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Benthopelagic habits of adult specimens of *Lampanyctus crocodilus* (Risso, 1810) (Osteichthyes, Myctophidae) in the western Mediterranean deep slope*

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SUMMARY: In an extensive survey of the middle and lower slope fish fauna of the Catalan Sea (western Mediterranean), the myctophid *Lampanyctus crocodilus* appeared as a common species despite using a semi-balloon otter trawl as sampling gear. All specimens captured were adults ranging from 5-18 cm. The peak abundance was located around 1200 m, the species becoming notably scarcer below this depth. No differences between day and night catches were found. These findings sharply contrast with the results obtained in the upper slope (544-710 m) using a commercial bottom trawl, where there are important differences in day/night catches. A study of the feeding habits of the specimens coming from the upper slope showed both a marked predominance of pelagic prey and a nocturnal foraging period centered in the BBL. The diet of those specimens collected in the middle and lower slope is markedly different, considering the great contribution of epibenthic mobile prey such as calanoid copepods and mysids. The diminishing influence of the mesopelagic fauna below 1000 m could be responsible of this change in diet and also may be the cause of the loss of a diel migration habit in adult specimens of *L. crocodilus*.

Key words: benthopelagic, diet, behaviour, *Lampanyctus crocodilus*, slope, western Mediterranean.

RESUMEN: HÁBITOS BENTOPELÁGICOS DE EJEMPLARES ADULTOS DE *Lampanyctus crocodilus* (RISSO, 1810) (OSTEICHTHYES, MYCTOPHIDAE) EN LA ZONA PROFUNDA DEL TALUD CONTINENTAL EN EL MEDITERRÁNEO OCCIDENTAL. *Lampanyctus crocodilus* resultó ser una de las especies más frecuentes entre las capturadas en un estudio exhaustivo de la ictiofauna del talud medio e inferior del mar Catalán (Mediterráneo occidental), en el que se utilizó como muestreador un «semi-balloon otter trawl». Todos los ejemplares eran adultos con tallas comprendidas entre 5 y 18 cm. La máxima abundancia se localizó sobre los 1200 m, disminuyendo notablemente a partir de esta profundidad. Asimismo, no se detectaron diferencias entre las capturas diurnas y nocturnas. Estos resultados contrastan con los obtenidos en el talud superior (544-710 m) mediante un arte de arrastre bentónico de tipo comercial, en donde sí se detectaron importantes diferencias entre capturas diurnas y nocturnas. El análisis de la dieta de ejemplares procedentes del talud superior indica el predominio de presas pelágicas y, por otra parte, una actividad depredadora nocturna a una cierta distancia del fondo, en el BBL. Por contra, la dieta en el talud medio e inferior presenta una alta proporción de presas epibentónicas móviles (p. ej. copépodos calanoideos y misidáceos). La menor influencia de la fauna mesopelágica por debajo de los 1000 m parece estar relacionada con este cambio de las preferencias tróficas y explicaría, además, la pérdida de una actividad migradora en los ejemplares adultos de *L. crocodilus*.

Palabras clave: bentopelágico, dieta, comportamiento, *Lampanyctus crocodilus*, talud, Mediterráneo occidental.

INTRODUCTION

Lampanyctus crocodilus (Risso, 1810) is one of the most abundant myctophids occurring in the Mediterranean Sea (TÅNING, 1918; HULLEY, 1984; BAUCHOT, 1987). While individuals caught in pelagic nets have allowed larval, postlarval and juvenile distribution to be relatively well established (TÅNING, 1918; GOODYEAR *et al.*, 1972; SABATÉS, 1988), this has not been the case for adults, where specimens appear almost exclusively in upper and middle slope bottom trawls to 700-800 m (DIEUZEIDE *et al.*, 1954; MAU-

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TABLE 1. — *Lampanyctus crocodilus* abundance values (indiv./h) for 36 OTSB14 trawls below a depth of 1000 m in the Catalan Sea. D: day samples; N: night samples. (Positions and other station data can be found in RUCABADO *et al.*, 1991).

