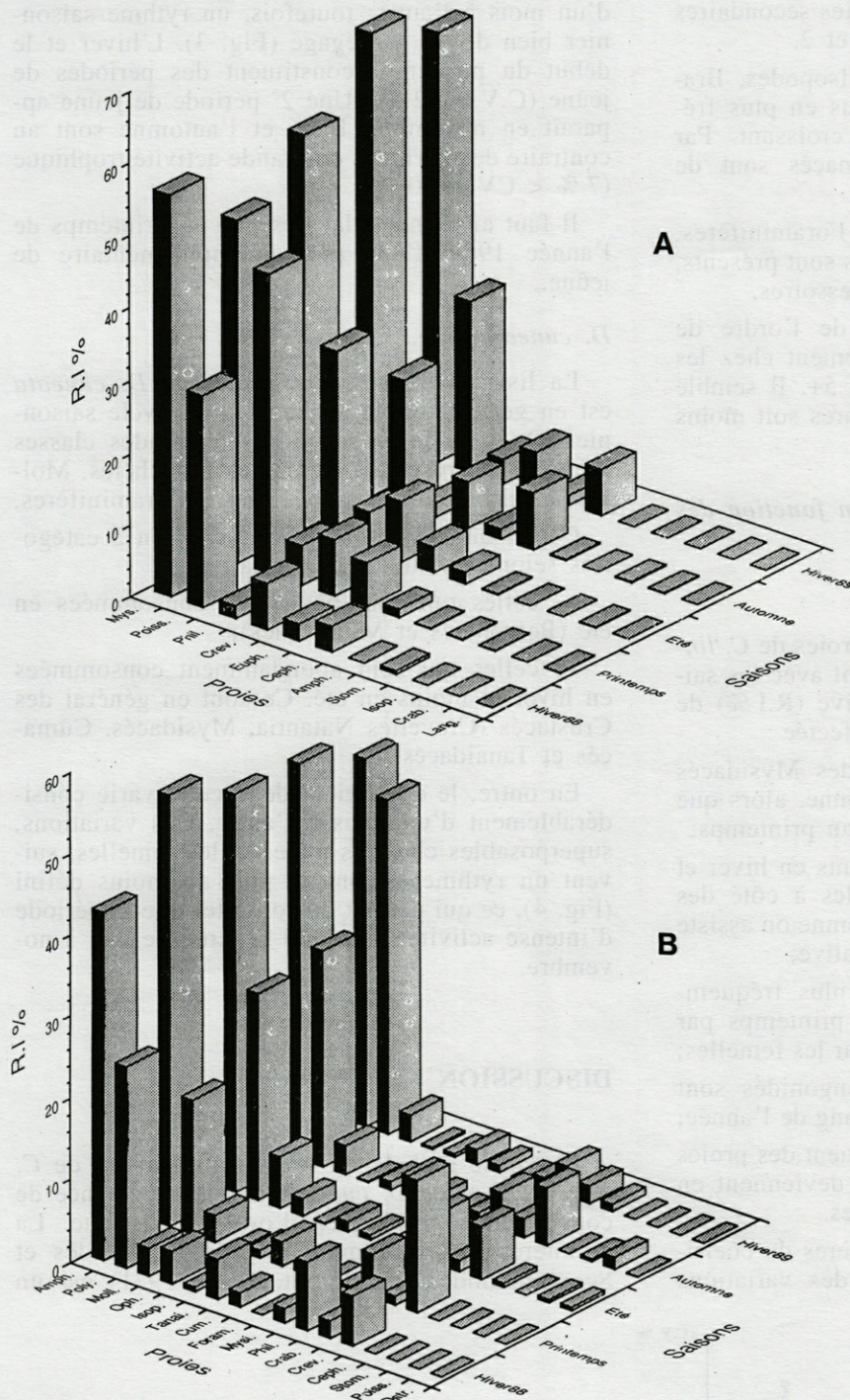


Fig. 3. – Variations du régime alimentaire en fonction des saisons. A : *Citharus linguatula*; B : *Dicologlossa cuneata*.

Seasonal variation in the diet. A : *Citharus linguatula*; B : *Dicologlossa cuneata*.

Amph. : Amphipodes, Ceph. : Céphalopodes, Crab. : Crabes., Crev. : Crevettes, Cum. : Cumacés, Euph. : Euphausiacés, Foram. : Foraminifères, Isop. : Isopodes, Moll. : Mollusques (Bivalves et Gastéropodes), Mys. : Mysidacés, Oph. : Ophiurides, Ostr. : Ostracodes, Phil. : *Philocheras sp.*, Pois. : Poissons, Poly. : Polychètes, Stom. : Stomatopodes, Tanai. : Tanaidacés.

les mâles : leur fréquence d'importance relative (RI %) passe respectivement de 54,71 à 43,86 et à 39,99 % chez les groupes d'âge 0-1-2, 3-4 et 5+.

Les Annélides polychètes sont toujours des proies secondaires quelle que soit la classe d'âge. On note cependant une légère diminution de leur importance relative chez les individus les plus âgés.

Les Crevettes *Natantia*, proies complémentaires chez les immatures des classes 0, 1 et 2, deviennent des proies secondaires chez les mâles et les femelles de plus de 3 ans.

Le reste des proies : Mollusques (Bivalves et Gastéropodes), Tanaidacés, Cumacés, Mysidacés, Brachyours, Isopodes et Ophiurides sont en général des proies complémentaires. Cependant certaines particularités méritent d'être signalées :



— les Brachyours sont des proies secondaires pour les femelles des classes 0, 1 et 2.

— les Bivalves, Gastéropodes, Isopodes, Brachyours et Tanaidacés sont de plus en plus fréquents chez les individus d'âge croissant. Par contre les Mysidacés et les Cumacés sont de moins en moins représentés.

Les Stomatopodes, Ostracodes, Foraminifères, Céphalopodes et Poissons, quand ils sont présents, ne représentent que des proies accessoires.

Le coefficient de vacuité est de l'ordre de 20,33, 13,46 et 10,71 % respectivement chez les individus des classes 0-1-2, 3-4 et 5+. Il semble que l'activité trophique des immatures soit moins intense que celle des adultes.

#### Variation du régime alimentaire en fonction des saisons

##### *C. linguatula* (Fig. 3 A)

La composition faunistique des proies de *C. linguatula* ne change pas profondément avec les saisons; cependant l'importance relative (R.I %) de chaque taxon est plus ou moins affectée :

— les fréquences importantes des Mysidacés sont enregistrées en été et en automne, alors que les faibles fréquences s'observent au printemps;

— les Poissons sont plus fréquents en hiver et constituent des proies préférentielles à côté des Mysidacés. En été et surtout en automne on assiste à un déclin de leur importance relative;

— les Crevettes *Natantia* sont plus fréquemment consommées en hiver et au printemps par les mâles et en été et à l'automne par les femelles;

— les Euphausiacés et les Crangonidés sont abondamment consommés tout au long de l'année;

— les Céphalopodes, qui constituent des proies accessoires en hiver et printemps, deviennent en automne des proies complémentaires.

L'analyse des variations saisonnières du coefficient de vacuité (Fig. 4), révèle des variations

d'un mois à l'autre; toutefois, un rythme saisonnier bien défini se dégage (Fig. 3). L'hiver et le début du printemps constituent des périodes de jeûne (C.V = 52 %). Une 2<sup>e</sup> période de jeûne apparaît en novembre. L'été et l'automne sont au contraire des périodes de grande activité trophique (7 % < CV < 30 %).

Il faut aussi noter la présence au printemps de l'année 1989 d'une période supplémentaire de jeûne.

##### *D. cuneata* (Fig. 3 B)

La liste faunistique des proies de *D. cuneata* est en général stable au cours d'un cycle saisonnier. On note la présence des 6 grandes classes de proies : Crustacés, Annélides Polychètes, Mollusques, Poissons, Echinodermes et Foraminifères.

Cependant, les proies se scindent en 2 catégories selon leur importance relative :

— celles qui sont davantage consommées en été (Polychètes et Mollusques);

— celles qui sont abondamment consommées en hiver et moins en été. Ce sont en général des Crustacés (*Crevettes Natantia*, Mysidacés, Cumacés et Tanaidacés).

En outre, le coefficient de vacuité varie considérablement d'un mois à l'autre. Ces variations, superposables chez les mâles et les femelles, suivent un rythme saisonnier plus au moins défini (Fig. 4), ce qui permet de constater que la période d'intense activité trophique se situe de mai à novembre.

## DISCUSSION

L'analyse globale du régime alimentaire de *C. linguatula* et de *D. cuneata* révèle l'existence de convergences trophiques d'ordre phylétique. La première espèce, comme tous les Citharidés et Scopthalmidés (De Groot, 1969, 1971) est un

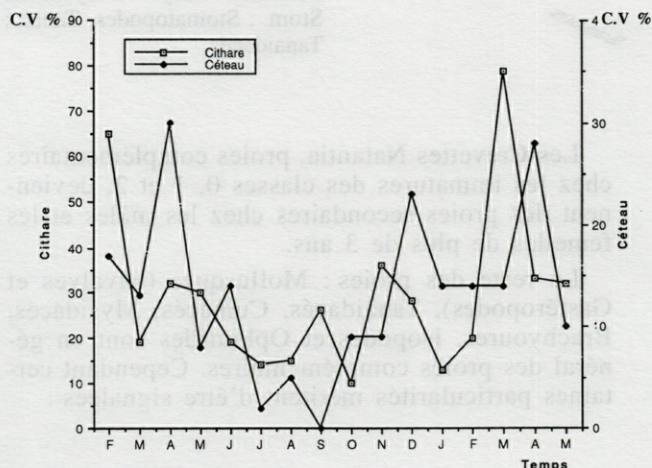


Fig. 4. — Analyse des variations saisonnières du coefficient de vacuité chez les deux espèces. Seasonal evolution of the coefficient of vacuity (CV) for the two species.



Poisson carnivore, planctonophage et ichthyophage et se nourrit surtout de Poissons, Céphalopodes et Crustacés (Mysidacés, Euphausiacés, Copépodes). Il s'agit d'une espèce relativement sténophage dans la mesure où *C. linguatula* se contente de quelques types de proies. Son régime alimentaire est de type pélagique, la fréquence d'occurrence de ce type de proies étant de l'ordre de 99 % (Geistdoerfer, 1978).

Par contre, *D. cuneata*, comme tous les Soleïdés, apparaît comme un prédateur benthophage (les proies de type benthique participent pour plus de 76 % à son alimentation), se nourrissant de proies immobiles ou peu vagiles (Polychètes, Bivalves, Gastéropodes, Amphipodes, Cumacés, Iso-podes, Tanaidacés, Mysidacés, Ostracodes, Natantia, Brachyours, Ophiurides...). *D. cuneata*, plus strictement benthique, a une alimentation plus diversifiée que *C. linguatula*, ce qui lui confère un caractère eurypage.

Le caractère necto-benthique des proies de *C. linguatula* nous permet de classer cette espèce parmi les Poissons chasseurs à vue se nourrissant pendant le jour, alors que *D. cuneata* dont le régime est à base de proies fixées, fousseuses superficielles ou mobiles en contact direct avec le fond, peut être considéré à la fois comme un carnassier et un brouteur de « sédiment ». Par ailleurs, comme la plupart des Soleïdés, *D. cuneata* se nourrit de nuit, les proies étant alors reconnues par olfaction (De Groot, 1971; Quiniou, 1978; Lagardère, 1982).

Bien qu'il n'apparaisse pas de différence profonde dans le régime alimentaire en fonction du sexe, chez *C. linguatula* comme chez *D. cuneata*, les femelles ont toujours des besoins trophiques et énergétiques supérieurs à ceux des mâles. Ce phénomène avait déjà été observé chez *D. cuneata* dans le Golfe de Gascogne (Lagardère, 1982).

Les préférences alimentaires changent aussi en fonction de l'âge. Les Mysidacés, Euphausiacés, Crangonidés et Amphipodes, proies de petite taille, caractérisent le régime alimentaire des jeunes individus mâles et femelles de *C. linguatula*, alors que les Poissons, Céphalopodes, Crevettes Natantia, Stomatopodes et Homaridés, proies plus volumineuses, sont typiques du régime alimentaire des adultes.

Ce passage progressif d'un régime à base de petites proies à un régime constitué de proies plus volumineuses (Poissons, Céphalopodes), bien marqué chez *C. linguatula*, est fréquent chez les Pleuronectiformes (Deniel, 1974; 1975 et 1981; Quiniou, 1978; Braber et De Groot, 1973; Lockwood, 1984). Ces changements qualitatifs du régime alimentaire en fonction de l'âge s'accompagnent de changements dans l'intensité de l'alimentation et doivent être interprétés comme des modifications dans le comportement

alimentaire des Poissons en relation avec l'accroissement des besoins énergétiques. En effet, les pourcentages des estomacs vides sont plus faibles chez les immatures de *C. linguatula*, preuve que ces derniers consacrent plus de temps que les adultes à la recherche de leurs proies. Cette intense alimentation des jeunes Poissons des classes d'âge 0,1 et 2 déjà signalée chez le Flet (Moore et Moore, 1976) trouve une explication dans le fait que la phase d'immaturité est une phase de forte croissance. Mais, elle peut être aussi une compensation au faible rendement énergétique des proies exploitées par ces classes d'âge.

Contrairement à *C. linguatula*, chez *D. cuneata*, la phase d'immaturité sexuelle ne semble pas être une période de forte activité trophique, les immatures de *D. cuneata* manifestant une intensité d'alimentation plus faible que les adultes.

Pour *D. cuneata*, alors que les Amphipodes et les Annélides Polychètes sont à la base de l'alimentation quel que soit l'âge des Poissons, les Brachyours, Mysidacés et Cumacés, proies de petite taille, ont tendance à disparaître du régime des Poissons âgés et sont remplacées par des proies plus volumineuses comme les Crevettes, Mollusques, Tanaidacés et Stomatopodes. Ces changements ne s'observent pas uniquement lors du passage du stade juvénile au stade adulte. Il s'agit en fait d'une évolution précoce qui débute au stade de postlarve. Lagardère (1982) dans le golfe de Gascogne observe que les larves de *D. cuneata* se nourrissent de Ciliés (Dinoflagellés et Tintinides), d'œufs et de nauplii de Crustacés, de larves de Bivalves et de Polychètes et de Copépodes, alors que le régime des juvéniles et des adultes est dominé par trois groupes d'Invertébrés benthiques : les Polychètes, Pélécy-podes et Crustacés (Amphipodes et Cumacés). Comme l'a montré Yasuda (1960 a et b), chez les Poissons, la taille des proies est proportionnelle à la taille du Poisson et plus spécialement à la largeur de la bouche.

Ainsi, il existe en fonction de la croissance du Poisson un système de relais dans la sélection des proies : le prédateur vise la même espèce de proie mais sélectionne les grands individus (relai intraspécifique) ou vise le même groupe taxonomique mais s'attaque à des espèces plus grosses (relai interspécifique) ou s'attaque à de nouveaux taxons (relai intertaxonomique).

Certaines variations du régime alimentaire constatées chez *C. linguatula* peuvent aussi être attribuées à l'évolution des peuplements benthiques au cours des saisons. En hiver, des proies, en général de petite taille, comme les Mysidacés, les Euphausiacés, les Crangonidés et les Crevettes Natantia, interviennent plus faiblement dans l'alimentation des poissons. Ces baisses sont avant tout corrélées aux faibles densités de la faune planctonique et benthique à cette période de l'année.



### Variations saisonnières et activité génésique

Chez *C. linguatula*, la faible activité alimentaire en hiver et au printemps est le reflet du jeûne trophique qui affecte les géniteurs pendant la période de frai. Si le frai est une vraie source de crise, comme de nombreuses espèces de Pleuronectiformes de la zone boréo-tempérée (*Pleuronectes platessa*, *Platichthys flesus* et *Solea vulgaris*) dont la reproduction est hivernale ou printanière, *C. linguatula* utilise la saison estivale pour croître et emmagasiner les réserves nécessaires à la maturation sexuelle et à la ponte.

L'activité alimentaire de *D. cuneata* montre aussi de profondes modifications au cours des saisons. En effet, celle-ci augmente très fortement du printemps au début de l'automne (mai à novembre). Cependant, les modifications saisonnières du régime alimentaire de *D. cuneata* se limitent à la plus ou moins grande prépondérance de l'un des quatre grands groupes d'Invertébrés, les Amphipodes étant en outre les proies les plus abondantes, quelle que soit la saison. Chez *D. cuneata*, à ces variations quantitatives s'ajoutent des différences qualitatives, comme le remplacement, au printemps, des Mysidacés et des Crangonidés par les Poissons et les Crevettes *Natantia* susceptibles de satisfaire, avec un meilleur rendement, les besoins énergétiques accrus des Poissons à cette période de l'année. Ce rythme alimentaire saisonnier, déjà observé par Lagardère (1982) dans le Golfe de Gascogne, apparaît lié à l'activité génésique du Poisson. Il convient cependant de noter que *D. cuneata* possède une reproduction étalée sur environ cinq mois fractionnée en deux cycles d'émission des gamètes (Belghyti, 1990). D'après Lagardère (1982), cette espèce ménage entre chaque cycle d'émission une phase de boulimie, ce qui se traduit par une allure en « dents de scie » du coefficient de vacuité. Ces variations du régime alimentaire s'accompagnent de migrations génésiques et trophiques. Au printemps, les populations se rapprochent de la côte pour se reproduire et s'en éloignent à la fin de l'automne, refoulées par les masses d'eaux froides, pour s'abriter à des profondeurs de 50 à 60 m où la température est relativement plus élevée (12°C).

L'analyse des fluctuations dans la composition du régime alimentaire des deux espèces de Pleuronectiformes nous permet de constater que ces deux espèces n'utilisent pour se nourrir qu'une partie des proies disponibles dans le milieu et prélèvent toujours des organismes qui appartiennent à un ensemble homogène. Le spectre de proies dont l'étendue apparaît fixée par l'ensemble des caractéristiques morphologiques et éthologiques liées à la recherche des proies constitue le cadre dans lequel s'exerce la sélection effective de l'espèce.

### Régime alimentaire et parasitisme

Le recensement dans les contenus stomacaux de *D. cuneata* de 16 espèces d'Amphipodes, parmi lesquelles *Phthisica marina* et *Pariambus typicus* qui occupent sur le littoral atlantique marocain la même niche écologique que *Caprella acutifrons*, hôte expérimental d'*A. canthocephaloides propinquus* (De Buron, 1986) nous amène à penser que ces deux espèces pourraient bien héberger les larves de ce parasite.

Par contre, pour *Bothriocephalus andresi*, parasite de *C. linguatula*, si la chute du parasitisme, concomitante du changement profond de régime alimentaire chez les Poissons de taille supérieure à 150 mm (Belghyti *et al.*) indique bien l'origine planctonique de l'hôte intermédiaire, l'absence de Copépodes hôtes habituels des Bothriocéphales (Robert et Gabrion, 1991) dans les contenus stomacaux de *C. linguatula* reste inexplicée. Un phénomène identique avait déjà été signalé par Dupont (1984) à propos de *B. claviceps* parasite de l'Anguille européenne.

### Peuplements littoraux et sélection des proies

Cependant, ainsi que l'ont montré Moore et Moore (1976) chez le Flet, le comportement trophique est déterminé, en fonction des possibilités ou des besoins de l'espèce, par le milieu et l'éventail des proies offertes. Pour De Groot (1971), le Céteau est avant tout un prédateur de Pélécy-podes et de Polychètes, alors que pour Sorbe (1972, 1981), il s'agit d'un consommateur d'Amphipodes. Une étude plus importante dans le temps et l'espace au niveau du Golfe de Gascogne (Lagardère, 1982) révèle que l'étendue des variations du régime alimentaire de cette espèce inclut les deux types de régimes. Néanmoins, l'auteur considère que les proies préférentielles du Céteau restent les Polychètes et les Pélécy-podes. L'étendue du spectre de proies entrant dans le régime alimentaire de *D. cuneata* sur le littoral atlantique marocain permet de couvrir les préférences alimentaires telles qu'elles ont été définies par ces différents auteurs avec cependant une nette prédominance des Amphipodes.

D'un point de vue qualitatif, la comparaison des espèces répertoriées sur le littoral atlantique marocain avec celles retrouvées dans le Golfe de Gascogne (Lagardère, 1982) révèle l'existence d'un certain nombre d'espèces communes au régime alimentaire du Céteau dans ces deux régions. Ces espèces appartiennent aux Amphipodes (*Ampelisca brevicornis*, *A. diadema*, *Apherusa* sp., *Pariambus typicus*, *Stenthoë* sp.), aux Cumacés (*Diastylis bradyi*, *D. laevis*), aux Annélides (*Nereis zonata*, *N. succina*) et aux Mollusques (*Cul-*



*tellus* sp., *Pharus legumen*). Cependant, globalement, le régime alimentaire du Céteau est moins diversifié sur le littoral atlantique marocain que dans le Golfe de Gascogne.

Par ailleurs, la comparaison des proies de *D. cuneata* et de *C. linguatula* permet de constater de profondes divergences dans le spectre de proies exploitées par chacune de ces deux espèces, le nombre d'espèces communes représentées essentiellement par les Crevettes Natantia (*Philocheras bispinosus*, *Processa canaliculata* et *Alpheus glaber*) étant particulièrement faible. Ces divergences ainsi que les stratégies déployées dans la recherche de la nourriture, évitent la compétition entre ces deux prédateurs et rendent possible leur coexistence.

La grande diversité des proies de ces deux espèces reflète la richesse de la faune profonde du littoral atlantique marocain. Cette diversité ainsi que la spécificité des proies consommées par les populations marocaines de *D. cuneata* comparées à celles du Golfe de Gascogne nous amènent à considérer que ces deux espèces constituent d'excellents traceurs naturels des peuplements littoraux dans lesquels se déroulent les principales étapes de leur cycle biologique.

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# MORPHOLOGICAL, GENETIC AND CHROMOSOMAL CHARACTERIZATION OF CORSICAN AND SPANISH *BACILLUS ROSSIUS* (INSECTA PHASMATODEA)

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DISTANCES GENETIQUES  
FUSION ROBERTSONIENNE  
OOTAXONOMIE  
RESTRUCTURATIONS  
CHROMOSOMIQUES  
SPANANDRIE

RESUME – L'ootaxonomie, l'électrophorèse des systèmes gène-enzyme et l'analyse chromosomique révèlent que le Phasmide *Bacillus rossius* de Corse, parthénogénétique, appartient à la sous-espèce *B. r. rossius*. Les distances génétiques et les caractéristiques chromosomiques, malgré une fusion Robertsonienne, indiquent une forte affinité avec les populations parthénogénétiques du Nord de la Sardaigne et de l'île d'Elbe; il est donc probable que toutes ces populations sont issues d'une dérive commune depuis le Tertiaire. L'analyse enzymatique de trois échantillons bisexués espagnols provenant de Catalogne (Tossa) et qui devraient être des *B. r. catalauniae*, indique au contraire qu'ils appartiennent également à la sous-espèce *B. r. rossius*.

GENETIC DISTANCES  
OOTAXONOMY  
REPATTERNED CYTOTYPES  
ROBERTSONIAN FUSION  
SPANANDRY

ABSTRACT – Chorionic pattern, allozymic and chromosomal analysis allow to assign the parthenogenetic Corsican *Bacillus rossius* to the *B. r. rossius* subspecies. Although some distinguishing chromosomal features have been detected (Robertsonian fusions), karyotype and general genetic characteristics indicate their high similarity to the parthenogenetic North-Sardinian and Elban demes, suggesting a common derivation during the Tertiary. Allozyme analysis of Spanish bisexual samples from *B. r. catalauniae* area (Tossa) reveals that these populations too belong to *B. r. rossius*.

## INTRODUCTION

The holomediterranean genus *Bacillus* has been widely investigated through multidisciplinary approaches (Scali & Mantovani, 1989; Bullini & Nascetti, 1990; Mantovani *et al.*, 1991 b). In addition to several thelytokous taxa, it includes two bisexual species. The first one, *B. grandii* (2n = 34 XX, female; 33 X0, male), is strictly bisexual and differentiated into 3 subspecies: *B. g. benazzii*, from North-western Sicily and Levanzo (Egadi Islands), *B. g. maretimi*, endemic of Marettimo (Egadi Islands) and *B. g. grandii*, found in a very limited area of South-eastern Sicily (Nascetti & Bullini, 1982; Scali & Mantovani, 1990; Mantovani *et al.*, 1991 a; Scali, 1991). The second one, *B. rossius* (2n = 36 XX, female and 35 X0, male), spreads into Central and Western Mediterranean basin also with many facultatively parthenogenetic demes. *B. rossius* is differentiated into 8 subspecies, recognized on ootaxonomical and electrophoretic grounds: *B. r. tripolitanus* A, *B. r.*

*tripolitanus* B, *B. r. lobipes*, *B. r. montalentii* and *B. r. medeae* (Northern Africa: Tunisia, Algeria); *B. r. catalauniae* (Spain: Catalonia); *B. r. rossius* (French and Western Italian coasts, Sardinia – except Sarrabus area – and Tuscan Archipelago); *B. r. redtenbacheri* (Sardinia – only in the Sarrabus area – Sicily, Eolie Islands, Southern Tyrrhenian, Adriatic and Ionian coasts of Italy, Yugoslavia, Greece (see Mantovani *et al.*, 1991 b for a review).

Many facultative parthenogenetic demes of *B. r. rossius* and *B. r. redtenbacheri* are known. They are always genetically more similar to the bisexual populations of the same area than to the parthenogenetic ones of the others (Gasperi *et al.*, 1983; Nascetti & Bullini, 1983; Scali *et al.*, 1987).

Investigations carried out on populations from Central and Western Mediterranean basin have considerably increased our knowledge about distribution, ootaxonomy, genetic structure, chromosomal complements and reproductive biology of *B. rossius* subspecies (Gasperi *et al.*, 1983;



Nascetti & Bullini, 1983; Scali & Marescalchi, 1987; Scali *et al.*, 1987; Tinti & Scali, 1990; Manaresi *et al.*, 1991; Mantovani & Scali, 1991; Tinti *et al.*, 1992).

Ootaxonomical investigations on the chorionic features in *B. rossius*, support a subspecific level of differentiation in agreement with the genetic structure (Scali *et al.*, 1987).

The subspecific values of genetic distance, obtained from gene-enzyme systems analysis at about 20 loci, range between  $D = 0.116$  (comparisons between Sardinian demes of *B. r. rossius* and *B. r. redtenbacheri*, Mantovani & Scali, 1991) and  $D = 0.543$  (Italian, Yugoslavian and Greek samples of *B. r. redtenbacheri* compared to *B. r. montalentii*, Nascetti & Bullini, 1983).

Nei's genetic distances between the *B. rossius* subspecies involved in the present paper are the following: *B. r. rossius* – *B. r. redtenbacheri*: 0.116 – 0.193; *B. r. rossius* – *B. r. catalauniae*: 0.161; *B. r. redtenbacheri* – *B. r. catalauniae*: 0.214 (Nascetti & Bullini, 1983; Mantovani & Scali, 1991; Tinti *et al.*, 1992). I would like to point out that no genotype or allele frequencies of *B. r. catalauniae* have been reported.

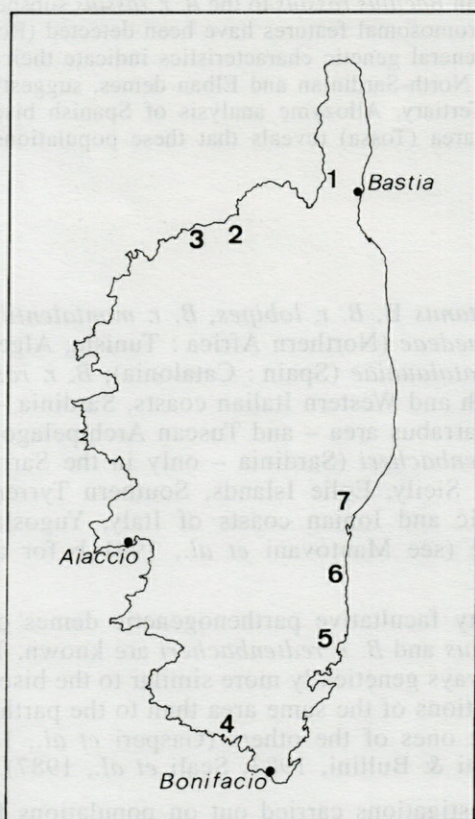


Fig. 1. – Map of Corsica showing the locations of the 7 analyzed *Bacillus rossius* demes (1: Albo, 2: Ile Rousse L, 3: Ile Rousse B, 4: Pianettoli, 5: S. Giulie, 6: Solenzara, 7: Ghisonaccia).

Chromosomal analyses of *B. rossius* show  $2n = 36$ , female and 35, male standard complement in all subspecies, with differences only in the number and position of secondary constrictions (Scali *et al.*, 1983; Scali & Marescalchi, 1987). However, instances of chromosomal repatterning (Robertsonian fusions or fissions, inversions and translocations) have been found to occur in some parthenogenetic demes from Sicily (Castelvetrano,  $2n = 38$ ; Scali & Marescalchi, 1987; Manaresi *et al.*, 1991) and from Northern Sardinia (Castelsardo,  $2n = 32$ ; Poglina,  $2n = 32, 34$ ; Tinti & Scali, 1990 and unpublished data).

No data about Corsica, the Balearic and others minor Mediterranean islands have been reported.

This paper deals with the systematic characterization of Corsican *B. rossius* through ootaxonomical, electrophoretic and karyological approaches, and the allozymic characterization of three samples from *B. r. catalauniae* area.

## MATERIALS AND METHODS

Seven all-females samples of *B. rossius* were collected in Corsica during September 1990 (Table I, Fig. 1). Also three amphigonic samples collected near Tossa (Catalonia, Spain; Table I) were analyzed. Morphological, allozymic and karyological investigations were carried out as reported below.

### Ootaxonomy

Only eggs of field collected females were used for SEM observations. After 80% ethanol fixation, eggs were washed, ultrasonicated to eliminate debris, air dried and mounted to specimen-holders with Bio-Rad silver-conducting paint. The eggs were coated with gold in a Ed-

Table I. – Collecting sites, sample sizes, sex-ratios and natural food-plants of the 7 Corsican and 3 Spanish populations of *Bacillus rossius*.

| POPULATIONS     | FEMALES | MALES | FOOD-PLANTS        |
|-----------------|---------|-------|--------------------|
| <b>Corsican</b> |         |       |                    |
| Albo            | 15      | 1     | Bramble, lentisk   |
| Ile Rousse L    | 3       |       | Lentisk            |
| Ile Rousse B    | 13      |       | Bramble            |
| Pianettoli      | 16      |       | Bramble            |
| S. Giulie       | 15      | 1     | Bramble, wild rose |
| Solenzara       | 6       |       | Bramble            |
| Ghisonaccia     | 30      |       | Bramble            |
| <b>Spanish</b>  |         |       |                    |
| Tossa 1         | 8       | 6     | Lentisk            |
| Tossa 2         | 7       | 7     | Bramble, lentisk   |
| Tossa 3         | 8       | 8     | Bramble            |



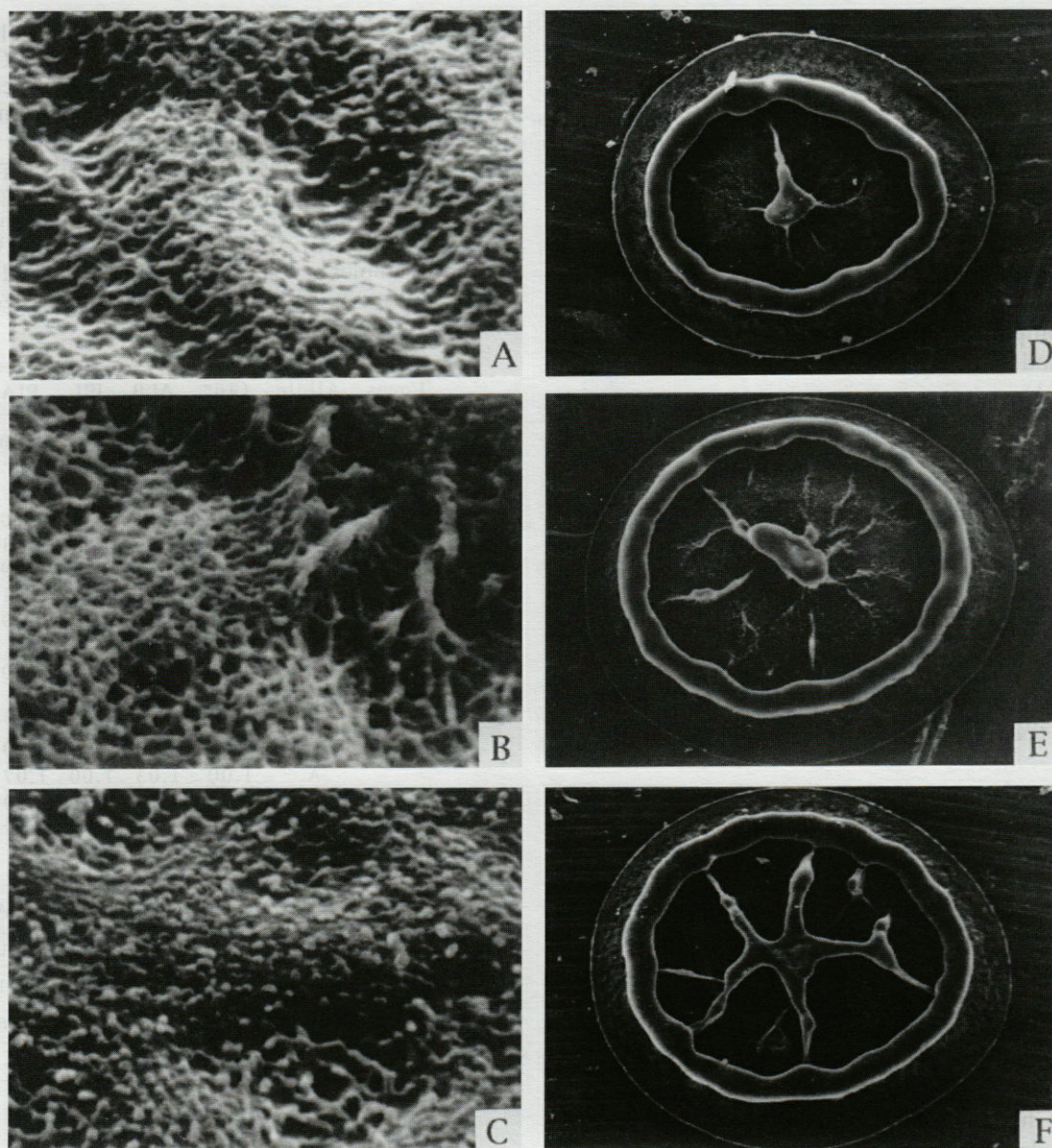


Fig. 2. – Fine capsule patterns (A : Solenzara, B : Ghisonaccia, C : Pianettoli; x 1300) and operculae (D : Ile Rousse L, E : S. Giulie, F : Pianettoli; x 60) of eggs laid by field-collected Corsican females.

wards S 150 A sputter coater and observed with a Philips 515 scanning electron microscope. The used terminology is according to Scali *et al.* (1990).

#### Allozyme analysis

Sample homogenates, electrophoretic runs and staining procedures were performed according to Mantovani *et al.* (1991 a). The following enzymes gave interpretable patterns in all analyzed populations:  $\alpha$  1 – GPDH (glycerophosphate dehydrogenase, E.C. : 1.1.1.08), MDH (malate dehydrogenase, E.C. : 1.1.1.37), IDH (isocitrate dehydrogenase, E.C. : 1.1.1.42), 6PGDH (6-phosphogluconate dehydrogenase, E.C. : 1.1.1.44), GOX (glucose oxidase, E.C. : 1.1.1.47), G6PDH

(glucose 6-phosphate dehydrogenase, E.C. : 1.1.1.49), G3PDH (glyceraldehyde 3-phosphate dehydrogenase, E.C. : 1.2.1.12), GOT (glutamate-oxaloacetate transaminase, E.C. : 2.6.1.1), HK (hexokinase, E.C. : 2.7.1.1), ADK (adenilate kinase, E.C. : 2.7.4.3), PGM (phosphoglucomutase, E.C. : 2.7.5.1), ALD (aldolase, E.C. : 4.1.2.13), FH (fumarase, E.C. : 4.2.1.2), MPI (mannose 6-phosphate isomerase, E.C. : 5.3.1.8), PGI (phosphoglucose isomerase, E.C. : 5.3.1.9). For MDH, IDH, GOT, HK, and ADK two systems were identified so that a total number of 20 loci were therefore studied.

The allozyme polymorphism indexes  $\bar{H}$ obs (mean observed heterozygosity),  $\bar{A}$  (mean effective number of allele per locus) and  $\bar{P}$  (frequency of polymorphic loci) were obtained following Mantovani *et al.* (1991 a).



Corsican and Spanish populations were compared with the two nearest Central Mediterranean *B. rossius* subspecies: *B.r. rossius* (samples from Sardinia, Elba Island, Tuscany, Latium) and *B.r. redtenbacheri* (samples from Sicily and Ionian-Adriatic coasts of Italy) (Mantovani & Scali, 1991; Tinti *et al.*, 1992).

Genetic distances (D) were calculated according to Nei's method (1972) on 20 loci for Corsican and Spanish samples and on 18 loci in intersub-specific comparisons. A dendrogram, based on D, was obtained with an UPGMA method (Sneath & Sokal, 1973).

### Karyology

Chromosome preparations of females and males were obtained from follicular cells and spermatogonia respectively, following Tinti & Scali (1991). Slides were stained with Giemsa stain (3% Giemsa solution in 0.1 M phosphate buffer pH 7.0) and mounted in Euparal.

For chromosome characterization, the criteria and terms suggested by Levan *et al.* (1964) were followed.

## RESULTS

### Ootaxonomy

In all samples, the capsule pattern is undulated. The net of indented ribbons present in South-eastern samples (S. Giulie, Solenzara, Ghisonaccia) becomes more faintly dented in the Western coastal ones; well developed cristae are found only in S. Giulie and Ghisonaccia (Fig. 2 A-B). A pattern given by isolated droplets is evident in Pianettoli samples (Fig. 2 C). The operculum is very similar in all demes and shows a well defined peripheral ring with variously developed internal cristae (Fig. 2 D-F); the differential developmental patterns of cristae does not follow any geographical cline.

### Electrophoretic analysis

Table II A gives the allelic frequencies of the Corsican demes at the 5 polymorphic loci (*6Pgdh*, *Got-1*, *Hk-1*, *Hk-2*, *Fh*), the other 15 loci being monomorphic for the same allele in all samples. Ile Rousse B, S. Giulie, Ghisonaccia, Solenzara demes showed an identical allele pattern and therefore they were pooled into one sample called GHI\*. At each locus, all samples show a homozygous genotype ( $\bar{H}_{obs} = 0.00$ ); consequently, the low polymorphism is also expressed by the low A and P values (1.00 - 1.07 and 0.00 - 0.10, respectively).

It is also to be noted that all populations show at all loci the 100 allele either as unique or most

Table II. - A, Allelic frequencies at the 5 polymorphic loci of the Corsican *Bacillus rossius* demes (GHI\*: Ile Rousse B, S. Giulie, Solenzara and Ghisonaccia; ALB: Albo; IRL: Ile Rousse L; PIA: Pianettoli). Sample sizes (n) and polymorphism indexes ( $\bar{H}_{obs}$ : mean observed heterozygosity; A: mean effective of allele per locus; P: frequency of polymorphic loci) are also reported. B, Nei's genetic distances (D) between Corsican *Bacillus rossius* samples. C, Allelic frequencies of the 3 bisexual Spanish samples at the 8 polymorphic loci (T1: Tossa 1; T2: Tossa 2; T3: Tossa 3) and sample sizes (n).

| A            |                 |      |      |      |      |
|--------------|-----------------|------|------|------|------|
| Locus        | Allele          | GHI* | ALB  | IRL  | PIA  |
| <i>6Pgdh</i> | 100             | 1.00 | 1.00 | -    | 1.00 |
|              | 105             | -    | -    | 1.00 | -    |
| <i>Got-1</i> | 95              | -    | 0.14 | -    | -    |
|              | 100             | 1.00 | 0.86 | 1.00 | 1.00 |
| <i>Hk-1</i>  | 100             | 1.00 | 1.00 | 1.00 | 0.71 |
|              | 102             | -    | -    | -    | 0.29 |
| <i>Hk-2</i>  | 100             | 1.00 | 1.00 | 1.00 | 0.71 |
|              | 102             | -    | -    | -    | 0.29 |
| <i>Fh</i>    | 97              | -    | 0.14 | -    | -    |
|              | 100             | 1.00 | 0.86 | 1.00 | 1.00 |
|              | n               | 53   | 14   | 3    | 14   |
|              | $\bar{H}_{obs}$ | 0.00 | 0.00 | 0.00 | 0.00 |
|              | A               | 1.00 | 1.03 | 1.00 | 1.07 |
|              | P               | 0.00 | 0.10 | 0.00 | 0.10 |

| B    |      |       |       |       |
|------|------|-------|-------|-------|
|      | GHI* | ALB   | IRL   | PIA   |
| GHI* | --   | 0.002 | 0.051 | 0.008 |
| ALB  |      | --    | 0.054 | 0.011 |
| IRL  |      |       | --    | 0.061 |
| PIA  |      |       |       | --    |

| C            |        |      |      |      |
|--------------|--------|------|------|------|
| Locus        | Allele | T1   | T2   | T3   |
| <i>6Pgdh</i> | 96     | 0.84 | 0.50 | 0.63 |
|              | 100    | 0.16 | 0.50 | 0.37 |
| <i>Gox</i>   | 100    | 0.65 | 0.75 | 0.81 |
|              | 105    | 0.35 | 0.25 | 0.19 |
| <i>G6pdh</i> | 98     | 0.17 | 1.00 | 1.00 |
|              | 100    | 0.83 | -    | -    |
| <i>Adk-1</i> | 97     | 0.50 | 0.79 | 0.56 |
|              | 100    | 0.50 | 0.21 | 0.44 |
| <i>Adk-2</i> | 96     | -    | -    | 0.13 |
|              | 100    | 1.00 | 1.00 | 0.81 |
| <i>Fh</i>    | 97     | 0.14 | 0.06 | 0.19 |
|              | 100    | 0.86 | 0.94 | 0.81 |
| <i>Mpi</i>   | 98     | -    | 0.13 | -    |
|              | 100    | 1.00 | 0.87 | 1.00 |
| <i>Pgi</i>   | 97     | 0.93 | 0.63 | 0.44 |
|              | 100    | 0.17 | 0.37 | 0.56 |
|              | n      | 14   | 16   | 16   |

common, the only exception being the Ile Rousse L population having the alternative 105 allele at the *6Pgdh* locus.



The high homogeneity deriving from the allele frequencies (Table II A), as well as the resulting low genetic distances ( $0.002 < D < 0.061$ , Table II B), clearly indicate a differentiation of only interpopulation level.

The same applies to the three Spanish samples which show a quite similar allelic structure at the 8 polymorphic loci (*6Pgdh*, *Gox*, *G6pdh*, *Adk-1*, *Adk-2*, *Fh*, *Mpi* and *Pgi*, Table II C); the remain-

ing 12 loci (see Materials and Methods) are monomorphic. Their low genetic distances ( $0.009 < D < 0.020$ , clearly of interpopulation degree) again suggest to pool them (TOSSA).

