LIFE-HISTORIES, SPECIATION, AND BIODIVERSITY IN MEDITERRANEAN PROSOBRANCH GASTROPODS

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SPECIATION
BIODIVERSITY
LARVAL ECOLOGY
MEDITERRANEAN
PALEOCLIMATE

ABSTRACT. – Marine gastropod molluscs are a very suitable group to study life-histories and speciation processes related to temporal and spatial patterns of biodiversity. Several developmental strategies have been adopted by marine prosobranch gastropods, that can fall into two fundamental categories : 1) planktotrophic development, with larvae feeding on plankton ; 2) non-planktotrophic development, with larvae that reach metamorphosis without feeding on plankton and usually spend less time or no time at all in the plankton. Presently, the Northeast Atlantic prosobranch fauna includes a large number of pairs of sibling species differing mainly or only in developmental strategy. A speciation model involving loss of planktotrophy as a leading factor, has been proposed to explain this pattern. Heterochronic changes during morphogenesis are considered the basis for such speciation events involving shifting of larval strategies, and epigenetic plasticity seems to explain some of the observed patterns rather well. In these cases environmental factors may have been responsible for "switching off" the pelagic larval phase in specific conditions, with a selection against planktotrophs. Restricted areas, higher predation rate, changes in food availability and temperature, are considered as some of the main selecting factors. The Mediterranean Sea proved to be a good laboratory to test the model. Comparison of palaeontological data, distribution patterns, molecular (allozyme) dating of some cladogenetic events, address the very Recent history of the basin. Quaternary palaeoclimatic fluctuations are very good candidates as responsible for having produced conditions (restricted areas, confinement, higher predation rate, fluctuating food availability etc.) unsuitable for the planktotrophs.

SPÉCIATION
BIODIVERSITÉ
ÉCOLOGIE LARVAIRE
MÉDITERRANÉE
PALÉOCLIMAT

RÉSUMÉ. – Les Mollusques Gastéropodes marins représentent un des groupes les plus appropriés à l'étude des cycles biologiques et des processus de spéciation, liés aux modèles temporels et spatiaux de biodiversité. Les Gastéropodes Prosobranches ont adopté plusieurs stratégies de développement, que l'on peut classer dans deux catégories : 1) planctotrophes, avec des larves qui se nourrissent de plancton, et 2) non-planctotrophes, avec des larves qui ne se nourrissent pas de plancton et qui ne sont pas planctoniques, ou qui le sont pour une période très brève. Dans la faune de l'Atlantique Nord-Est de nombreux couples d'espèces de Prosobranches ne diffèrent entre elles que par les stratégies de développement. Un modèle de spéciation, avec perte de la planctotrophie comme facteur guide, a été proposé pour expliquer ce phénomène. Des modifications hétérochroniques pendant la morphogenèse sont considérées comme la base de ces déplacements dans les stratégies larvaires et des phénomènes de spéciation qui en résultent, un certain degré de plasticité épigénétique peut aussi expliquer la dynamique du phénomène. Des facteurs environnementaux jouent un rôle décisif dans la suppression de la phase planctotrophe, avec la sélection négative des larves planctotrophes. Les principaux facteurs sont reconnaissables dans la limitation des aires, la prédation élevée, les changements de température et de sources alimentaires. La Mer Méditerranée se présente comme un bon laboratoire pour vérifier ce modèle. La comparaison des données paléontologiques, des types de distribution, des datations moléculaires (allozymiques) des divergences cladogénétiques, nous amène à considérer l'histoire récente du bassin. Les fluctuations paléoclimatiques du Quaternaire représentent les causes les plus probables des conditions environnementales (aires limitées, confinement, prédation élevée et fluctuation des ressources alimentaires, etc.) négatives pour les planctotrophes.