Station	*D/N*	*Depth (m)*	*Abundance (indiv./h)*	*Total Abundance (specimens)*
15BIII	D	986	1.9	7
24BIII	D	1001	3.4	12
10BV	N	1008	4.1	6
11BV	D	1010	2.6	8
17BV	D	1022	2.7	8
27BIII	D	1049	0.9	2
14BV	N	1075	0.3	1
4BV	D	1078	2.8	14
25BIII	D	1202	6.9	22
9BV	N	1212	9.0	27
16BIII	D	1225	1.3	5
10BIV	D	1264	0.8	4
6BII	D	1308	0.9	3
12BIV	D	1316	1.2	4
8BII	D	1326	1.1	3
17BIII	D	1409	0.9	3
11BIII	D	1468	1.8	1
11BIV	D	1488	1.2	4
18BV	N	1499	2.6	4
8BV	D	1568	1.7	5
7BIII	D	1584	0.3	1
2BV	D	1589	1.0	3
8BIII	D	1729	2.3	4
5BII	D	1734	1.0	2
7BV	D	1737	1.3	4
6BV	N	1739	0.3	1
26BIII	D	1748	0.9	3
3BV	D	1757	0.4	2
18BIII	D	1764	0.3	1
9BIV	D	1790	0.3	1
8BIV	D	1821	0.4	2
6BIII	D	1840	0.3	1
28BIII	D	1862	0.2	1
4BIV	D	2021	0.6	2
3BIV	D	2169	0.3	1
7BIV	D	2209	0.3	1

RIN, 1968; BINI, 1971; RELINI ORSI and RELINI, 1973; MATALLANAS, 1979; NADAL, 1981; ALLUÉ, 1985; etc.). Although distribution studies below this depth are virtually nonexistent the species does appear to be present below 1000 m (DIEUZEIDE *et al.*, 1954; MAURIN, 1968; CARPINE, 1970; FREDJ and MAURIN, 1987).

Studies on the diel cycle of *L. crocodilus* have detected migratory habits in juveniles of 13-33 mm, but not in larger juveniles or subadults (GOODYEAR *et al.*, 1972; HULLEY, 1984). Although relevant data for adults are not available, the existence of a nocturnal migration to shallower waters, as demonstrated for the closely related species *Lampanyctus cuprarius* Tåning, 1928 (MERRETT and ROE, 1974), cannot be excluded. Such migrations are trophic in nature (MARSHALL, 1960; VINOGRADOV and TSEITLIN, 1983 and references cited therein).

In this paper we present new data on the deep slope distribution of adult *L. crocodilus* and give clear evidence of benthopelagic behaviour (*sensu* MARSHALL and MERRETT, 1977) based on the analysis of the diet.

MATERIAL AND METHODS

All individuals were captured in the Catalan Sea continental slope (Northwestern Mediterranean, between 38°45' N and 42° N and the continental coast and the Balearic Islands), over a depth range of 544-2209 m (Tables 1 and 2).

Below 1000 m (Table 1) all material was obtained using a semi-balloon otter trawl —OTSB14— (RUCABADO *et al.*, 1991), during BATHOS III-V cruises (1988). To determine bathymetric distribution along the gradient, abundance values for 200 m strata were calculated and expressed as individuals/trawl hour.

Dietary composition of 98 from a total of 173 specimens was determined (Table 3). Immediately

TABLE 2. — Station data of two day/night cycles carried out in the upper slope using a commercial trawl. D: day samples; N: night samples.

