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A review of mechanically stimulated bioluminescence of marine plankton and its applications

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Bioluminescence is ubiquitous in marine ecosystems and found in uni- and multicellular organisms. Bioluminescent displays can be used to deter predators, attract mates, and lure and hunt prey. Mechanically stimulated flash kinetics of zooplankton and dinoflagellates are life stage-dependent and species-specific, and could prove effective at identification and monitoring biodiversity in bioluminescent species. Here, we provide a comprehensive review of mechanically stimulated bioluminescence for the main dinoflagellate and zooplankton clades in marine environments and assemble known flash kinetics and spectral emission data. Instruments and methods used in measuring bioluminescence are also discussed. Applications, research gaps, perspectives, and biases in approaches to studying bioluminescence are identified. Moreover, emission kinetics of most zooplankton are very poorly known and constitute a critical gap. Lastly, available knowledge is interpreted in terms of potential future changes in global bioluminescence driven by climate change.

KEYWORDS
bioluminescence, zooplankton, dinoflagellates, flash kinetics, wavelength, climate change

1 Introduction

Bioluminescence is a widespread mode of communication in marine environments. Lau and Oakley (2021) estimated that bioluminescence evolved at least 94 times across all taxa and is present in at least 760 genera (Herring, 1987; Haddock et al., 2010). Considering bioluminescent organisms are taxonomically widespread and present in most marine ecosystems (Lapota and Losee, 1984; Martini and Haddock, 2017), understanding its drivers, functions, and diversity is imperative and relevant to marine biologists, ecologists, and physical and biological oceanographers alike. Bioluminescence can be stimulated chemically by a change in water pH by adding specific chemicals, electrically by applying a voltage to the water volume, or mechanically by disturbing the flow (Hamman and Seliger,

1972; Herring, 1981). Mechanical stimulation is achieved when hydrodynamic external forces, e.g., waves, eddies, feeding currents of filtering organisms, etc., exert local stress on the cellular membrane, enabling an action potential and the bioluminescent chemical reaction to occur (Deane and Stokes, 2005). This review is focused solely on mechanically stimulated bioluminescence of marine planktonic organisms.

Mechanically stimulated bioluminescence (MSB) can often be seen on beaches with breaking waves, or in the wake of a moving ship or swimming nekton. As in all luminescent organisms, light emission is caused by a chemical reaction in specialized organelles or cells with the substrate luciferin catalyzed by the enzyme luciferase. Several different types of luciferin exist and vary between and within phyla (see Haddock et al. (2010) and Widder (2010a) for a taxonomic breakdown of chemical diversity). Euphausiids and dinoflagellates both use dinoflagellate luciferin. Cnidarians, ctenophores, some ostracods, copepods, decapod shrimps, chaetognaths, and larvaceans all use coelenerazine as their luciferin. *Cypridina* luciferin is found only in cypridinid ostracods and the midshipman fish *Porichthys*, their predator (Haddock et al., 2010). Every luciferin, when oxidized in a chemical reaction mediated by a corresponding luciferase, will emit at a wavelength spectrum that is unique to the luciferin and accessory proteins, thus resulting in varying spectral properties across bioluminescent organisms (Wilson and Hastings, 2012). Emissions may be further spectrally filtered by cellular contents and/or tissues.

