Cah. Biol. Mar. (1999) 40 : 57-63

Variation in bioluminescence with ambient illumination and diel cycle in a cosmopolitan ophiuroid (Echinodermata)

Dimitri DEHEYN[1*], Jérôme MALLEFET[2] and Michel JANGOUX[1, 3]
[1*] *Corresponding author: Laboratoire de Biologie marine (CP 160/15), Université Libre de Bruxelles, 50 av. F.D. Roosevelt, B-1050 Bruxelles, Belgium*
Fax: (32) 2 650 27 96 - e-mail: ddeheyn@ulb.ac.be
[2] *Laboratoire de Physiologie animale, Université Catholique de Louvain, 5 Place Croix du Sud, B-1348 Louvain-la-Neuve, Belgium*
[3] *Laboratoire de Biologie marine, Université de Mons-Hainaut, Avenue du Champ de Mars, Bâtiment des Sciences de la Vie, B-7000 Mons, Belgium*
Fax: (32) 2 650 27 96 - e-mail: ddeheyn@ulb.ac.be

Abstract: Luminescence intensity and kinetics of the small cosmopolitan ophiuroid *Amphipholis squamata* were measured in the laboratory from individuals collected in a bright intertidal environment and a dark subtidal environment (15 m depth). Luminescence was also measured during day and night for intertidal individuals only. Luminescence intensity was about 100 times higher for intertidal individuals than for subtidal individuals, and about 2 times higher during day time than at night for intertidal individuals. It is the first time that luminescence intensity has been shown to vary with depth and between day and night in a benthic invertebrate species. Conversely, luminescence kinetics, were always similar whatever the origin of the sample and time of measurement. Our results support the common belief that differences in luminescence intensity reflect differences in ambient illumination [obtaining enough contrast with the least signal] more than being related to any other environmental parameter.

Résumé : *Variation de la bioluminescence avec l'illumination ambiante et le cycle nycthéméral chez une espèce cosmopolite d'ophiure (Echinodermata).* L'intensité et la cinétique de luminescence de la petite ophiure cosmopolite *Amphipholis squamata* ont été mesurées en laboratoire sur des individus récoltés soit dans un environnement éclairé de la zone intertidale soit dans un environnement sombre du subtidal (15 m de profondeur). La luminescence a aussi été mesurée le jour et la nuit, mais seulement pour les individus de l'intertidal. L'intensité de la luminescence était ca. 100 fois plus élevée pour les individus de l'intertidal que pour ceux du subtidal et ca. 2 fois plus élevée pendant le jour que pendant la nuit pour les individus de l'intertidal. Pour la première fois il est montré que l'intensité de la luminescence varie avec la profondeur et entre le jour et la nuit pour une espèce benthique d'invertébré. La cinétique de luminescence, au contraire, a toujours été similaire, quelle que soit l'origine de l'ophiure (subtidale ou intertidale) et le moment de la mesure (jour ou nuit). Nos résultats semblent concorder avec la règle générale selon laquelle les différences d'intensité de luminescence traduisent des différences de luminosité ambiante (afin de garder un contraste de lumière suffisant à l'aide du signal le plus faible) plutôt qu'elles ne reflètent l'influence d'un autre paramètre de l'environnement.

Keywords : *Amphipholis squamata*; Luminescence; Ambient illumination; Diel variation; Adjustment; Light contrast.

Introduction

Luminescence, the ability to produce visible light, is a common feature among pelagic and benthic marine

Reçu le 6 mai 1998 ; accepté après révision le 16 novembre 1998.
Received 6 May 1998; accepted in revised form 16 November 1998.

organisms (Hastings & Morin, 1991). The production of light is influenced by temperature, salinity, pH and dissolved oxygen (Tett, 1969; Shimomura, 1985), parameters that can affect both luminescence intensity and kinetics. Light intensity indicates the amount of photogenous material involved in the luminescence process; it depends on the molecular reaction of the process and represents the energy that is available to produce the light (Shimomura, 1985; McCapra, 1990). Light kinetics characterizes the efficiency of biological pathway and cellular control leading to light production; it includes time of interaction between luminescence reagents and depends on the neuro-physiological condition of organisms, also on physico-chemical parameters of the environment (Dunlap et al., 1981; Hastings, 1983). In pelagic organisms that undertake diel vertical migration, the light produced varies in intensity according to ambient illumination and changes between depths and between day and night (Boden & Kampa, 1974; Young, 1983). The light production is associated with various visual functions (Herring, 1990). They are 'passive' when the intensity of the produced light is equal to that of surrounding illumination, or 'active' when it is higher (Morin, 1983; Young, 1983). Light signals with passive functions are undetectable since the light matches the background illumination and thus the emittor using this countershading technique becomes 'invisible' (Young & Roper, 1977; Latz, 1995). Light signals of active functions are produced to be detectable; they are associated with signals of defense that can stun, warn by aposematism or attract away using a luminescent sacrificial lure (Morin, 1983). In benthic organisms, luminescence is believed to be associated only with 'active' functions, but it is not known whether intensity of the produced light changes with ambient illumination.

