

Bioluminescence in marine and terrestrial organisms elicited through various kinds of stimulation

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Abstract

The term bioluminescence refers to a conspicuous light emission displayed by numerous aquatic and terrestrial organisms. This phenomenon has so far not been observed in several taxonomic groups like archaea, protista, platyhelminthes, chelicerata, cephalochordata, amphibians, reptiles, birds, plants, and mammals. However, some luminescent bacteria, fungi and microalgae like dinoflagellates are known. Bioluminescence has become a powerful biological tool and revolutionized several medical, physiological and biotechnological approaches, such as, for example, the study of metabolic pathways of bacteria to mammals. In 2008 O. Shimomura, M. Chalfie and R. Tsien were awarded the Chemistry Nobel prize for their discovery of the protein GFP, which is co-expressed with aequorin, the calcium-activated photoprotein involved in the bioluminescence reaction of the jellyfish *Aequorea victoria*. Some organisms are known to display bioluminescence only under certain kinds of stimulation and stress conditions; others appear to produce their light without prior stimulation either continuously or intermittently. Despite the discovery of more than 700 genera of bioluminescent organisms from marine, terrestrial, and freshwater environments, there is often still insufficient knowledge about their bioluminescence emission patterns under natural and stress conditions. Furthermore, there are no detailed reviews on stimulation techniques that can be used to test whether organisms previously not having been recognized to be luminescent are luminescent or not. This paper reviews various stimulants, such as chemical, mechanical, photic, thermal, magnetic and electrical ones, used in tests to elicit the emission of light in known bioluminescent organisms. This account should help researchers to extend their investigations to identify organisms hitherto not deemed to be luminescent.

Keywords: Bioluminescence; coelenterazine; fluorescent proteins; stimulation techniques; emission patterns; luminescence applications.

1. Introduction

Bioluminescence is the production of visible light generated by an oxidative reaction between an enzyme, generally referred to as a luciferase and a substrate, referred to as a luciferin. Both terms were first used by Raphaël Dubois (Anctil 2018), but chemically various different kinds of non-identical luciferases as well as luciferins exist.

The emissions of erratic, continuous, or flashing lights by several terrestrial and aquatic organisms have been a mesmerizing historical enigma since ancient times (Harvey 1940, 1952, 1957; Björn and Ghiradella 2008; Meyer-Rochow 2009; Anctil 2018). In nature, around 30 different bioluminescent systems are known, of which nine have been well studied for their luminous reaction mechanisms (Kaskova et al. 2016). In connection with the phenomenon of bioluminescence, various processes were studied and analyzed such as, for instance, the circadian rhythms in dinoflagellates (Hastings 2013), in bioluminescent fungi (Oliveira et al. 2015) or in New Zealand glowworms (Ohba and Meyer-Rochow 2005; Merritt and Aotani 2008; Merritt et al. 2012) and furthermore the ATP dependent luminescence system in fireflies (Jeng 2019), quorum sensing in the symbiotic relationship between the squid *Euprymna scolopes* and *Aliivibrio fischeri* (Nyholm and McFall-Ngai 2004) as well as the phylogenetic relationships of four *Vibrio* species (Urbanczyk et al. 2007, 2008).

However, the origins, ecological functions, and the chemical nature of many other bioluminescent systems often still remain largely unknown, although recently beautifully summarized for Brazilian bioluminescent beetles by Bechara and Stevani (2018). Evolutionary advantages of bioluminescence and associated fluorescent proteins in many luminous organisms are known to involve defensive and offensive functions such as repelling an attacker or attacking prey, to assist camouflage through counter illumination, and to assist inter as well as intra-specific communication (Lloyd 1965; Carlson and Copeland 1985; Haddock et al. 2010; Zarubin et al. 2012; Ramesh and Mohanraju 2019). Yet, other biological functions are still often unknown (Mallefet and Shimomura 1995).

The quorum sensing phenomenon is a well-known chemical signalling factor among luminous bacteria. However, some marine and terrestrial luminous bacterial species, *Photobacterium phosphoreum*, and *Photorhabdus* sp., do not exhibit quorum sensing (Ramesh and Mohanraju 2019; Tanet et al. 2019). That indicates that evolutionary adaptations are tailored to specific environments via their metabolic and genetic responses. Likewise, many non-luminous *Vibrio* species appear to have acquired *lux* genes via horizontal gene transfer and subsequently produced luminescence in earlier non-luminescent species (Dunlap and Urbanczyk 2013). Similarly, acquisition of luciferins

(e.g., euphausiids feeding on zooplankton, coelenterazine in non-luminous marine organisms and coelenterazine acquisition by cnidarians and ophiuroids) (Haddock et al. 2010; Wilson and Hastings 2013; Mallefet et al. 2020) through the food chain is also an exciting biological pathway leading to the emission of light.

Dietary acquisition of luciferins are well-known from five examples: (i) coelenterazine in the lophogastrid species *Gnathophausia ingens* (Frank et al. 1984), (ii) coelenterazine in the jellyfish species *Aequorea victoria* (Haddock et al. 2001), (iii) vargulin in the bony fish *Porichthys notatus* (Warner and Case 1980), (iv) coelenterazine in the ophiuroid *Amphiura filiformis* (Mallefet et al. 2020), and (v) “kleptoprotein bioluminescence” (acquisition of both luciferin and the luciferase enzyme from the luminous ostracod *Vargula hilgendorfii*) in *Parapriacanthus ransonneti* (Bessho-Uehara et al. 2020b). The occurrence of homologous luciferin contents in luminous and non-luminous beetles is also of interest for evolutionary studies (Oba et al. 2008, 2020). These intriguing incidents provoke researchers to extend their research, posing questions like why do some organisms exhibit phases with and without luminescence and why are others luminescent all the time. In order to test and activate the luminescence of inactive luminous organisms, one needs to have to one’s disposal a variety of methods that can be used as stimulants. It is in this context that this review on the various stimulating methods to induce bioluminescence has been written.

In the current scientific research on bioluminescence, the latter has widely been used to monitor and visualize biological processes in cells, tissues, and whole organisms (Kaskova et al. 2016). Bioluminescence has been a powerful biomarker to detect the propagation of numerous diseases, used as biosensors to detect a wide array of toxic pollutants, employed in the context of bioimaging of live organisms, involved in gene expression assays, immunoassays, and intracellular applications (Chudakov et al. 2010; Ramesh and Mohanraju 2015). The development of autoluminous plants as a natural source of light was also undertaken (Krichevsky et al. 2010; Mitiouchkina et al. 2020) and goes back to an idea that more than a hundred years Dubois (1914) had had (cited in (Anctil 2018)).

Approximately 8.7 million eukaryotic species are reported around the world (Mora et al. 2011), but bioluminescence is known for only approximately 10,000 species in 800 genera, representative of 13 phyla (Oba et al. 2017a). Therefore, it would be fair to say that bioluminescence and fluorescence traits have not yet been confirmed in the vast majority of the species on planet Earth and that the search to discover new luminous chemical systems in hitherto unexplored luminous organisms has not ended. Since many organisms belonging to different lineages appear to produce luminescence only after stimulation, finding the most appropriate stimulating method for

such organisms is essential. Therefore, it is hoped that the methods and techniques described in this review will benefit not just ongoing but future research as well in an endeavour to shed more light on the fascinating phenomenon of bioluminescence.

Why bioluminescence stimulation techniques?

Many of the stimulation techniques detailed in this paper were not at all necessary or used to discover novel bioluminescent mechanisms, but this review would benefit researchers who do not necessarily study bioluminescence, but study an organism or a group of organisms and then decide to check whether the possibility exists that the creature under investigation might not also be able to produce some biological light. This could be during a research cruise, as part of some field work or during a practical exercise with students.

Since luminous organisms have a variety of biotechnological applications, and investigating live samples under natural conditions in the field may unveil new chemical reactions that result in luminescence. In order to appropriately stimulate an organism to bioluminescence certain tools and chemicals are required (Fig. 1). Freshly caught specimens are often more likely to yield intense luminescence than stressed specimens that have exhausted their luminescent capacity. Therefore, maintaining fresh samples and avoiding stressful conditions (e.g., frequent handling and disturbing organisms) are important for obtaining superior photographic and emission records. Visible luminescence following appropriate stimulation can normally be photographed with high ISO (Ramesh 2020). Since some luminous organisms (e.g., jellyfish, *Aequorea victoria* and some deep-sea fish) possess fluorescent proteins, use of UV-blue light can help to identify the presence and absence of fluorescent proteins. However, it must be pointed out that fluorescence is not bioluminescence, because in the past there have been cases in which fluorescent organisms were described as being bioluminescent when in fact they weren't.

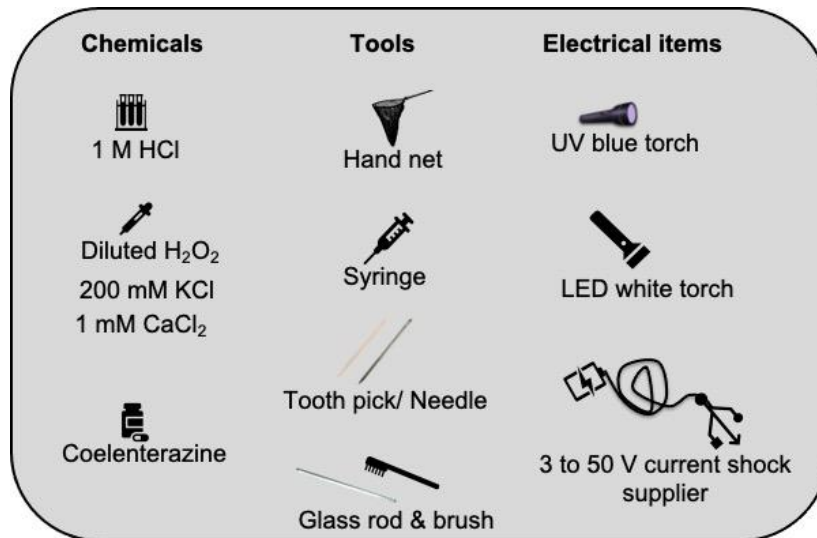


Fig. 1. Important tools and chemicals required for field investigations on stimulated bioluminescence. Note: Refer to sections and Tables below for when, where and how to use these stimulants.

