

Sensory constraints in temporal segregation in two species of anglerfish, *Lophius budegassa* and *L. piscatorius*

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ABSTRACT: The temporal segregation of 2 ecologically equivalent and sympatric species, the black anglerfish *Lophius budegassa* and white anglerfish *L. piscatorius*, was studied in relation to day–night behaviour and the underlying morphological variation in the sensory organs. Temporally scheduled trawl sampling was conducted on the western Mediterranean shelf, and diel fluctuations in catches were used as a proxy of behavioural rhythms. *L. budegassa* was more abundant at night than *L. piscatorius*, which mostly occurred in daytime catches. The observed differences in the timing of maximum activity (i.e. catches) were consistent with differences in otolith sagittae weight, eye/lens sizes and optical sensitivity. *L. budegassa* presented significantly heavier otolith sagittae than *L. piscatorius*, indicating that the behaviour of the black anglerfish is mostly acoustically driven (a typical characteristic of species living in dim light conditions). Preference for a dim light environment was also confirmed by the high optical sensitivity observed in this species achieved by enlarging the photoreceptors' diameter. In contrast, *L. piscatorius* showed larger eyes and lenses than *L. budegassa*, but only in individuals larger than 50 cm. Large eyes usually improve photon capture and the fineness with which the image is sampled; however, relatively low values of sensitivity and resolution were observed in large *L. piscatorius*. This indicates that a trade-off might exist between the increase in eye size as an adaptive response to the impending deep meso- and bathypelagic life and a visual constraint imposed by the quality of the water at the bottom level where contrast can be degraded by suspended particles. These results indicate that interspecific competition with sympatric and ecologically equivalent species may result in different adaptations to diurnal/nocturnal behaviour, which are sustained by morphological specialisations in sensory organs.

KEY WORDS: Sensory systems · Activity rhythm · Temporal segregation · Otolith · Eye · Anglerfish

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INTRODUCTION

Temporal segregation in activity rhythms of ecologically equivalent and sympatric species may promote their coexistence in overlapping distribution areas (Kronfeld-Schor & Dayan 2003). Thus, species reduce interspecific competition by segregating their timing of maximum behavioural activity into different windows of the day–night cycle (Pittman & McAlpine 2001).

Although activity patterns in fishes are often said to be plastic (Ali 1992), i.e. not always consistent either within species or between individuals, trawling can be considered a reliable method for assessing the behavioural rhythm in those fish living in deep water areas where direct observation is unfeasible (reviewed by Aguzzi & Company 2010). This method provides inter-

esting insight into species' biological clock regulation when catches are conducted concomitantly with measurements of physical factors that are key habitat parameters controlling rhythms (e.g. the light or tidal cycles as Zeitgeber; reviewed by Aguzzi et al. 2008). However, the field study of biological rhythms has to be supported by observations of the anatomy and functional mechanisms of the sensory capabilities that each species displays (Naylor 2005). In fact, to understand why a species occupies a temporal niche, it is crucial to identify the environmental characteristics under which individuals determine their appropriate period of activity.

Taking into account the fact that sensory systems represent the filters between environmental inputs and behavioural outputs, habitat choice will affect the

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environmental conditions under which sensory systems are employed, and the timing of behavioural activity may then be sustained by differences in sensory capabilities (Endler & McLellan 1988, Dusenbery 1992, Myrberg & Fuiman 2002, Weissburg 2005). Even though sensory modalities underlying spatial segregation phenomena have previously been highly documented in fish (Aguirre & Lombarte 2000, Bozzano & Catalán 2002, Lombarte et al. 2003, Sabatés et al. 2003, Schulz-Mirbach et al. 2008, Seehausen et al. 2008), there is still scant information on the role played by sensory modalities in relation to temporal segregation. Additionally, although the survival of a species demands some co-evolution of its sensory systems, adaptation to a temporal niche causes implementation of compensatory mechanisms that counterbalance the quality of each sensory modality, which means that the poor performance of one system is compensated for by the good performance of another (Schellart & Popper 1992).

With this in mind, 2 ecologically equivalent lophiid species, the black anglerfish *Lophius budegassa* and the white anglerfish *L. piscatorius*, represent a good example in which segregation can be analysed in relation to sensory modalities. In fact, these species show partial overlap in their bathymetric distribution range in the Mediterranean. Both species are present on the continental shelf but reach different depths on the slope. *L. budegassa* occurs down to a depth of 800 m (Carlucci et al. 2009), while *L. piscatorius* has been detected deeper, down to almost 2600 m (Afonso-Dias & Hislop 1996, Hislop et al. 2000). The black and white anglerfishes share common behavioural traits within the lophiids, especially in their feeding strategy, as they exhibit sit-and-wait ambush behaviour using their angling apparatus, the illicium, as a lure. In addition, both species show similar food preferences and therefore compete for similar prey items (Crozier 1985, Laurenson & Priede 2005, Preciado et al. 2006, Negzaoui-Garali et al. 2008).

Interspecific competition of ecologically equivalent species is reduced in sympatric zones by varying population densities and distributions, but also by varying the timing of their activity (Linnell & Strand 2000, Kronfeld-Schor & Dayan 2003). Accordingly, in the western Mediterranean, the reported overlap in the bathymetric range of lophiids indicates that there could be a concomitant process of morphological divergence occurring that may sustain species activity within different time windows (Seehausen et al. 2008). The activity rhythms of *Lophius piscatorius* and *L. budegassa* were analysed in the field using temporally scheduled trawl sampling and considering potential quantitative differences in the morpho-functionalities of their inner ears (acoustic and vestibular functions)

and eyes (visual functions), which are the sensory systems involved in remote detection of objects. With regard to the 3 otolithic organs of the fish's inner ear, the sacculus together with its otolith, the sagitta, shows the highest morphological variability, and this structure is located in the lower part of the inner ear, which is generally associated with the hearing sense (Platt & Popper 1981, Popper & Fay 1993, Popper & Lu 2000). The size and shape of this structure show adaptations to different environmental factors, such as depth, water temperature and substrate type (Lombarte & Fortuño 1992, Aguirre & Lombarte 1999, Paxton 2000, Torres et al. 2000, Gaudie & Crampton 2002, Volpedo & Echeverria 2003). With respect to vision, the capability to hunt at night or at the maximum depth at which a fish can operate seems very likely to be determined by its eye size, because large eyes both increase the retinal sampling frequency and therefore improve resolution, and capture more photons, improving sensitivity, although many exceptions to this exist (Land & Nilsson 2002).

