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# VIE ET MILIEU

## *Life and Environment*

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## RECRUITMENT IN THE LIGHT OF BIOLOGICAL- PHYSICAL INTERACTIONS IN COASTAL WATERS : RESULTS OF PNDR ACTION AT THE ARAGO LABORATORY IN 1994-1995

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POLYCHAETA  
RECRUITMENT  
LARVAE  
DISSEMINATION  
LIFE CYCLE  
INTERANNUAL VARIABILITY  
PHYSICAL PROCESSES  
CONSTRAINT  
FRENCH AND SPANISH CATALAN  
COAST  
ARCACHON BASIN  
EUPOLYMNIA NEBULOSA  
LANICE CONCHILEGA  
OWENIA FUSIFORMIS

**ABSTRACT** – This paper presents the work of the Arago Laboratory larval biology team developed close to the Laboratory but also in other areas which differ either by the dominant pattern of life cycle (subantarctic area) or by the conditions of water mass transport (Arcachon area on the Atlantic coast). The ultimate objective is the identification of the factors giving rise to the variability of populations. In this context, physical processes seem of primary interest for two reasons : a) they create a structure within which biological processes may proceed, and b) they influence the rate of these biological processes. Their identification and quantification form a fundamental point in our project. In Mediterranean populations of the target species *Eupolymnia nebulosa*, the mucilaginous egg mass sheltering larvae is related to the control of larval dissemination. Broadly speaking, development with reduction or suppression of the pelagic life, is considered as a response to the negative effects of dissemination. In this conceptual frame, life cycle evolution must have gone from benthoplanktonic to holobenthic development. The former is considered plesiomorphic, the latter is expressed by a very wide range of solutions.

A rough scheme of the seasonal variability of recruitment based on larval releasing has been elaborated : spring rise of temperature is of prime importance in the success of recruitment. The study of year to year variations in recruitment shows that short term perturbations may be at the root of the variable success of the species. The biomass level of *E. nebulosa* is determined during short periods of the year such as the prolongation or shortening of the thermocline, and the temporary fall of temperature breaking the smooth profile of the spring rising temperature curve. Consequently, in order to explain variation of recruitment, it is necessary to disregard the annual or monthly means which may suppress or seriously obscure short term deviations.

Larvae-substrate relationships are complex. Larvae settle on heterogeneous substratum. A solid basis or fulcrum is a requisite for coordination of movements which make possible manipulation of particles used for tube building and for feeding. This double constraint relative to the nature of substratum reflects living conditions of adults and not feeding processes. When considered as a whole, the main function of a life cycle is to secure the return of larvae to the adult habitat. This is achieved by several strategies among which the control of dissemination and the development of an elaborate larval behaviour can be pointed out.

POLYCHÈTES  
 RECRUTEMENT  
 LARVES  
 DISSÉMINATION  
 CYCLE DE VIE  
 VARIABILITÉ INTERANNUELLE  
 PROCESSUS PHYSIQUES  
 CONTRAINTES  
 CÔTES CATALANES ESPAGNOLES  
 ET FRANÇAISES  
 BASSIN D'ARCACHON  
*EUPOLYMNIA NEBULOSA*  
*LANICE CONCHILEGA*  
*OWENIA FUSIFORMIS*

**RÉSUMÉ** – Ce travail présente les activités de l'équipe de biologie larvaire du laboratoire Arago. Ces activités sont développées à proximité de ce laboratoire, sur la côte française catalane, mais aussi dans d'autres zones qui diffèrent par le type dominant du développement (province subantarctique) ou par les conditions de transport des masses d'eau (Bassin d'Arcachon sur la côte Atlantique). Le but essentiel est l'identification des facteurs à l'origine de la variabilité, ce qui suppose la connaissance précise des différentes étapes du développement. Dans ce contexte, les processus physiques apparaissent primordiaux pour deux raisons : a) ils créent des structures à l'intérieur desquelles les processus biologiques se développent et b) ils influencent la vitesse de ces mêmes processus. Leur identification et leur quantification constituent un point fondamental de notre programme. Chez les populations méditerranéennes de l'espèce cible *Eupolymnia nebulosa*, la structure mucilagineuse abritant les larves contrôle la dissémination de ces larves. De façon plus générale le développement avec réduction de la durée de la phase pélagique est considéré comme une réponse aux effets négatifs de la dissémination ; dans ce schéma conceptuel, l'évolution des cycles de vie part du développement benthoplanctonique représentant un caractère plésiomorphe en direction du développement holobenthique qui se manifeste par des solutions très diversifiées. Un schéma, encore simple de la variabilité saisonnière du succès du recrutement, a été élaboré à partir des modalités de libération des larves au cours de la saison de reproduction. Ces modalités dépendent fortement des variations de la température ambiante. L'étude des variations interannuelles du recrutement montre que des perturbations à court terme de la température, peuvent être à l'origine du succès variable d'une espèce. Ainsi le niveau de biomasse de *E. nebulosa* est déterminé durant de courtes fractions du cycle de variation de la température : lors d'une prolongation ou d'un raccourcissement de la période de thermocline ou lors de la chute provisoire de la température au cours de l'augmentation de la température printanière. En conséquence, il apparaît nécessaire, pour expliquer les variations du recrutement, de négliger les moyennes annuelles ou mensuelles qui suppriment ou gommement sérieusement les déviations à court terme. L'étude des relations de la larve et du substrat met en évidence la nécessité d'un substrat hétérogène au moment de la fixation ; une base stable est nécessaire pour la coordination des mouvements ; cette coordination rend possible la manipulation des particules les plus fines du substrat, utilisées pour la construction du tube et la nourriture. Cette double contrainte reflète l'habitat de l'adulte et non les procédés de nutrition. Considéré globalement, le cycle de vie a comme fonction fondamentale d'assurer le retour des larves dans l'habitat des adultes, ce qui est réalisé par différentes stratégies parmi lesquelles le contrôle de la dissémination et le développement d'un comportement larvaire élaboré.

## INTRODUCTION

Many of the facets of life-cycles of marine invertebrates are presently studied thoroughly, and lead to very fructifull synthesis. Study of larval settlement of soft-sediment invertebrates (Butman 1987) lead to two hypothesis : importance of active habitat selection and passive deposition of larvae. They were thought as exclusive but are probably compatible : larvae are passively deposited at a large spatial scale but are able to select actively over a much smaller scale. For organism distribution and animal-sediment relationships Snelgrove & Butman (1994) emphasize on hydrodynamic and sediment-transport processes, in addition to grain size, organic content, number of microorganisms and sediment stability. The pre- and post-settlement processes have been compared (Olafsson *et al.* 1994). Formerly Thorson (1946) stated that the longer duration of planktonic life for planktotrophic species induced a greater intrinsic variability in settlement rate and

adult population than that exhibited by lecithotrophic species. Presently (Beukema 1982) abundant evidence, based on demographic features, action of epibenthic predators or hydrodynamic disturbance, food limitation and carrying capacity, exists to show that post-settlement mortality is efficace in the density regulation of soft sediment invertebrates. Different perspectives have also been addressed to study the planktonic phase : identification (Bhaud & Cazaux 1987), dispersal (Bhaud 1993 ; Scheltema 1986), gene flux and its importance for evolution (Jablonski & Lutz 1983 ; Lenaers & Bhaud 1992 ; Scheltema 1981), plasticity of the planktonic life length (Bhaud 1990 ; 1993). Oocyte growth and process of adult maturity control the number of larvae available for the formation of the next generation. Consequently, environmental and endocrine controls of maturity have been thoroughly investigated (Olive 1984 ; Franke & Pfannenstiel 1984). However, in spite of perfectly cibled studies, tentatives of integration of isolated events of life-cycle are not numerous. At best, synthesis dealt with the

significance of variability in developmental patterns (Chia 1976; Giangrande *et al.* 1994; Grahame & Branch 1985; W.H. Wilson 1991) and processes related to a precise part of the life history are kept independent. For instance little is known about how initial patterns of larval settlement are related to the distribution of adults. However, we feel this point is a central problem which we suppose to link the disseminative ability of the larvae, the constraints when they settle, the kind of care brought to propagules, the potential fecundity, and the habitat of adults in terms of location and area. We know (Thorson 1966; Boesch *et al.* 1976; Marciano 1994) that numerous species settle in a much broader variety of habitats than in which they can survive. What means this difference between adult area and first benthic recruits? This paper presents some results related to this research field.

This paper may also draw attention to the activity of Arago Laboratory larval biology team, working close to the Laboratory but also in other areas which differ either by the dominant pattern of life cycle (subantarctic area) or by the conditions of water mass transport (Arcachon area on the Atlantic coast). The present results are for a large part a contribution to the French National Program on Determinants of Recruitment among which objectives, the identification of factors giving rise to numerical variability of populations can be pointed out. The methods are based on the analysis of "critical" phases of the life-cycle: oogenesis, larval settlement and first benthic juveniles. The starting point of our program was the presence of perfectly delimited benthic communities in the Bay of Banyuls (Fig. 1). The problem deals with the formation and perennity of these communities. How is the selection of larvae achieved in relation to their respective communities? How do these animal communities sustain themselves? Two complementary strategies were adopted: (1) to break down the life cycle of targeted species involving the comprehensive study of this life cycle; (2) to develop experimental studies on characteristic points, considered both in the field and in the laboratory. This second point required a large program which included the development of an automatic sampling station, a hydrodynamic canal and an actographic device. The limiting conditions of Mediterranean environments without tides induced us to integrate other conditions of transport by water masses far from Mediterranean Sea. We have not limited the location of studies to the Bay of Banyuls and we also have enlarged the range of developmental patterns and used different species of polychaete (from the families Terebellidae and Owenidae), for which a large body of knowledge already existed.

The main target species is the polychaetous annelid *Eupolyornia nebulosa* (Montagu), which is

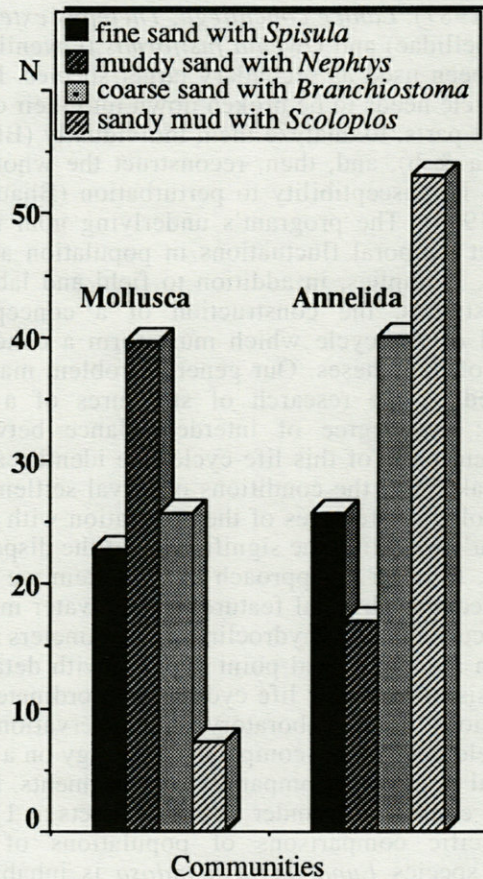


Fig. 1. – When visiting different communities in the bay of Banyuls, variation of number (N) of Annelids and Molluscs species is reversed, apart from fine sand with *S. subtruncata*. Segregation of species may take place through selective settlement of larvae from a common pool visiting all the communities or after settlement by progressive selection of benthic juvenile individuals. This situation is a typical example of one worth studying by larval biology, *in situ* and in the laboratory, with identification of settlement and dispersive constraints.

Fig. 1. – En se déplaçant dans différentes communautés de la Baie de Banyuls, le sens de variation du nombre (N) d'espèces d'Annélides et Mollusques est inverse, exceptés les sables fins à *S. subtruncata*. La ségrégation des espèces s'effectue-t-elle au stade larvaire qui constitue un pool commun visitant les différentes communautés ou au stade postérieur à la fixation par sélection progressive des individus benthiques juvéniles? Cette situation constitue l'exemple typique méritant d'être traité par étude de la biologie larvaire, en milieu naturel et au laboratoire, avec identification des contraintes de fixation et de dissémination.

widely distributed in the Bay of Banyuls (North Western Mediterranean Sea) but is also present throughout the world. An English Channel population has also been studied, allowing us to compare between different reproductive strategies: mucous egg-masses in the Mediterranean versus direct development in the English Channel (Bhaud

*et al.* 1987). *Lanice conchilega*, *Thelepus extensus* (Terebellidae) and *Owenia fusiformis* (Oweniidae) have been used as secondary target species. Each life-cycle needs to be broken down into their component parts, to analyze them individually (Bhaud 1994 a & b), and, then, reconstruct the whole to gauge its susceptibility to perturbation (Bhaud & Cha 1993). The program's underlying goal is to predict temporal fluctuations in population abundance. It implies, in addition to field and laboratory studies, the construction of a conceptual model of life-cycle which must form a coherent body of hypotheses. Our general problem may be defined as the research of structures of a life cycle: the degree of interdependence between different parts of this life-cycle, the identification of weak links, the conditions of larval settlement, the biological features of the population with year to year variability, the significance of the dispersal phase. In order to approach this problem we take into account physical features of the water mass: both currents and hydroclimatic parameters; we use an autoecological point of view with detailed analysis of a precise life cycle; we coordinate observations in the laboratory and observations in the field and we use comparative biology on a latitudinal transect. Comparative experiments have been considered under three aspects: 1) intraspecific comparisons of populations of the same species *Eupolyornia nebulosa* is inhabiting different climatic environments: the English Channel and the Mediterranean Sea. 2) interspecific comparisons of two species with different larval strategies: *Eupolyornia nebulosa* and *Lanice conchilega*. 3) comparisons and coordination of experiments in laboratory and in the field.

## MATERIAL AND METHODS

### 1. Lay-out of experiments in the laboratory

Larval potentialities have been studied in the laboratory with the aid of two technical devices: 1) a hydrodynamic canal for larval selection of sediments; 2) an actograph for recording passive and active displacements. The present study on mechanisms of accession to benthic life by planctonic larvae is indebted to the works of Wilson (1951, 1952, 1958) for relations between larvae and substratum; and to those of Nowell & Jumars (1984), Butman (1987), Butman *et al.* (1988), Jonsson *et al.* 1991, Andre (1994) for introduction of hydrodynamic conditions when larvae access to the bottom. Comparisons with several of these authors (see for instance Butman *et al.* 1988) command attention taking into account the similarity of goals and several differences with regard to the operative modalities. These differences affect specially the length of incubation (from 2 to 4 hours as opposed to several days in our protocol), modality of sowing larvae in the enclosure

from a precise location situated up-stream of the experiment tray – formed with 25 alternating small boxes filled with two types of sediments – and last, the simultaneous use of inert particles mimetic of larvae. Accordingly, two points are investigated: the nature of the final part of the fall curve and the possible rearrangement in the distribution of larvae between the sediments. However, experimental length is both too long in order to register the nature, either passive or active, of the larval fall, and also too short to estimate ability to choose among the sediments or to allow expression of benthic behaviour. For our part, we intended to be pragmatic and we searched for the possible existence of preferential situations during larval settlement (Bhaud 1990; Bhaud *et al.* 1991; Cha & Bhaud 1991). We saved a sufficiently long incubation time to allow for the demonstration of substratum selection which supposes the development of several tests by larvae eventually leading to a new spatial distribution. This length of experimentation also allowed the development of interindividual relations, which displayed for first built tubes contagious, neutral or negative distribution. Very possibly we did not study settlement (a biological step during development, independent from the observer) but recruitment (observer-defined) because, in the context of definitions given in literature, our first observed distributional pattern reflects a new organisation, considered by several authors as an indication of recruitment. However, the observer is not prevented from condensing the sampling method to try to get superposition of settlement and recruitment. This is what we have done; we analysed changes in spatial distribution and in mortality during access to benthic life, which allowed us to telescope first contact, settlement and recruitment (Cha 1990, 1994). Actography is a device used for studies of larval displacement in still water and flumes. A set of video cameras is attached on step motors driven by a 2 or 3-axis tracking system with a 12 microns resolution. The digitized signals are read by a video capture board and analyzed by a real time software developed by J.C. Duchêne. After shape extraction and recognition, the amount of detected movement is used by the computer to displace the cameras in order to keep the object in a central position within the working frame. Displacements are recorded on a real time basis by the computer. A working field corresponding to the overall length of the tracking translators may be defined with a starting point. In studies involving the use of a flume, this allows repetitive automatic recordings of sequences of larval displacement. The system is size independent: the ratio "object pixel size" on "video camera field width" depends on the optical lens used on the camera (Nozais 1991; Duchêne & Nozais 1993, 1994).

### 2. Experiments in the field integrating several topographic situations

A last point of method must be added. Limitation of the Mediterranean environment, particularly due to the absence of tides, induces the integration of specific topographic situations on the Atlantic coast. The presence of the Marine Station led us to study the influence of the topography formed by the Arcachon Basin and conditions of larval circulation through the channel con-

necting the Basin to the Ocean. Three reasons justify studies on recruitment in this site. It allows better than elsewhere; 1) the identification of hydrodynamic processes during recruitment; these processes are not always propitious to successful recruitment; 2) the integration of concepts of theoretical ecology, for instance significance of reproductive patterns in an ecological gradient developed over a short distance, or significance of plasticity of several developmental phases like metamorphosis not linked to a precise morphological stage; 3) development of natural experiments on larval sowing on varied substrata at the mercy of ocean water intake. This Basin is a lagunar environment communicating with the open sea. The tides originate an oscillatory movement of the water that can result in a larval exchange between both ecosystems. The Basin is characterized by a marked hydroclimatic gradient from the oceanic to the inner neritic waters. Also, an increasing number of species with benthic development is observed in the inner bottoms, associated with the reduced area of the specific adult habitat. The relationships between the mode of development and the range of larval dispersal can thus be fruitfully studied in this area (Bhaud & Duchêne, 1995). A comparative study on the delay of the metamorphosis can be done in this area in terms of stimulation by the charge with suspended particles; in the Basin, planktonic stages are submitted to benthic stimuli and their transfer to the benthos is fast; on the contrary the planktonic life is prolonged in the open sea where quite old larvae can be collected for the same species. This observation indicates a plasticity at the end of the planktonic life (Bhaud *et al.* 1990) showing that the size at metamorphosis is not constant in spite of the contrary hypothesis often advanced for the establishment of reproduction models (Grant 1983).

### 3. Two basic features of the target species

Before describing results, two aspects of the biology of our species must be considered because they are important elements of our method and are always present in the background of our research.

Firstly, a basic element in this research is the developmental pattern of the target species. Definition of several terms (larvae, juvenile, metamorphosis, as seen for settlement and recruitment) are subject to variation. This is the consequence of independence of states of developmental traits. In other words, they are not perfectly correlated, for instance pelagic development is associated with either feeding or non feeding development; likewise autonomous developmental pattern called "non-feeding development" is associated with direct development as well as indirect development. As it has been proposed formerly (Bhaud, 1987; Mc Edward & Janies 1993) three criteria or characters are used to define developmental patterns: 1) morphological change with or without a temporary structure specific to the larva depending on whether development is direct or indirect; 2) behaviour as in feeding or non feeding; and 3) ecology connected with spatial location of development: in the water column when pelagic, or close to the substrata when benthic. These three traits by combination allow to define 8 patterns. Application of these definitions to *E. nebulosa*, shows that this species changes its developmental pattern. At the begin-

ning of the reproductive period, development is indirect, pelago-benthic and endotrophic; larvae work on their own energy reserves when released; but when formed at the end of the reproductive period, the developmental pattern is direct, holobenthic and exotrophic; for feeding, larvae work on the environment after escaping from the egg mass. This species constitutes a model allowing us to understand the evolution from one developmental pattern to an other.

Secondly, we must distinguish between larval choice and opportunity. Throughout our present work we will use the expression larval choice, this is for simplicity rather task more than accuracy. A choice assumes a comparative action developed on short time and space scales which is exerted in the sensorial sphere of each individual, between alternative proposals simultaneously accessible. The analysis of the reorganisation of larval distribution indicates that this is not the case. The settling process is developed in time and it seems more correct to consider an ecological opportunity at the origin of the substratum selection. An other trait of the choice concept is the projection in the future and in this sense, choice constitutes an element of the reproductive strategy. But for *E. nebulosa* this strategy is missing: larvae must be confined in space to avoid a successful recruitment in the center of the Bay of Banyuls, followed by failure of benthic juveniles. Selection of sediment by larvae is accomplished on the short-term and does not assure the future of individuals. The result of the transition from the planktonic to the benthic phase is unrelated to the subsequent success or failure of recruitment. A contrast becomes visible between limited requirements in terms of grain size and shape defining a large potential zone for larval settlement, on the one hand, and a spatially limited adult area, on the other hand. These two features are made compatible by the existence of an egg mass in the life-cycle. Retention structures and larval plasticity are of great importance in the subantarctic environment found in Kerguelen archipelago, characterized by a narrow range of temperature variation and severe dissemination constraints (Duchêne, 1991, 1992).

## RESULTS

In the frame which has just been defined, we choose to expose some results on the following points: the importance of physical parameters of environment and particularly of water mass movements considered in different space scale; function of egg-mass in the life-cycle; selection of sediment by larvae during settlement; regulation and interannual variation of biomass with qualitative and quantitative modelisation, identification of connections between different features of the life-cycle.

### 1. Biological-physical interactions

Physical processes create the conditions for many important biological processes. They create

structures within which biological processes may proceed, and they influence the rate of these biological processes. Physical processes act on a large range of spatial scale. We have explored three of them: 1) physical conditions at the water-sediment interface, which determine the parameters of the benthic boundary layer, 2) physical conditions on the local scale of Banyuls Bay and 3) regional physical conditions in the subantarctic area.

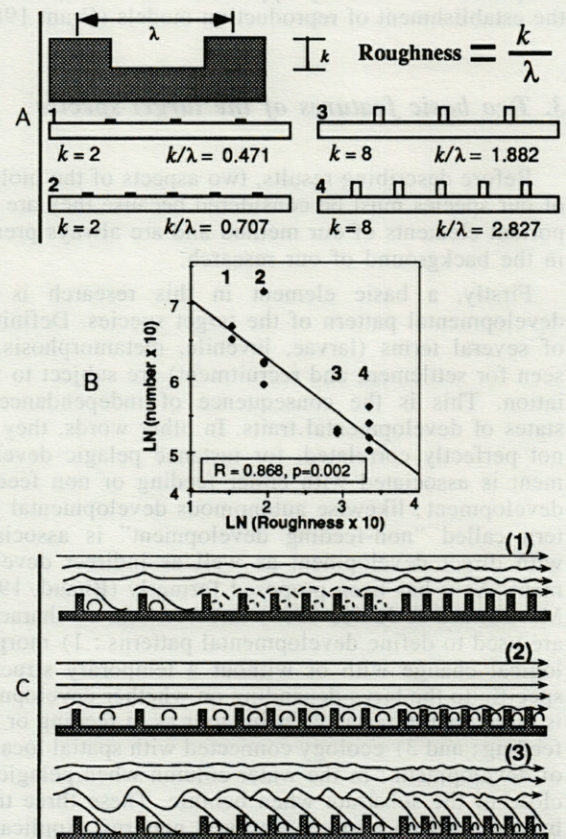
To approach physical conditions at the benthic boundary layer we firstly identified abilities of larvae to select substrata on a bottom subject to zero rugosity, and to a shear stress lower than  $0.15 \text{ cm.s}^{-1}$  (Cha 1994). In these conditions, larvae were able to reject an unsuitable substratum and to return to the water column. Secondly, roughness created by height and distance of a set of obstacles, was introduced. Sediment and larvae were introduced successively which represent natural conditions of a temporary high perturbation. Settlement areas were controlled by obstacles; larvae were limited in their exploratory space; they were obliged to stay close to the obstacles. They were not able to settle on the area covered with a reduced quantity of sediment. Consequently, tubes were observed only on areas with a thick layer of sediment. For an intermediate cur-

rent rate of  $8.6 \text{ cm.s}^{-1}$  a relation between roughness and number of settling larvae has been established (Fig. 2).

The specific situation of Banyuls Bay, sheltered from the dominant N-W winds, isolates partially internal water masses. The first thematic attempts to define the role of internal circulation in relation to the external general circulation of the western Golfe du Lion, on the dissemination of invertebrate larvae. The goal is the identification of spatial barriers in life-cycle in order to recognize spatial limitation of a population. The numeric modelling of currents in the Bay of Banyuls (Fig. 3) is based on flow simulation solving Navier-Stokes, 3 dimensional temperature and salinity equations, with a two equation closure model for the turbulence ( $\kappa$ - $\epsilon$  model). Several steps are in progress: a) the bay is considered during homogeneous sea conditions without wind and with a residual component of the liguro-provençal current; b) on the same basic scheme, dominant wind conditions from NW are added; c) the vertical circulation with upwelling is integrated. We dispose actually of the first model step which shows a bottom recirculation area and a surface flow going off the coast (ArnoUX & Fraunié 1994; Fraunié 1994).

Fig. 2. - Experimentation in two phases and simulating larval settling after a period of high turbulence (flow rate at the surface:  $18.5 \text{ cm.s}^{-1}$ ). Larvae are introduced after this turbulence (flow rate at surface:  $8.6 \text{ cm.s}^{-1}$ ). The bottom of the enclosure is furnished with obstacles defining the roughness (A). For conditions of flow rate in this experiment, there is a negative correlation (B) between roughness and number of settled larvae. C: illustration of the benthic boundary layer in terms of the flow rate at the surface when larvae are introduced; 1: average flow rate already illustrated in part B with number of settling larvae depending of roughness; this relation disappears when flow rates are higher (2) or lower (3); in these two situations the variation range of roughness is not large enough to differentiate larval settlement: with a high rate (2), larvae cannot pass between obstacles and with a low rate (3) larvae reach the bottom in all conditions of roughness.

Fig. 2. - Expérimentation se déroulant en deux phases et simulant la fixation des larves après une période de forte turbulence (vitesse de surface  $18.5 \text{ cm.s}^{-1}$ ). Les larves sont introduites après cette période de turbulence (vitesse de surface  $8.6 \text{ cm.s}^{-1}$ ). Le fond de l'enceinte expérimentale est garni d'obstacles définissant la rugosité (A). Pour les conditions de vitesse de l'expérience, il existe (B) une relation négative entre le facteur de rugosité et le nombre de larves fixées. C: illustration de la couche limite en fonction de différentes conditions de vitesse au moment de l'introduction des larves; 1: vitesse moyenne déjà illustrée par la partie B avec pénétration des larves en fonction de la rugosité; cette relation disparaît pour une vitesse plus forte (2) ou plus faible (3); dans ces deux cas la gamme de variation de la rugosité n'est pas suffisante pour différencier la réception larvaire; en vitesse élevée (2), les larves ne peuvent pénétrer entre les obstacles et en vitesse faible (3) les larves atteignent le fond dans toutes les conditions de rugosité.





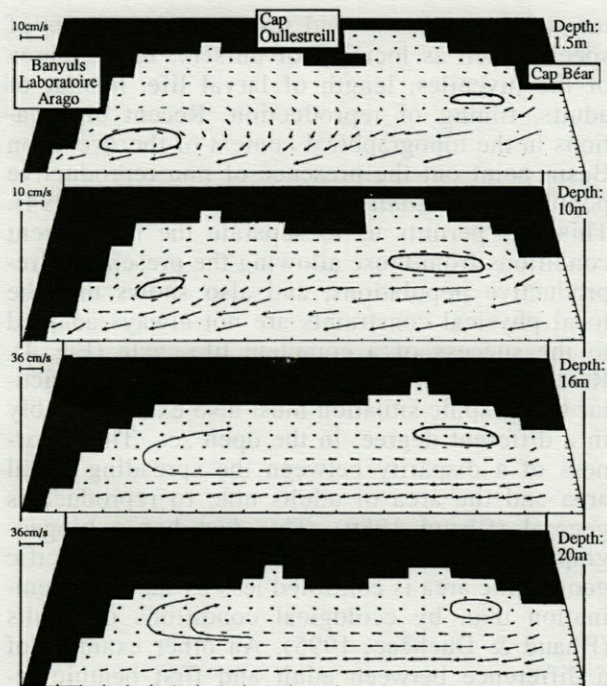


Fig. 3. – Numeric modelling of currents in the Bay of Banyuls. The graphs show the bay during homogeneous sea conditions without wind and with a residual component of the liguro-provençal current. The model shows a deep gyre and a current moving off the coast on the surface. For each depth, the length of the arrows is proportional to the scale on the left side but some arrows, too long if drawn in scale, are represented by points. The presence of rotary motion areas has been underlined.

Fig. 3. – Modélisation numérique de la circulation des courants en Baie de Banyuls. Les figures représentent la baie pour des conditions de mer homogènes, sans vent avec comme seul forçage, la présence du courant Liguro-Provençal. Le modèle met en évidence une zone de recirculation en profondeur et un flux qui s'éloigne de la côte en surface. Pour chaque profondeur, la longueur des flèches est proportionnelle à l'échelle présentée sur la gauche du plan mais les flèches qui auraient été trop longues sont remplacées par des points. La présence des gyres a été surlignée.

Physical environment considered on a regional scale controls several biological traits. For instance, the hypothesis of emergence of a direct development pattern governed by constraints of dissemination is perfectly illustrated by study of the Polychaeta from the Kerguelen province (Duchêne 1982, 1983, 1984, 1989; Bhaud & Duchêne 1988; Bhaud & Duchêne 1995). For species with known life-cycles, the most frequent development is direct, with large size eggs. This situation of the subantarctic area furnishes a strong correlation between direct development and the presence of exacerbated disseminative conditions. In the same area but for other groups (*i.e.* Crustacea), indirect

development is conserved. In this case, however, a retentive structure is formed by holdfasts of giant kelps like *Macrocystis* and *Durvillea* (Bhaud & Duchêne 1988). These examples of preservation of planktonic egg size in a structure of retention are particularly conclusive in an adaptation for reduced dissemination.

## 2. Function of egg masses in the life cycle of *E. nebulosa*

Laboratory experiments showed that larvae were able to use the finest fraction of the heterogeneous sediments present in the axis of the Bay of Banyuls (Bhaud & Cha 1994): muddy sand with *Nephtys hombergii* and fine sand with *Spisula subtruncata* community. However, adults are never been collected in these communities. They can be collected in a narrow belt (from 0 to 20 m depth) at the periphery of the Bay where blocks and boulders are progressively embedded in the soft substratum. Accordingly, it does not appear desirable that larvae by their dissemination reach the axis of the Bay which is not suitable for the adults. How then reconcile the absence of the species in the axis of the Bay with successful settlement on the same substratum? The negative aspect of this dissemination in the axis of the bay, followed by a successful larval settlement and a failure of juvenile grown, has been explained by studying the dragging of juvenile tubes built on soft substrata of *Nephtys hombergii* community in a hydrodynamic canal. According to the thickness of the sediment, tube anchorage is different. When tubes are arranged on a sedimentary bed, (*e.g.*, the center of the Bay), they can be easily washed away by hydrodynamic strength. On the other hand, when tubes are anchored on a thin layer of the same sediment, deposited on a hard substratum (*e.g.*, the periphery of the Bay), they offer a higher resistance to the erosion by currents (Cha 1994, Bhaud *et al.* 1995). These results transposed to the field suggest that the function of gelatinous egg-masses is to reduce the ability of larvae to spread and to prevent then settlement in the axis of the Bay. Even if larvae are able to settle on this area of Bay, it does not appear desirable that they reach this area which is an unsuitable habitat for adults. Mucilaginous structures shortened the length of the planktonic larval life thus securing settlement inside adult habitat areas. In the Kerguelen environment the egg masses reduce the pelagic life of *Thelepus* larvae to a maximum of 24 hours thus preventing larval drift off the coasts of this isolated island located in the westward currents of the southern Indian Ocean (Duchêne 1993).

### 3. Larvae-substratum relationship when settling

The transition from the plankton to the benthos has been investigated experimentally using *E. nebulosa* (Bhaud & Cha 1994). Tests on artificial and natural sediments lead to the following results. 1) Larvae are able to displace particles with a greater weight than their own, but this is possible only if larvae have access to a perfectly immobile platform. 2) Larvae require two kinds of substrata for settlement, one forming support and allowing coordination of movements, the other being tube-building material. This dual constraint, solid base plus manipulable building particles, is related to the nature of substrata. Such statement differs from previous conclusions, suggesting that only grain size was important for settlement. This has been demonstrated for the subantarctic terebellid *Thelepus extensus* (Duchêne 1982). Our observations also show the importance to settlement of the thickness of the sediment layer (Bhaud *et al.* 1995).

Larvae of a given stage of development are able to manipulate only a well defined size-range of particles. This range increased as development proceeded, and the result was the progressive utilisation of increasing grain sizes. This reduced selectivity of aged-larvae corresponded to an increasing ability to use particles. The older the larvae are when they touch the substratum for the first time, the weaker their ability to return to the water column is, when the substratum is unsuitable. In the same way, the suitable size range of particles increases with age, and the probability of a successful settlement increases. As a consequence, a delay in the contact of planktonic larvae with substrata is not necessarily a negative point, because the probability to settle successfully increases with this delay. *E. nebulosa* does not form the sole model for larva-substrate relationships. Recently, we observed that larvae of *O. fusiformis* are able to metamorphose on a very large range of sediments and even without soft substrata but in contact with hard substrata (notwithstanding numerous partially metamorphosed larvae collected in the water column). The acquisition of the first benthic morphology seems non related to the nature of substrata. The ability of larvae to select at a fine spatial scale seems non-existent. The first tube is secreted by the benthic worm and is made of mucus. From this step on, the nature of the sediment (size of grains, content in organic matter) may play a role in forming the definitive distribution of the adult population. In the case of *Thelepus* larvae released from the cocoons over a muddy substrate the presence of hard structures, mainly the adult tubes and *Macrocystis* canopy appears to be essential (Duchêne 1983).

Until now, we have worked with considering a perfect adjustment between the hydrologic struc-

ture of water masses and several characteristics of species such as location of nursery, feeding area of the juveniles, length of larval life, habitat of adults, timing of reproduction. Recent observations in the topographical context of the Arcachon Basin point out the presence of non reproductive populations of *Lanice conchilega* (Marcano 1994). This fact permits us to separate the recruitment conditions from those allowing the presence of reproductive populations, and also shows that the local physical constraints are not always adapted to the success of a complete life-cycle (Fig. 4). Retention process like that observed in a particular topographic situation must also exist, probably in a different degree, in the open sea. This clearness of a disparity between the spreading larval area and the area of adults able to reproduce is general (Bhaud 1989). This fact has a biogeographic consequence: variation of the specific geographic area is controlled less by larval dissemination than by ecological conditions of adults (Bhaud & Duchêne, 1995). An other example of a difference between adult and first benthic recruitment areas is given by a survey developed in the Bay of Blanes, Spanish Catalan coast (Pinedo *et al.* 1995; Sarda *et al.* 1995). The population structure of *Owenia fusiformis* from this Bay was studied from March 1992 to March 1993 (Fig. 5). Seasonal pattern in abundance was characterized by a peak during spring (recruitment period), a sharp decrease through summer and lower densities during autumn and winter. This population was stable from August to March with 500 ind m<sup>-2</sup> approximately. High density of small-sized individuals were observed at three stations during the recruitment period followed by high mortality. Adults were clearly detected at St 3 and more rarely at St 1; they disappeared completely at St 2. Area covered by young benthic recruits is larger than adult area. Settlement of larvae seems to be associated with a range of sediments larger than sediments associated with adults. As Thorson (1966) pointed out, many species set in a much broader variety of habitats than those in which they can survive (*cf* also Boesch *et al.* 1976). If there is not correspondence between distributional areas of both first benthic recruits and reproductive adult populations, the direct consequence is the obligation during benthic studies to specify the age of collected benthic specimens. Characteristics of a sediment containing young recruits or juvenile stages of a given species are not necessarily a specific trait; only the location of the reproductive phase is relevant.

### 4. Oocyte growth

From a long-term survey carried out in the Bay of Banyuls (North Western Mediterranean Sea),

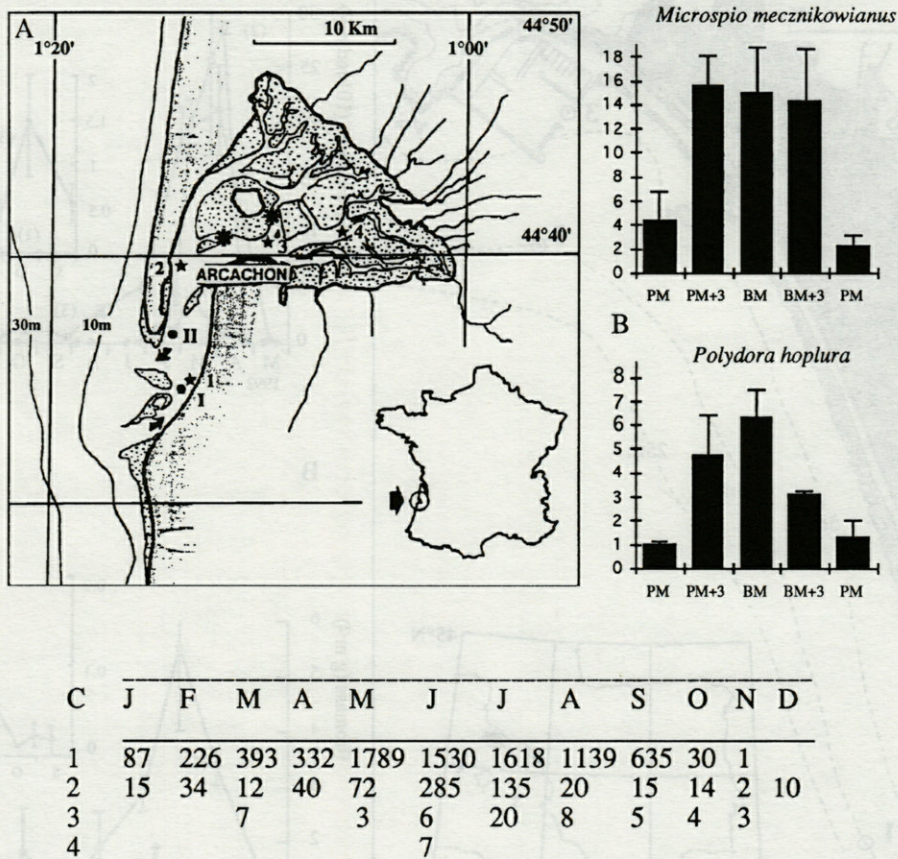


Fig. 4. – A, map of Arcachon Basin with position of sampling stations (1, 2, 3 and 4) of *L. conchilega* larvae (from Cazaux 1973) and position of two stations I and II at the entrance of the Basin for larval collection during tidal cycle. Two asterisks mark presence of young benthic *Lanice conchilega* inside the Basin. B, Variation during a tide cycle of larval density for *Microspio mecznikowianus* and *Polydora hoplura* collected in the entrance of the Basin. From high tide to low tide, the Basin empties then after low tide, it fills up. At the collecting station the timing of larval passage is connected with the distance of the water mass containing the larvae from the collecting station. Passage of *Microspio* larvae is registered at a maximum level as early as half flood or half ebb tide, indicating their position inside the Basin (external neritic area). On the other hand, *Polydora* larvae collected at a maximum level during low tide originate from the internal neritic area; they are last to leave the Basin and first to enter it. The symmetry of the collections indicates that the water mass leaving the Basin is recaptured by the tide wave for alimentation of the Basin during the following tide cycle. Each black block is the mean from two neighbouring stations I and II in the fairway entrance of the Basin and is based on 2 to 4 values (modified from Marcano 1994). C, Table of seasonal collect of *L. conchilega* larvae at stations 1, 2, 3 and 4 on the map A, indicating clearly their origin outside the Basin; some larvae will settle inside the Basin (stations marked by asterisks) but these individuals do not reach the reproductive step.

