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CHAPTER

3

Bioluminescence

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INTRODUCTION

The production of living light – bioluminescence, is a widespread but very unevenly distributed phenomenon among living organisms. As presently known, some five terrestrial and 14 marine phyla and more than 700 genera are known to have luminous species (Herring, 1987; Herring & Widder, 2001). The morphological diversity of luminous organs, physiology and taxonomic occurrence of bioluminescence in fishes is higher than in any other group of organisms and confined exclusively to marine habitats.

A significant body of information on fish bioluminescence is available from several detailed reviews (Herring & Morin, 1978; Herring, 1982; Haygood, 1993). Historically, the characterisation of fish bioluminescence was almost exclusively confined to adults. As emphasis on early ontogeny of fishes has increased in recent decades, the development of many species with bioluminescent properties has become increasingly well documented. According to these studies, bioluminescence often arises early in ontogeny. To date, however, very few studies have focused upon the early ontogeny of

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bioluminescence in the majority of marine fish groups. Ontogenetic aspects of bioluminescence are clearly needed for a better understanding of the mechanisms of light production in fishes, the different roles played by bioluminescence during a particular period of life, and the evolution of bioluminescence in particular groups and in fishes in general.

The purpose of this review is to synthesise the available information on various aspects of the development of bioluminescence during the early life history of marine fishes, to examine the functional significance and physiological basis for light production during early ontogeny, and to suggest directions for future studies.

PHYSIOLOGICAL BASIS FOR LIGHT PRODUCTION

Bioluminescence is an oxidative chemical reaction where the enzyme, known as luciferase and the substrate, known as luciferin, are synthesised by living organisms. Luciferin and luciferase are generic terms (derived from Lucifer, the light bearer) and require a taxon prefix to differentiate chemicals that have been isolated from different organisms. Chemically the luciferins and luciferases produced by different organisms are so dissimilar (Fig. 1) that it is apparent that bioluminescence has arisen independently multiple times during evolutionary history (Hastings, 1983). Substrates range from the simple, such as the aldehyde luciferin found in earthworms to the complex tetrapyrrole luciferin of dinoflagellates. The only commonality is that enzymes, although structurally dissimilar, are all oxygenases that require molecular oxygen to create the excited electron state that precedes light emission. Because of the reactivity of luciferins with reactive oxygen species, it has been proposed that these substrates originally evolved as detoxifiers of deleterious oxygen derivatives (Rees et al., 1998). According to this theory it was only after selection for antioxidative defense mechanisms lessened, possibly because of migration into deeper waters where oxidative stress is reduced, that transitions to light-emitting function occurred. Additionally, Seliger (1993) has proposed that the oxidative breakdown of pigment molecules could produce electronically excited states capable of emitting visible light. Therefore, as fish colonised the deeper, darker depths of the ocean any pigment spots that were used for visual signalling would be enhanced by a mutation that resulted in light emission and immediately selected for. Although the colours of bioluminescence cover the entire visible spectrum, the colour most commonly found in marine organisms is the blue (~475 nm) that penetrates farthest through seawater and is therefore capable of enhancing communication over the greatest distances (Widder et al., 1983).

Methods of controlling light emission are even more diverse than the light emitting chemicals. Bacteria are unusual in that their light emission is continuous rather than transient, apparently as a consequence of the light emitting reaction being a shunt of the respiratory pathway (Hastings, 1983). As a consequence, symbioses between animals and bacteria often involve the use of mechanical shutters to control the light emission. In non-symbiotic emitters, where the light emitting chemicals are intrinsic to the organism, light emission may be under either neural or hormonal control. Often a

Luciferins

Diplocardia

Latia

Firefly

Bacteria

Dinoflagellate
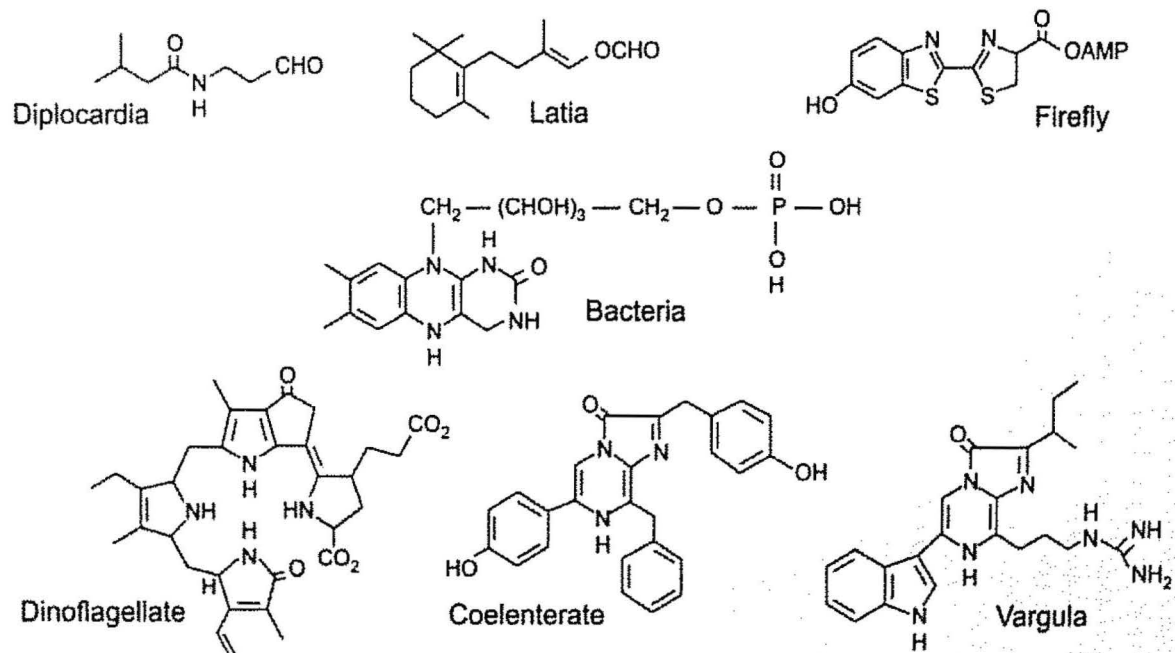
Coelenterate

Vargula

Fig. 1 Chemical structures of different luciferins redrawn from Hastings & Morin (1991). The simplest chemical structure is that of the earthworm, *Diplocardia*, while the most complex is the tetrapyrrolic luciferin extracted from photosynthetic dinoflagellates. Freshwater examples of bioluminescence are virtually unknown except for the limpet, *Latia*. Coelenterate luciferin, also known as coelenterazine because it was originally extracted from an anthozoan, is known to occur in at least seven different phyla. The ostracod, *Vargula*, releases its luciferin and luciferase into the water, while fishes exhibiting a dietary dependence on ostracod luciferin retain their light emitting chemicals internally.

co-factor is required in addition to the luciferin and luciferase, such as ATP in firefly luminescence or Ca^{2+} in coelenterates and in some cases another protein may serve as a secondary emitter that shifts the emission to longer wavelengths, such as the green fluorescent protein (GFP) extracted from some coelenterates.

Two major types of bioluminescence are known in marine fishes: 1) light production due to intrinsic luminescence, and 2) emission of light due to luminous bacteria harboured in special organs.

In the case of intrinsic luminescence the organism may either synthesise the enzyme and substrate *de novo* from basic biochemical building blocks or it may require an exogenous source of luciferin. When an exogenous source is required it is passed on maternally via the yolk or it is acquired by direct feeding later in the maturation process. Once an exogenous source of luciferin is acquired it can be recycled if the appropriate enzymes are present or if those enzymes are induced by the presence of the substrate. In such instances the exogenous source does not need to be replenished. However, if enzymes for recycling the substrate are not present, then the substrate must constantly be replenished through the diet. No examples of exogenously acquired luciferases are known, presumably because they are broken down by proteolytic enzymes during digestion.

The best documented example of dietary dependence of luminescence in fishes is in the midshipman (*Porichthys notatus*). Two factors have contributed to the extensive research that has been done on this species. The first is its accessibility. Female midshipman deposit their eggs subtidally, attached to abalone shells or in rock cavities. Males fertilise the eggs and then guard the nest throughout the approximately 40 days it takes for the juveniles to develop and become free-swimming (Anctil, 1977). This behaviour makes the nests relatively easy to find and transfer to a laboratory setting. The second is that the oxyluciferin produced by the light reaction is strongly fluorescent, a characteristic that is not shared by all bioluminescent reactions. Because fluorescence is much brighter and less transient than bioluminescence, it is easier to observe, thereby simplifying the process of monitoring dietary acquisition of the substrate.

Although near-shore bioluminescent fishes generally depend on luminous bacteria for light production (Morin, 1983), the midshipman is unusual in that its luminescence is intrinsic. Light originates from rows of hundreds of photophores distributed ventrally and ventro-laterally, along the head and trunk, and light emission is dependent on an exogenous source of luciferin derived from feeding on bioluminescent ostracods such as *Vargula hilgendorfii* and V. *tsujii* (Herring & Morin, 1978). The substrate, an imidazolopyrazine, is initially passed on maternally through the yolk, while the luciferase is synthesised *de novo* 28 days after the eggs are deposited (Tsuji et al., 1972). Luciferin reserves, present when juveniles detach from the nest, can be depleted within three weeks following repeated stimulation of bioluminescence (Mensinger & Case, 1991) indicating that the enzymes needed for recycling luciferin are not present. However, when members of a non-luminescent population of midshipman were fed a single dose of V. *hilgendorfii* luciferin, they became luminescent and remained so for two years, producing more photons than could be accounted for by the amount of luciferin that

was administered (Thompson et al., 1987). This was interpreted as being due to the exogenously supplied luciferin inducing the synthesis of enzymes required for recycling. These investigators inferred that the recycling mechanisms were not initially present because injection of oxyluciferin, i.e. spent luciferin, to dark fish did not result in luminescence, therefore it was not recycled back to luciferin. These results may be explained either by a developmental shift in the capacity for recycling that occurs sometime after the first three weeks following nest detachment or by a different metabolic pathway for dietary compared to maternally acquired luciferin.

A dietary dependence on Vargula-type luciferin may also exist in shallow-water apogonid fishes of the Far East as well as several species of the genera Parapriacanthus and Pempheris, all of which lack photophores, but have light organs associated with the digestive tract and elaborate accessory structures that function as reflectors, diffusers and light guides to produce a diffuse ventral glow. As in midshipman, their luciferin and luciferase extracts cross react with Vargula luciferin and luciferase, suggesting that they too may require this ostracod in their diet in order to remain luminescent (Herring & Morin, 1978).

