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Phenotypic plasticity of burrowing depth in the bivalve *Macoma balthica*: experimental evidence and general implications

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Abstract: Depth of burrowing in bivalves presents the individual with a trade-off: burrowing more deeply increases safety against predators but shallow burrowing increases food intake. Large variation in burrowing depth exists both between and within species. This study investigated whether part of this variation in depth in the tellinid *Macoma balthica* can be attributed to phenotypic plasticity. A predatory crab and food availability were either offered or withheld in separate aquaria and the response in burrowing depth measured. Individuals burrowed more deeply in the presence of a crab but only to shallow depths in the presence of food. This suggests that individuals can assess their environment and subsequently make decisions on their burrowing depth.

Phenotypic plasticity like this flexible anti-predation behaviour in *M. balthica* can have far-ranging effects. In the presence of predators burrowing depth increases, reducing energy uptake and subsequent growth and reproduction, whereas increased burrowing depths reduces mortality by predation, further affecting prey and predator population dynamics.

Many bivalves burrow in relatively soft substrata, like sand, mud, peat or even wood. Rapid burrowing probably evolved in the Silurian and became increasingly common, especially during the Cretaceous (Vermeij 1993). It is now widely distributed amongst several bivalve families (e.g. Stanley 1970). Burrowing reduces predation risk by decreasing visibility and accessibility to predators. Decreased visibility lowers the rate of detection and decreased accessibility increases handling times, making buried prey less profitable (e.g. Zwarts *et al.* 1996). Burrowing deeply may even provide a refuge against (some) predators (e.g. Blundon & Kennedy 1982; Zwarts & Wanink 1993).

But burrowing is not just beneficial; among the conceivable disadvantages, being buried deeply within the sediment reduces the access to food resources like suspended and deposited food particles. These resources are typically found in the water column or at the substrate–water interface, i.e. some distance away from the buried animal (Kamermans 1994). If buried deeper in the sediment, food uptake rates for a suspension feeder are likely to be reduced by the increased resistance of the currents through the outstretched siphons. For a deposit feeder, the sediment surface area available for deposit feeding will decrease owing to the limitations in extension of the siphon. When individual *M. balthica* were experimentally fixed at certain depths in the sediment, flesh growth decreased with increasing burrowing depth (Fig.1: linear regression; proportion flesh growth $= 0.15 - 0.049 \times$ burrowing depth (cm), $n = 126$, $R^2 = 0.11$, $p = 0.0005$ for constant, $p = 0.0001$ for slope). Zaklan & Ydenberg (1997) found that food intake decreased with an increase in burrowing depth when suspension-feeding *Mya arenaria* were positioned at fixed depths in the sediment, whereas De Goeij & Luttikhuizen (1998) found the same effect for growth in *M. balthica*.

Burrowing depth therefore can be regarded as a trade-off between predation risk (cost) and food intake (benefit). For successful reproduction an animal has to survive and have energy available for gamete production; lifetime reproductive success in a sequential reproducer is the summation of the reproductive output at age *i* times the probability to survive until age *i*, over all ages *i* (Stearns 1992). A rather generalized model shows this graphically (Fig. 2). Given general assumptions about the relationship between burrowing depth and food intake or survival (each monotonously decreasing and increasing, respectively, with increasing depth), reproductive output can be maximal at
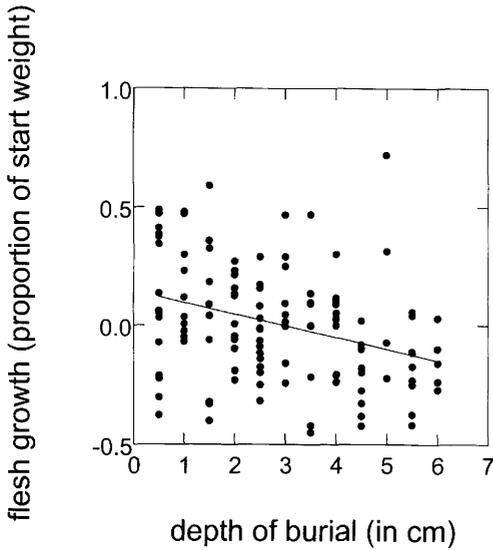
Fig. 1. The effect of experimentally fixed burrowing depth on flesh growth in *Macoma balthica*. Individuals collected in the field were positioned in a wire mesh frame and subsequently buried on an intertidal mudflat from 28 April 1999 until 18 May 1999. The frame enabled them to reach the sediment surface with their siphons for respiration and foraging, and to move horizontally, but prevented them from moving vertically, thus fixing the depth in the sediment at which they lived. Flesh growth was estimated by measuring the final ash-free dry weight (AFDW), and subtracting the estimated initial AFDW (based on a regression equation of AFDW measurements of subsamples taken at the start of the experiment v. shell length). Flesh growth was defined as the change in AFDW divided by the estimated initial AFDW. See text for statistics.

