

Parental care in the rocky intertidal: a case study of adaptation and exaptation in Mediterranean and Atlantic blennies

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Introduction

One of the important tools of behavioural ecology is the comparison of behaviour, social organization and life history of organisms that live in contrasting habitats (Reese and Lighter, 1978; Krebs and Davies, 1981). This kind of interhabitat comparison may help to identify contrasting ecological pressures and convergent adaptations of organisms that have colonized specific habitat types. One problem recognized in this kind of work is the need to choose adequate taxonomic levels in order to avoid the confounding effect arising from phylogenetic affinities among the organisms to be compared (Harvey and Pagel, 1992).

It is striking that, although many independent phyletic lines of fishes successfully colonized rocky intertidal habitats, their reproductive behaviour and life history falls into a very restricted range of patterns (as stressed by Gibson, 1969a, 1982, 1986). The majority of rocky intertidal fish species are of small (e.g. 30 mm total length (TL) in the clingfish *Diplecogaster bimaculata pectoralis* (Gobiesocidae): Patzner and Santos, 1992) to medium size (80–120 mm TL in several blennies: Santos *et al.*, 1989). Parental care, especially guarding of demersal eggs, is the most salient trait of their reproductive style. Most species live for several years (up to 13 years in *Lipophrys pholis* (Blenniidae): Dunne 1977) and are iteroparous. Dispersal is mainly achieved through planktonic larvae.

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In the present paper we discuss the role of reproductive characteristics in the colonization of rocky intertidal habitats by teleost fishes and the constraints that these habitats have imposed on the evolution of their reproductive styles. We will concentrate on blennies (Blenniidae), as a case study. Information on other families will be added when appropriate.

The following questions will be addressed:

1. To what extent are the features of this reproductive style specific to this habitat?
2. Did these patterns originate in different groups by convergent evolution in the process of colonization of rocky intertidal habitats, or are they an expression of pre-conditions (**exaptations** *sensu* Gould and Vrba, 1982) that made these groups successful in colonizing the rocky intertidal habitat?

In trying to answer these questions we will undertake two types of comparisons: (i) intrataxonomic and (ii) interhabitat.

We show: (i) parental care, especially egg guarding, occurs in the majority of fishes that inhabit rocky intertidal habitats; (ii) several features in this reproductive style are shared by members of each of the families that have colonized rocky intertidal habitat but live in different habitats; (iii) for most lineages, parental care must have evolved prior to colonization of the rocky intertidal habitat, and is an exaptation and not a true adaptation; (iv) in contrast, some details of displays found in the reproductive behaviour of intertidal blennies are best viewed as adaptations to intertidal life.

Material and methods

In the comparison that follows, attention will be concentrated on residents of rocky intertidal habitats. We consider residents those fishes that, after the larval stage, live permanently in the rocky intertidal habitat and spawn there (Gibson, 1982). Data on behaviour and depth range were gathered from the literature. Comparisons were centred on north-eastern Atlantic species. The number of species of each family that is represented in the rocky intertidal was compared with the number of species of the same families that occur subtidally. If the presence of parental care evolved, in each lineage, after the colonization of rocky intertidal habitats we would expect that only the intertidal species would show parental care. If parental care is present in both intertidal and subtidal species of each family that has some members in the intertidal, this can be taken as evidence that parental care evolved prior to the colonization of this habitat. In the case of Blennioidei (*sensu* Nelson, 1984) the details of courtship displays of species living at different depth ranges were compared. If the displays exhibited by intertidal species of different Blennioidei lineages contrast with those of their subtidal relatives, this can be taken in favour of the hypothesis that they evolved after colonization of the intertidal. If no contrast is found they could have evolved prior to colonization of the intertidal. This reasoning is only valid if intertidal forms evolved from non-intertidal ancestors. This assumption was adopted on the grounds of parsimony.

Comparative ethology of blennies

Among the main families of fishes found in the rocky intertidal and shallow subtidal habitats the ethology of blenniids is best known (Guitel, 1893; Qasim, 1956; Robins *et*

al., 1959; Fishelson, 1963, 1975; Abel, 1964; Wickler, 1965; Gibson, 1968b; Phillips, 1971, 1977; Heymer and Ferret, 1976; Losey, 1976; Nursall, 1977, 1981; Almada *et al.*, 1983, 1987, 1990b; Louisy, 1983; Heymer, 1985, 1987; Santos, 1985, 1987; Patzner *et al.*, 1986; Gonçalves, 1990).

