

# We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

185,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index  
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?  
Contact [book.department@intechopen.com](mailto:book.department@intechopen.com)

Numbers displayed above are based on latest data collected.  
For more information visit [www.intechopen.com](http://www.intechopen.com)



---

## Bioluminescent Fishes and their Eyes

---

José Paitio, Yuichi Oba and  
Victor Benno Meyer-Rochow

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/65385>

---

### Abstract

What shaped the evolution of vision in fish more than anything else is the need to see, be it to avoid obstacles or find shelters, and recognize conspecifics, predators and prey. However, for vision to be effective, sufficient light has to be available. While there is no shortage of light in shallow water depths, at least during the day, the situation for species occurring at greater depths is a different one: they live in an environment where sunlight does not reach, but which nevertheless, is not totally devoid of light. Numerous marine organisms, including fishes of at least 46 families, possess the ability to 'bioluminesce', i.e. they can produce biological light. This chapter focuses on the interaction between bioluminescence and specific photoreceptor adaptations in fishes to detect the biological light.

**Keywords:** bioluminescence, light, sea, eye, vision, fish

---

### 1. Introduction

Bioluminescence is rare, but widespread. This seemingly contradictory statement refers to the fact that there is almost no animal phylum that does not have at least a few bioluminescent species, even if the vast majority are non-luminescent. Freshwater contains the smallest number of bioluminescent species; terrestrial environments possess a slightly greater number, but the oceans are inhabited by a wide variety of bioluminescent creatures and the vertebrate class of Pisces represents one of the best examples of this [1]. When one thinks of the evolutionary plasticity of fishes and the fact that most of the ocean is dark, it is not surprising that these animals show a high degree of remarkable luminous features. In fact, fishes present the most diverse and complex examples of bioluminescent adaptations in the world [2].

---

In an environment where organic light is used for different biological purposes [1, 3], light perception may be a determinant factor for the survival and success of the species involved [4]. The eyes of all animals on the planet are adapted to the light regimes of the habitat they are meant to function in [5] and bioluminescent fishes are no exception. The visual capacities of oceanic fishes are adapted not only to the spectral properties and intensity of downwelling sunlight at depths the fish inhabit, but also to the bioluminescence in their environment [6]. Vision and bioluminescence (at least in fishes) are likely to share a common evolutionary history, which is reflected in the bioluminescent fishes’ ontogeny, behaviour and ecology.

2. Taxonomy of luminous fishes

While preparing this chapter, the authors found records of bioluminescence for around 1500 species of fish, but most likely this number is too low as some records of luminescent species may still be missing. The tally of luminescent fishes represents about 8% of the approximately 20,000 known species [7]. At least 43 families of 11 orders of bony fishes and 3 families of 1 order of sharks are luminous (**Table 1**). There are families with no luminescent representatives and there are families in which the luminescent species are more abundant than in some other families, which is often a reflection of the habitat that these species inhabit (see next section of this chapter).

Order (total number of families)	Family	Biolumine scent genus		Functions <sup>a</sup>
		Ratio <sup>b</sup>	Genus	
Cartilaginous fishes				
Squaliformes (7)	Dalatiidae	7/7	All [8]	L [8], CI [8]
	Etmopteridae	5/5	All [8]	M, CI, S <sup>c</sup> [92], A [67]
	Somniosidae	1/5	<i>Zameus squamulosus</i> [9]	?
Bony fishes				
Anguilliformes (16)	Congridae	1/30	<i>Lumiconger arafura</i> [16]	?
Aulopiformes (16)	Chlorophthalmidae	1/2	<i>Chlorophthalmus</i> [2]	S [60]
	Evermannellidae	2/3	<i>Cocorella atrata</i> [2], <i>Odontostomops normalops</i> [11]	?
	Paralepididae	2/12	<i>Lestidium</i> , <i>Lestroplepis</i> [23]	CI [4]
	Scopelarchidae	2/3	<i>Benthalbella</i> , <i>Scopelarchoides</i> [95]	R [95], CI [4]
	Batrachoidiformes (1)	Batrachoididae	1/22	<i>Porichthys</i> [21]

Order (total number of families)	Family	Biolumine scent genus		Functions <sup>a</sup>
		Ratio <sup>b</sup>	Genus	
Beryciformes (7)	Anomalopidae	6/6	All [12]	M, L [33], S, I, Br [62]
	Monocentridae	2/2	All [26]	L, I [53]
	Trachichthyidae	1/18	<i>Aulotrachiththys</i> [2]	CI [21]
Clupeiformes (7)	Engraulidae	1/17	<i>Coilia dussumieri</i> [15]	CI [33]
Gadiformes (10)	Macrouridae	14/23	<i>Cetonurus</i> , <i>Coelorinchus</i> , <i>Haplomacrurus</i> <sup>d</sup> , <i>Hymenocephalus</i> [23], <i>Kumba</i> [24], <i>Lepidorynchus</i> [23], <i>Lucigadus</i> [24], <i>Malacocephalus</i> , <i>Nezumia</i> , <i>Odontomacrurus</i> , <i>Sphagemacrurus</i> [23], <i>Spicomacrurus</i> [24], <i>Trachonurus</i> , <i>Ventrifossa</i> [23]	S [60], I [30]
	Merlucciidae		<i>Steindachneria argentea</i> [24]	?
Lophiiformes (18) (Suborder Ceratioidei)	Moridae	5/11	<i>Gadella</i> [23], <i>Physiculus</i> [23], <i>Salilota</i> [24], <i>Tripteryphycis</i> [23]	?
	Centrophrynidae	1/1	All [14]	M, L, I [14], Sa, Ss [41]
	Ceratiidae	2/2	All [14]	
	Diceratiidae	2/2	All [14]	
	Gigantactinidae	1/2	<i>Gigantactis</i> [14]	
Lophiiformes (18) (Suborder Ceratioidei)	Himantolophidae	1/1	All [14]	
	Linophrynidae	5/5	All [14]	
	Melanocetidae	1/1	All [14]	M, L, I [14], Sa, Ss [41]
	Oneirodidae	16/16	All [14]	
	Thaumatichthyidae	2/2	All [14]	
(non-Ceratioidei)	Ogcocephalidae	1/10	<i>Dibranchus atlanticus</i> [17]	?
Myctophiformes (2)	Myctophidae	34/34	All [11]	R [32], M [4], S [59], CI [2], I [1], Sa [2]
	Neoscopelidae	1/1	<i>Neoscopelus</i> [15]	CI [11], L [20]
Osmeriformes (14)	Alepocephalidae	4/19	<i>Microphotolepis</i> , <i>Photostylus</i> , <i>Rouleina</i> , <i>Xenodermichthys</i> [23]	CI [57], I [30]

Order (total number of families)	Family	Biolumine scent genus		Functions <sup>a</sup>
		Ratio <sup>b</sup>	Genus	
Perciformes (164)	Microstomidae	1/3	<i>Nansenia</i> [100]	?
	Opisthoproctidae	3/8	<i>Opisthoproctus</i> , <i>Rhynchohyalus</i> , <i>Winteria</i> [23]	CI [21]
	Platytroctidae	13/13	All [13]	R, CI, Ss [13]
	Acropomatidae	2/8	<i>Acropoma</i> [23], <i>Synagrops</i> [17]	CI [21]
	Apogonidae	5/32	<i>Apogon</i> , <i>Archamia</i> [23], <i>Jaydia</i> [18], <i>Rhabdamia</i> , <i>Siphamia</i> [23]	M, L, CI [51], I [33]
	Chiasmodontidae	1/4	<i>Pseudoscopelus</i> [23]	CI [21]
	Epigonidae	3/7	<i>Epigonus</i> , <i>Florenciella</i> , <i>Rosenblattia</i> [23]	?, Ss [2]
	Howellidae	1/3	<i>Howella</i> [23]	?
	Leiognathidae	7/7	All [18]	R, M, L, S, CI, I, Sa [53]
	Pempheridae	2/2	<i>Pempheris</i> , <i>Parapriacanthus</i> [23]	CI [33]
Saccopharyngiformes (4)	Scianidae	3/65	<i>Collichthys</i> [23], <i>Larimichthys</i> , <i>Sonorolux</i> [106]	CI [33]
	Eurypharyngidae	1/1	All [2]	?
Stomiiformes (4)	Saccopharyngidae	1/1	All [22]	L [15]
	Gonostomatidae	8/8	All [22]	CI [11]
	Phosichthyidae	7/7	All [22]	?
	Sternoptychidae	10/10	All [22]	CI [2]
	Stomiidae	27/27	All [22]	R [2], M [46], L [4], S [46], CI [2], I [48], A [46], Sa, Br [4]

<sup>a</sup>R—recognition; M—mate; L—lure; S—school; CI—counterillumination; I—illumination; A—aposematism; Br—blink and run; Sa—startle predators; Ss—smokescreen; ?—unreported functions in the references.

<sup>b</sup>Ratio, the number of the genera containing luminous species/the total number of the genera in the family; All, all the species are luminous.

<sup>c</sup>Etmopterids also seem to use its photophore patterns to coordinate hunting in schools [8].

<sup>d</sup>Bioluminescence in *Haplomacrurus* is only stated by Herring [23] and no other references found to contradict or agree with this information. The taxonomy used in this table is in accordance with the WoRMS Editorial Board, 2016 [7]. The taxonomic data used in this table are included and available online in the website of the Living Light List Project ([http://www3.chubu.ac.jp/faculty/oba\\_yuichi/Living%20Light%20List/](http://www3.chubu.ac.jp/faculty/oba_yuichi/Living%20Light%20List/)).

**Table 1.** Bioluminescent families and genera of fishes and respective suggested ecological functions.

In cartilaginous fishes, bioluminescence is not as common as in bony fishes. Only three families of luminous sharks are known, Dalatiidae, Etmopteridae and Somniosidae [8, 9]. Luminescence in rays and skates as well as in Holocephali seems non-existent or has not been confirmed. In the luminescent sharks, numerous small light organs are predominantly present in the ventral region of the body, but lower densities can even reach the dorsal areas in dalatiid species [10]. Luminous sharks, like the majority of fish species, possess external light organs with intrinsic light production, which are denominated as photophores [8, 11].

In bony fishes, bioluminescence reaches its zenith in terms of complexity and diversity of light organs and their corresponding biological and ecological functions. It is common to find whole families of bioluminescent species, such as the Myctophidae [11], Leiognathidae, Anomalopidae [12], Platytroctidae [13] and several families of anglerfishes [14]. In such cases, the patterns or shapes of the light organs are generally species-specific and can even be used for taxonomic purposes. Nevertheless, the most common scenario is that only some genera of fishes are bioluminescent as, for example, in families of the order Perciformes with very few luminescent species or in Macrouridae with considerably more luminescent species [2]. An uncommon scenario is when there is only a single luminous species known in an entire order as is the case with *Coilia dussumieri* in the Clupeiformes [15] and *Lumiconger arafura* in the order Anguilliformes [16, 17]. Equally uncommon is it to find only one luminescent species within a family as for the merlucciid *Steindachneria argentea* [2] and the ogcocephalid *Dibranchius atlanticus* [17]. On the other hand, we have the order Stomiiformes, in which all of its species produce their own light [1].

Generally speaking, the origin of the light emissions do not vary much within families, being either bacterial or intrinsic. Exceptions exist in the Apogonidae where only *Siphamia* species are known to have bacterial symbionts whereas the remainder of the luminescent species employ intrinsic bioluminescence with *Cypridina* luciferin [18]. A rare case is observed in anglerfishes of the families Lynophrinidae and Centrophrynidae which have an intrinsic bioluminescent barbel in addition to the symbiotic luminous lure of the first ray of the dorsal fin that projects from the dorsum of the anglerfishes and is known as the esca [14]. The location of the light organs is also generally similar within a family, but exceptions exist, namely in families where all the species are luminous. In Myctophidae, for example, only members of the genus *Diaphus* have head photophores and unlike fishes of some other genera do not possess caudal glands. Another example is that of luminous barbels, present in some species of Stomiidae [15]. Indirect bioluminescence is produced by internal luminous organs that depend on transparent tissues underneath to emit diffuse light from the ventral part of the body. Although this method is more common in the shallow-water species like those of the families Leiognathidae and Apogonidae [19], it can also be found in some fishes of greater depths as from the families of Opisthoproctidae [12] and Evermannellidae [2].

## 2.1. Dubious species

Misidentifications, confusion of non-luminous tissues and luminous bacteria on damaged specimens [20] are common sources of errors that led to reports of the luminous species, which do not exist or are not luminescent at all. Furthermore, unusual phylogenetic and habitat

placements in records for certain species claimed to be luminous, apparently backed up with dubious references, are suspicious vis-à-vis the phylogeny and habitat preferences of the accepted luminous species and therefore cast doubt on the validity of some records. Another problematic issue are contradictory statements, when some authors report a species to be luminescent and others contradict such statements. As the authors of this chapter did not have the chance to observe and confirm the status of luminosity of all the species mentioned, they decided to be neutral and include in the chapter cases that could be dubious.

The batoid *Benthobatis moresbyi* [20] is one of the most doubtful cases of bioluminescence reported in fishes. Sharks of the genus *Somniosus* were erroneously categorized as bioluminescent [2]. The megamouth shark possesses reflective tissue along its upper jaw, which can be used to attract its prey through reflecting the bioluminescence of other animals [1].

