Short communication

Temporal asymmetries in the feeding patterns along the tidal cycle in two sympatric littoral blennies

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1. Introduction

A salient feature of the animals that colonize the intertidal habitat is the prevalence on a wide spectrum of taxa of periodical oscillations, both physiological and behavioural, that are typically driven by internal clocks, and are entrained by external cues that keep them nearly in phase with the tidal cycle (e.g. Williams and Naylor, 1969; Gibson, 1967, 1970, 1973, 1982; Northcott et al., 1990; Northcott, 1991). These "tidal rhythms" seem to enable the organisms to track and anticipate physical, chemical and biotic oscillations that the tide imposes on intertidal organisms (for a review, see Gibson, 1999). Bhikajee and Green (2002) give an interesting extreme example of an amphibious blenny that remains almost constantly emersed, moving up and down with the tide, above the water level.

There is still very limited information on the interspecific variation of tidal rhythms that rocky intertidal fish of the same community may display. This is an important gap in our knowledge of the rocky intertidal fish communities. In a given assemblage fish typically vary in size, diet, preferred low-tide shelter and spawning site. They are likely to differ also in the extent of their high-tide excursions away from shelters and in the spatial and temporal patterns of exploitation of the available resources.

In Western Europe blennies, namely Lipophrys pholis and Coryphoblennius galerita are major components of the resident ichthyofauna of the rocky intertidal habitats (e.g. Gibson, 1972; Milton, 1983; Faria and Almada, 1999, 2001), and there have been attempts to access possible resource partitioning among them (e.g. Milton, 1983; O’Farrell and Fives, 1990; Faria and Almada, 2001). This resource partitioning may be expressed in trophic differences; however, it seems also to be expressed through differences in ontogeny: L. pholis grows faster and reaches a larger size than C. galerita, which leads the two species to use different types of shelter and prey (Milton, 1983; Faria and Almada, 2001; Monteiro et al., 2005). Indeed, L. pholis attains a much larger adult size than C. galerita (Zander, 1986). When they are about 1 year old, L. pholis reach the upper size of adult C. galerita (Faria et al., 1996). At this stage L. pholis leaves the pools that are shared by the juveniles of both species, seeking new shelters in crevices and spaces under boulders, in the lower shore, where they hide in groups (Qasim, 1957; Gibson, 1972; Faria and Almada, 2001). This shift in low-tide shelter is accompanied by a shift in diet, the larger L. pholis now eating larger prey (Monteiro et al., 2005).

Most studies on the ecology of these blennies have concentrated on observations made during low-tide, when their activity reached its minimum and fish congregate in shelters (e.g. Qasim, 1957; Gibson, 1972; Milton, 1983; Faria et al., 2001), so little consideration has been given to the possibility that partitioning of resources among the two species may occur through spatial and temporal differences in behaviour during high-tide. Burrows et al. (1999), using underwater TV observations, suggested that the shanny, Lipophrys pholis, shows the highest level of activity during the rising and high-tide periods, and that its feeding movements are concentrated around crevices. Faria and Almada (2006), based on

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visual underwater observations by snorkelling dives, described the
patterns of space utilization by _L. pholis_ and _Coryphoblennius galeraita_, along the tidal cycle. Whereas _C. galeraita_ seems to keep an
approximately constant position at a given shore level, probably in
the vicinity of the shelters used during low-tide, _L. pholis_, especially
the larger individuals, seems to move up and down with the tide,
maximising submersion time.

This paper addresses the following question: Do the patterns of
activity and vertical distribution of the two species along the tidal
cycle reflect their different patterns of space and microhabitat use?

### 2. Materials and methods

The study period ranged from June 2005 to October 2005. The
study site was a semi-exposed rocky platform, near the mouth of the
Tagus river, Avencas (38°41'N, 9°22'W).

The observations were based on visual censuses made by
snorkelling dives. On each day, two dives were always performed (with
a mean duration of 1 h 30 min to 2 h each), with intervals of
1–2 h between them, to cover two of the three distinct phases of
the same tidal cycle: the rising phase (which corresponds to the
submersion period that permits the diver to swim over the plat-
form up to 1 h before high-tide); the high-tide phase (defined as
the period 1 h before to 1 h after high-tide); and the ebbing phase
(defined as the period from 1 h after high-tide to the time when
water level no longer permitted the diver to swim over the plat-
form).

In each dive two transects were inspected on two different rock-
walls, almost parallel to the coast, that stay exposed during low-
tide (see _Faria and Almada, 2001_ for habitat descriptions). A diver
swam slowly and at a regular speed over each transect. Transects
length was 70 m and 80 m and inspection of each took about
45–60 min to be completed.