The aim of the present work was to determine whether anglerfish reduce competition in their overlapping distribution range by displaying temporal segregation in their behavioural activity and whether this is consistent with differences in their sensory modalities.

MATERIALS AND METHODS

Field sampling. Four days of temporally scheduled trawl sampling were carried out on the western Mediterranean lower continental shelf (100 to 110 m depth) during June 2000 at latitude 41°N to characterise the activity rhythms of the black and white anglerfishes. Thirty-two hauls were made along parallel and closely situated transects. The field survey was carried out onboard RV 'García del Cid' (38 m in length, 1200 HP), which was equipped with otter trawl nets of 27.5 mm headrope size (OTMS; Sardà et al. 1998).

The duration of the hauls was approximately 90 min, and their number, separated into day- and night-time trawls, is designated by 2 h time intervals in Table 1. A global positioning system (GPS) recorded the ship velocity and the initial and final position (latitude and longitude) for all hauls, while an echosounder provided depth measures. SCANMAR telemetric sensors connected to the mouth of the net recorded wing openings (m) and depths (m). Data were stored on an onboard computer. The setting and retrieving time of each haul were considered as the exact moment of the net landing and rising from the seabed, according to SCANMAR information.

Table 1. Numbers of trawl samples of *Lophius piscatorius* and *L. budegassa* and photon fluency rate (PFR) readings used for mean estimations at each 2 h time interval in the 24 h waveform analysis. -: no samples collected at the corresponding time interval during the 4 d of fishing activity; np: night period. Missing values at certain time intervals (i.e. -) were replaced by computing an average (\pm SD) estimate from all temporally adjacent values

Time interval (h)	No. of hauls	No. of PFR readings
12:00–14:00	3	–
14:00–16:00	1	1
16:00–18:00	3	2
18:00–20:00	5	4
20:00–22:00	4	np
22:00–00:00	–	np
00:00–02:00	3	np
02:00–04:00	1	np
04:00–06:00	4	4
06:00–08:00	4	4
08:00–10:00	4	2
10:00–12:00	–	4

Light intensity was directly sampled between consecutive hauls. The photometer (LI-193SA Spherical Quantum Sensor; LI-COR) was mounted on a conductivity, temperature and depth sensor (CTD), and it measured the light intensity as the photon fluency rate (PFR, $\mu\text{E m}^{-2} \text{s}^{-1}$) within the photosynthetic active radiation (PAR) range of 400 to 700 nm.

Activity rhythm determination. Fluctuations in the quantity of collected animals were used as a proxy of their behavioural rhythms when considering these as the product of their movement into and out of the sampling window. For each haul, all individuals of both *Lophius* spp. were counted. Because both species present overall similar morphological characteristics and colorations, animals were distinguished by the colour of the peritoneum and by the number of rays in the second dorsal fin (Caruso 1986): black peritoneum and 9 to 10 rays in *L. budegassa*; white peritoneum and 11 to 12 rays in *L. piscatorius*.

Time series of catches for each species were then elaborated by estimating the animals' bottom surface density variations over the 24 h cycle. A density value per haul was obtained by dividing the number of sampled animals by the swept area (km^2), as estimated by SCANMAR and GPS measures (Sparre et al. 1989).

Waveform analysis was conducted on time series of surface density and PFR estimates to assess the phase of the activity rhythms (i.e. the timing of peaks) in relation to the day–night cycle. A standard period of 24 h was subdivided into 2 h time intervals (Aguzzi et al. 2003a,b). All densities and PFR values computed from samplings that took place within a given 2 h time interval were averaged to obtain the 24 h con-

sensus waveform (see Table 1 for the number of hauls and PFR readings pooled in each 2 h time interval). The phase of the time series in surface density estimates was identified in each waveform plot by computing a daily mean as a threshold. This threshold was obtained by re-averaging all mean waveform values together. The resulting threshold value was represented as a horizontal line in the plot. Surface density estimates above that threshold indicated the presence of a significant increase in catches (adapted from Hammond & Naylor 1977). Mean density and light intensity estimates were plotted together in relation to the time of sunset and sunrise at the latitude of the study area (Greenwich Meridian Time: 19:27 and 04:19 h on 22 June).

Periodicity in the time series of density data was screened between 600 min (10 h) and 1800 min (30 h) using a chi-square periodogram analysis ('El temps'; A. Díez-Noguera pers. comm.). The periodogram analysis requires a series of data obtained at a constant time interval (for details on the procedure, see Hammond & Naylor 1977). This condition is difficult to satisfy in trawl-based sampling studies. Gaps in the time series were therefore replaced by the values obtained from waveforms at the corresponding 2 h time intervals (Aguzzi et al. 2003a,b). In the periodograms, the highest significant ($p < 0.001$) peak represented the maximum percentage of the total data variance fitted by the corresponding periodicity. The peak value was chosen for period attribution of the analysed time series.

