Bioluminescence: An investigation of the morphology, phylogenetic relationships, and adaptations of various fish taxa that possess photophores.

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Abstract

Present in over 460 marine fish species, bioluminescence is a multifaceted phenomenon that is adaptive for species that rely on camouflage to evade predators, for species to communicate with each other for mating events, as well as for prey and predator detection. Different wavelengths of light are present in various species as well as different mechanisms of production of bioluminescence within light organs. A review of the literature stresses the implications that bioluminescence has evolved more than once in fish and that the adaptations perceived in different species serve more than one purpose.

Introduction

Bioluminescence has been studied on mesopelagic fish in several different families of fish, from lantern sharks (Etmopteridae) of the Squaliformes to members of Myctophidae. A plethora of research exists with respect to the morphology of photophores, the main functional light-producing organ, as well as luminescent bacterial symbioses that occur in some fish species (Dunlap et al. 2007). What is particularly fascinating about the fishes' ability to produce and emit light at varying wavelengths is the underlying anatomy of the photophores and photocytes (Turner et al. 2009). In addition to the anatomy and physiology of luminescent fish, there is another dimension to origin of bioluminescence; many marine fish harbor luminescent bacteria symbionts within their light organs while other species produce light via endogenous reactions (Dunlap et al 2008). The goal of this review is to 1) introduce the importance of wavelengths in the environment and those produced by luminescing fishes; 2) discuss the morphology and anatomy of the light organs; 3) review recent research dealing with luminescent bacterial symbioses in fish; and 4) review the literature dealing with adaptive, evolutionary, and phylogenetic significance of bioluminescence.

Biochemistry and visual pigments of bioluminescent fishes

The fundamental workings behind bioluminescence involve wavelengths of light that organisms can perceive in relationship to their environment. Fish retinas contain visual pigments that are specific to absorbing a maximum wavelength of light (Hasegawa et al. 2008). In addition to visual pigments, neurotransmitters are necessary for the control of luminescence from the light organs (Krönström and Mallefet 2010). The

literature reviewed in this section covers the fascinating range of wavelengths produced and perceived by bioluminescent species, as well as the biochemical control of bioluminescence.

A study conducted in the Musician's Seamount region of the Pacific Ocean north of Hawaii investigated the visual pigments of Myctophid fish of the mesopelagic zone (Turner et al. 2009). The premise of the study was based on the light attenuation properties of water with increasing depth; as sunlight penetration decreases with depth, there is a narrow waveband of light available in the 470 nm to 490 nm zone (Turner et al. 2009). With this narrow waveband of light available, bioluminescence becomes an increasingly important selective pressure for mesopelagic fishes to maximize sensitivity to the available light. This means that in some mesopelagic leignathid fish, their visual pigments will have pigment absorption maxima that most closely resemble that of their ambient environment (Turner et al. 2009). The objective of this study was to characterize the visual pigment absorption maxima of myctophid fish, and a total of 40 species in the Myctophidae family was sampled. All species sampled exhibited absorption maxima in the range of 480 nm to 522 nm, with 522 nm being long-wave oriented for possible detection of dragonfish predators (Turner et al. 2009). This article was extremely thorough with explanations of why various fish species can detect certain wavelengths. It would have been valuable for more explanation or discussion as to why 3 species of the Myctophinae had a paired rhodopsin/porphyropsin system.

Similar to Turner et al. (2009), Herring and Cope (2005) studied three genera of mesopelagic dragonfish (Stomiidae) that emit red light. The three genera *Malacosteus*, *Aristostomias*, and *Pachystomias* have numerous small body photophores as well as large

suborbital photophores that emit red light and postorbital photophores that emit blue light (Herring and Cope 2005). The goal of this research was to compare the structure and fluorescent characteristics of the suborbital photophores of these three genera (Herring and Cope 2005). The researchers found that suborbital photophores of *Malacosteus sp.* are chocolate-brown and tear-drop shaped, and the organ consists of a large pigmented sac that is lined by a thick reflector (Herring and Cope 2005). In *Pachystomias sp.* the suborbital photophores are long and curve slightly upward, with a small additional photophore embedded in their ventral margins (Herring and Cope 2005). Photophores of *Aristostomias* were similar to those of *Malacosteus* but the color was more orange (Herring and Cope 2005). In all species sampled, the postorbital photophores comprised a near-spherical glandular mass inside a thin hemispherical reflector and an external pigment layer (Herring and Cope 2005).