In bony fishes, reports of luminescent members of opisthoproctids, *Dolichopteryx*, *Bathyllynops* and *Bathylagus* have been shown to be erroneous [2]. Some trachichthyid genera like *Hoplostethus* [21] and *Sorosichthys* [22] may have luminous members, but there is no convincing proof of their bioluminescence. In macrourids, the genera *Coryphaenoides*, *Mesobius*, *Pseudocentonus*, *Macrourus* and *Idiolorhynchus andriashevi* are stated as luminous by some, but not all investigators [21, 23, 24]. *Antimora* is another uncertain case among otherwise luminescent morids [2, 23].

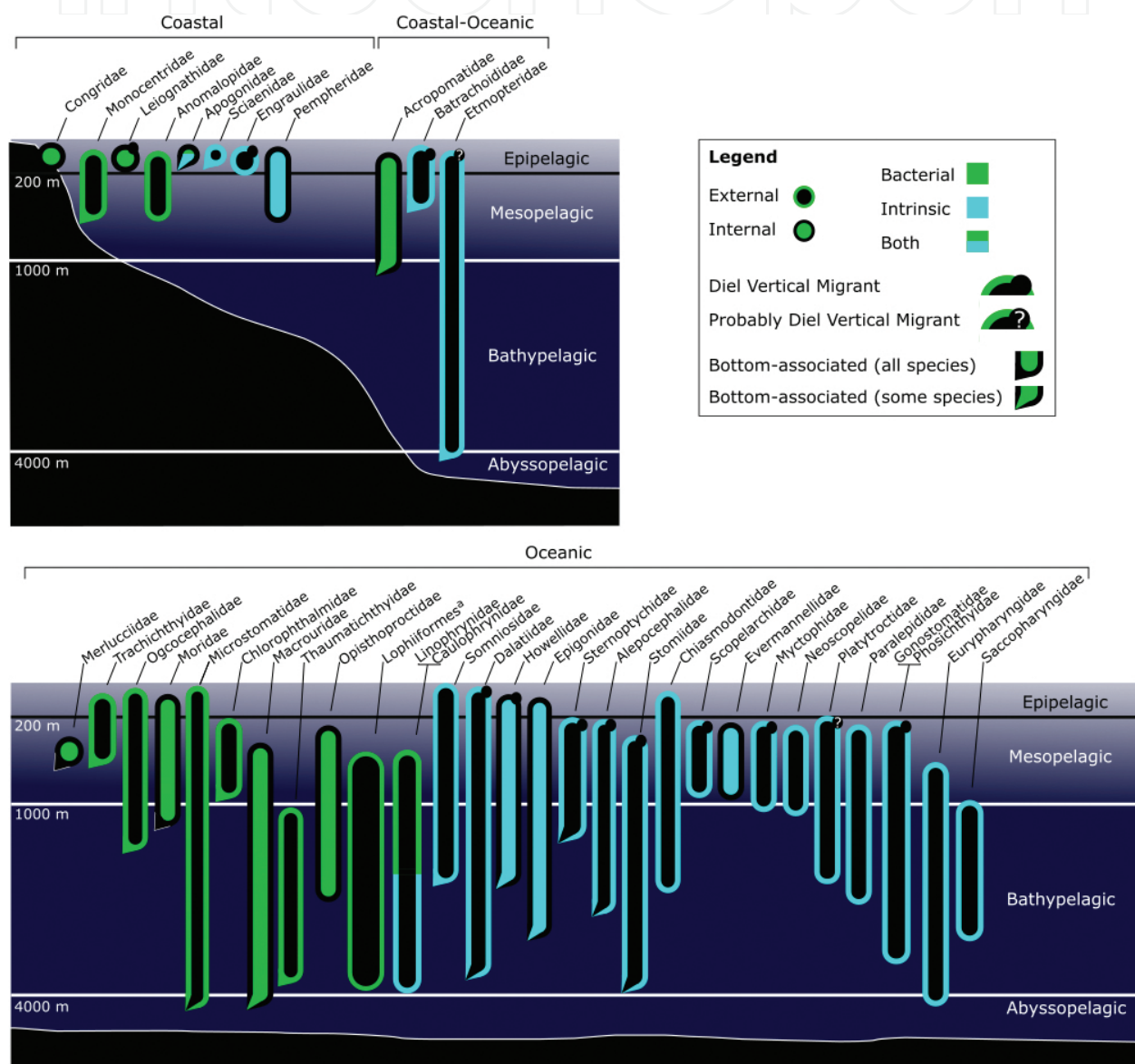
Apart from the well-known anglerfishes, two unrelated species of shallower water lophiiformes, *Antennarius hispidus* and *Chaunax* [20, 25] are described as luminous based on a single reference. There are also some species of ogocephalids, which have dubiously been reported as luminous [21, 23]. Bioluminescence in cetomimids has been stated by reference [21], but other authors disagree [26]. Reference [21] consider luminescence in the species of the families Halosauridae and Brotulidae and the gempylidae genus *Ruvettus* as dubious. The uncertainty of bioluminescence in *Kasidoron* and *Bathylagus* has been discussed [2] and possible luminescence in *Derichthys serpentinae* has been muted [27] but definitive proof is lacking. The silaginid *Sillago bassensis* was found with bioluminescent bacteria [28] probably attached to its skin; this might also have been the explanation for the dorsal luminescence of a flying fish reported in Japan [29].

### 3. Habitat dispersal of luminous fishes

Light penetrates the sea and is then subjected to scattering by air bubbles and water molecules [3], phytoplankton and zooplankton as well as suspended particles [30]. This essentially imposes limits on the use of vision in the aquatic environment [31]. Major light attenuation occurs in the epipelagic zone where the planktonic biomass, dissolved nutrients and floating debris 'filter' most of the light, reducing its intensity and altering its spectral composition. However, the angle of this light is almost completely vertical apart from very near the surface [32]. Not many bioluminescent fishes inhabit the epipelagic zone (**Figure 1**) and in those that are present, photoreceptive structures and visually induced behaviours seem less complex than that encountered in species inhabiting deeper habitats [33]. This seems likely to be related



to two main factors. Primarily, at these shallow depths light intensities, especially during the day, are too high for luminescence [4, 31] to be useful for ecological purposes without investing a considerable energy [32]. Secondly, if a very strong light were to be produced, it would readily be spotted by keen eyes of the abundant photopic predators around [32, 33]. The bioluminescent epipelagic species are mainly active at night [34] and use internal counterillumination to deter and avoid dusk-active piscivorous predators [19, 33]. Some exceptions are the headlights of anomalopid and monocentrid species [12, 35] and fishes with photophores, like the batrachoidid *Porichthys*.



**Figure 1.** Schematic representation of the spatial distribution of bioluminescent fish families and some ecological details.<sup>a</sup> Lophiiformes families other than Thaumichthyidae, Linophrynidae, Caulophrynidae and Ogcocephalidae. The data presented only refer to species that are known as bioluminescent. The order of disposition within the coastal, coastal-oceanic and oceanic categories is ecological and not spatial. References used for spatial distribution and diel vertical migrations [10, 13, 15, 26, 40, 65, 79, 95–99] and for bioluminescence [2, 9, 16, 21, 24, 47, 48, 50, 58, 60, 67, 100].



Only dim light from the short wavelength spectra of the blue–green component of sunlight (but no moonlight) reaches the mesopelagic zone [30]. In contrast to the epipelagic zone, the mesopelagic zone is characterized by a uniformity of light in all lateral directions and the highest intensity from above [4, 30]. This is the oceanic ‘bioluminescent hotspot’ where more than 80% of the species present are bioluminescent [32, 36] and biological light reaches its greatest splendour in diversity and complexity of structures and purposes [37]. In terms of fish biomass, it is the mesopelagic zone that stands out [38]. Myctophids are one of the families of teleosts with a very high number of species, representing the second most abundant taxon of mesopelagic fishes. In terms of sheer numbers, the gonostomatid genera *Vinciguerrria* and *Cyclothone* represent the most abundant fauna on the planet [11]. The mesopelagic zone is also the transference zone from an extended origin of light to a point source. The downwelling sunlight is the primary source of light in the upper mesopelagic zone (200–610 m depth) while bioluminescence takes over as the main source of light in the lower mesopelagic zone (610–1000 m depth). Under the essentially monochromatic scotopic light, the use of bioluminescence is far more advantageous for camouflage and vision, be it in the case of predators or prey, than at depths more brightly illuminated by a fuller spectrum of light. In the depths where silhouette distinction is of visual importance and it comes as no surprise that most of the bioluminescent fish species inhabit this realm. The colorations of the fish at greater depths are a reflection of the different light environment. In the upper mesopelagic silver bodies acting as mirrors and assisting in camouflaging are common [30]. The animals inhabiting the lower mesopelagic and bathypelagic tend to have darker bodies, preventing reflections of bioluminescence in these deeper realms [4, 21].

At 1000 m depth, sunlight is no longer strong enough to allow fishes to see in and that depth by definition corresponds to the beginning of the bathypelagic zone [30]. The latter is the aphotic zone where no sunlight is available [30] and complete homogeneity in terms of the light environment occurs in all directions [4, 31]. Here, light from above does not possess much relevance for the impoverished faunal assemblages present and the only source of photic stimulation, in contrast to that of the mesopelagic zone, is bioluminescence [3, 30]. Consequently, there is a drop in the number of bioluminescent species and individuals from that in the mesopelagic zone [2]. Even deeper living abyssal fishes, phylogenetically related to bathypelagic or mesopelagic luminous species, are not bioluminescent (e.g. macrourids) [4, 12].

It is not surprising that the majority of all bioluminescent fishes are oceanic and pelagic [33], as there are no structures blocking the path of the light in this environment, it seems to be optimal for the realization of many of the roles bioluminescence can ultimately be involved in [30, 37]. On the other hand, some bathypelagic species that are not known as vertical migrators possess ventral luminescence (e.g. morid species). These are puzzling cases of bioluminescence and its possible role [2], because emitting ventral light close to the bottom does not fulfil the purpose of camouflage. In fact, it may cause a reflection by the substrate and expose the fish [21]; however, there may be advantages too, which have not been looked into like, for instance, diverting attention and misguiding potential predators to the reflection rather than its originator. Coastal and benthic fishes more often employ bacterial luminescence while the pelagic species possess mostly intrinsic bioluminescence [2, 33, 39].

Diel vertical migrations are common among mesopelagic fishes [40] but are also known from some species of epipelagic [4, 41] and bathypelagic fish [4, 21]. These migrations do not always involve all taxa present [15] or genders in the same population and may vary geographically and seasonally. Generally speaking, the diel vertical migrant approaches surface waters at night to feed on zooplankton or other migrants when diurnally hunting visual predators are less active. The vertical movements of these individuals provide an important source of carbon (and other nutrients) to the deeper layers of the ocean [4].

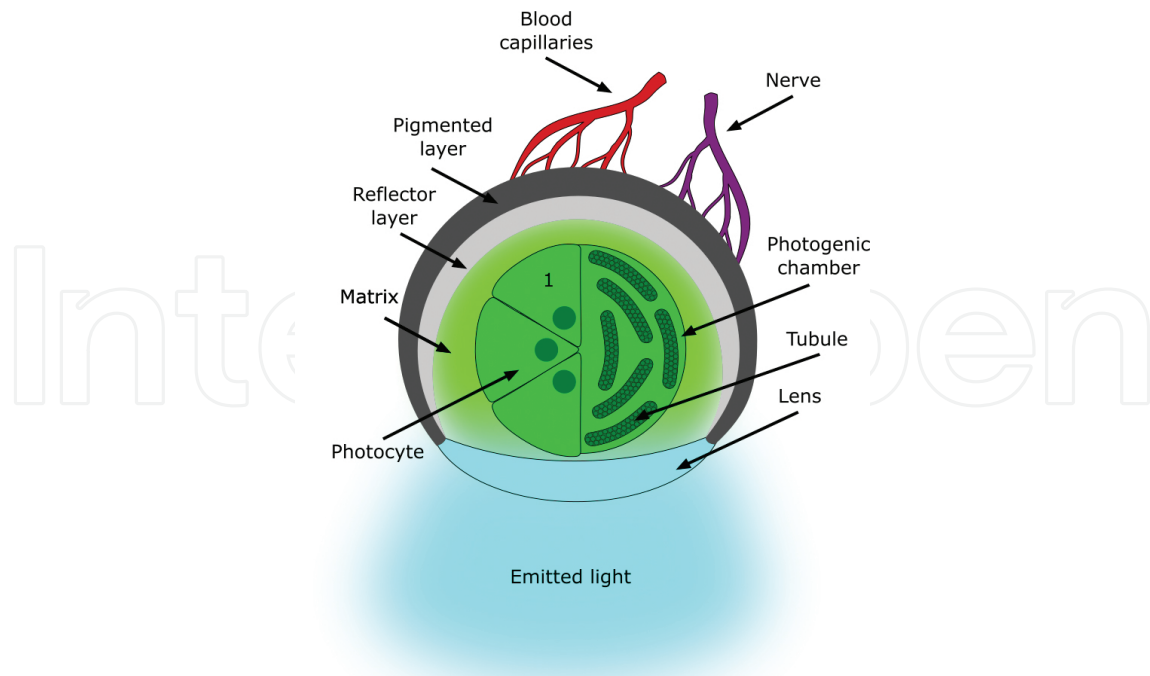
## 4. Bioluminescence purposes in fishes

### 4.1. Light organs and control

Despite the extensive diversity of luminous organs in fishes, the basic structure is rather uniform [37] irrespective of whether we deal with photocytes or bacterial symbionts (**Figure 2**). The photogenic mass is situated at the centre and is associated with an external lens. An internal reflector is enclosed by a pigmented layer. Innervation of blood capillaries is also a common feature [2, 37]. Bacterial light organs usually possess an opening to exterior allowing the release of excess bacterial cells to the environment [42]. Photophores, with the exception of those in neoscopelids, are closed [2, 4].

