

Depth of sojourn and niche differentiation of benthic blennies (Pisces, Blenniidae) in the Mediterranean Sea (Catalonia, NE Spain and Italian coast of the Tyrrhenian Sea)

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Depth of sojourn and niche differentiation of benthic blennies (Pisces, Blenniidae) in the Mediterranean Sea (Catalonia, NE Spain and Italian coast of the Tyrrhenian Sea).— The vertical distribution of nine species of combtooth blennies between the surface and 1.5 m depth was studied at selected rocky shore sections of the Mediterranean Sea in NE Spain and the W coast of Italy. Significant differences in mean depths of sojourn and the degree of depth overlap allow the distinction of species subgroups: species preferring the uppermost shore (*Coryphoblennius galerita*, *Aidablennius sphyinx* and *Lipophrys trigloides*), those mostly found in a middle stratum (*Lipophrys canevai*, *Scartella cristata*, *Parablennius incognitus*, *Parablennius gattorugine*) and two species with the lowest depth of sojourn (*Parablennius pilicornis*, *Parablennius zvonimiri*). The relative depth position showed little seasonal variation and was similar at both Spanish and Italian sites. The species of each subgroup which shows a high degree of spatial overlap is distinguished in other dimensions of its ecological niches, in particular by different feeding habits and differences in shelter characteristics. On the basis of exact depth distribution data the present study indicates that depth differences of Mediterranean blennies are very finely tuned and species-specific, even on a broad geographical and seasonal scale.

Key words: Vertical zonation, Rocky shore, Ecological niches, Overlap, Microhabitat, Fish assemblage.

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Introduction

Vertical zonation is one of the best studied phenomena in marine biology (NYBAKKEN, 1994), but relatively little is known about depth distribution of benthic fishes of the upper littoral. Many studies deal with intertidal fishes (overview in ZANDER et al., 1999), but in most cases depth distributions are expressed as occurrences in tide pools on different levels (e.g., GIBSON, 1972). Studies based on direct underwater observations of fish activity are rare: ILLICH & KOTRSCHAL (1990) deal with blennies in the Adriatic, LINDQUIST (1985) studied blennies in the Gulf of California and ZANDER (1996) gobies and blennies at Banyuls-sur-Mer, France. Depth distribution of blennies was treated in RODILLA (1998), but was only a marginal aspect in the papers of MACPHERSON (1994), SYMS (1995) and SPYKER VAN DEN BERGHE (1995).

On the other hand, depth of sojourn is relatively easy to observe and specific depth ranges have been used as a relatively constant characteristic of single species (e.g. in ZANDER, 1972). Furthermore, it is the most obvious spatial niche dimension in which ecologically similar species can be found in a community. This is particularly apparent in the Blenniidae which are usually abundant along the rocky shores of the Mediterranean (ZANDER, 1987). They are small fish (mostly around 8–10 cm maximum length) which feed on algae, sessile fauna or vagile meiofauna and use small holes and crevices of the rocky substrate as refuge, overnight shelter and egg deposit (KOTRSCHAL, 1988). Their abundance and diversity is typically concentrated in a very narrow zone near the water surface (ILLICH & KOTRSCHAL, 1990). There are, however, two species with deeper habitat depths (*Parablennius rouxi* and *Blennius ocellaris*). Up to nine species occur syntopically at a given site (ZANDER, 1972).

Whereas elsewhere blennies have been studied for their niche relationships (e.g. LINDQUIST & KOTRSCHAL, 1987), niche differentiation of the closely related and ecologically similar Mediterranean blennies is still relatively poorly investigated. Differential feeding behaviour of Adriatic blennies was analysed by GOLDSCHMID et al. (1980) and ZANDER (1980), that of western Mediterranean blennies by GIBSON (1968).

Seasonal variation of food niches of blennies was discussed by NIEDER (1997).

Spatial resource use as the other basic determinant of niche space was studied under the aspect of depth distribution by KOPPEL (1988) (only considering two blenny species) and ILLICH & KOTRSCHAL (1990). There are, however, very few studies dealing with depth distributions of littoral fishes near the sea surface, probably because observation there is much more inconvenient than at a greater depth where the impact of waves is negligible.

The aim of this paper is to present quantitative data of year-round depth distribution of blennies on a wider geographical scale. It intends to contribute to the ecological characterization of these benthic fishes of the upper littoral.

