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Ontogeny of photophore pattern in the velvet belly lantern shark, *Etmopterus spinax*

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Abstract

Bioluminescence is known to be of great ecological importance to a luminous organism but extremely few studies investigate the ontogeny of luminous capabilities. The photogenic pattern of the velvet belly lantern shark *Etmopterus spinax* was investigated over ontogeny (14.0–52.5 cm total length) to determine the scaling of the surface area and the photophore density of different luminous zones as well as the ecological consequences of ontogenetic variations in bioluminescence efficiency. According to the luminous zone considered, different scaling patterns were found for the surface areas while the photophore densities of all zones scale with negative allometry, even though photophore insertion occurs. No sexual differences in these relationships were found. Luminous zones can be placed in two morphologically different groups: the "coverage" and the "isolated" zones. While counter-illumination is certainly the function of the former, the latter are probably involved in intraspecific behaviours. Due to the discrepancy between luminous capabilities of these two luminous zone categories, there is an ontogenetic increase in the luminescence heterogeneity of the luminous pattern as it was shown by luminescence modelling and confirmed by direct observations of spontaneous luminescence in living sharks. This heterogeneity certainly represents a trade-off between an efficient ventral camouflage and a strong identification tool for intraspecific behaviours such as coordinate hunting, which would be particularly useful when *E. spinax* become fish eaters (>19 cm total length), and for sexual recognition in mature individuals.

Keywords: Elasmobranch; Etmopteridae; Bioluminescence; Luminous zones; Counter-illumination

Introduction

Bioluminescence is a widespread phenomenon in the deep-sea environment where many species from bacteria to fishes emit light for numerous purposes including predation, defence and reproduction (Buck, 1978; Wilson and Hastings, 1998; Herring, 2007). While the majority of deep-sea Osteichthyes (circa 70%) are luminous, only a small fraction (circa 6%) of deep-sea Chondrichthyes is endowed with this capability (Harvey, 1952; Herring and Morin, 1978; Compagno et al., 2004). This led some authors to consider this amazing property a burden on these fishes (Reif, 1985). Even though it is absent in Holocephali (chimaeras), the luminescence competence appeared at least three times

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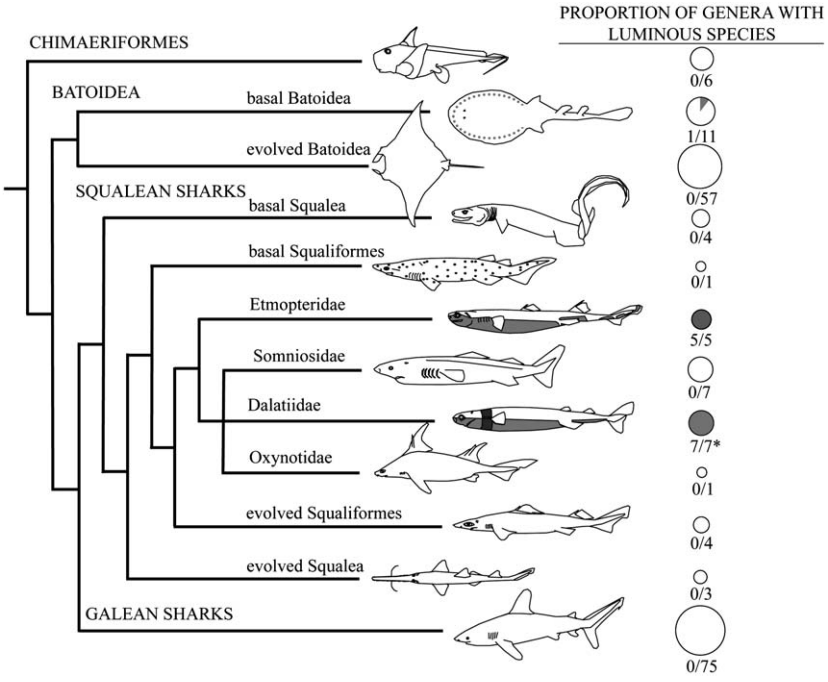

Fig. 1. Cladogram indicating the occurrence of bioluminescence in the cartilaginous fishes (grey shade represents photogenic tissues). Circles to the right indicate the proportion of luminous genera within a given taxonomic grouping (shaded, luminous; white, non-luminous; Harvey, 1952; Hubbs et al., 1967; Compagno et al., 2004). Circle size is proportional to the total number of genera in a given taxonomic grouping. The typology of the cladogram is based on Shirai (1996) and was improved following Naylor et al. (2005). One dalatid genus (*Mollisquama*) shows pectoral glands supposed to be luminous but more information is needed to confirm the luminous status of this very rare species (only known from one individual; Compagno et al., 2004).

independently in cartilaginous fishes, since three different phylogenetic groups harbour luminous species (Harvey, 1952; Hubbs et al., 1967; Fig. 1).

