BIOLUMINESCENT MARINE PLANKTON

Ramasamy Santhanam

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Bioluminescent Marine Plankton

Authored by

Ramasamy Santhanam

Fisheries College and Research Institute
Tamil Nadu Veterinary and Animal Sciences University
Thoothukudi
India

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Author: Ramasamy Santhanam

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PREFACE

Bioluminescence, the “cold living light” or the “cold fire of the sea,” is extremely common in all oceans at all depths. However, this phenomenon is nearly absent in freshwater, with the exception of a freshwater limpet. More than 75% of deep-sea creatures have been reported to produce their own light. The luminescent marine plankton such as dinoflagellate, radiolarians, jellyfish, comb jellies, annelids, copepods, ostracods, mysids, amphipods, euphausiids, and tunicates form an important component in the marine food chain. Research on luminescent marine plankton is gaining momentum now-a-days owing to its importance in human health. The glowing Green Fluorescent Protein (GFP) extracted from the North Pacific jellyfish, *Aqueorea victoria* (for which the Japanese biologist, Osamu Shimonmura won the Noble Prize in Chemistry in 2008) has helped shed light on key processes such as the spread of cancer, the development of brain cells, the growth of bacteria, damage to cells by Alzheimer's disease, and the development of insulin-producing cells in the pancreas. Furthermore, GFP has been “a guiding star for biochemists, biologists, medical scientists and other researchers” besides serving as an indispensable tool in cellular research and medicine. Recent research findings have also shown that the natural products of the bioluminescent marine plankton could be of great use in therapeutical and biotechnological applications. Further application of “bioluminescence imaging” has grown tremendously in the past decade, and it has significantly contributed to the core conceptual advances in biomedical research. This technology has provided valuable means for monitoring different biological processes for immunology, oncology, virology, and neuroscience. Bioluminescence imaging has also been successfully used to monitor infections caused by various microorganisms, particularly bacteria.

Though a few books are presently available on bioluminescence, a comprehensive volume dealing with the “Bioluminescent Marine Plankton ” has not so far been published. The first of its kind, this publication would answer this long-felt need. It deals with the chemistry of bioluminescence, types of bioluminescent displays, distribution of bioluminescence among marine plankton, ecological functions and uses/applications of planktonic bioluminescence; and the biology and ecology of about 200 species luminescent marine plankton of the different seas. It is hoped that the present publication, when brought out, would be of great use as a standard text-cum-reference for teachers, students, and researchers of various disciplines such as Marine Biology, Fisheries Science, and Environmental Sciences; and as a valuable reference for libraries of colleges and universities.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTEREST

The author declares no conflict of interest, financial or otherwise.

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Ramasamy Santhanam
Fisheries College and Research Institute
Tamil Nadu Veterinary and Animal Sciences University
Thoothukudi
India

CHAPTER 1

Introduction

Abstract: This chapter deals with the different types of luminescence: chemiluminescence, photoluminescence, fluorescence, phosphorescence, and bioluminescence; types of bioluminescence *viz.* extra cellular luminescence, intrinsic luminescence and extrinsic luminescence (bacterial luminescence); distribution of bioluminescence in different groups of marine plankton such as dinoflagellates, crustaceans, cnidarians, ctenophores and tunicates; biological functions of bioluminescence; interactions among luminescent marine zooplankton and fish; and commercial and therapeutic applications of bioluminescence.

Keywords: Applications of bioluminescence, Bioluminescent marine life, Cold living light, Extrinsic luminescence, Intrinsic luminescence.

The Greeks and Romans were the first to mention bioluminescent organisms, and Aristotle (384 – 332 BC) discovered self-luminosity in 180 marine species [1]. Bioluminescence, the cold living light, is a visible light produced by organisms. It is one form of chemiluminescence generated by a chemical reaction. Unlike fluorescence and phosphorescence, bioluminescence reactions do not need the initial absorption of sunlight by a molecule to emit light. A wide range of colours characterize bioluminescence. For example, it is blue in jellyfish, dinoflagellates, and ostracods; blue-green in bacteria and the limpet-like snail, *Latia*; and green-red in fireflies and railroad worms [2]. Some species of fungi are known to emit light continuously, and its glow is called foxfire. Most organisms, however, flash for periods of less than a second to about 10 seconds and these flashes occur in specific spots, such as the dots on a molluscan squid [3]. Bioluminescence has been reported to be very common in the water column of the ocean, less common on coral reefs and other places near the shore, rare on land, and nearly non-existent in freshwater (with the exception of a limpet-like freshwater snail, *Latia neritoides,* and a land snail, *Quantula striata*). The bioluminescence of the sea otherwise known as “cold fire of the sea” is present at all depths. It is estimated that 76% of the animals of the seas and oceans are bioluminescent. About 800 genera representing 13 phyla of marine animals are believed to be bioluminescent [4]. It is worth- mentioning here that for most of the well-known ocean glows, the dinoflagellate blooms are largely responsible.

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LUMINESCENCE AND ITS TYPES

Luminescence is the process of giving off light and is defined as any emission of light from a substance that does not arise from heating. There are many types of luminescence, *viz.* "Chemiluminescence" where a light emission is initiated by a chemical reaction; "photoluminescence " is the emission of light from a material following the absorption of light; "fluorescence" is prompt photoluminescence that occurs very shortly after photoexcitation of a substance; "phosphorescence" is long-lived photoluminescence that continues long after the photoexcitation has ceased; and "bioluminescence" is the production and emission of light by a living organism and it is otherwise known as "cold living light."

COLOURS OF BIOLUMINESCENT LIGHT

While most land organisms, including fireflies, glow in the yellow spectrum, almost all marine bioluminescence is blue due to two related reasons. Firstly, the blue-green light (wavelength around 470 nm) transmits furthest in water. Underwater photos are usually blue because water absorbs red light quickly as one descends. Secondly, most marine organisms are sensitive only to blue light, and they lack visual pigments that can absorb longer (yellow, red) or shorter (indigo, ultraviolet) wavelengths [5].

LIGHT EMISSION IN MARINE ANIMALS

While the bioluminescence of marine animals is invariably blue, the colour of the light can range from nearly violet to green-yellow (and very occasionally red), emitted in three different ways. In some species, the light is actually vomited from the animals. In other animals, the light is emitted by specialized cells called photocytes,sometimes grouped into lensed structures called photophores. On the other hand, some animals may have colonies of bioluminescent bacteria which glow continuously [6].

Types of Bioluminescence

Based on the source of illumination in marine animals, the luminescence may be classified as follows:

i. **Extracellular Luminescence**: In this type of luminescence, the light is generated by luminous secretion from the glandular tissues of animals. Extracellular luminescent organs are found in a very limited species of fish. For example, certain fish like rat tails emit light by secreting extracellular slime. These fish possess special glands near their anus, which secrete luminous slime sufficiently.

ii. **Intrinsic Luminescence (Intracellular Luminescence)**: In this type, light is produced intracellularly and the light is emitted by special cells called photocytes which form light producing photophores developed from the epidermis. This type of luminescence is mainly seen in teleost fish of the families, such as Sternoptychidae, Myctophidae, Halosauridae, Stomiatidae, Brotulidae, Lophiidae, and Zoarcidae.

iii. **Extrinsic Luminescence (Bacterial Luminescence**): In this type, symbiotic bacteria present in the photophores or luminous cells (photocytes) discharge light. The bacterial genera, Photobacterium and Achromobacterium, have been reported to contribute much to this type of luminescence. These bacterial species commonly found in dead fish or spoiling meat, have been isolated and grown in cultures.

Types of Bioluminescent Displays

Based on the appearance, the bioluminescent displays may be classified into three types *viz.* sheet type, spark type, and gloving-ball or globe type.

i. **Sheet-type Display**: This is the most common type in coastal waters and is caused by dinoflagellates or bacteria. It is also known as spilled or "milky" bioluminescence. During the formation of this type, the seawater is cloudy and may appear dully luminescent. The colour of the water is usually green or blue, and in many displays, it may also appear white when the organisms are present in great numbers *i.e*., during the bloom formation. Apart from the microscopic organisms, dense and extensive concentrations of large tunicate organisms, such as luminescent Pyrosoma (giving a flashing appearance during lower concentrations) or luminescent euphausiid species Nyctiphanes norvegica may also yield sheet-type display. The display of this euphausiid species was associated with large spots and long bands of milk-white water [7].

ii. **Spark-type Display:** This type of display is largely due to the appearance of large numbers of luminous euphausiids or copepods. This display occurs most often in colder waters and only when the waters are disturbed. The luminescence colour during this display is brilliant blue or white [7].

iii. **Glowing-ball- or Globe-type Display**: This display is normally observed in the warmer waters of the world. During this condition, the ocean may appear as full of balls or discs of light which may be flashing brightly when they are disturbed or dimming after the stoppage of the initial stimulus. Depending on the size of the luminescent organisms, the flashes of light may range in size from a few centimeters to a few meters in diameter. The colour of the light during this display is normally blue or green, and rarely it may be white, yellow, orange, or red. The light so emitted may rarely be continuous (Staples,1966). Combinations of either two or all three types of displays have

CHAPTER 2

Chemical Mechanism of Bioluminescence

Abstract: This chapter deals with the basic bioluminescence reactions, emission maxima, and colour of light in pelagic and deep-sea bioluminescent organisms, luciferins of planktonic organisms, types of intrinsic bioluminescence such as coelenterazine-based light production and cypridina luciferin-based light production, and extrinsic bioluminescence.

Keywords: Cypridina Luciferin, Emission Maxima, Extrinsic Bioluminescence, Intrinsic Bioluminescence Coelenterazine, Luciferin.