Materials and methods

The main study site was a stretch of rocky shore that forms the northeastern flank of a promontory (the "Punta de la Mora") pointing SE from the Playa de la Mora (8 km east of Tarragona, Spain). The study section is 78 m long and consists of almost the total length of one side of the promontory, excluding only the most shallow part (depth < 0.5 m). At the tip of the promontory the sandy bottom is at three metres depth. The rock wall is more or less vertical, the site is (apart from the outer tip of the promontory) moderately exposed.

The shore at La Mora was studied in 1989 and 1990, when visual censuses of randomly selected sections of 1.50 m length and 1.50 depth (in length and depth identical to those given at the following study sites; unless the site was not shallower) equivalent to 2.25 m² were carried out (10 sections in January, 24 in April, 37 in July, 18 in September, 20 in December). Fish on the surface of the substrate and those detectable in holes and crevices were counted. In order to minimise errors because of individuals entering or leaving the observed section, observation time was restricted to 10 minutes per section. Overlap of observed sections on successive days was sometimes unavoidable, but because the promontory offered relatively homogenous conditions the effect of possible multiple countings was not required.

In April 1989, the rocky shore at Ametlla de Mar (5 sections), Salou (6 sections) and La Mora (8 sections), Torredembarra (14 sections; all in the Province of Tarragona, Spain) and in July 1990 sections at Sa Riera (16 sections), L'Escala (13 sections) and Port Lligat (9 sections; all in the Province of Girona, Spain) were censused using the same method. In September 1990, Colera (9 sections; Province of Girona) and Banyuls (9 sections; France) were investigated (study sites indicated in fig. 1). All sites were moderately exposed and the rock surfaces more or less vertical. In July 1989, the same counting method was used for the coast of the Tyrrhenian Sea (fig. 2) at similar study sites (moderately exposed, approximately vertical rocks). Shore sections (from north to south) at Moneglia (9 sections), Livorno (13 sections), Castiglione (10 sections), Porto San Stefano (4 sections), San Marinella

(6 sections), Monte Circeo (25 sections), Sorrento (12 sections), Marina di Camerota (22 sections) and Capo Vaticano (12 sections) were studied.

Species and depth of sojourn of blenniid specimens were recorded underwater on plastic writing pads. Measuring tape was used to determine the length (1.5 m) and depth (1.5 m) of sections, and (unless the procedure was hindered by water turbulence) to estimate depth of specimens as precisely as possible. All censuses were done by the author. Two species were difficult but not impossible to distinguish: *Parablennius incognitus* and *Parablennius zvonimiri*. The latter usually has a more reddish colour. For a small distance, the feathery tentacles above the mouth are clearly recognizable in that species.

Due to varying and sometimes very difficult weather conditions with considerable

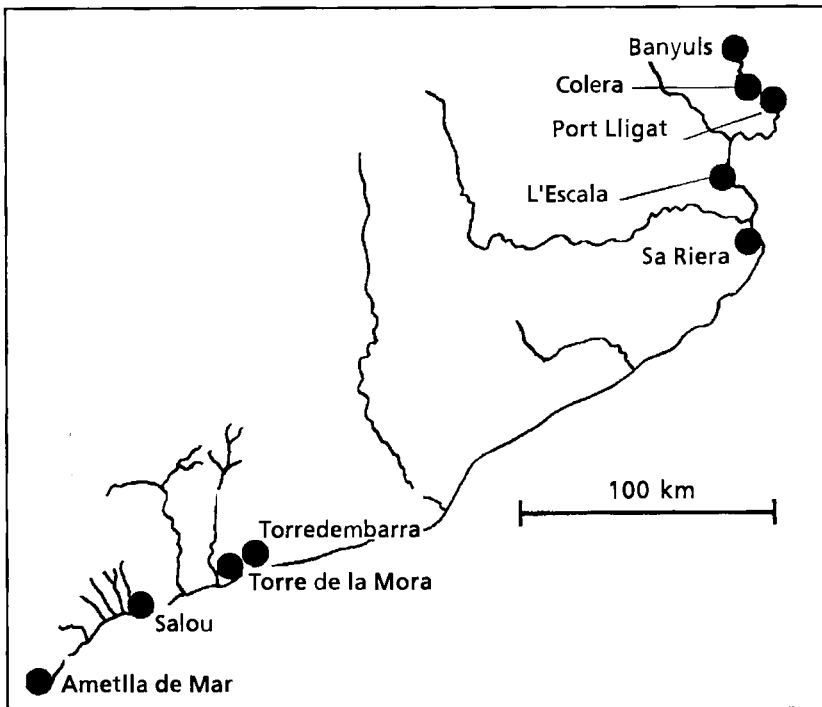


Fig. 1. Study sites in Catalonia and France.
Àrees de estudio en Catalunya y Francia.

wave action during observation periods in 1990, the total surface area of the La Mora sections studied differed between observation periods.

