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Phantom hunter of the fjords: Camouflage by counterillumination in a shark (*Etmopterus spinax*)

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ABSTRACT

Many midwater animals emit ventral light to hide their silhouette in the water column. This phenomenon known as counterillumination typically requires fine control over light emission since it needs a luminescence that closely matches the properties of downwelling light (intensity, angular distribution and wavelength). Here we provide evidence that, although lacking complex structures of counterilluminating animals, the deepwater luminescent shark *Etmopterus spinax* could, in Norwegian fjords, efficiently cloak its silhouette from downwelling ambient light to remain hidden from predator and prey. This represents the first experimentally tested function of luminescence in a shark and illustrates how evolution can take different routes to converge on identical complex behavior.

1. Introduction

Luminescent organisms are able to produce visible light via a chemical reaction. Luminescence's functions in animals are very diverse but mainly fall into intraspecific communication, predation help and predation avoidance (Buck, 1978). Many deepwater sharks (>50 species in 12 genera of two squalid families) harbor thousands of tiny (≈0.15 mm in diameter) epidermal photogenic organs called photophores (Compagno et al., 2004). Hypotheses regarding the function(s) of these organs have been proposed by different authors (Hubbs et al., 1967; Reif, 1985; Widder, 1998; Claes and Mallefet, 2008) but have never been tested due to the inherent difficulties of working with deepwater animals in good physiological condition.

The dense ventral photophore coverage and long-lasting glow of luminescent sharks has led to the idea that these fishes produce light to obliterate their silhouettes seen against the downwelling ambient light (Reif, 1985; Widder, 1998; Claes and Mallefet, 2008, 2009a). This camouflage mechanism, known as counterillumination, is documented for midwater organisms including crustaceans, mollusks (squids) and bony fishes that used it to virtually disappear in the water column (Clarke, 1963; Warner et al., 1979; Young et al., 1980). To achieve this illusion, the luminescence should however match the physical characteristics of the downwelling ambient light, i.e. intensity, angular distribution, and, if the viewer has a color vision, wavelength (Denton et al., 1985), which vary according to the radiating source (sun, moon, or stars) and the depth (Johnsen, 2003). Some counterilluminating animals have been shown to modulate the physical characteristics of their glow in response to these changes to remain cryptic in the water column (Warner et al., 1979; Young et al., 1980; Young and Mencher, 1980; Latz and Case, 1982; McFall-Ngai and Morin, 1991; Harper and Case, 1999; Jones and Nishiguchi, 2004). Light from the animal needs also to be emitted for extended period of time to make the camouflage efficient; flashes of light are not well adapted for counterillumination (Jones and Nishiguchi, 2004).

Shark photophores are intrinsic, i.e. they do not contain symbiotic luminous bacteria but instead an intrinsic luminous system. They are tiny and simple in structure, lacking the specialized reflectors and filters generally found in photophores of counterilluminating teleosts that allow them to control the angular distribution and wavelength of their luminescence (Hubbs et al., 1967; Denton et al., 1972, 1985). In addition, the luminescence spectrum of the cookie-cutter shark *Isistius brasiliensis* (the only available spectrum from the luminescence of a shark), peaks at a considerably shorter wavelength (455 nm) than that of the sunlight found in the oceanic water where it lives (470–480 nm), suggesting that either the photophores of this shark are not involved in camouflage by counterillumination or not well tuned for this purpose unless this camouflage is directed towards deep-sea organisms lacking specialized color vision (Herring, 1983). However, the recent discovery of a hormonal luminescence control in the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus 1758), fits in with counterillumination

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since it allows a long-lasting light production, which will be operating in a slowly changing or unchanging ambient light (Claes and Mallefet, 2009b).

Here, the lantern shark *E. spinax* was used in order to experimentally test the counterillumination hypothesis in a shark. We investigated the luminescence characteristics of this shark to determine if they comply with the required conditions to match the light characteristics of its environment (the Norwegian fjords in this case). In addition, we tested if this species was able to modulate the intensity of its glow in response to ambient light variations in intensity.

2. Materials and methods

2.1. Lantern shark luminescence

E. spinax specimens were collected at noon in winter by long lines lowered in a deep area (180–250 m) of the Raunefjord and brought to Espeland Marine Station where they were maintained in water tanks placed in a dark cold (6 °C) room where experiments were also performed. All the experiments were done in accordance with the Norwegian law for experimental fish care (fish handling approval #1664).