Fig. 4. – A, carte du Bassin d’Arcachon avec situation des stations de récolte des larves de *L. conchilega* 1, 2, 3 et 4 (d’après Cazaux 1973) et des stations I et II des passes d’entrée utilisées pour la récolte des larves au cours des cycles de marée; les deux astérisques figurent la présence de jeunes *Lanice conchilega* à l’intérieur du Bassin. B, Densités larvaires des deux espèces *Microspio mecznikowianus* et *Polydora hoplura* récoltées dans les passes d’entrée du Bassin. A partir de la pleine mer et jusqu’en basse mer, on assiste à une vidange du bassin puis entre la basse mer et la pleine mer à son remplissage. En une station donnée, l’ordre de passage des larves est lié à la distance de la masse d’eau qui contient les larves par rapport à la station d’observation. Le moment du plus fort passage des *Microspio* est situé dès la mi-marée montante ou descendante indiquant leur position à l’intérieur du bassin dans la zone néritique externe. En revanche le maximum des *Polydora* est enregistré en basse mer indiquant la présence des adultes dans la zone interne du bassin; ils sont les derniers à sortir et les premiers à entrer. Dans les deux cas, la symétrie des récoltes indique que la masse d’eau qui sort est reprise par la marée pour alimenter le bassin au cours d’un nouveau cycle. Chaque barre verticale noire représente la moyenne de deux à quatre valeurs obtenues aux stations I et II situées dans la passe d’entrée du Bassin (Marcano 1994, modifié). C, Tableau de récolte saisonnière des larves de *L. conchilega* aux stations 1, 2, 3 et 4 de la carte A indiquant clairement la source des larves à l’extérieur du Bassin; certaines larves se fixeront à l’intérieur du Bassin (station indiquée par les deux astérisques); cependant ces individus n’atteindront pas l’étape de la reproduction.

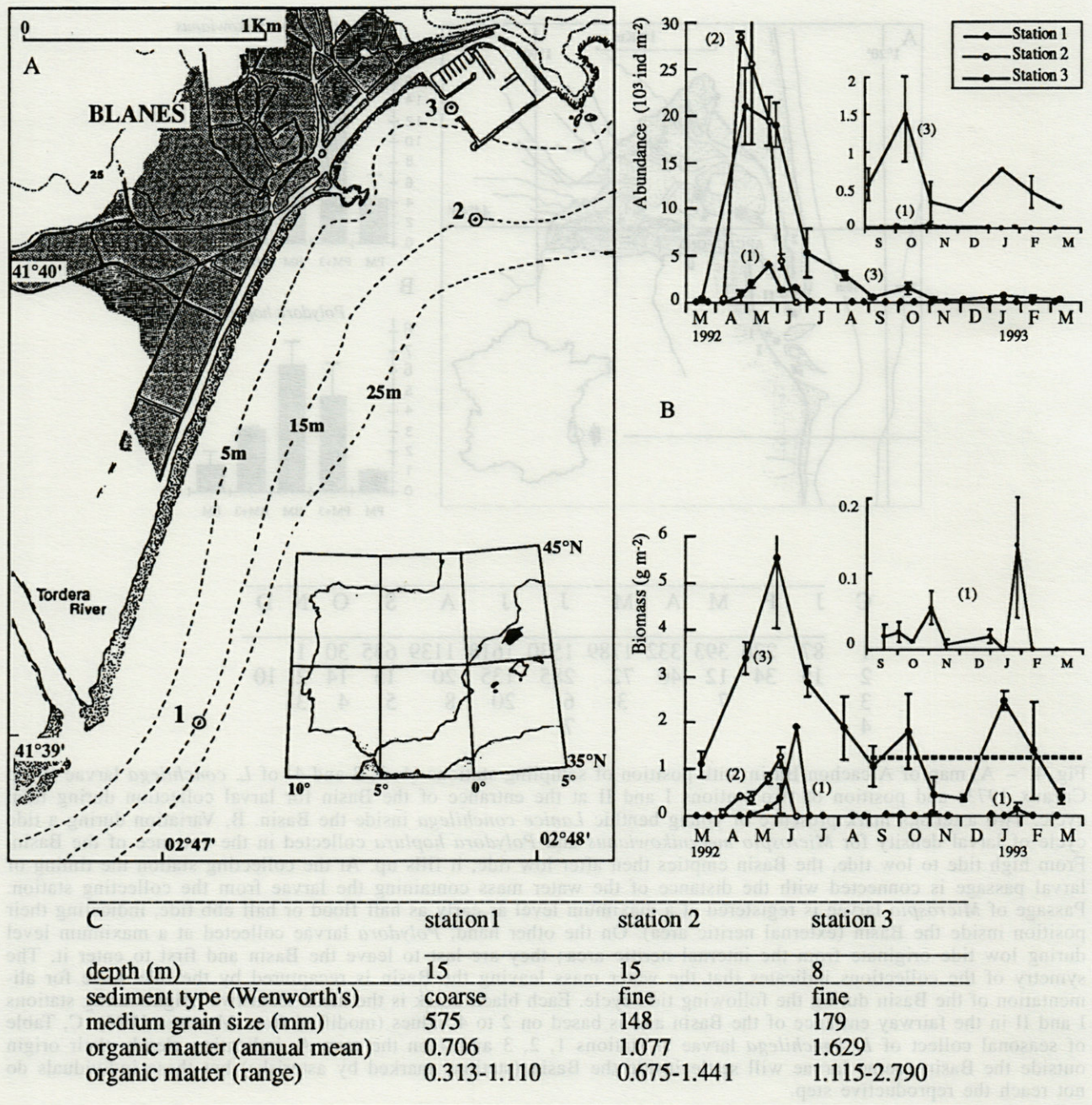


Fig. 5. – A, map of the area of Blanes with three sampling benthic stations. B, seasonal variation of abundance (above) and biomass (below) of *Owenia fusiformis*. The dotted curve superimposed from September to March on curve 3, bottom graph, shows as an hypothesis the mean of monthly biomass which is relatively stable. C, abiotic parameters of the three stations : mean and range of organic matter is given as % of dry weight.

Fig. 5. – A, carte de la zone de Blanes avec emplacement des trois stations de prélèvement benthique. B, variation saisonnière de l'abondance (graphique du haut) et de la biomasse (graphique du bas) d'*Owenia fusiformis*. Le trait en pointillé superposée sur la courbe 3, graphique du bas, indique à titre d'hypothèse la moyenne mensuelle de biomasse relativement stable. C, paramètres sédimentaires des trois stations : moyennes et extrêmes de matière organique sont exprimées en % du poids sec.

the coincidence of an advancement of the spawning period with a delay of the thermocline breakdown was described. These persistent high temperatures could act on the gamete development by stimulating oocyte growth, subsequently cau-

sing the advancement of cocoon release. To achieve a better understanding of this interactions between temperature and oocyte growth in *E. nebulosa*, an experimental approach to the individual level was applied (Cha, Martin & Bhaud 1995).

Three methodological steps were progressively used: 1) The identification of net growth component of intracoelomic oocyte population. 2) The identification of differential growth rates related to mean oocyte sizes. 3) The determination of statistically comparable pairs of oocyte size distributions at the onset of the experiment. Three main results were found: 1) A positive response of oocyte growth to the maintaining of high temperatures can be detected. 2) This positive response could not be demonstrated for all females but only for certain individuals. 3) The lack of non significant level population responses to changes of a given parameter should not be immediately attributed to the absence of any kind of response. It could eventually be related to the degree of variability among individuals. The existence of changes from discoid oocytes to spherical newly spawned eggs has also been noted for *E. nebulosa* (Martin, Cha & Bhaud 1995). Although there are not direct demonstrations, the existence of a size-dependent selection mechanism during the spawning process was strongly supported. This mechanism results in an effective selection of a short size-range of large mature oocytes and can be directly linked with the life-cycle strategy of the Mediterranean *E. nebulosa* populations. The implications of its existence in the English Channel populations remains unclear. The results underline the importance of considering the real form of gametes when dealing with the study of life history strategies viz. oocyte growth linked to different environmental or endogenous controllers or spawning mechanisms (Martin, Cha & Bhaud 1995).

##### 5. Age at first maturity

The comparative study of the English Channel and the Mediterranean Sea populations of *E. nebulosa* (Bhaud *et al.* 1987) displayed a difference in the age at first maturity which was 1 and 2 years, respectively. The origin of this difference remained unknown; it could be the consequence of a reversible adaptation or the expression of a genetic trait. Breeding experiments in the laboratory showed that age at first reproduction (2 years) estimated in the Mediterranean from the number of maxima in the frequency diagram of adult weight, was not a definitive feature. Effectively, his age has been put forward to 1 year by modification of breeding conditions. These modifications deals mainly with the quantity and quality of food (Cha 1994). These results incited us to propose 2 models, both able to take into account gonads development in terms of available food. 1) The energetic transfer to the gonads is only possible after soma reaches a given size limit; in this case morphological development and

size are always the same when first maturity is reached. 2) The second model is based on the accumulative rate of external energy; this input rate is variable; if reduced, the whole energy is attributed to somatic growth; above a given rate, a fraction of energy input is attributed to gonads, and consequently reproduction may occur early. In this model, the body size can be different from one individual to another when maturation begins. The choice between these two models will be dictated by examination of morphological structures at the time of first maturity.

##### 6. Life cycle regulation and year to year variation: qualitative model

The sequence of biological events in the life-cycle of *E. nebulosa* is superimposed on the hydroclimatic features of the seasons (Bhaud 1994b; Bhaud *et al.* 1995). The adjustment between these two series is governed by the placement of the growing period of juveniles during the spring rise of temperature. The demographic structure of juveniles is, then, distributed in a narrow range of sizes which involves weak competition between individuals. This regulation is open to external influences. A delay in the fall thermocline break down and an early rising of spring temperatures have two consequences: the displacement in time of the formation of egg masses and the lessening of the spring temperature gradient. The final result is a conservation of size structure of juveniles in a large range which produces interindividual competition. The sequence of events forming the life-cycle is the result of a long term developed balance. This balance is interpreted by two coordination processes identified in the life-cycle: 1) limitation of dispersal by egg masses, related to the narrow area of adult distribution; 2) size structure of juveniles. The need for reduced competition between juveniles, observed in the English channel as well as in the Mediterranean, controls the position of biological events on the hydrological calendar. Once this adjustment obtained, the remaining biological events are placed in relation to particular values of physical parameters but this situation may not be ideal. This allows to introduce the notion of imperfection or price to pay for instance existence of a spread period of larval formation apparently not coordinated with development of a mucous protection or poor success of early released larvae in spite of a protection. The coordination or adjustment of biological events on the hydroclimatic calendar is not insensitive to external influences. The oocyte growing phase and the period of releasing larvae from a cocoon are sensitive to temperature deviations in fall and spring, respectively. The earlier the cocoons develop, the more important the

spreading of larvae and the more limited their success. The source of year to year variability in settlement and adult biomass (the success of a life-cycle) appears to be located in the interference of two types of determinisms : 1) evolutionary biology, which addresses ultimate causes such as the specific adjustment of biological events superimposed on the climatic calendar; 2) functional biology which addresses proximate causes and deals with a physiological function on a short term scale such as oocyte growth linked with temperature. Absence (in the Atlantic and English channel) or presence (in the Mediterranean) of a mucous egg-mass in the life-cycle appears to be independent of the coordination setting in action the two circles representing biological and hydrological events. It seems to be linked to the control of dissemination. In the Mediterranean, where the adults are distributed in a very limited narrow belt perpendicular to the coast, a reduction of larval dissemination appears to be relevant. On the other hand, in the English channel, at the term of a maximal dissemination, larvae are still in an area where adults are collected and control of dissemination seems to be less significant.

**7. Year to year variation : quantitative model**

Study of year to year variations in recruitment shows that short term perturbations may be the root-cause of the variable success of species. The biomass level of *E. nebulosa* is determined during short periods of the year (Bhaud *et al.* 1995a). A methodological consequence obliges to disregard the analysis of annual means which may suppress or seriously obscure the short-term deviations. It is an obligation to use fine scale observations and to look at act precise periods of life-history when modeling. Our first models were proposed for a spawning period which extended during the spring increase of temperature (Fig. 6). In an earlier publication (Bhaud *et al.* 1995b) five reproductive traits were integrated in a first step model : 1) distribution of egg-masses during the spawning period with 4 peaks occurring during this period, at intervals of 28 days; 2) range from 30000 to 5000 larvae per egg-mass, at the beginning and end of the reproductive period, respectively; 3) temperature curve from January to June established from a 10 year series of observations; 4) the pattern of larval release from the mucilaginous masses (Duchêne & Nozais, 1992); and 5) the lo-

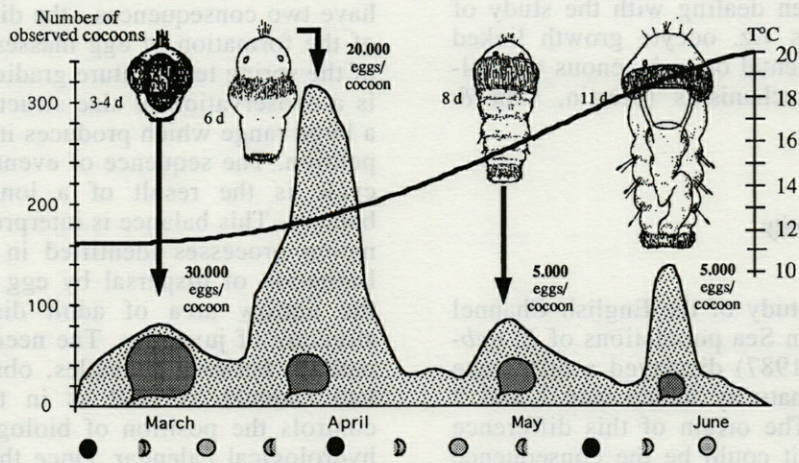


Fig. 6. - Variation during the reproductive period of the number of egg-masses (distributed in 4 distinct peaks), and variation of the morphology of larvae when escaping from mucilaginous masses. Morphological steps are function of the temperature. The mean number of larvae per egg-mass is given from five year observations. Variation of morphology and ability to disseminate when larvae are released is a factor of outstanding importance for success of recruitment. Timing of peaks of egg masses depends on moon phases which are not superposable from year to year; consequently border between months is not given. Variation of sea water temperature is given from four year observations (Bhaud 1991; Duchêne & Nozais 1993).

Fig. 6. - Variation au cours de la période de reproduction du nombre de masses mucilagineuses distribuées en 4 pics, et de la morphologie des larves au moment de leur libération; cette morphologie est fonction de la valeur de la température. Le nombre moyen d'œufs par masse muqueuse est donné à partir de cinq années d'observation. La variation de la morphologie et de la capacité de nage lors de la libération des larves est une composante essentielle du succès du recrutement. L'emplacement des maximums des masses d'œufs dépend des phases de la lune qui ne sont pas superposables d'une année à l'autre; en conséquence les limites entre les mois ne sont pas indiquées. La courbe de variation de la température de l'eau de mer repose sur quatre années d'observations (Bhaud 1991; Duchêne & Nozais 1993).

cation of the spawning period : the first peak more frequently located in early March, the latter at the end of May. Posteriorly, a modulation in the releasing period of larvae was introduced. The new model was based on 1000 cocoons distributed during the reproductive season following data already given (Bhaud *et al.* 1995) and derives from models developed on *Thelepus* (Duchêne 1990, 1992). Two steps were described (Fig.7). First, the seasonal variation of the number of larvae leading a planktonic life of 2 days at least can be estimated. Accordingly, these larvae were free to move away from the area inhabited by adults of the preceding generation. The seasonal variation of the number of larvae directly reaching the substratum after being released from cocoons is also represented (in Fig.7 with the graph between January and April on the top diagram and from March to June on the lower diagram). The earlier the formation period of the cocoon, the higher the number of released larvae at a planktonic stage, and the lesser the probability of a successful settlement. Thus, when the reproductive season begins in January, the number of swimming and benthic larvae reaches  $29 \times 10^6$  and  $0.45 \times 10^6$ , respectively. When reproduction is delayed until March, the same figures are  $23 \times 10^6$  (swimming larvae) and  $6.8 \times 10^6$  (benthic larvae). Secondly, we represent in rectangles A, B and C, the relative variation of protected larvae (inside the cocoon), planktonic larvae (free swimming larvae), and last, benthic larvae (or tubicolous larvae). The place of the maximum is given by a vertical straight line and the detail of the releasing by a bell shaped curve. During the reproductive season, the proportion of free larvae, at first important in A, decreases in B and disappears in C. In this last situation, this means that larvae when released reach the tubicolous benthic life directly.

Until now, a fixed number of oocytes was considered as well defined; and their distribution along reproductive period was modeled accordingly. In the future we will apply a refined model to the variation in oocyte formation by integration of the growing phase during fall; in this particular case, between year variations will depend on the duration of the thermocline.

## DISCUSSION

### 1. Significance of planktonic larval phase in a life-cycle

In attempting to understand the significance of planktonic larval life, we turned our research in the following direction : species does not select larval planktonic life as a dissemination mean ; on

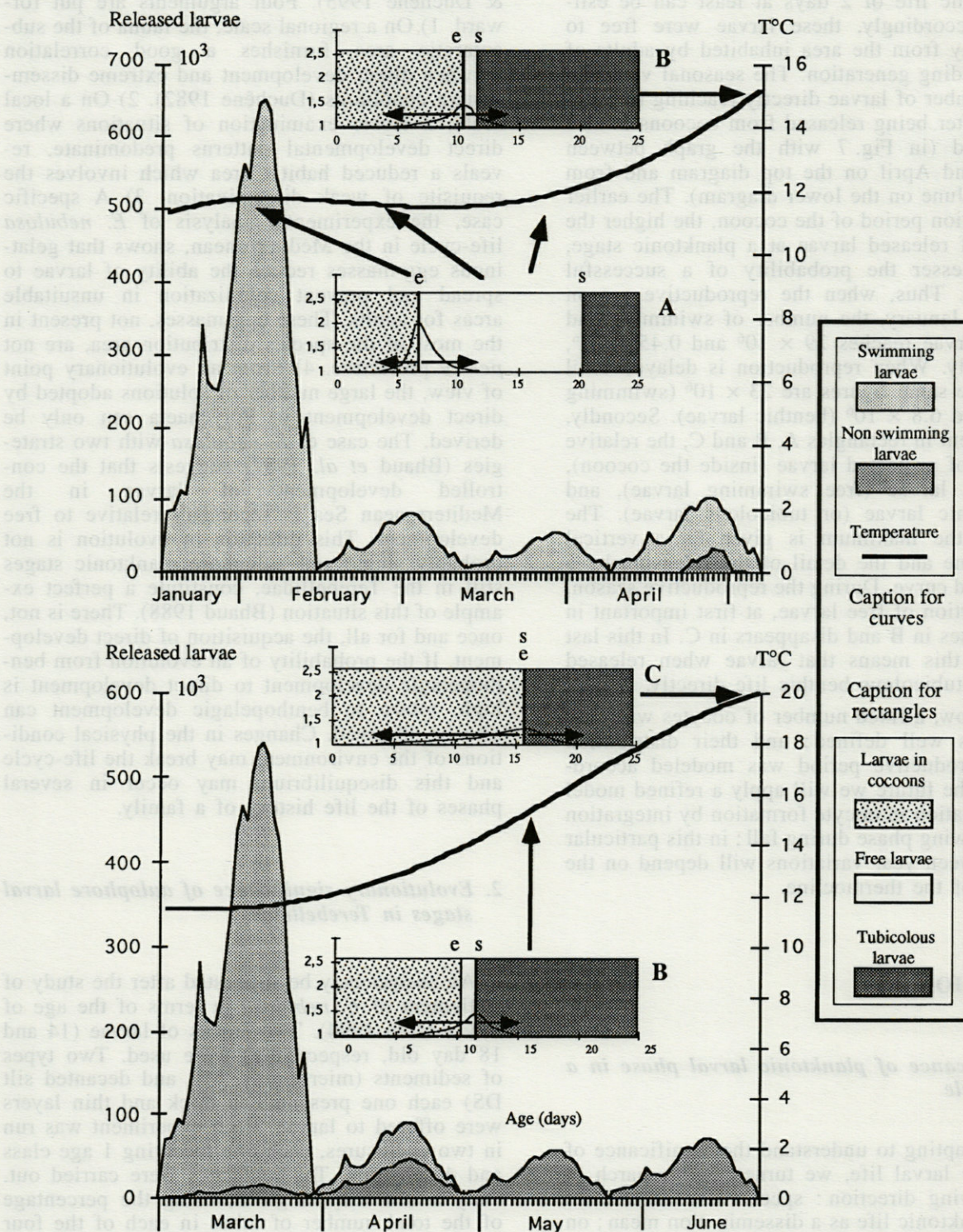
the contrary, species attempt to break free from this constraint. At the present time, research on recruitment is concerned, to a large extent, with the consequences of larval planktonic development within the physical structures of water masses which appear negative for a successful recruitment. On an evolutive time-scale, this coupling raises the question of the origin of direct development. This pattern has been considered as an answer to constraints of dissemination (Bhaud & Duchêne 1995). Four arguments are put forward. 1) On a regional scale, the fauna of the sub-antarctic area furnishes a good correlation between direct development and extreme disseminative conditions (Duchêne 1982). 2) On a local scale, a closer examination of situations where direct developmental patterns predominate, reveals a reduced habitat area which involves the requisite of weak dissemination. 3) A specific case, the experimental analysis of *E. nebulosa* life-cycle in the Mediterranean, shows that gelatinous egg-masses reduce the ability of larvae to spread and prevent colonization in unsuitable areas for adults. These egg-masses, not present in the most of the species distribution area, are not *per se* protective. 4) From an evolutionary point of view, the large number of solutions adopted by direct development in Polychaeta can only be derived. The case of *E. nebulosa* with two strategies (Bhaud *et al.* 1987) suggests that the controlled development of larvae in the Mediterranean Sea is secondary relative to free development. This direction of evolution is not probably single and aulophore planktonic stages still in the Terebellidae, constitute a perfect example of this situation (Bhaud 1988). There is not, once and for all, the acquisition of direct development. If the probability of an evolution from benthopelagic development to direct development is high, return to benthopelagic development can also be observed. Changes in the physical conditions of the environment may break the life-cycle and this disequilibrium may occur in several phases of the life history of a family.

### 2. Evolutionary significance of aulophore larval stages in Terebellidae

An answer may be suggested after the study of settlement of *E. nebulosa* in terms of the age of larvae (Cha 1994). Two stocks of larvae (14 and 18 day old, respectively) were used. Two types of sediments (microbeads, MB and decanted silt DS) each one presented in thick and thin layers were offered to larvae. Each experiment was run in two enclosures, each one receiving 1 age class and 4 substrata. Ten replicates were carried out. Only a summary is given, using the percentage of the total number of tubes in each of the four

sediments. Younger larvae preferred the thin layer of sediment. Presence (in DS) or absence (in MB) of organic matter was not a source of variance. The nature and the thickness of the sediment were of lesser importance for old than for young larvae. An age difference of four days resulted in highly modified settlement. Older larvae were less susceptible to differences between substrata; they had a greater settlement capability than younger

larvae, and they were distributed more evenly between different sediments. Likewise, observation of settlement during a prolonged time of incubation, in presence of several grain sizes of the same sediment, displays the progressive development of the ability to use this sediment. In this experiment, the sediment not used after 24 h is perfectly used at the end of 3 or 4 days (Cha 1994). This suggests the acquisition of new abilities by larvae.





Due to development larval size increase, parapodia are more numerous, first tentacles larger, mucous secretions more intensive and uncinal plates more numerous. These modifications explain why a sediment first unusable becomes usable (Fig. 8). These experiments show that a planktonic individual having an advanced developmental stage when contacting substrata for the first time, has a larger probability of settling than a younger one. Constraints linked to an uncompleted morphological organization are suppressed. Lengthening the planktonic life during stages with juvenile morphology results in the decrease of settlement constraints. The presence of mature *L. conchilega* in the Bay of Banyuls in a large range of sediments (sand with *Branchiostoma lanceolata*, muddy sand with *Nephtys hombergii*, detritic communities with *Venus ovata* and *Auchenoplax crinita*) is a consequence of this lengthening. The situation of aulophore larvae Terebellidae is interesting because: 1) It means a return towards a benthopelagic life-cycle. 2) The planktonic larva is not a trochophore but a postlarva; this is what Jägersten (1972) names a secondary planktonic larva. 3) The evolution does not come back throughout the same way used during the first transformation (Bhaud 1988); the second acquisition of a planktonic stage is made by a new

process (Dollo Law). 4) Conditions for recruitment are probably original. This last point is supported by three reasons: 1) the first contact with substrata is early and takes place when larvae build detritic tubes; 2) the second contact concerns a post larval or juvenile stage, from a morphological point of view; 3) the ability to use a large spectrum of sediment for building tubes is increased as showed formerly.

### 3. Planctonic larvae in the water mass

Planktonic larvae develop in a fluid, highly disseminating environment. In order to understand larval drift, an important element in recruitment and biogeography, a method could be used to track the water masses trajectory following the hypothesis that larval drift may be deduced from water flows. However, several difficulties arise.

1) It is generally accepted that pelagic larvae are able to control the level of their position in the water column. On the horizontal plan, swimming autonomy is clearly lower than the flow rate observed in the field. Consequently, it was proposed that horizontal dissemination is passive. This opinion is a simplification: by vertical migration, larvae are able to use different flow direc-

Fig. 7. — Model of seasonal variability in the planktonic larval emission from egg masses. The model is based on data collected over several years. The curves show the numeric variation of the number of larvae released from 1 000 egg masses for different spawning seasons and, accordingly, for variable temperatures. The upper graph presents the most common case: a spawning season starting in early March. The lower graph is for a spawning period starting in mid-January. The number of larvae with a longer planktonic larval life is more important when spawning occurs early in the year. Rectangular graphs present the length, (days), after egg-mass production of three steps: protected development in the egg mass, free planktonic stages and tubicolous life. The relative importance of these steps is given in terms of different temperatures: A, B and C are for 12 °C, 15 °C and 20 °C, respectively. The date of release (e) is variable and this variability is indicated by horizontal arrows. The associated curve indicates the intensity of larval releasing from the egg-masses. The onset of tubicolous life (s) is assumed from observations on behaviour of tube building and from the disappearance of larval vitelline reserves. Sensitivity of larval growth to varying temperatures is responsible to a large extent for the planktonic larval phase. It contributes defining the position of the metamorphosis, either within (when temperature is high) or outside (when temperature is low) the protected cocoon. In the first case, the local recruitment is particularly successful.

Fig. 7. — Modélisation de la variabilité saisonnière dans l'émission larvaire planctonique. A partir d'une situation moyenne obtenue sur plusieurs années d'observations, la modélisation permet de simuler la libération des larves à partir des cocons. Les courbes présentent la variation numérique du nombre de larves libérées à partir de 1 000 cocons en fonction des périodes de ponte et par conséquent de la température ambiante; de plus on a dissocié les larves planctoniques libres et les larves n'ayant pas ou plus de possibilité de nage. Le graphique du haut représente le cas le plus fréquent: celui d'une période de ponte qui débute au mois de mars. Le graphique du bas s'applique à une période de ponte qui débute en janvier. Le nombre de larves ayant une vie planctonique longue est plus important si la ponte débute tôt dans l'année. Les médaillons rectangulaires représentent la durée en jours, après la production du cocon, des trois phases dites protégée, libre et tubicole en fonction de la température: A, B et C correspondent respectivement à 12 °C, 15 °C et 20 °C. La date d'émission (e) est variable. Cette variabilité est figurée par deux flèches horizontales, qui matérialisent l'étendue de la libération, et par une courbe qui donne une idée de l'intensité de cette libération à partir des cocons. Le début de la phase tubicole (s) est déduit des observations comportementales liées à la construction du tube et aussi déduit de la disparition des réserves vitellines. La sensibilité de la croissance larvaire à la température est largement responsable de la durée de vie planctonique et contribue à positionner la période de métamorphose soit à l'intérieur de la masse mucilagineuse lorsque la température est élevée, soit à l'extérieur du cocon lorsque la température est basse. Dans le premier cas, la phase planctonique est supprimée ce qui favorise le recrutement local.

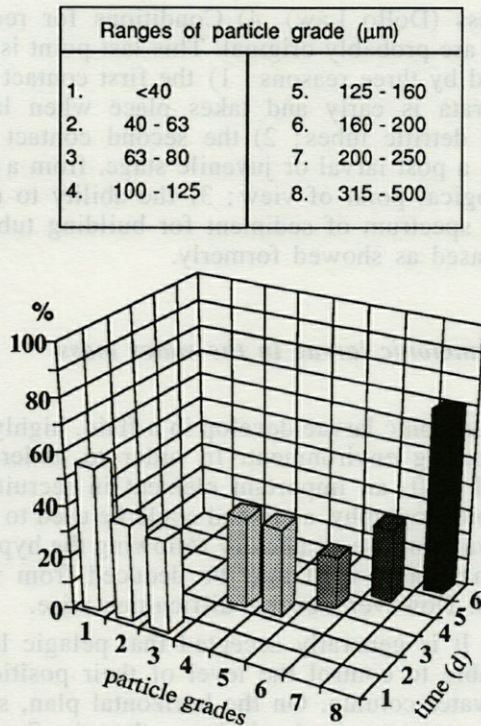


Fig. 8. - Progressive use by *E. nebulosa* of increasingly large sediment particles. Average of three experiments. For each size of sediment particle we have shown (%) the maximum number of tubes built and the time required to obtain this maximum after the introduction of larvae. The bigger the size of the particles, the later the tubes appear.

Fig. 8. - *Utilisation progressive de grains de sédiment de taille croissante par E. nebulosa. Moyenne de 3 expériences. Pour chaque taille de grain, on a indiqué (%) le nombre maximum de tubes construits et le délai de ce maximum après l'introduction des larves. Plus la taille des grains augmente et plus l'apparition des tubes est tardive.*

tions and on a regional scale there is a decoupling of the length of planktonic life and the distance covered from location of larval emission to settling point.

2) In order to include larvae in a model, we must define some characteristics of their displacement like size and density. However, displacement rates are difficult to determine when a visual or actographic recording clearly indicates something other than a direct run towards the bottom or the surface. Larval movements reveal slowing, acceleration, reversal, immobility, in quick alternation with upward and downward runs linked with mucous secretion or modification of behaviour (Nozais 1995). Larvae may vary its fall rate only by opening setigerous bundles after contact of a foreign particle. Finally, when at the proximity of substratum they can reach the water column after testing the sediment-water boundary if it is not clear enough supposing a fluid middle layer of

fine particles. Briefly, if each elementary segment of the run may be characterized by a given rate, it is only possible to chart the whole displacement at the price of a simplification based only on extreme points of the course.

3) We suppose now that the obstacle of the variability on a short-time scale and also the variability linked with morphological development, can be resolved by determining the relatively constant fall rates from narcotized specimens. This method allows the introduction of artificial particles with the same fall rate than larvae in a hydrodynamic enclosure. Active or passive fall of larvae when reaching two kinds of sediment arranged in different squares of a checker may then be tested. However, the use of these mimetic particles supposes a short length for incubation of living larvae in the experimental enclosure. It cannot pass beyond some minutes if we wish the distribution achieved at the end of the fall to be correlated only with active or passive falls and not altered by new benthic larval distribution following the fall. Accordingly, larvae do not appear as passive as it may be thought from rapid observations. Consequently, larval travel cannot be deduced from mean flow or residual vectors.

## CONCLUSION

We wish to emphasize only the two following points.

**How to consider life-cycle parameters?** It seems more interesting and profitable to examine the significance of the length of life of planktonic larvae integrated with other traits, rather than its absolute value. The level of this dissemination in the loss or the maintenance of individuals is probably connected with the size of the area suitable for larval reception, that is to say the size of the area suitable for adults. In such a situation, a species with a reduced distributional area and a weak capability to disseminate, would not work differently from another species which would lead a planktonic larval life for several weeks without going outside its adult distributional area, either because this adult area is very important or because larvae are put through antispreading hydrological structures. Life-cycles or life-histories have not got an unitary character but are composed by several groups of traits evolving for their own part. These traits are neither completely in concert nor completely independent. Our target species develops two groups of traits; from one group to another, these elements are independent. The coupling of these traits may be difficult. For instance, the existence of gelatinous egg-masses may be in connection with control of larval

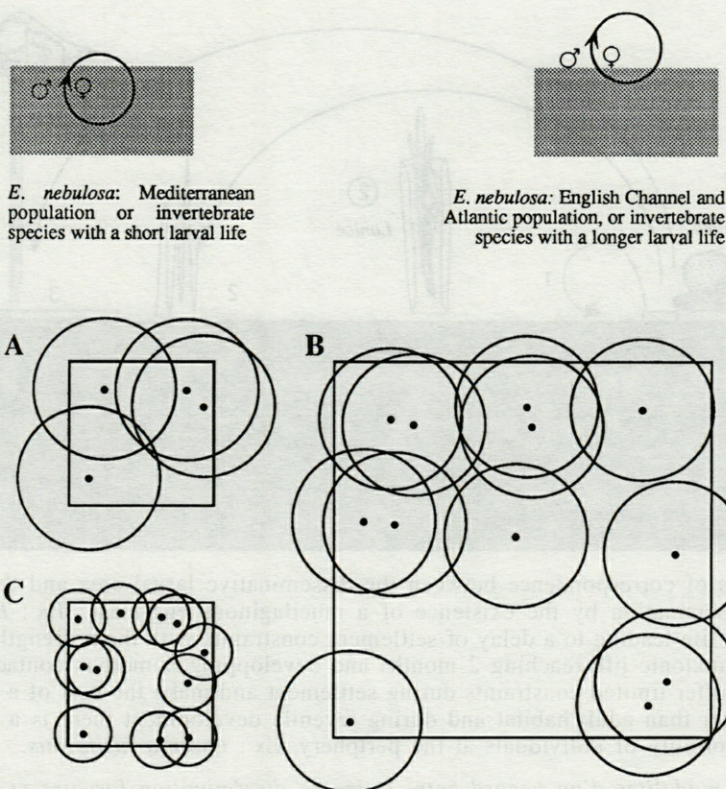


Fig. 9. – Co-ordination in *E. nebulosa* between surface area inhabited by adults (squares) and presence or absence of egg masses; these structures delay larval escaping therefore limit the ability to disseminate (circles). Supposing that the ability to disseminate in the Mediterranean populations (A), is similar to that of the Atlantic populations (B), the expected result would be : in A nearly all larvae would reach the borders of the habitat, thus the maintenance of the species would be unlikely. Species response is as follows : Mediterranean populations are able to overcome the constraint of small habitat by reducing the ability to disseminate (C); egg-masses become essential. This basic model does not take into account possible behavioural adaptations to hydrodynamic structures by larvae.

Fig. 9. – Co-ordination chez *E. nebulosa* entre la grandeur de l'aire des adultes (carrés) et la présence ou l'absence des masses d'œufs; ces structures retardent la libération des larves et par conséquent limitent la capacité de dissémination (cercles). En supposant que la capacité de dissémination des populations méditerranéennes (A) et d'Atlantique (B) soient similaires, le résultat prévisible est qu'en A l'ensemble des larves atteint la limite de l'habitat, ce qui rend improbable le maintien de l'espèce. La réponse de cette dernière en Méditerranée est la réduction de la dissémination (C) par l'existence de sac muqueux emprisonnant les larves.

spreading or with energy management. Only fine observations, experimental and comparative approaches allow one correct decisions.

**How to define the ultimate constraints of a life-cycle?** Organisms, through the game of selection, attempt to free themselves from advection, either by elaboration of larval behaviour or by suppression of the free larval stage with evolution towards a direct life-cycle. From the double set of solutions we can see there is not a direct relationship between area habitat and planktonic life length. However, the observation of a short larval life leads to the probably reduced area of adult habitat (Bhaud & Duchêne 1995). Our strategy is based on the hope of finding biological laws or features of general application. It could be put forward that the diversification and the variety of responses often observed could be a limitation in

this attempt of generalization. However, correctly used, this disadvantage is not real and leads to a better identification of the function. For instance, the ability of larvae to disseminate constitutes a numeric value to introduce in a conceptual model of the life-cycle of the species. Dissemination requirements are present in all species, and the large range of their values is not an obstacle to use a common model. If parameters are highly variable between species, the functional structures are not so varied and their identification must be exact. Comparison of Mediterranean and Atlantic populations of *E. nebulosa* (Fig. 9) perfectly indicates that the ultimate goal is the quest of an agreement between the adult habitat and the first recruitment area. Such a constraint secures a connection between the old benthic adult phase and the terminal planktonic larval phase by the link of the respective inhabited field area. The difference between

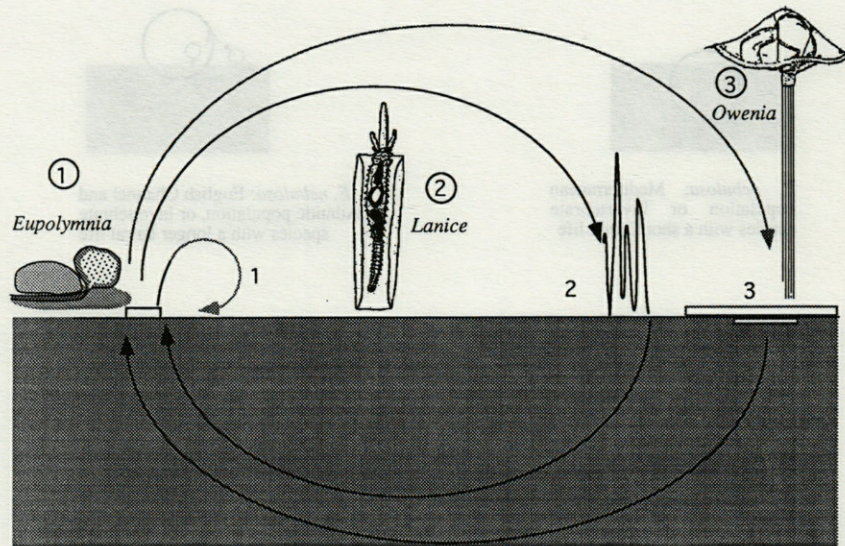


Fig. 10. – Several patterns of correspondence between the disseminative larval area and the habitat area of adults. 1) Checking of larval dissemination by the existence of a mucilaginous egg-mass; Ex : *Eupolymnia nebulosa*. 2) Prolongation of planktonic life leading to a delay of settlement constraints with their strength decreasing. Ex : *Lanice conchilega* with a long planktonic life reaching 2 months and developing numerous contacts with the sediment. 3) Larvae are passive; they suffer limited constraints during settlement and make the best of a large range of substrata; they settle on an area larger than adult habitat and during juvenile development there is a progressive reduction of the recruitment area by mortality of individuals at the periphery. Ex : *Owenia fusiformis*.