Another imidazolopyrazine luciferin, known as coelenterazine, because it was originally extracted from an anthozoan, is found in fishes as well as squids, radiolarians, a chaetognath and some crustaceans (Shimomura et al., 1980; Campbell & Herring, 1990; Haddock & Case, 1994). Although similar in structure to Vargula-luciferin, coelenterazine does not cross react with Vargula luciferase, nor does Vargula-luciferin cross react with coelenterate luciferase. Additionally these luciferins appear to be derived from different metabolic pathways, since Vargula luciferin is formed from the cyclisation of the three amino acids, tryptophan, isoleucine, and arginine, while coelenterazine is assembled from two tyrosines and a phenylalanine (Herring & Gruner, 2004). A dietary dependence on coelenterazine has been documented in the deep-sea lophogastrid shrimp (Gnathophausia ingens) (Frank et al., 1984). However, whether or not the coelenterazine that is found in fishes such as silver hatchetfish (Argyropelecus hemigymnus), viperfish (Chauliodus sloani), spotted lanternfish (Myctophum punctatum), slender lightfish (Vinciguerria attenuata) and Brauer's bristlemouth (Cyclothone braueri) (Mallafet & Shimomura, 1995) is acquired exogenously has yet to be established. Ironically, it was recently shown that a hydromedusa from which coelenterazine was extracted, Aequorea victoria (Shimomura et al., 1974), is itself dependent on an exogenous source of coelenterazine, raising the possibility that this substrate is misnamed (Haddock et al., 2001). Since the best evidence for de novo synthesis of coelenterazine is in the embryos of the decapod shrimp, Systellaspis debilis (Thomson et al., 1995), it is possible that, like the imidazolopyrazine required by midshipman, coelenterazine is actually of crustacean origin.

Fishes that depend on bacterial symbionts for light production are less common than intrinsic light emitters, but include such well known groups as the flashlight fishes (Beryciformes), ponyfishes (Perciformes), deep-sea anglerfishes (Lophiiformes) and rattails (Gadiformes). There are three culturable bacterial symbionts that have been isolated from specialised organs of fishes; Vibrio fischeri and Photobacterium leiognathi,

that grow best at warmer temperatures and have been isolated from shallow-water species, and *Photobacterium phosphoreum*, which thrives in cooler waters and has been isolated from deep-sea species. The taxonomy of luminescent bacteria has been revised often with *Vibrio* species, alternatively designated as *Photobacterium*, *Achromobacter*, *Lucibacterium*, *Neisseria* and *Beneckea* (Herring, 2002). The most recent contribution to the name game is the suggestion that *P. phosphoreum* in deep-sea fishes is an incorrect identification and should be replaced by *P. kishitanii* (Ast & Dunlap, 2005).

The primary means by which symbionts are transmitted between generations are either horizontal (environmental) or vertical (transovarian) (Nyholm & McFall-Ngai, 2004). Vertical transmission is known to occur in some insect species, but is generally rare compared to horizontal transmission, which includes the enteric microbiota found in all animal digestive tracts. Also known as cyclic transmission, because the symbionts must be reacquired from the environment with each new generation, horizontal transmission includes both direct and indirect transfer from the adult host. Direct transfer is relatively rare and requires the adult host to facilitate the transmission as, for example, when cows inoculate their calves with rumen microbiota while grooming them. Indirect transfer, where inoculation of the young is from the general environment, is the most common means of transmission, but one that requires a remarkable degree of co-ordination in order to insure that the host selects only desirable bacteria from the environment, rejects undesirable species and establishes growth conditions that favour the symbiont without allowing runaway growth (McFall-Ngai, 1998). The best documented case of environmental transmission of bioluminescent bacteria is in the Hawaiian bobtail squid (*Euprymna scolopes*) that systematically eliminates environmental intruders in favour of the bacterial symbiont, *Vibrio fischeri*, which then triggers developmental changes in the host, resulting in a functional light organ (Nyholm & McFall-Ngai, 2004). Inoculation of the juvenile light organ is facilitated by the daily expulsion into the water column of more than 90% of the adult light-organ symbionts, thereby augmenting their local concentration (Boettcher et al., 1996). A similar situation has been demonstrated in the ponyfish (*Leiognathus nuchalis*), which has a circumoesophageal light organ populated with the symbiont, *Photobacterium leiognathi* (Wada et al., 1999). Light emission is ventral through a complex series of reflectors and diffusers and apparently functions in counter-illumination (Hastings, 1971). In a study by Wada et al. (1999) it was found that juveniles that were reared separately from adults failed to become luminescent, indicating that bacteria were not transferred vertically. However, juveniles placed with adults or with homogenate from adult light organs became luminescent within 48 hours. During normal development juveniles became luminescent 45 days after hatching, apparently selecting the appropriate bacterial symbiont from the local environment, which is enriched with *Photobacterium leiognathi* expelled from adult light organs.

Similar examples of horizontal transmission of symbionts have been demonstrated in the monocentrid pineconefish (*Monocentris japonicus*), which has two small light organs located on the underside of the lower jaw that open to ambient seawater, and the sea urchin cardinalfish (*Siphamia versicolor*), which has a ventral light organ that

opens to the intestine. The symbiont in the monocentrids has been identified as *Vibrio fischeri* (Ruby & Nealson, 1976) while in sea urchin cardinalfish it appears to be *Photobacterium leiognathi* (Leis & Bullock 1986). Although the bacterial symbionts from the five species of flashlightfish, *Anomalops katoptron*, *Photoblepharon palpebratus*, *P. steinitzi*, *Kryptophanaron alfredi* and *Phthanophaneron harveyi*, have never been cultured or identified, there is evidence that they are acquired anew with each generation, via ducts that connect to the surrounding seawater. Interestingly, it appears that the flashlightfish symbionts vary between species and may have co-evolved with their hosts (Wolfe & Haygood, 1991). A similar situation may exist in deep-sea anglerfishes (Lophiiformes: Ceratioidea), which also have unculturable species-specific symbionts and a duct that connects the interior of the escal light organ with ambient seawater (Haygood & Distel, 1993). However, because deep-sea anglerfish larvae reside in surface waters and only descend into the depths at the start of metamorphosis, the question arises as to how the larvae can acquire the appropriate symbiont when there are no adults in proximity to provide the inoculum. One possible solution proposed by Haygood (1993) is that bacteria discharged from adult female escae during spawning might adhere to the eggs and then grow in the mucus layer that sheathes anglerfish larvae. During metamorphosis the esca develops as an ingrowth of epidermal cells that could therefore provide the required inoculum via the mucus sheath (Munk, 1999).

A TAXONOMIC SURVEY OF LARVAL BIOLUMINESCENCE

In order to simplify our survey, we will review the early development of fishes with luminescent properties by large taxonomic grouping (orders). The distribution of both bacterial and intrinsic bioluminescence in modern teleost fishes is presented in Figure 2 and follows the latest classification (Nelson, 2006).

Order Saccopharyngiformes

Among eels, two aberrant deep-sea families, Saccopharyngidae (swallower eels) and Eurypharingidae (gulpers or pelican eels), have been reported to have bioluminescent properties (Herring & Morin, 1978). However, the evidence of light production in these two families is still equivocal and is mainly based on indirect evidence.

For nine species of swallower eels, Nielsen & Bertelsen (1985) found it likely that the terminal caudal organ could serve as a bioluminescent lure for prey based on a single observation of a live specimen (Beebe, 1932) and the morphology of the organ itself, which bears numerous filaments hypothesised to aid in the luring process. Histological examinations of caudal organs in swallower eels have yielded no bacteria or tubular glands characteristic of bacterial light organs; thus, if caudal organs in the genus *Saccopharynx* are indeed photogenic, then they are likely non-bacterial. In addition, *Saccopharynx* species possess so-called "white line" organs, also called nuchal troughs, which run dorsally from just behind the head down the length of the body and tail (Herring & Morin, 1978; Nielsen & Bertelsen, 1985). Beebe (1932) described
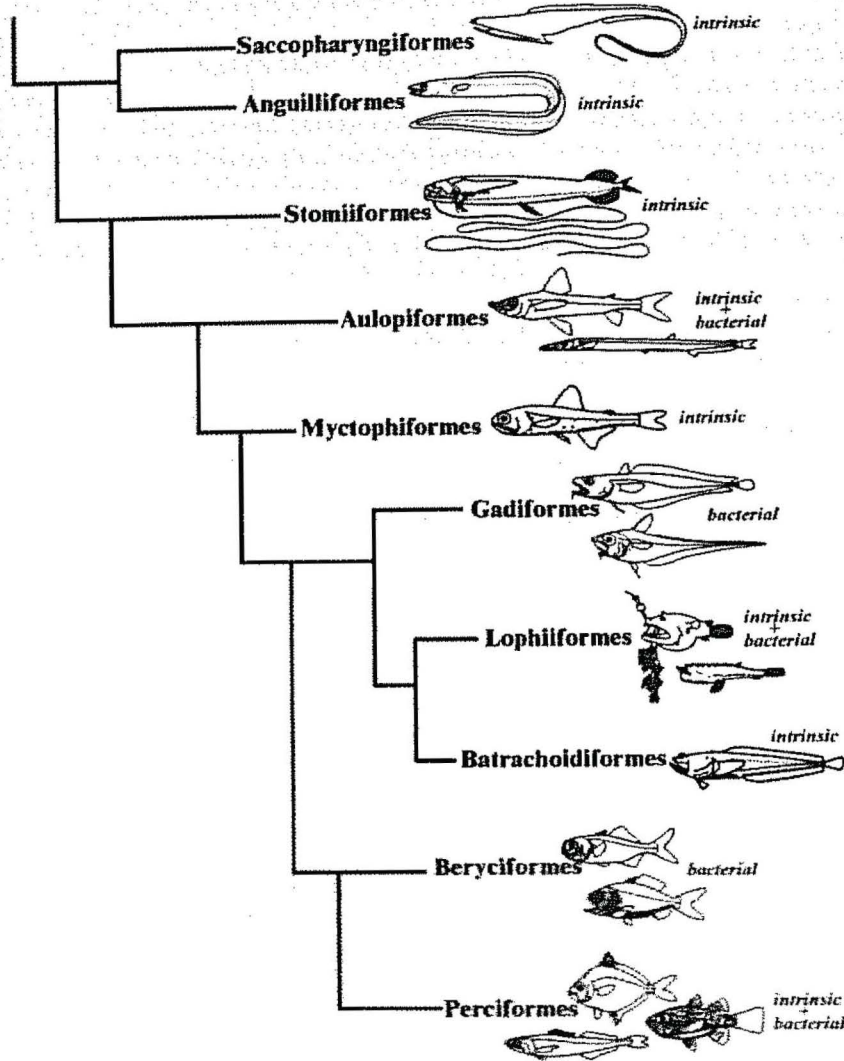
Fig. 2 Cladogram showing distribution of intrinsic and bacterial light production among various orders of teleostean fishes. Phylogeny after Nelson (2006).

these lines, running along both sides of the body below the dorsal midline as "filled with bluish luminous substance," although later studies failed to confirm bioluminescence of these structures (Nielsen & Bertelsen, 1985). The bioluminescent properties of the caudal organ of the pelican eel (*Eurypharynx pelecanoides*) are even less evident. It is

not equipped with filaments and observations on luminescence from this organ (Owre & Bayer, 1970) have not been confirmed (Nielsen et al., 1989). However, observations and video recordings of luminescence from the "white line" organs in the pelican eel have revealed them to be capable of brilliant luminescent flashes of such short duration that they are probably under neural control (E. Widder, unpublished data).

