

REVIEW

Sex with the lights on? A review of bioluminescent sexual dimorphism in the sea

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The reflected patterns and colours of terrestrial animals often show a sexual dimorphism associated with visual display, mate recognition and selection. In the sea the structures associated with bioluminescence may also show a marked sexual dimorphism. Some apparent bioluminescent dimorphisms (e.g. differences in photophore numbers) are probably secondary functions of sexual differences in size. A role in sexual communication is much more likely where specific photophores are developed or enlarged in mature specimens of one sex only but the presence of light organs in female anglerfishes (but not in males) is complicated by a significant size dimorphism. Dimorphisms in dragonfishes and lanternfishes primarily involve the relative enlargement of particular photophores in the males. A sexual role is assumed, but the morphological differences are often small. Most male ponyfishes have enlarged light organs; behavioural observations of free-swimming animals have clearly demonstrated that the males use them to generate bioluminescent sexual signals.

In the well-illuminated terrestrial and shallow water environments visual signals play a very important part in sexual recognition, attraction and mate selection. This is epitomized by the conspicuous sexual ornamentation of the males of many birds, reef fishes and insects (Andersson, 1994), whose striking visual characteristics are usually displayed to best advantage by specific behaviours. In a poorly lit or dark environment bioluminescence can be used for the same purpose. More than 99% of the volume of the earth's living space is contained in the oceans. Most of that space is dark and bioluminescence is a frequent occurrence. Its role is communication, whether defensive, attractive, or sexual (Herring, 1990a). This review examines the occurrence of bioluminescent sexual dimorphism in marine animals and the evidence for its role in sexual communication (Herring, 2000; Ruxton & Bailey, 2005).

The commonest examples of bioluminescent sexual dimorphism in the terrestrial environment (and associated observations of sexual selection) are dusk-active bioluminescent beetles, particularly the Lampyridae, or fireflies (Lloyd, 1979). The light organs in males and females may differ in size or position, or be lacking altogether in one of the sexes (usually the male). In a number of genera there is also a dramatic sexual difference in body form, with larviform wingless females contrasting with flying males, and visual adaptations that go hand-in-hand with the bioluminescent behaviours (Case, 1984). Equivalent dimorphisms are present in several groups of marine animals (e.g. Pietsch, 2005).

Primary anatomical dimorphism of external and/or internal reproductive tissues and structures is implicit in species with separate sexes. Bioluminescent sexual dimorphism con-

cerns secondary sexual characters. The complex, species-specific, role of bioluminescent dimorphism in the sexual signals of fireflies has been well documented. Nevertheless the assumption that sexual differences in bioluminescent structures necessarily translate into sexual messages and sexual selection (Andersson, 1994) remains largely unproven in the marine environment.

OCCURRENCE OF BIOLUMINESCENT SEXUAL DIMORPHISM

Gonad bioluminescence

In the simplest cases the ovaries or eggs of a species may be bioluminescent, when the testes are not. Examples of this situation are known in a few asteroids (*Benthopecten*, *Pectinaster*), ophiuroids (*Ophiomusium*) and medusae (*Atolla*, *Periphylla*) (Herring, 1990b, 1995). The phenomenon can be observed in moribund specimens and is enhanced by lysis, but there is no information on how often, or indeed whether, it occurs and is visible *in situ*.

Glandular bioluminescence

A second category of bioluminescent sexual dimorphism is that encountered in the small copepod *Oncaea conifera*. Males are considerably smaller than females. Both have numerous bioluminescent cuticular glands, but the males inevitably have fewer glands, and their distribution appears to be slightly different, though the latter aspect has not been studied in detail (Herring et al., 1993). There is, however, no sexual difference in the pattern of luminous glands in any other luminous copepod, including the much larger metridinid *Gaussia princeps* (Bowlby & Case, 1991).

Table 1. *Invertebrate bioluminescent sexual dimorphism.*

Taxon	Sexual dimorphism
CRUSTACEA	
Copepoda	
<i>Oncaea conifera</i>	Sexual differences in luminous cuticular glands
Euphausiacea	
<i>Nematoscelis</i>	♂♂ have one or more enlarged abdominal photophores
<i>Nematobrachion</i>	Atlantic <i>N. flexipes</i> : ♂♂ lack one abdominal photophore, ♀♀ lack two
Decapoda	
<i>Sergia</i>	Sexual differences in the distribution of ventral photophores
	<i>S. lucens</i> : maximum 184 photophores in ♂♂, 182 in ♀♀
MOLLUSCA	
Cephalopoda, Decapoda	
Enoploteuthidae	
<i>Watasenia</i>	Differences in numbers of mantle photophores (probably size-related)
Lycoteuthidae	
<i>Lycoteuthis</i> , <i>Selenoteuthis</i>	♂♂ have additional and/or some larger photophores
Ctenopterygiidae	
<i>Ctenopteryx</i>	♂♂ have an additional posterior visceral photophore
Cranchiidae	
<i>Cranchia</i> , <i>Liocranchia</i> , <i>Leachia</i> , <i>Egea</i> , <i>Teuthowenia</i> , <i>Megalocranchia</i>	Adult ♀♀ have arm tip (brachial) photophores
Cephalopoda, Octopoda	
Bolitaenidae	
<i>Japetella</i> , <i>Eledonella</i>	Adult ♀♀ have a circumoral photophore

Photophore distribution

Crustaceans (Table 1)

Different groups of midwater decapod shrimps have numerous ventrally directed photophores. Their primary role is believed to be that of counterillumination, for which there is some experimental support. Adult *Sergestes lucens* have up to 184 such photophores and Omori (1969) reported that while males have two pairs of photophores between the bases of the fifth pereopods, females have only one. He later examined a further 147 specimens, noting variability in the photophore number and location between individuals of the same size (Omori et al., 1996). Sexual differences also occur

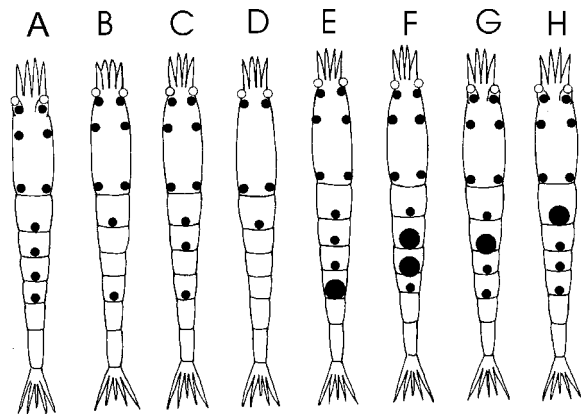


Figure 1. Position and sexual dimorphism of photophores in euphausiids: (A) photophore positions in most euphausiids; (B) *Nematobrachion flexipes* ♀; (C) *N. flexipes* ♂; (D) *Stylocheiron* spp. ♀♂; (E–H) position of enlarged photophores in ♂♂ of *Nematoscelis* spp. (see text).

in both the number of photophores and their pattern of distribution in *Sergestes richardi* and *S. robusta* (Dennell, 1955), and the differences are only slightly more distinctive than in *S. lucens*.