Orthogonal cancellate
intracapsular **non-planktotrophic**

Diagonal cancellate
planktotrophic veliger
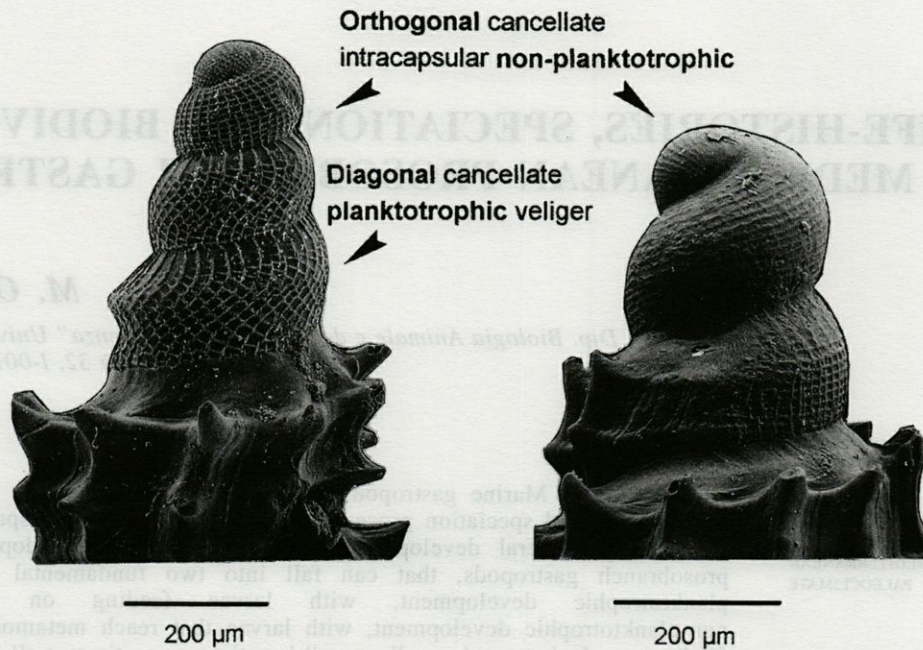
200 μm　　　　　　　　　　　　200 μm

Fig. 1. – Protoconchs of two prosobranch gastropods showing differences in the sculpture between a planktotrophic and a non-planktotrophic embryonic/larval shell. A, *Raphitoma hystrix* De Cristofori & Jan, from the Upper Pliocene of Tabiano (Italy) : 3 1/2 whorls, planktotrophic. B, *Raphitoma pseudohystrix* Sykes, from Central Tyrrhenian Sea – 80 m : 1 1/2 whorls, non-planktotrophic. Scale bar = 200 μm.

INTRODUCTION

Biodiversity is the product of a series of processes operating over time and space. In the past, attention has been mostly paid to the spatial patterns of biodiveristy. In several marine environments, the recent advances in taxonomy resulted in discovering a high number of sibling/cryptic species. This fact produced figures of diversity three to five times greater than previously recognised (Knowlton & Jackson, 1994), and we are probably looking only at the tip of an iceberg in most cases (Knowlton, 1993). More recently, the problem of a deeper understanding of dynamic processes producing biodiversity has been raised. Such processes have important components operating over a temporal scale, and speciation plays obviously a central role. Presently, interest is growing into aspects of speciation related to adaptation. The life histories of the involved organisms play an important role in the understanding of the speciation mechanisms. Particularly, larval ecology (long vs. short/absent pelagic life) exerts a remarkable influence on the life history of a species, especially as concerns their dispersal capability, the possibility and the extent of gene flow between populations, as well as the extinction/speciation rate (Mileikovsky, 1971; Scheltema, 1972, 1977; Shuto, 1974; Valentine and Jablonski, 1986; but see also Hedgecock, 1986).

Marine gastropod molluscs are a very suitable group to this aim. Likewise most of the marine invertebrates (see e.g. Jablonski & Lutz, 1983; Strathmann, 1978 a, 1978 b, 1985), several developmental strategies have been adopted by the marine prosobranchs. Regardless the uptake of dissolved organic material as an additional source of energy (Manahan, 1990; Jaeckle & Manahan, 1989), they can fall into two fundamental categories.

[P] planktotrophic development, with larvae feeding on plankton, spending a relatively long time in the planktonic stage;

[NP] non-planktotrophic development : in the most part lecithotrophic (but including also direct development, brooding, etc.) : larvae, if present (lecithotrophic), have at their disposal a more or less large yolk supply, reach metamorphosis without feeding on plankton and usually spend less time or no time at all in the plankton.

Features of embryonic/larval shells (protoconchs) are powerful tools to identify the mode of development of each individual (Fig. 1); if the protoconch is preserved in the adults, their larval development can be inferred from characteristics of the sculpture and by comparison of the dimensions (Thorson, 1950; Jablonski & Lutz, 1980). The developmental type of specimens in fossil material (Fig. 1A) can be also defined, when the protoconchs are preserved. It is a rare possibiliy in the Animal kingdom, that allows to study this biological feature along a temporal dimension.