Similar to other elopomorph fishes, all members of the Order Saccopharyngiformes pass through a unique leptocephalus larval stage and undergo extreme metamorphic changes prior to becoming juveniles. The leptocephali of Saccopharynx and Eurypharynx are known and possess no structures that can be attributed to incipient light organs.

Order Anguilliformes

The total absence of bioluminescent representatives among deep-sea anguilliform eels is perplexing, considering that a number of species thrive in the meso- and bathypelagic zones of the World Ocean. At present, no early life history information is available on the shallow-living, benthic congrid eel (Lumiconger arafura), the only species that has been shown to have bacterially induced bioluminescence (Castle & Paxton, 1984). We suspect, however, that the unique leptocephalus stage and the radical morphological changes taking place during metamorphosis preclude early bioluminescent capabilities in this species. Lack of incipient light organs in known larval saccopharyngiforms provides some credence to such views.

Order Clupeiformes

The only known bioluminescent species – the goldspotted grenadier anchovy (Coilia dussumieri, Engraulidae), with several dozen photophores along the isthmus, behind the eye and in four to six rows along the ventral and lateral surfaces of the body, is found from coastal India to Java (Whitehead et al., 1988). The bioluminescence of the goldspotted grenadier anchovy is apparently endogenous, but no information is available on the early ontogeny of photophores in this apparently unique engraulid species.

Order Argentiniformes

Suborder Argentinoidei   In the highly specialised deep-sea spookfishes of the genera Opisthoproctus, Winteria and Rhynchohyalus, light organs are of the open type and are a diverticulum of the gut, hosting luminous bacteria (Photobacterium phosphoreum) (Bertelsen & Munk, 1964; Bertelsen et al., 1965; Herring, 1975). In Opisthoproctus larvae (10.0-14.5 mm standard length, SL), the unusual light reflecting structure of the abdomen (sole) already shows precocious development and differentiation of parts (rectal bulb and parts of the reflector organ; Fig. 3a, b) found in adults (Bertelsen & Munk, 1964). The only record of a larval barreleye (Winteria telescopa) is that of a tentatively identified 12.0-mm specimen (Belyanina, 1982). Although no description was provided, an illustration shows an intensely pigmented terminal part of the intestine, the place for the developing rectal light organ (Fig. 3c). A similarly pigmented rectal
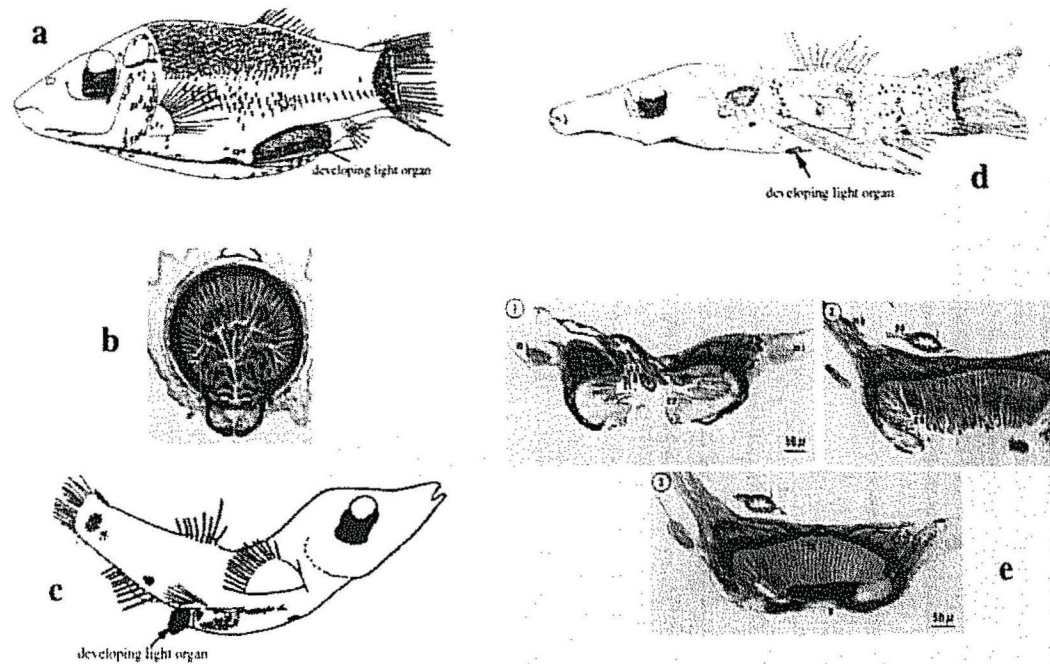
Fig. 3 The light organ development in Argentiniformes (suborder Argentinoidei). **a** – larva of barrel-eye (*Opisthoproctus soleatus*, Opisthoproctidae) 16.2 mm SL after Evseenko & Sunstov (1995); **b** – transverse section through rectal bulb of larval mirrorbelly (*Opisthoproctus grimaldii*, Opisthoproctidae) 10.0 mm SL after Bertelsen & Munk (1964); **c** – larva tentatively identified as *Winteria telescopa* (Opisthoproctidae) 12.0 mm SL with possible precocious development of a rectal bulb after Belyanina (1982); **d** – postlarva of *Rhynchohyalus natalensis* (Opisthoproctidae) 23.0 mm SL after Bertelsen *et al.* (1965); **e** – (1) transverse section through anterior, (2) middle and (3) posterior parts of the rectal bulb of *R. natalensis* 23.0 mm SL.

part of the intestine has also been noted for larval O. grimaldii and O. soleatus (Schmidt, 1918; Bertelsen & Munk, 1964; Evseenko & Suntsov, 1995). Thus, a precocious development of the rectal light organ in Winteria is also likely the case for Opisthoproctus.

An examination of a small post-larval specimen of the glasshead barreleye (Rhynchohyalus natalensis), still displaying a number of larval features (Fig. 3d, e), revealed the presence of a light organ (Bertelsen et al., 1965), a simple rectal bulb without lens cells or a reflector layer. Unlike Opisthoproctus and Winteria, which emit light indirectly, the light organ of Rhynchohyalus appears to emit light directly through the anus (Bertelsen et al., 1965; Herring, 1975).

Although information on the early stages of luminous spookfishes (Opistoproctidae) is very limited, it appears that their development is more or less gradual, similar to gradual development in related argentinoids (Ahlstrom et al., 1984). No actual bioluminescence in larval spookfishes has been observed, but precocious development of light organs could facilitate the initiation of the ventral camouflage, suggesting a deeper distribution than (shallower) larvae utilising transparency as primary camouflage. The two species of Opisthoproctus possess an elaborate abdominal reflecting structure, putatively assisting in bioluminescent counter-illumination, while Winteria and Rhynchohyalus develop less elaborate light organs.

Suborder Alepocephaloidei

Four genera of Alepocephalidae – Xenodermichthys, Photostylus, Rouleina and Microphotolepis, apparently forming a natural group, have been reported to have photophores (Herring & Morin, 1978). Subsequently, Sazonov (1995) mentioned the presence of photophores on the chin of the bathypelagic genera Bathyprion and Mirognathus. However, one of us (TT Sutton) has examined the latter species and did not detect the presence of photophores. Alepocephalid photophores show significant structural diversity, being sessile (Xenodermichthys, Rouleina), borne on stalks (Photostylus) or covered with scales (Microphotolepis) and the bioluminescence is endogenous.

For still unclear reasons, alepocephalid larvae and juveniles are rarely collected, and this naturally limits the available information on development of their light producing organs. At present, early ontogeny of photophores is known for the bluntsnout smooth-head (Xenodermichthys copei) and Schmidt's slickhead (Microphotolepis schmidti) (Badcock & Larcombe, 1980; Sazonov, 1995). In the bluntsnout smooth-head (Fig. 4a), first to appear are the primary photophores on the head (OpV, PO, OpD and Md) and ventral regions of the body (in series PV and VA), the latter being present in 9.0 mm SL larvae. The pattern of body photophore development is fairly constant and the first photophore in any given series is invariably ventral-most, with subsequent photophores added in a ventro-dorsal direction. Badcock & Larcombe (1980) found that the postflexion larva of another bioluminescent alepocephalid, the starry smooth-head (Photostylus pycnopterus) (11.8 mm SL), lacked photophores completely. Development of primary photophores in the smallest juveniles of M. schmidti
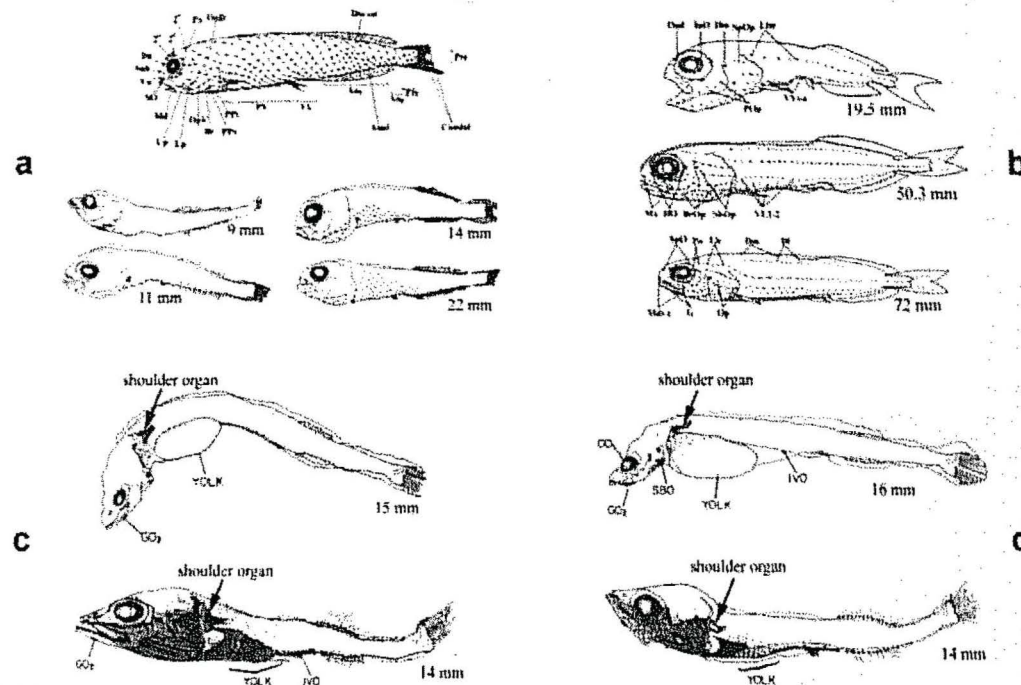
Fig. 4 The light organ development in Argentiniformes (suborder Alepocephaloidei). **a** – photophore terminology and sequence of photophore development in bluntsnout smooth-head (*Xenodermichthys copei*, Alepocephalidae), photophore acronyms: AOa – anterior anal; AOp – posterior anal; BR – branchiostegal; Dn – dorsonasal; LP – lower preopercular; Md – mandibular; OpD – latero-dorsal opercular; OpV – latero-ventral opercular; PO – postorbital; Prc – precaudal; PV – pectoral to pelvic series; SO – symphysial; Sub – suborbital; UP – upper preopercular; VA – pelvic to anal series; Vn – ventro-nasal; after Badcock & Larcombe (1980); **b** – sequence of photophore development in Schmidt's slickhead (*Microphotolepis schmidti*, Alepocephalidae), photophore acronyms: BrOp – branchiostegal; Dm – dorsomedian; DL – dorsolateral; G – gular; Hm – hyomandibular; IfO – infraorbital; InO – infraorbital ring; Llc – continuation of mediolateral series on head; Llm – mediolateral; Md_{1-2} – mandibular; Mx – maxillary; SpO – supraorbital; SpOp – supraopercular; Oad – antorbital; Op – opercular; PO – postorbital; Pop – preopercular; SbOp – subopercular; Vl_{1-2} – ventrolateral; Vl_{1-3} – three ventropelvic series. After Sazonov (1995); **c** – larval development in streaklight tubeshoulder (*Holtbyrnia latifrons*, Platytroctidae). GO_2 – posterior gular organ, IVO intraventral organ; **d** – larval development in shining tubeshoulder (*Sagamichthys abei*, Platytroctidae), OO – orbital organ, SBO – subopercular organ. After Matsui (1991).