The main discoveries of Herring and Cope (2005) include that the red-emitting photophores of *Pachystomias* and *Aristostomias* differ dramatically in morphology from those of *Malacosteus.* Photophores of *Malacosteus* contain a reflective cup that encloses a mass of glandular material, while the photophores of the former two genera have a main mass of glandular tissue that lies outside the reflector (Herring and Cope 2005). Fluorescence emission spectra were also measured for all three genera and the mechanisms of red light emission were different among the species (Herring and Cope 2005).

Retinal photoreceptors play a major role in the perception of bioluminescence. Turner et al. (2009) mentioned the wavelengths of light perceived by deep-sea and mesopelagic organisms depend on the visual pigments within the retinal photoreceptors

(Hasegawa et al. 2008). The visual pigments consist of two components, a light-absorbing chromophore and a protein called an opsin, to which the chromophore attaches (Hasegawa et al. 2008). Retinae can contain rhodopsin or porphyropsin, which is a long-wave sensitive visual pigment; porphyropsins are commonly found in rods and cones fishes that inhabit freshwater where long-waves predominate more than short-waves with increasing depth (Hasegawa et al. 2008). Conversely, in fishes inhabiting marine environments, these porphyropsins are rare due to the higher transmission of short waves, while diadromous fishes that migrate between marine and freshwater environments have both porphyropsins and rhodopsins so that they can adjust between both environments (Hasegawa et al. 2008). Most deep-sea fish have a single rhodopsin visual pigment that has maximum absorption in the blue-light wavelength range of 470 nm to 490 nm, which is due to the light attenuation that occurs in the ocean where short waves predominate (Hasegawa et al. 2008). However, a few marine fish possess porphyropsin in their retinae, such as members of the family Stomiidae, and can emit long-wave bioluminescence (Hasegawa et al. 2008).

Specimens of *Myctophum nitidulum* were caught in the Musician's Seamount region of the Pacific Ocean and the retinae were removed from hemisected eyes, from which extracted visual pigments were partially bleached under monochromatic light (Hasegawa et al. 2008). HPLC analyses showed distinct peaks for different chromophores that absorb at different light wavelengths (Hasegawa et al. 2008). Three partial bleaches were performed on each eye from individual specimens, and all revealed 2 visual peaks that fit templates for a porphyropsin and rhodopsin, showing that *M. nitidulum* specimens in this study possess paired rhodopsin/porphyropsin pigments

(Hasegawa et al. 2008). The significance of the discovery of the long-wave visual pigment reported in this study goes beyond the mere fact that this pigment is the most long-wave sensitive light pigment reported in any deep-sea fish to date; the presence of long-wave porphyropsins could enhance detection of bioluminescence produced by predators such as stomiids (Hasegawa et al. 2008). The discovery of a paired visual pigment system in this species could have far-reaching consequences for adaptations to evading stomiid predators and increased fitness.

A recent study was conducted on the luminous system of *Etmopterus spinax*, the velvet belly lantern shark, and the major focus was on the preys found in the diet of this shark and to determine which ones contained luciferin, the substrate required for light emission (Renwart and Mallefet 2013). Many bioluminescent fishes such as some teleosts have acquired luciferin through the food chain from coelenterazine, cyprinid luciferin, and dinoflagellates luciferin, so the researchers were interested if the luminous system of *E. spinax* contained luciferin from prey sources (Renwart and Mallefet 2013). Luciferins were extracted from the shark digestive tract and photophores were tested for their ability to react with different luciferases (Renwart and Mallefet 2013). Three prey taxa were identified as potential sources of luciferin: *Meganyctiphanes norvegica* (ephausiid), *Pasiphaea multidentata* (shrimp), and *Maurolicus muelleri* (teleost fish) (Renwart and Mallefet 2013). Despite the fact that this research did not find any luciferins that sharks could utilize from their food sources, the question still remains as to how these sharks produce bioluminescence. A possible mechanism for light emission could lie inside the shark as specific active or storage form of a known luciferin, or a new luciferin or photoprotein (Renwart and Mallefet 2013).