Luminous sharks are from two families, the Etmopteridae and the Dalatiidae, with distinct differences in the structure and the arrangement of their photophores (i.e. photogenic organs) (Hubbs et al., 1967; Reif, 1985; Fig. 1). While the Dalatiidae have an exclusively ventral pattern of photophores probably used for counter-illumination, the Etmopteridae show complex, species-specific patterns with photophore concentrations on the ventral part, but also on the flanks, tail, and sometimes on the upper eyelid (Iwai, 1960; Reif, 1985; Last et al., 2002; Yano et al., 2003; Fig. 1). The function of these patterns is still unknown but it is thought that they could play multiple roles, e.g. in schooling and counter-illumination (Reif, 1985; Claes and Mallefet, 2008).

If we assume that the function of the etmopterid bioluminescence is profoundly linked to the arrangement of their light organs, and knowing that these organs attain their maximum size at birth (Claes and Mallefet, 2008), the question arises as to how these sharks manage to maintain the integrity of their luminous pattern during growth.

The velvet belly lantern shark, *Etmopterus spinax*, Linnaeus 1758, is a good model to investigate the effect of growth on bioluminescence capabilities in a shark, as it is abundant in all size classes in the East Atlantic and the Mediterranean Sea and can be easily caught and maintained in captivity for long periods of time (>1 week; Compagno et al., 2004; Neiva et al., 2006; Claes and Mallefet, 2008). The luminous pattern of this shark is composed of nine luminous zones, which appear sequentially during embryogenesis and are already functional before birth (Claes and Mallefet, 2008).

The objectives of this study were (i) to investigate how the luminous capabilities of *E. spinax* are maintained during growth, (ii) to test for a potential sexual dimorphism in bioluminescence, (iii) to model the luminous pattern of this shark, and (iv) to discuss the results in relation to the ecology of this species.

Materials and methods

Experimental animals

Free-swimming specimens of *E. spinax* of 14.0–52.5 cm total length (TL) were obtained during three field trips (February 2007, December 2007, and April 2008) in the Raunefjord (longlines and bottom trawling) as well as in the Lysefjord (bottom trawling) in Norway, and brought alive to the Hoyteknologisenteret in Bergen

where they were kept in a tank placed in a dark cold room (4 °C).

Maturity of individuals was determined macroscopically following the maturity scale of Coelho and Erzini (2007) and rating all those able to reproduce or that had already reproduced in the past as mature (Conrath, 2004; Coelho and Erzini, 2008a). Immature individuals were divided into two categories according to their feeding preference: planktivorous ≤ 19 cm TL and piscivorous > 19 cm TL (Klimpel et al., 2003). Mature individuals were divided according to sex. All animals were sacrificed by a blow on the head, according to the experimental protocol of Hoyteknologisenteret in Bergen.

Morphological analysis

Digital pictures of the ventral and lateral sides of the sharks were taken with a digital camera (Canon D20; Canon Inc., Tokyo, Japan). The surface areas of the nine luminous zones of each individual were measured using ImageJ (National Institutes of Health, Bethesda, MD, USA). Photophore densities were estimated by counting photophores present on standard ($0.25\,cm^2$) skin patches placed under a binocular microscope in an isotonic shark saline following the method of Claes and Mallefet (2008). Since the small size of the caudal zone prevents precise measurement of photophore density, we considered the density in this zone the same as in the infra-caudal zone, of which it is an extension. The total number of photophores present in a shark was obtained by multiplication of the surface area of each zone by its specific density.

Luminometry

Excised luminous skin patches were placed in small perspex chambers with 200 µl of isotonic shark saline. Skin patches were stimulated by injecting hydrogen peroxide into the chambers to a final concentration of 0.1 M using a micropipette (200 µl). The chambers were placed inside a luminometer (Berthold FB 12; Berthold, Pforzheim, Germany) with the skin patches' exterior surface facing the photo-detector. The luminescence was recorded on a laptop computer for 5 min after stimulation, and characterised using the maximum intensity of light emission (L_{max}, in megaquantas per second (Mq s^{-1})) standardised by surface area (cm^2).