Morphometric measurements. Morphological measurements of the sensory organs were conducted on 274 *Lophius budegassa* and 137 *L. piscatorius*, ranging from 4.5 to 80 and 15 to 97.5 cm in total length (TL), respectively. Otolith sagittae were removed, mechanically cleaned (deprived of tissue debris with tweezers), dried at room temperature and finally weighed to the nearest 0.01 mg with a balance with a sensitivity of 0.001 mg. Otolith weight was used as a measure of size because in lophiids, otolith shape and area obtained by orthogonal projection are highly variable (Tuset et al. 2008). The eyes were enucleated, and their diameters were measured with callipers to the nearest 0.01 mm. The corneas were excised to extract the lenses, which were then measured using callipers to the nearest 0.01 mm. The vitreous was removed and the eye cups were fixed in a mixture of paraformaldehyde (2%) and gluteraldehyde (2%) in phosphate buffer (0.1 M). The caudal portion of the fixed retina from one small (*L. budegassa* of 14 cm TL and *L. piscatorius* of 15 cm TL) and one large individual of both species (*L. budegassa* of 66 cm TL and *L. piscatorius* of 77 cm TL) were embedded in resin (Technovit 7.0) and sectioned in the transverse and tangential planes.

Since the studied anglerfish stretch their distribution from shallow water to the deep mesopelagic zone, their visual systems encounter different light conditions; therefore, the optical sensitivity, i.e. the capability of seeing well in dim light conditions, was calculated both employing the Land (1981) sensitivity equation for monochromatic light at the preferred wavelength of the photoreceptor

$$S = (\pi/4)^2 A^2(d/f)^2(1 - e^{-kl}) \quad (1)$$

found in deep environments and the Warrant & Nilsson (1998) equation for white light

$$S = (\pi/4)^2 A^2(d/f)^2[kl/(2.3 + kl)] \quad (2)$$

visible in shallow waters. In these equations, sensitivity (S) is related to the diameter of the eye's aperture (A), the photoreceptor diameter (d), the focal length (f), the absorption coefficient of the photoreceptor (k) and photoreceptor length (l). In the present study, the eye's aperture, i.e. the diameter of the pupil, was considered equivalent to the lens diameter (Fernald 1990). Although these species show a pupil response, and hence the maximum pupil aperture should be employed in the sensitivity formulae, the analysed individuals were caught with diurnal commercial trawls and therefore the pupil was partially closed. The focal length (f), i.e. the distance from the centre of the lens to the retina, was calculated from Matthiessen's ratio, where $f = 2.55r$ and r is the radius of the lens. The absorption coefficient of monochromatic and white light is unknown in these species; therefore, the average k ($0.035 \mu\text{m}^{-1}$) for bony fish was employed (Warrant & Nilsson 1998). From f , the inter-receptor angle $\Delta\phi$, i.e. the feature of the eye's resolving power, can be calculated in accordance with Land & Nilsson (2002) where $\Delta\phi = s/f = L/(nf)$ and s is the photoreceptor spacing. The photoreceptor spacing is the inverse of the visual cell number (n) counted in the retinal linear transect L (3 linear $100 \mu\text{m}$ transects in the present study). Finally, the spatial frequency $1/2\Delta\phi$, a way of representing the optical resolution at the photoreceptor level, is obtained.

A comparative analysis of the relative increase of otolith weight and eye and lens diameters with respect to body length was performed for both species. Although the total size interval was 4.5 to 97.5 cm for both species, the range over which data on eye and lens diameter were available was 20 to 80 cm. To determine whether eye diameter and otolith weight presented isometric or allometric growth patterns, a comparison of the rate of their increase was performed according to different size classes. A t -test for the slopes

using normalised data (i.e. logarithmically transformed) was employed to test the significance of the differences between pairs of curves (Zar 1984). The presence of a significant relationship was assessed at a significance level of $p < 0.05$.

RESULTS

Activity rhythms

In total, 3810 individuals of *Lophius budegassa* and 2170 individuals of *L. piscatorius* were collected from our temporally scheduled trawling survey. Both species showed different temporal patterns in their catchability in relation to the measured light intensity cycle (Fig. 1). The outputs of a 24 h waveform analysis on the time series of surface density estimates and PFR (i.e. light intensity) data at depths of 100 to 110 m are shown in Fig. 2.