A 2010 study focused on the role and biochemical pathways of nitric oxide (NO) as a neurotransmitter in the control of bioluminescence in 7 mesopelagic fish species belonging to 3 different orders- Myctophiformes, Stomiiformes, and Batracoidiformes. The researchers used immunohistochemistry to detect the presence of NO-producing enzyme nitric oxide synthase (NOS) in the photophores of bioluminescent fish (Krönström and Mallefet 2010). To test for the presence of NOS, tissues containing photophores were dissected from the fish and incubated with antibodies and Eosin-Ehrlich hematoxylin solution. Major findings from this study include detection of strong NOS-like immunoreactivity in dot-like or stripe-like structures inside the photocytes of all myctophids (Krönström and Mallefet 2010). NOS-like immunoreactivity was found in different types of tissue, indicating that the functioning of nitric oxide may differ in each species (Figure 2) (Krönström and Mallefet 2010). Different species showed various arrangements of NOS immunoreactivity, and fish of the same family such as the Myctophidae, showed similar patterns of NO action, and fish of the same order did not share the same NOS-like immunoreactivity in the same photophore structures (Krönström and Mallefet 2010). This article presented the results of nerve cell densities within the photophores very well so that the reader could understand how the NO enters the photocytes, such as through lens or filter cells. However, the treatment and examination section in the methods was a bit tedious to read, especially when the authors went into great detail about the various staining methods and antibodies used for the tissue samples.

Morphology, anatomy, and development of photophores

A great diversity of form exists within the photophores of various species of fish. The anatomical diversity among different fish clades, families, and orders reflects the evolutionary diversity encompassed within bioluminescence (Dunlap et al. 2008). The following reviews of recent research on photophore development and morphology attempt to elucidate the luminous structures responsible for the production of bioluminescence.

Claes et al. (2008) investigated the onset of photogenic structures in the velvet belly lantern shark (*Etmopterus spinax*). The main objective was to determine how and when these species become luminous, as well as the size and density of light organs in different luminous zones (Claes et al. 2008). Pieces of skin containing photophores were placed in 50% ethanol and observed under a light microscope; after several shark embryos were observed, nine different luminous zones were noted and followed a precise order (Claes et al. 2008). The smallest embryos lacked luminous zones; however, spontaneous blue luminescence was observed in the embryos, which indicates that the luminous system functions prior to birth (Claes et al. 2008). The authors proposed the sequential appearance of luminous zones as follows: first is rostral, then ventral, caudal, infra-caudal, mandibular, pectoral, pelvic, lateral, and lastly, infra-pelvic (Claes et al. 2008). In addition to the discovery of luminous zones, Claes et al. (2008) also found that fluorescence was present in the yolk sac prior to photophore development in shark embryos, which suggests a maternal transfer of luminous compounds. Major implications of this research include that bioluminescence is not restricted to only one purpose in

luminescent species and that the development of light organs in *E. splendidus* is well-controlled (Claes et al. 2008).

A study conducted by Ikejima et al. (2008) investigated the sexually dimorphic light organ system (LOS) in the leiognathid fish *Photoplagios rivulatus*. In many leiognathid species, males possess larger light organs compared to females, in some cases leading to a distinctive transparent patch in males (Ikejima et al. 2008). The researchers investigated the possible coupling between sexual maturation and LOS enlargement in *P. rivulatus* by calculating the gonadosomatic index and percentage light organ weight to body weight (Ikejima et al. 2008). Major findings from this study support the hypothesis that gonad maturation and light organ development are synchronized in male *P. rivulatus* but not in females (Ikejima et al. 2008). Since the discovery of sexually dimorphic LOS in this species, it is postulated that bioluminescence could influence reproduction and sex-specific intra-species communication in leiognathid fishes. This article was well-written overall and the results seem like they should invite more research for reproductive roles of bioluminescence. One aspect of this article which was difficult to follow was the calculation and meaning of the gonadosomatic index; this method deserved more explanation because the results do not seem to discuss this index at all.