Statistical analysis

To highlight the scaling relationship in the different variables investigated (luminous zone surface area, photophore density, photophore number), they were $\log_{10}$ transformed and linearly regressed against $\log_{10}$-transformed TL. Slopes obtained for these scaling relationships were compared with theoretical isometrical slopes (−2 for photophore density, 0 for photophore number, and 2 for luminous surface area). For luminous zone surface areas and photophore densities, slopes obtained independently for the two sexes were compared and if no difference was detected, the analysis was performed on all animals without sexual distinction. Differences between slopes were only considered significant if none of the values present in the 95% confidence interval of the first was encompassed by the 95% confidence interval of the second slope.

Linear regressions between mean L_{max} values and mean photophore densities from the different luminous zones were performed in each shark category to identify the maximum intensity of light emission from a single photophore (i.e. the slope of the regression). These analyses were performed after removal of significant outliers ($> 2\sigma$). Statistical analyses were performed using the software SAS (SAS Institute Inc., Cary, NC, USA).

Results

In total, fifty free-swimming sharks were collected and used in this study. Immature specimens were mainly caught by trawl at shallower depths than adult individuals, which were only obtained with longline (Table 1).

Table 1. Summary of data for specimens of *Etmopterus spinax* collected for this study.

	n	TL			Collection depth	Collection method	
		Minimum (cm)	Maximum (cm)	Mean (cm)	(m)	Trawl	Longline
Immatures							
Planktivorous	10	14.0	18.5	16.4 ± 0.5	60–180	10	0
Piscivorous	12	20.5	34.0	25.2 ± 1.4	60–250	12	3
Matures							
Males	10	31.5	43.5	38.0 ± 1.3	180–250	0	10
Females	18	38.7	52.5	44.8 ± 1.0	180–250	0	18

Table 2. Results of scaling analyses on $\log_{10}$-transformed luminous zone surface areas of *E. spinax*.

Luminous zone	n^a	Regression equation ($\log LZ_S = a \log TL + b$)		r^2	p-value
		Slope (a)[b] [a_M/a_F]	Intercept (b)		
Rostral	45	**1.34** [**1.28**±0.17/**1.38**±0.10]	−1.17	0.96	<0.0001
Ventral	45	**2.42** [**2.31**±0.17/**2.15**±0.12]	−2.02	0.98	<0.0001
Caudal	44	**1.43** [**1.52**±0.34/**1.39**±0.22]	−2.91	0.87	<0.0001
Infra-caudal	45	1.92 [2.06±0.24/**1.84**±0.14]	−2.83	0.96	<0.0001
Mandibular	45	**1.75** [1.85±0.16/**1.71**±0.10]	−2.22	0.98	<0.0001
Pectoral	45	1.93 [1.99±0.28/1.82±0.18]	−3.17	0.93	<0.0001
Pelvic	45	**2.36** [**2.36**±0.22/**2.37**±0.17]	−2.99	0.97	<0.0001
Lateral	44	2.08 [2.18±0.23/2.08±0.16]	−3.85	0.96	<0.0001
Infra-pelvic	42	**2.52** [2.18±0.23/**2.42**±0.26]	−2.73	0.94	<0.0001

a_M, slope obtained for males (mean±S.E.M.); a_F, slope obtained for females (mean±S.E.M.); LZ_S, luminous zone surface area.

[a]Number of sharks used, i.e. 20 males and 25 females except for caudal, lateral, and infra-pelvic zones for which some female values were not available for calculation.

[b]When no differences between a_M/a_F were found, analysis was done on all data giving one slope value. Bold values indicate slopes deviating significantly from isometry.

The luminous zone surface areas of male and female specimens of *E. spinax* showed similar scaling patterns (Table 2). The surface area of some zones (rostral, caudal, and mandibular) showed negative allometry, while others (ventral, pelvic, and infra-pelvic) showed a positive allometry over ontogeny (Table 2, Fig. 2). The surface area of the infra-caudal, pelvic, and lateral zones showed isometric growth (Table 2, Fig. 2).

The luminous zone photophore densities showed similar scaling patterns in both sexes (Table 3). In all zones, photophore density scaled with positive allometry relative to the total length of *E. spinax,* which means that new photophores are continuously produced during growth (Table 3, Fig. 3A). However, the production rate is too low to keep a constant photophore density throughout ontogeny (i.e. to have a slope equal to 0).