SIBLING SPECIES

A recent study scored the presence in the Northeast Atlantic prosobranch fauna of a large number of pairs of sibling/cryptic "species" differing mainly or only in the developmental strategy (Oliverio, 1994 a). This world wide phenomenon (Hoagland and Robertson, 1988) has a particular relevance in this area. A particularly large number of such pairs are concentrated in the Mediterranean basin (Table I). In a few cases, the actual status of some such pairs of morphs (whether they might be considered as sibling species, or not) has still not been defined conclusively, although most of the "species" are currently accepted as such by European malacologists (e.g., Sabelli et al., 1990-1992; see also Hoagland and Robertson, 1988; Bouchet, 1989).

The existence of sibling species, differing only or mainly in their larval development witnesses in favour of a model of speciation involving loss of planktotrophy as a leading factor (Oliverio, 1991, 1996). In such a scenario the models of speciation, related in some way to larval ecology, are synthesised as follows :

I. Speciation within groups with planktotrophic development. Speciation usually occurs at the edges of the ancestral species range (Hansen, 1978; Shuto, 1974); often a peripatric model (Mayr, 1982) could explain the speciation events, notwithstanding the alleged homeostatic effect of the larval dispersal.

II. Speciation within groups with non-planktotrophic development. Usually because of the reduction or even absence of gene flow between populations (low dispersal capability), speciation appears like a classic allopatric event, and in some conditions, radiation may be favoured because of the isolation of the demes.

III. Speciation associated with the loss of planktotrophy (Oliverio, 1991, 1996). The mechanism of this type of speciation involves the modification of larval development. Environmental factors can be responsible for switching off the pelagic larval phase in specific conditions that select against planktotrophs. Restricted areas, higher predation rate, changes in food availability, etc., can be considered as the main factors (Strathmann, 1978 a, b).

Heterochrony is suggested to be an important prerequisite for evolutionary developmental transitions; it can explain the (presumably intraspecific) variation observed in some cases. Changes in timing (speed and sequence) of the developmental pathways underlie many aspects of organismal diversity (Gould, 1977; McKinney, 1988; Raff et al., 1990). Yet, little is known about the mechanisms ruling heterochronic variations

(Blackstone and Buss, 1993; Parks et al., 1993), and only recently theoretical models for the reaction norm are being tested (Gavrilets and Scheiner, 1993 a and b). Heterochronic changes in genes operating during oogenesis can result in changes (even dramatic) in the developmental pathway. According to Strathmann et al. (1992) heterochrony can account for at least the initial transition to non feeding larval development. Such epigenetic plasticity does not require the acceptance of a polymorphism and fits rather well with an approach of the problem under an "Alernative adaptation" perspective (West-Eberhard, 1986; see also Smith-Gill, 1983). Alternative developmental phenotypes produced by heterochrony can provide the basis for speciation.

The analysis of the distribution ranges of the "forms" within each pair provides useful insight for the comprehension of the mechanisms of Speciation III. An increasing dominance of the NP mode going eastward in the Mediterranean has been observed. Taking the Sicily Channel area as the boundary, exclusively eastern and western distribution are automatically defined. Prevalently eastern and western distribution are those of the species ranging slightly over the boundary, but with the main ranges centred East and West of the Channel, respectively. Out of the list in Table 1,21 NP vs. 7 P taxa have their prevalent or exclusive distribution in the Eastern basin; 9 NP vs. 20 P are prevalently or exclusively found in the Western basin.

THE WORKING HYPOTHESIS

During the last epochs, several geological events (e.g. closure of Tethyan and Atlantic connections, reopening of Gibraltar and the entry of cold water from the Atlantic in the Pleistocene) were important factors contributing to the modification of the Mediterranean faunas in the period from Miocene to Pleistocene (see Di Geronimo, 1990, for a comprehensive review). It can be considered that one or more of the Late Tertiary to Quaternary geological events that characterised Mediterranean history, could have operated on a number of species, at different times, providing speciation opportunities. This is partly confirmed by the analysis of the evolution of larval development in some prosobranch lineages in the Mediterranean area (Oliverio, 1994 a; Oliverio and Sabelli, unpublished). The paleontological data set indicates a clear trend toward the loss of planktotrophy in those lineages, with P NP transitions located in few points along the temporal scale. Paleoclimatic fluctuations also produced important changes on Mediterranean faunal assemblages, and in very recent times. Levels of genetic