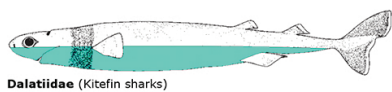
The majority of the bioluminescent fishes have luminous tissues capable of generating light by themselves, but others maintain a culture of luminous symbiotic bacteria in their light organs [4, 39, 43]. The light organs of the species with symbiotic bacteria possess ducts in which they culture extracellular luminous bacteria [39]. In most cases, these bacteria are species like *Photobacterium*, but *Aliivibrio fischeri* and possibly *Vibrio harveyi* can also be found as symbionts in light organs of some luminous fishes [42]. Intrinsically luminescent fish possess photocytes with *Cypridina* luciferin and coelenterazine. *Cypridina* luciferin is only used by coastal fishes of the families Batrachoididae, Pempheridae and Apogonidae while coelenterazine has been suggested to occur in Stomiiformes, Myctophiformes and Platytrichtidae [44]. The remainder of intrinsically bioluminescent fishes may belong to coelenterazine or unknown luciferin types.

A pigmented layer of cells surrounds the light organs internally to absorb stray light [2]. Below the light organ, there usually is a layer of cells with a reflecting material that redirects the light towards the lens [45]. Some species lack reflectors [20, 21], and in others, the reflectors may not be present in all types of luminous tissues, as stomiids [46]. In fishes with indirect bioluminescence, the reflector is located above the ventral diffusive tissues (see **Figure 3**) instead of being inside the light organ [47]. Reflectors affect the emission spectra in some fishes, as in alepocephalids, and myctophids that lack pigmented lenses in front of the light organ [48, 49]. When the light produced by the photogenic chamber is emitted to the outside of the photophores, it passes through the lens [45], whose pigments filter the emitted light and adjust its spectrum to match that of the downwelling light [3, 48]. Some fishes like the monocentrids lack lenses. In the case of *Cleidopus gloriamaris*, a red-orange skin tissue external to the light organ alters the spectrum of the light emission [12].

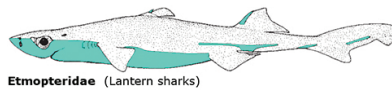


**Figure 2.** Schematic representation of the general structure of light organs in fishes. External side with light emission and internal side with blood capillaries and nerve supply. Matrix represents the space between the photogenic chamber and other structures. The right half of the photogenic chamber represents an intrinsic light organ with photocytes. The left half of the photogenic chamber represents a symbiotic light organ with transverse section of tubules filled with luminous bacteria.

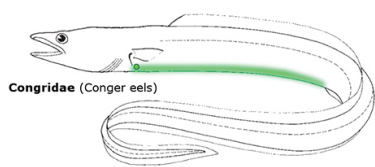
Fishes with luminous symbiotic bacteria emit light continuously, but may have some control over the light by chromatophores [34] and nutrient supply to the bacteria [34, 43, 45]. Shutters are tissue patches with chromatophores that can partially or totally cover the light organs and are under muscular control [41, 50]. These shutters are different across genera of the same family and may occlude internal organs as in leiognathids and *Siphamia* or may be restricted to external organs as in anomalopids [41, 50, 51]. It is suggested that anglerfishes possess a similar mechanism to control the light emission from the escae [41]. Skin chromatophores can be used to control light emissions in bioluminescent fishes with internal bacterial symbiotic organs (leiognathids [50], pempherids [47], acropomatids [19], evermannellids [2]) or externally (Gadiformes [52], Trachichtidae [12]), and bacterial symbionts in the lower jaw organs as in monocentrids [34]. There are some exceptions like *Opisthoproctus*, which may regulate light with ventral scale movements [2] and thaumatichthyids [41] and *Cleidopus gloriamaris* [12] that have light organs inside the mouth closing it to block the light emission. Leiognathids use branchiostegals to control their light emissions [53], and according to the observations of one of the authors (Yuichi Oba), the pigmented pelvic fins of *Chlorophthalmus* may serve the same purpose. The regulation of bacterial luciferase by oxygen and ion supply from the blood has been stated as a possibility, but there are no clear conclusions on this [39]. Observations by Meyer-Rochow [43] on *Anomalops katoptron* have shown that their bacterial light organs become successively dimmer when the fish starves.



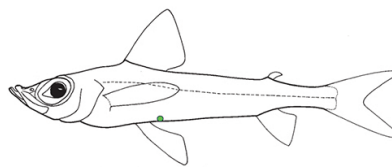
**Dalatiidae** (Kitefin sharks)



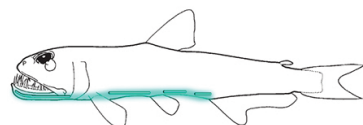
**Etmopteridae** (Lantern sharks)



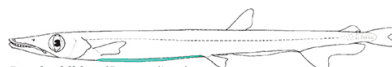
**Congridae** (Conger eels)



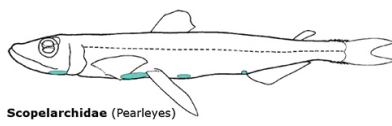
**Chlorophthalmidae** (Greeneyes)



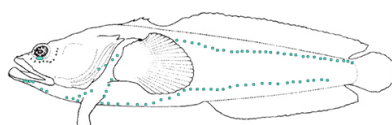
**Evermannellidae** (Sabertooth fishes)



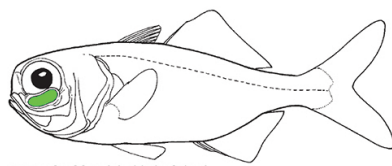
**Paralepididae** (Barracudinas)



**Scopelarchidae** (Pearleyes)



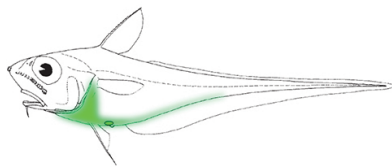
**Batrachoididae** (Toadfishes)



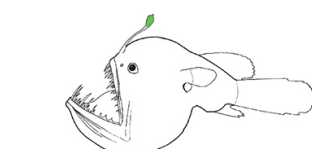
**Anomalopidae** (Flashlight fishes)



**Engraulidae** (Anchovies)



**Macrouridae** (Grenadiers)  
<sup>a</sup>**Merlucciidae** (Merluccid hakes), **Moridae** (Moras)



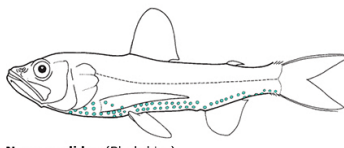
**Lophiiformes, Ceratioidei** (Anglerfishes)



**Lophiiformes, Ogcocephalidae** (Batfishes)<sup>b</sup>



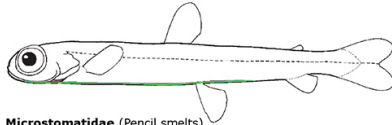
**Myctophidae** (Lanternfishes)



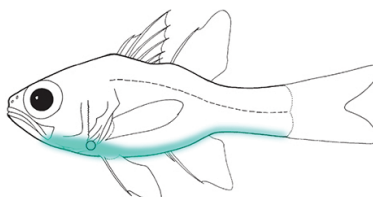
**Neoscopelidae** (Blackchins)



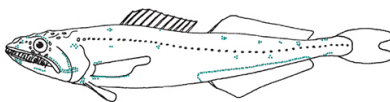
**Alepocephalidae** (Slickheads)



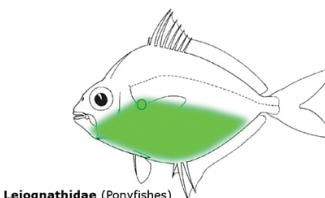
**Microstomatidae** (Pencil smelts)



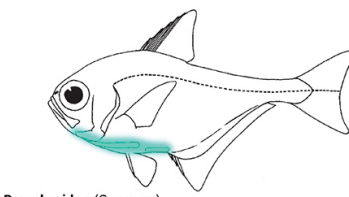
**Apogonidae** (Cardinalfishes)  
<sup>a</sup>**Epigonidae** (Deepwater cardinalfishes),  
**Howellidae** (Ocean basslets)



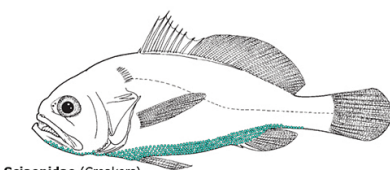
**Chiasmodontidae** (Swallowers)



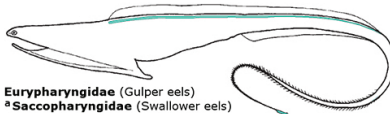
**Leiognathidae** (Ponyfishes)



**Pempheridae** (Sweepers)



**Sciaenidae** (Croakers)

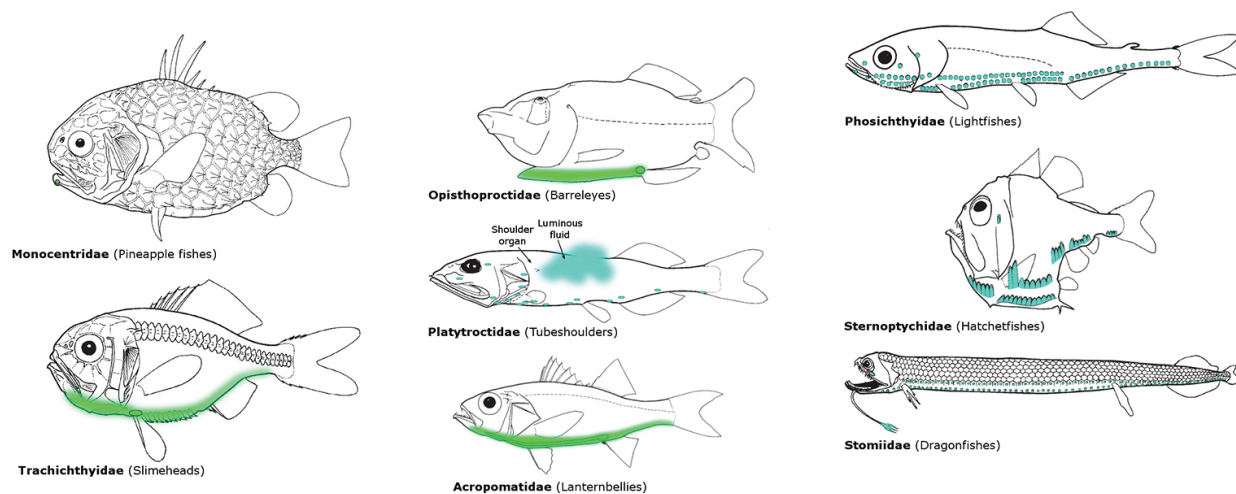


**Eurypharyngidae** (Gulper eels)  
<sup>a</sup>**Saccopharyngidae** (Swallower eels)



**Gonostomatidae** (Bristlemouths)





**Figure 3.** Light organs in fishes per family. Intrinsic bioluminescence in blue and symbiotic in green. The light organs are represented in coloured bands or circles delimited by a black outline. Blur coloured forms represent internal bioluminescence through diffusive tissues. <sup>a</sup>Used in cases that bioluminescent emissions and organs are very similar between families of the same order. <sup>b</sup>Crane [101] also found luminescence in skin samples of the ventral surface of the fish. Images are representative for the families and are not on scale. Same references used for bioluminescence in **Figure 1** plus [10, 13, 15, 95]. Source of drawings: Food and Agriculture Organization of the United Nations [15, 26, 96, 102–105]. Reproduced with permission.

Neural light emission control of intrinsic bioluminescence occurs in sharks [54], Stomiiformes [46, 55], myctophids, *Porichthys* [55] as well as alepocephalids [49] and proceeds through neurons in scopelarchids [56] and other coastal fishes besides *Porichthys* [33]. Neurons may be able to individually regulate light outputs of single photophores as in myctophids [55]. However, blood supply has also been suggested to be involved, at least in the control of the linophrynid's intrinsically luminous barbels [41].

Exceptions are platytrichtids, which excrete luminous liquids; a process that invokes muscular control [2, 41]. In some anglerfishes, the liquid may not actually be secreted by the Escae, but from small symbiotic luminous bulbs (the so-called caruncles) that in the family Ceratiidae are dorso-posteriorly positioned from the escae [14].

Luminous organs are predominantly ventral [21, 37] (**Figure 3**) but some light tissues can be dorsal, as in the escae of anglerfishes and photophores in dalatiid sharks. Some fishes have buccal light organs like in the apogonids *Siphamia* spp. [18], the myctophid genus *Neoscopelus* [20] and thaumatichthyids and *Cleidopus*. Light organs are present in or on the heads of some fish especially deep-sea species like alepocephalids [57], platytrichtids [13], myctophids, stomiids, and the chiasmodontid *Pseudoscopelus* [58], but also the shallow-water anomalopids and monacanthids [12]. Apart from these organs, there are other types of luminous tissues in fishes. Besides the 'normal' photophores, i.e. primary photophores, some species also possess secondary photophores that are smaller and of less complex structure [57]. These small photophores are then, rarely with some degree of preference, distributed all over the body of the fish, cf. platytrichtids, alepocephalids, myctophids and stomiids [13, 15, 57]. Myctophids possess caudal glands that usually present sexual dimorphism [2] and glandular light organs can also be found in the Stomiiformes [2, 46] and dalatiid species [8]. Luminous tissue with a

similar structure to photophores can be found in the body of myctophids [2] and stomiids [46] and barbels, while luminous mucus clinging to teeth was seen in some stomiids [20] and anglerfishes [2]. Some studies suggest the existence of bioluminescent skin in *Himantolophus azurlucens* and *Cryptopsaras couesii* [41].