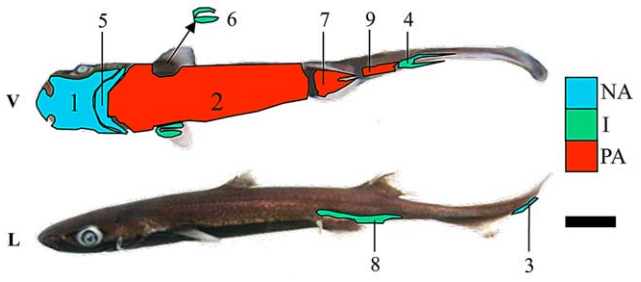

Fig. 2. Ventral (V) and lateral (L) views of a specimen of *E. spinax* (22 cm TL) showing how the surface area of the different luminous zones scales over ontogeny. I, isometry; NA, negative allometry; PA, positive allometry. 1 = rostral zone; 2 = ventral zone; 3 = caudal zone; 4 = infra-caudal zone; 5 = mandibular zone; 6 = pectoral zone; 7 = pelvic zone; 8 = lateral zone; 9 = infra-caudal zone. Scale bar = 2 cm. Results of scaling analyses of luminous zone surface areas are available in Table 2.

Not all zones decreased in density to the same degree; for example, there was a large decrease in the ventral zone, while the pectoral zone showed only a slight decrease (Table 3, Fig. 3A).

Similar relationships between total length and total number of photophores were found for males (slope = 1.2±0.46) and females (slope = 1.12±0.15), and the slope obtained for the regression on all specimens was significantly higher than 0, showing a significant ontogenetic increase in the total number of photophores (Fig. 3B). The total number of photophores ranged from 67,105 units (in a male of 15.5 cm TL) to 439,227 units (in a female of 52 cm TL).

In all categories, a significant relationship was found between mean peroxide-induced L_{max} and mean photophore densities (Table 4; Fig. 4).

A theoretical relative bioluminescence model for the luminous pattern of each category of *E. spinax* at different sizes (planktivorous immatures, piscivorous immatures, mature males, and mature females) was realised (Fig. 5A). This model assumes that the luminescence of a luminous zone is directly dependent on its photophore density. Photophore density of each zone was determined using the mean size of sharks from each category as input in the regression equations presented in Table 3. Zonal density was normalised to the photophore density of the ventral luminous zone and expressed relative to L_{max}. In this model, the heterogeneity of luminescence capabilities between luminous zones increases throughout ontogeny (Fig. 5A). Direct observation of long-lasting (>one hour) spontaneous luminescence from *E. spinax* confirmed the results obtained with the theoretical model (Fig. 5B). The two sexes showed dimorphism in the shape of their luminous pelvic zone (Fig. 5C).

Table 3. Results of scaling analyses on $\log_{10}$-transformed luminous zone photophore densities of *E. spinax*.

Luminous zone	n[a]	Regression equation ($\log PD = a \log TL + b$)		r^2	p-value
		Slope (a)[b] [a_M/a_F]	Intercept (b)		
Rostral	50	**−0.73** [**−0.74** ± 0.31/**−0.71** ± 0.25]	4.73	0.59	< 0.0001
Ventral	50	**−1.57** [**−1.31** ± 0.51/**−1.74** ± 0.33]	5.79	0.75	< 0.0001
Infra-caudal (and caudal)	50	**−0.69** [**−0.44** ± 0.37/**−0.82** ± 0.30]	4.89	0.45	< 0.0001
Mandibular	50	**−1.14** [**−1.07** ± 0.23/**−1.14** ± 0.20]	5.26	0.84	< 0.0001
Pectoral	46	**−0.25** [**−0.05** ± 0.27/**−0.39** ± 0.32]	4.27	0.12	0.0189
Pelvic	50	**−0.60** [**−0.47** ± 0.35/**−0.57** ± 0.29]	4.60	0.40	< 0.0001
Lateral	50	**−0.93** [**−0.99** ± 0.32/**−0.92** ± 0.26]	5.00	0.69	< 0.0001
Infra-pelvic	49	**−0.66** [**−0.22** ± 0.32/**−0.81** ± 0.32]	4.75	0.38	< 0.0001

a_M, slope obtained for males (mean ± S.E.M.); a_F, slope obtained for females (mean ± S.E.M.); PD, photophore density.