Echinoderms include numerous bioluminescent species, mostly ophiuroids (Herring, 1995). Luminescence is triggered by mechanical stimulation and intensity of the luminescent reaction varies according to magnitude of the stimulus: glows of weak intensity are produced in response to weak stimulation and series of intense flashes in response to strong stimulation (Basch, 1988). *Amphipholis squamata* (Delle Chiaje, 1828) is a small bioluminescent ophiuroid, in which adult specimens have a disc diameter of about 3 mm and an arm length of about 15 mm. Only the arms are luminescent in this ophiuroid (Brehm & Morin, 1977). The species is cosmopolitan and distributed from the intertidal zone to depths of 2000 m (Gage et al., 1983); individuals reside in all kind of habitats regardless of substrate granulometry, but never in anoxic ones (Johnson, 1972).

The present study investigates the luminescence of *A. squamata* from different depths in a bay characterized by the fact that the sea water is fully mixed from bottom to surface, conditions of ambient illumination being the only parameter clearly changing with depth. Luminescence of individuals was investigated both in day light and at night.

Material and methods

Amphipholis squamata was collected in July 1995 in Hansa Bay (Madang Province, Papua-New Guinea (PNG)). We sampled two stations (Fig. 1), Laing Island (4°10' S, 144°52' E; station 1) and Sushimaru wreck (4°09' S, 144°50' E; station 2). Studied individuals were adults of similar size (2.01 ± 0.01 mm, disc diameter ± confidence limit). Individuals were collected by hand at low tide from four large tide pools on the eastern shore of Laing Island (Claereboudt et al., 1989). The pools are shallow (5 to 100 cm depth) and exposed to day light (i.e. a bright environment). The sea water they contain has the same characteristics as the open sea water, except for some abrupt variations of temperature and salinity during low tides on sunny or rainy days (Claereboudt et al., 1989). July is the dry season in PNG, and temperature and salinity in the pools sometimes increase from 29 to 34 °C and from 29 to 31 P.S.U., respectively. The tide pools contain abundant encrusting coralline algae and boulders of living coral colonies on a sandy substrate (Claereboudt & Bouillon, 1987; Claereboudt et al., 1989), and blocks of dead coral from under which ophiuroids were collected. Individuals from the Sushimaru wreck (station 2) were collected from under shell fragments subtidally at 12-15 m depth by SCUBA diving. The substrate at the subtidal site is a hard structure (the wreck) covered with a thin layer of sand mixed with silt. Coral and algae are absent as light penetration in sea water at Hansa Bay is poor due to high turbidity (i.e. a dark environment). This is caused by circulating water currents around the bay that create a fully mixed water column from the bottom up to the surface (Claereboudt & Bouillon, 1987; Claereboudt et al., 1989).

Individuals from stations 1 and 2 were transported to the King Léopold III Biological Laboratory (Laing Island) where their luminescence was measured either soon after collecting, to reduce exposure to other illumination conditions or, after maintenance for 8 to 12 hrs in an outdoor open marine aquarium containing boulders for night measurements. Light measurements were taken between 14.00-18.00 h (day measurements) for individuals from both stations, and between 00.00-04.00 h (night measurements) for individuals of station 1 (intertidal zone). For comparison between day and night luminescence, the ophiuroids were investigated on three successive moonless nights and on the three preceeding daytime periods. Individuals were collected on each of these days between 11.00 to 13.00 h for day measurement and between 16.00 to 17.00 h for night measurement.

