Diet preference reflects the ontogenetic shift in microhabitat use in *Lipophrys pholis*

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Based on the heterogenous nature of *Lipophrys pholis* diet, the stage of the species' ontogenetic development when major niche shifts occurred was identified, and the causes that force this blennid to change its feeding behaviour, vertical distribution and shelter occupation were considered. The diet analysis of the different size classes consistently showed two clusters, grouping individuals < or >8 cm total length. This shift occurred simultaneously with the onset of reproduction; it seemed to be independent of inter- and intraspecific competition and reflected a quantitative and qualitative alteration of the dietary constituents. The analysis of the diet of other sympatric intertidal blennids, *Lipophrys trigloides* and *Coryphoblennius galerita*, showed that, apart from the first developmental stages, there seemed to be no important dietary overlap. The inevitability of this niche alteration could be explained by the combination of at least two different factors: the development of the scraping capability that enabled the fish to feed on large benthic prey, together with the limited number of suitable shelters that were available in rock pools. © 2005 The Fisheries Society of the British Isles

INTRODUCTION

There are few habitats as accessible and rich as rocky shores. The rocky intertidal, however, is a harsh environment with its regular alteration of physical conditions, mainly due to more or less prolonged periods of emersion and submersion (Lewis, 1964; Barlow, 1999), forcing specific adaptations in its colonizing fauna and flora. Nevertheless, many independent fish phyletic lines have settled in this particular habitat with their reproductive behaviour and life history falling into a narrow range of strategies (Gibson, 1982, 1999; Almada & Santos, 1995; Zander *et al.*, 1999). Considerable interest has been devoted to the general structure of rocky intertidal fish communities, especially to blennioids

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(one of the most abundant fish groups in tropical and warm temperate habitats), focusing on specific dimensions of their niches (*e.g.* diet, vertical distribution and shelter availability) or important ecological relationships, such as competition or predation (Gibson & Yoshiyama, 1999; Norton & Cook, 1999). In spite of all available data, information on intraspecific variation of niche occupation is scarce, namely amongst different sex and size classes, regardless of its more than probable importance on the distribution of fish populations along the intertidal zone. Indeed, the few published studies that addressed this issue confirm that intraspecific variation in niche occupation patterns due to size, sex and phase of breeding cycle may be quite substantial and may affect multiple niche dimensions, namely diet, type of shelter and vertical distribution (Gibson, 1967, 1968, 1972).

Lipophrys pholis (L.) is a common inhabitant of the north-eastern Atlantic rocky intertidal, from Mauritania to Norway (Zander, 1986; Almada *et al.*, 2001), usually found in rock pools, crevices or under boulders, from where it emerges at high tide to forage. As one of the most abundant intertidal fish species, its important trophodynamic role is well established. An increasing body of literature is being published concerning *L. pholis* ecology and behaviour (Qasim, 1956; Gibson, 1967, 1972; Shackley & King, 1977; Laming *et al.*, 1982; Almada *et al.*, 1990*a*, *b*, 1992; Northcott, 1991; Morgan & Cordiner, 1994; Faria *et al.*, 1996, 1998; Dodd *et al.*, 2000), some of them specifically aimed at describing its dietary habits from several locations along its geographical distribution (Qasim, 1957; Dunne, 1977; Carvalho, 1982; Milton, 1983; Wyttenbach & Senn, 1993; Mazé *et al.*, 1999). Apart from particular differences, all findings converge on the generalist nature of this species that forages on heterogeneous diet. All studies agree on the importance of mussels, barnacles and limpets as major components of the diet of this fish.

Faria & Almada (2001*a*) demonstrated that when juveniles of *L. pholis* reach a total length (L_T) of *c.* 7 cm they initiate a radical shift in their pattern of microhabitat occupation. While smaller juveniles are predominantly found within rock pools at low tide, larger individuals leave the pools and begin to occupy crevices and narrow spaces that often remain emersed when the tide is low. Burrows *et al.* (1999) showed, based on high tide video observations, that *L. pholis* performed limited excursions into the area surrounding their low tide shelter. The niche shift referred to above must make available to the fish many areas, located far from pools, which cannot be exploited by smaller juveniles. Thus, this change in shelter occupation and available feeding areas may affect the diet of the fish. In this paper, the stage of ontogenetic development at which the major niche shift occurs in this species was identified, and the possible causes that force this intertidal blenny to undergo changes in its feeding behaviour, vertical distribution and shelter occupation were considered.

MATERIAL AND METHODS

From October 1998 to April 1999, during ebb tides, 338 *L. pholis* were captured in Aguda (northern Portugal), a typical exposed rocky shore. In addition, 166 *Coryphoblennius galerita* (L.) and 45 *Lipophrys trigloides* (Valenciennes) were captured for subsequent comparisons of diet composition.

Fishes were killed with an overdose of the anaesthetic quinaldine (4%, in ethanol) and frozen ($-20°$ C) until used for gut content analysis. Each fish was measured (L_T) to the nearest mm and the sex was determined by examining the gonads. In the case of *L. pholis*, eleven size classes were defined, at 1 cm intervals. Due to a low number of individuals on both edges of the distribution, specimens <4 cm or >13 cm were pooled in the '0–4' and '13–17' cm class, respectively [number of individuals per size class (n) were: '0–4', 27; '4 –5', 40; '5–6', 68; '6–7', 48; '7–8', 14; '8–9', 36; '9–10', 40; '10–11', 24; '11–12', 16; '12–13', 11; '13–17', 14]. A similar approach was used for the other two blennid species.