The physical characteristics of lantern shark luminescence were determined by analyzing the spontaneous glow observed in some sharks immediately after the catch (Fig. 1a).

The spectrum of the glow of three *E. spinax* specimens was measured with the optical fiber (model A976201, core diameter = 0.6 mm, length = 1.5 m with SMA905D connectors at both ends) of a mini-spectrometer (Hamamatsu photonics K. K. TM-VIS/NIR: C10083CA, Hamamatsu-City, Japan; precision = 6 nm) positioned perpendicularly to the photogenic tissue at a distance of 1 mm. As it is generally done, we used the function "Gaussian smoothing" of the spectrometer to present the data with more clarity.

In order to be able to record the intensity of the ventral luminescence of the sharks, we coupled an optical fiber (model FFO3914, International Light Technologies, Peabody, MA, USA; core diameter = 3 mm, length = 0.9 m) to a luminometer (Berthold FB12, Pforzeïm, Germany), by placing one extremity into the entrance slit of the luminometer in front of its photomultiplier tube (effective spectral range 300–600 nm), and the other extremity placed towards the surface area of the photogenic tissue (Fig. 1b). The transmission power of the optical fiber was calculated using a standard 470 nm light source (Beta light; Saunders Technology, Hayes, UK), which was measured once with the optical fiber, coupled to the luminometer, as well as with the luminometer alone. The ratio between the two measures [130 000 vs. 960 000 relative light units (RLU)] gave us the transmission power of the fiber (14%). RLU were converted into absolute values using our calibrated Beta-light source (emission of 29 megaquanta (Mq) s^{-1} in December 2008).

The luminescence intensity of the shark was measured in different experimental conditions: (i) immediately after catch, to measure the intensity and angular distribution of spontaneous glows, and (ii) after an overhead light stimulation, some days after catch, to test the response of the sharks to light stimuli.

The glow intensity from twenty-one sharks (9 adult males, 9 adult females and 3 sharks born in our tank), was measured by placing the optical fiber perpendicularly to the surface area of the photogenic tissue at a distance of 1 mm. In some animals, the intensity of the glow was monitored for a long period of time (up to 1 h) to test its stability over time.

This optical fiber was then used to generate a polar diagram of the angular distribution of the luminescence in three sharks. The optical fiber was positioned at different positions around the shark (every 10°, Fig. 1b) and the light intensity was measured for 5 s at each position at a distance of 10 cm. For each shark, the values were standardized by the intensity value of the luminescence taken vertically [angle from vertical (θ) = 0°] below the shark (perpendicular to the photogenic tissue)