Station	*Date*	*Situation*	*Time (GMT)* *Initial*	*Final*	*D/N*	*Depth (m)*	*Abundance (indiv./h)*	*Total Abundance (Specimens)*
DN1/1	13/07/1989	41°07' N - 02°03' E	17.30	19.45	D	668	6.2	14
DN1/2	13/07/1989	41°07' N - 02°03' E	21.43	23.51	N	655	2.8	6
DN1/3	14/07/1989	41°07' N - 02°03' E	01.35	03.46	N	646	2.8	6
DN1/4	14/07/1989	41°07' N - 02°03' E	05.23	07.26	D	710	13.7	28
DN1/5	14/07/1989	41°07' N - 02°03' E	08.40	11.05	D	622	11.6	25
DN2/1	20/10/1990	41°07' N - 01°56' E	19.45	21.00	N	550	0.8	1
DN2/2	20/10/1990	41°07' N - 01°56' E	22.08	23.23	N	553	0	0
DN2/3	21/10/1990	41°07' N - 01°56' E	00.15	01.25	N	546	0.9	1
DN2/4	21/10/1990	41°07' N - 01°56' E	02.25	03.30	N	544	0.9	1
DN2/5	21/10/1990	41°07' N - 01°56' E	04.25	05.30	N	559	1.9	2
DN2/6	21/10/1990	41°07' N - 01°56' E	06.16	07.30	D	546	1.6	2
DN2/7	21/10/1990	41°07' N - 01°56' E	08.15	09.35	D	553	5.3	7
DN2/8	21/10/1990	41°07' N - 01°56' E	10.22	11.37	D	546	4.8	6
DN2/9	21/10/1990	41°07' N - 01°56' E	12.23	13.40	D	546	7.0	9

TABLE 3. — Composition of the diet of *Lampanyctus crocodilus* in two different bathymetric ranges along the slope.

Lampanyctus crocodilus	*550-700 m* % F	*550-700 m* % N	*1000-2200 m* %F	*1000-2200 m* %N
SIPHONOPHORA	—	—	4.2	2.1
CRUSTACEA				
Decapoda				
Sergestes arcticus	12.0	7.3	2.1	1.0
Sergia robusta	—	—	4.2	2.1
Sergestidae unidentitified	—	—	4.2	2.1
Acanthephyra pelagica	—	—	2.1	1.0
Acanthephyra sp.	—	—	2.1	1.0
Pasiphaea sivado	8.0	3.6	—	—
Pasiphaea multidentata	—	—	2.1	1.0
Mysis larvae	4.0	1.8	—	—
Euphausiacea	4.0	1.8	2.1	1.0
Mysidacea				
Eucopia hanseni	—	—	6.3	3.1
Boreomysis arctica	16.0	10.9	18.8	10.4
Unidentified	4.0	1.8	6.3	3.1
Amphipoda				
Gammaridea				
Eusirus longipes	—	—	2.1	1.0
Rhachotropis caeca	—	—	2.1	1.0
Scopelocheirus hopei	4.0	1.8	—	—
Oediceropsis brevicornis	4.0	1.8	—	—
Pardalisca sp.	—	—	2.1	1.0
Pseudotiron bouvieri	—	—	2.1	1.0
Stegocephalidea	—	—	2.1	1.0
Hyperiidea				
Scina sp.	—	—	2.1	1.0
Vibilia sp.	8.0	3.6	—	—
Euprimo sp.	4.0	1.8	2.1	1.0
Isopoda				
Ilyarachna sp.	—	—	2.1	1.0
Cumacea				
Bodotriidae	—	—	2.1	3.1
Iphinoe sp.	4.0	1.8	—	—
Copepoda Calanoidea	20.0	9.1	43.8	25.0
Unidentified crustacea	20.0	9.1	2.1	1.0
ECHINODERMATA				
(Echinoidea)	—	—	2.1	1.0
CHAETOGNATA	4.0	1.8	—	—
OSTEICHTHYES				
Cyclothone braueri	4.0	1.8	—	—
Unidentified	44.0	20.0	29.2	14.6
Unidentified debris	8.0	3.6	2.1	1.0
Scales (Unidentified)	28.0	16.4	—	—
(Mora moro)	—	—	18.8	14.6
Plant debris	—	—	2.1	1.0
Plastic	—	—	4.2	2.1
FORAMINIFERA	4.0		4.2	
Bolivina sp.	4.0		—	
Ammolagena sp.	—		2.1	
Benthic foraminifera	—		2.1	
Number of specimens analyzed	25		98	
Number of prey (excluding foraminiferans)		55		96
Percentage fullness	84.6		50.5	