(~ 19.5 mm SL) parallels that of the bluntsnout smooth-head (Fig. 4b), with the first appearance on the lower parts of the body and head. Secondary photophores appear later in ontogeny, at 35-40 mm SL (Sazonov, 1995).

All genera of tubeshoulders (Platytroctidae) are characterised by a unique shoulder organ, containing blue-green luminous cells that can be ejected into the water (Herring, 1972). In addition to shoulder organs, most species of platytroctids have variously developed body photophores, primarily found on the ventral surface of the body (Matsui & Rosenblatt, 1987).

Similar to alepocephalids, early stages of platytroctids are uncommon in plankton collections. Earlier studies noted distinct ontogenetic changes in the orientation of photophores in platytroctids, where larvae and juveniles are characterised by horizontally oriented light organs, changing to ventrally directed in adults (Matsui & Rosenblatt, 1971). Detailed development from yolk-sac larvae to juveniles was subsequently described for two platytroctids – the streaklight tubeshoulder (*Holtbyrnia latifrons*) and the shining tubeshoulder (*Sagamichthys abei*) (Matsui, 1991). Shoulder organ and head photophores in both species show extremely precocious development (Fig. 4c, d), being already distinct in yolk-sac larvae (15-16 mm SL). Photophores in the ventral series on the body develop in late larvae and juveniles (Matsui, 1991). The description of another, tentatively identified platytroctid species, the palegold tubeshoulder (*Maulisia argipalla*), also reports the precocious development of the shoulder organ (John *et al.*, 2000).

Order Stomiiformes

Fishes in this order (4-10 families depending on the classification scheme), along with lanternfishes (Order Myctophiformes), form the vast majority of luminous pelagic ichthyofauna of the oceanic midwaters. All representatives of this primarily deep-water assemblage are self-bioluminescent. Larvae of numerous stomiiform families are quite common in plankton collections, but complete development is documented mostly for zooplanktivorous families.

Zooplanktivorous stomiiforms (Diplophidae, Gonostomatidae, Phosichthyidae and Sternoptychidae) mostly possess large "primary" photophores on the head and ventral surface of the body, with infrequent occurrence of smaller secondary photophores in some species. Primary photophores can be separate or in groups.

In stomiiforms in general, light organs form during a sometimes prolonged metamorphosis and are laid down as "white photophores," which are apparently non-functional. Transformation length and patterns of light organ development vary significantly in different stomiiform families and are detailed by Moser (1996). Ventral photophores of diplophids, gonostomatids and phosichthyids develop rapidly and simultaneously during a "white photophore" stage, while lateral photophores form later and more gradually. In *Cyclothone* spp. (Gonostomatidae), first to form are photophores of the BR and VAV series, while in *Gonostoma* and *Sigmops* spp. (Gonostomatidae) and *Diplophos* spp. (Diplophidae) the OP_1 is first (Ahlstrom, 1973; Watson, 1996a).

Species of Sternoptychidae have photophores within at least some of the photophore groups united in common glands and are characterised by gradual acquisition of both photophore groups and photophores within each group (Fig. 5b, e) during metamorphosis (Watson, 1996b).

Light organ diversity is higher in barbeled stomiiforms (Stomiidae, *sensu* Fink, 1985). In addition to the regular series of ventral and lateral photophores, most piscivorous stomiiforms have bioluminescent barbels and minute secondary photophores scattered over the body. Also present in a few species are pre-, sub-, and postorbital photophores which can be sexually dimorphic, as well as species-specific luminous patches or spherules on the body and fins (O'Day, 1973; Jorgensen & Munk, 1979; Parin & Borodulina, 2003). In addition, three stomiid genera (*Aristostomias*, *Malacosteus*, and *Pachystomias*) have developed extremely rare long-wavelength (red) bioluminescence (Widder et al., 1984; Herring & Cope, 2005).

The reference to larval length at the time of development of light organs in predatory stomiiforms can often be misleading, since their larvae are known to undergo significant shrinkage during metamorphosis. Thus, less advanced larvae with "white photophores" are significantly larger than more developed transitional specimens (30-40 mm SL) with pigmented and probably functional photophores. Similarly, larvae with "white photophores" may be smaller than early larvae with no photophores.

The early development of predatory stomiiforms has been documented in detail in very few cases, precluding broad generalisations on time and order of photophore formation. In the viperfish (*Chauliodus sloani*), photophores appear at 33-37 mm SL after significant shrinkage of up to 30% of its previous size. The shrinkage is complete at 25-27 mm SL, by which time a barbel with a terminal photophore is present. Small secondary photophores subsequently appear on the head and body (Belyanina, 1977), and the barbel later regresses to form a vestigial nub. In the longfin dragonfish (*Tactostoma macropus*), photophores in the ventral series appear at 47-49 mm SL and development of the primary photophores precedes that of the smaller secondary photophores (Kawaguchi & Moser, 1993). In another stomiid fish (*Astronesthes spatulifer*), branchiostegal photophores (BR series) are first to form, appearing at 40-41 mm SL, followed by almost simultaneous development of "white photophores" in other ventral series (PV, VAV, AC) at 46-47 mm SL (Suntsov, 1999). A review of the published information on the larvae of barbeled stomiiforms indicates that specialised luminous organs and structures appear much later in ontogeny (Kawaguchi & Moser, 1984; Moser, 1996).

Order Aulopiformes

Bioluminescence is not widespread in this diverse group of primarily deep-sea fishes (15 families), of which only four families – the benthopelagic greeneyes (Chlorophthalmidae), and the pelagic pearleyes (Scopelarchidae), barracudinas (Paralepididae) and sabertooth fishes (Evermannellidae) have few bioluminescent representatives. Rarity and morphological disparity of light organs in this group suggest
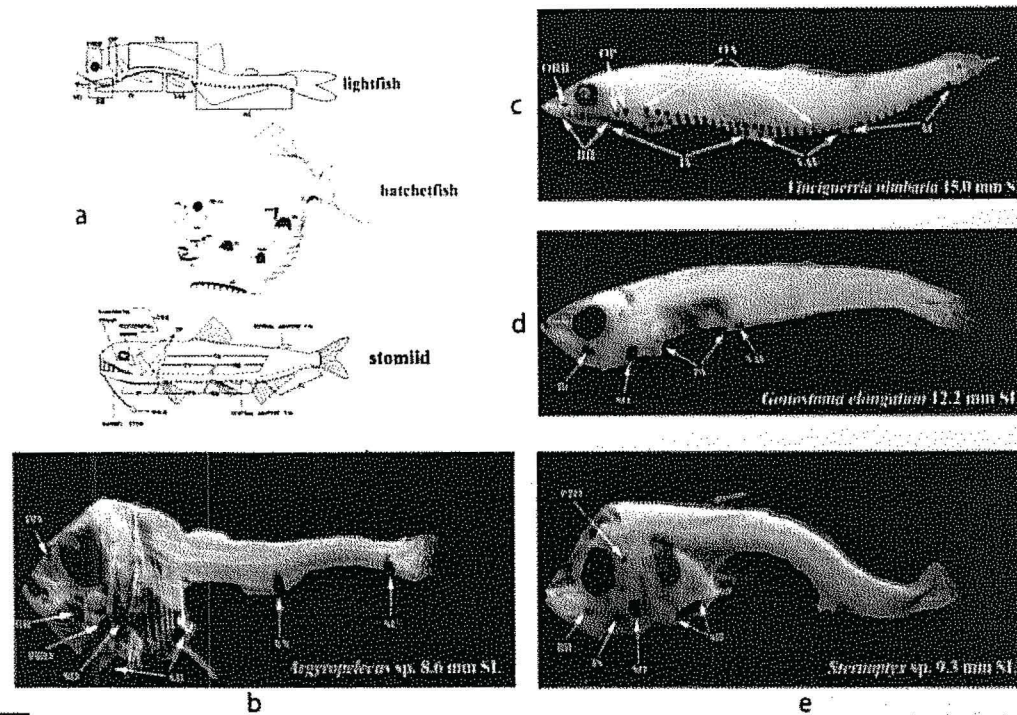
Fig. 5 Development of light organs in the order Stomiiformes. **a** – photophore terminology for different stomiiform groups. After Moser & Watson (1996); **b**, **e** (Sternoptychidae), **c** (Phosichthyidae), **d** (Gonostomatidae) – representatives of larval stomiiforms showing precocious development of light organs. AB – abdominal photophores; AC – photophores from the anal fin base to caudal fin base; AN – anal; Br – branchiostegal; Is – isthmal; IV – isthmus to pelvic series; PAN – preanal; OA – lateral series from the opercle to anal fin base; ORB – orbital; OP – opercular; PO - preorbital; PTO – postorbital; PRO – preopercular; SAN – supraanal; SC – subcaudal; SO – subopercular; SP – suprapectoral; VAV – pelvic to anal fin base series.

that the ability to produce light may have evolved multiple times due to similar selection pressure in the oceanic midwaters.

