Species abundance, sexual encounter and bioluminescent signalling in the deep sea

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The problems faced by deep-sea animals in achieving sexual and other encounters require sensory and effector systems the synergy of which can span the often very substantial distances that separate individuals. Bioluminescent systems provide one of the links between individuals, and the sexual dimorphism of some photophores suggests that they are employed to attract a mate. However, nearest-neighbour values for many deep-sea animals put them beyond the effective range of bioluminescent signals and it is therefore likely that these signals are employed at intermediate ranges, once an initial contact (perhaps olfactory) has been made.

Keywords: photophores; bioluminescence; sexual dimorphism; encounter probability; mate attraction; chemosensory systems

1. INTRODUCTION

Deep-sea animals have to be able to locate each other, either for predator–prey interactions or for sexual or social aggregation. Plankton and nekton biomass declines logarithmically with depth, with the consequence that it becomes increasingly difficult for one animal to encounter another. Active searching (for a mate or for prey) requires the possession of appropriate sensory systems to process the signals that are generated (either deliberately or accidentally) by other individuals. Chemo-, mechano- and photoreceptors fulfil this requirement.

Sexually dimorphic sensory systems, such as the enlarged olfactory lamellae in the males of some meso- and bathypelagic fishes, are complemented by similar sexual dimorphism in certain effector systems. The powerful drumming muscles of the males of some brotulid and macrourid fishes provide one example, while the enlargement of particular photophores in either males or females of fishes or squid provides another. In the search for a mate, the task facing one partner is clearly greatly simplified by the broadcasting of sexually specific signals by the other.

2. BIOLUMINESCENT SIGNALS

For many deep-sea animals bioluminescence provides one such type of signal. In shallow marine environments, some of these signals have been known for many years (e.g. the luminous sexual swarming of syllid fireworms and its lunar periodicity). The elaborate nature of others has only recently become apparent. Species of the ostracod *Vargula* (and related genera) have very elaborate luminous courtship signals, based on repeated puffs of luminescence squirted into the water. The specific identities of the (male) signallers are encoded in the frequency and timing of the puffs and in the trajectory and location of the swimming paths along which they are produced (Morin 1986). The puffs are recognized by the appro-

priate female, which then swims up off the bottom to encounter the target male. The light puffs are bright and produced only a metre or so above the waiting females. The visual task of the female is to resolve the individual puffs and she has then to decode centrally their spatial and temporal patterns. The eyes of many of these species are also sexually dimorphic, but curiously it is the male that has the larger eyes, perhaps in response to the more difficult task of recognizing a non-luminous female.

These examples can be observed *in situ*. This is not yet possible for their deep-sea equivalents. Bright bioluminescent flashes, as measured from deep-sea animals, usually have a maximum photon flux in the range 10^{10}–10^{12} photons s^{-1} (Mensinger & Case 1990). This would provide an irradiance in the clearest oceanic water of *ca.* 8×10^2 to 8×10^4 photons cm^{-2} s^{-1} at a range of 10 m assuming no scattering or absorption. These values are within the likely sensitivity ranges of the eyes of most deep-sea fish, squid and shrimp. The irradiance at 1 m will be 100 times greater. But it is most unlikely that the individuals will usually be within that distance of each other. The abundances of deep-sea species reflect the much lower biomass at depth. A midwater trawl filters tens of thousands of cubic metres at each tow, but many species are taken only very occasionally. Nearest-neighbour distances (based on the closest packing of equal spheres (Mackie & Mills 1983)) can be calculated from the observed abundances. Available data are limited but representative examples of the commonest bioluminescent species of fish, shrimp and (for comparison) copepods are shown in table 1. All data are from hauls in the upper 1500 m and all show the maximum observed abundance of each species at the sampling site, usually derived from a series of samples at 100 m depth horizons.

The data demonstrate that, at their maximum abundances, a number of these species have nearest-neighbour distances of less than 10 m, clearly within the visual range of the likely photon fluxes from bright bioluminescent flashes. The numbers, however, distinguish neither adults

1273

Table 1. *Abundance and nearest-neighbour distance of some representative deep-sea fishes and crustaceans*

(Numbers in bold are theoretical; abundance data are for individual species. Crustaceans: *C. pacificus*, *M. lucens*, *P. gracilis*, copepods; *S. debilis*, *G. elegans*, decapods.)