More definitive differences have been reported in some euphausiid shrimp. Most species have ten photophores, consisting of an ocular pair, two thoracic pairs and four pleonal organs, although both sexes of the genus *Stylocheiron* lack three of the pleonal organs (Figure 1D). Females of Atlantic *Nematobrachion flexipes* have only two of the four pleonal photophores, while males have three (P.T. James, cited by Herring & Locket, 1978). In the genus *Nematoscelis* all males of *N. megalops* and *N. difficilis* have pleonal photophores similar in size to those of females. However, some male *N. gracilis* and *N. microps* have the first pleonal photophore enlarged. In two other species of the genus (*N. atlantica* and *N. tenella*) some males have either the 2nd and 3rd or the 4th pleonal photophore enlarged (Figure 1). In each of these species the two different forms with enlarged photophores are geographically separated (Einarsson, 1942; James, 1973; Gopalakrishnan, 1975). If increased photophore size indicates an increased light intensity it is feasible that the differences in pattern could act as a signal of sexual identity.

Cephalopods (Table 1; Figure 2)

A similar situation to that in the decapod shrimps occurs in some cephalopods. Sasaki (1914) reported that females of *Watasenia scintillans* had more ventral mantle photophores (566–687) than did males (450–543). Males are slightly smaller than females (mean dorsal mantle lengths 49 mm and 60.5 mm, respectively). When adjusted for mantle

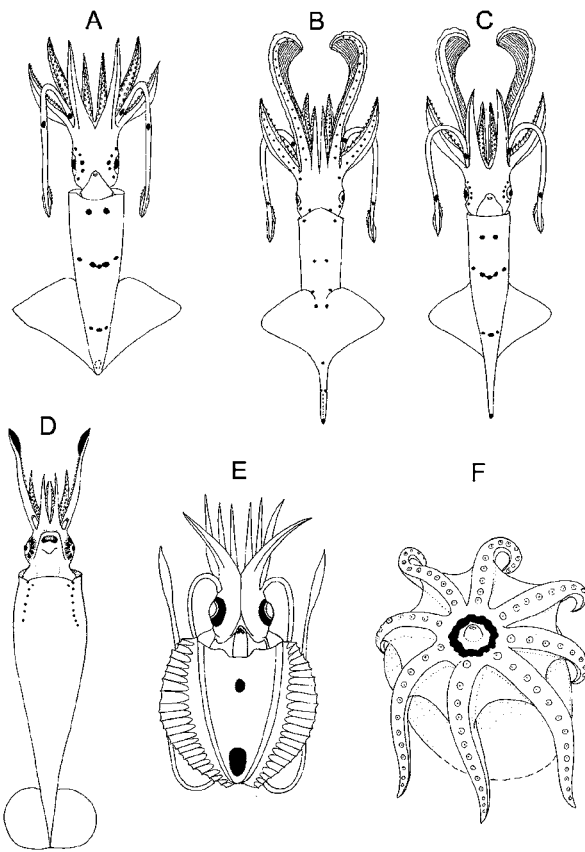


Figure 2. Examples of sexual dimorphism in the photophores of cephalopods. (A) *Lycoteuthis diadema* ♀ in ventral view; (B, C) *L. diadema* ♂ in dorsal and ventral views, respectively. Males have many more dorsal photophores than females, particularly on the arms; (D) *Leachia cyclura* ♀ with a pair of large brachial photophores; (E) *Ctenopteryx sicula* ♂, showing the additional large posterior visceral photophore; and (F) the octopod *Japetella diaphana* ♀, showing the large circumoral photophore.

length the photophore numbers hardly differ, nor could Sasaki detect any visible sexual differences in luminescing animals. Other examples of sexual dimorphism among the photophores of cephalopods are much more likely to have a directly communicative role (Herring, 1988). Male *Lycoteuthis diadema* were originally described as a different genus (*Oregoniateuthis*), and differ from females in having more posterior photophores and additional dorsal integumental photophores extending on to arms II and III (Figure 2A–C) (Toll, 1983). Male *Selenoteuthis scintillans* have both a larger terminal mantle photophore than females, and arm tip photophores. Male *Ctenopteryx sicula* have a large visceral photophore, which females lack (Figure 2E). Although only males of *Psychroteuthis* have glandular structures on their arm tips there is no certainty that they are photophores (M. Vecchione, personal communication).

There are some cephalopods in which particular photophores are present only in mature females. In seven of the 13 genera of the family Cranchiidae mature females develop large arm tip (brachial) photophores (Voss, 1980), structurally quite different to the other photophores on the eye or in the mantle (Figure 2D) (Herring et al., 2002). Similarly females of the octopod genera *Japetella* and

Table 2. Ceratioid bioluminescent sexual dimorphism (all genera have dwarf males).

Taxon	Sexual dimorphism
Caulophryinae	
<i>Caulophryne</i> , <i>Robia</i>	♂♂ lack an esca (<i>Caulophryne</i> ♀♀ may have a non-luminous esca)
Melanocetidae	
<i>Melanocetus</i>	♂♂ lack an esca
Himantolophidae	
<i>Himantolophus</i>	♂♂ lack an esca
Diceratiidae	
<i>Diceratias</i> , <i>Bufoceratias</i>	♂♂ lack an esca
Oneirodidae	
<i>Oneirodes</i> , <i>Bertella</i>	♂♂ of all genera lack an esca
<i>Leptacanthichthys</i>	
<i>Lophodolos</i> , <i>Chaenophryne</i>	
<i>Dolopichthys</i>	
<i>Microlophichthys</i>	
<i>Phyllorhinichthys</i>	
<i>Danaphryne</i> , <i>Spiniphryne</i>	
<i>Dermatias</i> , <i>Ctenochirichthys</i>	
<i>Puck</i> , <i>Tyrannophryne</i>	
<i>Pentherichthys</i> , <i>Chirophryne</i>	
Thaumataichthyidae	
<i>Thaumataichthys</i> , <i>Lasiognathus</i>	♂♂ lack an esca
Centrophrynidae	
<i>Centrophryne</i>	♂♂ lack an esca
Ceratiidae	
<i>Ceratias</i> , <i>Cryptopsaras</i>	♂♂ lack the esca and the luminous caruncles
Gigantactinidae	
<i>Gigantactis</i> , <i>Rhynchactis</i>	♂♂ lack an esca (<i>Rhynchactis</i> ♀♀ may have a non-luminous esca)
Neoceratiidae	
<i>Neoceratias</i>	No bioluminescent structures in either sex
Linophryinae	
<i>Linophryne</i> , <i>Haplophryne</i>	♂♂ of all genera lack an esca;
<i>Acentrophryne</i> , <i>Borophryne</i>	those of <i>Linophryne</i> also lack the
<i>Photocorynus</i>	luminous barbel characteristic of that genus.

Eledonella develop a large circumoral photophore (Robison & Young, 1981), which degenerates after spawning (Figure 2F). Males of these two genera have no photophores. None of these female-specific photophores has been seen illuminated *in situ*, but the clear implication is that they are involved in sexual communication.