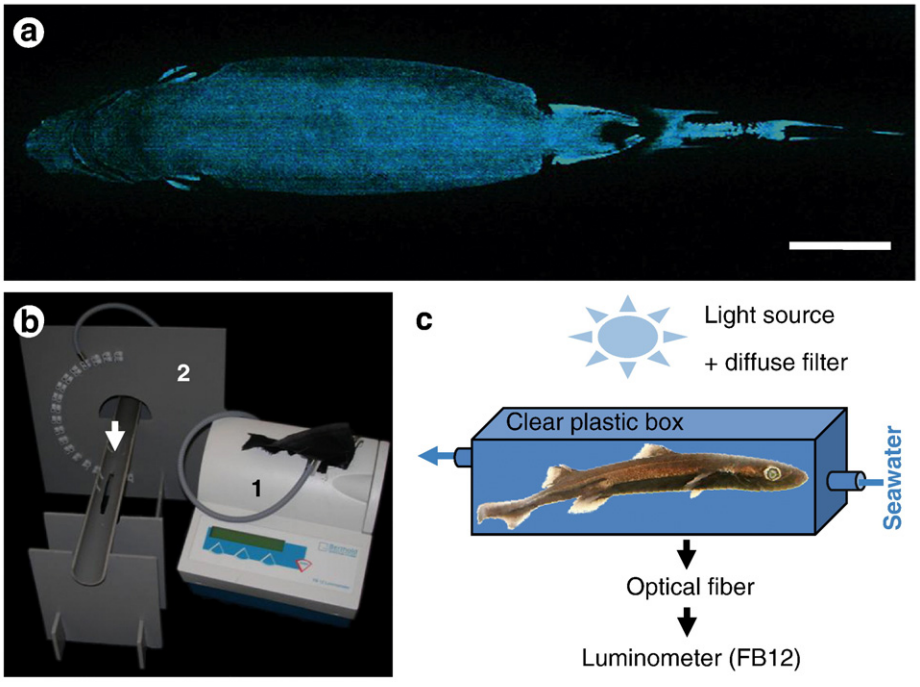

Fig. 1. (a) Spontaneous ventral luminescence in an adult specimen of *E. spinax*. (b) Experimental PVC set-up (1) to measure the angular distribution of *E. spinax* luminescence. Sharks were positioned (belly-up) on a plastic channel (arrow) and luminescence was recorded on a circle around the animal (in a perpendicular plane) by means of clips placed every 10° that were able to hold the optical fiber coupled to the luminometer (2). (c) Experimental set-up to measure the intensity of the luminescence of the sharks in response to light stimuli (overhead illumination of variable intensity). The sharks were positioned in clear water-filled plastic boxes with running seawater and surmounted by a diffuse light source. A 480 nm filter allowed us to restrict the wavelengths of the source in the range of the wavelengths found in the environment of the sharks, while the intensity of the source was modulated by neutral density filters. The luminescence was measured by the optical fiber coupled to the luminometer.