The intensity of light emission in fishes can vary individually depending on the type of organ, depth and function (see further). Nevertheless, it seems that intensity is higher in coastal and shallow rather than mesopelagic, deep water species. Light spectra of the emitted lights usually peak in the blue-green, but are to some extent variable mostly in relation to depth. Coastal and epipelagic fishes produce light principally in the green and meso- and bathypelagic in the blue [3, 4, 33]. A rare case is the red light emission of some stomiids. Regarding angular distribution, bioluminescence starts to exceed downwelling light in the lower mesopelagic zone. At that depth, luminescence signals change from a ventral direction to a point-light scenario with bioluminescence emitted in all directions. The angle of the light emitted by an individual depends on the position of the light organ and its reflector in the body of the fish [2, 48], on the kind of transmission tissue involved and the body position of the light-emitting fish in the water column [37, 50]. Some shallow-water fishes like anomalopids and leiognathids can control the angle of the emitted lights [41, 50]. The light emitted also depends on the trophic level and nutritive state of the fish [43] and whether the light-emitting individual is looking at a conspecific side by side in a school, or, for example, prey above or a predator below.

## 4.2. Functions of light organs and likely roles of the emitted lights

A bioluminescent signal is defined by its intensity, spectral peak(s), temporal and spatial characteristics [3]. To what extent the degree of polarization, if any, plays a role has never been examined. The same luminous tissue may serve multiple kinds of functions, and the locations of the light organs are generally related to the roles the emitted lights are expected to play. The light generated can be used by a fish to communicate with its congeners, attract prey or avoid and startle predators. The range of functions of biological light is less complex in the coastal species than that in the deep water species, but even in the former, the emitted light has a variety of different biological roles.

### 4.2.1. Intraspecific communication

Fishes use light signals for intraspecific recognition, schooling and mating. Some fishes possess species-specific structures that purely on account of their placement and position may also assist specific recognition, as the photophore patterns in myctophids apparently do [59]. As aggregations of bioluminescent fishes help confusing predators, light emission may also assist school-forming species of etmopterids [10, 54], chlorophthalmids and macrourids [60].

A role in reproduction seems to be the part of the bioluminescence repertoire of at least some luminescent fishes including leiognathids, with their complex system of controlled light emission, and stomiids [2, 3]. Light organs are sexually dimorphic in some species of *Gazza*,



*Secutor* and *Leiognathus*, and courtship behaviours using light signals have been observed in these fishes [61].

#### 4.2.2. Interspecific communication

Some fishes use luminous organs located in or on the head to illuminate their surroundings, in search of prey and to detect predators. The bright headlights of anomalopids illuminate their surroundings, help them to avoid predators [62] and allow them to spot zooplankton [35]. Luminescence may be used for illumination in alepocephalids and macrourids in search of prey on the seafloor [30].

Many fish seem to attract their prey with bioluminescent lures. The escae of anglerfishes have been suggested to mimic faecal pellets with luminous bacteria [32]. Monocentrids have been assumed to attract prey with their light organs [53], but the cephalic photophores of *Diaphus* may be used to stun preys with bright flashes [1]. *Malacosteus niger* has small greenish light-emitting spots near its mouth and larger red light-emitting patches below its eyes. It is believed that the small greenish lights attract prey and the red light, invisible to most deep water organisms, is used by the fish to visually detect the approach of the unsuspecting prey in order to seize it when sufficiently close [2, 30, 48, 63].

Bioluminescent fishes can also use their lights in various ways to distract predators and avoid to be seen by them. Counterillumination is widespread and particularly common in the mesopelagic species, which emit light ventrally to match the downwelling light from above. In that way these often strongly laterally compressed species become camouflaged and almost invisible as silhouettes to the eyes of a predator below [37, 50]. This notion of the use of bioluminescence is strongly supported by biological and ecological facts. Photophores tend to be larger in the species of mesopelagic fishes occurring at shallower depths [2, 4], but the intensity of the ventral light emission from some fishes may change according to the light they find themselves in as from leiognathids [50] and myctophids [64]. Extraocular photophores in Stomiiformes, myctophids [2] and sharks [65] are located in optimal positions for comparisons of the downwelling sunlight with their own light in order to adjust it, a scenario that has also been suggested for apogonids [51]. Counterillumination appears to be of importance to the vast majority of luminous shallow water [33, 35] and mesopelagic teleosts [4, 21, 57] and sharks [66]. Whether the control of the matching luminescence involves eyes and ocular feedback or whether the light organs and cells within them are able to independently and directly regulate photic output of the light organ are questions yet to be answered.

Aposematism is a likely reason for the bioluminescent dorsal spines in etmopterids [67]. Aposematism is one of the proposed functions for bioluminescence in Porichthys as these species possess venomous dorsal spines [2]. When a possible predator is close by and ready to attack, other methods have to be used for luminous fishes to escape. One possible strategy for prey to evade a predator's attack is to emit a brief and blindingly bright flash of light right before changing its swimming direction. This has been suggested for the post-orbital photophores of anomalopids [62] and stomiids [4]. As most of the predators of these fishes have eyes adapted to dim light, very bright flashes may have a temporary effect of rendering them incapable of vision [32, 33]. In addition to the species already mentioned,

this survival strategy also seems to be employed in cases of the brief and bright flashes of leiognathids [53], the cephalic photophores in *Diaphus* [1] and the caudal organs of various myctophids [2]. A very similar defence has been proposed in cases in which a bioluminescent liquid is secreted into the water, acting as a luminous smokescreen and confusing the predator while the prey escapes [4]. Luminous liquids or mucoid secretions are produced in the 'shoulder organ' of platytroctids [57], the gill slits of the epigonid *Florenciella* [2], the anal gland of the macrourid *Malacocephalus* [21] and the escae and caruncles of some anglerfishes [21, 41].

#### 4.2.3. Unreported functions

For the bioluminescence in several families of fish, no particular reason for the biological light is known (**Table 1**). Nevertheless, most of these unreported cases deserve some attention. As for the majority of other pelagic species, counterillumination is probably the most important function in Somniosidae, Evermannellidae, Microstomatidae, Phosichthyidae, Epigonidae and Howellidae as well as in some other families of the same order. Eurypharyngidae may use their luminescence as a lure to attract food items as with members of Saccopharyngidae. The fact that bioluminescence characteristics exhibit considerable similarities within the families of the order Gadiformes may be used as evidence that functions suggested for Macrouridae can apply equally to Moridae and Merlucciidae.

## 5. Vision in bioluminescent fishes

Light enters the eye through the cornea (**Figure 4**), passes the pupil and is refracted by the lens and focussed on the retina. Photons are absorbed by pigments in the photoreceptor cells, transformed into synaptic signals, the latter being transmitted through interneurons to the retinal ganglion cells [30, 68, 69]. The axons of these cells are grouped together and form the optic nerve which passes the visual information to the optic areas in the brain [70]. The basic structure of the eye in fish conforms to that of other vertebrates, but there are features that differ, depending on the life style of the fish involved (predator or prey) and on the photic environment [3], i.e. essentially the epipelagic and mesopelagic zones, in which the fish eyes are supposed to operate [30]. The most obvious differences in the structure and function of the fish eye accompany differences in the light intensities prevailing along the depth gradient of the oceanic zones. The majority of the bioluminescent species inhabit deeper waters and their vision is adapted to dim light conditions [30]. The luminescent crepuscular or nocturnal epipelagic fishes [33, 34, 39] have photoreceptors that, too, are mainly adapted to function under low light conditions [68, 70, 71].

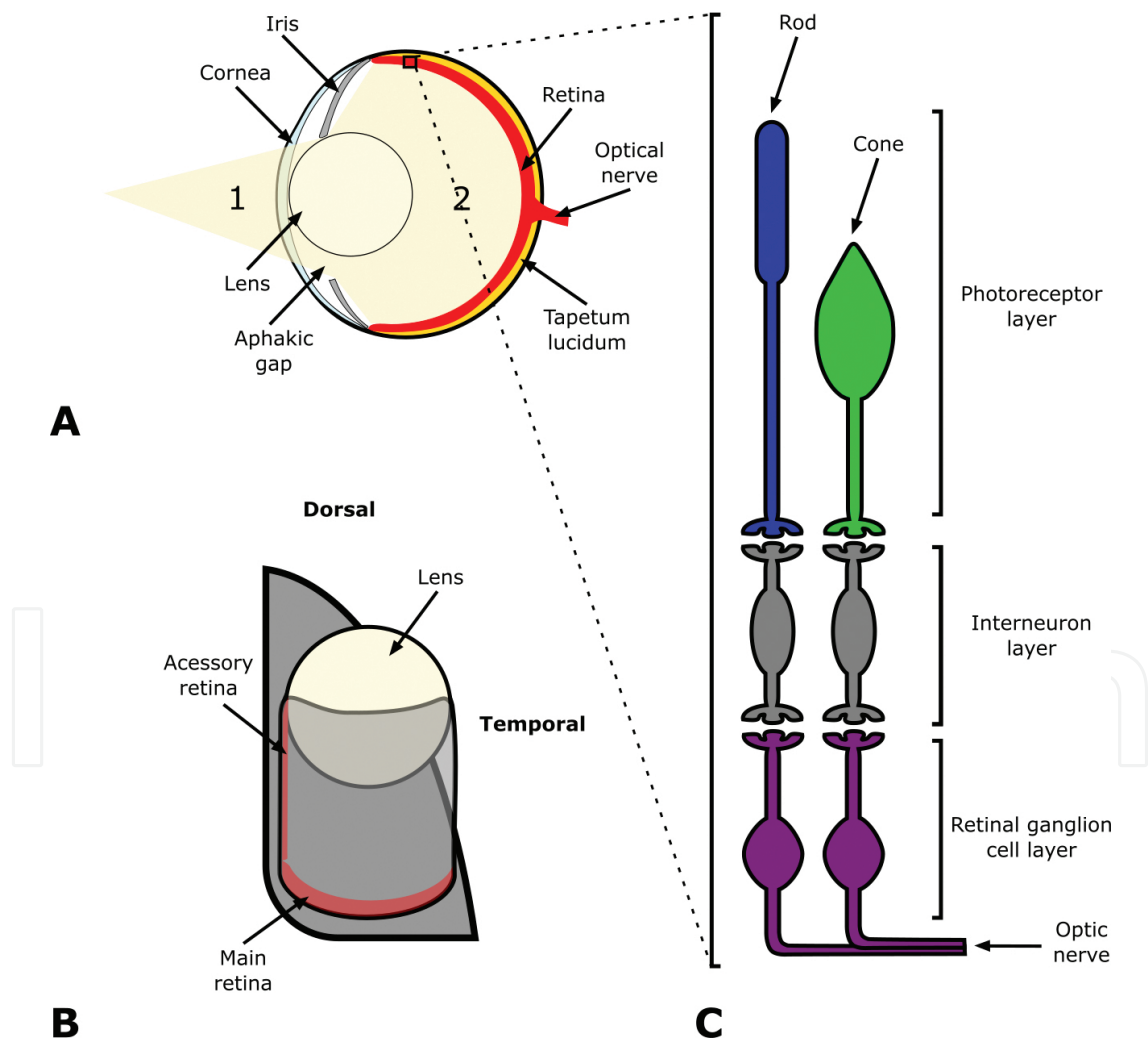
### 5.1. Eye (structure, size and position)

There are no bioluminescent fishes with degenerated eyes and all possess binocular vision [3]. Epipelagic [4, 33] and mesopelagic fishes [30] inhabit environments that can be reached by sunlight and they usually possess large laterally positioned eyes. In contrast, the aphotic

bathypelagic species often have smaller eyes [4, 30]. The majority of the bioluminescent fishes have typical single lens, camera-type eyes, but some mesopelagic fishes possess tubular eyes. The latter are cylindrical eyes located at the top of the head and on account of their position allow the fish to distinguish silhouettes against downwelling sunlight. In these eyes, their binocular overlap provides high quantum capture, and accessory retinae and additional visual structures allow them to also detect a certain amount of light coming from lateral and ventral regions [68].

5.2. Lens, pupils and gaps

Fish lenses present little spherical aberration and a gradient of refractive index with the highest value in the centre guarantees that the focus of the light is sharp [4]. Lens transparency helps sensitivity [3], but lens pigments may influence the colour of the light reaching the retina [36]. Large pupils corresponding to wide apertures allow the admission of more photons, increasing



**Figure 4.** Schematic representations of the eye structure in fishes. (A) Camera-eye representing light entering the eye (1) and refracted by the lens focused on the retina (2). (B) Front-view of a left tubular eye in the head of a fish. (C) Basic retinal structure by cell layers.

visual sensitivity [30]. Aphakic gaps can enhance sensitivity by allowing light capture from specific oblique areas of the visual field [3, 4]. Such gaps are more commonly rostrally placed and extend binocular frontal vision in the lateral eyes. Light passing through gaps may get focussed in specialized retinal areas [30, 31, 72].