In temperate waters, blennies are among the best-adapted species, especially for living in exposed turbulent waters subject to wave action (Gibson, 1986; Horn and Gibson, 1988). This capability to live in exposed turbulent waters does not, however, mean that they are predominantly intertidal. Even if we limit our attention to temperate fauna, leaving aside the many tropical species, we find that intertidal species form only about 50% of the total number of Blenniidae species in the same geographic area (Table 1).

Both intertidal and subtidal species use cavities as nests (except for several tripterygiids, clinids and labrisomids) where males guard the eggs. Cavities include the holes made by burrowing molluscs (e.g. used by *Acanthemblemaria crockeri*: Lindquist, 1985; *Lipophrys canevae* and *Parablennius incognitus*: Koppel, 1988; *Lipophrys dalmatinus*, *Lipophrys adriaticus*, *Parablennius zvonimiri* and *Parablennius tentacularis*: Kotschal, 1988), the tests of barnacles, such as *Megabalanus tintinnabulum* (e.g. used by *Acanthemblemaria balanorum*: Lindquist, 1985; *Coryphoblennius galerita* and *Parablennius incognitus*: personal observations in the Azores), bivalve shells (e.g. used by *Omobranchus anolius*: Thomson and Bennett, 1953), crevices and spaces under stones (e.g. used by *Parablennius sanguinolentus parvicornis*: Santos, 1985; *C. galerita*: Almada *et al.*, 1983), and, in *Salaria basiliscus*, spaces among *Posidonia* sp. (Heymer, 1985).

The males possess a well-developed sexual repertoire that is convergent with that of many other crevice-spawning fishes of widely diverse families and habitats (Gibson, 1969a; Wirtz, 1978). In blennies from rocky intertidal and subtidal habitats, the initial phase of male courtship involves stereotyped signalling movements including vertical and lateral movements with or without back-and-forth actions of the head and/or all the body. In subtidal species, these movements may involve pronounced elevations of the whole fish up to several body lengths off the substratum (e.g. *Ecsenius bicolor*: Wickler, 1965; *Meiacanthus nigrolineatus*: Fishelson, 1975; *Parablennius rouxi*: Heymer and Ferret, 1976; *P. pilicornis*: Almada *et al.*, 1987; *Ophioblennius atlanticus*: Marraro and Nursall, 1983; *O. a. atlanticus*: personal observations). The males of the species of the

Table 1. Number of intertidal and subtidal Blenniidae species in some temperate north-eastern Atlantic regions

Region	Subtidal	Intertidal	Authors
Azores	4	4	Patzner <i>et al.</i> (1992); Oliveira <i>et al.</i> (1992)
Canaries	3	3	Brito (1991)
Madeira	4	3	Oliveira <i>et al.</i> (1992)
Portugal	6	7	Oliveira <i>et al.</i> (1992)
France	3	4	Zander (1986)
Great Britain	2	2	Wheeler (1978)
Ireland	2	2	Wheeler (1978)

$\chi^2 = 0.34$; no difference (ACTUS simulations: Eastabrock and Eastabrock, 1989).

genus *Tripterygion* (Wirtz, 1978), which are related to blenniids, also show those elevatory movements off the substratum. In intertidal species the displays are predominantly performed without loss of contact with the substratum (e.g. *C. galerita*: Guitel, 1893; Almada *et al.*, 1983; *Lipophrys pholis*: Qasim, 1956; Almada *et al.*, 1990b). In the subtidal *P. rouxi* (Heymer and Ferret, 1976) and in *Parablennius pilicornis* (Denoix, 1984; Almada *et al.*, 1987), whose range begins immediately below the intertidal, and initial phase of courtship includes an up-and-down element that projects the body out of the nest (Denoix, 1984; Almada *et al.*, 1987). This same type of movement was observed in *Parablennius ruber* (Santos, 1987). *P. pilicornis* also performs swimming displays, hovering head-up in the water column several centimetres off the substratum with sustained, exaggerated swimming movements with unpaired fins spread (Almada *et al.*, 1987). In *Parablennius incognitus* (Abel, 1964) and *P. zvonimiri* (Wirtz, 1978), which live just below the intertidal zone, the head-up courtship signal is still well developed. It is worth noting that *P. rouxi*, *P. incognitus*, *P. pilicornis*, *P. zvonimiri* and *P. ruber* are thought to be very closely related (Bath, 1976, 1982; Zander, 1986).