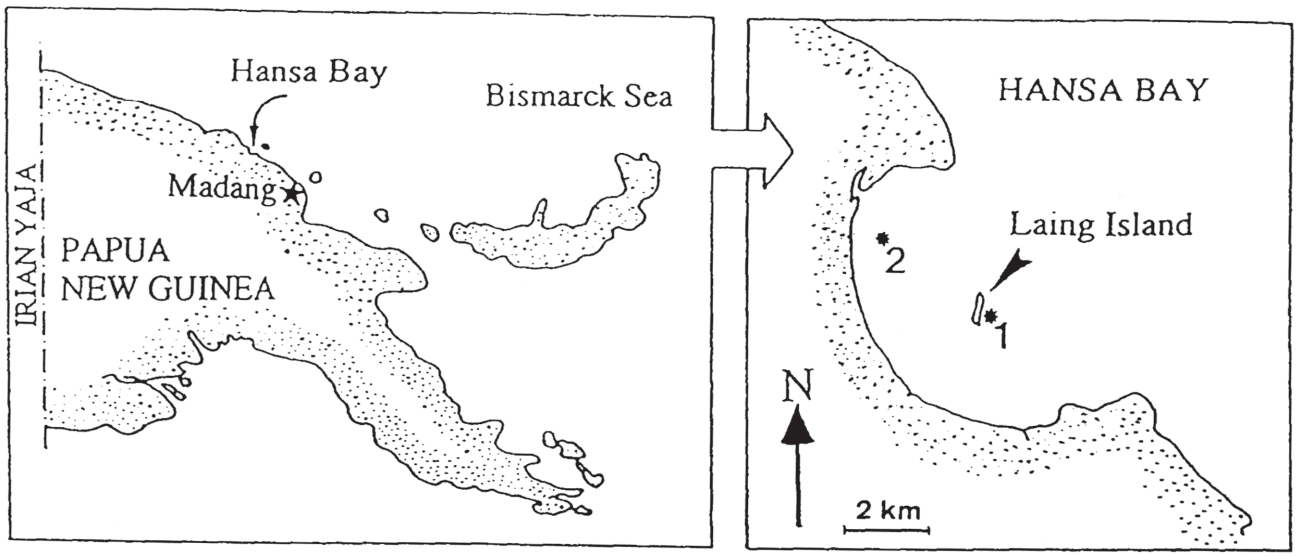


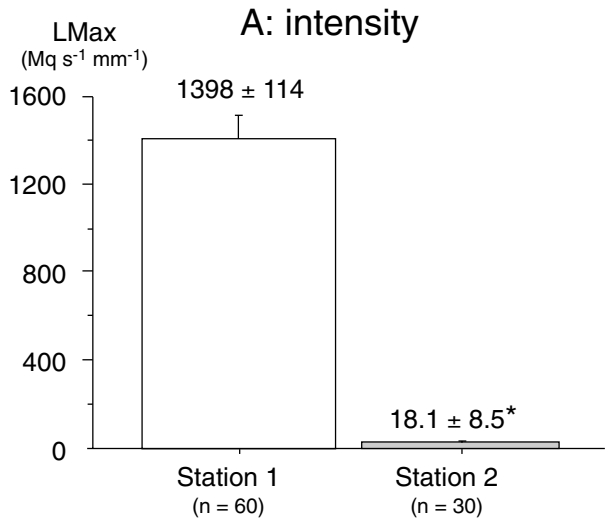
Figure 1. Sample sites (1 and 2).
Figure 1. Sites d'échantillonnages (1 et 2).

For arm luminescent measurements, individuals were anaesthetized in a 3.5% w/w $MgCl_2$ solution and dissected using a fine scalpel under a binocular microscope: their disc bursae were opened to check for embryo and/or juveniles and their arms were separated from the disc (Deheyn et al., 1997). Each of the five isolated arms was tested for luminescence in a dark room at constant temperature (25°C), the luminescence being triggered using 200 mM KCl to maximize the individual's light production (Mallefet et al., 1992). The latter starts around 2 s after the KCl addition, the luminescence then being unimodal and lasting for around 120 s. The luminescence was detected using a phototube (type IP21-S20) with maximal spectral sensitivity from 400 to 600 nm (*A. squamata* luminescence spectrum is maximal from 480 to 520 nm; Brehm & Morin, 1977). The light record thus always included the maximal spectral band of the ophiuroid luminescence. The light detected by the phototube was transformed into an electric signal using a IL 760 radiometer and amplified (Amplifier IL 1700) before being recorded graphically (Deheyn et al., 1997). The light was not monochromatic and was not therefore expressed in terms of emitted photons but in terms of total energy produced (Hastings & Morin, 1991). The same measurement technique was applied to all specimens and the experimental device was calibrated every week using a tritium-phosphor source whose light production (energy flux in Megaquanta per second) is known and maximal from 470 to 510 nm (Deheyn et al., 1997).