Table I. – Pairs of "morphs" and their distribution. A = Atlantic; M = Mediterranean; W = Western Mediterranean (W to the Sicily Channel); E = Eastern Mediterranean (E to the Sicily Channel); * = Localized, endemic to (...). **Bold capitals** indicate the preferential distribution.

planktotrophic	distribution		non-planktotrophic
Alvania rudis (Philippi, 1844)	WE	WE	*A. litoralis* (Nordsieck F., 1972)
Alvania cimex (Linné, 1758)	W	WE	*A. mamillata* Risso, 1826
Alvania testae (Aradas & Maggiore, 1844)	WE	WE	*A. subsoluta* (Aradas, 1847)
		WE	*A. elegantissima* (Monterosato, 1875)
Alvania cancellata (Da Costa, 1778)	WE	W	*A. hirta* Monterosato, 1844
Alvania discors (Allan, 1818)	WE	WE	*A. lineata* Risso, 1826 group
Rissoa labiosa (Montagu, 1803)	AWE	E*(Gabes)	*R. paradoxa* (Monterosato, 1844)
		AE	*R. membranacea* (Adams, 1800)
Rissoa radiata Philippi, 1836	W	WE	*R. munda* (Monterosato, 1884)
Rissoa guerini Recluz, 1846	WE	WE	*R. lia* (Monterosato, 1844)
Rissoa ventricosa Desmarest, 1814	WE	WE	*R. variabilis* (Von Muehlfeldt, 1824)
R. splendida Eichwald, 1830	E		
Rissoa pulchella Philippi, 1836	WE	E	*R. marginata* Michaud, 1832
Rissoa monodonta Philippi, 1836	WE	E	*R. auriformis* Pallary, 1904
Rissoa auriscalpium Linné, 1758	WE	W*(Tyrrh.)	*R. italiensis* Verdun, 1985
		E	*R. rodhensis* Varduin, 1985
Rissoa similis Scacchi, 1836	WE	E	*R. scurra* (Monterosato, 1918)
Rissoa violacea Desmarest, 1814	WE	E	*R. sp.*
Vitreolina curva (Monterosato, 1974) group	WE	E	*V. levantina* Oliverio *et al.*, 1994
Columbella adansoni Menke, 1853	A	AM	*C. rustica* (Linné, 1758)
Nassarius circumcinctus (Adams, 1851)	WE	E	*N. gibbosulus* (Linné, 1758)
Nassarius caboverdensis Rolàn, 1984	A	M	*N. ferrusaci* Payraudeau, 1826
Mangelia rugulosa (Philippi, 1844)	W	E	*"Mangiliella" barashi* Aartsen & Fehr-de Wal, 1978
Mangelia paciniana (Calcara, 1839)	W	E	*"Mangiliella" sandrii* (Brusina, 1865)
Mangelia costulata (Blainville, 1826)	WE	E*Gabès	*"Mangiliella" pallaryi* (Nordsieck, 1977)
Mangelia scabrida (Monterosato, 1890)	WE	E	*"Mangiliella" secreta* Aartsen & Fehr-de Wal, 1978
Bela nebula (Montagu, 1803)	WE	E	*"Fehria" taprurensis* (Pallary, 1904)
Bela nana (Scacchi, 1836)	WE	E	*"Fehria" zenetouae* Aartsen, 1988
Raphitoma laviae (Philippi, 1844)	WE	WE	*"Philbertia" philberti* (Michaud, 1829)
Raphitoma echinata (Brocchi, 1814)	WE	WE	*"Philbertia" horrida* (Monterosato, 1844)
Headropleura sp.	A	M	*H. septangularis* (Montagu, 1803)

divergence, based on allozymic data from a few case-studies (Oliverio, 1994a, b, 1996; Munksgaard, 1990) address relatively recent events of separation of the entities within each pair.

The Atlantic neogastropod *Columbella adansoni* (with planktotrophic development) is separated from the mainly Mediterranean *Columbella rustica* (its sibling/sister with non-planktotrophic development) at a genetic distance of ca D = 0.4; this level allows dating (Nei, 1987) the cladogenetic event at ca. 2 MY bP. Noteworthy, this estimate indicates the period following the onset of the glaciations and their southward extension (Tunnell and Douglas, 1983; Thunnell *et al.*, 1984). Confinement of the Mediterranean basin during cool phases probably supported the specia-

tion event. The present distribution pattern recalls the glacial southward faunal shifts (Taviani *et al.*, 1991), with boreal species moving from North, and thermophilic species (as *C. adansoni* appears to be, according to its tropical-subtropical range) being often pushed southward along the African coasts (Oliverio, 1994 a, 1995).