Figure 1 shows a typical first flash response of the dinoflagellate *Pyrocystis fusiformis*, obtained through mechanical stimulation in the Underwater Bioluminescence Assessment Tool (UBAT; SeaBird Electronics, Bellevue, WA). For those organisms able to flash multiple times, the first flash is usually most intense. Since the kinetics associated with the first emission are often species-specific (Nealson et al., 1986; Johnsen et al., 2014), they have potential for differentiating between species *in situ*. Typical flash kinetic parameters for an individual organism are generally the peak intensity (PI) in photons/s, the rise time (RT) in ms, the decay time (DT) in ms, the flash duration (FD) in ms, and the first flash of mechanically stimulated light (FF-MSL) in photons/flash. The peak intensity is measured as the highest instantaneous intensity during the first flash. The rise time is measured as the time between the first emission above baseline to the peak intensity. Similarly, the decay time is measured from the peak intensity to its return to baseline. The flash duration is measured as the time at which emissions are above baseline for a single emission. It is also equal to the sum of RT and DT. FF-MSL is the total amount of photons emitted in a single flash, based on the time period established by the flash duration. FF-MSL and often other kinetic parameters are highly dependent on the applied shear level, physiological state of the organism, and the instrument used for measurement (Latz and Rohr, 2013). The e-folding time (EF, in ms) is the time needed for the decaying emission intensity to reach 1/*e* of the maximum intensity, starting from the emission peak timestamp. For bathyphotometer mechanically stimulated light (BP-MSL) and total mechanically stimulable light (TMSL), we follow the descriptions of Latz and Rohr (2013). BP-MSL is defined as the average bioluminescence intensity measured in a specific bathyphotometer (photons/s), but is more specifically expressed in photons/s/L when taking into account the bathyphotometer's chamber volume and flow rate. This parameter or similar derived parameters have been used to characterize a water system based on MSL and to uncover associated seasonal and spatial variations in emission capacity (see Section 5 for ecological applications). Importantly, BP-MSL is instrument-specific since every bathyphotometer has different incident shear stresses affecting the MSL and its flash kinetics. Additionally, residence times for organisms in a photometer measurement cavity vary between sensors, so measurements can only be effectively compared when using the same instrument

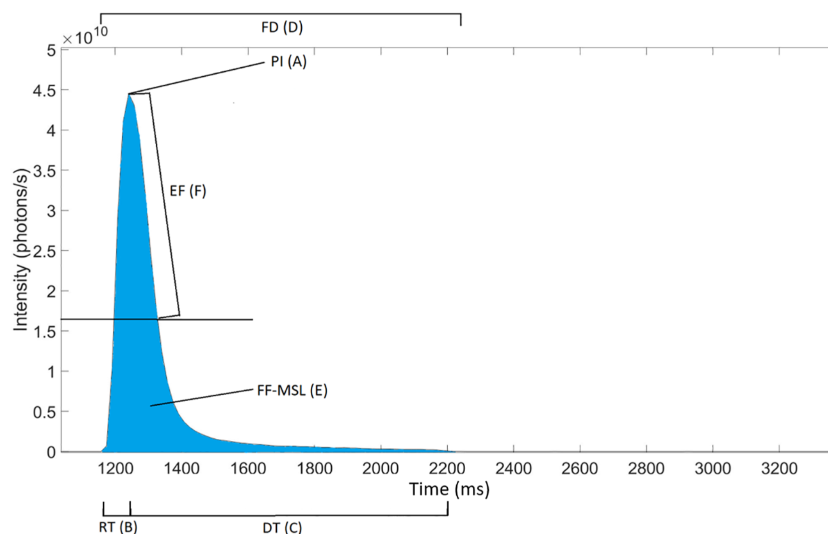

FIGURE 1
Typical first flash emission of the dinoflagellate *Pyrocystis fusiformis* obtained with the UBAT, with annotated flash kinetics. (A) Peak intensity (PI). (B) Rise time (RT). (C) Decay time (DT). (D) Flash duration (FD). (E) First flash of mechanically stimulated light (FF-MSL). See text for details.

(more detail provided in Section 3). TMSL is typically determined in a controlled laboratory setting and can be described as the total amount of mechanically stimulated light (or luminescence) for a single individual or cell under maintained stimulation until light emission exhaustion, with units photons/cell or photons/ind. Bioluminescence potential (BP) is the absolute maximal amount of photons that can be produced by an organism, typically measured through acid treatment and is expressed in photons/cell or photons/ind. This is the terminology that will be used to discuss kinetics, as there are significant inconsistencies in the literature (see Section 6).