Some species like *Lipophrys canevae*, which in the Atlantic is intertidal (personal observations) and in the Mediterranean lives in very shallow water, display to females by lateral undulations of the body without loss of contact with the substratum (Abel, 1964). In deeper-water blenniids, the performing of elevatory and swimming displays does not mean that nodding (which involves only up-and-down rhythmic movements of the head) is lacking in the species' repertoire. *P. rouxi* uses nodding in a more advanced stage of courtship (Heymer and Ferret, 1976). *P. pilicornis* uses nodding in agonistic contexts (Almada *et al.*, 1987). Nodding, lateral head-shaking, and back-and-forth movements at the nest entrance take the dominant role in the repertoire of intertidal species (e.g. *C. galerita*: Guitel, 1893; Almada *et al.*, 1983; *L. pholis*: Qasim, 1956; Almada *et al.*, 1990b; *Salaria pavo*: Patzner *et al.*, 1986; Almada, 1989; Gonçalves, 1990).

Two interesting exceptions are *Istiblennius zebra* (Phillips, 1977) and *P. s. parvicornis* (Santos, 1992). Both species show patterns of behaviour with elevation above the substratum. It is interesting to note that *I. zebra*, although living in the intertidal zone, inhabits pools that are isolated from the sea, thus being in waters without turbulence for long periods. *P. s. parvicornis* in the Azores is an intertidal species with well-developed signal swimming (Santos, 1992). In the Mediterranean, *P. s. sanguinolentus* lives in protected shallow waters (Abel, 1962; Gibson, 1969b; Zander, 1972; Illich and Kotschal, 1990). In the Azores, despite being an intertidal resident, it always stays and breeds in pools where the water remains calm for many hours. In contrast, males of *C. galerita*, *L. pholis* (Santos *et al.*, 1989; Almada *et al.*, 1990a, b, 1992) and *S. pavo* (Santos *et al.*, 1989; Almada, 1989; Gonçalves, 1990) of the Portuguese coast spend the low tide hours in crevices and holes that are out of the water. This means that for these species mating can only occur when the tide is high, and wave action is an important problem to contend with.

C. galerita (Almada *et al.*, 1983) presents a pattern of nod-swimming that is probably homologous with the signal swimming of other blenniids (Santos, 1988). However, in this species, living in a habitat exposed to wave action, the elevatory component of this movement is very brief and the fish keeps in contact with the substratum.

We suggest that during the colonization of rocky intertidal habitats, especially in those species that inhabit areas exposed to stronger wave action, behavioural displays have

been subjected to modifications. These tend to minimize swimming time and loss of contact with the substratum. We also suggest that those signalling activities performed by some deeper-water blennies in the absence of females, tend to be eliminated. In rocky intertidal habitats, males stay longer in the nests and initiate courtship displays only when females enter their visual field. All this contrasts, not only with subtidal blennies, but also with species from other families (e.g. the pomacentrids *Abudefduf luridus* and *Chromis limbata*: Mapstone and Wood, 1975; some Labridae: Lejeune, 1985) which in some cases, invest a substantial proportion of time in signalling displays performed even in the absence of females. This reduction of self-advertisement provides support for the idea that turbulence is one of the most important selective pressures with which rocky intertidal blennies have to cope. The immediate subtidal zone is also exposed to strong water movement, but with increasing depths wave action decreases rapidly. The range of subtidal species normally extends several metres below the tide marks (Table 2). This means that for the great part of their vertical range most subtidal species live in relatively calm water, at least for most of the time. While intertidal species have small vertical ranges subjected to wave action, subtidal species are only subjected to strong turbulence in the extreme upper part of their ranges or, episodically, during storms.

The subtidal species *P. pilicornis* may be found and even breed in waters very near the low-tide mark in sheltered places while in places subjected to strong wave action it only breeds in deeper water (Almada *et al.*, 1987). The reduction of activities involved in self-advertisement also gives support to the hypothesis that, in rocky intertidal habitats, females must have a decisive role in searching for and locating the nests of the males.