after capture examples were fixed in 10 % formalin. In the laboratory individuals were weighed and stomach contents analysed. Fullness coefficient was defined as percentage of stomach contents having food remains. Prey were classified to the lowest possible taxonomic group, noting also occurrence frequency (F) and numerical proportion (N).

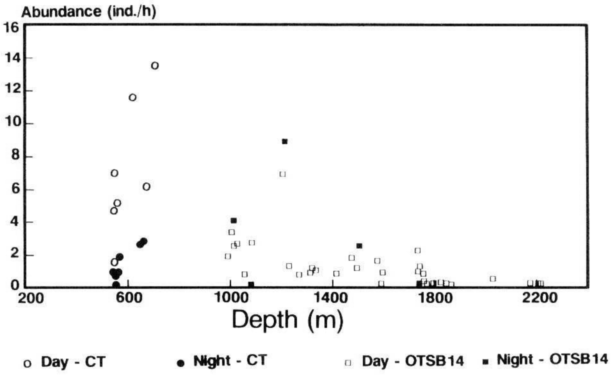

FIG. 1. — Abundance values of *Lampanyctus crocodilus* along the slope of the Catalan Sea, in day/night samples taken with an OTSB14 and a Commercial Trawl (CT).

For comparative purposes and to contrast behavioural patterns along the slope, data for two day/night cycles collected from commercial bottom trawls in the upper slope (544-710 m) were also considered (Table 2). To detect any possible trophic diel migration, degree of digestion was also considered. Method and four step digestive scale was that described in ALONCLE and DELAPORTE (1970) and AMEZAGA (1988).

RESULTS

In the middle and lower slope, *L. crocodilus* appeared in 36 of a total of 48 samples (see Table 1 and STEFANESCU, 1991), which represents an incidence frequency of 0.75.

Abundance values along the studied depth range are shown in Figure 1. Below 1000 m peak abundance value (9 indiv./h) was observed around 1200 m, specimens becoming notably scarcer (0-2 indiv./h) below this depth. Despite less data being available for nocturnal catches (5 samples), results did not appear to deviate from diurnal values.

Diurnal abundance values for the upper slope (5-14 indiv./h) were notably higher than the corresponding night values (0-3 indiv./h). The only diurnal catch registering an abnormally low value (1.6 indiv./h, DN2/6) was, in fact, taken at dawn (Table 2).

Figure 2 shows length frequency for 105 specimens taken below 1000 m. The observed distribution is bimodal, with an overall average length of 10.5 cm (±3.4 cm SE) and minimum and maximum values of 5.5 and 18 cm respectively.

Differences in diet were detected along the slope

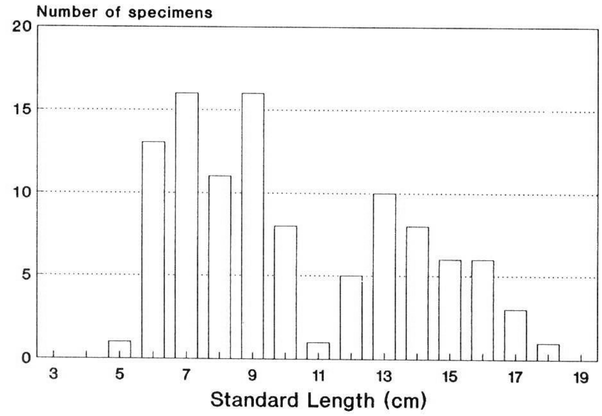

FIG. 2 — Length-frequency distribution of 105 specimens of *Lampanyctus crocodilus* trawled below a depth of 1000 m in the Catalan Sea.