Herein, we discuss current knowledge and gaps for MSB of dinoflagellates and the main zooplankton clades. We outline the various functions attributed to biologically emitted light and discuss what is known regarding the role of MSB. We provide an extensive and updated review of MSB flash kinetics of several species measured over the past few decades. Since several hundred bioluminescent species exist, we discuss every major planktonic group of interest for which flash kinetics were measured, or at least discussed. For a comprehensive inventory of bioluminescent species, we recommend the works of Esaias and Curl (1972); Herring (1983); Poupin et al. (1999), and Widder et al. (1983). We then describe multiple instruments used to study MSB in laboratory conditions and *in situ*. The scientific applications in ecology, diversity, oceanography, climate change, autonomous sensing, and other fields are explored. Finally, we identify gaps in the literature regarding bioluminescence research and provide an assessment of the biases that can occur when collecting data on bioluminescent organisms. This effort builds upon previous reviews and research by Haddock et al. (2010); Herring (1983); Latz et al. (1988); Marcinko et al. (2013b); Martini and Haddock (2017); Moline et al. (2013); Widder et al. (1983), and Widder (2010a), with a focus on zooplankton and dinoflagellate clades. Key objectives are to assess remaining gaps, to evaluate the potential for bioluminescence as a tool to study diversity, and to identify pathways forward for research and technology development.

2 Bioluminescence emissions in plankton

MSB in marine species is thought to enhance survivability by luring or finding prey and warding off predators (Haddock et al., 2010). MSB can either be intrinsic, semi-intrinsic or extrinsic (Mirza and Oba, 2021). Intrinsic bioluminescence occurs when an organism produces both the luciferin and the luciferase needed for the chemical reaction. Inversely, an organism that obtains these molecules through predation and diet will display extrinsic bioluminescence. An individual with semi-intrinsic bioluminescence will obtain one of the components through their diet, sometimes facultatively.

Bioluminescence is present in at least 14 phyla, most having marine species (Morin, 1983; Widder, 2002). In some groups such as cnidarians, nearly all described species produce light (Martini and Haddock, 2017). Since the ability to bioluminesce seems to have evolved several times (Haddock et al., 2010; Lau and Oakley, 2021), one can expect significant variability in ecological value and emission flash kinetics from one group to another and within species. In the following section, we discuss emission characteristics, functions, and ecology of bioluminescence for the main clades of zooplankton and dinoflagellates.

2.1 Dinoflagellata

Dinoflagellates are autotrophic, heterotrophic, or mixotrophic single-cell organisms that are abundant in coastal and open ocean environments in the photic zone. They are known for their bioluminescent displays along the shore, i.e., *Noctiluca scintillans* and *Lingulodinium polyedra*, and some species are responsible for toxic red tides, i.e., *Karenia brevis*, *Pyrodinium bahamense*, and *L. polyedra* (Fleming et al., 2011). Haddock et al. (2010) and Poupin et al. (1999) counted at least 18 genera of bioluminescent dinoflagellates in five orders (Gymnodiniales, Noctilucales, Peridiniales, Prorocentrales, and Pyrocystales). Marcinko et al. (2013b) reviewed a total of 68 species of confirmed bioluminescent dinoflagellates. Because of their ecological role and the possibility to keep clonal cultures in laboratory, the bioluminescence of dinoflagellates has been extensively studied since the 1950s (Haxo et al., 1955). Indeed, first flash kinetics of several species have been characterized (Widder and Case, 1981; Latz and Lee, 1995; Cussatlegras and Le Gal, 2005; Cussatlegras and Le Gal, 2007), and their response to shear stress has been measured in fully developed pipe flow and other characterized flow fields (Latz et al., 2004b; Maldonado and Latz, 2007; Watanabe et al., 2012).