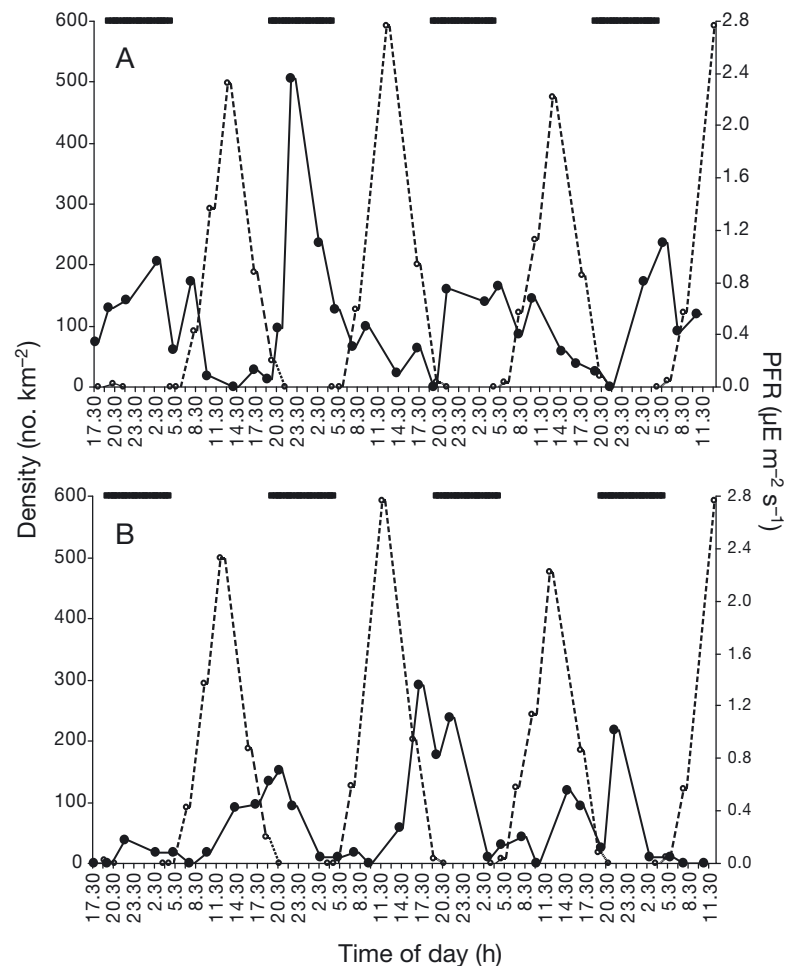


Fig. 1. *Lophius budegassa* and *L. piscatorius*. Density (no. km^{-2} ; continuous lines) estimates of (A) *L. budegassa* and (B) *L. piscatorius* in relation to the light intensity cycles (i.e. photon fluency rate, PFR, in $\mu\text{E m}^{-2}\text{s}^{-1}$; dashed line) as recorded during 4 d of fishing activity at 100 m around the summer solstice (i.e. June). Black top bars indicate the night duration

Lophius budegassa chiefly presented a nocturnal catch pattern. A significant increase in catches occurred over a temporal amplitude that started between 20:00 and 22:00 h and ended between 04:00 and 06:00 h. A decrease in catches occurred for PFR values above $0.93 \mu\text{E m}^{-2} \text{s}^{-1}$.

Lophius piscatorius showed a significant increase in catches (i.e. values above the daily mean) at daytime. The resulting temporal amplitude of the catch peak spanned from 12:00–14:00 to 22:00–00:00 h. Increased catches were observed for PFR values above $1.25 \mu\text{E m}^{-2} \text{s}^{-1}$. Catches decreased within a few hours after the onset of darkness, and the onset of this decrement occurred for PFR values below $0.87 \mu\text{E m}^{-2} \text{s}^{-1}$.

Both species showed a significant ($p < 0.001$) diel periodicity very close to a 24 h cycle (Fig. 3). *Lophius budegassa* presented a significant increase in catches that repeated itself every 1430 min, which is equal to

23 h and 50 min. A similar temporal pattern was detected for *L. piscatorius* with a period of 1455 min, which is equal to 24 h and 15 min, in catch fluctuations.

Morphometric relationships in sensory organs

Otolith weight increased progressively during fish growth, ranging from 2.7 to 102.6 mg in *Lophius piscatorius* and from 0.6 to 107.3 mg in *L. budegassa* (Fig. 4). For equivalent fish lengths, *L. budegassa* had 50% heavier otoliths than *L. piscatorius*, and with increasing length, the difference between the species was observed to be fairly constant. A significant difference between the curves depicting this relationship for these 2 species was observed ($p < 0.05$).

During fish growth, progressive eye and lens enlargement was observed in both anglerfish species (Fig. 5). However, a shift in their trends was observed during growth. In fact, the eye diameters of small *Lophius budegassa* (TL < 50 cm) were larger than those of *L. piscatorius* of comparable size, with a mean value (\pm SD) of 20.7 ± 3.7 mm ($n = 82$) in the former group and 17.5 ± 3.6 mm ($n = 37$) in the latter. In larger individuals (TL \geq 50 cm), the mean eye diameters (\pm SD) of *L. budegassa* measured 26.8 ± 2.8 mm ($n = 24$), and those of *L. piscatorius* measured 29.8 ± 2.2 mm ($n = 22$). When the eye diameters of small individuals of both species were plotted separately from the diameters of large individuals, significant differences were observed in both cases ($p < 0.05$).

A similar trend was observed for lens diameter, although the shift was recorded at 58 cm. The mean lens diameter (\pm SD) of small individuals of *Lophius budegassa* and *L. piscatorius* measured 7.9 ± 1.5 mm ($n = 59$) and 6.4 ± 1.4 mm ($n = 37$), respectively, while large individuals had lenses of 9.9 ± 1.0 mm ($n = 21$) and 10.7 ± 0.8 mm ($n = 19$), respectively. Although significant differences ($p < 0.05$) between the slopes of lens diameter were observed over the total size range of the individuals examined, when the 2 size groups were plotted separately, no significant differences were found ($p > 0.05$).

The anglerfishes showed duplex retinas where rods and single and double cones were visible. Single cones were the predominant cone type, and their density and the size of their outer segments were employed to calculate the spatial frequency and the optical sensitivity, respectively. Although a