Species of *Chlorophthalmus* spp. were reported to have a bacterial light organ associated with a peri-anal groove (Somiya, 1977). Available information on the early ontogeny of *Chlorophthalmus* indicates that a light organ is not present in the larvae (Okiyama, 1984). Among pearleyes (Scopelarchidae), only Zugmayer's pearleye (*Benthalbella infans*) and *Scopelarchoides kreffti* are known to have ventral luminescent organs (four and two, respectively) and are considered self-bioluminescent (Merrett et al., 1973). The photogenic tissue of Zugmayer's pearleye is unique among teleosts because of its derivation from muscle cells (Johnston & Herring, 1985). Light organs are barely visible as whitish areas in 20-mm postlarvae of Zugmayer's pearleye and are fully developed only in adults (Merrett et al., 1973). The ontogeny of most scopelarchids is well known, but no information on the larvae of *S. kreffti* is available and the possibility of early development of light organs remains open (Johnson, 1984a).

Of the three genera of sabertooth fishes (Evermannellidae), only the Atlantic sabertooth (*Coccorella atrata*) and possibly *C. atlantica* have light organs as part of the gut wall of the intestine, the rectum and the anterior pyloric caecae (Herring, 1977). Light organs do not appear early in the development of *Coccorella* species (Johnson, 1984b). Two genera of barracudinas (Paralepididae) – *Lestrolepis* and *Lestidium*, are self-bioluminescent, having either single (*Lestidium*) or double (*Lestrolepis*) abdominal bands of luminous tissue. In addition, some species are reported to have ventral photophores (Herring & Morin, 1978). The early development of barracudinas is still poorly known and no incipient light organs are evident in published accounts of paralepidid ontogeny (Rofen, 1966; Okiyama, 1984).

Order Myctophiformes

Bioluminescence is found in both families of this rather morphologically homogenous group, the blackchins (Neoscopelidae) and the lanternfishes (Myctophidae). Of the blackchins, which includes three genera and six species, three species of *Neoscopelus* have large primary photophores in horizontal rows on the body and tongue. No additional luminous organs are present. Available information on the development of *Neoscopelus* suggests that no photophores are present in the larvae (Okiyama, 1984).

All 235 currently known species of lanternfishes are luminous. In addition to large primary photophores arranged in distinct groups on the head and body (Fig. 6a), various species of myctophids possess small secondary photophores on the head and body, supra- and infracaudal glands, photophores associated with the eyes, and a variety of luminous patches (Paxton & Hulley, 1999). Unlike neoscopelids, all species of myctophids show relatively early development of photophores (Fig. 6b-f). Early myctophid ontogeny is well documented and the sequence of photophore development in different genera can be significantly different (Table 1). However, the initial light organs to form are always the middle pair (Br_2) of branchiostegal photophores. The only exception to this rule is peculiar larvae of *Diaphus* from the western Pacific,
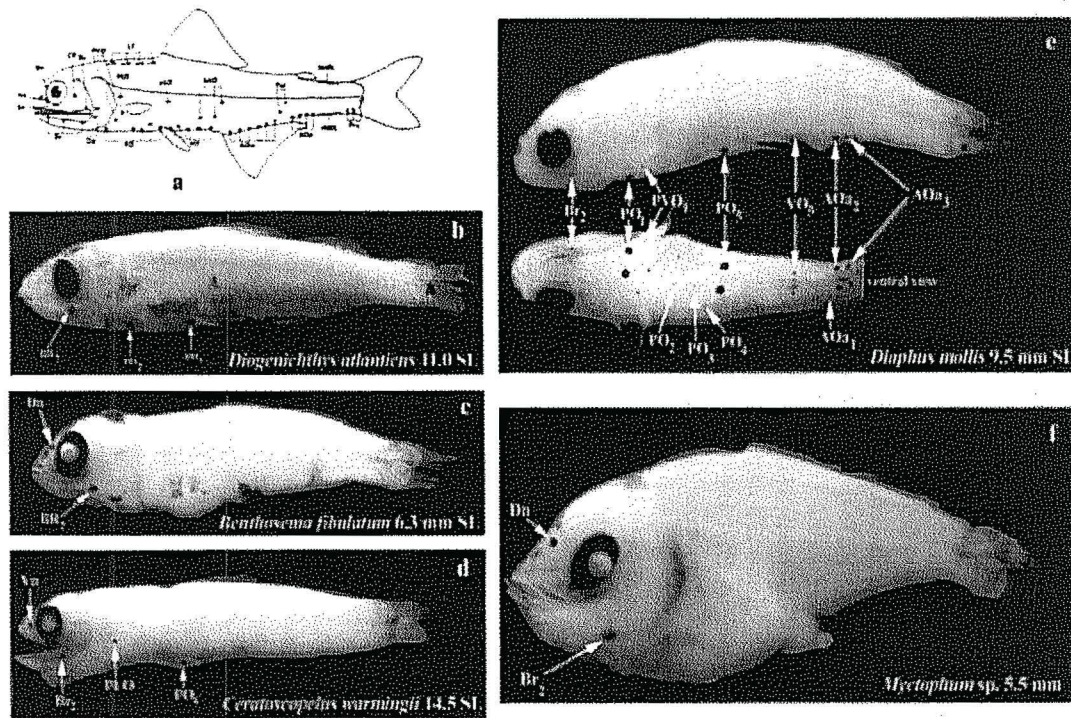
Fig. 6 a – The general distribution and terminology of the luminous organs (photophores) in the family Myctophidae. After Paxton (1972); b-f – representative larval myctophids showing early appearing photophores. Photophore acronyms: AOa – anterior anal; AOp – posterior anal; Br – branchiostegal; Bu – buccal; Cp – cheek; Dn – dorsonasal; INGL – infracaudal luminous gland; Lt – patches of luminous tissue; Op – opercular; PLO – suprapectoral; PO – thoracic or pectoral; Pol – posterolateral; Prc – precaudal; PVO – subpectoral; SAO – supraanal; So – suborbital; SUGL – supracaudal luminous gland; VLO - supraventral; Vn – ventronasal; VO – ventral.

Table 1 Sequence of formation of photophores in selected genera of Myctophidae. The Br appear first in all genera listed. Parentheses indicate late appearing photophores after Moser et al. (1984).

	Br_1	Br_3	Dn	Vn	OP_2	PO_1	PO_2	PO_3	PO_4	PO_5	PVO_1	PVO_2	PLO	VLO	VO_1	VO_5	AOa_1	AOa_2
Benthosema																		
suborbitale	2	2	—	—	2	1	1	3	3	3	—	—	—	—	—	—	3	3
glaciale	—	—	—	—	(1)	(1)	(1)	(1)	(1)	(1)	—	—	—	—	—	—	—	—
pterota	—	—	1	—	4	6	—	—	—	2	3	5	—	—	5	—	6	—
fibulatum	—	—	1	—	—	3	5	—	—	2	—	—	—	6	—	—	4	6
Diogenichthys																		
laternatus	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
atlanticus	—	—	—	—	—	—	1	—	—	2	—	—	—	—	—	—	3	—
Myctophum																		
spinosum	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
lychnobium	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
asperum	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
brachygnathum	—	—	1	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—
obtusirostre	—	—	1	—	—	3	—	—	—	—	—	—	2	—	—	—	—	—
selenops	—	—	—	—	—	3	—	—	—	—	—	—	2	—	—	—	—	—
Lobianchia	—	—	—	—	—	1	—	—	—	2	3	4	—	—	—	—	—	—
Diaphus																		
theta	—	—	—	—	(5)	2	(4)	(7)	(8)	1	—	—	—	(9)	(3)	(6)	—	—
pacificus	—	—	—	—	—	2	(3)	(5)	—	1	(4)	—	—	—	(6)	—	—	—
Gymnoscopelus	—	—	—	—	—	2	4	—	—	1	—	—	—	—	3	—	—	—
Lampanyctodes	—	—	—	1	—	4	—	—	—	2	—	—	3	—	—	—	—	—
Scopelopsis	—	—	—	2	—	—	—	—	—	1	—	—	—	3	—	—	—	—
Lampichthys	—	—	—	2	—	4	—	—	—	1	—	—	3	—	—	—	—	—
Notoscopelus	—	—	—	2	—	—	—	—	—	1	—	—	3	—	—	—	—	—
Lampadena	—	—	—	3	—	3	—	—	—	2	—	—	1	—	—	—	—	—
Ceratoscopelus	—	—	—	1	—	—	—	—	—	3	—	—	2	—	—	—	—	—
Lepidophanes	—	—	—	1	—	—	—	—	—	1	—	—	1	—	—	—	—	—
Bolinichthys	—	—	—	(1)	—	—	—	—	—	(1)	—	—	(1)	—	—	—	—	—

designated as *Diaphus* sp. XII, which never develop Br_2 photophores even during metamorphosis (Ozawa, 1986). In the multispot lanternfish (*Scopelopsis multipunctatus*), Br_2 are visible at 5.4 mm SL and are well formed in 10.8-mm larvae. In the same species, the posterior-most pair of PO photophores is next to form, followed by Vn and VLO photophores (Moser & Ahlstrom, 1972). The functional state of the larval photophores in myctophids has not been investigated to date.

Order Gadiformes

Bioluminescence is widespread in this primarily benthopelagic group and is most commonly found in fishes inhabiting continental slopes between 100-500 m (Marshall & Cohen, 1973). Among the grenadiers (Macrouridae), all species in 10 (out of 27 total) genera have a ventral light organ in front of the anus, and the light is produced by luminous bacteria (Herring & Morin, 1978). Although certain developmental stages in several bioluminescent genera (e.g. *Coelorhynchus*, *Malacocephalus*, *Nezumia*, *Ventrifossa*) are described, no special attention is usually given to development of luminous organs (Fahay & Markle, 1984; Merrett, 1989; Ambrose, 1996). A macrourine alevin, with a head length (HL) of 19 mm, was found with a light organ with two separate dermal windows (Fig. 7a) between the pelvic bases (Merrett, 1989). Pelagic larvae of Sagami grenadier (*Ventrifossa garmani*) (5.1 mm HL, 90+ mm total length, TL) appear to initiate the development of its two dermal windows (Fig. 7b) as part of the anal light organ (Fukui & Tsuchiya, 2005).

Species of *Hymenocephalus* have a long, tubular, abdominal light organ, with two (anterior and posterior) light glands (Fig. 7c) equipped with lenses and connected by a common duct (Haneda, 1951). The light organ of *Hymenocephalus* is accompanied by fine skin striae ventrally and laterally, probably serving as indirect diffusers of light (Marshall & Iwamoto, 1973). Larvae of *Hymenocephalus* sp. (3.6 mm HL, 20.5 mm TL) display a light organ similar to that of the adult, with anterior and posterior lenses connected by a duct, but with no apparent striations on the ventral portion of the abdomen (Endo et al., 1992). Light organs in the species of *Coelorhynchus* display significant structural variation, ranging from simple bulbous light glands near the anus to tubular organs similar to that of *Hymenocephalus* (Okamura, 1970). There is some evidence that in some species of *Coelorhynchus* bioluminescence may be restricted or better developed in juveniles than adults (Haneda, 1951)

The only bioluminescent merlucciid species, the luminous hake (*Steindachneria argentea*, Merlucciidae) (Fig. 7d), has a doughnut-shaped light gland surrounding the anus, with bacterially produced light emitted through the striated skin and hypaxial abdominal musculature (Cohen, 1964). Although no special attention has been given to the exact time of the development of bioluminescent structures, published illustrations of early development in luminous hake show that the light organ system is probably developed by 24.0 mm SL (Fahay, 1989).