species	abundance (no. m^{-3} × 10^4)	nearest-neigh-bour distance (m)
Calanus pacificus	up to 2.7×10^{11}[f]	
	10^5	**0.5**
Metridia lucens	84 360[b]	
	10^4	**1.1**
Pleuromamma gracilis	5570[b]	
	10^3	**2.4**
Cyclothone acclinidens	470[e]	
Vinciguerria attenuata	210[e]	
	10^2	**5.2**
Diaphus arabicus	90[c]	
Systellaspis debilis	65[a]	
Cyclothone braueri	62.5[c]	
Gennadas elegans	20[a]	
Benthosema glaciale	11.8[c]	
	10^1	**11.2**
Argyropelecus hemigymnus	5.9[c]	
Chauliodus sloani	1.5[d]	
	10^0	**24**
Stomias affinis	1.0[d]	
Stomias boa	0.8[c]	
Photostomias guernei	0.8[d]	

[a]Roe 1984*a*; [b]Roe 1984*b*; [c]Roe & Badcock 1984 (eastern N. Atlantic); [d]Sutton & Hopkins 1996 (Gulf of Mexico); [e]P. J. Herring, unpublished data (Gulf of Oman); [f]Alldredge *et al.* 1985 (Santa Barbara Basin, N. Pacific).

from juveniles, nor males from females. If all the specimens are adult and the two sexes are equally abundant, the nearest-neighbour distance remains the same but there is only a 50% chance of any particular encounter being between different sexes. If the sex ratio departs significantly from 1:1, the chances are reduced for the most abundant sex, as they are for both sexes if the population includes juveniles. For less common species, and even for those species listed in table 1 when their abundances are lower than the local maxima, nearest sexual partner distances will frequently be in (or exceed) the 50–100 m range. This is beyond the effective reach of a bioluminescent flash. A single flash carries specific information only in its spectral and kinetic characteristics. Additional information can be transmitted to the observer through the characteristics of the flash frequency and/or the spatial pattern of the signal (as in the ostracod *Vargula*). Unfortunately, these characteristics are very poorly known for bioluminescence from deep-sea photophores, let alone from the sexually specific ones.

3. SEXUAL DIMORPHISM OF PHOTOPHORES

The expression of sexual dimorphism in photophores of deep-sea animals ranges from their presence and absence

in female and male anglerfishes, respectively (and in some pelagic cephalopods), to either variations in the relative sizes of particular orbital or caudal photophores (e.g. some melanostomiid and myctophid fishes) or the presence of one or two additional ventral photophores among the suite of *ca.* 180 in some sergestid shrimps (figure 1). Although this morphological sexual dimorphism is recognizable by taxonomists, there is still no evidence that it is similarly recognizable by the sexes of the species concerned. The benefit of a larger postorbital photophore in many male melanostomiids may well be that it produces a greater photon flux than does the smaller female organ; it will therefore be more clearly recognizable at a greater distance. If the female perceives the male flash at long range and responds with a weaker flash of her own, there will be a 'dead zone' in the separation between the two, over which the male will be unable to see the response flash (their eyes are of similar size). She can best respond by swimming towards the male, or by releasing some other signal that will enable him to locate her more easily. In most cases, the males of these fishes are smaller than the females; if postorbital bioluminescent signals are the *sole* key to mate recognition, it seems likely that the female will be the active partner in the final approach. Female selection (as occurs in many birds) may also apply in some instances in the deep sea. Indeed, there may be an analogy between enlarged male melanostomiid photophores and striking sexual plumage.

More certain evidence for the use of bioluminescent signals for sexual recognition, albeit still circumstantial, is the late development of secondary light organs in adult females of some squid and octopods. As they mature, females of certain cranchiids (e.g. *Liocranchia*) develop additional light organs at the tips of some of the arms; these sexual photophores are structurally quite different from the others. For most of their lives females of the octopod *Japetella* are, like the males, not luminous, but ripe females develop a ring of bioluminescent tissue around the mouth (figure 1*b*) and this tissue atrophies once the eggs are spent. Nothing is known about the characteristics of their signals. Sexual dimorphism of the photophores occurs in a few other squid, but the differences are much less extreme and not so clearly related to sexual maturity.