The gut was carefully excised and its contents analysed under a Leica stereomicroscope. Prey items were counted, measured, identified to the lowest possible taxonomic level and grouped into the following 23 classes for statistical analysis: *Mytilus galloprovincialis*; other Bivalvia; Polyplacophora; *Patella* spp.; *Gibbula* spp.; other Archaeogastropoda; *Melaraphe neritoides*; other Mesogastropoda; Neogastropoda; *Skeneopsis planorbis*; *Chthamalus* spp.; Isopoda; Amphipoda; Copepoda; Decapoda; Picnogonida; Insecta; Rhodophyta; Chlorophyta; Errantia; *Sabellaria alveolata*; other Sedentaria; Echinodermata. These specific classes were created in order to represent the taxonomical diversity of *L. pholis* diet, emphasizing, nevertheless, the more frequent prey items. Certain prey items, such as algae, *Sabellaria alveolata* spines or *Chthamalus* spp. cirri (when the wall plates were not present) were registered only as present.

A principal component analysis (PCA) based on correlations was conducted on the average number of prey items per size class (Statistica 6.0). A cluster analysis (linkage rule: group average; distance measure: Euclidean distance), multidimensional scaling (MDS) and ANOSIM analysis were conducted (Primer 5.2.2), also based on the average number of prey items per L_T class.

The maximum length and width were recorded from 894 *M. galloprovincialis*. In order to calculate an approximate measure of the mussel volume, taking its shape into account, it was compared to a prolate spheroid (volume $= 4/3\pi ab^2$; where a is the major axis and b the minor axis). A piecewise regression was conducted in order to detect the breakpoint where mussel consumption markedly differed among *L. pholis* L_T classes.

RESULTS

The proportion of males and females, in the class groups where sex differentiation was possible (>8 cm L_T), did not differ (Wilcoxon matched pairs test; $n = 6$, $T = 7$, $P = 0·893$). The average consumption of the different prey items for each size class is represented in Fig. 1. Copepoda and Insecta are not represented since they both appeared in only one size class (4–5 cm). A preliminary analysis of Fig. 1 shows that prey items could be categorized into three groups (represented in the graph by different column shading), depending on the frequency distribution of the different graphs. Thus, some prey items were increasingly consumed as the fish grew (*e.g. Chthamalus* spp, Rhodophyta and Chlorophyta); other items tend to be consumed less (*e.g.* Isopoda, Amphipoda and *Melaraphe neritoides*) while the intake of some seems to be more or less constant across the range of sizes (*e.g. Mytilus galloprovincialis* and *Sabellaria alveolata*).

A PCA analysis of the data (Fig. 2) supported the interpretation of the previous results shown in Fig. 1. The three extracted factors explained 71% of the total variance (factor 1: 40·18%; factor 2: 16·99%; factor 3: 13·86%). The projection of the different prey items on the factor-plane (factor 1×2 and factor 1×3) and the projection of the size classes (also using factor 1×2 and factor 1×3) are also displayed in Fig. 2. On both projections, two clusters are discernable, grouping individuals < and >8 cm. Considering the projection of these
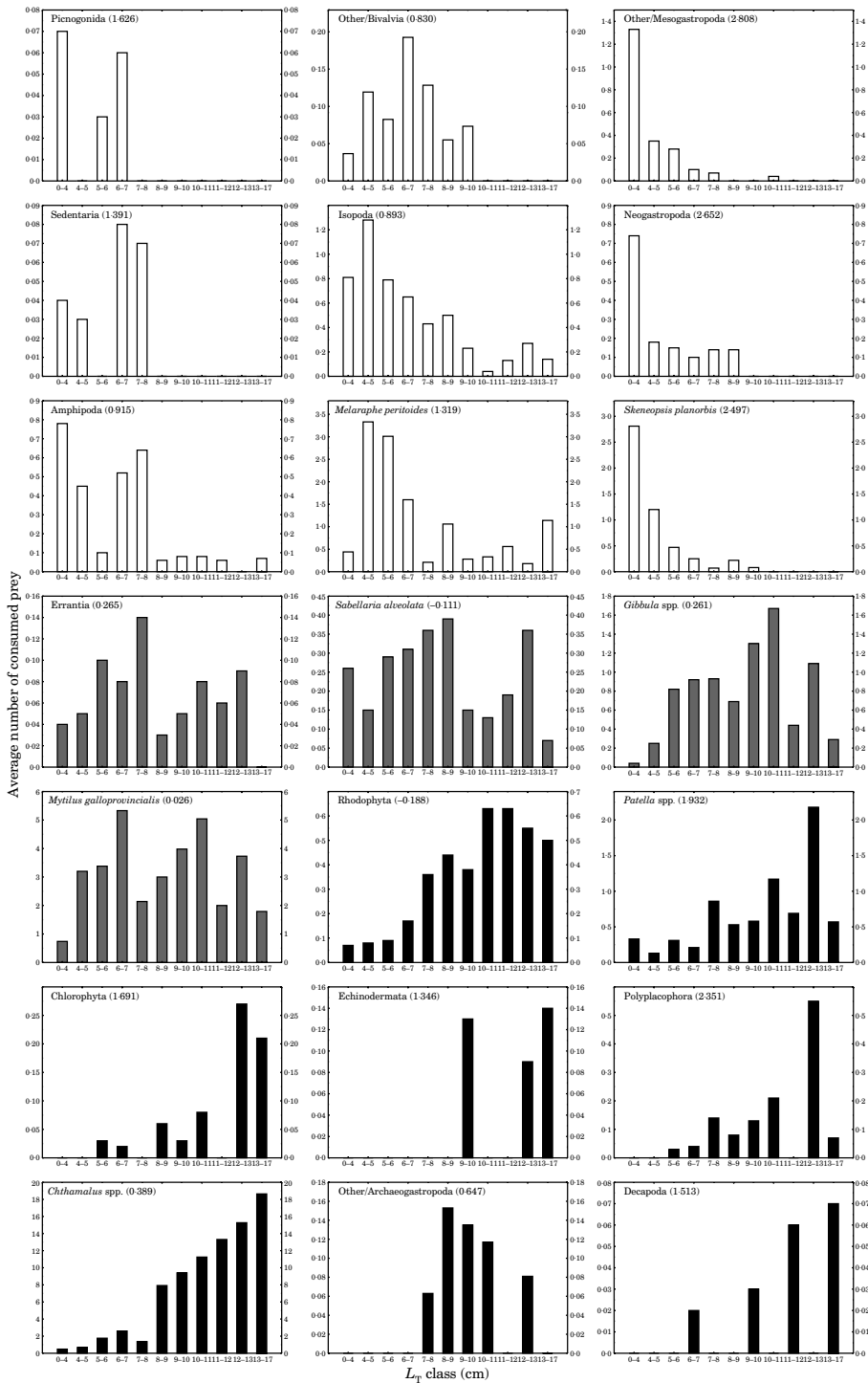
FIG. 1. The diet of *Lipophrys pholis*. The average consumption of the major prey items for each total length class considered [increasing (■), decreasing (□) or partially stable (▨) consumption tendencies]. Skewness values are given in parentheses.