(Table 3). Whereas on the upper slope the diet of *L. crocodilus* consisted mainly of bony fishes, mesopelagic decapods (e.g. *Sergestes arcticus, Pasiphaea sivado)* and mysids *(Boreomysis arctica),* preferred prey on the middle slope were calanoid copepods, mysids (e.g. *B. arctica, Eucopia hanseni*) and bony fishes, in this order. Percentage fullness showed a marked decrease with depth, from a value of 84.6 % for the upper slope to 50.5 % for the middle and lower slopes.

DISCUSSION

L. crocodilus, a Mediterranean and North Atlantic species traditionally considered as mesopelagic (KREFFT and BEKKER, 1973; HULLEY, 1984), is one of the most abundant myctophids taken in pelagic samples in the western Mediterranean (TÅNING, 1918; SABATÉS, 1988; I. Palomera pers. comm.). Nevertheless, these samples are almost exclusively comprised of small individuals from larval, postlarval or juvenile stages, and any adults, if represented, form only a small part of the total catch. Thus, although larval, postlarval and juvenile bathymetric distribution has been well documented (cf. TÅNING, 1918; GOODYEAR *et al.,* 1972), details on adult distribution have not been available (HULLEY, 1984).

The paucity of adult individuals in pelagic samples stands in marked contrast to their abundance in slope bottom trawls. The popular denomination "mare d'amploia" by Catalan fishermen is, in itself, an indication of a frequent appearance in commercial bottom trawls. Moreover, *L. crocodilus* is also regularly caught on the lower slope, its capture frequency being comparable to that of many demersal fish having their distribution centered around this depth (STEFANESCU *et al.,* 1992).

It has already been suggested by some authors (for example, BINI, 1971; HAEDRICH and POLLONI, 1974; MARSHALL, 1979) that, unlike most pelagic myctophids, adult *L. crocodilus* probably live near the sea-bed. This would explain their absence in pelagic catches to 1000 m (GOODYEAR *et al.,* 1972; KARNELLA, 1987). Further direct observations made from submersibles in the Northwest Atlantic (KARNELLA, 1987) appear to confirm such benthopelagic behaviour. As suggested by the presence of individuals around 10 cm length close to the sea-bed, there seems to be an ontogenic shift in relation to preferred habitat.

Moreover, the length at which *L. crocodilus* acquires benthopelagic behaviour might be situated between 5-6 cm, this being the minimum length recorded in bottom trawls from either the upper slope (MATALLANAS, 1982) or middle and lower slope (present work), and corresponding to the maximum observed length taken in pelagic samples in the Northwest Atlantic (KARNELLA, 1987).

A consideration of diet and behaviour in detected prey meant the hypothesis that individuals might have been caught at mid waters, during pay out or retrieval of the warp, could be rejected. Moreover, in spite of not being the most suitable sampling gear, bottom trawls can provide useful information about pseudoceanic species distribution in the sea-bed vicinity, given a high rate of capture (MERRETT, 1986).

The upper slope diet of *L. crocodilus* has been shown to be predominantly pelagic (MATALLANAS, 1982), with any incidence of benthic prey considered as accidental. Our present work agrees with this author, while further reaffirming the presence of benthic prey. Effectively, *L. crocodilus* is feeding on mobile epibenthic prey such as the gammaridean amphipods *Scopelocheirus hopei* and *Oediceropsis brevicornis,* the cumacean *Iphinoe* sp. and the mysid *Boreomysis arctica.*

In the middle and lower slope, a high incidence of epibenthic peracarid crustaceans was found, even though the predominant prey at this depth are calanoid copepods. There is some evidence to suggest that these copepods would be considered "suprabenthic" (*sensu* BRUNEL *et al.,* 1978) or, in a wider sense, benthopelagic (*sensu* MARSHALL and MERRETT, 1977). Thus, for example, they form the principal component of the diet for species belonging to genus