Two parameters were used to characterize the light production, (a) the maximum light intensity (LMax), expressed in megaquanta emitted per second per millimeter of arm (Mq s^{-1} mm^{-1}) and which indicates the maximal flux of energy quanta associated with the produced photons (intensity parameter), and (b) the latency time (TLMax) which is the time (s) to reach the maximum light intensity (kinetic parameter). Luminescence intensity and kinetics between stations 1 and 2 and between day and night were analysed using nested Analysis of Variance (arms nested within individual) and multiple mean comparisons tests (Tukey), with the α=0.05 for all analyses, which were run using Systat 5.2.1.

Results and Discussion

Amphipholis squamata showed no signs of stress (i.e., no autotomy) either when collected or after 8-12 hrs of maintenance in aquarium. Light was always produced following stimulation, whatever the individuals' origin (intertidal or subtidal zone) or the time of measurement (day or night). Light intensity (LMax) varied significantly ($P<0.0001$) according to depth (Fig. 2), subtidal luminescence being about 100 times less intense than intertidal luminescence, and according to time (Fig. 3), night time luminescence being around 2 times less intense than day time luminescence. Light kinetics (TLMax) did not vary significantly between station 1 and 2, nor between day and night (Figs. 2 and 3). This suggests that the amount of photogenous material involved in luminescence differed between stations and time, but that all individuals produced light using the same mechanism and following the same biological pathway. Constancy in kinetics also supports the fact that individuals were in similar physico-chemical conditions of sea water, or if these conditions were different, that they had no influence on luminescence. Sea water



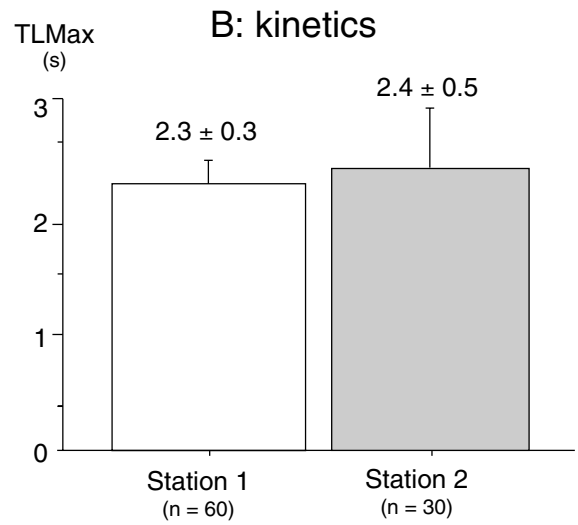
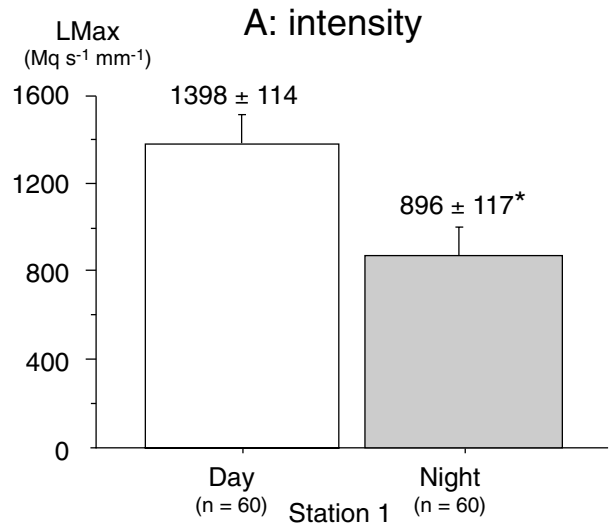


Figure 2. *Amphipholis squamata*. Luminescence parameters of individuals from stations 1 and 2. (**A**) maximal light intensity (LMax in Mq s^{-1} mm^{-1}); (**B**) time to reach maximal light intensity (TLMax in s) (mean ± 95 % confidence limit); n = number of stimulated arms from 12 (station 1) and 6 (station 2) individuals; * significantly different.