The allelic frequencies at the 14 polymorphic loci of *B. r. rossius* and *B. r. redtenbacheri* reference samples (split into amphigenics and parthenogenetics), pooled Corsican and Spanish *B. rossius* samples are presented in Table III. The  $\alpha$ -

Table III. - Allelic frequencies at the 14 polymorphic loci of *Bacillus rossius rossius* reference samples (ROSUC, unisexual continental demes; ROSBC, bisexual continental populations; ROSEL, Elban populations; ROSUS, unisexual Sardinian demes; ROSBS, bisexual Sardinian populations), pooled Corsican (CORSI), pooled Spanish (TOSSA) *B. rossius* samples and *B. r. redtenbacheri* reference samples (REDU, unisexual demes; REDB, bisexual populations). Allelic frequencies of *B. rossius* reference samples were desumed from Mantovani & Scali, 1991 and Tinti *et al.*, 1992.

| Locus        | Allele | ROSUC | ROSBC | ROSEL | ROSUS | ROSBS | CORSI | TOSSA | REDU | REDB |
|--------------|--------|-------|-------|-------|-------|-------|-------|-------|------|------|
| <i>Mdh-1</i> | 100    | -     | -     | -     | -     | -     | -     | -     | 1.00 | 0.85 |
|              | 110    | 1.00  | 1.00  | 1.00  | 1.00  | 0.95  | 1.00  | 1.00  | -    | 0.15 |
|              | 116    | -     | -     | -     | -     | 0.02  | -     | -     | -    | -    |
|              | 125    | -     | -     | -     | -     | 0.03  | -     | -     | -    | -    |
| <i>Mdh-2</i> | 100    | 1.00  | 1.00  | 1.00  | 0.84  | 1.00  | 1.00  | 1.00  | 1.00 | 1.00 |
|              | 111    | -     | -     | -     | 0.16  | -     | -     | -     | -    | -    |
| <i>Idh-1</i> | 96     | -     | -     | -     | -     | 0.01  | -     | -     | -    | -    |
|              | 100    | 1.00  | 1.00  | 1.00  | 1.00  | 0.97  | 1.00  | 1.00  | 1.00 | 1.00 |
|              | 103    | -     | -     | -     | -     | 0.01  | -     | -     | -    | -    |
| <i>6Pgdh</i> | 107    | -     | -     | -     | -     | 0.01  | -     | -     | -    | -    |
|              | 96     | -     | -     | -     | -     | -     | -     | 0.64  | -    | 0.10 |
|              | 100    | 1.00  | 1.00  | 1.00  | 1.00  | 0.92  | 0.93  | 0.36  | 1.00 | 0.88 |
|              | 103    | -     | -     | -     | -     | 0.03  | -     | -     | -    | -    |
| <i>Gox</i>   | 105    | -     | -     | -     | -     | 0.05  | 0.07  | -     | -    | -    |
|              | 107    | -     | -     | -     | -     | -     | -     | -     | -    | 0.02 |
|              | 94     | -     | 0.06  | -     | -     | 0.06  | -     | -     | -    | 0.02 |
|              | 100    | 1.00  | 0.66  | 1.00  | 1.00  | 0.88  | 1.00  | 0.76  | 1.00 | 0.86 |
|              | 102    | -     | -     | -     | -     | -     | -     | -     | -    | -    |
| <i>G6pdh</i> | 105    | -     | -     | -     | -     | 0.03  | -     | 0.24  | -    | 0.01 |
|              | 107    | -     | 0.26  | -     | -     | -     | -     | -     | -    | -    |
|              | 110    | -     | -     | -     | -     | 0.03  | -     | -     | -    | 0.09 |
|              | 115    | -     | -     | -     | -     | -     | -     | -     | -    | 0.02 |
|              | 121    | -     | 0.02  | -     | -     | -     | -     | -     | -    | -    |
|              | 98     | -     | -     | -     | -     | -     | -     | 0.05  | -    | 0.02 |
| <i>Got-1</i> | 100    | 1.00  | 1.00  | 1.00  | 1.00  | 0.96  | 1.00  | 0.95  | 1.00 | 0.98 |
|              | 105    | -     | -     | -     | -     | 0.04  | -     | -     | -    | -    |
| <i>Got-2</i> | 93     | -     | 0.04  | -     | -     | -     | -     | -     | -    | -    |
|              | 95     | -     | -     | -     | -     | -     | 0.02  | -     | -    | -    |
| <i>Hk-1</i>  | 100    | 1.00  | 0.96  | 1.00  | 1.00  | 1.00  | 0.98  | 1.00  | 1.00 | 1.00 |
|              | 96     | -     | -     | -     | -     | 0.04  | -     | -     | -    | -    |
| <i>Hk-2</i>  | 100    | 1.00  | 0.88  | 1.00  | 1.00  | 0.96  | 1.00  | 1.00  | 1.00 | 1.00 |
|              | 103    | -     | 0.12  | -     | -     | -     | -     | -     | -    | -    |
|              | 104    | -     | 0.02  | -     | -     | -     | -     | -     | -    | -    |
| <i>Adk-1</i> | 100    | 1.00  | 0.98  | 1.00  | 1.00  | 1.00  | 0.95  | 1.00  | 1.00 | 1.00 |
|              | 102    | -     | -     | -     | -     | -     | 0.05  | -     | -    | -    |
|              | 104    | -     | 0.02  | -     | -     | -     | -     | -     | -    | -    |
|              | 94     | -     | -     | -     | -     | 0.03  | -     | -     | 0.04 | 0.40 |
| <i>Adk-2</i> | 97     | 1.00  | 0.95  | 1.00  | 1.00  | 0.87  | 1.00  | 0.53  | 0.03 | 0.11 |
|              | 100    | -     | 0.05  | -     | -     | 0.10  | -     | 0.47  | 0.90 | 0.49 |
|              | 103    | -     | -     | -     | -     | -     | -     | -     | 0.03 | -    |
| <i>Mpi</i>   | 96     | -     | -     | -     | -     | -     | -     | 0.05  | -    | -    |
|              | 100    | 0.97  | 1.00  | 0.83  | 1.00  | 0.94  | 1.00  | 0.95  | 1.00 | 1.00 |
|              | 104    | 0.03  | -     | 0.17  | -     | -     | -     | -     | -    | -    |
|              | 110    | -     | -     | -     | -     | 0.06  | -     | -     | -    | -    |
|              | 96     | -     | -     | -     | -     | 0.25  | -     | -     | -    | 0.04 |
|              | 98     | -     | -     | -     | -     | -     | -     | 0.04  | -    | -    |
| <i>Pgi</i>   | 100    | 1.00  | 1.00  | 1.00  | 1.00  | 0.69  | 1.00  | 0.96  | 1.00 | 0.86 |
|              | 105    | -     | -     | -     | -     | 0.03  | -     | -     | -    | 0.03 |
|              | 108    | -     | -     | -     | -     | -     | -     | -     | -    | 0.02 |
|              | 109    | -     | -     | -     | -     | 0.03  | -     | -     | -    | -    |
|              | 110    | -     | -     | -     | -     | -     | -     | -     | -    | 0.02 |
| <i>Pgi</i>   | 112    | -     | -     | -     | -     | -     | -     | -     | -    | 0.02 |
|              | 84     | -     | -     | -     | -     | 0.02  | -     | -     | -    | -    |
|              | 95     | -     | -     | -     | -     | 0.03  | -     | -     | -    | 0.02 |
|              | 97     | 0.22  | 0.83  | 1.00  | 1.00  | 0.70  | 1.00  | 0.66  | -    | 0.04 |
| 100          | 0.78   | 0.17  | -     | -     | 0.25  | -     | 0.34  | 1.00  | 0.94 |      |



*Gpdh*, *Idh-2*, *G3pdh* and *Ald* loci are monomorphic. Within all samples, the number of alleles ranges from 2 (*Mdh-2*) to 8 (*Gox* and *Mpi*). All samples share the 100 allele at 10 out of the 14 polymorphic loci either as the unique or the most common allele (*Mdh-2*, *Idh-1*, *Gox*, *G6pdh*, *Got-1*, *Got-2*, *Hk-1*, *Hk-2*, *Adk-2*, *Mpi*). However, while at *Mdh-1* and *Adk-1* loci, *B. r. rossius* samples present the same allele (*Mdh-110* and *Adk-197*) as the unique/most common one, the *B. r. redtenbacheri* show alternative alleles (*Mdh-1100* and *Adk-194* or *Adk-1100*). Corsican and Spanish *B. rossius* generally show either as the unique/most frequent allele that of the reference *B. r. rossius*, the only exception being the *6Pgdh*<sup>96</sup> allele of the Spanish sample, where it is the most common one.

Genetic distances (Table IV) clearly indicate an interpopulation level of differentiation between reference *B. r. rossius* samples and pooled Corsican demes ( $0.002 < D < 0.037$ ). The same applies to Spanish samples ( $0.038 < D < 0.053$ ). On the other hand, D values obtained from the comparisons *B. r. rossius* - *B. r. redtenbacheri* ( $0.085 < D < 0.178$ ), Corsican samples - *B. r. redtenbacheri* ( $0.142 < D < 0.178$ ) and Spanish samples - *B. r. redtenbacheri* ( $0.103 < D < 0.132$ ), clearly fall into a subspecific differentiation range.

Table IV. - Nei's genetic distances (D) between of *Bacillus rossius rossius* reference samples, pooled Corsican samples, pooled Spanish samples and *B. r. redtenbacheri* reference samples (for captions see Table III).

|       | ROSUC | ROSBC | ROSEL | ROSUS | ROSBS | CORSI | TOSSA | REDU  | REDB  |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| ROSUC | --    | 0.028 | 0.036 | 0.037 | 0.021 | 0.036 | 0.053 | 0.115 | 0.085 |
| ROSBC |       | --    | 0.010 | 0.010 | 0.011 | 0.009 | 0.044 | 0.161 | 0.126 |
| ROSEL |       |       | --    | 0.003 | 0.012 | 0.002 | 0.049 | 0.178 | 0.144 |
| ROSUS |       |       |       | --    | 0.012 | 0.002 | 0.050 | 0.178 | 0.144 |
| ROSBS |       |       |       |       | --    | 0.011 | 0.038 | 0.141 | 0.106 |
| CORSI |       |       |       |       |       | --    | 0.046 | 0.178 | 0.142 |
| TOSSA |       |       |       |       |       |       | --    | 0.132 | 0.103 |
| REDU  |       |       |       |       |       |       |       | --    | 0.012 |
| REDB  |       |       |       |       |       |       |       |       | --    |

The most likely phyletic relationships among analyzed samples are figured in the dendrogram (Fig. 3).

### Karyology

Females from Ghisonaccia, Solenzara, S. Giulie and Pianettoli share the same standard  $2n = 36$  (XX) *B. rossius* complement. The large elements of the karyotype (1st pair, large metacentrics; 2nd pair, acrocentrics; 3rd pair, submetacentrics - sexual chromosomes -) and also others small chromosomes, such as the smallest, are clearly recognizable; minor differences related to second-

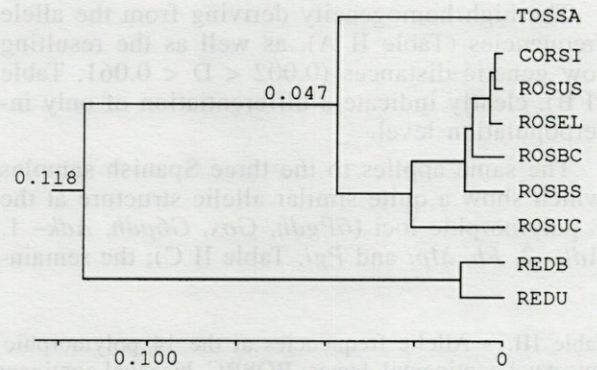


Fig. 3. - Dendrogram showing the most likely phyletic relationships among the here analyzed Corsican and Spanish *Bacillus rossius*, *B. r. rossius* and *B. r. redtenbacheri* reference samples (for captions see Table III).

ary constrictions (see f.i. pairs 13 and 16) are however noticeable (Fig. 4 A).

On the other hand, all the Ile Rousse L females share a  $2n = 34$  cytotype, which differs from the standard one for a submetacentric pair, ranking as the 2nd in size (Fig. 4 B). It appears to be derived from the Robertsonian fusion of acrocentric pairs 4 and 5, since they are missing as separate elements from this cytotype. Ile Rousse B deme shares both the standard and the repatterned cytotype.

The two odd males collected at Albo and S. Giulie (one each from among otherwise all females demes, see Table II), show a standard  $2n = 35$  (XO) karyotype, regular meiotic processes and normal spermatogenesis (Fig. 4 C-E).

### DISCUSSION

Ootaxonomical and electrophoretical results indicate a remarkable level of homogeneity within Corsican *B. rossius* demes, although some minor differences occur in Pianettoli and Ile Rousse L samples.

The undulated net-like capsule pattern, sometimes faintly dented, observed in all demes, excepting Pianettoli, is actually the same as the already described for *B. r. rossius* (Scali *et al.*, 1987). The chorionic features of Pianettoli, already evidenced in a few Sardinian demes (Scali *et al.*, 1983 and unpublished data) suggest a certain degree of variability in ootaxonomic details, even within subspecific taxa, which make the Pianettoli deme a *redtenbacheri* - like one, from the chorionic point of view.

Allelic constitution, genetic structure and distances unequivocally assign Corsican *B. rossius* to the *B. r. rossius* subspecies. Furthermore, the low



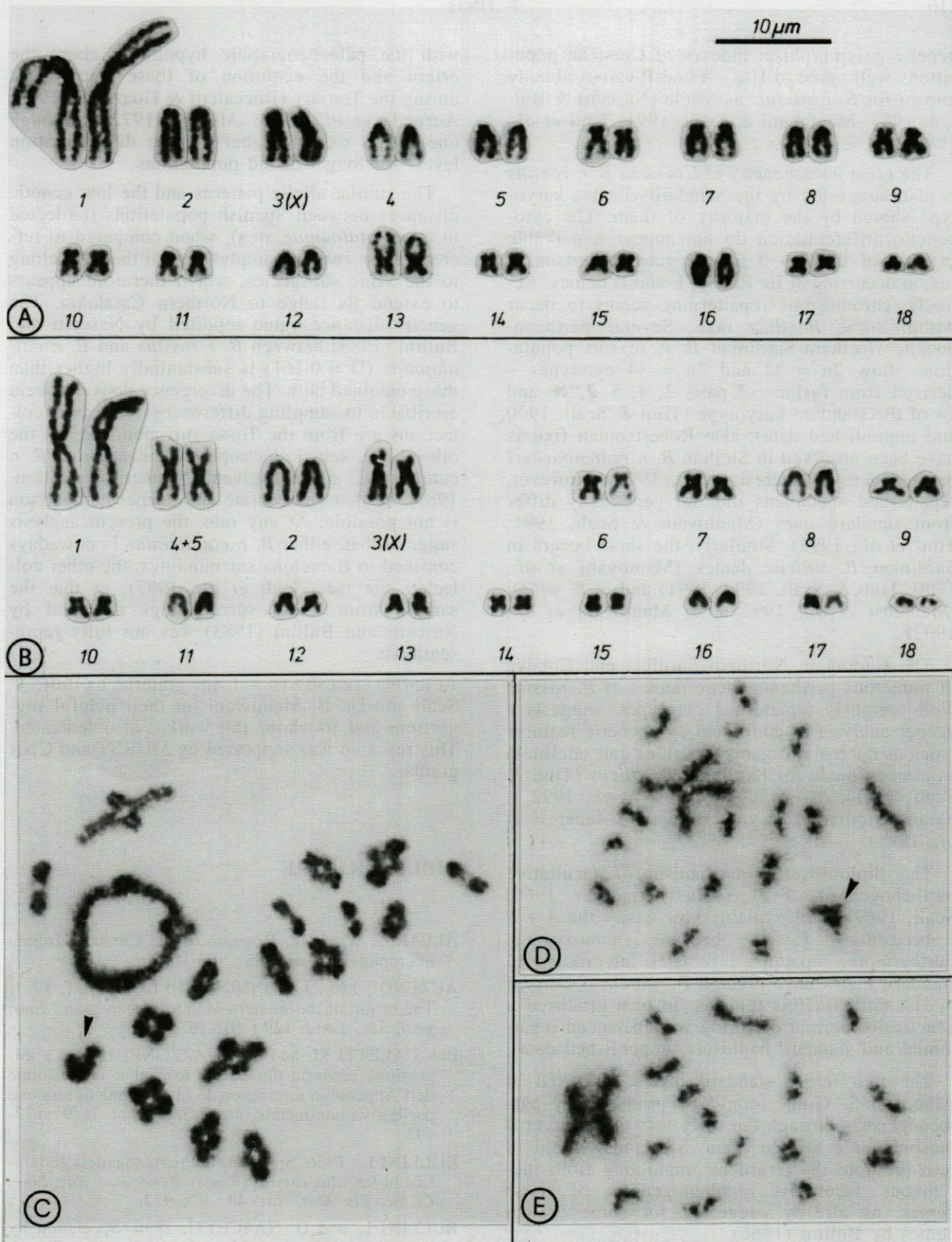


Fig. 4. - A : The standard karyotype ( $2n = 36$ ) shared by the majority of Corsican demes. In this karyotype (Solenzara), two evident homozygous satellites are present on the pairs 13 and 16. B : The  $2n = 34$  cytotype found in Ile Rousse L and Ile Rousse B demes. Note the large submetacentrics (2nd pair in size) derived from the homozygous Robertsonian fusion of pairs 4 and 5, here missing. C : A regular metaphase I, with 17 bivalents and 1 univalent (X, arrowhead) found in Albo male. D and E : Regular metaphases II showing 18 (X, arrowhead) and 17 diads, respectively, found in S. Giulie male.



genetic polymorphism indexes of Corsican populations well agree to  $H_{obs}$ , A and P values already known for *B. r. rossius* as whole (Nascetti & Bullini, 1983; Mantovani & Scali, 1991; Tinti *et al.*, 1992).

The great homogeneity of Corsican *B. r. rossius* is also suggested by the standard Giemsa karyotype shared by the majority of them. The cytogenetic differentiation do not appear remarkable in spite of the 4 + 5 homozygous Robertsonian fusion occurring at Ile Rousse L and B demes. Actually, chromosome repatterning seems to occur within some *Bacillus* taxa. Several parthenogenetic Northern-Sardinian *B. r. rossius* populations show  $2n = 32$  and  $2n = 34$  cytotypes – derived from fusions of pairs 2, 4, 5, 7, 10 and 14 of the standard karyotype (Tinti & Scali, 1990 and unpublished data); also Robertsonian fixions have been observed in Sicilian *B. r. redtenbacheri* parthenogens (Manaresi *et al.*, 1991). However, repatterned specimens did not genetically differ from standard ones (Mantovani & Scali, 1991; Tinti *et al.*, 1992). Similarly, the same occurs in Sardinian *B. atticus* demes (Mantovani *et al.*, 1990; Tinti & Scali, 1990, 1991) and in *B. whitei* (Manaresi *et al.*, 1992 a, b; Mantovani *et al.*, 1992).

The finding in Northern Sardinia and Corsica of numerous parthenogenetic demes of *B. rossius* with variously repatterned cytotypes, suggests a deeper analysis of additional cytogenetic features (such as nucleolar organizer regions and satellites) as already made for Sardinian *B. atticus* (Tinti & Scali, 1991), *B. whitei* (Manaresi *et al.*, 1992 a, b) and Sicilian *B. r. redtenbacheri* (Manaresi *et al.*, 1991).

The diploidization mechanism of facultative parthenogenesis of *B. rossius* (Pijnacker, 1969; Scali, 1969), well explains how easily the 4 + 5 Robertsonian fusion became homozygous. Furthermore, repatterned females lab-crossed to standard males have given a  $F_1$  which, if crossed to standard *Bacillus* females, in turn produced a genetically normal offspring with balanced repatterned and standard haplosets (unpublished data).

The two fertile standard males, collected at Albo and S. Giulie, could be produced by parthenogenesis through the early loss of an X chromosome of a female germ. Spanandry could in turn promote the return to amphigony from thelytokous facultative parthenogenesis of these demes, as already suggested for some French demes by Bullini (1966).

On the whole, Corsican *B. r. rossius* appear – either on chromosome and allozymic grounds – more similar to the geographically close Sardinian and Elban parthenogenetic demes than to other *B. r. rossius*, suggesting that these samples may have had a parallel evolution. This observation is in line

with the paleogeographic hypothesis about the origin and the evolution of these microplates during the Tertiary (Boccaletti & Guazzone, 1970; Auzende *et al.*, 1971; Alvarez, 1972), although one would expect higher genetic differentiation levels for long isolated populations.

The similar allelic patterns and the low genetic distances between Spanish populations (collected in *B. r. catalauniae* area), when compared to reference *B. r. rossius* samples, reveal that all belong to the same subspecies, which therefore appears to extend its range to Northern Catalonia. The genetic distance value reported by Nascetti and Bullini (1983) between *B. r. rossius* and *B. r. catalauniae* ( $D = 0.161$ ) is substantially higher than those obtained here. The divergence does not seem ascribable to sampling differences, since both collections are from the Tossa surroundings. On the other hand, actual electrophoretic data about *B. r. catalauniae* are not given (Nascetti & Bullini, 1983), so that an accurate and deeper comparison is not possible. At any rate, the present analysis suggests that, either *B. r. catalauniae* is nowadays confined to Barcelona surroundings, the other collected site (see Scali *et al.*, 1987), or that the sample from Tossa surroundings analyzed by Nascetti and Bullini (1983) was not fully representative.

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## MOVEMENT OF *ABAX ATER* (COL. CARABIDAE) : DO FOREST SPECIES SURVIVE IN HEDGEROW NETWORKS ?

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HEDGEROW NETWORK  
FOREST CARABID BEETLES  
*ABAX ATER*  
METAPOPULATION  
MARK - RECAPTURE METHOD  
CONSERVATION BIOLOGY

RÉSEAU BOCAGER  
CARABIQUES FORESTIERS  
*ABAX ATER*  
MÉTAPOPULATION  
CAPTURE - RECAPTURE  
BIOLOGIE DE LA CONSERVATION

**ABSTRACT** – Some forest carabid beetles can be found far from the forest although they have a very low power of dispersal. This study focuses on the movements of individuals of *Abax ater* living at the intersection of three lanes bordered by two wooded banks. Using the mark–recapture method, it is shown that individuals are resident and reproduce in this study site. This proves that a small population of *Abax ater* can settle in a node of a hedgerow network and survive there, at least for some time. From the point of view of conservation biology, this study provides guidelines for landscape management.

**RÉSUMÉ** – Certains Carabiques forestiers sont trouvés à une distance importante de la forêt la plus proche malgré un pouvoir de dispersion très limité. Cette étude porte sur les mouvements individuels chez *Abax ater*, individus vivant sur l'intersection de trois chemins bordés chacun de deux talus boisés. En utilisant la méthode de capture – recapture, il a été possible de montrer que les individus sont résidents et qu'ils se reproduisent sur le site. Cela signifie que de petites populations d'*Abax ater* peuvent s'installer sur les nœuds du réseau bocager et y survivre au moins à court terme. Du point de vue de la biologie de la conservation, ces résultats fournissent quelques orientations pour une meilleure gestion de l'espace.

### INTRODUCTION

In north America and Europe, the temperate forest has become fragmented so that patches of forest are scattered throughout a cultivated matrix. In these landscapes, the survival of populations living in isolated forest habitats has become of interest from the point of view of conservation biology. Presence of woodlots has a positive effect on biodiversity (Whittaker, 1972; Pielou, 1975) because they can allow the survival of some forest species which otherwise would have disappeared. For some species, it has been shown that, in fragmented habitats, several populations of woodlots can be connected by dispersal movements (Fahrig and Merriam, 1985; Van Dorp and Opdam, 1987; Den Boer, 1990; Murphy *et al.*, 1990; Verboom *et al.*, 1990). These populations are considered as subpopulations of a metapopulation (Levins, 1970).

Carabids are a well known biological material (Thiele, 1977). Studies on carabids made probable that a local population may go extinct rapidly (30

or 40 years) when isolated (Den Boer, 1985). Dispersal movements, which can lead to the colonization of empty patches is thus of prime importance for the regional survival of these species. In this study, we focus on forest carabid species. For us, a forest species is a species that is more often found in mature forests than in other elements of the landscape. But, one may distinguish the "interior forest species" (Forman et Godron, 1986) as for example *Abax parallelus*, which are limited to the interior of the forest (Clavreul, 1984; Burel, 1987) from others, which are more eurytopic species.

In western France, the landscape "bocage" is characterized by the presence of a hedgerow network. The spatial distribution of carabids has been studied in several hedgerow networks in England (Pollard, 1968) and France (Deveaux, 1976): the assemblages in hedgerows are characterized by the presence of some forest species which are also present in the landscape surrounding the forest (Burel, 1987, 1989). Some species, "corridor forest species" are found far from the forest in hedgerow network. For these species, the wooded



linear elements of the landscape may act as corridors if their internal structure is suitable. Burel (1989) noticed that corridor forest species are particularly abundant when two hedgerows border a lane. For forest species living in hedgerows, the question is whether they use both forests and hedgerows which then might be considered as complementary habitats, or they may realize their whole life cycle within hedgerows. Corridor forest carabids may be present far (10 km) from the forest (Burel, 1989) although most of them are unable to fly (Den Boer, 1985). Thus, it appears unlikely that they use hedgerows only as corridors and return to the nearest forest for reproduction. To test this hypothesis, we studied the movements of individuals in a hedgerow.

In this paper, we focus on the behaviour of such species in a hedgerow network. The two main questions are :

- Are there local populations of corridor forest carabid species present in the hedgerow network ?
- What is the pattern of movements of individuals ?

## THE STUDY AREA

The study area is located in a hedgerow network, near St Aubin du Cormier, 30 km West of Rennes, France. In this typical bocage area, land use is mainly meadows grazed by cows, and some fields cultivated for cereal crops. There are also some patches of coniferous forest and heath.

The study site is the intersection of three lanes, each bordered by two wooded banks (fig. 1). It is surrounded by two meadows and one crop field. None of the lanes is maintained or used by the resident farmers so that the study site, between the banks, is becoming wooded. The herbaceous layer is dense and the shrub layer is dominated by Blackberry bushes (*Rubus fruticosus*). Trees are mainly present on the banks. They are Oak (*Quercus pedunculata*), Chestnut (*Castanea sativa*) and Aspen (*Populus tremula*). This site is characterized by a dense cover of vegetation and the presence of leaf litter.

## MATERIALS AND METHODS

Studying the spatial distribution of a population requires a study of the movements of individuals. Thus, we used the mark-recapture method. We chose *Abax ater* among several "corridor" forest species because it is common and of medium size (16-22 mm) which allows to apply marking tech-

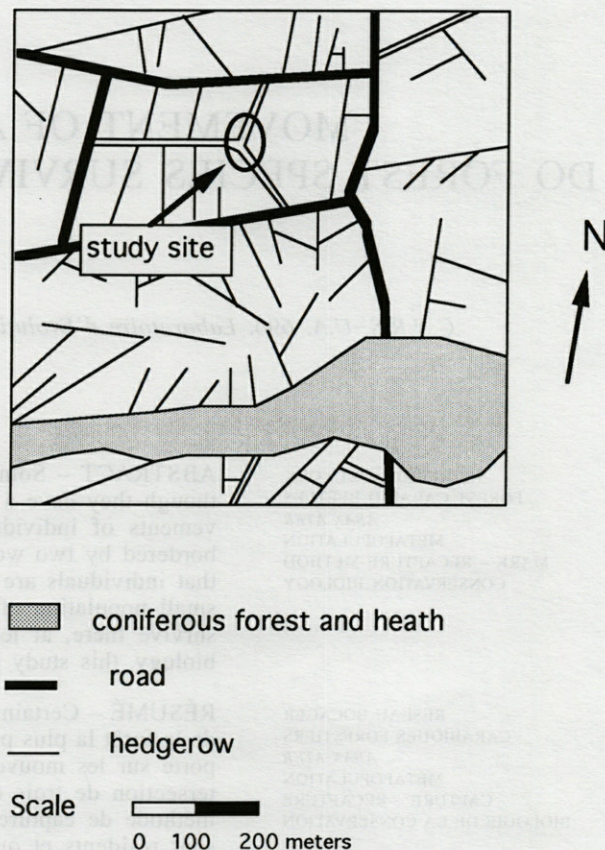


Fig. 1. – The study site and its surrounding.

niques easily. It is active between April and October and reproduction occurs between April and July (Greenslade, 1965; Turin *et al.*, 1977; Drach, 1980). Like many other carabids, it is a polyphagous predator (Loreau, 1983).

Twenty seven pitfall traps, 13 cm diameter by 25 cm deep, were spread over the site, the top of the wooded banks included. Trapping occurred from the beginning of June to the beginning of August 1991. The pitfall traps were emptied every two days and individuals were marked by scraping certain positions on the elytra so that each one had a unique number (Murdoch, 1963). Individuals were sexed and individuals with soft elytra, which are only a few days old, were distinguished from the others. All of them were released at a distance of one meter from the trap where they were caught.

For each beetle, the distances covered between two captures and the time taken to cover these distances were recorded as well as the value of the mean duration of residence was estimated. This is the mean time of residence observed between trappings of the same individual. It was compared with the maximal residence i.e. the period of residence in the case where all individuals caught during the experiment would have been still present at the end of the study.



In order to characterize quantitatively the movements of individuals, we used a method originating from the diffusion model (Box 1) (Drach and Cancela da Fonseca, 1990).

#### Box 1 :

Method of calculation of the coefficient of diffusion of individuals originating from the diffusion model (Drach and Cancela Da Fonseca, 1990) :

At a time 0, individuals are considered to be concentrated at one spot, then they scatter over the site. After a given time, the proportion of individuals located at a distance lower than a distance  $R$  from the center of diffusion is called  $g(R)$ . This model permits to determine an indicator of activity level for the population, called  $D$ , coefficient of diffusion, which is the square of the mean displacements of individuals per time unit  $t$ . The diffusion model gives the equation

$$\ln(1-g(R)) = -R^2/4Dt$$

$g(R)$  is the proportion of individuals that are recaptured at a distance lower than a distance  $R$  from the pitfall trap where they were released.

$R$  is the distance from the pitfall trap where they were released.

$D$  is the coefficient of diffusion = the square of the mean displacements of individuals per time unit  $t$ . It is an indicator of activity level.

$p$  is the probability that an individual stands fixed where it was released. It is an indicator of inactivity level.

$t$  is the time unit.

$D$  and  $p$  can be calculated with a linear regression  $\ln(1-g(R))$  on  $R^2$  of the form

$Y = A + BX$ ; where  $Y = \ln(1-g(R))$ ;  $X = R^2$ ;  
 $A = \ln(1-p)$ ;  $B = 1/4Dt$  is the regression coefficient.

## RESULTS

More than fifty individuals were marked individually at the study site and 61,4 % was recaptured. The sex ratio was 0,5 for marked individuals and 0,45 for recaptured individuals. Some individuals were caught 5 times and one even 6 times. Population size was estimated with the Jolly-Seber stochastic model (1965); for the whole trapping period, density was about 0.15 individuals per square meter.

All the movements recorded during the trapping period are given in figure 2. This figure clearly reveals a spatial heterogeneity in captures and it appears that traps set at the top and near the banks remained almost empty. Figure 3 shows the movements during two months of the male that was re-

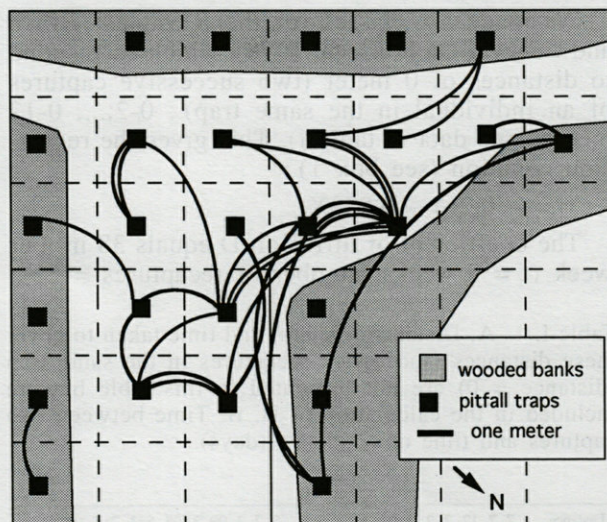


Fig. 2. - Trajectories recorded on the study site between the 12/06/91 and the 14/08/91.

captured 6 times. It was often caught in the same traps and it moved around the centre of the study site without a preferred direction.

Distances between two captures (in meters) and the time taken to cover these distances (in days) are listed in table IA. The time between two captures and the observed time of residence are known for every individual; the minimal, maximal and mean values are recorded in table IB. The value of the mean time of residence (27 days) equals 2/3 of the maximal period of residence (40 days). The Pearson coefficient of correlation between distances covered and the time needed by carabids to cover these distances is not significant ( $n = 45$ ;  $r = 0,232$  NS).

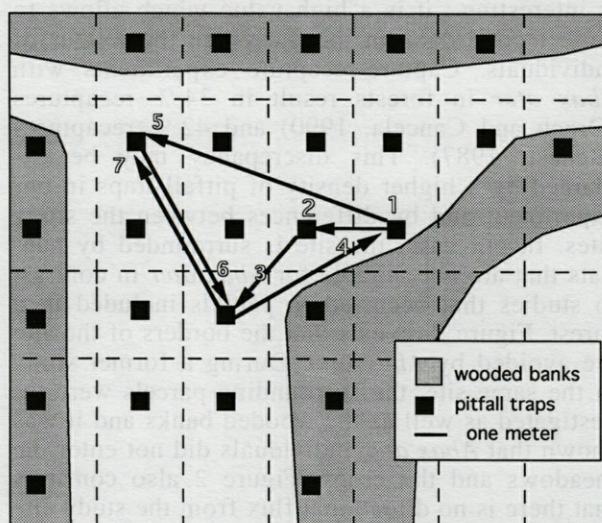


Fig. 3. - Dated trajectory of the male which was recaptured six times.  
 1 = 12/06/91; 2 = 14/06/91; 3 = 18/06/91; 4 = 27/06/91;  
 5 = 07/08/91; 6 = 13/07/91; 7 = 14/08/91.



We made six classes for the R values (Drach and Cancela Da Fonseca, 1990), which correspond to distances of 0 meter (two successive captures of an individual in the same trap) : 0-2;..., 0-12 meters (see data in table I). This gives the regression equation (see box 1) :

$$Y = - 0,261 - 0,023X$$

The coefficient of diffusion D equals 38 m<sup>2</sup> per week (t = 9 weeks, number of recaptures = 52).

Table I. – A, Distance (meters) and time taken to cover these distances (successive recaptures in the same trap (distance = 0) are not presented in this table but are included in the calculation of D. B, Time between two captures and time of residence (days).

| A                          |  |
|----------------------------|--|
| Distance (meters)          | 7. 7. 12. 2. 2. 2. 07. 5. 08. 5. 8. 5. 2. 2. 09. 3. 05. 5. 3. 7. 5. 03.  |
| Time (days)                | 2. 9. 27. 2. 2. 2. 22. 2. 48. 2. 32. 2. 2. 6. 19. 2. 25. 7. 2. 9. 5. 30. |
| Distance (meters)          | 3. 3. 1. 1. 01. 04. 10. 10. 11. 9. 04. 02. 2. 4. 9. 07. 08. 7. 05. 3. 3. |
| Time (days)                | 2. 2. 2. 6. 19. 22. 14. 13. 15. 2. 31. 52. 2. 6. 2. 30. 27. 4. 21. 2. 2. |
| B                          |  |
|                            | Mean      Minimal      Maximal   |
| Time between two captures  | 13            2            51  |
| Observed time of residence | 27            2            63  |

## DISCUSSION

Density of *Abax ater* in the study site, of 0.15 individuals per square meter is comparable to those found in forests by Thiele (1956) and Loreau (1984) which vary from 0.03 to 0.28. The fact that more than 60 % of the individuals was recaptured is interesting : it is a high value which allows to collect good data on the movement behaviour of individuals. Capture-recapture experiments with *Abax ater* in forests result in 34 % recaptures (Drach and Cancela, 1990) and 42 % recaptures (Benest, 1987). This discrepancy may be explained by a higher density of pitfall traps in our experiment and by differences between the study sites. In our case, the site is surrounded by habitats that are not suitable for *Abax ater* in contrast to studies that occurred in parcels included in a forest. Figure 2 reveals that the borders of the site are avoided by *Abax ater*. During a former study in the same site, the surrounding parcels were investigated as well as the wooded banks and it was shown that *Abax ater* individuals did not enter the meadows and the crops. Figure 2 also confirms that there is no directional flux from the study site to the surrounding parcels and furthermore, apparently no significant flux to other parts of the three lanes included in the hedgerow network (fig.1). Movements of individuals are clearly restricted to the interior of the site.

The high proportion of recaptures also contradicts the possible hypothesis of a continuous passage of individuals from elsewhere through the site. Also the lack of a relation between distances and the time needed to cover these distances indicates that the beetles did not walk uninterruptedly with a preferred direction. A striking point is that the coefficient of diffusion, 38 m<sup>2</sup> per week, is similar to the 36 m<sup>2</sup> per week calculated for *Abax ater* inside a forest (Drach and Cancela da Fonseca, 1990). This means that individuals of a forest population and those of this hedgerow network show the same intensity of movement. This pattern of movement resembles that of others carabids described by Baars (1979) and Rijnsdorp (1980) called random walk by these authors ie small displacement, moderate velocity and random choice of direction. This locomotory activity is apparently mainly motivated by foraging or egg laying and seems to occur only in habitats suitable for the species.

The value of the mean time of residence is high if we take into account mortality in the site during the two months of study. As the high proportion of recapture, it indicates that most individuals are sedentary in the interior of the site during this period and probably during the whole season of activity. The sex ratio did not change during the experiment and reveals the presence of females in the site during the entire trapping period, which is also the reproduction period of *Abax ater*. The fact that some new hatched individuals were caught at the end of the study indicates that reproduction occurred and was successful in the study site; apparently, individuals did not have to return to the nearest forest for reproduction.

All these elements support the opinion that the study site is a real suitable habitat for *Abax ater*, where individuals behave as if they were in a forest. They show the same pattern of movement and succeed in reproducing. In Brittany, forests and woodlots are not so common; at the landscape level survival of the kind of species we studied is mainly related to the presence of the hedgerow network and to the nodes of this network. Such small habitats composed of intersections of hedgerows and lanes are very common and allows to expect that this species occurs frequently, even far from a forest. An important question now becomes how this set of populations can maintain itself in the bocage. In a forest, populations are large or may be composed of several small populations so that they can face demographic stochasticity easily. But small populations of carabids, as those in the hedgerow network may go extinct rapidly if isolated from others populations. Den Boer (1990) estimated the average life expectancy of small isolated populations of *Abax ater* to be about 100 years. Analysis of old cadastral survey (1833) proves the temporal stability of landscape



structure in the study area since the forest boundaries did not change and the three lanes were already present 150 years ago and possibly before. This means that the population of *Abax ater* we studied and probably some others present in nodes of the network are not remnant of a large forest population recently fragmented but rather the result of some colonization processes. For other populations resulting of an ancient fragmentation, we can suppose that they are not isolated from a source of colonizers otherwise they would have become extinct. Individuals of corridor forest species are commonly trapped in hedgerows internal structure of which is suitable. It would be interesting to know whether single hedgerows can support carabid populations comparable to those in the nodes of the network or they are only used by individuals dispersing between local populations.

As a study dealing with relationships between landscape structure and species survival, the results provide some guidelines for landscape management of the bocage in a conservation perspective for the kind of forest species we studied. It appears clearly that the hedgerow network can support populations of some forest species and that these populations have to be interconnected for the long term survival of the species. Connectivity between populations is ensured by individuals using hedgerows as corridors for their movements through the network. In practical terms, species conservation at the landscape level requires to avoid breaks in the bocage and preservation of good connections between hedgerows.

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## BIOLOGY AND POPULATION DYNAMICS OF *IDOTEA BALTICA* (CRUSTACEA, ISOPODA) IN THE GULF OF NAPLES, THE TYRRHENIAN SEA

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IDOTEA BALTICA  
ISOPODE  
CYCLE DE VIE  
DYNAMIQUE DE POPULATIONS  
VARIATION SAISONNIÈRE

**RÉSUMÉ** – La biologie et la dynamique d'une population d'*Idotea baltica* (Crustacea, Isopoda) de la Mer Méditerranée centrale sont étudiées pour la première fois, sur le terrain et au laboratoire. Les prélèvements ont été effectués dans une station du Golfe de Naples, dans la Mer Tyrrhénienne. Le cycle de reproduction de cette espèce est continu. Au laboratoire, la différenciation sexuelle est atteinte après 60 jours et le taux de croissance est plus grand pour les mâles : la taille maximale est de 26 mm pour les mâles et de 16 mm pour les femelles. La longévité ne dépasse pas 10-12 mois. La sex ratio est d'environ 1 au laboratoire, tandis que dans la population naturelle, elle est toujours en faveur des femelles. Le nombre d'embryons est proportionnel à la longueur totale de la femelle. La durée du développement des embryons varie en fonction des saisons. Pendant l'année la population se compose surtout de mâles et femelles de taille moyenne : de fin août à début novembre, les plus grands individus disparaissent et la plupart des Isopodes restants sont de petite taille. Du point de vue biogéographique, il était très intéressant de comparer nos résultats aux données obtenues pour une population d'*Idotea baltica* vivant à des latitudes plus élevées. Les corrélations suggèrent que la plasticité de l'activité reproductrice est la stratégie la plus importante utilisée par cette espèce pour s'adapter aux différentes latitudes.

IDOTEA BALTICA  
ISOPODA  
LIFE-CYCLE  
POPULATION DYNAMICS  
SEASONAL VARIATION

**ABSTRACT** – Field and laboratory studies were conducted for the first time on the life cycle and population dynamics of *Idotea baltica* (Crustacea, Isopoda) from the middle Mediterranean Sea. The sampling site was a station of the Gulf of Naples in the Tyrrhennian Sea, where this species shows a continuous reproductive cycle over the year. At the laboratory, the sexual differentiation appeared on the 60th day in juveniles, and growth rate was higher in males, which attained their maximal length at 26 mm, while females reached it at about 16 mm. The lifespan was about 10-12 months. The sex ratio measured in the laboratory was about 1, while females were always more numerous in the natural population for most of the year. Egg production was related to ovigerous female length. Embryo development time appeared strictly season-dependent. Middle-sized males and females were the most numerous throughout the year, except from August to early November when small-sized isopods prevailed and the largest ones that had overwintered disappeared completely. From the biogeographical point of view, it appeared interesting to compare our results with those reported on an *I. baltica* population living at higher latitudes. The correlations observed suggest that the flexibility of the reproductive activity may be the most important strategy by which this species adapts itself to diverse latitudes.

### INTRODUCTION

The Idoteinae are isopod crustaceans widespread on both the Atlantic and Pacific coasts of America (Brusca and Wallerstein, 1977), in the northern European Seas (Segerstråle, 1944; Nay-

lor, 1955; Tinturier-Hamelin, 1963; Sywula, 1964) and the Mediterranean Sea, where they inhabit littoral areas and lagoons. When abundant, they play a fundamental role in the marine ecosystem, being voracious detritus-feeders and prey for many invertebrates and fish species. They help to transform the masses of macroalgae, in particular when



the latter are driven ashore by wave action (Gaevskava, 1958; Nicotri, 1980; Salemaa, 1987).

*Idotea baltica* is one of the most widespread Idoteinae in the European Seas; nevertheless, its reproductive biology and population dynamics have only recently been studied systematically. However, literature data are mostly concerned with localities of the Baltic Sea (Salemaa, 1979) and the coastal lagoons of southern France (Kouwenberg & Pinkster, 1984, 1985; Kouwenberg *et al.*, 1987), whereas nothing is known about the Tyrrhenian Sea. The data show that many species of Idoteinae may coexist in the same habitat; however, different species of *Idotea* dominate different littoral habits (Horlyck, 1973; Shaeder, 1977; Salemaa, 1979; Kouwenberg & Pinkster, 1984; Salemaa, 1986; Kouwenberg *et al.*, 1987).

The aim of the present work, carried out in 1990-92, is to study the reproductive biology and population dynamics of *Idotea baltica* inhabiting a bay of the Gulf of Naples and preliminarily investigated by us in 1988 (Guarino and de Nicola, 1992). This locality was chosen for its quite stable hydrographical conditions and the slight variations in chemical-physical factors.

## MATERIALS AND METHODS

Samples were taken weekly over a 3-year period, from January 1990 to July 1992, in the same station (Bacoli) of the Gulf of Naples (Fig. 1) as 1988's preliminary observations (Guarino and de Nicola, 1992). This site is characterized by sheltered and shallow waters (1-2 m deep), and is

covered with a vast bed of filamentous algae *Gracilaria* sp. (Rhodophyceae) which constantly provides *Idotea baltica* with food and a refuge from the predation of littoral fishes and marine invertebrates. Females, juveniles and small-sized males live attached to the alga filaments, whereas medium- and large-sized males swim freely, though within a limited range.