### 5.3. Tapeta

Animals that live in dim environments often possess *tapeta lucida*, which consist of a reflective layer positioned behind the photoreceptors acting as a mirror [30, 71]. This layer reflects the photons that are not captured by the photoreceptors, sending them back to the photoreceptors [68] and doubling quantum capture success; thus improving the sensitivity of the eye [31]. The spectral reflection peak of the tapetal regions in some fish species is thought to coincide with the absorption peaks of the visual pigments in the photoreceptors of the fish, but in some cases specific tapetal areas reflect spectrally different light thereby fulfilling specific visual tasks [36, 72].

### 5.4. Retina

Photoreceptor cells are responsible for the perception of light and their anatomical and ultrastructural make up, organization, dimensions, density, and distribution, and visual pigment is what has to match the behavioural visual tasks required of them by their owners in the specific photic habitats [69]. Like other vertebrates, fishes have two anatomically distinguishable types of photoreceptors. Cones, of which physiologically different two, three or more kinds with non-identical peak spectral sensitivities may be present, perceive different colours under conditions of bright light. Contrary to cones, rods are monochromatic photoreceptors, but provide the fish with high sensitive vision under low levels of light [36]. Cones occur in some bioluminescent fishes but are often reduced in total number and/or size even in the shallow-water species [60, 68, 70, 71, 73, 74]. Deep-sea fishes have mostly pure rod retinas of high cell density, for there is little need for them to be able to distinguish colours. For them the priority is to possess high sensitivity in a blue-light dominated nearly monochromatic dim, almost dark environment. High sensitivity of the rods is achieved by longer and wider cells. Sensitivity is also enhanced when rods are arranged in groups or are arranged in multi-layers called banks [30].

The differences in function between rods and cones are due to different kinds of photopigments in the visual cells. Rods possess either rhodopsin, a visual pigment with maximum absorbance at short wavelength (chemically a retinaldehyde, retinal 1 or vitamin A<sub>1</sub>-based compound) or porphyropsin (i.e. chemically a 3,4-dehydroretinal, retinal 2 or vitamin A<sub>2</sub>-based compound) [36]. Deep-sea fishes usually have high concentrations of rhodopsin giving the fish broad sensitivity to blue-green wavelengths [69]. However, some deep-sea fish have rod types containing different wavelength-sensitive rhodopsins or in addition may also have porphyropsins, the latter with longer-wavelength peak absorbances. The variety of receptor types and the development of banked retinas to increase absolute sensitivity can provide deep-water fish with the potential to make use of a wide range of photic stimuli [36, 75].

The density of retinal ganglion cells and, in particular, the ratios between receptors to ganglion cells define visual acuity and sensitivity. A high ratio of rods to retinal ganglion cells is indicative of high absolute sensitivity, while a low ratio would favour acuity. Most of the deep-water fishes possess unspecialized retinae and retinal cell ratios typical of sensitivity improvement [30, 31]. However, even so slight regional enhancements of acuity may be found in some species [68, 76].

Retinal specializations are regions of concentric increases in visual cell densities that enhance the visual sensitivity (rods) or acuity (retinal ganglion cells). These specializations seem to be related to visual behavioural tasks [72, 76]. In bioluminescent fishes, *areae centralis* and foveas can usually be identified as areas with higher visual acuity than the rest of the retina [30, 68], but it is possible that such specialized retinal regions change during the lifetime of a fish [77].

## 6. Evolution of bioluminescence and vision

The eyes of bioluminescent fishes evolved as adaptations to a dim light environment, in which bioluminescence provided important visual stimuli to perceive predators, prey items and mates. The fact that the bioluminescence in these species shares optical properties with the light pervading the environment the fish inhabit indicates the role selective pressures must have played [4]. Nevertheless, one cannot discount the idea that light emission and reception together represent a mutual and progressive adaptation [3].

In fishes, the adaptation of rhodopsin pigments to dim-light vision occurred in 12 separate occasions, suggesting that dim-light vision was a subject to considerable adaptive evolution [5]. In deep-sea fishes, these pigments were already shifted and adapted to the same visual environment as today in the Early Triassic. This shift was an adaptation to maximize the quantum capture of the dim sunlight and the biologically generated light in the deeper water of the sea. Along the way, convergent evolution seemed to have occurred with regard to rhodopsins of deep-sea fishes for adaptation to specific light regimes. This would explain the variation of wavelength sensitivities in these fishes, some adapted to specific bioluminescence peaks [75, 78]. Diversity in the pigmentation of the lenses of deep-water fishes suggests that it too has been the subject of separate evolutionary events a number of times [36]. Much later than vision, and assumed to have happened from the Early Cretaceous to the Late Cenozoic, bioluminescence appears to have evolved in teleosts [17]. A total of 27 independent occurrences are regarded to have left representatives in the marine teleosts assemblage, appearing first in the Stomiiformes [17]. Bioluminescence in the three closely related families containing luminescent species of sharks is also thought to have evolved from a common ancestor during the Cretaceous [9, 10, 17]. Bioluminescent patterns could have contributed to speciation in fishes [9, 11].

### 6.1. Bioluminescence evolution

An exposure to different light regimes powerfully influences the type of bioluminescence characteristics in the species of different habitats. This can express itself through different



spectral emission peaks and intensities of the biologically generated lights matching the photic environment of a species' habitat. The angle and direction of the emitted light are also subject to evolutionary pressures as most of luminescence glows ventrally in epipelagic and mesopelagic zones [2, 21, 33], where traces of sunlight from above are still discernible. No light from above, on the other hand, reaches the bathypelagic zone where the bioluminescent species exhibit a reduction in the number and sizes of photophores [2]. A good example of this tendency is the bathypelagic myctophids of the genus *Taaningichthys*, in which only the deepest living species, *T. paurolychnus* [79], lacks photophores (but still possesses caudal glands) [15].

#### 6.1.1. Functions

Bioluminescence plays major roles in the ecology of the luminescent fish species. The evolutionary history of bioluminescence in fishes shows that the ability to generate light arose dozens of times in unrelated clades [17] and yet, the basic structure of the light organs is nearly the same in all cases, independent of substrate, position and functions of the organ [20, 37]: counterillumination seems an excellent example. Fishes developed different ways to hide their silhouette from predators, using their ventral light emission. Some species make use of rows of photophores for that purpose, whereas others use indirect luminescence, but each case arose repeatedly and independently during evolution [17, 21].

An example of different structures employed in counterillumination can be seen in shallow-water species. In that environment, all the fishes use an indirect form of bioluminescence for camouflage with the exception of *Porichthys*, sciaenids and *C. dussumieri* that have photophores for that purpose [2, 33]. Different photogenic origins (i.e. symbiotic and intrinsic) may have led to the evolution of counterillumination, and some excellent examples are those that involve indirect bioluminescence. Some shallow (e.g. pempherids) and deep-water (e.g. *Coccorella atrata*) fishes use intrinsic light organs for indirect ventral bioluminescence, but the majority of species with this kind of light emission are employing symbiotic bacteria [2, 19, 39]. This divergence of photogenic origins can also be observed within apogonids [2]. Ventral luminescence in diel vertical migrants must also have come under selective pressures to conceal the silhouettes of the migrants from predators, when ascending into shallower and more illuminated waters [21, 37]. It is also conceivable that light signals in interspecific schools of diel vertical migrants play a role in keeping individuals together [3]. Although we focussed on counterillumination, there are other less well studied examples of structures of photogenic as well as non-photogenic origins serving identical functions in bioluminescent fishes. What immediately comes to mind are the symbiotic lures in anomalopids [53] and ceratiids [14] and the intrinsic barbels of stomiids [4] and photophores in sharks [8].

#### 6.1.2. Acquisition

Whether we deal with cases of intrinsic or symbiotic bioluminescence in fishes, the acquisition of the bioluminescence must have appeared at some point in the evolutionary history. It is still not clear how and when this happened, but based on some widely accepted suggestions the process behind it is thought to have involved the higher availability of luminous bacteria in coastal areas as a cause for the widespread use of symbiotic bacteria in the bioluminescence



of fishes inhabiting seashore-near habitats [80]. Similar kinds of constraints could have acted upon the *Cypridina* luciferin containing species of intrinsic luminous fish. These fishes are coastal species [33, 44] and the ostracods, which produce *Cypridina* luciferin, *Vargula* and *Cypridina* are benthic species and seem to inhabit mainly coastal and shallow waters [81–83]. It is well established that fishes like apogonids, pempherids and *Porichthys* have obtained the *Cypridina* luciferin from ostracods they ingested [18, 47, 84]. As there are no records that fish can synthesize coelenterazine, dietary acquisition seems a plausible scenario. This suggestion is supported by the widespread occurrence of coelenterazine also in luminous mid-water fishes and the fact that this substance is most abundant in the tissues of the digestive tracts of these fishes [85].

On the other hand, we have the symbiotic luminous fishes, in which light-producing bacteria are responsible for the bioluminescent capacity of the host. In return, the host provides protection, a place to grow, nutrition and oxygen to the bacteria [42]. This symbiotic relation could have started with facultative luminous bacteria in the gut of fishes (e.g. leiognathids), evolving into the obligatory symbiosis we now witness in anglerfishes and anomalopids [39, 41]. Hosts are ecologically dependent on the bacterial light and 'host family-bacterial specificity' seems to be the trend [42]. However, contrary to what had been believed for decades, nowadays coevolution between facultative symbiont and the host fish species is regarded as an unlikely scenario [41] as different fish host the same bacterial species and different species of bacteria can be co-symbionts of fish species. Moreover, evolutionary divergence in the bacterial species is unrelated to that of the host species [86]. Nevertheless, the absence of non-luminous bacteria in the organs indicates that some selection must have taken place [42] and associations could have arisen (or been bolstered) through environmental factors like the depth that the metamorphosing larvae inhabit. Support for this notion comes from *Photobacterium leiognathi* and *Photobacterium mandapamensis* found in organs of fishes that inhabit warmer and shallower waters and *Photobacterium kishitanii* that is found in deeper and colder waters [39, 42, 86].

## 6.2. Visual adaptation to bioluminescence

Vision in fishes evolved primarily as an adaptation to light intensity changes to extended or point sources in the near and far field of vision and secondarily to species-specific ecological needs [30, 31]. Bioluminescence has, to a large extent, affected the evolution of the optical system in luminescent fishes, which is obvious when one compares the eyes of fishes inhabiting the mesopelagic and bathypelagic realms. In the mesopelagic zone, animals use counterillumination to match the dim background light [36] and under such conditions fish evolved certain adaptations like tubular eyes [68], yellow lenses and retinae with banked receptor cells. In terms of their function, such eyes had to be sensitive, able to distinguish small spectral discrepancies from background light and to detect camouflaged prey [36]. For bathypelagic fishes, on the other hand, the only light sources available to them would have been of bioluminescent origins, restricting the range of their visual adaptational possibilities [31]. The bathypelagic species therefore tend to have larger aphakic gaps than mesopelagic species even within the same genus [3, 68]. As food is scarce at these greater depths, fishes living there

evolved less energetically expensive small eyes [4]. Nevertheless, these fishes do possess eyes with visual acuities capable of distinguishing point-source bioluminescence. Moreover, the eyes of the bathypelagic bioluminescent species show overall fewer regressed features than the eyes of the non-luminescent bathypelagic species do, indicating that the former rely more on vision than the latter. There are even some bottom-dwelling deep-sea fishes that have severely degenerated eyes, which are likely to detect no more than the presence or absence of bioluminescence of perhaps invertebrates in the seabed [31].

The types of visual pigments [5] and the balance between visual acuity and sensitivity are the results of millennia of selective pressures stemming from the diverse light regimes and visual tasks fishes had to contend with [4]. Visual pigments evolved primarily to light from the sun, perhaps to guide specimens to darker regions and shelters away from the light or to seek illuminated areas, but in deep-sea fishes photopigments seem to be much more attuned to bioluminescence spectra [4, 6, 30, 36]. The eyes of most of the deep-water species have high concentrations of rhodopsin giving them a broad sensitivity to the blue-green range of the spectrum [69], comprising wavelengths that seem ideally suitable for perceiving bioluminescence emissions of prey, predators and conspecifics [6]. Potential colour vision in some deep-sea fishes may be an adaptation to identify species by differences in their bioluminescence hues [69, 75].

## 7. Ontogeny of bioluminescence and vision

### 7.1. Metamorphosis of eye and luminous tissues

During larval metamorphosis in fishes, the eyes change in shape, size, structure and even location [27]. The best examples among bioluminescent species are the tubular eyes, which are formed from laterally placed camera-type eyes in the larvae that become tubular in shape and migrate dorsally during metamorphosis. The lens remains unchanged but the retina suffers many alterations [87]. Retinae in larvae of the deep-water species, whether or not luminescent, are poorly specialized and vision, generally, is much less developed than in adults [88]. Almost all fish larvae have pure-cone retinae that are totally or partially substituted by rods during metamorphosis. The only exceptions in bioluminescent fish larvae are Saccopharyngiformes and *Lumiconger arafura*, in which pure rod retinae are the rule. In retinae with rod multilayers, the number of banks increases throughout development [68, 87, 88].

Photophores are formed during metamorphosis of a fish [22, 27, 87] and some are then already functional [2]. The luminous organs of symbiotic fishes also develop during larval metamorphosis [39]. This is the case of other luminous tissues too, as for example, the caruncles of ceratiids [41] and the caudal glands of myctophids [27]. Furthermore, the barbels of stomiids seem to arise during metamorphosis [27] and continue to elaborate throughout the fish's development [4].