An earlier study from 1997 focused on understanding mid-water teleost luminescence by quantifying and comparing the kinetic and quantum emission data for similar species of 4 teleost families from two distinct geographical regions: Hawaiian waters and the nearshore California basins (Mensinger et al. 1997). Flash kinetics and photon emission were quantified using an integrating sphere quantum counting photometer, and individual fish collected from the California coast were placed in

transparent containers where spontaneous luminescence was recorded. Researchers found that orbital, caudal, and oral organs emitted discrete flashes spontaneously and during mechanical stimulations (Mensinger et al. 1997). Four specimens of Myctophidae were recorded to luminesce spontaneously from body photophores and caudal tissue, with the caudal organs emitting a wide range of flash patterns (Mensinger et al. 1997). An interesting find between Hawaiian teleosts and Southern Californian teleosts was that in both regions the myctophid caudal flash durations were significantly shorter than stomiatoid orbital photophore flashes. One aspect of this study which could be improved was knowledge on the sample size of the collected fish; how many replicates from each species were conducted? This article was organized appropriately and the discussion took into account how the characteristics of light emission, visual systems, and optical environment all play a role in bioluminescence.

Claes et al. (2011) studied the organization and structure of photophores, as well as the physiological control of light emission in the splendid shark *Etmopterus splendidus.* Three specimens were studied by testing physiological control of photophores with test substances for neurotransmitters such as nitric oxide and hormones (Claes et al. 2011). After organization and structure of photophores was analyzed, Claes et al. (2011) found a luminous pattern that was divided into 9 luminous zones and a dark, non-luminous zone between the infrapelvic and infracaudal zone (Figure 1). In addition, application of nitric oxide on ventral skin patches showed little to no light response, while prolactin stimulated significant light responses (Claes et al. 2011). Similar to *Etmopterus spinax,* the non-luminescent photophores appeared as black dots while luminescent ones exhibited an iris-like morphology (Claes et al. 2011).

Symbiotic associations with luminescent bacteria

The following studies investigated fish symbioses with luminescent bacteria. The fish harbor luminescent bacteria inside of their light organs, thereby providing the bacteria with oxygen and nutrients for luminescence and reproduction (Dunlap et al. 2008). In return, the host fish uses the bacterial light for signaling, attracting prey, and avoiding predators (Dunlap et al. 2008). At least 4 different luminescent bacteria species have been identified as either obligate or facultative symbionts of fish.

Researchers were interested in the specificity and codivergence in bioluminescent symbioses, with the study of interest based on extensive background research on obligate versus facultative bacterial symbioses within the light organ tissues of bioluminescent teleosts (Dunlap et al. 2007). Thirty-five species in 7 teleost families were examined by extraction of DNA from tissues, isolation of bacterial endosymbionts through culturing light organ homogenate on various agar plates, and phylogenetic analyses of sequencing the 16S ribosomal RNA gene and the cytochrome oxidase subunit I gene (Dunlap et al. 2007). Results from parsimony analyses of different bacterial strains of *Photobacterium leiognathi* and *Vibrio fischeri* show that some symbiotic bacterial associations occur consistently at certain fish family levels, while some such as *V. fischeri* which was harbored by different species of macrourids (Dunlap et al. 2007). The authors conclude that bacterial symbiosis within luminescent organs is not limited to strict host-symbiont specificity (Dunlap et al. 2007). The phylogenetic differences found in the bacterial bioluminescent fishes, as well as differences in morphology and anatomical locations of

fish light organs suggests that bioluminescent symbioses arose independently and multiples times in fish.

Another study was interested in identifying the developmental stage at which luminescent bacterial symbiosis begins in the leiognathid fish *Nuchequula nuchalis* (Dunlap et al. 2008). The goal of this study was to determine whether light organ ontogeny precedes bacterial colonization of the internal supraesophageal light organs; this was accomplished by dissecting light organs from larval specimens, isolating bacterial symbionts from adult and larval specimens, performing DNA fingerprint analysis on bacterial strains, and amplification of the *luxA* region from *Photobacterium leiognathi*, the bacterial symbiont of this fish (Dunlap et al. 2008). Results included that all specimens contained light organ tissue that partially wraps around the esophagus and covered dorsally with a layer of pigment; in specimens that were 6.0 to 6.5 mm long, the swim bladder was small and had not established the interface with the light organ, which is characteristic of leiognathids (Dunlap et al. 2008). The researchers also found that in specimens of 6.0 to 6.5 mm in length there were no luminous or nonluminous bacterial colonies, but in all specimens that were 6.6 mm long or larger harbored large populations of luminous bacteria; from these findings the authors surmise that light organ inception precedes the host's acquisition of symbiotic bacteria (Dunlap et al. 2008). From the *luxA* sequencing, all examined bacterial strains in the light organs were members of *P. leiognathi*, and in one examined fish specimen, *Vibrio harveyi* was identified in the light organs along with *P. leiognathi* (Dunlap et al. 2008). Major implications from this study include that high diversity of bacterial strains exists within the light organs of members of the same fish species such as *N. nuchalis*; the local environment plays a role with regard