Data analyses were designed following ZAR (1984). Statistical calculations were performed by means of the computer program Statistica 5 (StatSoft Inc., 1995).

The differences in mean depth distribution were tested using a Kruskal–Wallis non-parametric ANOVA. For a comparison of niche overlap, Morisita's index of similarity (MORISITA, 1959) was used. This index was chosen because it has a very low bias at all sample sizes and multiple resources (KREBS, 1999). Distribution along the depth gradient of littoral blennies could be considered to correspond to the use of a niche dimension. Depth zones were treated as representing resource states, and niche width was additionally calculated on the basis of the Shannon–Wiener index of diversity (H). The indices were calculated with Excel (Microsoft Office 5.0). Because of rounding to four digits, complete overlap (given as "1" in table 3) was calculated as a number above 1 (from 1.0218 to 1.0609).

Along with the countings, 212 specimens (usually 12 per investigation period) of *Lipophrys trigloides* (Cuv. & Val. 1836), *Parablennius pilicornis* (Cuvier 1829) and *Scartella cristata* (Linné 1758) were caught at La Mora in plastic bags, sacrificed and fixed in 4% formalin immediately after the dive for study of gut contents and precise length determination. The results of the gut content analysis were published in NIEDER (1997).

Species names follow ZANDER (1987).

Results

On the basis of the observation area covered, the total number and absolute densities of blennies at La Mora was calculated (table 1). A seasonal pattern emerged, with maximum numbers and maximum density of all blenniid species in July 1990. Length measurements of the specimens caught for gut content analysis (NIEDER, 1992) showed that juvenile specimens of *L. trigloides* could be found in December, juvenile *P. pilicornis* in July and juvenile *S. cristata* in September. Large individuals of *L. trigloides* became less numerous in July, those

of *P. pilicornis* in September, and those of *S. cristata* in December.

At Torre de la Mora in 1990 a total of 1,614 sightings was recorded (table 2). For each species, different mean densities and significantly different mean depths (table 3) resulted. Figure 3 illustrates the depth distribution pattern of nine blenniid species at the study site La Mora on the basis of all observations in 1990.

Coryphoblennius galerita (Linnaeus 1758) shows by far the narrowest niche width in depth distribution ($H = 0.8843$). *Aidablennius sphynx* follows ($H = 1.6850$), and then all other species with much wider niche widths (from $H = 2.0909$ to $H = 2.5114$).

The extremes (fig. 3) are rather similar for the two species occurring above the others (*C. galerita* and *A. sphynx*) and for six species occurring in lower depths (*L. trigloides* to *P. pilicornis*), respectively. *P. zvonimiri* is confined to the lower part of the upper littoral, otherwise its distribution is similar to that of *P. pilicornis*.

The Kruskal–Wallis non-parametric ANOVA showed that the depth of sojourn means for each species were significantly different ($H = 543.4036$; $p = 0.000$). Table 3 gives overlap indices according to Morisita's index of similarity. Overlap indices mirror the significances of depth differences. The emerging structure of differences allows the distinction of species groups (consisting of one or several species) within the blenny assemblage at La Mora, according to their preference of depths of sojourn and distribution patterns.

The depth range of *C. galerita* is extremely narrow (fig. 3). A large number of *C. galerita* were observed between 0 to 0.2 m depth. Most individuals (63%) were seen at water level or above the surface. Mean depth of sojourn at La Mora was only 5.3 cm. The species was frequently found above the water, indicating that *C. galerita* was practically amphibious.

A. sphynx and *L. trigloides* occurred slightly deeper than *C. galerita* (fig. 1). Mean depths at La Mora were 0.22 m and 0.29 m (table 2), respectively. Niche breadth of depth of sojourn was similar (table 3), compared to other species.

S. cristata, *Lipophrys canevai*, *P. incognitus* and *Parablennius gattorugine* had mean

depths between 0.45 m and 0.59 m at La Mora (table 2). The depth distribution of *P. gattorugine* was, however, slightly more irregular (fig. 3). The vertical niche breadth of all four species was relatively large (Shannon–Wiener index of diversity in the order of the species named: 2.3250, 2.4774, 2.2815, 2.3242).

P. pilicornis and *P. zvonimiri* occurred deeper than the other seven species (at La Mora 0.86 m and 0.98 m mean depths), and their depth distribution was irregular (fig. 3). Whereas *P. pilicornis* had the widest vertical niche breadth (Shannon–Wiener index of diversity: 2.5114) of all species, *P. zvonimiri* had a rather narrow one (Shannon–Wiener index of diversity: 2.2179).