Bioluminescence emissions originate from scintillons, organelles containing the luminescent chemistry that are activated by a pH change following deformation of the plasma membrane, i.e., mechanical stimulation (Figure 2). This deformation is usually caused by a flow gradient present in the water column, i.e., shear, originating from waves, currents, other organisms swimming close by, or the feeding current of a predator. Dinoflagellates have a species-specific shear stress threshold, below which they will not typically bioluminesce. Peak bioluminescence emissions and TMSL typically exhibit a graded response to shear stress levels, i.e., higher shear stress typically produces a higher bioluminescence intensity (Latz et al., 1994; Latz and Rohr, 1999; Maldonado and Latz, 2007). Latz et al. (2004b) found that the shear stress threshold for four species of dinoflagellates varied from 0.02 to 0.3 N/m^2 with fully developed pipe flow experiments. Species where shear-induced bioluminescence has been studied include *L. polyedra* (Anderson et al., 1988; Dassow et al., 2005), *Pyrocystis noctiluca* (Cussatlegras and Le Gal, 2004), *Pyrocystis lunula*, (Jarms et al., 2002; Cussatlegras and Le Gal, 2007; Watanabe et al., 2012), *P. bahamense* (Biggley et al., 1969), *Ceratocorys horrida* (Latz and Lee, 1995; Latz et al., 2004a), *Gonyaulax spinifera* (Vishal et al., 2021), and *Tripos fusus* (Latz et al., 2004b), although thresholds have rarely been established. Table 1 summarizes the shear stress thresholds of available species along with the method or instrument used to quantify it. Shear stress thresholds for bioluminescence also vary between coastal or open ocean species (Marcinko et al. (2013b); coastal species tend to have higher thresholds, presumably because

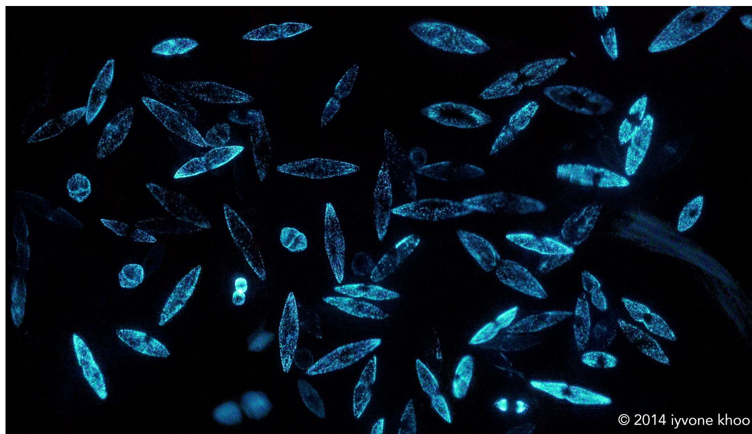

FIGURE 2
Mechanically stimulated bioluminescence in the dinoflagellate *Pyrocystis fusiformis*. Photo courtesy of Iyvone Khoo.

they live in a high-energy environment, which prevents unnecessary energetic expenditure.

Flash kinetics of dinoflagellates vary by several orders of magnitude among different species. For example, FF-MSL was 2.50×10^{11} photons/flash for *N. scintillans* using mechanical stimulation in an integrating light chamber (Buskey et al., 1992) and 3.35×10^{8} photons/flash for *P. bahamense* using mechanical stimulation through stirring and bubbling (Biggley et al., 1969). Indeed, TMSL varies based on organism size and the ability to produces several flashes repeatedly (Biggley et al., 1969). There is a positive correlation between TMSL of dinoflagellates and cell surface area; indeed, the approximate ratio of 10^{11} photons mm^{-2} is referred to as Seliger's rule (Buskey et al., 1992). When mechanically stimulated, the rise time of dinoflagellates is usually less than 50 ms, shorter than most other bioluminescent phyla (Widder, 1991; Latz and Lee, 1995). Widder and Case (1981) observed that *P. fusiformis* produces two types of flashes when mechanically stimulated for prolonged periods, where the second flash is dimmer and longer in both duration and rise time. Changes in flash responses upon repeated stimulation appear to be a feature of *Pyrocystis* species (Tesson and Latz, 2015). Other dinoflagellate species likely can produce variable flash kinetics upon secondary stimulation. Mean emission wavelengths for dinoflagellate species vary from 471 to 480 nm (Widder et al., 1983; Latz and Lee, 1995; Poupin et al., 1999). Emitted wavelength maxima are highly conserved across different genera of dinoflagellates, which is not the case for other phyla (Section 2.9).