2. Stimulation methods on bioluminescence

A review of the literature shows that many organisms produce luminescence when subjected to a variety of stimulations. Directly or indirectly, the stimulants trigger the proton channels or regulating genes to generate the luminescence. Thus, understanding stimulation techniques is helpful in the quest to explore excitatory luminescence and its possible applications. Thus far seven ways to stimulate bioluminescence of inactive luminous organisms have been described in the literature, including chemical, mechanical/physical, electrical, thermal, photonic, genetic, and biological means (Table 1; Fig. 2). In each stimulation category, the taxonomical grouping was made based on the availability of information from the literature and personal study.

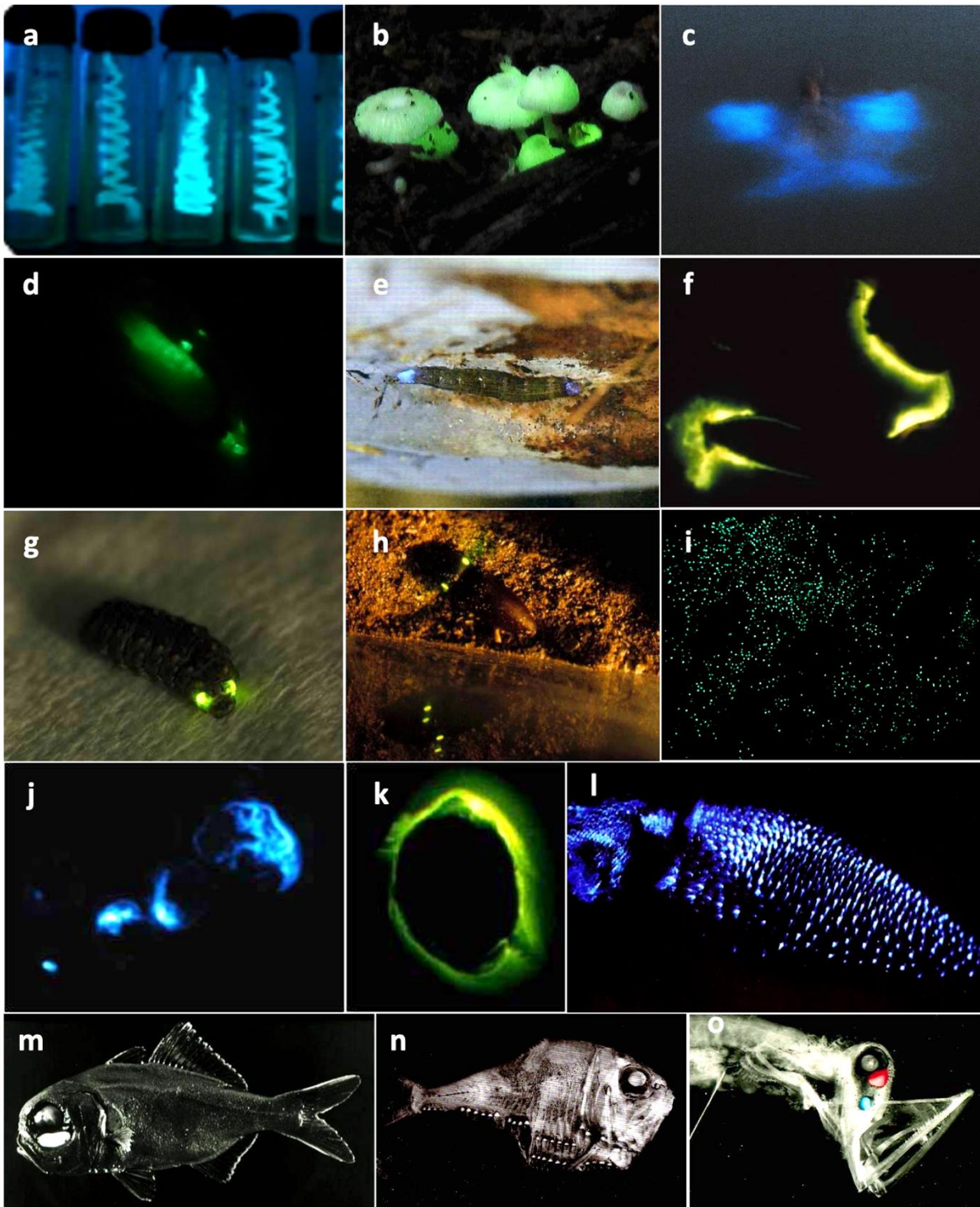


Fig. 2. Some examples of bioluminescent organisms. Luminous bacteria (a), luminescent fungi (b), dinoflagellate bloom (c), fireworm *Odontosyllis* sp. (d), larval fungus gnat *Keroplatus nipponicus* (e), New Zealand megascolycid earthworm (f), firefly larva, courtesy of M. Hironaka (g), Luminous elaterid beetle (h), *Arachnocampa luminosa* of Waitomo glowworm cave (i), Ostracod *Cypridina* sp. (j), freshwater limpet *Latia neritoides* (k), *Watasenia* sp., courtesy of N. Ohba (l), flashlight fish *Anomalops katoptron* (m), hatchetfish *Argyropelecus* sp. (n) and dragonfish *Malacosteus niger* (retouched) (o).

Obviously, the categories are not clear-cut and there are overlaps between them as, for example, when one considers communication with photic signals by fireflies, which involves biologically-created stimulation, but which could also be assigned to the category of photostimulation given that it can be elicited by artificial light signals. When in the case of *Pyrocystis fusiformis* their cells touch or bump against those of another individual and then respond to that with a flash of light, this could have involved a physical or chemical stimulation by another organism and could also be interpreted as a biological stimulus (Sweeney 1979). Despite these difficulties to always assign bioluminescent responses unambiguously to a stimulus category, it can be helpful to know which kind of stimulation works best in eliciting a bioluminescent response from a species.

There is a vast literature on bioluminescence and this paper cannot claim to cite or refer to all of the interesting research that has been conducted on luminescent organisms. It focuses on the most important taxa and presented examples that can be considered representative for other related species that may not necessarily be mentioned.

2.1. Chemical stimulation

2.1.1. Bacteria

Chemically stimulated luminescence (CSL) is a widely used method in connection with many stimulus-dependent luminous organisms. In naturally luminous bacteria, the longevity of luminescence depends on cell density, environmental conditions, and acid production in the growth medium. Many luminous strains appeared to be luminous upon primary isolation but turn dim very quickly or even become non-luminous and end up contaminated (Dunlap 2009). Diminishing luminescence over time has also been observed in luminous bacteria (Wolfe et al. 2004; Flodgard et al. 2005; Figge et al. 2014) and at least in the symbiotic luminescent bacteria of the light organ of the Indonesian fish *Anomalops katoptron* the loss of luminescence appeared to have been caused by the starving fish being unable to supply its luminescent bacteria with essential nutrients to maintain the light production (Meyer-Rocchow 1976).

It is known that sometimes a pure and viable luminous strain can enter into an unculturable condition (Ramaiah et al. 2002), but that the luminescence of such dim or some dark strains as well as some viable and non-viable states of *Vibrio* species can occasionally be retrieved by adding one of the following reagents: fresh medium (Nealson et al. 1970; Barak and Ulitzur 1981), 3-oxo-C6 HSL (Wollenberg et al. 2012), tetradecanal or myristic acid (Ulitzur and Hastings 1979), long-chain aliphatic aldehyde or autoinducer (Fidopiastis et al. 1999; Anetzberger et al. 2009), arginine

(Nealson et al. 1970), cyclic AMP (400 µg/ml) (Ulitzur and Yashphe 1975), phosphate ions (0.03-0.05 g/ml) (Adoki and Odokuma 2006), various concentrations of NaCl (3-6%), CaCO₃ (0.3-1.0%), MgSO₄ (0.3-0.7%), glycerol (0.3-1.0%), K₂HPO₄ (0.3-0.5%) (Ramesh et al. 2014), and by introducing additional luminescent bacterial colonies to the culture (Ruby and Asato 1993) and finally by adding non-luminescent allo-bacterial extracellular products (Ravindran et al. 2011). In certain strains of *V. harveyi* and *A. fischeri*, luminescence occurs only late in the exponential growth phase due to peak accumulation of quorum sensing molecules (Wilson and Hastings 1998).

2.1.2. Fungi

Approximately 80 species of fungi are known to be bioluminescent and to emit a continuous greenish light (O’kane et al. 1990; Vydryakova et al. 2011). The only species for which a circadian rhythmicity of the light emission has been described is the South American *Neonothopanus gardneri* (Oliveira et al. 2015). If one suspects a mushroom or its mycelium to have the capacity to produce light (but one cannot see any), it was reported that an addition of boiled cell-free liquid cultures of three non-related species of basidiomycetes to an *Armillaria borealis* culture can evoke a hugely augmented luminescence emission due to the precursor of fungal luciferin present in the non-luminescent basidiomycetes (Puzyr et al. 2019). But usually, when a mushroom does not emit light, it means it does not have the whole cluster of genes related to the Caffeic Acid Cycle (CAC) responsible for fungal bioluminescence (Kotlobay et al. 2018). Hence, there’s nothing much one can do to elicit bioluminescence. However, in some cases according to Stevani (pers. comm.) the light is dim because the fungus produces low amounts of luciferin (3-hydroxyhispidin). This fact was confirmed by measuring the amount of luciferin precursor (hispidin) in different fungi (Oba et al. 2017b). In this case one can try to spray hispidin or luciferin on the surface of either the culture or the mushroom. The addition of caffeic acid in the agar with other nutrients may also help.