Figure 2. *Amphipholis squamata*. Paramètres de luminescence des individus des stations 1 et 2. (A) intensité maximale de lumière (LMax en Mq s^{-1} mm^{-1}) ; (**B**) temps nécessaire pour atteindre l'intensité maximale (TLMax en s) (moyenne ± intervalle de confiance à 95 %) ; n = nombre de bras stimulés à partir de 12 (station 1) et de 6 (station 2) individus; * est significativement différent.



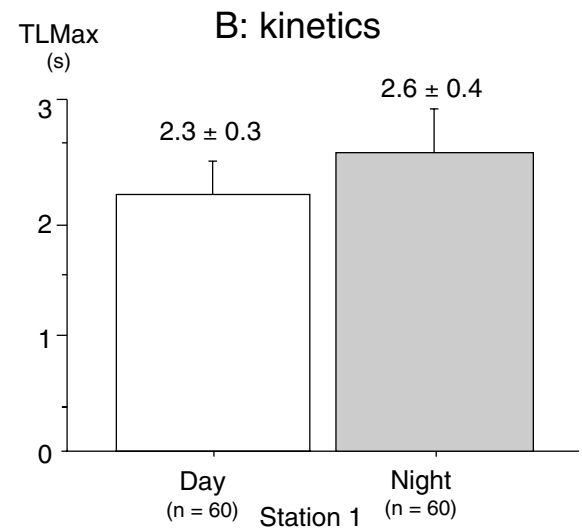


Figure 3. *Amphipholis squamata*. Luminescence parameters of individuals from station 1 at day (14.00-18.00 pm) and night (00.00-04.00 am). (A) maximal light intensity (LMax in Mq s^{-1} mm^{-1}); (B) time to reach maximal light intensity (TLMax in s) (mean ± 95 % confidence limit); n=number of stimulated arms from 12 individuals each time; * is significantly different.

Figure 3. *Amphipholis squamata*. Paramètres de luminescence des individus de la station 1 le jour (14.00-18.00 h) et la nuit (00.00-04.00 h). (**A**) intensité maximale de lumière (LMax en Mq s^{-1} mm^{-1}) ; (**B**) temps nécessaire pour atteindre l'intensité maximale (TLMax en s) (moyenne ± intervalle de confiance à 95 %) ; n = nombre de bras stimulés provenant de 12 individus à chaque fois ; * est significativement différent.

parameters are known to vary little from the bottom to the surface in Hansa Bay, due to the particular hydrogeographic conditions of the area (Bouillon et al., 1986; Claereboudt et al., 1989). Therefore, any observed variation in luminescence intensity must be related to other biological or environmental factor(s).

As the population investigated here is homogenous for colour (all individuals had pale beige disc and finely pigmented white arms) and for brooding state (all individuals considered were brooding), the luminescence cannot possibly be influenced by colour variety or brooding state, as shown for another population (Deheyn et al., 1997).

Luminescence intensity can be influenced by availability and quality of food since substances involved in photogenous reactions are possibly of exogenous origin (Hastings & Morin, 1991; Thompson & Rees, 1995). The availability of food does not appear likely to be an influencing parameter here, as luminescence differs between day and night. Moreover, the availability of food does not appear to be an important factor that could affect biology of the species, since individuals may use various feeding strategies being either omnivorous, detrivorous, deposit or suspension feeder depending upon their environmental conditions (Johnson, 1972; Emson & Whitfield, 1989; Emson et al., 1989; Jones & Smaldon, 1989).

Two complementary features are necessary to support the possible influence of the quality of food on the luminescence property. The first is assuming that some photogenous material is of exogenous origin. The second is implying a wide variability of luminescence among individuals from a given station, or from a given time of collecting, as luminescence depends both on equal presence of food at all stations and on individuals' ingestion rates (Hastings, 1983; Thompson & Rees, 1995). However, in the present study, the luminescence showed little variability at a station and between times of collecting, as indicated by the low confidence limit associated with mean values (Figs. 2 and 3). Moreover, photogenous material has been suggested to be of endogenous origin in *A. squamata* (Deheyn et al., 1997). Therefore, we can say that the quality of the food probably does not have any impact on the luminescence.