Anglerfishes (Table 2)

The condition in the octopods (above), where bioluminescence is confined to a single sex, predominates in the ceratioid anglerfishes (Bertelsen, 1951). In all but one of the 11 families and 35 recognized genera of these fishes (the exception is *Neoceratias*) the females have a bulbous luminous esca (or lure), which is lacking in the dwarf males (Figures 3 & 4). The esca is a complex structure, which often bears numerous protuberances and filaments as well as reflector systems, and is borne on the first fin ray (the illicium). The

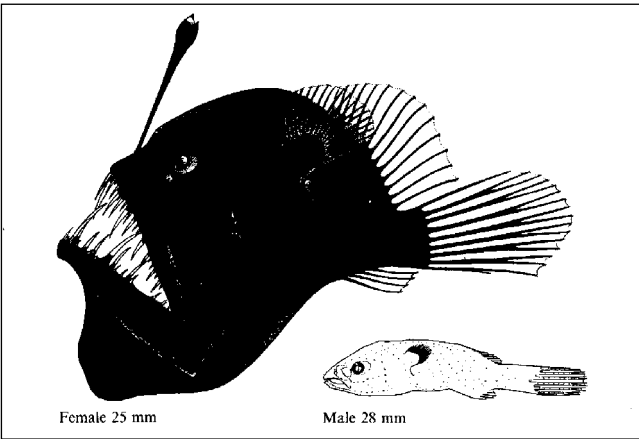


Figure 3. *Melanocetus johnsoni*, 25 mm ♀ and 28 mm ♂ (from Bertelsen, 1986).

bulb opens to the exterior by a pore, contains a core of symbiotic luminous bacteria, and light emission is under the host's control. Escal luminescence has been observed in only a minority of species, but it is generally assumed that females of all species have the same light-emitting capability (this is doubtful in *Caulophryne* and *Rhynchactis*, in which the esca lacks both a pore and the bacterial core). In addition to the esca, females of species of the genera *Ceratias* and *Cryptopsaras* have, respectively, two and three dorsal sacs (caruncles) containing luminous bacteria. Female *Linophryne* have an additional species-specific luminous barbel, bearing numerous intrinsic (non-bacterial) photophores.



Figure 4. *Melanocetus johnsoni*, 75 mm ♀ with attached ♂.

Males lack all these structures, and there is a remarkable homology between the pterygiophore that supports the illicium in the female and the basal bone in the male, which allows it to bite on to the female (Pietsch, 2005).

Dragonfishes (Table 3)

The dragonfishes (family Stomiidae) have many different kinds of intrinsic (non-bacterial) photophores distributed over most parts of the body, and females are frequently larger than males (Figure 5). Sexual dimorphism of bioluminescent organs occurs in 17 of the 24 genera but is restricted to the paired postorbital and preorbital photophores and (rarely) the barbel. In all affected genera the postorbital photophores of females are relatively smaller or absent (with one exception,

Table 3. Sexual dimorphism of luminous structures in dragonfishes (Stomiidae).

Genus	Dimorphism of postorbital (p-o) and antorbital or preorbital (a-o) photophores and barbel
<i>Chauliodus</i>	P-o larger in ♂♂ <i>C. macouni</i> , smaller in ♂♂ <i>C. danae</i>
<i>Stomias</i>	P-o (postorbital) larger in ♂♂, especially in species where ♂♂ are significantly smaller than ♀♀
<i>Astronesthes</i>	<i>A. cyaneus</i> : barbel is about headlength in ♂♂, minute in ♀♀ <i>A. macropogon</i> : p-o larger in ♂♂ of >100 mm standard length
<i>Borostomias</i>	No reported dimorphism
<i>Diploplychnus</i>	No reported dimorphism
<i>Heterophotus</i>	No reported dimorphism
<i>Rhadinesthes</i>	No reported dimorphism
<i>Neonesthes</i>	No reported dimorphism
<i>Melanostomias</i>	<i>M. biserialatus</i> and <i>M. melanopogon</i> : terminal filament present on the barbel of ♀♀, absent in ♂♂
<i>Chirostomias</i>	P-o variable size in ♂♂, absent in ♀♀ (present in juveniles, then atrophies)
<i>Trigonolampa</i>	No reported dimorphism
<i>Pachystomias</i>	P-o larger in ♂♂
<i>Eustomias</i>	P-o minuscule in ♀♀
<i>Flagellostomias</i>	P-o absent in ♀♀
<i>Leptostomias</i>	P-o minuscule in ♀♀
<i>Thysanactis</i>	No reported dimorphism
<i>Grammatostomias</i>	P-o minuscule in ♀♀
<i>Bathophilus</i>	P-o in ♂♂ much larger than in ♀♀
<i>Echiostoma</i>	P-o in ♂♂ larger and less tapering in shape than in ♀♀
<i>Photonectes</i>	P-o relatively larger in ♂♂ of some species
<i>Idiacanthus</i>	♂♂ have no barbel and a large p-o; ♀♀ have a barbel and small p-o
<i>Photostomias</i>	P-o in ♂♂ larger than in ♀♀; a-o (antorbital or preorbital) small in ♂♂, minute in ♀♀
<i>Malacosteus</i>	♂♂ have relatively larger p-o and a slightly different shape
<i>Aristostomias</i>	P-o larger in ♂♂ of some species

Data largely from Badcock & Merrett (1976), Berry & Perkins (1966), Bigelow et al. (1964), Gibbs (1969), Goodyear & Gibbs (1969), Krueger & Gibbs (1966), Marshall, (1979) and personal communications from T. Sutton and C. Kenaley.

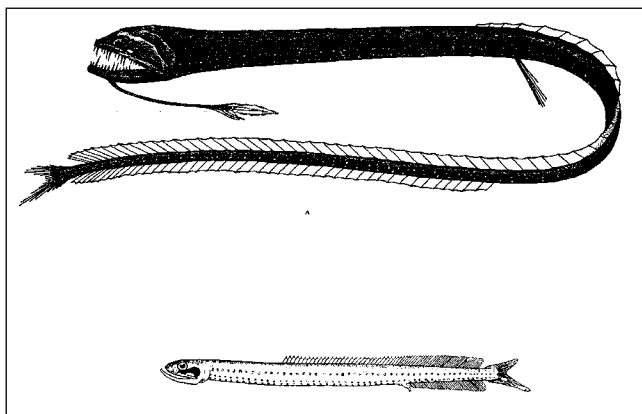


Figure 5. *Idiacanthus fasciola* ♂ and ♀. Adult ♀♀ are up to four times the length of adult ♂♂; the latter have greatly enlarged postorbital photophores, and lack barbel, teeth and pelvic fins (from Nafpaktitis et al., 1977 and Marshall, 1954).

the report that the postorbitals of female *Chauliodus danae* are larger than those of the males (Badcock & Merrett, 1976)). In *Echiostoma barbatum* the sexual size and shape differences are apparent only in specimens greater than 200 mm standard length (Krueger & Gibbs, 1966) (Figure 6).

The differences do not necessarily apply to all species in a genus. In *Stomias* the postorbitals of females are significantly smaller only in those species in which there is also a dimorphism of body size (smaller males), while in *Astronesthes macropogon* only males above a certain size have larger postorbitals than females (Gibbs, 1969; Goodyear & Gibbs, 1969). A large, red-emitting, suborbital photophore is present in a few genera (*Malacosteus*, *Pachystomias*, *Aristostomias*) but is not dimorphic. A preorbital (or antorbital) photophore is present in male *Photostomias*, but is smaller and subcutaneous in females (T.T. Sutton, personal communication). A red-emitting preorbital is also present in *Pachystomias*, but no dimorphism has been reported.