For each dive, the species and size class, <7 cm and >7 cm for
=Lipophrys pholis_, of each observed fish were recorded on an
underwater writing pad. In addition, fish were classified as being
feeding or not feeding, and either as active (when they were out of
shelters) or inactive (when they were found in refuge). Both species
fed by a very rapid action in which the fish turned its head to the
prey and grasped it, followed by a strong jerking movement that
pulled the food item from the rock. Size was visually estimated
taking as reference a ruler drawn in the writing pad. Separation of
L. pholis in these two size classes was made because it is known that
at this size a major ontogenetic shift in type of food consumed and
kind of shelter used takes place in this species (_Faria and Almada,
2001; Monteiro et al., 2005_).

Additional dives were undertaken to perform focal observations
(sensu _Martin and Bateson, 1993_), in which an individual fish was
continually observed for 5 min or until the fish moved out of sight
of the observer. For each fish, the behaviours exhibited and the
distances travelled (estimated by eye) were recorded. A total of
47 fish were followed (30 _Lipophrys pholis_ and 17 _Coryphoblennius
galerita_). Although an eventual influence of the observer is almost
impossible to disprove, the fact that the fish did not hide or escape
and continued to feed actively, and move around, strongly suggests
that they were not seriously affected by the presence of the diver.

A total of 40 dives were performed (10 during the rising-tide and
10 during the high-tide of the same day; 10 during the high-tide
and 10 during the ebbing-tide of the same day). As this kind of dives
was only possible when sea conditions were very favourable, the
number of dives per month varied (June: 10 dives, July: 20 dives,
October: 10 dives).

Statistical analysis involved two types of tests. Contingency
tables were built for each species, and size class for _Lipophrys pholis_.
In each table, the number of fish recorded as feeding and non-
feeding at each tidal phase (rising, high and ebbing-tide) was in-
cluded. The contingency table analysis was performed using the
program ACTUS (_Estabrook and Estabrook, 1989_), which imple-
ments a statistical simulation procedure designed to analyse con-
tingency tables that is not limited by the assumptions of
conventional Chi-Square Tests and that, apart from assessing the
overall significance of the table, allows assessment of the signifi-
cance of deviations of each individual cell. In addition, the numbers
of fish of each species, and size class for _L. pholis_, observed feeding
at each dive were analysed, as a function of the tidal phase, with
a Kruskall–Wallis test, using the software Statistica 5.0 for Win-
dows (_Statsoft, 1995_). As the overall result was significant, multiple
comparisons were performed with Dunn test ( _Siegel, 1956_).

### 3. Results

Both _Lipophrys pholis_ and _Coryphoblennius galeraita_ were ob-
served feeding on barnacles, limpets and algae (or organisms that
grew on them). _Lipophrys pholis_ was also observed feeding on
mussels and small dead crabs. Normally individuals moved around
a small area ( _L. pholis_ average = 83.22 cm, s.d. = 45.07, range: 10–
500, n = 30; _C. galeraita_: average = 47.74 cm, s.d. = 21.12, average:
5–150, n = 17), performing a series of small bites ( _L. pholis;
average = 7.64 per 5 min., s.d. = 3.83, range: 1–13x, n = 11; _C.
galeraita_: average = 7.43 per 5 min., s.d. = 6.55, range: 1–22x,
n = 14).

The number of active fish in the different tidal phases and the
proportion of this number observed feeding are given in Table 1. Concerning feeding activity, in general a higher proportion of fish
dead during the rising-tide (38%) or the high-tide (56%), than during
the ebbing phase (6%) (_C. galeraita_: $\chi^2 = 15.01$, d.f. = 2, $p < 0.001$;
_Lipophrys pholis_ (>7 cm) $\chi^2 = 56.06$, d.f. = 2, $p < 0.001$; _L. pholis_
(>7 cm) $\chi^2 = 17.06$, d.f. = 2, $p < 0.001$).