The factors remaining to potentially influence luminescence are water pressure and ambient illumination. Pelagic luminous organisms do vertical migration in the water column and the luminescence then changes with depth (Tett & Kelly, 1973). Swift et al. (1981) considered that the change in pressure occurring along a vertical migration did not explain the variation of luminescence and that the main factor of influence appeared to be the ambient illumination (see also Young & Roper, 1977; Latz, 1995). It seems that in the present study, the parameter playing a major role in Hansa Bay is more likely to be the changes in ambient illumination. The latter varies between station 1 and 2 and between day and night. Individuals from station 2 (subtidal zone) lived in dark conditions and produced weak luminescence, those from station 1 (intertidal zone) lived in bright conditions and produced intense luminescence. Similarly, luminescence was weak at night and intense during the day. This suggests a diel variation in the ophiuroid luminescence. Dinoflagellates are the only organisms that have been found to show diel variation of luminescence independent from diel vertical migration (Kelly & Tett, 1978; Swift et al., 1981; Hastings, 1986). During the day dinoflagellates do photosynthesize which is in accordance with (photo)inhibition of their luminescence. The luminous signal they produce thus is weaker in day light (Swift et al., 1981; Hastings et al., 1991). Dinoflagellates produce luminescence following mechanical stimulation and the light produced is then used for defense (see the 'burglar alarm effect'; Morin, 1983), the defense being more efficient during dark nights (Kelly & Tett, 1978; Hastings & Morin, 1991). There is only one species of dinoflagellate (*Noctiluca scintillans* Kofoid & Swezy, 1921) that is not inhibited by day light and in which luminescence is adapted to ambient level of illumination, the produced light therefore being more intense during the day than at night (Bityukov et al., 1967). The luminescence then supposedly remains defensive. The situation appears similar in *A. squamata* in which luminescence is different according to day or night and is associated with a defensive function (Deheyn et al., 1998; Mallefet et al., 1998). Biological mechanisms controlling this diel luminescence variation are not known. It might be regulated genetically by a biological clock in phase with diel variation of ambient illumination, as it is for dinoflagellates (Hastings et al., 1991; Roenneberg, 1996) or might be modulated neurophysiologically by the level of ambient illumination, as it is for pelagic organisms (Boden & Kampa, 1974; Latz, 1995).

Dubuisson (1995), working in experimental conditions on *A. squamata* from a French location, proposed a neurophysiologically modulated diel variation of luminescence for this ophiuroid. Individuals were maintained for two weeks in close-circuit marine aquaria under 3 illumination conditions: 12:12 light:dark regime, constant light, or constant darkness. When in 12:12 light:dark regime, luminescence was intense in light conditions (ca. 9 Mq s^{-1} mm^{-1}) and weak in dark conditions (ca. 6 Mq s^{-1} mm^{-1}). Under constant light, the luminescence was more intense (ca. 60 Mq s^{-1} mm^{-1}); it was weaker under constant darkness (ca. 6 Mq s^{-1} mm^{-1}). Our results thus confirmed in the field Dubuisson's experimental observation. However we found that the luminescence measured at night was higher than the one measured in dark conditions (subtidal zone). This suggests a progressive adjustment of luminescence to changes in environmental light depending on the original value of intensity and the length of time during which the changes occur.

Irrespective of the control mechanism, producing less light when ambient illumination is weaker must be advantagous for the ophiuroid. The luminescence is a function of considerable metabolic cost (McCapra, 1990) that is nonetheless found in many organisms, where it plays a role in visual communication. The luminescence in ophiuroids is associated with "active" signals of defense, the light signal being functional when of higher intensity than the surrounding illumination (Basch, 1988; Grober, 1988). We suggest that it would be (energetically) advantagous for the ophiuroid to modulate the intensity of its luminescence

with changes in ambient illumination. Our results indicate that *A. squamata* can adjust its intensity of luminescence to contrast with the ambient illumination and be detectable. Further investigation should now consider whether photoregulation of luminescence could be possible also in luminous benthic organisms, as well as in pelagic ones.

Acknowledgments

Funds for this research were provided by the King Léopold III Foundation, a FRIA grant to D. Deheyn, an Academy of Sciences grant to J. Mallefet and by the FRFC convention ref. 6.231.85. We are grateful to Ch. Spirlet, T. Feldstein and anonymous referees for criticism on the manuscript, and to G. Seghers (ULB, Laing Island) and I. Cogneau (UCL) for technical assistance. This is a contribution of the "Centre Interuniversitaire de Biologie Marine" (CIBIM). J. Mallefet is a Research Associate of the National Fund for Scientific Research (FNRS, Belgium).