Several genera of morid cods (Moridae), *Physiculus*, *Brosmiculus*, *Gadella*, *Tripterophycis*, and perhaps *Antimora* and *Lotella*, are known to have bioluminescent
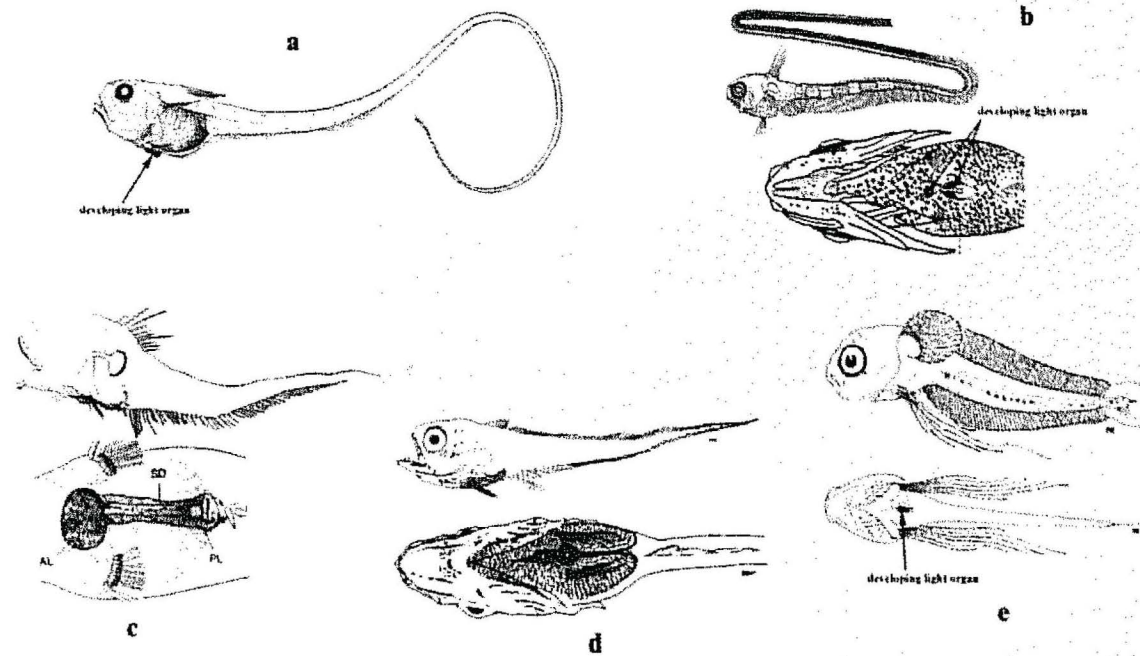
Fig. 7 Development of light organs in the order Gadiformes. **a** – unidentified macrourid alevin (19 mm HL) with a developing light organ (after Merrett, 1989); **b** – pelagic larva of Sagami grenadier (*Ventrifossa garmani*, Macrouridae) 5.1 mm HL (90 + mm TL). Lateral view and ventral view of the abdomen showing incipient light organ modified after Fukui & Tsuchiya (2005); **c** – larval *Hymenocephalus* sp. (Macrouridae) 20.5 mm TL, lateral and ventral views of developing light organs after Endo *et al.* (1992); **d** – late larva of luminous hake (*Steindachneria argentea*, Merluciidae) 24.0 mm SL, showing developing light organ and striated abdominal musculature after Fahay & Markle (1984); **e** – larva of charcoal mora (*Physiculus nematopus*, Moridae) 9.2 mm SL and ventral view of larva 14.1 mm SL after Fahay & Markle (1984). Abbreviations: SL – standard length, TL – total length, HL – head length, AL – anterior lens, PL – posterior lens, SD – secondary duct.

organs (Marshall & Cohen, 1973). Early life history information on morid species is scarce, but similar to other bioluminescent gadiform representatives, the published larval descriptions (e.g. *Physiculus*, Fig. 7e) indicate rather early development of luminous structures (Fahay & Markle, 1984).

Order Batrachoidiformes

Within this order, bioluminescence occurs only in the genus *Porichthys*, with 14 species found in coastal waters of North and South America. The midshipman has served as a model organism in a variety of bioluminescence studies (Nicol, 1957; Baguet & Case, 1971). In this species, numerous photophores (up to 850) in rows are found along the lateral lines and light production is endogenous (Herring & Morin, 1978).

During early ontogeny, photophores are first externally visible in larvae 12-13 mm SL and display an asynchronous development, spreading from head to tail. First to appear are the mandibular photophores, followed by differentiation of body photophores. There are two distinct stages in the functional development of midshipman photophores. At around 18-21 mm SL (28 days after hatching), when the yolk is nearly or fully resorbed, larvae emit a green fluorescence from most photophores under ultraviolet light and exhibit strong and fluctuating luminescence upon application of hydrogen peroxide. A luciferin and luciferase are detected in larvae at this stage (Tsuji *et al.*, 1972). However, the endogenous control of the bioluminescence, i.e. when luminescence is induced by electrical stimulation or norepinephrine injection, is observed somewhat later, at 32-33 days post hatching. Detailed anatomical studies indicate that the photophore anlage originates as an outgrowth from the basal cell layer of the epidermis and thus is of ectodermal origin. Conversely, the reflector is of mesodermal origin, developing from the fibroblast layer enveloping the dermal aspect of the developing photophore (Anctil, 1977).

Order Lophiiformes

The remarkable assemblage of deep-sea anglerfishes (superfamily Ceratioidea), currently with ~158 species in 11 families, represents the most diverse group of bioluminescent bathypelagic fishes. In addition to extreme sexual dimorphism in size (females greatly larger than males) and some other unique morphological trends, only female ceratioids (except *Neoceratias* and *Caulophryne*) are known to produce light (Bertelsen, 1951; Pietsch, 2005). The most common and widespread type of bioluminescence in ceratioids is due to non-culturable luminous bacteria hosted in the esca – the terminal bulbous part of the ilicium (a modified dorsal ray). Some studies suggest that each ceratioid species may have its own species of luminous bacterium (Haygood & Distel, 1993). Furthermore, females of the family Ceratiidae possess caruncles – additional bacterial light organs in front of the soft dorsal fin (Bertelsen, 1951). Females of the genus *Linophryne* (Linophrynidae) display a dual bioluminescent system, with both a bacterial light organ within the esca as well as a self-luminescent hyoid (chin) barbel (Hansen & Herring, 1977).

The larvae of ceratioids, similar to many deep-sea fish groups, primarily live in the productive epipelagic zone and descend rapidly to deeper levels at the start of their metamorphosis. A club-shaped, rudimentary ilicium is formed early in ontogeny and is present in numerous larval female ceratioid species (Bertelsen, 1984). The early development of escal light glands was studied in larval *Melanocetus* spp. and triplewart seadevil (*Cryptopsaras couesii*), and metamorphosing bulbous dreamer (*Oneirodes eschrichtii*), soft leafvent angler (*Haplophryne mollis*), and Murray's abyssal anglerfish (*Melanocetus murrayi*) specimens. No or few luminous bacteria were found in the larvae and light glands of recently metamorphosed specimens (Munk and Herring, 1996; Munk et al., 1998). Thus, the functionality of the luminous glands appears to be postponed until the end of metamorphosis, at which time morphological differentiation of intraglandular lumina occurs and a duct to the exterior is formed (Munk, 1999). Furthermore, metamorphosis is associated with an accelerated morphological development of the esca (Munk & Herring, 1996).

The acquisition of the right type of luminous symbiotic bacteria apparently occurs around the time of metamorphosis, a view corroborated by the presence of partly-colonised light glands in juvenile soft leafvent angler (Herring and Munk, 1994). A similar situation was described for the caruncles found in ceratiid species (Munk & Herring, 1996). The self-luminescence found in the hyoid barbels of the genus *Linophryne*, where 10-mm larvae possess only rudimentary thickening of the skin in the place of the barbel, is also apparently confined to adults (Bertelsen, 1984).

The only other lophiiform representative known to have bioluminescent properties is the batfish (*Dibranchus atlanticus*, Ogcocephalidae), reported to have dorsal skin luminescence (Crane, 1968). No further information on bioluminescence in this species is available.

Order Beryciformes

Three families of this order have bioluminescent representatives – the slimeheads (Trachichthyidae), the flashlightfishes (Anomalopidae) and the pinecone or knight fishes (Monocentridae). Bioluminescence is of bacterial origin and light organs can be variously placed near the anus, on the lower jaw, or beneath the eyes (Herring & Morin, 1978).