The acquisition of the photogenic substrate in fishes is not well known. The luminous organs of symbiotic fishes start to develop prior to their being colonized by bacteria. Colonization

occurs during metamorphosis and it seems that each new generation of fish needs to acquire its symbiont afresh from the environment. The larvae of the shallow-water species are spatially close to adults, which suggests that bacteria may be released from the adult light organ and transferred to the young [39]. This does not seem to apply to the deep-sea species as the larvae are planktonic and hundreds of metres away from the adults. In these cases, it was suggested that larvae are infected when they migrate to coastal areas where luminous bacteria are more abundant [42, 80]. For ceratioids, the secretory cells that are common only in young fish may liberate pheromones to attract the right bacterial symbiotic species [41]. In intrinsic species, maternal transference of *Cypridina* luciferin was observed in *Porichthys* [84]. The same mechanism was suggested to apply to other teleosts and etmopterid sharks [89, 90].

## 7.2. Ecology and ontogeny: vision and bioluminescence in young fishes

Most symbiotic and intrinsically bioluminescent fishes have epipelagic larvae that will inhabit mid- or deep-waters as adults [4, 12, 15, 22, 26, 39]. During this ontogenic vertical migration to deeper waters, the visual habitat changes to an increasingly dim and monochromatic light scenario. These changes in the light environment require the modifications of the fish's photoreceptive as well as luminescent structures (described above) to coincide with the larvae undergoing metamorphosis. The migration to deeper waters and the metamorphic changes previous to the habitat change are believed to be completed in a relatively short time [87]. The development of rods and the changes in photoreceptor arrangements prepare the metamorphosing larvae to a life as a juvenile or adult in an environment where superior visual sensitivity is paramount. The transformations provide the young fish with visual capabilities for recognizing conspecifics, forming schools, engaging in predation and tracking and evading predator advances. In multi-layered retinæ, a greater development of banks appears to coincide with the greater depths juvenile fish seek to spend their lives in as adults. In shark species, a metamorphosis similar to that seen in teleost is not present and the ontogenesis of photogenic organs or eyes in bioluminescent sharks has not been studied in much detail [68, 87].

In teleosts, the development of luminous organs is also affected by the changes in the photic environment and the behaviour of the young fishes. In some Stomiiformes and myctophids, the early development of cephalic photophores suggests that they are used to lure crustacean prey at night [22]. The more common scenario is that in the species whose larvae occur in dimly illuminated waters, photophores develop on the body first [2, 22, 91] and then gradually become functional as the migration to deeper water proceeds [22]. Larvae tend to develop photophores earlier in the species that inhabit deeper water as adults. For juveniles, light emission changes during growth and maturation [22]; ventral luminescence develops rapidly during that phase of the life of many teleosts [2, 4, 12, 52]. Ventral photophores also appear to be more developed in juvenile etmopterid sharks that inhabit shallower depths than the adults [8]. Considered together, these observations highlight the importance of counterillumination in young fishes while they migrate to deeper waters [2, 22].

Not only do photophores and light organs change in relation to a fish's developmental stage, the role or roles bioluminescence is to play in the life of a fish may also change with age. This

has been suggested for etmopterid sharks as ventral patterns of photophores used for mating and schooling are more developed in adults [8, 92]. Photophores of young platytroctids are horizontally placed on the body and are probably used to illuminate prey, while distracting predators. These photophores, however, do acquire more vertical positions as the ontogenic development proceeds [13] and this very likely implies a similar explanation to that seen in scopolarchids in which luminescence is limited to the adults [2]. In both cases, the use of the ventral lights only in adults is strong evidence for its function as counterillumination devices to help camouflage silhouettes of larger adult bodies.

## 8. Visual ecology

Considering bioluminescence as a means for communication and vision may help us understand its origins in fishes. Luminous species exhibit adaptations for a wide range of visual tasks [30] as light organs are multi-purpose and in most cases their predators and preys are also bioluminescent [2, 30]. Most bioluminescent signals are of rather low intensity, but bioluminescent fishes frequently possess rod-dominated retinæ, conferring to them high visual absolute sensitivity [68, 70, 71] allowing them to perceive even very dim lights.

### 8.1. Bioluminescence detection

The optical characteristics, i.e. 'quality and quantity' of the light emitted by the vast majority of mid and deep-water luminescent species of fish relate to the downwelling light of their habitats. Vision accompanies this tendency. All of the luminescent species, whether shallow or deep-water fishes, possess eyes with at least some visual overlap, i.e. binocular vision, and that enhances sensitivity to and detection of distant point sources in dimly lit environments [68]. Bioluminescent fishes, moreover, frequently exhibit large pupils, which help them to detect bioluminescent flashes against a wider background [30]. The visual pigments present in the eyes of deep-sea bioluminescent fishes seem to be perfectly adapted to the bioluminescence spectra they encounter [2, 6, 30, 36].

Additionally to these more general adaptations, bioluminescent fishes evolved numerous visual particularities in order to improve detection of bioluminescence signals. Large eyes in epipelagic and in particular mesopelagic species admit greater amounts of photons, banded photoreceptors further improve the photon yield and efficient tapeta permit an at least two-fold photon catch. Such adaptations are critically important if sensitivity improvement in order to use bioluminescence is the goal. Different spatial relation of aphakic gaps, retinal specializations and tapeta are particularly well developed among the myctophid species [72] and luminous sharks [65]. Most deep-sea fishes can detect bioluminescence signals up to 30 m away [6, 48]. Some are even able to see bioluminescence up to 51 m as in bathypelagic fishes [21]. Bioluminescent bathypelagic fishes possess small eyes with wide pupils, rostral aphakic gaps and acute foveas. Although these eyes are less sensitive than those of the mesopelagic species, their resolving power is better and they seem perfectly adapted to spot point sources of biological lights in their environment. Contrary to non-luminescent bathy-

pelagic fishes, the eyes of the luminous species are not widely separated, aiding them in distances estimation [31, 68].

## 8.2. Intraspecific communication

In many bioluminescent fish species, their luminescence seems to play a role in communication between conspecifics. The eyes of these species are by necessity optimally adapted to their own bioluminescence. In shallow-water species, anomalopids seem to have eyes and retinæ adapted to their own lights [74] and the visual pigments of *Porichthys* are also a good match to the emission spectrum in this species [73].

In deeper species, the eyes of *Chlorophthalmus*, with yellow tainted lenses and a specialized retina with some cones seem specifically adapted to their own blue-green light emissions [60]. Myctophids also possess visual pigments adapted to the spectra of their own light emissions [6]. Most male anglerfishes possess relatively large laterally positioned eyes with aphakic gaps [14] and long rods for heightened absolute sensitivity, adaptations that may be linked to the use of the female's esca to attract the attention of a male [3]. The genera *Malacosteus*, *Photostomias* and *Aristostomias* possess sub-ocular photophores, which emit red-light used as a 'private waveband'. These species evolved long-wavelength pigments in their rods and possessed tapeta and lenses that allow them to see their own red light [36].

Dalatiid sharks do not school, contrary to etmopterids [10]. In bioluminescent sharks, only the etmopterids seem to use their light emissions for intraspecific purposes, specifically the lateral patterns of the photophores [8, 92]. These patterns are more nasal and temporal in *Etmopterus lucifer* and seem to be detected by specific sensitive and acute zones in the nasal and temporal areas of the retina of this species [65].

## 8.3. Hunting

The use of bioluminescence in the context of food procurement in luminescent fishes is common. Photic lures to attract prey are one of the better known examples of luminous hunting devices. In order to be seen by and attract prey, the light tissue of the predator needs to be brighter than the background and has to be located in a visible place of the predator body, preferably the head and near the mouth [21]. Indeed, the most luminous structures of fishes that are likely to act as lures are easily spotted and emit an intense light, as the escae of anglerfishes [41], the barbels of stomiids [4] and the head organs of anomalopids [33], monacanthids [12] and *Diaphus* [1]. Most of their prey organisms possess highly sensitive eyes [30], so that the perception by them of the lights emitted by the photic lures is not an issue.

Some luminous fishes use their light to illuminate their surroundings, helping them in the search and seizure of prey, as suggested for anomalopids [35, 62] and *Diaphus* [1]. The same is possible for the benthopelagic deep-sea fishes, as alepocephalids and macrourids, that have uncommonly well-developed eyes, which might serve them to search for prey with their ventrally aimed luminescence [31].

It is common for bioluminescent fishes to prey on other luminous organisms. A good indication of this is the acquisition of *Cypridina* luciferin by fish through the consumption of luminous



ostracods [18, 33] and the high amount of coelenterazine in the digestive tissues of bioluminescent fishes [85]. The eyes of these predators, exhibit characteristics that help them perceive the bioluminescence of their prey. The highly sensitive retinae of fishes like myctophids, ensures that light from prey reaching them over relative long distances, i.e. several metres, is registered [72, 76]. Luminous sharks have retinal specializations, aphakic gaps and tapeta that also seem to be used for the detection of luminescent prey. In the specific case of the dalatiid *Squaliolus aliae*, the shortwave sensitive pigments in its retina seem to be more adapted to prey emitting blue-luminescence [65].

The fact that the prey of luminous fishes is frequently bioluminescent can create problems for the predator as most prey may employ counterillumination for concealment [4]. Bioluminescent fishes therefore appear to have evolved visual mechanisms allowing them to distinguish light emissions of prey from the downwelling surrounding lights. Most of the predators seeking to capture fish that employ counterillumination have large eyes that can disrupt the prey's counterillumination at close range [32]. Other species have evolved tubular eyes which possess acute retinal areas [30] perfect to detect at greater distances even silhouettes camouflaged through counterillumination [21, 46] and diverticula and accessory retinae to detect lateral luminescent stimuli [3, 31]. Some predators use yellow eye lenses to cut-off blue spectra, and to recognize the minimal green mismatches revealing the luminous silhouettes of prey [36]. Aphakic gaps 'lined' with retinal specializations of photoreceptor and ganglion cells as in myctophids may further help detecting counterilluminated prey [72, 76]. The enhancement of binocular resolution by foveas in deep-sea fish may also aid in breaking luminescent camouflages [68]. Different visual pigments and banks in rods that potentiate colour vision in deep-sea fishes are probably involved in breaking counterillumination [36, 75] and the translucent skin area above the eyes in etmopterid sharks may filter the spectra of luminescent prey, thereby compromising the camouflage of the latter [65].

#### 8.4. Predator avoidance

One of the major functions of bioluminescence is defence [4, 33]. It is therefore not surprising to see such a vast number of different self-protective mechanisms in luminescent fishes. The trick is to avoid being seen by predators and in the case that has already happened, to deceive the predator and 'to go on the run'. The method of defence as well as vision of the predator and prey is always involved. We already stated the possibility for the predators to be luminous and that the eyes of bioluminescent fishes serving as prey are sufficiently sensitive to detect the predator. Curiously, except for the purpose of camouflage, smaller species tend to produce faster and shorter flashes than the larger predators [93]. This seems a strategy to reduce the risk to be accepted by a predator. A predator cannot afford the effort and risk of checking out every single flash it encounters, so that the predator would probably use the size and duration of a flash it encounters in deciding whether pursuit is worthwhile and the emitter of the luminescence is large or small [32].

The spectrum of a luminescent species' light used in counterillumination is not always a perfect match of the downwelling light [30]. This is not a problem for the deep-sea species as most of their predators do not possess colour vision [4, 48] and intensity rather than spectral matching



is most important and apparently within the capability of most species that employ counter-illumination concealment [4, 30, 32, 64]. On the other hand, epipelagic predators of bioluminescent fish have eyes more capable than those of deeper waters [94] to disrupt counterillumination [33]. The majority of coastal luminescent fishes exhibit internal light organs providing them a kind of disruptive luminescence that is more effective in turbid and dynamic near-shore waters than the uniform glow [33, 50] of deep-water species that live in more homogeneous and optically transparent photic environment [4].

Since both nocturnal predators of shallow-water bioluminescent fishes [94] and deep water predators [30] possess highly sensitive eyes, luminescent 'smokescreens' and very bright, brief flashes can temporarily confuse or even blind a predator and allow potential prey to flee [33].

Bioluminescence is not always straightforward and what seems to be an advantage can become a disadvantage under certain conditions. The 'private waveband' of the red light in stomiids seems an outstanding evolutionary trait for a predator, but some prey like scopelarchids [69], gonostomatids [75] and myctophids [6] have retinae with additional long-wave sensitive photopigments enabling the potential prey to see the stomiids red light. Fishes with 'head lamps' to illuminate the surroundings may be coastal and nocturnal or midwater inhabitants. Their bright emissions may be an advantage to pick up prey, but they are also a disadvantage as predators can easily spot these fishes and be attracted to them [12, 32, 33]. Nevertheless, the risks of that happening appear to be reduced as these species feed in schools from which predators usually find it more difficult to focus on an individual fish and seize it [12, 33, 94]. Moreover, the luminescent anomalopid also can rapidly and repeatedly occlude their lights [35, 41, 43].