[a] Number of sharks used, i.e. 20 males and 30 females except for pectoral and infra-pelvic zones for which some female values were not available for calculation.

[b] When no differences between a_M/a_F were found, analysis was done on all data giving one slope value. Bold values indicate slope deviating significantly from isometry.

Discussion

The size range of the velvet belly lantern shark specimens used in this study (14.0–52.5 cm TL) encompasses more than 75% of the absolute size range observed in wild individuals (9.0–60.0 cm TL); our sample is therefore suitable for an ontogenetic study of photogenic structures in this luminous shark species (Borges, 2002; Compagno et al., 2004; Gennari and Scacco, 2007). Our fishing results confirm those of a study on Mediterranean individuals which shows that small specimens are mainly captured by trawl fishing while bigger specimens are principally caught with baited longline (Coelho and Erzini, 2008b). The total absence of mature individuals in trawl catches, which were realised at shallower depths (≤180 m) than longline catches (≥200 m), may indicate size-related depth stratification in fjord-inhabiting populations of Norwegian velvet belly lantern shark, as it is the case in the Mediterranean Sea, with immature individuals principally occurring in the upper part of the water column and mature individuals living in greater depths (Coelho and Erzini, 2007).

The bioluminescence modelling presented in this study is a first attempt to determine the functional morphology of the complex luminous pattern of a lantern shark. The validity of our approach is demonstrated by the fact that luminous pattern models obtained for the different shark categories are similar to the luminescent patterns observed in spontaneously glowing specimens of *E. spinax*.

Ontogeny of photogenic structures

The complex luminous patterns observed in Etmopteridae are often used for species determination as they are assumed to be species-specific and to stay identical over ontogeny (Reif, 1985; Springer and Burgess, 1985; Schofield and Burgess, 1997; Last et al., 2002). Recently, Claes and Mallefet (2008) showed variations in the luminous structures of *E. spinax* during embryogenesis. Our work demonstrates for the first time that the luminous pattern of *E. spinax* is not constant during growth in free-swimming specimens.

In *E. spinax*, as in other etmopterid sharks, the luminous pattern is formed by different luminous zones, which are aggregations of numerous tiny (<200 μm) photophores (Hubbs et al., 1967; Compagno et al., 2004; Claes and Mallefet, 2008). This explains why, in a lantern shark species, luminous pattern variations can occur at different levels: (i) the relative surface area covered by each luminous zone, (ii) the photophore density of the luminous zones, and (iii) the size of the photophores present in the luminous zones. Even if no ontogenetic differences occur at the third level (Claes and Mallefet, 2008), we demonstrate that growth-linked variations do occur at the two first levels, as different zones (rostral, ventral, caudal, mandibular, pelvic, and infra-pelvic zones) show an allometric growth of their surface area and all zones show a decrease in photophore density, in spite of the continuous insertion of new photophores during growth. This ontogenetic decrease in photophore density is probably due to a space conflict between growing placoid scales and photophores (which are epidermal organs; Reif, 1985; Raschi and Tabit, 1992).

Two morphologically distinct types of zones can be distinguished: (i) coverage zones (rostral, ventral, and mandibular), which represent circa 75% of the ventral surface of the shark and in which the photophore insertion rate is low; and (ii) isolated zones (caudal, infra-caudal, pectoral, pelvic, lateral, and infra-pelvic), which are well-defined zones located either ventrally,