Seasonal variation of depth at La Mora in each species (table 4) was usually minimal and not significant, according to a Kruskal–

Wallis ANOVA. Only *S. cristata* ($H = 27.76864$, $p = 0.0000$) and *L. trigloides* ($H = 21.46012$, $p = 0.0003$) had significantly different mean depths in the course of 1990.

At other Catalanian sites mean depths of species were roughly similar to those found at La Mora (table 2). Again *C. galerita* was found at shallow depths, on a lower level *L. trigloides* and *S. cristata* followed. *A. sphyinx*, *L. canevai* and *P. incognitus* formed a group of species at middle depths, and *P. gattorugine*, *P. pilicornis* and *P. zvonimiri* formed the blenny species assemblage predominant in the lower littoral.

Even Italian and Spanish sites were strikingly similar (table 2). Though absolute depths of single species were different, we found the same order of mean depths (with *P. pilicornis* missing) as in the Catalanian study sites.

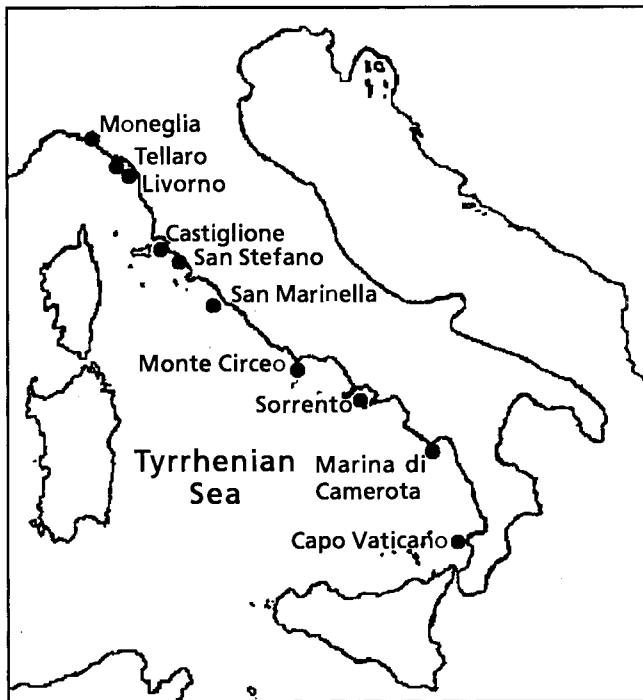


Fig. 2. Study sites along the coast of the Tyrrhenian Sea.
Àreas de estudio en la costa del Mar Tirreno.

Table 1. Countings of blennies at the La Mora study site in 1990: Jn. January; Ap. April; Jl. July; Sp. September; Dc. December; T. Total; SD. Standard deviation. A Kruskal-Wallis ANOVA showed that all mean densities were significantly different ($H = 11.081$; $p = 0.0257$). (Mean densities are calculated per section of 1.5 m length.)

Contajes de blénidos en el área de estudio de La Mora en 1990: Jn. Enero; Ap. Abril; Jl. Julio; Sp. Septiembre; Dc. Diciembre; T. Total; SD. Desviación estándar. La ANOVA de Kruskal-Wallis mostró que todas las densidades medias fueron significativamente diferentes ($H = 11,081$; $p = 0,0257$).

	Jn	Ap	Jl	Sp	Dc	T
Total length of littoral (m)	15	36	57	20.5	40	168.5
Area (m ²)	22.5	54	85.5	30.75	60	252.75
Number of sections (of 1.5 m length)	10	24	37	18	20	109
Number of individuals	106	348	661	214	278	1,607
Mean densities (1.5 m / section)	10.6	14.7	17.7	11.9	14.3	-
Min. / Max.	3/23	5/27	7/39	5/23	4/35	-
SD	7.07	4.54	9.54	4.66	8.30	-

Table 2. Blennies at Torre de la Mora (1990), other Catalanian sites (1990) and Italian sites (1989), in descending order of depths at La Mora: N. Number of fish individual sightings; Mdn. Mean densities (individuals / m²); Mdp. Mean depths (m); SD. Standard deviation.

Blénidos de Torre de la Mora (1990), otros lugares de estudio en Cataluña (1990) y lugares de estudio en Italia (1990), en orden descendente de profundidades de La Mora: N. Número de observaciones individuales de peces; Mdn. Densidades medias (individuos / m²); Mdp. Profundidades medias (m); SD. Desviación estándar.