INTRODUCTION

In the seas and oceans, there is an amazing diversity of organisms that emit light, wherephytoplankton and zooplankton play a significant role in the ecology and food chain of these marine environments. While the bioluminescence chemistryis diverse an enzyme-mediated reaction between molecular oxygen and an organic substrate is vital in light emission. The different components of plankton occupying the surface, are presented in the chemical aspects of a major bioluminescence process.

Bioluminescence is considered a "cold light" (*i.e.* cold living light) which states that only a small percentage of this light contains heat, unlike the light produced by the sun's rays or fire (Tampier, 2017).

Luciferase

(A) Luciferin (substrate) + O_2 -------------------→ Oxyluciferin + CO_2 + hv (light)

(B) Photoprotein + Ca^{2++} ---------------→ Protein- coelenteramide *+ CO_2 = hv (light)

* = Protein-bound oxyluciferin

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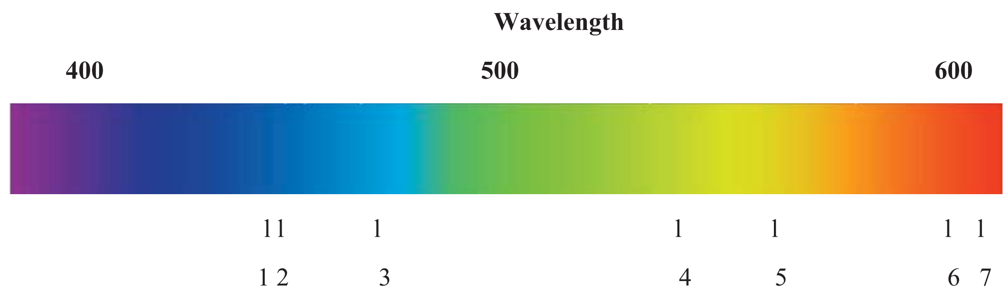
COLOURS OF BIOLUMINESCENCE

Light at shorter wavelengths, such as blue (400-500 nm) and green (500-600 nm), travels farther down in the ocean (deeper than 100 m). This may be why most marine organisms that emit blue or green lighthide in their surroundings. Further, marine organisms of coastal areas typically produce green light (490-520 nm), whereas the vast majority of pelagic and deep-sea bioluminescent organisms emit blue light with emission maxima (λ_{max}) ranging from 450 to 490 nm [21]. Unlike blue or green light, red light with wavelengths (600-700 nm) are absorbed quickly in the ocean *i.e.*, they travel across the shallower sea but fail to reach the deep-sea zone. Therefore, some deep-sea organisms use red pigmentations on their skin to make them invisible. Further, this red colouration helps deep-sea animals camouflage in the depths where they appear black and disappear into the darkness [22]. The spectral properties in terms of emission maxima of certain marine bioluminescent species are compared with that of terrestrial species in Fig. (**1**).



1. Copepod, *Gaussia princeps*; Wavelength, λ max 460 nm (Blue)
2. Ostracod, *Cypridina noctiluca*; Wavelength, λ max 465 nm (Blue)
3. Cnidarian, *Renilla renifromis* and Dinoflagellates; Wavelength, λ max 480 nm (Blue)
4. Euphausiid, *Thysanoëssa raschii*; Wavelength, λ max 540 nm (Green)
5. Arthropod firefly (terrestrial), *Photinus pyralis* ; Wavelength, λ max 560 nm (Green)
6. Fish, *Tripterygion delaisii*; Wavelength, 600 nm (Red)
7. Arthropod fire beetle (terrestrial), *Pyrophorus plagiophthalmus*; Wavelength, 613 nm (Red)

Fig. (1). Spectral properties of marine and terrestrial animals.

Emission Maxima of Marine Organisms

The values of the emission spectra of protozoans , zooplankton, and fishes measured are given in Table **1**. It is worth mentioning here that with few exceptions, emission maxima of these organisms ranged between 440 and 500 nm, in the blue region of the spectrum Table **1** [23].

Table 1. Emission maxima (λmax) values of marine organisms.

Phyla / Class	λmax (nm) range
Protozoa	443- 458
Cnidaria	444- 488
Ctenophora	478- 496
Annelida	565
Crustacea	444- 492
Mollusca	449 - 514
Tunicata	471, 493
Pisces	477 – 689

BIOLUMINESCENCE IN MARINE PLANKTON

Among all bioluminescent marine planktonic organisms, the cnidarians (formerly coelenterates) have been reported to give the brightest luminescence when they were mechanically stimulated. Further, the hydrozoan medusae and siphonophores of these cnidarians emitted at the shortest wavelengths, with emission maxima between 444 and 466nm. The siphonophore *Arnphicaryon* species showed peak emissions at longer wavelengths (maximum at 487nm; and the scyphozoan medusae had peak emissions at wavelengths between 450 and 480 nm. On the other hand, the longest wavelength emissions for the ctenophores, had an emission maxima between 480 and 490 nm. It is also reported that light emission in cnidarians was intracellular, except for the scyphomedusa, *Chrysaora hysosceles*, which produced a luminescent slime. Besides the siphonophores, other short-wavelength emitters are colonial radiolarians which had an emission maxima ranging from 440 to 460 nm. Euphausiids showed narrow bandwidth and the mean observed emission maximum was 461 nm, with shoulders at about 485 and 505 nm. Copepods and ostracods were found to show secreted bioluminescence with emission maxima ranging from 470 to 490 nm. The pelagic polychaete, *Tomopteris nisseni* was found to produce yellow light of intracellular origin within its parapodia and had maximum emission at 565 nm. In some of these organisms both mechanical and electrical stimulations were found to induce luminescence [23]. The groups of planktonic organisms possessing luciferin are shown in Table **2**.

Luciferins

The first luciferin (from the Latin lucifer, “light-bearer”), the vital evidence for our understanding of today’s bioluminescence was isolated by Green and McElroy in 1956 [25]. There are five known distinct chemical classes of luciferins

CHAPTER 3

Bioluminescent Marine Dinoflagellates

Abstract: This chapter deals with the identified luminescent species of marine dinoflagellates and their description, emission maxima, total stimulable luminescence (TSL) in observed species of dinoflagellates. and their mechanism of bioluminescence.

Keywords: Dinoflagellates, Emission maxima, HABs, Seafood poisoning, Tetrapyrrole luciferin, TSL.

INTRODUCTION

If one sees luminous sparkles in the wake of a boat or in splashing waves on the beach, they are mostly from the dinoflagellates, an important component of marine phytoplankton. Indeed, these dinoflagellates are responsible for most of the bioluminescence observed on the ocean's surface and are known to occur globally. They are very abundant during red tides and are believed to use their light as a burglar alarm to attract predators to animals grazing on them. Though these dinoflagellates play an important role in the food chain of marine ecosystems, the ecological importance of their bioluminescence is highlighted in this chapter.

The dinoflagellates or fire algae are members of phytoplankton and are generally yellow-brown in color. Typically these organisms contain some photosynthetic and possess two different flagella, which are ribbon-shaped. Of about 2000 known species of dinoflagellates, 1,555 (90%) free-living species are found in the seas and oceans. These dinoflagellates are mostly microscopic ranging from 15 to 40 microns. The largest species *Noctiluca scintillans* (sea sparkle, sea ghost, or fire of the sea), may have a size of about 2 mm in diameter. Several species of marine dinoflagellates have been reported to cause harmful algal blooms (HABs) like anoxia red tides, believed to cause direct effects on fish in oceans worldwide, by damaging their gills or by promoting low dissolved-oxygen concentrations. Further, these red tides may also negatively effect the economy and human health. Seafood poisoning in humans is invariably caused by consuming toxin-containing seafood contaminated with marine dinoflagellates. According to the species of

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toxigenic dinoflagellates, the poisoning syndromes are named as paralytic (PSP), diarrhetic (DSP), neurotoxic (NSP), azaspiracid shellfish poisoning (AZP) and ciguatera fish poisoning (CFP). Besides these well-known poisoning types, new dinoflagellate toxins, such as yessotoxin (YTX) and palytoxin (PTX), have also been reported from certain species of marine dinoflagellates [14, 37].

BIOLUMINESCENCE IN DINOFLAGELLATES

One of the fascinating characteristics of the marine dinoflagellate is that they can produce and emit blue light during night hours in response to mechanical stimulation, which may even be the turbulence produced by a small air bubble popping. The intracellular bioluminescence of these dinoflagellates is due to its tetrapyrrole luciferin, which is enzymatically oxidized in the presence of dinoflagellate luciferase [38]. Bioluminescence has been reported in 81 species (Table **1**) of 18 dinoflagellate genera [13] and the emission of light is very common among the species of *Alexandrium* such as *Alexandrium affine, Alexandrium acatenella, Alexandrium catenella, Alexandrium fundyense, Alexandrium tamarense, Alexandrium monillatum, Alexandrium ostenfeldii* and *Alexandrium fraterculus*. In these dinoflagellate species, the capacity for bioluminescence is said to remain almost constant throughout the night and is completely restored in 1 hour after exhaustive stimulation [39]. The values of total stimulable luminescence in these dinoflagellates have been reported to range from 10^7 to10^{10} photons per cell [40]. These dinoflagellates are very sensitive to motion induced by ships or fish-like organisms, and they are said to respond with rapid brilliant flashes, and the glow (Fig. **1**) thus caused is sometimes seen in the wake of a ship.

Table 1. Bioluminescent marine dinoflagellates [13].