2.1.3. Dinoflagellates

Many dinoflagellates such as *Gonyaulax polyedra* (= *Lingulodinium polyedra*), *Pyrodinium bahamense*, and several *Pyrocystis* species produce short and spontaneous luminescent flashes (ranging from dim to bright) without any need for mechanical or chemical stimulation. However, upon chemical or mechanical stimulation, dinoflagellates display intense and continuous luminescence for a prolonged duration of time (Sweeney 1979). In *G. polyedra*, luminescence can, for instance, be stimulated 55 fold with 5-methoxylated indoleamines (Balzer and Hardeland 1991). In short, bioluminescence in dinoflagellates, like *G. polyedra*, *Pyrodinium bahamense*, *Pyrocystis fusiformis*, *P. noctiluca*, and *P. lunula* can be elicited through addition of Ca²⁺, NH₄⁺, K⁺, or H⁺ ions

(Hamman and Seliger 1982; Widder and Case 1982), with concentration ranging between 0.1 to 0.4 M (Sweeney 1979). Luminescence of unialgal cultures of *Ceratocorys horrida* was augmented by using 0.1 ml 4 M acetic acid (Latz 1995), while acetic acid or calcium chloride worked for *Gonyaulax* species (Esaias et al. 1973). Adding 0.2 ml of 1 M HCl (Hardeland and Nord 1984) or citric acid (Behrmann and Hardeland 1999) to *P. noctiluca* culture medium placed in scintillation vials caused emission of bioluminescence. Stimulated luminescence was also successful in connection with different undefined plankton organisms (referred to as luminous dinoflagellates and some zooplanktons) using buffered 5% formaldehyde solution (Losee et al. 1985). In *Lingulodinium polyedrum*, luminescence was elicited by using Ca^{2+} (von Dassow and Latz 2002) and 1 mM benzyl alcohol (Jin et al. 2013).

2.1.4. Cnidarians and Ctenophora

In the comb-jelly, *Mnemiopsis leidyi*, $10 \mu\text{M l}^{-1}$ atropine, $100 \mu\text{M l}^{-1}$ propranolol, and 1 mM l^{-1} serotonin stimulated luminescence (Anctil 1985). In the deep-sea siphonophore genus *Erenna*, tentacles of the polyps produced photophore-mediated luminescence when ruptured in CaCl_2 solution (Haddock et al. 2005). Aequorin, a light-emitting photoprotein obtained from the jellyfish *Aequorea victoria*, produces light upon the addition of Ca^{2+} , even in the absence or presence of oxygen molecules (Shimomura and Yampolsky 2019).

2.1.5. Annelida

Luminescence of the earthworm *Lampito (=Megascolex) mauritii* was induced using a dilute solution of ammonia and hydrogen peroxide (Ismail and Kaleemurrahman 1981), glucose oxidase (12 mg ml^{-1}), and 2 mM glucose in phosphate buffer (Haram et al. 1996), 50 mM Fe^{2+} ions solution (Santhanam and Limaye 1989a), K_2SO_4 or phosphate buffer (Santhanam and Limaye 1989b), or by immersing the worms in methylated spirits and a weak solution of ammonium hydroxide or chloretone (Gates 1925). The use of 50% ethanol was reported by Pes et al. (2016) for *Eisenia lucens* luminescence (Pes et al. 2016). In the case of the luminescent earthworms *Henlea* spp., Ca ions of a concentration of $1.3 \times 10^{-4} \text{ M}$ triggered luminescence reliably (Rodionova et al. 2002).

In the marine parchment tubeworm *Chaetopterus* sp., the addition of peroxide and Fe^{2+} solutions elicits luminescence (Shimomura and Yampolsky 2019). KCl (200 mmol l^{-1}) is an effective stimulant to stimulate luminescence in worms like *Odontosyllis* (Deheyn and Latz 2009). The parapodia of the planktonic worm *Tomopteris helgolandica* produced yellow light upon stimulation with 200 mmol l^{-1} of KCl and 1 mmol l^{-1} carbachol (Gouveneaux and Mallefet 2013). For deep-sea worms like *Flota flabelligera* and *Tomopteris* spp., 7.5% KCl appears to work as a one time eliciting

stimulus (Francis et al. 2016). Different planktonic worms such as *Tomopteris planktonis*, *T. septentrionalis*, and *T. pacifica* produced intense luminescence in response to chemical stimulants like 200 mM KCl, 1% Triton X-100, and 500 mM KCl, respectively (Gouveneaux et al. 2016).

2.1.6. Arthropoda

In the copepod *Oncaea conifera*, luminescence was induced by immersing individuals in seawater containing eserine, acetylcholine, or carbamylcholine (Herring et al. 1993). Nitric oxide (70 ppm) is also known to inhibit mitochondrial respiration in the photocytes of *Photuris* sp. fireflies, thereby releasing oxygen molecules for producing a long lasting luminescence (Trimmer et al. 2001). Injection of *Neoditomiya* larvae with 5 μ l of *Orfelia* luciferase and 5 μ l of 100 mM DTT resulted in intense blue luminescence and fluorescence (Viviani et al. 2020). In this case, *Neoditomiya* emitted luminescence due to the presence of a precursor (*Orfelia*'s luciferin). Serotonin and nitric oxide are known to control the bioluminescence in northern krill, *Meganyctiphanes norvegica* (Fregin and Wiese 2002; Krönström et al. 2007).

2.1.7. Mollusca

Saturated NaCl solution triggered and stimulated luminescence in different marine gastropod species (Schultz and Oba 2014). Induction of luminescence in homogenized tissues of midwater cephalopods and octopuses was achieved by passing air into vials containing homogenate, and treating homogenized samples with photophore extracts containing luciferase (Young et al. 1979).

2.1.8. Echinodermata

Arm segments of some luminous ophiuroid species responded to stimulation with KCl, acetylcholine, carbachol, dopamine, 5-HT, and taurine (Dewael and Mallefet 2002). Arms of coelenterazine-fed specimens produced light upon stimulation using 400 mM KCl solution (Mallefet et al. 2020).

2.1.9. Fish and Pyrosomes

Nitric oxide is known to trigger luminescence by photocytes of several fish species, e.g., *Argyrolepecus hemigymnus*, *Hygophum benoiti*, *Myctophum punctatum*, *Electrona risso*, *Cyclothone braueri*, *Vinciguerria attenuata*, *Maurolicus muelleri*, and *Porichthys notatus* (Krönström et al. 2005; Krönström and Mallefet 2009). In deep-sea luminescent sharks (Etmopteridae and Dalatiidae), melatonin (10^{-6} M) was reported to cause a long-lasting glow production (Claes and Mallefet 2009a; Claes et al. 2012; Duchatelet et al. 2020a, b). Another hormone, prolactin (10^{-6} M), triggers a rapid emission of light in Etmopteridae, such as *Etmopterus spinax*, *E. splendidus*, and *E. molleri* (Claes

and Mallefet 2009a, 2015; Duchatelet et al. 2020a). Hormonal control of light emission is specific to luminous Chondrichthyans (Claes and Mallefet 2009a, b, 2015; Claes et al. 2011).

In bony fishes, light emission is triggered by nervous control (Baguet and Case 1971; Mallefet et al. 2019). Turquoise luminescence was observed in the stomiatoid fish *Maurolicus muelleri* by injecting it with 0.2 cc of epinephrine (adrenaline) 1:200 in isotonic saline (Anctil 1972). Intraperitoneal injections (0.1-0.4 cc) and external applications (0.2-0.6 cc) of 3% hydrogen peroxide evoked luminescence in the Atlantic lanternfishes *Benthoosema glaciale*, *Myctophum punctatum*, and *Notoscopelus kroeyeri* (Anctil 1972). The midshipman fish *Porichthys* displayed intense luminescence when placed in seawater containing a little ammonia (Tsuji et al. 1971). Cross reaction experiments on tissues of fishes with known luciferins and luciferases of other luminous organisms would likely result in luminescence according to Renwart and Mallefet (2013). A recent study showed that mixing coelenterazine luciferin with pyrosome homogenate and PyroLuc produced blue luminescence (Tessler et al. 2020) (Table 1).

Table 1. Summary of various chemical stimulants used to induce luminescence in selected representative organisms.