The population investigated consisted of a single species, *Idotea baltica* (Pallas), which was strikingly polychromatic. The phenotypes observed were the same as those described by Salemaa (1978); the *uniformis* morph was the most widespread, accounting for about 80 %.

For sampling, 10 l algae were taken weekly at depths ranging from 0 to 1 meter, and transferred to the laboratory in few hours. Animals larger than 6 mm were measured and inspected for size and sex. Juveniles smaller than 7 mm were not taken into consideration, due to the absence of sexual characteristics.

In order to obtain information on their reproductive activity, *I. baltica* females were divided into ovigerous, non-ovigerous and mating individuals. Sex ratio and the relation between egg number and females' body length were determined.

Altogether a total of 9952 individuals was examined, 5627 of which were females.

In addition, mating animals were collected and kept in the laboratory. When mating was over, females were separated from males and fed until hatching, so that embryo development time could be measured. Newly born juveniles were then counted, separated from one another and reared singly for 5 months in order to evaluate growth

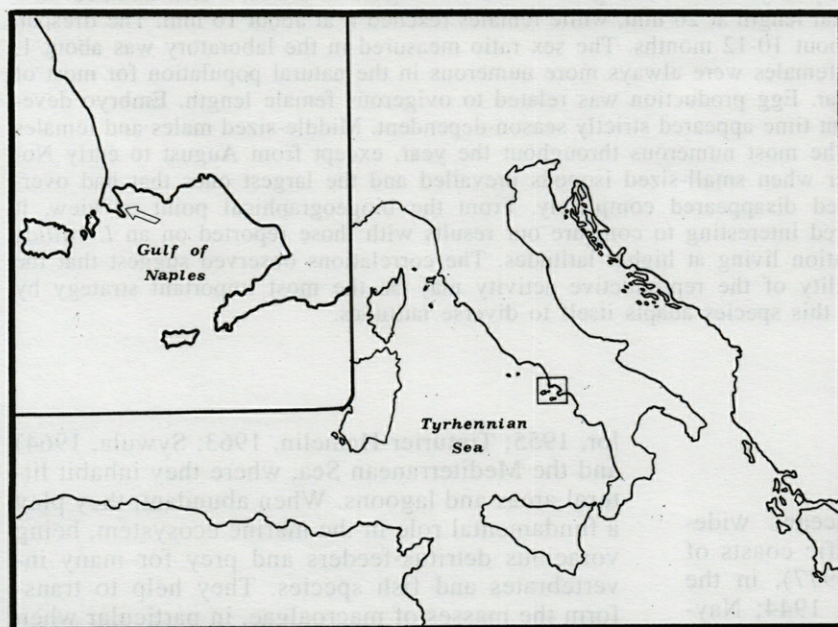


Fig. 1. — Location of the sampling site in the Gulf of Naples.



rate and sex ratio. A total of 3653 animals was used in these experiments.

The standard laboratory conditions were 15°C and 12/12 LD, and the food was *Gracilaria*.

In order to obtain significant data, a large number (2460) of gravid females were collected in the field, and the number and development stages of their embryos were determined.

From January 1990 to July 1992, a total of 16055 animals was examined altogether.

Post-marsupial growth was followed in the laboratory for 5 months, appearing constant in the early 2 months of life, when external sex characteristics were absent in juveniles. Subsequently, growth rate appeared more rapid in males (Fig. 2) until the 90th day, afterwards it was identical for both sexes.

**a. sex ratio**

Sex ratio, expressed as the number of females divided by the number of males, was around 1.0

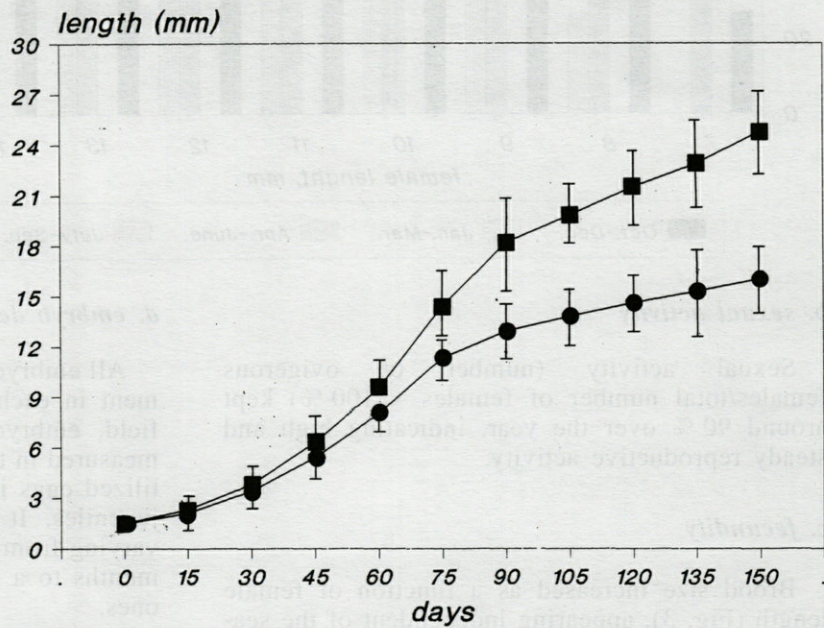


Fig. 2. - Body growth (as mm length) of *Idotea baltica* juveniles bred in laboratory; (= females, = males).

**RESULTS**

After mating (3-8 days), females laid eggs in the marsupium, where embryo development took place. The juveniles just released from the marsupium were about 1.5 mm; males attained their maximum size at 26 mm, and females at 16 mm.

in individuals born and bred in the laboratory. In the natural population, in 1990-1992 (Table I), this value was observed only from late August to early November, when the population consisted mostly of small-sized isopods; females instead prevailed in the rest of the year.

Table I. - *Idotea baltica* field sex ratios over the years.

| year | J    | F    | M    | A    | M    | J    | J    | A     | S     | O     | N    | D    |
|------|------|------|------|------|------|------|------|-------|-------|-------|------|------|
| 1990 | 1.29 | 1.37 | 1.21 | 1.27 | 1.40 | 1.31 | 1.22 | 0.96* | 1.05* | 1.03* | 1.30 | 1.10 |
| 1991 | 1.62 | 1.33 | 1.18 | 1.45 | 1.30 | 1.10 | 1.44 | 1.01* | 1.03* | 0.98* | 1.40 | 1.35 |
| 1992 | 1.28 | 1.55 | 1.50 | 1.32 | 1.28 | 1.50 | 1.27 |       |       |       |      |      |

\* This quarter is significantly different (p < 0.01) in comparison with the others quarter.



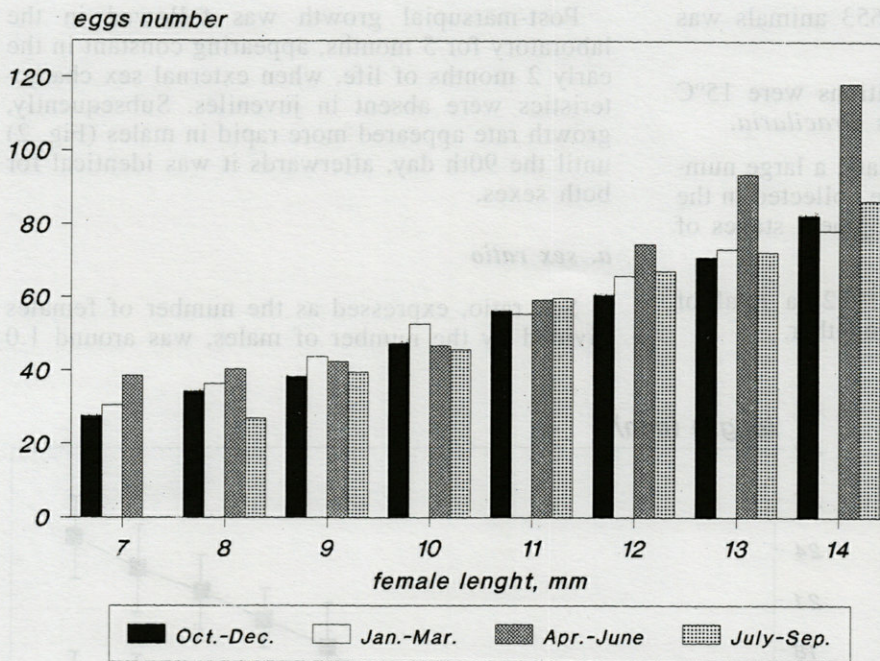


Fig. 3. – Seasonal mean number of eggs per ovigerous female of *I. baltica* of different size classes.

#### b. sexual activity

Sexual activity (number of ovigerous females/total number of females  $\times$  100 %) kept around 90 % over the year, indicating high and steady reproductive activity.

#### c. fecundity

Brood size increased as a function of female length (Fig. 3), appearing independent of the season, whereas only large-sized females produced more eggs in the period May-August ( $p < 0.05$  for 12-13 mm, and  $p < 0.01$  for 14 mm).

#### d. embryo development time

All embryos were at the same stage of development in each brood. In females collected in the field, embryo development time (Table II) was measured in the laboratory from the release of fertilized eggs into the marsupium until hatching of juveniles. It appeared strictly season-dependent, varying from a maximum of 30 days in the winter months to a minimum of 10 days in the summer ones.

There was a little loss of embryos from the marsupium as development proceeded. Five stages of embryo development could be observed, as al-

Table II. – Mean embryo development time (in days) of *I. baltica*.

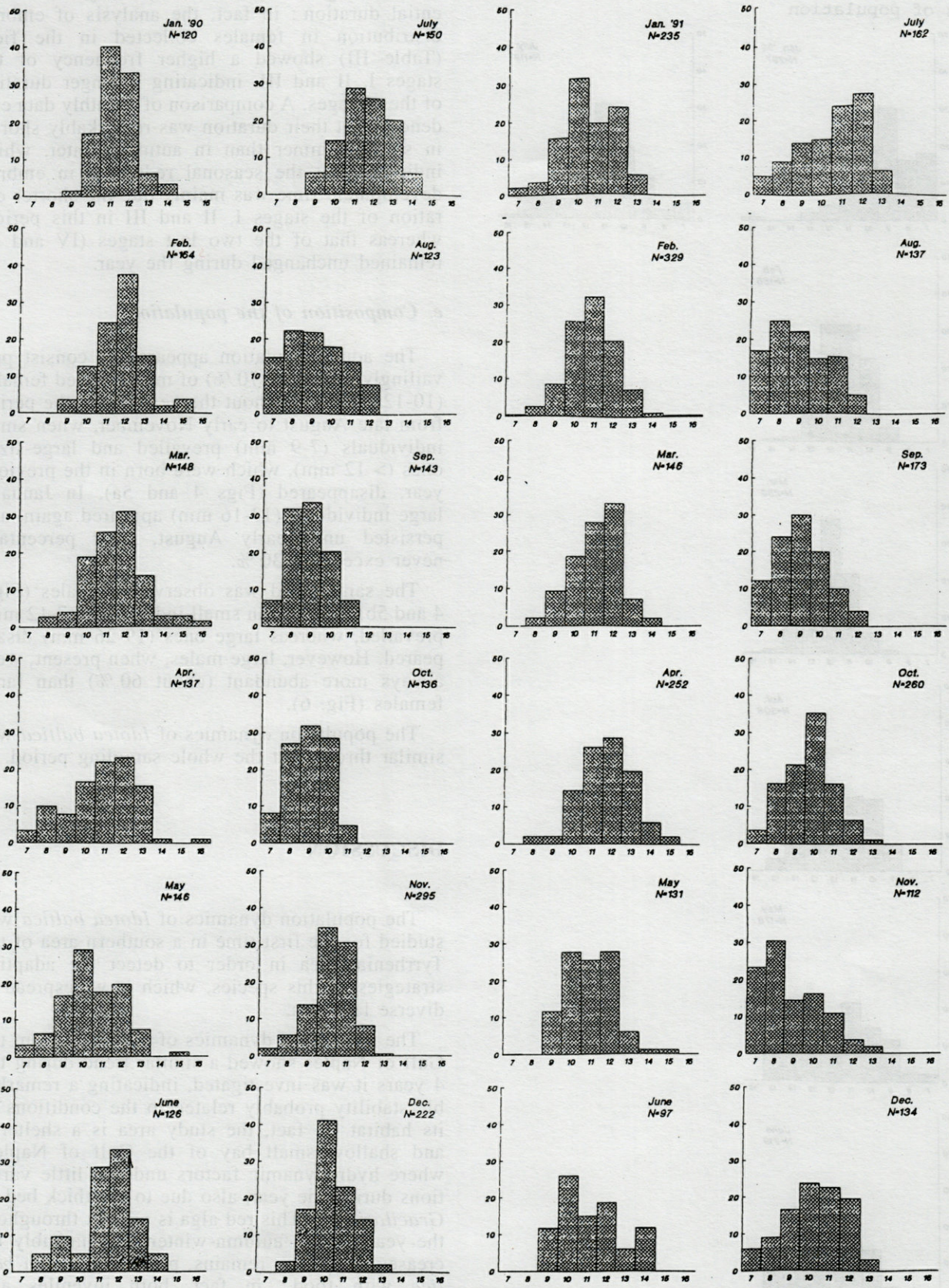
| year | Jan.           | Feb.           | Mar.           | Apr.           | May            | June           | July           | Aug.           | Sep.           | Oct.           | Nov.           | Dec.           |
|------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| 1988 | 22.5 $\pm$ 4.1 | 21.0 $\pm$ 3.7 | 21.0 $\pm$ 4.4 | 21.5 $\pm$ 3.0 | 14.0 $\pm$ 2.1 | 9.0 $\pm$ 1.3  | 9.0 $\pm$ 1.9  | 10.0 $\pm$ 1.5 | 8.0 $\pm$ 0.9  | 30.0 $\pm$ 5.5 | 31.2 $\pm$ 3.8 | 28.8 $\pm$ 4.7 |
| 1990 | 20.8 $\pm$ 3.8 | 22.1 $\pm$ 3.2 | 23.2 $\pm$ 5.1 | 21.1 $\pm$ 2.9 | 13.8 $\pm$ 1.9 | 10.5 $\pm$ 1.2 | 11.2 $\pm$ 2.1 | 9.9 $\pm$ 1.7  | 10.3 $\pm$ 1.7 | 29.4 $\pm$ 3.5 | 30.5 $\pm$ 6.1 | 30.9 $\pm$ 3.9 |
| 1991 | 22.4 $\pm$ 3.5 | 22.2 $\pm$ 3.8 | 22.5 $\pm$ 4.2 | 21.6 $\pm$ 4.1 | 14.5 $\pm$ 2.2 | 8.8 $\pm$ 1.7  | 10.5 $\pm$ 1.8 | 11.1 $\pm$ 1.4 | 10.8 $\pm$ 1.5 | 30.2 $\pm$ 4.1 | 31.0 $\pm$ 4.2 | 30.7 $\pm$ 4.5 |
| 1992 | 21.7 $\pm$ 2.8 | 22.8 $\pm$ 4.5 | 22.1 $\pm$ 3.1 | 22.4 $\pm$ 3.5 | 13.5 $\pm$ 2.5 | 10.2 $\pm$ 1.8 | 9.9 $\pm$ 1.7  |                |                |                |                |                |

Table III. – Mean stages of embryonic development in *I. baltica*.

| period              | total | STAGE          |               |               |               |               |
|---------------------|-------|----------------|---------------|---------------|---------------|---------------|
|                     |       | I              | II            | III           | IV            | V             |
| OCT-DEC             | 30    | 12.3 $\pm$ 2.4 | 6.2 $\pm$ 1.8 | 7.2 $\pm$ 2.1 | 2.5 $\pm$ 0.9 | 1.2 $\pm$ 0.8 |
| JAN-APR             | 22    | 8.1 $\pm$ 2.1  | 4.7 $\pm$ 1.5 | 5.2 $\pm$ 1.6 | 2.4 $\pm$ 1.1 | 1.6 $\pm$ 1.2 |
| MAY                 | 14    | 4.3 $\pm$ 1.1  | 2.6 $\pm$ 0.9 | 3.9 $\pm$ 0.8 | 2.0 $\pm$ 0.7 | 1.3 $\pm$ 0.7 |
| JUN-AUG             | 10    | 1.1 $\pm$ 0.5  | 1.6 $\pm$ 0.8 | 3.0 $\pm$ 0.6 | 2.5 $\pm$ 1.0 | 2.0 $\pm$ 0.7 |
| X <sup>2</sup> test | <0.01 | <0.01          | <0.01         | <0.05         | n.s.          | n.s.          |



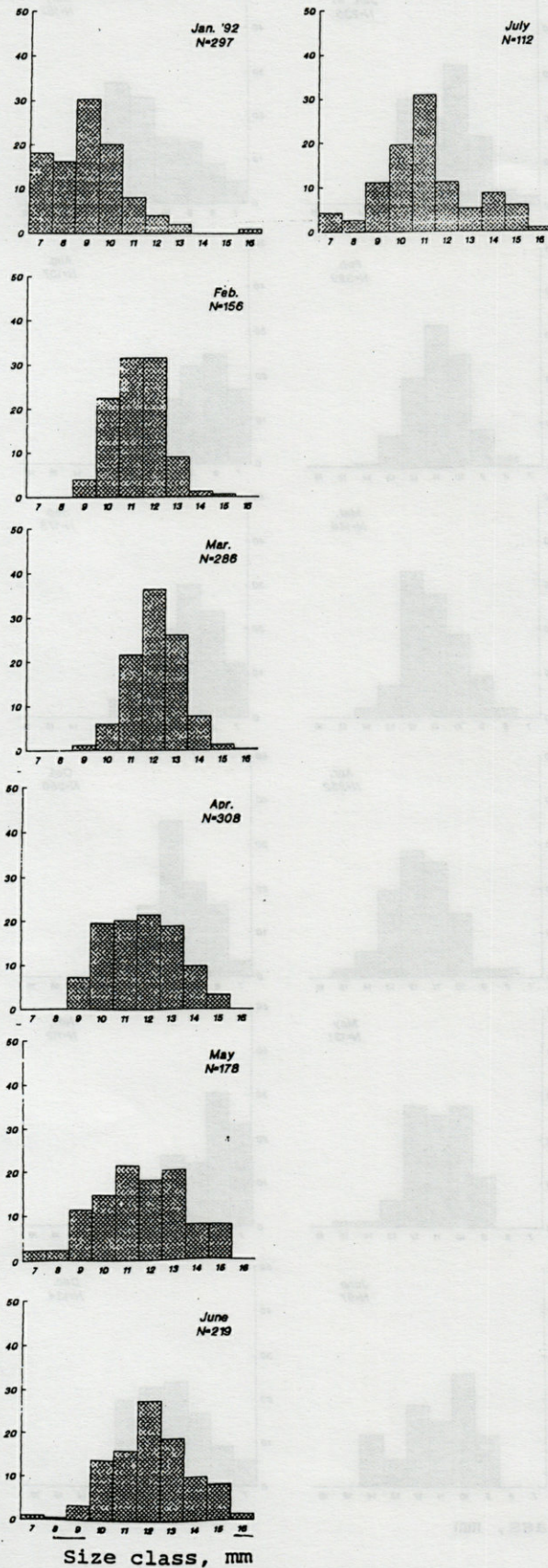
% of population



Size class, mm



% of population



ready described in the literature (Naylor, 1955; Kouwenberg & Pinkster, 1985). They had differential duration: in fact, the analysis of embryo distribution in females collected in the field (Table III) showed a higher frequency of the stages I, II and III, indicating a longer duration of these stages. A comparison of monthly data evidenced that their duration was remarkably shorter in spring-summer than in autumn-winter, which indicates that the seasonal reduction in embryo development time was mainly due the shorter duration of the stages I, II and III in this period, whereas that of the two last stages (IV and V) remained unchanged during the year.

#### e. Composition of the population

The adult population appeared to consist prevalently (about 60-70 %) of middle-sized females (10-12 mm) throughout the year but in the period from late August to early November, when small individuals (7-9 mm) prevailed and large-sized ones (> 12 mm), which were born in the previous year, disappeared (Figs 4 and 5a). In January, large individuals (13-16 mm) appeared again, and persisted until early August, their percentage never exceeding 30 %.

The same trend was observed in males (Figs. 4 and 5b): in autumn small individuals (7-12 mm) prevailed, whereas large ones (19-26 mm) disappeared. However, large males, when present, were always more abundant (about 60 %) than large females (Fig. 6).

The population dynamics of *Idotea baltica* was similar throughout the whole sampling period.

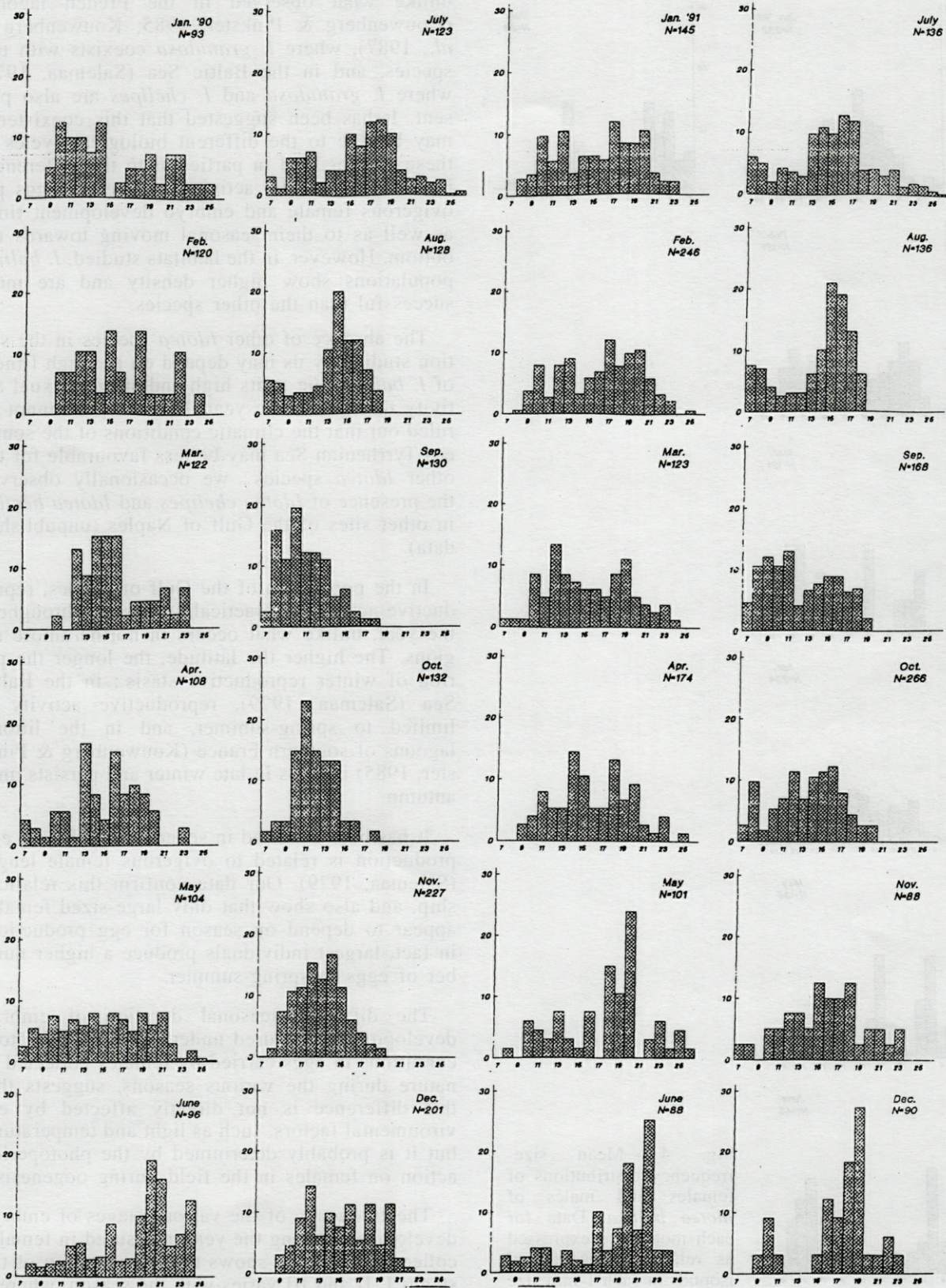
## DISCUSSION

The population dynamics of *Idotea baltica* was studied for the first time in a southern area of the Tyrrhenian Sea in order to detect the adaptive strategies of this species, which is widespread at diverse latitudes.

The population dynamics of *I. baltica* from the Gulf of Naples showed a similar trend during the 4 years it was investigated, indicating a remarkable stability probably related to the conditions of its habitat. In fact, the study area is a sheltered and shallow small bay of the Gulf of Naples, where hydrodynamic factors undergo little variations during the year, also due to the thick bed of *Gracilaria* sp.. This red alga is present throughout the year, and in autumn-winter it remarkably increases vegetation remains, providing *Idotea baltica* with food: in fact, both juveniles and females, particularly the gravid ones, are always attached to the alga filaments. The males, though



% of population



Size class, mm



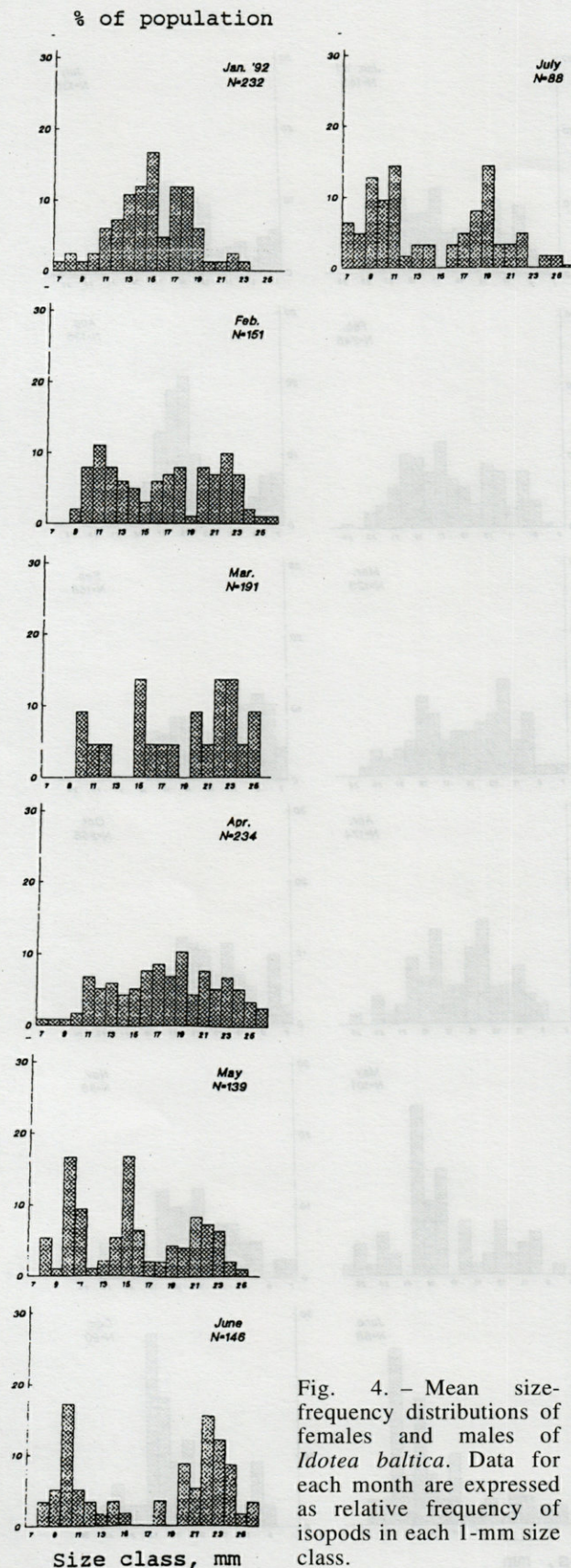


Fig. 4. — Mean size-frequency distributions of females and males of *Idotea baltica*. Data for each month are expressed as relative frequency of isopods in each 1-mm size class.

being free, never move too far from the bed of *Gracilaria*. The alga provides also a safe shelter from predation of littoral fishes. The only species of Idoteinae present in this habitat is *I. baltica*, unlike what observed in the French lagoons (Kouwenberg & Pinkster, 1985; Kouwenberg *et al.*, 1987), where *I. granulosa* coexists with this species, and in the Baltic Sea (Salemaa, 1979) where *I. granulosa* and *I. chelipes* are also present. It has been suggested that this coexistence may be due to the different biological cycles of these species, and in particular to the differences in sex ratio, sexual activity, number of eggs per ovigerous female and embryo development time, as well as to their seasonal moving towards the bottom. However, in the habitats studied, *I. baltica* populations show higher density and are more successful than the other species.

The absence of other *Idotea* species in the station studied by us may depend on the high fitness of *I. baltica* due to its high and steady sexual activity throughout the year. However, it cannot be ruled out that the climatic conditions of the southern Tyrrhenian Sea may be less favourable for the other *Idotea* species: we occasionally observed the presence of *Idotea chelipes* and *Idotea hectica* in other sites of the Gulf of Naples (unpublished data).

In the population of the Gulf of Naples, reproductive activity is practically constant throughout the year, unlike what occurs in northernmore regions. The higher the latitude, the longer the period of winter reproductive stasis: in the Baltic Sea (Salemaa, 1979), reproductive activity is limited to spring-summer, and in the littoral lagoons of southern France (Kouwenberg & Pinkster, 1985) it starts in late winter and persists until autumn.

It has been reported in several isopods that egg production is related to ovigerous female length (Salemaa, 1979). Our data confirm this relationship, and also show that only large-sized females appear to depend on season for egg production; in fact, largest individuals produce a higher number of eggs in spring-summer.

The different seasonal duration of embryo development, measured under standard laboratory conditions in eggs carried by females collected in nature during the various seasons, suggests that this difference is not directly affected by environmental factors, such as light and temperature, but it is probably determined by the photoperiod action on females in the field during oogenesis.

The frequency of the various stages of embryo development during the year, measured in females collected in nature, shows that the duration of the stages I, II and III varies with the season, whereas that of the stages IV and V remains unchanged.



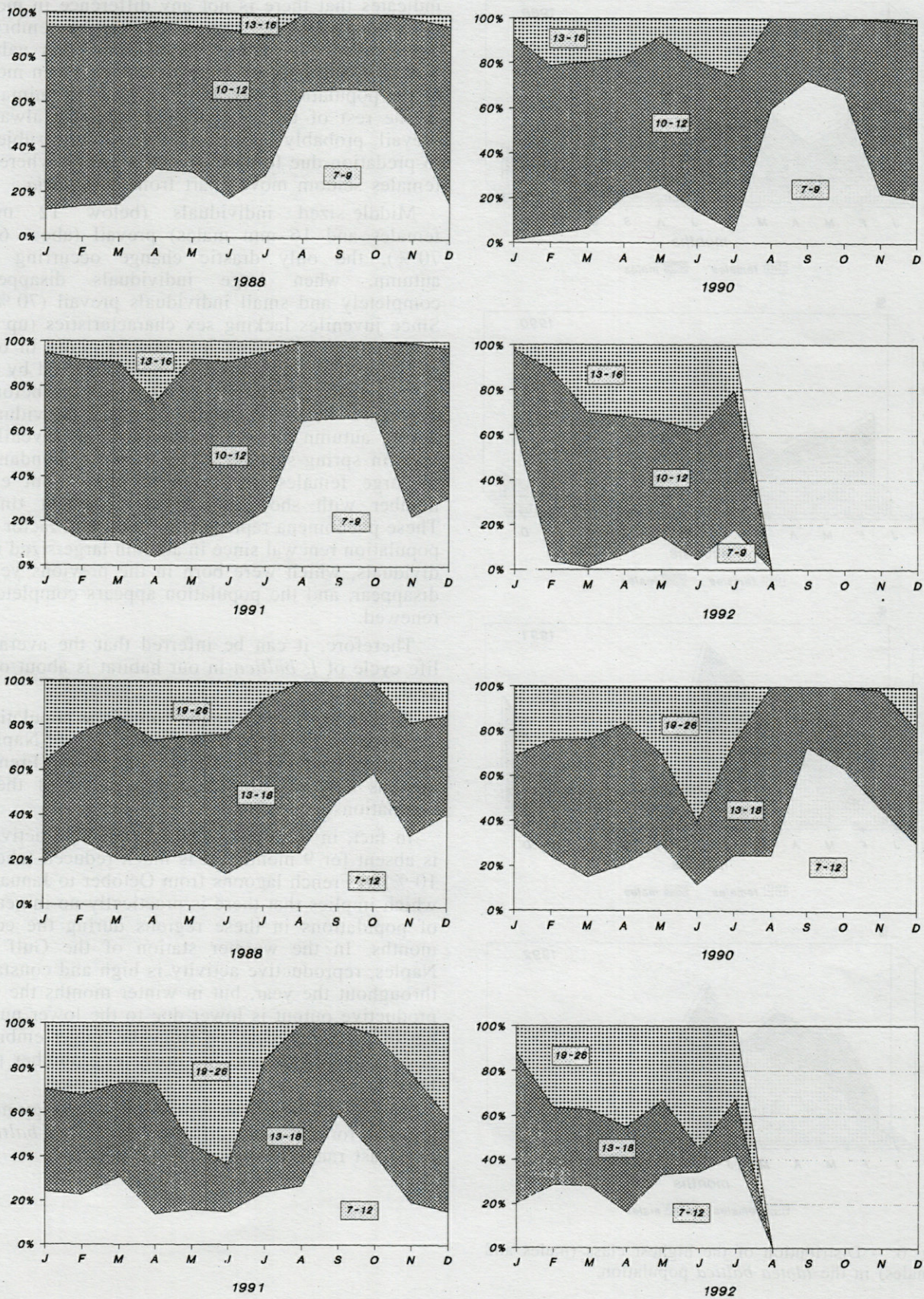


Fig. 5. – The composition of *Idotea baltica* population expressed as size-classes frequency : a), females, b, males.



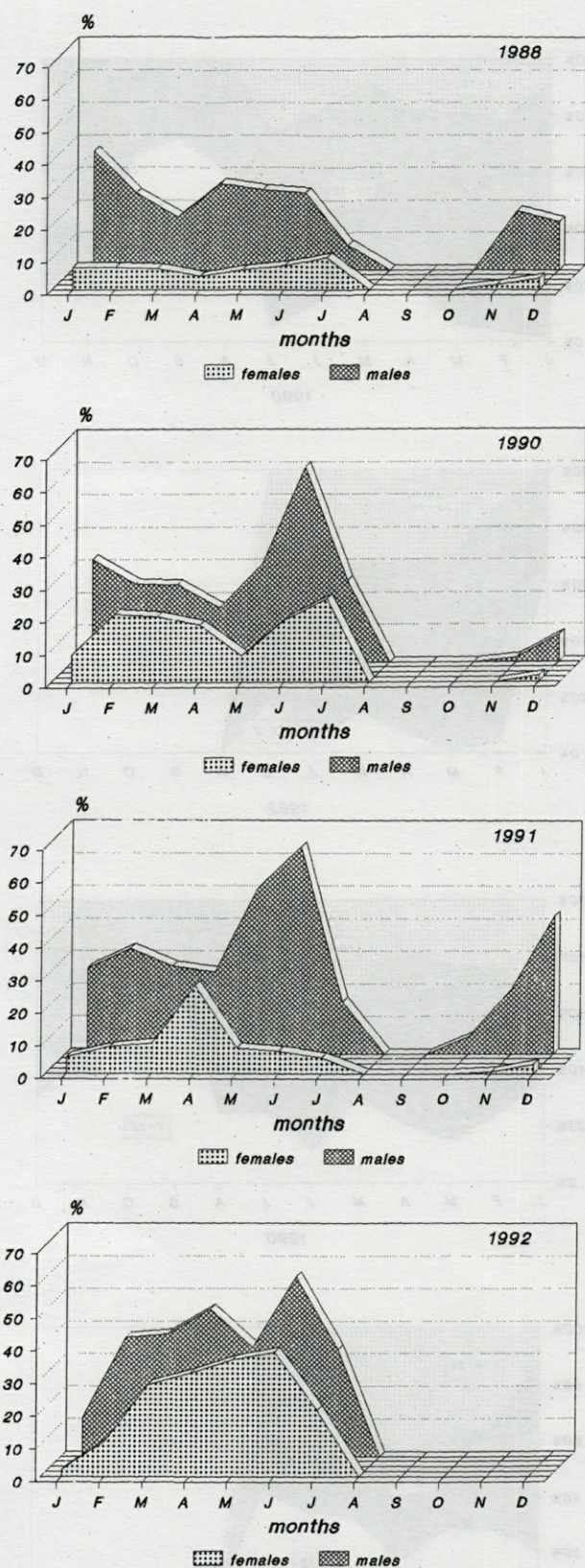


Fig. 6. - Distribution of the highest class (males and females) in the *Idotea baltica* population.

Sex ratio was about 1 in the laboratory, which indicates that there is not any difference in mortality between the two sexes during embryo development. In natural populations, this value was observed only in August-October, when most of the population consists of newly born animals. In the rest of the year, instead, females always prevail, probably because males are more subject to predation due to their greater vagility, whereas females seldom move apart from *Gracilaria*.

Middle-sized individuals (below 12 mm females and 16 mm males) prevail (about 60-70%), the only drastic change occurring in autumn, when large individuals disappear completely and small individuals prevail (70%). Since juveniles lacking sex characteristics (up to 7 mm) were not taken into consideration in our sampling, the small-sized animals observed by us were actually born two or three months before. Therefore the large amount of small individuals during autumn months is the result of juveniles born in spring-summer when there is abundance of large females producing the maximum egg number with short embryo development time. These phenomena represent an important factor of population renewal since in autumn large-sized individuals, which were born in the previous year, disappear, and the population appears completely renewed.

Therefore, it can be inferred that the average life cycle of *I. baltica* in our habitat is about one year.

In conclusion, the comparison of the population dynamics of *I. baltica* living in the Gulf of Naples and those living in the Baltic Sea and the French lagoons suggests similar trends in all of these populations.

In fact, in the Baltic Sea, reproductive activity is absent for 9 months; it is much reduced (about 10%) in French lagoons from October to January, which implies that there is practically no increase of populations in these regions during the cold months. In the warmer station of the Gulf of Naples, reproductive activity is high and constant throughout the year, but in winter months the reproductive output is lower due to the lower number of juveniles resulting from the longer embryo development time and the lower egg number per female.

The flexibility of the reproductive strategy may account for the wide diffusion of *Idotea baltica* in a vast range at different latitudes.



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# DESCRIPTION PRÉLIMINAIRE DE QUATRE NOUVEAUX GENRES ET TROIS NOUVELLES ESPÈCES DE CYCLODORIPPOIDEA AMÉRICAINS (Crustacea, Decapoda, Brachyura)

*Preliminary description of four new genera and three new species  
of Cyclodorippoidea from the Americas (Crustacea, Decapoda, Brachyura)*

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DECAPODES  
BRACHYURES BATHYAUX  
PODOTREMATA  
CYCLODORIPPIDAE  
CYMONOMIDAE

RÉSUMÉ – Nous adjoignons quatre nouveaux genres et trois nouvelles espèces aux cinq genres connus auparavant de la faune cyclodorippoïdienne du nouveau monde, à savoir deux nouveaux genres et trois nouvelles espèces de Cyclodorippidae Ortmann, 1892 : *Cyclodorippe manningi* sp. nov.; *Neocorycodus* gen. nov. (pour *Clythrocerus stimpsoni* Rathbun, 1937); *Clythrocerus moreirai* sp. nov.; *Deilocerus* gen. nov. (pour *Clythrocerus perpusillus* Rathbun, 1900); *Deilocerus hendrickxi* gen. nov., sp. nov.; deux nouveaux genres de Cymonomidae Bouvier, 1897 : *Cyonomoides* gen. nov. (pour *Cyonomus guinotae* Tavares, 1991); *Curupironomus* gen. nov. (pour *Cymopolus agassizii* A. Milne Edwards et Bouvier, 1899).

DECAPODS  
BATHYAL BRACHYURANS  
PODOTREMATA  
CYCLODORIPPIDAE  
CYMONOMIDAE

ABSTRACT – As a result of a review of all known species of cyclodorippoid crabs from the New World, four new genera and three new species are herein described. The present paper increases the number of known genera in the area from five to nine. Two new genera and three new species are added to the Cyclodorippidae Ortmann, 1892 : *Cyclodorippe manningi* sp. nov.; *Neocorycodus* gen. nov., for *Clythrocerus stimpsoni* Rathbun, 1937; *Clythrocerus moreirai* sp. nov.; *Deilocerus* gen. nov., for *Clythrocerus perpusillus* Rathbun, 1900; *Deilocerus hendrickxi* gen. nov., sp. nov.; and two new genera to the Cymonomidae Bouvier, 1897 : *Cyonomoides* gen. nov., for *Cyonomus guinotae* Tavares, 1991; *Curupironomus* gen. nov., for *Cymopolus agassizii* A. Milne Edwards et Bouvier, 1899.

## INTRODUCTION

Les Cyclodorippoidea Ortmann, 1892 américains renferment au total cinq genres. Trois genres appartiennent aux Cyclodorippidae : *Cyclodorippe* A. Milne Edwards, 1880; *Corycodus* A. Milne Edwards, 1880; *Clythrocerus* A. Milne Edwards et Bouvier, 1899. Deux genres appartiennent aux Cymonomidae Bouvier, 1897 : *Cyonomus* A. Milne Edwards, 1880, et *Cymopolus* A. Milne Edwards, 1880. Sauf *Corycodus*, qui compte trois espèces dans l'Indo-Ouest-Pacifique, tous ces genres sont entièrement américains.

Récemment (Tavares, 1991a), nous avons commencé une série de travaux consacrés à la révision des Cyclodorippidae et des Cymonomidae à l'échelon mondial. L'ensemble des Cyclodorip-

pidae et des Cymonomidae indo-ouest-pacifiques, à l'exclusion du genre *Cyonomus*, a été revu par Tavares (1991b, 1992a, 1992b, sous presse), ce qui a permis d'établir quatre genres nouveaux et treize espèces nouvelles dans l'Indo-Ouest-Pacifique.

Dans la présente note, nous adjoignons aux Cyclodorippoidea américains deux genres nouveaux et trois espèces nouvelles de Cyclodorippidae ainsi que deux genres nouveaux de Cymonomidae. Les taxons établis ici sont les suivants : *Cyclodorippe manningi* sp. nov.; *Neocorycodus* gen. nov., pour *Clythrocerus stimpsoni* Rathbun, 1937; *Clythrocerus moreirai* sp. nov.; *Deilocerus* gen. nov., pour *Clythrocerus perpusillus* Rathbun, 1900; *Deilocerus hendrickxi* gen. nov., sp. nov.; *Cyonomoides* gen. nov., pour *Cyonomus guinotae* Tavares, 1991; *Curupironomus* gen. nov., pour Cy-



*mopolus agassizii* A. Milne Edwards et Bouvier, 1899.

Au cours de cette étude, nous avons fait appel aux collections de divers musées, dont les abréviations sont les suivantes : Museum of Comparative Zoology, Massachusetts (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Nationaal Natuurhistorisch Museum, Leiden (RMNH); Collection Carcinologique de l'Universidade Santa Ursula, Rio de Janeiro (USU); Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Estación Mazatlan (EMU).

La terminologie utilisée pour les différentes structures de la carapace est celle de Tavares (1991b). Les mesures données pour les spécimens correspondent respectivement à la longueur (rostre inclus) et à la largeur maximales de la carapace, exprimées en millimètres (mm).

## CYCLODORIPPIDAE Ortmann, 1892

### Genre *Cyclodorippe* A. Milne Edwards, 1880

Espèce-type. *Cyclodorippe agassizii* A. Milne Edwards, 1880, par désignation subséquente. Genre féminin.

Espèces incluses. *Cyclodorippe agassizii* A. Milne Edwards, 1880; *C. antennaria* A. Milne Edwards, 1880; *C. bouvieri* Rathbun, 1934; *C. ornata* Chace, 1940; *C. angulata* Tavares, 1991; *C. manningi* sp. nov., décrite ci-dessous.

### *Cyclodorippe manningi* sp. nov. Fig. 1 A, B

Matériel examiné. Cuba : « Blake », st. 754, au large de La Havane, 315 m : ♂ holotype 5,5 x 6 mm (USNM-68292).

Types. Holotype : mâle 5,5 x 6 mm (USNM-68292). Localité-type. Cuba, au large de La Havane, 315 m.