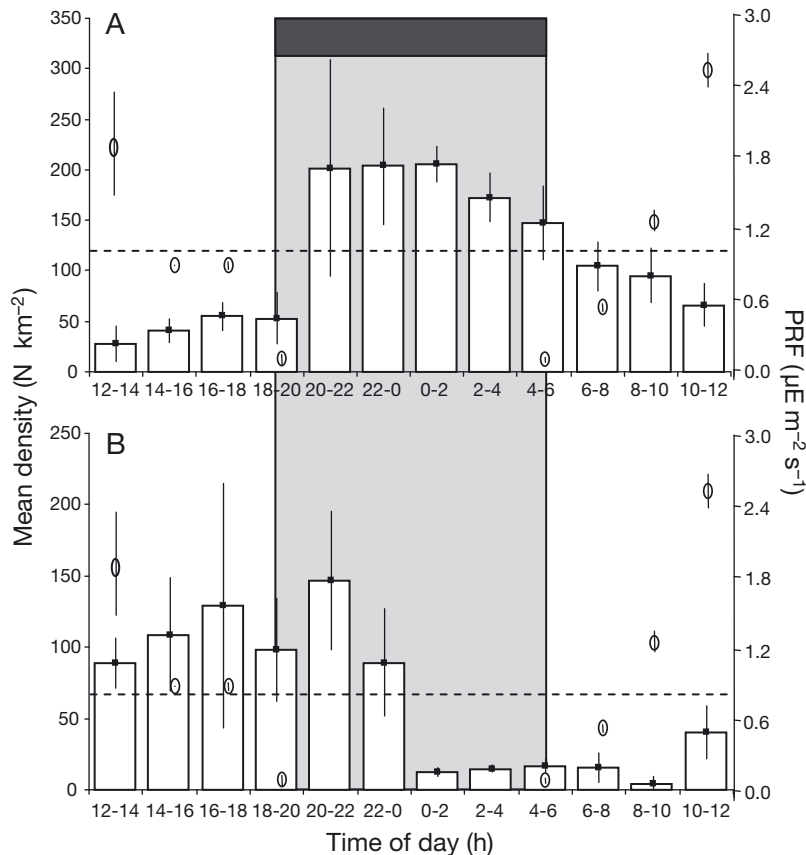


Fig. 2. *Lophius budegassa* and *L. piscatorius*. Waveform analysis outputs from time series of catches depicting mean estimates in abundance (no. km^{-2} , bars) of (A) *L. budegassa* and (B) *L. piscatorius* and light intensity measures (photon fluency rate, PFR, circles) as recorded during 4 d at 100 to 110 m depth around the summer solstice (22 June to 3 July 2000). The recorded light intensity ranged between 0.0038 and $2.77 \mu\text{E m}^{-2} \text{s}^{-1}$. The vertical shaded area with the dark grey bar on the top indicates the night duration. Daily means (horizontal dashed lines as computed by averaging all waveform values; no. km^{-2}) are 114 for *L. budegassa* and 64 for *L. piscatorius*

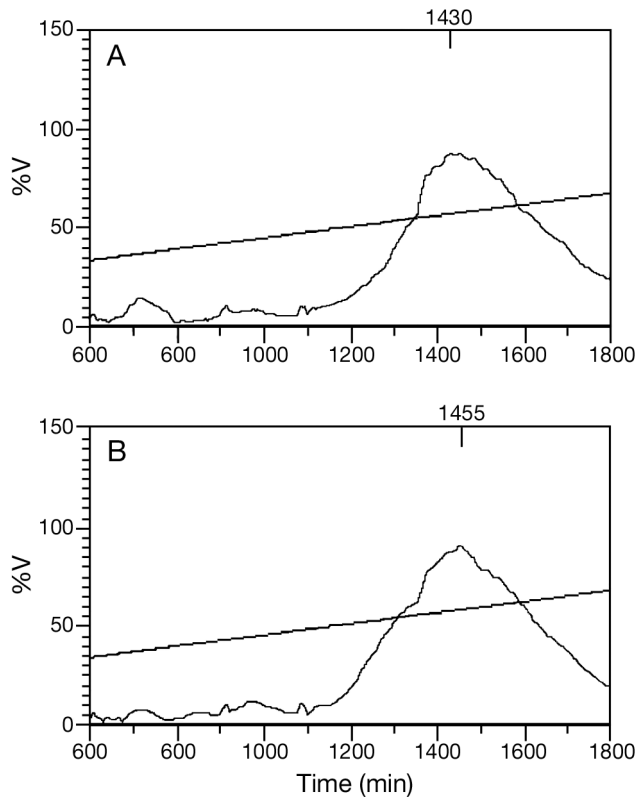


Fig. 3. *Lophius budegassa* and *L. piscatorius*. Outputs of periodogram analysis conducted on the time series of catches of (A) *L. budegassa* and (B) *L. piscatorius* as recorded during 4 d at 100 to 110 m depth around the summer solstice (22 June to 3 July 2000). Periodogram units (%V) refer to the percentage of variance explained by fitting to the data set of modelled harmonics of increasing periodicity. The straight sloping line in each panel indicates the significance threshold for periodicity determination ($p < 0.001$)

more accurate method for calculating sensitivity would be to use rod size, the use of the single cones is partially due to the fact that the rod diameter was difficult to measure accurately in the retina of the analysed individuals. In addition, since a large number of single cones was observed in these species, the role of these photoreceptors in improving sensitivity is highly probable. The measurements taken from the anglerfish eyes are sum-

marised in Table 2. Using obtained data and the sensitivity equations, the eye of the anglerfish showed an increase in sensitivity with growth both to white and monochromatic light. While a small increase in sensitivity was observed for *Lophius piscatorius*, in *L. budegassa* the sensitivity values of the large individual were triple those of the small individual for both types of light (Table 2). These increases seem to be attributable to the considerable enlargement of the photoreceptor diameter during growth. The retinal receptor spacing and the relative spatial frequency were similar in the 2 species (Table 2).

Because interspecific differences of a sensory organ cannot be interpreted in isolation from other sensory systems, otolith weight and eye diameter were compared, and the allometric coefficient values indicated that in *Lophius budegassa*, otolith weight increased more than eye size, while an opposite trend was observed for *L. piscatorius* (Fig. 6). A comparison of the slopes showed significant ($p < 0.05$) differences between the species.