Among trachichthyids, only species of *Aulotrachichthys* (formerly a subgenus of *Paratrachichthys*) are bioluminescent. However, the presence of characteristic striated areas in other representatives (e.g. *Sorosichthys*) can be an indication of a more frequent occurrence of bioluminescence in these fishes (Kotlyar, 1996). In *Aulotrachichthys* sp., a light organ surrounding the anus first appears in 3.6-mm larvae and is well-developed and heavily pigmented by 4.9 mm SL (Fig. 8b). Striated tissue, probably serving as a light guiding structure similar to that found in some gadiform fishes, is developed somewhat later, by 7.9 mm SL (Jordan & Bruce, 1993). Similarly, Konishi & Okiyama (1997) reported developed light organs in a 4.6-mm larva and the development of striated tissue in 7.4-mm larva of this species.
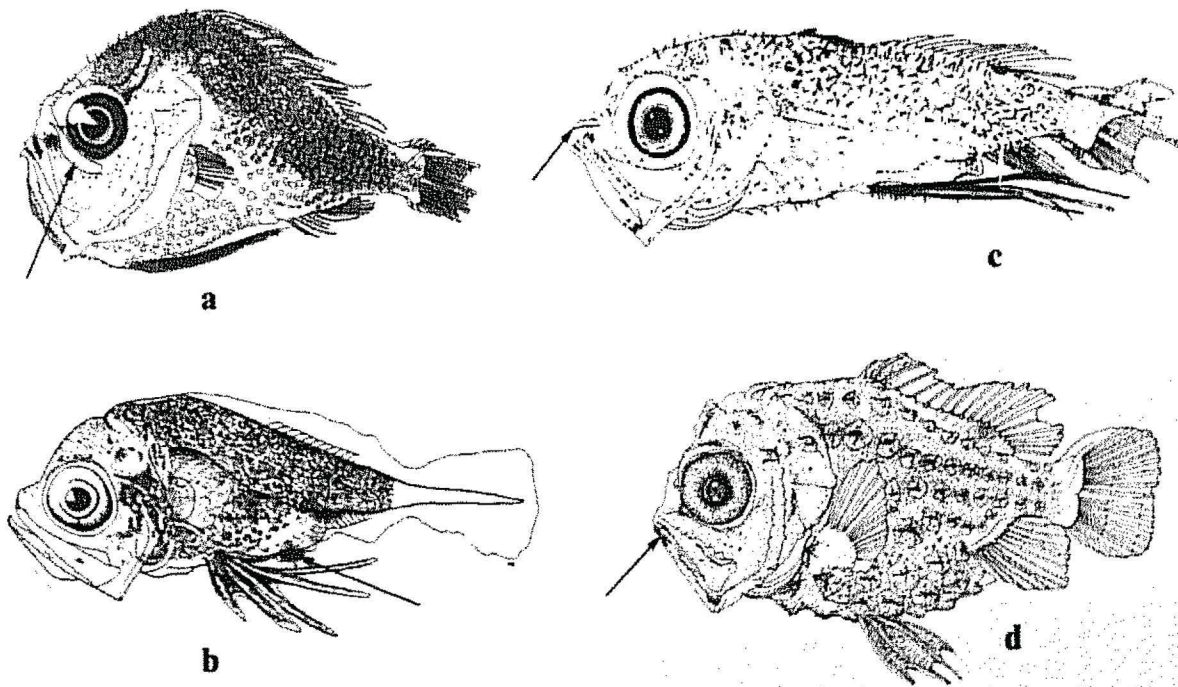
Fig. 8 Development of light organs in the order Beryciformes. **a** – larva of splitfin flashlightfish (*Anomalops katoptron*, Anomalopidae) 5.8 mm SL after Konishi & Okiyama (1997); **b** – larva of *Aulotrachichthys* sp. (Trachichthyidae) 4.4 mm SL after Jordan & Bruce (1993); **c** – larva of Atlantic flashlightfish (*Kryptophanaron alfredi*, Anomalopidae) 6.2 mm SL after Baldwin & Johnson (1995); **d** – larva of pineconefish (*Monocentris japonicus*, Monocentridae) 6.5 mm SL after Okiyama (1988). Arrows indicate developing light organs.

All five genera and six species of anomalopids are bioluminescent, bearing prominent subocular light organs packed with luminous bacteria (Kotlyar, 1996). In splitfin flashlightfish (*Anomalops katoptron*) larvae, incipient light organs appear as rod-shaped projections on the ascending process of the premaxilla in flexion-stage larvae (Fig. 8a), subsequently becoming crescent-shaped and migrating below the eye (Konishi & Colin, 2000). The exact state of bacterial inoculation of the developing light organ in postflexion larva of splitfin flashlightfish 5.8 mm SL is not clear, since it was not examined histologically, but the developing light organ was referred to as "incipient" (Konishi & Okiyama, 1997). In the only known larva of Atlantic flashlightfish (*Kryptophanaron alfredi*) (6.2 mm notochord length), the light organ develops as an anteriorly directed, rod-like projection on the snout (Fig. 8c), with internal invaginations similar to adult light organs. At this stage, no luminous bacteria are present (Baldwin & Johnson, 1995).

Three species of nocturnal, bottom-living monocentrids are unusual in having luminous organs located on the lower jaw. The incipient black-coloured light organ in pineconefish appears on the symphysis of the lower jaw (Fig. 8d) by 6.5 mm SL (Konishi, 2000). No information on the early development of the western Australian pineapplefish (*Cleidopus gloria-maris*) is available.

Order Perciformes

Bioluminescence is a rare phenomenon in this largest assemblage of modern teleost fishes (160 families). Only six distantly related families contain bioluminescent representatives, with both endogenous (some Apogonidae, Pempheridae, Sciaenidae, Chiasmodontidae) and bacterially induced light production (some Apogonidae, Acropomatidae, Leiognathidae). Nocturnal lifestyles (Apogonidae, Pempheridae), as well as certain environmental conditions such as deep-sea darkness (Chiasmodontidae, some Acropomatidae) or turbid estuarine or coastal waters (Leiognathidae, Sciaenidae) have made light emitting properties in certain perciform groups selectively advantageous.

The bacterial luminescence in cardinalfishes (Apogonidae) is apparently restricted to the genus *Siphamia* (Herring & Morin, 1978). The small luminous gland of *Siphamia* is found ventrally in the anterior part of the abdominal cavity and is connected to the gut (Iwai, 1971). An additional orobranchial luminous organ in the same genus was described recently by Fishelson *et al.* (2005). Three other genera of luminous apogonids (*Apogon*, *Archamia* and *Rhabdamia*), with endogenous (*Cypridina*-like) bioluminescence, show diversity in the morphology of their internal light organs, ranging from pouch-like protrusions of the intestine, rectum or even a modified pyloric caecum (Haneda *et al.*, 1969).

To date, only the larvae of the sea urchin cardinalfish (*Siphamia versicolor*) have been studied closely in terms of the early ontogeny of luminous organs (Leis and Bullock, 1986). In this species, the light gland develops as a pigmented gut diverticulum at 2.4 mm SL and moves to a more anterior position near the cleithrum with larval growth (Fig. 9a). The final positioning of the light gland, reached by 2.8 mm SL, is accompanied by the development of associated light diffusers, which gradually spread
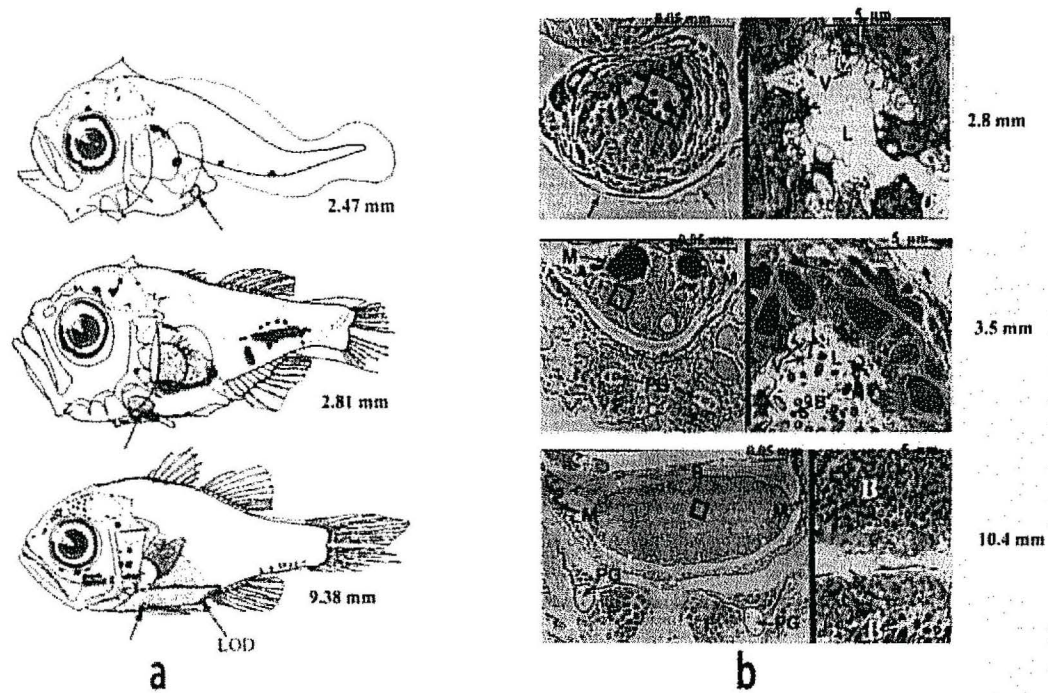
Fig. 9 Development of light organ in sea urchin cardinalfish (*Siphamia versicolor*, Apogonidae, Perciformes) modified after Leis & Bullock (1986). **a** – Migration of the light organ in developing larvae of sea urchin cardinalfish. Arrows point to developing light gland. LOD – light organ diffuser. **b** – phase contrast photographs of transverse sections of the light organ in larval sea urchin cardinalfish 2.8 mm, 3.5 mm and 10.4 mm SL. Regions similar to those shown within boxes are enlarged on right. Scale 0.05 mm. Muscle fibres (F) of the light diffuser surround the developing bones of pelvic girdle (PG). R – dorsal layer of fibrous tissue. The light organ contains many densely packed vesicles packed with bacteria. V – microvilli, M - melanin bodies, L – lumen, B – bacteria.

anterior and posterior to the light organ itself. Symbiotic bacteria (*Photobacterium leiognathi*) were observed in the larval light organs starting at 3.5 mm SL and the gross morphology of the light organ in 10.4-mm larva is basically identical to that of the adults (Leis & Bullock, 1986). This study suggests that the light organ of sea urchin cardinalfish should be functional before reaching 10.4 mm SL, when associated reflector and diffusers are already fully developed and while the larvae are still pelagic. Luminous bacteria are apparently acquired *de novo* from the environment by developing larvae, but when this happens is still a matter of conjecture (Leis and Bullock, 1986). The presence of a recently described oral light organ in a second species of *Siphamia* (Fishelson *et al.*, 2005), as well as its early development, remains to be confirmed. Although a number of other forms of apogonid larvae have been described, few have been ascribed to particular species and no developing light organs are evident from available illustrations and descriptions (Leis & Rennis, 2000a).

The early stages of development are known for at least some species in the remaining bioluminescent perciforms – e.g. Acropomatidae (*Acropoma*), Leiognathidae (*Leiognathus*), Pempheridae (*Pempheris, Parapriacanthus*) – but no references to developing light organs are made in available descriptions and no precocious light organs are evident from published illustrations (Haque & Ozawa, 1995; Sandknop & Watson, 1996; Leis & Rennis, 2000b; Trnski & Leis, 2000). Thus, more detailed studies of larval ontogeny, including histological investigations, are needed to confirm the presence or absence of light organs in the larvae of perciform fishes with internal light organs.

The self-luminescent perciform genera *Pseudoscopelus* (Chiasmodontidae) and *Collichthys* (Sciaenidae), unlike perciforms with internal light glands, possess numerous small photophores on lower parts of the body (Herring & Morin, 1978). The early ontogeny of *Pseudoscopelus* species is barely known, but the absence of light organs in available illustrations suggests that development of photophores is postponed until probably the juvenile stage (Watson & Sandknop, 1996). No early life history information is available on luminous species of *Collichthys*, but late development of body photophores is most likely the case in this genus as well.