Three primary roles for MSB in dinoflagellates have been hypothesized to enhance survival. The first function is likely to startle predators with a bright and rapid flash when entrained in a feeding current. Dinoflagellate cultures displaying brighter bioluminescence emissions were less preyed upon by the copepod *Acartia tonsa* (White, 1979). Esaias and Curl (1972) measured reduced ingestion rates by copepods on dinoflagellate cultures with higher bioluminescence potential. The swimming patterns of copepods are also altered in the presence of bioluminescent flashes caused by dinoflagellates, appearing as a startle response that can be interpreted as a fleeing behavior from a predator that would be attracted by this light (Buskey et al., 1983). This second function is described as the burglar alarm hypothesis, in which a dinoflagellate flash will cause the copepod to jump away to possibly avoid any visual predator that could capture it. Dinoflagellate bioluminescence reduced their predation by the mysid *Holmesimysis costata* via secondary predation by fish on *H. costata* (Mesinger and Case, 1992). Cusick and Widder (2014) and Hanley and Widder (2017) provided nuance to this theory in comparing bright and dim dinoflagellates and their ability to deter predators by flashing. Their results suggest that flashes of dimmer species like *Alexandrium* spp. and *L. polyedra* will hinder predator grazing (via secondary predation), but only above a certain cell concentration. This was not the case for brighter species, e.g., *P. fusiformis*, where this effect can be attained at high and low cell concentrations. The third function for dinoflagellate MSB is thought to be aposematism. In these cases, the bright blue flashes would act as a colorful warning to predators of the toxic nature of that particular species (Hanley and Widder, 2017).

For a predator, ingesting a flashing dinoflagellate is also risky, since light emitted from the digestive gut of the predator can alert other predators. Considering entire populations of some dinoflagellates are clones of a single organism, ingestion by a predator is not always detrimental to the population (Abrahams and Townsend, 1993). Thus, the cost of losing a few individuals may in fact be tolerable to the clonal colony, making bioluminescence a viable strategy to enhance survival of the population.

Some species of dinoflagellates can significantly contribute to the bioluminescence of a given ecosystem. For example, up to 30% of the bioluminescence measured at stations in the Sargasso Sea was caused by *P. noctiluca* (Swift et al., 1985). This is due both to the bright flashes it creates and its abundance in the water column when conditions allow. Under bloom conditions, which may be highly persistent in locations such as the bioluminescent bays of Puerto Rico, the dinoflagellate *P. bahamense* can completely dominate bioluminescence (Sastre et al., 2013; Soler-Figueroa and Otero, 2016). *N. scintillans* is a major contributor to bioluminescence

TABLE 1 Shear stress thresholds for dinoflagellates and zooplankton, along with the method used for quantifying the shear levels.

Group	Shear stress threshold (Nm^{-2})	Technique used	Reference
Dinoflagellata			
Ceratocorys horrida	0.039	Fully developed laminar pipe flow	(Latz et al., 2004b)
Tripos fusus	0.123	Fully developed laminar pipe flow	(Latz et al., 2004b)
Lingulodinium polyedra	0.1	Simple Couette chamber	(Latz et al., 1994)
Lingulodinium polyedra	0.15	Laminar pipe flow	(Rohr et al., 1997)
Lingulodinium polyedra	0.241	Simple Couette chamber	(Maldonado and Latz, 2007)
Lingulodinium polyedra	0.298	Fully developed laminar pipe flow	(Latz et al., 2004b)
Lingulodinium polyedra	0.32	Fully developed laminar pipe flow	(Latz et al., 2004b)
Pyrocystis fusiformis	0.06	Simple Couette chamber	(Latz et al., 1994)
Pyrocystis fusiformis	0.106	Fully developed laminar pipe flow	(Latz et al., 1994)
Pyrocystis fusiformis	0.6	Pipe flow	(Blaser et al., 2002)
Pyrocystis lunula	0.2	Couette chamber	(Cussatlegras and Le Gal, 2007)
Pyrocystis noctiluca	0.06	Simple Couette chamber	(Latz et al., 1994)
Copepod assemblage	0.51	Unavailable	(Hartline et al., 1999)
Sargasso Sea surface plankton	0.11	Simple Couette chamber	(Latz et al., 1994)
Sargasso Sea 100-m-depth plankton San Diego Bay and San Clemente Island, CA	0.2	Simple Couette chamber	(Latz et al., 1994)
L. polyedra, C. fusus, and *Protoperidinium* spp.	0.1	Laminar pipe flow	(Rohr et al., 1997)
Mixed plankton			
San Diego Bay, CA	0.13	Laminar pipe flow	(Rohr et al., 2002)
San Diego Bay, CA, Spring 1994	0.08	Laminar pipe flow	(Rohr et al., 2002)
San Diego Bight, CA, Summer 1994	0.09	Laminar pipe flow	(Rohr et al., 2002)
Scripps Pier, La Jolla, CA	0.09	Laminar pipe flow	(Rohr et al., 2002)