The submental barbel contains luminous tissues in most, if not all, species. Barbel dimorphism therefore affects bioluminescence capability. In *Astronesthes cyaneus* the barbel is present in males but minute in females. In two species of *Melanostomias* the male barbel lacks a terminal filament that is present in the female. *Idiacanthus* males show the greatest size reduction and lack a barbel altogether (Figure 5). The barbel structure is extremely complex in species of *Eustomias* and it was originally thought that there was a marked sexual dimorphism of both structure and tissue colour. Recent studies (Gibbs et al., 1983; Sutton & Hartel, 2004) have concluded that there is no real sexual dimorphism and that the supposed cases arose from comparisons between previously synonymized forms that are now regarded as different species (115 species are now recognized in the genus).

Lanternfishes (Table 4)

Lanternfishes (family Myctophidae) provide the most extensive evidence of bioluminescent sexual dimorphism among oceanic animals, and illustrate great variation within this globally distributed family. The main sexual differences are in the presence and/or size of specialized photophores



Figure 6. Adult ♂ *Echiostoma barbatum* with a typically enlarged postorbital photophore.

at the base of the tail. These are known as the supra- and infracaudal organs and are formed from separate or coalesced luminous scales. Nevertheless three of the 33 accepted genera in the family lack these organs altogether (*Diaphus*, *Gymnoscopelus* and *Hintonia*) and in a further eight genera they exhibit no sexual dimorphism (*Ceratoscopelus*, *Lampadena*, *Lampichthys*, *Lepidophanes*, *Metelectrona*, *Parvilux*, *Stenobranchius*, *Triphoturus*).

Relatively minor dimorphism occurs in some species of *Bolinichthys*, *Lampanyctodes*, *Lampanyctus* and *Taaningichthys*, largely involving a greater degree of development of the male caudal organs (Table 4). Mature males of *Lampanyctodes hectoris* have slightly larger, better-developed, infra- and supracaudal luminous scales than have females, and in two species of *Bolinichthys* the infracaudal scales are larger in males (P.A. Hulley, personal communication). Most species of *Lampanyctus* show no sexual dimorphism, but in one, *L. photonotus*, the supracaudal is larger in males, and in another, *L. alatus*, a luminous gland at the base of the adipose fin is also larger in males (Nafpaktitis et al., 1977). Similarly, in just one species of *Taaningichthys* (*T. minimus*) the supracaudal is slightly longer in males than in females.

In the simplest cases of marked dimorphism a supracaudal organ is present only in males and neither sex has an infracaudal organ (*Loxosteira*, *Notoscopelus*, *Scopelopsis*, *Tarletonbeania*) although one female specimen of *S. multipunctatus* was found to have a small infracaudal organ (Hulley, 1981) and male *Tarletonbeania crenularis* do occasionally have an infracaudal. Curiously, males of *Notoscopelus bolini*, unlike other species in the genus, have no supracaudal organ, but have instead a large patch of luminous tissue, absent in females, on either side of the head (Figure 7). Dimorphic patches of glandular luminescent tissue are also present in some species of *Bolinichthys* and *Gymnoscopelus* (Table 4).

In other genera a large supracaudal is present in males and a smaller infracaudal in females (*Benthosema*, *Centrobranchus*, *Diogenichthys*, *Electrona*, *Gonichthys*, *Hygophum*, *Idiolychnus*, *Krefflichthys*, *Lobianchia*, *Myctophum* (Figure 8), *Protomyctophum*). Again there are occasional exceptions. A few mature female *Hygophum benoiti* also have a minute supracaudal organ and some specimens of *Benthosema glaciale* have both supra- and

Table 4. Sexual dimorphism of luminous structures in lanternfishes (Myctophidae).

Genus	Sex	Head	Gland patches	Supra-caudal	Infra-caudal	Comments
Myctophinae						
<i>Benthosema</i>	♂ ♂			+	(+)	Occasional specimens of <i>B. gladiale</i> have both, supracaudal larger in males and vice versa
<i>Centrobranchus</i>	♂ ♂			+	-	
<i>Diogenichthys</i>	♂ ♂	Dn>		-	+	Dn enlarged in <i>D. paucispinus</i> and <i>D. lateralis</i>
<i>Electrona</i>	♂ ♂			+	+	<i>E. paucispinus</i> : male has large supracaudal, female tiny supracaudal plus infracaudal. <i>E. rissoi</i> (and <i>E. carlsbergi</i>): both males and females may have a supracaudal, or an infracaudal or both. <i>E. subasperus</i> : males have a supracaudal, females have a supracaudal and/or infracaudal
<i>Goniichthys</i>	♂ ♂			+	-	
<i>Hygophum</i>	♂ ♂			+	-	
<i>Kieffichthys</i>	♂ ♂			(+)	+	Occasional mature <i>H. benoiti</i> also have a tiny supracaudal
<i>Larveina</i>	♂ ♂			+	-	Two small unsexed specimens with both supracaudal and infracaudal (Hulley, 1981)
<i>Metellectrona</i>	♂ ♂			+	-	
<i>Myctophum</i>	♂ ♂			+	+	
<i>Protonyctophum</i>	♂ ♂			+	-	<i>M. punctatum</i> , <i>M. asperum</i> , <i>M. selenops</i> has supracaudal in both, larger in males, no infracaudal in either sex
	♂ ♂			+	(+)	Supracaudal only (e.g. <i>P. bolini</i>), or both, with smaller infracaudal (e.g. <i>P. gemmatum</i> , <i>P. luciferum</i> , <i>P. audriashevii</i>).
	♂ ♂			+	(+)	Some spp. with small supracaudal and tiny infracaudal (e.g. <i>P. gemmatum</i> , <i>P. luciferum</i>) others with only an infracaudal (e.g. <i>P. tenisoni</i> , <i>P. normani</i>)
<i>Symbolophorus</i>	♂ ♂			+	(+)	or males with supracaudal only
<i>Tartarobea</i>	♂ ♂			+	(+)	or females with infracaudal only
				-	-	infracaudal may be absent or present
Lampanyctinae						
<i>Bolinichthys</i>	♂ ♂		(+)	+	+	Inter-orbital (possibly luminous) tissue in male <i>B. longipes</i> better developed and more extensive than in females. Probably also in <i>B. indicus</i> and <i>B. photolhorax</i> , but inter-orbital tissue is absent in other species. Length and development of infracaudal scales is sexually dimorphic in <i>B. indicus</i> and <i>B. longipes</i> —longer and better developed in males
<i>Cardioscopelus</i>	♂ ♂		(+)	+	+	