Species	Torre de la Mora				Catalonian sites			Italian sites		
	N	Mdn	Mdp	SD	N	Mdn	Mdp	N	Mdn	Mdp
<i>C. galerita</i>	56	0.22	0.05	0.09	18	0.06	0.08	101	0.24	0.10
<i>A. sphyinx</i>	45	0.18	0.22	0.14	17	0.05	0.41	55	0.13	0.31
<i>L. trigloides</i>	155	0.61	0.29	0.25	131	0.40	0.19	157	0.37	0.24
<i>S. cristata</i>	365	1.44	0.45	0.30	54	0.17	0.29	87	0.21	0.40
<i>P. incognitus</i>	327	1.29	0.48	0.30	27	0.83	0.24	234	0.55	0.53
<i>L. canevei</i>	244	0.97	0.51	0.35	122	0.37	0.41	163	0.38	0.31
<i>P. gattorugine</i>	42	0.17	0.59	0.40	237	0.73	0.51	52	0.12	0.89
<i>P. pilicornis</i>	354	1.4	0.86	0.38	23	0.70	1.10	-	-	-
<i>P. zvonimiri</i>	26	0.12	0.98	0.32	13	0.04	0.94	85	0.20	0.78

Table 3. Morisita's measure of overlap for depths of sojourn of blennies at the Torre de la Mora study site: Cg. *C. galerita*; As. *A. sphynx*; Lt. *L. trigloides*; Lc. *L. canevali*; Sc. *S. cristata*; Pi. *P. incognitus*; Pg. *P. gattorugine*; Pp. *P. pilicornis*; 1. Complete overlap.

Morisita's medida de solapamiento de las profundidades de estancia de blénidos en el área de estudio de Torre de la Mora: Cg. C. galerita; As. A. sphynx; Lt. L. trigloides; Lc. L. canevali; Sc. S. cristata; Pi. P. incognitus; Pg. P. gattorugine; Pp. P. pilicornis; 1. Solapamiento total.

	Cg	As	Lt	Lc	Sc	Pi	Pg	Pp
<i>C. galerita</i>	-							
<i>A. sphynx</i>	0.4675	-						
<i>L. trigloides</i>	0.5408	1	-					
<i>L. canevali</i>	0.1915	0.8393	0.8779	-				
<i>S. cristata</i>	0.1877	0.8430	0.8945	0.9989	-			
<i>P. incognitus</i>	0.1107	0.8230	0.8440	0.9975	0.9721	-		
<i>P. gattorugine</i>	0.1120	0.7511	0.8109	1	1	1	-	
<i>P. pilicornis</i>	0.0152	0.2150	0.8753	0.6234	0.5728	0.6392	0.7483	-
<i>P. zvonimiri</i>	0.2029	0.0624	0.1938	0.4801	0.3800	0.4467	0.5958	1

Table 4. Seasonal variation of mean depths of sojourn of blennies at Torre de la Mora: Jn. January; Ap. April; Jl. July; Sp. September; Dc. December; N. Number of fishes observed; Mdp. Mean depth. Mean depths were not significantly different (according to a Kruskal-Wallis ANOVA), except for *S. cristata* ($H = 27.76864$, $p = 0.00$) and *L. trigloides* ($H = 21.46012$, $p = 0.0003$).

Variación estacional de profundidades medias de los blénidos de Torre de la Mora: Jn. Enero; Ap. Abril; Jl. Julio; Sp. Septiembre; Dc. Diciembre; N. Número de individuos observados; Mdp. Profundidad media. Las profundidades medias no fueron significativamente diferentes (Kruskal-Wallis ANOVA), excepto en los casos de S. cristata ($H = 27,76864$; $p = 0,00$), y L. trigloides ($H = 21,46012$; $p = 0,0003$).

Species	Jn		Ap		Jl		Sp		Dc	
	N	Mdp	N	Mdp	N	Mdp	N	Mdp	N	Mdp
<i>L. trigloides</i>	15	0.25	48	0.25	48	0.22	18	0.19	26	0.55
<i>S. cristata</i>	17	0.42	53	0.38	163	0.53	38	0.37	85	0.36
<i>P. incognitus</i>	26	0.44	87	0.48	134	0.51	43	0.43	37	0.43
<i>L. canevali</i>	16	0.46	59	0.48	99	0.51	36	0.48	34	0.51
<i>P. pilicornis</i>	21	0.91	57	0.79	139	0.87	55	0.83	69	0.80

Discussion

The changes of blenny numbers and densities at La Mora (table 1) indicated a seasonal pattern of abundance, with a maximum in July. The length measurements of the 3 species which were caught for gut analysis (*L. trigloides*, *P. pilicornis* and *S. cristata*; see NIEDER, 1997) suggested that in summer the juvenile specimens were recruited while the largest adult specimens had not yet died. This explains the elevated density of individuals compared to the winter season.