Apart from ecological differences, display patterns also reflect phyletic affinities, as is shown by each of the three species groups – i.e. the genera *Parablennius*, *Lipophrys* and *Hypsoblennius* (Table 3). Subtidal forms of each different group of species show a variety of display forms that must surely be linked with pressures other than turbulence, such as density of females, risk of predation, and also size and shape of the body.

What seems important is the fact that, despite the variety of their probable origins, the species that live in very turbulent intertidal waters show a more limited degree of self-advertisement and movements off the substratum. These traits could be achieved by gradual adaptation to intertidal life, or be an exaptation present in the ancestors of the colonizers. Only detailed cross phylogenetic and ecological studies can help to solve this question.

Courtship displays involving active swimming off the substratum are found not only in blenniids but also in the closely related families Chaenopsidae (Thresher, 1984) and Tripterygiidae (Wirtz, 1978; Thresher, 1984). Within the Blenniidae they are distributed in three of the five tribes: Salariini, Blenniini, Nemophini (Nelson, 1984). This argues in favour of the view that off-ground displays represent the primitive condition, the displays without loss of the contact being derived characters.

Interhabitat comparisons

Parental care is almost universal in species that breed in rocky intertidal habitats. It is not only more frequent there than in other biotopes of the same area, but it is also more common than in coral reefs (Table 4).

As a very general rule, each of the main families that have colonized the rocky intertidal habitat contains an important fraction of subtidal species that have essentially

Table 2. Vertical distribution of Blennioidei species

Littoral preference*	Extent of vertical distribution (m) ^{††}	Authors
Intertidal species		
<i>Scartella cristata</i>	1.5	Zander (1972); Wirtz (1980)
<i>Salaria pavo</i>	0.9	Zander (1972); Almada (1989)
<i>Aidablennius sphynx</i>	1.1	Gibson (1968a); Zander (1972); Illich and Kotschal (1990)
<i>Lipophrys trigloides</i>	1.1	Illich and Kotschal (1990); Patzner and Santos (1993)
<i>Lipophrys pholis</i>	0.5	Milton (1983); Santos <i>et al.</i> (1989); Almada <i>et al.</i> (1990a,b)
<i>Lipophrys velifer</i>	1	Wirtz (1980)
<i>Lipophrys canevae</i>	1.5	Zander (1972); Illich and Kotschal (1990)
<i>Coryphoblennius galerita</i>	1.5	Gibson (1968a); Zander (1972); Almada <i>et al.</i> (1983); Milton (1971)
<i>Parablennius s. parvicornis</i>	0.5	Brito and Lozano (1981); Santos (1985)
Transition species		
<i>Parablennius ruber</i>	5	Almeida and Vivien (1983); Santos (1987); Patzner and Santos (1993)
<i>Parablennius s. sanguinolentus</i>	1	Gibson (1968a); Illich and Kotschal (1990)
<i>Parablennius incognitus</i>	6	Almeida and Vivien (1983); Illich and Kotschal (1990); Patzner and Santos (1993)
<i>Lipophrys nigriceps</i>	3.8	Abel (1962); Illich and Kotschal (1990)
<i>Lipophrys dalmatinus</i>	4	Illich and Kotschal (1990)
Subtidal species		
<i>Blennius ocellaris</i>	28	Albuquerque (1954–1956)
<i>Parablennius gattorugine</i>	35	Gibson (1968a); Dunne and Byrne (1979)
<i>Parablennius zvonimiri</i>	6	Abel (1962); Zander (1972); Illich and Kotschal (1990)
<i>Parablennius pilicornis</i>	10	Almada <i>et al.</i> (1987)
<i>Ophioblennius atlanticus</i>	15	Wirtz (1980); Patzner and Santos (1993)
<i>Tripterygion delaisi</i>	8	Wirtz (1978)
<i>Tripterygion tripteronotus</i>	6	Wirtz (1978)
<i>Tripterygion xanthesoma</i>	37	Wirtz (1978)
<i>Tripterygion melanurus</i>	18	Wirtz (1978)

*Intertidal species, species that breed at intertidal habitats, including pools; transition species, species which often occur in the intertidal/ shallow subtidal as adults; subtidal species, species whose distribution is strictly subtidal.