	♂	Vn> Ant> Dn> So> (Vn) (Ant) (Dn) (So)		—	—	
<i>Diaphus</i>				—	—	Vn shows greatest differences in most species (<i>D. hudsoni</i> , <i>D. fragilis</i> , <i>D. holli</i> , <i>D. meadi</i> , <i>D. mollis</i> , <i>D. rafinesquii</i> , <i>D. problematicus</i> , <i>D. splendidus</i> , <i>D. taeningsi</i> , <i>D. dumerilii</i>). Vn shows a marked difference in <i>D. diadematus</i> , less apparent in <i>D. termophilus</i> , <i>D. luetkeni</i> and <i>D. diademophilus</i> . Ant may be present only in the male and is the main distinction in <i>D. fragilis</i> , <i>D. perspicillatus</i> , <i>D. vanhoeffeni</i> . Dn sexually dimorphic in <i>D. malayanus</i> . So sexually dimorphic in <i>D. hudsoni</i> , <i>D. meadi</i> , <i>D. holli</i> , etc. (the So group)
<i>Gymnoscopelus</i>	♂	+		—	—	<i>G. fraseri</i> : antorbital tissue well developed in males, poorly in females
<i>Hintonia</i>	♂	(+)		—	—	
<i>Idiobrychus</i>	♂			—	—	
<i>Lampadena</i>	♂		+	—	—	
<i>Lampanyctodes</i>	♂		+	+	+	Mature males of <i>L. hectoris</i> have slightly larger caudal luminous scales than females
<i>Lampanyctus</i>	♂	+		+	+	Larger supracaudal in <i>L. photonotus</i> . Luminous gland at base of adipose fin larger in males of <i>L. alatus</i>
<i>Lamplichthys</i>	♂	(+)		+	+	Very small or absent in both sexes
<i>Lepidophanes</i>	♂			—	—	Infra-caudal better defined; similar to several other glandular sites
<i>Lobianchia</i>	♂			+	+	Little or no development of either caudal organ in expatriate <i>L. gemellari</i>
<i>Nannobranchium</i>	♂			—	—	
<i>Notobrychus</i>	♂			+	+	
<i>Notoscopelus</i>	♂			+	(+)	Two head patches, and no supracaudal, in <i>N. bolini</i>
<i>Parulux</i>	♂	(+)		—	—	
<i>Scopelopsis</i>	♂	(only <i>N. bolini</i>)		(+)	(not <i>N. bolini</i>)	One specimen with a small infra-caudal (Hulley 1981)
<i>Stenobrachius</i>	♂	—		—	—	Supracaudal relatively slightly longer in males of <i>T. minimus</i>
<i>Taeningsichthys</i>	♂			+	+	
<i>Triphlopterus</i>	♂			+	+	

+, present; -, absent; (+) signifies that the particular head or caudal organ may be reduced or absent. **Dn** signifies that Dn or other photophore may be enlarged in this sex. Data largely from Nafpaktitis et al. (1977), Hulley (1981, 1986, 1990 and personal communication), Paxton (1972) and Paxton et al. (1984).

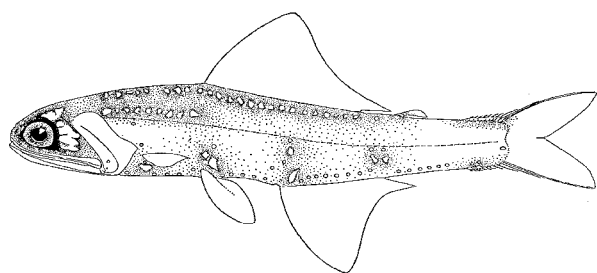


Figure 7. Adult ♂ *Notoscolopelus bolini*, showing the large patch of dimorphic luminous tissue behind the eye (from Nafpaktitis et al., 1977).

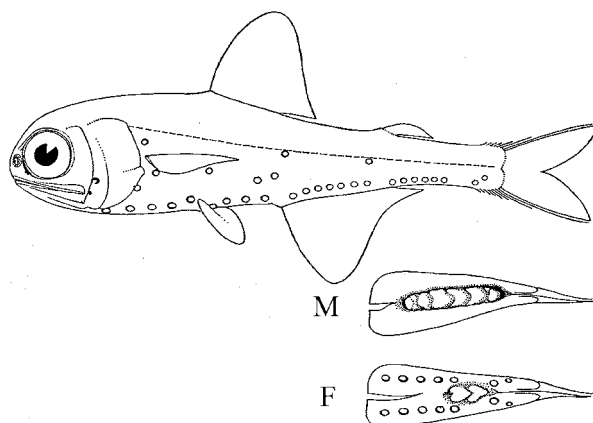


Figure 8. *Myctophum asperum*, young ♀ (top), and the supra-caudal and infra-caudal organs of, respectively, adult ♂ and ♀ (from Nafpaktitis et al., 1977).

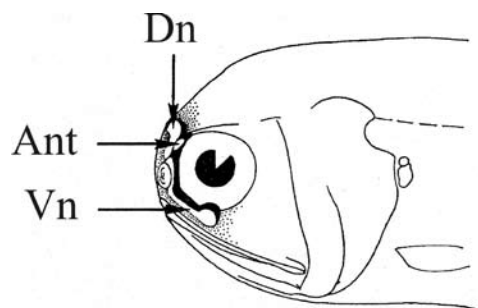


Figure 9. The main dimorphic head photophores of *Diaphus* species. Dn, dorsonasal; Ant, antorbital; Vn, ventronasal (from Nafpaktitis, 1978).

infra-caudal organs, the supracaudal larger in males and the infra-caudal larger in females. Some females of both *Myctophum asperum* and *M. punctatum* have additional, very small, supracaudal organs. Both males and females of *Myctophum selenops* have only a supracaudal organ, but it is larger in males. Male and female *Symbolophorus* usually have both caudal organs, but in some species males may lack the infra-caudal and some females the supracaudal organs (Table 4). Even greater variability is shown by species of *Protomyctophum* and *Electrona* (e.g. Duhamel et al., 2005).

Species of *Diaphus* do not have caudal organs but instead exhibit a very pronounced sexual dimorphism of at least one of the head photophores (Figure 9), usually the ventronasal organ (Vn) and the suborbital organ (So) (in those species

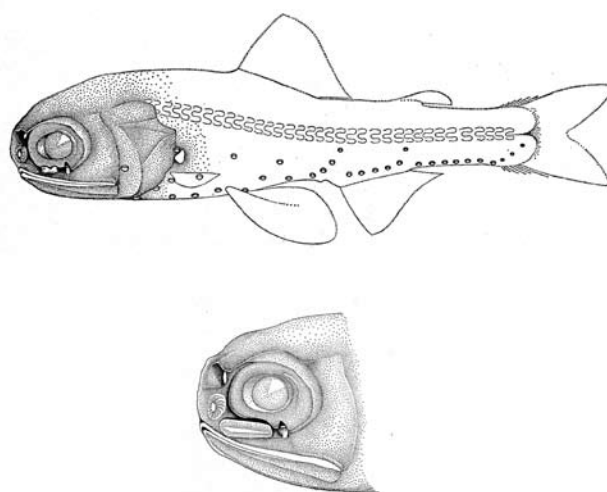


Figure 10. *Diaphus subtilis* ♀ and the head of an adult ♂, with greatly enlarged Vn photophore. The So, at the posterior end of the Vn, is not dimorphic in this species but is in several others (from Nafpaktitis et al., 1977).

with this organ). These are always larger in males (Figure 10) (Nafpaktitis, 1968, 1978).

The dorsonasal organ (Dn) is also enlarged in male *Diaphus malayensis*. The anteronasal photophore (Ant) may be present only in males of some species, and is the prime sexual distinction in *Diaphus fragilis*, *D. elucens*, *D. perspicillatus* and *D. vanhoeffeni*. Several species (e.g. *Diaphus phillipsi*, *D. effulgens* and *D. metoplocampus*) apparently lack any sexual dimorphism of the head photophores (Nafpaktitis, 1968, 1978). Males of *Diogenichthys panurgus* and *D. laternatus* also have an enlarged Dn, in addition to the dimorphic caudal organs.