interactions (not all genotypes respond identically to a particular environment); specific environmental effects (random deviation due to individual uniqueness in time and space; i.e. unexplained variation) (Lynch & Walsh 1998). Phenotypic adjustment to environmental variation is possible for an individual if the common environmental effects and/or genotype × environment interaction statistically explain part of the variation in phenotype between individuals. This can be summed under the term phenotypic plasticity. If such plasticity does not exist, changes in the environment can only be tracked by natural selection on genotypic values. Thus, phenotypic plasticity can be viewed as any individual response to environmental change with respect to morphology, physiology or behaviour (also including phenotypic flexibility; Piersma & Lindström 1997).

Appropriate adjustments can only be made if the means to sense and process environmental information and the decision-making tools have evolved (Dusenbery 1992). It is known that burrowing depth differs widely between species (e.g. Stanley 1970), but to what extent has phenotypic plasticity in this behaviour evolved? Can bivalves respond to environmental changes that affect the costs and benefits of this behaviour?

M. balthica, a small tellinid bivalve, is found mainly in intertidal areas and the shallow subtidal

some intermediate burrowing depth. As a result of natural selection, burrowing depth may have evolved towards those values that maximize fitness.

Figure 2 reflects the situation in a constant environment. More realistically, environmental conditions vary both on ecological and evolutionary timescales. The trait value that maximizes fitness will therefore vary too. The question of interest is whether individual organisms can adjust to changes in optimum trait value by modifying their phenotype (like depth of burrowing). Following the framework of quantitative genetics, the phenotype of an individual is usually divided into the following additively contributing components: genotypic value (all additive, dominant and epistatic genetic effects); common environmental effects (general effects working on all individuals of a population equally); genotype × environment
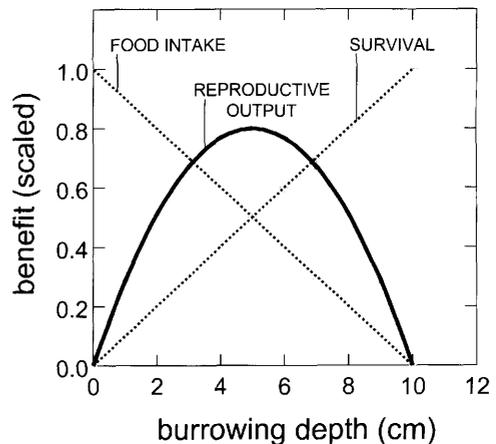

Fig. 2. Hypothetical relationship between burrowing depth and survival, food intake and reproductive output. Burrowing increases survival by reduction of predation risk but decreases food intake. Reproductive output is a multiplication of survival and energy investment, so reproductive output is non-linearly related to burrowing depth. The burrowing depth that maximizes reproductive output will be at some intermediate value.

(at least in Europe). It burrows in soft sediments, usually muddy sands, and feeds both on suspended food particles, mainly microalgae, as well as on deposited food particles and diatoms growing on the sediment surface (Kamermans 1994). Predators on adults include fishes, crabs and birds. Predation is often linked to the size of the predators, with smaller predators taking smaller *M. balthica* due to preference or even foraging constraints (e.g. Zwarts & Wanink 1993; Seed & Hughes 1995). Burrowing depth shows extreme variability in the field, both between and within sites (Zwarts & Wanink 1989; Piersma *et al.* 1994). It is not clear to what extent this phenotypic variation represents individual responses to environmental fluctuations (phenotypic plasticity).

In the section 'Experimental evidence' (below), this study first explores whether the burrowing depth of *M. balthica* represents flexible behaviour, responsive to food and predators, or behaviour that is constant for individuals. Implications of plasticity in depth of burrowing for shell formation, population dynamics and (in general) evolution of traits and species will then be discussed in 'General implications'.