Class	Order	Family	Species
Dinophyceae	Prorocentrales	Prorocentraceae	*Prorocentrum micans*
-	Gymnodiniales	Gymnodiniaceae	*Gymnodinium flavum*, G.sanguineum
-	-	Polykrikaceae	*Polykrikos kofoidii,, P. schwartzii*
-	Noctilucales	Noctilucaceae	*Noctiluca scintillans`*
-	Pyrocystales	Pyrocystaceae	*Dissodinium pseudolunula, Pyrocystis acuta, P.lunula,P.fusiformis,P.noctiluca*
-	Peridiniales	Pyrophacaceae	*Fragilidium heterolobum, Pyrophacus horologium*
-	-	Ceratocorythaceae	*Ceratocorys horrida*
-	-	Ceratiaceae	*Ceratium furca, C.candelabrum,C.furca,C.fusus,C.gibberum,C.horridum, C.lunula, C.tripos*

(Table 1) cont.....

Class	Order	Family	Species
-	-	Goniodomataceae	*Alexandrium acatenella,A.catenella, A.fraterculus, A.monilatum, A.ostenfeldii, A.tamarense, Pyrodinium bahamense, Triadinium polyedricum*
-	-	Gonyaulacaceae	*Gonyaulax digitali, G.excavta, G. grindleyi, G.hyalina, G. monacantha, G.monilata, G.parva, G.polygramma, G. scrippsae, G. sphaeroida, G.spinifera, Lingulodinium polyedrum, Peridiniella catenate*
-	-	Peridiniaceae	*Glenodinium sp., Protoperidinium antarcticum, P,bipes, P.brevipes, P.pyrifore, P.brochii, P.creasus, P.claudicans, P.conicoides, P.conicus, P.curtipes, P.crassipes, P.depressum, P.divergens, P.elegans, P.eugrammum, P.excentricum, P.exiquipes, P.globulum, P.granii, P. heteracanthus,P.huberi, P. leonis, P.minutum, P.nudus, P.oceanicum, P.ovatum, P.pacificum, P.pallidum, P.pellucidum, P.pentagonum, P. punctulatum, P.pyriforme, P.saltans, P.seta, P. punctulatum,P.sournia, P. steinii, P. subinerme, P. thulesense, P.tubum*

Fig. (1). Bioluminescence due to dinoflagellates. Image credit: Josh Myers, Florida Adventure (Reproduced with permission).

CHAPTER 4

Bioluminescent Marine Radiolarians

Abstract: This chapter deals with the identified luminescent species of marine, colonial radiolarians, emission maxima in observed species of marine radiolarians, the description of luminescent marine radiolarian species and their mechanism of bioluminescence.

Keywords: Colonial radiolarians, Emission maxima, Stimulated bioluminescence.

INTRODUCTION

Radiolarians (single-celled marine protists), the members of silica-secreting zooplankton, are like amoebae living in glass houses and are common in shallow oceanic gyres of deep oceans worldwide. However, some species are limited to certain regions and serve as temperature, salinity, and total biological productivity indicators. The skeletal remains of some radiolarians make up a fairly large part of the cover of the ocean floor as siliceous ooze. It is interesting to note that these organisms use calcium-activated photoproteins much like hydromedusae in their bioluminescence. Radiolarians that inhabit great depths in the water column where light is limited or absent typically lack algal symbionts.

Radiolarians (Phylum: Protozoa) are incredibly diverse in their skeletons, ranging from spherical to rod-shaped and radial to bilaterally symmetrical. Their cytoplasmic mass is divided into two regions separated by a perforated membrane. The first of these regions is the central mass or the central capsule, and the second is the extracapsulum, a peripheral layer of cytoplasm surrounding the central capsule. The central capsule contains the organelles such as the mitochondria and vacuoles, while the extracapsulum is characterized by its thread-like extensions of the cytoplasm, *i.e.*, the rhizopodia. It is reported that both the solitary and colonial species of radiolarians can produce light with multiple flashes [38]. A total of 9 taxa of radiolarians (Table **1**) have been reported to possess the characteristic, bioluminescence which is largely due to the mechanical stimuli and their luciferin (coelenterazine) and Ca^{2+-} activated photoprotein [27]. Light emission in these organisms is deep blue with peak

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emissions between 443 and 456 nm wavelengths. Single flashes are 1–2 seconds in duration with species-dependent flash kinetics. Colonies of different species (even families) may display different flash kinetics. The quantal content of single flashes averaged 1×10^9 photons flash-1, and the colonies have shown prolonged light emission. The mean value of bioluminescence potential in these luminescent radiolarians based on total mechanically stimulated bioluminescence has been reported to be 1.2×10^{11} photons colony-1. It is also estimated that colonial radiolaria have the capacity to produce $\approx 2.8 \times 10^{12}$ photons $\cdot$ m^{-2} of sea surface [53].

Table 1. Bioluminescent marine radiolarians [13].

Class	Order	Family	Species
Radiolaria	Phaeogromia	Tuscaroridae	*Tuscaridium cygneum*
-	Spumellarida	Thalassicolidae	*Thalassicola nucleata, Thaiassicolla sp.*
-	-	Thalassothamnidae	*Cytocladus major*
-	-	Sphaerozoidae	*Rhaphidozoum acuferum*
-	-	Collosphaeridae	*Acrosphaera murrayana*, *Collosphaera huxleyi,* Myxosphaera coerulea, *Siphonosphaera tenera*,
-	Phaeosphaerida	Aulosphaeridae	*Aulosphaera triodon*

Emission Maxima in Luminescent Marine Radiolarians

The emission maxima (λmax) of the different species of luminescent marine radiolarians have been reported to vary from 443 to 458 nm (Table **2**).

Table 2. Emission maxima (λmax) of luminescent marine radiolarians.

Species	λmax (nm)	Ref
Acrosphaera murrayana	443 nm	[23]
Collosphaera huxleyi	456 nm	[23]
Collosphaera spp.	443, 445, 452 nm	[23]
Myxosphaera coerulea	453 nm	[23]
Rhaphidozoum acuferum	458 nm	[23]
Siphonosphaera tenera	450 nm	[23]
Thalassicola nucleata	446 nm	[54]
Thaiassicolla sp.	450nm	[10]

LUMINESCENT MARINE RADIOLARIANS

Acrosphaera murrayana

The shell of this luminescent species (Fig. **1**) is spherical, with large circular or roundish pores of unequal size. Ten to twelve pores are seen in the half meridian of the shell. The margin of every pore is with a coronal of six to nine short and acute spines. No spines are present between the pores. Shell diameter varies from 70 to 190 µm.

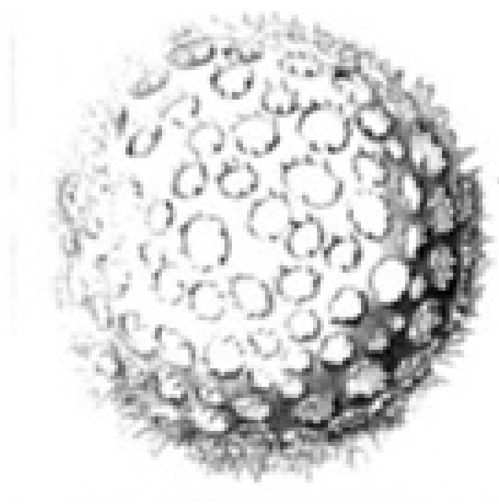

Fig. (1). *Acrosphaera murrayana*. Image credit: Wikipedia

Aulosphaera triodon

The shell of this luminescent species is spheroidal to ellipsoidal with triangular (sometimes square) mesh openings. Its radial tubes are generally smooth and are with 2-4 (rarely 3, seldom 4) straight or slightly curved terminal branches. The diameter of the shell varies from 1.2 to 4.0 mm.

Collosphaera huxleyi

The shells of this luminescent species (Fig. **2**) have small to medium-sized pores that are scattered about the surface only. There are no spines or tubes. The shell diameter varies from 80 to 150 µm.

CHAPTER 5

Bioluminescent Marine Cnidarians

Abstract: This chapter deals with the total luminescent fauna of planktonic hydrozoa and scyphozoa, emission maxima in observed species of planktonic hydrozoa and scyphozoa, the description of luminescent marine species of planktonic hydrozoa and scyphozoa and their mechanism of bioluminescence.

Keywords: Emission maxima, Luminescent hydrozoan medusae, Luminescent scyphozoan medusae, Luminescent siphonophores.

INTRODUCTION

Cnidarians which include four main groups *viz.* the almost wholly sessile Anthozoa (sea anemones, corals, sea pens), swimming Scyphozoa (jellyfish), Cubozoa (box jellies), and Hydrozoa (that includes all the freshwater cnidarians), as well as many other marine forms. They were all formerly grouped with ctenophores under the common phylum *viz.* Coelenterata, but their differences in morphology and biology caused them to be placed in a separate phylum *i.e.*, Cnidaria, which was recognized in 2007. Cnidarians are mostly predators, but certain species may also scavenge dead animals or obtain nourishment from intracellular, photosynthetic unicellular algae, called zooxanthellae. Among the cnidarians, several species are venomous, causing human mortalities worldwide. Bioluminescence as a common phenomenon has also been widespread in cnidarians. This chapter deals with the biology and ecology of bioluminescent cnidarians.

All members of the phylum Cnidaria (formerly Coelenterata) are radially symmetrical with a two-layered body made up ofan ectoderm and an endoderm. The three classes of this phylum consist of the Hydrozoa in which the animals have a lifecycle with two phases *viz.* a sessile polyp phase and a free-floating medusoid stage, the class Scyphozoa which includes the medusae thatonly have the medusoid stage in their life cycle, and the class Anthozoa in which the animals are non-planktonic and only have a polyp stage in their life cycle.