Fig. 10. – Les différentes modalités d'un accord entre l'aire de dissémination larvaire et l'habitat des adultes. 1) Le contrôle de la dissémination larvaire s'effectue par développement d'une structure mucilagineuse. Ex : *Eupolymnia nebulosa*. 2) La prolongation de la vie planctonique entraîne un retard des contraintes sédimentaires avec diminution de leur intensité. Ex : *Lanice conchilega* avec une vie planctonique très longue (2 mois) qui se termine par des touchers sédimentaires nombreux. 3) La dissémination des larves est passive; elles subissent peu de contraintes au moment de leur établissement; elles s'accrochent d'une large variété de substrats et se fixent sur une aire qui dépasse largement l'habitat des adultes reproducteurs; l'accord se fait progressivement au cours du développement de la phase juvénile par mortalité des individus de la périphérie de l'aire de recrutement. Ex : *Owenia fusiformis*.

both areas is an estimation of the mortality rate during the juvenile phase. However, the fundamental constraint in a life-cycle is not to reduce the ability of dissemination but to return to the adult habitat or to preserve this habitat, the ultimate goal being to ensure mating. This is achieved by different strategies, the control of dissemination and the development of elaborate larval behaviour, among them. Strategies reported in Fig. 10 may be schematized as follows. 1) The future of larvae is secured by controlling their dissemination as soon as they are formed. 2) The species does not control dissemination, and what's more, they use their dissemination by transforming it in advantage through prolongation of life in open water or through the development of a return process supported by physical structures of water masses. These two solutions aim to delay settlement constraints and, as a consequence, to diminish the strength of these constraints when larvae settle on the substratum. Moreover, the test of substrata are made possible by ballooning

processes. 3) A generalized dissemination allows to an overlapping of the adult area, and, accordingly, to a renewal of individuals in adult area but the price is a large loss after the overflowing of the adult area by larvae. Consequently, a general and fruitful idea emerges : the place of the largest loss of individuals is probably located during the benthic phase and is represented by the difference between the area receiving first recruits and the area where mature individuals are limited.

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# NEMATODE TAIL-SHAPE GROUPS RESPOND TO ENVIRONMENTAL DIFFERENCES IN THE DEEP SEA

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NEMATODA  
DEEP-SEA BENTHOS  
FUNCTIONAL GROUPS

**ABSTRACT** – Although it has been proposed that tail shapes could be used as the basis for ecologically useful functional groups of nematodes, the proposition has not been tested. We used data from three sites in the deep North Atlantic for such a test. In a pretest, we found that nematode functional groups based on buccal morphology differed significantly in their proportional representation among the sites, indicating that for nematodes the sites differed ecologically. Results of similar tests involving tail-shape groups were significant, indicating that there is ecological information in the tail-shape groups, and a further test revealed that the information in the shape of the tail was not a simple reflection of information in the buccal-morphology groups. Distribution of functional groups formed by combining tail shape and buccal morphology also differed significantly among sites. We conclude that both the tail-shape and buccal-morphology-by-tail-shape approaches hold promise for the ecological analysis of deep-sea nematode assemblages.

NEMATODA  
BENTHOS PROFOND  
GROUPES FONCTIONNELS

**RÉSUMÉ** – Bien que la forme de la queue des Nématodes ait été proposée pour constituer des groupes fonctionnels sur le plan écologique, cette hypothèse n'a pas été testée. Nous avons utilisé des données provenant de trois sites de prélèvements de l'Atlantique nord profond pour de tels tests. Dans un test préliminaire, nous avons trouvé que les groupes fonctionnels de Nématodes basés sur la morphologie buccale présentaient des différences significatives dans leurs proportions relatives entre les sites, ce qui montre que les sites sont différents sur le plan écologique pour les Nématodes. Les résultats d'analyses similaires impliquant les groupes constitués à partir de la queue sont significatifs, indiquant qu'il existe une information d'ordre écologique à partir de ces groupes et une analyse ultérieure montre que l'information provenant de la forme caudale ne correspond pas à une simple redondance de l'information obtenue à partir des groupes basés sur la morphologie buccale. La distribution des groupes fonctionnels obtenus en combinant la forme caudale et la morphologie buccale diffère également de façon significative entre sites. En conclusion, les deux approches, forme caudale et morphologie buccale – forme caudale seront intéressantes à exploiter lors des analyses écologiques des communautés de Nématodes profonds.

## INTRODUCTION

That nematodes are an important component of the deep-sea soft-bottom fauna can be argued many ways. They are by far the most abundant metazoans, and they constitute a nonnegligible portion of the biomass (Gage & Tyler, 1991). They are thought to feed primarily on microbes (Jensen, 1988), although predators are known (Jensen, 1992). They are probably food for larger organisms and so play a role in deep-sea food chains, but only inferential evidence is available (Lambshead *et al.*, in press). In shallow water, they alter the sea bed by adding mucus (Riemann

and Schrage, 1978), by creating burrows (Cullen, 1973), and by tube-building (Nehring *et al.*, 1990; Nehring, 1993); deep-sea nematodes may have similar effects. Despite the importance of nematodes, our understanding of their ecology in the deep sea lags that of other groups; we are still in the pattern-recognition stage. One reason for this situation is that deep-sea nematodes are extremely diverse (Lambshead, 1993), and most species are rare, making the acquisition of ecological information difficult.

One approach to this problem has been to combine species into functional groups. Functional groups consist of species that share morphological

traits thought (or known) to imply similarity in an important ecological function. For nematodes, Wieser (1953) proposed that buccal morphology could be used to group by feeding type. This scheme has been widely used in ecological work (see references in Jensen, 1987, and Tietjen, 1989). Thistle and Sherman (1985) noted that nematode tails could be important in locomotion and reproduction and proposed a second functional grouping of nematodes based on tail shape. To date, the ecological utility of nematode tail-shape groups has not been tested. In this paper, we first use the buccal-morphology approach to show that our sites differ ecologically from the perspective of nematodes. We then test the ability of tail-shape groups to detect differences among the sites that are not simply those reflected by the buccal-morphology groups. We also tested the proposition that tail-shape grouping and buccal-morphology grouping could be combined to give an ecologically useful, two-way classification for nematodes analogous to that for polychaetes (Jumars and Fauchald, 1977).

## METHODS

### Site descriptions

Two of the sites are in the northeast Atlantic and were studied as part of the MAST-funded, multidisciplinary investigation into the effects of seasonal flux of phytodetritus to the sea floor. The sites were chosen to differ as little as possible except for the depth of winter mixing in the overlying water and are described in detail by Rice and Lamshead (1993, see their Fig. 15.2), Lamshead and Hodda (1994), Rice *et al.* (1994), and Lamshead *et al.* (in press). The Porcupine Abyssal Plain site (PAP) is located to the southwest of Ireland at 4850 m depth (48° 50' N, 16° 30' W). It receives a major seasonal input of aggregated phytodetritus. The second station (MAP) is located on the Madeiran Rise at 4950 m depth (31° 05' N, 21° 10' W). Time-series bottom photographs show that MAP lacks the phytodetritus flux experienced at PAP and has lower biological activity. Standing stocks at MAP are also lower than those at PAP (Thurston *et al.*, 1994).

The site we will refer to as "HEBBLE" is located in the northwest Atlantic at the base of the Scotian Rise at 4626 m depth (core 1, 40° 24.0' N, 63° 07.4' W; core 2, 40° 24.3' N, 63° 09.6' W). It was the location of preliminary studies for the High Energy Benthic Boundary Layer Experiment (Hollister and Nowell, 1991); the actual HEBBLE site was 69 km away at 4820 m and is described by Thistle *et al.* (1991). The two locations have similar environments, so we have used information from both in this description. The productivity of the overlying water is relatively high (Berger, 1989, his Fig. 11), and some evidence suggests that the food supply to the benthos is abundant (Hollister and Nowell, 1991). The near-bottom hydrodynamic regime is dramatically different from that of quiescent

deep-sea sites. In particular, the site is exposed to benthic storms during which maximum velocities at 10 m above bottom reach 15-40 cm s<sup>-1</sup> (Weatherly and Kelly, 1982; Hollister and Nowell, 1991). Eight to 10 storms occur annually. During storms, millimeters of sediment can be eroded; during interstorm periods, similar amounts are deposited.

### Sampling

At both PAP and MAP, one core (5.7 cm internal diameter) was chosen from each of six multiple-corer lowerings (Barnett *et al.*, 1984). The top 1-cm layer of sediment was immediately fixed in buffered, seawater formalin (9:1, v:v). In the laboratory, the nematodes were extracted by a modification of the Ludox-TM-decantation method (de Jonge and Bouwman, 1977) (45- $\mu$ m sieve), placed in functional groups, and enumerated (Tables I and II).

Table I. - Porcupine Seabight nematodes by buccal morphology and tail shape. See text for the meaning of abbreviations. Samples are from station 11908 (Rice *et al.*, 1994).

Tail	Sample						Buccal Morphology
	1	2	3	4	5	6	
1	18	19	18	23	6	6	
2	61	41	51	90	17	10	1A
3	9	21	49	13	3	6	
4	29	22	52	29	2	8	
1	1	1	0	2	0	1	
2	27	55	25	42	6	7	1B
3	1	0	1	1	0	0	
4	5	5	2	8	1	0	
1	0	0	0	0	0	0	
2	2	0	23	4	1	2	2A
3	52	29	47	24	5	15	
4	34	27	64	51	14	31	
1	0	0	0	0	0	0	
2	0	0	0	5	2	0	2B
3	1	0	0	0	0	0	
4	6	5	6	4	2	3	

Table II. – Madeira Abyssal Plane nematodes by buccal morphology and tail shape. See text for meaning of abbreviations. Samples are from station 12174 (Rice *et al.*, 1994).

Tail Shape	Sample						Buccal Morphology
	1	2	3	4	5	6	
1	0	1	0	0	1	0	
2	36	53	21	24	13	13	1A
3	4	13	5	5	1	3	
4	6	23	3	7	5	2	
1	0	0	0	1	0	0	
2	24	41	16	9	8	7	1B
3	1	1	0	0	0	0	
4	3	3	3	0	4	1	
1	0	0	0	0	0	0	
2	11	7	7	4	4	8	2A
3	6	5	5	3	5	1	
4	9	10	10	7	4	11	
1	0	0	0	0	0	0	
2	0	0	2	1	0	0	2B
3	0	0	0	0	0	0	
4	26	30	8	8	18	7	

The HEBBLE samples were taken with a 0.25-m<sup>2</sup> box corer (Hessler and Jumars, 1974); two box cores were taken 3 km apart. We studied the central nine 10-cm-by-10-cm subcores (Thistle *et al.*, 1985, their Fig. 3) from each box core. Because each subcore contained a subsubcore for use by another investigator, 77 cm<sup>2</sup> per subcore was sampled for nematodes. At sea, the water overlying each subcore was drawn off and passed through a 45- $\mu$ m sieve. The top 1 cm of each subcore and the sieve residue were preserved in sodium-borate-buffered seawater formalin (4:1, v:v). In the laboratory, each sample was washed on a 62- $\mu$ m sieve (the fraction passing a 62- $\mu$ m sieve and caught on a 44- $\mu$ m sieve from two subcores selected at random contained < 1% of the nematodes; this fraction was not considered further.) Thistle and Sherman (1985) described how a random 25% subsample of the nematodes in each sample was obtained (Tables III and IV).

Because the HEBBLE samples were collected with a box corer and the MAP and PAP samples with a multiple corer, the possibility that faunal differences could arise from differences in sampler performance had to be confronted. Bett *et al.* (1994) point out that, in general, box corers collect nematodes less efficiently

than multiple corers, at least in part because the pressure wave that precedes a box corer displaces material of low specific gravity (*e.g.* nematodes) from the surface of the sediment before the sample is taken (Jumars, 1975). However, the box corer employed had been modified to reduce bow-wave effects (see Thistle and Sherman, 1985, for details). Also, the HEBBLE site frequently experiences strong benthic storms that reduce the amount of easily displaced material on the sediment surface (*in situ* photographs, personal observation, D.T.). Thistle and Sherman (1985) tested for evidence of the displacement of nematodes from the HEBBLE samples and found no evidence for it, implying that the samples were taken during one of the many periods when the HEBBLE-site sediments cannot be eroded, even by benthic storms (Gross and Williams, 1991). Bow-wave-induced bias appears to have been minimal.

### Morphological groups utilized

Wieser (1953) proposed that buccal morphology could be used to group marine nematodes into four groups that fed in similar ways: 1A = small/absent buccal cavity without teeth, 1B = medium/large buccal cavity without teeth, 2A = small/medium cavity with teeth, and 2B = large buccal cavity with large teeth/mandibles. This classification has proved to be of great value and has often been employed in shallow-water (*e.g.* see references in Heip *et al.*, 1985, and Jensen, 1987) and deep-sea studies (Rutgers van der Loeff and Lavaleye, 1986). In the deep sea, Wieser's groups have been used primarily to explore the responses of nematodes to differences in sediment texture and composition (Tietjen, 1989, and included references).

Wieser (1953) suggested four functions for the feeding groups – 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistrate feeders, and 2B = omnivore-predators – but additional information on the feeding behavior of shallow-water (*e.g.* Tietjen and Lee, 1977; Jensen, 1979, 1982, 1986, 1987; Romeyn and Bouwman, 1983; Romeyn *et al.*, 1983, Nehring, 1992a, b) and deep-sea nematodes (Jensen, 1992) has become available. These observations, albeit on a limited number of species, have not entirely supported the originally suggested feeding behavior for Wieser's groups. For example, Romeyn and Bouwman (1983) reported that some species with 1A buccal-cavity types (*e.g.* *Monhystera microphthalma*) were actually nonselective feeders. Information on feeding in the 2B group has indicated that it includes both true predators, which ingest prey, and scavengers. The latter are the families Oncholaimidae and Enchelidiidae, which are only partially predatory as adults (without ingesting prey) and not at all predatory as juveniles (Jensen, 1987, and references therein; Riemann and Schrage, 1978).

These observations have led to suggested modifications to Wieser's morphological groups. Romeyn and Bouwman (1983) and Bouwman *et al.* (1984) included sensory organs as additional characters for delineating trophic groups, but this approach has not been widely supported and is rejected by Jensen (1986, 1987). Jensen (1986, 1987) suggested splitting the 2B group into true predators and scavengers. He also recommended

Tail Shape	Sample									Buccal Morphology
	7	8	9	12	13	14	17	18	19	
1	0	0	0	0	0	3	1	0	0	
2	6	3	11	6	15	15	28	21	14	1A
3	5	2	3	3	5	6	8	9	6	
4	8	4	12	23	17	16	19	14	17	
1	0	0	0	0	0	0	0	0	0	
2	9	1	2	3	3	0	5	1	6	1B
3	0	1	4	0	0	0	4	7	2	
4	27	5	27	44	18	26	35	50	23	
1	0	0	0	0	0	0	0	0	0	
2	0	0	15	13	24	23	42	19	12	2A
3	8	5	9	10	6	16	15	22	28	
4	4	3	1	16	5	9	6	5	1	
1	0	0	0	0	0	0	0	0	0	
2	2	5	4	8	8	20	7	7	5	2B
3	0	0	0	0	0	0	0	0	0	
4	0	2	2	7	2	4	9	5	4	

Table III. - Nematodes from the first HEBBLE box core. The sample numbers refer to the position of the subcores in the corer box (see Thistle *et al.*, 1985, their Fig. 3). See text for meaning of abbreviations.

combining groups 1A and 1B on the grounds that the morphological distinction between the two groups was arbitrary and not indicative of a fundamental trophic distinction.

In this paper, we elected to use the original buccal-morphology groups of Wieser. This approach allowed us to test whether it is useful to preserve the distinction between the 1A and 1B groups. Also, although the case for dividing the 2B group into scavengers and true predators (Jensen, 1986, 1987) is strong, at our sites, as in other deep-sea studies (Jensen, 1988), scavengers were extremely rare; we therefore retained the 2B classification as a single group for statistical purposes.

Thistle and Sherman (1985) proposed that nematodes could also be usefully grouped by tail shape, given that tail shape plays an important role in nematode biology, *e.g.* for locomotion (Adams and Tyler, 1980) and reproduction (J.L. personal observation). However, the functional significance of only one of their groups was known. That is, Riemann (1974) reported that long-tailed nematodes were hemisessile, spending substantial periods anchored by the tip of the tail to the substrate by an adhesive secreted by the caudal glands. Note that long-tailed nematodes have been considered to be an ecological group by other workers (*e.g.* Fegley, 1987).

Thistle and Sherman (1985) created 11 morphological tail-shape groups based on the HEBBLE specimens.

In attempting to apply this scheme to the PAP and MAP specimens, we realized that many of the categories intergraded (see also Bussau, 1993) and that the eleven tail-shape groups could be reduced to four (Fig. 1). These are the "rounded" tail type, with a blunt end (tail-shape 1; Thistle and Sherman's category A); the "clavate-conicocylindrical" tail type, initially conical with an extension to the tip (tail shape 2; Thistle and Sherman's categories B and E); the "conical" tail type, with a pointed tip and tail length less than five body widths (tail shape 3; Thistle and Sherman's categories D, F, H, J, and K); and the "long" tail type, with a tail longer than five body widths (tail shape 4; Thistle and Sherman's categories C, G, and I).

**Statistical analysis**

For a given method of grouping (by buccal morphology, tail shape, or both simultaneously), we tested the null hypothesis that the nematodes at the three sites were distributed in the same proportion among the categories of the group with a row-by-column test of independence using the *G*-test (Sokal and Rohlf, 1969). We explored the data by calculating bootstrap (Efron and Gong, 1983) 95% confidence intervals (N = 1000) for the median of the percent abundance of each category

Tail Shape	Sample									Buccal Morphology
	7	8	9	12	13	14	17	18	19	
1	1	0	0	0	0	0	0	0	0	
2	9	9	14	13	13	14	9	12	23	1A
3	5	8	8	7	5	9	8	6	28	
4	4	10	17	12	13	14	15	17	17	
1	0	0	0	0	0	0	0	0	0	
2	7	6	2	5	4	8	3	4	1	1B
3	12	1	1	7	3	2	5	6	15	
4	11	29	36	18	25	16	16	18	39	
1	0	0	0	0	0	0	0	0	0	
2	15	37	17	38	35	21	27	32	37	2A
3	6	12	25	17	25	16	14	13	18	
4	5	6	7	1	4	0	2	0	11	
1	0	0	0	0	0	0	0	0	0	
2	9	16	8	12	27	12	13	18	18	2B
3	2	0	0	0	0	0	0	1	0	
4	7	3	4	4	5	8	4	4	7	

Table IV. - Nematodes from the second HEBBLE box core. The sample numbers refer to the position of the subcores in the corer box (see Thistle *et al.*, 1985, their Fig. 3). See text for meaning of abbreviations.

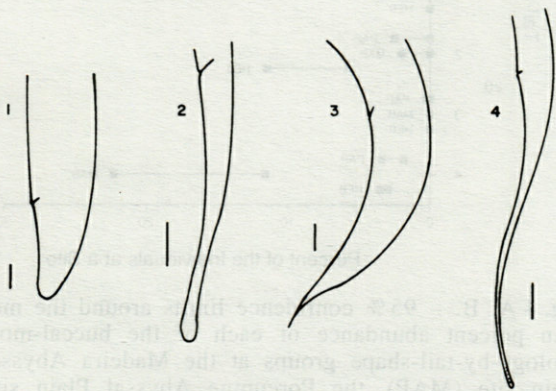


Fig. 1. - Representative tails from each of the tail-shape groups (modified from Thistle and Sherman, 1985): 1 = rounded, 2 = clavate-conicocylindrical, 3 = conical, 4 = long. Scale lines: 1, 2, and 4 = 20 µm; 3 = 50 µm.

for each station using Resampling Stats (Bruce, 1991). If the 95% confidence intervals for two medians did not overlap, the medians were considered to be significantly different. In this exploratory analysis, the HEBBLE subcores were treated as independent samples. Also, we did not adjust the alpha level to correct for the increased probability of rejecting a true null hypothesis when multiple tests were performed.

RESULTS

Our test of the utility of the tail-shape approach required that our three sites differ ecologically from the perspective of nematodes. We tested this assumption using the buccal-morphology groups. The test of independence detected a significant ( $p < 0.005$ ) departure from proportional representation. The sites differed in their buccal-morphology-group composition, as expected if the sites differed ecologically from the perspective of nematodes. By examining the 95% confidence intervals (Fig. 2), we found that the proportion of group 2B was significantly greater at MAP and at HEBBLE than at PAP and that the proportion of group 1A was significantly less at HEBBLE than at either MAP or PAP.

To test the efficacy of the tail-shape grouping, we repeated the analysis that we had done on the buccal-morphology grouping. The tail-shape groups were not distributed proportionally among the sites ( $p < 0.005$ ), as expected if the tail-shape groups responded to ecological differences among the sites. In the 95%-confidence-interval analysis (Fig. 3), we found that the proportions of tail-

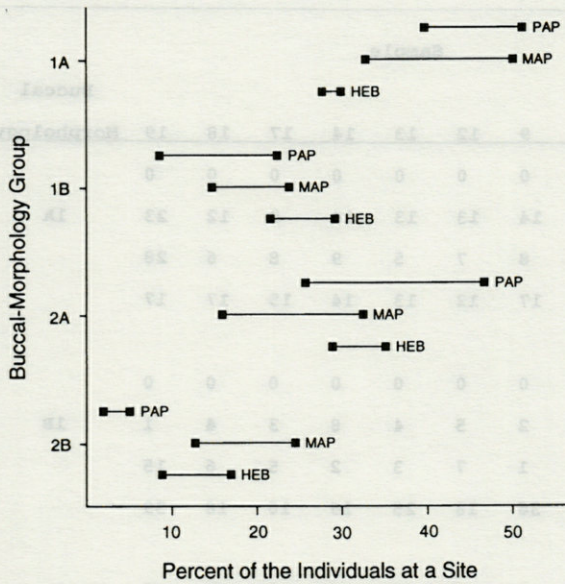


Fig. 2. - 95% confidence limits around the median percent abundance of each of the buccal-morphology groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See text for explanation of buccal morphology groups. 1A = small or absent buccal cavity without teeth. 1B = medium or large buccal cavity without teeth. 2A = small or medium buccal cavity with teeth. 2B = large buccal cavity with large teeth or mandibles.

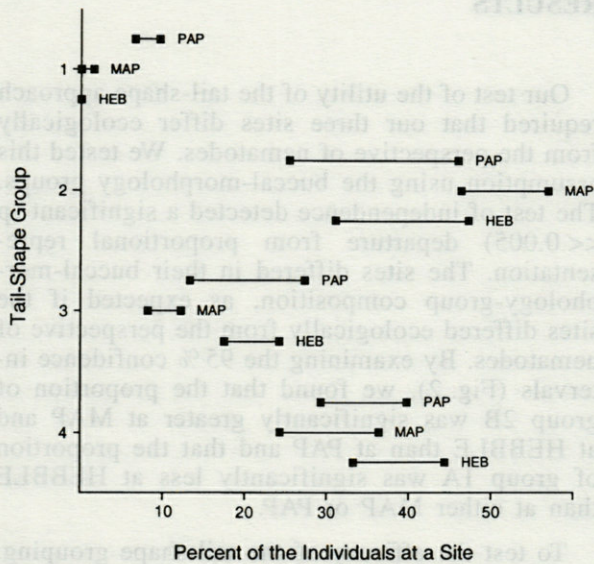


Fig. 3. - 95% confidence limits around the median percent abundance of each of the tail-shape groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See text for explanation of tail-type groups. 1 = rounded tail, 2 = clavate-conicocylindrical tail, 3 = conical tail, 4 = long tail.

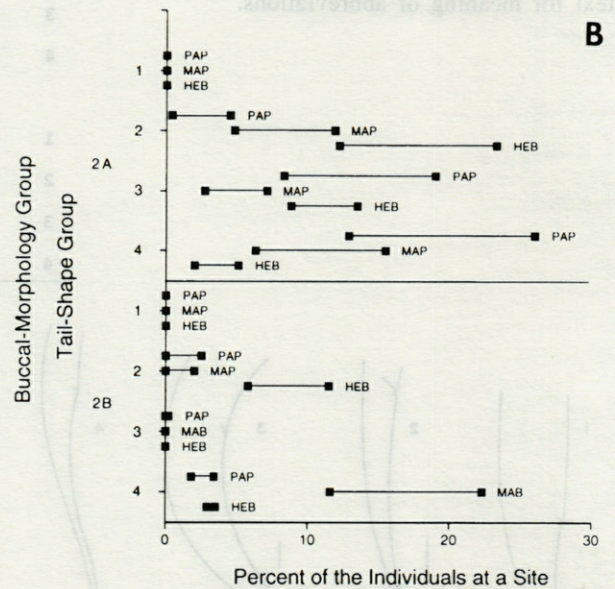
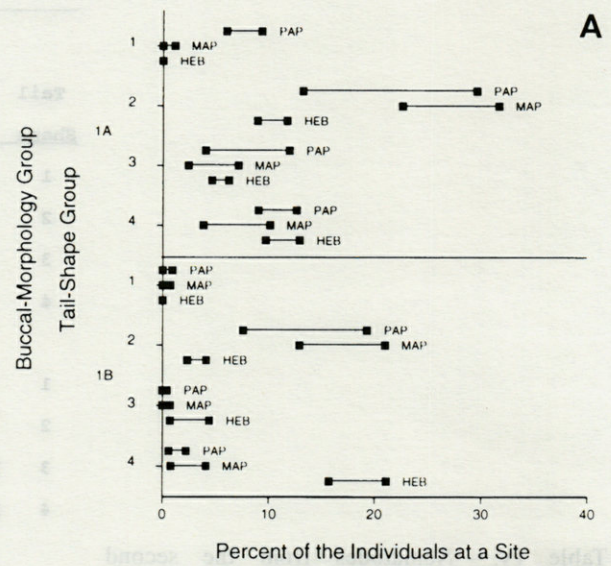


Fig. 4 A, B. - 95% confidence limits around the median percent abundance of each of the buccal-morphology-by-tail-shape groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See Fig. 2 for explanation of buccal-morphology-group labels. See Fig. 3 for explanation of tail-shape group labels.

shape 1 (rounded) at HEBBLE and at MAP were significantly less than that at PAP, that the proportional representation of tail-shape 2 (clavate-conicocylindrical) was significantly greater at MAP than at PAP, and that the proportional representation of tail-shape 3 (conical) was significantly less at MAP than at PAP or HEBBLE. Five of 12 possible differences (42%) were significant for tail shape, as were 4 of 12 (33%) for buccal morphology.

To determine whether the tail-shape groups revealed ecological information not present in the buccal-morphology groups, we proceeded as follows. For a given buccal-morphology group, we ranked the abundance of the individuals by tail-shape group for each of our three sites. If there were no new information in the tail shapes, these rankings should match. We then counted the number of mismatches and repeated the process for each of the buccal-morphology groups. Given four buccal-morphology groups and three sites, there were a total of 12 possible matches. Of these, there were 7 instances of mismatched ranks. The probability of 7 mismatches occurring by chance is much less than 0.005, supporting the inference that there is new information in the tail-shape groups.

To investigate the ecological utility of the two-way grouping, we classified the specimens from each site simultaneously by buccal morphology and tail shape and tested the null hypothesis of proportional representation among the sites. The null hypothesis was rejected ( $p \ll 0.005$ ). The plots of 95% confidence intervals (Fig. 4A, B) revealed that, in 21 of 48 possible pair-wise comparisons among sites (44%), there was a significant difference.

Because of concerns about the comparability of multiple corer (MAP, PAP) and box corer (HEBBLE) samples, we repeated the three tests of independence omitting the HEBBLE data. For all three methods of grouping, the tests remained significant ( $p \ll 0.005$ ), suggesting that the results had not been caused by sampling differences.

## DISCUSSION

The sites differed significantly in their buccal-morphology-group composition, suggesting that the sites do differ ecologically from the perspective of marine nematodes, so it was meaningful to use these sites to test the ecological utility of the tail-shape groups. The buccal morphology analysis also showed that the distinction between Wieser's groups 1A and 1B contains ecological information (1A's are significantly rarer at HEBBLE than at the other sites). We recommend retaining this distinction until additional natural-history information allows more biologically meaningful categories to be erected.

Interpretations of the observed differences among sites in relative abundances of buccal morphologies were not the thrust of this paper, but the small representation of 1A's at HEBBLE is suggestive. That is, observations on estuarine 1A nematodes (Romeyn and Bouwman, 1983) suggest that they feed on bacteria by means of continuous

oesophageal pulsations. Feeding can be passively selective, in that the food particles must be small enough to enter the tiny buccal cavity, or more actively selective, in that individual bacteria are chosen. Repeated exposure to benthic storms at HEBBLE may wash from the sediments many of the small particles on which these animals feed.

Our tests revealed that tail-shape groups differed between sites as much as did the established, buccal-morphology groups and that tail-shape groups contained ecological information not incorporated by the buccal-morphology groups, making them potentially useful as ecological tools. A first step toward providing a natural-history underpinning for interpreting tail-shape-group patterns might be to determine how well mode of locomotion is predicted by tail shape (see Adams and Tyler, 1980, and references therein). Until such natural-history information is available, speculation on distribution differences is fruitless except that the absence of a difference in proportional representation of the long-tailed group between HEBBLE and the other sites brings into question Thistle and Sherman's (1985) notion that the hemisessile life style is favored in high-energy areas.

The two-way approach is not more powerful, on a percentage basis, than the single-classification analyses, but it is of interest. First, it shows that tail shape incorporates new information because the two-way classification reveals that particular tail shapes are not restricted to particular buccal morphologies (Fig. 4A, B). Second, with the two-way classification, we discovered some groups to which no species belonged at our sites; there were no 2A's or 2B's with rounded tails. These combinations are known from other environments (e.g. *Comesa*, *Pontonema*). Are they absent from the abyss or present in the abyss though absent from our sites? Answers to these questions are relevant to the ecology and evolution of deep-sea nematodes. Finally, the most informative system of functional groups will be the one that corresponds most closely to nematode guilds. Given the diversity of nematodes, the four-subdivision guilds based on buccal morphology and tail shape almost surely underresolve the guild structure. The buccal-morphology-by-tail-shape system may be a step toward this "best" system of functional groups.

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# GENETIC DIFFERENTIATION IN THE GENUS ACARTIA FROM THE LAGOON OF VENICE

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CALANOIDA  
ACARTIA  
ENZYME POLYMORPHISM  
GENETIC DISTANCE

**ABSTRACT** – The genus *Acartia* is a dominant zooplankton, widespread in the Lagoon of Venice. The distribution and abundance of the two most representative species are related to the degree of salinity. *A. clausi* Giesbrecht, a coastal species, predominates in areas characterized by good turnover with sea water. *A. margalefi* Alcaraz is more abundant in the inner lagoon, where salinity is lower. In order to evaluate the genetic relationships between the species and to find genetic markers to flank morphological determinations of zooplankton collections, research on nine gene-enzyme systems was carried out: AMY, APK, DIA, FH, G6PDH, GPI, MDH, ME and XD. Distribution of allele frequencies indicates important qualitative genetic differentiation between *A. clausi* and *A. margalefi*. Six loci may be considered as diagnostic characters, as none of the alleles overlaps. Genetic differentiation of the two species was confirmed by different levels of protein polymorphism and distribution. *A. margalefi* has higher genetic variability than *A. clausi*. Moreover, some patterns scored on APK and GPI gels indicate the existence of a third species, closely related to *A. margalefi* from the morphological viewpoint.

CALANOIDA  
ACARTIA  
POLYMORPHISME ENZYMATIQUE  
DISTANCE GÉNÉTIQUE

**RÉSUMÉ** – Les Copépodes du genre *Acartia* constituent la fraction dominante et la plus largement distribuée dans la lagune de Venise. La répartition et l'abondance des deux espèces les plus représentatives sont liées à la salinité. L'espèce côtière *Acartia clausi* Giesbrecht est bien répandue dans les zones ayant un bon renouvellement en eau marine. *Acartia margalefi* Alcaraz est plus abondante dans le milieu lagunaire intérieur, où la salinité moyenne est plus faible. Afin d'évaluer le degré de divergence génétique et trouver des marqueurs de nature génétique qui peuvent simplifier l'identification des espèces, neuf systèmes gène-enzyme ont été étudiés par électrophorèse: AMY, APK, DIA, FH, G6PDH, GPI, MDH, ME et XD. Les distributions des fréquences alléliques calculées indiquent une notable différenciation génétique entre *A. clausi* et *A. margalefi*. On a montré des allèles exclusifs de chaque espèce pour six loci que l'on peut vraisemblablement considérer comme discriminatifs. Les différences observées par le degré de variabilité protéique et par leur distribution soulignent la distinction entre les deux espèces. Chez *A. margalefi* on a remarqué une variabilité plus élevée que chez *A. clausi*. Enfin, les phénotypes particuliers mis en évidence pour les loci APK et GPI laissent supposer l'existence d'une troisième espèce dans la lagune de Venise, morphologiquement très semblable à *A. margalefi*.

## INTRODUCTION

The Lagoon of Venice is a complex coastal ecosystem in the Northern Adriatic. Water exchange with the open sea takes place through three channels: Lido, Malamocco and Chioggia. Tides flowing through these port mouths have created two sills (Avanzi *et al.*, 1979) which, from a hydrological viewpoint, subdivide the entire area

into three basins. Freshwater output is poor; the Dese is the only river with a relatively high flow (Sfriso *et al.*, 1988). As water from inland comes principally from agricultural and industrial discharges, a pollution gradient occurs from inland to the open sea (Zingales *et al.*, 1980).

Zooplankton abundances strongly decrease from the outer to the inner areas of the Lagoon (Comaschi Scaramuzza, 1987; Socal *et al.*, 1987). Copepods are the most representative group, and

species belonging to the genus *Acartia* have the greatest abundances (Comaschi *et al.*, in press). A similar zooplankton composition has often been described in estuarine and lagoonal ecosystems (e.g., Alcaraz, 1983; Ferrari *et al.*, 1982).

Taxonomic classification of *Acartia* species is mainly based on the morphology of the fifth pair of legs (P5) and the last cephalothoracic segment: the presence or absence of spinules or fine hairs on them is very important. Length/width ratios and other biometric measurements are also employed (Bradford, 1976). These differences, based on a few morphological traits and often observed only in a few specimens, may be expressed anomalously in relation to environmental factors (Brylinski, 1984). Furthermore, populations from different habitats belonging to the same species may be classified as different species when separately studied. Descriptions of new poorly differentiated species emphasize the limitations of approaches based only on morphology and suggest that the genetic structure of populations should be studied (McKinnon *et al.*, 1992). For comparisons of closely related species, electrophoresis has proved to be a most effective technique (Gosling, 1992). By identifying allozyme polymorphism and evaluating gene frequencies, the degree of genetic similarity may be assessed and phylogenetic relationships identified (Avisé, 1983; Nevo, 1990).

The aim of this research was to study some gene-enzyme systems in samples of two species of the genus *Acartia*, *A. clausi* and *A. margalefi*, from the Lagoon of Venice. Genetic markers may be suitable for evaluating the dynamics of *Acartia*

populations (Meneghetti *et al.*, 1991), since they are influenced by a variety of environmental factors (Comaschi Scaramuzza, 1987; Socal *et al.*, 1987).

## MATERIALS AND METHODS

This research was carried out during summer 1988. Three sampling areas were established (Fig. 1): Station A near the port mouth of Lido; Station B along the Burano-Dese channel, between the islands of Crevan and Torcello; Station C in Valle di Brenta, a hydrologically separate area in the southern basin of the Lagoon.

Specimens of zooplankton were caught using a Clarke-Bumpus horizontal sampler, transferred into glass bottles containing sea water, and transported to the laboratory. Each specimen was isolated in a glass cuvette, classified while still alive by means of stereomicroscopy and then immediately frozen at  $-80^{\circ}\text{C}$ . Specimens were preserved at this temperature until electrophoretic analysis.

Each single copepod was prepared for electrophoretic analysis on acrylamide gel according to the methods described by Bisol *et al.* (1981) for animals of small size. A Hoefer Mighty Small II System was used for migration runs. Two acrylamide gel thicknesses were used, 0.75 mm for *A. clausi* and 0.50 mm for the smaller *A. margalefi*. Specimens of the two species were alternately used as controls. Electrodes and gel buffer was Tris-Glycine pH 8.3 (Tris, 3 g/l; glycine 14.40 g/l).