from tropical oceans to northern seas, and is often responsible for red tide events, causing fish and invertebrate mortality through rapid eutrophication creating hypoxic conditions (Zahir et al., 2023). Chen et al. (2023) measured decreasing bioluminescence intensity with increasing salinity and temperature, but intensity remained unchanged with varying levels of nutrients. See Marcinko et al. (2013b) for a more complete discussion on the applications and modeling of dinoflagellate bioluminescence emissions and their relative contributions to the water column's bioluminescence.

2.2 Arthropoda

2.2.1 Copepoda

Copepods are one of the most abundant invertebrate clades in marine and freshwater systems, both in biomass and abundance (Le Borgne, 1982; Webber and Roff, 1995; Blaxter et al., 1998). They are an important link between primary production and higher trophic levels such as larval fish and macroinvertebrates. Although the most abundant species are not bioluminescent, several copepod species of ecological importance are bioluminescent (Herring, 1988) and can be important proxies for secondary production estimates and ecosystem health assessments.

The majority of bioluminescent copepods are in the *Augaptilidae, Heterorhabdidae, Lucicutiidae*, and *Metridinidae* families, though several species belonging to other families have been documented (Clarke et al., 1962; Herring, 1988; Takenaka et al., 2012). Copepods do not have light-producing organs *sensu stricto*, e.g., photophores. Instead, luciferin-luciferase-mediated light emissions are produced in glandular cells, for which the quantities and locations are highly variable among species (Herring, 1988). Light-emitting gland contents are usually excreted out of pores into the water column, although some species retain light emission in the glands. The latter is the case for the calanoid *Oncaea conifera* displaying peak emissions of $6.90{\times}10^{8}$ photons/s/ind on average (mechanically stimulated

through stirring in an integrating sphere) (Herring et al., 1993). *M. lucens* has been shown to synthesize all needed components for bioluminescence emissions, i.e., intrinsic bioluminescence, but it is believed that most copepods acquire at least one of the compounds (luciferin/luciferase) through predation (Mirza and Oba, 2021). Light-producing cells of copepods have been found in a small cluster on the head between the antennules, on the ventral side, on the exopods of swimming legs, and on the caudal rami (Clarke et al., 1962; Takenaka et al., 2017). Peak emission wavelengths for planktonic copepods range from 469 to 492 nm (Herring, 1983; Takenaka et al., 2012; Santhanam, 2022). Some species will not excrete clouds of bioluminescent secretions and light will be constrained to the glands.

The main function for bioluminescent displays by copepods is antipredatory. By secreting luminescent fluids into the water column or by quickly flashing, copepods presumably hope to distract, disorient, and cloud the vision of predators long enough for them to be able to produce a swimming burst and escape (Porter and Porter, 1979; Hartline et al., 1999). Indeed, the well-studied copepod *Metridia lucens* will only flash on its own, i.e., without mechanical or chemical stimulation, when in the presence of the predator, *Meganyctiphanes norvegica* presumably from visual and chemical recognition (David and Conover, 1961). *M. lucens* may also flash to alert other individuals of potential danger, essentially acting as an alert system (Buskey and Swift, 1985). Copepods are also thought to use MSB as a "burglar alarm" as previously mentioned for dinoflagellates, as the planktonic polycheate *Tomopteris septentrionalis* showed increased swimming speeds when *M. lucens* flashed, perhaps to reduce their own predation (Buskey and Swift, 1985). For freshwater copepods, however, no change in behavior can be observed when bioluminescent flashes are present (Buskey et al., 1987), showing potentially different ecological roles in different environs.