[†]Extent of vertical distribution of strictly intertidal species, transition species and subtidal species.

^{††}Kruskall–Wallis analysis of the differences of the extent of vertical distribution of intertidal, transition and subtidal species: $H(2, N = 24) = 17.34$; $p < 0.001$.

Table 3. Habitat and ethological features of some species of Blennioidei

Genus	Species	Habitat	Displays above the bottom in the absence of females	Authors
<i>Parablennius</i>	<i>sanguinolentus</i>	ST (Medit.)	?	Taborsky and Limberger (1980)
		IP (Atlantic)		Santos (1985)
	<i>pilicornis</i>	ST	Yes	Almada <i>et al.</i> (1987)
	<i>rouxi</i>	ST	Yes	Heymer and Ferret (1976)
	<i>incognitus</i>	SZ/ST	Yes	Abel (1964)
<i>Salaria</i>	<i>ruber</i>	SZ/ST	Yes	Santos (1987)
	<i>pavo</i>	I	No	Fishelson (1963); Patzner <i>et al.</i> (1986)
	<i>basiliscus</i>	ST	No	Heymer (1985)
<i>Aidablennius</i>	<i>sphynx</i>	I/SZ	No	Guitel (1983)
<i>Lipophrys</i>	<i>pholis</i>	IT/IP	No	Qasim (1956); Almada <i>et al.</i> (1990a,b)
	<i>velifer</i>	IT/IP	No	Wirt (1980)
	<i>canevae</i>	I/IZ	No	Abel (1964)
<i>Coryphoblennius</i>	<i>galerita</i>	IP/IT/SZ	No	Guitel (1893); Almada <i>et al.</i> (1983)
<i>Istiblennius</i>	<i>zebra</i>	IP	Yes	Phillips (1977)
<i>Ophioblennius</i>	<i>atlanticus</i>	SZ/ST	Yes	Nursall (1977)
<i>Hypsoblennius</i>	spp.	I/SZ/ST	Yes	Losey (1976)
<i>Tripterygion</i>	spp.	ST	Yes	Wirtz (1978)

*Habitat range: I, intertidal; IP, intertidal pools; SZ, upper subtidal; ST, subtidal.

Analysis design: intertidal versus subtidal species / species with displays above the substratum versus species which do not display above the substratum: $\chi^2 = 5.53$; $p < 0.05$ (ACTUS simulations: Eastabrock and Eastabrock, 1989).

the same reproductive style as their rocky intertidal relatives. In our study area, all but one of the families that have intertidal species with parental care are represented by greater number of species in other biotopes (Table 5). Therefore it is possible to conclude that parental care probably evolved before colonization of rocky intertidal habitats.

The almost universal occurrence of demersal eggs and parental behaviour in rocky intertidal fishes, in contrast to its relative rarity amongst all marine species (Table 6 based on Breder and Rosen, 1966; Blumer, 1979, 1982; Almada, 1990), suggests that these reproductive characters played an important pre-adaptive role in the colonization of this habitat. Among the 20 families of the north-eastern Atlantic and Mediterranean area (Whitehead *et al.*, 1984, 1986) exhibiting parental care, only 10 are not represented on the rocky intertidal. This reproductive style, together with small size, negative buoyancy, ability to get quickly to shelter and to keep close to the substratum form a complex of traits valuable in other habitats, namely many subtidal fish living among barnacles and many coral reef inhabitants. It seems reasonable to assume that these traits had evolved before intertidal habitats were colonized. The fact that in coral reefs most families with

Table 4. Number of intertidal and subtidal teleost families from the north-eastern Atlantic and Mediterranean (Whitehead *et al.*, 1984, 1986) with and without parental care. Coral reef teleost families are classified on the same categories (based on Thresher, 1984). At least one species of the family must be able to reproduce in the intertidal for the family to be included in that category. Maximum depth considered was 100 metres. At least one species must be present at that depth range for the family to be included in the subtidal category

Parental care	Habitat		
	A: Intertidal	B: Subtidal	C: Coral reefs
With	10	10	18
Without	1	75	36

A versus B: $\chi^2 = 36.99$; $p < 0.001^*$

B versus C: $\chi^2 = 9.55$; $p < 0.002$

A versus C: $\chi^2 = 12.35$; $p < 0.001^*$

*ACTUS simulations: Eastabrock and Eastabrock (1989).