Description. Carapace à peine plus longue que large, granulation des flancs assez accusée, envahissant les régions hépatique et branchiales; régions frontale, gastriques et cardiaque avec seulement quelques granules. Région frontale légèrement déprimée en son milieu. Nodosités protogastriques très basses. Régions gastriques et cardiaque délimitées latéralement par un sillon peu profond et présentant chacune une nodosité assez basse ornée de granules. Saillies antéro-latérales (les seules sur la carapace) vestigiales. Front à contour semi-circulaire, bordé de denticules assez gros. Dent exorbitaire pointue. Bord supérieur de l'orbite très large et rectiligne. 3<sup>e</sup> maxillipède orné, sur l'ensemble de sa face ex-

terne, de minuscules épines clairsemées, très aiguës. Chélipèdes égaux; mérus, carpe et propode munis de fortes épines sur la face externe; bord interne du carpe avec une grosse dent triangulaire, elle-même bordée de dents plus petites; doigts allongés; dactyle avec une rangée d'épines sur le bord supérieur et des petits granules sur la face externe; bords préhensiles dépourvus de dents. P2 et P3 similaires; ensemble du mérus orné de nombreux tubercules; carpe à bords supérieur et inférieur bordés de denticules et garnis sur les côtés de quelques granules; propode avec le bord supérieur et les côtés munis de granules, le bord inférieur inerme; dactyle entièrement lisse, sauf sur la partie proximale de son bord supérieur quelque peu granulée. Sternum thoracique muni d'épines minuscules et clairsemées. Chez le mâle, tergites abdominaux 1 à 4 et partie proximale du tergite 5 munis de nombreuses petites épines.

Distribution. Cette espèce n'est connue actuellement que de sa localité-type : Cuba, au large de La Havane, 315 m de profondeur.

Remarques. *Cyclodorippe manningi* est similaire à *C. angulata* Tavares, 1991, par le bord supérieur de l'orbite très large et rectiligne ainsi que par les saillies de la carapace vestigiales. Cependant, ces deux espèces se distinguent par les caractères suivants : chez *C. manningi*, aspect plus spinuleux de la carapace et des appendices; carapace plus longue que large (chez *C. angulata* la carapace est beaucoup plus large que longue); front bordé de denticules assez gros (tandis que chez *C. angulata* le front est bordé de denticules minuscules); enfin, mérus, carpe et propode des chélipèdes armés d'épines fortes (tandis que chez *C. angulata* l'ensemble du chélipède est orné de tubercules émoussés).

### Genre *Clythrocerus* A. Milne Edwards et Bouvier, 1899

Espèce-type. *Cyclodorippe nitida* A. Milne Edwards, 1880, par monotypie. Genre masculin.

Espèces incluses. *Clythrocerus nitidus* (A. Milne Edwards, 1880); *Clythrocerus granulatus* (Rathbun, 1898); *Clythrocerus edentatus* Garth, 1966; *Clythrocerus carinatus* Coelho, 1973; *Clythrocerus moreirai* sp. nov., décrite ci-dessous.

Remarques. Nous démembrons le genre *Clythrocerus* en deux genres nouveaux (cf. ci-dessous) : *Neocorycodus* gen. nov., créé pour *Clythrocerus stimpsoni* Rathbun, 1937, et *Deiloceris* gen. nov., établi pour les espèces suivantes : *Clythrocerus perpusillus* Rathbun, 1900, son espèce-type, *Cyclodorippe plana* Rathbun, 1900 (transférée dans le genre *Clythrocerus* par Rathbun, 1904 et y étant maintenue par Rathbun, 1937); *Clythrocerus decorus* Rathbun, 1933; *Clythrocerus laminatus* Rathbun, 1935; et *Clythrocerus analogus* Coelho, 1973. En outre, le nouveau



genre *Deilocerus* reçoit *Deilocerus hendrickxi* sp. nov., décrite ci-après.

***Clythrocerus moreirai* s.p. nov. Fig. 1 C, D, E**

Matériel examiné. Rio de Janeiro : « Prof. W. Besnard », st. MBT197, 23°47'N-44°44'30''W, 65 m : 2 ♂ 2 ♀ ovigères paratypes (RMNH D 30894). st. MBT211, 23°59'N-43°01'W, 220 m : ♂ holotype 3 x 3,5 mm, 3 ♀ paratypes (RMNH D 30895). *Ibidem* : 1 ♂ 1 ♀ paratypes (USU 408).

Types. L'ensemble des types (mâle holotype, 3 mâles et 5 femelles paratypes) sont déposés à Leiden, sauf pour un mâle et une femelle paratypes conservés dans la collection carcinologique de l'Universidade Santa Ursula.

Localité-type. Rio de Janeiro, 23°59'N-43°01'W, 220 m.

Étymologie. Nous avons le plaisir de dédier cette espèce au regretté Carlos Moreira (1869-1946), l'un des pionniers de la Carcinologie au Brésil.

Description. Carapace beaucoup plus large que longue, régulièrement couverte de gros granules à sommet aplati, légèrement plus petits sur la région frontale. Bord latéral de la carapace armé d'épines, qui se développent davantage sur la portion postéro-latérale. Flancs ornés de gros granules et de quelques tubercules plus allongés et à sommet aplati. Région frontale déprimée en son milieu. Nodosités protogastriques à peine développées. Régions gastriques et cardiaque délimitées latéralement par un sillon peu profond. Saillies antéro-latérales (les seules sur la carapace) bien nettes. Front découpé en quatre dents; dent frontale médiane plus courte que la dent frontale latérale. Avancée de l'endostome visible en vue dorsale entre les dents frontales médianes. Dent orbitaire très développée, en forme d'auvent. Bord supérieur de l'orbite avec une profonde encoche; sur le bord inférieur, un lobe assez proéminent, cachant une partie de l'œil quand celui-ci est couché dans la cavité orbitaire. Troisième maxillipède orné de granules sur l'ensemble de sa face externe. Chélipèdes égaux, presque trois fois plus longs que la longueur maximale de la carapace, régulièrement couverts dans leur ensemble d'assez denses granules, à sommet aplati. Doigts environ deux fois plus courts que le propode, avec les bords préhensiles armés de dents. Sternum thoracique densément couvert de granules aplatis. Tergites abdominaux mâles 1-5 couverts de granules. Chez la femelle, tergites abdominaux 1-6 ornés de granules denses.

Distribution. A l'heure actuelle, *Clythrocerus moreirai* sp. nov. n'est connue que de la côte brésilienne, en l'occurrence au large de Rio de Janeiro, entre 65 et 220 m.

Remarques. *Clythrocerus moreirai* sp. nov. est voisine de *C. granulatus* (Rathbun, 1898). La nouvelle espèce a la particularité d'avoir, sur le bord inférieur de l'orbite, un lobe assez proéminent, cachant une partie de l'œil quand celui-ci est couché dans la cavité orbitaire (fig.1 D). Chez *C. granulatus*, le bord inférieur de l'orbite est bordé de quelques épines de taille variable, mais il n'y a jamais formation d'un gros lobe. Chez *Clythrocerus moreirai* sp. nov., le bord supérieur de l'orbite possède souvent une profonde encoche; sur la carapace la saillie antéro-latérale est bien nette, tandis que chez *C. granulatus* le bord supérieur de l'orbite n'est pas interrompu par une encoche et la saillie antéro-latérale de la carapace est vestigiale.

***Neocorycodus* gen. nov.**

*Clythrocerus* Rathbun, 1937 : 109 (pro parte) [non *Clythrocerus* A. Milne Edwards et Bouvier, 1899; espèce-type : *Cyclodorippe nitida* A. Milne Edwards, 1880].

Description. Carapace à contour subpentagonal, très renflée, surtout au niveau des régions gastrique et branchiales. Céphalothorax très épais. Saillie antéro-latérale de la carapace présente. Limites entre la face dorsale et les flancs de la carapace assez nettes. Largeur fronto-orbitaire égale à la moitié de celle, maximale, de la carapace. Orbites profondément creusées, à bords supérieur et inférieur bien délimités. Cavités orbitaire et antennaire complètement séparées; lobe infra-orbitaire très développé, cloturant totalement la cavité orbitaire. Antennes beaucoup plus courtes que la moitié de la longueur maximale de la carapace; segment 2 valviforme, obturant totalement la cavité antennaire et cachant l'antennule lorsque celle-ci est repliée. Avancée de l'endostome en forme de gouttière, plus étroite vers l'avant, dépassant le bord frontal de la carapace et donc visible en vue dorsale. Exopodite des 3 paires de maxillipèdes dénué de flagelle. 3<sup>es</sup> maxillipèdes avec l'ischion et le mérus bien plus longs que larges; palpe inséré sur la face interne du mérus. Chélipèdes de longueur égale; doigts assez grêles, armés d'épines longues et aiguës. P2 et P3 avec le propode et le dactyle ornés de soies courtes et peu denses; dactyle légèrement comprimé latéralement. Spermathèques presque contiguës. Abdomen femelle formé de six segments; pléopodes articulés sur la face ventrale des segments abdominaux 2 à 5.

Étymologie. Nom générique formé par la combinaison du nom masculin *corycodus* et du mot grec *neo*, nouveau, par allusion à la ressemblance entre les genres *Corycodus* et *Neocorycodus* gen. nov. Genre masculin.

Espèce-type. *Clythrocerus stimpsoni* Rathbun, 1937.



Espèces incluses. *Neocorycodus stimpsoni* gen. nov., comb. nov. (Rathbun, 1937). Fig. 1 F, G.

Remarques. Le genre nouveau *Neocorycodus* est créé ici pour abriter *Clythrocerus stimpsoni* Rathbun, 1937, originalement incluse dans le genre *Clythrocerus*. Chez *Neocorycodus stimpsoni* gen. nov., comb. nov., la carapace beaucoup plus large que longue, offre un contour subpentagonal, très renflé, surtout au niveau des régions gastrique et branchiale (fig. 1 F) (tandis que chez *Clythrocerus* la carapace est subcirculaire et légèrement plus longue que large); la largeur fronto-orbitaire est égale à la moitié de celle, maximale, de la carapace (chez *Clythrocerus* la largeur fronto-orbitaire est supérieure à la moitié de la largeur maximale de la carapace); les doigts des chélicères sont cylindriques, longs et assez grêles, comme deux baguettes armées d'épines longues et aiguës (fig. 1 G) (chez *Clythrocerus* les doigts des chélicères sont courts, aplatis et creusés sur leur face interne).

*Neocorycodus* gen. nov. est proche du genre *Corycodus* A. Milne Edwards, 1880, dont il se sépare aisément par la largeur de la région fronto-orbitaire qui est égale à la moitié de la largeur maximale de la carapace (elle est bien inférieure chez *Corycodus*); par les cavités orbitaire et antennaire complètement séparées par un lobe infra-orbitaire très développé (chez *Corycodus* ces deux cavités communiquent entre elles, et le lobe infra-orbitaire est très petit); par l'endostome avancé vers l'avant, dépassant le bord frontal de la carapace et donc visible en vue dorsale (chez *Corycodus* l'endostome ne dépasse pas le bord frontal de la carapace et il n'est pas visible en vue dorsale); par les 3 paires de maxillipèdes dépourvues de flagelle (chez *Corycodus* le Mxp3 seulement est dépourvu de flagelle); par les spermathèques presque contiguës (tandis que chez *Corycodus* elles sont assez séparées); enfin, par l'abdomen femelle de six segments (l'abdomen femelle compte sept segments chez *Corycodus*).

#### *Deilocerus* gen. nov.

*Clythrocerus* Rathbun, 1937 : 109 (pro parte) [non *Clythrocerus* A. Milne Edwards et Bouvier, 1899; espèce-type : *Cyclodorippe nitida* A. Milne Edwards, 1880].

Description. Carapace à contour subcirculaire et aplatie sur le dessus. Saillies hépatique et antéro-latérale présentes. Limites entre la face dorsale et les flancs de la carapace assez nettes. Largeur fronto-orbitaire égale à la moitié de celle, maximale, de la carapace. Orbites profondément creusées, à bords supérieur et inférieur bien délimités. Cavités orbitaire et antennaire communiquant librement; lobe infra-orbitaire petit. Antennes plus courtes que la moitié de la longueur maximale de la carapace; segment 2 légèrement aplati. Avancée

de l'endostome en forme de gouttière, plus étroite vers l'avant, dépassant le bord frontal de la carapace et donc visible en vue dorsale. Exopodite de la 3<sup>e</sup> paire de maxillipède dénué de flagelle; palpe inséré sur la face interne du mérius.

Étymologie. Nom formé par les mots grecs *deilos*, faible, réduit, et *keros*, antenne, par allusion au segment 2 de l'antenne non valviforme. Genre masculin.

Espèce-type. *Clythrocerus perpusillus* Rathbun, 1900.

Espèces incluses. *Deilocerus perpusillus* (Rathbun, 1900); *Deilocerus planus* (Rathbun, 1900); *Deilocerus decorus* (Rathbun, 1933); *Deilocerus laminatus* (Rathbun, 1935); *Deilocerus analogus* (Coelho, 1973); *Deilocerus hendrickxi* sp. nov.

Remarques. *Deilocerus* gen. nov. se caractérise par des antennes assez courtes, dont le segment 2 est légèrement aplati (au lieu d'être valviforme comme chez *Clythrocerus*), et par un lobe infra-orbitaire plus petit que chez *Clythrocerus*.

Nous établissons le nouveau genre *Deilocerus* pour les espèces suivantes : *Clythrocerus perpusillus* Rathbun, 1900, son espèce-type; *Cyclodorippe plana* Rathbun, 1900 (transférée dans le genre *Clythrocerus* par Rathbun en 1904 et y étant maintenue par Rathbun en 1937); *Clythrocerus decorus* Rathbun, 1933; *Clythrocerus laminatus* Rathbun, 1935; et *Clythrocerus analogus* Coelho, 1973. En outre, le nouveau genre *Deilocerus* reçoit *Deilocerus hendrickxi* sp. nov., décrite ci-dessous.

#### *Deilocerus hendrickxi* gen. nov., sp. nov. Fig. 1 H, I

Matériel examiné. Golfe de Californie : « *El Pluma* », st. 68, 29°35'N-113°33'W, 162-175 m : ♂ holotype 6,5 x 7,8 mm, 1 ♀ ovigère paratype (MNHN-B 22664). *Ibidem* : 1 ♀ paratype (USNM). *Ibidem* : 1 ♂ paratype (USU-407). *Ibidem* : ♂ paratype (EMU-2722).

Types. La série-type de *Deilocerus hendrickxi* gen. nov., sp. nov. est composée d'un mâle holotype, de deux mâles et de deux femelles (une ovigère), paratypes.

Localité-type. Golfe de Californie, 29°35'N-113°33'W, 162-175 m.

Étymologie. Espèce dédiée à M. E. Hendrickx, Universidad Nacional Autónoma de México, toujours prêt à apporter son aide lorsque des prêts de matériel lui sont demandés.

Description. Carapace un peu plus large que longue, presque lisse sur le dessus, sauf par quelques granules présents sur les régions hépatique et métabrancheiale. Carapace munie de tubercules de même taille sur toute la longueur du bord latéral. Région frontale déprimée en son milieu. Ré-



gions gastriques et cardiaque délimitées latéralement par un sillon peu profond. Saillies hépatiques et antéro-latérale assez développées, l'antéro-latérale bien plus grande que la saillie hépatique. Front découpé en deux dents, entre lesquelles l'avancée de l'endostome apparaît, en vue dorsale, comme une projection triangulaire. Dent exorbitaire très développée, en forme d'auvent. Bord supérieur de l'orbite avec une très profonde encoche. Troisième maxillipède orné de petits granules spinuleux sur l'ensemble de sa face externe. Chélicères égaux, l'ensemble de la face externe régulièrement couvert de petits granules. Bord interne du dactyle, du propode et du carpe longé par des épines aiguës. Sternum thoracique couvert de petits granules pointus. Chez le mâle, tergites abdominaux 1-5 couverts de granules, tergite 1 faiblement orné. Chez la femelle, tergites abdominaux 1-6 munis de granules minuscules, surtout les deux premiers; tergite 6 avec une fente longitudinale sur presque toute son étendue.

Distribution. Actuellement, *Deilocerus hendrickxi* gen. nov., sp. nov. est connue seulement du Golfe de Californie, entre 162-175 m.

Remarques. *Deilocerus hendrickxi* gen. nov., sp. nov. est voisine de *D. decorus* gen. nov., comb. nov. (Rathbun, 1933). La nouvelle espèce se distingue aisément par sa carapace presque lisse sur le dessus, sauf par la présence de quelques granules sur la région hépatique, la région métabran-chiale et sur les bords latéraux, ainsi que par l'ornementation beaucoup moins accusée de son chélicère (tandis que chez *D. decorus* la carapace comme les chélicères sont ornés d'assez gros granules).

## CYMONOMIDAE Bouvier, 1897

### *Cyonomoides* gen. nov.

*Cyonomus*. (pro parte) Chace, 1940 : 18; Griffin et Brown, 1975 : 251; Tavares, 1991a : 635 [non *Cyonomus* A. Milne Edwards, 1880; espèce-type : *Cyonomus quadratus* A. Milne Edwards, 1880].

Description. Carapace à contour subquadratique. Orbites absentes. Rostre vestigial ou très court. Pédoncules oculaires orientés dans un sens longitudinal par rapport à l'axe de la carapace, assez longs, fortement divergents, très calcifiés et complètement soudés entre eux à la base. Cornée inexistante. Endostome assez court. 3<sup>e</sup> maxillipède avec le mérus très saillant en avant; exopodite avec un flagelle bien développé. Chélicères égaux. Pleurites thoraciques au niveau des P2 et P3 apparaissant toujours à découvert. P2 et P3 à dactyles comprimés dorso-ventralement; P4 et P5 subdorsaux. Sternite 8 chevauchant partiellement

le sternite 7 au niveau de la spermathèque, en ménageant une sorte de poche située à l'extrémité du sillon sternal 7/8. Abdomen mâle et femelle formé de 7 segments.

Étymologie. Nom générique formé par la combinaison du nom masculin *cyonomus* et du mot grec *eidos*, *oid*, *oides*, ressemblance, par allusion aux affinités entre les genres *Cyonomus* et *Cyonomoides* gen. nov. Genre masculin.

Espèce-type. *Cyonomus guinotae* Tavares, 1991.

Espèces incluses. *Cyonomoides cubensis* gen. nov., comb. nov. (Chace, 1940); *Cyonomoides delli* gen. nov., comb. nov. (Griffin et Brown, 1975); et *Cyonomoides guinotae* gen. nov., comb. nov. (Tavares, 1991).

Remarques. Le nouveau genre *Cyonomoides* est créé ici pour 3 espèces décrites auparavant dans le genre *Cyonomus* A. Milne Edwards, 1880 : *Cyonomus cubensis* Chace, 1940, *Cyonomus delli* Griffin et Brown, 1975, et *Cyonomus guinotae* Tavares, 1991.

Chace (1940) a décrit *Cyonomus cubensis* de la mer des Caraïbes, première espèce à abdomen mâle et femelle de 7 segments. A cette occasion, il mentionne que ce caractère pourrait revêtir une signification qui dépasserait le niveau spécifique. Plus tard, Griffin et Brown (1975) ont découvert, au large de la côte est-australienne, une 2<sup>e</sup> espèce, *Cyonomus delli* qui, comme *C. cubensis*, a l'abdomen mâle et femelle formé de 7 segments. Ces deux auteurs partagent l'avis de Chace quant à la possibilité de séparer les espèces à 7 segments abdominaux dans un nouveau genre. Récemment, nous avons entrepris une série de travaux en vue d'une révision des *Cyonomidae* et des *Cyclodorippidae*. Tavares (1991a) a décrit 3 nouveaux *Cyonomus* du Brésil, dont une espèce, *C. guinotae*, présentait 7 segments abdominaux, chez le mâle comme chez la femelle. C'est seulement après l'avancement des travaux de révision que nous avons pu décider que les singularités de ces trois espèces nécessitaient l'établissement d'un genre particulier, nommé ici *Cyonomoides*.

Le nouveau genre a la particularité d'avoir l'abdomen mâle et femelle formé de 7 segments; les pédoncules oculaires fortement divergents, immobiles, très calcifiés, complètement soudés entre eux à la base et totalement dépourvus de cornée; le rostre peut être vestigial ou, sinon, très court. Les 3 espèces de *Cyonomoides* gen. nov. sont aveugles et habitent à des profondeurs comprises entre 592 et 900 m.

### *Curupironomus* gen. nov.

*Cymopolus*. A. Milne Edwards et Bouvier, 1902 : 74 (pro parte) [non *Cymopolus* A. Milne



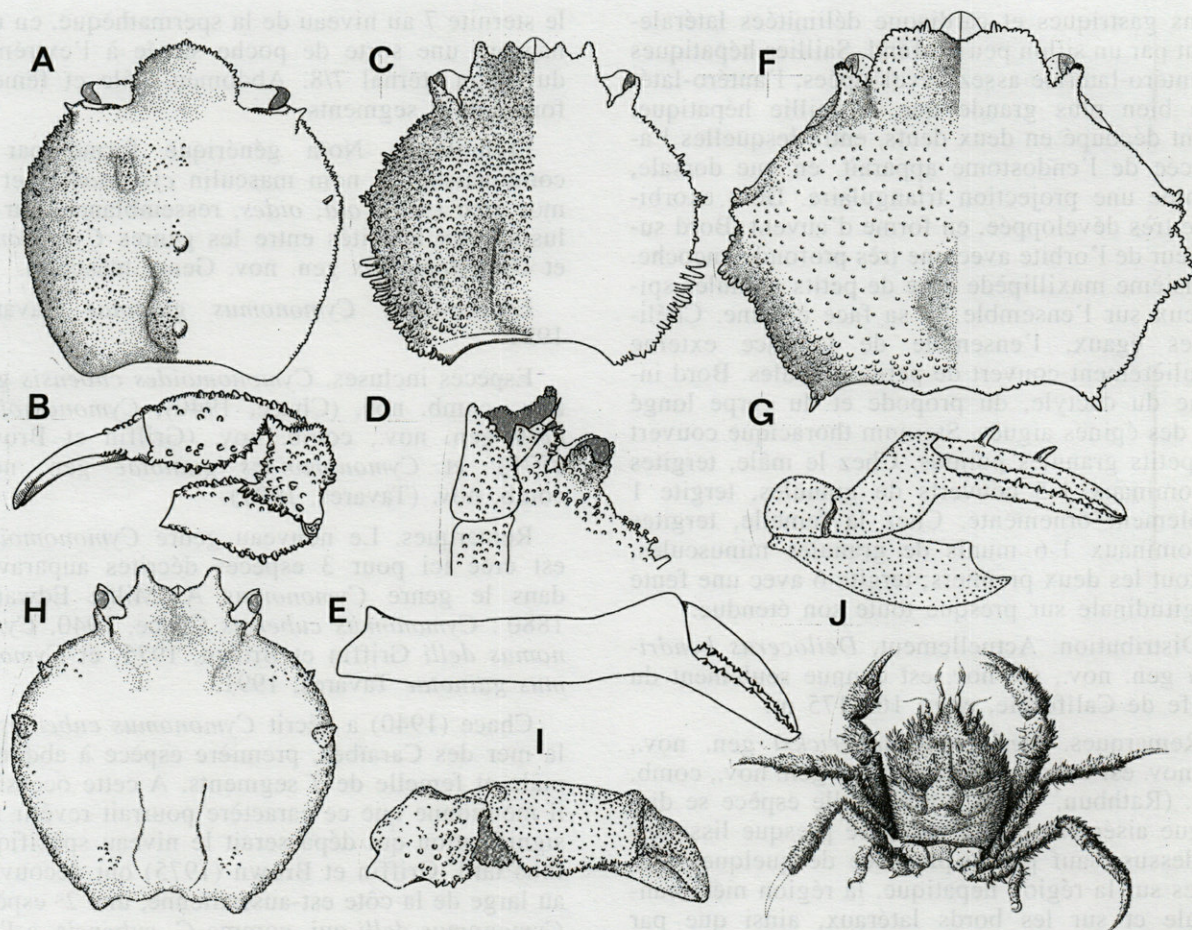


Fig. 1. A-B. *Cyclodorippe manningi* sp. nov. Cuba : « Blake », st. ?54, au large de La Havane, 315 m : ♂ holotype 5,5 x 6 mm (USNM-68292) : A, face dorsale de la carapace; B, chélicèpe. C-E. *Clythrocerus moreirai* sp. nov., Rio de Janeiro : « Prof. W. Besnard », st. MBT211, 23°59'N-43°01'W, 220 m : ♂ holotype 3 x 3,5 mm (RMNH D 30895) : C, face dorsale de la carapace; D, vue ventrale de la région orbitaire; E, chélicèpe d'un ♂ paratype 2,8 x 3,0 mm (ornementation non représentée) (RMNH D 30895). F-G. *Neocorycodus stimpsoni* gen. nov., comb. nov. (Rathbun, 1937). Côte ouest de la Floride : « Bache », 22 Avril 1872, W. Stimpson coll., 180 m : ♀ holotype 3,5 x 5 mm (MCZ-8261) : F, face dorsale de la carapace. G, chélicèpe. H-I. *Deilocerus hendrickxi* gen. nov., sp. nov. Golfe de Californie : « El Pluma », st. 68, 29°35'N-113°33'W, 162-175 m : ♂ holotype 6,5 x 7,8 mm (MNHN-B 22664) : H, face dorsale de la carapace. I, chélicèpe. J. *Curupironomus agassizii* gen. nov., comb. nov. (A. Milne Edwards et Bouvier, 1899), d'après A. Milne Edwards et Bouvier (1902 : planche XV, fig. 1).

Edwards, 1880; espèce-type : *Cymopolus asper* A. Milne Edwards, 1880].

Description. Carapace un peu plus élargie vers l'avant, hérissée d'épines très obtuses et arquées sur les flancs. Régions gastriques et cardiaque délimitées de chaque côté par un sillon profond. Rostre à peine incurvé vers le bas. Pédoncule oculaire presque complètement visible en vue dorsale. Surface cornéenne assez réduite, semblant dégénérée. Bord antérieur de l'endostome très légèrement incurvé vers l'avant. Région épistomienne assez courte. Exopodite du troisième maxillipède avec un flagelle rudimentaire. Chélicèdes forts et égaux. P2 et P3 similaires, garnis d'épines obtuses. P4 et P5 subdorsaux.

Étymologie. Nom générique formé de *curupira*, tiré d'un folklore brésilien mentionnant un person-

nage qui aurait les deux pieds retournés vers l'arrière du corps, et du substantif néo-latin *gnomus*, nain, petit. C'est une allusion aux péréiopodes subdorsaux 4 et 5 de ce Crabe. Genre masculin.

Espèce-type. *Cymopolus agassizii* A. Milne Edwards et Bouvier, 1899.

Espèces incluses. *Curupironomus agassizii* gen. nov., comb. nov. (A. Milne Edwards et Bouvier, 1899), fig. 1J.

Remarques. Le nouveau genre *Curupironomus* est établi ici pour une seule espèce, *Cymopolus agassizii* A. Milne Edwards et Bouvier, 1899, connue de la mer des Caraïbes (Floride et Porto Rico). *Curupironomus* gen. nov. se distingue surtout par le pédoncule oculaire bien long et presque complètement visible en vue dorsale (tandis que chez *Cymopolus* il est presque entièrement caché



par un auvent formé par le rostre); par le bord antérieur de l'endostome légèrement incurvé vers l'avant (chez *Cymopolus* le bord antérieur de l'endostome est assez incurvé et possède une crête médiane); par la région épistomienne assez courte (chez *Cymopolus* cette région est allongée); par l'abdomen formé de 7 segments (l'abdomen est formé de 6 segments chez *Cymopolus*); par le rostre à peu près droit (chez *Cymopolus* le rostre est fortement incurvé vers le bas).

REMERCIEMENTS – Nous exprimons nos plus vifs remerciements à A. B. Johnston (Museum of Comparative Zoology, Massachusetts), toujours prête à apporter son aide lorsque des recherches de matériel lui sont demandées : elle a mis à notre disposition les riches collections de matériel-type de Cyclodorippidae et de Cymonomidae conservées dans son institution.

Nous sommes très reconnaissant à R. B. Manning (Smithsonian Institution, Washington), qui nous a accordé une bourse de « Short Term Visitor » à la Smithsonian Institution et nous a donné toutes les possibilités de travail lors de notre séjour. Son aide a été indispensable pour compléter la révision des Cyclodorippidae et Cymonomidae américains, dont la présente note comporte les premiers résultats. L. K. Manning a très aimablement préparé la reproduction de la figure originale d'A. Milne Edwards et E.-L. Bouvier (1902), représentée comme fig. 1J. Tout au long de ce travail, les discussions avec R. B. Manning et F. A. Chace Jr. (Smithsonian Institution, Washington) nous ont été d'un grand secours.

Nous exprimons également notre sincère gratitude à C. H. J. M. Franssen et à L. B. Holthuis (Nationaal Natuurhistorisch Museum, Leiden); à M. Hendrickx (Estación Mazatlan, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México), qui nous ont aimablement envoyé des spécimens conservés dans leur institution.

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## THREE NEW *MIXTACANDONA* (OSTRACODA) SPECIES FROM CROATIA, AUSTRIA AND FRANCE

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OSTRACODA  
MIXTACANDONA  
EUROPE  
TAXONOMY

**ABSTRACT** – Three new species, *Mixtacandona lattingerae* n. sp. (from the alluvial sediments of the river Sava in Croatia), *M. spandli* n. sp. (from the groundwaters of the Danube wetland Lobau at Vienna) and *M. coineauae* n. sp. (from the karstic system in southern France) are described. The 3 new taxa belong to the group of species *hvarensis*. A comparative morphological analysis of the 5 species belonging to this group is synthetically presented.

OSTRACODES  
MIXTACANDONA  
EUROPE  
TAXONOMIE

**RÉSUMÉ** – Trois nouvelles espèces, *Mixtacandona lattingerae* n. sp. (provenant des sédiments alluviaux de la Sava en Croatie), *M. spandli* n. sp. (provenant des eaux souterraines de Lobau, plaine alluviale du Danube près de Vienne) et *M. coineauae* n. sp. (provenant d'un système karstique dans le sud de la France) sont décrites. Les trois nouveaux taxa appartiennent aux espèces du groupe *hvarensis*. Une analyse morphologique comparative de cinq espèces appartenant à ce groupe est présentée de manière synthétique.

### A. INTRODUCTION

Ostracods are one of the common crustacean groups in freshwater subterranean waters in Europe (Danielopol, 1985). The genus *Mixtacandona* Klie is a primitive member of the Candoninae group which contains 20 hypogean living species and possibly one fossil representative (Danielopol, 1972, 1978 and 1985).

Here we describe three new species assigned to the species group *hvarensis* sensu Danielopol 1977/1978. A detailed analysis of their ecology and biogeography is presented elsewhere (Rogulj *et al.*, 1993 and in print). The material is deposited in the Limnological Institute of the Austrian Academy of Sciences (Mondsee, Austria).

### B. TAXONOMIC DESCRIPTION

Description is following the model Broodbakker and Danielopol (1982)

*Abbreviations used in text and figures :*

Soft parts : A, anterior; A1, antennula; A2, antenna 2; D, distal; E, endopodite; Ex, exterior; Exo, exopodite; Fu, furca; G, claw at A1 and T1;

G<sub>a</sub>, G<sub>p</sub>, anterior and posterior claw of Fu; G<sub>m</sub>, G<sub>M</sub>, minor and major claws at A2 : EIV; G<sub>1</sub>, G<sub>2</sub>, G<sub>3</sub>, claws at A2 : EIII; I to VII, first to seventh segment; In, interior; l, long; m, medium; P, posterior; S<sub>a</sub>, S<sub>p</sub>, anterior and posterior setae of Fu; s, short; T1 (2), thoracopod 1 (2); t<sub>1</sub> to t<sub>4</sub>, 4 setae at A2 : EIII; Y, aesthetasc at A2 : EI; Ya, aesthetasc at A1 print VII; Y1 to Y3, 3 aesthetascs at A2 : EII, EIII, EIV; z<sub>1</sub> to z<sub>3</sub>, three setae at A2;

*Valves* : H, height of valves; L, length of valves; R, right valve; L, left valve.

#### 1. *Mixtacandona lattingerae* n. sp.

##### 1.1. Derivatio nominis

Species dedicated to Dr. R. Lattinger (University of Zagreb) who provided the material and helped in many ways one of us (B.R.) during the completion of this project.

##### 1.2. Material (leg. R. Lattinger)

**Holotype** : One dissected female mounted in glycerine on slide and valves kept in ethanol.

**Paratype** : One undissected female kept in ethanol.



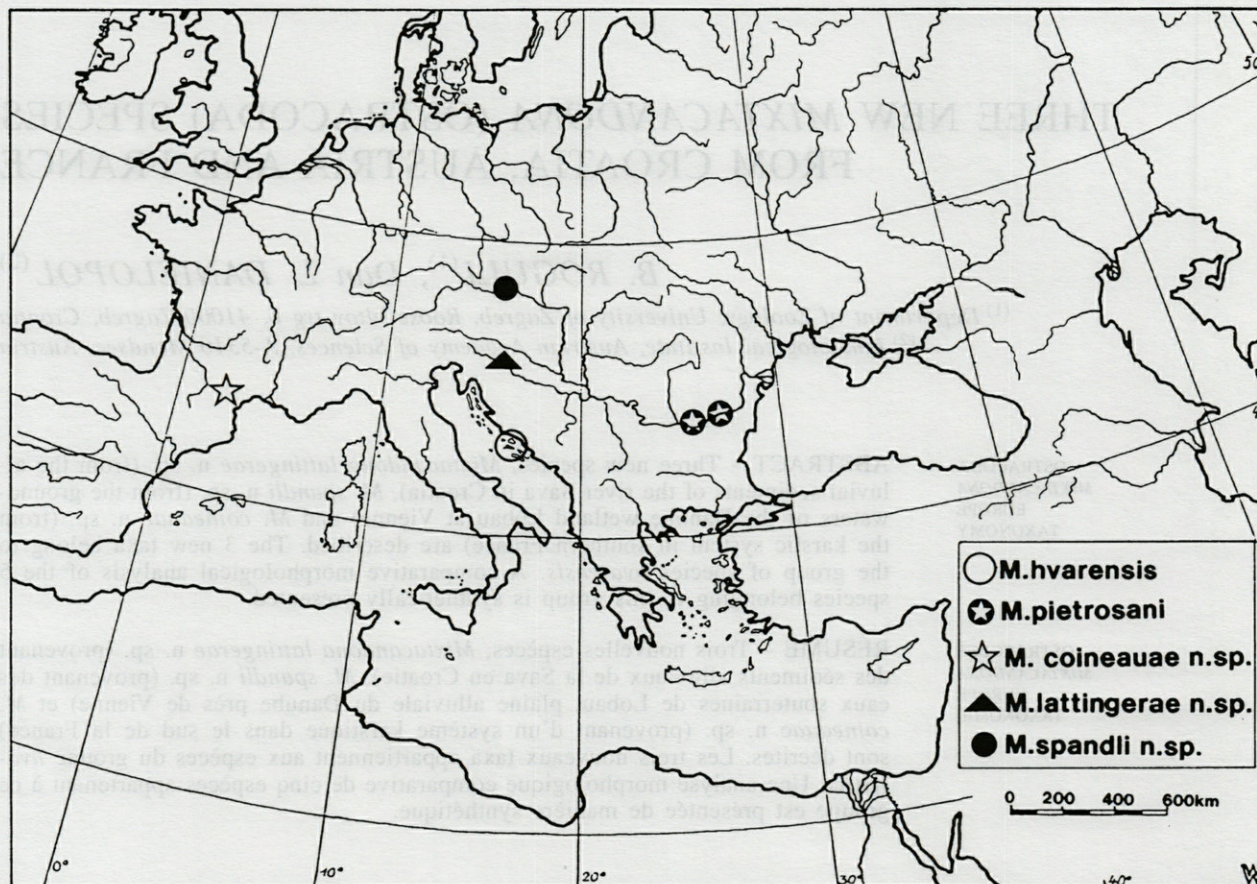


Fig. 1. – Biogeographical distribution of the species group *Mixtacandona hvarensis*.

Type locality: Opatovina, gravel bar at the river Sava near Zagreb, Croatia (Fig. 1 and 2). Detailed description of the site is given in Mestrov *et al.* (1983) and Rogulj *et al.* (in print).

Additional material: Samples from the same locality were taken on 3 occasions from 21 piezometer wells fixed to various depths between 0.5 and 7 m. Site B (25 m from the river): depth 0.5 m = 3 adults; 1 m = 15 ad., 3 juveniles; 2 m = 1 ad; Site C (75 m): depth 1 m = 1 ad., 2 juv.; 2 m = 713 ad. and juv.; 3 m = 7 ad., 5 juv.; Site D (135 m): depth 7 m = 2 ad., 2 valves.

### 1.3. Description

Carapace smooth and thin. Maximal height in the middle, comprising 48-52 % of total length. Maximal width less than 1/3 of the carapace length. Anterior and posterior margins curved, ventral margin straight. Left valve triangular and slightly higher, dorsal margin of the right valve centrally straighter. Internal calcareous lamella wider in anterior and posterior parts (maximal width of the lamella – carapace length proportion of the anterior part = 7.5 % for the RV and 6 % for the LV; the same proportion of the posterior part = 5 % for the both valves.

Carapaces display no sexual dimorphism.

Dimensions (n = 10): Length = 0.74-0.79 mm; height = 0.36-0.40 mm.

*Antennula* (Fig. 4A)

I: P-1 m-11, A-1m/II: A-1s/III: P-1s/IV: A-11, P-1s/V: A-21, P-1s/VI: A-21, P-2 m/VII: 21-1G-Ya.

*Second antenna* (Fig. 4 D and Fig. 5)

Female (Fig. 5B): Pr: 11/Exo: 11/EI: P-Y-11-1s/E (II + III): A-2s, P-Y1-2m (t<sub>1-4</sub>), D-21 (G<sub>1,3</sub>)-1m (G<sub>2</sub>), In-3s (z<sub>1-3</sub>), P-Y<sub>2</sub>/EIV: 11 (G<sub>M</sub>)-1m (G<sub>m</sub>)-Y<sub>3</sub>

Male (Fig. 5A): Pr: 11/Exo: 11/EI: P-Y-11-1s/EII: A-2s, P-Y1-2m (t<sub>1-2</sub>), Ex-1m (t<sub>3</sub>)-1s(t<sub>4</sub>)/EIII: A-21 (G<sub>1,2</sub>) – 1 m (G<sub>3</sub>), A-3 m (z<sub>1-3</sub>)-Y<sub>2</sub>/EIV: 11 (G<sub>M</sub>)-1m (G<sub>m</sub>)-Y<sub>3</sub>

Mean value of the ratio of Y – aesthetasc and interodistal margin of EI is 129 % for the female and 145 % for the male.

*First thoracopod* (Fig. 4F):

Pr/EI: A-1s/EII: 1s/EIII: A-1s/EIV: 11 (G) – 2s

*Second thoracopod* (Fig. 4G):



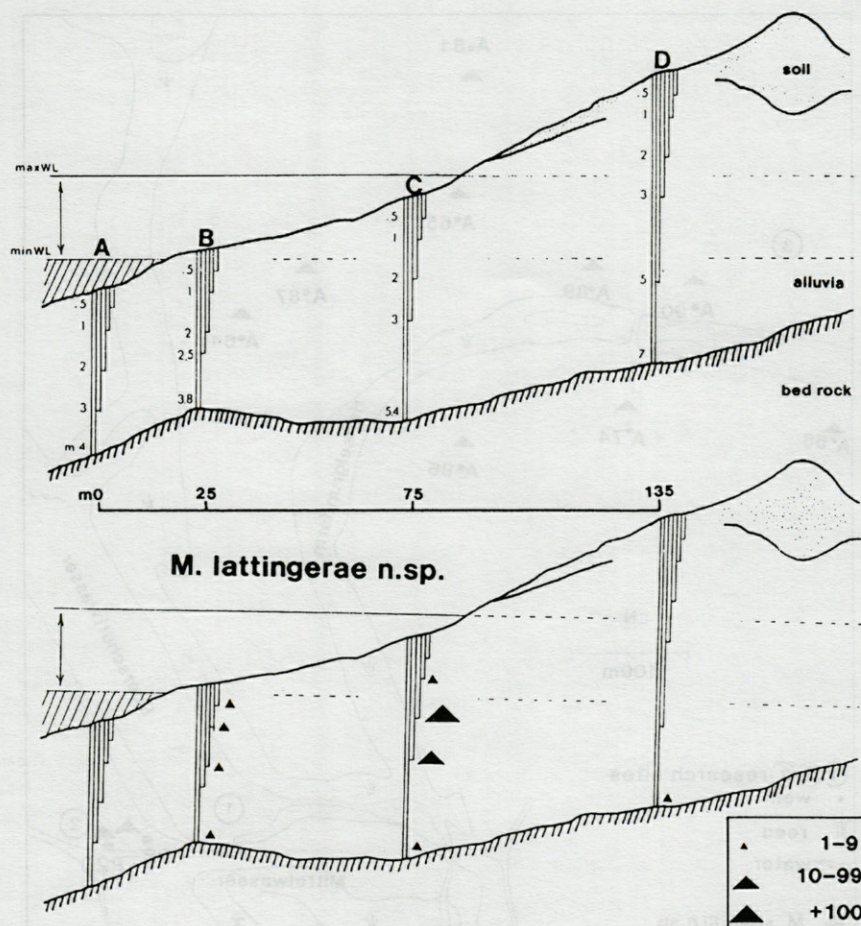


Fig. 2. - Location of the gravel bar at the river Sava near Zagreb with the abundance of *M. lattingerae* n. sp. specimens in three samples, each 336 l of groundwater (see Rogulj *et al.*, in print).

Pr : A-1m, P-2m/EI : P-1s/E (II + III) : P-2s/EIV : 11-2s

*Furca* (Fig. 4H)

Distal claws (GA, Gp) equally long; anterior and posterior setae short (about 1/7 of the length of the distal claw). The length of distal claw represents about 65 % of the anterior margin's length (measured between the anterior seta and the point of furcal attachment).

Additional information of female :

Ovocyte : Maximal diameter = 113  $\mu$ m. Ovocyte diameter - carapace length ratio = 14,3 %.

Additional information of male :

Prehensile palp (Fig. 7A) : slightly asymmetrical internal margin of the terminal segment due to the well developed protuberance on the left palp.

Hemipenis : D-lobe rounded.

## 2. *M. spandli* n. sp.

### 2.1. Derivatio nominis

Species dedicated to the viennese carcinologist Hermann Spandl, who contributed to the launching of the modern groundwater evolutionary ecology through his monography "Die Tierwelt der unterirdischen Gewässer", Speläol. Inst. Verlag, Wien (1926).

### 2.2. Material (leg. P. Pospisil and F. Moeszlacher)

Holotype : One male mounted in glycerine on slide with valves kept in a micropalaeontological slide.

Paratype : One female and 1 male, undissected and kept in ethanol.