Experimental evidence

Methods

Individual *M. balthica* were collected at five locations in the Dutch Western Wadden Sea and were kept for three months for acclimatization in outdoor containers filled with sand and supplied with unfiltered seawater. Suspended food was thus available, but predators were excluded.

At the beginning of the experiment, thin nylon threads, length of 10 cm and with individually numbered labels, were glued to the right valve of a total of 480 individuals with shell lengths of 10–25 mm, following the method of Zwarts (1986). Subsequently, four randomly assigned individuals of each of the five populations were released in each of 24 aquaria (40 × 50 × 30 cm), containing 15 cm of sandy sediment and 15 cm of filtered (food-free) water. No renewal of water occurred during the experiment but the water was oxygenated continuously. The individuals were free to burrow in the sand. Burrowing depth was measured by gently pulling the thread until it was perpendicular to the sediment surface and under tension, and then pulling the individual out of the sand and measuring the length of thread which was buried underneath the sediment. The same individuals were used during two manipulations, the first with predators present, and then with food present. Individuals that failed to burrow successfully in

either of the two manipulations were excluded from the analyses (33 out of 480, i.e. < 7% – this was due to poor condition, damage during handling or the valves becoming inadvertently glued together).

Comparing the first and second depth of burrowing of each individual in the two controls (i.e. no predators or food present), it is clear that it is very consistently maintained in these completely extracted individuals (Fig. 3: Pearson's $r = 0.86$, $n = 111, p < 0.001$). This indicates that this method of measurement does not cause disturbance and that the measured depth yields relevant information concerning the depth in the sediment that an individual occupies at any point in time during the experiment.

The predator manipulation consisted of exposing the buried *M. balthica* to cues from feeding shorecrabs (*Carcinus maenas*). Separate small mesh cages with a closed floor were placed in the aquaria and were stocked with either a crab or no crab, yielding $n = 12$ replicate aquaria for each manipulation. Water was free to move between the crab cage and the rest of the aquarium, but the crab was prevented from reaching the bivalves. All crabs were fed with two *M. balthica* each day. Excrement and prey remains were prevented from falling onto the sediment surface as the closed floor of the crab cage was fitted with a small ledge. Burrowing depth was first measured after seven days.
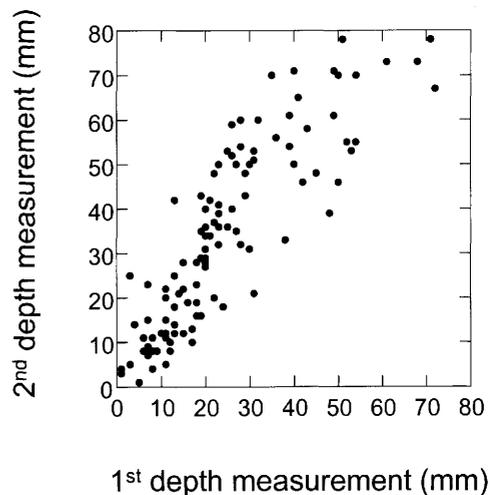

Fig. 3. Repeatability of burrowing depth in *Macoma balthica*. Only individuals that were not subjected to food or a crab in both manipulations were selected. Individuals were free to burrow twice for seven days and burrowing depth was measured by extracting the individuals completely. See text for statistics.

Subsequently, the crabs and cages were removed and the bivalves were replaced in their aquarium and allowed to re-burrow. Water was completely replaced and flowed freely in order to remove potential chemical predation cues. After six days, food was provided to the *M. balthica* in 12 out of the 24 aquaria (balanced with regards to the previous manipulation to avoid unwanted correlation between the food and predator manipulations). Food was provided by adding 0.5 g of finely pulverized dried spinach to 100 mL of filtered seawater and pouring this suspension into the aquarium. Pilot experiments showed that *M. balthica* uses these fine particles as food: the water was cleared, and inspection of the intestines showed that the spinach was accepted as food, and not just removed as pseudo-faeces. The control manipulation consisted of the addition of 100 mL of filtered seawater only. After two days, burrowing depth was measured and all individuals were stored frozen for subsequent analyses.