4. BIOLUMINESCENT DIALOGUES

Fireflies are known to have complex luminescent courtship dialogues, involving the recognition of at least flash frequency, response delay and flight trajectory. No such complexity has been identified in deep-sea animals; the shallow-water ostracod *Vargula* has the most elaborate pattern yet identified in a marine animal, and this is a display rather than a dialogue. There are other marine animals that respond (like a firefly) to a flash of light with their own flash. Ostracods, copepods, euphausiids, *Pyrosoma*s and lanternfish have all been reported to respond to illumination by luminescing in return. Many of the observations of these responses involved illumination with artificial lights of very much greater intensity than natural bioluminescent sources, but several did note that the luminescence of one animal could stimulate another. This indicates the potential for the employment of a
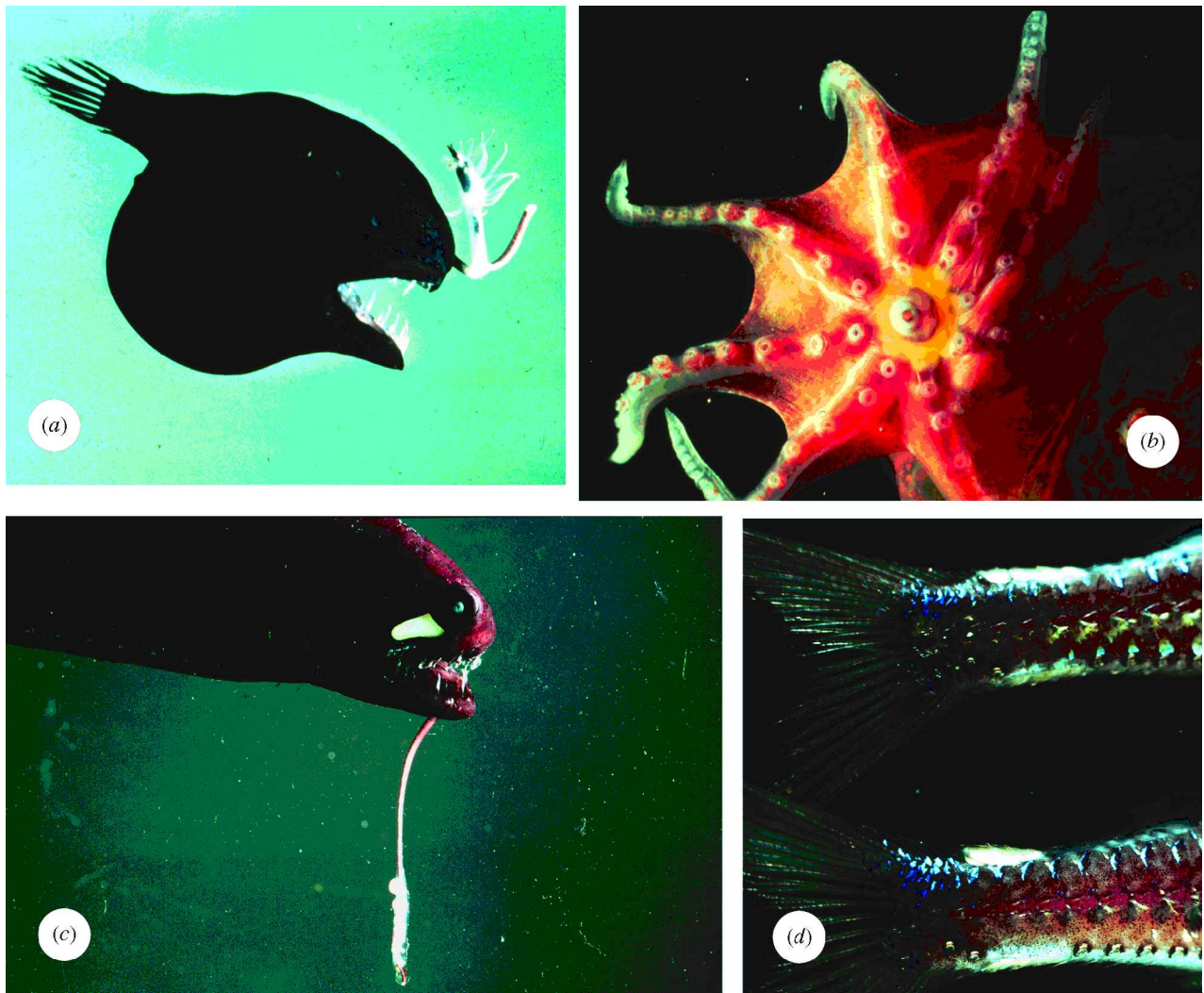
Figure 1. Examples of sexual dimorphism of photophores. (*a*) Females of the anglerfish *Chaenophryne draco* have a very elaborate luminous lure; males have no photophore. (*b*) Mature females of the octopod *Japetella diaphana* (shown here) develop a yellow circumoral photophore; males have no photophore. (*c*) In species of the deep-sea fish *Melanostomias*, the postorbital photophores are larger in males (as shown here) than in females. (*d*) Many lanternfishes (Myctophidae) have special dorsal and ventral photophores on the caudal peduncle, which differ in size or position between males and females. In many cases males have only supracaudal organs and females only infracaudals; in others, one or both sexes may have photophores in both positions (as shown here for *Myctophum* sp.).