for which strains will colonize the light organ tissue. This article was very cohesive in terms of the methods and presentation of the results. There was a discussion on merodiploidy near the end of the article, which was difficult to connect with the main premise of the research study.

Urbanczyk et al. (2012) investigated whether the limited geographic distribution of merodiploid *Photobacterium leiognathi* in northern Japan is attributed to physical barriers or to fish preferentially forming symbioses with single *lux-rib* strains. Merodiploid refers to symbiotic bacteria that have multiple *lux-rib* operons; these operons are responsible for the bacterial bioluminescent phenotype (Urbanczyk et al. 2012). *Photobacterium leiognathi* strains were isolated from light organs of captured fish as well as amplification and sequencing of *lux* genes (Urbanczyk et al. 2012). Results from this study indicate that merodiploid *P. leiognathi* strains were only found in Japan near Honshu and Kyushu islands (Urbanczyk et al. 2012). While 20 merodiploid strains were found in specimens of *Nuchequula nuchalis* and *Equulites rivulatus*, both bioluminescent fish, only single-copy strains were found in specimens of *Secutor indicius* caught near Kyushu Island (Urbanczyk et al. 2012). It appears that *S. indicius* preferentially forms symbioses with *P. leiognathi* bearing a single *lux-rib* operon, which has implications for the role of additional luciferase activity and host tissue osmolarity on light organ symbiosis (Urbanczyk et al. 2012). Where Dunlap et al. (2008) left off on merodiploid strains of *P. leiognathi*, Urbanczyk et al. (2012) elaborated and gave great insight into the role of genes in controlling bioluminescence in host tissues.

Similar to the research of Urbanczyk et al. (2012) and Dunlap et al. (2008), Wada et al. (2006) investigated whether or not *Photobacterium leiognathi spp. mandapamensis*,

a strain of *P. leiognathi* that possesses the *lux*F operon, forms light organ symbioses in non-leiognathid fish. The *lux* F operon codes for a nonfluorescent flavoprotein and can be used to distinguish between *P. leiognathi spp. leiognathi* and *P. leiognathi spp. mandapamensis*, two distinct clades within the *P. leiognathi* population. Researchers sequenced the luciferase gene, *lux*A, and 16 rRNA of symbiotic *P. leiognathi* from the light organs of acropomatid and apogonid fish, which are non-leiognathid fish; this was of interest because *mandapamensis* isolates had been taken from sea water or dead bioluminescent fish that do not form bacterial symbioses (Wada et al. 2006). Results from the *lux*A sequencing showed that symbionts of the acropomatid and apogonid fish shared more than 90.5% similarity with each other, compared to 72 to 75% similarity to leiognathid symbionts (Wada et al. 2006). These results strongly suggest that the symbionts of the non-leiognathid fish were of the *mandapamensis* clade, whereas symbionts of leiognathid fish belonged to the *leiognathi* clade (Wada et al. 2006). Evolutionary significance from this study includes divergent evolution within the *P. leiognathi* population that resulted from specific associations in which symbionts may have diverged in parallel with their hosts (Wada et al. 2006).

Phylogeny, adaptations and evolutionary significance of bioluminescent fishes

The previous sections have dealt with bioluminescence on individual topics of morphology, bacterial symbioses, biochemical pathways, and visual pigments. The research articles in this final section will amalgamate these topics into a review of how the form and function of bioluminescence is adaptive and evolutionarily significant within and among various fish species.