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Hydromedusae: Generally, the hydromedusae are small, and they are either transparent or lightly pigmented, although some of the deep-sea species are dark red in coloration. Hydromedusae are often common in coastal habitats but they are usually believed to be seasonal. Most coastal hydromedusae are asexually budded off their single-sexed parent hydroids. Each hydroid colony that produces medusae generates only male or female medusae, but not both. The female or male medusae then produce eggs and sperm free-spawned into the sea; the fertilized eggs develop into new hydroids, which are usually benthic (bottom-living). The hydromedusae, therefore, represent only part of the life cycle of each animal. Some open ocean hydromedusae also have hydroids, which may live deep on the sea floor, but some of these oceanic hydroids have found highly specialized substrates to live on, such as little floating clumps of algae, the skin of fishes, or the shells of pelagic snails. Other hydromedusae (typically oceanic or deep water species) do not have a hydroid but have a life cycle in which the fertilized eggs produced by medusae instead develop directly into the next generation of medusae. Such species are sometimes described as "holoplanktonic" carrying out their entire life cycle in the plankton.

Siphonophores: These polymorphic planktonic marine cnidarians inhabit the deep pelagic ocean at depths from ~200 m to the abyssal seafloor (>4,000 m). A typical siphonophore consists of a pneumatophore, nectosome (with nectophores) and siphosome (with its constituents such as bract, gonodendron, tentaculozooid and gastrozooid) . Each loop of the siphosome is called cormidium. Siphonophore colonies have a modular body plan with different zooids performing different functions. Some species of siphonophores have elaboratefluorescent or bioluminescent lures to attract prey.

BIOLUMINESCENT MARINE HYDROZOAN MEDUSAE AND SIPHONOPHORES

A total of about 80 species of hydrozoans are listed below in Table **1**. Both hydrozoan medusae and siphonophores have been reported to be luminescent [13]. In all the planktonic cnidarians, bioluminescence is due to their imidazolopyrazine (coelenterazine) and Ca^{2+-} activated photoprotein. Light production in these organisms is limited to the blue-green wavelengths *i.e.* from 440 to 506 nm. Further, no significant difference has been reported in the mean wavelength between scyphomedusae (474.0 nm) and hydromedusae (473.7 nm). All the luminous hydrozoans possess a photoprotein system of light production (where the luciferin is coelenterazine) *e.g.* obelin in *Obelia geniculata* and clytin in *Clytia hemisphaerica*. As all bioluminescent hydrozoans are believed to possess green fluorescent protein (GFP) in their photocytes, their bioluminescent flash is green [27]. The mean emission max for all the observed species of hydromedusa was found to be 473.8 nm (range 443 - 505 nm). Among the hydromedusae, the four shortest-wavelength species were found to be the Trachymedusae of the family Halicreidae. On the other hand, the longest-wavelength medusae are Leptomedusae such as the common and well-known, *Aequorea forskalea* and *Phialidium (=Clytia) hemisphaerica,* which bear GFP. Narcomedusae such as *Aegina citrea* and *Solmissus* spp. produced intermediate luminescence spectra, with emission max between 460 and 478 nm [57]. The siphonophore spectra were found distributed bimodally with modes centered at 450.5 nm and at 486 nm (range 442 - 500 nm). The light from deep-dwelling siphonophore species showed significantly shorter wavelengths than light from shallow species as in the case of the medusae [57]. Among the siphonophores, the shortest wavelengths have been recorded from the species of *Apolemia* and *Bargmannia*, whereas the light with the longest wavelength was from the epipelagic *Muggiaea* sp. Further, in the siphonophores, there was no significant relation between luminescence and species. For example calycophorans and physonects are more or less equally well represented by species of short and long wavelengths . Three species of siphonophores, *Abylopsis tetragona, Bargmannia elongata,* and *Frillagalma vityazi*, were observed to produce multiple colors of luminescence. In *Abylopsis tetragona*, a major peak with 489 nm, and a secondary peak at 450 nm have been recorded. *Vogtia glabra* produced a unimodal emission with an emission max near 450 nm. It is worth noting that the posterior end of some species of siphonophores produced predominantly green light while the anterior end produced more blue light [57].

Table 1. Bioluminescent marine cnidarians: Hydrozoan medusae and siphonophores [13]

Class	Order	Family	Species
Hydrozoa	Hydroida	Tubulariidae	*Euphysora valdiviae*
-	-	Bougainvilliidae	*Bougainvillia carolinensis*
-	-	Calycopsida	*Bythotiara depressa*
-	-	Pandeidae	*Leuckartiara octona, Pandea conica*
-	-	Mitrocomidae	*Cosmetira pilosella, Halistaura cellularia, Halopsis ocellata, Mitrocoma cellularia, Mitrocomella polydiademata*
-	-	Campanulariida	*Obelia lucifera, Phialidium (=Clytia) hemisphaerica, Phialidium gregarium*
-	-	Aequoreidae	*Aequorea forskalea, Aequorea macrodactyla, Aequorea victoria, Aequorea vitrina*
-	-	Phialuciidae	*Octophialucium funerarium*
-	-	Eutimidae	*Eutonina indicans, Tima bairdi, Tima saghalinensis*

CHAPTER 6

Bioluminescent Ctenophores

Abstract: This chapter deals with the total luminescent fauna of the phylum, Ctenophora,; the emission maxima in observed species of ctenophores, the description of luminescent species of ctenophores, and their mechanism of bioluminescence.

Keywords: Emission maxima, Luminescent nudans, Luminescent tentaculates.

INTRODUCTION

Ctenophores or comb jellies which are probably common members of the zooplankton are presently classified under a separate phylum *viz*. Ctenophora. The latter once formed a major component of the erstwhile phylum Coelenterata. Ctenophores are exclusively marine, and they can be found in most marine habitats, from polar to tropical, inshore to offshore, and from near the surface to the very deep ocean. They are characterized by their eight rows of cilia, which are mainly used for locomotion. These organisms may be seasonally much more abundant in the spring and early summer. Almost all ctenophores are bioluminescent, with the exception of the sea-gooseberry, *Pleurobrachia*, and some benthic species. Like hydrozoans, these comb jellies use photoproteins with coelenterazine to make light. Some species secrete luminous material into the water when they are disturbed. Though there are about 100-150 species of ctenophores throughout the world's oceans, the existing information on about 50 species of bioluminescent ctenophores is scanty [87]. The present topic deals with the biology and ecology of common bioluminescent species of ctenophores.Coastal ctenophores: The common coastal ctenophore representatives of the order Cydippida are round or oblong in shape and are usually below 3 cm in diameter. These ctenophores are distinguished by their more or less solid bodies, eight radial comb rows, which are helpful in their locomotion, and two-branched tentacles for capturing small planktonic prey. The most common cydippid ctenophore species, distributed worldwide are the non-luminescent species of the genus *Pleurobrachia* andthe most common luminescent representatives of the order, Lobata include the species of the genera *Bolinopsis* and *Mnemiopsis*.

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Oceanic ctenophores: Many species of ctenophores are found only far offshore near the surface, mid-water, or in the deep sea. Unlike the coastal ctenophores, oceanic ctenophores are much more fragile because they do not need to tolerate heavy wave action or the sediment load of coastal waters. Notable species of open ocean near-surface ctenophores include the Venus' girdle, *Cestum veneri*s and the lesser known species include that of *Ocyropsis*.

Bioluminescence in ctenophores: Among the ctenophores, 31 species have been reported to be luminescent (Table **1**). In luminescent ctenophores, both luciferin (coelenterazine) and Ca^{2+-} activated photoprotein are present [27]. One of the most important characteristics of ctenophores is their light-scattering produced by beating the eight ctenes (comb rows) of locomotory cilia. This light scattering appears as a changing rainbow of colors running down the comb rows and this is simple light diffraction or scattering of light by the moving cilia. Several species of ctenophores are also bioluminescent, but their light (usually blue or green) can only be seen in darkness. This bioluminescence is invariably caused by activating the calcium-activated proteins called photoproteins in cells called photocytes, which are normally confined to the meridional canals that underlie the eight comb rows. Species averages of maximal wavelengths for these ctenophores ranged from 440 to 506 nm. Deep-dwelling ctenophores produce light with shorter wavelengths compared to shallow-dwellers [57].

Table 1. Bioluminescent ctenophores [13].

Class	Order	Family	Species
Tentaculata	Cydippida	Haeckeliidae	*Aulacoctena acuminata, Haeckelia beehleri, H. bimaculate,H.rubra*
-	-	Bathyctenidae	*Bathyctena chuni*
-	-	Lampeidae	*Lampea lactea, L. pancerina*
-	-	Pleurobrachiidae	*Hormiphora luminosa*
-	-	Incertae Sedis	*Tizardia phosphorea*
-	-	Euplokamidae	*Euplokamis stationis*
-	-	Mertensiidae	*Charistephane fugiens, Mertensia ovum*
-	Thalassocalycida	Thalassocalycidae	*Thalassocalyce inconstans*
-	Lobata	Bathocyroidae	*Bathocyroe fosteri*
-	-	Bolinopsidae	*Bolinopsis infundibulum, B.vitrea, Mnemiopsis leidyi*
-	-	Eurhamphaeidae	*Deiopea kaloktenota, Eurhamphaea vexilligera, Kiyohimea aurita*
-	-	Leucotheidae	*Leucothea multicornis, L. pulchra*
-	-	Ocyropsidae	*Ocyropsis maculata immaculata, O.fusca*

(Table 1) cont.....

Class	Order	Family	Species
-	Cestida.	Cestidae	*Cestum veneris, Velamen parallelum*
Nuda	Beroida	Beroidae	*Beroe abyssicola, B. cucumis, B. forskalii, B.gracilis, B.ovata*

Emission maxima in luminescent ctenophores: The emission maxima (λmax) of the different species of marine hydrozoan medusae and siphonophores have been reported to vary from 443 to 550 nm (Table **2**).