variables, in the diet of the smallest *L. pholis* (classes 0–4 and 4–5 cm), a contribution of small prey is visible, such as *S. planorbis*, Neogastropoda (especially very small *Nucella lapillus*), Isopoda (*Sphaeroma serratum, Dynamene magnitorata* and *Ischyromene lacazei*), Amphipoda (*Hyale perieri, Parajassa pelagica* and *Caprella acanthifera*), Copepoda and other Mesogastropoda (*Rissoa parva, Tricolia pullus, Barleia rubra* and *Bittium reticulatum*). As *L. pholis* grew, there was an increase in the relative importance of sessile prey. Adult individuals (>8 cm) tended to eat large quantities of
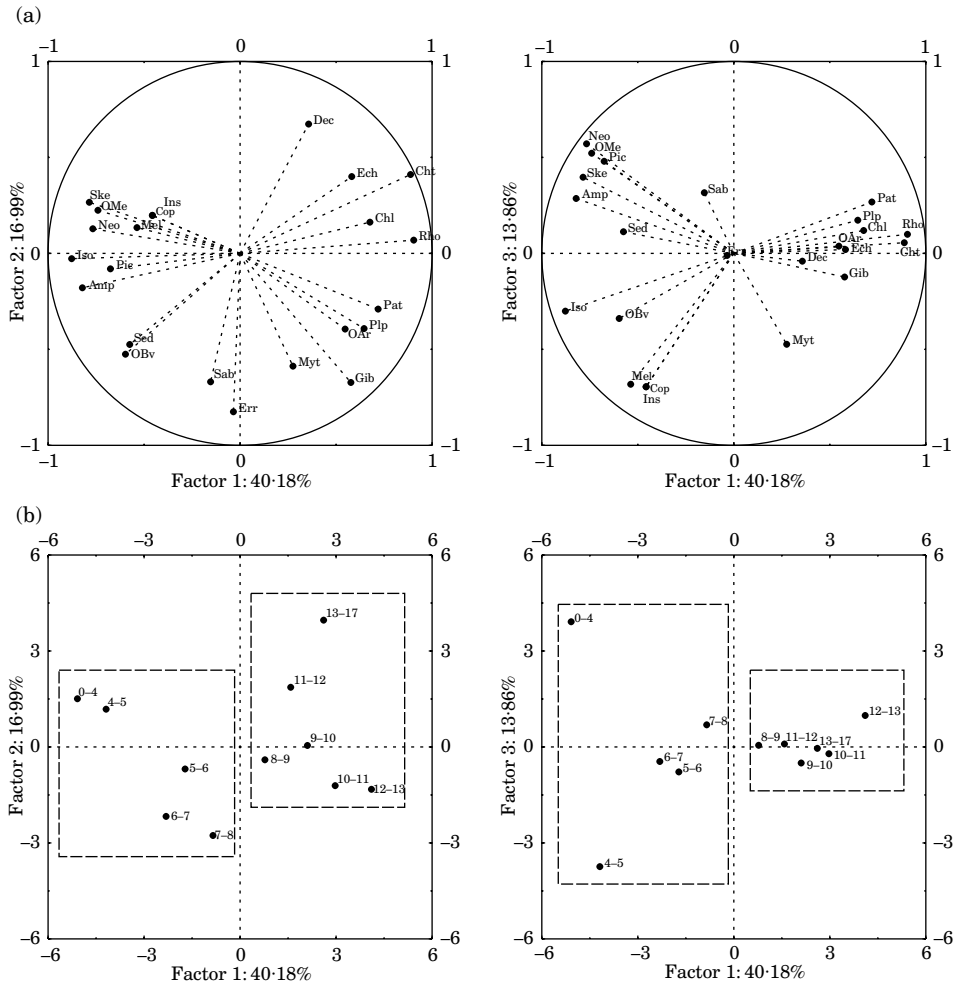