Research conducted in Norwegian fjords used the lantern shark *Etmopterus spinax* to test the counter-illumination hypothesis, which states that organisms will produce persist light from the ventral photophores in order to camouflage their silhouette against down-welling light (Claes et al. 2010). The researchers tested whether this shark could produce luminescence that matched the light characteristics of the fjord and if this species could adjust the intensity of its glow in response to ambient light intensity changes of its environment (Claes et al. 2010). Using an optical fiber, luminescence intensity of *E. spinax* was tested under two experimental conditions: immediately after capture to measure intensity of spontaneous glows, and after an overhead light stimulation several days after capture (Claes et al. 2010). After the stimulations, only 2 individuals exhibited responses to overhead illumination, and directly after capture a majority of the organisms produced long-lasting spontaneous luminescence, with the luminescence spectrum showing a peak at 486 +/- 1 nm (Claes et al. 2010). The major findings from this study include that *E. spinax* can produce ventral luminescence with a wavelength spectrum that closely matches the wavelength range found in the deep waters of Norwegian fjords (Claes et al. 2010).

Claes et al. (2010) speculated that the ability of this lantern shark to produce luminescence that resembles ambient light characteristics present in its environment is advantageous not only for evading predators but also for being able to become invisible to prey such as krill (Claes et al. 2010). This article was relatively easy to follow, and the results appear to be in favor of the counter-illumination hypothesis. One aspect of the methods section that was weak included the sample size for the sharks; only 7 sharks were used for the overhead light stimulations. A larger sample size could have made the

results more reliable, and also a wider range of size and age classes of the sharks would be ideal since only one newborn was used. Otherwise, this article has great potential for showing the ability of organisms to fine-tune their luminescent spectra.

Straube et al. (2010) also examined bioluminescence within lantern sharks using phylogenetic analyses such as maximum parsimony and PCR. The main objectives of this study were to test for independent development of bioluminescence within Squaliformes (dogfish sharks) and to identify the sister group of Etmopteridae among Squaliformes (Straube et al. 2010). Bioluminescence is limited to only two families of dogfish sharks: the Etmopteridae and Dalatiidae (Straube et al. 2010). Results of the phylogenetic analyses supported evidence for the monophyly of Squaliformes and Etmopteridae but did not identify the sister group of Etmopteridae (Straube et al. 2010). Results from the phylogenetic analysis show that a monophyletic clade Dalatiidae evolved independently from Etmopteridae, which supports the hypothesis that bioluminescence evolved twice and independently (Straube et al. 2010). In particular, the authors speculate that the great diversity within Etmopteridae could be due to species-specific bioluminescent flank markings, which could aid in schooling and cooperative hunting (Straube et al. 2010). This article placed much emphasis on phylogenetic and morphological relationships among lantern sharks, and could have incorporated more information on bioluminescence in lantern sharks.

A phylogenetic study on Apogonidae, the cardinalfishes, examined the structure and evolution of the visceral bioluminescent system (Thacker and Roje 2009). Within Apogonidae there are species that have symbiotic luminescent bacteria within the buccal cavity and others that lack symbiotic bacteria, and instead have specialized luminescent

sections of the alimentary canal (Thacker and Roje 2009). For this study 47 individuals representing 32 apogonid species were sequenced using NADH –dehydrogenase subunits and cytochrome oxidase subunit one (COI); for light organ histology, light organs and associated tissues were dissected and dehydrated through a series of ethanols (Thacker and Roje 2009). For the results, 20 individuals of *Archamia, Jaydia, Rhabdamia, Siphamia, Parapriacanthus, Pempheris,* and *Acropoma* were dissected; in *Archamia, Jaydia,* and *Rhabdamia* the light organ was a portion of the intestinal tract, while in *Siphamia, Pempheris,* and *Parapriacanthus* light organs consisted of masses of tubules in thoracic organs (Thacker and Roje 2009). The different morphologies and locations of light organs of the examined species, along with the deep divergences inferred from the phylogenetic tree analyses, suggests that each instance of luminescence in Apogonidae evolved independently (Thacker and Roje 2009). One aspect of this study that the authors could have improved upon was keeping the species that were dissected consistent with those that were sequenced; some of the discussion revolved around sub-families and genera that were not used in the dissections, which made the discussion difficult to follow.