The statistical unit used for two-factor ANOVA was the burrowing depth averaged over all individuals in a single aquarium. This is necessary because individuals were grouped within a single aquarium and the measured burrowing depths cannot be considered as independent. Inspection of the mean depths revealed that their distributions were skewed. Transforming the data by calculating the logarithm resulted in very acceptable normal distributions and these transformed values were used for subsequent parametric statistical analyses. Testing for the effect of crab and food was performed by two-factor ANOVA on the mean burrowing depths of both manipulations. Both factors, crab and food, were included in the test of each of the two manipulations in order to use the appropriate degrees of freedom. Additionally, testing for the effect of food was performed by testing for a difference between the two categories of the food manipulation in the change in average burrowing depth. This change in depth was used since it represents a much more sensitive measurement. Because burrowing depth was highly correlated between the two depth measurements in individuals (Fig. 3), the same is true for the mean burrowing depths of the aquaria, but variation between aquaria was large. By taking the change in burrowing depth as the response variable, this large but consistent variation is accounted for (as in a paired t-test).

Results

The average depths of the first and second measurements for each aquarium are plotted in Fig. 4. The output of the two-factor ANOVA on the first depth measurement, the second measurement and the change in burrowing depth between the two measurements are given in Table 1. It should be noted that in the ANOVA of the first depth measurement, the effect of food is expected to be non-significant since this was not manipulated; it tests for systematic errors in the initial design that might explain later significant results of the food manipulation.

In the first measurement, individuals burrowed more deeply when in the presence of a crab (mean = 38.7 mm) compared to no crab present (mean = 24.6 mm) (Fig. 4: triangles v. circles). In
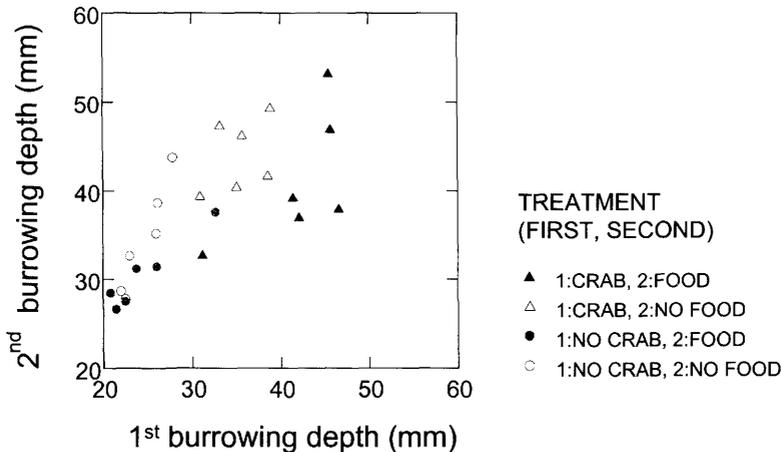

**TREATMENT
(FIRST, SECOND)**

▲ 1:CRAB, 2:FOOD
△ 1:CRAB, 2:NO FOOD
● 1:NO CRAB, 2:FOOD
○ 1:NO CRAB, 2:NO FOOD

Fig. 4. Aquarium mean burrowing depths – first depth measurement v. second depth measurement for each of the four treatments. In the first manipulation, crabs were either present (triangles) or absent (circles). In the second manipulation, food was either present (closed symbols) or absent (open symbols). See text for statistics.

Table 1. F- *and* p-*values of two-factor ANOVA on first and second depth measurement, and on the change in burrowing depth* (n = *24 for all tests*)

Treatment	First burrowing depth	Second burrowing depth	Change in depth
Crab	$F_{1,20} = 73.6$ $p < 0.0001$	$F_{1,20} = 20.8$ $p = 0.0002$	$F_{1,20} = 20.3$ $p = 0.0002$
Food	$F_{1,20} = 2.18$ n.s.	$F_{1,20} = 2.63$ n.s.	$F_{1,20} = 19.4$ $p = 0.0003$
Crab × food	$F_{1,20} = 2.85$ n.s.	$F_{1,20} = 0.11$ n.s.	$F_{1,20} = 3.06$ n.s.

n.s., non significant.

the second measurement, *M. balthica* overall burrowed more deeply (i.e. 92 out of 111 for the individuals of Fig. 3). There was no significant effect of the food manipulation on burrowing depth but, despite the fact that the crabs had been removed, the effect of crab presence was still significant. When the change in burrowing depth was tested for the effect of food, it was found that the change in depth was not identical for individuals from the two feeding categories; individuals burrowed less deeply in the presence of food compared to food not being present (Table 1 and Fig. 4: closed v. open symbols).

