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Intertidal habitat: does the shore level affect the nutritional condition of the shanny (*Lipophrys pholis*, *Teleostei*, *Blenniidae*)?

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Abstract. The nutritional condition of the shanny (*Lipophrys pholis*, *Teleostei*, *Blenniidae*), an intertidal fish, is affected by the shore level on which it dwells. Depending on the altitude within the intertidal zone access to food is restricted for a certain time. A progressive decrease in the feeding time for an individual remaining on an increasingly higher shore level leads to a poorer nutritional condition compared to an individual staying at a lower shore level. Trade-off mechanisms between the feeding time and competition for space and/or predation pressure seem to be responsible for the still high abundance of *L. pholis* on the upper shore. Possible consequences for growth and reproduction as well as distribution patterns are discussed.
Key words. Blenniidae; condition factor; shore level; feeding time.

Blenniid fishes in the intertidal fringe offer an outstanding subject for studies in behavioural ecology. Inhabiting a domain characterised by the greatest variations in environmental factors of any marine area, they should be expected to develop a wide set of behavioural strategies. The intertidal habitat in many parts of the world is subjected to a semidiurnal tide cycle. Hence fish living on the sea shore encounter a twice-daily cycle of approximately 6 h of exposure to air and submersion in seawater. During exposure to air blennies survive low tide in tidal rockpools or among boulder and gravel where they are easily accessible. The semidiurnal emersion/submersion sequence sets up a whole series of secondary effects that may themselves play an important part in limiting particular intertidal species to their characteristic zone on the shore[1]. One such factor is the time available for feeding.

The shanny (*Lipophrys pholis*), a semi-amphibious blenny (*Teleostei: Blenniidae*), is common on shores of the North Sea and the North Atlantic coasts of Europe[2]. *L. pholis* has a restricted home range and shows an ability to home to a particular tide pool[3,4]. Being a poor swimmer *L. pholis* does not migrate downshore with the ebbing tide, thereby conserving energy. This advantage is counterbalanced by the disadvantage of having less time available for feeding, since during low tide access to food (mainly barnacles) is restricted. Available feeding time, which depends on the daylight submersion time, is therefore shorter on the upper shore compared to lower positions. Hence individuals lower on the shore might show a better nutritional condition than individuals of upper shore levels.

The nutritional condition of intertidal animals is the result of a complex interaction between the effects of environmental and endogenous factors of energy gain and energy loss. A net gain from the environment supplies the energy which is available for growth and reproduction. The energy-demanding reproductive machinery of an organism is directly affected by the nutritional state of an individual as well as by other factors. For example Almada et al.[5] showed that since a breeding male of *L. pholis* (which exhibits male parental care) stays in its nest for 92% of the time it is submerged, time available for other activities (mainly feeding) is restricted to about 27 min per day. Massive fat reserves (good nutritional condition) are therefore necessary for males entering into the reproductive period in order to maximise reproductive success. For females, a good nutritional condition at the beginning of the spawning season could enhance its gonad weight resulting in the production of more eggs in comparison to females in a poorer nutritional state. A decrease in the nutritional condition can follow restricted feeding as was shown for several gobiids[6] and the blenniid *Parablennius sanguinolentus*[7]. So far studies on feeding time (food intake) in relation to the shore level have all been carried out on (semi-) sessile invertebrates[8-11]. The present study therefore investigates whether individuals of *L. pholis* at a lower tidal level, having a higher mean submersion and greater access to food, are indeed in better condition than individuals staying at an upper shore level.

Material and methods

Data were collected on the Atlantic coast of Brittany (France) near Erquy (48°37′N/2°29′W) between April 5 and May 10 1991. The study site can be characterised as a rocky terrain where the tidal range varies maximally from 0.45 m at neap tides to 12.3 m above the hydrographic zero at spring tides.

476 individuals of *L. pholis* were caught with a small hand net from 2.5 to 10 m above the hydrographic zero. The capture position on the shore was noted. All fish

were measured to the nearest millimeter (total length) and weighed (wet weight) to a degree of accuracy of 0.1 gram using a digital scale (Tanita, Model 1476). Data on the length and weight of the animals were used to compute the condition factor. The condition factor, or 'ponderal index', is routinely used in fisheries ecology to assess the nutritional condition (fatness) of a fish and is regarded as a good indicator of the general well-being of teleost fishes[12]. It assumes that, for a given length, the heavier fish is in better condition. If the condition factor is applied to characterise habitat-specific differences one should use the 'relative' condition factor (Kb) which is independent of length and constant for equally nourished fishes and calculated by $K_b = \text{weight (g)} \times 100/\text{length (cm)}^b$ where b is a constant[13]. The constant b is determined by calculating the regression line of the logarithmic length-weight relationship for the whole population. This takes into account the usually allometric growth of fishes.