The number of fish observed on the rock-walls during the three
different phases of the tidal cycle differed (Table 1). The number of
_Coryphoblennius galeraita_ observed during the ebbing phase was
smaller compared to the high-tide phase or the rising phase
(_Kruskall–Wallis test: H(2, N = 40) = 22.632, p < 0.001_; Dunn test:
rising phase versus ebbing phase, $Q = 4.256$, $p < 0.001$; high-tide

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Rising-tide (n = 10)</th>
<th>High-tide (n = 20)</th>
<th>Ebbing-tide (n = 10)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. pholis</em> (&lt;7 cm)</td>
<td>51.70</td>
<td>26.20</td>
<td>39.10</td>
</tr>
<tr>
<td><em>C. galeraita</em></td>
<td>39.10</td>
<td>16.08</td>
<td>18.29</td>
</tr>
<tr>
<td><em>L. pholis</em> (&gt;7 cm)</td>
<td>25–61</td>
<td>19–42</td>
<td>32–45</td>
</tr>
<tr>
<td><em>C. galeraita</em></td>
<td>5–9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Panel A*

| Mean | 0.23 | 0.04 | 0.25 | 0.14 | 0.06 | 0.25 | 0.10 | 0.04 | 0.11 |
| s.d. | 0.07 | 0.03 | 0.15 | 0.11 | 0.06 | 0.17 | 0.09 | 0.05 | 0.09 |
| Range | 0.150–0.29 | 0.00–0.05 | 0.05–0.47 | 0.05–0.47 | 0.01–0.22 | 0.07–0.44 | 0.01–0.25 | 0.01–0.17 | 0.00–0.29 |
phase versus ebbing phase, $Q = 4.169, p < 0.001$. On the contrary, the number of larger individuals of *Lipophrys pholis* (>7 cm) was higher in the rock-walls during the ebbing phase than in the preceding high-tide or rising phase (Kruskall–Wallis test: $H(2, N = 40) = 9.486, p < 0.01$; Dunn test: rising phase versus ebbing phase, $Q = −2.668, p < 0.01$; high-tide phase versus ebbing phase, $Q = −2.788, p < 0.01$). For small *L. pholis* (<7 cm) there were no statistical differences (Kruskall–Wallis test: $H(2, N = 40) = 4.682, p > 0.05$).

4. Discussion

The results suggest that the patterns of activity observed in *Lipophrys pholis* and in *Coryphoblennius galerita* during the different tidal phases are probably related to feeding activities. Both species feed mainly on gastropods, barnacles and algae, with a minor proportion of other invertebrates like amphipods, copepods and isopods (Qasim, 1957; Gibson, 1972; Milton, 1983; Monteiro et al., 2005). As suggested by Burrows et al. (1999), these fish may be hungrier during the rising-tide, since in the previous tidal phase (low-tide) they have been confined to small refugia, like tide-pools and crevices, where the typical prey of both species (e.g. barnacles and mussels) are usually unavailable (Gibson, 1972; Faria and Almada, 2001). Indeed, both barnacles and mussels tend to occur out of the pools, thus being available only when the rocks are covered by water. Our observations support this interpretation and show that the feeding patterns are especially intense during the rising-tide, when compared to the ebbing-tide. This means that the tidal variation of the feeding pattern is asymmetrical in nature. Similar evidence was provided by Ralston and Horn (1986) for *Cebidichthys violaceus*, a fish of a different taxonomic group (Stichaeidae). Apparently, pelagic fish that visit the intertidal during high-water to feed also show this asymmetry in the use of this area (e.g. Carlisle, 1961).

From a functional point of view, the pattern described in the present paper makes sense if one assumes that fish start feeding as soon as there is enough water, and that they also must be able to return to their low-tide shelter in time to avoid the risk of getting stranded in unsuitable locations. This hypothesis would explain why a fish ceases to feed and begins to seek shelter while there is still enough water to move around.

This interpretation is also consistent with the differences observed between *Coryphoblennius galerita* and small *Lipophrys pholis* on one hand and larger *L. pholis* on the other. As shown by Faria and Almada (2001, 2006), both *C. galerita* and small *L. pholis* feed on the rock-platforms which are typically in the vicinity of the tide-pools where they shelter during low-tide. On the contrary, *L. pholis* larger than 7–8 cm, move up and down with the tide, and spend the low-tide time in crevices often located in the lower shore. This would explain why their relative abundance on the rock-wall increased at the beginning of the ebbing-tide, as we were likely observing fish that had moved to the highest levels of the platform and were in their downward movements as the tide ebbed. This increase could also occur if part of the population migrated to the subtidal. In that case, we would be observing the congregation of fish coming both from above and below. This possibility is however, very unlikely, as very few *L. pholis* occur subtidally in any tidal phase (Faria and Almada, 2006).

One limitation of our observations stems from the fact that they were made from June to October. It would be interesting to study the behaviour of this fish in winter, when sea conditions and the entire ecology of the intertidal are radically altered. However, in this area of the Atlantic, winter conditions make regular dives very hard to achieve. The same applies to very exposed shores, where

the behaviour of intertidal fish during high-tide is virtually unknown. This work emphasizes the need of more field studies that cover the entire tidal cycle to get a full understanding of the ecology of intertidal fish assemblages.

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References


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