In the North Sea the *Rissoa labiosa* [P]/*R. membranacea* [NP] pair has been studied by Munksgaard (1990). She scored evidence of genetic isolation in sympatric populations of the two species. The genetic distance between them was ca. D = 0.056 dating the speciation to ca. 200-250 000 years bP.

Much lower levels have been scored (Oliverio, 1994 b) in the populations of two rissoid
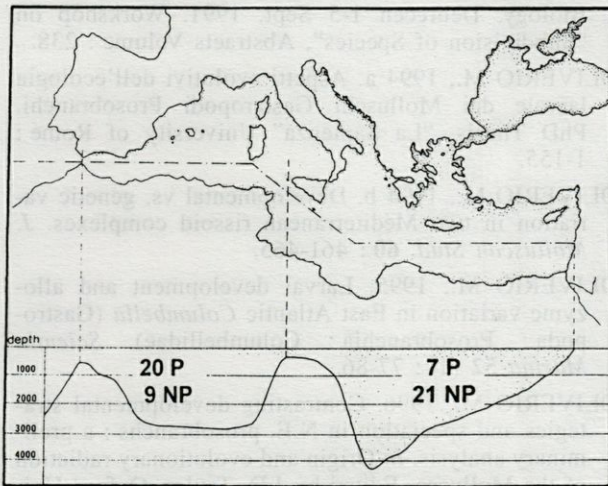
Fig. 2. – Schematic representation of the Mediterranean basin showing the figures of P Vs. NP with distributions exclusive or prevalent in one of the two subbasins (Table I).

complexes (*Rissoa auriscalpium* and *R. violacea*). Such figures indicate (comparing Aegean [NP] and Tyrrhenian [P] populations in both cases) times of divergence of 5-6.000 years and 40-50.000 years, respectively.

Quaternary paleoclimatic fluctuations are normally regarded as the main factor having affected land and freshwater biodiversity in the Mediterranean region (see e.g. La Greca, 1984). Their effects also on the marine assemblages are probably not fully acknowledged.

The peculiar physiognomy of the Mediterranean Sea (Fig. 2) played an important role during that time. The Mediterranean Sea is in fact, a concentration basin separated from the main ocean by the Gibraltar threshold. Internally it consist of two main sub-basins (eastern and western) also separated by a sill (the Siculo-Tunisian channel). During glacial periods the Mediterranean vs. the Atlantic, and the eastern vs. the western basin, underwent a strong isolation due to hydrographic factors. Inversion of water flows at both sills (Gibraltar and the Siculo-Tunisian one) contributed perhaps seasonally to such confinement, and sea level lowering produced reductions of the Sicily Channel up to three quarter width (Bethoux, 1979, 1984). Such conditions promoted the main factors suggested to counter select the planktotrophic larvae (Strathmann, 1978 a, b) : fluctuations in the energy (food) input, restricted areas, higher predatory pressure.

The model proposed is a working hypothesis, which needs to be carefully tested on the basis of research focusing on taxonomy, palaeobiogeography, morphology and physiology. Comparisons with other areas (Baltic Sea, Red Sea, Arabian Gulf) and/or animal groups (Annelida and Echi-

nodermata should prove to be good fields : Guérin and Kerambrun, 1984 ; Levin *et al.*, 1991 ; Strathmann *et al.*, 1992) could help in detecting if there are common patterns of the model in animals with similar life strategies (Hasgprunar *et al.*, 1995).

The most correct approach to the study of biodiversity must focus (also) on the dynamic processes operating and having operated to produce present patterns. Speciation processes reveal obviously important aspects, and their study must include the definition of the adaptive factors in the speciation events. Speciation is presently even more seen as a non-random event, not only a by product of geographic separation and/or of genetic drift. Selection and adaptation probably play more important roles than commonly suggested and the analysis of aspects related to life-histories, connected with speciation will yield important results in the definition of the underlying mechanisms of speciation. This will allow to asses a more general model for Speciation III, relating environmental and life-histories changes, and will result in a better understanding of the processes producing biodiversity in the ocean.

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