FIG. 2. Principal component analysis of the diet of *Lipophrys pholis* showing the projection of (a) the different prey items according to the three main factors and (b) the total length classes (cm) considered. (Myt, *Mytilus galloprovincialis*; OBv, other Bivalvia; Plp, Polyplacophora; Pat, *Patella* spp.; Gib, *Gibbula* spp.; OAr, other Archaeogastropoda; Mel, *Melaraphe neritoides*; OMe, other Mesogastropoda; Neo, Neogastropoda; Ske, *Skeneopsis planorbis*; Cht, *Chthamalus* spp.; Iso, Isopoda; Cop, Copepoda; Amp, Amphipoda; Dec, Decapoda; Pic, Picnogonida; Ins, Insecta; Rho, Rhodophyta; Chl, Chlorophyta; Sed, Sedentaria; Ech, Echinodermata.)

M. galloprovincialis, *Patella* spp. (especially *P. depressa*), *Gibbula* spp. (*G. umbillicalis*, *G. penanti* and *G. cineraria*), other Archaeogastropoda (*Acmaea virginea*) and Polyplacophora (*Trachydermon cinereus* and *Acanthochiton crinita*). Older individuals tended to eat large quantities of red and green algae (*Osmundea pinnatifid*a and *Ulva* sp., respectively). In the stomach of large *L. pholis* a considerable quantity of *Chthamalus* spp. (*C. stellatus* and *C. montagu*i) was sometimes visible, still interconnected, suggesting that these fish scraped the rock, ingesting large clutches of barnacles (in some cases, several *M. neritoides* were still visible inside empty barnacle plates).

Tree diagrams [Fig. 3(a)] and a MDS [Fig. 3(b)] ordination of the intake of the various food items by the different size classes indicate intra-and interspecific diet relationships between *L. pholis*, *C. galerita* and *L. trigloides*. The cluster analysis and MDS show that the difference between large and small *L. pholis* was greater than the differences between the group composed of *C. galerita*, small *L. pholis* and *L. trigloides*, although the four groups did not overlap. These results are corroborated by the data from the ANOSIM pair-wise test (Table I) that indicates that the four groups considered [small ($L_T < 8$ cm) and large ($L_T > 8$ cm) *L. pholis*, *C. galerita* and *L. trigloides*] in the analysis are homogeneous, with no apparent overlaps. The diets of very small blennies tended to be similar [Fig. 3(a)].

The relationship between the size of preyed mussels and fish L_T is shown in [Fig. 4(a)]. Both the major and minor axis of the prey were positively correlated with L_T ($r = 0.713$, $P < 0.001$ and $r = 0.686$, $P < 0.001$, respectively). Using the formula to calculate the volume of a prolate spheroid (similar shape), the predicted volume of the measured mussels is given in Fig. 4(b). In Fig. 4(c), the average consumed volume (average number of preyed mussels × average mussel volume per L_T class) is presented, showing significant differences between the average consumed volume of the two considered groups of *L. pholis* (< and >8 cm: piecewise regression;
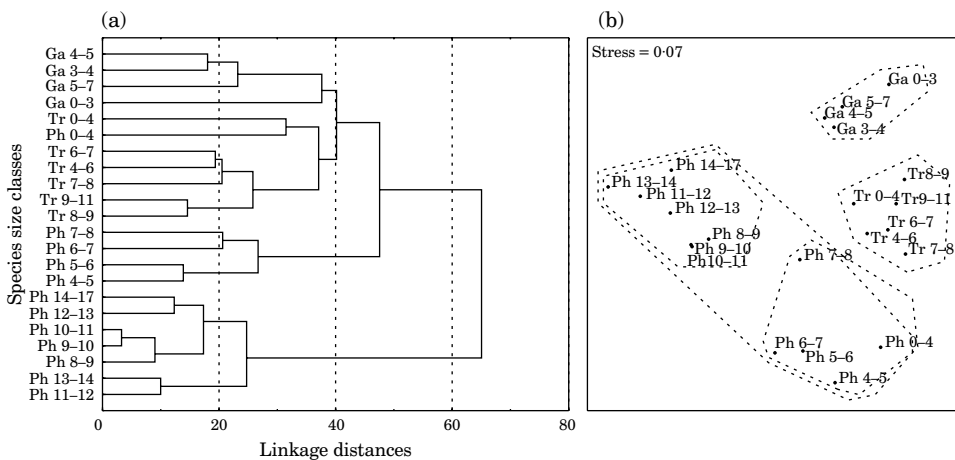

FIG. 3. (a) Cluster analyses and (b) multidimensional scaling based on a similarity matrix constructed on the average prey consumption of *Lipophrys pholis* (Ph), *Lipophrys trigloides* (Tr) and *Coryphoblennius galerita* (Ga) of different total length classes (cm).