To find the mean daylight submersion time of each location where individuals of *L. pholis* were captured, the height to the hydrographic zero was determined during low tide. With the help of a tide table[14] the mean submersion time within the daylight hours for the tidal cycles from April 5 to May 10 1991 was calculated. The formulae used for the computation of tidal waves are based on a sinusoidal oscillation. The required data are: time of day at which low and high tide occur, tidal amplitude and the time of sunrise and sunset. To determine the exact time of sunrise and sunset of the study site, a computer program was worked out using parameters given in the almanac for computers[15]. These calculations showed a progressive decrease in the mean daylight submersion time for an increasingly higher shore level.

Results

The logarithmic relationship between the lengths and weights from all individuals of the population of *L. pholis* resulted in the regression $Y = 3.105\,x - 2.04$, ($n = 476$). The regression coefficient was used to compute the relative condition factor (Kb).

In the table the mean Kb for individuals captured on 24 different height-levels, the corresponding height and the mean daily submersion/emersion time, are listed. A significant positive correlation between the means of the Kb and of the daily submersion time was found (Spearman rank correlation, rho = 0.696, $p < 0.001$) (fig. 1). This result suggests that the shore level, and consequently the mean daily submersion/emersion time, is an important environmental component controlling the nutritional condition of *L. pholis*.

At the very highest shore level the nutritional condition of *L. pholis* is expected to deteriorate heavily since tide pooles are uncovered by the water for considerably long periods. Figure 2 shows the tidal cycles of Erquy from April 1991. At the beginning of the study period several individuals of *L. pholis* were detected in tidal rockpools 10.5 m above the hydrographic zero. The first bar (fig. 2) shows that these fishes could not leave the tide pool for feeding 9 consecutive days.

Table.

Height	Mean Kb	SD (Kb)	N	MDS	SD (mds)	MDE	SD (mde)
2.50	0.996	0.134	30	790	105	58	71
3.50	0.981	0.109	9	744	105	108	94
4.62	0.954	0.127	142	625	69	222	83
5.40	0.899	0.095	7	505	35	347	41
5.42	0.93	0.07	30	501	34	350	42
5.54	0.938	0.064	8	489	36	363	44
5.55	0.966	0.184	25	487	37	364	44
5.60	0.92	0.171	22	481	38	371	46
5.91	0.914	0.119	7	452	47	399	54
5.96	0.934	0.05	7	448	51	405	56
6.15	0.903	0.067	13	427	52	422	61
6.24	0.894	0.08	27	418	55	434	67
6.33	0.925	0.044	7	410	58	443	79
6.75	0.904	0.067	6	371	73	484	90
7.17	0.884	0.078	9	330	92	520	100
7.22	0.91	0.104	26	325	95	529	108
7.40	0.897	0.094	25	301	109	551	125
7.82	0.862	0.078	7	252	138	596	143
7.88	0.891	0.061	9	245	139	605	145
8.13	0.889	0.118	23	221	139	625	147
8.45	0.877	0.082	11	189	141	658	149
8.51	0.906	0.073	7	186	139	664	150
8.85	0.838	0.057	12	151	142	697	152
9.68	0.931	0.116	7	93	119	754	132

Height, height above the hydrographic zero (m); Mean Kb, mean relative condition factor; SD, standard deviation; MDS, mean daylight submersion time (min); MDE, mean daylight emersion time (min).

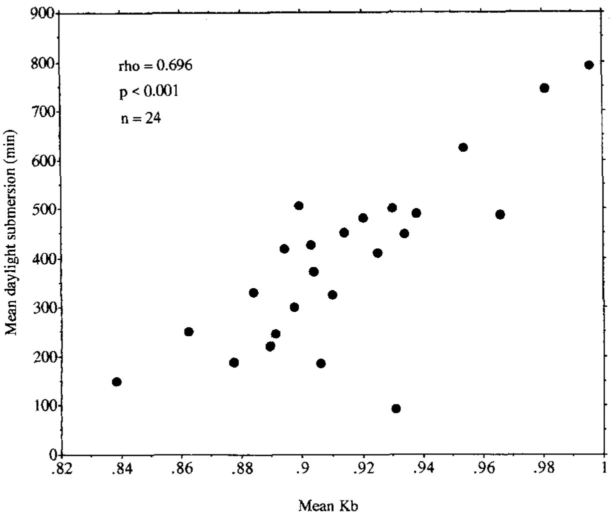

Figure 1. Correlation between the mean relative condition factor (Kb) and the mean daylight submersion time (min). Spearman rank correlation coefficient rho = 0.696, $p < 0.001$, $n = 24$.