References

Basch L.V. 1988. Bioluminescent anti-predator defense in a subtidal ophiuroid. In: *Echinoderm Biology* (R.D. Burke, P.V. Mladenov, P. Lambert & R.L. Parsley eds), pp. 565-573. A.A. Balkema: Rotterdam.

Bityukov E.P., Rybasov V.P. & Shaida V.G. 1967. Annual changes in the bioluminescence field intensity in the neritic zone of the Black Sea. *Okeanologiya,* **7**: 1087-1099.

Boden B.P. & Kampa E.M. 1974. Bioluminescence. In: *Optical aspects of oceanography* (N.G. Jerlov & E. Steeman Nielsen eds), pp. 448-469. Academic Press: London.

Bouillon J., Claereboudt M. & Seghers G. 1986. Hydroméduses de la baie de Hansa (Mer de Bismarck; Papouasie-Nouvelle-Guinée) - Répartition, conditions climatiques et hydrologiques. *Indo-Malayan Zoology,* **3**: 105-152.

Brehm P. & Morin J.G. 1977. Localization and characterization of luminescent cells in *Ophiopsila californica* and *Amphipholis squamata* (Echinodermata: Ophiuroidea). *Biological Bulletin,* **152**: 12-25.

Claereboudt M. & Bouillon J. 1987. Coral associations, distribution and diversity on Laing Island reef (Papua New Guinea). *Indo-Malayan Zoology,* **4**: 11-25.

Claereboudt M., Massin C. & Bouillon J. 1989. A general survey of Laing Island environment (Papua New Guinea). *Indo-Malayan Zoology,* **6**: 1-23.

Deheyn D., Mallefet J. & Jangoux M. 1997. Intraspecific variations of bioluminescence in a polychromatic population of *Amphipholis squamata* (Echinodermata: Ophiuroidea). *Journal of the Marine Biological Association of the United Kingdom,* **77**: 1213-1222.

Deheyn D., Mallefet J. & Jangoux M. 1998. Bioluminescence in *Amphipholis squamata*: an anti-predator aposematic deterrent function? In: *Echinoderms: San Francisco* (R. Mooi & M. Telford eds), p. 351. AA Balkema: Rotterdam.

Dubuisson M. 1995. *Influence des facteurs abiotiques (température-photopériode-oxygène) sur la luminescence d'Amphipholis squamata (Echinodermata: Ophiuroidea).* Master thesis, Louvain-la-Neuve Catholic University, Belgium, 40 p.

Dunlap J.C., Taylor W. & Hastings J.W. 1981. The control and expression of bioluminescence in dinoflagellates. In: *Bioluminescence Current Perpectives* (K.H. Nealson ed), pp. 108-124. Burgess Publishing: Minneapolis.

Emson R.H., Jones M.B. & Whitfield P.J. 1989. Habitat and latitude differences in reproductive pattern and life-history in the cosmopolitan brittle-star *Amphipholis squamata* (Echinodermata). In: *Reproduction, genetics and distributions of marine organisms* (J.S. Ryland & P.A. Tyler eds), pp. 75-81. Olsen & Olsen: Fredensborg.

Emson, R.H. & Whitfield P.J. 1989. Aspects of the life history of a tide pool population of *Amphipholis squamata* (Ophiuroidea) from South Devon. *Journal of the Marine Biological Association of the United Kingdom*, **69**: 27-41.

Gage J.D., Pearson M., Clark A.M., Paterson G.L.P. & Tyler P.A. 1983. Echinoderms of the Rockall Trough and adjacent areas. 1. Crinoidea, Asteroidea and Ophiuroidea. *Bulletin of the British Museum of Natural History (Zoology)*, **45**: 263-308.

Grober M.S. 1988. Brittle-star bioluminescence functions as an aposematic signal to deter crustacean predators. *Animal Behaviour,* **36**: 493-501.

Hastings J.W. 1983. Biological diversity, chemical mechanisms, and the evolutionary origins of bioluminescent systems. *Journal of Molecular Evolution*, **19**: 309-321.

Hastings J.W. 1986.. Dinoflagellate bioluminescence: biochemistry, cell biology and circadian cycle. In: *Bioluminescence and chemiluminescence* (J. Scholmerich, R. Andreesen, A. Kapp, M. Ernst & W.G. Woods eds), pp. 343-350. John Wiley & sons: Chichester.