FUNCTIONAL SIGNIFICANCE OF BIOLUMINESCENCE IN LARVAL FISHES

Although a significant body of information has accumulated on the early development of teleost fishes with bioluminescent properties as adults, numerous aspects of the early ontogeny of light production, such as the exact timing when photophores become functional, possible changes in physical properties of the emitted light during growth and maturation, and/or ontogenetic variations in light organ development between different ecological groups remain unknown. In addition, although a significant number of observations of live bioluminescence is available for adult fishes, such data for larval stages are almost completely lacking. In fact, only the larvae of coastal midshipman have been closely studied to date in this respect (Anctil, 1977).

Despite the numerous gaps in our knowledge of early light production in fishes, certain clues to its possible function and biological significance can be deduced from the accumulated ecological and developmental information on marine fish larvae. This is especially true for the most diverse and abundant bioluminescent teleost representatives, the midwater ichthyofauna, where in some cases 97% of the individuals and 75% of the fish species can be bioluminescent (Badcock & Merrett, 1976). Due to the abundance and ubiquity of mesopelagic fish larvae in various oceanic regions, more information on their development and habitat preferences is available than for any other bioluminescent fish group.

Unlike shallow-living and coastal species, where adult and larval lives are spent in relatively similar depth strata, most deep-sea pelagic fishes initially develop in the productive surface waters, forming a significant portion of the zooplankton assemblage (the ichthyoplankton). With growth and approaching the juvenile stage, these larvae initiate their descent to deeper levels common for adults, a phenomenon known as ontogenetic vertical migration. Most oceanic ichthyoplankton are found within the upper 200 m and the bulk is composed of larvae of light-producing fishes such as stomiiforms and myctophids (Loeb, 1979; Suntsov, 2000; Sassa et al., 2002).

The available information on the development of deep-sea fishes reveals a significant variation in developmental timing of particular photophores or photophore groups. It is not clear, however, whether these developing photophores actually produce light, and to date no live bioluminescence at these early stages has been reported. In adult deep-sea fishes, the uses of bioluminescence are manifold and often several functions can be attributable to a single light organ. Among most commonly cited functions of light production in fishes are ventral counter-illumination to match the downwelling light, attraction or illumination of prey, intra- and inter-specific communication, and deterrence of predators (Herring, 1982; Widder, 1999). One can hypothesise a number of similar uses in fish larvae, but at least some known functions (e.g. attracting a mate) can be excluded from early ontogeny with confidence. In addition, the full diversity of adult light organs is not acquired until the completion of metamorphosis, making the larval bioluminescent repertoire intrinsically more limited.

Ventral photophores are the first to develop in certain midwater fishes and the use of bioluminescence for counter-illumination seems to be the most plausible explanation. According to experimental data, the effective upper depth limit for counter-illumination is approximately 400 m (Young et al., 1980). Thus, during daytime, light production is of limited value in the well-lit epipelagic zone, because no light organ can match the high intensity of downwelling irradiance.

In oceanic lanternfishes, whose larvae develop primarily at depths less than 100 m (Loeb, 1979), first to develop are the Br_2 photophores, followed by some other photophores on the head (Fig. 6). The acquisition of photophores on the ventral surface of the body is postponed to later stages and is gradual. This particular feature, as well as the occurrence of lanternfish larvae in the upper levels of the water column, suggests that ventral counter-illumination is likely not to occur during early development of myctophids. An apparently similar situation exists in the larvae of some other luminous

fishes that develop in well-lit levels of the upper water column. For example, only non-functional, white photophores are found in the larvae of *Cyclothone* spp. occurring above 200 m, with photophore completion and metamorphosis occurring at depths greater than 350 m (Ahlstrom, 1973; Loeb, 1979).

The early appearance of some light organs in myctophid larvae could potentially be an indication of other uses of bioluminescence at low light levels, such as at night. For example, early forming head photophores (Br_2, Dn, Vn and others) could offer a certain selective advantage (if functional) and be used for attraction of prey organisms such as copepods (Moser, 1981), most of which are known to have positive phototaxis. Interestingly enough, development of light organs on the head (e.g. Br, So) in larval stomiiforms, also precedes the appearance of body photophores (Watson, 1996a, b; Suntsov, 1999), possibly indicating a common ecological cause in both groups. However, the production of light has its own metabolic costs and for such a strategy to be effective the advantages should outweigh the possible losses. There is also the possibility that certain patterns of light organ development could be a reflection of specific phylogenetic patterns and have little or no functional significance in early ontogeny.

Interestingly, the timing in photophore development seems to have a positive correlation with different ecological preferences in different groups of myctophid larvae. Two currently recognised subfamilies of oceanic lanternfishes, Myctophinae and Lampanyctinae, have markedly different larval morphologies and also vary in their habitat preferences, with larvae of the former subfamily usually found deeper in the water column, while most larval lampanyctines inhabit shallower depths (Ahlstrom, 1959; Loeb, 1979; Sassa *et al.*, 2002). Available information on the development of deeper dwelling lanternfish larvae (subfamily Myctophinae) indicates that more photophores develop early and have more advanced development in this subfamily than in the other group with shallow dwelling larvae (subfamily Lampanyctinae) (Moser & Ahlstrom, 1996). It is possible that lower irradiance as well as lower prey abundance at deeper strata would render precocious development in light organs and their early functional state more useful and advantageous for early life.

The larvae of oceanic hatchetfishes (Sternoptychidae) display strikingly precocious development of photophores in the ventral series. The adult hatchetfishes, with their extremely flattened bodies, silvery flanks, and clusters of abdominal photophores, are exemplary deep-sea fishes utilising ventral counter-illumination in oceanic midwaters (Denton *et al.*, 1972). Larvae of *Argyropelecus* and *Sternoptyx* (and possibly some other genera) are unusual among other types of oceanic ichthyoplankton in developing at markedly deeper levels of the water column. Larvae of *Sternoptyx* are found between 500-1000 m and *Argyropelecus* between 100-500 m in the eastern Atlantic (Badcock & Merrett, 1976). In the central Pacific the situation is somewhat different with larval *Sternoptyx* occurring at 100-350 m and *Argyropelecus* at 350-600 m, but this still reflects deeper dwelling preferences (Loeb, 1979). It seems plausible that early developing clusters of ventral photophores in hatchetfish larvae could well be functional and used for counter-illumination at low irradiance levels in deeper water. At the opposite end of the vertical distribution spectrum, the larvae of *Diplophos* (Diplophidae), whose

adults have well-formed abdominal photophores, develop at very shallow depths (0-25 m; Loeb, 1979). The formation of photophores in this genus is not apparent during the larval stage and evidently quite delayed.

Data on the early development of another deep-pelagic fish family, the Platytroctidae, suggest a similar trend in light organ development, i.e. deeper water levels - early forming photophores. A number of platytroctid species with documented early ontogeny display very precocious development of certain body photophores as well as the tube shoulder organ (Fig. 4). This is in agreement with present knowledge on their vertical distribution, where larvae occur at deeper strata – 300-1000 m (Matsui, 1991), than the majority of larval fishes in the open ocean. Although the functional state of these early forming light organs is also a matter of conjecture, dim downwelling light of the mesopelagic zone could be a factor, making the early emission of light from larval photophores selectively advantageous.

One point to consider is that if light production is indeed present in the larvae of some bioluminescent mesopelagic fishes, this light could be quite different from that of adults. Fully developed photophores can be quite complex structures, equipped with reflectors, screens, filters, diffusers or light conducting channels, which modulate the spectrum and angular distribution of the emissions (Herring, 1982; Widder et al., 1983). Thus, the final state of a particular light organ is probably achieved only after metamorphosis, and before that, the emission of light may not be tuned as in adults.

It is apparent from previous accounts of fish bioluminescence (Herring & Morin, 1978; Herring, 1982) that the multiple origins of light production in unrelated teleost groups indicate a great degree of convergence in evolution of both bacterial and endogenous light organs due to common selection pressures. Intrinsic luminescence is usually confined to single cutaneous light organs or photophore groups and is found in both ancient deep-water fishes (sensu Andriashev, 1953) such as stomiiforms, myctophiforms and alepocephaloids as well as more phylogenetically recent deep-sea families, e.g. swallowers (Chiasmodontidae). Although both "primary" and "secondary" deep-sea fishes possess multiple body photophores as adults, only ancient deep-water forms display early the appearance of light organs in larvae. Evidently, longer evolutionary periods under deep-sea conditions have not only produced an array of unique morphological and physiological adaptations in primitive teleosts, but also influenced their early ontogeny, warranting early development of light organs in larvae.

FUTURE PERSPECTIVES

It is apparent that bioluminescence has played a significant, if not pivotal, role in the evolution of certain teleost groups, facilitating a number of adaptive radiations in a diversity of habitats ranging from deep-sea to coastal waters and coral reefs. To date, the research emphasis in studies of fish bioluminescence has been on the adult stage. Ideally, however, every adaptive feature or function should be investigated in its entirety, from earliest appearance to fully developed state, if we are to gain a true understanding of its biological significance. Considering the still nascent state of larval

bioluminescence research, the prospects for incorporating data from early ontogeny in the studies of light production in fishes are very promising and this largely unexplored field will no doubt yield many important insights and discoveries in the future.

One of the primary goals of future research should be to document the functional ontogeny of light producing organs or structures. This information, coupled with available data on various developmental patterns in different teleost lineages, could supply valuable insight into environmental adaptations, developmental constraints and/or ecological and behavioural factors relevant to light production during early life stages. A taxonomically broad approach in such studies will also likely provide insight into convergent evolution of bioluminescent phenomena.

Differential rates of development of photophores, changes in intensity and spectral composition of light during development would also be important and interesting aspects to address in future studies. For example, heterochrony has been a common evolutionary mechanism in the long history of teleost fishes. It is intriguing to consider the potential role of changes in the order and timing of developmental events in reference to developing photophores and other specialised light organs. Another important and equally demanding component of larval bioluminescence research will be to understand the exact pathways and origins of luciferins in self-luminescent groups and also mechanisms and timing of bacterial acquisition in species with bacterial bioluminescence.

Detailed morphological, physiological and histological studies of the early ontogeny in a few bioluminescent "oddballs" – e.g. rare species in otherwise non-bioluminescent groups, could be particularly promising in gaining understanding of the independent evolution of light production, possible limiting factors precluding its development, as well as mechanisms or morphologies which overcome such restrictions. Similarly, detailed comparison of light producing structures in phylogenetically "old" and "modern" teleost groups would be valuable in deciphering the degree of convergence of bioluminescent phenomena.

Several of these avenues of research would clearly require a great deal of experimental field work and laboratory study. Such research would be particularly interesting for pelagic deep-sea fishes considering their outstanding diversity. However, deep-sea fishes are rarely maintained in captivity because of their strict physiological and ecological demands. In this regard, experimental work on larvae might prove more realistic, considering their often less strict physiological requirements.

In conclusion, teleost larvae are incredibly diverse morphologically, behaviorally and ecologically and the body of knowledge in this area is impressive. Capitalising on this wealth of information to understand the early ontogeny of bioluminescence is a challenging task which should prove rewarding for any researcher ready to take on the challenge.

Acknowledgements

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