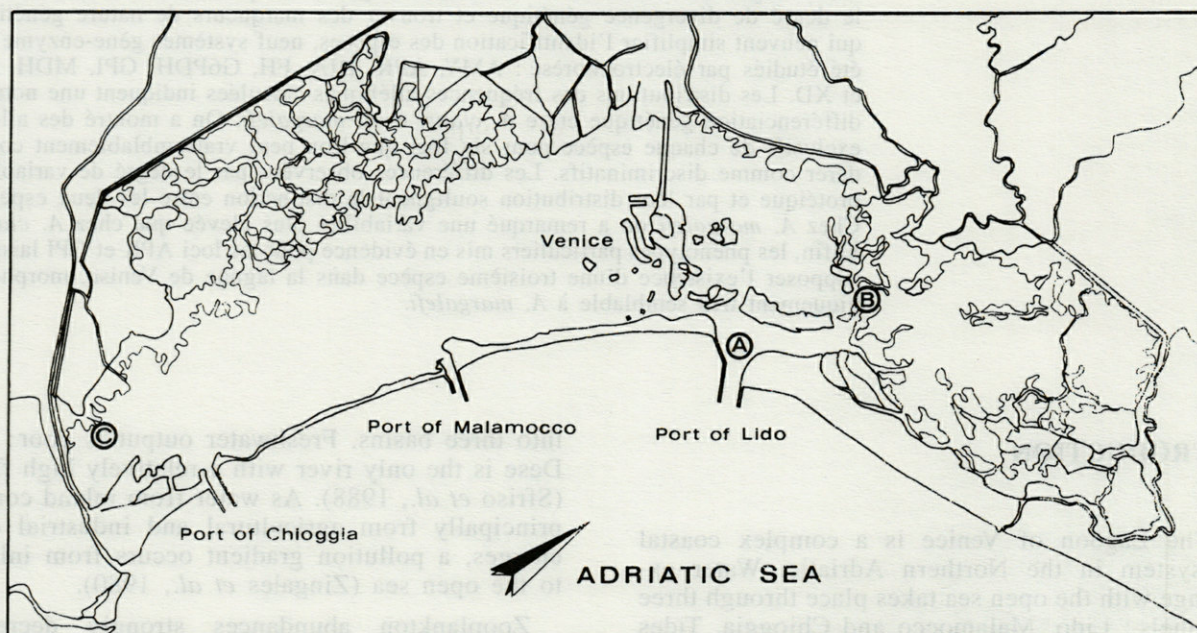


Fig. 1. - Lagoon of Venice with sampling stations (A, port mouth of Lido; B, Burano-Dese channel; C: Valle di Brenta).

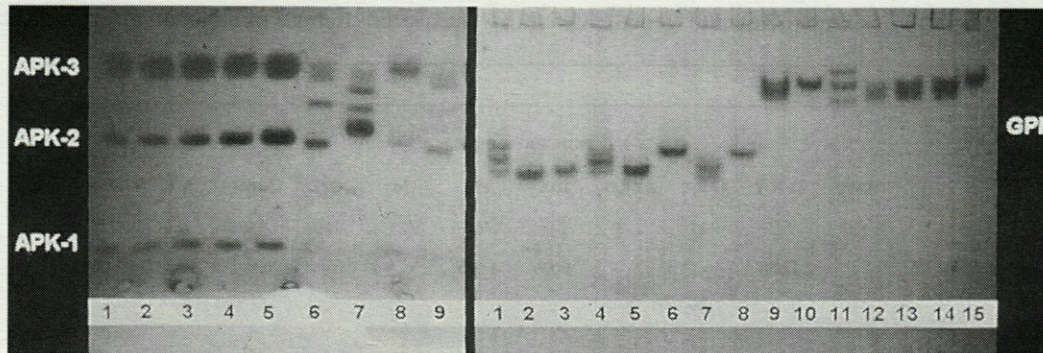


Fig. 2. — Electrophoretic patterns of APK and GPI systems in *Acartia*. APK; items 1-5 and 8 *A. margalefi* (APK-1 : all B/B; APK-2 : all B/B; APK-3 : all C/C); item 7 *A. clausi* (APK-1 : A/A; APK-2 : C/C; APK-3 : A/A); items 6 and 9 *A. sp.* (APK-1 : all C/C; APK-2 : all A/A; APK-3 : all B/B). GPI; items 1-8 *A. margalefi* (1 : B/E; 2, 3, 5 : B/B; 4 : B/D; 6, 8 : D/D; 7 : A/C); items 9-15 *A. clausi* (9, 12-14 : I/J; 10-15 : J/J; 11 : I/K).

The gene-enzyme systems studied were: Amylase (AMY), Arginine phosphokinase (APK), Diaphorase (DIA), Fumarate hydratase (FH), Glucose-6-phosphate dehydrogenase (G6PDH), Glucose phosphate isomerase (GPI), Malate dehydrogenase (MDH), Malic enzyme (ME), and Xanthine dehydrogenase (XD).

Staining techniques were those described by Shaw and Prasad (1970), with modifications in pH and quantities of substrate. The amylase system was studied according to Bisol (1980).

Electrophoretic phenotypes were classified according to the Mendelian law of monohybrid segregation (Fig. 2). The alleles were codominant. When no variation was detected in the zones of enzymatic activity of one population, it was assumed this as a locus controlled by a single gene without allele variation in the population. Different loci in an enzyme system were identified by a number code and the alleles by a letter, designating the relative anodal mobility: for instance, APK-1 is the most anodal locus of the Arginine phosphokinase system and, at this locus, A is the fastest allele.

All alleles of each enzyme system were designated with regard to the mobility of observed bands, independent of sampling or species, as if only one sample had been examined.

The Hardy-Weinberg equilibrium was verified by the  $X^2$  test, and genotypes were pooled when the expected values were less than one.

## RESULTS

Examination of the protein relationships between the two species of *Acartia* was influenced by some difficulty in collecting samples. The copepods were very small, so that only one enzyme could be scored per specimen. In practice samples size useful for the electrophoretic analysis should be about 100 specimens per species per enzyme.

During summer 1988, the Lagoon of Venice was severely affected by an anoxia crisis due to extensive blooming of the macrophyte *Ulva* sp. The abundance of zooplankton was reduced to about 200 individuals  $m^{-3}$ , whereas in previous years numbers had ranged from 1,000 to 10,000 individuals  $m^{-3}$  in the same area and season.

In order to obtain a sufficient number of specimens, catches were replicated in different areas many times, but in spite of this, only a few specimens of *A. margalefi* were collected each time. Only samplings in the southern basin of the Lagoon (Valle di Brenta) in autumn provided a representative number of *A. margalefi*.

The results of electrophoretic analyses are shown in Table I.

Of the eleven loci scored, eight were invariant in *A. clausi* and seven in *A. margalefi*. Loci AMY, MDH and GPI were polymorphic in *A. clausi*, while loci AMY, APK-2, APK-3 and GPI were polymorphic in *A. margalefi*. Loci DIA, FH, ME and XD were identical in all specimens. APK-1 and G6PDH were monomorphic, but for different alleles in the two species. Frequency distributions agreed with the Hardy-Weinberg equilibrium, with the exception of GPI in *A. margalefi*. The average levels of genetic variability are reported in Table II. For all parameters, *A. margalefi* had higher values than *A. clausi*.

The distribution of allele frequencies indicated important qualitative genetic differentiation between *A. margalefi* and *A. clausi*. Six loci proved to be diagnostic, as none of the alleles overlapped. The probability of assigning a specimen to the correct taxon was in agreement with the criteria of Ayala and Powell (1972).

Genetic similarity and differentiation between species were evaluated by I (genetic identity), which estimates the proportion of genes remaining identical in two populations, and D (genetic dis-

Table I. – Allele frequencies and genetic variability measures. Items : number of individuals.

<i>Acartia clausi</i>											
Locus and sample size											
	AMY	APK-1	APK-2	APK-3	DIA	FH	Gd	GPI	MDH	ME	XD
Items	127	175	175	175	141	109	125	129	130	160	126
Allele A	-	1.000	-	-	1.000	1.000	-	-	0.977	1.000	1.000
B	0.008	-	-	1.000	-	-	1.000	-	0.023	-	-
C	-	-	1.000	-	-	-	-	-	-	-	-
D	0.984	-	-	-	-	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-
F	0.008	-	-	-	-	-	-	0.016	-	-	-
G	-	-	-	-	-	-	-	0.043	-	-	-
H	-	-	-	-	-	-	-	0.093	-	-	-
I	-	-	-	-	-	-	-	0.558	-	-	-
J	-	-	-	-	-	-	-	0.209	-	-	-
K	-	-	-	-	-	-	-	0.062	-	-	-
L	-	-	-	-	-	-	-	0.019	-	-	-
H exp.	0.031	-	-	-	-	-	-	0.630	0.045	-	-
H obs.	0.031	-	-	-	-	-	-	0.643	0.046	-	-

<i>Acartia margalefi</i>											
Locus and sample size											
	AMY	APK-1	APK-2	APK-3	DIA	FH	Gd	GPI	MDH	ME	XD
Items	114	60	97	46	89	95	61	128	116	121	149
Allele A	0.009	-	-	-	1.000	1.000	1.000	0.453	-	1.000	1.000
B	-	1.000	0.897	-	-	-	-	0.246	-	-	-
C	0.947	-	-	0.880	-	-	-	0.238	1.000	-	-
D	0.031	-	0.103	0.120	-	-	-	0.059	-	-	-
E	0.013	-	-	-	-	-	-	0.004	-	-	-
H exp.	0.101	-	0.185	0.211	-	-	-	0.674	-	-	-
H obs.	0.105	-	0.165	0.196	-	-	-	0.469	-	-	-

Table II. – Genetic variability at 11 loci common to *A. clausi* and *A. margalefi* from the Lagoon of Venice (s.e. in brackets).

Species	Mean sample size per locus	Mean number of alleles per locus	Percentage of polymorphic loci	Mean heterozygosity	
				Direct count*	Hardy-Weinberg expected**
<i>A. clausi</i>	142.4 (7.2)	1.8 (0.6)	9.1	0.066 (0.058)	0.064 (0.057)
<i>A. margalefi</i>	97.7 (9.6)	1.8 (0.4)	36.4	0.084 (0.043)	0.107 (0.062)

\* Loci are considered polymorphic if frequency of most common alleles does not exceed 0.95.

\*\* Unbiased estimate (see Nei, 1978).

tance), which estimates the proportion of gene substitutions (Nei, 1987). These were respectively 0.301 and 1.200.

These statistics exclude some homozygous phenotypes scored in the summer sample of *A. margalefi* from station C, consisting of alleles never observed in heterozygous combinations with the others. Specimens with these "special" phenotypes were observed in the electropherograms of loci APK-1, APK-2, APK-3 and GPI. No peculiar

phenotype was found in AMY locus. In particular, examination of the three APK patterns, which were simultaneously visible, showed a striking distribution: the 17 specimens homozygous for a slower allele at locus APK-1 were also the only homozygotes for faster alleles at loci APK-2 and APK-3. The lack of heterozygotes, together with this distribution of genotypes, suggests that the summer samples consisted of three species of *Acartia*.

In addition, a relationship was found between these special biochemical patterns and specimen size. The specimens collected in June which had the special allele phenotypes, were often the smallest. This tendency, and the presence in samples of *A. margalefi* from the northern basin, may confirm a previous suggestion by Bradford (personal communication) who, on the basis of our drawings, hypothesized the coexistence of *A. teclae* and *A. margalefi* in this area.

Although further data are necessary, specially for the AMY locus, the above elements seem to be reasonably sufficient to exclude these phenotypes from the *A. clausi* and *A. margalefi* species.

## DISCUSSION

The principal aims of this work on *Acartia* were identification of genetic markers and evaluation of the degree of differentiation between the two species *A. clausi* and *A. margalefi*. Despite difficulties in sampling and the relatively small number of gene-enzyme systems studied, a preliminary comparison between the two species may be made. Firstly, the genetic distances is high, corresponding to those of "good" species distinguishable by morphological structure (Battaglia *et al.*, 1985; Nei, 1987). Genetic differentiation was confirmed by the different levels and distribution of protein polymorphism: *A. margalefi* has higher genetic variability than *A. clausi*.

Polymorphisms scored at four loci in *A. margalefi* and two in *A. clausi* may play a role on the different ecological requirements which characterize the two species in the Lagoon of Venice. *A. clausi*, a coastal-water euryhaline species, may be sampled in all seasons and in all parts of the lagoon. Its abundances increase in water characterized by high salinity and low nutrient contents, that is, near the port mouths and in areas characterized by good water turnover with the open sea. Instead, *A. margalefi*, not found in coastal waters, is abundant in the inner lagoon, where salinity is lower and the variability of hydrological parameters is higher (Comaschi Scaramuzza, 1987).

Study of gene frequencies in samples collected from different areas at different times may reveal the role of natural selection and genetic drift. Moreover, analysis of polymorphism dynamics may allow estimates of important phenomena like migration, recruitment, and seasonal changes in population.

Lastly, the results validate the biochemical approach to the problem of *Acartia* species and contribute to their classification. Due to the difficulty in dissecting all specimens for biometrical pur-

poses, and the limitations of quick classification by stereomicroscopy of closely related species, electrophoretic analysis for diagnostic systems such as arginine phosphokinase turns out to be a valuable method for qualitative and quantitative zooplankton estimates.

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# INTRASPECIFIC AGONISTIC BEHAVIOUR IN THE POLYCHAETE *PERINEREIS CULTRIFERA* (GRÜBE)

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AGONISTIC BEHAVIOUR  
FIGHTING  
TERRITORY  
GALLERY  
POLYCHAETE

**ABSTRACT** – The polychaete annelid *Perinereis cultrifera* living in a network of galleries at the interface between soft and hard substrates is spontaneously active when it is kept under constant conditions ; it can be distinguished from other nereid species by the low frequency of the reversal and searching sequences. It is a territorial species with its territory restricted to the burrow. It presents a very marked intraspecific agonistic behaviour, never tolerating a congeneric species within its burrow. Acclimatization-period, position of the individuals (Head to Head “H-H” or Head to Tail “H-T”) and initial distance between the anterior end of the established worm and the intruder do not influence the outcome of encounters. The fighting patterns in “H-T” encounters are more complex. All these behaviours may be interpreted as adaptative responses to the occupation of a very specific biotope implying a certain mode of life.

COMPORTEMENT AGONISTIQUE  
COMBAT  
TERRITOIRE  
GALERIE  
POLYCHÈTE

**RÉSUMÉ** – L'Annélide Polychète *Perinereis cultrifera* habitant à l'intérieur d'un réseau de galeries et de gouttières à l'interface substrats durs-substrats meubles est spontanément actif lorsqu'il est placé sous conditions constantes ; néanmoins, il peut être distingué des autres membres de la famille des *Nereidae* par la faible fréquence des séquences de retournement et de prospection. C'est une espèce manifestant un comportement territorial, son territoire étant limité à la galerie. Il présente un comportement agonistique intraspécifique très prononcé, ne tolérant jamais la présence d'un congénère à l'intérieur de son terrier. La période d'acclimatation, la position des individus (Tête-Tête “T-T” ou Tête-Queue “T-Q”) ainsi que la distance initiale séparant la partie antérieure du Ver établi de l'intru n'influencent pas l'issue des rencontres. L'analyse comportementale des scénaris de combat montre que les rencontres T-Q engendrent les réponses comportementales les plus complexes. Tous ces comportements peuvent être interprétés comme des réponses adaptatives à l'occupation d'un biotope très spécifique impliquant un certain mode de vie.

## INTRODUCTION

According to Evans (1971) polychaetes are particularly useful for behaviour investigations. Since they have relatively simple repertoires of behaviour (Wells, 1955) and comprise many species and a variety of modes of live, they make excellent subjects for comparative studies of behaviour.

The endobenthic nereid *Perinereis cultrifera* which inhabits heterogenous sediments of the *Fucus serratus* horizon is tubicolous. It builds U or Y shape burrows connected with horizontal galleries at the interface between the soft substrate and an overlying stone (Scaps *et al.*, in press). Behaviour in nereid polychaetes is a well studied subject (Reish and Alosi, 1968; Goerke, 1971;

Evans, 1973; Evans *et al.*, 1974; Cram and Evans, 1980); however, no study exists on *Nereidae* occupying a specific biotope like that of *Perinereis cultrifera*. Previous work by Scaps (1992) seems to indicate that the territory of *Perinereis cultrifera*, similar to those of *Nereis diversicolor* (Lambert and Retière, 1987) and *Nereis virens* (Miron *et al.*, 1991 a and b), is restricted to the burrow and that feeding areas may overlap. On the northern coast of Brittany, juvenile individuals of *Perinereis cultrifera* are distributed in the upper portion of the *Fucus serratus* horizon while adults are found in the lower levels of that area (Scaps *et al.*, 1992). Juveniles migrate downshore during their heavy growth while swarming epitokous individuals migrate upshore. These migrations may lead to an encounter between a worm

inhabiting a burrow and an intruder as observed in the field by Miron *et al.* (1992) for *Nereis virens*. So, the goal of this work was to study the organisation of the spontaneous and agonistic behaviours which could take place during the growth and structuring of the population. These observations will be of value for comparisons with related species and for understanding any influences of the biotopes on the behaviour of the species.

## METHODS

### Collection of individuals

Individuals were collected during autumn of 1990 from l'anse du Pissot near Dinard (France). Individuals had an average ( $\pm$  SD) fresh towel-dried-weight of  $0.90 \pm 0.17$  g. The worms were kept in running sea water in the laboratory.

### Spontaneous behaviour

Worms were provided with glass tubes varying in diameter from 4 to 6 mm and varying in length from about 20 to 25 cm. Worms in tubes were transferred to the bottom of glass tanks measuring  $28.5 \times 21.5 \times 8.0$  cm; these were filled with sea water to a depth of about 5 cm. Temperature varied between 11 and 13 °C and photoperiod was natural. Sources of extraneous stimulation (vibrations) were kept to a minimum. Worms were observed individually and continuous recordings of their behaviour were made for periods of 30 minutes or more. Like Evans *et al.* (1974), activities were recorded as single behavioural units. The following activities were recorded: AM (Anterior Movements), PM (Posterior Movements), HM (Head Movements), I (Irrigation), R (Reversal sequence), S (Searching sequence) and Inact (Inactivity).

The conditions of observation for the spontaneous behaviour were similar to those described by Evans *et al.* (1974). Recordings were made of the behaviour of 15 specimens maintained individually which had been kept under constant conditions for periods of up to 4 days. During the preceding 4 day period they were fed with Tetramin. Observation periods lasted 90 minutes, records concerned occurrence and duration of different activities.

### Agonistic behaviour

At first, to verify if an individual showed an agonistic behaviour to protect only its gallery or also the area adjacent to the burrow orifices, encounters between two worms in glass tubes and also in Petri dishes were observed. The procedures used were similar to those described by Reish and Alosi (1968) and Evans (1973). Petri dishes (diameter 9 cm) were filled with sea water 6 mm high. Vessels with glass tubes and Petri dishes were left undisturbed for a period of 30 min. Each intruder was guided with a paint brush to the entrance of the established worm's tube or so that it crawled round the edge of the dish towards the anterior end of

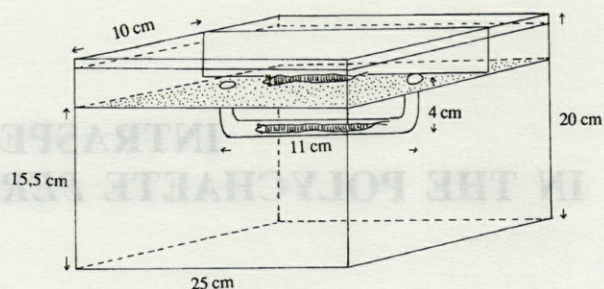


Fig. 1. – Experimental aquarium to study the agonistic behaviour of *Perinereis cultrifera*.

the resident worm. The influence of the size class of the individuals was also tested. Encounters between worms of the same sizes, small/small (300 to 600 mg), large/large (1000 to 1500 mg) and between worms of different sizes, large/small, were carried out.

In order to examine the different fighting patterns used in the protection of the territory, the behaviour of *Perinereis cultrifera* maintained in aquaria was watched. A plastic plate (representing the searching area) in which two holes were drilled fixed an artificial U-shape burrow (glass tube, 6 mm diameter) in the experimental tank (Fig. 1). Each worm was acclimated to its glass tube for at least 48 hours, before it was fixed to the plastic plate. After a waiting period of 15 min, an intruder was disposed on the surface. An additional wall was set up near the burrow orifices to guide the intruder to the resident (Fig. 1). Residents had a maximum of "1 fight" and the same individuals never met twice. When the established worm was evicted a new acclimatization period of 48 hours was provided. Each encounter was filmed with a videocamera. The responses previously defined by Evans *et al.* (1974) and those described by Reish and Alosi (1968) and Miron *et al.* (1992) were recorded: RC (Recognition Contacts), Ret (Retreat), EP (Eversing Proboscis), B (Biting), P (Pushing) and LB (Leave Burrow). 30 encounters were analysed according to the position of the worms during the first contact (Head to Head: "H-H" or Head to Tail: "H-T") and the initial distance between the anterior end of the established worm and the intruder.

### Data analysis.

According to Siegel (1956), it was more convenient to use a non-parametric test for the statistical analysis of behavioural data because of the high variability of the responses observed. Outcome and frequency of encounters involving fighting according to experimental procedure, individual size-class, acclimatization-period, position of the worms ("H-H" or "H-T") and initial distance between the two protagonists were analysed with the likelihood ratio test (G test). William's correction was applied when the sample size was small (Scherrer, 1984); but when the total number of data was too small, we used the Fischer's exact test. Finally, the Wilcoxon-Mann-Withney test was employed to compare the length of fights as a function of each type of encounter ("H-H" versus "H-T"). Sequential data were expressed in the form of transition matrices. Significant transitions related to the position of the worms or the distance between each individual were identified by simple ap-

proximation derived from Castellan's (1965) method of partitioning contingency tables (Miron *et al.*, 1992). The expected frequency of each cell was calculated by dividing the product of the corresponding column and row by the total number of acts. The restriction of utilisation of the  $\chi^2$  test (80% of the expected frequencies must be superior to the value 5: Cochran's rule, in Scherrer, 1984) requires regrouping of data when the sample size is too small.

**RESULTS**

*Spontaneous behaviour*

The individuals were spontaneously active when they were kept under constant conditions, but all worms did not perform the full range of response during the observation time; sometimes Searching and Reversal sequences were not recorded (Fig. 2B). In contrast, the other modes of behaviour were always recorded, periodically the worms crawled anteriorly, posteriorly, performed head movements or irrigated their tubes. Brief inactivity periods (less than 5 min) during the behavioural sequences and long inactivity periods (more than 5 min) between behavioural sequences were distinguish. Behaviour was frequently organised in cycles of activity and rest (Fig. 2). Sometimes worms had their proboscis eversed during inactivity (5 observations) or irrigation (1 observation).

*Agonistic behaviour*

**Outcome of encounters**

When individuals had the same weight (large/large or small/small) encounters led to the intruder's eviction during fighting between worms in glass tubes or to the intruder's retreat during fighting between worms in Petri dishes (Table I A). Fights with proboscis eversions occurred significantly ( $P < 0.05$ ) less often between worms crawling round Petri dishes than between those in tubes (Tables I A, B). Cohabitation was possible between worms in Petri dishes but it never occurred in tubes. When the intruder was bigger than the resident, the established worm was preferentially evicted (Tables I A and B). A 30 min or a 48 hour-acclimatization period of the worm to its artificial burrow did not significantly influence the rate of resident eviction nor the percentage of encounters with fighting (Table II A). The eviction rate of the established worm was more important in "H-T" encounter but the difference was not significant (Gc test). The percentage of encounters with fighting did not significantly change (Table II B). Fights, were settled, on average ( $\pm$  SD), after  $1.16 \pm 1.17$  minutes in "H-H" encounters ( $N = 17$ ) and in  $5.06 \pm 5.46$  minutes in "H-T" encounters ( $N = 13$ ). The difference was significant ( $P < 0.05$ ). Variability was, however, very high. The longest fight lasted more than 15 minutes ("H-T") while the shortest lasted 6 se-

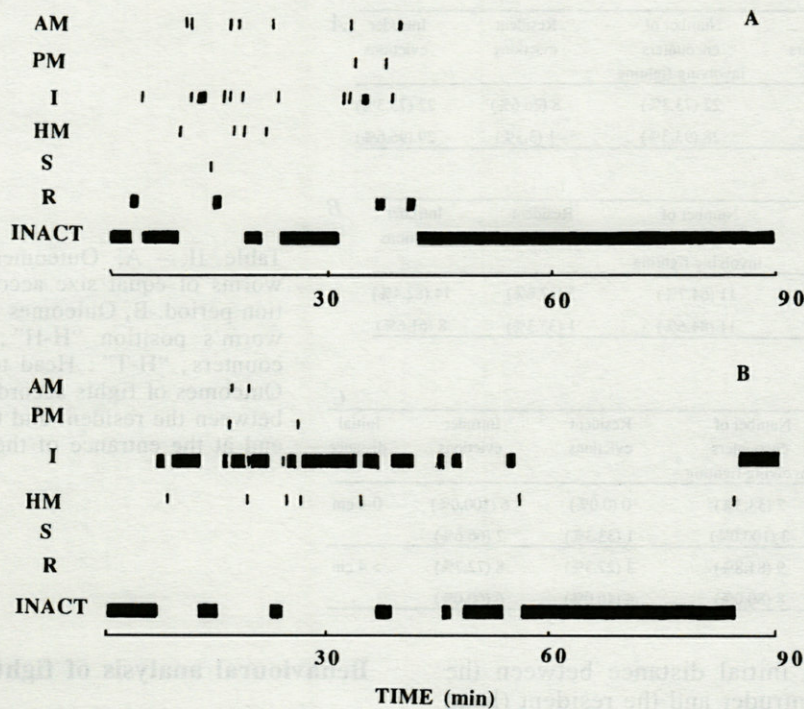


Fig. 2. - Spontaneous behaviour in two individuals (A and B) of *Perinereis cultrifera* kept under constant conditions. AM: Anterior Movements; PM: Posterior Movements; I: Irrigation movements; HM: Head Movements; S: Searching sequence; R: Reversal sequence; Inact: Inactivity.

	Number of encounters	Evictions or retreat		Cohabitations	Proboscis eversions	
		Established	Intruder		Established	Intruder
<b>Petri dishes</b>						
small-small	30	2	13	15	2	1
large-large	30	4	20	6	3	2
small-large <sup>1</sup>	30	23	2	5	2	5
<b>Glass tubes</b>						
small-small	30	5	25	0	20	15
large-large	30	1	29	0	23	13
small-large <sup>1</sup>	30	26	4	0	23	24

1 intruder A

Place of encounter	Type of encounter	Number of encounters	Number of encounters	% of encounters
			involving fighting	involving fighting
<b>Worms of the same size</b>				
<b>Glass tubes</b>	small-small	30	24	80.00
	large-large	30	28	93.33
	total	60	52	86.66
<b>Worms of different size</b>				
		30	27	90.00
<b>Worms of the same size</b>				
<b>Petri dishes</b>	small-small	30	3	10.00**
	large-large	30	5	16.66**
	total	60	8	13.33**
<b>Worms of different size</b>				
		30	7	23.00**

**B**

Table I. - A, Outcomes of interspecific encounters between worms in glass tubes and worms crawling in Petri dishes. B, Relative occurrence of fighting (with proboscis eversions) during interspecific encounters between worms in glass tubes and worms crawling in Petri dishes (\* P < 0.05, \*\* P < 0.01).

Acclimatization period	Number of encounters	Number of encounters involving fighting	Resident evictions	Intruder evictions
30 minutes	30	22 (73.3%)	8 (26.6%)	22 (73.3%)
48 hours	30	28 (93.3%)	1 (3.3%)	29 (96.6%)

**A**

Type of encounter	Number of encounters	Number of encounters involving fighting	Resident evictions	Intruder evictions
"H-H"	17	11 (64.7%)	3 (17.6%)	14 (82.4%)
"H-T"	13	11 (84.6%)	1 (33.3%)	8 (61.6%)

**B**

Type of encounter	Number of encounters	Number of encounters involving fighting	Resident evictions	Intruder evictions	Initial distance
"H-H"	6	2 (33.3%)	0 (0.0%)	6 (100.0%)	0-4 cm
"H-T"	3	3 (100.0%)	1 (33.3%)	2 (66.6%)	
"H-H"	11	9 (81.8%)	3 (27.3%)	8 (72.7%)	> 4 cm
"H-T"	10	8 (80.0%)	4 (40.0%)	6 (60.0%)	

**C**

Table II. - A, Outcomes of fights between worms of equal size according to acclimatization period. B, Outcomes of fights according to worm's position "H-H": Head to Head encounters; "H-T": Head to Tail encounters. C, Outcomes of fights according to initial distance between the resident and the intruder's anterior end at the entrance of the burrow.

conds ("H-T"). The initial distance between the anterior end of the intruder and the resident (head or tail) was not significant in determining contest outcome nor the percentage of encounters with fighting (Table II C).

**Behavioural analysis of fighting patterns**

In "H-T" encounters two pathways led to resident (18%) or intruder (82%) evictions. The eviction sequence began by Recognition Contacts with

cirri (25%) or palps (75%). This contact led to an intruder passive eviction (12%) or was followed by Pushing-Retreat-Proboscis Eversions series. Proboscis eversions succeeded one another (30%) or were interrupted by Anterior Movements (12%) or Biting (12%). Evictions of the residents (18%) occurred when these retreated and evictions of the intruders (70%) followed from Pushing by the resident.

In "H-T" encounters, behavioural sequences of established worms were more complex. Recognition contacts between the two individuals led to an intruder passive eviction (15%) or a new behavioural activity: Reversal sequence (85%) of the resident. Then, the established worm left the burrow spontaneously (8%) or entered one of the two major pathways: Pushing (40%) or Recognition Contacts (40%) with palps (73%) or cirri (27%). This led to Pushing-Retreat-Proboscis Eversions series broken by Anterior Movements. Proboscis eversions succeeded one another (16%). As for "H-H" encounters, evictions of the residents (30%) were observed after Retreat and evictions of the intruders (47%) after Pushing by the resident.

Behavioural sequences of intruders were more complex than those of residents. In "H-H" encounters, intruders entered the glass tube and performed Irrigation movements (6%) and Recognition Contacts with cirri (5%) or palps (95%). RC led to Retreat (59%) or Pushing and to Pushing-Retreat-Proboscis Eversions series (59%). Evictions of the residents were noticed after Biting (6%) or Pushing (12%) and evictions of the intruders after Retreat (82%).

In "H-T" encounters, Anterior Movements were interrupted by spontaneous behaviour phases. Recognition contacts with palps (79%) or cirri (21%) led to Pushing-Retreat-Proboscis Eversions series broken by Biting (40%) or by spontaneous pauses. During this pause individuals could again enter into contact and start again fighting. Proboscis eversions succeeded one another (31%). Evictions of the intruders (62%) were noticed after Retreat, and resident evictions after Pushing (38%).

## DISCUSSION

Marine invertebrates show, in general, spontaneously activity when they are kept under constants conditions of temperature and light (Evans, 1971). Polychaetous annelids and specifically nereids are in concordance with this rule. The spontaneous behaviour of *Perinereis cultrifera* is very similar to that described for other members of the *Nereidae* – in particular *Nereis diversicolor*, *Nereis fucata*, *Platynereis dumerilii* and *Nereis*

*virens* (van Dam, 1937 in Evans, 1973; Lindroth, 1938 in Wells and Dales, 1951; Evans *et al.* 1974; Evans and Downie, 1986; Evans and Rogers, 1978) – in which, the frequency and the duration of a response are variable according to the species (Cram and Evans, 1980). So, *Perinereis cultrifera* can be distinguished by the low frequency of the Reversal and Searching sequences. The structure of the galleries of *Perinereis cultrifera* is very complicated. The burrows are connected with a network of horizontal galleries at the interface between the soft substrate and an overlying stone (Scaps *et al.*, in press). This network offers a great number of pathways and possibly results in the individual turning round less frequently compared to one in a more simple burrow.

Nereidae are well known to be aggressive: *Nereis caudata* (Herpin, 1925), *Neanthes arenaceodentata*, *Nereis grubei*, *Nereis latescens*, *Nereis succinea*, *Platynereis bicanaliculata* (Reish and Alosi, 1968), *Nereis diversicolor*, *Nereis pelagica*, *Platynereis dumerilii* (Evans, 1973), *Nereis fucata* (Cram and Evans, 1980), *Nereis virens* (Miron *et al.*, 1992) and *Perinereis cultrifera*. These laboratory experiments demonstrate that the individuals of *Perinereis cultrifera* are more aggressive when they are put in glass tubes rather than in Petri dishes and this is in agreement with observations by Evans (1973) on *Nereis diversicolor*, *Nereis pelagica* and *Platynereis dumerilii* but differs from observations of Reish and Alosi (1968) on *Neanthes arenaceodentata*, *Nereis grubei*, *Nereis latescens*, *Nereis succinea* and *Platynereis bicanaliculata*. These results confirm Clark's observations (1959) who noticed the rareness of fights during contacts between individuals of *Nereis pelagica* outside the tubes and those of Lambert and Retière (1987) on *Nereis diversicolor* where contact on the sediment surface systematically leads to retraction or avoidance. The territory of *Perinereis cultrifera* is restricted to the burrow. Fights between *Perinereis cultrifera* to defend territories are very violent: the species never tolerates another individual in its glass tube.

If resident and intruder have the same size, fights lead, generally, to an intruder eviction but fights between worms of different size favour the largest individuals. In 1975, Roe made the same observation concerning *Platynereis bicanaliculata* and *Nereis vexillosa*. The position of adults (males or females) of *Perinereis cultrifera* do not influence the results of encounters as also shown by Cram and Evans (1980) in *Nereis diversicolor* and *Platynereis dumerilii*. On the other hand, Miron *et al.* (1992) demonstrated with *Nereis virens* that "H-T" encounters tended to increase the resident's vulnerability whereas data of Cram and Evans (1980) for *Nereis fucata* indicated that "H-T" encounters were more favourable in expelling intruders. Acclimatization period and initial

distance separating the intruder's anterior end from the resident (head or tail) do not modify the course of fights. According to Miron *et al.* (1992) a 24-hour acclimatization period increased the tendency of *Nereis virens* to defend its burrow successfully particularly in "H-H" encounters. Vulnerability was greater in this species if residents were placed at a distance greater than 15 cm from the intruders.

Fighting sequences are shorter for "H-H" encounters: 1'16" against 5'06". This last value is similar to that noticed by Clark (1959) on *Nereis pelagica* (3 to 4') but is shorter than that found by Miron *et al.* (1992) in *Nereis virens*. "H-T" encounters increase the complexity of the fighting sequence because the individual has to turn round before it can face the intruder. Moreover, fighting sequences are often interrupted by spontaneous behaviour pauses. As for *Nereis virens* (Miron *et al.*, 1992) fighting sequences are more complex in "H-T" encounters. The stone covering the entrance to the burrow provides a protection against mobile macrofauna predators, while the gallery assures the function of refuge proper. The pronounced agonistic behaviour could play a role in fights with other macroendobenthic species (for example *Nephtys caeca*) and in space partitioning.

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# ÉTUDE DE LA VARIABILITÉ DE L'INDICE GONADIQUE DE L'OURSIN COMESTIBLE *PARACENTROTUS LIVIDUS* (ECHINODERMATA : ECHINIDAE) EN MÉDITERRANÉE NORD-OCCIDENTALE

*Study of gonad index variability of the edible sea-urchin Paracentrotus lividus (Echinodermata : Echinidae) in the North-Western Mediterranean*

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PARACENTROTUS LIVIDUS  
ECHINIDAE  
INDICE GONADIQUE  
MARSEILLE  
BIOTOPE  
PROFONDEUR  
TEMPÊTE

**RÉSUMÉ** – Les variations de l'indice gonadique (IG) de *Paracentrotus lividus* ont été suivies dans la région de Marseille de mars à juillet 1992, à trois profondeurs (1-3 m, 6-8 m, 12-15 m) sur roche et dans l'herbier à *Posidonia oceanica*, et en fonction de l'abondance des populations d'Oursins exprimée en « volume d'Oursins » (50-300 cm<sup>3</sup>/m<sup>2</sup> et 300-900 cm<sup>3</sup>/m<sup>2</sup>). Sur roche, des mesures ont été réalisées avant et après le passage d'une tempête. Des différences statistiquement significatives ont été observées entre les valeurs de l'IG des individus des deux biotopes, les valeurs les plus élevées étant pour ceux de l'herbier à *P. oceanica*. Dans l'herbier, les Oursins ont des gonades dont le développement n'est pas affecté par la profondeur, alors que sur roche, la profondeur de 6-8 m semble être plus favorable à la croissance des gonades. Dans l'herbier, le « volume d'Oursins » le plus favorable au développement des gonades serait de 50-300 cm<sup>3</sup>/m<sup>2</sup> (ce qui équivaut à 1-6 individus/m<sup>2</sup> de diamètre moyen égal à 4,5 cm sans les piquants). Sur roche, nous n'avons pas décelé de différences significatives entre les deux « volumes » considérés. Enfin, la variation des valeurs de cet indice à 6-8 m de profondeur sur roche, ne présente pas de différences significatives après le passage d'une tempête; par contre on note une chute significative de l'abondance de *P. lividus* entre le premier et le troisième jour après la tempête.

PARACENTROTUS LIVIDUS  
ECHINIDAE  
GONAD INDEX  
MARSEILLES  
BIOTOPE  
DEPTH  
STORM

**ABSTRACT** – Variations of the gonad index (IG) of *Paracentrotus lividus* were investigated in the area of Marseilles from March to July 1992, at three levels of depth (1-3 m, 6-8 m, 12-15 m), on rocky substrates and in *Posidonia oceanica* beds, and according to a population abundance expressed in « sea-urchin volume » (50-300 cm<sup>3</sup>/m<sup>2</sup> and 300-900 cm<sup>3</sup>/m<sup>2</sup>). On rocky substrates, measurements were taken before and after a storm. Statistically significant differences were observed between IG values in individuals of both biotopes, the highest values being in the *P. oceanica* beds. In these sea-grass beds, the development of sea-urchin gonads is not affected by depth, whereas, among rocks, 6-8 m seems to be the most favourable depth for the development of gonads. In the *P. oceanica* beds, the « sea-urchins volume » most favourable for the development of gonads would be 50-300 cm<sup>3</sup>/m<sup>2</sup> (which is equivalent to 1-6 individuals/m<sup>2</sup> with mean diameter of 4.5 cm without spines). On rocks, no difference between the two « volumes » considered was noted. Finally, the variation of this index at 6-8 m depth on rocks does not show any significant variations after a storm; on the other hand, we observed a significant reduction in numbers of *P. lividus* between the first and the third day after the storm.