Taxonomic group	Group/Organism name	Chemical stimulant & concentration	Emission colour /λ_{max}	Reference
Bacteria	<i>Aliivibrio fischeri</i> (= <i>Vibrio fischeri</i>)	3-oxo-C6 HSL	Blue	(Wollenberg et al. 2012)
	<i>A. fischeri</i>	Arginine	Blue	(Nealson et al. 1970)
	<i>A. fischeri</i>	Addition of luminescent bacterial colonies	Blue	(Ruby and Asato 1993)
	<i>A. fischeri</i>	Non-luminescent allo-bacterial extracellular products	Blue	(Ravindran et al. 2011)
	<i>A. fischeri</i>	Zn (II)	Blue	(Christofi et al. 2002)
	<i>Vibrio</i> sp., <i>Photobacterium</i> sp.	Fresh media	Blue	(Nealson et al. 1970; Barak and Ulitzur 1981)
	<i>Vibrio campbellii</i> STF1	NaCl (3-6%), CaCO ₃ (0.3-1.0%), MgSO ₄ (0.3-0.7%), Glycerol (0.3-1.0%), & K ₂ HPO ₄ (0.3-0.5%)	Blue	(Ramesh et al. 2014)
	<i>Vibrio harveyi</i>	Autoinducers	Blue	(Anetzberger et al. 2009)

	<i>V. harveyi</i>	cyclic AMP (400 µg/ml)	Blue	(Ulitzur and Yashphe 1975)
	<i>V. harveyi</i>	Tetradecanal or myristic acid	Blue	(Ulitzur and Hastings 1979)
	<i>V. harveyi</i> , <i>A. fischeri</i> , <i>Photobacterium leiognathi</i> and <i>Photobacterium phosphoreum</i>	Phosphate (0.03-0.05 g/ml)	Blue	(Adoki and Odokuma 2006)
	<i>Vibrio salmonicida</i>	Long-chain aliphatic aldehyde	Blue	(Fidopiastis et al. 1999)
	<i>Photobacterium leiognathi</i>	Acriflavine, Proflavine, Ethidium bromide, Nalidixic acid, & Cinodine	Blue	(Steinberg et al. 1985)
Fungi	<i>Neonothopanus nambi</i>	Mn ²⁺ ions, H ₂ O ₂ and EDTA cause increase	527-535 nm	(Bondar et al. 2011)
Dinoflagellates	<i>Ceratocorys horrida</i>	0.1 ml 4 M acetic acid	478 nm	(Latz 1995)
	Dinoflagellates	Buffered 5% formaldehyde solution	480 nm	(Losee et al. 1985)
	<i>Gonyaulax</i> sp.	Acetic acid or calcium chloride	~480 nm	(Esaias et al. 1973)
	<i>Lingulodinium polyedra</i> (= <i>Gonyaulax polyedra</i>)	5-methoxylated indoleamines	Blue	(Balzer and Hardeland 1991)
	<i>Lingulodinium polyedra</i>	Amitriptyline, Indoleamines, Kynuramine, and Pargyline (10 ⁻⁴ - 10 ⁻⁶ M)	Blue	(Balzer and Hardeland 1989)
	<i>Lingulodinium polyedra</i> , <i>Pyrodinium bahamense</i> , <i>Pyrocystis fusiformis</i> , <i>Pyrocystis noctiluca</i> , and <i>Pyrocystis lunula</i>	Ca ²⁺ , NH ₄ ⁺ , K ⁺ , or H ⁺ (0.1 to 0.4 M)	Blue	(Sweeney 1979; Hamman and Seliger 1982)
	<i>P. noctiluca</i>	1 M HCl (0.2 ml)	Blue	(Hardeland and Nord 1984)
	<i>P. noctiluca</i>	Citric acid	Blue	(Behrmann and Hardeland 1999)
	<i>P. lunula</i>	Various chemicals	Blue	(Lambert 2006)

	<i>Lingulodinium polyedra</i>	Ca ²⁺ (1 mmol l ⁻¹ ionomycin)	Blue	(von Dassow and Latz 2002)
	<i>Lingulodinium polyedra</i>	1 mM benzyl alcohol	Blue	(Jin et al. 2013)
Ctenophora	<i>Mnemiopsis leidyi</i>	10 µM l ⁻¹ Atropine, 100 µM l ⁻¹ Propranolol, 1 mM l ⁻¹ Serotonin	Blue	(Anctil 1985)
	<i>Mnemiopsis leidyi</i>	96% ethanol	Blue	(Tokarev et al. 2008b, a; Mashukova and Tokarev 2013)
	<i>Mnemiopsis</i> sp.	Coelenterazine and O ₂ , pH 9.0.	Blue	(Anctil and Shimomura 1984)
Cnidaria	<i>Aequorea victoria</i>	Calcium	Blue-green	(Shimomura 2006)
	Deep-sea anthozoans	KCl, 50 mM CaCl ₂	475-507 nm	(Bessho-Uehara et al. 2020a)
	<i>Erenna</i> sp.	CaCl ₂ solution	410 nm	(Haddock et al. 2005)
	<i>Renilla koellikeri</i>	Adrenaline	480 nm	(Anctil et al. 1982)
Annelida	<i>Lampito mauritii</i>	Ammonia and H ₂ O ₂ diluted solutions	Blue	(Ismail and Kaleemurrahman 1981)
	<i>L. mauritii</i>	Glucose oxidase (12 mg ml ⁻¹) and 2 mM glucose in phosphate buffer	267 nm	(Haram et al. 1996)
	<i>L. mauritii</i>	50 mM Fe ²⁺ solution	270 and 410 nm	(Santhanam and Limaye 1989a)
	<i>L. mauritii</i>	K ₂ SO ₄ or phosphate buffer	270 and 410 nm	(Santhanam and Limaye 1989b)
	<i>L. mauritii</i>	Methylated spirits and weak solution of ammonium hydroxide or chloretone	Blue	(Gates 1925)
	<i>Eisenia lucens</i>	50% ethanol	493 nm	(Pes et al. 2016)
	<i>Henlea</i> sp.	Ca ions (1.3×10 ⁻⁴ M)	Blue	(Rodionova et al. 2002)
	<i>Tomopteris carpenteri</i>	200 mM KCl	564 nm	(Gouveneaux et al. 2016)
	<i>Tomopteris</i>	200 mM KCl or	573	(Gouveneaux et al.

	<i>helgolandica</i>	1 mM carbachol	nm	2017)
	<i>Tomopteris pacifica</i>	500 mM KCl	549 nm	(Gouveneaux et al. 2016)
	<i>Tomopteris planktonis</i>	200 mM KCl; 10 ⁻³ M carbachol	450 nm	(Gouveneaux et al. 2016)
	<i>Tomopteris septentrionalis</i>	1% Triton X-100	557 nm	(Gouveneaux et al. 2016)
Arthropoda	<i>Neoditomiya</i> larvae	5 µl of <i>Orfelia</i> luciferase and 5 µl of 100 mM DTT	~460 nm	(Viviani et al. 2020)
	<i>Photuris</i> sp.	70 ppm Nitric oxide	Yellow	(Trimmer et al. 2001)
	<i>Luciola praeusta</i>	Ethyl acetate vapors	Yellow	(Gohain Barua and Rajbongshi 2010)
	Copepoda	Buffered 5% formaldehyde solution	480 nm	(Losee et al. 1985)
	<i>Triconia conifera</i> (= <i>Oncaea conifera</i>)	Eserine, acetylcholine or carbamylcholine	469 nm	(Herring et al. 1993)
	<i>Meganyctiphanes norvegica</i> , <i>Thysanoessa raschii</i>	5-Hydroxytryptamine	Blue	(Kay 1962; Doyle and Kay 1967)
	<i>Meganyctiphanes norvegica</i>	Serotonin and nitric oxide	Blue	(Krönström et al. 2007)
Mollusca	Marine gastropods	Saturated NaCl solution	Blue	(Schultz and Oba 2014)
Echinodermata	Ophiuroid species	KCl, acetylcholine, carbachol, dopamine, 5-HT, and taurine	Blue	(Dewael and Mallefet 2002)
Tunicata	<i>Clavelina miniata</i>	K ⁺ ions or Hypotonic	Green	(Aoki et al. 1989)
Hemichordata	<i>Ptychodera flava</i>	Diluted H ₂ O ₂	528 nm	(Kanakubo and Isobe 2005)
Chordata	<i>Argyropelecus hemigymnus</i>	Nitric oxide	Blue	(Krönström et al. 2005; Krönström and Mallefet 2009)
	Etmopteridae and Dalatiidae	Melatonin (10 ⁻⁶ M)	Blue	(Claes and Mallefet, 2009b; Claes et al., 2012; Duchatelet et al., 2020a)
	Etmopteridae	Prolactin (10 ⁻⁶ M)	Blue	(Claes and Mallefet 2009a, 2015; Duchatelet et al. 2020a)
	Bony fishes	Nervous control	460-470	(Baguet and Case 1971; Anctil 1972;

			nm	Malfet et al. 2019)
	<i>Argyrolepecus hemigymnus</i>	Epinephrine	470 nm	(Baguet et al. 1980)
	<i>Porichthys notatus</i>	Epinephrine	475 nm	(Mensing and Case 1990, 1991)
	<i>Mauroliticus muelleri</i>	0.2 cc of epinephrine 1 :200 in isotonic saline	Blue-green	(Anctil 1972)

2.2. Mechanical stimulation

Among the various known kinds of stimulation, mechanically induced luminescence has gained the most attention by scientists and beach watchers. During sunset or at night, walking on the sandy shores containing washed up luminous dinoflagellates, produces instant bioluminescence due to the mechanical disturbance caused by the feet on the sand. Similarly, striking seawater with an oar or watching how leaping fish or dolphins leave a trail of light behind are other manifestations of mechanically induced luminescence. Gently touching or brushing against some bioluminescent dorids, sea pens, and various mid- and deep-water luminous creatures often results in an intense blueish light emission. In deep-sea submersibles, researchers are using a splat screen to check mechanically stimulated luminescence (MSL) in planktonic forms. MSL is an effective technique used in several of the bathyphotometer systems. Sometimes, MSL has acted as an early warning sign of toxic bloom formation (Le Tortorec et al. 2014). In this section, the bioluminescence response of various animals to different mechanical stimulants are being detailed.

2.2.1. Dinoflagellates

Dinoflagellates display something akin to a piezoelectric effect, in which various mechanical conditions may generate an electric charge that triggers their luminescence (Sweeney 1979; Latz 1995), but a distinct structure involved in this has not been identified and the entire cell body may be involved. Each dinoflagellate species responds differently to MSL (Latz et al. 1994) and in the natural environment, the red tide forming dinoflagellate *G. polyedra* is known to display flashes of spontaneous luminescence (Sweeney 1979). The green tide forming *Noctiluca scintillans* is also known to produce flashes of light spontaneously (Author Information). Often small planktonic microorganisms, including dinoflagellates and calanoid copepods, display luminescence triggered by mechanical stimulation. This can be due to an agitation of the water caused by turbulently moving seawater or the gentle swell, bubbles in the water, wind churning up the waves, breaking waves and their splashes, water currents, action of grazers (Blaser et al. 2002; Latz et al. 2004a, 2008;

Cussatlegras and Le Gal 2005, 2007; Deane et al. 2016), or by forces creating laminar fluid shear, turbulent pipe flow (Anderson et al. 1988; Latz et al. 2004b; Watanabe et al. 2012), by towing nets, swimming, rowing, boat propellers and moving ships, porpoising dolphins, seals, and leaping fish as well as sudden directional changes of whole fish shoals (Daniel et al. 1979; Williams and Kooyman 1985; Losee et al. 1985; Latz et al. 1990, 1994, 2004b, a; Webster et al. 1991; Rohr et al. 1998; Jamieson et al. 2006; Maldonado and Latz 2007; Deane et al. 2016; Vishal et al. 2021).