## 9. Final remarks

### 9.1. Methodology

To understand the inter-relationship between vision and bioluminescence in luminescent species, detailed information on eyes and light organs of these animals is paramount. Spectral properties and intensities of the emitted lights, development, organization, structure and function of photophores as well as photoreceptors have to be studied and behavioural correlates need to be identified. None of that is easy; accessibility is difficult, measurements of the light emissions in luminescent fishes can be a tricky undertaking (especially for deep-sea teleosts and sharks) and when caught, these animals are more than often moribund and in most cases have to be stimulated to glow. This is possible using electricity and/or certain chemicals [34, 55]. The intensity and spectra of such induced light emissions can be measured using a spectrometer and a photo detector, but the data may not exactly reveal their properties in the way the fish use their luminescence in their natural environment. The angle of the light emissions depends on the light organ's position on the body and the internal angle of the organ, both analysable to a fair degree of accuracy using histological techniques [46]. Chemical analyses of the chemical compounds involved in the generation of the biological light would help understand the underlying mechanism involved, but control of the light emissions,

whether direct by the photophores themselves, through nervous signals or hormonal mediators requires living, healthy specimens.

Anatomical details of the eye, cell topography, photoreceptor cell types, cell ultrastructures and distributions as well as certain visual parameters can be gleaned from histological investigations, but while functional parameters like sensitivity, acuity, angular acceptance, etc. can to some extent be deduced from the anatomical details, electrophysiological techniques or the use of microspectrophotometry must be the methods of choice when it comes to functional questions. Spectral sensitivity peaks of the visual pigments obtained spectrophotometrically or electrophysiologically ought to be connected with chemical analyses of the photopigments involved and opsin gene analyses [36]. Chemical and optical studies like refractive indices, focal lengths, etc. on the dioptric structures of the fish eye ought to complement the other investigations so that predictions can be made on the way a fish uses its eyes.

Evolutional studies of vision receive support from investigations on the mutagenesis of the visual pigments [5] and genetics of nuclear and mitochondrial gene fragments can also be used in studies on phylogenetic relationships between species [17]. Often lacking first-hand direct observational evidence of vision/luminescence interactions in the natural environment, the next best approach would involve realistic analyses of the underwater transmission of bioluminescence in specific cases and ecological modelling, based on the information available [48].

## 9.2. Future prospects

Communication by light is a subject of considerable interest to ethologists and ecologists, chemists, geneticists, anatomists, physiologists, opticians and vision researchers. Biotechnologists, too, become increasingly interested in bioluminescence generally and communication by light in particular. For the comparative zoologist it is important to realize that behaviour exhibited by individual luminescent fish in captivity may not be the same as that in the fish's natural environment. This is even more important to keep in mind when interpreting the induced light emissions obtained from nearly dead deep-sea species. Moreover, vision and bioluminescence are only part of a bigger picture. There is evidence that pineal photoreceptors support light perception and are even involved in light output regulation in deep-sea fish [64]. Therefore in analyses of the ecological role, i.e. overall biological significance that bioluminescence plays, we must not ignore the fact that other sense organs like, for instance the lateral line system, semicircular canals, otoliths, chemo, electro and magnetoreceptors, etc. may also be involved [4].

Regarding the eco-ethological roles of the relationship between bioluminescence and vision, some questions have been answered but many more remain to be solved. Remotely operated underwater vehicles (ROVs) can be expected to help in this task and should provide new *in vivo* insights into the various eco-ethological roles of bioluminescence while advances in genetic techniques can be expected to shed further light onto the phylogeny and evolution of these 'brightest creatures of the animal world'.

## Acknowledgements

The authors are grateful to the Food and Agriculture Organization of the United Nations for the authorization of the drawings in **Figure 4** and Dr. Hayato Tanaka for the information on luminous ostracods.

## Author details

José Paitio<sup>1</sup>, Yuichi Oba<sup>1\*</sup> and Victor Benno Meyer-Rochow<sup>2,3</sup>

\*Address all correspondence to: yoba@isc.chubu.ac.jp

1 Department of Environmental Biology, Chubu University, Kasugai, Japan

2 Department of Genetics and Physiology, Oulu University, Finland

3 Research Institute of Luminous Organisms, Hachiojima, Japan

## References

- [1] Haddock SHD, Moline MA, Case JF. Bioluminescence in the sea. *Annual Review of Marine Science*. 2010;2:443–493. DOI: 10.1146/annurev-marine-120308-081028.
- [2] Herring PJ, Morin JG. Bioluminescence in fishes. In: Herring PJ, editor. *Bioluminescence in Action*. London: Academic Press; 1978. pp.273–329.
- [3] Nicol JA. Bioluminescence and vision. In: Herring PJ, editor. *Bioluminescence in Action*. London: Academic Press; 1978. pp. 367–408.
- [4] Herring P. *The Biology of the Deep Ocean*. New York: Oxford University Press Inc.; 2002. 314 p.
- [5] Yokoyama S. Evolution of dim-light and color vision pigments. *The Annual Review of Genomics and Human Genetics*. 2008;9:259–282. DOI: 10.1146/annurev.genom.9.081307.164228.
- [6] Turner JR, Whit EM, Collins MA, Partridge JC, Douglas RH. Vision in lanternfish (Myctophidae): Adaptations for viewing bioluminescence in the deep-sea. *Deep-Sea Research I*. 2009;25:1003–1017. DOI: 10.1016/j.dsr.2009.01.007.
- [7] WoRMS Editorial Board. *World Register of Marine Species* [Internet]. [Updated: 2016]. Available from: [www.marinespecies.org](http://www.marinespecies.org) [Accessed: 20/06/2016].

- [8] Claes JM, Mallefet J. Bioluminescence of sharks: First synthesis. In: Meyer-Rochow VB, editor. *Bioluminescence in Focus - A Collection of Illuminating Essays*. Kerala: Research Signpost; 2009. p. 51–65.
- [9] Straube N, Li C, Claes JM, Corrigan S, Naylor GJP. Molecular phylogeny of Squaliformes and first occurrence of bioluminescence in sharks. *BioMed Central Evolutionary Biology*. 2015;15:162. DOI: 10.1186/s12862-015-0446-6.
- [10] Reif W-E. Function of scales and photophores in mesopelagic luminescent sharks. *Acta Zoologica*. 1985;66(2):111–118.
- [11] Davis MP, Holcroft NI, Wiley EO, Sparks JS, Smith WL. Species-specific bioluminescence facilitates speciation in the deep sea. *Marine Biology*. 2014;161:1140–1148. DOI: 10.1007/s00227-014-2406x.
- [12] Herring PJ. Aspects of the bioluminescence of fishes. In: Barnes H, Barnes M, editors. *Oceanography and Marine Biology. An Annual Review. Volume 20*. Aberdeen: Aberdeen University Press; 1982. pp. 472–541.
- [13] Matsui T, Rosenblatt RH. Review of the deep-sea fish family Platytroctidae (Pisces: Salmoniformes). *Bulletin of the Scripps Institution of Oceanography*. 1987;19:1–159.
- [14] Pietsch TW. *Oceanic Anglerfishes. Extraordinary Diversity in the Deep Sea*. Berkeley: University of California Press; 2009. 557 p.
- [15] Carpenter KE, Niem VH, editors. *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 3: Batoid Fishes, Chimaeras and Bony Fishes Part 1 (Elopidae to Linophrynidae)*. Rome: Food and Agriculture Organization of the United Nations; 1999. pp.1407–2068
- [16] Castle PHJ, Paxton JR. A new genus of luminescent eel (Pisces: Congridae) from the Arafura Sea, Northern Australia. *Copeia*. 1984;1:72–81.
- [17] Davis MP, Sparks JS, Smith WL. Repeated and widespread evolution of bioluminescence in marine fishes. *PLoS One*. 2016;11(6):e0155154. DOI: 10.1381/journal.pone.0155154.
- [18] Thacker CE, Roje DM. Phylogeny of cardinalfishes (Teleostei: Gobiiformes: Apogonidae). *Molecular Phylogenetics and Evolution*. 2009;52:735–746. DOI: 10.1016/j.ympev.2009.05.017.
- [19] Haneda Y. Luminous organs of fish which emit light indirectly. *Pacific Science*. 1950;4:214–227.
- [20] Harvey EN. Pisces. In: Harvey EN, editor. *Bioluminescence*. New York: Academic Press; 1952. pp. 494–553.
- [21] McAllister DE. The significance of ventral bioluminescence in fishes. *Journal of the Fisheries Research Board of Canada*. 1967;24(3):538–554.

- [22] Suntsov AV, Widder EA, Sutton TT. Bioluminescence. In: Finn RN, Kapoor BG, editors. *Fish Larval Physiology*. Enfield: Science Publishers; 2008. pp. 51–88.
- [23] Herring P. Systematic distribution of bioluminescence in living organisms. *Journal of Bioluminescence and Chemiluminescence*. 1987;1:147–163.
- [24] Cohen DM, Inada T, Iwamoto T, Scialabba N. *FAO Species Catalogue. Gadiform Fishes of the World (Order Gadiformes). An Annotated and Illustrated Catalogue of Cods, Hakes, Grenadiers and Other Gadiform Fishes Known to Date*. FAO Fisheries Synopsis. Number 125. Volume 10. Rome: Food and Agriculture Organization of the United Nations; 1990. 442 p.
- [25] Ramaiah N, Chandramohan D. Occurrence of *Photobacterium leiognathi*, as the bait organ symbiont in frogfish *Antennarius hispidus*. *Indian Journal of Marine Sciences*. 1991;21:210–211.
- [26] Carpenter KE, Niem VH, editors. *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 4: Bony Fishes Part 2 (Mugilidae to Carangidae)*. Rome: Food and Agriculture Organization of the United Nations; 1999. pp. 2069–2790 .
- [27] Moser HG, editor. *The Early Stages of Fishes in the California Current Region*. Atlas number 33. La Jolla: California Cooperative Oceanic Fishery Investigations; 1996. 1505 p.
- [28] McKay RJ. *FAO Species Catalogue. Sillaginid Fishes of the World. (Family Sillaginidae). An Annotated and Illustrated Catalogue of Sillago, Smelt or Indo-Pacific Whiting Species Known to Date*. FAO Fisheries Synopsis. Number 125. Volume 14. Rome: Food and Agriculture Organization of the United Nations; 1992. 87 p.
- [29] Terao A. Photophore in flying fish. *Zoological Magazine*. 1950;13(40):59–60.
- [30] Warrant EJ, Locket NA. Vision in the deep sea. *Biological Reviews*. 2004;79:671–712. DOI: 10.1017/S1464793103006420.
- [31] Warrant EJ, Collin SP, Locket NA. Eye design and vision in deep-sea fishes. In: Collin SP, Marshall NJ, editors. *Sensory Processing in Aquatic Environments*. New York: Springer-Verlag; 2003. pp. 303–320.
- [32] Young RE. Oceanic bioluminescence: An overview of general functions. *Bulletin of Marine Science*. 1983;33(4):829–846.
- [33] Morin JG. Coastal bioluminescence: Patterns and functions. *Bulletin of Marine Science*. 1983;33(4):787–817.
- [34] Harvey, EN. The luminous organs of fishes. In: Brown ME, editor. *The Physiology of Fishes*. Volume II. Behaviour. New York: Academic Press; 1957. pp. 346–366.
- [35] Meyer-Rochow VB. Some observations on spawning and fecundity in the luminescent fish *Photoblepharon palpebratus*. *Marine Biology*. 1976;37:325–328.



- [36] Douglas RH, Partridge JC, Marshall NJ. The eyes of deep-sea fish I: Lens pigmentation, tapeta and visual pigments. *Progress in Retinal and Eye Research*. 1998;17(4):597–636.
- [37] Clarke WD. Function of bioluminescence in mesopelagic organisms. *Nature*. 1963;198:1244–1246.
- [38] Sutton TT. Vertical ecology of the pelagic ocean: Classical patterns and new perspectives. *Journal of Fish Biology*. 2013;83:1508–1527. DOI: 10.1111/jfb.12263.
- [39] Haygood MG. Light organ symbioses in fishes. *Critical Reviews in Microbiology*. 1993;19(4):191–216.
- [40] Salvanes AGV, Kristoffersen JB. Mesopelagic fishes. In: Steele JH, Thorpe SA, Turekian KK, editors. *Encyclopedia of Ocean Sciences*. Volume 3. 2nd ed. San Diego: Academic Press; 2001. pp. 748–754.
- [41] Karplus I. The associations between fishes and luminescent bacteria. In: Karplus I, editor. *Symbiosis in Fishes: The Biology of Interspecific Partnerships*. New Jersey: John Wiley and Sons; 2014. pp. 7–57.
- [42] Urbanczyk H, Ast JC, Dunlap PV. Phylogeny, genomics, and symbiosis of *Photobacterium*. *Federation of European Microbiological Societies*. 2011;35(2):324–342. DOI: 10.1111/j.1574-6976.2010.00250.x.
- [43] Meyer-Rochow VB. Loss of bioluminescence in *Anomalops katoptron* due to starvation. *Experientia*. 1976;32:1175–1176.
- [44] Thompson EM, Rees J-F. Origins of luciferins: Ecology of bioluminescence in marine fishes. In: Hochachka PW, Mommsen TP, editors. *Biochemistry and Molecular Biology of Fishes*. Amsterdam: Elsevier Science; 1995. pp. 435–466.
- [45] Cavallaro M, Mammola CL, Verdiglione R. Structural and ultrastructural comparison of photophores of two species of deep-sea fishes: *Argyropelecus hemigymnus* and *Maurolicus muelleri*. *Journal of Fish Biology*. 2004;64:1552–1567. DOI: 10.1111/j.905-8649.2004.00410.x.
- [46] O'Day WT. Luminescent silhouetting in stomiatoid fishes. *Contributions in Science from the Natural History Museum of Los Angeles*. 1973;246:1–8.
- [47] Haneda Y, Johnson FH. The photogenic organs of *Parapriacanthus beryciformes* franz and other fish with the indirect type of luminescent system. *Journal of Morphology*. 1962;110(2):187–198.
- [48] Denton EJ, Herring PJ, Widder EA, Latz MF, Case JF. The roles of filters in the photophores of oceanic animals and their relation to vision in the oceanic environment. *Proceedings of the Royal Society of London B: Biological Sciences*. 1985;225:63–97.
- [49] Best ACG, Bone Q. On the integument and photophores of the alepocephalid fishes *Xenodermichthys* and *Photostylus*. *Journal of the Marine Biological Association of the United Kingdom*. 1976;56:227–236.