## INTRODUCTION

Selon les statistiques de pêches de la F.A.O. (1988, 1991), la pêche professionnelle des Oursins dans le monde est passée de 40 000 tonnes en 1980 à 80 000 tonnes actuellement, ce qui représente une augmentation de 100% en dix ans. La quasi-totalité des Oursins commercialisés proviennent des stocks naturels car l'échinoculture est encore peu développée au niveau mondial, même dans les pays ayant une tradition dans l'aquaculture des organismes marins comme le Japon (Ogawa, 1988).

En France, la pêche aux Oursins concerne principalement l'espèce *Paracentrotus lividus* (Lamarck) (Le Gall, 1987; Le Direac'h, 1987, 1988) qui est très commune en Méditerranée occidentale. Le quartier maritime de Marseille est le principal quartier en France pour la pêche de *P. lividus* (Le Direac'h, 1987).

Depuis quelques années, cette ressource baisse dangereusement et de nombreux auteurs ont souligné la grave situation que traverse cette pêcherie (Allain, 1975; Gras, 1987; Le Direac'h, 1987; Le Gall, 1987; Régis, 1987; Byrne, 1990). Les causes invoquées pour expliquer la chute de ces stocks sont diverses : la surexploitation (Allain, 1971, 1975; Gras, 1987; Le Gall, 1987), la pêche peu et/ou mal réglementée (Allain, 1975; Le Direac'h, 1987), les techniques de pêches très destructives (Allain, 1971), les mortalités massives dues à une maladie (Boudouresque *et al.*, 1980), ou à des conditions météorologiques extrêmes (Allain, 1972), et enfin le changement du degré d'eutrophisation du milieu ainsi que l'accroissement des aménagements littoraux (Régis, 1987). Cette espèce a fait l'objet de nombreuses études en Méditerranée occidentale, notamment sur son écologie (Kempf, 1962), son cycle annuel de reproduction (Fenaux, 1968; Régis, 1978), sa dynamique de populations (Azzolina *et al.*, 1983; Azzolina, 1988), ainsi que son impact sur le phytobenthos (Verlaque, 1987) et enfin sa physiologie par Frantzis et Grémare en 1992. Les gonades, constituent la partie consommée et celle qui intéresse les professionnels de la pêche. Au cours de l'année, le volume des gonades (et donc l'indice gonadique, qui en est une mesure) subit des variations saisonnières importantes décrites surtout par Fenaux (1968) et Régis (1979).

Les pêcheurs professionnels cherchent à mettre sur le marché, non seulement des Oursins dont l'indice gonadique est le plus élevé possible, mais aussi des lots aussi homogènes que possible : à une saison donnée en effet, des individus à indice gonadique élevé et à indice gonadique faible sont pêchés simultanément, or un pourcentage d'individus à gonades peu développées diminue considérablement la valeur commerciale du produit.

Dans le présent travail, on se propose donc d'étudier les variations de l'indice gonadique (IG) chez *Paracentrotus lividus* en fonction de 4 paramètres : (1) la profondeur, facteur dont l'action n'a été étudiée que sur des espèces non méditerranéennes (Dix, 1977; Nichols 1981); (2) le biotope (herbier à *Posidonia oceanica* (Linnaeus) Delile et la roche avec algues); (3) l'abondance des individus (en utilisant une nouvelle expression de l'abondance : «le volume d'Oursins»); (4) les conditions météorologiques (certains pêcheurs d'Oursins considèrent en effet que l'indice gonadique chute après une tempête). Nous avons choisi d'étudier ces variations sur la période de mars à juillet. En effet, les travaux des auteurs indiquent de façon concordante, que pendant cette période, il y a un pic de l'IG suivi d'une ponte (Fenaux, 1968; Régis, 1978, 1979). Une meilleure connaissance des causes de la variabilité de l'IG permettrait aux pêcheurs d'Oursins de mieux organiser leur récolte, en vue d'une qualité meilleure et plus homogène du produit.

## MATERIEL ET METHODES

### Présentation du site

Les prélèvements ont été effectués à Carry-le-Rouet (Fig. 1) à l'Ouest de Marseille (Bouches-du-Rhône, France). L'échantillonnage s'est fait en plongée en scaphandre autonome dans plusieurs stations représentant deux biotopes différents. Le premier est un substrat rocheux couvert par un peuplement riche en algues macroscopiques; les espèces dominantes sont les suivantes : les Florideophyceae *Asparagopsis armata* Harvey, *Corallina elongata* Ellis et Solander, *Jania rubens* (Linnaeus) Lamouroux, *Sphaerococcus coronopifolius* Stackhouse; Les Fucophyceae *Cladostephus hirsutus* (Linnaeus) Boudouresque et Perret, *Dictyota dichotoma* (Hudson) Lamouroux, *Dilophus fasciola* (Roth) Howe, *Padina pavonica* (Linnaeus) Thivy, *Halopteris scoparia* (Linnaeus) Sauvageau et les Ulvophyceae *Codium bursa* (Linnaeus) C. Agardh, *Codium effusum* (Rafinesque) Delle Chiaje et *Codium vermilara* (Olivieri) Delle Chiaje. Le second biotope est l'herbier à *Posidonia oceanica* (Phanérogame).

Les prélèvements ont été effectués entre mars et juillet 1992. Dans chaque station, plusieurs lots de 20 Oursins de 4.5-5.5 cm de diamètre horizontal, mesurés sans les piquants, ont été récoltés. Ce diamètre est estimé *in situ* et vérifié au laboratoire grâce à un pied à coulisse (précision : 1 mm) et correspond à l'intervalle de taille des Oursins les plus pêchés par les professionnels. Les Oursins sont pesés à 0,01 g près (poids total humide) et disséqués, les gonades sont retirées, égouttées et pesées (poids des gonades humides). Le traitement statistique des données utilise le test non paramétrique de comparaison des moyennes par rangs de Kruskal et Wallis (Dagnelie, 1975; Elliot, 1977; Siegel et Castellan, 1988) ainsi que le test non paramétrique de comparaisons multiples (Zar, 1984; Siegel et Castel-



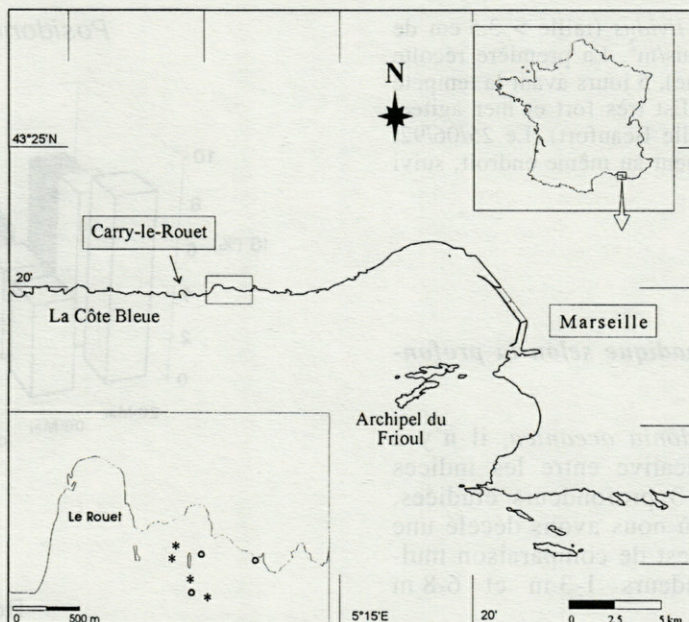


Fig. 1. – Sites de prélèvements (\* : herbier à *Posidonia oceanica* ; o : roche avec algues).

Sites of sampling (\* : *Posidonia oceanica* beds ; o : rocky substrate).

lan, 1988). Nous n'avons pas utilisé de méthodes paramétriques car les conditions d'homogénéité des variances (Test de Cochran :  $P \ll 0,01$ ) ainsi que la normalité de la distribution des données n'étaient pas respectées (même après une transformation arcsinus des données, qui est la plus communément utilisée pour des rapports comme l'indice gonadique).

#### Calcul de l'indice gonadique

L'indice gonadique (IG) est une relation entre un descripteur quantitatif de l'appareil reproducteur et un descripteur quantitatif des organes somatiques. Parmi les indices gonadiques proposés par les différents auteurs (Moore, 1934 ; Fenaux, 1968 ; Régis, 1978 et Semroud et Kada, 1987) nous avons opté pour celui utilisé par Lawrence *et al.* (1965), Cameron (1986) et San Martin (1990), qui est le rapport exprimé en pourcentage du poids frais des gonades (PHG) sur le poids frais total de l'Oursin (PT) :  $IG = \frac{PHG}{PT} \cdot 100$ . Ce choix s'explique par le fait que les Oursins sont vendus frais, et donc cet indice permet une approche plus claire de la qualité des Oursins en tant que produit de consommation. Les individus mâles et femelles ont été séparés ; toutefois, les valeurs des indices gonadiques n'étant jamais significativement différentes entre les deux sexes (test de Kruskal et Wallis,  $P > 0,1$ ), nous les avons réunis dans la présentation des résultats.

#### Etude de l'effet du biotope et de la profondeur sur l'indice gonadique

Quatre prélèvements d'Oursins, à intervalle plus ou moins régulier (26/03/92, 07/04/92, 06/05/92, 03/06/92, 27/06/92), ont été effectués à 3 profondeurs différentes

(1-3 m, 6-8 m, 12-15 m) dans les 2 biotopes (herbier à *Posidonia oceanica* et roche avec algues).

#### Etude de l'effet de l'abondance d'Oursins sur l'indice gonadique

L'objectif est d'étudier l'abondance des Oursins sur l'indice gonadique. Le descripteur à utiliser ne peut être la densité des Oursins, car elle ne tient pas compte de leur diamètre ; or l'IG augmente avec le diamètre (Semroud et Kada, 1987). C'est la raison pour laquelle nous avons opté pour un descripteur qui intègre le nombre et le diamètre des Oursins présents. Nous avons considéré pour cette étude que le test est assimilable à une sphère, dont le volume se calcule comme suit :

$V = \frac{4}{3} \pi R^3$ , R = diamètre horizontal du test / 2 ; et nous avons calculé le « volume d'Oursins » par unité de surface ( $m^2$ ) :  $V_T = \sum \frac{4}{3} \pi R^3$

Nous avons prélevé à 3 reprises (15/05/92, 18/06/92, 28/07/92) des individus correspondant à des abondances (exprimées en terme de « volume d'Oursins ») différentes : 50 à 300  $cm^3$  et 300 à 900  $cm^3$ . Ainsi, avant chaque prélèvement, nous avons calculé à plusieurs reprises (3 à 4 fois) le volume d'Oursins existant dans un quadrat de 1  $m^2$  disposé au hasard, puis une moyenne est calculée pour chaque station afin de voir à quel intervalle de volume elle appartient et ce dans les 2 biotopes étudiés ; la profondeur étant toujours la même : 6 à 8 m.

#### Etude de l'effet d'une tempête sur l'indice gonadique

Pour l'étude de cet effet, l'échantillonnage s'est déroulé sur fond rocheux uniquement, à une profondeur

de 6-8 m; la densité de *P. lividus* (taille > 3.5 cm de diamètre) était de 5 individus/m<sup>2</sup>. La première récolte a été faite (par mer très calme), 5 jours avant la tempête des 23 et 24/06/92 (vent d'Est très fort et mer agitée, entre force 6 et 7 de l'échelle Beaufort). Le 25/06/92, nous avons fait un prélèvement au même endroit, suivi de 2 autres, 2 et 4 j après.

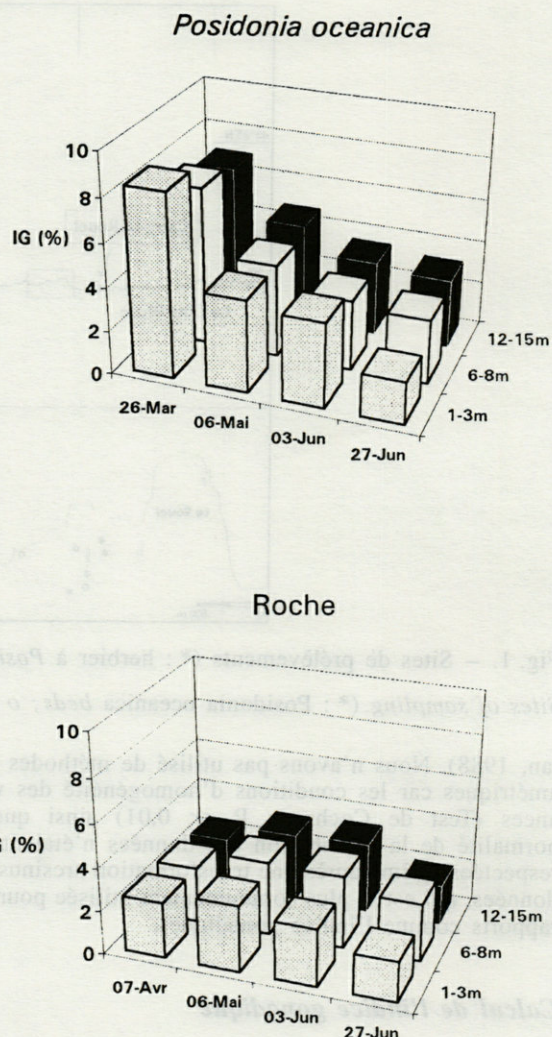
## RESULTATS

### Variation de l'indice gonadique selon la profondeur

Dans l'herbier à *Posidonia oceanica*, il n'y a pas de différence significative entre les indices gonadiques moyens aux 3 profondeurs étudiées, sauf fin juin (Tabl. IA) où nous avons décelé une différence significative (test de comparaison multiple), entre les profondeurs 1-3 m et 6-8 m (Fig. 2).

Sur roche, il n'y a pas de différence dans les valeurs moyennes de l'indice gonadique en fonction de la profondeur (Fig. 2), excepté fin juin où on retrouve des variations significatives (Tabl. IA) entre les profondeurs de 1-3 m et 6-8 m ainsi qu'entre 6-8 m et 12-15 m (test de comparaison multiple).

Fig. 2. – Indice gonadique moyen de *Paracentrotus lividus* par biotope, en fonction de la profondeur et de la date d'échantillonnage.



Tabl. I. – A, Résultats du test de Kruskal et Wallis ( $\chi^2$ ) pour tester l'effet de la profondeur sur l'indice gonadique de *Paracentrotus lividus*. NS : non significatif; [] : niveau de signification. B, Indice gonadique moyen de *Paracentrotus lividus* en fonction du biotope, la profondeur et la date d'échantillonnage et résultats du test de Kruskal et Wallis ( $\chi^2$ ). () : écart-type; [] : niveau de signification; NS : non significatif.

A, Results of the Kruskal-Wallis test ( $\chi^2$ ) for the effect of depth on gonad index of *Paracentrotus lividus*. NS : not significant; [] : significance level. B, Mean gonad index of *Paracentrotus lividus* according to biotope, depth and sampling date and results of Kruskal-Wallis test ( $\chi^2$ ). () : standard deviation; [] : significance level; NS : not significant.

	Date		<i>Posidonia oceanica</i>		Roche		Résultats du test
	1 - 3 m	6 - 8 m	12 - 15 m				
Test pour les profondeurs à chaque date de prélèvement	26 mar/7avr		1.06 [P >0.05] NS		1.14 [P >0.05] NS		
	6 mai		0.61 [P >0.05] NS		0.24 [P >0.05] NS		
	3 juin		3.31 [P >0.05] NS		4.45 [P >0.05] NS		
	27 juin		15.88 [P <0.001]		9.94 [P <0.01]		
	1 - 3 m		6 - 8 m		12 - 15 m		Résultats du test
	<i>P.oceanica</i>	Roche	<i>P.oceanica</i>	Roche	<i>P.oceanica</i>	Roche	
26 mar/7avr	8.44(3.40)	2.58(1.29)	7.29(1.75)	2.58(0.68)	6.89(2.80)	2.45(1.35)	69.57 [P <0.001]
06 mai	4.27(1.21)	3.07(0.82)	4.27(1.63)	3.44(1.11)	4.68(1.52)	3.21(1.20)	22.12 [P <0.001]
03 juin	3.90(1.12)	2.65(0.86)	3.24(1.32)	3.36(1.09)	3.48(1.31)	3.32(1.52)	3.71 [P=0.05] NS
27 juin	1.93(0.69)	1.86(0.65)	2.96(1.11)	2.68(1.11)	3.18(1.19)	1.87(0.78)	9.11 [P <0.01]

### L'indice gonadique selon le biotope

La profondeur n'ayant pas souvent d'effet significatif, nous avons réuni les données des différentes profondeurs. L'indice gonadique des individus vivant dans l'herbier à *Posidonia oceanica* est en général significativement plus important que celui des individus de la roche (Tabl. IB, Fig. 2). L'IG moyen calculé sur tous les prélèvements donne une valeur de 4.45 (s = 2.47) pour les individus de l'herbier à *Posidonia oceanica* et une valeur de 2.75 (s = 1.17) pour ceux de la roche. Ces deux valeurs diffèrent significativement (test de Kruskal et Wallis :  $P < 0.01$ ,  $\chi^2 = 74.04$ ).

### L'indice gonadique selon l'abondance des Oursins

Dans l'herbier à *Posidonia oceanica*, l'indice gonadique moyen est significativement plus élevé chez les populations clairsemées (« volume d'Oursins » de 50-300 cm<sup>3</sup>/m<sup>2</sup>, qui équivaut à une densité d'Oursins de 1-6 ind/m<sup>2</sup> de 4.5 cm de diamètre moyen) que chez les populations denses (« volume » de 300-900 cm<sup>3</sup>/m<sup>2</sup>, qui équivaut à une densité de 6-18 ind/m<sup>2</sup>), excepté en juin (Tabl. IIA).

Lorsque les Oursins sont clairsemés (50-300 cm<sup>3</sup>/m<sup>2</sup>), la densité des faisceaux de *Posidonia oceanica* est importante et les feuilles sont longues, alors que les populations denses (300-900 cm<sup>3</sup>/m<sup>2</sup>) vivent dans un herbier plus clairsemé

à feuilles plus courtes : il est possible d'y voir la conséquence d'un surpâturage et/ou le signe d'une ressource alimentaire limitante.

Sur roche, les valeurs moyennes de l'indice gonadique sont faibles par rapport à celles de l'herbier à *Posidonia oceanica* (ce qui confirme les résultats de la comparaison de ces deux biotopes) et la variation selon le « volume d'Oursins » n'est jamais significative (Tabl. IIA).

### Effet d'une tempête sur l'indice gonadique

Dans un biotope rocheux avec Algues à une profondeur de 6-8 m, nous n'avons pas trouvé de différences significatives (test de Kruskal et Wallis :  $P = 0.739$ ,  $\chi^2 = 1.25$ ), dans la variation de l'indice gonadique moyen avant, immédiatement après et quelques jours après la tempête des 23 et 24/06/92 (Tabl. IIB).

Par contre, 5 jours avant la tempête (18 juin), nous avons observé une densité moyenne de 5 *P. lividus*/m<sup>2</sup> (taille > 3.5 cm de diamètre) à 6-8 m, le 25 juin, cette densité a diminué (Tabl. IIB) et les Oursins sont descendus vers 10-12 m de profondeur. Dès le 2<sup>e</sup> jour après la tempête, la densité des Oursins à 6-8 m est revenue à son état initial.

### Le coefficient de variation de l'indice gonadique

L'IG varie chez les Oursins d'un même échantillon (prélevés à une date, une profondeur, un bi-

Tabl. II. – A, Indice gonadique moyen de *Paracentrotus lividus* en fonction du biotope, « volume d'Oursins » et date d'échantillonnage et résultats du test de Kruskal et Wallis ( $\chi^2$ ). ( ) : écart-type; [ ] : niveau de signification; NS : non significatif. B, Indice gonadique moyen de *Paracentrotus lividus* avant et après la tempête des 23 et 24 juin. n : taille de l'échantillon; D : diamètre moyen des Oursins (cm); d : densité (ind/m<sup>2</sup>, individus > 3.5 cm diamètre); ( ) : l'écart-type.

A, Mean gonad index of *Paracentrotus lividus*, according to biotope, « sea-urchin volumes » and sampling date and results of Kruskal-Wallis test ( $\chi^2$ ). ( ) : standard deviation; [ ] : significance level; NS : not significant. B, Mean gonad index of *Paracentrotus lividus* before and after the storm of 23 and 24 June. n : sample size; D : mean diameter of sea-urchins (cm); d : density (ind/m<sup>2</sup>, individuals > 3.5 cm diameter); ( ) : standard deviation.

	Posidonia oceanica			Roche		
	50-300 (cm <sup>3</sup> /m <sup>2</sup> )	300-900 (cm <sup>3</sup> /m <sup>2</sup> )	Résultats du test	50-300 (cm <sup>3</sup> /m <sup>2</sup> )	300-900 (cm <sup>3</sup> /m <sup>2</sup> )	Résultats du test
15 mai	4.24(0.96)	3.01(0.98)	12.93 [P < 0.001]	3.17(1.28)	2.94(1.22)	0.53 [P > 0.05] NS
18 juin	2.69(1.04)	2.59(1.51)	0.94 [P > 0.05] NS	2.48(0.61)	2.40(1.03)	0.45 [P > 0.05] NS
28 juillet	4.55(1.47)	2.80(1.08)	16.02 [P < 0.001]	2.99(1.08)	2.58(1.16)	1.28 [P = 0.05] NS

	n	D	d	IG
18 juin	20	4.69(0.17)	5	2.48(0.61)
25 juin	22	4.96(0.23)	< 3	2.52(1.12)
27 juin	20	4.75(0.15)	5	2.68(1.11)
29 juin	20	4.97(0.36)	5	2.75(0.92)

Table III. – A, Coefficient de variation (%) de l'indice gonadique de *Paracentrotus lividus* en fonction de la profondeur, du biotope et de la date d'échantillonnage. B, Coefficient de variation (%) de l'indice gonadique de *Paracentrotus lividus* en fonction du biotope, « volume d'Oursins » et date d'échantillonnage.

Table III. – A, Coefficient of variation (%) of the gonad index of *Paracentrotus lividus* according to depth, biotope and sampling date. B, Coefficient of variation (%) of the gonad index of *Paracentrotus lividus* according to biotope, « sea-urchins volume » and sampling date.

	1 - 3 m		6 - 8 m		12 - 15 m	
	<i>Posidonia oceanica</i>		<i>Posidonia oceanica</i>		<i>Posidonia oceanica</i>	
	<i>Posidonia oceanica</i>	Roche	<i>Posidonia oceanica</i>	Roche	<i>Posidonia oceanica</i>	Roche
26 mars/7 avr	40.28	50.00	24.00	26.35	40.63	55.10
6 mai	28.33	26.71	38.17	32.26	32.47	37.78
3 juin	28.71	32.45	40.74	32.44	37.64	45.78
27 juin	35.75	34.94	37.50	41.41	37.42	36.87

	<i>Posidonia oceanica</i>		Roche	
	50-300 cm <sup>3</sup> /m <sup>2</sup>	300-900 cm <sup>3</sup> /m <sup>2</sup>	50-300 cm <sup>3</sup> /m <sup>2</sup>	300-900 cm <sup>3</sup> /m <sup>2</sup>
	15 mai	22.64	32.55	40.37
18 juin	38.66	58.30	24.59	42.91
28 juillet	32.30	38.57	36.12	44.96

otope et un « volume d'Oursins » identiques). Nous avons donc calculé le coefficient de variation (CV = [écart-type/moyenne].100), afin de vérifier si cette variabilité est plus importante selon l'un des facteurs étudiés. La variabilité de l'IG ne diffère pas en fonction de la profondeur ni en fonction du biotope (Tabl. IIIA), mais elle augmente avec le « volume d'Oursins » (Tabl. IIIB) (elle est plus grande au « volume » 300-900 cm<sup>3</sup>/m<sup>2</sup>).

## DISCUSSION ET CONCLUSIONS

Afin de mieux comprendre la variabilité de l'indice gonadique, chez *Paracentrotus lividus*, nous discuterons les résultats obtenus pour chacun des biotopes.

**Herbier à *Posidonia oceanica*** : Dans ce biotope, l'indice gonadique ne varie généralement pas en fonction de la profondeur (1-3 m, 6-8 m, 12-15 m). Dix (1977) montre que, chez l'Oursin de Tasmanie *Heliocidaris erythrogramma*, la taille de la gonade et l'indice gonadique ne varient pas avec la profondeur. En revanche, Nichols *et al.* (1983) trouvent que, chez *Echinus esculentus* en Grande Bretagne l'indice gonadique est souvent plus élevé chez les populations d'Oursins des eaux peu profondes (8 m) que chez celles vivant plus profondément (20-22 m).

L'abondance des Oursins (exprimée au terme de « volume d'Oursins ») influe significativement sur l'indice gonadique dans l'herbier à *Posidonia oceanica* : celui-ci diminue avec l'abondance des

Oursins. Donc, un « volume » de 50-300 cm<sup>3</sup>/m<sup>2</sup> (ce qui équivaut à une densité de 1-6 individus/m<sup>2</sup> de 4.5 cm de diamètre moyen) semble plus favorable à l'accroissement des gonades. Dans ce cas, les Oursins bénéficieraient d'une quantité de nourriture importante (ressources non limitantes). En effet, l'indice gonadique et l'indice de réplétion sont en relation car, plus l'Oursin se nourrit plus il développe ses gonades (Semroud et Kada, 1987). Moore (1934), trouve une étroite corrélation entre la croissance du test, le développement des gonades et l'abondance de la nourriture chez *Echinus esculentus*; cela est valable également pour les adultes de *Strongylocentrotus intermedius* (Fuji, 1967) ainsi que pour *Strongylocentrotus droebachiensis* (Keats *et al.*, 1983). D'après Gonor (1972) le développement gonadique peut être utilisé comme un indice des conditions de nutrition chez *S. purpuratus*. Cette relation entre le développement gonadique et la nourriture paraît être générale chez les Oursins (Lawrence, 1975; Mottet, 1976). Nos résultats corroborent ceux de Byrne (1990) qui remarque, en Irlande, une relation inverse entre la densité de *P. lividus* et la taille des gonades.

**Roche avec peuplement algal riche** : Comme pour l'herbier à *P. oceanica*, nous n'avons pas trouvé de variations significatives de l'indice gonadique en fonction de la profondeur, excepté fin juin, où la profondeur de 6-8 m paraît plus favorable que les autres au maintien d'un indice gonadique relativement élevé. Des indices élevés ont déjà été signalés à cette profondeur de 6-8 m (Nichols *et al.*, 1981, 1983) chez une autre espèce d'Oursin, *Echinus esculentus*. D'autres auteurs (Keats *et al.*, 1983, 1984) mettent en évidence une

variation de l'indice gonadique moyen en fonction de la profondeur, sur substrat rocheux, chez *Strongylocentrotus droebachiensis*, qui serait surtout due à la variation de l'abondance des Algues préférées selon la profondeur. Or, dans notre cas, la plus grande concentration en Algues préférées par *P. lividus*, telles que *Dictyota dichotoma* et *Halopteris scoparia* (Verlaque, 1987) s'observe en juin à 6-8 m, ce qui pourrait expliquer cette valeur plus élevée de l'indice gonadique.

En revanche, l'indice gonadique moyen des Oursins vivant dans l'herbier à *P. oceanica* est plus important que celui des individus de la roche avec Algues. Les Algues consommées dans le biotope rocheux ne permettent donc pas un développement des gonades aussi important que dans l'herbier à *Posidonia oceanica*. Cela s'expliquerait par le fait que la majorité des Algues du biotope rocheux étudié sont évitées par *P. lividus* à l'exception de *Dictyota dichotoma* et *Halopteris scoparia* (Frantzis *et al.*, 1992). Mais ces mêmes auteurs indiquent que, dans des conditions expérimentales, cet Oursin évite la Phanérogame *P. oceanica*, ce qui apparemment n'est pas notre cas puisque l'indice gonadique est élevé dans l'herbier. Ces plus fortes valeurs seraient dues plutôt à la préférence par *P. lividus* des extrémités épiphytées de cette plante (Verlaque, 1987). Ce dernier et Sellem (1990) trouvent une ration alimentaire journalière beaucoup plus grande chez les Oursins de l'herbier que chez ceux du substrat rocheux, Fernandez (1990) arrive aux mêmes résultats, mais dans les pelouses d'une autre Phanérogame *Cymodocea nodosa* (Ucria) Aschinson.

Toujours dans le biotope roche, l'indice gonadique ne varie pas selon l'abondance d'Oursins (qui équivaut à 1-6 et à 6-18 ind/m<sup>2</sup>) de diamètre moyen : 4.5 cm. Il ne semble pas y avoir d'effet de la densité de la population. Verlaque (1987), calcule pour le même biotope une densité critique<sup>1</sup> (densité responsable de la destruction complète du peuplement algal) pouvant faire régresser des phytocénoses photophiles (surpâturage) et par conséquent le développement des gonades, de 22-28 individus/m<sup>2</sup> (très supérieure à celles que nous avons utilisées), pour des Oursins ayant un diamètre de 4.5 cm.

D'une façon générale, l'indice gonadique des Oursins de l'herbier diminue de la fin de mars jusqu'en juin; sur roche, cette diminution est moins marquée. Cette diminution est le résultat des pontes qui ont eu lieu durant cette période (Fenaux, 1968; Régis, 1979).

L'indice gonadique de *P. lividus* vivant à 6-8 m de profondeur ne présente pas d'évolution signi-

ficative après le passage d'une tempête, tout au moins pour juin, où les indices moyens sont déjà relativement faibles. Par contre, la densité de cet Oursin à cette profondeur est affectée car, pendant la tempête, les Oursins descendent se réfugier à une profondeur plus importante (10-12 m). De telles descentes d'Oursins pendant une tempête ont été observées chez *P. lividus* par Dance (1987) et chez *Echinus esculentus* par Nichols (1979, 1981). Donc, si la tempête n'a pas eu d'influence sur l'indice gonadique des Oursins, elle en a eu sur leur densité. Nichols *et al.* (1983) remarquent qu'il n'y a pas de différence significative dans l'effort de reproduction entre sites exposés et sites protégés des tempêtes chez *Echinus esculentus*. Par contre, Bennett et Giese (1955) indiquent que les conditions climatiques peuvent avoir un important effet sur l'écologie de *Strongylocentrotus droebachiensis* et de *S. franciscanus*; ceci est confirmé par Keats *et al.* (1984) chez *S. droebachiensis* et suggèrent l'hypothèse qu'à court terme, une tempête peut avoir un effet négatif sur les Oursins car ils arrêtent de se nourrir, mais à long terme elle pourrait être positive car elle augmente la quantité d'Algues en dérive. Dix (1970) suggère que les conditions climatiques influencent le développement des gonades d'*Evechinus chloroticus* de Nouvelle Zélande (le volume des gonades étant faible quand la mer est calme et augmentant quand la mer est agitée et les algues en dérive abondantes).

Au total, il apparaît donc que l'indice gonadique de *P. lividus*, dont l'intérêt économique pour la région et l'importance dans le fonctionnement des écosystèmes benthiques méditerranéens sont bien connus, est le plus élevé chez les individus vivant dans l'herbier à *Posidonia oceanica*, avec une abondance faible d'Oursins (1-6 individus/m<sup>2</sup> de taille commerciale). En outre, cette faible abondance s'accompagne d'une plus grande homogénéité de l'indice gonadique, ce qui augmente la valeur commerciale du produit.

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# POPULATION BIOLOGY OF *ELEDONE CIRRHOSA* (MOLLUSCA, CEPHALOPODA) IN THE NORTH AEGEAN SEA (EASTERN MEDITERRANEAN SEA)

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CEPHALOPODA  
BIOLOGY  
REPRODUCTION  
AEGEAN SEA  
MEDITERRANEAN SEA

**ABSTRACT** – The present paper deals with data on the population biology of *Eledone cirrhosa* in the North Aegean Sea (Eastern Mediterranean Sea) collected during eight trawl surveys carried out from 1990 to 1992 as part of an E.E.C. project on demersal resources of this area. The length frequency distributions exhibited gaussian components the progression during time of which was used to model the growth of *Eledone cirrhosa* according to the parabolic equation :  $DML (mm) = 8.18 + 1.75 t + 0.13 t^2$ , where  $t =$  month. On the basis of this model, individuals of *Eledone cirrhosa* in the North Aegean Sea should reach the greatest sizes at a maximum age of about 22 months from hatching. Ripe gonads in males were found in June and August-September whereas mature females were almost exclusively caught during the August-September period. The sizes at first maturation in males and females were 77 mm DML and 89 mm DML respectively. The juveniles were mainly found in the upper 100 m of depth where a nursery area for the species is probably present while mature individuals were mostly fished at a depth greater than 200 m which represents the spawning area of *Eledone cirrhosa* in the North Aegean Sea.

CEPHALOPODES  
BIOLOGIE  
REPRODUCTION  
MER EGÉE  
MER MEDITERRANÉE

**RÉSUMÉ** – Les auteurs analysent quelques aspects de la biologie des populations du Mollusque Céphalopode *Eledone cirrhosa* vivant dans la Mer Egée du Nord. Les données ont été relevées au cours de huit campagnes expérimentales de chalutage, effectuées de 1990 à 1992 en vue d'évaluer les ressources halieutiques démersales. L'analyse a concerné la structure de la population en âge et en taille, la croissance et la reproduction de cette espèce encore peu connue dans ce bassin. Les distributions de fréquence des tailles montrent des composantes gaussiennes et le modèle de croissance est le suivant :  $DML (mm) = 8.18 + 1.75 t + 0.13 t^2$  où  $t =$  mois. Des mâles mûrs ont été trouvés en juin et en août-septembre et les femelles matures en août et en septembre. La taille de première maturité des individus mâles est 77 mm DML et celle des femelles 89 mm. Les juvéniles ont été récoltés entre 60 et 100 m de profondeur où il existe probablement une "aire de nurserie". Les individus mûrs ont été surtout capturés à une profondeur supérieure à 200 m où se trouve "l'aire de ponte" de cette espèce.

## INTRODUCTION

Cephalopods are short-lived fast-growing animals for which difficulties of modelling population parameters, such as growth and mortality, are recognized (Caddy, 1983). However, the knowledge on such population parameters comes from both laboratory and field studies.

Some authors point out the unreliability of the field studies in modelling and forecasting population because of the bias in the samples and the lack of population structure analysis techniques (Boyle, 1983; Forsythe & Van Heukelem, 1987; Wurtz *et al.* 1988) while, on the other hand, sampling optimization and frequency distribution separator methods have been described and applied (Caddy, 1983; Ehrhardt *et al.* 1983; Pauly, 1985; Matricardi *et al.* 1989).

Most studies on biology (reproduction, growth, etc.) in the field population of *Eledone cirrhosa* (Lam., 1798), are related to the western Mediterranean whereas the knowledge on population biology of this octopus in the eastern basin is rather scarce. In fact, until some years ago, even the presence of *Eledone cirrhosa* was considered uncertain in some areas, such as the Aegean Sea (Mangold & Boletzky, 1987).

In this paper some results which have been obtained from a field study on population biology of *Eledone cirrhosa* in the North Aegean Sea are presented and discussed.

## MATERIALS AND METHODS

In the context of a study project on demersal resources financed by the E.E.C., the Institute of Zoology and Comparative Anatomy of the University of Bari (Italy) in collaboration with the National Centre for Marine Research of Athens (Greece), carried out eight seasonal trawl surveys from June 1990 to February-March 1992 in the North Aegean Sea (Fig. 1). A professional trawler of 115 tons gross tonnage, equipped with a 250 Hp engine was hired. The nylon net had a mesh size of 16-18 mm at the cod-end.

The statistical design of sampling, for biological and statistical reasons (Fogarty, 1985), was random-stratified and there were on average 32 hauls, lasting about 1 hour, for each trawl survey. The hauls were planned between 60 and 490 m in depth in the following bathymetrical strata: 0-100 m; 100-200 m; > 200 m. For each haul, the temperature and salinity of the water column were measured.

Dorsal mantle length (DML), expressed in mm, was measured for each individual of *Eledone cirrhosa*. In general sex and maturity stage of gonad were recorded for the whole population sampled. However, for practical reasons, only representative samples were recorded for the individuals caught during August-September 1990 and 1991 and November-December 1990.

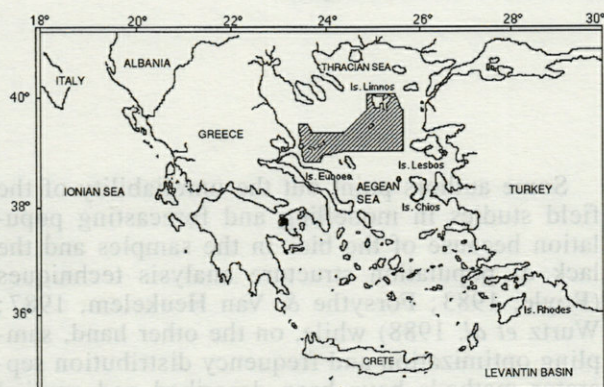


Fig. 1. - Area investigated during eight trawl surveys carried out in the North Aegean Sea from 1990 to 1992.

The maturity stage of the gonad was assessed in relation to the size of the testis and presence of spermatophores in the males, and to the size of eggs in the females (Mangold-Wirz, 1963). In particular, four stages of maturity were defined both in females and in males as follows: 1) immature (in both sexes the gonad is very small, ovary and testis are transparent and membranous); 2) maturing (females with small and medium eggs; males with white testis and forming spermatophores); 3) maturing (females with large reticulated eggs; males with more bulky testis and underdeveloped spermatophores); 4) mature (female with large eggs ready to be spawned, the reticular system on their surface disappears; males with fully formed spermatophores for which a slight pressure on the spermatophoric sac will discharge them through the penis to the mantle cavity).

Analysis of length-frequency distributions was carried out by means of the "steepest descent method" (Hasselblad & Tomlinson, 1971). Such a method permits the identification of the various modes in the length frequency distribution and the goodness of fit is provided by chi-squared criterion.

## RESULTS

The length frequency distribution of the sampled population of *Eledone cirrhosa* exhibited, in each survey, two modal components and a wide range between minimum and maximum length observed (Fig. 2).

Individuals, sizes (DML) of which ranged between 23 and 125 mm, were found during August-September in both years of research.

Very small specimens (between 20 and 38 mm DML), belonging to the new generation and constituting a definite gaussian component, were caught, in the first survey (June, 1990), together with a remarkable number of larger specimens (on average 74 mm DML) representing the second modal peak in the size frequency distribution.

In the successive seasons, a size modal progression of recruits and a decrease of adult individuals was observed. These exhibited an increase in length during warm seasons, from June to August-September, and they were totally missing in the catches of February-March 1991. The smallest individuals fished in June completely replaced the adults in the stock in this latter season.