Ponyfishes (Table 5)

Ponyfishes (family Leiognathidae) are coastal fishes with an Indo-West Pacific distribution and have a bioluminescent system whose light source is the luminous bacterium *Photobacterium leiognathi*. The bacteria are maintained in extracellular symbiosis in a circumoesophageal light organ. Their light is directed into the silvered swimbladder from where it is reflected out along the ventral margin, as a counterillumination camouflage, or laterally through translucent areas on the flanks or head region, serving a variety of suggested functions (Hastings, 1971; Haneda & Tsuji, 1976; Jayabalan, 1989; Jayabalan & Ramamoorthi, 1985; McFall-Ngai & Dunlap, 1983, 1984; McFall-Ngai & Morin, 1991). In some species there is a pronounced internal sexual dimorphism in the size, shape and pigmentation of the light organ, which may be up to 100 times larger in the male than in the female. In a subset of these species there is also external dimorphism in the presence or absence of the lateral windows (McFall-Ngai & Dunlap, 1984; Sasaki et al., 2003; Ikejima et al., 2004; Sparks et al., 2005) (Figure 11).

A recent detailed re-examination of the comparative morphology of the light organ system and of the molecular phylogeny of the group by Sparks and others (Ikejima et al., 2004; Sparks & Dunlap, 2004; Sparks et al., 2005; Sparks, 2006) has confirmed the earlier hypothesis (McFall-Ngai & Dunlap, 1984) that the dimorphisms would contribute to the taxonomy and phylogeny of the family. They have

Table 5. Sexual dimorphism of light organs in ponyfishes (*Leiognathidae*).

Genus	Sexual dimorphism
<i>Gazza</i> (Clade F)	Internal dimorphism: ♂♂ have a larger volume l.o. (light organ)
<i>Secutor</i> (Clade D)	Internal dimorphism: ♂♂ have a larger volume l.o.
<i>Leiognathus</i> (Clades I, J, (K?))	No dimorphism (insufficient material for Clade K)
“ <i>Leiognathus</i> ” (Clades G, H)	Internal dimorphism: ♂♂ have a larger volume l.o.
<i>Photoplagios</i> (Clades C, L, M)	Internal and external dimorphism: ♂♂ have a translucent lateral patch and hypertrophied dorsolateral lobes of the l.o., extending into the gas bladder. The lobes are enormously enlarged in <i>P. elongatus</i> and <i>P. rivulatus</i>
<i>Photopectoralis</i> (Clade E)	Internal and external dimorphism: ♂♂ have a translucent patch in the axil of the pectoral fin and the l.o. has greatly enlarged dorsolateral lobes, which abut the patch

From Sparks et al. (2005).

shown that the presence of such dimorphism is closely linked with other characters useful for reconstructing the phylogeny of the family, and helps to provide a robust generic separation of different groups of species (Table 5). One non-monophyletic group of species (*Leiognathus* s.s.) lacks any sexual dimorphism of the light organs. The remaining leiognathid species (comprising species of *Gazza*, *Secutor*, ‘*Leiognathus*’, *Photoplagios*, and *Photopectoralis*) are monophyletic and exhibit internal dimorphism in which the light organs are enlarged in males. The last two genera, which were recently recognized (Sparks et al., 2005; Sparks, 2006), have both internal and external dimorphism. Males of *Photoplagios*

have enlarged light organs and a translucent window or stripe on the flank (Figures 12–14); males of *Photopectoralis* also have enlarged light organs, but the translucent window is located in the axil of the pectoral fin.

SEXUAL DIMORPHISM AND SEXUAL SIGNALS

The existence of sexual dimorphism in bioluminescent structures (as outlined above) begs the question of whether it invariably indicates a sexual signal. Certainly such dimorphism can provide different intensities and/or spatial patterns of luminescence in the two sexes. Nevertheless ovarian luminescence in animals without image-forming abilities (e.g. medusae and echinoderms) clearly would not provide an effective sexual signal (if it is indeed a natural phenomenon). The developing eggs of a number of terrestrial species are luminescent, including the British glowworm, *Lampryris noctiluca*, but this phenomenon has no sexual significance.

Invertebrates

Glandular bioluminescence of female *Oncaea conifera* (and other copepods such as *Gaussia*) is interpreted as a defensive response to a potential predator. There is no reason to doubt that the luminous glands of the male have precisely the same purpose, and that the differences lack any sexual significance beyond the dimorphism of body size. In the shrimp *Sergia lucens* it is equally improbable that the minor variation in sexual pattern of the photophores, within the ‘noise’ of individual variability, can be used as a specific sexual signal. In other species of *Sergia* a sexual significance is possible, albeit still very unlikely, given the limited visual acuity of these shrimp and the very small separation of the photophores. This is exacerbated by the fact that the photophores are directed downwards and would be invisible other than to an observer from immediately below (their primary role is in counterillumination camouflage). The same argument applies to the size-related minor differences in the number of ventral mantle photophores in the firefly squid *Watasenia scintillans*, although the visual acuity of its camera eye is likely to be greater than that of the compound eyes of decapod and euphausiid crustaceans.

This analysis assumes that all the photophores are illuminated together. If the different sexes are able to select

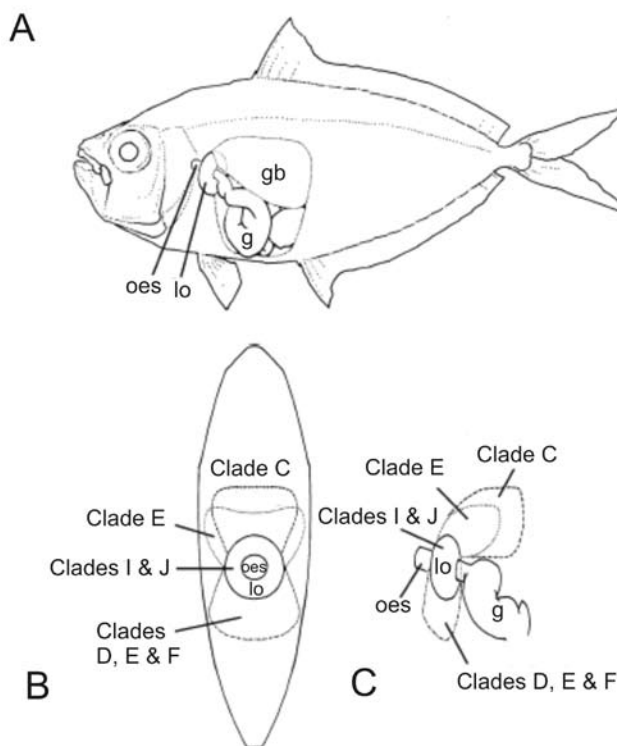


Figure 11. (A) A generalized leiognathid showing the circum-oesophageal position (oes) of the light organ (lo), the gas bladder (gb) and the gut (g); (B, C) the light organ in section and plan view, showing its extent in the non-dimorphic Clades I and J (solid line) and the enlargement found in ♂♂ of Clades C, D, E and F (dotted lines) (from Sparks et al., 2005).