Table 2. Emission maxima (λmax) of luminous ctenophores.

Species	λmax	Ref
Aulacoctena acuminata	458nm	[57]
Bathocyroe fosteri	459 to 492nm	[57]
Bathyctena chuni	492 nm	[57]
Bathyctena spp.	488,490nm	[13]
Beroe abyssicola	491nm	[57]
Beroe cucumis	489nm	[57]
Beroe forskalii	491nm	[57]
Beroe gracilis	495nm	[88]
Beroe ovata	493nm	[57]
-	494,500nm	[10]
Bolinopsis infundibulum	488nm	[57]
-	505nm	[10]
Bolinopsis vitrea	490nm	[57]
Cestum veneris	493nm	[57]
-	490 nm	[23]
Charistephane fugiens	468nm	[57]
Clytia bakeri	508nm	[10]
Clytia edwardsi	508nm	[10]
Clytia hemisphaerica	504nm	[57]
Clytia gregaria	460, 494 nm	[60]
Deiopea kaloktenota	489nm	[57]
Euplokamis stationis	467 nm	[13]
Euplokamis sp.	483nm	[57]
Eurhamphaea vexilligera	496nm	[57]
Haeckelia beehleri	500nm	[57]

CHAPTER 7

Bioluminescent Planktonic Marine Annelids

Abstract: This chapter deals with the luminescent species of planktonic annelids such as *Tomopteris* spp and syllid larva, the emission maxima in observed species of *Tomopteris*, the description of luminescent species of planktonic annelids and their mechanism of bioluminescence.

Keywords: *Chaetopterus*, Emission maxima, *Tomopteris*.

INTRODUCTION

The annelids (also called “ringed worms”) (Phylum: Annelida) are segmented worms, with about 17,000 species, including polychaetes, clitellates, ragworms, earthworms, and leeches. They are found in marine environments from tidal zones to hydrothermal vents, in freshwater, and in moist terrestrial environments. Among the 13 known families of annelids, eight of which are marine, with both benthic and pelagic animals producing bioluminescence. These eight marine families include the well-studied, charismatic, displays from Chaetopteridae, Tomopteridae, and Syllidae. Some notable examples are the benthic “fireworms”(*Hermodice* spp) which use luminescence as part of their mating display, and planktonic *Tomopteris*, which makes yellow light. On land, some oligochaetes (earthworms) produce luminous secretions. Among the marine polychaetes, the species of *Alciopina* and *Rhynchonereella* (Alciopidae), *Tomopteris* (Tomopteridae), *Chaetopterus* (Chaetopteridae), *Poeobius* (Flabelligeridae) and larvae of *Odontosyllis* (Syllidae) are the planktonic, luminescent marine organisms. However, the luciferin and luciferase of the benthic adult fireworm *Odontosyllis* have only been identified and purified though the light emission process within annelids and seems to be distinct in each family. Among the wide range of taxa, annelid bioluminescence in general and planktonic annelid bioluminescence is one of the least studied. This chapter deals with the findings relating to planktonic, luminescent annelids.

Of the holopelagic polychaete families of the phylum Annelida, only 13 species have been reported to be luminescent (Table **1**). Of these species, the members of

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Tomopteridae are well-known. Most of these tomopterids are known to produce a golden yellow bioluminescent light under nervous control,b species that emit blue light have also been reported in this family [98]. Though photogenic organs have not been reported in the Alciopidae, some species of this family have been reported to be luminescent. In general, the structure and function of the photogenic organs and the associated luminescent products are incompletely known in these pelagic polychaetes [99].

Table 1. Bioluminescent planktonic annelids [13]

Class	Order	Family	Species
Polychaeta	Phyllodocida	Alciopidae	*Alciopina* sp., *Rhynchonereella* sp.
-	-	Syllidae	*Odontosyllis* sp. (larva)
-	-	Tomopteridae	*Tomopteris pacifica, T.carpenteri, T.helgolandica, T.nisseni, T. septentrionalis, T.planktonis, T.mariana, T.nationalis*
-	Spionida	Chaetopteridae	*Chaetopterus pugaporcinus*
-	Terebellida	Flabelligeridae	*Poeobius meseres*

Bioluminescence in tomopterids: The holoplanktonic tomopterids (Annelida: Polychaeta) have a maximum size of 10 cm and are found distributed worldwide from the near-shore waters to about 3000 meters in depth. A total of twelve species of *Tomopterisviz.*: *Tomopteris anadyomene, Tomopteris apsteini, Tomopteris elegans, Tomopteris helgolandica, Tomopteris kefersteini, Tomopteris krampi, Tomopteris mariana, Tomopteris nationalis, Tomopteris nisseni, Tomopteris planktonis, Tomopteris rolasi,* and *Tomopteris septentrionalis* have been reported topossess photogenic organs in their parapodial glands and emit golden-yellow colored light (Fig. **1**) with an emission maximum (λmax) of 565-570 nm. In the yellow-colored light emitting system of these animals, a photoprotein probably activated by superoxide anion is believed to be involved. Further, the presence of cœlenterazine (28 pmol in one specimen) and a fluorescent emitter has also been documented from the tissue homogenates of these tomopterids. The bioluminescent system components of tomopterids have also been reported to be Aloe-emodin/luciferase . Although the luminescence of these tomopterids was thought to be intracellular, a secretory activity has also been suggested in several species of *Tomopteris* which release the luminous exudate while trying to escape from a collecting device [21]. It is reported that the luminescence emission of polychaetes is due to the oxidation reaction of luciferin and oxygen catalyzed by the enzyme luciferase or species-specific protein [100].

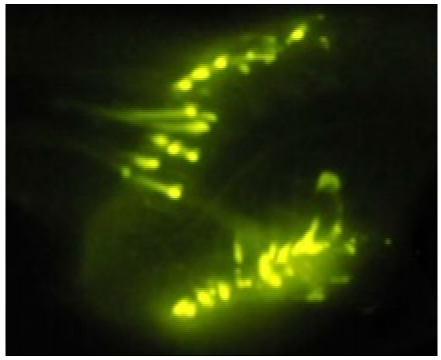

Fig. (1). Yellow light produced by *Tomopteris* spp.

Image credit: The Oceanography Society (Reproduced with permission)

Emission maxima in luminescent marine planktonic annelids: The emission maxima (λmax) of the different species of luminescent marine planktonic annelids have been reported to vary from 450 to 574 nm (Table **2**).

Table 2. Emission maxima (λmax) of luminescent planktonic marine annelids.

Species	λmax	Refs.
Tomopteris carpenteri	565-570nm	[21]
-	574nm	[98]
Tomopteris helgolandica	565-570 nm	[21]
-	573nm	[98]
Tomopteris nationalis	550, 570nm	[102]
Tomopteris nisseni	565nm	[98]
Tomopteris pacifica	565-570 nm	[21]
-	549nm	[98]
Tomopteris planktonis	450 nm	[21]
Tomopteris septentrionalis	565-570 nm	[21]
-	557nm	[98]
Tomopteris spp.	565nm	[98]
-	493nm	[98]
Poeobius meseres	495nm	[101]

CHAPTER 8

Bioluminescent Chaetognaths

Abstract: This chapter deals with the luminescent species of Chaetognatha *viz*. *Caecosagitta macrocephala* and *Eukrohnia fowleri*,their emission maxima and mechanism of bioluminescence.

Keywords: *Caecosagitta macrocephala*, Emission maxima, *Eukrohnia fowleri*.

INTRODUCTION

The phylum Chaetognatha, commonly known as arrow worms, contains about 200 species and about 80% of them are planktonic, bilaterally symmetrical, coelomate and worm-like organisms. Chaetognaths may be found in all marine environments, from tropical surface waters and shallow tide pools to the deep sea and polar regions. While most chaetognaths are transparent and torpedo-shaped, some deep-sea species are orange. Among the arrow worms, very few species like *Caecosagitta macrocephala* and *Eukrohnia fowleri* have been reported to be luminescent by using the luciferin coelenterazine to make their light. This chapter deals with such luminescent species of chaetognaths and their light emission associated with luciferin–luciferase reaction.

The phylum Chaetognatha (meaning bristle-jaws) are commonly known as arrow worms. These marine planktonic organisms are distributed worldwide and are found in all marine environments from surface tropical waters to the deep sea and polar regions. Most chaetognaths are transparent and are torpedo-shaped, but some deep-sea species are orange. They range in size from 2 to 120 millimetres. Though there are more than 120 modern species of Chaetognatha, only two species *viz*. *Caecosagitta macrocephala* and *Eukrohnia fowleri* are known to luminescent. In these species, the bioluminescent organs are present on their fins. These chaetognatha use luciferase and coelenterazine to shed light during an escaping response [107].

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Caecosagitta macrocephala

Image credit: WoRMS

This deep-sea (200 - 5000 m) luminescent species (Fig. **1**) has a cosmopolitan distribution and is commonly seen in the north-western Pacific and the centre-east of southern Atlantic Oceans. It has been reported to have a very wide distribution that ranges from the Subantarctic to the Subarctic Ocean. It has a large head. Along with its eyes, its gut or intestine has orange pigmentation and a luminous organ that flashes light due to bioluminescence, unlike other species of Sagittidae. Its body length may range from 16 to 22 mm. Its hooks and teeth are deep browns. It is worth mentioning that the individuals living near the bottom may be morphologically slightly different from those in the upper water column. Animals of the latter may possess foamy collarette on the entire body, long anterior fins and no traces of eyes.