C. galerita, *A. sphynx* and *L. trigloides* were the species found immediately beneath the water surface at La Mora and the other study sites (table 2), forming the uppermost species group in the vertical blenny structure.

The semi-amphibian behaviour of *C. galerita* has been known since SOLJAN (1932). Its (mainly nocturnal) terrestrial sojourns above water level were investigated by ZANDER (1983). GIBSON (1972), ARRUDA (1979). FIVES (1980) found this species in little depth at surf-exposed rocks in the Atlantic. The results of the present study confirm that *C. galerita* is the blenny occurring highest on shore at different sites in its respective blenny assemblage.

A. sphynx was described as frequent on rocks in shallow water (ABEL, 1962; PAPA-CONSTANTINOU, 1974; PATZNER, 1984; SEGANTIN, 1968 and ZANDER, 1972). At La Mora, *L. trigloides* is another species that in most cases can be observed close to the surface. This matches the observations of ILLICH & KOTRSCHAL (1990), PATZNER (1984) and ZANDER (1972, 1983).

Beneath the 3 above-mentioned species, *L. canevei*, *S. cristata*, *P. incognitus* formed what can be called the "middle stratum" of blennies. *L. canevei* was found in depths around or little above 0.5 m by ILLICH & KOTRSCHAL (1990), PATZNER (1984, 1985), SEGANTIN (1968), ZANDER (1972, 1980). *S. cristata* was described as most frequent in the same shallow depth zone (BALMA & DELMASTRO, 1984; DE LEO et al., 1976; PATZNER, 1984). The average depth of sojourn of *P. incognitus* at La Mora (between 0.4 m and 0.6 m) is slightly above that given in KOPPEL (1988) (0.86 m) and ZANDER (1972) (0.6 m to 1.0 m).

The preference for deeper habitats in *P. gattorugine* has been pointed out since VINCIGUERRA (1879); PATZNER (1984), RIEHL (1978)

and ZANDER (1972) agree in this respect. At La Mora, where mostly juveniles under 80 mm total length were sighted, mean depth of sojourn was relatively shallow in comparison. *P. pilicornis* and *P. zvonimiri* prefer the deepest zones of the rocky shore habitat. In North Africa ZANDER (1972) found the biggest abundance of *P. pilicornis* at sites with deep rocky shores. A similarly deep occurrence (1–3 m) was noted by BRITO (1982). *P. zvonimiri* is a facultative cave-dweller (ZANDER & HEYMER, 1976) that normally keeps away from the surface (ABEL, 1962; PATZNER, 1984). At La Mora, this species had the greatest mean depth of sojourn.

In conclusion, interspecific differences in depth distributions emerge. Each species has a preferred depth which should correspond to the mean depth of all sightings. Chosen depths should reflect the ability of each species to cope with the physical properties of the uppermost littoral, e.g. the impact of wave action. This environmental factor has long been supposed to have a decisive influence on fishes in the intertidal zone (GOSLINE, 1965). In extreme cases benthic fishes can be cast onto the shore (FOLLETT, 1970). Intertidal fishes have been observed to shift their distribution to deeper water in times of strong wave action (GIBSON, 1982). The anatomical features of blennies which allow them to keep their position in even massive currents are the pectoral fin anatomy and the surface structure of their cuticle (ZANDER, 1973). It seems very likely that these features serve in an optimal way at a certain depth and thus help to withstand a certain quantity of wave force.

Why don't littoral fish retreat into deeper water, if water turbulence is such a problem? Predation pressure is probably greater in lower depth zones. At La Mora and other sites, *L. trigloides* could be found in even shallower depths at night than during daytime, and numerous piscivore *Scorpaena* spp. in depths of less than 2 m could be observed (NIEDER & ZANDER, 1993–1994). It has been suggested that the turbulent surge zone screens littoral fish from potential piscivores (ILLICH & KOTRSCHAL, 1990).