Table 5. Number of species with parental care in eleven teleost families which breed either in rocky intertidal habitats or in other habitats in the north-eastern Atlantic and the Mediterranean (data from Whitehead *et al.*, 1984, 1986, but primary sources were also verified, when justified)

Family	Number of species that breed in rocky intertidal habitats	Number of species that breed in habitats other than rocky intertidal habitats	Number of species whose breeding habitat could not be confirmed
Blenniidae	10	12	
Pholididae	1	0	
Zoarcidae	1	26	
Cottidae	1	15	
Cyclopteridae	2	14	
Gobiesocidae	2	3	3
Gobiidae	10	58	2
Syngnathidae	1	15	
Labridae	1	23	
Gasterosteidae	1	3	
Atherinidae	1	3	

small-size species tend to exhibit parental care argues in favour of this interpretation (Barlow, 1981; Thresher, 1984).

Discussion

The prevalence of parental care in rocky intertidal species is to be viewed as an exaptation because it is present in species related to each intertidal resident species but living in other places.

Of the diverse array of reproductive styles of shallow-water marine fishes, only parental care of demersal eggs and, on a much smaller scale, viviparity are to be found in the rocky intertidal habitat. Apparently this habitat offers abundant opportunities for fishes that require cavities as nests, provided that the eggs and adult parent are able to resist the marked fluctuations in physical conditions prevailing here. Dando (1984) points out that estuaries pose difficult problems for the development of fish eggs mainly due to the high quantities of organic matter, low levels of dissolved oxygen and high risks of microbial infection which are very commonly found in estuary waters. On the contrary, for larvae and postlarvae, estuaries provide favourable conditions due to the richness in plankton they usually possess.

It can be suggested that for rocky intertidal habitats the situation is reversed. Conditions are favourable for the development of eggs if they are adequately sheltered and cared by a parent and quite unfavourable for free-swimming larval stages. This does not mean that true adaptations to rocky intertidal habitat do not exist. Display modification in blennies may prove to be an example of adaptation to shallow water with high wave energy.

At the behavioural level, other areas where true adaptations may be expected include: (i) the co-ordination of courtship and spawning with tidal rhythms (Gibson, 1986) and changes in the patterns of social interactions and socio-spatial relationships also linked to endogenous and exogenous factors related to tidal rhythms (as proposed for *Lipophrys pholis* by Gibson, 1968b); (ii) modifications of frequency of different breeding behaviour patterns and of the time allocated to each of them: for example, Almada *et al.* (1990b, 1992) have shown that *L. pholis*, which breeds high in the middle littoral zone, in exposed areas, shows quite low interspecific agonistic behaviour, and very few attempts at nest intrusions and egg predation by other species were noted, whereas in contrast *P. pilicornis* (Almada *et al.*, 1987), which breeds subtidally, and *P. s. parvicornis* (Santos,

Table 6. Number of marine teleost families with and without parental care (Almada, 1990) in comparison with the same categories of intertidal north-eastern Atlantic and Mediterranean families (Whitehead *et al.*, 1984, 1986)

	NE Atlantic and Mediterranean intertidal teleost families	All marine teleost families
With parental care	10	47
Without parental care	1	277

$\chi^2 = 43.98$; $p < 0.001$ (ACTUS simulations: Eastabrock and Eastabrock, 1989).

1985, 1992), which breeds in pools often connected with the sea, have to face frequent attempts of intrusion by many fish species, and egg predation is quite high soon after the parental male is removed (similar results were also found for *Tripterygion* spp.: Wirtz, 1978); (iii) possible behavioural mechanisms in larvae allowing them rapid transfer to the plankton after hatching, minimization of offshore dispersal and quick postlarval settlement (Marliave, 1977, 1986).