In dinoflagellates, mechanically induced luminescence differs from species to species (Latz et al. 2004b). Usually, dinoflagellates exhibit a 24-hour light intensity rhythm, with the greatest luminescence occurring at night and dips during the day (Hastings 2013). In the laboratory, dinoflagellate cells show luminescence when cells are accelerated in a centrifuge or passed through a capillary tube, and with a mechanical pulse from piezoelectric crystal (Sweeney 1979; Latz 1995). A study focusing on *Noctiluca* sp. demonstrated stimulated bioluminescence using a screw propeller (Han et al. 2015). Various other MSL techniques used included vigorously pouring seawater from one bucket into another container in a dark room (Meyer-Rochow 1986), using the suction of a vacuum pump in connection with luminescent copepods (Clarke et al. 1962), or making use of a piezoelectric suction pipette as in connection with *Gonyaulax* bioluminescence (Reynolds et al. 1969), and stirring the cell contents of *Ceratocorys horrida* in a vial (Latz et al. 1990; Latz 1995), either by hand or with a motor-driven paper clip as for *Gonyaulax* species (Esaias et al. 1973). Luminescence of *Noctiluca* sp. increased in parallel with the noise made by ships, because of the vibro-acoustic transducer frequencies and increasing energy (Jing et al. 2014). Cells of *Pyrocystis lunula* held in a micropipette displayed stimulated luminescence when subjected to fluid flow and direct physical indentation (Jalaal et al. 2020). Some luminous *Vibrio* species also produce intensive luminescence only upon stirring or vigorous shaking of a culture of them (Ramesh 2016).

2.2.2. Porifera, Cnidaria and Ctenophora

A demosponge, *Suberites domuncula* has been reported to possess a different luminescence mechanism from that of other animals, consisting of inorganic light converting silica spicules and organic luciferase enzymes (Wang et al. 2012; Martini et al. 2021). A deep sea carnivorous sponge, *Cladorhiza* sp. nov. collected from the Northeast Pacific Ocean, emitted light upon repetitive mechanical stimulation (Martini et al. 2021). Poking deep-sea scyphozoans with a mounted steel needle resulted in luminescence (Herring and Widder 2004). Luminescence in some species of ctenophores, medusae, and siphonophores was also inducible with a mesh screen or by gentle prodding (Haddock and Case 1999). In the ctenophore *Beroe ovata*, MSL resulted in twice the strength of luminescence than that produced by chemical stimulation (Tokarev et al. 2012), although

the latter was more effective in *Mnemiopsis leidyi* than MSL (Olga and Yuriy 2012; Tokarev and Mashukova 2016). Tactile stimulation in the sea pansy *Renilla* sp. generated waves of luminescence travelling down this organism (Nicol 1955). Brushing against a golden coral bush of the species *Keratoisis flexibilis* in deep water resulted in the emission of blue-green light; likewise, poking flytrap-anemones and other cnidarian species has been reported to lead to a blue luminescence (Johnsen et al. 2012). Squeezing the stalk of the sea pen *Stylatula*, using forceps, stimulated the propagation of light from stalk to plume or vice versa, depending on the squeezing point in relation to the stalk's or center or tip. Squeezing the stalk of an *Umbellula* species of sea pen, produced a change of coloration from green to blue light from stalk to plumes (Johnsen et al. 2012). Many deep-sea soft bodied organisms and plankton produce intense luminescence when coming into contact with the screen mesh (Widder et al. 1989). Agitation of deep-sea anthozoan specimens with a ROV's robotic arm has been noted to cause some of the specimens touched to produce luminescence (Bessho-Uehara et al. 2020a).

2.2.3. Annelida

Mechanically elicited luminescence in deep-sea polychaete worms was observed upon bumping or brushing against the worm's sides with a pipette or by aiming a jet of seawater at them or by tapping the sieve against water tank (Francis et al. 2016). A gentle touch given to the burrowing parchment worm *Chaetopterus* elicited luminescence but the large and luminous earthworms of New Zealand (e.g., *Octochaetus multiporus*) need to be handled roughly or even have to be physically injured before they produce their brightly luminescent, yellow-green secretions (Rota 2009). Species of the genus *Henlea* releases an intense blue slime at their body ends upon mechanical, chemical or thermal stimulation (Rota et al. 2018). Rough handling of planktonic worms via pinching, using forceps, pipetting (i.e., hydro-mechanical stimulation), and emersion using dipnetting are all known to cause spontaneous light production (Gouveneaux et al. 2018). Likewise, luminescence in the terrestrial luminous earthworm *Pontodrilus*, was stimulated via rough handling with a motor pestle (Seesamut et al. 2021). Placing seaweed samples with an attached *Odontosyllis* sp. into a bowl of freshwater usually resulted in the detached worms floating in the water and emitting an intense luminescence that lasted for 30 to 60 seconds (Ramesh et al. 2017).

2.2.4. Arthropoda

Production of copious luminescence from the urosomes of copepods like *Metridia longa* was observed in plankton net hauling (Lapota et al. 1986). Copepods, *Calanus* and *Gaussia* species all exhibit stimutable luminescence upon disturbing them with a rod by stirring (Barnes and Case 1972)

or prodding them by hand (Bowlby and Case 1991). Captured ostracods (e.g., *Vargula norvegica*) would produce pale blue luminescence upon agitation or shaking (Heger et al. 2007) and some ostracods are known to release clouds of luminescence if mechanically stimulated (Angel 1968). Blowing a gentle puff of air over luminescent springtails (*Collembola*) causes them to luminesce according to Prof. Marcel Koken (Pers. Comm.). MSL in the mysid shrimp, *Gnathophausia* resulted in luminescent secretions of bright blue coloration (Frank et al. 1984). The entire body of *Motyxia* millipedes displays a bright greenish-white glow either spontaneously or upon physical stimulation (Rosenberg and Meyer-Rochow 2009).

Interestingly, bioluminescence of *Arachnocampa flava* responded to noise, vibration, light exposure, and prey movements (Mills et al. 2016). In the Mid-Atlantic Ridge, zooplankton exhibited luminescence when they hit protruding rocky substrate areas (Craig et al. 2011). Similarly, many deep-sea pelagic organisms are observed to display luminescence when they collided with the telescopic infrastructure of a ROV (Aguzzi et al. 2017) or with pointed rocky substrates (Craig et al. 2011).

2.2.5. Echinodermata

Bioluminescent events (77%) observed on non-bioluminescent crinoids, e.g., *Anachalypsicrinus nefertiti* were likely due to defensive reactions of luminous zooplankton trapped on or colliding with the filtration arms (Craig et al. 2011). A gentle touch using fingers or stressing arms of the black brittle-star *Ophiocomina nigra* with a small pair of forceps for 5 minutes or so to mimic the action of the claw of a crab, resulted in the release of intensive bioluminescence localized in the stimulated area (Jones and Mallefet 2012).

2.2.6. Pyrosomes and Fishes

Repetitive MSL, using 1 cm diameter fiberglass rod with a solenoid, was used to elicit rhythmic high and low flashing luminescence displays in the pyrosomes *Pyrosoma atlanticum* and *P. verticillata* (Bowlby et al. 1990). Squeezing lanternfish species gently provoked brief repetitive flashes up to 1 to 2 s⁻¹, while rough handling resulted in more rapid flashes lasting 3-4 sec (Barnes and Case 1974). Mechanically damaged light organs or tissues did not produce luminescence (Barnes and Case 1974) (Table 2).

Table 2. Summary of various mechanical stimulants used to induce luminescence in some selected representative organisms.

Taxonomic group	Group/Organism name	Stimulant	Emission colour/λ_{max}	Reference
Bacteria	<i>Vibrio</i> , <i>Photobacterium</i>	Agitation or air bubbling	475-495 nm	(Ramesh 2016)
Fungi	<i>Armillaria</i> spp.	Pressure	515-525 nm	(Mihail 2015)
Dinoflagellates	Dinoflagellates	Seawater perturbation (see text)	478 nm	(Sweeney 1979; Losee et al. 1985; Latz et al. 1990, 1994; Latz 1995; Jamieson et al. 2006; Deane et al. 2016)
	Dinoflagellates	Zooplankton & nekton movements	Blue	(Buskey et al. 1990)
	Dinoflagellates	Motor acceleration	475 nm	(Stolzenberg et al. 1995)
	<i>Gonyaulax</i> sp.	Piezoelectric suction pipette	Blue	(Reynolds et al. 1969)
	<i>Alexandrium ostenfeldii</i> , <i>Lingulodinium polyedra</i> , <i>Pyrodinium bahamense</i> , and <i>Pyrocystis lunula</i>	Bubbling & stirring	470 nm	(Biggley et al. 1969; Kauko 2013)
	<i>Lingulodinium polyedra</i>	Shear, acceleration, and pressure	Blue	(Anderson et al. 1988)
	<i>Ceratocorys horrida</i>	Stirring	478 nm	(Latz et al. 1990; Latz 1995)
	<i>Alexandrium catenella</i> (= <i>Gonyaulax catenella</i>)	Stirring with a motor-driven paper clip	Blue	(Esaias et al. 1973)
	<i>Gonyaulax spinifera</i>	Shear, hand splash, oar and swimming movements	Blue	(Vishal et al. 2021)
	<i>Noctiluca</i> sp.	Acoustic transducer	Blue	(Jing et al. 2014)
	<i>Noctiluca</i> sp.	Screw propeller	498 nm	(Han et al. 2015)
	<i>Pyrocystis fusiformis</i>	Bump with container or cells	Blue	(Sweeney 1979)
	Zooplankton	Protruding rocky	Blue	(Craig et al.