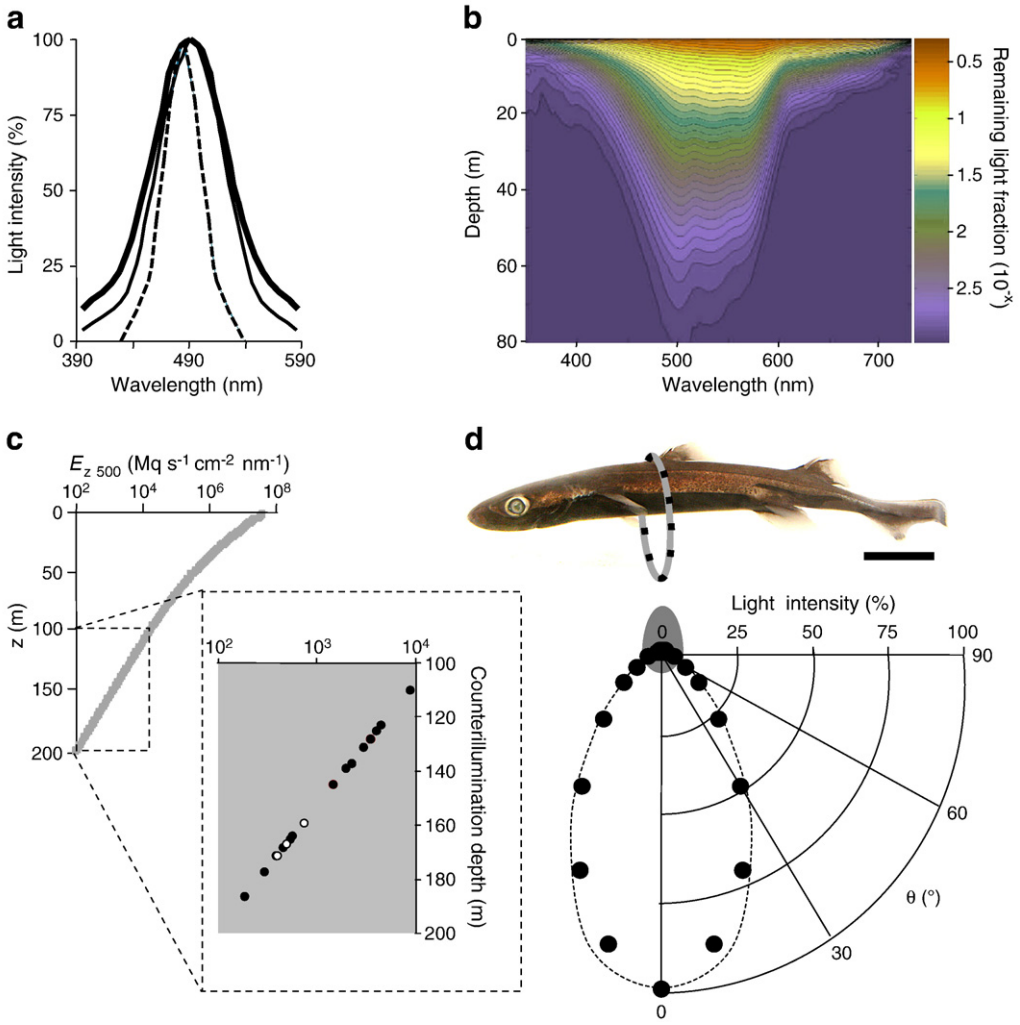

Fig. 2. (a) Luminescence spectrum (Gaussian smoothing) of 3 adult specimens of *E. spinax* (dashed, thin and thick line). (b) Light spectrum according to the depth in the Masfjord (unpublished data given with the courtesy from Stein Kaartvedt and Thor Klevjer). Below 80 m wavelengths around 500 nm dominate. (c) Irradiance at 500 nm according to the depth (z) ($E_{z\ 500}$) calculated for the Raunefjord. Insert, ventral luminescence intensities of 21 different sharks plotted against the depth at which these intensities are found in the Raunefjord. (d) Polar diagram representing the angular distribution of luminescence just in front of the first dorsal fin. Dots are mean values from 3 adult *E. spinax* specimens (due to low variation between individuals s.e.m. are smaller than dots' size). The dotted line represents the near-asymptotic angular distribution of the light at 66.1 m depth in the Lake Pend Oreille (modified from Tyler, 1960). The light intensity decreases as the angle from vertical (θ) increases. Scale bar, 5 cm.

which always gave the highest luminescence intensity following the method of Harper and Case (1999).

The effect of a light stimulation on shark luminescence was tested after two days of captivity in constant darkness in order to let the sharks recover from the stress from the catch and to obtain behaviors as natural as possible in laboratory conditions. Seven sharks (6 adult sharks and one newborn) were placed in water-filled clear plastic boxes that were approximately of their size and width in order to restrict their movements (Fig. 1c). A diffuse light source (with a filter restricting the wavelength around 480 nm and neutral density filters for intensity modulation) was used and projected on a portion of the room's white ceiling situated about 50 cm above the shark and intensity was recorded with the optical fiber coupled to the luminometer. To quantify downwelling light intensities, the optical fiber was placed directly below the plastic box without the shark present. To measure the luminescence intensity, the optical fiber was placed just beneath the ventral photogenic area of the shark when the overhead light was switched off. This experimental device allowed us (i) to test if an overhead illumination would induce luminescence in the sharks, and (ii) if the sharks would be able to modulate the intensity of their glow in response to variation of overhead light intensity. The overhead light intensities were in the range of spontaneous glow intensities of the sharks, except for one intensity that was ten times higher than the most intense recording. Each overhead light stimulation (when the light was suddenly switched on) lasted at least 1 h in order to allow the sharks to acclimate themselves to the light regime, and the luminescence measurement was done just after the end of the light stimulation, when the light was suddenly switched off.

2.2. Environmental light

To estimate the physical characteristics of the light environment encountered by the sharks, we used data from three Norwegian fjords situated close to each other: the Masfjord, the Raunefjord and the Samnangerfjord.

The wavelength distribution of the downwelling irradiance at 80 m depth was measured using a hyperspectral radiometer (RAMSES ACC, Trios-optical sensors, Oldenburg, Germany) in the Masfjord (see Aksnes et al., 2009 for method).

The amount of downwelling irradiance in the Raunefjord was calculated by a proxy method. Aksnes et al. (2009, their Eqs. 2 and 3) report the observed relationship between the attenuation of downwelling irradiance at 500 nm [$K_{d\ 500}$, in m^{-1}], salinity (S), chlorophyll concentration (C, in mg Chl$a$ m^{-3}), and dissolved oxygen concentration

for several western Norwegian fjords in winter time when chlorophyll *a* (Chl*a*) concentrations were low (<0.6 mg Chl*a* m^{-3}):

$$K_{d500} = 0.62 - 0.017S + 0.16C$$
(for a dissolved oxygen concentration of 5 ml l^{-1})

This relationship was used to obtain an estimate of the attenuation of downwelling irradiance ($E_{z\ 500}$, in quanta $m^{-2}\,s^{-1}\,nm^{-1}$) as a function of depth (z) from the salinity and chlorophyll concentrations obtained from *in situ* fluorescence measured using a fluorometer (Seapoint chlorophyll fluorometer, Seapoint Sensores, Inc., Exeter, NH, USA) coupled to a mini CTD (model SD204, SAIV/AS, Bergen, Norway) in the Raunefjord on 11th of December 2007 (at the same time and location of the shark catch) according to:

$$E_{z\ 500} = E_{0\ 500}\exp[-K_{i\ 500}z]$$

where $K_{i\ 500}\,z$ is the integrated attenuation between the surface and the depth z (ranging from 0 to 200 m). We assumed a surface irradiance ($E_{0\ 500}$) corresponding to $5 \cdot 10^7$ Mq $s^{-1}\,cm^{-2}\,nm^{-1}$) reflecting the low solar irradiance at wintertime in Raunefjord. This value corresponds to a clear sky noon irradiance as measured by the Geophysical Institute, University of Bergen, Bergen, Norway.