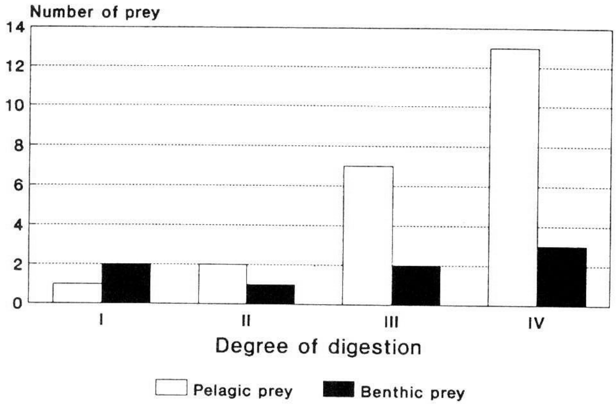

FIG. 3. — Digestive degree for benthic and pelagic prey ingested by 24 *Lampanyctus crocodilus* taken during the day in the upper slope (scales and unidentified prey have been excluded). Scale of digestion increases from I to IV.

Bathypterois, sedentary fish which remain on the sea-bed supported by their caudal and pelvic fin rays (SULAK, 1977). Concordantly, CARRASSÓN and MATALLANAS (1990) found the diet of *Bathypterois mediterraneus*, the dominant lower slope fish species in the Catalan Sea (STEFANESCU, 1991; STEFANESCU *et al.*, 1992) to be almost exclusively composed of such copepods. The previously described numerical importance of calanoid copepods within the near sea-bed (MARSHALL, 1965; HARGREAVES *et al.*, 1984) has recently been further confirmed along the slope of the study area, from epibenthic sled samples (unpublished data) taken with a modified Macer-Giroq epibenthic sled (DAUVIN and LORGERE, 1989). In fact, they were found to be the dominant suprabenthic crustaceans in the water layer immediately above the sea bottom (from 10-130 cm above the sea-bed). Thus, if this prey group can be considered benthic, at least 57 % of the diet of *L. crocodilus* in the middle and lower slope is of benthic origin, providing clear evidence of benthopelagic behaviour in this species.

On the upper slope, benthic prey play a diminished role in a predominantly pelagic diet. Furthermore, in those specimens taken in diurnal samples, pelagic prey showed an advanced degree of digestion (Fig. 3). This is indicative of a prior period of nocturnal foraging where *L. crocodilus* leaves the sea-bed, further supported by its reduced occurrence in nocturnal catches taken with a commercial bottom trawl (Fig. 1), whose mouth opens to a vertical height of 5.5 m aprox.

In the light of these results, together with the absence of large individuals in pelagic samples, the authors suggest that in the upper slope adult *L. crocodilus* of more than 5-6 cm move nocturnally away from the sea bottom to feed within the so-called Benthic Boundary Layer (cf. WISHNER, 1980; HARGREAVES *et al.*, 1984). Moreover, many of the detected prey, such as *Sergestes arcticus* and *Eucopia hanseni*, constitute an important part of the BBL fauna (HARGREAVES, 1984; unpublished data).

On the other hand, *L. crocodilus* exhibits similar diurnal behaviour to that described for other mesopelagic species, such as the decapod *Pasiphaea multidentata* (CARTES, 1991). This diel migration does not appear to occur at greater depth, where no difference in day/night catches are observed (Fig. 1). This could be attributed to the diminishing mesopelagic fauna influence below 1000-1200 m (BERNARD, 1958; FRANQUEVILLE, 1971; CARTES, 1991; MAUCHLINE and GORDON, 1991; STEFANESCU, 1991; amongst others), with the consequent reduction in BBL density and the trophic availability. The decrease found in fullness percentage with depth (MATALLANAS, 1982; present work) is also in accordance with this tendency.

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