Discussion

Variation in burrowing depth can be as large as two orders of magnitude (Fig. 3). Most of this variation is probably explained by differences in size and condition, as is true in field samples (Zwarts & Wanink 1993; pers. obs.). Since the individuals were randomly assigned to the aquaria, no systematic differences between manipulation categories were expected and indeed they were statistically far from significant in the analyses. More interesting is the fact that burrowing depth is highly consistent (Fig. 3). Some mechanism may be constraining burrowing depths or perhaps a preferred depth for each individual exists. When comparing the second measurement of burrowing depth with the first one, it was found that most individuals burrowed more deeply the second time. Burrowing depth of the first measurement was therefore not (completely) constrained, indicating that depth is open to individual decision making. It is possible that individuals burrowed more deeply the second time as a result of the experience of being completely extracted from the sediment and handled outside the water. Such experiences may indicate risk of predation or erosion.

These experiments show that, through varying their burrowing depth, individuals respond to exposure to food and predators. Shallow burrowing became beneficial as food was added, with the animals staying closer to the surface. Adding a predator to the aquarium increased the (perceived) costs of shallow burrowing, and the animals buried, on average, 57% deeper. Is it difficult to say how much the increase in survival rate would be as depth increases from 25 to 39 mm, since this is completely dependent on the foraging behaviour of the predator – a complex function of profitability and density of many classes of potential prey types (e.g. Krebs & Davies 1987). However, it seems highly likely that it will increase survival rate, as was found in other studies concerned with burrow depth and predation risk of various predators (e.g. Blundon & Kennedy 1982; Zwarts & Wanink 1993; Zwarts *et al.* 1996). This is especially so as shorecrabs forage mainly in the upper few centimetres of the sediment (pers. obs.).

However, the presence of a crab feeding on *M. balthica* may not be directly causally related to the increased burrowing depth. For instance, the condition of the water in the tank may have changed in biotic or abiotic parameters. As feeding remains and crab excrement were prevented from falling onto the sediment, it is unlikely that *M. balthica* will have fed on them. It is possible that bacterial loads increased, but since bacteria are also utilized as food source by *M. balthica* (Kamermans 1994), a decrease in burrowing depth would have been expected (i.e. as in the food addition manipulation). In contrast, an increase in burrowing depth when crabs were present was observed, and therefore this possibility was dismissed. Similar reasoning is valid for potential confounding by abiotic variables such as oxygen saturation and detrimental chemicals. Due to the aeration, oxygen would not have been limiting. It is known that *M. balthica* is very able to cope with stressful situations without large changes in survival or functioning (Jahn *et al.* 1997; Modig & Olafsson 1998). Moreover, when the chemical environment deteriorates the usual response is to reduce burrowing depth, or even to leave the sediment completely (pers. obs.), and not to increase it.

Individuals of *M. balthica*, as has been demon-
strated before in many other species (Lima & Dill
1990), seem to have the capacity to adaptively
respond to changes in the environment that affect
the trade-off between food and predation risk.
Without dismissing the possibility that this trade-
off is open to natural selection on a longer,
evolutionary, timescale (Stearns 1992), the
experiments show that this trade-off is open to
individual decision making (i.e. a behavioural
response to environmental input; Krebs & Kacelnik
1991). This may seem unexpected for a 'sluggish'
creature like a bivalve. However, there is one other
study documenting increased burrowing depth
under stimuli of increased risk of predation. Here,
Mya arenaria responded to various stimuli that
mimicked increased risk of predation by red rock
crabs (Zaklan & Ydenberg 1997). Exactly how
bivalves sense (chemically?) and process the cues
presented to them is unclear (cf. Dusenbery 1992).
Also, it is not clear whether *M. balthica* responded
solely to the presence of crabs, the presence of
crushed and eaten conspecifics, or a combination of
the two. This distinction is not an issue here as each
of these sources of information indicates an
increased risk. Rather then speculating about the
mechanism, further discussion will focus on the
repercussions of behavioural plasticity on
ecological and evolutionary processes.