The near asymptotic angular distribution of light in these fjords was considered to be similar to the distribution obtain by Tyler (1960) for the Lake Pend Oreille, since this lake shows a similar ratio of scattering to absorption which is similar to the ratio found in the Samnangerfjord (Hamre et al., 2003). The angular structure of the underwater light field approaches an asymptotic state with increasing depth, and below 1% light depth there are only small changes in the angular distribution (Kirk, 1994). The actual shape of the asymptotic distribution is determined by the ratio of scattering to absorption. At a high ratio the shape of the angular distribution (plotted as a polar diagram such as in Fig. 2d) tends towards a circle, while at a low ratio the polar diagram takes on the form of a narrow pencil (Kirk, 1994). Hamre et al. (2003) measured seasonal variations in absorption and scattering down to 50 m depth in the Samnangerfjord. Their results (their Fig. 1) indicate a scattering to absorption ratio close to 2 in the deepest part (40–50 m), which is near the value (2.4) reported for Lake Pend Oreille by Tyler (1960) that is discussed by Kirk (1994, his Figs. 5.11 and 6.12).

2.3. Statistical analysis

The statistical analyses (Student's *t*-test, linear regression) were performed using the software SAS/STAT (STAT Institute Inc., 1990, Cary, NC, USA) and considered to be significant when *P*-value was lower than 0.05.

3. Results

Directly after catch, the vast majority of specimens produced a spontaneous long-lasting (sometimes more than 1 h) luminescence. The physical characteristics of this glow were very similar to those of the ambient light environment encountered by the sharks.

The luminescence spectrum showed a peak at 486 ± 1 nm (Fig. 2a), which falls in the small range of wavelengths (around 500 nm) detected at 80 m in the Masfjord (Fig. 2b). The luminescence intensities (295–8620 Mq $s^{-1}\,cm^{-2}$) of tested sharks were stable over time (variations of less than one order of magnitude) and corresponded to $E_{z\ 500}$ between 110 and 186 m in the Raunefjord at time of the catch (Fig. 2c). Adult male and female sharks did not show any significant difference in the intensity of their glow (*t*-test, $P = 0.22$), or in the depth at which the intensity of their glow was theoretically capable of matching the ambient light intensity present in the fjord (*t*-test, $P = 0.33$).

The angular distribution of *E. spinax* luminescence was also very close to that present in its environment, with a polar diagram showing a near-asymptotic angular distribution slightly narrower than the one found in the lake Pend Oreille, with the majority of the light emitted downward (Fig. 2d).

After two days of captivity, spontaneous luminescence was only observed in two animals and in a transitory manner. Two sharks (an adult and a newborn) responded to an overhead illumination by switching on their luminescence at an intensity level falling into the range of the spontaneous glows recorded the day of the catch (Fig. 3). The five other tested sharks did not luminesce even after different trials with variable light intensities. However, the adult shark that started to produce light was not able to modulate the intensity of its glow in response to an increase in the overhead light intensity (Fig. 3), it continued to emit light at a relatively constant intensity (from 74 to 160 Mq $s^{-1}\,cm^{-2}$) during the entire experiment (which last more than 5 h). No correlation was therefore found between the intensities of shark luminescence and overhead light (linear regression, $r^2 = 0.07$, $P = 0.67$).

4. Discussion

Here we show that in the southern Norwegian fjords velvet belly lantern sharks (*E. spinax*) emit a ventral luminescence whose physical characteristics are very close to those of the light present in their environment. This is the first evidence that sharks could use camouflage by counterillumination.

E. spinax photophores produce a luminescence whose spectrum has a narrow peak which is closer to the wavelength range found in the deep waters of the fjords than the spectral luminescence of the dalatiid shark *I. brasiliensis* (Herring, 1983). The origin of such a difference in the luminescence spectrum of these two shark species is unknown but may be linked to a difference in the luminous substrate of the chemiluminescent reaction as well as to the presence of pigments in the photophore lens that alter the spectral characteristics of luminescence (Denton et al., 1985).