TABLE I. ANOSIM permutation results (global $R = 0.942$, $P \leq 0.001$; number of permutations $\geq R = 0$)

Groups	Statistic	P	Possible permutation	Used permutation	Number $\geq$ observed
Small *Lipophrys pholis v.* large *Lipophrys pholis*	0.948	0.001	792	792	1
Small *Lipophrys pholis v.* *Coryphoblennius galerita*	0.919	0.008	126	126	1
Small *Lipophrys pholis v.* *Lipophrys trigloides*	0.827	0.002	462	462	1
Large *Lipophrys pholis v.* *Coryphoblennius galerita*	1	0.003	330	330	1
Large *Lipophrys pholis v.* *Lipophrys trigloides*	1	0.001	1716	1716	0
Coryphoblennius galerita v. *Lipophrys trigloides*	0.806	0.005	210	210	1

$R = 0.970$, explained variance $= 94.182\%$, breakpoint $=$ between size classes '7–8' and '8–9'). This difference was not detectable if only the number of preyed mussels (Mann–Whitney *U*-test, $Z = -0.183$, $P = 0.855$) was compared. The correlation between L_T and average mussel volume consumed was also much higher than the corresponding values for linear measurements of the mussels ($r = 0.987$, $P < 0.001$).

DISCUSSION

During the ontogenetic development of *L. pholis*, a quantitative and qualitative alteration of the dietary constituents was clearly visible. Some prey items, such as amphipods or isopods, important for the smallest size classes, tended to disappear from the diets of larger individuals, being progressively replaced by different prey items. This substitution pattern followed a consistent pattern: 1) smaller prey tended to be gradually replaced by larger prey items, 2) mobile prey species were replaced by sessile ones and 3) prey items usually found inside rock pools during the low tide tended to be replaced by prey that occupied substrata periodically exposed to the air.

It is possible that, for an increasingly larger fish, small prey (*e.g. S. planorbis* and small *N. lapillus*) start to be energetically less profitable while the increase of mouth size allows for the intake of larger prey items. Data concerning the consumption of mussels seem to support this hypothesis. The consumption of ubiquitous and abundant species, such as mussels and limpets, that present a considerable range in size, should be analysed in the future taking into account the ingested volume rather than its number.

Sessile prey, such as mussels, limpets and barnacles, may attain densities of several thousand specimens per m^2 (Lewis, 1964). They constitute a very abundant resource that may be easily collected provided that the fish displays adequate behaviour and sufficient force to detach the organisms from the rock. Interestingly, the head of *L. pholis* displays a number of unique anatomical
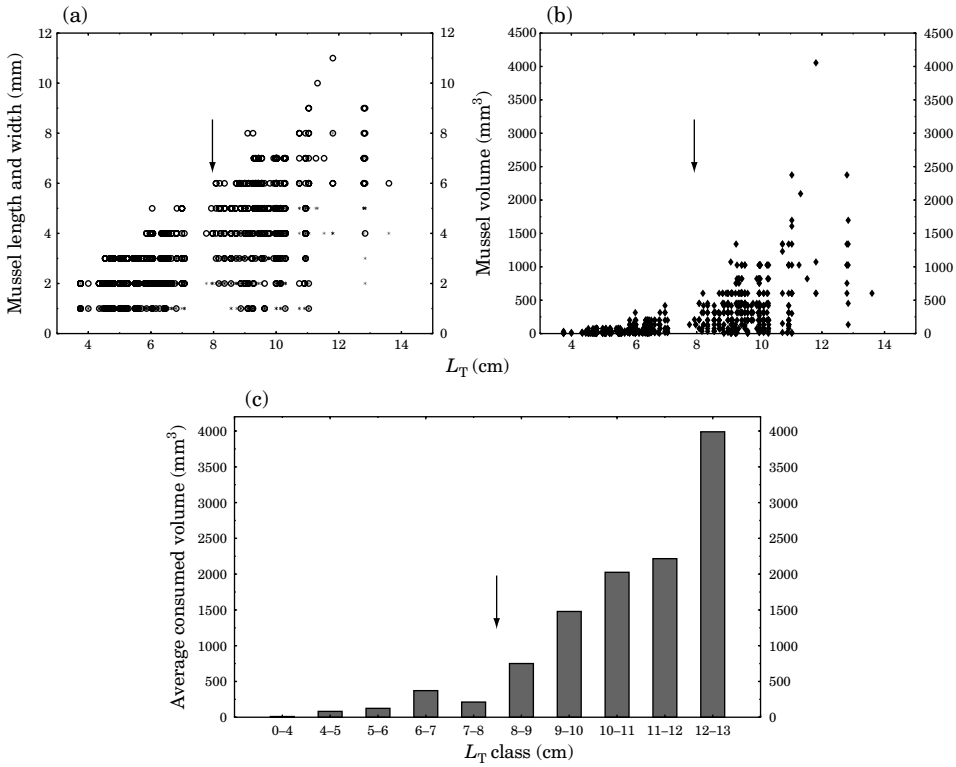
FIG. 4. Mussel (*Mylitus galloprovincialis*) consumption. (a) Relationship between mussel length ($\bigcirc$) ($r = 0.741$, $P < 0.05$) and width ($\bullet$) ($r = 0.713$, $P < 0.05$) and fish total length (L_T). (b) Relationship between mussel approximated volume and L_T. (c) Average mussel volume consumption per L_T class (average number of preyed mussel multiplied by the average mussel volume per L_T class). $\downarrow$, division between the two groups at 8 cm.