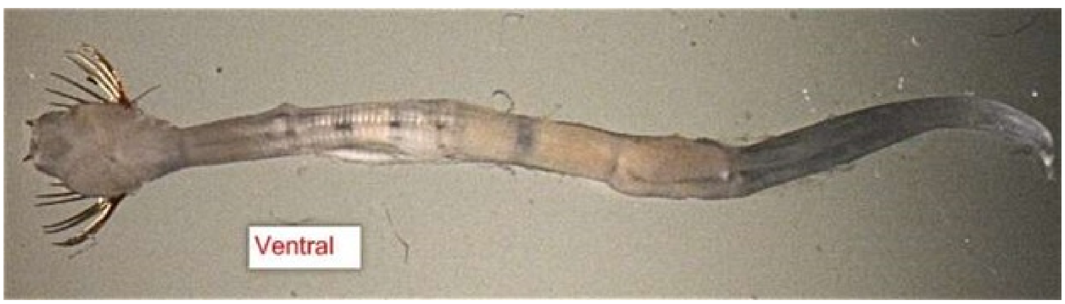

Fig. (1). *Caecosagitta macrocephala*.

Eukrohnia fowleri

Image not available

It is a bathy or mesopelagic oceanic species found mainly below 700 meters throughout the world. The body of this species is firm and broad with a large head . It has partially rayed long fins that originate at the level of the ventral ganglion. The alimentary diverticula are absent,the gut is usually reddish, and the eyes are provided with triangular pigment spots. The animals are brown in coloration with straight tips. There are 2-31 teeth, with short and broad ovaries, large and ovoid seminal vesicles, and a maximum body length of 4 cm.

Bioluminescence: In these species, their bioluminescence is based on a coelenterazine-luciferase reaction [13]. The luminescent organ of *Caecosagitta macrocephala* (Fig. **2**) is located on the ventral edge of each anterior lateral fin, whereas that of *Eukrohnia fowleri* (Fig. **3**) runs across the center of the tail fin on both dorsal and ventral sides [108]. Further, they reported that the bioluminescent organs of both species consisted of hexagonal chambers containing elongated ovoid particles called the organelles, which are believed to hold bioluminescent materials. The transmission electron microscopy of these particles from *Caecosagitta macrocephala* revealed a densely packed paracrystalline matrix punctuated by globular inclusions, which seemed to correspond to luciferin and luciferase, respectively. Further, both species used unique luciferases in conjunction with coelenterazine for light emission. While the luciferase of *Caecosagitta macrocephala* became inactive after 30 minutes, luciferase of E. fowleri was found to be highly stable. Although *Caecosagitta macrocephala* had about 90 times fewer particles than *Eukrohnia fowleri*, it had a more or less similar bioluminescent capacity (total particle volume) due to its larger particle size. *In situ* observations of *Caecosagitta macrocephala* revealed that the released luminous particles formed a cloud.

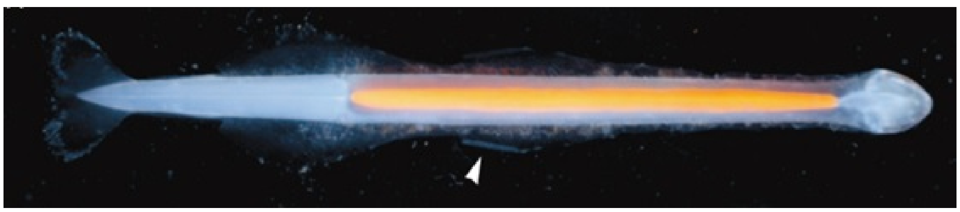

Fig. (2). Bioluminescent organ of *Caecosagitta macrocephala* (arrow-locating).

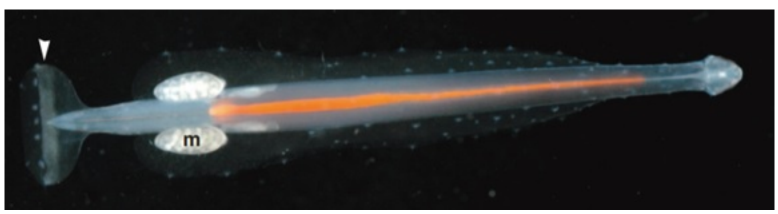

Fig. (3). Bioluminescent organ of *Eukrohnia fowleri* (arrow-locating). Image credit: Erik V. Thuesen, Ph.D. (Reproduced with permission)

CONCLUSION

The functional mechanics of light emission in chaetognaths remain largely unknown. Although the photocytes of luminous organs are stimulated to luminescence by nervous conduction in other organisms, the luminescence mechanism in these chaetognaths is unique in the fact that these photocytes will flash and glow even once they detached from the chaetognath. It indicates that these photo particles are passively disrupted when exposed to seawater. Further, intensive research on the diversity of luminescent chaetognaths and the characterization of the novel luciferases from these chaetognath species will thereforebe a fascinating glimpse into the evolution of coelenterazine-based bioluminescence.

CHAPTER 9

Bioluminescent Marine Crustaceans

Abstract: This chapter deals with the luminescent species of planktonic marine crustaceans such as ostracods, copepods, amphipods, mysids, euphausiids and decapods; and their emission maxima and mechanism of bioluminescence.

Keywords: Amphipods, Copepods, Emission maxima, Euphausiids, *Lucifer*, Mysids, Ostracods.

INTRODUCTION

Marine crustaceans form a very diverse group of invertebrate animals including planktonic members such as krill, copepods, amphipods, nektonic lobsters,shrimp, benthic crabs and more sessile creatures like barnacles. These crustaceans play a key role as an important source of nutrition for a wide range of marine vertebrates such as fish, birds and mammals (seals, whales). Most planktonic crustacean groups (with the exception of isopods) such as copepods, ostracods, amphipods, decapod shrimp and euphausiids (krill) possess luminous members. Uniquely, three of the major marine luciferins *viz.* ostracod-type luciferin, dinoflagellate-type luciferin, and coelenterazine are used in various crustaceans in the chemical reactions associated with the production of light. Further, crustaceans have been reported to produce coelenterazine and they are believed to be the major source for coelenterazine in the sea. Among crustaceans, luminous species are especially remarkable in the copepods, shrimps, and ostracods. Some shrimp (*Hoplophorus*) emit a luminous secretion from luminous organs, while others possess true light organs (photophores), which may be internal or superficial and glow steadily. These photophores consist of a lens, reflector, and light-emitting photogenic cells.

BIOLUMINESCENT MARINE OSTRACODS

Ostracods occur in all oceans from polar to tropical waters and at all depths (surface to about 4,000 meters). About 50% of the hither-to described 300 species of marine ostracods as luminescent (Table **1**). Like copepods, these organisms possess luminescent glands which release light-producing substances into the water. Among the ostracods, the species of *Cypridina* possess a large luminous

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gland in which two types of gland cells are present. While one type secretes the substrate “luciferin” the other secretes the putative photoprotein, luciferase. On stimulation, these organisms squirt both the luciferin and luciferase into seawater. The mixing of these two substances produces a blue cloud of luminescence in the seawater [13].

Table 1. Bioluminescent marine ostracods [13].

Class	Order	Family	Species
Ostracoda	Myodocopida	Cypridinidae	*Cypridina americana, C. dentata, C. noctiluca, C.serrata, Vargula antarctica, V. bullae, V.harveyi, V. hilgendorfii, V. norvegica, V. tsujii*
-	-	Halocyprididae	*Conchoecia acuminata, C. alata, C. ametra, C.atlantica, C. belgicae, C.bispinosa, C. borealis, C. concentrica, C. curta, C . daphnoides, C. echinate, C.elegans, C. haddoni, C.hyalophyllum, C. imbricata, C. kampta, C. lophura, C. loricata, C. macrocheira, C.magna, C. oblonga, C. parthenoda, C.procera, C. rhynchena, C.secernenda, C.spinifera, C. spinirostris, C.subarcuata, Euconchoecia chierchiae*

Emission Maxima in Luminescent Marine Planktonic Ostracods: The emission maxima (λmax) of the different species of luminescent marine planktonic ostracods have been reported to vary from 459 to 481nm (Table **2**).

Table 2. Emission maxima (λmax) of luminous marine ostracods.

Species	λ max	Ref
Conchoecia imbricata	474nm	[13]
Conchoecia secernenda	481nm	[13]
Vargula antarctica	475nm	[109]
Vargula hilgendorfii	459-465nm	[10]
-	465-469nm	[13]

Bioluminescent Marino Ostracods

Family: Cypridinidae

Cypridina noctiluca (= *Pyrocypris noctiluca*)

Image credit: Dr. Yuichi Oba, Ph.D. (Reproduced with permission)

This luminescent species (Fig. **1**) is widely distributed in the coastal waters of the western Pacific (from southern Japan to Hawaii, Australia, and Southeast Asia) and in the Indian Ocean. It is a large ostracod, measuring about 2 mmand has a cylindrical tail, posteriorly and anteriorly with a very shallow incisure. The dorsal and ventral margins are not broadly rounded, the surface of the shell is smooth, and the uropodal lamellae haveeight claws.

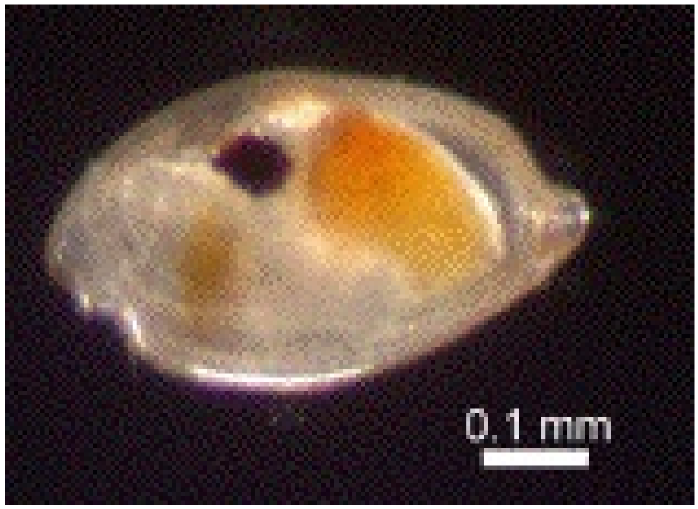

Fig. (1). *Cypridina noctiluca*.