- [50] McFall-Ngai M, Morin J. Camouflage by disruptive illumination in leiognathids, a family of shallow-water, bioluminescent fishes. *Journal of Experimental Biology*. 1991;156:119–138.
- [51] Dunlap PV, Nakamura M. Functional morphology of the luminescence system of *Siphamia versicolor* (Perciformes: Apogonidae), a bacterially luminous coral reef fish. *Journal of Morphology*. 2011;272:897–909. DOI: 10.1002/jmor.10956.
- [52] Haneda Y. The luminescence of some deep-sea fishes of the families Gadidae and Macrouridae. *Pacific Science*. 1951;5(4):372–378.
- [53] McFall-Ngai MJ, Dunlap PV. Three new modes of luminescence in the leiognathid fish *Gazza minuta*: Discrete projected luminescence, ventral body flash, and buccal luminescence. *Marine Biology*. 1983;73:227–238.
- [54] Claes JM, Mallefet J. Comparative control of luminescence in sharks: New insights from the slendertail lanternshark (*Etmopterus molleri*). *Journal of Experimental Marine Biology and Ecology*. 2015;467:87–94. DOI: 10.1016/j.jembe.2015.03.008.
- [55] Baguet F. Excitation and control of isolated photophores of luminous fishes. *Progression in Neurobiology*. 1975;5(2):97–125.
- [56] Case JF, Strause LG. Neurally controlled luminescent systems. In: Herrin PJ, editor. *Bioluminescence in Action*. London: Academic Press; 1978. pp. 331–366.
- [57] Sazonov YI. Morphology and significance of the luminous organs in alepocephaloid fishes. *Biosystematics and Ecology Series*. 1996;11:156–163.
- [58] Tatsuta N, Imamura H, Nakaya K, Kawai T, Abe T, Sakaoka K, Takagi S, Yabe M. Taxonomy of mesopelagic fishes collected around the Ogasawara islands by the T/S Oshoro-Marui. *Memoirs of the Faculty of Fisheries Sciences, Hokkaido University*. 2014;56(1):1–64.
- [59] Nicol JA. Spectral composition of the light of the lanternfish *Myctophum punctatum*. *Journal of Marine Biological Association of the United Kingdom*. 1960;40:27–32.
- [60] Somiya, H. Bacterial bioluminescence in chlorophthalmid deep-sea fish: a possible interrelation between the light organ and the eyes. *Experientia*. 1977;33:906–909.
- [61] McFall-Ngai MJ, Dunlap PV. External and internal sexual dimorphism in leiognathid fishes: Morphological evidence for sex-specific bioluminescent signaling. *Journal of Morphology*. 1984;182:71–83.
- [62] Morin JG, Harrington A, Neilson K, Badlwin TO, Hastings JW. Light for all reasons: Versatility in behavioural repertoire of the flashlight fish. *Science*. 1975;190:74–76.
- [63] Meyer-Rochow VB. Light of my life – Messages in the dark. *Biologist*. 2001;48(4):163–167.

- [64] Young RE, Roper CFE, Walters JF. Eyes and extraocular photoreception in midwater cephalopods and fishes: Their roles in detecting downwelling light for counterillumination. *Marine Biology*. 1979;51:381–390.
- [65] Claes JM, Partridge JC, Hart NS, Garza-Gisholt E, Ho H-C, Mallefet J, Collin SP. Photon hunting in the twilight zone: Visual features of mesopelagic bioluminescent sharks. *PLoS One*. 2014;9(8):e104213. DOI: 10.1381/journal.pone.0104213.
- [66] Claes JM, Ho H-C, Mallefet J. Control of luminescence from pygmy sharks (*Squaliolus aliae*) photophores. *The Journal of Experimental Biology*. 2012;215:1691–1699. DOI: 10.1242/jeb.066704.
- [67] Claes JM, Dean MN, Nilsson D-E, Hart NS, Mallefet J. A deepwater fish with “light-sabers” – a dorsal spine-associated luminescence in a counterilluminating lanternshark. *Scientific Reports*. 2013;3:1308. DOI: 10.1039/srep01308.
- [68] Wagner H-J, Fröhlich E, Negishi K, Collin SP. The eyes of deep-sea fish II. Functional morphology of the retina. *Progress in Retinal and Eye Research*. 1998;4:637–685.
- [69] Douglas RH, Hunt DM, Bowmaker JK. Spectral sensitivity tuning in the deep-sea. In: Collin SP, Marshall NJ, editors. *Sensory Processing in Aquatic Environments*. New York: Springer-Verlag; 2003. pp. 323–342.
- [70] Ali MA. *Retinas of Fishes: An Atlas*. Berlin: Springer-Verlag; 1976. 284 p. DOI: 10.1007/978-3-642-66435-9.
- [71] Warrant E. Vision in the dimmest habitats on earth. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioural Physiology*. 2004;190:765–789. DOI: 10.1007/s00359-004-0546-z.
- [72] de Busserolles F, Fitzpatrick JL, Marshall NJ, Collin SP. The influence of photoreceptor size and distribution on optical sensitivity in the eyes of lanternfishes (Myctophidae). *PLoS One*. 2014;9(6):e99957. DOI: 10.1381/journal.pone.0099957.
- [73] Fernandez HR, Tsuji FI. Photopigment and spectral sensitivity in the bioluminescent fish *Porichthys notatus*. *Marine Biology*. 1976;34:101–107.
- [74] Meyer-Rochow VB, Barburina V, Smirnov S. Histological observations on the eye of the two luminescent fishes *Photoblepharon palpebratus* (Boddaert) and *Anomalops katoptron* (Blkr). *Zoologischer Anzeiger – A Journal of Comparative Zoology*. 1982;209(1/2):65–72.
- [75] Douglas RH, Partridge JC. On the visual pigments of deep-sea fish. *Journal of Fish Biology*. 1997;50:68–85.
- [76] de Busserolles F, Marshall NJ, Collin SP. Retinal ganglion cell distribution and spatial resolving power in deep-sea lanternfishes (Myctophidae). *Brain, Behaviour and Evolution*. 2014;84(4):262–276. DOI: 10.1159/000365960.

- [77] Miyazaki T, Iwami T, Meyer-Rochow VB . The position of the retinal area centralis changes with age in *Champscephalus gunnari* (Channichthyidae), a predatory fish from coastal Antarctica. *Polar Biology*. 2011;34:1117–1123. DOI: 10.1007/s00300-011-0969-2.
- [78] Hunt DM, Dulai KS, Partridge JC, Cottrill P, Bowmaker JK. The molecular basis for spectral tuning of rod visual pigments in the deep-sea fish. *The Journal of Experimental Biology*. 2001;204:3333–3344.
- [79] Froese R, Pauly D. Fishbase [Internet]. [Updated: 2015]. Available from: fishbase.org [Accessed: 15/06/2016]
- [80] Dunlap PV, Davis KM, Tomiyama S, Fujino M, Fukui A. Developmental and microbiological analysis of the inception of bioluminescent symbiosis in the marine fish *Nuchequula nuchalis* (Perciformes: Leiognathidae). *Applied and Environmental Microbiology*. 2008;74(24):7471–7481. DOI: 10.1128/AEM.01619-08.
- [81] Tsuji FI, Lynch III RV, Haneda Y. Studies on the bioluminescence of the marine ostracod crustacean *Cypridina serrata*. *Biological Bulletin*. 1970;139(2):386–401.
- [82] Cohen AC, Morin JG. Six new luminescent ostracodes of the genus *Vargula* (Myodocopida: Cypridinidae) from the San Blas region of Panama. *Journal of Crustacean Biology*. 1989;9(2):297–340.
- [83] Morin JG. Firefleas of the sea: Luminescent signaling in marine ostracode crustaceans. *The Florida Entomologist*. 1986;69(1):105–121.
- [84] Mensinger AF, Case JF. Bioluminescence maintenance in juvenile *Porichthys notatus*. *Biological Bulletin*. 1991;181:181–188.
- [85] Shimomura O, Inoue S, Johnson FH, Haneda Y. Widespread occurrence of coelenterazine in marine bioluminescence. *Comparative Biochemistry and Physiology – Part B. Biochemistry & Molecular Biology*. 1980;65:135–138.
- [86] Dunlap PV, Ast JC, Kimura S, Fukui A, Yoshino T, Endo H. Phylogenetic analysis of host-symbiont specificity and codivergence in bioluminescent symbioses. *Cladistics*. 2007;23:507–532. DOI: 10.1111/j.1096-0031.2007.00157.x.
- [87] Evans BI, Fernald RD. Metamorphosis and fish vision. *Journal of Neurobiology*. 1990;21(7):1038–1052.
- [88] Evans BI, Browman HI. Variation in the development of the fish retina. *American Fisheries Society Symposium*. 2004;10:146–166.
- [89] Claes JM, Mallefet J. Early development of bioluminescence suggests camouflage by counter-illumination in the velvet belly lantern shark *Etmopterus spinax* (Squaloidea: Etmopteridae). *Journal of Fish Biology*. 2008;73:1337–1350. DOI: 10.1111/j.1095-8649.2008.02006.x.
- [90] Mallefet J, Shimomura O. Presence of coelenterazine in mesopelagic fishes from the Strait of Messina. *Marine Biology*. 1995;124:381–385.

- [91] Badcock J, Larcombe RA. The sequence of photophore development in *Xenodermichthys copei*. Journal of the Marine Biological Association of the United Kingdom. 1980;60:277–294.
- [92] Claes JM, Mallefet J. Ontogeny of photophores pattern in the velvet belly lantern shark, *Etmopterus spinax*. Zoology. 2009;112:433–441. DOI: 10.1016/j.zool.2009.02.003.
- [93] Mensinger AF, Case JF. Luminescent properties of deep-sea fish. Journal of Experimental Marine Biology and Ecology. 1990;144:1–15.
- [94] Munz FW, McFarland WN. Evolutionary adaptations of fishes to the photic environment. In: Crescitelli F, editor. Handbook of Sensory Physiology, Volume VII/5. The Visual System in Vertebrates. Berlin: Springer-Verlag; 1977. pp. 193–274. DOI: 10.1007/978-3-642-66468-7
- [95] Merret NR, Badcock J, Herring PJ. The status of *Benthalbella infans* (Pisces: Myctophidae), its development, bioluminescence, general biology and distribution in the eastern North Atlantic. Journal of Zoology, London. 1973;170:1–48.
- [96] Carpenter KE, Niem VH, editors. FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 5: Bony Fishes Part 3 (Menidae to Pomacentridae). Rome: Food and Agriculture Organization of the United Nations; 2001. pp. 2791–3390 .
- [97] Fernandez I, Devaraj M. Dynamics of the gold-spotted grenadier anchovy (*Coilia dussumieri*) stock along the northwest coast of India. Indian Journal of Fisheries. 1996;43(1):27–39.
- [98] Roe HSJ, Badcock J. The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 5. Vertical migrations and feeding of fish. Progress in Oceanography. 1984;13:399–424.
- [99] Badcock J. The vertical distribution of mesopelagic fishes collected on the SOND Cruise. Journal of the Marine Biological Association in the United Kingdom. 1970;50:1001–1044.
- [100] Poulsen JY. A new species of pencil smelt *Nansenia boreacrassicauda* (Microstomatidae, Argentiniformes) from the North Atlantic Ocean. Zootaxa. 2015;4030(3):517–532. DOI: 10.11646/zootaxa.4020.3.6.
- [101] Crane Jr JM. Bioluminescence in the batfish *Dibranchius atlanticus*. Copeia. 1968;2:410–411.
- [102] Carpenter KE, Niem VH, editors. FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 2: Cephalopods, crustaceans, holothurians and sharks. Rome: Food and Agriculture Organization of the United Nations; 1998. pp. 687–1406.
- [103] Carpenter KE, Niem VH, editors. FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 6: Bony

Fishes Part 4 (Labridae to Latimeriidae), Estuarine Crocodiles, Sea Turtles, Sea Snakes and Marine Mammals. Rome: Food and Agriculture Organization of the United Nations; 2001. pp. 3391–4218 p.

- [104] Carpenter KE, editor. FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Atlantic. Volume 2: Bony Fishes Part 1 (Acipenseridae to Grammatidae). Rome: Food and Agriculture Organization of the United Nation and American Society of Ichthyologists and Herpetologists. Special Publication Number 5; 2002. pp. 601–1374.
- [105] Carpenter KE, editor. FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Atlantic. Volume 3: Bony Fishes Part 2 (Opistognathidae to Molidae), sea turtles and marine mammals. Rome: Food and Agriculture Organization of the United Nation and American Society of Ichthyologists and Herpetologists. Special Publication Number 5; 2002. pp. 1375–2127 .
- [106] Sasaki K. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty of Fisheries Hokkaido University*. 1989;36(1–2):1–138.