		surface, mesh, baits		2011)
Porifera	<i>Cladorhiza</i> sp. nov.	Mechanical	Blue	(Martini et al. 2021)
Ctenophora	Ctenophores	Mesh screen or gentle prodding	465–470 nm	(Haddock and Case 1999)
	<i>Beroe ovata</i> , <i>Mnemiopsis leidyi</i>	Poke or touch	Blue	(Tokarev et al. 2008a, 2012)
Cnidaria	Deep-sea anthozoans	Agitation using robotic arm of ROV, hand touch, & gentle pipette touch	475-538 nm	(Bessho-Uehara et al. 2020a)
	Deep-sea scyphozoans	Prodding with a mounted steel needle	465–470 nm	(Herring and Widder 2004)
	Medusae and siphonophores	Mesh screen or gentle prodding	465–470 nm	(Haddock and Case 1999)
Annelida	Deep-sea polychaete worms	Bumping with a pipette or squirting with seawater	493-497 nm	(Francis et al. 2016)
	<i>Henlea</i> sp.	Mechanical, chemical, thermal	Blue	(Rota et al. 2018)
	<i>Tomopteris</i> sp.	Touch with dissection needle	565-570 nm	(Gouveneaux et al. 2016)
	Luminous earthworms and parchment worm, <i>Chaetopterus</i> sp.	Gentle touch	Blue	Author Information
	<i>Pontodrilus</i> sp.	Rough handling (motor pestle)	524–528 nm	(Seesamut et al. 2021)
Arthropoda	<i>Motyxia</i> sp.	Physical stimulation	Greenish-white	(Rosenberg and Meyer-Rochow 2009)
	<i>Geophilus electricus</i>	Poke with finger or needle	Green	Author Pers. Comm.
	Copepoda (unspecified)	Vacuum suction	482 nm	(Clarke et al. 1962)
	<i>Metridia longa</i>	Plankton net hauling	Blue	(Lapota et al. 1986)
	<i>Pleuromamma xiphias</i>	Hydrodynamic stimuli	Blue	(Hartline et al. 1999)
	<i>Vargula norvegica</i>	Shaking	Blue	(Heger et al. 2007)
	<i>Collembola</i> sp.	Blowing a gentle air	Blue	Prof. Marcel Koken, Unpublished data

	<i>Meganyctiphanes norvegica</i>	Gentle squeeze		(Mauchline 1960)
	<i>Meganyctiphanes norvegica</i>	Water oscillation (3–150 Hz)	480 nm	(Fregin and Wiese 2002)
Echinodermata	<i>Ophiocomina nigra</i>	Gentle touch or nudging with forceps	Blue	(Jones and Mallefet 2012)
Tunicata	<i>Pyrosoma atlanticum</i> and <i>Pyrosomella verticillata</i>	Prodding with fiberglass rod	475 nm	(Bowlby et al. 1990)

2.3. Electrical and Magnetic stimulation

Although these kinds of stimulation are less frequently practiced, methods such as these have resulted in the elicitation of luminescence in scyphozoans and earthworms and appear to have been able to affect luminescent displays in fireflies and glowworms.

2.3.1. Radiolarians and Dinoflagellates

In radiolarians, train of flashes were detected in response to repetitive electrical stimuli (Herring 1979). The electrical stimulation of bioluminescence via the insertion of a microelectrode into the vacuole of *Noctiluca miliaris* and *P. fusiformis* resulted in flashes of luminescence (Sweeney 1979).

2.3.2. Cnidaria

Treatment of deep-sea scyphozoans with 20 V current for 5 ms resulted in visible stimulated bioluminescence (Herring and Widder 2004). Light emission in the sea pansy *Renilla* was induced by stimulation with 0.1 msec pulses of 5–15 V, with a Grass S4 stimulator using an A.C. amplifier (Anderson and Case 1975).

2.3.3. Annelida and Arthropoda

In the Indian luminescent earth worm *Lampito mauritii* a display of bioluminescence was initiated upon stimulating it with a 4 V electric shock (Ismail and Kaleemurrahman 1981). Copepods held in chambers of wax or lucite, containing platinum or carbon electrodes produced luminescence when supplied with short bursts of alternating current (60 hz) or condenser shocks (up to 20 V, 0–5/ μ F) (Clarke et al. 1962; Herring et al. 1993). Pulses of 50 V, 5 ms current shocks elicited luminescence in the copepod *Gaussia princeps* (Bowlby and Case 1991). A range of electrical stimuli from 4 – 8 V, provided by an ac-generator that supplied pulses of a range of voltages and durations, was used to elicit bioluminescence in the larvae of the Japanese fungus gnat *Keroplatus nipponicus* (Osawa et al.

2014). The most intense luminescence occurred when the larvae were subjected to a one minute long 6 V exposure.

The effects of a strong pulsed train magnetic field (PMF) and a 10 Tesla order of static magnetic field on the flash repetition rates in the Japanese fireflies *Luciola cruciate* and *L. lateralis* (Iwasaka et al. 2011) as well as the Indian *L. praeusta* (Gohain Barua et al. 2012) were studied and it could be shown that flashing became more rapid, occasionally producing broad compound flashes, as a response to the magnetic field exposure. The emitted light from *L. cruciate* and *L. lateralis* also showed a tendency of being red-shifted in the range of 540 to 580 nm when the fireflies emitted their pulses under the magnetic field (Iwasaka et al. 2011).

2.3.4. Pyrosomes and Fishes

In the pyrosomes *P. atlanticum* and *P. verticillata*, luminescence was elicited using a Grass S48 stimulator and tungsten electrodes (0.5-50 Hz, 5 ms duration, 50 V) (Bowlby et al. 1990). Stimulation of the spinal cords of Atlantic lanternfishes *Benthosema glaciale*, and *Myctophum punctatum* with pulses of 3-5 V for 5 to 10 s⁻¹ evoked flashes of luminescence (Anctil 1972). Photophores of the bathypelagic fish *Chauliodus sloanei* emitted erratic luminescence flashes when stimulated with 50 V and slower flashes with 10 V anodic stimuli (Christophe et al. 1979). Photophores of *Arqyropelecus*, *Diaphus*, and *Ichthyoeoccus* species also responded with brief flashes to 20-80 V (4-15 msec) electrical stimulation (Baguet and Marechal 1976; Baguet et al. 1980). Luminous tissue patches and photophores of lanternfishes reacted to an electrical impulse (15-40 V, 3-5 ms) with the production of spontaneous luminescence of variable light intensity (Barnes and Case 1974) (Table 3).

Table 3. Summary of electrical and magnetic stimulants used to induce luminescence in some selected representative organisms.

Taxonomic group	Group/Organism name	Stimulant & Concentration	Emission colour/λ_{max}	Reference
Dinoflagellates	<i>Noctiluca scintillans</i> (= <i>Noctiluca miliaris</i>) and <i>Pyrocystis fusiformis</i>	Microelectrode	Blue	(Sweeney 1979)
Cnidaria	Deep-sea scyphozoans	20 V current, 5 ms	465–470 nm	(Haddock and Case 1999; Herring and Widder 2004)
	<i>Renilla</i> sp.	5-15 V current, 0.1 ms	480 nm	(Anderson and Case 1975)
Annelida	<i>Lampito mauritii</i>	4 V electric shock	Blue	(Ismail and Kaleemurrahman 1981)
	<i>Tomopteris carpenteri</i>	9 V current	572 nm (yellow)	(Gouveneaux et al. 2016)
	<i>Polycirrus</i> sp.	Inductorium shocks	Blue	(Johnson and Johnson 1959)
	<i>Pontodrilus</i> sp.	Electricity	524–528 nm	(Seesamut et al. 2021)
Arthropoda	Copepoda (unspecified)	Alternating current (60 hz) or condenser shocks (up to 20 V)	469-483 nm	(Clarke et al. 1962; Herring et al. 1993)
	<i>Gaussia princeps</i>	50 V, 5 ms	Blue	(Bowlby and Case 1991)
	<i>Keroplatus nipponicus</i>	6 V, 1 min	460 nm	(Osawa et al. 2014)
	<i>Luciola crucita</i> , <i>Luciola lateralis</i> , <i>Luciola praeusta</i>	Pulsed train magnetic fields (10T and 250–325 T/s at 1.3–10 Hz)	540-580 nm	(Iwasaka et al. 2011; Gohain Barua et al. 2012)
Tunicata	<i>Pyrosoma atlanticum</i> and <i>Pyrosomella verticillata</i>	50 V, 0.5-50 Hz, 5 ms	475 nm	(Bowlby et al. 1990)
Chordata	<i>Argyropelecus</i> , <i>Diaphus</i> and <i>Ichthyococcus</i>	20-80 V (4-15 msec)	Blue	(Baguet and Marechal 1976; Baguet et al. 1980)
	<i>Bentho sema glaciale</i> , and <i>Myctophum punctatum</i>	3-5 V at 5 to 10/s	Blue	(Anctil 1972)
	<i>Chauliodus sloani</i>	10 V (1 ms) & 50 V (4-8 ms)	Blue	(Christophe et al. 1979)

2.4. Photostimulation

Different kinds of spectral lights ranging from the UV to red wavelengths delivered as brief pulses, or longer exposures were used in connection with several groups of organisms to induce luminescence. In this context the combination of lights (strobe light vs. steady light, lasers vs. strobes, etc.) and their most effective spectral range in stimulating or eliciting luminescence need to be studied in more detail, especially with regard to the role that the luminescent organisms' photoreceptors play in this. In this section, brief details of various photo-stimulants used to induce luminescence of different organisms are garnered.