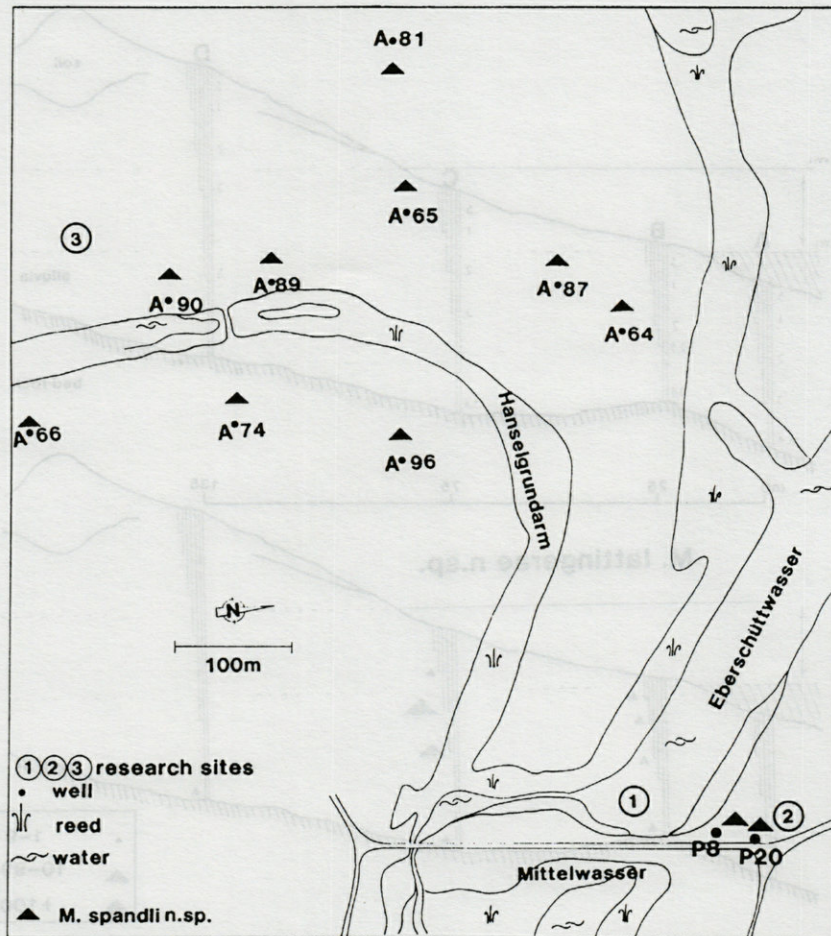


Fig. 3. – Distribution of *M. spandli* n. sp. in the wetland Lobau near Vienna. 1) 30 m<sup>2</sup> area in the gravel sediments of the Eberschüttwasser (Danielopol, 1991); 2) groundwater area described by Danielopol *et al.* (1992); 3) The Hanselgrundarm area (Rogulj *et al.*, 1993).

Type locality: Lobau, the wetland area of the Danube at Vienna, Austria (Fig. 1 and 3). Detailed description of the site is given in Danielopol *et al.* (1992) and Rogulj *et al.* (1993, in print).

Additional material: The samples were extracted with a Bou-Rouch pump fixed to a double packer. The specimens were found in various wells used as piezometers and for groundwater ecological purposes at site 3 (Fig. 3): A64 = 17 adults; A65 = 3 valves; A66 = 4 ad.; A74 = 1 ad.; A81 = 9 ad. and valves; A87 = 3 juveniles; A89 = 34 ad.; A90 = more than 100 ad. and juv.; A96 = 4 ad. and several valves; P8 = 1 valve; P20 = 1 empty carapace.

### 2.3. Description

#### Carapace

Carapace, smooth, thin, with the height/length proportion between 44 and 48 % in the left valve and 44 and 46 % in the right valve. Maximal width less than 1/3 of the carapace length. Anterior and posterior parts of the inner calcified lamella wider;

maximal width of the lamella – carapace length proportion is 14 % in the anterior part and 9 % in the posterior part.

Dimensions: (n = 5): length = 0.65-0.68 mm; height = 0.29-0.32 mm.

Antennula (Fig. 6G)

I: P-1m-1l, A-1m/II: A-1s/III: P-1s/IV: A-1l, P-1s/V: A-2l, P-1s/VI: A-2l, P-2m/VII: 2l-1m-Y.

Antenna (Fig. 6G)

Female: Pr: 1l/Exo: 1l/EI: P-Y-1l-1s/E (II + III): A-1s, P-Y1-2m (t1-4), D-2l (G1,3)-1m(G2), In-3s (z1-3), P-Y2/EIV: 1l (GM)-1m(Gm)-Y3

Male: Pr: 1l/Exo: 1l/EI: P-Y-1l-1s/EII: A-1s, P-Y1-2m (t1-2), Ex-1m (t3)-1s (t4)/EIII: A-2l (G1,2)-1m (G3), A-3m (z1-3)-Y2/EIV: 1l (GM)-1m(Gm)-Y3

Mean value of the ratio Y aesthetasc and interodistal margin of EI is 94.7 % for the female and 104 % for the male.

First thoracopod (Fig. 6I):

Pr/EI/EII: A-1s/EIII: A-1s/EIV: 1l (G)-2s.



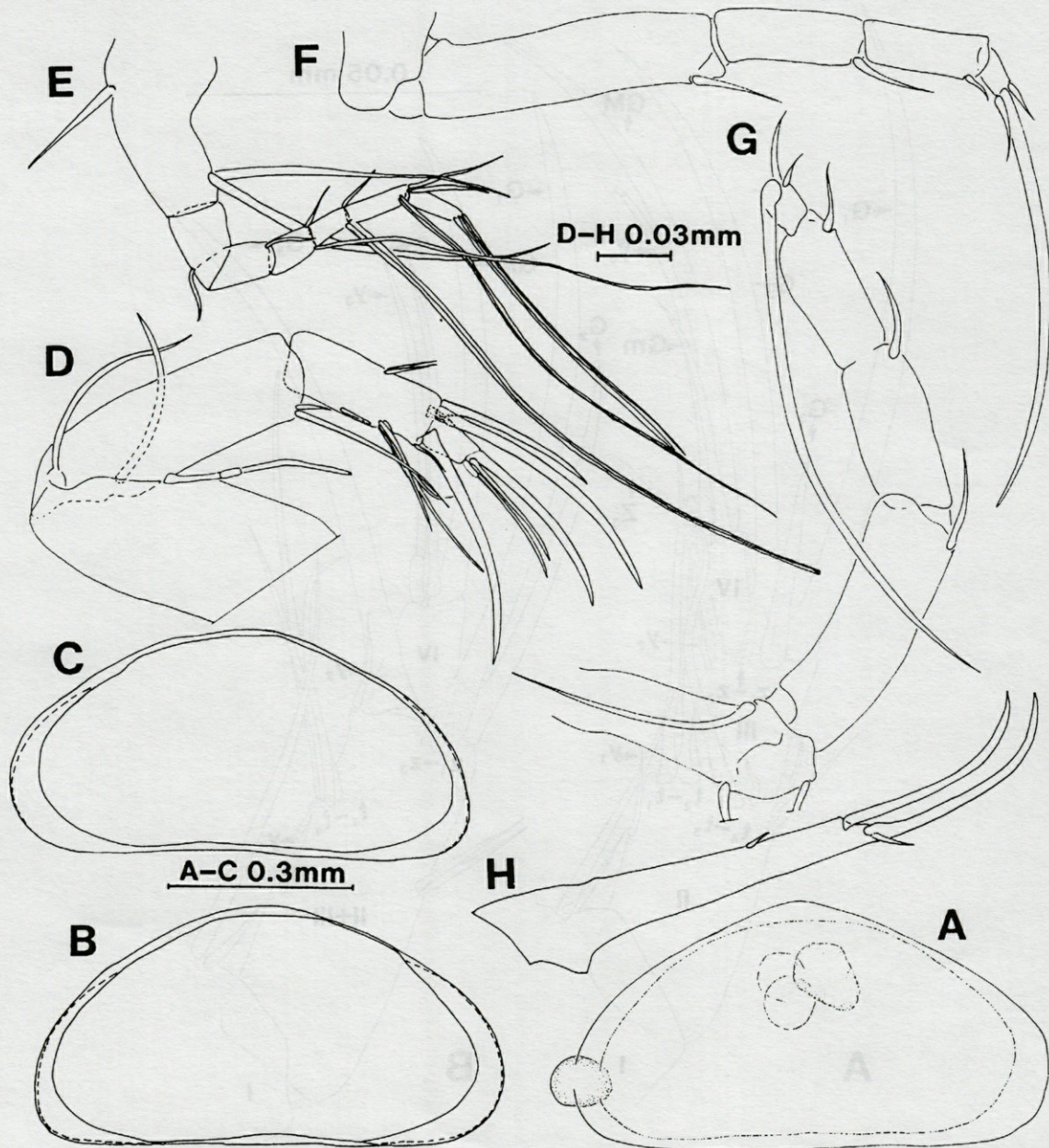


Fig. 4. – *Mixtacandona lattingerae* n. sp.: A, D, E female; B, C, F-H male; A, RV; B, LV; C, RV; D, A2; E, A1; F, T1; G, T2. Abbreviations for limbs and carapace see text.

*Second thoracopod* (Fig. 6H) :

Pr : A-1m, P-2m/EI/E (II + EIII) : 1s/EIV : 1l-2s

*Furca* (Fig. 4H)

Distal claws unequally long, the anterior one (Ga) comprising 50% of the length of furcal ramus and the posterior one (Gp) about 50% of the anterior one.

Additional information of female :

Ovocyte : Maximal diameter was 123  $\mu$ m.  
Ovocyte diameter – carapace length ratio = 18,9%.

Additional information of male :

Prehensile palp (Fig. 7A) : slightly asymmetrical, with slight protuberance of terminal segment's internal margin.

Hemipenis : D-lobe rounded.

3. *M. coineauae* n. sp.

3.1. *Derivatio nominis*

Species dedicated to Dr. N. Coineau (Observatoire Océanologique, Banyuls-sur-Mer) in recognition for her multiple contributions to the understanding of the complex problems about the



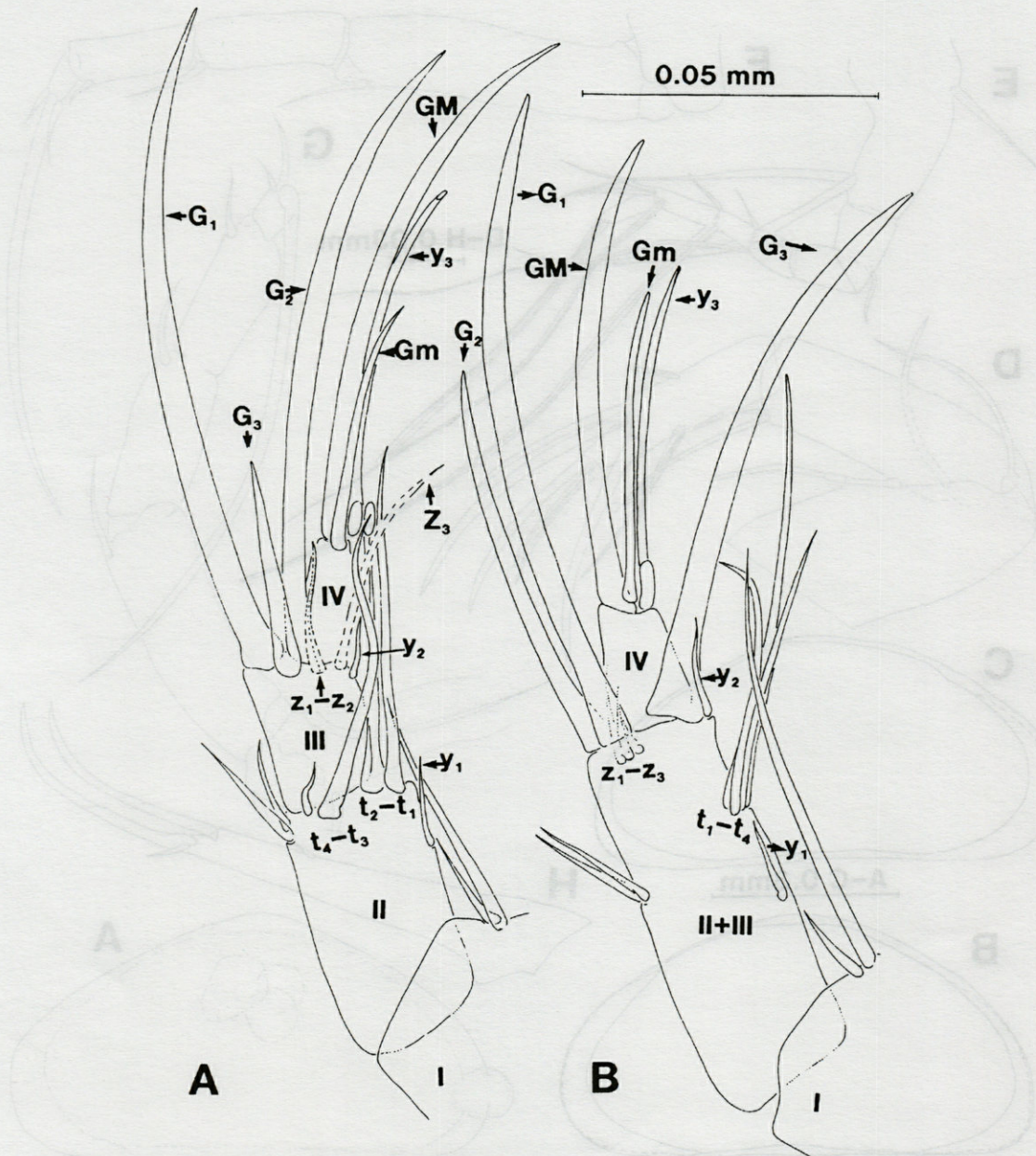


Fig. 5. – *M. lattingerae* n. sp.: A2, A – male, B – female. Abbreviations for limbs and carapace, see text.

origin and evolution of the aquatic subterranean Crustacea.

### 3.2. Material (leg. C. Juberthie and R. Rouch)

Holotype – One dissected male with limbs mounted in glycerine on slide and valves kept in ethanol.

Type locality – Karstic spring located below the entrance into the cave La Clamouse near Pont du Diable (Herauld), southern France (Fig. 1). Sample was obtained filtrating the karstic water during 15 hours for drifting organisms which leave passively the subterranean system (Rouch pers. comm.).

### 3.3. Description

#### Carapace

Carapace smooth, thin. Maximal height in the middle, comprising 47.2 % of the height in the left valve and 46.9 % in the right valve, the left valve slightly higher and moderately triangular. Maximal width less than 1/3 of the carapace length. Inner calcified lamella wider in the anterior part (maximal width of the lamella – carapace length proportion = 11 % in both valves) and in lesser extent in the posterior part (the above mentioned proportion = 7.7 % for the RV and 3.3 % in the LV).

Dimensions (n = 1): Length = 0.59 mm, height = 0.28 mm.



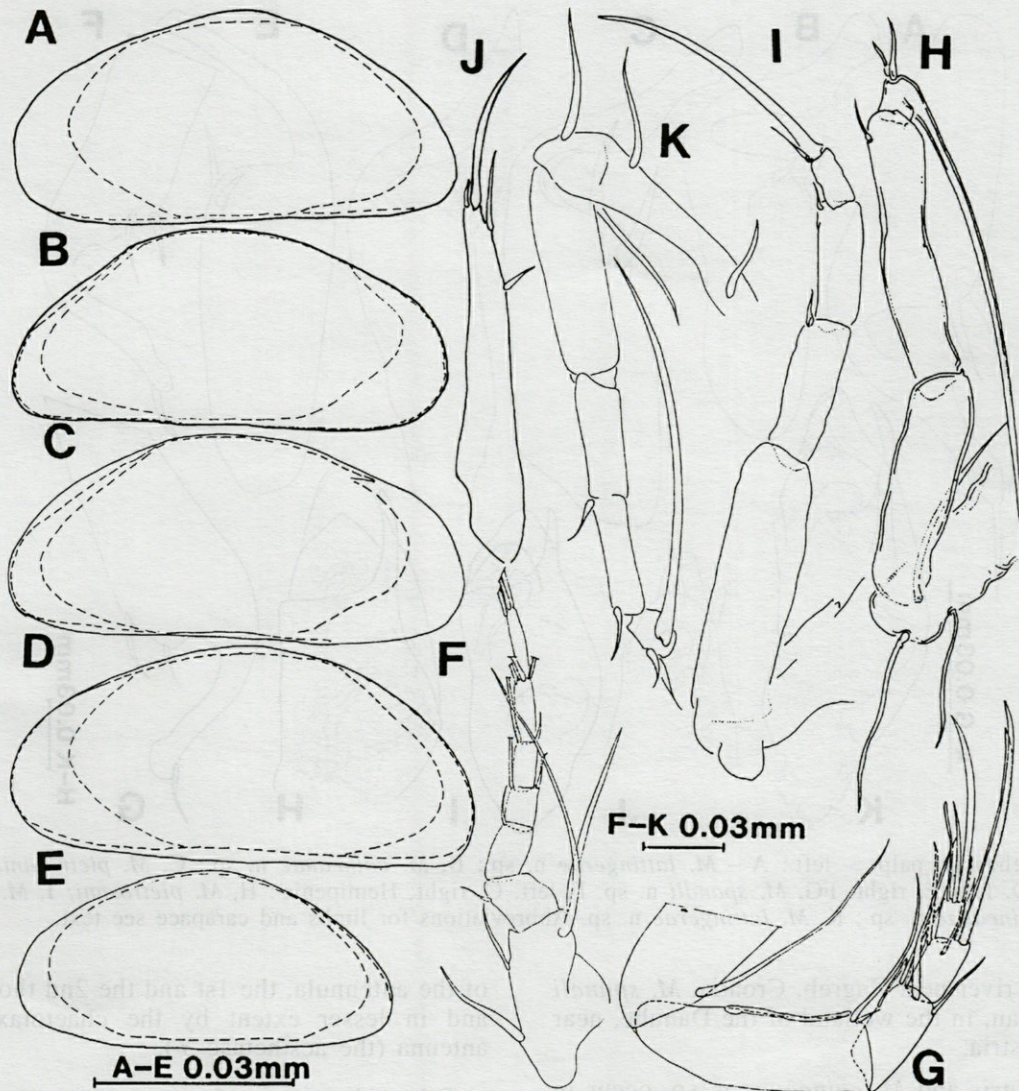


Fig. 6. – *M. spandli* n. sp. : C, D, G-J male; A, B, F female; A, LV; B, RV; C, RV; D, LV; E, juvenile, LV; F, A1; G, A2; H, T2; I, T1; J, Fu; K, *M. coineauae* n. sp., male – T2. Abbreviations for limbs and carapace, see text.

#### Antenna (Fig. 8H)

Pr : 11/Exo : 11/EI : P-Y-11-1s/EII : A-1s, P-Y1-2m (t1-2), Ex-1m (t3)-1s (t4)/EIII : D-11 (GM)-1m (Gm)-Y3.

Mean value of the ratio Y aesthetasc and interodistal margin of EI : 250 %.

#### First thoracopod (Fig. 6I)

Pr/EI/EII : A-1s/EIII : A-1s/EIV : 11-2s

#### Second thoracopod (Fig. 6H)

Pr : A-1m, P-2m/EI : P-1s/EII : P-1s/EIII : 1s/EIV : 11-2s

#### Furca

Distal claws equally long.

Additional information of male :

Prehensile palp (Fig. 7 D) : sensory organs on the basal segment shorter than in other species

described here, internal margin's protuberance on the terminal segment rounded and rather well developed.

Hemipenis : D-lobe rounded.

## C. DISCUSSION

All the species *Mixtacandona* of the group *hvarensis* are endemic, with a restricted geographical distribution (Fig. 1). *M. hvarensis* : city of Hvar on the island of Hvar in the south Adriatic sea, Croatia (Danielopol, 1969). *M. pietrosani* : villages Pietrosani and Chiselet near the Danube, south Romania (Danielopol, Cvetkov, 1979). *M. coineauae* n. sp. : karstic system La Clamouse in southern France. *M. lattingerae* n. sp. : Opatovina,



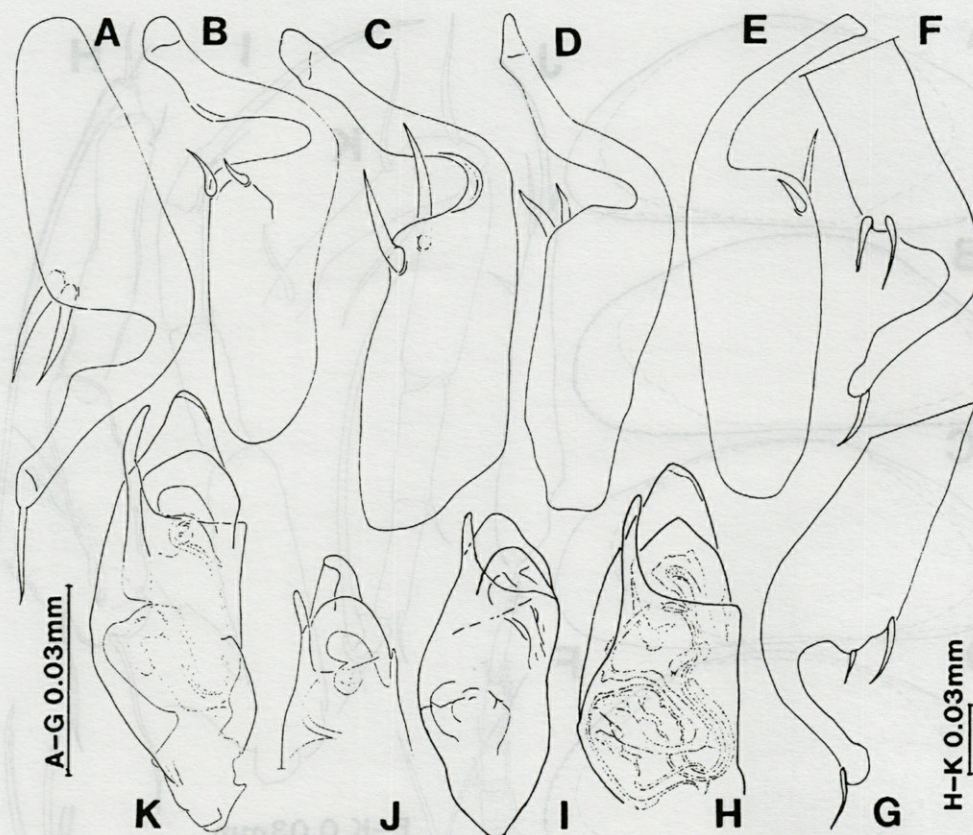


Fig. 7. – Prehensile palps – left : A – *M. lattingerae* n. sp.; B, *M. coineauae* n. sp.; C, *M. pietrosani*; D, E, *M. hvarensis*, D, left, E, right; FG, *M. spandli* n. sp. F, left, G, right; Hemipenis : H, *M. pietrosani*; I, *M. spandli* n. sp.; J, *M. coineauae* n. sp.; K, *M. lattingerae* n. sp. Abbreviations for limbs and carapace see text.

at the Sava river near Zagreb, Croatia. *M. spandli* n. sp. : Lobau, in the wetland of the Danube, near Vienna, Austria.

*M. hvarensis* and *M. coineauae* n. sp. occur in karstic habitats while *M. pietrosani*, *M. lattingerae* n. sp. and *M. spandli* n. sp. live in alluvial sediments of the large rivers (Danube, Sava). The latter three species prefer habitats with low temperature fluctuations. These species never occur in subsurface sediments of rivers e.g. the Sava or the riverbed sediments of the Danube.

Table I displays the differential morphological features of the *Mixtacandona* of the group *hvarensis*. The major morphological characters which define these species are displayed by the chaetotaxy

Table I. – Differential diagnosis of the species of the group *Mixtacandona hvarensis*. M.l. : *M. lattingerae* n. sp.; M.s. : *M. spandli* n. sp.; M.c. : *M. coineauae* n. sp.; M.p. : *M. pietrosani*; M. h. : *M. hvarensis*. Abbreviations for limbs and setae see text.

|             | M.l.  | M.s.    | M.c.  | M.p.  | M.h.  |
|-------------|-------|---------|-------|-------|-------|
| A1 (EV)     | A-2l  | A-1l    | A-1l  | A-1l  | A-1l  |
| A2 (EII)    | A-2s  | A-1s    | A-1s  | A-2s  | A-1s  |
| T1 (EI)     | 1s    | 0       | 0     | 1s    | 1s    |
| T2 (EI)     | 1s    | 0       | 0     | 1s    | 0     |
| T2 (EII)    | 1s    | 0       | 1s    | 1s    | 0     |
| Fu (Ga, Gp) | equal | unequal | equal | equal | equal |

of the antennula, the 1st and the 2nd thoracic legs and in lesser extent by the chaetotaxy of the antenna (the aesthetasc Y).

Other characters of minor importance are the shape of the hemipenis lobe “D” (Fig. 7), rounded in all the five species except *M. pietrosani* which is characterized by an acuminate D-lobe, and the distal fingers of the male clasping organs (prehensile palps) which are variously bent, with markedly larger protuberance of the internal margin of the left palp in *M. lattingerae* n. sp., *M. coineauae* n. sp. and *M. pietrosani* and less protruded in the case of *M. hvarensis* and *M. spandli* n. sp.

*M. spandli* is unique within this group through a short distal claw on the posterior side of the furca (Fig. 6J).

Within the *Mixtacandona hvarensis* group, *M. pietrosani* and *M. lattingerae* n. sp. appear the most primitive species with the largest carapace size and a complete chaetotaxy, comparable to other primitive Candoninae e.g. those of *Cryptocandona*. *M. spandli* n. sp. displays the most derived characters (see the reduced thoracopod and furcal chaetotaxy as well as the small carapace size).



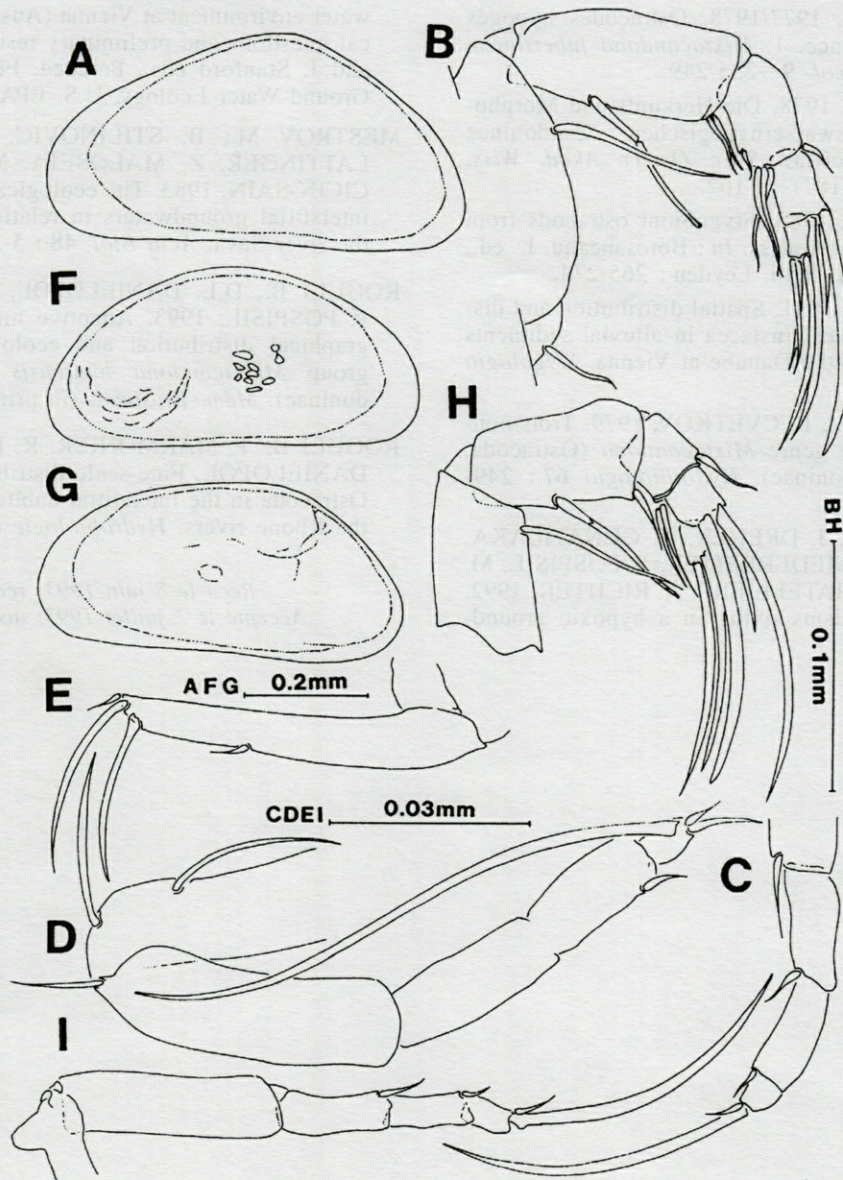


Fig. 8. - ABCE, *M. hvarensis*: A, E male; F-I *M. coineauae* n. sp., male; A, RV; B, A2; C, T1; D, T2; E, Fu; F, LV; G, RV; H, A2. Abbreviations for limbs and carapace see text.

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Fig. 8 - ABCD, M. hvarensis: A, E, male; F-M, candoninae n. sp., male; A, RV; B, AS; C, TL; D, TS; E, PL; F, LV; G, RV; H, AS. Abbreviations for limbs and cangae see text.

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## NEREIPHYLLA PUSILLA (POLYCHAETA, PHYLLODOCIDAE) REDISCOVERED AND REDESCRIBED FROM SICILY

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POLYCHÈTES  
PHYLLODOCIDAE  
NEREIPHYLLA PUSILLA  
REDESCRIPTION  
MÉDITERRANÉE

RÉSUMÉ – Redescription de *Nereiphylla pusilla* (Claparède, 1870). Un néotype est désigné parmi des spécimens récoltés sur la côte est de la Sicile. Cette espèce se distingue des autres espèces de *Nereiphylla* européennes par la combinaison de la petite taille à la maturité (3-5 mm), de la grande dimension des œufs (environ 150 µm), et de cirres dorsaux, ventraux et pygidiaux courts et gonflés. Elle est connue du nord-est de la Méditerranée seulement. *Phyllodoce nana* Saint-Joseph, 1906, décrite de Cannes, est considéré comme un synonyme plus récent. L'espèce est comparée avec d'autres espèces de *Nereiphylla*, et *N. mimica* Eibye-Jacobsen, 1992, de Belize, est considérée comme l'espèce la plus proche.

POLYCHAETA  
PHYLLODOCIDAE  
NEREIPHYLLA PUSILLA  
REDESCRIPTION  
MEDITERRANEAN

ABSTRACT – *Nereiphylla pusilla* (Claparède, 1870) is redescribed and a neotype designated from newly collected specimens from eastern Sicily. It is distinguished from other European members of the genus by the combination of small size at maturity (3-5 mm long), possession of large eggs (about 150 µm in diameter) and short swollen dorsal, ventral and pygidial cirri. The species is currently known only from the north-western Mediterranean, *Phyllodoce nana* Saint-Joseph, 1906 from Cannes being a junior synonym. Comparisons with other species of *Nereiphylla* are provided, and *N. mimica* Eibye-Jacobsen, 1992 from Belize is considered the closest related species.

### INTRODUCTION

*Anaitis pusilla* was originally described from Naples by Claparède (1870). Since then the species has rarely been reported. This is probably due, at least in part, to a lack of both type material and of subsequent descriptions. In addition, its generic affinities have been uncertain; the species being variously referred to *Phyllodoce* (in Fauvel 1923), *Paranaitis* (in Hartman 1959) and *Genetyllis* (in Campoy 1982).

Dredge samples taken during scientific investigations off eastern Sicily in May 1990 yielded numerous specimens which correspond well to Claparède's original description, and the species is redescribed below as *Nereiphylla pusilla* comb. nov.

### MATERIALS AND METHODS

Most specimens were relaxed in 7 % magnesium chloride, fixed in 4 % formaldehyde in sea-

water for a few days, rinsed in fresh water and subsequently transferred to 70 % alcohol. A few specimens (NMW.Z.1992.002.6, 9 & 11) were fixed (approx. 10 % formaldehyde in seawater) in unsorted samples without being relaxed, while several others (NMW.Z.1992.002.7-8) were relaxed using menthol. In both cases the specimens were later rinsed and preserved in alcohol as above. All drawings were prepared with the aid of a camera lucida.

The holotype of *Phyllodoce nana* Saint-Joseph, 1906, was examined in the Muséum National d'Histoire Naturelle, Paris (MNHN). For comparative purposes, type materials of other species referable to *Nereiphylla* were also examined: holotype of *Phyllodoce magnaoculata* Treadwell, 1901 (USNM 15951), syntypes of *Phyllodoce ferruginea* Moore, 1909 (USNM 17361) and *Phyllodoce fragilis* Webster, 1879 (USNM 535) from the National Museum of Natural History, Smithsonian Institution, Washington D.C.; holotype of *Prochaetoparia gruai* Rullier, 1973 from the Université Catholique, Angers (UCA); syntypes of *Genetyllis lutea* Malmgren, 1865 (BMNH 1865.9.23.5 and SMNH 2416) from the Natural History Museum, London, and the Swedish Mu-



seum of Natural History, Stockholm. Non-type material of other *Nereiphylla* species was also examined: *Carobia castanea* Marenzeller, 1879 (NMW.Z.1986.079. 134-141; 13 specimens from Hong Kong) from the collections of the National Museum of Wales, and *Nereiphylla paretii* Blainville, 1828 (about 20 specimens from around the British Isles and the western Mediterranean) and *Phyllodoce* (*Carobia*) *rubiginosa* Saint-Joseph, 1888 (about 50 specimens from western Ireland, English Channel, west-coasts of France and Spain, Italy, Yugoslavia and Greece) from a number of polychaete collections (including those of the MNHN, SMNH & NMW).

## SYSTEMATICS

### *Nereiphylla pusilla* (Claparède, 1870) (Figs. 1-3)

*Anaitis pusilla* Claparède, 1870 : 460-461, pl. IX, fig. 6.

*Phyllodoce pusilla*. Fauvel, 1923 : 157, fig. 56f.

?*Phyllodoce nana* Saint-Joseph, 1906 : 223-224, pl. V, figs. 96-98. Fauvel, 1923 : 156, fig. 55h-i.

*Genetyllis* cf. *pusilla*. Campoy, 1982 : 144-146.

Non *Phyllodoce pusilla*. Cazaux, 1965 : 1-15, pl. 2-5 [= *Nereiphylla rubiginosa* (Saint-Joseph, 1888)]

### Material examined

France : Cannes, holotype of *Phyllodoce nana* (MNHN). ITALY, eastern Sicily : sample T1, off Capo Mulini (near Aci Trezza), 37°34.35'N 15°11.65'E, large rock blocks, 30-40 m, 8 specimens (SMNH), 12.5.90; sample T14, off Capo Mulini (near Aci Trezza), 37°34.45'N 15°11.8'E, base of rock face, 40 m, 2 specimens (NMW.Z.1992.002.6), 17.5.90; sample T19/20, off Capo Mulini (near Aci Trezza), 37°34.45'N 15°11.8'E, large rock blocks, 35 m, 1 specimen (SMNH), 1 specimen (NMW.Z.1992.002.7), 18.5.90; sample T33, off Capo Campolato (NE of Brucoli), 1-3 m, neotype (NMW.Z.1991.002.5), 2 specimens (SMNH), 22.5.90; sample T36/40, off Capo Campolato (NE of Brucoli), 37°17.1'N 15°15.55'E, rock, 24 m, 1 specimens (NMW.Z.1992.002.8), 1 specimen (SMNH), 23.5.90; sample T46/49, off Valtur (NW of Brucoli), 37°17'N 15°11'E, boulders/muddy sand/sea-grasses, 17-24 m, 19 specimens (SMNH), 3 specimens (NMW.Z.1992.002.9-10), 25.5.90; east of Cozzo dei Turchi, 37°17'N 15°10.1'E, algae/coarse sand, 2-4 m, 4 specimens (NMW.Z.1992.002.11), 29.5.90.

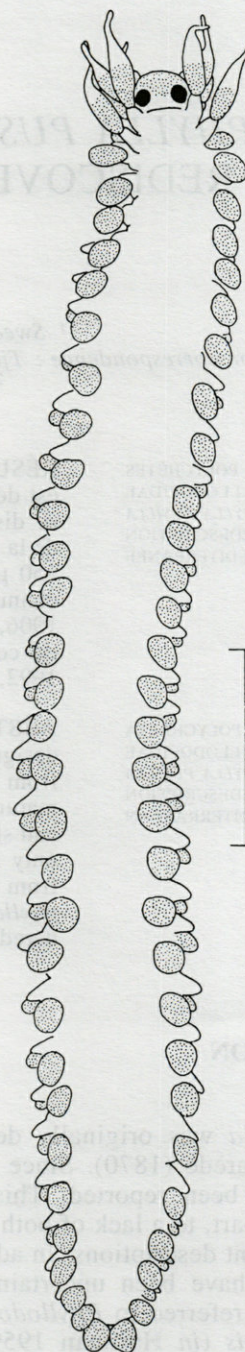


Fig. 1. – *Nereiphylla pusilla*. Neotype, dorsal view of entire animal. Scale line 0.5 mm.

### Description

Prostomium anteriorly rounded (Figs. 1, 2A). Paired antennae all basally swollen, widest subproximally, with distinct drawn-out tips (Fig. 2B). Ventral pair slightly smaller than dorsal, ventrally displaced and not usually visible from above. Eyes very large, rounded. Nuchal organs not observed. Proboscis long and thin, with diffusely distributed blunt conical papillae (Fig. 2C). Distal part not observed. Segment 1 dorsally fused with segment



2 (i.e. distinct delineation absent). All tentacular cirri similar; ampulliform, proximally swollen with distinct drawn-out tip. Dorsal pair of segment 2 longest, reaching about segment 5 if directed posteriorly; dorsal ones of segment 3 slightly shorter. Ventral pair of segment 2 and those of segment 1 shortest, of equal length (Fig. 2A). Several setae evident on segment 2, arising from small setigerous lobe fused to each cirrophore (Fig. 2B). Dorsal cirri of median segments swollen, but slightly flattened, semi-globular to ovoid, almost as long as wide (Fig. 2D). Setigerous lobes small, symmetrical. Setae about 10-12 per parapodium, all compound. Rostrum of setal shaft truncate with large number of acuminate teeth. Ventral cirri swollen, slightly longer than wide, obliquely oriented. Pygidial cirri swollen, almost

as wide as long, ovoid (Fig. 2E). Median pygidial papilla present. No ciliation observed.

#### Colour

Eyes of live specimens red, body bright yellow with darker yellow prostomium and cirri. Tentacular cirri only with proximal swollen part pigmented. Eggs of mature females dull pink. Acicula distinctly black. Preserved specimens with body light yellow and orange to dark brown cirri. Eyes brown.

#### Reproduction

Mature specimens found on eastern Sicily in May. Diameter of eggs about 150  $\mu\text{m}$ , possibly

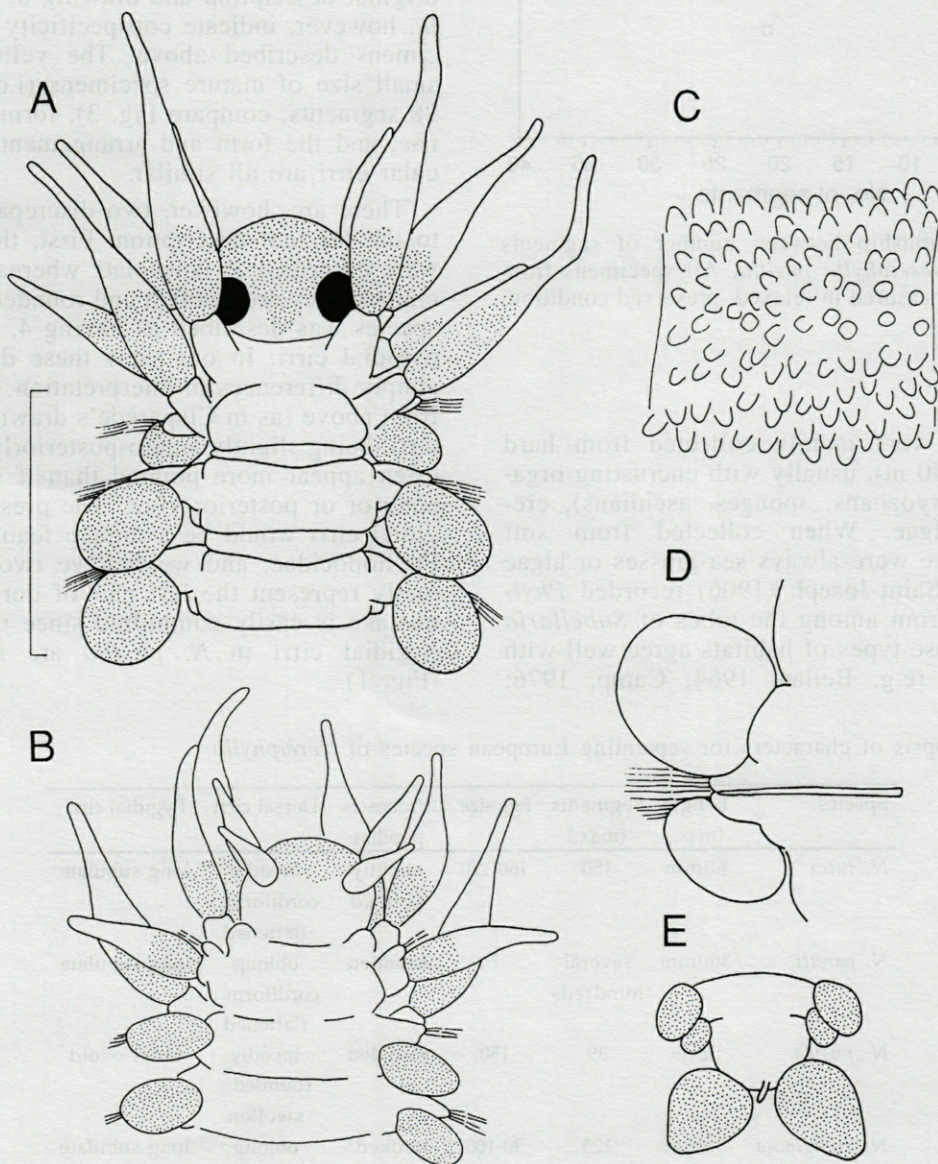


Fig. 2. - *Nereiphylla pusilla*. A, C, D & E specimens from Brucoli, Sicily, B from Acitrezza, Sicily. Scale line 0.25 mm. A. Anterior end, dorsal view. B. Anterior end, ventral view. C. Proboscis, subproximal part, dorsal view. D. Median parapodium, anterior view. E. Posterior end, ventral view.



indicating a lecithotrophic larval development. In the studied material mature specimens occurred from a size of about 3 mm, corresponding to about 30 segments.

### Measurements

No specimens found with more than 39 segments and 5.0 mm long (Fig. 3).

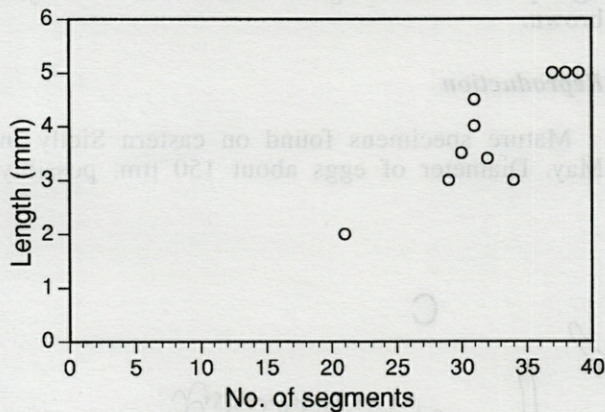


Fig. 3. — Relationship between number of segments and length in *Nereiphylla pusilla*. All specimens from eastern Sicily, measured in relaxed, preserved condition.

### Habitat

Specimens were mainly collected from hard substrates (1-40 m), usually with encrusting organisms (e.g. bryozoans, sponges, ascidians), crevices and algae. When collected from soft sediments there were always sea-grasses or algae present also. Saint-Joseph (1906) recorded *Phyllodoce nana* from among the tubes of *Sabellaria alveolata*. These types of habitats agree well with other records (e.g. Bellan, 1964; Camp, 1976;

Campoy, 1982; Giangrande, 1986, 1988; Sardá-Borroy, 1987; Somaschini, 1988).

### Distribution

Presently known only from the Mediterranean coast of France and the east coast of Sicily.

### Remarks

As far as we are aware, there is no extant type material. Claparède strongly believed that the examination of live specimens was paramount and regarded the study of preserved museum material as a useless exercise (Claparède, 1868: 318). His original description and drawing of *Anaitis pusilla*, however, indicate conspecificity with the specimens described above. The yellowish colour, small size of mature specimens (i.e. 2.8 mm for 28 segments; compare Fig. 3), form of the antennae, and the form and arrangement of the tentacular cirri are all similar.

There are, however, two discrepancies relative to the original description. First, the dorsal cirri were described as lanceolate whereas, in our specimens, they are swollen and rounded. Second, the species was described as having 4, rather than 2, pygidial cirri. In our view these differences are simply differences in interpretation. When viewed from above (as in Claparède's drawing) the dorsal cirri, being slightly antero-posteriorly compressed, often appear more pointed than if seen in direct anterior or posterior view. The presence of 4 pygidial cirri would be a unique feature within the Phyllodocidae, and we believe two of these actually represent the last pair of dorsal cirri. This mistake is easily committed since the dorsal and pygidial cirri in *N. pusilla* are rather similar (Fig. 1).

