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 (Blenniiidae), 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 Blenniodei (*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 Blenniodei 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*