Besides the feeding time, other parameters which influence the nutritional state of *L. pholis* must be kept in mind. Figure 3 summarises schematically the impact of the shore level on the nutritional condition of *L. pholis*.

Discussion

It could be shown that the mean daylight submersion time, and therefore the shore level, does affect the nutritional condition of the shanny. The trend towards a significantly better nutritional state in individuals staying at the sublittoral fringe (low on the shore) is considered to be a result of the enhanced feeding time resulting from an increased mean daylight submersion. If the better nutritional condition of an individual on the lower shore has a positive effect on growth and reproduction, the strategy 'stay low on the shore to maximise the feeding' should be favoured. However *L. pholis* is also abundant on intermediate and upper shore levels (table). Gibson[3] showed that on exposed shores

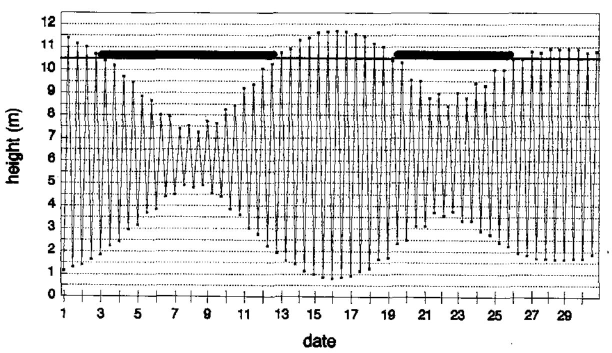

Figure 2. Tidal cycles at Erquy from April 1991. Bars show the period for which a tide pool 10.5 m above the hydrographic zero is uncovered by water.

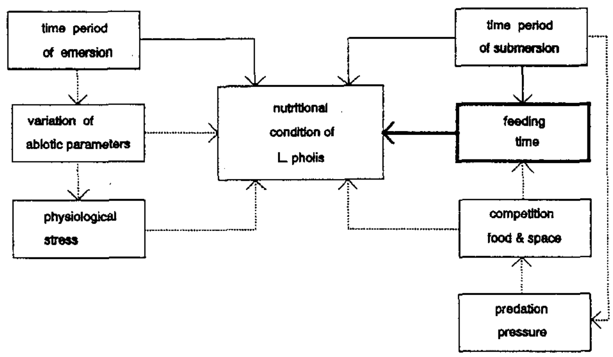

Figure 3. Possible parameters affecting the nutritional condition of *L. pholis*. Boxes on the right contain parameters which decrease with higher shore level. Parameters listed on the left increase with higher shore level.

the vertical distribution of *L. pholis* reaches a maximum frequency in tide pools from 5 m to 7 m above the hydrographic zero. On sheltered shores its upwards vertical distribution extends even further. The most likely explanation for why *L. pholis* is particularly abundant in upper shore levels although it faces a shorter feeding time is some sort of trade-off between the feeding time and competition for space and/or predation pressure. Biological interactions such as competition for space are thought to be strongest low on the shore where species diversity is highest[1,16]. Similarly the time when *L. pholis* is vulnerable to sea predators (predation pressure) is prolonged as the daily submersion time increases with lower shore level. Gibson[17] also pointed out that *L. pholis* possibly reduces competition for food and space by being spread out over the whole littoral zone.

Food abundance is a further possible component influencing the vertical distribution patterns of *L. pholis*. Barnacles, which were shown to be the main food resource for *L. pholis*[18,19], were in rich supply from the sublittoral up to the supralittoral fringe at the study site. Therefore it is very unlikely that *L. pholis* prefers a particular shore level to exploit food resources. As shown in figure 2, tide pools on the very upper shore can be uncovered by water for considerable periods (in this case 9 days). The physiological stress arising from the highly varying abiotic parameters in the rockpool water (e.g. temperature)[4,20,21] is another important factor which may affect the nutritional state of individuals choosing such rockpools to survive low tide.

The finding of individuals in poor condition on the upper shore could be because fish in poor condition may not be able to compete for good sites low on the shore. However, this implies that the lower shore is a better habitat for *L. pholis*. Making this assumption, the results show that the distribution of *L. pholis* is highly determined by species interactions such as competition. Further studies must be carried out to elucidate how environmental factors combined with species interactions operate on the behavioural mechanism of animals in the intertidal habitat. A comparative approach could contribute to a better understanding of how various parameters (see fig. 3) affect the behaviour of intertidal animals.

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