On the other hand, blennies occurring at any given site show significant interspecific differences in distribution on a very fine

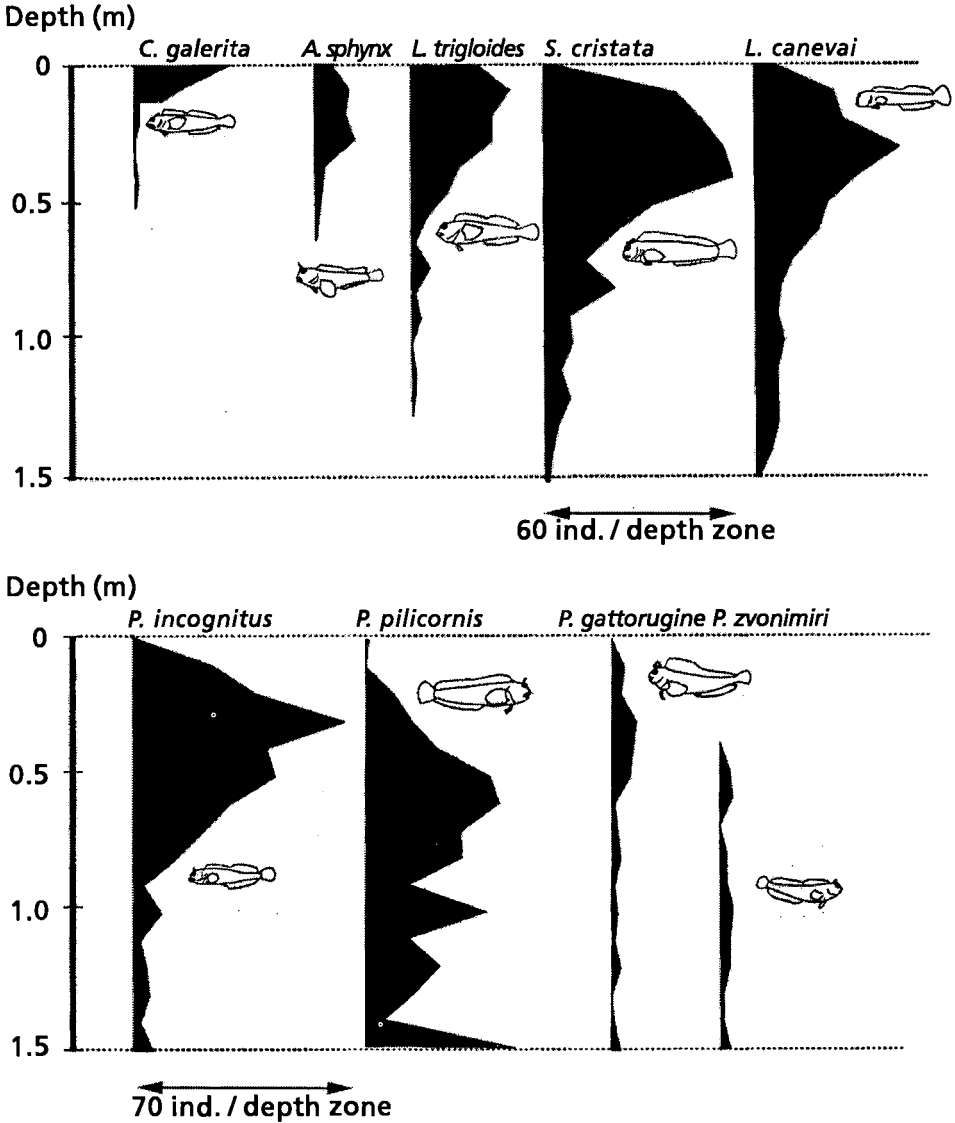


Fig. 3. Depth distributions of blennies at Torre de la Mora in 1990. The width of the black silhouettes indicates the numbers of blenny individuals.
Distribuciones de profundidad de blénidos en Torre de la Mora en 1990. El ancho de las siluetas negras indica el número de individuos.

scale, in the case of the study site at La Mora within the first metre of depth. Is this perhaps the result of vertical niche differentiation, preventing competitive exclusion?

Figure 4 illustrates the niche differentiation of the blenny assemblage at the Torre de la Mora site, indicating approximate depth preference (following the results of this