2.4.1. Bacteria

A variety of studies demonstrated that when the luminous *Photobacterium leiognathi*, *P. phosphoreum*, *Aliivibrio fischeri*, and *V. harveyi* (Czyz et al. 2002) and *V. campbellii* (Ramesh et al. 2014) were exposed light of a UV emitting source, they responded with a predictable and intense luminescence.

2.4.2. Dinoflagellates

The unicellular dinoflagellates, *Gonyaulax polyedra* (= *Lingulodinium polyedra*), *Pyrocystis fusiformis*, and *P. lunula* exhibited stimulated luminescence (478 nm) under red light upon irradiation of cell suspensions treated with various chemical components (Sweeney et al. 1983). Under controlled conditions, stimulated luminescence was observed in the dinoflagellate *Protoperidinium depressum* (Lapota et al. 1986). Stimulated bioluminescence at various temperatures was observed in the dinoflagellate *Pyrocystis lunula* using a pulsed dye laser and rhodamine 6G dye with an optimum laser wavelength of $586 \pm 30\text{nm}$ (Hickman et al. 1984).

2.4.3. Cnidaria and Ctenophora

Bioluminescent responses of soft bodied deep-sea organisms like hydromedusa and pelagic worms were recorded at high frame rates upon light stimulation (Phillips et al. 2016a). The illumination of other luminous organisms appears to cause a decrease or even total disappearance of luminous ability (e.g., photoinhibition in the ctenophore *Mnemiopsis* due to a dissociation of coelenterazine and oxygen from the photoprotein mnemiopsin) (Anctil and Shimomura 1984). Under controlled conditions light flashes were also found to stimulate luminescence in the siphonophore *Vogtia serrata* (Lapota et al. 1986).

2.4.4. Annelida and Arthropoda

A recent experimental study demonstrated that *Tomopteris helgolandica* produces yellow and blue emission signals in response to yellow and blue lights as stimuli, supporting the hypothesis of intraspecific communication (Gouveneaux et al. 2018). The black body segments of the luminescent *Orfelia fultoni* displayed blue fluorescence under UV (375 nm) irradiation (Viviani et al. 2020). Ostracods such as *Cypridina noctiluca* and *C. serrata*, the mesopelagic shrimp *Sergestes similis* (Lapota et al. 1986), the euphausiids *Meganyctiphanes norvegica* (Kay 1965) and *Thysanoessa raschii* (Tett 1969), copepods (Buskey and Swift 1985), as well as chaetognaths have been reported to respond to illumination and/or flashes of light with a bioluminescent reaction (Buskey and Swift 1985).

The group most thoroughly studied in terms of responses to photic stimulation by emitting their own lights are fireflies as shown, for example by Carlson et al. (1977), Buck and Case (1986), Carlson and Copeland (1985) and several others summarized by Ohba (2004), Lewis (2009) and Bechara and Stevani (2018).

2.4.5. Tunicata

Pyrosomes such as *P. atlanticum* and *P. verticillata* provide some of the best examples of light-induced luminescence. Experiments with photic stimulation were carried out using Bausch and Lomb monochromator with a tungsten light source (Bowlby et al. 1990), and using Nikon Speedlight SB-910 strobe (Tessler et al. 2020). The maximum spectral response was detected at 475 nm with a mean photon emission of 1.1×10^7 in *P. atlanticum* and 9.3×10^7 in *P. verticillata* (Bowlby et al. 1990) (Table 4).

Table 4. Summary of photostimulants used to induce luminescence in some selected representative organisms.

Taxonomic group	Group/Organism name	Stimulant & Concentration	Emission colour/λ_{max}	Reference
Bacteria	<i>Aliivibrio fischeri</i> , <i>Photobacterium leiognathi</i> , <i>Photobacterium phosphoreum</i> , and <i>Vibrio harveyi</i>	UV light	Blue (475-495 nm)	(Czyz et al. 2002)
	<i>Vibrio campbellii</i>	UV light	Blue	(Ramesh et al. 2014)
Fungi	<i>Omphalia flavida</i>	UV-light	530 nm	(Cormier and Trotter 1966)
	<i>P. stipticus</i>	X-radiation	530 nm	(Wassink 1979)
Dinoflagellates	<i>Lingulodinium polyedra</i> (= <i>Gonyaulax polyedra</i>), <i>Pyrocystis fusiformis</i> and <i>Pyrocystis lunula</i>	Red light	478 nm	(Sweeney et al. 1983)
	<i>P. lunula</i>	Pulsed dye laser	Blue	(Hickman et al. 1984)
	<i>P. lunula</i> , <i>P. fusiformis</i> and <i>P. noctiluca</i>	Light	Blue	(Swift and Meunier 1976)
	Planktonic forms	White light, blue-green light	340-740 nm	(Neshyba 1967)
	Dinoflagellate, <i>Protoperidinium depressum</i>	Flashes of light	Blue	(Lapota et al. 1986)
Cnidaria	Hydromedusa and pelagic worms	Strobe light	Blue	(Neshyba 1967; Phillips et al. 2016a)
	<i>Vogtia serrata</i>	Flashes of light	Blue	(Lapota et al. 1986)
	<i>Lepidisis</i> sp.	Red light	477 nm	(Bessho-Uehara et al. 2020a)
Arthropoda	<i>Orfelia fultoni</i> black bodies	UV (375 nm)	~460 nm	(Viviani et al. 2020)
	Likely shrimp	Strobe light	~500 nm	(Phillips et al. 2016b)
	<i>Meganyctiphanes norvegica</i> & <i>Thysanoessa raschii</i>	Flashes of light	Blue	(Kay 1965; Tett 1969)
	<i>Cypridina noctiluca</i> and <i>C. serrata</i>	Flashes of light	Blue	(Lapota et al. 1986)
	<i>Eusergestes similis</i> (= <i>Sergestes similis</i>)	Flashes of light	Blue	(Lapota et al. 1986)
Tunicata	Pyrosomes	Bausch and Lomb monochromator	475 nm	(Bowlby et al. 1990)

2.5. Thermal stimulation

Luminous bacterial species are known to produce blue to blue-green luminescence. However, the *Aliivibrio fischeri* strain Y-1 emits yellow light at 18°C and blue luminescence at higher temperatures (>18°C) (Herring 2002). Lowering the environmental temperature from 22 to 17°C had a stimulatory effect on the luminescence of *Noctiluca scintillans* (Sato and Hayashi 1998). However, this was not observed in another *Noctiluca* sp., whose bioluminescence was triggered by MSL (Han et al. 2013). In *G. polyedra*, an increased intensity of luminescence was observed when the ambient temperature was gradually increased from 20°C to 25°C (Sweeney 1979) (Table 5).

Table 5. Summary of thermal stimuli used to induce luminescence in some selected representative organisms.

Taxonomic group	Group/Organism name	Stimulant & Concentration	Emission colour/λ_{\max}	Reference
Bacteria	<i>Aliivibrio fischeri</i> Y-1	Temperature	Yellow (540 nm at 18°C) and blue (475 nm at >18°C)	(Herring 2002)
Dinoflagellates	<i>Noctiluca scintillans</i>	Lowering temperature (22 to 17°C)	Blue	(Sato and Hayashi 1998)
	<i>Noctiluca</i> sp.	Increasing temperature (15 to 19°C)	Blue	(Han et al. 2013)
	<i>Lingulodinium polyedra</i> (= <i>Gonyaulax polyedra</i>)	Raising temperature (20° to 25°C)	Blue	(Sweeney 1979)

2.6. Biological stimulation

Under this heading we include forms of mechanical and other forms of stimulation, which are delivered by other organisms through contacts, attack, startle, arousal, and feeding.

2.6.1. Bacteria and Dinoflagellates

Free-living strains of *A. fischeri* start to emit luminescence when they colonize squids (Reen et al. 2006). Some bacteria exhibit an increase in luminescence in the presence of other microorganisms (e.g., *Aliivibrio fischeri* found to produce brighter luminescence in the presence of *Pseudoaltermonas piscicida*) (Berleman 2009). Either non or normally only dimly luminescent pathogenic species emit increasingly brighter light following the colonization of what is usually a non-luminescent species of

a host arthropod. For example, in cases that out of about 14 colonizing bacterial species mainly involved *Vibrio harveyi*, the latter can cause major damage to cultured penaeid shrimps like *Penaeus monodon*, in which the affected non-luminescent individuals turn luminescent, become limp and placid, and then die (Azizunnisa and Sreeramulu 2013). For terrestrial insects we can refer to a study by Pfeiffer and Stammer, who investigated the role of a pathogen known to them as *Bacterium haemophosphoreum* in rendering a caterpillar of the moth *Mamestra oleracea* brightly luminescent (Pfeiffer and Stammer 1930). However, a more detailed examination in this anecdotally reported case was not carried out.

2.6.2. Cnidaria and Ctenophora

Scyphozoans are known to produce luminescence when in contact with another animal (Herring and Widder, 2004). Non-luminous *Aequorea* produced luminescence when fed with the bioluminescent ctenophore *Bathocyroe fosteri* and the hydromedusa *Mitrocoma cellularia*. In these cases, the light emission lasted for up to two weeks upon a single feeding event even after repeated stimulations (Haddock et al., 2001).

2.6.3. Annelida and Arthropoda

Luminescent earthworms appear not to emit light unless they are being attacked and physically damaged by a predator (Sivinski and Forrest 1983; Rota 2009).