specializations that enable the fish to exploit benthic prey by a very powerful biting ability. Since *C. galerita* and *L. trigloides* do not possess the behavioural and anatomical capability to remove strongly attached prey, *L. pholis* benefits by increasing in size since it becomes able to exploit this new resource.

The increase in the proportion of prey species that are not pool residents suggests that larger fish probably undertake migrations outside rock pools during the high tide whilst smaller fish mainly feed inside a confined space, probably corresponding to the same rock pool occupied during the low tide. Faria & Almada (2001*a*) showed that when *L. pholis* of both sexes reach *c.* 7 cm they begin to leave the pools occupying channels and crevices. This shift in shelter occupation means that large fish may find low tide refuge even when in areas far from rock pools. Even if they feed near the shelter, as suggested by Burrows *et al.* (1999), they will get access to a different and much wider area of rocky shore in which to forage at high tide than if they were confined to rock pools.

Diet alterations were visible in all results (Figs 2 and 3), with the L_T classes 7–8 and 8–9 cm assuming a boundary position between the two major groups. Inter- or intraspecific competition does not seem to be the cause of this shift. The high

density of each preferred prey item along the rocky intertidal suggests that these resources are underexploited. Furthermore, as stated by Carvalho (1982) and Milton (1983), and confirmed in Fig. 3(b) and Table I, overlaps in the diet of intertidal fish species were scarce and probably negligible. Even though *C. galerita* and *L. trigloides* share some diet similarities, their vertical distributions do not overlap (Gibson, 1972; Carvalho, 1982; Zander *et al.*, 1999). Agonistic interactions with other fish species also do not seem to explain microhabitat migration in *L. pholis*. In fact, the coexistence of juvenile *L. pholis* and *C. galerita* in tidepools is common, even though *C. galerita* shows higher rates of agonistic interactions and overt aggression (Faria & Almada, 2001*b*), being dominant over *L. pholis* of similar sizes (Faria *et al.*, 1998). It is unlikely that *L. pholis* are aggressively forced to abandon tidepools since they migrate only when they are larger than *C. galerita*, that is to say, when they assume a dominant position. Concerning intraspecific aggression, Gibson (1968) demonstrated that juveniles of *L. pholis* engage in agonistic interactions where larger fish tend to be dominant over smaller ones. Finally, Faria & Almada (2001*b*) using removal and addition experiments in pools, demonstrated that the removal of one species is not followed by an increase of the proportion of fish of the remaining species. Rather, recolonization tends to re-establish the number of each species existing prior to the experiment. Thus, the evidence presented above seems to argue against a significant role of competition as a mechanism forcing the fish to leave the pools when they reach a given size. Two non-exclusive hypotheses, more likely to explain this phenomenon than competition, can be proposed. The first hypothesis ('tool usage maximization') assumes that when fish attain a critical size their scraping capability reaches a point where it becomes more profitable to feed on large benthic prey than to hunt for small mobile organisms. The second hypothesis ('pool load capability') is based on the observation that according to its micro-topography each pool presents a limited number of shelter sites available to a limited size of fish. This would explain the concordant pattern found by a considerable number of studies which show that rocky intertidal fish communities tend to be highly resilient despite the harsh nature of their environment and the occurrence of important disturbances like those resulting from storms (Bohnsack, 1983; Lassig, 1983). For instance, Faria & Almada (1999) show that the number of fishes (*L. pholis*, *C. galerita* and *Gobius cobitis* Pallas) found in a set of pools in periods of several years show very high interannual correlations that may reach values of up to 0·8. These correlations do not represent the permanence of the same individuals because *L. pholi*s and *G. cobitis* change shelter as they grow and juveniles recruit each year to the pools. These findings rather suggest that in every year, each pool is occupied by the number of fishes of each size class that it can shelter. The results of addition and removal experiments (Faria & Almada, 2001*a*), pointing also to a given number of fishes of each size class in each pool, seem to support this view as well.

Therefore, migration may just be inevitable, with 7–8 cm being the limiting size for the adequate usage of 'higher' or very shallow tidepools. These rock pools, presenting a complex substratum, with numerous small holes and crevices, and generally low water volumes, could provide higher protection from predators during the low tide, but are only suitable for small fishes. Probably due to specific mechanisms of rock erosion on the intertidal platform, the number of

hiding places suitable for larger fishes is scarce in these rock pools (N.M. Monteiro, pers. obs.), forcing individuals above a certain threshold to migrate downwards to larger pools, crevices and channels, as observed not only for *L. pholis*, but also for some gobiid species (Faria & Almada, 2001*a*).