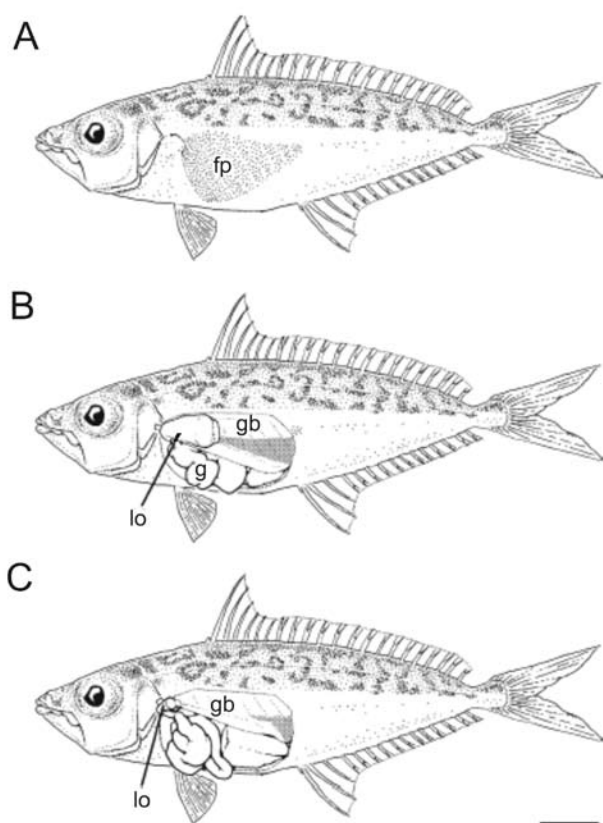


Figure 12. *Photoplagios elongatus*. (A) External view of ♂, showing the dimorphic translucent flank patch (fp); (B) diagram of the enlarged light organ in the ♂; and (C) the equivalent light organ in the ♀ (from Sparks et al., 2005). Scale bar: 10 mm.

particular patterns of illumination from among the available photophores then a sexually explicit signal is perfectly feasible, as it is for the sexually distinctive spatial pattern of photophores described above in *Lycoteuthis*, *Selenoteuthis* and *Ctenopteryx*. The very numerous mantle photophores of enoploteuthid squids such as *Watasenia* comprise not only several separate morphologies but also the ability to produce light of different wavelengths (Young & Mencher, 1980; Young & Bennett, 1988; Herring et al., 1992). A spectrally selective sexual signal is therefore a possibility, given that these squid have visual systems that are capable of discriminating the different wavelengths.



Figure 13. *Photoplagios elongatus*: live ♀, not luminescing. (Photograph: A. Sasaki).

A much clearer case for a sexual signal is provided by the unique photophores developed at maturity in some female cranchiid squids and midwater octopods, and their resorption in the latter after spawning.

Anglerfishes

Superficially the extreme bioluminescent dimorphism of ceratioid anglerfishes encourages the assumption that it is involved with sexual signalling. Nevertheless sexual dimorphism in ceratioid anglerfishes is not confined to the bioluminescent system, but is expressed particularly in their size, females always being much larger than the (dwarf, and often attached) males (Bertelsen, 1951; Pietsch, 2005) (Figure 4). Females may well be using their luminous lures to attract the males, but it is assumed (on the basis of observations of shallow water anglerfishes) that the lure is at least as important in the capture of prey (Pietsch & Grobecker, 1978). It is essential for the growth and development of the large, relatively immobile, females that they have some mechanism for the capture of sufficient prey. The tiny males have much more limited requirements.

The escal morphology of different species provides valuable taxonomic clues to their identities. Complex reflector systems make for potentially different patterns of light emission, whereas multiple filaments and protuberances are probably indicative of variations in mechanosensory and/or chemosensory abilities, and the esca should not be regarded solely as a luminous organ. The visual and olfactory systems of many male ceratioids are relatively enlarged when compared with those of the females, and both systems are probably employed in the search for mates. Female pheromones may provide a long-distance signal while escal bioluminescence may allow species discrimination at closer range (Herring, 2000). However, this generalization ignores some key examples that challenge the concept of visually directed male searches. *Neoceratias* females have no bioluminescent structures and the eyes of attached males are degenerate, while the eyes of male *Himantolophus*, *Centropryphne*, *Gigantactis* and *Rhynchactis* are also very small. If escal bioluminescence has no sexual significance in these genera why should it have any in other ceratioids? Yet the eyes of male *Ceratias* and *Cryptopsaras* are particularly large and suggest a visual search, perhaps compensating for the poorly developed nostrils (Pietsch, 2005). Females of *Haplophryne* have been taken with up to eight attached males (Pietsch, 2005) suggesting



Figure 14. *Photoplagios elongatus*: live ♂, luminescing through the transparent patch on the flank. (Photograph: A. Sasaki).

the possibility of male/male competition if their arrival is approximately synchronous, though bioluminescence cannot be involved in any such interactions.

If escal luminescence is regarded as the source of a potential sexual signal, the same argument can be applied to the caruncles of female ceratiids (Bertelsen, 1951), and to the barbels of female *Linophryne*, but is harder to sustain insofar as multiple sources of bioluminescent sexual signals in a single individual seem an unnecessary complication when others have none. Caruncles are able to secrete luminous bacteria into the surrounding seawater, which could perhaps be associated with a pheromone. There is no information on the normal employment of luminescence in the *Linophryne* barbel, which is analogous to the barbel of many dragonfishes.

Dragonfishes

Information on dragonfish bioluminescent sexual dimorphism is limited by the fact that only immature specimens are represented in most collections (T.T. Sutton, personal communication), so for many species it has not yet been possible to compare adult males and females. The increased size of the postorbital photophore in males of several genera is the most consistently dimorphic character, though adult females of some genera (e.g. *Idiacanthus*, *Chauliodus*, *Photostomias*) are larger than the males. The postorbital photophore flashes readily in response to a mechanical stimulus, so it is unlikely that its only role is that of sexual communication. Nevertheless a larger postorbital organ implies a more intense bioluminescent signal, potentially visible at longer range. If the visual sensitivity of the two sexes is similar, the consequence is that a female could be attracted to such a signal before she was close enough to return it (Herring, 2000). Alternatively, but not exclusively, the intensity of the male postorbital photophore could be taken by the female as an indication of the male's general fitness, although she would also need a means of determining its distance. The visible colour of the postorbital luminescence is invariably blue, despite minor variations in the colour of the photophore itself, so it is unlikely that any sexual value could accrue from spectral differences. There is no indication of any sexual dimorphism in the large, red-emitting, suborbital photophores of the three genera, *Malacosteus*, *Pachystomias* and *Aristostomias* and any role they may have in intraspecific communication remains speculative (Herring & Cope, 2005).

Lanternfishes

The complexity and variety of sexual dimorphism in lanternfish caudal photophores provides strong circumstantial evidence for their involvement in sexual signalling. Where a caudal organ is present only in the male (*Loweina*, *Notoscopelus*, *Scopelopsis*, *Tarletonbeania*) any signal can only be a male monologue, but when both sexes have caudal organs there is the potential for a bioluminescent dialogue, akin to that which takes place in many fireflies. The kinetics of caudal organ flashes are quite different from those of the ventrolateral counterillumination photophores. Caudal organs can produce volleys of very fast, high intensity flashes, whereas the ventrolateral photophores

have a more continuous emission (Barnes & Case, 1974; Mensinger & Case, 1997). Much has been made of the possibilities of species recognition by lanternfishes, based on the different patterns of lateral photophores (e.g. Beebe, 1935) but Mensinger & Case (1997) regard this as visually improbable. Sexual recognition of a volley of fast caudal organ flashes would anyway be quite separate from any potential pattern recognition of flank photophores. The flashes from glandular patches present elsewhere on some lanternfishes (e.g. *Ceratoscopelus*, *Diaphus*) have similar fast kinetics. It is perhaps indicative of the significance of sexual signals that *Notoscopelus bolini*, though lacking caudal organs, has sexually dimorphic head patches, which probably have similar fast flash kinetics.