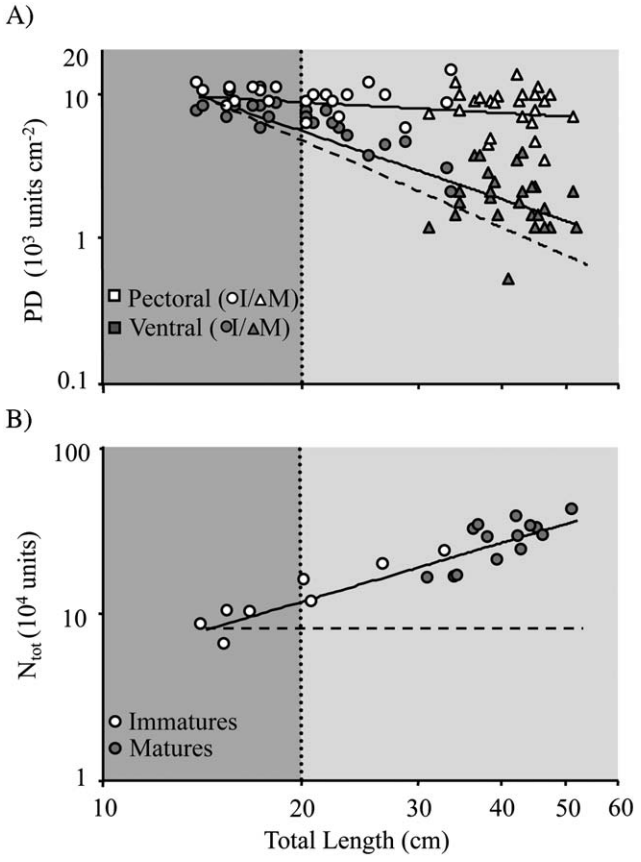

Fig. 3. (A) Photophore density of the ventral and the pectoral zones of *E. spinax* plotted versus total length on logarithmic axes. The dashed line indicates an isometric slope of −2, while the solid lines are regression lines of data (see Table 3 for details). Results of scaling analyses of luminous zone surface densities are available in Table 2. (B) Total number (N_{tot}) of photophores of *E. spinax* plotted versus total length on logarithmic axes. The solid line is the regression line for all specimens ($\log N_{tot} = 1.19 \log TL + 3.54$; $n = 22$; $r^2 = 0.85$; $P < 0.0001$), while the dashed line indicates an isometric slope of 0. Shading indicates the feeding transition occurring around 20 cm TL in this species; dark shading = planktivorous; light shading = piscivorous.

showing higher photophore insertion rates during ontogeny, or laterally. The observed morphological differences indicate different luminous capabilities of these two groups of zones, and hence different uses of luminescence.

Bioluminescence ecology

Numerous adaptative benefits have been suggested for bioluminescence, highlighting the perceived importance of this phenomenon in the ecology of luminous organisms (Harvey, 1952; Buck, 1978; Hastings, 1983). In teleost fishes, bioluminescence is thought to be used for different purposes: (i) interspecific ones such as camouflage by counter-illumination (and disruptive illumination), predator jamming, decoying (to approach prey), prey attraction (luminous lure), prey illumination and (ii) intraspecific ones such as sexual signalling and schooling (Clarke, 1963; Young and Roper, 1976; Young, 1977; Buck, 1978; McFall Ngai and Morin, 1991; Herring, 1985, 2000, 2007). Though often quite plausible, these hypotheses have never been tested due to the difficulty of working with luminous fishes (Buck, 1978; Wetherbee, 2000). Only camouflage by counter-illumination has been relatively well documented by behavioural experiments in the myctophid *Myctophum obtusirostrum* and in the juveniles of the midshipman fish *Porichthys notatus* (Young et al., 1980; Harper and Case, 1999).

Our work allows us to establish strong hypotheses about the ecology of bioluminescence in *E. spinax* and to propose that morphologically divergent luminous zones play different roles. At first sight, the coverage zones are designed for camouflage by counter-illumination. Indeed, having similar photophore densities, these zones form a large homogeneous luminescent surface emitting a long-lasting blue glow that is a good match for down-welling light, so the fish disappears from the sight of its predators (Harper and Case, 1999; Claes and

Table 4. Results of regression of photophore density against L_{max} for different *E. spinax* categories.

Shark group	n[a]	Regression equation ($L_{max} = a\,PD + b$)		r^2	p-value
		Slope (a)	Intercept (b)		
Immatures					
Planktivorous	10	62.39 ± 51.70	−365.56	0.59	0.0255
Piscivorous[b]	12	65.54 ± 27.04	−290.96	0.89	0.0016
Matures					
Males	10	19.84 ± 9.86	−37.64	0.80	0.0026
Females	17	15.97 ± 6.05	−26.52	0.87	0.0007

PD, photophore density in 1000 units cm^{-2}.
[a]Number of sharks used to determine the PD and the L_{max} of each luminous zone.
[b]In this group, the regression was performed without the infra-caudal zone which gave a very weak luminescence.