The onset of reproduction takes place immediately after migration from very shallow tide pools to lower, larger pools, crevices and channels. The observation of the gonads of *L. pholis* confirmed that individuals measuring *c*. 8 cm started to present mature ovaries and testis. This is in agreement with the breeding size reported for *L. pholis* in Portugal by Almada *et al.* (1990*a*). Thus, reproduction, diet change and microhabitat shift appear to be intimately related. A more energetically profitable diet, preyed upon with considerably lower effort (mainly abundant sessile organisms), might be essential to compensate and maximize the reproductive effort (Fig. 4). Also, suitable areas for reproduction are found mainly outside the particular pools occupied by *C. galerita* and young *L. pholis* (N.M. Monteiro, pers. obs.). Faria & Almada (1999) demonstrated that the proportion of males of *C. galerita* in pools temporarily decreases during the breeding season because many of them occupy nest holes outside the pools. Many of the nests of *L. pholis* are also located in holes that are out of water during low tide (N.M. Monteiro, pers. obs.). It could be argued that the results could be an artefact due to unequal sampling of both sexes as the period of fish collection coincided with the breeding season where males are inside nesting holes, and are hence more difficult to capture. Since the proportion of both sexes was similar in the fish sample ($\chi^2 = 0.341$, $P = 0.58$, $n = 176$ sexed individuals), it seems likely that bias was avoided. It is possible, however, that parental males which in many blennies differ in diet, eating much smaller quantities of food (Almada *et al.*, 1994) may be underrepresented in the sample. Even if this is the case, the results presented will hold for females and for those males that are not guarding eggs.

The diet analysis in the present study proved to be an objective, yet indirect, tool to understand *L. pholis* life-history patterns, reflecting the major niche change occurring during the ontogenetic development of this fish. It also indicated with relative precision at what L_T individuals moved out of the rock pools to channels, crevices and deeper pools in the vicinity of the subtidal. This migration, occurring at *c*. 8 cm was also correlated with the onset of reproduction.

References

Almada, V. C. & Santos, R. S. (1995). Parental care in the rocky intertidal: a case study of adaptation and exaptation in Mediterranean and Atlantic blennies. *Reviews in Fish Biology and Fisheries* **5,** 23–37.

Almada, V. C., Barata, E. N., Gonçalves, E. J. & Oliveira, R. F. (1990*a*). On the breeding season of *Lipophrys pholis* (Pisces: Blenniidae) at Arrábida, Portugal. *Journal of the Marine Biological Association of the United Kingdom* **70**, 913–916.

Almada, V. C., Oliveira, R. F., Barata, E. N., Gonçalves, E. J. & Rito, A. P. (1990*b*). Field observations on the behaviour of the breeding males of *Lipophrys pholis* (Pisces: Blenniidae). *Portugaliae Zoologica* **1**, 27–36.

Almada, V. C., Gonçalves, E. J., Oliveira, R. F. & Barata, E. N. (1992). Some features of the territories in the breeding males of the intertidal blenny *Lipophrys pholis* (Pisces: Blenniidae). *Journal of the Marine Biological Association of the United Kingdom* **72**, 187–197.

Almada, V. C., Gonçalves, E. J., Santos, A. & Baptista, C. (1994). Breeding ecology and nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. *Journal of Fish Biology* **45**, 819–830.

Almada, V. C., Oliveira, R. F., Gonçalves, E. J., Almeida, A. J., Santos, R. S. & Wirtz, P. (2001). Patterns of diversity of the north-eastern Atlantic blenniid fish fauna (Pisces: Blenniidae). *Global Ecology & Biogeography* **10**, 411–422.

Barlow, G. W. (1999). Fish life on the littoral edge. In *Behaviour and Conservation of Littoral Fishes* (Almada, V. C., Oliveira, R. F. & Gonçalves, E. J., eds), pp. 3–32. Lisboa: ISPA.

Bohnsack, J. A. (1983). Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal Fish kill. *Environmental Biology of Fishes* **9**, 41–53.

Burrows, M. T., Kawai, K. & Hughes, R. N. (1999). Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies, *Lipoprhys pholis*, and crabs, *Carcinus maenas*. *Marine Ecology Progress Series* **187**, 237–250.

Carvalho, F. P. (1982). Ethologie alimentaire de trois poissons blenniidae de la côte Portuguaise. *Boletim da Sociedade Portuguesa de Ciências Naturais* **21**, 31–43.

Dodd, J., Gibson, R. N. & Hughes, R. N. (2000). Use of cues by *Lipophrys pholis* L. (Teleostei, Blenniidae) in learning the position of a refuge. *Behavioural Processes* **49**, 69–75.

Dunne, J. (1977). The biology of the shanny, *Blennius pholis* L. (Pisces) at Carna, Connemara. *Proceedings of the Royal Irish Academy* **77**, 207–338.

Faria, C. & Almada, V. C. (1999). Variation and resilience of rocky intertidal fish in western Portugal. *Marine Ecology Progress Series* **184**, 197–203.