Based on knowledge of sexual dimorphisms in the light-organ system (LOS) of leignathids (pony fishes), a study examined whether sexual selection acting on the LOS tempo and mode of pony fish diversification (Prosanta et al. 2011). Researchers asked the question, are increased rates of diversification associated with sexually dimorphic clades? Twenty-one outgroups were chosen to examine interrelationships of Leignathidae and 44 leiognathid species were used for the ingroup; nucleotide characters were sampled from 7 mitochondrial and 2 nuclear genes (Prosanta et al. 2011). In the methods section the

researchers discussed diversification rate variation with AIC, which was difficult to comprehend due to the copious jargon and rate-constant models that I am not familiar with; it was hard to understand how these models tied into the phylogenetic tree analyses. Major results from this study include that taxonomic richness was greater in sexually dimorphic pony fish lineages than in lineages lacking sexually dimorphic LOS (Prosanta et al. 2011). The subfamily Gazzinae was found to have more disparate external features of its LOS than non-externally sexually dimorphic sister clades (Prosanta et al. 2011). Important conclusions from this study involve the role of sexual selection on the LOS in creating genetic isolation mechanisms that permit the continued diversification of pony fishes (Prosanta et al. 2011).

Conclusion

Without a doubt, extensive research on the mechanisms and integral components of bioluminescence show that this phenomenon has not only species-specific roles but also multifarious ecological roles across species. Knowledge on the fundamental morphology of photophores and the role of neurotransmitters in producing light are fascinating and should serve as a solid foundation for future research on the obscured mechanisms of how some fish can change the wavelength of emitted light. In addition, the symbiotic relationships that leiognathid fish and other marine teleosts have formed with luminescent bacteria demonstrate the diversity and evolutionary history of bioluminescence. Recent literature suggests bioluminescence plays a vital role in mesopelagic fishes with respect to mating, evading predators, and prey capture mechanisms; as more research is conducted, hopefully more insight can be evolved as to how different fish species produce light and how bacterial symbioses developed.

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Figures

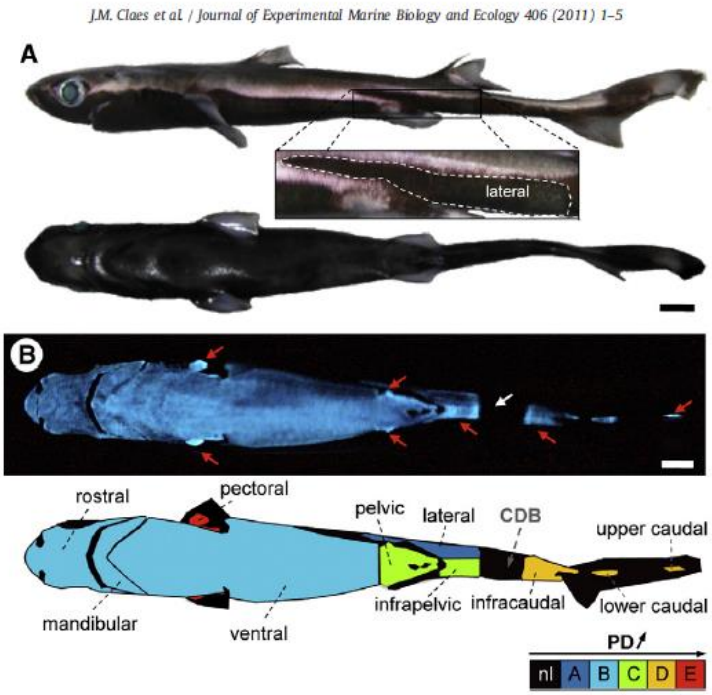

Figure 1. Luminous pattern of *Etmopterus splendidus.* (A) Lateral (top) and ventral (bottom) view of an adult specimen showing a typical pelagic habitus with a cylindrical morphology and the lateral luminous markings, which support its affiliation to "*Etmopterus pusillus"* clade. (B) Spontaneous luminescence of a freshly caught specimen (top) and description of the different photogenic zones composing the luminous pattern (bottom). Red and white arrows on top indicate bright luminescence and non-luminous caudal dark band (CDB), respectively. Photogenic zones shown in same color have similar photophore density (PD). nl, not luminous. Scale bars: 2 cm. (Claes et al. 2011).