During the second year of research, both structure and dynamics of the stock was similar to that in the previous year. In fact, in June, a new generation joined the preceding one on the fishing grounds. The adult individuals showed further growth during summer and a decrease during autumn until the sampled population was mainly made up of young individuals in February-March 1992.

The progression of each mode in the length frequency distributions over time ( $29 \pm 3.1$  mm in June 1990;  $35.3 \pm 7.2$  mm in August-September;  $46.5 \pm 6.5$  mm in November-December;  $65.3 \pm 10.7$  mm in the February-March and  $77.4 \pm$

$9.3$  mm in June 1991) was used to model the growth of *Eledone cirrhosa* in the North Aegean Sea. In this respect, the smallest specimens fished in June were considered to be 6 months from hatching (Mangold *et al.*, 1971).

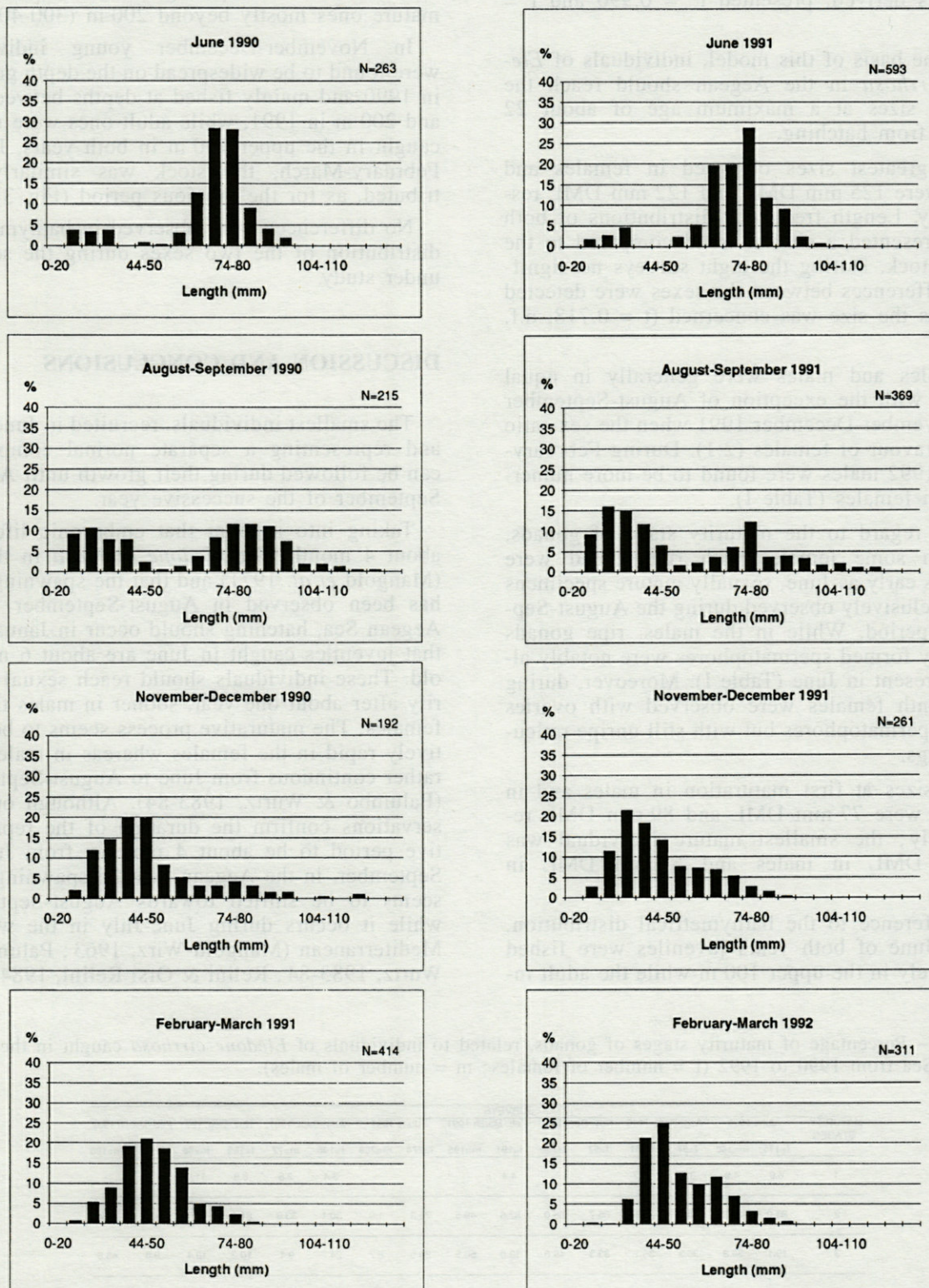


Fig. 2. – Length frequency distributions related to individuals of *Eledone cirrhosa* caught in the North Aegean Sea from 1990 to 1992.



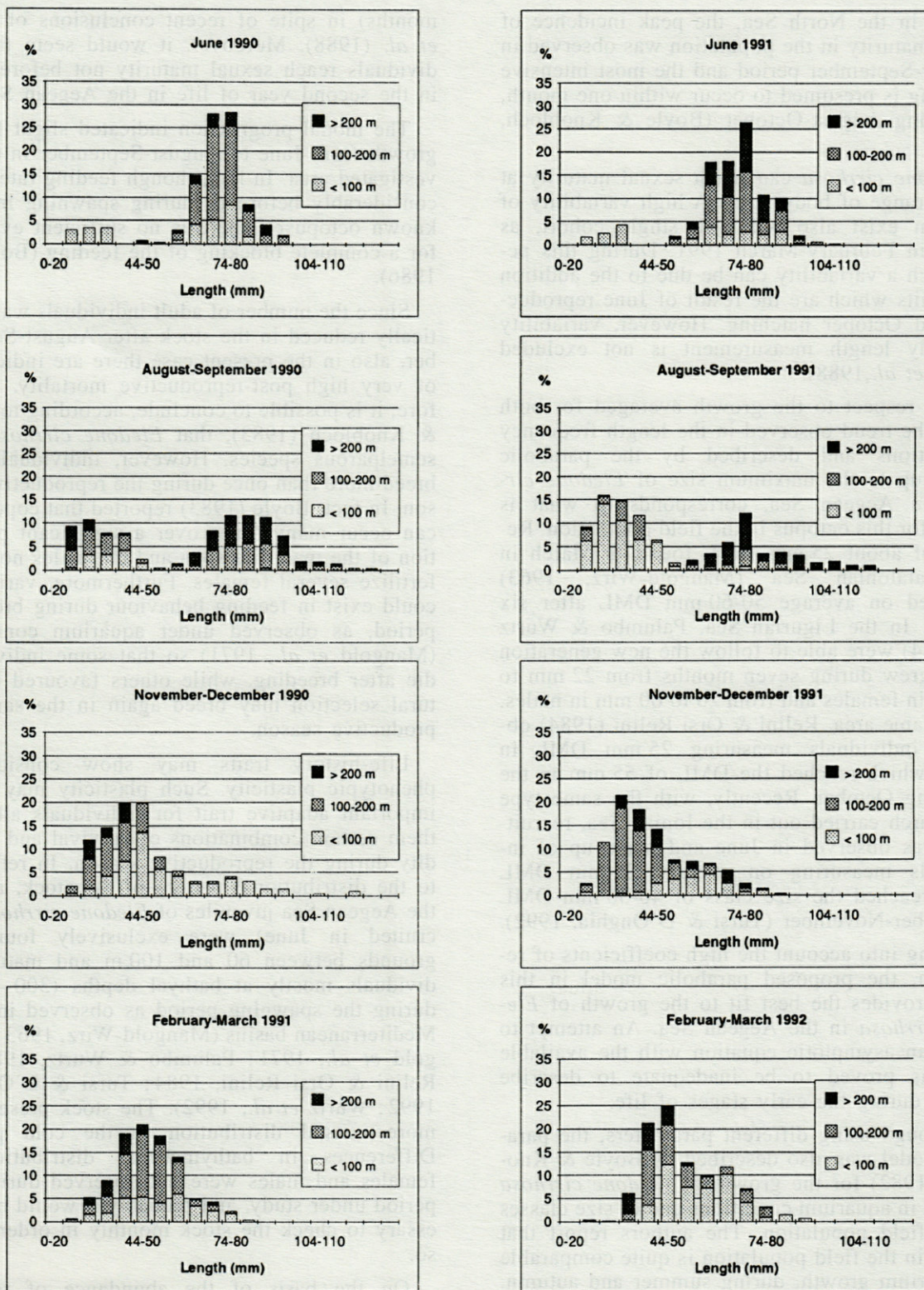


Fig. 3. – Length frequency distributions, related to depth, of individuals of *Eledone cirrhosa* caught in the North Aegean Sea from 1990 to 1992.

spawning peak in August-September determines the recruitment peak in June in the Aegean Sea whereas the spawning peak in June-July leads to

a recruitment peak in early spring in the western Mediterranean Sea.

Also in the North Sea, the peak incidence of sexual maturity in the population was observed in the July-September period and the most intensive spawning is presumed to occur within one month, i.e. during August-October (Boyle & Knobloch, 1983).

*Eledone cirrhosa* can reach sexual maturity at a wide range of body sizes. A high variability of size can exist also within a single cohort, as shown in February-March 1991. During this period such a variability can be due to the addition of recruits which are the result of June reproduction and October hatching. However, variability for body length measurement is not excluded (Baino *et al.*, 1988).

With respect to the growth averaged for both sexes, the trend observed in the length frequency distributions and described by the parabolic model, up to the maximum size of *Eledone cirrhosa* in Aegean Sea, corresponds to what is known for this octopus in the field population. Recruits of about 25 mm DML found in March in the Catalanian Sea (Mangold-Wirz, 1963) measured on average 50-60 mm DML after six months. In the Ligurian Sea, Palumbo & Wurtz (1983-84) were able to follow the new generation which grew during seven months from 22 mm to 55 mm in females and from 20 to 60 mm in males. In the same area, Relini & Orsi Relini (1984) observed individuals measuring 25 mm DML in March which reached the DML of 55 mm in the following October. Recently, with the same type of research carried out in the Ionian Sea, recruitment was observed in June and made up of individuals measuring on average 25 mm DML which reached the size class of 40-50 mm DML in October-November (Tursi & D'Onghia, 1992).

Taking into account the high coefficients of regression, the proposed parabolic model in this paper provides the best fit to the growth of *Eledone cirrhosa* in the Aegean Sea. An attempt to define an asymptotic equation with the available data has proved to be inadequate to describe growth during the early stages of life.

Although using different parameters, the parabolic model was also described by Boyle & Knobloch (1982) for the growth of *Eledone cirrhosa* isolated in aquarium conditions and of size classes in the field population. The authors report that growth in the field population is quite comparable to aquarium growth, during summer and autumn.

In this respect, temperature conditions in the water column beyond 50 m in depth in the Aegean is about 14 °C with very little fluctuation, the same as the temperature conditions maintained in the aquarium by Mangold *et al.* (1971) who studied mediterranean *Eledone cirrhosa*.

On the basis of growth observed it is possible to confirm a life-span of about two years (21-22

months) in spite of recent conclusions of Boyle *et al.* (1988). Moreover, it would seem that individuals reach sexual maturity not before April in the second year of life in the Aegean Sea.

The modal progression indicated slight further growth from June to August-September in the investigated area. In fact, though feeding rates drop considerably before or during spawning in most known octopuses, there is no sufficient evidence for a complete blocking of the feeding (Boletzky, 1986).

Since the number of adult individuals was drastically reduced in the stock after August-September, also in the present case there are indications of very high post-reproductive mortality. Therefore, it is possible to conclude, according to Boyle & Knobloch (1983), that *Eledone cirrhosa* is a semelparous species. However, individuals may breed more than once during the reproductive season. In fact, Boyle (1983) reported that copulation can occur many times over a significant proportion of the male life span and the males normally fertilize several females. Furthermore, variability could exist in feeding behaviour during brooding period, as observed under aquarium conditions (Mangold *et al.*, 1971) so that some individuals die after breeding, while others favoured by natural selection may breed again in the same reproductive season.

Life-history traits may show considerable phenotypic plasticity. Such plasticity may be an important adaptive trait for individuals allowing them certain combinations of survival and fecundity during the reproductive season. In reference to the distributional pattern of the stock, also in the Aegean Sea juveniles of *Eledone cirrhosa* (recruited in June) were exclusively found on grounds between 60 and 100 m and mature individuals mostly at bathyal depths (300-400 m) during the spawning period as observed in other Mediterranean basins (Mangold-Wirz, 1963; Mangold *et al.*, 1971; Palumbo & Wurtz, 1983-84; Relini & Orsi Relini, 1984; Tursi & D'Onghia, 1992; Wurtz *et al.*, 1992). The stock presented a more coastal distribution in the cold period. Differences in bathymetrical distribution of females and males were not observed during the period under study, and probably it would be necessary to check the stock monthly in order to do so.

On the basis of the abundance of recruits Morales (1960) claimed that a spawning area near Blanes (Spain) was at a depth of 100 m while Mangold *et al.* (1971) asserted that, because the hatched *Eledone cirrhosa* are truly planktonic larvae, the only reliable indication for spawning area is the presence of fully mature females.

Therefore, as shown in the Ligurian Sea (Relini & Orsi Relini, 1984), the investigated upper level

(60-100 m) could represent a nursery area for *Eledone cirrhosa* in the Aegean Sea while the deeper grounds (300-400 m) might constitute a spawning area for this octopus.

Finally, since very small specimens were occasionally caught in August-September 1990 at a depth greater than 200 m and taking into account the planktonic phase of hatched individuals, we can conclude that the nursery area can be defined less exactly than the spawning area for this species.

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## TWO RELICT TETHYAN COPEPODS NEW FOR THE MEDITERRANEAN SEA : *EXUMELLA POLYARTHRA* AND *PARAMISOPHRIA AMMOPHILA* (COPEPODA : CALANOIDA)

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COPEPOD  
*EXUMELLA*  
*PARAMISOPHRIA*  
MEDITERRANEAN  
RELICT

**ABSTRACT** – The copepod *Exumella polyarthra* Fosshagen, 1970, previously only reported from the Bahamas, has been recordered in three different submarine caves of Minorca (Balearic Islands, Western Mediterranean). Two females of *Paramisophria ammophila* Fosshagen, 1968 and two copepodids V have been also recordered. The description of the copepodid V of *Paramisophria ammophila* is included. Relationship between this interesting case of biogeographic distribution and the possible relict tethyan character of these species are discussed.

COPÉPODE  
*EXUMELLA*  
*PARAMISOPHRIA*  
MÉDITERRANÉE  
RELICTE

**RÉSUMÉ** – Les Copépodes calanoïdes *Exumella polyarthra* Fosshagen, 1970 et *Paramisophria ammophila* Fosshagen, 1968, décrits des Bahamas, ont été observés dans des grottes sous-marines à Minorque (Iles Baléares). Les caractères morphologiques sont donnés, ainsi que la description du copépodite V de *Paramisophria ammophila*. La distribution géographique et le caractère relict de ces formes en Méditerranée occidentale sont évoqués.

### INTRODUCTION

Cave faunas have drawn great attention because they are inhabited by numerous Tethyan relicts and endemic organisms (Iliffe *et al.* 1984; Wilkens *et al.* 1986; Boxshall 1989; Ohtsuka *et al.* 1993). Diverse biological communities have been found in totally or partially submerged marine caves, and several groups of high taxonomic value have been described (Sket & Iliffe 1980; Yager 1981; Iliffe *et al.* 1984; Bowman & Iliffe 1985).

A carefull examination of some cave-dwelling copepods from the Mediterranean Sea revealed the presence of some interesting species in the caves of Minorca Island.

The copepod family Ridgewayiidae M.S. Wilson, 1958 includes four genera: *Ridgewayia* Thompson & A. Scott, 1903; *Exumella* Fosshagen, 1970; *Placocalanus* Fosshagen, 1970; and *Brattstromia* Fosshagen, 1991. All the species of these genera are characteristic of shallow waters, coastal areas and submarine caves of tropical and sub-tropical regions.

The genus *Ridgewayia* includes nine species (three males not described) with a wide geographic range. The genera *Exumella* and *Placocalanus* include two species each, and the genus

*Brattstromia* is known only from the type species (Table I).

The eight genera included in the family Arietelidae G.O. Sars, 1902 are pelagic, except *Paramisophria* T. Scott, 1897 which is epibenthic and inhabitant of caves or hypersaline bays.

The present paper includes the record of *Exumella polyarthra* and *Paramisophria ammophila*, and the description of the stage V of *P. ammophila*, both species inhabiting different marine caves on Minorca Island. Their presence represents the first record for the Mediterranean Sea. A discussion of the possible relation between these Mediterranean populations and those described on the Bahamas region is also included, considering the relict character of these species and their possible origin in the Tethys Sea.

### MATERIAL AND METHODS

Samples were obtained using diving techniques, with a net of mesh size 0.250 mm and square mouth of 900 cm<sup>2</sup>. Two females and two copepodids of *Paramisophria ammophila* and 116 females, 229 males and 10 copepodids of *Exumella polyarthra* were collected in

Genus	Species	Locality
<i>Ridgewayia</i>	<i>canalis</i> (Gurney, 1927)	Suez Canal (Kabret, Ismailia)
	<i>flemingeri</i> Othman & Greenwood, 1988	Australia (Gulf of Carpentaria)
	<i>fosshageni</i> Humes & Smith, 1974	Panama, Bahamas
	<i>gracilis</i> M.S. Wilson, 1958	Florida (SW coast)
	<i>krishnaswamyi</i> Ummerkutty, 1963	Indian Ocean
	<i>marki</i> (Esterly, 1911)	Bermuda Islands (marine caves)
	<i>shoemakeri</i> M.S. Wilson, 1958	Panama, Florida
	<i>typica</i> Thompson & Scott, 1903	Ceylon
	<i>wilsonae</i> Fosshagen, 1970	Bahamas
	sp. (Krishnaswamy, 1953) sp. Yeatmann 1969	India (Madras) Bermuda Islands
<i>Exumella</i>	<i>polyarthra</i> Fosshagen, 1970	Bahamas (Exuma Islands), Minorca
	<i>tuberculata</i> Grahame, 1970	Jamaica (Kingston Harbour)
<i>Placocalanus</i>	<i>insularis</i> Fosshagen, 1970	Bahamas
	<i>namnus</i> Fosshagen, 1970	Bahamas
<i>Brattstromia</i>	<i>longicaudata</i> Fosshagen, 1991	Belize (Giant Cave, Caye Caulker)

Table I. – Geographic distribution of the species within the family Ridgewayiidae.

Table II. – Station data of the marine caves where individuals of *Exumella polyarthra* and *Paramisophria* sp. were collected.

Cave	Locality	Mean Depth (m)	Temperature (°C)
Cap d'en Font	39°49'43''N, 4°12'20''E	14	17.1
Cova Sa Gamba			
Cala'n Porter	39°52'07''N, 4°07'33''E	6	23

different marine caves on Minorca (Balearic Islands, Western Mediterranean). Station data for the specimens described here are resumed in Table II.

Samples were preserved in 5% formalin solution.

All measurements and dissections were made on specimens in lactic acid, following the method used by Humes & Gooding (1964). The length of the body does not include the caudal rami. The morphological terminology of copepods is based on Huys & Boxshall (1991), Fosshagen & Iliffe (1989).

## THE SPECIES DESCRIPTIONS

### FAMILY RIDGEWAYIIDAE M.S. Wilson, 1958

#### Genus *Exumella* Fosshagen, 1970

#### *Exumella polyarthra* Fosshagen, 1970 (Fig. 1A-E)

#### Material examined

116 adult females (38 on 19 June 88 and 75 on 30 October 82 from Sa Gamba cave; 2 on 19 June 88 from Cap d'en Font cave; and 1 on 10 July 88 from Calau Porter cave), 229 adult males (49 on 19 June 88 and 180 on 30 October 82 from Cova Sa Gamba) and 10 copepodids. Some specimens have been dissected and mounted on slides. All the samples and slides are deposited in the Laboratoire Arago (Banyuls-sur-Mer, France).

#### Adult female (Fig. 1 A-E)

The total length of 10 individuals ranged between 0.80 and 0.89 mm with an average of 0.84 mm (std = 0.035).

Some of the females (Fig. 1A-B) had a long spermatophore (Fig. 1C) reflecting a recent copulation.

No differences have been observed between the individuals of Minorca and those of Bahamas described by Fosshagen (1970). For that reason, only some appendages are represented here (Fig. 1D-E), as a complement of the description by Fosshagen (1970).

### FAMILY ARIETELLIDAE G.O. Sars, 1902

#### Genus *Paramisophria* T. Scott, 1897

#### *Paramisophria ammophila* (Fig. 2A-Q)

#### Taxonomy

Among the 8 genera included in the family Arietellidae, *Paramisophria* T. Scott, 1897 was re-described by Krishnaswamy (1959), Ohtsuka *et al.* (1991) and Ohtsuka *et al.* (1993). There are 11 species and 1 juvenile form described: *P. ammophila* Fosshagen, 1968; *P. cluthae* T. Scott, 1897; *P. fosshageni* Othman & Greenwood, 1992; *P. galapagensis* Ohtsuka, Fosshagen and Iliffe, 1993; *P. giselae* (Campaner, 1977); *P. itoi* Ohtsuka, 1985; *P. japonica* Ohtsuka, Fosshagen & Go, 1991; *P. platysoma* Ohtsuka & Mitsuzumi, 1990; *P. reducta* Ohtsuka, Fosshagen and Iliffe, 1993; *P. spooneri* Krishnaswamy, 1959; *P. variabilis* McKinnon & Kimmerer, 1985; *Paramisophria* sp. Ohtsuka, Fosshagen & Go, 1991. The species described by Tanaka (1966) as *P. cluthae* is different from that described by T. Scott (1897). Nevertheless, as all the authors have emphasized, it is difficult to consider it as a different species from *P. cluthae* T. Scott, 1897 because of the absence of males. *P. cluthae* T. Scott, 1897, described from Lake Fyne (Scotland), was found later by Sars (1902) near the west coast of Norway. It was reported also by Sars (1925) from

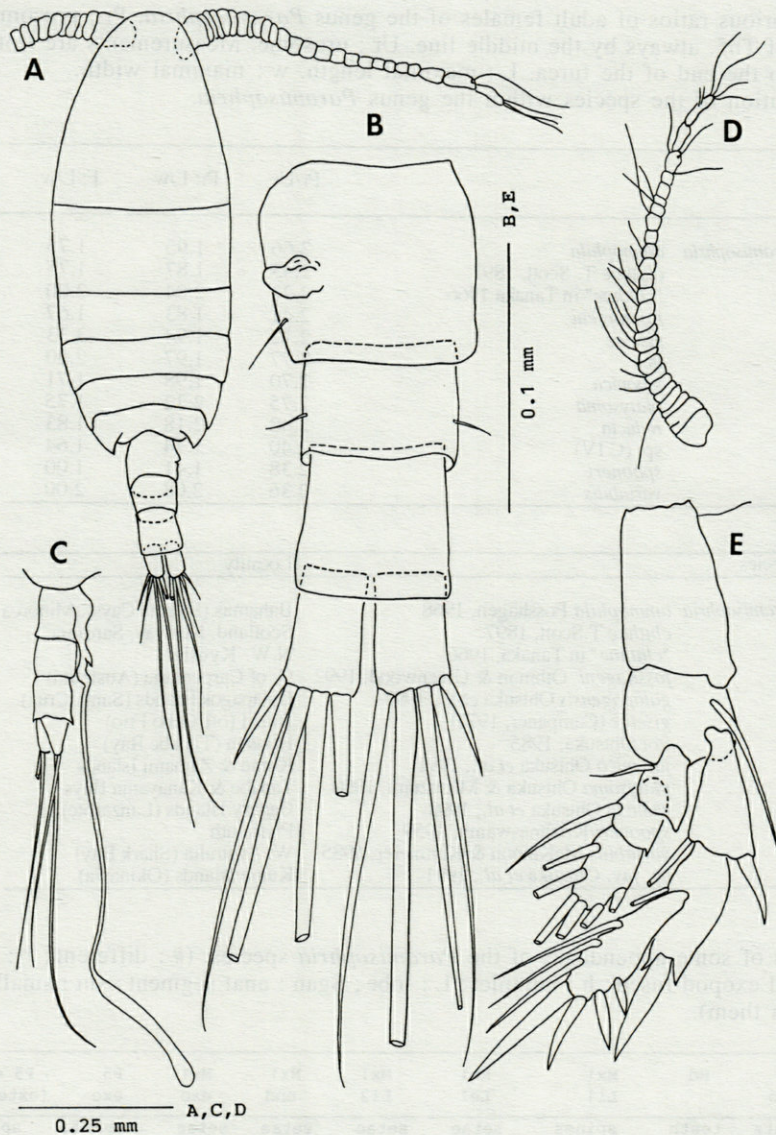


Fig. 1. - *Exumella polyarthra* Fosshagen, 1970, adult female. A, Dorsal view. B, Urosome in ventral view. C, lateral view of the spermatophore and urosome. D, Antennule (A1). E, Fifth leg.

Sardinia (Porto Conte) and by Tanaka (1966) from the coastal waters of the north-west coast of Kyushu (Japan).

The different proportions of the body and the furca of all the species of *Paramisophria* having been described so far are included in Table III A. Their geographical distribution is summarized in Table III B.

#### Material examined

2 females and 2 female copepodids were re-recorded from Sa Gamba cave, 30 Oct. 88. All are deposited in the Laboratoire Arago (Banyuls-sur-Mer, France).

#### Female copepodid stage V (Fig. 2A-J, 3 A-E)

Body (Fig. 2A) Total length = 1.20-1.22 mm; Prosome (length/width) = 2.03-2.09; ratio of length of Prosome/Urosome = 2.51.

Head (Fig. 2B): rounded (dorsal view); rostrum invisible from dorsal view, with two filaments.

Antennule (Fig. 2C): short, extends to approximately half the cephalosome; 21-segmented, the first segment elongated.

Antenna (Fig. 2D): exopod with 4 segments.

Mouth appendages (see Remarks, Table IV and Figs. 2E-H).

Table III A. – List of various ratios of adult females of the genus *Paramisophria*. Pr : prosome. Measures forehead to the posterior margin of Th5, always by the middle line. Ur : urosome. Measurements are from the anterior margin of the genital segment to the end of the furca. L : maximal length. w : maximal width.

B. – Geographic distribution of the species within the genus *Paramisophria*.

A		Pr/Ur	Pr. L/w	F. L/w
<i>Paramisophria</i>	<i>ammophila</i>	2.66	1.95	1.75
	<i>cluthae</i> T. Scott, 1897	2.43	1.87	1.75
	" <i>cluthae</i> " in Tanaka 1966	2.22	2.04	2.00
	<i>fosshageni</i>	2.41	1.83	1.67
	<i>giselae</i>	2.12	1.94	3.33
	<i>itoi</i>	2.77	1.97	2.00
	<i>japonica</i>	2.70	1.98	1.71
	<i>platysoma</i>	2.75	2.32	1.75
	<i>reducta</i>	2.48	2.18	1.83
	sp. (C IV)	2.40	1.74	1.64
	<i>spooneri</i>	2.38	1.41	1.00
	<i>variabilis</i>	2.36	2.08	2.00

B		Locality
<i>Paramisophria</i>	<i>ammophila</i> Fosshagen, 1968	Bahamas (Exuma Cays), Minorca
	<i>cluthae</i> T. Scott, 1897	Scotland, Norway, Sardinia
	" <i>cluthae</i> " in Tanaka, 1966	N.W. Kyushu
	<i>fosshageni</i> Othman & Greenwood, 1992	G. of Carpentaria (Australia)
	<i>galapagensis</i> Ohtsuka <i>et al.</i> , 1993	Galapagos Islands (Santa Cruz)
	<i>giselae</i> (Campaner, 1977)	Brazil (off Cabo Frio)
	<i>itoi</i> Ohtsuka, 1985	Honshu (Tanabe Bay)
	<i>japonica</i> Ohtsuka <i>et al.</i> , 1991	Kume & Zamami Islands
	<i>platysoma</i> Ohtsuka & Mitsuzumi, 1990	Tanabe & Kanayama Bays
	<i>reducta</i> Ohtsuka <i>et al.</i> , 1993	Canary Islands (Lanzarote)
	<i>spooneri</i> Krishnaswamy, 1959	Plymouth
	<i>variabilis</i> McKinnon & Kimmerer, 1985	W. Australia (Shark Bay)
	sp. juv. Ohtsuka <i>et al.</i> , 1991	Kume Islands (Okinawa)

Table IV. Characteristics of some appendages of the *Paramisophria* species. (# : different ; \* : trace of suture ; ? : no data ; Bexo : basipod and exopod fused ; h : humplet ; L : lobe ; Sgan : anal segment ; sm : small ; vis / invis : visible ; ≈ : very similar between them).

Species	A1 N. segments	A2 exo	Md teeth	Mx1 Li1 spines	Mx1 Le1 setae	Mx1 Li2 setae	Mx1 end setae	Mx1 exo setae	P5 exo segments	P5 exo (external) spines	P5 endo setae	Sgan
<i>ammophila</i>	21	4	1+h+3	4≈	5+3	0	1+1sm	3	1+*	3	1	<< Ur
<i>cluthae</i>	21	6	1+3	5≈	4+3	0	1	3	1	3	1	< Ur
<i>cluthae</i> in Tanaka 1966	21	4?/6	1+h+2	3≈	6+1	?	2sm	3	1	3	1	< Ur
<i>fosshageni</i>	21	7	1+3	4+1sm	5+2sm	0	1+1sm	3	1	3	1	< Ur
<i>giselae</i>	22	7	1+h+2	4+2sm	6+2	1 long	1	3	Bexo	2	2	± vis
<i>itoi</i>	21	6	1+3	4+1sm	5+3	0	1+1sm	3	2	3	1	<< Ur
<i>japonica</i>	22	6	1+3	4+1+1	6+2	1 acute	1+1sm	3	2+*	3	2	± vis
<i>platysoma</i>	21	6	1+h+3	4≈+1sm	6+2	0	2#	3	1	3	0	< Ur
<i>reducta</i>	22	8*	1+3	4+1+1	5+1	0	2#	3	1	2	1	< Ur
sp. (C IV)	22	6	1+3	4≈+1+1	6+2	1 long	1	3	1	3	2	invis
<i>spooneri</i>	20	2	? 3≈	5+2sm	?	1+1sm	2	1	3	1	< Ur	
<i>variabilis</i>	21	3	1+3	4≈	5+3	0	2	3	1	3	1	< Ur

Cephalosome & Th1 : separated.

Th4 & Th5 : fused.

Th5 (Fig. 2I) : posterior margins symmetrical and characteristic of the genus, with a sub-dorsal right point that in lateral view forms a large rounded indentation.

Urosome (Fig. 2J) : 4-segmented. Proportional length of urosomal segments and furca (% = 21.6 / 12 / 19.9 / 20 / F = 26.5).

Genital segment (Fig. 2K-K') : slight median anterior prominence. Spermatheca not clearly visible.

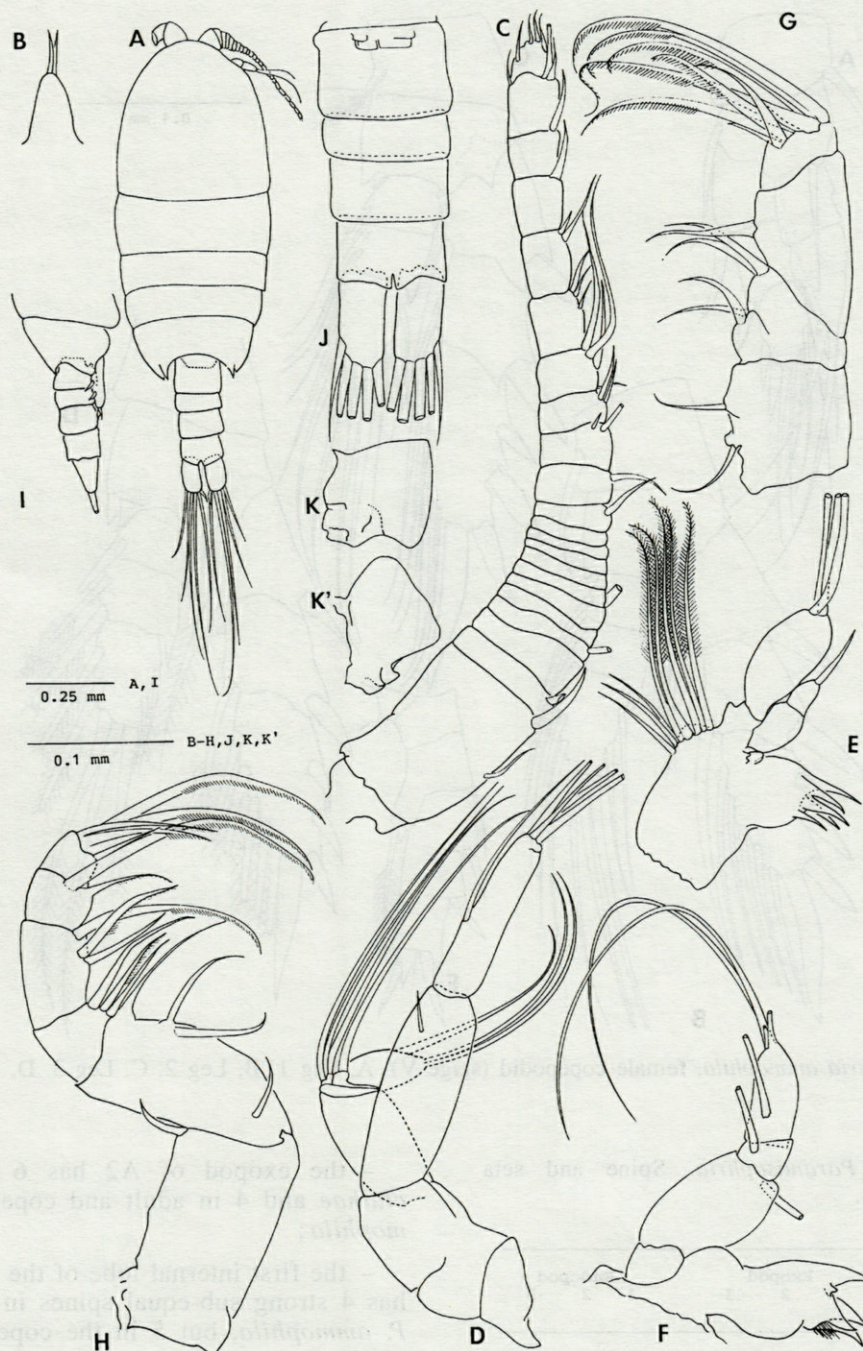


Fig. 2. - *Paramisophria ammophila*, female copepodid (stage V). A, Dorsal view. B, Rostrum. C, Antennule (A1). D, Antenna (A2). E, Maxilla 1 (Mx 1). F, mandible (Md). G, maxilla 2 (Mx 2). H, maxilliped. I, lateral view of Th 5 and urosome. J, Ventral view of the urosome. K-K', Lateral view of the genital segment.

Anal segment (Fig. 2J): well visible, with almost the same length as the preceding segment.

Caudal rami (Fig. 2J): asymmetrical (slightly longer on right side). Length/width ratio = 1.86 (on right side).

Legs 1-4 (Fig. 3A-D): like those drawn by Sars (1902, Pl. 87), although there is a doubt about the presence of one setae at the basis of the leg 4 (Table V).

Leg 5 (Fig. 3E): intercoxal sclerite visible (suture line with the coxa not well marked); coxa clearly separated from basis, which has an external setae. Endopod totally fused to basis. A fine suture is partially marked between exopodal segments 1 and 2, as hint in Fig. 2F in Fosshagen, 1968. Exopodal segment 1 has a strong spine at the distal external margin; exopodal segment 2 has only one spine near the middle of the external margin, none sub-distal.

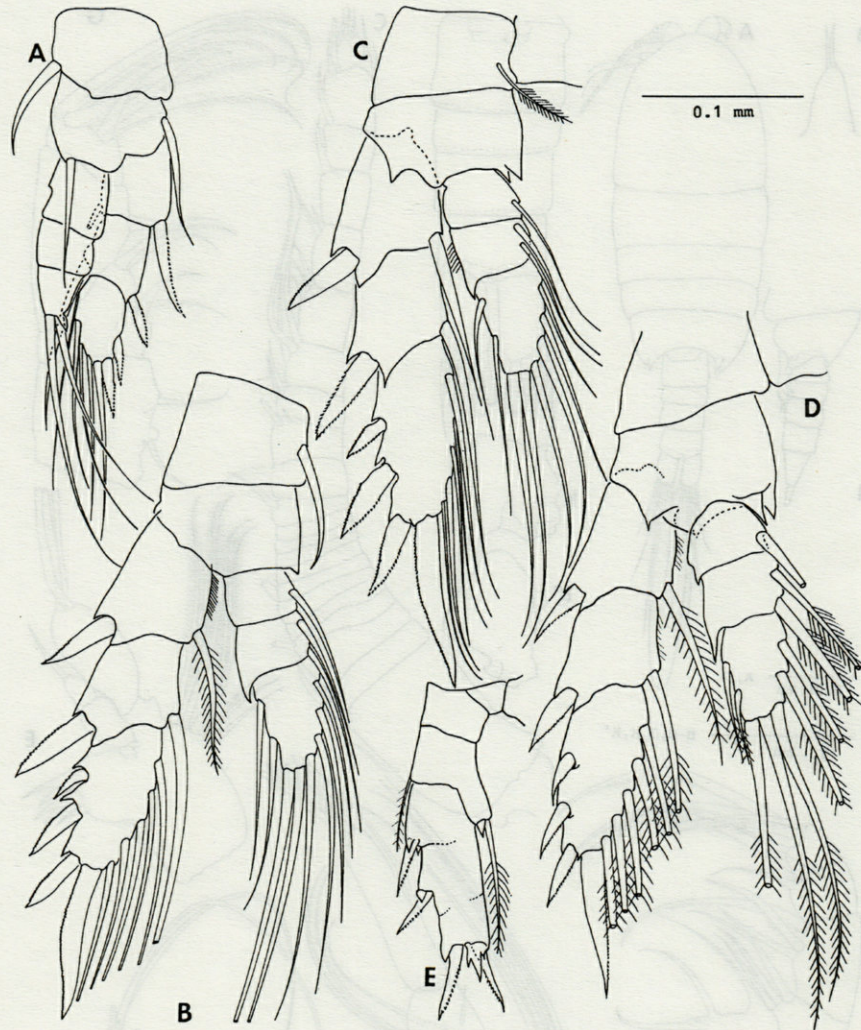


Fig. 3. – *Paramisophria ammophila*, female copepodid (stage V). A, Leg 1. B, Leg 2. C, Leg 3. D, Leg 4. E, Leg 5.