Faria, C. & Almada, V. C. (2001*a*). Microhabitat segregation in three rocky intertidal fish species in Portugal: does it reflect interspecific competition? *Journal of Fish Biology* **58**, 145–159. doi: 10.1006/jfbi.2000.1434

Faria, C. & Almada, V. C. (2001*b*). Agonistic behaviour and control of access to hiding places in two intertidal blennies, *Lipophrys pholis* and *Coryphoblennius galerita* (Pisces: Blenniidae). *Acta Ethologica* **4**, 51–58.

Faria, C., Almada, V. C. & Gonçalves, E. J. (1996). Juvenile recruitment, growth and maturation of *Lipophrys pholis* (Pisces: Blenniidae), from the west coast of Portugal. *Journal of Fish Biology* **49**, 727–730.

Faria, C., Almada, V. C. & Nunes, M. C. (1998). Patterns of agonistic behaviour, shelter occupation and habitat preference in juvenile *Lipophrys pholis*, *Coryphoblennius galerita* and *Gobius cobitis*. *Journal of Fish Biology* **53**, 1263–1273.

Gibson, R. N. (1967). Experiments on the tidal rhythm of *Blennius pholis*. *Journal of the Marine Biological Association of the United Kingdom* **47**, 97–111.

Gibson, R. N. (1968). The food and feeding relationships of littoral fish in the Banylus region. *Vie et Milieu* **19**, 447–456.

Gibson, R. N. (1972). The vertical distribution and feeding relationship of intertidal fish on the Atlantic coast of France. *Journal of Animal Ecology* **41**, 189–207.

Gibson, R. N. (1982). Recent studies on the biology of intertidal fishes. *Oceanography and Marine Biology: an Annual Review* **20**, 363–414.

Gibson, R. N. (1999). Movement and homing in intertidal fishes. In *Intertidal Fishes: Life in Two Worlds* (Horn, M. H., Martin, K. L. M. & Chotkowski, M. A., eds), pp. 97–125. San Diego, CA: Academic Press.

Gibson, R. N. & Yoshiyama, R. N. (1999). Intertidal fish communities. In *Intertidal Fishes: Life in Two Worlds* (Horn, M. H., Martin, K. L. M. & Chotkowski, M. A., eds), pp. 264–296. San Diego, CA: Academic Press.

Laming, P. R., Funston, C. W., Roberts, D. & Armstrong, M. J. (1982). Behavioural physiological and morphological adaptations of the shanny (*Blennius pholis*) to the intertidal habitat. *Journal of the Marine Biological Association of the United Kingdom* **62,** 329–338.

Lassig, B. R. (1983). The effects of a cyclonic storm on coral reef fish assemblages. *Environmental Biology of Fishes* **9,** 55–63.

Lewis, J. R. (1964). *The Ecology of Rocky Shores.* London: English Universities Press Ltd.

Mazé, R. A., Dominguez, J. & Pérez-Cardenal, D. (1999). Diet of *Lipophrys pholis* (Teleostei, Blenniidae) in Cantabrian coastal waters (Spain). *Acta Oecologica* **20,** 435–448.

Milton, P. (1983). Biology of littoral blenniid fishes on the coast of south-west England. *Journal of the Marine Biological Association of the United Kingdom* **63,** 223–237.

Morgan, E. & Cordiner, S. (1994). Entrainment of a circa-tidal rhythm in the rock-pool blenny *Lipophrys pholis* by simulated wave action. *Animal Behaviour* **47,** 663–669.

Northcott, S. J. (1991). A comparison of circatidal rhythmicity and entrainment by hydrostatic pressure cycles in the rock goby, *Gobius paganellus* L. and the shanny, *Lipophrys pholis* (L.). *Journal of Fish Biology* **39,** 25–33.

Norton, S. F. & Cook, A. E. (1999). Predation by fishes in the intertidal. In *Intertidal Fishes: Life in Two Worlds* (Horn, M. H., Martin, K. L. M. & Chotkowski, M. A., eds), pp. 223–263. San Diego, CA: Academic Press.

Qasim, S. Z. (1956). The spawning habits and embryonic development of the shanny (*Blennius pholis* L.). *Proceedings of the Royal Society of London* **127,** 79–93.

Qasim, S. Z. (1957). The biology of *Blennius pholis* L. (Teleostei). *Proceedings of the Royal Society of London* **128,** 161–208.

Shackley, S. E. & King, P. E. (1977). The reproductive cycle and its control: frequency of spawning and fecundity in *Blennius pholis* L. *Journal of Experimental Marine Biology and Ecology* **30,** 73–83.

Wyttenbach, A. & Senn, D. G. (1993). Intertidal habitat: does the shore level affect the nutritional condition of the shanny (*Lipophrys pholis*, Telesotei, Blenniidae)? *Experientia* **49,** 725–728.

Zander, D. (1986). Blenniidae. In *Fishes of the North-eastern Atlantic and the Mediterranean.* (Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E., eds), pp. 1096–1112. Paris: UNESCO.

Zander, C. D., Nieder, J. & Martin, K. (1999). Vertical distribution patterns. In *Intertidal Fishes: Life in Two Worlds* (Horn, M. H., Martin, K. L. M. & Chotkowski, M. A., eds), pp. 26–53. San Diego, CA: Academic Press.