General implications

Flexibility in anti-predation behaviour resulting in,
for example, increased burrowing depth may have
far ranging ecological consequences. If individuals
find themselves exposed to greater danger, con-
tinued increased burrowing depth results in
decreased food intake (Zaklan & Ydenberg 1997).
With less energy available, growth slows down
(Fig. 1; De Goeij & Luttikhuizen 1998). In species
with growth rings spaced in time, this effect should
be visible, even after the death of the individual.
Decreased growth can affect shape and thickness of
the shell (Vermeij 1978). Moreover, shell size,
shape and thickness have been found to be flexible
anti-predation traits too (e.g. Appleton & Palmer
1988; Crowl & Covich 1990; Trussell 1996).
Palaeontologists and neontologists should avoid
interpreting such phenotypic differences between
populations as genetic differences without due
acknowledgment of the possibility of phenotypic
plasticity. Nor should they attribute such differ-
ences to the wrong environmental variables, such
as a low food availability that constrains growth
instead of high predator density resulting in the
choice to grow slowly but remain safe. Information
on predator abundance is usually collected directly

(e.g. catches, fossil counts) or indirectly (e.g. by
determining the proportion of predated shells). Yet,
the level of predator-induced damage on shells is
not necessarily a reliable estimator of predator
density, as a few predators may be very successful
in a situation where bivalves do not benefit in
taking refuge at the cost of reduced food intake.

Besides the effects of flexibility in behaviour on
individuals, population dynamics can also change
(Komers 1997). Adaptive anti-predation behaviour
changes outcomes of simple population dynamic
models as a consequence of changed predation
mortality rates (Fryxell & Lundberg 1997). In more
complex models, even without any substantial
predation mortality, a population can even become
extinct if reduced reproductive rates due to reduced
food intake cannot compensate adult mortality
(Matsuda & Abrams 1994). Especially in situations
where fertilization, larval survival, settlement, spat
and adult survival, or other demographic variables,
are density dependent, adaptive changes in anti-
predation behaviour can seriously change prey
and/or predator population dynamics (e.g. Matsuda
et al. 1993; Jennings 1997; McCann *et al.* 1998). In
summary, modellers of predator–prey interactions
that have included flexibility of behaviour have
stressed its importance in model outcomes.

Unfortunately, hardly any field measurements
and experiments have focused on these longer-term
population consequences of behavioural flexibility.
Long-term experiments are hard to fund and prone
to failure, and it is almost impossible to design an
experiment that only affects the behaviour of a
focal organism and not all other interacting
organisms too. Untangling the total response of the
populations into the causal components is thus
extremely difficult; measuring only the final overall
change is hardly enlightening. Here lies a major
task with which to further integrate the fields of
behavioural and community ecology.

Finally, is there an effect of phenotypic plasticity
on the evolution of biodiversity? Plasticity helps
organisms to cope with changes in the environment
(Via *et al.* 1995). If plasticity came without costs
and limits, life would still have evolved but not as
we know it (DeWitt *et al.* 1998). Costs and limits
can be found and measured in organisms in genetic,
ontogenetic and energetic terms. In a completely
stable environment, adaptive plasticity is expected
to be selected against, as maintaining the genetic
coding for all aspects of plasticity, as well as
maintaining the sensory systems for monitoring
potential change in the environment, would be
energetically wasteful (DeWitt *et al.* 1998). The
mere presence of plasticity in an organism therefore
already points out that its environment varies
sufficiently and predictably enough to 'justify' its
evolution (e.g. Pijanowska *et al.* 1993; Via *et al.*

1995; Storfer & Sih 1998). Indeed, plasticity is higher in species that live in more variable environments (Komers 1997).

Plasticity can increase adaptiveness in more then one environment (Via *et al.* 1995). When plasticity is perfect, variation in time or space of a particular potential selective force does not result in evolution by means of natural selection. In effect, the fossil record documents that species with (assumed) high levels of adaptive phenotypic plasticity are more resilient and less responsive to changes in selective regimes (Sheldon 1990). Highly plastic species are diverging at a lower rate and are evolutionary longer lived then less plastic species. Intriguingly, in a recent review, Jackson & Cheetham (1999) found that new species of marine biota arise not by gradual change but by 'punctuated equilibria'; quick shifts in morphology with no intermediate types found in the fossil record. This indicates that speciation comes about by sudden changes in the environment, like the occurrence of geographic barriers with subsequent allopatric speciation, whereas the inevitable minor environmental changes apparently did not result in speciation. This is in line with the thought that plasticity prevents speciation. The study of plasticity of traits (by means of experimental manipulations) of living taxa might therefore explain some of the evolutionary patterns of stasis v. adaptive radiation between different groups (Soares *et al.* 1998). As many species of bivalves have a larval phase with a potentially very high dispersal capacity, high levels of plasticity may indicate realized high levels of dispersal and gene flow (e.g. Parsons 1997, 1998), thus preventing local adaptation and speciation.

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