The angular distribution of *E. spinax* luminescence is remarkably similar to the near-asymptotic distribution found in its environment as well as in other counterilluminating animals (Denton et al., 1972; Harper and Case, 1999). This shows that a diffuse pattern of photophores differentially organized around the axis of the animal is another way to achieve an appropriate angular distribution of the light field. A gradual transverse change in the orientation of the photophore axis was already observed by Hickling (1928) in this species.

Luminescence intensities for 500 nm light measured in *E. spinax* fall in the range of downwelling irradiance at 110–186 m deep in its environment. Counterilluminating animals are generally able to

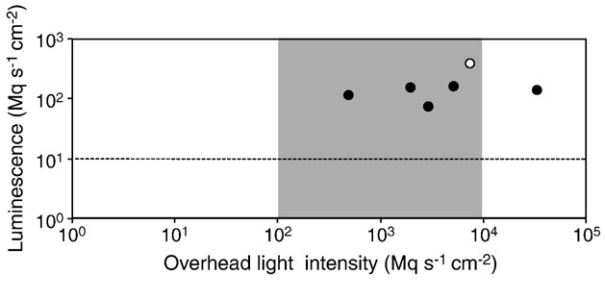

Fig. 3. Relationship between overhead light intensity and *E. spinax* luminescence. The dashed area represents the range of intensities of spontaneous glows measured the day of the catch. The dotted line represents the background level of luminescence found in the sharks two days after the catch. Two sharks switched on their luminescence in response to overhead light. Open symbol, shark 1 (newborn); filled symbols, shark 2 (adult). Shark 2 maintained its luminescence intensity during all the experiment at a relatively constant level, even when the overhead light intensity changed.

modulate the intensity of their luminescence in response to ambient light changes by comparing visually their luminescence output and the ambient light intensity (Warner et al., 1979; Young et al., 1979, 1980; Jones and Nishiguchi, 2004). The temporal stability of *E. spinax* glow intensity after the capture and in response to different light intensities suggests that this animal maintains a diel vertical migration pattern in the Norwegian fjords to stay in a constant light level at a wavelength of 500 nm. This idea is supported by observations of *E. spinax* at very shallow depth (up to 15 m) at night in some Norwegian fjords (Moen and Svensen, 2004; Heidler, 2006). The poor ability of this shark to rapidly adjust its luminescence on a wide range of intensities is probably a consequence of the hormonal control of luminescence present in this species (Claes and Mallefet, 2009b). Indeed, the intensity of prolactin and melatonin-induced luminescence from *E. spinax* photophores does not vary much even if a wide range of concentrations is applied on the tissue (Claes and Mallefet, 2009b). In this study, however, some sharks showed small variations in their luminescence intensity (always less than one order of magnitude). One cannot exclude the possibility that these variations represent temporary adjustments of luminescence intensity that would allow the shark to move in the water column to stay in an isolume. It is likely that this shark uses both the eyes and pineal gland to monitor information on downwelling light during their vertical migrations as it has been already suggested in lantern sharks (Clark and Kristof, 1990) and in other animals including fishes and cephalopods that use camouflage by counterillumination (Young et al., 1979; Jones and Nishiguchi, 2004). In this case the information would be directly transmitted to the photophores by hormonal inputs.

Counterilluminating animals generally use their luminescence to disappear from their predator's sight, and this is probably also the case in *E. spinax*, especially at small size when it is more vulnerable. The ability of newborn individuals to match intensities found in their environment, to switch on their luminescence in response to overhead light illumination, and the high photophore coverage of their ventral surface area (Claes and Mallefet, 2008, 2009a) supports this hypothesis. However, as with almost all sharks, this animal captures its prey with a ventral mouth. A ventral camouflage by counterillumination may therefore double the adaptive advantage in this species since it would make the shark invisible not only to its predator but also to its prey. The main Norwegian preys of *E. spinax* are krill and pearlfish (Klimpel et al., 2003), which are also luminous and undergo diel vertical migrations in Norwegian fjords (Kaartvedt et al., 1988). This also supports the idea that, in Norwegian fjords, this shark is an isolume follower that performs diel migrations in the water column to remain hidden from predator and prey. It remains to be determined, however, if this capability to disappear in a world with no place to hide might also be present in other lantern sharks with ventral photophores or even in other populations of *E. spinax*, such as those present in the Mediterranean Sea, for example, whose biotic (predator and prey) and abiotic (light level, depth, temperature) environments are different.

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