luminous dialogue in order to identify a mate. It also demonstrates that a luminous signal could be propagated through a population if the individuals are within responsive range of one another (as occurs in some fireflies). The possibility has been carefully analysed in the responses of two species of *Pyrosoma* to light stimuli (Bowlby *et al.* 1990). The photon flux that elicits a maximum luminescent response from these colonial animals is equivalent to the flux from that response at a range of 17 m. Recorded population densities reach 85 per 10 000 m^3, equivalent to a nearest-neighbour distance of 5.5 m and thus well within the range required for a propagated response. Waves of light have been observed to propagate through shallow-water ostracod populations, showing that the effect can indeed occur *in situ*. Night-time aggregations of the reef-living flashlight fishes *Photoblepharon* and *Anomalops* (Anomalopidae) probably develop and are maintained by bioluminescent signals, but the prospect of an equivalent behaviour in any deep-sea species remains wholly theoretical.

5. MATE LOCATION AND PERCEPTION DISTANCES

Sexual encounters in the deep sea are certainly facilitated by sexual dimorphism of signalling and sensory systems. An analysis of the problem of mate location in hatchetfishes (among the commoner of mesopelagic fishes) has modelled the role of olfaction in facilitating the process in *Argyropelecus hemigymnus* (whose males are macrosmatic). Bioluminescence may have an equivalent function in *Sternoptyx diaphana* (in which both sexes are microsmatic, i.e. they have tiny olfactory systems). The olfactory model used assumes that a slowly decaying female pheromone spreads in a two-dimensional patch, which is located by searching males. A male moves initially at some mean speed in purely random directions, but must maintain a vertical velocity component to encounter a horizontal odour patch, where he then undertakes active searching for the source of the odour. The results of the model show that reasonable encounter rates can be achieved with known population densities and swimming

speeds. *Sternoptyx diaphana* is less abundant (and lives deeper) than *A. hemigymnus*, and also lacks the olfactory dimorphism. In two populations (Gulf of Mexico and Hawaii), with stock sizes of 5000 and 11 000 km^{-2}, respectively, the sex ratios were assumed to be 1 : 1, adults comprised 20–25% of the totals and the average male densities over the 200 m depth of maximum abundance were 0.38 and 0.88 m$^{-3} \times 10^4$, giving average male–female separations of 29 and 22 m, respectively. Given that both sexes move randomly and at equal velocity, with a uniform probability distribution in three dimensions, it is possible to model how differences in population abundance, swimming speed and perception distance would affect the likelihood of an encounter in a given time (Baird & Jumper 1995). The results show that at low combinations of abundance and velocity there is a nonlinear increase in the numerical perception distance required for a probable encounter. For the average Hawaiian populations, a perception distance of 4 m gives a 95% probability of encounter in one day, reducing to 6 h with a perception distance of 7.5 m. If the perception distance is reduced to 1.0 and 0.5 m, the encounter times increase to 10 and 40 days, respectively. If only one sex is actively swimming, the encounter delay increases by one-third. Diel vertical migration will enhance the encounter opportunities for many mesopelagic animals if the population distributions are biased towards horizontal layers.

The simulations show the critical importance of increasing the perception distances; for *S. diaphana*, in the absence of chemical cues, bioluminescence may be the key. For species that are much less abundant (e.g. the hatchetfishes *Sternoptyx pseudobscura*, *S. obscura* and *Argyropelecus aculeatus* off Hawaii) nearest-neighbour distances may exceed 200 m. The problems posed to deep-sea animals by these very low abundances may well limit their reproductive success. The sensory mechanisms that make mate encounter a survivable probability in these circumstances are not either one system or another but the combination of the sensory suite of each species. Bioluminescence and vision undoubtedly play an impor-

tant role for many deep-sea animals, but their employment may come after the detection of a long-range chemical cue and precede close-range mechanosensory recognition. Sensory processing of this aquatic environment for sexual encounters is a challenge requiring integrated solutions.

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