Table V. – Genus *Paramisophria*. Spine and seta formula for legs 1-4.

Leg	Coxa	Basis	Exopod			Endopod		
			1	2	3	1	2	3
Leg 1	0-1	1-1	I-1; I-1;	II-I-4		0-1; 0-2;	1-2-2	
Leg 2	0-1	0-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-4	
Leg 3	0-1	0-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-4	
Leg 4	0-0	1?-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-3	

### Remarks

The most important differences between adult females of *P. cluthae*, *P. ammophila*, and the copepodid stage V of *P. ammophila* are as follows (Fig. 2, 3, 4):

– the exopod of A2 has 6 segments in *P. cluthae* and 4 in adult and copepodid of *P. ammophila*;

– the first internal lobe of the Mx1 (maxillule) has 4 strong sub-equal spines in adult female of *P. ammophila*, but 5 in the copepodid and in *P. cluthae*;

– the first external lobe of the Mx1 has 7 setae in *P. cluthae*, and 8 in the adult female and copepodid of *P. ammophila*;

– the endopod of the fifth leg has one long seta and one smaller in the adult female of *P. ammophila*, but a single long one in the copepodid and in *P. cluthae*;

– the endopod of the fifth leg is slightly longer in the adult female of *P. ammophila* than in the copepodid and in *P. cluthae*;

– the distal part of the exopod of the fifth leg of the adult female of *P. ammophila* has an external spine much longer than the inner one. In

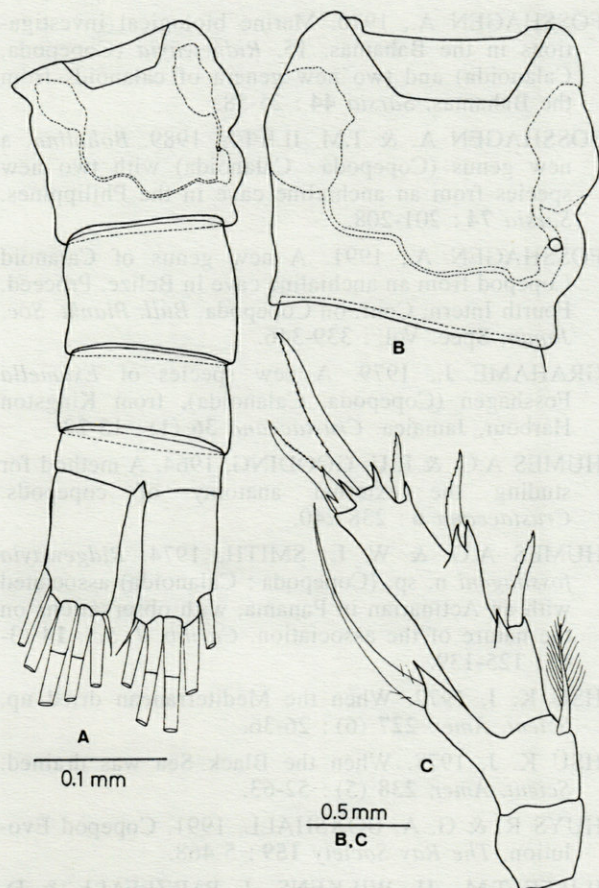


Fig. 4. *Paramisophria ammophila*, adult female. A, Ventral view of the urosome. B, Ventral view of the genital segment. C, Leg 5.

the copepodid and in *P. cluthae* both spines have similar length.

– the anal segment of the adult female of *P. ammophila* is very small compared with the preceding urosomal segment; in the copepodid and in *P. cluthae* both segments are similar in length and longer than in the adult *P. ammophila*.

– in the copepodids of *P. ammophila* the masticatory blade has a small tiny tooth at the internal basal part of the external tooth. This characteristic has been also described in the adult female of *P. ammophila*, but not in *P. cluthae*.

The only copepodid of *Paramisophria* described in the literature is that of Ohtsuka *et al.* (1991) from the Kume Islands (South Japan). It is a copepodid IV of an unknown species. The legs 1-4 have 2 segments on both the endopod and the exopod, and the fifth leg has a well separated intercoxal plate. According to these authors, the last copepodid stages are characterized by the length of the antennule, which does not extend farther than the first pedigerous segment, and by the fusion of segments in the fifth leg. In this genus the number of segments of the

antennule seems to be fixed after stage IV, as was shown by the structure of this cephalic appendage.

According to the complete number of segments of the swimming legs (Table V) the copepodid found in Minorca would correspond to an elder stage than the copepodid IV described by Ohtsuka *et al.* (1991).

## DISCUSSION

The record of *Exumella polyarthra* and *Paramisophria ammophila* from Minorca is particularly interesting from a biogeographic point of view. It not only reflects their not strictly tropical distribution, but also poses the problem of their origin.

The geographic isolation of the two populations by the Atlantic Ocean, one from the western region of the Atlantic (Bahamas) and the other from the Mediterranean Sea (Minorca), lends support to a Tethyan population with gene exchange, predating a relative narrow separation of the Atlantic Ocean. This origin followed by separation and isolation of the species by continental drift, could explain their present characteristic habitat limited to coastal and hyperbenthic areas (Table I and III).

Geologically, there are some relationships between the Caribbean and the South Spanish-Morocco areas since the continental drift and the formation of the Atlantic Ocean (Sclater & Tapscott 1979). It is plausible that the original populations of both, *Exumella polyarthra* and *Paramisophria ammophila*, inhabited the Tethys sea before the drift (200 million years ago). During the following periods (182-112 million years ago; see Dercourt *et al.* 1985) the Tethys sea began an intrusion to the Pangea, which separated Laurasia from Gondwana. The areas occupied now by the Mediterranean Sea and the Florida-Bahamas region were close and connected by that sea; this event allowed the Tethyan fauna to colonize all these regions. Posterior gradual aperture of the Atlantic (6-92 million years ago) forced the separation of the West and the East Atlantic coasts and the geographic isolation of populations at different regions. The interruption of gene flow between populations separated geographically may eventually result in the formation of evolutionarily independent units that can be recognized by genotypic differences.

For a comprehensive analysis of the biogeography of specific taxa, we do not only need data on ecology and biology of the species in question, and on the local geology and history, but also its phylogenetic relationships. Future work with molecular techniques (mtDNA, isoenzymes, or ribo-

somal RNA), would provide phylogenetic information for inferring evolutionary history.

The hypothesis of a recent origin of these species at both the western Atlantic and the Mediterranean Sea would have required convergent evolution to produce the same species in both regions. The chance of convergence producing such similarity is unlikely. Since more species of different groups show the same distribution than these two copepods cited in this manuscript (see Iliffe *et al.* 1984), the hypothesis of the Tethyan origin followed by separation and isolation of the species by continental drift is the most plausible explanation.

The Miocene partial drying of the Mediterranean (Hsü 1972, 1978) could have caused the extinction of some of the species from the open sea. Nevertheless, those inhabiting deep basins which did not dry, and perhaps also caves, could have survived.

New prospecting and discoveries in different places are required to make a satisfactory analysis. By the moment, all considerations remain partially speculative.

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# LIFE-HISTORY PATTERNS AND SPATIAL SEPARATION EXHIBITED BY THE ODONATES FROM A MEDITERRANEAN INLAND CATCHMENT IN SOUTHERN SPAIN

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ODONATES  
LIFE HISTORY  
SPATIAL AND TEMPORAL  
SEPARATION  
MEDITERRANEAN INLAND  
CATCHMENT

**ABSTRACT** – Population dynamics of the most abundant odonate species in a mediterranean inland catchment (*Calopteryx virgo*, *Lestes viridis*, *Cercion lindeni*, *Gomphus pulchellus*, *Onychogomphus uncatatus*, *O. forcipatus*, *Boyeria irene* and *Cordulegaster boltoni*) are analysed. At least five different life-history patterns are exhibited by the odonates that inhabit the basin of the River Yeguas. In the river basins of southern Europe seasonal changes are very marked in seasonal streams and middle and lower reaches of the main channel. Spatial separation among species by occupying different habitats through the catchment was evident. Temporal separation due to life-history displacement seems to decrease competition among co-existing populations. In the basin studied, a progressive increase in the seasonal variation of abiotic factors (temperature, current velocity) going downstream along the main channel, correlates with a progressive decrease in faunal richness, and appears to give rise to the dominance of *C. lindeni*, a species with partly bivoltine life history in the Sierra Morena.

ODONATES  
CYCLE BIOLOGIQUE  
SÉGRÉGATION SPATIALE ET  
TEMPORELLE  
BASSIN INTÉRIEUR  
MÉDITERRANÉEN

**RÉSUMÉ** – Cette étude traite de la dynamique de populations des espèces d'Odonates les plus abondantes dans un bassin intérieur méditerranéen (*Calopteryx virgo*, *Lestes viridis*, *Cercion lindeni*, *Gomphus pulchellus*, *Onychogomphus uncatatus*, *O. forcipatus*, *Boyeria irene* et *Cordulegaster boltoni*). Les Odonates qui peuplent le bassin de la rivière Yeguas présentent au moins cinq modèles différents de cycles biologiques. Dans les bassins fluviaux du Sud de l'Europe les changements de saison sont remarquables dans les ruisseaux saisonniers et dans les tronçons moyen et bas de l'axe principal. Cette étude montre une ségrégation spatiale parmi les espèces, qui se répartissent entre les différents habitats le long du bassin. Parmi les espèces qui cohabitent la séparation temporelle due aux décalages des cycles vitaux peut contribuer à diminuer la concurrence. L'accroissement progressif de la variation saisonnière des facteurs abiotiques (température, vitesse du courant) vers l'aval, le long de l'axe, est corrélée à une baisse de la richesse faunistique et peut aussi entraîner la dominance progressive d'une espèce, *C. lindeni*, à cycle biologique partiellement bivoltin dans la Sierra Morena.

## INTRODUCTION

In the river basins of southern Europe that run through mountains of medium altitude, in general, and in the river system studied here, seasonal changes are very marked (Prat *et al.* 1984, Giudicelli *et al.* 1985) and environmental conditions vary a great deal among the different locations along the basin (Graça *et al.* 1989). These differences are especially evident in summer and early autumn. In many streams of the Mediterranean basin which carry large amounts of water during

the rainy season in winter and spring, the flow is interrupted in summer and autumn. For four or five months of the year, only isolated pools of water remain in the river bed (Giudicelli *et al.* 1985). The spatial distribution of species that allows them to take advantage of different habitats is clearly evident in this type of river.

Most of rheophilous insects (e.g. Plecoptera, Trichoptera, Ephemeroptera) that inhabit rivers with these characteristics have adapted their life-history to the seasonal variations in flow (Petts 1984) such that larvae are confined to winter and

spring, and the emergence (of adults) occurs in spring or beginning of summer. Compared with other aquatic insects, the Odonata exhibit great variety in life-history patterns (Corbet 1962, Norling 1984). Some species that inhabit rivers and streams of southern Europe have a larval stage that lasts for more than a year (Prodon 1976, Suárez *et al.* 1986); some complete their development in a year; and others complete more than a generation per year (Ferrerias-Romero 1991). In all species, except a few in the second (univoltine) category of life-history, larvae occur throughout the year.

On the other hand, whereas in northern and central Europe dragonflies and damselflies occupy, by preference, lentic environments, in the Mediterranean basin these insects represent an important part of the macroinvertebrate communities that inhabit streams and rivers (Carchini and Rota 1982, 1985, Jurzitza 1965, 1993).

The major aims of this study were to find out how the Odonata were distributed in space and time in the varied habitats represented in the River Yeguas, and to evaluate the change taking place in the odonate populations during the year. The River Yeguas runs through a mountainous region in a forested valley that has no industry and negligible agricultural and urban pollution. The models of associations found in the different habitats, especially of those associations that exist during the drier phases of the annual cycle, may be useful in future studies on biological monitoring throughout the year (Armitage *et al.* 1990) or for restoration of rivers in the Mediterranean basin in areas that have characteristics similar to those of the Sierra Morena.

## STUDY AREA

The River Yeguas system can be physiographically divided into three distinct habitat types. *a) Streams with permanent flow.* In the upper part of the catchment, a naturally vegetated area, are stable streams that always have a current. Their banks are lined by deciduous trees – *Alnus glutinosus* (L.), *Ulmus minor* Miller – and, except in winter, sunlight rarely reaches the stream bed. Water temperature never exceeds 20 °C. The origin of the river's main channel is found in two streams of this description: the Cereceda and Pradillo. *b) Seasonal streams.* The middle and lower portions of the catchment are also well vegetated, but this is in part due to human influence by conifer plantings. In this area the tributaries are seasonal, intermittent streams that lack surface water in summer and early autumn. Their banks are populated only by shrubby greenery – *Nerium oleanders* L., *Securinega tinctoria* (L.) – that allows sunlight to reach the riverbed readily.

*c) Main channel.* The main channel of the river flows southward from its origin and after 85 km empties into the River Guadalquivir between Montoro and Marmolejos. Although in the upper reaches the flow is not completely interrupted, closer to the river's mouth seasonality increases progressively such that below 500 m a.s.l., after July, there remain only pools of water in the river bed. The volume of these pools gradually decreases during the summer until the rainy season begins again in mid-autumn (November). The width of the upper river and lower river is 6-10 m and 25-30 m respectively. Marginal trees are sparsely distributed and thus the bottom of the river receives direct and abundant sunlight.

This system drains an area of approximately 828 km<sup>2</sup> and has an annual average volume of 160 hm<sup>3</sup>. The average gradient of the main channel is between 1.8% in the upper tract and 0.3% near the river's mouth.

## METHODS

### Sampling sites

From May 1983 to April 1984, chemical and biological samples were collected monthly in the last week of each month at 8 sampling sites along the catchment (Fig. 1). Two sampling sites were established in the headwater streams. Site 1 was on the stream Cereceda (700 m a.s.l.) and Site 2 was on the stream Pradillo (660 m a.s.l.). Two other sampling sites were established in seasonal tributaries. Site 4 was on the stream Los Términos (570 m a.s.l.) and Site 7 was on the stream Fresnedoso (220 m a.s.l.). Four sampling points were established on the main channel of the River Yeguas. The uppermost, Site 3, was situated 2 km below the confluence of two headwater streams (600 m a.s.l.). Sites 5, 6 and 8 were established downstream at 550, 300 and 200 m a.s.l. respectively. The last site, located near the mouth of the River Yeguas at the Guadalquivir is affected by a dam upstream.

### Chemical and Physical Features

Current velocity and water temperature were recorded monthly at each site. Alkalinity, pH, dissolved oxygen (Winkler method), and Cl<sup>-</sup> concentration were also measured monthly at all sites. Moreover, at two extremes phases of the annual cycle, July and January, Ca<sup>++</sup>, Mg<sup>++</sup>, Na<sup>+</sup>, K<sup>+</sup>, SO<sub>4</sub><sup>=</sup> and P<sub>2</sub>O<sub>5</sub> concentrations were measured.

### Odonata Collection

Insect samples were collected with two 0.5 mm-mesh needed handnets, one with a triangular mouth (30 cm each side of the frame) and the other with a square

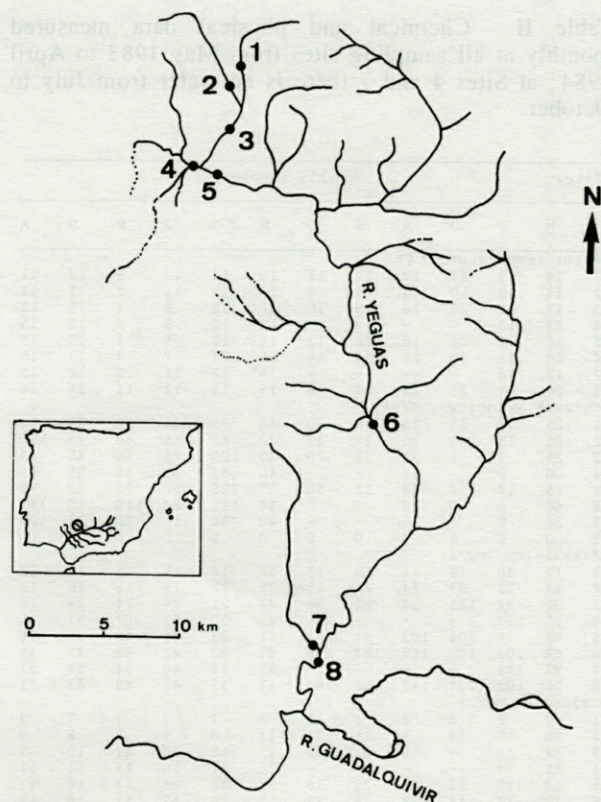


Fig. 1. – Location of the study area on the Iberian Peninsula. The number are the sites of the catchment where physical, chemical and biological samples were collected monthly from May 1983 to April 1984. 1, stream Cereceda; 2, stream Pradillo; 4, stream Los Términos; 7, stream Fresnedoso; 3, 5, 6 and 8, main channel of River Yeguas.

mouth (15 cm each side of the frame). The nets were used simultaneously for 45-60 minutes, collecting larvae in everyone of the habitats existing in each sampling sites. Similar sampling techniques have been used successfully for odonate population studies by Macan (1964), Lawton (1970), Johannsson (1978) and Crowley and Johnson (1982). This method does not necessarily provide high numbers of larvae in each sample, but a sufficient number of samples can allow different environments to be compared (Castella 1987); moreover, it appears to be the best method for collecting larvae of all the species that inhabit sampling sites such as those in this study (Carchini and Rota 1985). A circular aerial insect net, 30 cm in diameter and 80 cm in length of handle, was used to collect adults. Larvae and exuviae were preserved in the field in 70% ethanol for later identification in the laboratory.

#### Data Analysis

Species diversity for each sampling point was assessed using the Shannon-Weaver function (larvae only have been used). The abundance values (larvae only) were distributed among five classes, each of which is given a value of between 1 and 5, according

to Verneaux's method (1973). Furthermore, by using this method, species having an ubiquitous distribution but a very low level of occurrence are easily shown. 85% of odonates collected were larvae.

The terms 'spring' and 'summer' species, applied to life-history patterns, are used throughout the text in the sense defined by Corbet (1954, 1962).

## RESULTS

### Physical-Chemical Characteristics

For most of this fluvial system the physical-chemical characteristics varied significantly from winter to summer. Whereas the headwater streams showed high stability, the summer-to-winter differences in the main channel were very pronounced, especially for the seasonal tributaries that lacked surface water from July to early November. For several parameters the range of variation is greater for sampling sites on the River Yeguas than for those on headwater streams. Notwithstanding this, the variation was especially high for the first site on the upper river (Site 3), where the highest  $\text{Na}^+$ ,  $\text{SO}_4^-$ ,  $\text{Cl}^-$  and  $\text{P}_2\text{O}_5$  concentrations were measured during the summer (Table I). This is the only area on the river which is affected by urban pollution, coming from Fuencaliente, a small riverside village.

The River Yeguas is slightly alkaline at all sampling sites (Table II), although the alkalinity increases downstream. Mean annual values for sampling sites were 16, 21, 51, 66, 63, 89, 75 and 90  $\text{mg/l HCO}_3^-$ . The dissolved oxygen levels were high, most of them exceeding 7.0  $\text{mg/l}$ , except for July's samples in the upper river where Sites 3 and 5 showed 2 and 3  $\text{mg/l}$  respectively. In general, there is a progressive increase in instability along the main channel of the catchment which is due to the very clearly seasonal nature of this type of river basin (Fig. 2). Whereas in the

Table I. – Concentration of ions at the sampling sites in July (s) and January (w); at Sites 4 and 7 (seasonal streams) there is no water in July.

Samples	Water concentration ions (mg/l)							
	Ca	Mg	Na	K	$\text{HCO}_3^-$	$\text{SO}_4^-$	Cl	$\text{P}_2\text{O}_5$
S-1 (s)	20.0	12.2	2.3	0.0	18	0.8	8	0.12
S-1 (w)	12.0	2.4	3.3	0.0	15	3.0	7	0.00
S-2 (s)	20.0	14.6	5.6	1.0	33	28.8	13	0.35
S-2 (w)	16.0	4.9	3.5	0.9	15	22.9	9	0.00
S-3 (s)	40.1	9.7	25.4	9.7	125	44.3	30	0.56
S-3 (w)	12.0	4.9	5.7	1.1	24	19.9	10	0.00
S-4 (w)	20.0	4.9	10.7	1.1	51	19.9	15	0.00
S-5 (s)	36.1	7.3	16.0	2.8	109	3.0	21	0.20
S-5 (w)	20.0	7.3	7.3	1.0	36	34.9	13	0.10
S-6 (s)	44.1	9.7	16.0	3.3	115	17.0	18	0.00
S-6 (w)	16.0	7.3	8.7	0.9	42	31.9	12	0.17
S-7 (w)	20.0	4.9	10.7	0.0	48	5.7	12	0.12
S-8 (s)	40.1	7.3	22.0	2.1	134	1.3	18	0.00
S-8 (w)	16.0	7.3	9.4	0.9	42	7.8	12	0.15

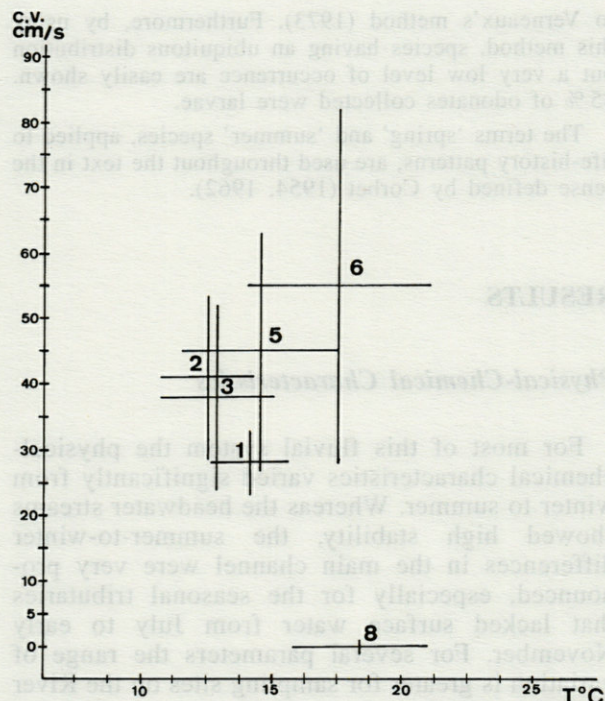


Fig. 2. - Distribution of sampling sites (except seasonal streams, sites 4 and 7) according to annual mean values of temperature and current velocity. Standard deviation is indicated. Current velocity in Site 8 (affected by a dam upstream) was imperceptible on days when this locality was visited. A progressive increase in instability along the main channel (sites 3, 5 and 6) is evident.

upper parts of the river the flow is not interrupted in summer and the maximum water temperature was less than 20 °C, the pools which remain in the middle and lower reaches of the river may experience water temperatures of 30 °C in summer.

**Odonates species richness, abundance and diversity analysis**

The greatest species richness (larvae, exuviae and adults have been used) occurred in the upper part of the main channel where 14 species were collected at Sites 3 and 5 (Fig. 3). Many fewer species were found in the permanent headwater streams : eight and six species were found at Sites 1 and 2 respectively. In seasonal streams at Sites 4 and 7, 8 and 5 species respectively were found. Near the river's mouth only seven species were found. Abundance values are shown in the Table III A.

Although the richness was slightly different at Sites 1 and 2, which are on headwater streams, when diversity for those sites was calculated the Shannon-Weaver index value was similar for the two streams (Fig. 3). At Site 1 the most abundant

Table II. - Chemical and physical data measured monthly at all sampling sites from May 1983 to April 1984; at Sites 4 and 7 there is no water from July to October.

Sites	Monthly samples											
	M	J	J	A	S	O	N	D	J	F	M	A
<b>Water temperature (°C)</b>												
1	14	17	17	17	17	11	15	14	13	8	13	11
2	14	18	19	15	14	9	12	13	11	5	11	11
3	17	18	20	16	15	10	12	12	8	4	10	12
4	23	19	-	-	-	-	10	10	9	6	10	15
5	22	19	24	18	20	12	11	10	9	4	10	15
6	20	21	30	25	24	16	15	13	7	7	17	15
7	17	24	-	-	-	-	14	12	11	10	12	15
8	20	27	25	23	24	18	15	13	12	11	16	16
<b>Current velocity (cm/s)</b>												
1	25	15	15	25	18	30	30	35	35	30	33	50
2	25	15	20	30	18	30	30	60	65	60	45	100
3	25	6	1	20	38	25	40	100	45	40	45	80
4	30	0	-	-	-	-	40	83	55	55	55	65
5	15	17	1	18	15	30	55	125	50	70	70	75
6	60	0	0	0	0	0	60	110	80	110	110	140
7	30	0	-	-	-	-	40	140	55	70	70	100
8	0	0	0	0	0	0	0	0	0	0	0	0
<b>Alkalinity (mg/l)</b>												
1	12	30	18	21	12	15	12	12	15	15	15	21
2	27	32	33	24	21	18	21	12	15	15	18	12
3	30	94	125	94	61	54	42	21	24	24	24	18
4	82	137	-	-	-	-	45	30	51	67	51	61
5	48	79	109	103	91	73	61	33	36	42	39	36
6	67	103	115	158	167	176	67	33	42	48	45	45
7	97	149	-	-	-	-	85	48	48	64	54	57
8	70	103	134	149	152	189	67	33	42	48	45	51
<b>Chloride (mg/l)</b>												
1	7	8	8	8	9	8	8	7	7	7	7	7
2	10	10	13	9	11	10	11	8	9	9	8	9
3	12	18	30	19	21	15	17	12	10	11	10	9
4	12	24	-	-	-	-	16	11	15	16	11	11
5	13	19	21	28	28	19	17	12	13	14	10	11
6	12	17	18	22	26	27	15	10	12	11	10	11
7	12	18	-	-	-	-	15	11	12	11	10	12
8	12	16	18	21	34	36	15	10	12	11	10	11
<b>Dissolved oxygen (mg/l)</b>												
1	7	7	7	8	8	9	8	8	9	8	8	8
2	8	7	7	7	8	9	8	8	9	10	9	8
3	7	5	2	4	6	8	8	9	10	9	9	8
4	7	5	-	-	-	-	9	10	11	10	8	8
5	6	6	3	6	7	9	9	10	11	11	9	8
6	7	6	9	8	9	9	9	9	10	9	8	8
7	8	9	-	-	-	-	9	9	10	9	8	7
8	7	6	8	7	8	10	8	9	11	9	8	7

species were *Onychogomphus uncatus* (Charpentier) (35% of larvae collected) and *Boyeria irene* (Fonscolombe) (26%); the value of the dominance index (McNaughton and Wolf 1970) was 61%. At Site 2, 46% of larvae collected were *B. irene* and 28% were *Cordulegaster boltoni* (Donovan); dominance index 74%.

The richness also differed in the two seasonal streams studied, but in this case the values obtained for diversity differed even more (Fig. 3). At Site 4 on a stream in the middle part of the catchment, *Coenagrion coerulescens* (Fonscolombe) was the most abundant species, making up 50% of the larvae taken. At Site 7 on a stream in the lower part of the catchment, however, 84% of the larvae captured were *Lestes viridis* (Van der Linden). The massive appearance of this species in spring and its clear dominance gave this stream the lowest diversity along the catchment.

The two sites on the upper reach of the main channel showed the greatest richness, 14 species, whereas at Sites 6 and 8 (on the middle and lower reaches) 12 and 7 species respectively were found. When the diversity for the two sites on the upper

Table III. - A, Species found in this study; *Calopteryx* spp. include *C. haemorrhoidalis* and *C. xanthostoma*; *Platycnemis* spp. include *P. acutipennis* and *P. latipes*. Abundance values have been transformed into semi-quantitative data according to Vernaux's method (1973), thus reducing the influence on the calculations of the most abundant species and eliminating species with ubiquitous distribution or with a very low level of occurrence.  $i/N$  is the upper limit of class three (see explanation in text). B, Larval body-length in millimetres, two age-groups are separated.

A		Sites								$i/N$
Species		1	2	3	4	5	6	7	8	
<i>C. virgo</i> (L.)		5	1	2	-	-	-	-	-	7
<i>Calopteryx</i> spp. Leach		4	-	3	-	4	1	-	-	7
<i>L. viridis</i> (V.d.Linden)		-	-	-	1	-	1	5	-	13
<i>Platycnemis</i> spp. Burm.		-	-	1	-	4	4	-	-	2
<i>P. nymphula</i> (Sulzer)										low level of occurrence (2)
<i>I. graellsii</i> (Rambur)										ubiquitous distribution (3)
<i>C. lindeni</i> (Sélys)		-	-	-	1	5	4	1	4	53
<i>C. coerulea</i> (Fonsc.)		-	-	-	5	2	-	-	-	7
<i>G. pulchellus</i> Sélys		-	-	-	-	2	4	-	4	7
<i>O. uncatus</i> (Charp.)		5	4	3	-	1	-	-	-	34
<i>O. forcipatus</i> (L.)		-	1	4	1	5	4	1	-	6
<i>B. irene</i> (Fonsc.)		4	5	1	-	1	-	-	-	35
<i>A. imperator</i> Leach										low level of occurrence (1)
<i>C. boltoni</i> (Donovan)		4	4	1	-	-	-	-	-	31
<i>M. splendens</i> (Pictet)										low level of occurrence (2)
<i>P. depressum</i> (L.)		-	-	3	-	-	-	-	-	6
<i>O. coerulea</i> (F.)		-	-	4	-	3	1	-	-	4
<i>O. chrysostigma</i> (Burm.)										low level of occurrence (1)
<i>C. erythraea</i> (Brullé)										low level of occurrence (3)
<i>S. striolatum</i> (Charp.)										low level of occurrence (2)
<i>T. annulata</i> (Pal.Beauv.)		-	-	-	-	-	3	-	4	5

B		<i>Onychogomphus forcipatus</i>		<i>Gomphus pulchellus</i>
May 1983	10.0	18.3-22.2		17.5
June	10.0-16.8	21.3-24.4		21.3
July	10.6-15.4		10.9-16.5	21.3
August	10.7		17.0	22.0-22.6
September	14.0-14.6			21.6-27.9
October	9.0	18.7		
December			12.7	25.2
January 1984	11.8			28.3
February	13.4			
March	10.9-11.0		14.4	
April	12.5	19.7-24.2		

reach was calculated we found that, although the same number of species had been collected, the diversity was clearly lower at Site 5. The dominance index at site 3 was 43%, the lowest along the catchment. The decrease in diversity values continued progressively toward the mouth of the river. This fact is due to two circumstances: the decrease in species found at each site as one proceeds downriver; and the progressive effect of the dominance of one species, *Cercion lindeni* (Sélys). Of the larvae collected at Sites 5, 6 and 8, 59%, 63% and 79% respectively were *C. lindeni*.

### Temporal variation in community structure

Among the 23 species found during this study, 79.4% of the individuals collected belong to only six species (*L. viridis*, *C. lindeni*, *O. uncatus*, *O. forcipatus*, *B. irene* and *C. boltoni*). Two other species, *C. virgo* and *G. pulchellus*, are less abundant but of significance to the structure of associations.

Larvae of *O. uncatus*, *B. irene* and *C. boltoni* were found on headwater streams throughout the year. The range in size of these larvae, featuring a bimodal instar-distribution of overwintering larvae, demonstrates that these species are semi-voltine. Adults of these three species were collected only in June and July. In general, *O. uncatus* and *B. irene* can be regarded as typical summer species. 76.5% of final-instar larvae of *B. irene* were collected from late January to late May; 52.9% were collected between March and

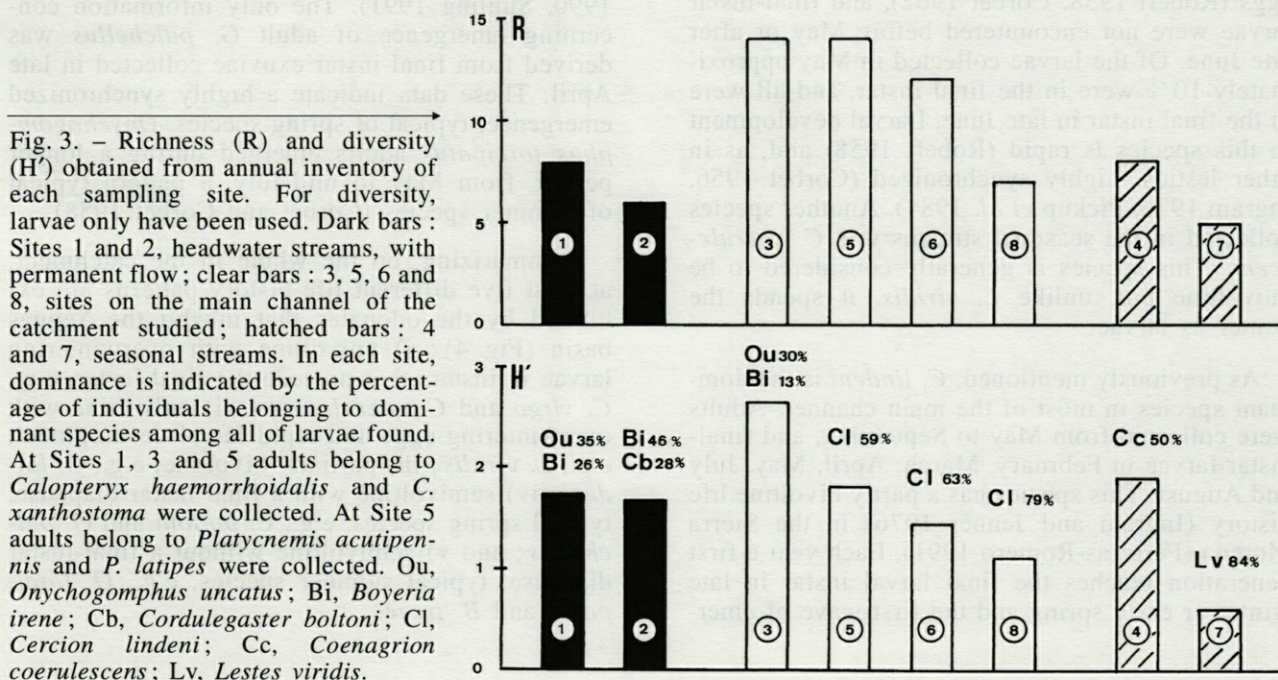


Fig. 3. - Richness (R) and diversity ( $H'$ ) obtained from annual inventory of each sampling site. For diversity, larvae only have been used. Dark bars: Sites 1 and 2, headwater streams, with permanent flow; clear bars: 3, 5, 6 and 8, sites on the main channel of the catchment studied; hatched bars: 4 and 7, seasonal streams. In each site, dominance is indicated by the percentage of individuals belonging to dominant species among all of larvae found. At Sites 1, 3 and 5 adults belong to *Calopteryx haemorrhoidalis* and *C. xanthostoma* were collected. At Site 5 adults belong to *Platycnemis acutipennis* and *P. latipes* were collected. Ou, *Onychogomphus uncatus*; Bi, *Boyeria irene*; Cb, *Cordulegaster boltoni*; Cl, *Cercion lindeni*; Cc, *Coenagrion coerulea*; Lv, *Lestes viridis*.

May. From late January to late May 73.9% of the final-instar larvae of *O. uncatius* were collected and 60.8% between March and May. However, 4 of the 10 *O. uncatius* larvae collected in October were in the final instar; the fact that a certain number of larvae enter the final instar during autumn suggests that this species does not have a very clearly defined life-history pattern, as in some other Odonata (Paulson and Jenner 1971, Norling 1984). On the contrary, *C. boltoni* is a typical spring species: between January and May only 53.3% of final-instar larvae of this species were collected. From late March to late May only 13.3% of the final-instar larvae were collected.

Another species found principally in headwater streams was *C. virgo*. Adults of this species were collected in May, June and July, and final-instar larvae were collected only in February and March. The larvae of this species collected in December were from penultimate and antepenultimate instars. Although our data for this species are not numerous and more extensive studies are required, it is possible that the life history in the south of the Iberian Peninsula differs from that in Britain (Corbet 1957a) and Switzerland (Robert 1958). In our study area it may be that the life history is completed in a year and the final instar is not a diapause stage. This insect appears to function as a summer species.

Dominant in astatic environments (Castella 1987), *L. viridis* is the most characteristic species of the seasonal streams of the Sierra Morena (Ferrerias-Romero 1984, 1988a, Ferrerias-Romero and Gallardo-Mayenco 1985). Adults were collected in June and October and larvae between April and June. This species has overwintering eggs (Robert 1958, Corbet 1962), and final-instar larvae were not encountered before May or after late June. Of the larvae collected in May approximately 10% were in the final instar, and all were in the final instar in late June. Larval development in this species is rapid (Robert 1958) and, as in other lepidoptera, highly synchronized (Corbet 1956, Ingram 1976, Pickup *et al.* 1984). Another species collected in the seasonal streams was *C. coerulescens*. This species is generally considered to be univoltine but, unlike *L. viridis*, it spends the winter as larvae.

As previously mentioned, *C. lindeni* is the dominant species in most of the main channel. Adults were collected from May to September, and final-instar larvae in February, March, April, May, July and August. This species has a partly bivoltine life history (Ingram and Jenner 1976) in the Sierra Morena (Ferrerias-Romero 1991). Each year a first generation reaches the final larval instar in late winter or early spring and the first wave of emer-

gence occurs in spring. The first final-instar larvae were collected in late February at Site 8; at Sites 5 and 6, however, final-instar larvae were not collected before late March. By May many adults were collected. The second generation resulting from cohort splitting consists of individuals that had hatched in spring from eggs laid by the earliest emerging adults. These individuals had grown rapidly, and within a single summer had completed development and emerged in late July, August or September. Other members of the same cohort experienced slow growth such that they were destined to overwinter and then emerge as the first wave the following year.