Bioluminescence: The luminous ostracods of the genus *Cypridina* (family Cypridinidae), commonly called sea fireflies, produce blue light with an emission maximum (λmax) ranging between 448 and 463 nm. In the bioluminescent reaction of *Cypridina* spp. the Cypridina luciferin (now cypridinid luciferin) (also known as Vargulin) is oxidized in the presence of Cypridina luciferase (CLase) (now cypridinid luciferase) and molecular oxygen (oxidation step), followed by generation of the oxyluciferin in the excited state (excitation step) and subsequent change to the ground state with light emission (light production step). The luminescent reaction in cyprinids is detailed below [110].

$$\text{Cypridinid luciferase + cypridinid luciferin + } O_2 \quad \textbf{(1)}$$

$$\text{Cypridinid luciferase-cypridinid luciferin-dioxetanone intermediate} \quad \textbf{(2)}$$

$$\text{Cypridinid luciferase-cypridinid oxyluciferin* + } CO_2 \quad \textbf{(3)}$$

$$\text{Cypridinid luciferase + cypridinid oxyluciferin + hv } (\lambda max \sim 462nm) \quad \textbf{(4)}$$

Cypridina noctiluca has been reported to synthesize Cypridina luciferin de novo (anew) from three amino acids *viz.* L-tryptophan, L-isoleucine, and L-arginine [4]. The luciferase of this species has been utilized for biochemical and molecular

CHAPTER 10

Bioluminescent Marine Mollusc

Abstract: This chapter deals with the only luminescent species of planktonic marine nudibranch mollusc *viz*. *Phylliroe bucephala*,and its emission maxima and mechanism of bioluminescence.

Keywords: Emission maxima, Luminescent mollusc, *Phylliroe bucephala*.

INTRODUCTION

Molluscs are the most noteworthy group of marine organisms. They account for 7% of all the animals, while the phylum Mollusca is considered the second most important animal phylum with more than 52,000 identified and characterized species. The phylum Mollusca is gaining attention from the scientific community due to the number of their nutraceuticals of health importance. The promising potential of molluscs and products thereof the mitigation of human health problems call for more exploration and validation to fully utilize this enormous source of food drugs. Unlike freshwaters, where only a freshwater limpet (*Latia neritoides*) is bioluminescent, marine habitats are known for various luminescent molluscs such as nudibranchs, clams, cephalopods, and octopods. Amazingly, cephalopods possess the most advanced luminescence systems, and squids, particularly have been reported to have three or more types of luminous organs. Though several nektonic and benthic marine molluscs are luminescent, planktonic adult molluscs are rarely seen. This chapter, therefore, deals with the only species of planktonic nudibranch mollusc *viz*. *Phylliroe bucephala* (Fig. **1**).

Class: Gastropoda; Order: Nudibranchi; Family: Phylliroidae

Phylliroe bucephala

Image credit: Lydekker R., Wikimedia

This highly modified planktonic nudibranch is a deep water species found throughout the world and is common in the Atlantic, Pacific, and Mediterranean. The body of this luminescent species is laterally compressed, totally transparent, elongated, and fish or leaf-like. The tail is long and more than 16% of the body's

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length. It lacks papillae, but has one pair of well-developed tentacles (the rhinophores). The foot is reduced to a pedal gland and the anus is situated on the right lateral side in the centre of the body. It has 3 to 5 gonads and a parasitic life cycle. Its larval form attaches to the bell of the hydrozoan medusa *Zanclea costata* with its foot, where it feeds on the tissues of the bell. As the nudibranch reaches its maximum size of 550mm, this medusa shrinks in size, resulting in the adult nudibranch outgrowing the medusa after 10 days. This nudibranch then eats the host's tentacles and gets separated to live independently. Lastly, ithas a maximum length of 550 mm.

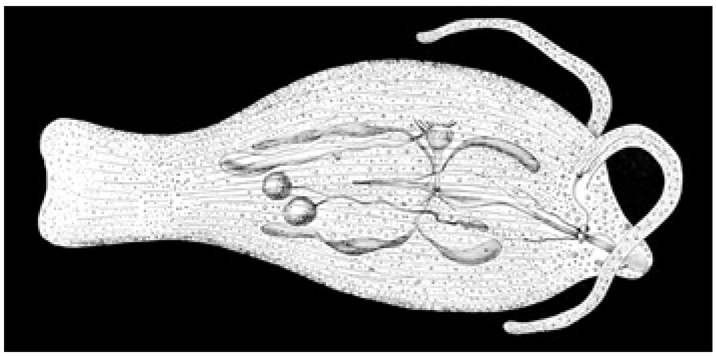

Fig. (1). *Phylliroe bucephala*.

Bioluminescence: It has bioluminescent markings on its body that are highly bioluminescent and emit flashes of light when disturbed, especially in the dark. In the luminescent molluscs, colenterizine (as luciferin) is present but there is no Ca2 – activated photoprotein [27].

CONCLUSION

Though several species of nektonic and benthic molluscs have been reported to be bioluminescent, reports on the bioluminescent species of planktonic marine molluscs are scanty except in a few species like the nudibranch, *Phylliroe bucephala*. This calls for intensive research on the diversity of planktonic, luminescent molluscs, their light organs, and light emission mechanisms.

CHAPTER 11

Bioluminescent Tunicates

Abstract: This chapter deals with the luminescent species of appendiculatians and thaliaceans; their emission maxima and mechanism of bioluminescence.

Keywords: Doliolid, Emission maxima, *Oikopleura*, *Pyrosoma*, Salp.

INTRODUCTION

The tunicates are small marine invertebrate animals, members of the subphylum, Tunicata of the Phylum, Chordata, found in great numbers throughout the seas of the world. Adult members are commonly embedded in a tough secreted tunic containing cellulose. While the bottom-dwelling and sessile (benthic) animals are less modified, the floating and swimming (planktonic and nektonic) animals are more advanced. While certain species of ascidians of Tunicata are consumed as food worldwide, several species of tunicates have been reported to contain a host of potentially useful chemical compounds such as didemnins, which are effective against various types of cancer, as antivirals, and as immunosuppressants. Bioluminescence takes different forms in the different groups of tunicates. Among the planktonic tunicates, Pyrosomes produce very brightly, long-lasting light by using bacteria to glow. On the other hand, most planktonic larvaceans embed luminous particles into their mucus "houses". Among the planktonic luminescent tunicates, the biology and ecology of certain species of *Folia* and *Oikopleura* (Oikopleuridae), *Pyrosoma* (Pyrosomatidae), *CycIosalpa, Helicosalpa* (Salpidae), *Doliolula* (Doliopsidae), *Pseudusa* (Doliolunidae) and *Paradoliopsis* (Paradoliopsida) are presented in this chapter.

Among these classes, Appendicularia and Thaliacea possess luminescent species of about 30 species (Table **1**). Special attention must be paid to identify the bioluminescent urochordates because they may trap luminous microorganisms, such as luminous dinoflagellates or luminous bacteria, which may induce extrinsic luminescence in these urochordates. For example, the brilliant blue-green luminescence of the colonial tunicate, *Pyrosoma* was earlier attributed to luminous bacteria, though, this symbiotic relationship is currently rejected. Its

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luciferin–luciferase reaction has not been demonstrated to date. Further, the bioluminescence of the appendicularians has been briefly reported currently., and It is considered as the coelenterazine-related luciferin–luciferase system of *Oikopleura labradoriensis* [4]. This calls for intensive research on the mechanism of bioluminescence in the planktonic urochordates.

Table 1. Bioluminescent tunicates [13]

Class	Order	Family	Species
Appendicularia	Copelata	Oikopleuridae	*Folia gracilis, Oikopleura albicans, O. cophocerca, O. dioica, O. drygalskii, O. gaussica, O. labradoriensis, O. mediterranea, O. parva, O. rufescens, O. valdiviae, O. weddelli, Stegosoma magnum*
Thaliacea	Pyrosomatida	Pyrosomatidae	*Pyrosoma atlanticum, P. spinosum, Pyrosomella verticillata*
-	Salpida	Salpidae	*CycIosalpa affinis, C. floridana, C. pinnata, C.polae, C.bakeri, C. foxtoni, C. ihlei, C. quadriluminis f. paralleJa, C.q.f. quadriluminis, C. sewelli, HelicosaJpa komaii, H. virgula, H. younti,*
-	Doliolida	Doliopsidae	*Doliolula equus*
-		Doliolunidae	*Pseudusa bostigrinus*
-		Paradoliopsidae	*Paradoliopsis harbisoni*

Table 2. Emission maxima (λmax) of luminescent tunicates.

Species	Colour of light	(λmax)	Ref
Oikopleura dioica	Green	400 to 500 nm	[141]
O. labradorien	Green	400 to 500 nm	[141]
O. rufescens	Blue-green	---	[142]
Stegosoma magnum	Blue-green	---	[142]
Pyrosoma atlanticum	----	493nm	[10]
---	---	482 nm	[13]
P. a. giganteum	--	493 nm	[13]
P. spinosum	--	483-487nm	[10]
Pyrosoma spp.	---	490(540); 485-503nm	[10]
Pyrosomella verticillata	--	491, 483 nm	[13]
Doliolula equus	Blue	----	[143]

Emission Maxima in Luminescent Tunicates: The emission maxima (λmax) of the different species of luminescent tunicates have been reported to vary from 400 to 540 nm (Table **1**).