Table I. — Synopsis of characters for separating European species of *Nereiphylla*.

| Species              | Length (max.) | Segments (max.)  | Egg size | Proboscis papillae | Dorsal cirri                  | Pygidial cirri |
|----------------------|---------------|------------------|----------|--------------------|-------------------------------|----------------|
| <i>N. lutea</i>      | 60mm          | 150              | 160-170  | slightly pointed   | broadly cordiform ; flattened | long subulate  |
| <i>N. paretii</i>    | 300mm         | several hundreds | ?        | rounded            | oblong cordiform ; flattened  | long subulate  |
| <i>N. pusilla</i>    | 5mm           | 39               | 150      | rounded            | broadly rounded ; swollen     | short ovoid    |
| <i>N. rubiginosa</i> | 35mm          | 125              | 90-100   | hooked*            | oblong cordiform ; flattened  | long subulate  |

\*hooked papillae occurring on proximal part of proboscis



Brucoli on the east coast of Sicily is not too far from Claparède's original locality of Naples and, since the species is common in the area, we find this an appropriate place from which to select a neotype. The holotype of *Phyllodoce nana* Saint-Joseph, 1906, is in poor condition, but examination of the specimen and the original description suggests that it is a junior synonym of *Nereiphylla pusilla*. Our slight doubt as to this synonymy is due to Saint-Joseph's description of enormous (400 µm) eggs in an animal 480 µm wide including cirri! Such a large egg size differs markedly from those of all the other European species of *Nereiphylla* (Table 1), as well as from other phyllococids.

Taking this synonymy into account, *N. pusilla* has been recorded from several widespread localities: Italy (Claparède, 1870; Cantone, 1971; Giangrande, 1986, 1988; Somaschini, 1988), south of France (Saint-Joseph, 1906; Bellan, 1964), northeast Spain (Camp, 1976; Campoy, 1982), Gibraltar Strait (Sardá-Borroy, 1987), Atlantic coast of France (Cazaux, 1965), Canary Islands (Nuñez *et al.*, 1991), Senegal (Rullier, 1964) and Ivory Coast (Intes & Le Lœuff, 1977). The descriptions provided by Saint-Joseph, Claparède, Campoy, Rullier and Nuñez *et al.* indicate a distribution throughout the western Mediterranean and along the northwest coast of Africa. The description of *Phyllodoce pusilla* from Arcachon (Cazaux, 1965), however, clearly relates to *N. rubiginosa*.

## DISCUSSION

Following the proposed phylogeny of Pleijel (1991), the possession of the two shared derived characters (sub-proximally swollen frontal antennae and obliquely oriented ventral cirri) indicate membership within the subfamily Notophyllinae, and the absence of median antenna membership within the genus *Nereiphylla*.

Three other species of *Nereiphylla* occur in European waters: *N. lutea* (Malmgren, 1865), *N. paretii* Blainville, 1828 and *N. rubiginosa* (Saint-Joseph, 1888). Descriptions of these are provided in Pleijel and Dales (1991) and Pleijel (1993), and a summary of all four species is given in Table 1. *Nereiphylla pusilla* is readily distinguished from these species by its small size and possession of swollen (almost globular) dorsal, ventral and pygidial cirri. As to their distribution, *N. paretii* and *N. rubiginosa* partly occur sympatrically with *N. pusilla* with a distribution from the northern Mediterranean up to the British Isles, whereas *N. lutea* has a more northern distribution, ranging from the Irish Sea to northern Norway.

An additional European species that probably belongs to *Nereiphylla* is *Phyllodoce lugens* Eh-

lers, 1864. This species, described from the northern Adriatic, is known only from the original description. According to this, it is similar to *N. pusilla* in its small size at maturity and in the size of its eggs. It differs in being dark olivebrown to green, in having green eggs, and in having pointed flattened pygidial cirri. We have been unable to locate any type material and, for the present, consider this a *nomen dubium*.

Only five non-European phyllococid species can be referred, with any degree of confidence, to *Nereiphylla* (checklist in Pleijel 1991): *N. castanea* (Marenzeller, 1879), *N. ferruginea* (Moore, 1909), *N. fragilis* (Webster, 1879), *N. gruai* (Rullier, 1973) and *N. mimica* Eibye-Jacobsen, 1992. An additional species, *Phyllodoce magnaoculata* Treadwell, 1901, may belong in the genus but the condition of the holotype does not permit any certain assignment. Of the aforementioned species, only *N. mimica* from Belize approaches *N. pusilla* in body size and form of the dorsal, ventral and pygidial cirri. It differs in having abruptly tapered tentacular cirri, the widths of which are almost uniform along their entire lengths, and in the pigmentation pattern of both live and preserved material. *Nereiphylla castanea*, *N. ferruginea* and *N. fragilis* all differ in their much greater size (40–50 mm maximum), their pigmentation, and in having large flattened foliaceous and cordiform dorsal cirri.

In its small size and thickened dorsal cirri, *Nereiphylla gruai* from the Kerguelen Islands appears superficially to resemble *N. pusilla*. Examination of the slide-mounted holotype proved inconclusive. The specimen was not sexually mature and its general aspect was very suggestive of it being a juvenile specimen of a larger species. In this respect we would like to advise caution when identifying small specimens of any *Nereiphylla* species. The thickness of the dorsal and ventral cirri is, to a certain degree, size-dependant. For example, the dorsal cirri of small specimens of *N. rubiginosa* can be somewhat swollen, but they become more flattened as the animals grow larger. This character should therefore not be used in isolation.

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## SOME ASPECTS OF THE BIOLOGY OF *BATHYPOLYPUS SPONSALIS* (MOLLUSCA, CEPHALOPODA) IN THE NORTH AEGEAN SEA (EASTERN MEDITERRANEAN SEA)

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CEPHALOPODA  
NEW RECORDS  
BIOLOGY  
AEGEAN SEA  
MEDITERRANEAN SEA

**ABSTRACT** – The presence of the Cephalopod *Bathypolypus sponsalis* (P. & H. Fischer, 1892) in the North Aegean Sea (Greece) is recorded. Specimens of this species were found during four trawl surveys carried out from 1990 to 1991 in the Aegean Sea. Some biological aspects of the species are reported.

CÉPHALOPODES  
MER ÉGÉE  
MÉDITERRANÉE  
BIOLOGIE

**RÉSUMÉ** – La présence du Céphalopode *Bathypolypus sponsalis* (P. & H. Fischer, 1892) dans la Mer Egée septentrionale (Grèce) est signalée pour la première fois. De nombreux exemplaires (94) de cette espèce ont été capturés pendant quatre croisières effectuées de 1990 à 1991 dans la Mer Egée. Quelques aspects de la biologie de cette espèce ont été analysés.

### INTRODUCTION

Although the presence of *Bathypolypus sponsalis* (P. & H. Fischer, 1892) in the Mediterranean Sea was first recorded in 1954 (Wirz, 1954), there are some areas, mostly in the eastern basin, in which the species had not been previously recorded and its presence was therefore considered uncertain (Mangold & Boletzky, 1987).

Recent research, aiming at the assessment of the demersal resources of the Aegean Sea, has led to the finding of some rare species including *B. sponsalis*.

This report gives some information on the biology of this species.

### MATERIALS AND METHODS

The following data were collected during four trawl surveys carried out, respectively, in August-September 1990, November-December 1990, February-March 1991 and June 1991 within the EEC financed programme "Investigation of the abundance and distribution of demersal stocks of primary importance to the Greek fishery in the North Aegean Sea (Greece)", with which the Institute of

Zoology and Comparative Anatomy of the University of Bari (Italy) and the National Center for Marine Research of Athens (Greece) cooperate.

The area investigated, shown in Fig.1, covers two zones of the North Aegean Sea. One lies near the Sporades Islands and has an area of 1 800 km<sup>2</sup>; the other, in the eastern area south of the island of Limnos, has a surface of about 6 000 km<sup>2</sup>.

A professional trawler of 115 tons, equipped with a nylon net with 16 mm meshes to the cod-end, was hired.

The sampling was random-stratified and the area investigated was divided into three depth strata: 0-100 m, 100-200 m, 200-500 m. The minimum and maximum depths trawled were 60 and 440 m respectively in the western area and 32 and 437 m in the eastern one.

The hauls, 11 in the western area and 21 in the eastern one, lasted each about 1 hour.

The specimens of *B. sponsalis* found during the surveys were kept aboard in 5 % formol and their dorsal mantle length (DML) in mm and weight (in grams) were measured. For the specimens for which it was technically possible, sex and stage of maturity of the gonads (Mangold-Wirz, 1963) were assessed and the eggs or spermatophores present in mature individuals were counted.



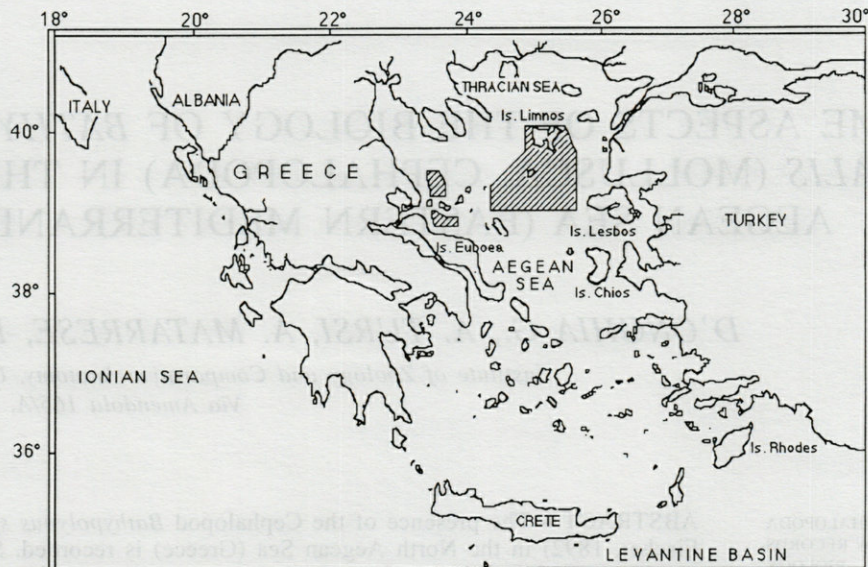


Fig. 1. – Areas investigated during four trawl surveys carried out in the North Aegean Sea during 1990-91.

## RESULTS

The 94 individuals of both sexes caught during the trawl surveys are listed in table I with the geographical position, depth of the station, body size of the individuals and stage of maturity of their gonads.

*Bathypolypus sponsalis* was found in both areas on muddy bottoms starting from 300 m to the maximum depth investigated (440 m). In the catches, together with this octopod, the species *Sepietta oweniana*, *Rossia macrosoma*, *Octopus salutii* and, in deeper stations, *Neorossia caroli*, *Todarodes sagittatus* and *Pteroctopus tetracirrhus* were frequently present. Sometimes *Sepia orbignyana*, *Illex coindetii* and *Eledone cirrhosa*, which have a wide bathymetrical distribution, were also found together with *B. sponsalis*.

The minimum and maximum dorsal mantle lengths were 20 and 50 mm for females and 18 and 40 mm for males, respectively. The number of females and males found in each trawl survey and their average sizes are given in table II. Because in the first two surveys only a few specimens were fished, the comparison between the mean sizes of the two sexes is reliable only with regard to the last two surveys. Evidence arises from the comparison that females have a greater mean size than males ( $t = 4.17$ , d.f. = 39,  $p < 0.001$  in February;  $t = 2.28$ , d.f. = 35,  $p = 0.029$  in June). The specimens fished in the Aegean Sea had rather stumpy mantles, nearly as wide as long, comparable to the type of the Balearic Islands (Wirz, 1955) which are also found in the Tuscan archipelago (Lumare, 1970).

In mature females, fished during the surveys carried out in February-March and in June, up to

60 pear-shaped eggs were found, ranging from 6 to 13 mm in length. Sometimes smooth eggs were found together with eggs with longitudinal striping. In sexually mature male individuals from 4 to 8 spermatophores were counted, their maximum length was 22 mm, i. e. over 50 % of the dorsal mantle length.

The smallest mature female individual had a size of 30 mm and the smallest male a size of 27 mm. The hectocotylus arm was distinct, with developed *ligula* and *calamus*, even in immature individuals, and its length was 60 % of that of the opposite arm.

The size/weight ratio for *B. sponsalis* was calculated pooling both sexes, because of the small number of individuals fished and also to be able to compare data with those recently reported by some authors for individuals fished in the Tyrrhenian Sea and in the Channel of Sicily (Jereb *et al.*, 1989). The ratio was:  $W = 0.005201 \cdot L^{2.37}$ , from which the allometric nature of the growth of *B. sponsalis* can be recognized. The size/weight ratio calculated separately for each sex, although it must be considered as scarcely reliable due to the small number of individuals for which it was established, stresses the tendency that, females tend to weigh more than males with equal mantle length.

## DISCUSSION AND CONCLUSIONS

The finding of *Bathypolypus sponsalis* in the North Aegean Sea broadens its geographical distribution in the Mediterranean Sea. Within this distribution a geographical void exists in the Ion-



Table I. - List of specimens of *Bathypolypus sponsalis* found during four trawl surveys carried out in the North Aegean Sea from 1990 to 1991, with indication of fishing zone, depth, individual size (in mm DML) and reproductive stage in both females and males. I = immature; m = maturing; M = mature.

| Survey        | Latitud./Longitud. | Depth (m) | Females |             | Males   |             |
|---------------|--------------------|-----------|---------|-------------|---------|-------------|
|               |                    |           | DML(mm) | Repr. Stage | DML(mm) | Repr. Stage |
| Aug./Sept.'90 | 39°23'/23°18'      | 385       | 34      | m           | 31      | M           |
|               |                    |           | 39      | M           | 32      |             |
| Nov./Dec.'90  | 39°13'/24°37'      | 437       | 35      |             | 35      | I           |
|               |                    |           | 40      |             | 30      |             |
|               |                    |           | 30      |             | 32      |             |
|               |                    |           | 25      |             | 36      |             |
|               |                    |           | 25      |             | 30      |             |
|               |                    |           | 29      |             |         |             |
| Feb./Mar.'91  | 39°23'/23°18'      | 385       | 20      |             |         |             |
|               |                    |           | 35      | M           | 35      | M           |
|               |                    |           | 38      | M           | 40      | M           |
|               |                    |           | 45      | M           | 38      | M           |
|               |                    |           | 40      | M           | 35      | M           |
|               |                    |           | 40      | M           | 35      | M           |
|               |                    |           | 25      | I           | 30      | M           |
|               |                    |           |         |             | 30      | M           |
|               |                    |           |         |             | 30      | m           |
|               |                    |           |         |             | 25      | m           |
|               |                    |           |         |             | 25      | I           |
|               |                    |           |         |             |         |             |
|               |                    |           |         |             |         |             |
| 39°20'/25°08' | 300                | 50        |         |             |         |             |
|               |                    | 42        |         |             |         |             |
|               |                    | 35        | m       |             |         |             |
|               |                    | 40        | M       | 35          | M       |             |
|               |                    | 30        | M       | 32          | M       |             |
|               |                    | 35        | M       | 35          | M       |             |
|               |                    | 32        | M       | 22          | m       |             |
|               |                    | 42        | M       | 22          | m       |             |
|               |                    | 37        | M       | 27          | M       |             |
|               |                    | 33        | m       | 22          | m       |             |
|               |                    | 32        | M       | 28          | m       |             |
|               |                    | 30        | m       | 18          | m       |             |
|               |                    |           |         | 28          | M       |             |
|               |                    | 22        | m       |             |         |             |
|               |                    | 25        | m       |             |         |             |
|               |                    | 23        | m       |             |         |             |
| June '91      | 39°17'/23°26'      | 440       | 37      | m           | 34      | M           |
|               |                    |           | 45      | M           | 32      | M           |
|               |                    |           | 32      | m           | 36      | M           |
|               |                    |           | 33      | m           | 31      | m           |
|               |                    |           | 35      | M           | 25      | m           |
|               |                    |           | 30      | m           | 25      | m           |
|               |                    |           | 28      | m           | 28      | m           |
|               |                    |           | 36      | m           | 28      | m           |
|               |                    |           | 28      | m           | 23      | m           |
|               |                    |           | 42      | M           | 24      | m           |
|               |                    |           | 38      | M           | 35      | M           |
|               |                    |           | 30      | m           | 35      | M           |
|               |                    |           | 30      | m           | 36      | M           |
| 28            | m                  | 32        | M       |             |         |             |
|               |                    | 31        | M       |             |         |             |
|               |                    | 31        | M       |             |         |             |
|               |                    | 29        | m       |             |         |             |
|               |                    | 23        | m       |             |         |             |
|               |                    | 35        | M       |             |         |             |
|               |                    | 25        | m       |             |         |             |
|               |                    | 27        | m       |             |         |             |
| 39°13'/24°37' | 437                | 38        |         | 38          | M       |             |
|               |                    |           |         | 22          | m       |             |

ian Sea in which the species has not yet been found even after nine experimental trawl surveys carried out with the same sampling techniques as used in the Aegean Sea (Tursi and D'Onghia, 1992). The reasons for the absence of *B. sponsalis* from the Ionian Sea, while it is present in two neighbour areas, namely the Channel of Sicily and the Aegean Sea, are still unknown. In the Aegean Sea in particular, the water temperature at depths greater than 200 m ranges over the seasons between 13°C and 14°C and its salinity is nearly always around 38.7 ‰ reaching, in some stations, the maximum value of 39.0 ‰. Such chemical-physical values, being only slightly different from those found in the western Mediterranean Sea

Table II. - Number of individuals of *Bathypolypus sponsalis*, with average size (DML) and standard deviation, found during four trawl surveys carried out in the North Aegean Sea from 1990 to 1991.

|          | Aug.-Sept. '90 | Nov.-Dec.'90 | Feb.-March '91 | June '91 |
|----------|----------------|--------------|----------------|----------|
| Females  | 2              | 7            | 18             | 14       |
| DML (mm) | 36.5±3.5       | 28.7±6.4     | 36.7±6.1       | 33.7±5.4 |
| Males    | 3              | 4            | 23             | 23       |
| DML (mm) | 32.7±2.1       | 32.0±2.8     | 28.8±6.0       | 29.8±4.9 |

(Wirz, 1955), should not ban any species of cephalopod from the Aegean Sea. Moreover, although only a small number of individuals of *B. sponsalis* have been found, its presence at greater depths than those investigated, should not be excluded. Its bathymetrical distribution does not seem to be related to sex, as far as our data suggest.

The bathymetrical distribution of *B. sponsalis* in the North Aegean Sea is also limited to the bathyal zone; yet this species, rather than being bathy-benthic as reported by Mangold-Wirz (1973), seems to be distributed on epi- and meso-bathyal bottoms, in accordance with the findings of Torchio (1968), Perez-Gandaras and Guerra (1978) and Jereb *et al.* (1989). Furthermore, this cephalopod is rather uncommon in the environment in which it lives, as are *Neorossia caroli* and other bathyal species living in the investigated area (D'Onghia *et al.*, in press). *B. sponsalis* was rather uncommon in the demersal catches carried out in the Italian seas (AA. VV., 1988), possibly due to the fact that a trawl net, if not suitably equipped, might not be the best method to fish small cephalopods.

Females are generally larger than males. The mean lengths observed on the individuals of the Aegean Sea are, however, inferior to those reported by the aforementioned authors. Such smaller dimensions might be caused by contraction in formol that, according to Nixon (1971), can lead, in *Octopus vulgaris*, to a reduction of the mantle length by about 26 % compared to that of fresh specimens. Jereb *et al.* (1989) assert that in both specimens of *B. sponsalis* preserved in alcohol and in those preserved at -20°C, the weight reduction compared to that of fresh specimens is approximately 40 %.

The size/weight ratio reported for *B. sponsalis* in the Aegean Sea shows a greater allometry ( $b = 2.37$ ) compared to that of the specimens fished in the Tyrrhenian Sea ( $b = 2.49$ ) and in the Channel of Sicily ( $b = 2.79$ ) (Jereb *et al.*, 1989).

The reproduction of this cephalopod in the North Aegean Sea takes place in late winter and in spring. The small number of individuals found in August-September and November-December does not however allow us to define exactly the length of the reproduction period. A good correspondence with the data reported by Wirz (1954; 1955), Mangold-Wirz (1963) and Perez-Gandaras and Guerra (1978) was noted for the number and



dimensions of eggs and spermatophores of *B. sponsalis* found in the North Aegean Sea.

The low number of eggs produced by mature females, which can be as low as 25 in *Octopus joubini* (Boyle, 1990), as well as their large dimensions can be considered as reflecting a reproductive strategy also adopted by many other species of cephalopods (Caddy, 1983). Often these species spawn more eggs than those present at the onset of egg-laying (Boletzky, 1986). Large eggs, rich in yolk, together with parental care of the eggs themselves, ensure higher larval survival as compared to that of other marine organisms having a higher fertility. Moreover, many species of the family Octopodidae, to which *B. sponsalis* belongs, reduce aggregation during the reproductive stage and females show solitary behaviour during to the preparation of the den (Hatanaka, 1979). Obviously this behaviour results in the species being less vulnerable during the reproductive period to predators and fishing activities. Considering the territorial nature of octopus, *B. sponsalis* may create its den in holes and pits it digs in the mud, as is known for other octopus species from experiments carried out in the laboratory, for example *Octopus defilippi* (Hanlon *et al.*, 1985). Finally, it can not be excluded that *B. sponsalis* might use structures of a different nature already existing on the bottom, including those of anthropic origin, in order to build its den.

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## POPULATION DYNAMICS AND SECONDARY PRODUCTION OF THE SPIONID POLYCHAETE *PRIONOSPIO CASPERSI* IN FRONT OF THE PO RIVER DELTA

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POLYCHAETES  
DYNAMIQUE DE POPULATIONS  
PRODUCTION SECONDAIRE  
DELTA DU PO

**RÉSUMÉ** – Dynamique de population et production secondaire du Spionidé *Prionospio caspersi* Laubier, 1962 face au delta du Pô. Une population de *Prionospio caspersi* a été échantillonnée pendant un cycle annuel, par carotages dans les fonds meubles infralittoraux face au delta du Pô. L'abondance, la biomasse et la microdistribution ont été mesurées, ainsi que quelques paramètres du milieu. L'abondance maximale (16.094 individus m<sup>-2</sup>) a été enregistrée en septembre; elle a été suivie par une chute très rapide au mois d'octobre. L'analyse des histogrammes de distribution des tailles a été utilisée pour l'estimation de la production secondaire (somatique) par deux méthodes différentes. La première (méthode des accroissements de poids) donne une estimation de 2,53 g m<sup>-2</sup> an<sup>-1</sup> (poids sec sans cendres) avec un rapport P/B de 6,02. La deuxième (méthode de la cohorte moyenne) donne une valeur de 3,28 g m<sup>-2</sup> an<sup>-1</sup> avec un P/B de 7,81. Ces résultats sont discutés par rapport aux données de l'année précédente et les réductions d'abondance, de biomasse et de production sont mises en relation avec la baisse d'oxygène dans les eaux proches du fond en septembre.

POLYCHAETES  
POPULATION DYNAMICS  
SECONDARY PRODUCTION  
PO RIVER DELTA

**ABSTRACT** – The population of the Spionid Polychaete *Prionospio caspersi* Laubier, 1962 has been studied by means of core samplings in the sandy bottoms off the Po river delta, during an annual cycle. Numerical density, biomass and spatial dispersion have been assessed, together with physical-chemical parameters. The maximum numerical abundance (16,094 ind. m<sup>-2</sup>) was reached in September, followed by a sudden decrease in October. The analysis of size-frequency distributions has been used for the estimate of secondary production (somatic growth) with two different methods. The former (weight increment method) gives an estimate of 2.53 g m<sup>-2</sup> year<sup>-1</sup> ash free dry weight, with a production/biomass ratio of 6.02. The second (average cohort method) gives 3.28 g m<sup>-2</sup> year<sup>-1</sup> and P/B 7.81. The results have been discussed in comparison with the data of the preceding year, and the reduction in abundance, biomass and production has been related to the low oxygen content in the bottom water during fall.

### INTRODUCTION

This research is part of investigations on the main macrobenthic populations in the marine area of the Po Delta (Ambrogi and Occhipinti Ambrogi 1987, 1988) to provide a more accurate description of the biological mechanisms which are at the basis of the structural modifications in the communities. This paper aims at continuing the observations on the population of the Spionid

Polychaete *Prionospio caspersi* Laubier, 1962, a species which is numerically dominant in the sandy bottoms facing the delta. An annual cycle (July 1986 – July 1987) in the same area has already been described by Ambrogi (1990).

The population dynamics of *P. caspersi* is confronted with the physical-chemical data collected during the sampling cruises, with the specific composition and with the abundance of the macrobenthic population.



## MATERIALS AND METHODS

The samples were taken in the marine area facing the Po delta, at a depth of 5 metres. A central point (Y5) was fixed (Fig. 1), corresponding with the previously described research station 5C (Ambrogi, 1990) around which, within a radius of 25 metres to the north, east, south and west, other sampling points, indicated as Y1, Y2, Y3 and Y4, were placed.

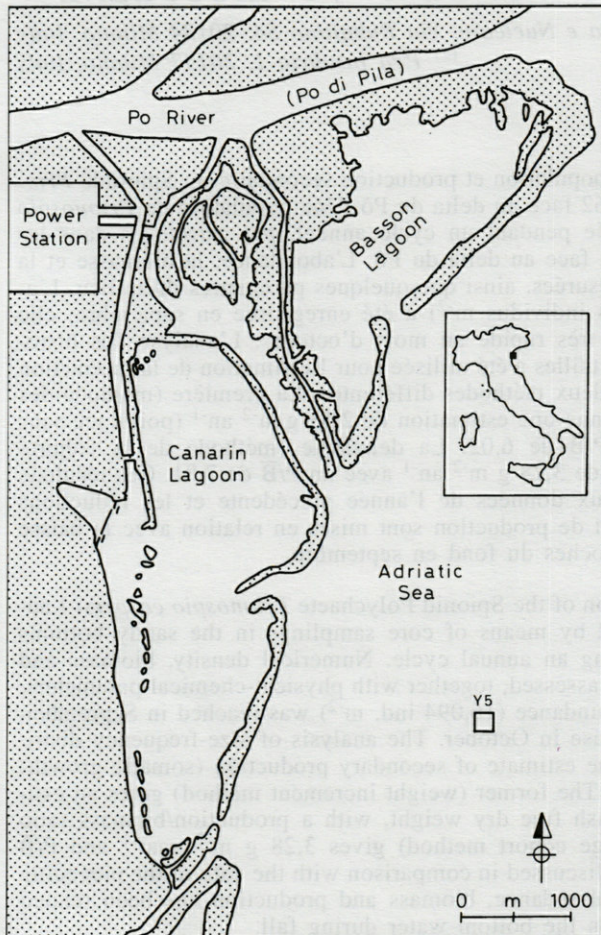


Fig. 1. - The area of the Po River Delta showing the site of the sampling station (Y5).

Samplings were performed from July 1987 to June 1988 on 8 sampling dates. The samples were taken by an underwater operator using plexiglass cores having an inner diameter of 6.63 cm. Two or three core samplings were taken at each sampling point. The first samples, taken in July 1987, involved only the central point Y5. The newly obtained samples were sieved on a screen with square mesh of 0.5 mm and were immediately fixed with previously neutralised 10 % formalin.

In the laboratory the specimens of *P. caspersi* were all isolated and counted and subsequently the area of the anterior part, from the prostomium to

the tenth setiger, was measured using the Kontron-Zeiss IBAS 1 image analysis system, according to the method described by Ambrogi *et al.* (1985) and Ambrogi (1990). Frequency bar graphs were plotted using class intervals of 0.1 mm<sup>2</sup>. For more accurate information on the spatial microdistribution of *P. caspersi* in the area being sampled, the dispersion index or mean variance ratio (Elliot, 1971) and the Morisita index (1959) were calculated.

In order to estimate the ash-free dry weight and the biomass, the procedure was as follows: only the entire individuals were divided into size classes of 0.1 mm<sup>2</sup>, dried in a stove at 105°C for an hour, weighed on an electronic ultramicrobalance and later incinerated in a muffle at 550°C for 12 hours (Crisp, 1984). The secondary production was then calculated by means of the weight increment method (Crisp, 1984). As a further estimate, for comparison purposes, the so-called Hynes or average cohort method was used (Hamilton, 1969), following the formula indicated by Cornet (1986).

$$P = \left[ \sum_{j=i}^i i (\bar{N}_j - \bar{N}_{j+1}) (\bar{w} \cdot \bar{w}_{j+1})^{0.5} + \bar{N}_i \bar{w}_i \right] \frac{12}{CPI}$$

where:  $\bar{N}_j$ , number of individuals in class  $j$ ;  $(\bar{W}_j * \bar{W}_{j+1})^{0.5}$ , geometric mean of the ash-free dry weight of two successive size classes;  $i$ , number of size classes;  $(\bar{N}_j - \bar{N}_{j+1})$ , loss of individuals when changing from one class to the next;  $P_j$ , production of size class  $j$ ; CPI, cohort production interval (life of the cohort expressed in months).

As far as the physical-chemical parameters are concerned, at the sampling point Y5, near the bottom, the temperature of the water, salinity and the concentration of dissolved oxygen (Winkler titration) were measured. Moreover the grain size composition of the sediment, the Chemical Oxygen Demand (C.O.D.) and the Total Organic Carbon (T.O.C.) were determined. The methods and the detailed data are set out by Fontana *et al.* (1989).

## RESULTS

### Physical-chemical parameters (Fig. 2)

The flow rate of the Po measured at Pontelagoscuro (some 100 km upstream) showed a trend which does not depart greatly from the monthly average calculated over a period of 70 years. The average annual flow rate was 1678 m<sup>3</sup> s<sup>-1</sup>, comparable to the long-term average of 1500 m<sup>3</sup> s<sup>-1</sup>.

The salinity at the bottom is not significantly affected by the fluctuations in flow rate, always



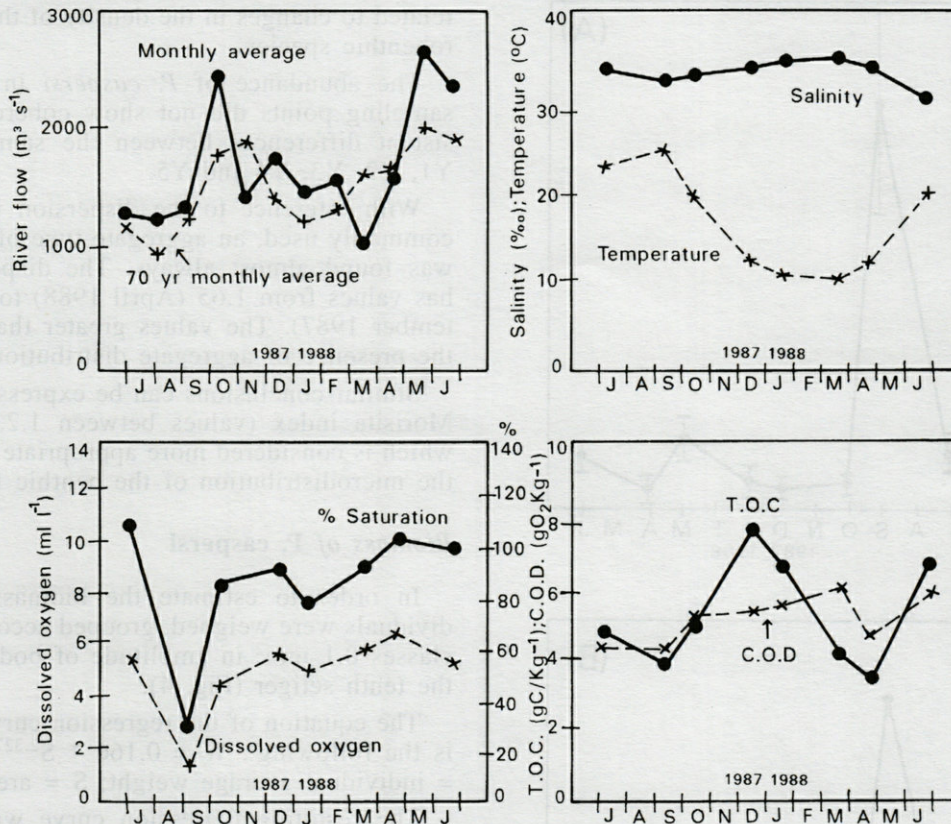


Fig. 2. – Physical-chemical parameters recorded during the sampling campaigns. The monthly average flow rate is recorded at Pontelagoscuro (Ferrara), courtesy of Ufficio Idrografico del Po, Parma. Temperature, salinity and oxygen are measured in the water layer immediately over the bottom. T.O.C. and C.O.D. are measured on sediment samples.

remaining above 31 ‰ (min. 31.1 max 36 ‰). The thermal cycle shows a maximum in the September sample (25°C) and winter temperatures of between 10 and 12°C. Severe winter temperatures (as low as 5°C) were not recorded as on previous occasions. The dissolved oxygen is characterised by a sharp drop in September (1.3 ml l<sup>-1</sup> and 27 % saturation) which witnesses the onset of an acute dystrophic crisis at the end of the summer. Data on the sediments demonstrated that the sandy fraction is prevalent (average of the fraction 0.074 mm = 93 %). The median diameter of the grains is between 0.125 and 0.150 mm. The chemical properties of the sediments confirm a certain stability of the C.O.D. at around values of 4 g O<sub>2</sub> kg<sup>-1</sup> of dry sediment as in the previous year. On the contrary, the fluctuations in T.O.C. are somewhat broad. The winter months, December and January, record the maximum values of 7.8 and 6.8 g C kg<sup>-1</sup> of dry sediment, unlike the findings of the previous year (maximum values in the summer).

#### Distribution of *P. caspersi* and numerical density trend

The numerical density (average of all the cores taken in the sampling station), exhibited an

anomalous time trend compared to the previous year (Ambrogi, 1990) (Fig. 3).

In fact, with the exception of the September 1987 sample (16,094 ind.m<sup>-2</sup>) very low values were obtained overall, from 805 ind. m<sup>-2</sup> to 2743 ind. m<sup>-2</sup>, whereas during the previous year's cycle maximum summer values were recorded at around 18,000 ind. m<sup>-2</sup> and the minimum value (March 1987) was 6822 ind. m<sup>-2</sup>.

In order to compare the trend of abundance of *P. caspersi* with those of other macrobenthic species identified from the core samples, Table I shows the top-ranking species and the relevant density in the various samples.

Apart from the high density of *Lentidium mediterraneum* in the July 1987 sample, the species which were constantly present at a high density were *Magelona papillicornis* and *Owenia fusiformis*, polychaetes which are larger in size as compared to *Prionospio caspersi* and therefore with greater biomass. On the other hand, the numerical densities of these species in seasonal samples in the previous annual cycle were similar to those found in our samples (Ambrogi and Fontana, 1989). In conclusion, the difference in abundance of *P. caspersi* between the year 1986-1987 and the year 1987-1988, would not appear to be



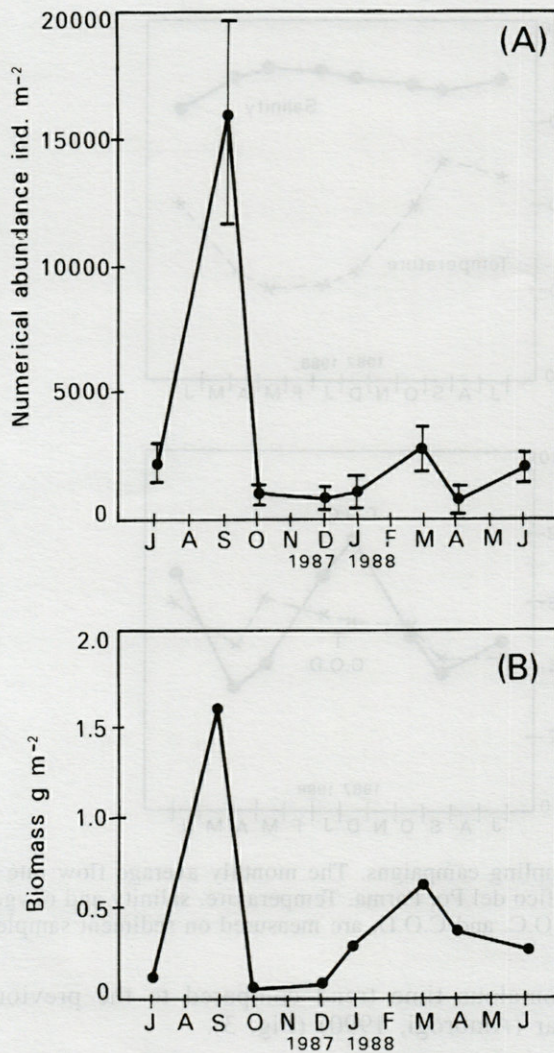


Fig. 3. – Seasonal fluctuations of numerical abundance (A) and biomass (B) values on the 8 sampling dates. Vertical bars in (A) represent one standard deviation.

Tabl. I. – Most abundant macrobenthic species present in the various sampling dates at station Y5. Values expressed as ind.m<sup>-2</sup>.

|                                | JUL 87 | SEP   | OCT | DEC  | JAN 88 | MAR  | APR | JUN  |
|--------------------------------|--------|-------|-----|------|--------|------|-----|------|
| <i>Prionospio caspersi</i>     | 2073   | 16094 | 945 | 805  | 1179   | 2743 | 798 | 1195 |
| <i>Spio decoratus</i>          | 2438   |       |     |      |        |      |     | 266  |
| <i>Polydora ciliata</i>        | 3048   |       |     |      |        |      |     |      |
| <i>Owenia fusiformis</i>       | 488    | 146   | 366 | 1500 | 284    | 805  | 299 | 599  |
| <i>Magelona papillicornis</i>  |        | 146   | 274 | 914  | 650    | 475  | 266 | 432  |
| <i>Lentidium mediterraneum</i> | 57913  |       |     |      |        |      |     | 233  |
| <i>Cylope neritea</i>          |        | 390   |     | 256  | 284    | 256  | 100 |      |
| <i>Tellina fabula</i>          |        | 122   | 91  | 183  | 163    | 146  | 100 |      |
| <i>Corbula gibba</i>           |        |       | 91  | 183  | 203    |      |     | 233  |

related to changes in the density of the main macrobenthic species.

The abundance of *P. caspersi* in the various sampling points did not show coherent and consistent differences between the sampling points Y1, Y2, Y3, Y4 and Y5.

With reference to the dispersion indices most commonly used, an aggregate type of distribution was found almost always. The dispersion index has values from 1.65 (April 1988) to 11.56 (September 1987). The values greater than 1 indicate the presence of aggregate distribution.

Similar conclusions can be expressed using the Morisita index (values between 1.23 and 4.03), which is considered more appropriate for studying the microdistribution of the benthic fauna.

#### Biomass of *P. caspersi*

In order to estimate the biomass, entire individuals were weighed, grouped according to size classes 0.1 mm<sup>2</sup> in amplitude of body area up to the tenth setiger (Fig. 4).

The equation of the regression curve ( $r = 0.99$ ) is the following:  $W = 0.166 * S^{2.327}$ , where:  $W$  = individual average weight;  $S$  = area.

The resulting regression curve was compared with that relating to the previous year (Ambrogi, 1990). Non-significant difference between the slopes of the two curves was found ( $p = 0.05$ ), following Student's t-test (value  $t = 0.74$  for 19 degrees of freedom).

The individual average weight of each size class derived from the regression equation was



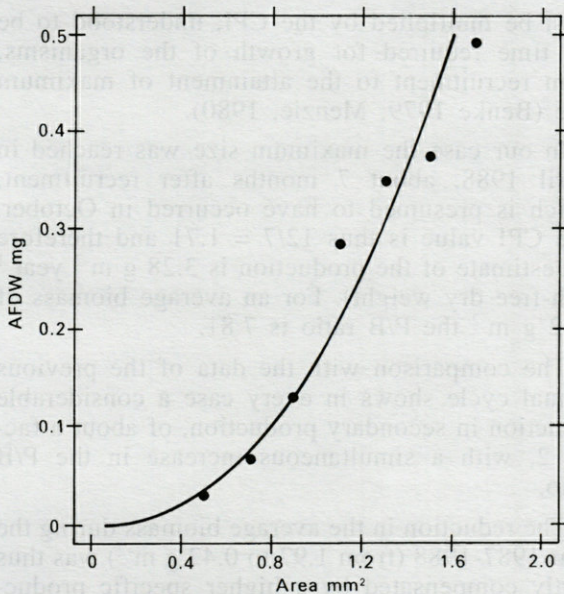


Fig. 4. - Area-weight regression curve. The points represent a pool of entire individuals having the same area of the anterior end.

used to calculate the total biomass. The trend of the biomass (Fig. 3 B) follows that of the numerical density, with a peak in September 1987 ( $1.6 \text{ g m}^{-2}$ ) and a sharp fall in October. A later and smaller peak occurred in March. The trend differs from that of the previous year in that the highest biomass appeared in April 1987 ( $3.7 \text{ g m}^{-2}$ ).

**Size distribution**

Three separate cohorts can be hypothesised by examining the bar graphs (Fig. 5). The first cohort appears in July 1987 with quite small abundance. The second sample (September 1987) shows the density maximum and a rapid growth. This cohort (cohort 1) disappears almost completely after the September sample.

The second cohort identified (with a density lower than the former) appears in October, and continues its growth until June 1988. In the same month (June 1988) the bimodal distribution of the size of the individuals indicates the recruitment of a new spring cohort (third cohort).

The spring recruitment, appearing as a new cohort in June-July, is a similar feature of this year-cycle and of the previous year-cycle, started in

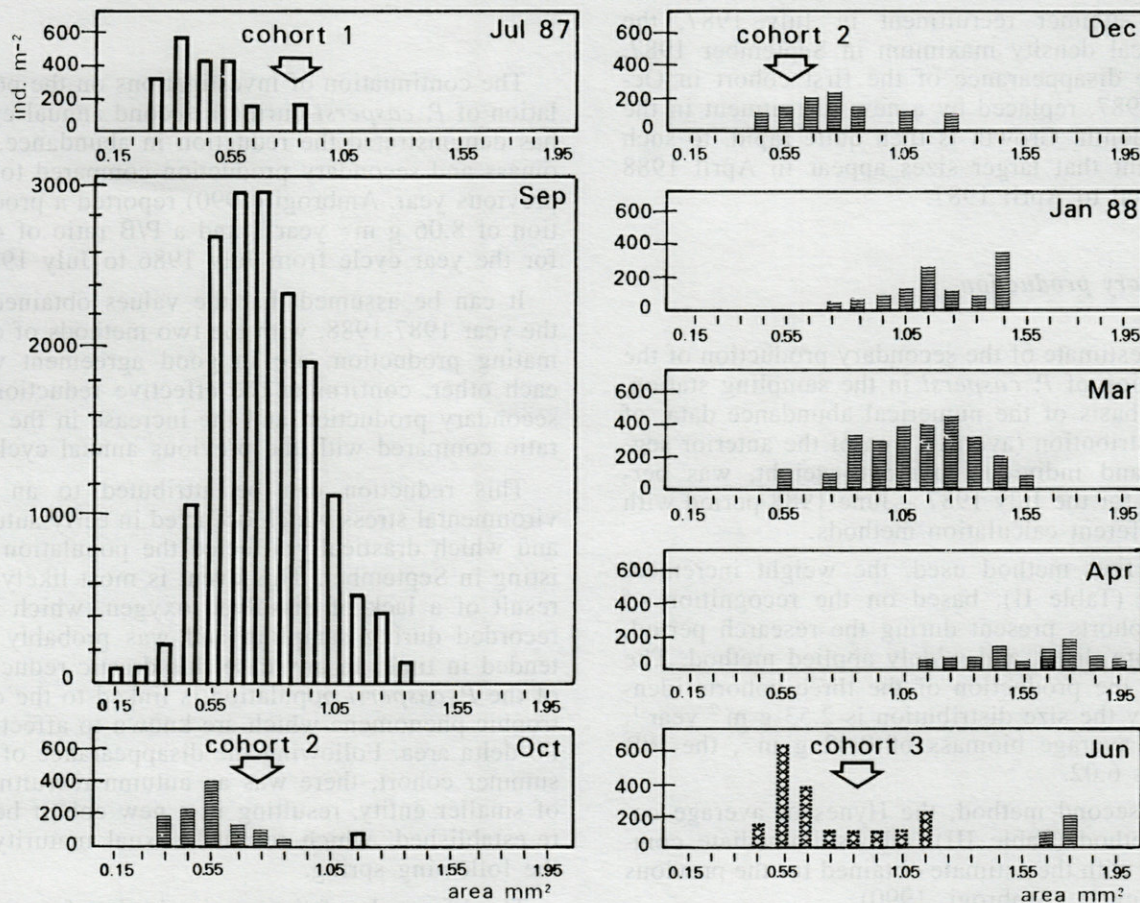


Fig. 5. - Size-frequency histograms based on surface area of the anterior end. The size-class interval is  $0.1 \text{ mm}^2$ . Three successive cohorts are shown.