Hastings J.W. & Morin J.G. 1991. Bioluminescence. In: *Neural and integrative animal physiology* (C.L. Prosser ed), pp. 131-170. Wiley-Liss Inc.: Cambridge.

Hastings J.W., Rusak B. & Boulos Z. 1991. Circadian rythms: the physiology of biological timing. In: *Neural and Integrative animal physiology* (C.L. Prosser ed), pp. 435-546. Wiley-Liss Inc.: Cambridge.

Herring P.J. 1990. Bioluminescent communication in the sea. In: *Light and Life in the Sea* (P.J. Herring, A.K. Campbell, M. Whitfield & L. Maddock eds), pp. 245-264. Cambridge University Press: Cambridge.

Herring P.J. 1995. Bioluminescent echinoderms: Unity of function in diversity of expression? In: *Echinoderm research* (R.H. Emson, A.B. Smith & A.C. Campbell eds), pp. 9-17. A.A. Balkema: Rotterdam.

Johnson J. 1972. *The Biology of Amphipholis squamata Delle Chiajei (Echinodermata: Ophiuroidea).* PhD thesis, University of Newcastle upon Tyne, England, 186 p.

Jones M.B. & Smaldon G. 1989. Aspects of the biology of a population of the cosmopolitan brittlestar *Amphipholis squamata* (Echinodermata) from the Firth of Forth, Scotland. *Journal of Natural History*, **23**: 613-625.

Kelly M.G. & Tett P. 1978. Bioluminescence in the ocean. In: *Bioluminescence in action* (P.J. Herring ed), pp. 399-417. Academic Press: London.

Latz M.I. 1995. Physiological mechanisms in the control of bioluminescent countershading in a midwater shrimp. *Marine and Freshwater Behaviour and Physiology,* **26**: 207-218.

Mallefet J., Vanhoutte P. & Baguet F. 1992. Study of *Amphipholis squamata* luminescence. In: *Echinoderm Research* (L. Scalera-Liaci & C. Canicatti eds), pp. 125-130. A.A. Balkema: Rotterdam.

Mallefet J., Dupont S., Vandemeulebroecke G., Baguet F. & Deheyn D. (1998). Study of *Amphipholis squamata* luminescence function(s). *EOS transaction (American Geophysical Union)*, **79**: p. 175.

McCapra F. 1990. The chemistry of bioluminescence: origins and mechanism. In: *Light and Life in the Sea* (P.J. Herring, A.K. Campbell, M. Whitfield & L. Maddock eds), pp. 265-278. Cambridge University Press: Cambridge.

Morin J.G. 1983. Coastal bioluminescence: patterns and functions. *Bulletin of Marine Science,* **33**: 787-817.

Roenneberg T. 1996. The complex circadian system of *Gonyaulax polyedra*. *Physiologia Plantarum,* **96**: 733-737.

Shimomura O. 1985. Bioluminescence in the sea: photoprotein systems. *Society for Experimental Biology Symposium,* **39**: 351-371.

Swift E., Meunier V.A., Biggley W.H., Hoarau J. & Barras H. 1981. Factors affecting bioluminescent capacity in oceanic dinoflagellates. In: *Bioluminescence Current Perpectives* (K.H. Nealson ed), pp. 95-106. Burgess Publishing: Minneapolis.

Tett P.B. 1969. The effects of temperature upon the flash-stimulated luminescence of the euphausiid *Thysanoessa raschi*. *Journal of the Marine Biological Association of the United Kingdom,* **49**: 245-258.

Tett P.B. & Kelly M.G. 1973. Marine bioluminescence. *Oceanography and Marine Biology Annual Review,* **11**: 89-173.

Thompson E.M. & Rees J.-F. 1995. Origins of luciferins: ecology of bioluminescence in marine fishes. In: *Biochemistry and molecular biology of fishes, Vol 4* (P.W. Hochachka & T.P. Mommsen eds), pp. 435-466. Elsevier Science: Amsterdam.

Young R.E. 1983. Oceanic bioluminescence: an overview of general functions. *Bulletin of Marine Science,* **33**: 829-845.

Young R.E. & Roper C.F.E. 1977. Intensity regulation of bioluminescence during countershading in living midwater animals. *Fishery Bulletin,* **75**: 239-252.