At the physiological and life history levels, promising areas to search for adaptations include: (i) the evolution of mechanisms, both in adults and eggs, that enable them to stay out of water during low tide and to face the marked changes in physical conditions characteristic of these habitats (Gibson, 1969a, 1982, 1986; Milton, 1971; Nonnotte and Kirsch, 1978; Nonnotte *et al.*, 1979; Heymer, 1982; Laming *et al.*, 1982; Zander, 1983; Bridges *et al.*, 1984; Louisy, 1987; Horn and Gibson, 1988); (ii) the possible different bioenergetic demands for the parental males, because, although parental behaviour may reduce feeding opportunities, this may be partly compensated for by long periods of immobility and reduced metabolic rates during low tide when the nests stay out of water (Laming *et al.*, 1982).

The search for true adaptations in these areas requires, however, that much more detailed quantitative data become available for a wide range of species and that the phylogenetic relationship between intertidal fishes and their subtidal relatives are worked out in detail.

When an interhabitat comparison indicates that a number of taxa that have colonized the given habitat show clear similarities in their behaviour and their biology, adaptation is not necessarily demonstrated. The spectrum of potential colonizers of a particular habitat may be quite wide, but only a fraction of the species possess a minimum of features that make life in the habitat possible. The results of an interhabitat comparison may thus reflect the constraints imposed by the environments upon the kinds of life styles that can be successful in each biotope. Thus many of the features found in organisms of a given habitat may represent exaptations that made colonization possible, rather than true adaptations. Adaptation must only be claimed if we have strong evidence that the ancestors of the colonizers did not possess the features in question and that these features evolved after the colonization process began.

It is useful to distinguish exaptations that were relevant in the process of colonization of the rocky intertidal habitat from other correlated traits that are related to the coherence of a particular reproductive style but had no special role in the colonization process. The prevalence of parental care of demersal eggs in crevices in rocky intertidal habitats may be a case in point.

Only fishes that are benthic, and relatively small, are apparently able to establish themselves as residents in these habitats. The reproductive style that they show may reflect an adaptation to benthic life and was exaptive in the colonization of the rocky intertidal habitat.

Another example of correlation between features of the reproductive style that apparently have little to do with the colonization process is the common occurrence in courtship behaviour of signalling the nests and leading the female to the entrance in species with uniparental male care and nesting in cavities. This type of courtship pattern apparently evolved convergently in many groups (e.g. Gasterosteidae, Centrarchidae, Percidae, Labridae, Pomacentridae, etc.) with male parental care of demersal eggs, in a wide variety of biotopes (Keenleyside, 1979).

In conclusion it seems useful, in interhabitat comparisons of reproductive styles, to distinguish clearly between adaptations, exaptations and correlations of traits that make each reproductive style effective and are not, in themselves, linked to specific ecological factors.

Summary

The main features of the behavioural ecology of rocky intertidal species are compared both within families – though concentrated on blennies – and between habitats. It is suggested that, at the behavioural level, the reduction of vertical and swimming elements in the male sexual and agonistic displays of Blennioidei may constitute an adaptation to typical intertidal conditions, especially in those species that inhabit areas exposed to strong wave action. The other aspect which is discussed is the prevalence of parental care in rocky intertidal fishes. In these fishes parental care is much more frequent than for marine fishes as a whole. Taken alone, this could also suggest that guarding evolved as an adaptation during the process of colonization of these habitats. The hypothesis proposed in this paper is that guarding was already present in the ancestors of the resident species, at least in the majority of cases. Many differences in interhabitat studies may express the action of the environment, not as an agent of natural selection, but as a filter, which prevented some groups from invading a given habitat and, at the same time, made colonization easier for other groups. When a number of taxa that colonized a given habitat display clear similarities in their behaviour and their biology, adaptation is not necessarily demonstrated. There is evidence in the literature to support the hypothesis that those traits were already present in the ancestors of the rocky intertidal resident fishes, thus being best viewed as exaptations.

Acknowledgements

An early enlarged version of this paper has benefited from comments of Robin Gibson (Dunstaffnage Marine Research Laboratory, UK), Anthony Underwood (Sydney University, Australia), Stephen J. Hawkins (University of Liverpool, UK), Jeffrey Marliave (Vancouver Aquarium, Canada), Robert Patzner (University of Salzburg, Austria), Paul Dando (Marine Biological Association of the UK) and George Barlow (University of California, Berkeley, USA), to whom we are deeply grateful. We also acknowledge Tony J. Pitcher and Charles Hollingworth, editor and technical editor of *RFBF*, respectively, and two anonymous referees, whose comments and criticism helped to improve the current version of the paper.

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