Tabl. II. – Estimation of secondary production with the weight increment summation method. N = cohort numerical abundance;  $\bar{W}$  = average individual AFDW; NW = biomass;  $\bar{N}$  = average value of N over the sampling interval;  $\Delta\bar{W}$  = weight increment since previous sample;  $\Delta P$  = production increment; B = average biomass over the year.

|            | N     | $\bar{W}$ | NW      | $\bar{N}$ | $\Delta\bar{W}$ | $\Delta P$ |
|------------|-------|-----------|---------|-----------|-----------------|------------|
| I cohort   |       |           |         |           |                 |            |
| JUL 87     | 1935  | 0.03      | 0.05805 |           |                 | 0.05805    |
| SEP        | 16094 | 0.10      | 1.60940 | 9015      | 0.07            | 0.63102    |
| OCT        | 33    | 0.23      | 0.00759 | 8064      | 0.13            | 1.04826    |
|            |       |           | 1.67504 |           |                 | 1.73733    |
| II cohort  |       |           |         |           |                 |            |
| OCT 87     | 912   | 0.04      | 0.03740 |           |                 | 0.03740    |
| DEC        | 805   | 0.10      | 0.08050 | 859       | 0.06            | 0.05065    |
| JAN 88     | 1179  | 0.26      | 0.30654 | 992       | 0.16            | 0.15872    |
| MAR        | 2743  | 0.23      | 0.63089 | 1961      | -0.03           | -0.05883   |
| APR        | 798   | 0.48      | 0.38304 | 1771      | 0.25            | 0.44262    |
| JUN        | 272   | 0.51      | 0.13872 | 535       | 0.03            | 0.01605    |
|            |       |           | 1.57709 |           |                 | 0.64661    |
| III cohort |       |           |         |           |                 |            |
| JUN 88     | 1723  | 0.08      | 0.14300 |           |                 | 0.14300    |

July 1986 (Ambrogi, 1990). The most noticeable differences between the two annual cycles are: the scanty summer recruitment in July 1987, the numerical density maximum in September 1987, and the disappearance of the first cohort in October 1987, replaced by a new recruitment in the same month. Growth is then quite rapid, to such an extent that larger sizes appear in April 1988 compared to April 1987.

### Secondary production

The estimate of the secondary production of the population of *P. caspersi* in the sampling station, on the basis of the numerical abundance data, of size distribution (average area of the anterior segment) and individual average weight, was performed for the July 1987 – June 1988 period with two different calculation methods.

The first method used, the weight increment method (Table II), based on the recognition of three cohorts present during the research period, is a more direct and widely applied method. The sum of the production of the three cohorts identified by the size distribution is  $2.53 \text{ g m}^{-2} \text{ year}^{-1}$ . For an average biomass of  $0.42 \text{ g m}^{-2}$ , the  $P/\bar{B}$  value is 6.02.

The second method, the Hynes or average cohort method (Table III), allows immediate comparison with the estimate obtained for the previous annual cycle (Ambrogi, 1990).

The value of the sum of the production of each size class amounts to  $1.92 \text{ gm}^{-2} \text{ year}^{-1}$ . This value

must be multiplied by the CPI, understood to be the time required for growth of the organisms, from recruitment to the attainment of maximum size (Benke 1979; Menzie, 1980).

In our case the maximum size was reached in April 1988, about 7 months after recruitment, which is presumed to have occurred in October. The CPI value is thus  $12/7 = 1.71$  and therefore the estimate of the production is  $3.28 \text{ g m}^{-2} \text{ year}^{-1}$  (ash-free dry weight). For an average biomass of  $0.42 \text{ g m}^{-2}$  the  $P/\bar{B}$  ratio is 7.81.

The comparison with the data of the previous annual cycle shows in every case a considerable reduction in secondary production, of about a factor 2, with a simultaneous increase in the  $P/\bar{B}$  ratio.

The reduction in the average biomass during the year 1987-1988 (from  $1.97$  to  $0.42 \text{ g m}^{-2}$ ) was thus partly compensated by a higher specific production. A similar observation was made on populations of the bivalve *Spisula subtruncata*, in the same area (Ambrogi and Fontana, 1990).

### CONCLUSIONS

The continuation of investigations on the population of *P. caspersi* during a second annual cycle has demonstrated the reduction in abundance, biomass and secondary production compared to the previous year. Ambrogi (1990) reported a production of  $8.06 \text{ g m}^{-2} \text{ year}^{-1}$ , and a  $P/\bar{B}$  ratio of 4.09 for the year cycle from July 1986 to July 1987.

It can be assumed that the values obtained in the year 1987-1988, with the two methods of estimating production, are in good agreement with each other, confirming the effective reduction in secondary production and the increase in the  $P/\bar{B}$  ratio compared with the previous annual cycle.

This reduction can be attributed to an environmental stress which occurred in early autumn and which drastically affected the population existing in September. This event is most likely the result of a lack of dissolved oxygen, which was recorded during sampling and was probably extended in time. In any case this drastic reduction of the *P. caspersi* population is linked to the dystrophic phenomena which are known to affect the Po delta area. Following the disappearance of the summer cohort, there was an autumn recruitment of smaller entity, resulting in a new cohort being re-established, which reached sexual maturity in the following spring.

The life cycle of the species is therefore modified in relation to the previous year, due to the presence of two separate recruitments.



Tabl. III. - Estimation of secondary production with the average cohort method (the so-called Hynes method).  $N_j$  = average number of individuals in class  $j$ ;  $(N_j - N_{j+1})$  = number of individuals lost when changing from one class to the next;  $W_j$  = AFDW of individuals belonging to class  $j$ ;  $N_j W_j$  = biomass of class  $j$ ;  $\text{Avg } \bar{W} = (\bar{W}_j * \bar{W}_{j+1})^{0.5}$  = geometric mean of AFDW of two successive size classes; Biomass lost =  $(N_j - N_{j+1}) * \text{Avg } \bar{W}$ ;  $P_j$  = production; CPI = cohort production interval;  $\bar{B}$  = average biomass over the year.

| Class           | $\bar{N}_j$         | $\bar{N}_j - \bar{N}_{j+1}$ | $\bar{W}_j$ | $\bar{N}_j \bar{W}_j$ | Avg $\bar{W}$ | Biomass lost       | $P_j$              |
|-----------------|---------------------|-----------------------------|-------------|-----------------------|---------------|--------------------|--------------------|
| mm <sup>2</sup> | ind m <sup>-2</sup> | ind m <sup>-2</sup>         | mg          | mg                    | mg            | mg m <sup>-2</sup> | mg m <sup>-2</sup> |
| 0.15            | 4                   |                             | 0.0020      | 0.0082                |               |                    |                    |
| 0.25            | 43                  | -38.6                       | 0.0066      | 0.2819                | 0.0036        | -0.1403            | -2.67              |
| 0.35            | 118                 | -75.3                       | 0.0144      | 1.6996                | 0.0097        | -0.7343            | -13.95             |
| 0.45            | 235                 | -117.0                      | 0.0259      | 6.0870                | 0.0193        | -2.2593            | -42.93             |
| 0.55            | 532                 | -297.1                      | 0.0413      | 21.9782               | 0.0327        | -9.7182            | -184.65            |
| 0.65            | 457                 | 75.0                        | 0.0610      | 27.8880               | 0.0502        | 3.7634             | 71.51              |
| 0.75            | 428                 | 29.5                        | 0.0851      | 36.3922               | 0.0720        | 2.1283             | 40.44              |
| 0.85            | 383                 | 44.3                        | 0.1139      | 43.6681               | 0.0985        | 4.3565             | 82.77              |
| 0.95            | 301                 | 82.6                        | 0.1475      | 44.3739               | 0.1296        | 10.6998            | 203.30             |
| 1.05            | 228                 | 73.0                        | 0.1862      | 42.4238               | 0.1657        | 12.0979            | 229.86             |
| 1.15            | 182                 | 46.0                        | 0.2302      | 41.8527               | 0.2070        | 9.5298             | 181.07             |
| 1.25            | 141                 | 41.2                        | 0.2795      | 39.2977               | 0.2537        | 10.4531            | 198.61             |
| 1.35            | 90                  | 50.1                        | 0.3343      | 30.2441               | 0.3057        | 15.3235            | 291.15             |
| 1.45            | 83                  | 7.9                         | 0.3948      | 32.6144               | 0.3633        | 2.8555             | 54.25              |
| 1.55            | 30                  | 52.4                        | 0.4611      | 13.9437               | 0.4267        | 22.3444            | 424.54             |
| 1.65            | 36                  | -5.4                        | 0.5333      | 19.0281               | 0.4959        | -2.6976            | -51.25             |
| 1.75            | 22                  | 14.0                        | 0.6116      | 13.2595               | 0.5711        | 7.9955             | 151.92             |
| 1.85            | 9                   | 13.0                        | 0.6961      | 6.0352                | 0.6525        | 8.4888             | 161.29             |
| 1.95            | 4                   | 4.3                         | 0.7869      | 3.4151                | 0.7401        | 3.2047             | 60.89              |
|                 |                     | 4.3                         |             |                       | 0.7879        | 3.4151             | 64.89              |
| Total           | 3325                |                             |             | 424.48                |               |                    | 1921.02            |

$$\text{CPI} = 7 \quad P = \Sigma P_j * 12/\text{CPI} = 1.92 * 1.71 = 3.28 \text{ g m}^{-2} \text{ year}^{-1}$$

$$\bar{B} = 0.42 \text{ g} \quad P/\bar{B} = 7.81$$

The data given for *P. caspersi* are in addition to those already obtained for the bivalve *Spisula subtruncata* (Ambrogi and Fontana, 1990) highlighting the response to the environmental conditions of the two dominating species in the area investigated. In fact, a tendency to decline in density and production was also found for *Spisula subtruncata* in the same period. The den-

sity data of the community overall do not indicate other species which are capable of benefitting from the documented reduction of the two dominant ones.

In order to understand the mechanisms and the causes for this reduction, it will be important to develop a specially designed research on the first phases of recruitment to the substratum of the

Tabl. IV. - Literature data on secondary production of Spionid Polychaetes. Data expressed as ash-free dry weight.

| Species                            | P (g m <sup>-2</sup> yr <sup>-1</sup> ) | P/ $\bar{B}$ | Reference                 |
|------------------------------------|---|--------------|---------------------------|
| <i>Spiophanes kroyeri</i>          | 0.20                                    | 1.40         | Buchanan & Warwick, 1974  |
| <i>Spiophanes bombyx</i>           | 3.34                                    | 4.86         | Warwick et al., 1978      |
| <i>Spiophanes bombyx</i>           | 0.08                                    | 1.31         | Warwick & George, 1980    |
| <i>Polydora quadrilobata</i>       | 2.06                                    | 6.20         | Lambeck & Valentjin, 1987 |
| <i>Paraprionospio pinnata</i>      | 4.53                                    | 2.40         | Carrasco & Arcos, 1980    |
| <i>Prionospio caspersi</i>         | 8.06                                    | 4.09         | Ambrogi, 1990             |
| <i>Prionospio caspersi</i> (met.1) | 2.53                                    | 6.02         | Ambrogi et al., this work |
| <i>Prionospio caspersi</i> (met.2) | 3.28                                    | 7.81         |                           |



main species, by means of investigations on temporary meiobenthos during specific samplings. A preliminary survey on meiobenthos was conducted in the same sampling dates as for macrobenthos cores, enabling to find only a few juvenile stages of *P. caspersi* in the summer samples (Ceccherelli pers. comm.).

This change in the structure of the benthic community is worth paying some attention as to the consequences on the overall productivity of the sandy bottom of the marine area of the Po delta, which provides a considerable source of food for a number of fish species, including those of commercial importance.

The production data on this Spionid Polychaete, regardless of the method of estimation, and considering the two annual cycles investigated, can be compared with literature data only in a limited number of cases (Table IV). In fact Spionid Polychaetes, even if they are important members of the macrobenthic communities, especially in disturbed areas, where they are considered opportunistic species (Rhoads and Germano, 1986), had not been extensively studied in terms of their production ecology. Our data suggest that they may contribute to a significant part of the total production of infralittoral sand communities, in spite of their small size, and that their life-cycle can be adapted to wide environmental fluctuations, that are very frequent in coastal waters, particularly near river outlets.

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**DIPLOSOMA LAFARGUEAE N. SP., NOUVELLE ESPÈCE  
DE DIDEMNIDAE (ASCIDIENNES COMPOSÉES)  
DES CÔTES ATLANTIQUES IBÉRIQUES**

*Diplosoma lafargueae n. sp., a new species of the Didemnidae family  
(compound ascidians) in the Iberian atlantic coast*

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NOUVELLE ESPÈCE  
DIDEMNIDAE  
GALICIA  
ESPANA

NEW SPECIES  
DIDEMNIDAE  
GALICIA  
SPAIN

**RÉSUMÉ** – Une nouvelle espèce du genre *Diplosoma* (Famille Didemnidae), récoltée à la Ría de Ferrol (NW Péninsule Ibérique), est décrite. Ses affinités avec les autres espèces du genre sont discutées.

**ABSTRACT** – The description of a new species belonging to the genus *Diplosoma* (Family Didemnidae) collected in the Ría de Ferrol (NW Iberian Peninsula) is given. The affinities with other species of the genus are discussed. A tabular key of the *Diplosoma* on the european coast is presented.

**MATÉRIEL EXAMINÉ**

Deux colonies récoltées sur une roche granitique verticale à 9 m de profondeur dans la Ría de Ferrol (Galicia, NW Péninsule Ibérique) (Fig. 1). Les colonies mesurent 60 x 50 mm et 30 x 20 mm. L'holotype est déposé au Museo Nacional de Ciencias Naturales à Madrid (n° 31.01/2) et le paratype dans la collection du Département de Biologie Animale à l'Université de Santiago.

**DESCRIPTION**

Les colonies sont minces; l'épaisseur moyenne est de l'ordre de 3 mm.

La tunique, dépourvue de spicules est de couleur orange pâle (avant la fixation).

Les zoïdes (Fig. 2 a) sont de grande taille; ils mesurent 2-3 mm environ. Ils ne se présentent pas en systèmes nets.

Le thorax est muni de 6 lobes buccaux. La branche comprend 4 rangs de stigmates. De chaque côté on compte 10 stigmates sur le premier rang, 9 sur le deuxième, 8 sur le troisième et 8 sur le quatrième.

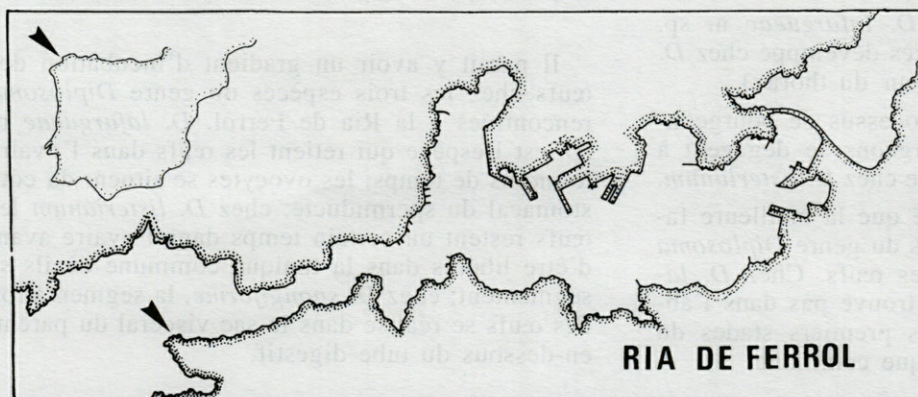


Fig. 1. – Situation de la station à la Ría de Ferrol

*Location of the station in the Ría the Ferrol*



L'ouverture cloacale est très grande; la paroi péribranchiale, très rudimentaire, laisse voir les 2 rangs centraux de stigmates; il n'y a pas de languette cloacale. Le ganglion nerveux est très marqué. Il n'y a pas d'organes thoraciques latéraux.

Appendice fixateur absent. Pédoncule oesophago-rectal assez long. Anse intestinale serrée; estomac volumineux, perpendiculaire à l'intestin terminal; l'intestin antérieur est dilaté dans sa partie proximale; intestin moyen long et coudé; intestin terminal parallèle à l'oesophage. L'anus s'ouvre au niveau du 3<sup>e</sup> rang de stigmates.

Le testicule, bilobé, est situé sur le côté gauche du corps. Le spermiducte est droit, large sur le testicule, il se rétrécit en allant vers l'intestin terminal. Il n'y a pas de glande « surtesticulaire ». L'ovaire n'a qu'un ovocyte en maturation sur le testicule et spermiducte.

Nous n'avons pas trouvé de larves.

Les colonies, récoltées en août, contenaient des zoïdes mûrs.

## ÉCOLOGIE

Il s'agit d'une espèce de la zone infralittorale (9 m de profondeur), située sur les parois verticales sur les côtes semi-battues de l'horizon à *Laminaria hyperborea*.

## DISCUSSION

L'espèce se rapproche de *Diplosoma listerianum* mais avec les différences suivantes: la couleur extérieure des colonies vivantes de *D. lafargueae* n. sp. est orange, couleur jamais signalée par les autres auteurs, ni observée par nous dans les colonies de la Ría de Ferrol. Les zoïdes de *D. lafargueae* n. sp. sont plus grands (2-3 mm environ) que ceux *D. listerianum* (1-2 mm). La différence de taille entre le thorax et l'abdomen est 1 : 1.8 chez *D. lafargueae* n. sp. et 1 : 0.7 chez *D. listerianum*.

L'appendice fixateur de *D. lafargueae* n. sp. n'existe pas alors qu'il est très développé chez *D. listerianum* (égal à la longueur du thorax).

En ce qui concerne le processus de bourgeonnement (Fig. 2 b), les bourgeons se dégagent à un stade moins développé que chez *D. listerianum*.

Lafargue (1968) a signalé que la meilleure façon de distinguer les espèces du genre *Diplosoma* est le mode d'incubation des œufs. Chez *D. lafargueae* n. sp. l'œuf ne se trouve pas dans l'abdomen, il est libéré dès les premiers stades du développement dans la tunique commune.

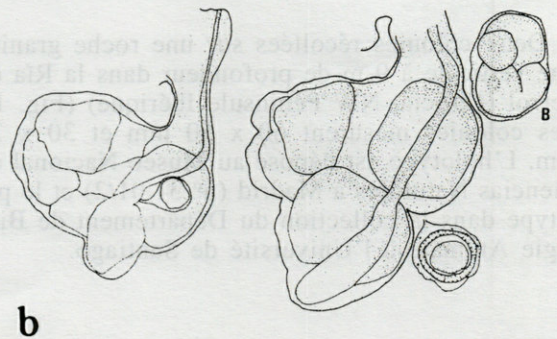
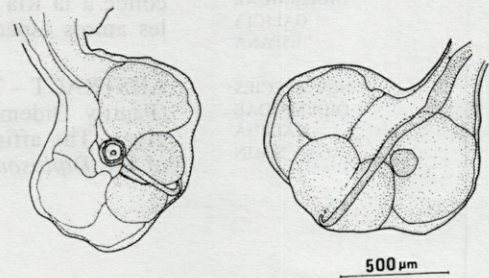
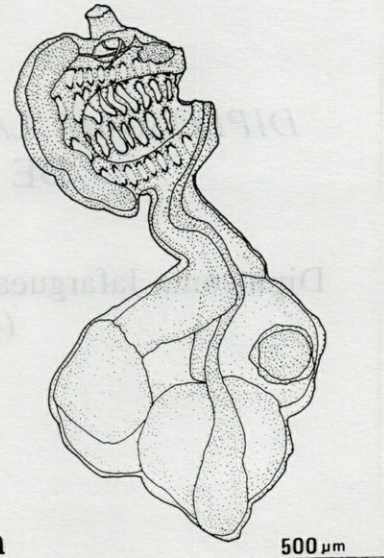


Fig. 2.— a, zoïde; b, 4 stades de développement de l'ovocyte. B, bourgeon.

a, zooid; b, four stages of the oocyte development.

Il paraît y avoir un gradient d'incubation des œufs chez les trois espèces du genre *Diplosoma* rencontrées à la Ría de Ferrol. *D. lafargueae* n. sp. est l'espèce qui retient les œufs dans l'ovaire le moins de temps; les ovocytes se situent du côté stomacal du spermiducte; chez *D. listerianum* les œufs restent un certain temps dans l'ovaire avant d'être libérés dans la tunique commune où ils se segmentent; chez *D. spongiforme*, la segmentation des œufs se réalise dans le sac viscéral du parent, en-dessous du tube digestif.



*D. lafargueae* se distingue également par son écologie : il habite l'infralittoral à 9 m de profondeur tandis que *D. listerianum* se trouve dans la zone de marées et dans le premier mètre de l'étage infralittoral.

*D. lafargueae* se différencie des autres espèces du genre *Diplosoma* des côtes européennes. *Diplosoma carnosum* Von Drasche, 1883 (décrit de l'Adriatique) possède un appendice fixateur très long et une glande subtesticulaire près de chaque lobe du testicule (Lafargue & Valentincic, 1973). *Diplosoma singulare* Lafargue, 1968 (des Glénan) possède une gonade située à droite du corps et un testicule simple dépourvu de lobes (Lafargue, 1968).

### COMPLÉMENT À LA CLÉ TABULAIRE DES ESPÈCES DE *DIPLOSOMA* D'EUROPE DE LAFARGUE & VALENTINCIC (1973)

- Présence ou absence d'appendice fixateur :  
P-présent; A-absent
- Glande « pylorique » : une paire de glandes de part et d'autre du post-estomac  
N-de taille normale plus ou moins visible; E-de taille énorme toujours visible.
- Glande « surtesticulaire » : une glande sur chaque testicule reposant contre l'intestin.  
P-présente; A-absente.
- Nombre de testicules  
1, 2, 2-5
- Position de l'ovaire : (considérer les ovocytes de petite taille).  
S-sur testicule et spermiducte;  
IT-entre testicule et intestin terminal.
- Nombre d'ovocytes :  
1-un, rarement 2;  
p-plusieurs
- Paires de prolongements ectodermiques chez la larve :  
2, 3, 2-7, 4-5.
- Incubation des larves :  
TC-dans la couche basale de la tunique;  
TCC-dans la couche centrale de la tunique.  
Z-par le zoïde géniteur dans la tunique basale.
- Forme de l'anse intestinale :  
L-lâche;  
S-serrée.
- Position de l'estomac par rapport à l'intestin terminal :  
Pa-parallèle;  
Pe-perpendiculaire.

L'emplacement du point de contact de l'estomac avec l'intestin terminal complète l'observation de ce caractère. Il se situe sur la face ventro-latérale gauche dans le premier cas et dans la région cardiaque dans le second.

11. Position de l'oesophage et de l'intestin terminal;

C-oesophage et intestin terminal croisés;

P-oesophage et intestin terminal parallèles.

12. Positions des gonades par rapport au zoïde :

D-à droite;

G-à gauche.

|   |   |   |     |    |   |     |     |   |    |    |    |   |
|---|---|---|-----|----|---|-----|-----|---|----|----|----|---|
| 1 | 2 | 3 | 4   | 5  | 6 | 7   | 8   | 9 | 10 | 11 | 12 |   |
| P | N | A | 2   | S  | 1 | 2-7 | Z   | S | Pa | C  | G  | <i>Diplosoma spongiforme</i><br>(Giard, 1872)         |
| P | N | P | 2   | S  | P | 2   | TC  | S | Pa | C  | G  | <i>Diplosoma listerianum</i><br>(Milne Edwards, 1841) |
| P | N | A | 2-5 | IT | P | 3   | TCC | L | Pe | P  | D  | <i>Diplosoma carnosum</i><br>(Von Drasche, 1883)      |
| P | E | A | 2   | IT | P | 2   | TC  | L | Pe | P  | D  | <i>Diplosoma migrans</i><br>(Menker et Ax, 1970)      |
| A | N | A | 1   | IT | P | 4-5 | TC  | L | Pe | P  | D  | <i>Diplosoma singulare</i><br>Lafargue, 1968          |
| A | N | A | 2   | S  | 1 | ?   | ?   | S | Pe | P  | G  | <i>Diplosoma lafargueae</i> n.sp.                     |

Cette espèce est dédiée à Françoise Lafargue.

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# INTERTIDAL MACROBENTHIC COMMUNITIES STRUCTURE IN THE MONDEGO ESTUARY (WESTERN PORTUGAL): REFERENCE SITUATION

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COMMUNAUTÉS ESTUARIENNES  
MACROBENTHOS  
SITUATION DE RÉFÉRENCE

**RÉSUMÉ** – L'estuaire du Mondego, divisé en deux bras, nord et sud, hydrologiquement très différents, subit un stress environnemental sévère. Une étude des communautés intertidales a été effectuée en décembre 1986 et juillet 1987, pour caractériser une situation de référence et servir de base à des travaux ultérieurs sur l'impact des activités humaines. L'analyse structurale des communautés a mis en évidence des différences entre les deux bras de l'estuaire, notamment en ce qui concerne la densité des populations et la biodiversité, ce qui est en accord avec l'analyse des facteurs physiques et chimiques. Le bras sud semble moins perturbé, présentant des conditions plus favorables au développement de populations abondantes d'espèces typiquement estuariennes. La salinité semble être le premier facteur qui conditionne la répartition des organismes sur substrats durs, tandis que la granulométrie et le pourcentage de matière organique, la salinité et l'oxygène dissous dans l'eau sont les plus importants pour les organismes de substrats meubles. Les aires à *Spartina maritima* et à *Zostera noltii*, surtout localisées au milieu du bras sud, sont les plus riches, présentant des populations plus denses et une biodiversité plus élevée. Des travaux ultérieurs seront nécessaires pour suivre les tendances évolutives des communautés macrobenthiques.

ESTUARINE COMMUNITIES  
MACROBENTHOS  
REFERENCE SITUATION

**ABSTRACT** – The Mondego estuary, consisting of two arms, north and south, with very different hydrographic characteristics, is under severe environmental stress. In December 1986 and July 1987, a study was carried out over the intertidal communities in order to provide reference data on which further studies on the impact of human activities could be based. The analysis of the communities structure revealed differences between the two estuarine arms for populations densities and biodiversity, which is consistent with results from the analysis of physico-chemical data. The southern arm appears to be less affected by human activities, presenting more favourable conditions for the development of abundant populations of typical estuarine species. Salinity appears to be the most important factor controlling the distribution of hard substrates organisms, while granulometry and organic matter contents of sediments, salinity, and dissolved oxygen in the water column are the most important factors for soft substrates organisms. *Spartina maritima* and *Zostera noltii* marshes, mainly located in the middle section of the southern arm, present the richest macrofaunal composition with regard to both abundance and biodiversity. Further work will be necessary in order to monitor changes and to understand the evolutive trends of macrobenthic communities.

## INTRODUCTION

The Mondego river drains a hydrological basin of nearly 6670 km<sup>2</sup> and its estuary (Fig. 1) is the location of Figueira da Foz, a commercial harbour of regional vital importance. Besides the harbour facilities and dredging activities, causing physical disturbance of the bottoms, the Mondego estuary supports industrial activities, many salt-works,

and aquaculture farms. It also receives the nutrient and chemical discharge from agricultural areas in the river valley, which can be especially significant in rainy periods. All these factors contributed to a severe increase of environmental stress.

Despite the increasing pressure, until 1985 there was no reference data on the Mondego estuary on which further studies on the impact of human activities over the structure and functioning of the ecosystem could be based.



From 1985 to 1990 a reference study on the benthic communities was carried out, regarding both the intertidal and subtidal zones. The aims of the study were :

a) To characterize the macrobenthic communities structure in relation to physicochemical environmental factors;

b) To identify the most important species, which could play a key role in the ecosystem functioning.

Results regarding the characterization of the intertidal communities are presented in this paper.

## MATERIAL AND METHODS

### Study site

The Mondego estuary is located in a warm-temperate climate. It consists of two arms, north and south (Fig. 1), with very different hydrographic characteristics. The northern arm, where the harbour is located, is deeper and the freshwater flows essentially by the northern arm, while the southern arm is almost silted up in the upstream section. Consequently, the water circulation in the southern arm is mostly due to tides

and to the usually small freshwater input of the Pranto river (Fig. 1). In addition, due to differences in depth, the tidal penetration tends to be faster along the northern arm causing stronger daily salinity changes, while daily temperature changes are more significant in the southern arm (Marques, 1989).

In both estuarine arms hard substrates are covered primarily by *Enteromorpha* and *Fucus* species, which form eulittoral macroalgae belts. Near the mouth of the estuary *Fucus* spp. appear clearly mixed with marine elements (e.g. *Chthamalus stellatus* and *Mytilus galloprovincialis*), and *Ulva* sp. shows a significant development in the upper limits of the sublittoral zone. Hard substrates result essentially from human occupation (e.g. harbour facilities, aquaculture farms, salt works), corresponding to about half of the estuarine perimeter. An important area of the intertidal zone, especially along the southern arm of the estuary, is still unchanged, presenting sediments from sand to mud, and in these areas *Spartina maritima* and *Zostera noltii* can cover a significant part of the eulittoral zone. Uncommon macroalgae blooms of *Enteromorpha* spp. have been observed in the southern arm, probably as the result of excessive nutrients release from the river valley into the estuary.

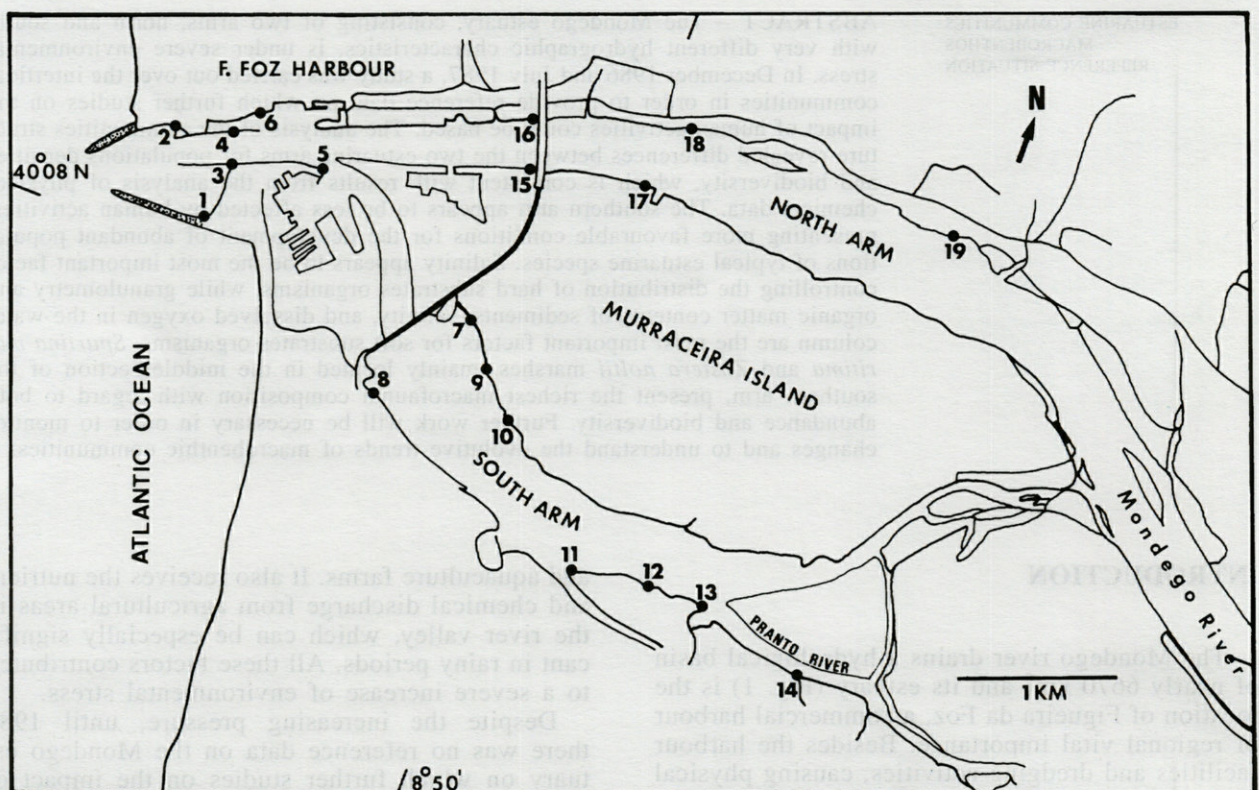


Fig. 1. - The Mondego estuary. Localization of the intertidal sampling stations.



### Field program

In December 1986 and July 1987 quantitative samples were carried out in 19 sampling stations (Fig. 1), in order to characterize the communities structure in winter and summer situations. Each time, sampling took place in five consecutive days, always in the morning and during a 3 hours period in low water. This allowed samples to be carried out in approximately uniform conditions.

Both hard and soft substrates were frequently found in the same sampling station, and depending on the intertidal slope the sampling area was quite variable. On soft substrates, *Spartina maritima* and *Zostera noltii* marshes could be present or not, depending on the sampling station.

In order to establish an uniform sampling criterion, in each station the intertidal zone was stratified, taking into consideration different eulitoral levels, and the type of macroalgae or macrophytes covered areas. This criterion allowed to consider three approximately equidistant levels between high water and low water levels. On hard substrates, depending on the sampling site, the two upper levels corresponded approximately to *Enteromorpha* spp. and *Fucus* spp. algal belts, whereas the lower level in stations located near the mouth of the estuary presented also a significant population of *Mytilus galloprovincialis* (mussels). On soft substrates with vegetal covered areas the two upper levels frequently corresponded respectively to the marsh-grass *Spartina maritima* belt and to the eel-grass *Zostera noltii* meadows, while the lower level corresponded mainly to sandy or muddy substrates without macrophytes.

Two different sampling techniques were used as a function of the type of substrate. On hard substrates three replicates of 625 cm<sup>2</sup> were randomly sampled in each level by scratching out organisms with a chisel. On soft substrates we adapted the technique described by Dexter (1979; 1983) for sandy beaches, and eight replicates were randomly sampled in each level by using a manual corer, each core corresponding to 141 cm<sup>2</sup> and approximately 3 liters of sediment.

All the biological samples were sieved *in situ* using a 1 mm mesh size sieve, and then fixed in 4 % neutralized formol. This mesh size was considered suitable for this study, regarding the types of sediment we expected to find along the estuary.

Each time and for each station, several physicochemical factors were determined, respectively salinity, temperature, pH, dissolved oxygen (measured *in situ*), nitrites, nitrates, and phosphates (analysed in the laboratory). The analysis of water samples followed the methods described in Strickland & Parsons (1968). Sediment samples were also collected and sub-

Tabl. I. - Particle-size categories used to classify sediment types in present study.

| Size class | Diameter (mm)  | Sediment classification |
|------------|----------------|-------------------------|
| 1          | > 2            | Gravel                  |
| 2          | 1 to 2         | Coarse sand             |
| 3          | 0.5 to 1       | Medium sand             |
| 4          | 0.250 to 0.5   |                         |
| 5          | 0.125 to 0.250 | Fine sand               |
| 6          | 0.063 to 0.125 | Silt                    |
| 7          | 0.002 to 0.063 |                         |
| 8          | < 0.002        | Clay                    |

sequently analysed for granulometry, organic matter and carbonate contents.

For each sediment sample particles were ranked into eight size categories (table I) :

The organic mater contents in the sediments was calculated after destruction in a muffle furnace (24 hours at 500°C).

In the laboratory the organisms were separated, preserved in 70 % ethanol or in 4 % neutralized formol, according to the presence or absence of calcareous parts, and identified and counted.

### Data analysis

Data on both hard and soft substrates and on winter and summer situations were assumed to correspond to different ecological conditions, and therefore were analysed separately.

With regard to biological data, species x stations matrices were analysed, considering data on each sampling site as a whole. The goal of the analysis was to study the horizontal distributional ecology of the species along the estuary, and to reveal differences between the two estuarine arms with regard to communities structure. A first analysis was achieved taking into consideration all the species, and a second one overlooking the species found only once (Legendre & Legendre, 1984).

On hard substrates, since it was not possible to collect water in each sampling level, water samples for determination of physicochemical factors were always taken from the water column (one sample per station). On soft substrates, because of water retention in pools during low tide, it was always possible to get water and sediment samples in each sampling level. Consequently, in the first case, we analysed factors x stations matrices, while in the second case the analysis was based upon factors X samples matrices.



Data underwent principal component analysis (PCA), using the sampling stations or the samples as operational units in the space of biological or physicochemical variables. Sediment granulometric fractions (expressed in %) and dissolved oxygen (% of saturation) were submitted to angular transformation. Eigenvalues and eigenvectors of correlation matrices between variables were computed after centering and reduction to unit variance (Legendre & Legendre, 1984). Correlation matrices were computed using the Pearson's correlation index. In addition, biological data was submitted to cluster analysis, using the Chi-Square distance coefficient (Lebart *et al.*, 1984). (Q mode analysis) and the unweighted pair group mean of analysis (UPGMA) clustering method (Legendre & Legendre, 1984). Data treatment was performed with the NTSYS-PC 1.60 software system (Rohlf, 1990).

Finally, in order to get information on species richness and evenness in different estuarine areas, the values of the Shannon-Wiener heterogeneity index (Legendre & Legendre, 1984; Peet, 1974) were calculated for each sampling station in winter and summer situations.

## RESULTS

We identified 90 macrofaunal species from samples carried out in winter and summer situations (table II). A first look to data confirmed our primary assumptions for data analysis, showing that 34 taxa (38 %) were found only in the winter, while 19 (21 %) were found exclusively in the summer, reflecting a seasonal variation in the species composition. Moreover, 36 taxa (40 %) were found exclusively on hard substrates, while 24 (27 %) occurred only in soft substrates, exhibiting a different species composition as a function of the type of substrate.