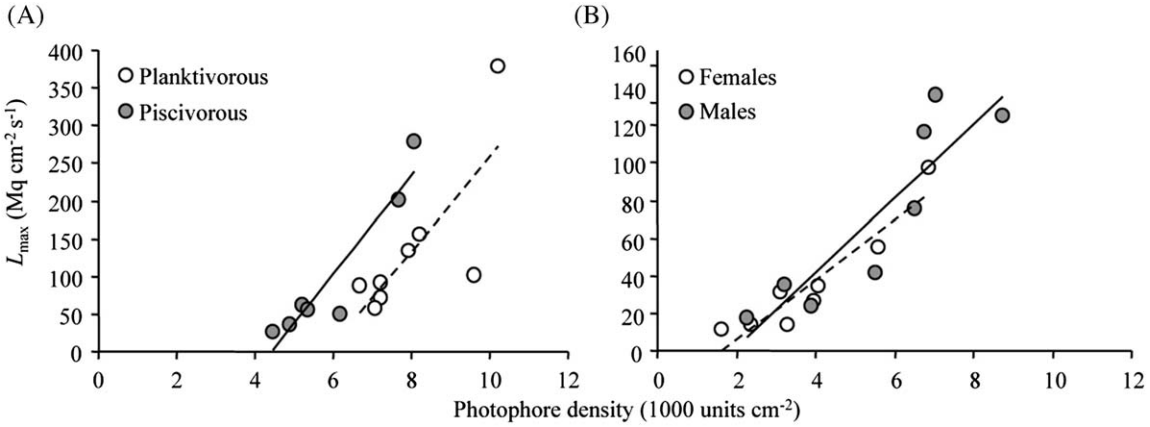

Fig. 4. L_{max} plotted versus photophore densities of the different luminous zones of (A) immature and (B) mature specimens of *E. spinax*. Solid and dashed lines represent regression lines of the data (dashed lines = open circles; solid lines = filled circles). Results of the regressions are available in Table 4.