DISCUSSION

Temporal segregation

The black and white anglerfishes coexist on the Mediterranean shelf, but their relative abundance was observed to vary on a diel scale, with *Lophius budegassa* more abundant at night and *L. piscatorius* more abundant during the day. In general, species sharing important traits related to their ecological niches can coexist in the same area due to temporal segregation in the phase of their maximum behavioural activity (Carothers & Jaksic 1984). Although trawling is an active method of sampling that collects all animals down to the seabed independently of their level of behavioural activation, rhythmic catch variations in trawl hauling at a certain location can be considered to be the product of rhythmic displacements of marine populations into and out of the sampling window

Table 2. *Lophius piscatorius* and *L. budegassa*. Morphological parameters taken from 1 ind. for each size, employed to calculate sensitivity for the preferred wavelength (λ_{\max}) and white light and for the spatial frequency in anglerfish

Species	Size (cm)	Lens diameter (mm)	Focal length (mm)	Cone length (μm)	Cone diameter (μm)	Sensitivity white ($\mu\text{m}^2 \text{sr}$)	Sensitivity (λ_{\max}) ($\mu\text{m}^2 \text{sr}$)	Inter receptor angle (degrees)	Spatial frequency (cycle per degree)
<i>L. budegassa</i>	14	3.88	4.95	9.7	4.12	0.83	1.85	0.14	3.56
<i>L. budegassa</i>	77	12.05	15.36	12.85	6.44	2.57	5.7	0.08	6.15
<i>L. piscatorius</i>	15	3.78	4.82	8.4	3.53	0.54	1.2	0.14	3.66
<i>L. piscatorius</i>	63	10.91	13.91	12.96	4.01	1.01	2.2	0.09	5.57

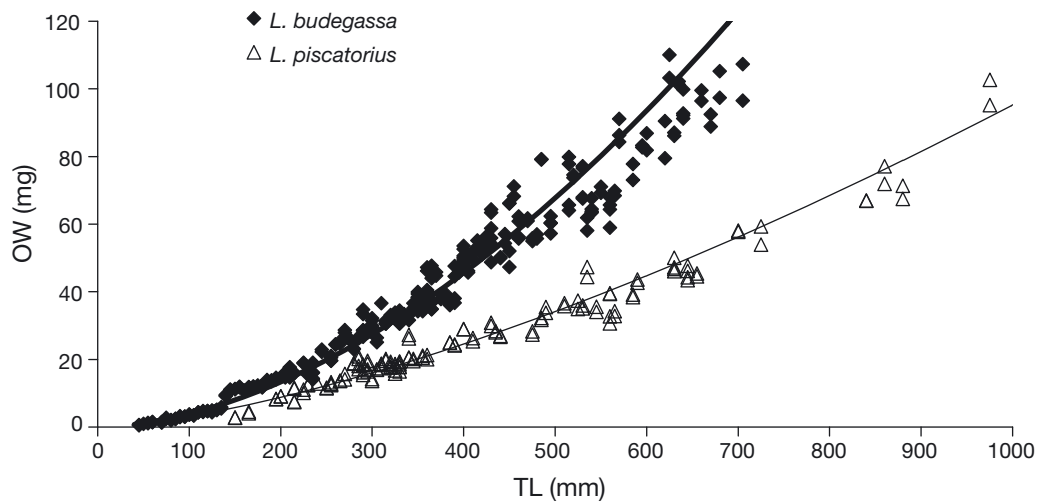


Fig. 4. *Lophius budegassa* and *L. piscatorius*. Relationship between otolith weight (OW) and total length (TL): *L. budegassa* ($OW = 0.0011 TL^{1.7725}$; $r^2 = 0.9813$; $n = 274$) and *L. piscatorius* ($OW = 0.0035 TL^{1.4802}$; $r^2 = 0.9417$; $n = 137$)