In the glowworms of the genus *Arachnocampa*, luminescence is stimulated by feeding (Meyer-Rochow 2007; Willis et al. 2011; Merritt et al. 2012), but they have also been seen to respond with luminescence when a predator attacks them and especially when a non-luminescent pupa or female adult is touched by a male. Most thoroughly studied under both field and laboratory conditions by, to name but a few, Buck and Buck (1966), Lloyd (1986), Ohba (2004), Lewis (2009), Faust (2017), has been the flash communication between male and female fireflies, in which photic signals emitted by one individual and perceived by the photoreceptors of another (Lall 1981; Eguchi et al. 1984; Lall et al. 2009) can lead to a luminescence response in the receiving individual.

The ostracod *Vargula norvegica* has been observed to release luminescence as an anti-predation defence against attacks by the eel *Synaphobranchus kaupii* (Gillibrand et al. 2007a, b; Heger et al. 2007). Copepod luminescence is also often a response to stimulation by their predators' (e.g., euphausiids) attacks on them (David and Conover 1961). Artificial food falls in the form of bait (mackerel, *Scomber scombrus*) observed to indirectly promote the luminescence in *V. norvegica* (Heger et al. 2007) or other deep-sea animals (Priede et al. 2006). The deep-sea shrimp *Acanthephyra purpurea* spews or squirt out a bioluminescent cloud at the approach of a predator in

order to escape from predators (Widder 2010) and similar behavioural reactions have been credited to luminescent squids. The brackish water amphipod, *Pontogammarus maeoticus*, has been reported to emit a steady green light from its whole body, which is postulated to be of bioluminescent bacterial origin (Copilas-Ciocianu and Pop 2020).

2.6.4. Mollusca, Echinodermata, and Fishes

Several deep-sea non-luminous cephalopods and octopods were noticed to become luminous upon obtaining dietary luciferin (Young et al. 1979). The tissues (e.g., kidney, blood, digestive gland) of some squid and octopus, when exposed to air, treated with H₂O₂ or treated with photophore extract containing luciferase, can turn intensely luminous (Young et al. 1979). The bobtail squid *Euprymna scolopes* (Nyholm and McFall-Ngai 2004) as well as especially mid-water species of squid (Young et al. 1979) eject a cloud of bacterial luminescence at the approach of predators in order to temporarily overstimulate the sensitive eyes of the latter and render them blind.

A recent study demonstrated the role of coelenterazine-supplemented pellets and non-coelenterazine-supplemented pellets in the induction of light in the ophiuroid *Amphiura filiformis* (Mallefet et al. 2020). Many luminescent fishes and crustaceans obtain dietary luciferin for their own luminescence emission (Frank et al. 1984). Brittle stars release luminescent flashes when injured by a crab's pincers (Deheyn et al. 2000; Jones and Mallefet 2013), and as a common result the startled crab avoids the brittle star (Grober 1990). Flashlight fish school display coordinating behavior via each other's light stimulation (Gruber et al. 2019). For the luminescent freshwater limpet *Latia neritoides* it has been reported that a sticky greenish luminescent slime is released when attacked by an eel or dragonfly nymph and that the attackers take a long time to remove the luminous sticky substance (Meyer-Rochow and Moore 1988). The luminous fish *Parapriacanthus ransonneti* acquires its luciferase and luciferin by preying on the luminous ostracod *Vargula hilgendorfi* (Bessho-Uehara et al. 2020b) (Table 6).

Table 6. Summary of biological stimulants involved in stimulated luminescence in some selected representative organisms.

Taxonomic group	Group/Organism name	Stimulus	Emission colour/λ_{\max}	Reference
Bacteria	<i>A. fischeri</i>	Colonization with squid	Blue	(Reen et al. 2006)
	<i>A. fischeri</i>	<i>Pseudoalteromonas piscicida</i>	Blue	(Berleman 2009)
Dinoflagellates	Dinoflagellates	Predator contact or grazing	Blue	(Latz and Rohr 1999; Latz et al. 2004b)
Cnidaria	Scyphozoans	Contact with another animal	465–470 nm	(Herring and Widder 2004)
	<i>Aequorea victoria</i>	Dietary luciferin	Blue	(Haddock et al. 2001)
Annelida	<i>Pontodrilus</i> sp.	Insect bites	524–528 nm	(Seesamut et al. 2021)
Arthropoda	<i>Arachnocampa</i> spp.	Feeding activity	Blue	(Willis et al. 2011)
	<i>Acanthephyra purpurea</i>	Predators	~475 nm	(Widder 2010)
	<i>Pontogammarus maeoticus</i>	Luminous bacteria	Green	(Copilas-Ciocianu and Pop 2020)
	<i>Metridia lucens</i>	Predators	482 nm	(David and Conover 1961)
Mollusca	Shrimps	Dietary coelenterazine	Blue-green	(Shimomura et al. 1980)
	<i>Euprymna scolopes</i>	Predators	Blue	(Nyholm and McFall-Ngai 2004)
	Non-luminous cephalopods	Uptake of dietary preluciferin	Blue	(Young et al. 1979)
	Squids	Dietary coelenterazine	Blue-green	(Shimomura et al. 1980)
	<i>Latia neritoides</i>	Attack by predator	505 nm and 535 nm	(Shimomura and Johnson 1968; Meyer-Rochow and Moore 1988)
Echinodermata	Brittle stars	Crab pincers bite	Blue	(Jones and Mallefet 2013)
Chordata	Some fishes	Dietary coelenterazine	Blue-green	(Shimomura et al. 1980)
	<i>Parapriacanthus ransonneti</i>	Preying on ostracod <i>Vargula hilgendorffii</i>	456 nm	(Bessho-Uehara et al. 2020b)

2.7. Gene acquisition or nucleotide deletion mediated luminescence

It has now been demonstrated repeatedly that many micro and macro-organisms can be transformed into a glowing state through genetic engineering by the use of genes responsible for light emission. For instance, many non-luminous bacterial and fungal species are known to produce luminescence upon the cloning of *lux* and *luc* genes (Ramesh 2021). But there are, however, exceptional cases in the natural environment where, as one example, a freshwater bacterium known as *Vibrio cholerae* biovar *albensis* displayed luminescence due to two nucleotide deletions in the *luxO* gene (Kasai 2006). In this strain, the operon is regulated by the 4,5-Dihydroxy-2,3-pentanedione inducer (Kasai 2006). Conversely, many non-luminous bacterial members of the genus *Vibrio* and *Photobacterium* are known to become luminous by acquiring *lux* genes through the phenomenon of horizontal gene transfer (HGT) phenomenon (Dunlap and Urbanczyk 2013) or by losing or modifying certain specific genes (Ramesh and Mohanraju 2017) (Fig. 3; Table 7). To date these processes have only been identified in *Vibrio* and *Photobacterium* species; thus, it remains an open question as to whether other group of bacteria could turn into emitting species by *lux* gene acquisition.

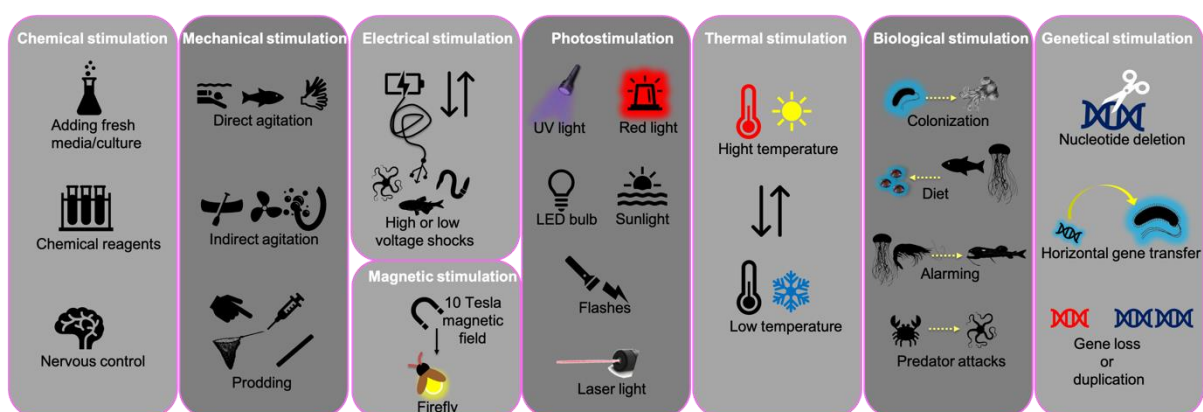


Fig. 3. An overview of stimulation methods leading to the emission of bioluminescence.

Table 7. Summary of gene acquisition or nucleotide deletion mediated luminescence in bacteria.

Taxonomic group	Organism	Stimulus	Emission colour/ λ_{max}	Reference
Bacteria	<i>Vibrio cholerae</i> biovar <i>albensis</i>	Two nucleotides deletion in <i>luxO</i>	Blue	(Kasai 2006)
	<i>Photobacterium</i> and <i>Vibrio</i>	HGT of <i>lux</i> genes	Blue	(Urbanczyk et al. 2008)
	<i>Photobacterium</i> and <i>Vibrio</i>	Loss or duplication of <i>lux</i> genes	Blue	(Dunlap and Urbanczyk 2013; Ramesh and Mohanraju 2017)

4. Future perspectives

Many terrestrial and aquatic organisms are yet to be tested to affirm their ability to emit biological light under natural or stress conditions. Various methods and techniques are available to test whether or not an organism can be termed bioluminescent. Approaches using the outlined stimulations may help to discover organisms with unknown biochemical reactions underlying bioluminescence. The rate of stimuli, stimuli-dependent luminescence patterns, flash types, flash frequencies, kinetics of luminescence, duration, depletion rate, and quantum emission aspects as well as biochemical background should then be studied for any stimulus-dependent luminous emissions. Questions, for example, when and how and under what environmental conditions the light emissions take place and to what extent lack and quality of food, age and sickness of an individual affect the generation of the biological light should then be asked and tackled in order to more fully understand the role of biological light emissions in ecology and biodiversity contexts.

Conflict of interest

The author does not have any conflict of interest to declare.

Ethical Statement

Not applicable.

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