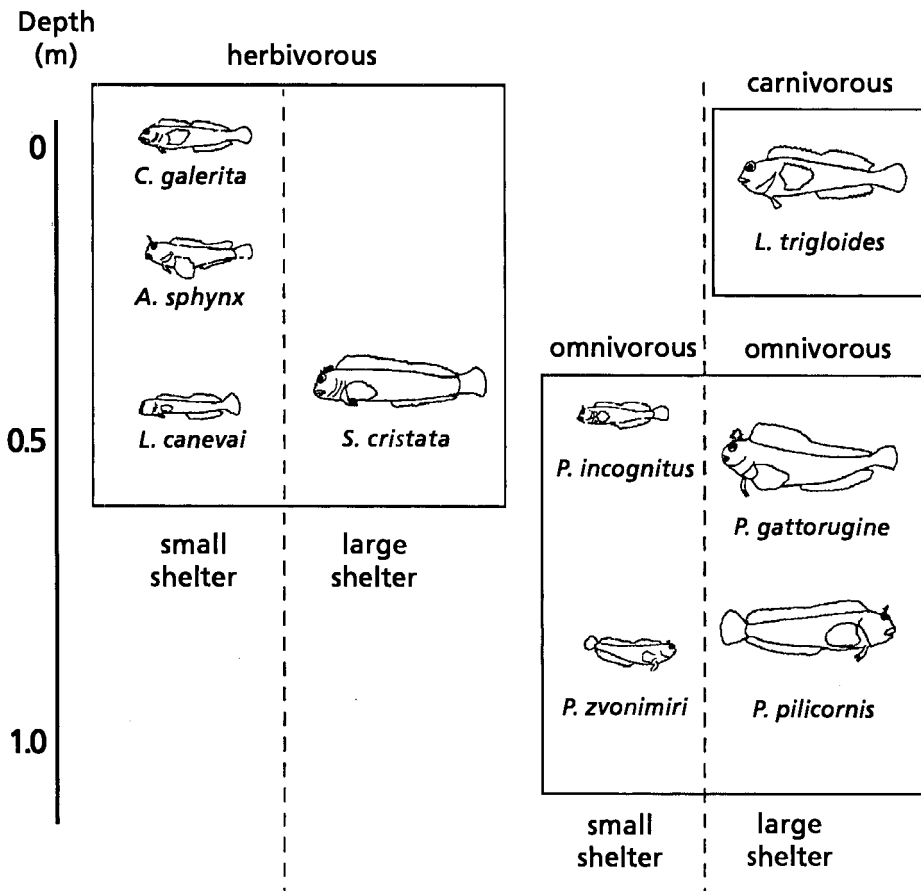


Fig. 4. Depth preferences and differences in food and shelter requirements in different blenny species (schematic illustration based on the data presented in this study and literature, see Discussion). Note the ecological separation of species occurring in the same depth zone. "Shelter" refers to the holes and fissure of rock surfaces which all the blennies use as temporary retreat and breeding holes.

Preferencias de profundidad y diferencias en la alimentación en diferentes especies de blénidos (ilustración esquemática, basada en los datos de esta publicación y bibliografía, ver Discusión). Hay una separación ecológica entre las especies presentes en la misma zona de profundidad. "Shelter" se refiere a los agujeros y fisuras en las rocas que los blénidos utilizan como refugio.

study) and ecological separation according to food preferences (GOLDSCHMID et al., 1980; 1984; NIEDER, 1997) and shelter requirements (KOPPEL, 1988; KOTRSCHAL, 1988). The ecological distinction is particularly obvious in those species which do not occupy different depth zones (*A. sphynx*/*L. trigloides*; *L. canevai*/

S. cristata / *P. incognitus*; *P. pilicornis* / *P. zvonimiri*).

Some species are well separated in their food preferences: *A. sphynx* is a predominantly herbivore species (ABEL, 1962; GOLDSCHMID et al., 1984). Some studies indicate, however, a variable diet in this species (GIBSON, 1968;

ZANDER & BARTSCH, 1972). *L. trigloides*, on the other hand, is a carnivore. *L. canevai* is predominantly herbivorous, *P. incognitus* omnivorous, and the same is true for *P. zvonimiri* and *P. pilicornis* (feeding data from GOLDSCHMID et al., 1984; NIEDER, 1997).

Body size differences help to explain the remaining overlap (*S. cristata* and *L. canevai* / *P. incognitus*; *P. gattorugine* and *P. pilicornis*). An important component of the spatial niche dimension for blennies is the size of boreholes of endolithic bivalves. Studies concerning shelter characteristics and trophic niches *L. canevai*, *P. incognitus*, *A. sphyinx* and *P. zvonimiri* (KOPPEL, 1988; KOTRSCHAL, 1988) show that even small differences in body size result in differential uses of shelter holes. The size differences of *S. cristata* and *L. canevai* / *P. incognitus* on the one hand and *P. gattorugine* and *P. pilicornis* on the other are marked (GOLDSCHMID et al., 1984; NIEDER, 1988; NIEDER, 1992) and suggest differential use of shelter holes in the habitat.

Further investigation is necessary to fully understand the complex web of niche relationships of Mediterranean blennies. The fine-tuning of the spatial niche, e.g., the preferred depth of sojourn, is possibly one of the factors responsible for the adaptive success of Mediterranean blennies, expressed in the large number of species occurring in one habitat.

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