### Hard substrates community

#### Winter situation

PCA of species x stations data (Fig. 2 A) shows a clear separation between stations located near the mouth (group A) and stations located inside the estuary (groups B and C) along the first axe. A separation between stations from the southern arm (group C) and stations from the northern arm, together with a few stations located near the mouth (group B), is evident along the second axe. Near the mouth, sessile marine species like *Chthamalus stellatus* and *Mytilus galloprovincialis* are very abundant, and significant populations of *Montacuta ferruginosa*, *Idotea*

Tabl. II. – List of the *taxa* identified in winter and summer situations, and on both hard and soft substrates. For each *taxa*, the average density (number of individuals.m<sup>-2</sup>) is given.

| TAXA                               | WINTER          |                 | SUMMER          |                 |
|------------------------------------|-----------------|-----------------|-----------------|-----------------|
|                                    | Hard Substrates | Soft Substrates | Hard Substrates | Soft Substrates |
| <b>TURBELLARIA</b>                 |                 |                 |                 |                 |
| <i>Convoluta</i> sp.               |                 | 0.7             | 0.4             | 0.6             |
| <b>NEMERTINI</b>                   |                 |                 |                 |                 |
| <i>Lineus</i> sp.                  | 4.2             |                 |                 |                 |
| <i>Oerstedtia</i> sp.              |                 | 2.8             | 0.4             |                 |
| <i>Tritasiemna</i> sp.             |                 | 3.5             | 2               | 0.6             |
| <i>Palaeonemertea</i>              |                 |                 |                 | 0.6             |
| <b>OLIGOCHAETA</b>                 |                 | 0.7             |                 |                 |
| <i>Eteone picta</i>                |                 | 6.3             |                 |                 |
| <i>Glycera convoluta</i>           |                 | 4.2             |                 |                 |
| <i>Lepidonotus clava</i>           |                 |                 | 0.4             |                 |
| <i>Nephtys cirrosa</i>             |                 | 0.7             |                 |                 |
| <i>Hediste diversicolor</i>        | 10.8            | 66.1            | 13.2            | 890             |
| <i>Neanthes irrorata</i>           |                 | 2.8             | 0.4             |                 |
| <i>Phyllodoce</i> sp.              | 1.4             |                 |                 |                 |
| <i>Polydora</i> sp.                |                 |                 | 2.9             |                 |
| <i>Amage adpersa</i>               |                 | 34.6            | 2               | 128             |
| <i>Amphicheus gunneri</i>          |                 | 17              |                 |                 |
| <i>Capitella capitata</i>          |                 | 4.8             | 0.8             | 30.3            |
| <i>Cirratulus cirratus</i>         | 0.5             |                 |                 |                 |
| <i>Heteromastus filiformis</i>     |                 | 72.9            |                 |                 |
| <i>Lagis koreni</i>                |                 | 2.8             |                 |                 |
| <i>Mercierella enigmatica</i>      |                 |                 | 4.4             |                 |
| <i>Pomatocerus triquetus</i>       | 9.4             | 0.7             |                 |                 |
| <i>Pseudomuriceoceros cantabra</i> |                 | 8.4             |                 |                 |
| <i>Pyrosospio elegans</i>          |                 | 0.7             |                 |                 |
| <i>Sabellaria alveolata</i>        | 2.4             |                 |                 |                 |
| <i>Spio filicornis</i>             |                 | 3.5             |                 | 3.7             |
| <i>Sireblosipio dekhuyzeni</i>     |                 | 24.5            | 2.4             | 23.9            |
| <i>Sabellaria</i>                  |                 |                 | 0.4             |                 |
| <b>POLYPLACOPHORA</b>              |                 |                 |                 |                 |
| <i>Lepidochitona cinereus</i>      | 0.5             |                 |                 |                 |
| <b>GASTROPODA</b>                  |                 |                 |                 |                 |
| <i>Bitium reticulatum</i>          |                 |                 |                 | 0.6             |
| <i>Cerithium vulgatum</i>          |                 |                 |                 | 0.6             |
| <i>Gibbula umbilicalls</i>         |                 |                 |                 | 0.6             |
| <i>Hamia hydatis</i>               | 30              | 200             |                 | 0.6             |
| <i>Hydrobia ulvae</i>              | 52.2            | 1980            | 181             | 859             |
| <i>Littorina littorea</i>          | 0.5             | 15.4            |                 | 10              |
| <i>Littorina neritoides</i>        | 2.8             |                 |                 |                 |
| <i>Littorina saxatilis</i>         |                 |                 |                 | 0.6             |
| <i>Murex trunculus</i>             | 0.9             |                 |                 |                 |
| <i>Nassarius reticulatus</i>       |                 |                 |                 | 5               |
| <i>Nucella lapillus</i>            |                 |                 | 0.4             |                 |
| <i>Odostomia unidentata</i>        | 0.9             |                 |                 |                 |
| <i>Patella aspera</i>              | 0.5             |                 |                 |                 |
| <i>Patella lusitanica</i>          | 1.4             |                 |                 |                 |
| <i>Rissoa membranacea</i>          | 0.5             |                 |                 |                 |
| <i>Rissoa parva</i>                | 0.9             |                 |                 |                 |
| <i>Cerastoderma edule</i>          |                 | 66.6            | 2.8             | 36              |
| <i>Montacuta ferruginosa</i>       | 32.9            | 0.7             |                 |                 |
| <i>Mytilus galloprovincialis</i>   | 5790            | 4.9             | 1390            |                 |
| <i>Scrobicularia plana</i>         | 1.9             | 283             | 4.8             | 103             |
| <b>ANOSTRACA</b>                   |                 |                 |                 |                 |
| <i>Artemia salina</i>              |                 | 0.7             |                 |                 |
| <b>CIRRIPEDIA</b>                  |                 |                 |                 |                 |
| <i>Ballanus perforatus</i>         | 11.8            |                 |                 |                 |
| <i>Chthamalus stellatus</i>        | 764             |                 | 1470            |                 |
| <b>ISOPODA</b>                     |                 |                 |                 |                 |
| <i>Cyathura carinata</i>           | 0.9             | 322             | 11.2            | 128             |
| <i>Dynamene bidentata</i>          | 0.5             |                 | 2.4             |                 |
| <i>Gnathia vorax</i>               | 0.5             |                 |                 |                 |
| <i>Eurydice pulchra</i>            |                 |                 |                 | 0.6             |
| <i>Eurydice spinigera</i>          |                 |                 |                 | 0.6             |
| <i>Idotea chelipes</i>             | 3.8             | 0.7             |                 |                 |
| <i>Idotea granulosa</i>            | 3.3             |                 | 1.6             | 0.6             |
| <i>Idotea pelagica</i>             | 64.9            | 0.7             | 37.6            |                 |
| <i>Jaera forsmanni</i>             | 9.9             |                 | 63.6            |                 |
| <i>Sphaeroma hookeri</i>           | 24.4            | 0.7             | 10.4            | 1.8             |
| <b>AMPHIPODA</b>                   |                 |                 |                 |                 |
| <i>Amphithoe valida</i>            | 1.4             |                 |                 |                 |
| <i>Amphithoe ramondi</i>           | 3.3             |                 |                 |                 |
| <i>Amphithoe rubricata</i>         | 3.4             |                 |                 |                 |
| <i>Bathyporeia sarsi</i>           |                 | 1.4             |                 | 1.3             |
| <i>Corophium insidiosum</i>        | 33.1            |                 | 2.8             |                 |
| <i>Corophium multisetosum</i>      |                 | 3.4             |                 | 5.7             |
| <i>Echinogammarus marinus</i>      | 196             | 12.6            | 95.1            | 3.1             |
| <i>Echinogammarus stevenseni</i>   |                 |                 | 68.4            | 1.6             |
| <i>Gammarus chevreuxi</i>          | 1.4             | 1.4             |                 |                 |
| <i>Gammarus locusta</i>            | 2.6             |                 | 6.4             |                 |
| <i>Hauistorius arenarius</i>       |                 | 0.7             |                 |                 |
| <i>Hyale crassipes</i>             | 3.3             |                 |                 |                 |
| <i>Hyale perieri</i>               | 2.8             |                 |                 |                 |
| <i>Hyale stebbingi</i>             | 184             |                 |                 | 117             |
| <i>Jassa marmorata</i>             |                 |                 |                 | 0.4             |
| <i>Leptocheirus pilosus</i>        | 44.7            |                 |                 | 88.4            |
| <i>Melita palmata</i>              | 88.9            | 19.1            |                 | 66.8            |
| <i>Talorchestia</i> sp.            |                 |                 |                 | 8.4             |
| <b>MYSIDACEA</b>                   |                 |                 |                 |                 |
| <i>Parameysis helleri</i>          |                 |                 |                 | 1.9             |
| <b>DECAPODA</b>                    |                 |                 |                 |                 |
| <i>Carcinus muenes</i>             | 13.2            | 13.3            | 80              | 15              |
| <i>Crangon crangon</i>             |                 | 2               | 7.6             | 11.3            |
| <i>Pachygrapsus marmoratus</i>     | 6.6             |                 | 1.2             |                 |
| <i>Pulmonometes varians</i>        | 0.9             | 0.7             | 2.8             | 1.8             |
| <b>INSECTA</b>                     |                 |                 |                 |                 |
| Diptera larvae                     | 4.2             | 9.1             | 86.4            | 3.7             |
| Lepidoptera larvae                 |                 |                 |                 | 1.6             |
| <b>PISCES</b>                      |                 |                 |                 |                 |
| <i>Blennius</i> sp. 1              | 0.5             |                 |                 |                 |
| <i>Blennius</i> sp. 2              | 0.5             |                 |                 |                 |
| <i>Pomatoschistus</i> sp.          | 0.5             | 0.7             |                 | 1.9             |

*pelagica*, and *Hyale stebbingi*, all marine species, together with less important populations of *Littorina neritoides*, *Ballanus perforatus*, *Idotea chelipes*, *I. granulosa*, *Jaera forsmanni*, *Amphithoe ramondi*, *A. rubricata*, and *Pachygrapsus marmoratus* are also found. In the inner areas of the



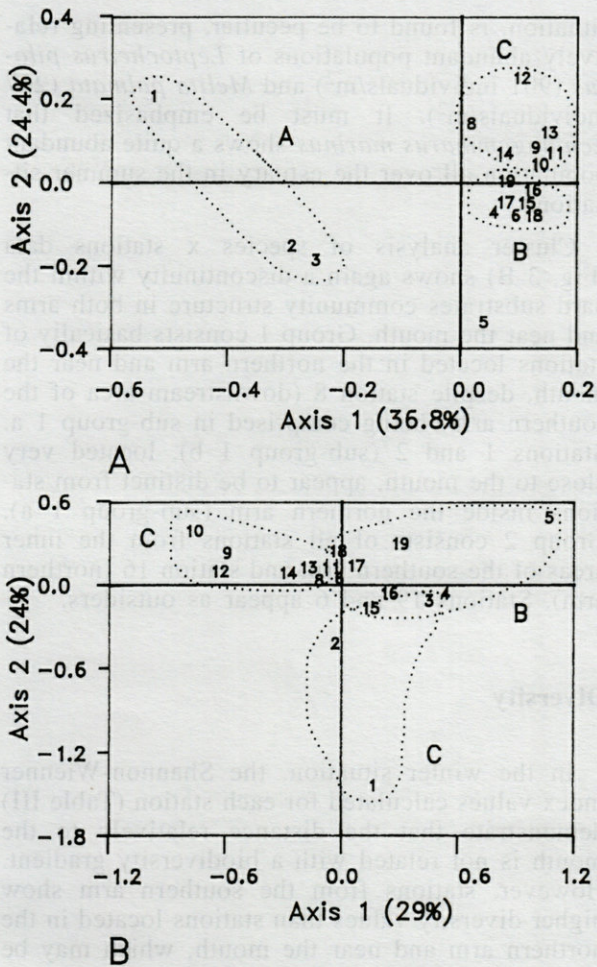


Fig. 2. - Analysis of hard substrates community structure from PCA of species x stations matrices overlooking species found only once. A - winter situation : Projection of stations against the first two axes,  $r = 0.88934$ . B - summer situation : Projection of stations against the first two axes,  $r = 0.85206$ . The percentage of variability explained by the principal axes is given. Groups of stations pointed out are discussed in the text.

estuary, *Mytilus galloprovincialis* and *Chthamalus stellatus* populations become much less dense, and the presence of other typical marine species is inconspicuous. Station 1, which exhibits the strongest marine influence (typical estuarine species are represented only by sparse populations of *Echinogammarus marinus* and *Carcinus maenas*), presents dense populations of *Mytilus galloprovincialis*, *Chthamalus stellatus*, and *Hyale stebbingi*. The separation of stations from both estuarine arms along the second axis is mainly due to the preferential occurrence of *Leptocheirus pilosus* and *Melita palmata*, followed by *Sabellaria alveolata*, in stations from the northern arm, and of *Echinogammarus marinus*, *Sphaeroma hookeri*, and *Hediste diversicolor* (frequently found in sediment deposits over rock), followed by *Idotea chelipes*, *I. pelagica*, *Amphithoe ra-*

*mondi*, *A. rubricata*, and *Carcinus maenas*, in stations from the southern arm.

Station 5, located near the connection of the two arms, appears to be peculiar, exhibiting significant densities of *Melita palmata* (704 individuals/m<sup>2</sup>) and *Leptocheirus pilosus* (437 individuals/m<sup>2</sup>) populations. Typical estuarine species like *Hydrobia ulvae*, *Echinogammarus marinus*, *Sphaeroma hookeri*, and *Carcinus maenas* show higher abundances in the southern arm, while *Mytilus galloprovincialis* and *Chthamalus stellatus* populations are significant in

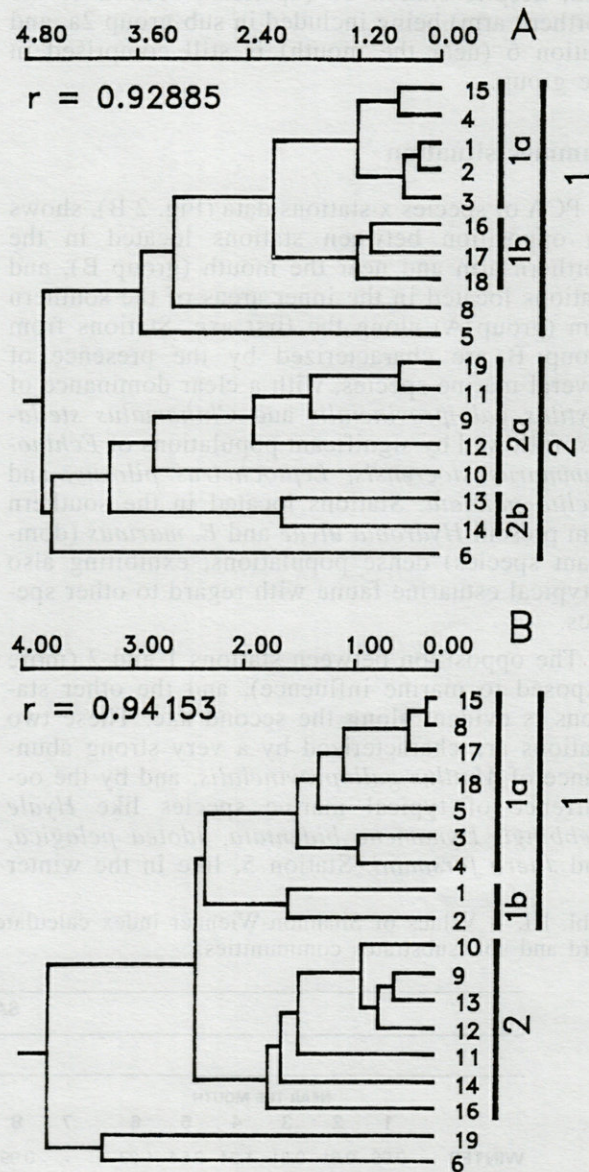


Fig. 3. - Hard substrates community structure : Cluster analysis of species x stations matrices overlooking species found only once. Data analysed using the Chi-Square distance coefficient (Q mode analysis) and the UPGMA clustering method. A - winter situation; B - summer situation. Values of cophenetic correlation coefficients are indicated.



the northern arm (although less abundant than in stations located near the mouth) and very scarce in the southern arm.

Cluster analysis of species x stations data (Fig. 3 A) allows to recognize a structural discontinuity in the communities from both arms and near the mouth, corroborating therefore the results from ordination. Group 1 consists of stations located near the mouth (basically sub-group 1a) and inside the northern arm (sub-group 1b), together with stations 8 and 5, located in the down stream section of the southern arm. Group 2 consist primarily of stations from inner areas of the southern arm, despite station 19 (upstream section of the northern arm) being included in sub-group 2a, and station 6 (near the mouth) is still comprised in the group.

### Summer situation

PCA of species x stations data (Fig. 2 B), shows an opposition between stations located in the northern arm and near the mouth (group B), and stations located in the inner areas of the southern arm (group A) along the first axe. Stations from group B are characterized by the presence of several marine species, with a clear dominance of *Mytilus galloprovincialis* and *Chthamalus stellatus*, followed by significant populations of *Echinogammarus stoerensis*, *Leptocheirus pilosus*, and *Melita palmata*. Stations located in the southern arm present *Hydrobia ulvae* and *E. marinus* (dominant species) dense populations, exhibiting also a typical estuarine fauna with regard to other species.

The opposition between stations 1 and 2 (more exposed to marine influence), and the other stations is evident along the second axe. These two stations are characterized by a very strong abundance of *Mytilus galloprovincialis*, and by the occurrence of typical marine species like *Hyale stebbingi*, *Dynamene bidentata*, *Idotea pelagica*, and *Jaera forsmanni*. Station 5, like in the winter

situation, is found to be peculiar, presenting relatively abundant populations of *Leptocheirus pilosus* (901 individuals/m<sup>2</sup>) and *Melita palmata* (267 individuals/m<sup>2</sup>). It must be emphasized that *Echinogammarus marinus* shows a quite abundant population all over the estuary in the summer situation.

Cluster analysis of species x stations data (Fig. 3 B) shows again a discontinuity within the hard substrates community structure in both arms and near the mouth. Group 1 consists basically of stations located in the northern arm and near the mouth, despite station 8 (downstream area of the southern arm) being comprised in sub-group 1 a. Stations 1 and 2 (sub-group 1 b), located very close to the mouth, appear to be distinct from stations inside the northern arm (sub-group 1 a). Group 2 consists of all stations from the inner areas of the southern arm and station 16 (northern arm). Stations 19 and 6 appear as outsiders.

### Diversity

In the winter situation, the Shannon-Wiener index values calculated for each station (Table III) demonstrate that the distance relatively to the mouth is not related with a biodiversity gradient. However, stations from the southern arm show higher diversity values than stations located in the northern arm and near the mouth, which may be due to the combined effects of tides and stronger fresh water discharge along the northern arm, creating a significant daily environmental stress for environmental factors.

On the other hand, in the summer situation, the Shannon-Wiener index values calculated for each station (Table III) reveal several differences as compared to the winter situation. In the summer, the highest values for diversity are found near the mouth of the estuary, while the lowest values are found inside the southern arm.

Tabl. III. – Values of Shannon-Wiener index calculated for each station in winter and summer situations and for hard and soft substrates communities.

|        |  | SAMPLING STATIONS |      |      |      |      |      |           |      |      |      |      |      |      |           |      |      |      |      |      |
|--------|--|-------------------|------|------|------|------|------|-----------|------|------|------|------|------|------|-----------|------|------|------|------|------|
|        |  | Hard substrates   |      |      |      |      |      |           |      |      |      |      |      |      |           |      |      |      |      |      |
|        |  | NEAR THE MOUTH    |      |      |      |      |      | SOUTH ARM |      |      |      |      |      |      | NORTH ARM |      |      |      |      |      |
|        |  | 1                 | 2    | 3    | 4    | 5    | 6    | 7         | 8    | 9    | 10   | 11   | 12   | 13   | 14        | 15   | 16   | 17   | 18   | 19   |
| WINTER |  | 0.98              | 0.61 | 0.81 | 1.24 | 2.54 | 1.23 | -         | 0.99 | 1.07 | 1.21 | 1.26 | 2.31 | 1.16 | 1.94      | 1.11 | 2.27 | 0.35 | 0.62 | 1.2  |
| SUMMER |  | 1.55              | 2.09 | 2.22 | 2.12 | 1.58 | 2.2  | -         | 0.41 | 0.78 | 1.21 | 1.4  | 0.73 | 1.12 | 1.07      | 0.78 | 0.99 | 0.97 | 1.5  | 3.0  |
|        |  | Soft substrates   |      |      |      |      |      |           |      |      |      |      |      |      |           |      |      |      |      |      |
|        |  | NEAR THE MOUTH    |      |      |      |      |      | SOUTH ARM |      |      |      |      |      |      | NORTH ARM |      |      |      |      |      |
|        |  | 1                 | 2    | 3    | 4    | 5    | 6    | 7         | 8    | 9    | 10   | 11   | 12   | 13   | 14        | 15   | 16   | 17   | 18   | 19   |
| WINTER |  | 1.0               | 1.39 | -    | -    | -    | 1.52 | 2.32      | 1.5  | 2.69 | 2.19 | 1.96 | 1.43 | 1.91 | 1.71      | 2.13 | 3.08 | 1.6  | 2.01 | 1.52 |
| SUMMER |  | 0.92              | 0.76 | -    | -    | -    | -    | 2.65      | 1.83 | 2.3  | 1.6  | 2.08 | 1.36 | 1.19 | 1.62      | 1.51 | 1.45 | 0.66 | 1.38 | 0.54 |

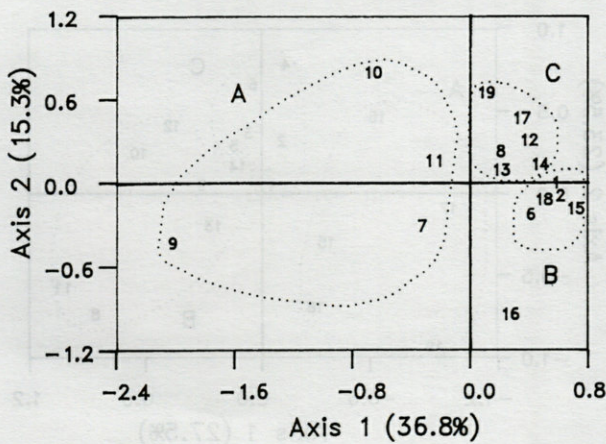


With regard to hard substrates community, a decrease in diversity was observed in the southern arm from winter to summer, while an increase occurred in the northern arm and near the mouth. The decrease in diversity observed in the southern arm may be explained by the change in biological activity of *Echinogammarus marinus*, which becomes extremely abundant in the summer situation (average about 3 000 individuals/m<sup>2</sup> in the southern arm on the *Fucus* covered areas), affecting species evenness.

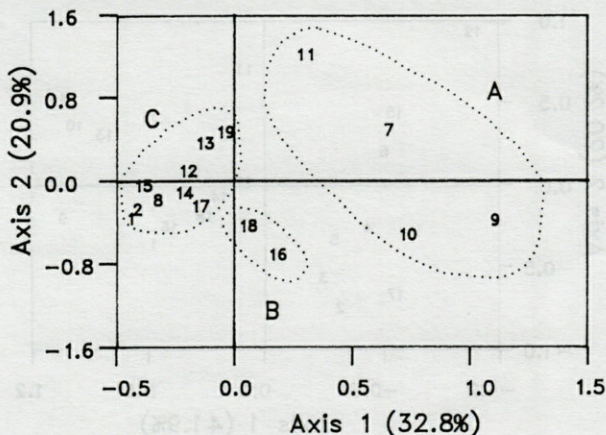
### Soft substrates community

#### Winter situation

PCA of species x stations data (Fig. 4 A) shows the opposition between stations 7, 9, 10, and 11



A



B

Fig. 4. - Analysis of soft substrates community structure from PCA of species x stations matrices overlooking species found only once. A - winter situation: Projection of stations against the first two axes,  $r = 0.80878$ . B - summer situation: Projection of stations against the first two axes,  $r = 0.87681$ . The percentage of variability explained by the principal axes is given. Groups of stations pointed out are discussed in the text.

(group A), located in the southern arm, corresponding to *Spartina maritima* and *Zostera noltii* marshes, and stations without vegetal covered areas (groups B and C) along the first axe. These stations differ from the others in that several species (e.g. *Amage adspersa*, *Heteromastus filiformis*, *Hediste diversicolor*, *Hydrobia ulvae*, *Cerastoderma edule*, *Scrobicularia plana*, and *Cyathura carinata*) present considerably higher population abundances. Along the second axe we can distinguish between stations located in the southern arm (8, 12, 13, and 14), followed by stations 17 and 19 (northern arm) (group C), and stations located in the northern arm and near the mouth of the estuary (group B). Stations from the southern arm, even those located in areas without vegetal cover, present higher population abundances than stations from the northern arm, namely with regard to common species like *Hediste diversicolor*, *Hydrobia ulvae*, *Scrobicularia plana*, and *Cyathura carinata*. Station 16, located in the northern arm, is clearly separated along the second axe, which is explained by the sporadic occurrence of several rare species in the estuary like *Eteone picta*, *Glycera convoluta*, and *Spio filicornis*.

Cluster analysis of species x stations data (Fig. 5 A) does not reveal a clear discontinuity within the soft substrates community. Actually, a single main group of stations is recognizable (group 1), consisting of stations from both estuarine arms, while stations 1, 2 and 6, located near the mouth, appear as outsiders. Nevertheless, stations 9, 11, 10 and 7, located in *Spartina maritima* and *Zostera noltii* marshes, are clearly assembled (sub-group 1 b), which agrees with results from ordination.

#### Summer situation

PCA of species x stations data (Fig. 4 B) shows once more the opposition between stations corresponding to *Spartina maritima* and *Zostera noltii* marshes (group A) and stations without vegetal covered areas (groups B and C) along the first axe. Like in the winter situation, the most important species contributing to the observed variability are *Amage adspersa*, *Heteromastus filiformis*, *Hediste diversicolor*, *Hydrobia ulvae*, *Cerastoderma edule*, *Scrobicularia plana*, and *Cyathura carinata* (positive side of factor 1), which populations are much more abundant in stations from group A as compared to other areas. Contrarily to the winter situation, differences between stations located in the southern arm and stations located in the northern arm are not evident. This may be due to the increase of marine influence inside the estuary in the summer, determining the occurrence of more uniform conditions.



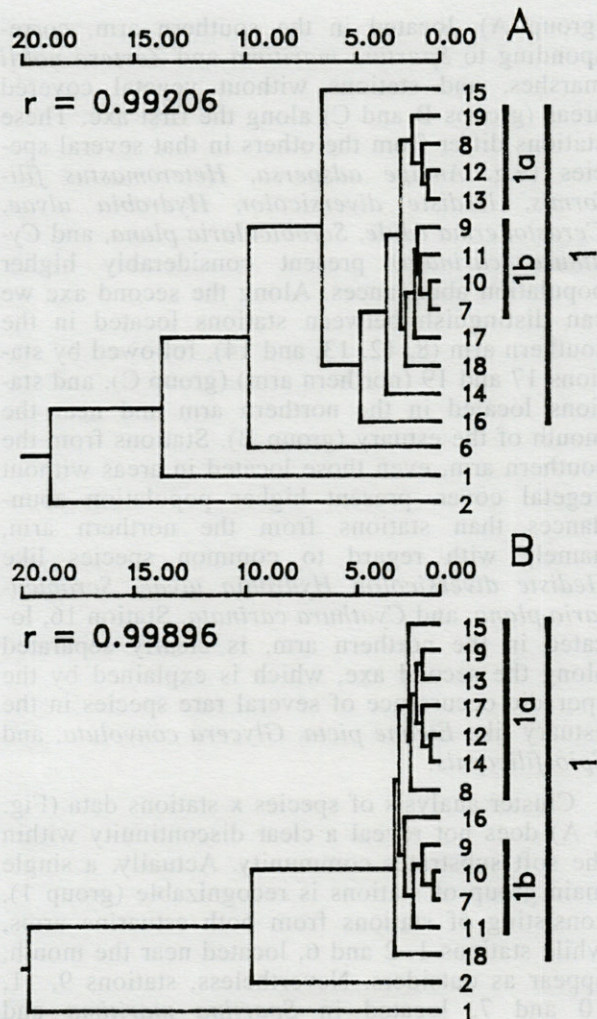


Fig. 5. - Soft substrates community structure : Cluster analysis of species x stations matrices overlooking species found only once. Data analysed using the Chi-Square distance coefficient (Q mode analysis) and the UPGMA clustering method. A - winter situation; B - summer situation. Values of cophenetic correlation coefficients are indicated.

Cluster analysis of species x stations data (Fig. 5 B), like in the winter situation, does not bare a discontinuity within the soft substrates community, and again a single group of stations is recognizable (group 1), consisting of stations from both estuarine arms. Stations 2, and 1, located very close to the mouth, appear as outsiders. Again like in the winter situation, stations 9, 10, 7 and 11, located in *Spartina maritima* and *Zostera noltii* marshes, are assembled (sub-group 1 b), corroborating results from ordination.

### Diversity

The Shannon-Wiener index values calculated for each station in both winter and summer situations (Table III) are consistently higher in stations

located in *Spartina maritima* and *Zostera noltii* marshes, which emphasizes their favourable conditions for the development of abundant populations and higher biodiversity. However, differences between other estuarine areas and seasonal variations in diversity are not outstanding.

### Physical and chemical parameters

With regard to the winter situation, PCA of water physicochemical factors x stations matrices (Fig. 6 A) reveals a clear separation between stations from the northern and southern arms (groups A and B respectively) along the first axis, and a gradient from the mouth (group C) to inner areas of the estuary along the second axis. The variability along the first axis is mainly explained by the distribution pattern of dissolved oxygen and nitrates concentration values (negative side of factor 1),

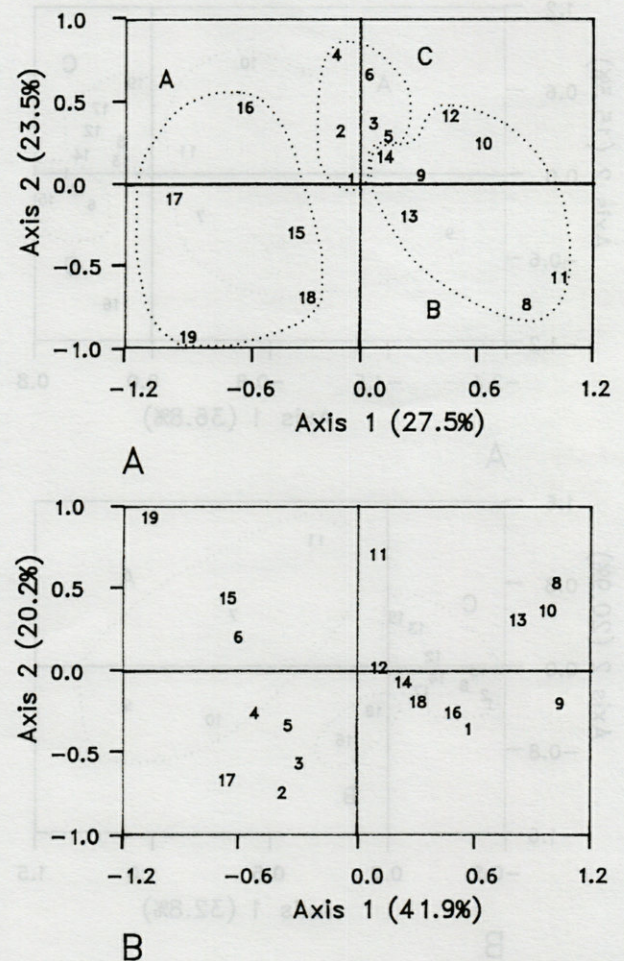


Fig. 6. - Analysis of physicochemical factors of the water from PCA of factors x stations matrices. A - winter situation : Projection of stations against the first two axes,  $r = 0.94057$ . B - summer situation : Projection of stations against the first two axes,  $r = 0.93314$ . The percentage of variability explained by the principal axes is given. Groups of stations pointed out are discussed in the text.



and of salinity and temperature values (positive side of factor 1). Along the second axe, variability is mainly explained by the distribution of salinity, temperature and nitrites values (negative side of factor 2), and of pH (positive side of factor 2). Actually, it is very clear the opposition along the first axe between stations from the northern arm, presenting lower salinities ( $20.8 \pm 6.8 \text{ ‰}$ ) (average  $\pm$  standard deviation) more stable temperatures ( $12 \pm 0.5^\circ\text{C}$ ) and higher concentrations of dissolved oxygen ( $76.5 \pm 11.6 \text{ ‰}$  of saturation) and nitrates ( $0.32 \pm 0.18 \text{ mg liter}^{-1}$ ) during low tide, and stations from the southern arm, presenting higher salinities ( $22.9 \pm 6.7$ ), more variable temperatures ( $12.9 \pm 24^\circ\text{C}$ ), and lower dissolved oxygen ( $70.6 \pm 7.1 \%$ ) and nitrates concentrations ( $0.16 \pm 0.09 \text{ mg.liter}^{-1}$ ).

These results can be explained taking into consideration the hydraulic circulation in the estuary. In the northern arm, the water circulation depends on tides and on the freshwater discharge, determining a faster renewal of the water mass, and consequently higher values of dissolved oxygen. Moreover, since samples were taken during low tide, the river discharge (transporting nutrients from agricultural areas) determined the occurrence of lower salinities and higher nitrates concentration in the northern arm and areas near the mouth. The smaller depth may explain larger temperature ranges found in the southern arm. Finally, the lower concentration of nitrates in the southern arm may be a function of the smaller freshwater discharge.

Due to marine influence, temperature and pH values seem to be more uniform near the mouth of the estuary ( $7.4 \pm 0.4$ ), and nitrites concentration to be low ( $0.006 \pm 0.002 \text{ mg.liter}^{-1}$ ) (probably as a function of stronger oxygenation of the water column).

In the summer situation, the analysis of physicochemical factors of the water do not show conspicuous differences between stations located in both estuarine arms and near the mouth (Fig. 6 B). Stations 2, 3, 4, 5, 6, 15, 17 and 19 (in the northern arm and near the mouth) are opposed to stations 1, 8, 9, 10, 11, 12, 13, 14, 16 and 18 (in the northern arm, southern arm, and near the mouth) along the first axe. The variability along the first axe is mainly explained by lower salinities ( $25 \pm 2.1 \text{ ‰}$ ) and higher values of dissolved oxygen ( $92.8 \pm 6.1 \%$ ), pH ( $7.8 \pm 0.3$ ) and nitrites ( $0.01 \pm 0.002 \text{ mg.liter}^{-1}$ ) found in stations from the negative side of factor 1, and by higher salinities ( $27.3 \pm 2.4 \text{ ‰}$ ) found in stations from the positive side of factor 1.

Along the second axe, stations from the inner areas of both arms (8, 10, 11, 12, 13, 15 and 19) are partially separated from stations located in the downstream section of the northern arm and near the mouth. Temperature is the factor that con-

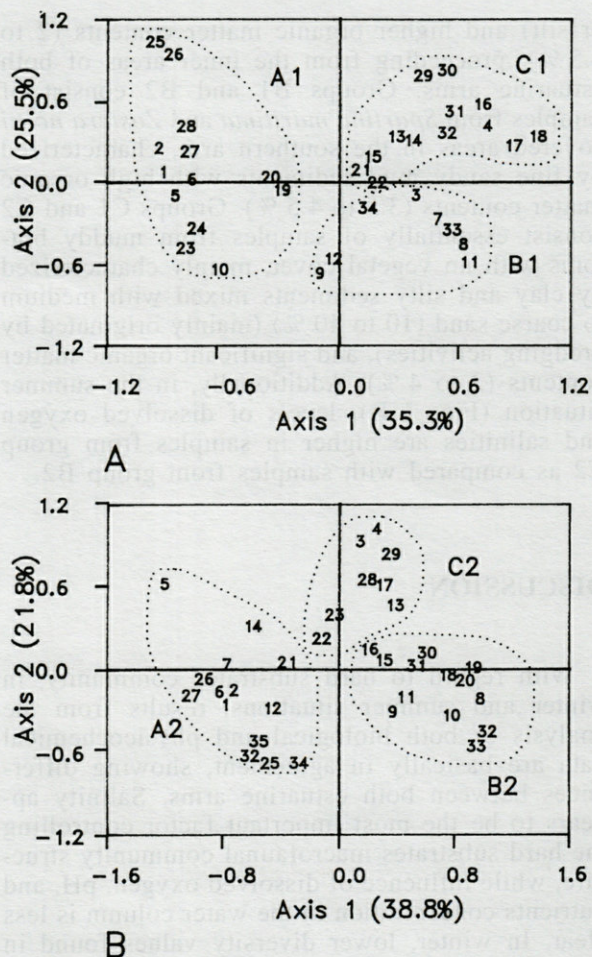


Fig. 7. - Analysis of physicochemical factors of water and sediments from PCA of factors x samples matrices. A - winter situation : Projection of samples against the first two axes,  $r = 0.91314$ ; B - summer situation : Projection of samples against the first two axes,  $r = 0.94261$ . The percentage of variability explained by the axes is given. Groups of samples pointed out are discussed in the text.

tributed the most for this partial separation. Actually, higher temperatures of the water found in estuarine inner areas may be explained by the smaller depth as compared to areas near the mouth.

PCA of water sediments physicochemical factors x samples matrices shows similar results with regard to winter (Fig. 7 A) and summer (Fig. 7B) situations. In both cases, projection of samples against the first two axes of variability allow to consider three distinct equivalent groups. Groups A 1 and A 2 correspond mainly to samples obtained on fine or medium sand bottoms with small organic matter contents (0 to 1.5 %), proceeding from the lower limits of the eulittoral zone (low water level) in the downstream sections of both arms and near the mouth (sand pole). Groups B1, B2, C1 and C2 correspond to samples from bottoms with large fractions of fine particles (clay



or silt) and higher organic matter contents (2 to 4.5 %), proceeding from the inner areas of both estuarine arms. Groups B1 and B2 consist of samples from *Spartina maritima* and *Zostera noltii* covered areas in the southern arm, characterized by fine sandy mud sediments with high organic matter contents (3.5 to 4.5 %). Groups C1 and C2 consist essentially of samples from muddy bottoms with no vegetal cover, mainly characterized by clay and silty sediments mixed with medium to coarse sand (10 to 40 %) (mainly originated by dredging activities), and significant organic matter contents (2 to 4 %). Additionally, in the summer situation (Fig. 7 B), levels of dissolved oxygen and salinities are higher in samples from group C2 as compared with samples from group B2.

## DISCUSSION

With regard to hard substrates community, in winter and summer situations, results from the analysis of both biological and physicochemical data are basically in agreement, showing differences between both estuarine arms. Salinity appears to be the most important factor controlling the hard substrates macrofaunal community structure, while influence of dissolved oxygen, pH, and nutrients concentration in the water column is less clear. In winter, lower diversity values found in the northern arm and near the mouth of the estuary may be due to the combined effects of tides and freshwater discharge, causing strong daily variations in physicochemical factors. From winter to summer, the decrease in freshwater discharge, and consequently the easier tidal penetration, seems to favour the incursion of epifaunal marine species (e.g. *Dynamene bidentata*, *Echinogammarus stoerensis*, *Jassa marmorata*, *Pachygrapsus marmoratus*) inside the estuary and especially along the northern arm. Despite their sparse populations, the intrusion of these species may explain the observed increase in diversity.

The hydraulic circulation in the southern arm depends essentially on tides and on the freshwater discharge of the Pranto river. Consequently, in the summer situation, due to evaporation during low water, salinity values are higher in the southern arm as compared with the northern arm and areas near the mouth. Both daily and seasonal salinity changes are less important in the southern arm (Marques, 1989), which can nevertheless change through the year, from mesohaline (winter situation) to polyhaline conditions (summer situation). The southern arm presents therefore favourable environmental conditions for true estuarine organisms, as defined in McLusky (1989). That is the case of *Echinogammarus marinus*, a key species in the *Fucus spp.* covered areas (Marques &

Nogueira, 1991), which exhibits important population abundances all over the estuary during summer, although appearing more limited to the southern arm in the winter. Therefore, the small decrease in species diversity observed from winter to summer in the southern arm does not correspond to a reduction in species richness, but apparently to an increase of biological activity, since the enhancement of *Echinogammarus marinus* population undoubtedly decreased species evenness.

With regard to soft substrates community, we found also a good agreement between results from the analysis of biological and physicochemical data in both winter and summer situations. The sediment particles size appears to be the most important factor controlling organisms distribution, although organic matter contents, salinity, and dissolved oxygen still seem to play an important role. In fact, higher fractions of fine particles (0.125 mm) and higher organic matter contents tend to correspond to enhanced populations of the most common and abundant species in the estuary (e.g. *Hediste diversicolor*, *Hydrobia ulvae*, *Scrobicularia plana*, and *Cyathura carinata*). Whereas involving other species, a similar situation was observed in other estuaries (Andrade, 1986; Dauer *et al.*, 1987). Temperature, pH, and nutrients concentration in the water seem to have little influence. Nevertheless, although all the water samples were taken over periods of 3 hours around low water time, sampling was not really simultaneous, which surely introduced a bias into the results since tidal effects, especially near the mouth, can change very rapidly the values of physicochemical factors.

In the *Spartina maritima* and *Zostera noltii* marshes, primarily located in the middle section of the southern arm, the most common and abundant species (e.g. *Amage adspersa*, *Heteromastus filiformis*, *Hediste diversicolor*, *Hydrobia ulvae*, *Cerastoderma edule*, *Scrobicularia plana*, and *Cyathura carinata*) present enhanced populations as compared to other areas, and biodiversity is higher. A similar trend have also been observed in other estuarine systems, particularly in *Zostera* covered areas (Almeida, 1988; Whitfield, 1989). Actually, *Zostera sp.* is a macrophyte with roots which can only take up nutrients from the sediments. Consequently, the formation of hydrogen sulphide in the sediments becomes much less important in these areas, and the redox discontinuity layer occurs deeper in the sediments. Therefore, although living *Zostera* is normally not an important food item for macroinvertebrates (Whitfield, 1989), it may provide good conditions for zoobenthos populations.



## CONCLUSIONS AND OUTLOOKING

The analysis of both hard and soft substrates communities structure showed clear differences between the two arms of the Mondego estuary, namely with regard to populations abundance and biodiversity. In both cases a good agreement was found between results from the analysis of biological and physicochemical data.

The observed differences are most probably due to very dissimilar hydrographic characteristics of the two arms. The southern arm is still less affected by human activities and presents more favourable environmental conditions for the development of enhanced populations of true estuarine species. Nevertheless, the southern arm is also shallower than the northern arm, and water circulation depends widely on tides, especially in the summer. For these reasons, we consider that the southern arm appears potentially much more exposed to environmental changes.

Salinity appears to be the most important factor controlling the hard substrates community structure, while sediments granulometry is the most important factor controlling the distributional ecology of soft substrates macrofauna, followed by organic matter contents, salinity, and dissolved oxygen. Other studied factors seem to play a less important role with regard to macrofauna distribution.

*Spartina maritima* and *Zostera noltii* marshes appear to be the richest areas with regard to macrofauna abundance and biodiversity. However, occasional blooms of *Enteromorpha* spp. have been observed in the southern arm, probably as a function of excessive nutrients release into the estuary. Since macrophytes have roots and are only able to take up nutrients from the sediments, it seems possible that macroalgae like *Enteromorpha*, which is able to take up nutrients directly from the water, can take advantage from this situation. Therefore, it seems also likely that an eutrophication process might take place in the southern arm, and in such a case a shift in the benthic primary producers could occur, affecting the structure and functioning of the trophic chain and ultimately the species composition in the community. The present results concern a limited period, and therefore further work will be necessary in order to monitor changes and determine the evolutive trends of the macrobenthic communities in the Mondego estuary.

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## ANALYSES D'OUVRAGES BOOK REVIEWS

L. de VOS, K. RUTZIER, N. BOURY-ESNAULT, C. DONADEY & J. VACELET, 1991. Atlas of sponge morphology (Atlas de Morphologie des Sponges). Smithsonian Institution Press, Washington & London : i-ix, 1-117, US\$35.00 (Benelux, France and Scandinavia : order through Academic Book Promotions, Brouwersgracht 288, 1013 HG Amsterdam, the Netherlands).

What does a sponge look like inside ? There is now an atlas of the anatomy of "the" sponge consisting of stereo SEM images of microscopical and ultrastructural details of its inner space and outer surfaces.

Sponges are way out on a limb in the classification of multicellular organisms through their possession of a unique waterpumping system, absence of clearly definable tissues and great regenerative properties. It is debatable whether sponges constitute colonies of individual cells with task partitioning or whether they are a clonal individuals with a low grade of cellular coordination. Recent molecular studies have suggested that sponges are possibly polyphyletic, although evidence is thin and in view of important synapomorphies of all sponges is probably false. Sponges are exclusively aquatic and largely marine. They contribute significantly to all aquatic ecosystems as filterfeeders of the smallest organic fractions in the open water column, as major space competitors on hard substrates at all depths, as carbonate recyclers through the excavating properties of some specialized groups, as producers of important chemical substances with pharmaceutical properties, and as primary producers through symbiosis with photosynthesizing bacteria. They have been successful as a group since the dawn of multicellular life in the Precambrian and – if present diversity and abundance is a sign at all – will continue to do so in the foreseeable future.

Anatomical studies of sponges are seriously complicated by the loose organization of the sponge cells. Up till a few dozen years ago, only the possession of distinct skeletal arrangements and skeletal elements of most sponges made it possible to make reproducible descriptions of sponges and the systematics is thus entirely dominated by skeletal characters. The occurrence of some taxa without skeletons spurred on the search for additional criteria for sponge recognition. However, light microscope histology revealed relatively few details because of the low cellular of

the paraffin cuts. Transmission electron microscope studies were also complicated and relatively uninformative. In physiological studies better results were obtained by phase-contrast microscopic observations of living sponge fragments or newly hatched juveniles grown between glass slides (so called sandwich cultures).

Scanning electron microscopy, and more especially in combination with careful fixations, the so called freeze fracture technique, followed by critical point drying, has altered all this and it is now possible to include ultrastructural anatomical details to sponge descriptions and classifications. Many of these ultrastructural details appear informative in the classification of sponges.

The Atlas of Sponge Morphology is the harvest of a great number of such studies presented in the form of detailed anatomical SEM photos of all parts of "the" sponge, with alternative images in cases where distinct diversity is found among various sponge groups.

The page sized or half-page pictures are presented with a line drawing on the opposing page which also includes an explanation and discussion. An introductory colour plate and several black and white plates of in situ photographed reef sponges precede a total of 55 black and white plates arranged in the "chapters" Surface, Canal System, Choanocyte Chambers, Mesohyl, Microsymbionts, Reproduction and Skeleton. All three classes of sponges are represented. The photos are of superb quality and give a wonderfully clear understanding of how sponges are built and with very little imagination one may see how the various parts would function in living sponges.

The text is bilingual (English and French), which may seem a bit overdone at first glance. However, it gives credit to the predominantly French input in this particular field of science (four of the five authors are francophone) and at the same time provides English translations of the predominantly French terms for the various parts of the anatomy of sponges.

Through its clear and abundant illustrations, which at the same time provide a wealth of details, the book is a useful buy for general biologists including teachers as well as for sponge specialists; at US\$35.00 it is a bargain.

Dr. R.W.M. Van Soest



DIMENTMAN, Ch., H.J. BROMLEY & F.D. POR, 1992. Lake Hula. Reconstruction of the fauna and hydrobiology of a lost lake. I. Ferber Edit., The Israel Academy of Sciences and Humanities, Jerusalem, 170 p (augmentée de la version en hébreux, 24 p).

Le lac Hula et les marais adjacents, situés dans la célèbre vallée du Jourdain, ont été drainés dans les années 50 en vue d'assainir la région, d'exploiter les ressources naturelles et d'y développer l'agriculture par irrigation.

Ces écosystèmes avaient été activement prospectés au siècle dernier, ainsi qu'avant les travaux de drainage (Hula expéditions) par des scientifiques de nombreux pays, mais les résultats restaient dispersés ou non publiés et n'avaient pu faire l'objet de publication de synthèse avant la réalisation des travaux d'ingénierie de drainage.

Le but des auteurs est donc de rassembler et de synthétiser dans cet ouvrage toutes les connaissances disponibles datant d'avant 1958 (date des premiers aménagements) pouvant constituer l'"état zéro" pré-drainage. Les résultats principaux portent sur les plantes vasculaires, les Poissons, les Amphibiens et les Oiseaux aquatiques; la documentation est moindre en ce qui concerne les Invertébrés aquatiques. Néanmoins, l'inventaire faunistique recense plus de 700 espèces d'Invertébrés et de Vertébrés et en indique la distribution.

Outre cet inventaire et un chapitre sur l'histoire des recherches sur le lac, le livre contient des données au sujet de l'hydrographie, des caractéristiques physico-chimiques de l'eau et des sédiments, de l'écologie des différents biotopes de la vallée, des aspects biogéographiques et des activités traditionnelles de la vallée Hula. Un chapitre indique les phases successives de l'aménagement et fournit une liste des 119 taxons qui n'ont plus été retrouvés depuis l'exécution des projets de drainage. A elle seule, cette liste faunistique souligne la perte en bio-diversité et l'impact désastreux des

aménagements irrationnels. Vient ensuite un court chapitre relatant la mise en réserve naturelle d'une petite partie du lac Hula et des marais les plus voisins et l'eutrophisation progressive de ses eaux. Le livre se termine par une note d'espoir, avec l'éventualité d'une restauration partielle de plans d'eau à l'emplacement du lac et des anciens marais.

La compréhension du fonctionnement des divers écosystèmes et la connaissance de la diversité biologique qui prévalaient avant 1958 exposées dans cet ouvrage pourraient servir de base pour des études ultérieures de ces écosystèmes et permettre des recommandations pour les aménagements des futurs projets de restauration.

La bibliographie mentionne 524 titres; elle est suivie de 3 index (auteurs, taxons, géographie). Des cartes, des photographies et des plans anciens et récents illustrent l'ouvrage.

N. COINEAU

#### Complément à l'article J. ROCHE/To be added to the paper by J. ROCHE

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