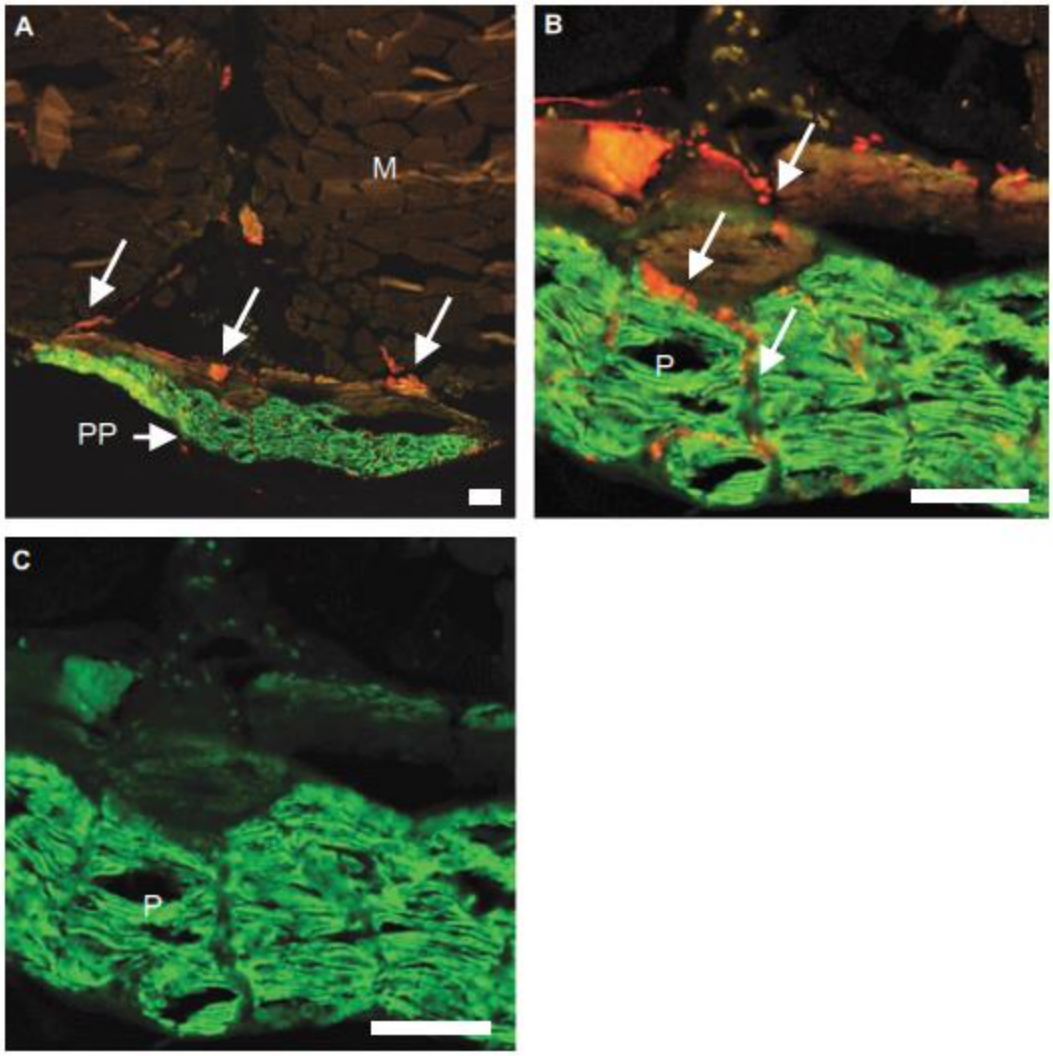

Figure 2. Cross section of caudal photophore (PP) from *Myctophum punctatum*. **A**. Thick nerve bundles approach the photophore (red, AcT, arrows) and nerve fibers are crossing the reflector (**B**, arrows). **B.** The fibers branch and follow the capillaries inside the photophore (arrows). **A-C**. Strong NOS-like immunoreactivity was detected in the numerous flattened photocytes (P) throughout the whole photophore (green, nNOSsc1025). **A, B.** Double labeling showing NOS-like immunoreactivity (green, nNOSsc1025) and nerve fibers (red, AcT). NOS-like immunoreactive fibers turn up orange in the picture. PP, photophore; P, photocyte; M, muscular tissue; bars are 50 µm. (Krönström and Mallefet 2010).