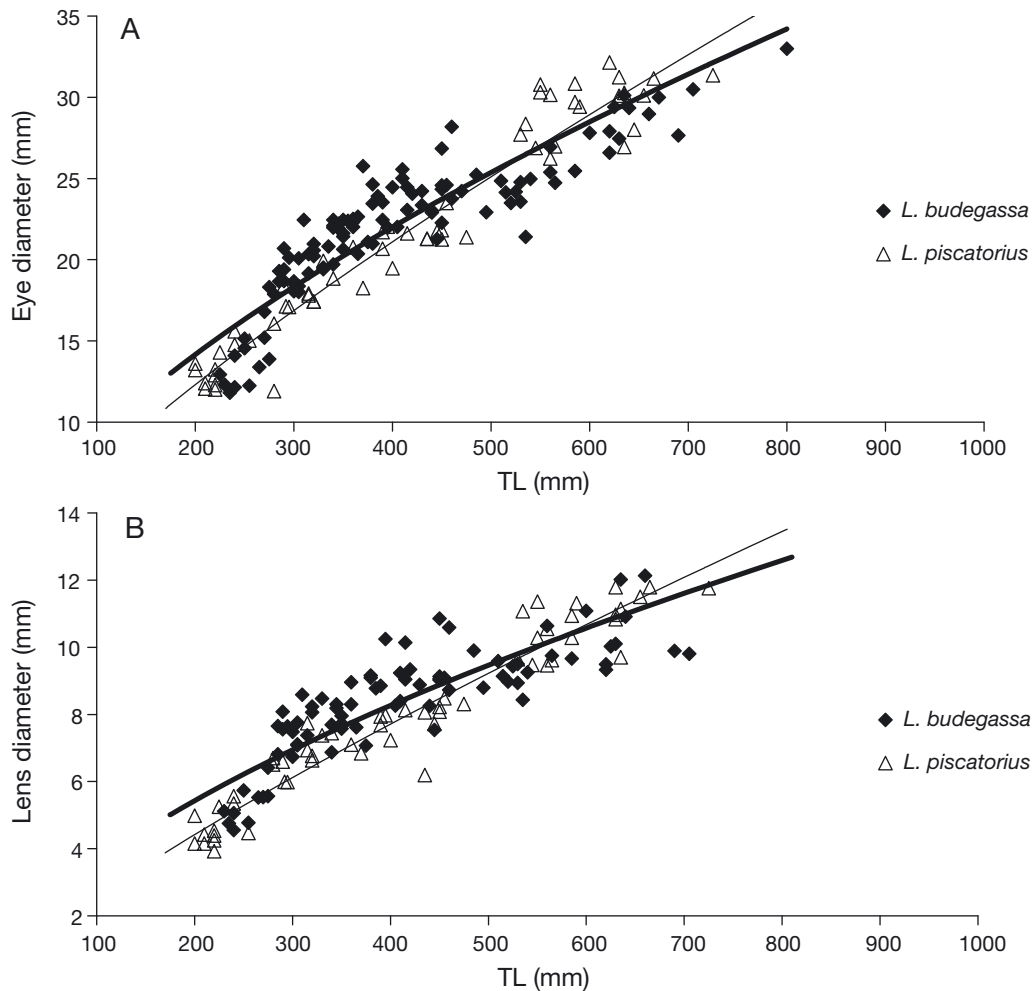


Fig. 5. *Lophius budegassa* and *L. piscatorius*. (A) Relationship between eye diameter and total length (TL): *L. budegassa* (eye diameter = $0.4882 TL^{0.6357}$; $r^2 = 0.7745$; $n = 106$) and *L. piscatorius* (eye diameter = $0.1998 TL^{0.7778}$; $r^2 = 0.9472$; $n = 59$). (B) Relationship between lens diameter and TL: *L. budegassa* (lens diameter = $0.2186 TL^{0.6063}$; $r^2 = 0.7138$; $n = 80$) and *L. piscatorius* (lens diameter = $0.0628 TL^{0.8027}$; $r^2 = 0.9231$; $n = 56$)

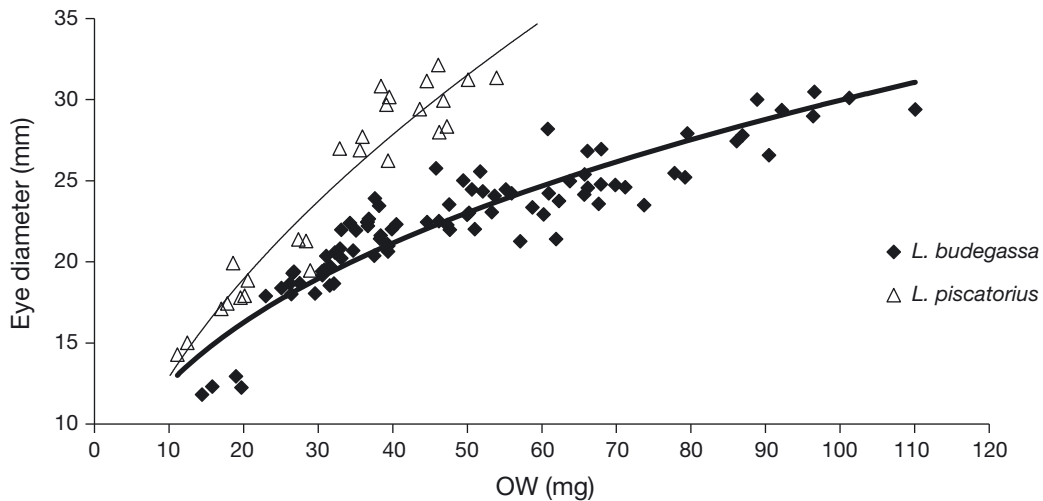


Fig. 6. *Lophius budegassa* and *L. piscatorius*. Relationship between eye diameter and otolith weight (OW): *L. budegassa* (eye diameter = $5.2128 \text{ OW}^{0.3798}$; $r^2 = 0.8215$; $n = 87$) and *L. piscatorius* (eye diameter = $3.5919 \text{ OW}^{0.5551}$; $r^2 = 0.9289$; $n = 26$). Total lengths of individuals ranged from 22.5 to 80 cm

(reviewed by Aguzzi & Company 2010). When that sampling window consistently occurs at a certain depth and location, catchability rhythms can be precisely studied in relation to the light intensity fluctuation at the site. Rhythmic population movements occur over the day–night cycle in several different ways: within the water column (i.e. vertical–bentholeagic), in and out from the substrate (i.e. endobenthic), or at the benthic boundary layer, along bathymetric gradients (i.e. horizontal–nektobenthic). Anglerfishes do not burrow and rarely display vertical migration (Hislop et al. 2000), but they do possess some swimming capability (Velasco et al. 2008). The flattened morphology typical of demersal fish (Caruso 1986) allows us to assume that the activity rhythms of these species occur as nektobentic displacements. In fact, tagged and recaptured *L. piscatorius* demonstrated in- and offshore movements in the northeastern Atlantic (Laurenson et al. 2005, Landa et al. 2008). Therefore, these species may rhythmically swim between the shelf and the slope, with the main part of the population moving into shallow water areas during 2 opposite times in the day–night cycle.

Although prey species are known to shift their activity patterns to avoid predation (Fenn & Macdonald 1995, Fraser et al. 2004), it is also common to observe a similar phenomenon among predators that compete for the same prey (Schoener 1986, Soria-Barreto & Rodiles-Hernández 2008). While this competition is reduced for species of mixed predatory and scavenging activity, pressure is likely to be stronger for more specialised piscivores such as anglerfish. Both *Lophius piscatorius* and *L. budegassa* generally mainly prey on whiting *Micromesistius poutassou*, cod *Gadus morhua* and other gadids (Crozier 1985, Laurenson & Priede

2005, Preciado et al. 2006, Negzaoui-Garali et al. 2008). Because they show similar food preferences and compete for the same available resources, their temporal segregation seems to occur to avoid interference competition.