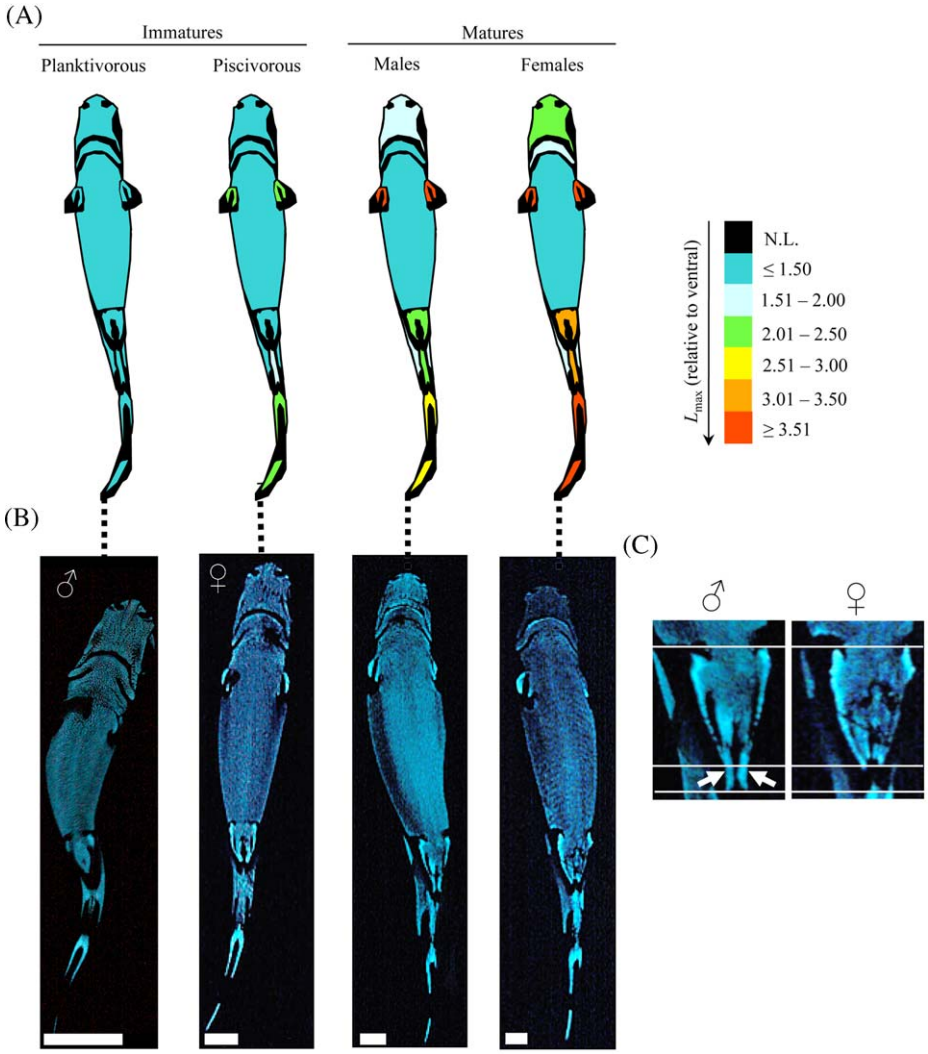

Fig. 5. (A) Luminous pattern modelling of the different *E. spinax* categories investigated in this study. In each shark category, the luminescence of the luminous zones is expressed in relation to the luminescence of the ventral zone. N.L. = non-luminous tissue. (B) Spontaneous luminescence of different specimens. Scale bars = 2 cm. Dashed lines link the pictures to the luminous pattern models to which they are supposed to correspond. (C) Close-up of pelvic areas of an adult male and an adult female specimen of *E. spinax*. Presence of a high photophore density in this body region allows the two sexes to be distinguished in the dark: only male sharks exhibit luminous pterygopods (white arrows), which are used for mating.

Mallefet, 2008). The positions of the isolated zones as well as their luminous characteristics render these zones more visible in adults, which favours intraspecific signalling. It is known that numerous non-luminous sharks probably live and reproduce in deep waters with the help of pheromonal signals (Wourms, 1977; Johnson and Nelson, 1978; Pratt and Carrier, 2001; Compagno et al., 2004). One cannot exclude, however, that the presence of brighter luminescence in the sexually dimorphic pelvic areas of mature specimens of *E. spinax* might facilitate sexual recognition, comparable to lantern fishes (Osteichthyes: Myctophidae) where sexual dimorphism of caudal photophores provides circumstantial evidence for sexual signalling (Herring, 2007). The high luminous capabilities of isolated zones could also serve as visual clues helping to coordinate swimming and/or hunting since it is known that teleost fishes and other shark species frequently use visual information for intraspecific behaviours (Myrberg, 1990; Grégoire and Chaté, 2004). Springer (1967) already suggested that luminescence in the green lantern shark (*Etmopterus virens*) is a schooling aid and that this species predates in groups. He based his hypothesis on the fact that the prey consumed by this shark is too big to be hunted and killed by a single shark. Based on the same observations, Macpherson (1980), and more recently Neiva et al. (2006), formulated the same hypothesis for *E. spinax*. Bright luminous markings on flanks, tail, and pectoral fins would give helpful visual clues for such coordinated movements in the darkness of the deep sea.

Shift in photophore pattern organisation

Our results show that the luminous capabilities of a zone are dependent on its photophore density. The low photophore insertion rates of coverage zones, and the constant size of photophores in free-swimming specimens of *E. spinax* (Claes and Mallefet, 2008) strongly suggest that small sharks of this species can counter-illuminate at shallower depths than bigger ones. This assumption is totally in accordance with recent findings of Coelho (2007), who showed that depth stratification occurs in Mediterranean *E. spinax*, with larger individuals occurring predominantly in deep waters, and females migrating vertically to give birth at shallower depths. A similar trend was observed in this study, with no mature specimens caught above a depth of 180 m and only few (13%) immature sharks found below this depth. Isolated zones, on the other hand, face a pressure to have their luminescence capabilities maintained over ontogeny. This is conclusive if we consider that these zones help sharks to dominate large prey such as large fishes and squids which only start to be part of the alimentation when the shark grows over 19 cm TL (Klimpel et al., 2003; Neiva et al., 2006), the size at which coverage and isolated luminous zones start to diverge in terms of luminous capabilities. The luminous pattern heterogeneity observed in fish-eating sharks would thus represent the answer to the trade-off faced by this shark that tries to keep an efficient ventral luminescent camouflage when faced with the need for a visual tool for intraspecific behaviours. Krill-eating sharks ($\leq$19 cm TL) do not need to increase the visibility of their isolated zone and have a homogeneous luminous pattern (with only slight differences in photophore density between luminous zones), which covers a very large part of the ventral surface area, thus giving a nearly perfect camouflage. This confirms the adaptative advantage of ventral counter-shading in young specimens of this species, as is the case for *Porichthys notatus*, a luminous teleost (Mensinger and Case, 1991; Claes and Mallefet, 2008).

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