BIOLUMINESCENT APPENDICULARIANS (LARVACEANS)

Folia gracilis

Image not available

It is a circumglobal (except the Arctic) species. The body has an elongated trunk which is up to 0.5 mm long. Its buccal glands are very small, the endostyle is short, and the esophagus is long, entering the upper genital corner of the stomach. Moreover, the gonads are cup-shaped and parallel to the posterior wall of the genital cavity, and the tail is with a group of small spherical subchordal cells.

Bioluminescence: In this species, luminescence is assumed due to the presence of its photogenic oral glands [13].

Oikopleura albicans

Image not available

It is found distributed in the Indo-Pacific, Atlantic Ocean, and the Mediterranean. The trunk of this species is elongated and up to 5.0 mm long, the buccal glands are large, and the gonads are located adjoining the coil of the gut as a semicircular clasp protruding dorsally when ripe. The tail musculature is moderately broad with numerous, small, and stellar subchordal cells arranged in 2 lines over half of the tail length.

Bioluminescence: Certain oikopleurids possess paired oral glands that are considered the source of a “fluorescent” secretion. This secretion gets incorporated into the house and is responsible for the bioluminescence of the tunicate and its house. This species has been reported to give off spontaneous flashes of light while erecting a new house. Further, the finished house itself produces point sources of a fight when agitated [142]. This species also secretes long luminous filaments [13].

Oikopleura dioica

Image credit: Dr.David Fenwick (Reproduced with permission)

Bioluminescence: In luminescent larvaceans such as *Oikopleura dioica* (Fig. **1**), *Oikopleura labradoriensis, Oikopleura albicans, Oikopleura vanhoeffeni, Oikopleura rufescens,* and *Stegosoma magnum,* the granular inclusions which are probably present in their expanded house, accounted for the multiple, point-sources of light observed in flashing houses. In all these species, mechanical stimulation produced multiple, summated blue-green flashes from free individuals invested by house rudiments and from empty houses which were thoroughly free from exogenous luminescent bacteria or other luminescent microorganisms. Further in these species, the light is produced by clusters of 1 to 2 μm fluorescent granules that form intricate, species-specific patterns of inclusions in the house rudiment [141]. All the six known luminescent species of larvaceans possess fluorescent and luminescent house rudiment inclusions and oral glands [142].

Fig. (1). *Oikopleura dioica*.

Oikopleura labradoriensis

Image not available

This medium-sized, luminescent appendicularian is found distributed in the Arctic, northern North Atlantic, and northern North Pacific Oceans. The trunk is elongated, the tail has a long series of sub-chordal cells near the tip, the left lobe of the stomach is trapezoidal, and the buccal glands are slightly large and oval in shape. Moreover, a single ovary and two paired testes are seen posteriorly in the trunk and tts body length can go up to 2.6 mm.

Bioluminescence: This species uses a coelenterazine+luciferase system to produce of light [8].

Oikopleura rufescens

Image not available

This species is found distributed in the Indo-Pacific, the Atlantic Ocean and the Mediterranean. The trunk is compact and can go up to 2.3 mm long. The buccal glands are spherical and fairly large, and the gonads are located adjoining the gut coil protruding dorsally, and tapering toward the posterior end. Lastly, the tail has a spindle-shaped subchordal cell, and its musculature is narrow.

Bioluminescence: It is endogenously luminescent and gives blue-green flashes upon stimulation of free animals with house rudiments [142].

CHAPTER 12

Marine Bioluminescence and Biotechnology

Abstract: The role of bioluminescent marine plankton in the fisheries and the health of the oceans is fairly well known. Recent research has shown that this light could be of great use in therapeutic and biotechnological applications. While the marine bioluminescent, planktonic crustaceans are helpful in the treatment of cancers, other groups of marine plankton have their potential biotechnological applications, including hygiene control and mapping out pollution in ecosystems. However, further intensive research is needed on this vital aspect, especially when identifying lesser-known bioluminescent planktonic groups and their biomedical and biotechnological applications for the benefit of human society.

Keywords: ATP sensing, Bioluminescent imaging, CAR T-cell therapy, Hygiene control, Marine pollution.

INTRODUCTION

The phenomenon of bioluminescence has been reported to be helpful in biomedical applications, especially wheninvestigating and monitoring cell health and the impact of drug treatments. For instance, if one compares the light given off by cells in treated wells against untreated wells (light is a proxy for the number of live cells), the amount of light given off by the untreated samples would be higher than the treated wells if the chemotherapeutic is effective. The bioluminescent proteins, including the luciferases may serve as biosensors in the targets of drugs used to treat a wide array of disorders and diseases, including diabetes, allergies, pain, and hypertension [149]. Further, these biosensors could have a major impact on new drug development. Additionally, bioluminescence can also be used within biological systems for monitoring water systems to ensure high-quality drinking water, for detecting proteins, for determining whether a patient's blood sample contains antibodies to COVID-19, and for vaccine research and development. These findings may lead up to the developments in synthetic luciferins and engineered luciferases for other biotechnological applications, including ATP sensing, hygiene control in the fish and milk industries, mapping out pollution in ecosystems *etc*. It can also be reasonably expected that developments in these areas will feed into the research and applications of bioluminescence in biotechnology.

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THE ROLE OF MARINE BIOLUMINESCENT PLANKTONIC CRUSTACEANS IN CANCER IMMUNOTHERAPIES

The marine bioluminescent planktonic crustaceans have been reported to play a major role in the treatment of cancers. The enzyme, luciferase from these organisms, when introduced into cancer cells relating to chronic myelogenous leukemia, acute myelogenous leukemia, and Burkitt lymphoma, was found to leak out as the cells die, leaving a visible glow. This assay has been reported to accurately recognize the death of a single cancer cell in 30 minutes [149]. It is also reported that this technique can also be employed in CAR T-cell therapy (chimeric antigen receptor T-cell therapy) in which a patient's T-cells (a type of immune system cell) taken from his blood are changed in the laboratory so they can attack cancer cells. In the development of CAR T cells, the proteinof bioluminescent crustaceans' luciferase can play a leading role in the future (chimeric antigen receptor T-cell therapy [150].

Bioluminescent Imaging

The green fluorescent protein (GFP), first isolated from jellyfish and subsequently from corals, sea anemones, zoanthids, copepods, and lancelets, exhibits bright green fluorescence when exposed to light in the blue to ultraviolet range. This GFP has a wide application in bioluminescent Imaging (BLI) to study the interaction of infectious bacteria and fungi with living cells [151].

MARINE BIOLUMINESCENT PLANKTON AND THEIR BIOTECHNOLOGICAL APPLICATIONS

Though a total of about 30 bioluminescent systems have been identified, the luciferin-luciferase pairs of only 11 systems have been characterised to date. As the different luciferin-luciferase pairs have different light emission wavelengths they are deemed suitable for various applications [152]. Bioluminescent organisms may also serve as a target for many areas of research. Presently, luciferase systems are widely used in the field of genetic engineering. Certain applications of engineered bioluminescence include: i) glowing trees to light up highways and save electricity, ii) crops and domestic plants which luminesce when they need watering, and iii) novelty pets that luminesce (rabbits, mice, fish *etc*.) [153].

Hygiene Control

The ATP-bioluminescence assay based on the firefly bioluminescence system is presently used in applications relating to hygienic control. This technology is applied to monitor the cleanliness of surfaces in healthcare facilities such as hospitals and clinics; and food and dairy industries.Similar applications would also be made possible in the future with bioluminescent marine plankton if and when adequate research is attempted [152].

MAPPING OUT POLLUTION IN ECOSYSTEMS

The common application of bioluminescence in ecotoxicology and pollutant monitoring is ATP quantification using the firefly bioluminescence ATP assay in the marine environment. Similar applications would also be made possible in the future with bioluminescent marine plankton [152].

FUTURE ISSUES IN MARINE BIOLUMINESCENCE

i): Though the genes for many luciferases derived from marine-luminescent organisms are known, the mechanisms of luciferin biosynthesis are yet to be known. This will be a promising area for future research in marine bioluminescence.

ii): The chemistry of luminescence for many organisms such as planktonic polychaetes and tunicates, is still completely unknown. Intensive research is therefore needed on this aspect.

iii): In order to thoroughly understand the marine ecosystem dynamics, harmful algal blooms, and how and why plankton populations fluctuate over time, improvements in remote and automated methods of detecting oceanographic-scale bioluminescence (satellites and bathyphotometers) are the need of the hour.

CONCLUSION

It is worth mentioning here that the function of bioluminescence has been investigated much less than any other topic in the field. Though bioluminescence has been found to be very useful in various fields, including medicine, biology, physics, and engineering, intensive research is greatly needed on aspects such as the origins and mechanisms of bioluminescence, luciferin and luciferase systems, in less studied luminescent marine organisms, to derive advanced applications of bioluminescence in biotechnology across various fields and make them accessible to particular target groups.

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RAMASAMY SANTHANAM

Ramasamy Santhanam is the former dean of the Fisheries College and Research Institute, Tamil Nadu Veterinary and Animal Sciences University, India. He has 50 years of teaching and research experience in Marine Planktonology and Fisheries Environment. He has served as a fisheries expert for various government and non-government organizations in India and abroad. Dr. Santhanam has published 33 books on various aspects of aquatic life and aquaculture. He was a member of the American Fisheries Society, United States; World Aquaculture Society, United States; Global Fisheries Ecosystem Management Network GFEMN), The United States; and the IUCN's Commission on Ecosystem Management, Switzerland.