Species of *Diaphus* (and *Diogenichthys*) have sexually dimorphic head photophores, particularly the Vn (and So). As in most cases where the photophore is present in both sexes, enlargement occurs in the male. There is no information on the flash kinetics of these photophores, but the conservative assumption is that they would have the same slower kinetics as other ventrolateral photophores.

The variety of sexually dimorphic photophores in lanternfishes demonstrates the intense selection pressure for sexual recognition and discrimination over a distance of several metres. The group is divided into two subfamilies; the myctophine genera tend to have a supracaudal organ in males and an infracaudal organ in females, while the lampanyctines more often have both supra- and infracaudals (or none) in both sexes, but there is no clear division between the two (Table 4). *Idiolychnus* is believed to be the basal genus (Stiasny, 1996) but despite being a lampanyctine it has a supracaudal in the male and an infracaudal in the female. The absence of caudal organs in three genera is regarded as a derived character (Paxton et al., 1984). In male myctophids there is generally either a relative enlargement of the dimorphic caudal and head photophores, or they are present only in males. This contrasts with those cephalopods in which additional sexual photophores are present in the females of particular species.

Individual anomalies in the development of sex-linked characters in myctophids probably account for occasional individuals of the same species and sex exhibiting differences in caudal organ distribution, just as there is frequent meristic variation in the numbers of serial lateral photophores (e.g. Nafpaktitis, 1968).

There have been no observations of sexual signalling by lanternfishes, so the interpretation of the use of photophore dimorphisms remains speculative. An alternative, and not necessarily exclusive, role for male caudal organs was proposed by Bolin (1961), based on differences in the sex ratios of *Tarletonbeania crenularis* taken in nets and from the stomachs of albacore caught in the same area. The ratio of males to females in net hauls was approximately equal, but the albacore stomachs contained predominantly males. Only males have caudal organs and Bolin suggested that they used the flashes from these photophores to attract the tuna predators to themselves as sacrificial decoys, and away from the females. Male flashing would have had no effect on the capture of both sexes by nets. However, altruistic sacrifice has no adaptive value, so this argument cannot be sustained

in evolutionary terms unless there is close kinship between the apparently altruistic males and the surviving females.

There are more species of lanternfish (238) than of any other meso- and bathypelagic family of fishes, and it is far more likely that the great variety of sexual dimorphism in the family is an indication of an intense sexual selection that is responsible for, and maintains, the separation of the many sympatric species. Bioluminescent sexual dimorphism may also contribute to the variety of dragonfishes (Stomiidae) (228 species) and ceratioid anglerfishes (162 species) but lanternfishes are considerably more abundant than either of these two groups. Certainly bioluminescent sexual signals would be contributors to the Specific Mate Recognition System mechanism of speciation proposed by Paterson (1985).

Ponyfishes

The near-shore ponyfishes are the only sexually dimorphic fishes whose bioluminescent behaviour has been observed in the field (albeit fleetingly), and examined in more detail in the laboratory. Woodland et al. (2002) reported synchronized flashing among all the fish in schools of *Leiognathus splendens*, a species that has no external dimorphism but whose internal light organs are larger in males (Clade H, Table 5). The authors considered the possibility that the schools consisted only of males and that the display was sexual in nature, analogous to the synchronized flashing of the males of some fireflies, but could not rule out other possible functions involving feeding, predator evasion and social cohesion. Field observations of *Photoplagios* (*Leiognathus*) *elongatus* (Sasaki et al., 2003) indicate a more definitive role in sexual communication. External dimorphism in this species involves a 'window' on the flanks of males. Males produced rhythmic pulses of light, with occasional synchrony, and were observed to chase non-luminous individuals (females). Azuma et al. (2005) recorded the bioluminescence of free-swimming specimens of *L. nuchalis* (Clade G, Table 5) in large aquaria, during both the breeding and the non-breeding seasons. Luminescence from adult fishes was only detected during the breeding season, and flashing had a diel periodicity, being greatest during the nocturnal spawning period of 2000–2400 h. The males of this species have enlarged internal light organs but no external dimorphism. Further support for a sexual role for the bioluminescence of males of *Photoplagios* (*Leiognathus*) *rivulatus* has been provided by Ikejima et al. (2005), who showed that during the breeding season the light organs of males increase in size relative to body weight. This increase was significantly correlated with a similar increase in gonad size. The gonads of females also showed a seasonal weight increase, but their light organs showed no equivalent changes.

All the observations noted above, combined with the detailed analysis of the family and its bioluminescent systems by Sparks and his colleagues, support their conclusion that 'the degree of species-specific morphological specialization and strong sexual dimorphism of the light organ and associated structures...., suggest a system of mate recognition based on male species-specific luminescent signaling' (Sparks & Dunlap, 2004; Sparks et al., 2005). Although there are

only about 40 species of ponyfishes, and all are restricted to a shallow coastal habitat, bioluminescent sexual signalling has probably contributed to the diversification of the family and to the maintenance of specific identity, given the opacity of the waters in which many of them live and the close similarity of body form in sympatric species (Sparks et al., 2005).

This discussion has focused on the importance of sexual dimorphism in the production of sexually specific bioluminescent signals. Such signals contribute to the reproductive success of an individual and are thus examples of sexual selection, which could take the form of female selection or interactions between competing males. Population densities in the ocean are generally low (Herring, 2000) and male competition is much less likely than female selection. A recent simulation (Ruxton & Bailey, 2005) suggests that it may take only a few hours for a male to arrive once a female has begun signalling.

It is also perfectly feasible for animals to produce sexually specific bioluminescent signals without any sexual dimorphism of the bioluminescent structures (as may be the case in some lanternfishes and ponyfishes). One well-documented marine example is the mating display of syllid worms (Markert et al., 1961; Erdman, 1965). In Bermuda females swim at the surface producing bioluminescent secretions. Males are attracted to the display, circle the females, and produce their own luminous secretions. In California the males are the first to appear (Tsuiji & Hill, 1983). Another example, also involving luminous secretions, is the very complex pattern of species-specific bioluminescent signals produced by males of the ostracod genus *Vargula*, to which the females are attracted (Morin, 1986). The displays involve pulsed secretions along specific swimming trajectories and provide a close analogy with firefly signals, except that the females remain dark (Morin & Cohen, 1988, 1991; Cohen & Morin, 1990). It is very likely that other animals with no apparent sexual dimorphism of the bioluminescent organs are nevertheless able to produce specific signals by means of sexual differences in flash kinetics, spatial patterns, spectral emissions or associated movements. Many fish and squid have numerous photophores of very different morphologies, giving them the potential for a great variety of different displays and functions. Ponyfishes can use a single pair of internal light organs in at least four different ways (McFall-Ngai & Dunlap, 1984) and flashlight fishes (Anomalopidae) use their paired suborbital light organs similarly, including sexual dialogue (Morin et al., 1975). An immense variety of signals are potentially available from the multiple photophores of other marine animals.

Sexual dimorphism provides evidence (still largely circumstantial) for sexually specific bioluminescent signals in a number of marine animals, but many more are certainly capable of generating sexually explicit signals without any equivalent dimorphism. There are immense difficulties inherent in observing normal bioluminescent behaviour in the ocean and one consequence is that our awareness of most species' signalling potential is still rudimentary. However, the complexity of bioluminescent sexual dimorphism that has been identified does emphasize the important contribution that light signals make to sexual selection in a dark environment (Herring, 2000).

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