Two other species that were relatively abundant in the main channel are *O. forcipatus* and *G. pulchellus*, the first of which is found more frequently upstream and the latter downstream. Both species are semivoltine, as demonstrated by the bimodal size-distribution of larvae (Table. III). However, the life-history patterns seen in these insects are not the same in both species. The great majority of *O. forcipatus* larvae collected in autumn and winter were in the antepenultimate instar or were even smaller. Only one larva, collected in October at Site 5, was in the penultimate instar. From July to March no final-instar larvae were collected. Final-instar and penultimate-instar larvae were often collected in April and May. Thus this species is a typical summer species. Final-instar larvae of *G. pulchellus*, on the other hand, were collected in September, December and February. The senior cohort attained the final instar at the beginning of autumn and overwintered in that instar. *Gomphus pulchellus* is a typical spring species. Similar results have been obtained in Lower Saxony (Germany) (Müller and Suhling 1990, Suhling 1991). The only information concerning emergence of adult *G. pulchellus* was derived from final-instar exuviae collected in late April. These data indicate a highly synchronized emergence, typical of spring species. *Onychogomphus forcipatus* adults emerged during a longer period, from May to mid-July, a pattern typical of summer species (Corbet and Corbet 1958).

Summarizing, on the whole in the catchment, at least five different life-history patterns are exhibited by the odonates that inhabit the Yeguas basin (Fig. 4): i) univoltine with overwintering larvae in instars that precede the final instar, e.g., *C. virgo* and *C. coerulescens*; ii) univoltine with overwintering eggs and rapid larval development, e.g., *L. viridis*; iii) partially bivoltine, e.g., *C. lindeni*; iv) semivoltine with a final-instar diapause, typical spring species, e.g., *C. boltoni* and *G. pulchellus*; and v) semivoltine without a final-instar diapause, typical summer species, e.g., *O. forcipatus* and *B. irene*.



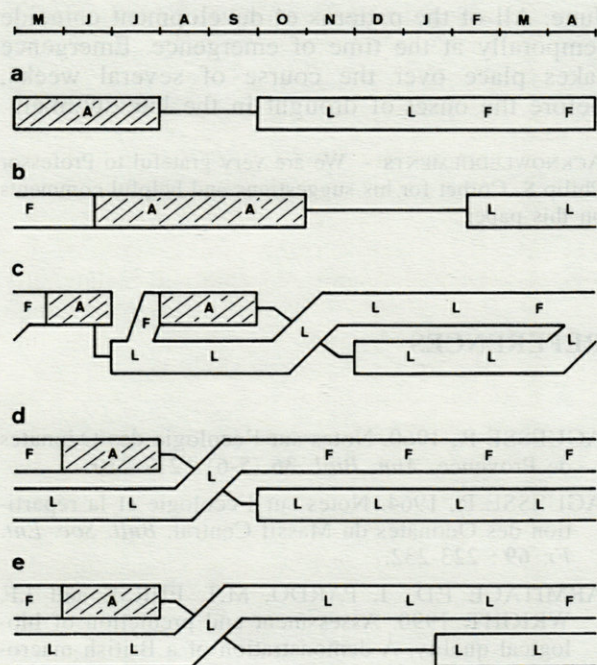


Fig. 4. - Life-history patterns exhibited by the odonates that inhabit the Yeguas basin: a and b, univoltine; c, partially bivoltine; d and e, semivoltine. A in hatched area, adult stage; in clear area, F final-instar larvae, L larvae of smaller instar; line, eggs.

## DISCUSSION

The few studies that have been carried out on the structure and functioning of the odonate community of an entire river basin (Perry 1981) show that the species are distributed according to models that are easily explained as a function of the physiognomy of the river's successive reaches. This is determined by factors such as slope, current-velocity and stability or seasonality of flow (Jarry and Vidal 1969, Aguesse 1960, Voshell and Simmons 1978), parameters that largely dictate the type of river bottom and determining the annual variation in water temperature and the concentration of dissolved oxygen in the water.

In this study highest abundance values correspond to the headwater streams (Sites 1 and 2) and the second half of the upper reach of the main channel (Site 5). Several semivoltine Anisoptera (*O. uncatius*, *B. irene* and *C. boltoni*) find their optimal ecological situation in the headwater streams, and a relatively important population of *C. lindeni* was encountered at Site 5, where *O. forcipatus* also has its ecological optimum.

The uppermost part of the main channel (Site 3) was the only area in the catchment that experiences some level of eutrophication of the water in summer, highest concentration of ions

$\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{SO}_4$ ,  $\text{Cl}^-$ ,  $\text{P}_2\text{O}_5$  (Table. I) and low levels of dissolved oxygen (Table. II). The influx of nutrients at this point on the river is explained by the fact that the only source of urban pollution in the catchment is found some 2.5 km upstream. According to Aguesse (1964), a certain level of eutrophication in the water leads an increase in the variety of odonate species in a given area. The high richness in this site (Fig. 3) must also be explained because some larvae belong to rheophilous species (*O. uncatius*, *B. irene*, *C. boltoni*) must arrive by drift at this area, in winter and spring, from points upstream.

A progressive decrease in richness and diversity were observed going downstream along the main channel. This decrease seems to correspond to a progressive increment in the seasonal variation of abiotic factors (temperature, velocity of current) which, in turn, appears to give rise to the dominance of one species, in this case *C. lindeni*. This insect is partially bivoltine and completes two generations each year (Ferrerias-Romero 1991). *Cercion lindeni* is, probably, the species best adapted to the particular environmental conditions of the rivers of the Sierra Morena (Ferrerias-Romero 1982, 1984, 1988b, Ferrerias-Romero and Gallardo-Mayenco, 1985), conditions characterized by marked seasonality and interrupted flow during several months each year.

Besides *C. lindeni*, in the main channel, two semivoltine species (*G. pulchellus* and *O. forcipatus*) are also abundant. These last species, besides appearing to be partially separated spatially, also exhibit different life histories which in turn are different from the model shown by the more abundant *C. lindeni*. Similarly, in the headwater streams, *B. irene*, *C. boltoni* and *C. virgo* have different life histories. This is probably a useful strategy for counteracting interspecific competition (Butler 1984), because differences in temporal patterns, developmental rates of larvae and, in general, the temporal separation of life cycle events may be important in enabling the species to exist sympatrically (Ingram and Jenner 1976).

The co-existence of several species of Odonata with high abundance levels and different modes of larval development is apparently frequent in ponds (Benke and Benke 1975, Ingram and Jenner 1976) and lakes (Crowley and Johnson 1982). For certain communities the spatial separation of populations occupying different microhabitats appears to be more important to their co-existence than temporal separation (Johannsson 1978). However, among species with similar ecological characteristics, such as odonates, the temporal separation due to life-cycle displacement works importantly to decrease or eliminate competition among populations (Benke 1970), thus favouring their co-existence (Johannsson 1978). Moreover, a niche differentiation in foraging behaviour (a sit

and wait or an active mode) may be one of several ways to reduce food competition between co-existing species (Johansson 1991).

According to Crowley and Johnson (1982), larval habitat and seasonality are important factors in the odonate communities. The results obtained in the Yeguas basin clearly support Crowley and Johnson's conclusions for lentic environments, but here for a river system. The distribution of populations across the catchment seems to reduce the interaction among dominant populations, whereas the seasonal distribution reduces the overall intensity of these interactions. In each of the different types of habitat in the catchment where this study was carried out there exist two or more species with different patterns of life history.

The life-history pattern of *O. uncatius* is unclear because in southern Europe some species that inhabit streams that are highly stable in terms of water temperature, flow and food availability, probably not enter winter diapause in the no-final instars. Although the winter diapause in the larval stage is a well known feature of insects at higher latitudes (Corbet, 1962; Norling, 1984), in southern Europe certain species may only become quiescent in winter. If this is indeed so, the growth of the cohort may be continuous until the larvae reach the final instar. Depending on the season in which a larva reaches the final instar, either it will proceed quickly to maturity (in spring and early summer), or its development will temporarily stop (in late summer, autumn and winter). Such a facultative diapause was first recognised in *Anax imperator* Leach (Corbet 1957b); it permits larvae that have spent their last winter in the latest larval instars (the last two in the case of *A. imperator* in England) to emerge in the same year.

How semivoltine species (*G. pulchellus*, *O. forcipatus*) can complete their life cycles in watercourses that are reduced to a series of isolated ponds from July to October, with elevated water temperature (> 30 °C) and, consequently, very low dissolved oxygen level, is a subject requiring further investigation. Our working hypothesis is that the larvae remain, perhaps in quiescence, in the hyporheic zone. The ecological significance of the hyporheic habitat in rivers has been discussed for several aquatic insects (Williams 1984, Stanford and Ward 1988, Puig *et al.* 1990) including dragonflies (Reygrobelle and Castella 1987, Strommer and Smock 1989). The hyporheic zone offers protective advantages for benthic invertebrates during the dry season (Bishop 1973, Williams 1977).

The diversity in life-history patterns contrasts with the uniformity in the time of year in which almost all of the species studied here are on the wing. All of the species collected as adults were found from May to July; 74% being collected in

June. All of the patterns of development coincide temporally at the time of emergence. Emergence takes place over the course of several weeks, before the onset of drought in the late summer.

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# ECOLOGICAL CORRELATES OF REPRODUCTIVE MODE IN REPRODUCTIVELY BIMODAL SNAKES OF THE GENUS *CORONELLA*

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EVOLUTION OF VIVIPARITY  
SNAKES  
*CORONELLA*  
SEXUAL SIZE  
REPRODUCTION  
ACTIVITY  
COLD CLIMATE

**ABSTRACT** – The snake genus *Coronella* (Colubridae) includes two species, a live-bearing (*C. austriaca*) and an oviparous taxon (*C. girondica*). Data were gathered on several life-history traits of both *Coronella* species in order to shed some light on the selective forces that favoured viviparity, or on subsequent adaptations to the shift in reproductive mode. These data clearly revealed that oviparous and viviparous species are not significantly different in most of the factors that were predicted as favouring the evolution of reptilian live-bearing, including adult body sizes and sexual size dimorphism, offspring sizes, ovulation timing and female frequency of reproduction. Interspecific differences were found in activity patterns, the live-bearing taxon being more heliothermic than the oviparous congener. Moreover, the live-bearing taxon is characterized by its occupancy of colder climates in comparison with the oviparous congener, namely of higher altitudes and latitudes. Our results on *Coronella* strongly agree with those obtained on the Australian elapid snakes *Pseudechis*, but falsify several hypotheses on the ecological consequences of the shift in reproductive mode.

ÉVOLUTION DE LA VIVIPARITÉ  
SERPENTS  
*CORONELLA*  
DIMORPHISME SEXUEL  
REPRODUCTION  
ACTIVITÉ  
CLIMATS FROIDS

**RÉSUMÉ** – Les serpents du genre *Coronella* (Colubridae) comprennent deux espèces, *C. austriaca*, vivipare, et *C. girondica*, ovipare. Les données proviennent de travaux relatifs à la biologie des deux espèces pour mettre en évidence les forces de sélection qui favorisent la viviparité, ou les adaptations consécutives au changement du mode de reproduction. Ces données montrent que les espèces ovipares et vivipares ne diffèrent pas significativement en ce qui concerne les facteurs prédictifs en vue de favoriser l'évolution des Reptiles ovipares, comme la taille de l'adulte et de la différenciation sexuelle, la taille de la descendance, la fréquence de l'ovulation et de la reproduction. Des différences interspécifiques ont été détectées dans les modes d'activité, les taxons vivipares étant plus héliothermes que leurs congénères ovipares. En outre, les formes vivipares se caractérisent par leur présence dans des régions plus froides que celles occupées par les ovipares, en particulier à plus haute altitude et à des latitudes plus élevées. Nos résultats sur *Coronella* sont en accord avec ceux portant sur les Serpents australiens elapidae *Pseudechis*, mais infirment plusieurs hypothèses à propos des conséquences écologiques du changement du mode de reproduction.

## INTRODUCTION

Evolution of viviparity (live-bearing, including both "ovoviviparity" and "eu viviparity" in this term), being a central feature of reptilian reproductive biology, has been a subject of strong debate among evolutionary ecologists since several decades (Packard *et al.*, 1977; Blackburn, 1982, 1994; Shine, 1985, 1987 a).

According to the general opinion, reptilian viviparity probably derived from oviparity by means

of gradual evolutionary processes (Shine and Bull, 1979) and a continuum oviparity-viviparity has been hypothesized (Shine, 1983a; Xavier and Gavaud, 1986). Very recently, some evidence supporting this hypothesis has been found by observing intermediate reproductive characters in the hybrids of oviparous and viviparous *Lacerta vivipara* (Heulin *et al.*, 1992).

Although many hypotheses on the environmental or species characteristics having important roles in the evolution of viviparity have been proposed, the selective forces favouring this process

are not yet well known (Shine, 1987a). Many reptilian genera, in which both viviparity and oviparity occur, could provide ideal models for comparing closely related species having different reproductive modes (Guillette *et al.*, 1980; Guillette, 1982). According to Shine (1987a), such comparisons may shed light on the evolutionary processes that favoured viviparity or on the subsequent adaptations to the changing reproductive mode.

Amongst the European snakes, the bimodality in the reproductive mode is known in the genus *Vipera* (Viperidae) and in the genus *Coronella* (Colubridae). The former genus is composed by a predominant number of live-bearing taxa, while the latter one by one oviparous (*Coronella girondica*) and one live-bearing (*Coronella austriaca*) species. As for the oviparous taxon, Naulleau (1984, p. 31) hypothesized the occurrence of viviparous populations ("avec tous les intermédiaires possibles entre l'oviparité et l'ovoviviparité"), which, however, have not been discovered up to now.

This paper provides information on the ecological correlates of reproductive mode within the two *Coronella* species.

## MATERIALS AND METHODS

This research relies both on bibliography and original data.

Available published data on both *Coronella* species are reviewed, and are discussed where relevant to the predictions analysed in the paper. Additional original information is also given.

Original data on *C. austriaca* were obtained especially from the following three areas:

— (1) Tarvisio Forest (province of Udène Carnic Alps, 900-1100 m a.s.l., north-eastern Italy). This is a mountainous territory characterized by the presence of vast coniferous woods and by typical Alpine climate with rainy spring, cool summer and cold winter with very prolonged snow-covering (Pignatti, 1979). *C. austriaca* is widespread in this area, especially in rocky-stony spots, and at the edges of the coniferous woods. Other snake species are *Vipera berus* and *Natrix natrix*.

— (2) Tolfa mountains (province of Rome, central Italy, 250-500 m a.s.l.). This is a hilly territory characterized by a complex sedimentary basement crossed and overlaid by eruptive rocks related to different volcanic cycles. Climate and vegetation are of Mediterranean type (Pignatti, 1979). *C. austriaca* occurs with scattered populations in this area, usually at the edges of *Quercus* and *Fagus* forests. The snake fauna is very diversified. Common species are *Coluber viridiflavus*, *Elaphe longissima*, *E. quatuorlineata*, *Natrix natrix* and *Vipera aspis*.

— (3) Sagittario Valley (Abruzzi, central Apennines, about 800 m a.s.l.). This is a mountainous area with sub-continental climatic characteristics, i.e. with strong seasonal fluctuations, high temperatures and rare rains during summer, cold and prolonged snow covering during winter. In this latter area the smooth snakes were captured in spots belonging to the *Quercetalia pubescentis*. The snake fauna is very diversified. Widespread species are *Coluber viridiflavus*, *Elaphe longissima*, *E. quatuorlineata* and *Vipera aspis*.

Data on *C. girondica* were recorded in the territory of Tolfa mountains (see area (2) of *C. austriaca*). In this area *C. girondica* is found only with scattered populations. One of these populations (found in the Rio Fiume Valley, about 300 m a.s.l.) was previously surveyed during the course of an ecological study on this taxon (see Agrimi and Luiselli, 1994, for a description of this locality).

Data on *C. austriaca* from areas (1) and (2) were collected during the course of long-term studies on ecological strategies of the snakes of these areas (Luiselli and Agrimi, 1991; Luiselli, 1992, 1993; Luiselli and Rugiero, 1993; Capula and Luiselli, 1994 a, 1994 b). Data on *C. austriaca* from study area (3) were collected by one of the authors (LR) during the years 1991-1993.

As proximate environmental factors are known to strongly influence several snake life-history traits, where possible we compared data carried out from the population of *C. girondica* from Tolfa mountains with (1) data carried out from *C. austriaca* populations living in "contiguous parapatry" with the oviparous congener (at about one km each from the other) and under identical climatic conditions, and (2) with data on *C. austriaca* living under different bioclimatic regimes. This could permit us comparisons of some relevance from an ecological point of view.

Statistical analyses were performed by using a SYSTAT computer package, all tests being two tailed. Significance was assessed at a probability level of 0.05. For the choice of the statistical tests, we followed recommendations in Siegel (1956) and in Sokal and Rohlf (1969).

## RESULTS

There are many hypotheses about factors important for the evolution of reptilian viviparity, and these hypotheses yield a remarkable array of predictions on ecological characteristics of oviparous versus viviparous congeners.

### 1. Is reptilian viviparity correlated with harsh climate conditions?

The principal prediction on the ecological correlates of viviparity in reptiles is that viviparous taxa should occur under climatic conditions different from those of oviparous ones

(colder, hotter, wetter, drier, more unpredictable), as viviparity is an adaptation to increase survivorship of embryos in populations living under harsh conditions (Shine, 1987a). This hypothesis is based on three principal assumptions: (i) pregnant female body temperatures are higher than nest temperatures because of behavioral thermoregulations; (ii) embryonic development is accelerated by this temperature difference; (iii) probability of survival increases in offspring because they hatch before the beginning of autumnal cold (Shine, 1983).

*C. austriaca* is found both at higher latitudes (Fig. 1 and 2; Arnold and Burton, 1978; Saint Girons, 1982; Rage and Saint Girons, 1990) and at higher elevations than the oviparous congener (Saint Girons 1990a), thus broadly confirming such a prediction. For instance, mountainous populations of *C. austriaca* occur also above 2000 m a.s.l., in the alpine pastures beyond the wooded zone (e.g. in the central Apennines [Du-

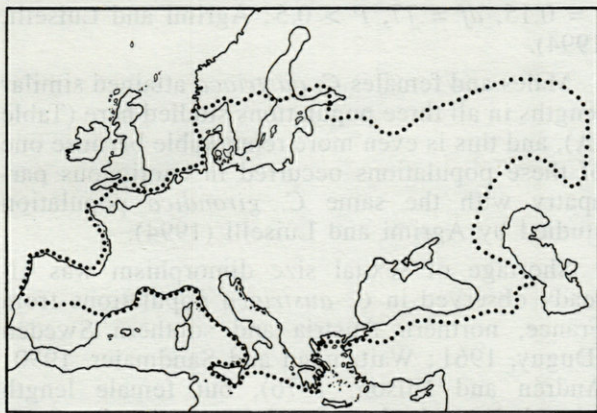


Fig. 1. - European distribution of *Coronella austriaca*.

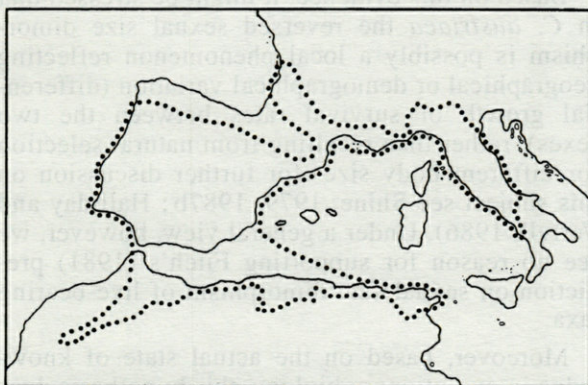


Fig. 2. - European distribution of *Coronella girondica*. Note that this oviparous taxon is found mainly in the Mediterranean region, and that it does not occur in Britain, Scandinavian peninsula, and in other north-European regions where, conversely, its live-bearing congener is actually present.

chessa and Velino mounts, Capula *et al.*, legit] and in the central Alps [Alpe di Siusi, Capula *et al.*, legit]), while *C. girondica* populations do not occur at altitudes higher than 1100 m a.s.l. (Saint Girons 1990b), and are more common at elevations lower than 500 m a.s.l. (Mazzotti and Stagni, 1993; Agrimi, Capula and Luiselli, unpublished).

It is also interesting to note that, when the two species inhabit the same areas, they are never sympatric. In the hilly area of Tolfa mountains, for instance, scattered populations of both taxa inhabit the valley of the stream "Rio Fiume", but the populations of the one species are found at least some hundreds of meters far from those of the other species. Moreover, the two species exhibit different habitat preferences. On the one hand *C. austriaca* inhabits damp-bushy spots bordering the wooded zones (e.g. *Quercus* and *Fagus* forests); on the other hand *C. girondica* inhabits dry pastures with stones and scattered bushes. Though further data are required before stressing firm conclusions, we suspect that such habitat differences may depend on the exigence to reduce interspecific competition between two ecologically similar species (both taxa are similar in body size and dietary habits). In reptile communities, in fact, habitat separation has been shown to be usually the main factor minimizing competition (Pianka, 1966; Jenssen, 1973; Schoener, 1975, 1977), and the distribution of ecologically similar snakes is often complementary (Saint Girons, 1975; 1986).

## 2. Does body size of viviparous taxa exceed that of oviparous ones?

A second prediction, proposed by Neill (1964), suggests that body sizes should be larger in viviparous than in oviparous species, since females of large species should have less risk of predation than small sized ones during pregnancy.

Adult body size of three *C. austriaca* populations were measured. Data in Table IA reveal that the interpopulation variation in average lengths is small (TL ranging from about 47 to about 52 cm), and that body sizes of these Italian *C. austriaca* are similar to adult body sizes of *C. austriaca* from southern Britain (e.g., see Goddard, 1984). Moreover, contrary to the prediction, adult *C. austriaca* did not differ from adult *C. girondica* in terms of average body length ( $P > 0.5$  in all cases).

Gravid females of all *C. austriaca* populations studied here tended to be significantly smaller than gravid females of their oviparous congener ( $P < 0.05-0.01$ , see Table IB, and compare these data with those given by Spellerberg and Phelps, 1977 and Goddard, 1984, for smooth snakes from southern Britain). Also this occurrence is contrary

Table I. – A, Body sizes (TL, mean  $\pm$  SD, in cm) and sexual dimorphism (analysed by two-tailed Student *t*-test) of three *Coronella austriaca* and one *C. girondica* populations from the Italian peninsula. B, Body sizes (TL, mean  $\pm$  SD, in cm) of gravid females of three *C. austriaca* and one *C. girondica* populations from the Italian peninsula. All means did not differ at two-tailed Student *t*-test (in all cases,  $P > 0.5$ ). C, Body sizes (TL, mean  $\pm$  SD, in cm) of offspring *Coronella austriaca* from three study areas of the Italian peninsula.

A		
<i>Coronella austriaca</i>		
	Tolfa Mountains	
adult males:	$x = 50.72 \pm 3.39$ cm	$n = 10$
adult females:	$x = 48.94 \pm 4.96$ cm	$n = 10$
	$t = 0.93, df = 18, P = 0.362$	
	Tarvisio Forest	
adult males:	$x = 51.14 \pm 6.35$ cm	$n = 14$
adult females:	$x = 48.75 \pm 5.83$ cm	$n = 12$
	$t = 0.99, df = 24, P = 0.330$	
	Sagittario Valley	
adult males:	$x = 47.36 \pm 4.09$ cm	$n = 11$
adult females:	$x = 47.30 \pm 3.02$ cm	$n = 11$
	$t = 0.04, df = 20, P = 0.960$	
<i>Coronella girondica</i>		
	Tolfa Mountains	
adult males:	$x = 52.40 \pm 7.89$ cm	$n = 42$
adult females:	$x = 50.80 \pm 7.50$ cm	$n = 37$
	$t = 0.15, df = 77, P > 0.5$	
B		
<i>Coronella austriaca</i>		
Tolfa Mountains:	$x = 48.03 \pm 5.20$ cm	$n = 8$
Tarvisio Forest:	$x = 49.00 \pm 7.37$ cm	$n = 7$
Sagittario Valley:	$x = 48.28 \pm 2.93$ cm	$n = 6$
<i>Coronella girondica</i>		
Tolfa Mountains:	$x = 56.81 \pm 4.28$ cm	$n = 15$
C		
Tolfa Mountains:	$x = 15.31 \pm 0.85$ cm	$n = 39$
Tarvisio Forest:	$x = 15.37 \pm 0.83$ cm	$n = 30$
Sagittario Valley:	$x = 15.27 \pm 1.02$ cm	$n = 32$

to the prediction. However, similar findings were already reported for Australian elapid snakes *Pseudechis*, in which females of the viviparous taxon (*P. porphyriacus*) are smaller than females of most of their oviparous congeners (Shine, 1987a).

Maximum body sizes of *Coronella* species is similar: the longest *C. girondica* known measured 86 cm (Duguy, 1960), while *C. austriaca* individuals exceeded sporadically 80 cm (Arnold

and Burton, 1978). With regard to adult body sizes of natural populations of snakes, however, one should remark that they may depend on several proximate factors – e.g. mortality rates, prey availability, duration of the active period due to climatic conditions, etc. – rather than on precise evolutive trends, so that our indications merely seem to represent a tendency.

### 3. Is sexual size dimorphism more pronounced in viviparous rather than in oviparous taxa?

Fitch (1981) predicted that females should be significantly larger than males in the viviparous species, since the infrequent reproduction of live-bearing females favours increases in body size – and, consequently, in fecundity – at each reproduction.

Sexual size dimorphism was not evident in *C. girondica* from Tolfa mountains, as males ( $n = 42$ ) averaged almost the same total lengths as females ( $n = 37$ ) ( $\bar{x} = 52.4 \pm 7.89$  cm vs  $50.8 \pm 7.50$  cm,  $t = 0.15, df = 77, P > 0.5$ ; Agrimi and Luiselli, 1994).

Males and females *C. austriaca* attained similar lengths in all three populations studied here (Table IA), and this is even more remarkable because one of these populations occurred in contiguous parapatry with the same *C. girondica* population studied by Agrimi and Luiselli (1994).

Shortage of sexual size dimorphism was already observed in *C. austriaca* populations from France, northern Austria and southern Sweden (Duguy, 1961; Waitzmann and Sandmaier, 1990; Andr n and Nilson, 1976), but female length exceeded greatly that of males ( $t = 1.98, P < 0.05$ ) in *C. austriaca* from southern Britain (Goddard, 1984).

Based on this evidence, it might be stressed that in *C. austriaca* the reversed sexual size dimorphism is possibly a local phenomenon reflecting geographical or demographical variation (differential growth or survival rates between the two sexes), rather than resulting from natural selection for different body size (for further discussion on this subject see Shine, 1979, 1987b; Halliday and Verrell, 1986). Under a general view, however, we see no reason for supporting Fitch's (1981) prediction on sexual size dimorphism of live-bearing taxa.

Moreover, based on the actual state of knowledge in evolutionary biology, this hypothesis does not appear convincing to us, as it does not take into any account the current theories on the evolution of sexual dimorphism, either under an eco-ethological point of view (relations with the reproductive system – monogamy/polygamy) or under an ecological point of view (intra- / inter-



specific competition). Sexual size dimorphism is often correlated with the occurrence of male combats for access to females during the mating season (Shine, 1978). Males of both *C. girondica* (Agrimi and Luiselli, unpublished observations) and *C. austriaca* (Davis, 1936; Rollinat, 1947) however, are involved in such combats during the reproductive season.

Moreover, sexual size dimorphism may be strongly influenced by, and depend on, differential growth and survivorship rates between the two sexes, rather than resulting from natural selection for different body sizes (Shine, 1979, 1987b; Haldiday and Verrell, 1986). Alternative hypotheses also include ecological niche partitioning (Shine, 1980), in which intraspecific competition is reduced by each sex using a different resource (Shine, 1986; Houston and Shine, 1993).

#### 4. Are viviparous taxa more heliothermic than oviparous ones?

Shine (1985) suggested that viviparous taxa should be heliothermic rather than thigmothermic, because oviductal egg retention in cold areas accelerates the embryonic development. Thus, live-bearing taxa should be more heliothermic than their oviparous congeners.

This hypothesis seems to be confirmed by our own observations on *Coronella* species. The oviparous taxon, in fact, spends almost all daylight hours under the stones (about 75% [ $n = 141$ ]) of *C. girondica* specimens encountered during daylight hours in the territory of Tolfa mountains were under flat stones; for similar findings see also Saint Girons and Saint Girons, 1956; Saint Girons, 1971; Agrimi and Luiselli, 1994), while *C. austriaca* is a diurnal heliotherm, which exhibits precise thermoregulation at relatively high environmental temperatures ( $> 30^{\circ}\text{C}$ ) (Gaywood and Spellerberg, 1989).

In this regard it is interesting to note that, though in most live-bearing species the gravid females usually maintain higher body temperatures than non-reproductive females and males for accelerating embryogenesis that is temperature-dependent (Shine, 1980; Beuchat, 1988; Schwarzkopf and Shine, 1991; Capula and Luiselli, 1993, etc.), in other species the gravid females do maintain lower temperatures for avoiding developmental accidents. This is the case of the common lizard, *Lacerta vivipara*, in which the mean body temperature of pregnant females is about  $28^{\circ}\text{C}$ , while that of males and non-pregnant females is about  $30\text{--}32^{\circ}\text{C}$  (Patterson and Davies, 1978; Heulin, 1987). Also the regression line  $TC = f(TS)$  calculated for pregnant females appears to be significantly different from those calculated for males and non-pregnant females (Heulin, 1987).

#### 5. Are offsprings of viviparous taxa larger than those of oviparous ones?

According to a popular hypothesis (Shine, 1978), newborn snakes should be larger in viviparous than in oviparous taxa because higher survivorship of eggs in utero than in the nest may favor an evolutionary increase in size of neonates according to the "safe harbor" hypothesis.

On the one hand, mean body length of *C. girondica* offsprings was about 15 cm (ranging from 12 to 20 cm) in central Italy (Agrimi and Luiselli, 1994), and nearly the same in France (Naulleau, 1984).

On the other hand, *C. austriaca* offsprings averaged about 15 cm in either central or northern Italy (Table IC) and about 13 cm (range = 11/19 cm) in southern Britain (Fig. 4 in Goddard, 1984).

In both species, moreover, offspring mass is usually lower than 4 g (Goddard, 1984; Agrimi and Luiselli, 1994).

Based on these data, no positive support to the "safe harbor" hypothesis has derived, though relatively important interpopulation variations of mean offspring size may possibly occur within the genus *Coronella*.

#### 6. Do ovulation and reproduction timing start earlier in viviparous rather than in oviparous taxa?

A popular hypothesis predicts that the seasonal timing of reproduction may shift, resulting in earlier ovulation in the live-bearing taxon because of the relevant advantages of maternal thermoregulation (Guillette, 1982).

In the territory of Tolfa mountains, where both *Coronella* species inhabit areas with identical climate conditions (see methods), a remarkable similarity between the two species was found to occur. Late May was the earliest period in which ova were detected (by palpation) in the oviducts of potentially pregnant females of both species.

On the other hand, in mountainous areas (Alps and Apennines, where the duration of the snake annual cycle is considerably shortened due to strong extrinsic constraints), first ova were detected at the beginning of June, as in northern latitudes (Goddard and Spellerberg, 1980; Naulleau, 1984).

*C. austriaca* gave birth from mid-August (Tolfa mountains) to the beginning of September (Tavrisio Forest and Sagittario valley), while *C. girondica* laid eggs in late June, and egg hatched generally at mid August (Agrimi and Luiselli, 1994).

Fecundity parameters of the two species are rather different.

*C. girondica* was found to produce a low number of eggs ( $X = 2.53 \pm 0.83$ ,  $n = 15$ , range = 1-4), fecundity and female size (length in cm) being slightly positively correlated (Pearson's  $r = 0.38$ , Agrimi and Luiselli, 1994).

*C. austriaca* was found to produce a higher number of young (Duguy, 1961; Appleby, 1971; Andr n and Nilson, 1976). Clutch size was highly positively correlated to female size (Table II for original data; but see also Duguy, 1961; Spellerberg and Phelps, 1977; Goddard and Spellerberg, 1980; Goddard, 1984, for comparisons). Slopes of regressions relative to all smooth snake populations studied here differed significantly from that relative to *C. girondica* from Tolfa mountains (heterogeneity of slopes test,  $P < 0.01$ ). The reasons for such differences are not completely clear, but it appears rather reasonable that either the scarce correlation between female size and fecundity or the lower number of eggs produced by *C. girondica* depend on its semi-fossorial habits (Agrimi and Luiselli, 1994).

Table II. – Results of regression analysis and ANOVA on the relationships between female size (TL, in cm) and fecundity in three Italian populations of *Coronella austriaca*. For comparison with *C. girondica*, see Agrimi & Luiselli (1994).

Population	Analysis of regression		ANOVA			
	$r$	$r^2$	Mean Square	$F$	$df$	Signf. $P$
Tolfa Mountains	.98	96.07%	16.21	146.55	1,8	.00002
Tarvisio Forest	.95	91.20%	14.59	41.45	1,7	.003
Sagittario Valley	.94	89.10%	8.31	32.68	1,6	.004

### 7. Is there a lower number of clutch per female per year in viviparous females?

According to Fitch (1970), the number of clutches produced per female per year should be lower in live-bearing rather than in oviparous taxa, because of the longer duration of burdening of the female.

Because female frequency of reproduction depends essentially on energy available and remarkable differences are accomplished to local factors (e.g., at higher altitudes or latitudes the female frequency of reproduction is lower than at lower altitudes or latitudes, Saint Girons, 1957; Capula and Luiselli, 1992), the ideal system for testing eventual differences in this reproductive parameter is comparing sympatric or contiguously al-

lopatric populations living under identical or very similar environmental and climatic conditions.

We have exactly done this for stressing our conclusions about *Coronella* snakes from Tolfa mountains.

80% of the female *C. austriaca* ( $N = 10$ ) and about 78% of the female *C. girondica* ( $N = 15$ ) captured in late June were pregnant (differences between the two samples:  $\chi^2$  test with  $df = 1$   $P > 0.5$ ). Thus, in both species the female frequency of reproduction appears to be normally annual in Mediterranean environments, and the prediction tested is strongly refused. Moreover, contrary to oviparous lizards such as *Podarcis* species (Barbault and Mou, 1988; Capula *et al.*, 1993), *Coronella* species are unable to reproduce more than once within a season because of insufficient fat body reserves. Also observations carried out in outdoor enclosure support this conclusion.

However, whereas *C. austriaca* was found to mate both in spring and in the early autumn (Luiselli, unpublished observations; Duguy, 1961), the oviparous congener was found to have only a intense spring mating season (Agrimi & Luiselli, 1984).

With regard to the female frequency of reproduction of *C. austriaca*, it must be stressed that this species exhibits annual cycle in central France (Duguy, 1961), and prolonged breeding cycle in more northerly latitudes (e.g. in Sweden and Britain, Andr n and Nilson, 1976; Spellerberg and Phelps, 1977).

Other predictions, for example those proposed by Fitch (1970) and Seigel and Fitch (1984), have not been considered in this note and will be analysed more detailedly in a further paper.

## DISCUSSION AND CONCLUSIONS

The overall analysis of the ecological correlates of reproductive mode within the studied snake genus clearly shows that the live-bearing taxon is remarkably similar to the oviparous congener in most of the studied variables that were considered as possible factors stimulating the evolution of viviparity in squamates. Within *Coronella*, in fact, little variation between live-bearing and oviparous species is evident in, e.g., adult body sizes, sexual size dimorphism, reproductive seasonality and hatching sizes. An almost identical result has been obtained by Shine (1987a) in comparing the ecological correlates of reproductive mode within reproductively bimodal Australian snakes of the genus *Pseudechis*. We retain that the similar results obtained by both us and Shine (1987a) are strongly indicative for understanding general patterns in the evolution of reptilian viviparity, be-

cause (1) *Coronella* and *Pseudechis* belong to two distinct phylogenetic lineages (the former is a genus of Colubridae, the latter of Elapidae) and (2) they inhabit very different areas in terms either geographic or environmental.

Most of the hypotheses which have been suggested as factors stimulating live-bearing evolution have not been confirmed by either studies, while only a few predictions have been supported. For instance, the "climate hypothesis" has been supported by both the studies, as live-bearing taxa of either groups inhabit areas much colder than oviparous taxa. However, the prediction that viviparous species should live in unpredictable habitats (Tinkle and Gibbons, 1977) remains rather untestable at the actual state of the knowledge, at least because it is rather difficult to identify the variables for which predictability is to be assessed. If we consider temperatures and precipitations as the more relevant of these variables, we are lead to agree with Shine (1987a) that the results on both *Coronella* and *Pseudechis* are against the above-exposed hypothesis of Tinkle and Gibbons (1977). In fact, these two variables are more predictable at higher than at lower altitudes or latitudes (e.g., see Zammuto and Millar, 1985), so that live-bearing taxa seem to inhabit predictable rather than unpredictable environments. In regard to the "climate hypothesis", we agree with Shine (1987 a, p. 561) that the occupancy of cold climates by live-bearing squamates, though being the most consistent correlate of viviparity within reproductively bimodal reptiles, "could mean either that viviparity has usually evolved in cold climates, or that species in which viviparity has evolved are then likely to invade cold climates".

Another point in which studies on either *Coronella* or *Pseudechis* does agree is in regard to the heliothermicity of the live-bearing taxa. We retain that this characteristic may be a consequence of the shift in the reproductive mode rather than a factor stimulating viviparity, but no definitive proof has been produced in this regard. Thus, we can consider the greater heliothermicity of viviparous species both as cause and as effect of the change in reproductive means. Moreover, although this prediction has been confirmed by the observations on *Coronella*, we are not convinced that most of the viviparous reptiles are more heliothermic than their oviparous congeners.

The theoretical assumption that live-bearing taxa should have a lower number of clutch per female per year than their oviparous congeners has not been supported by our data. However, one should consider that other reptiles with reproductive strategies and parental investment different from these snakes may also verify such a prediction. For instance, Heulin and associates (1994) demonstrated that, because of a second clutch in

one year, annual fecundity is higher in lowland oviparous populations than in lowland viviparous populations of the lizard *Lacerta vivipara*. However, the birth dates of viviparous *Lacerta vivipara* populations are similar to the dates at which early eggs of mountainous oviparous populations hatched (Heulin *et al.*, 1991).

At the same time, although some lines of evidence have been found in a few squamate groups (e.g., see Heulin *et al.*, 1992), we do not remain completely convinced that viviparity, which has evolved independently at least 95 times in squamates and in some cases more than once within a single genus (Shine, 1983; 1984), always evolved gradually. The absence of intermediate forms in *Coronella* as well as in numerous other reptile genera with reproductive bimodality, in fact, lead us to think that, at least in some cases, live-bearing might be the result of a relatively rapid and sudden change (e.g., see Eldredge and Gould, 1972; Gould and Eldredge, 1977).

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