Sensory specialisation

The observed differences in the timing of maximum activity of *Lophius piscatorius* and *L. budegassa* were consistent with differences in their otolith weight and eye size. Otoliths represent an important part of the fish's hearing apparatus, and they are an indicator of how the teleostean inner ear works (Platt & Popper 1981, Paxton 2000). The inner ear in species that live in poor light environments, such as sea slope-dwelling fishes (Paxton 2000, Lombarte & Cruz 2007), nocturnal species, such as holocentrids (Smale et al. 1995), and cave-adapted species (Schulz-Mirbach et al. 2008), are characterised by relatively large otolith sagittae. Furthermore, sound-producing species, which are specialised in acoustic communication, such as sciaenids, are also characterised by bigger otoliths than species that are not sound producers (Cruz & Lombarte 2004). The heavier otoliths found in *L. budegassa* confirm this as a preferentially nocturnal species compared to *L. piscatorius*. In fact, species that are predominantly active at night or that dwell in deep water have been found to have large (and therefore heavy) otoliths, indicating that their behaviour is mostly acoustically driven, which is a characteristic usually found where light is insufficient to support visual communication (Lychakov & Rebane 2000, Paxton 2000, Parmentier et al. 2001, Lombarte & Cruz 2007, Tuset et al. 2010).

However, the visual systems of many organisms have evolved to see well in dim light conditions by employing different optical strategies to enhance the perception of an image, both in terms of spatial resolution (by increasing the focal length as a consequence of enlarging the axial diameter of the eye) and sensitivity (improving photon capture, which is mostly achieved by having a large pupil; Warrant 1999). Although the major adaptation for improving sensitivity is having a low F-number (focal length divided by the pupil diameter), most fish have an F-number close to 1 as their optics adhere to Matthiessen's ratio. Therefore, large eyes may reflect a need for increasing spatial resolution (Land & Nilsson 2002). Because better resolution and sensitivity are achieved with bigger eyes, evolution has benefited animals that must perform considerable visual tasks with large eyes. Although there are many exceptions, epipelagic fishes with nocturnal activity or species inhabiting mesopelagic waters tend to have bigger eyes than diurnal shallow water species (Marshall 1971, Warrant & Locket 2004, Pulcini et al. 2008, Antonucci et al. 2009). In this context, the data we present here fit well with observations of the eye design in other diurnal and nocturnal teleosts. In fact, *Lophius piscatorius*, the species exhibiting a preference for diurnal activity, had a significant smaller eye and lens than *L. budegassa*, the species captured mainly at night. The preference for diurnal activity of *L. piscatorius* was clearly reflected in the retinal anatomy of this species, especially in the cone diameter that was smaller than that of *L. budegassa*. This characteristic was responsible for the low optical sensitivity observed in this species. Instead, *L. budegassa* showed a sensitivity higher than 1, typical of crepuscular or mid-water species (Land & Nilsson 2002). Optical sensitivity increased greatly with size in this species, confirming the possibility of seeing well in dim light. In fact, a similar sensitivity of $5.7 \mu\text{m}^2 \text{sr}$ was found in the blue marlin *Makaira nigricans*, a species whose eyes are adapted to the severe change in light intensity that this species encounters during its diving that may stretch several hundred metres (Fritsches et al. 2003).

The interspecific comparison of the eye size of *Lophius piscatorius* and *L. budegassa* was reversed when *L. piscatorius* reached 50 to 55 cm TL, and above this threshold, *L. piscatorius* showed significantly larger eyes than *L. budegassa*. This trend reversal probably reflects important changes in the life history of *L. piscatorius*. Even though there are uncertainties about several key events during the life history of *L. piscatorius*, many authors agree that this species spawns in deep or very deep water (>1000 m) (reviewed by Hislop et al. 2001). At these depths, mature males of 50 to 60 cm are commonly observed

(Duarte et al. 2001), whereas females of *L. piscatorius* reach their first maturity at a larger size. In addition, changes in the feeding behaviour of *L. piscatorius* have also been observed at this size (Laurenson & Priede 2005). The change in the visual scenery with depth, from being extended in the epipelagic zone to semi-extended in the mesopelagic zone and even to point-source light (bioluminescence) in the bathypelagic zone, could be one of the driving forces in the evolution of larger eyes in large *L. piscatorius*. Instead, the relatively low resolution obtained for this species is quite surprising, as larger fish with larger eyes usually have higher resolving power (Collin & Pettigrew 1989, Shand 1997, Bozzano & Catalán 2002). Probably, for a species living on the bottom where the water is often full of suspended particles, the environment acts as a constraint for increasing acuity. Similarly, an unexpected low resolution was also observed in the blue marlin, a species with a huge eye size (Fritsches et al. 2003).

Although interspecific temporal segregation is one of the mechanisms employed by different fish species to allow their coexistence, there is still little information on how it occurs and its adaptive value. In other groups, such as birds, adaptations to night vision include large eye size, and it has been demonstrated that birds with large eyes become active earlier (at low light intensity) than birds with small eyes (Thomas et al. 2002). In fishes, spatial segregation is a more common mechanism of coexistence, and concomitant spatial segregation in activity rhythms and different eye sizes has been observed in several ecologically equivalent and sympatric species. In cichlids of African lakes, vision greatly contributes to their habitat segregation and even to their speciation (Seehausen et al. 2008, Hofmann et al. 2009). In this family, 2 highly morphologically similar species, *Haplochromis hiatus* and *H. iris*, prey on similar food items and inhabit different depths. Accordingly, the deeper water species (*H. iris*) has larger eyes compared to the shallower species (van der Meer & Anker 1983). However, eye size and visual capability in fish are likely to be determined by a number of different selection pressures and constraints, and therefore, the existence of large eyes does not necessarily mean that they have evolved only to see better in dim light conditions. For example, fast swimming also requires good vision, and hence, large eyes are also found in swordfish and tuna. The association of evolutionary changes in eye size with different behavioural and ecological traits in *Lophius* spp. needs to be further investigated by morphological and physiological analyses to trace the history of changes in the relationship between morphological characters and activity.

However, sensory constraints appear to be an important feature enhancing partitioning in time by enabling closely related species such as *Lophius piscatorius* and *L. budegassa* to inhabit the same area at different times of the day. Although these species rely on a combination of sensory stimuli to perform their daily tasks, under the paradigm of compensatory specialisation, their sensory systems experience high interspecific pressure that may lead to different diurnal or a nocturnal behaviour.

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