Consistent with the taxonomic and morphological diversity of copepods, the flash kinetics of bioluminescence emissions, when described, are highly variable. With flashes of 0.2 to 30 s in duration for *M. lucens*, copepods can produce some of the longest flashes of all crustacean zooplankton (Herring, 1988). Among the brightest is the centimeter-long calanoid *Gaussia princeps* living in temperate and tropical waters. This copepod can sustain PI emissions at 483 to 488 nm for up to 3 s, resulting in a very high TMSL (4.30×10^{11} photons/ind measured through mechanical stimulation in an integrating sphere) (Barnes and Case, 1972; Widder et al., 1983; Latz et al., 1990). According to Bowlby and Case (1991), PI for this species averaged 3.5×10^{10} photons/s, and the FF-MSL was estimated at 1.8×10^{11} photons/ind when measured in an integrating sphere. However, results showed that four types of flash responses can be obtained via electrical stimulation, i.e., one with relatively fast rise time, one with a long total duration, one with a slow rise time and long duration, and a compound emission with a fast or long flash followed by a slow flash.

Species with very broad distributions can display large variations in kinetics. Indeed, for *Oncaea conifera* stimulated in an integrating sphere, Herring et al. (1993) noted significantly longer RT and FD for the North American population (64.9 ms and 213 ms, respectively) compared to the Mediterranean population (26.2 ms and 88.5 ms, respectively), although no statistical differences were observed for PIs and FF-MSLs. Similar results were obtained by Latz et al. (1987a) when studying the copepod *Pleuromamma xiphias*. With PI of 3.32×10^{11} photons/s (Latz et al., 1990), three different sets of flash kinetics and peak emissions were obtained when mechanically stimulating at three different shear levels, i.e., fast rise and decay, slow rise and decay, and a compound flash of a fast and a slow flash (Latz et al., 1987a; Latz et al., 1990). The fact that multiple flash signatures can be obtained for one species via mechanical stimulation may increase the difficulty to adequately identify and quantify zooplankton species in the water column based on their flash kinetics since it is more likely that one of these flash emissions closely match bioluminescent signatures of other organisms (Johnsen et al., 2014; Cronin et al., 2016). Moreover, the temporal aspect of the measurement, level of mechanical stimulation, and well-defined kinetics are all crucial to be repeatable and comparable data. Latz et al. (1990) noted collection and handling of the copepods decreased the available TMSL by 85%, so sufficient recovery time must be allowed (typically 24 h). Variation in PI for different life stages of *Pleuromamma piseki* and *Pleuromamma gracilis* was observed by Herring (1988), although interpretation is difficult since the organisms were chemically stimulated through a pH shift.

2.2.2 Amphipoda

Bioluminescence has been reported in at least 39 species of amphipods (Copilas-Ciocianu and Pop, 2020). Photophore emissions in the majority of marine amphipods species are thought to act as a predator repellent by startling an aggressor (Herring, 1981). Indeed, bioluminescent displays are usually triggered when an organism is either handled or disturbed, i.e., mechanically stimulated, though it is possible that bioluminescence serves as counter-illumination camouflage in *Parapronoe crustulum*. Individuals of the genus *Scina* will also adopt a rigid defensive posture while activating their photophores (Herring, 1981). In most species of *Scinidae*, the photophores are present in the antennae, at the tip of the fifth pereiopod and on the uropods. Both the location of the photophores and the behavior of the organism while flashing hint to an anti-predatory response since these appendages are at conspicuous extremities. The duration of a bioluminescent flash is quite variable and further complicated by the fact that amphipods will often flash several times sequentially when disturbed (Bowlby et al., 1991). For species from the genus *Cyphocaris*, length of flash sequences can reach 9 s and clouds of bioluminescent secretions can also be released (Bowlby et al., 1991). *Cyphocaris faurei* emits light at two peak wavelengths, 475 and 595 nm with the latter being rarely seen in zooplankters (Bowlby et al., 1991). Additionally, amphipods of the genus *Scina* emit light at 435 to 444 nm, which are some of shortest wavelengths measured for bioluminescent arthropods (Widder et al., 1983; Latz et al., 1988).

Not unlike other arthropod clades described here, peak intensities of bioluminescence flashes vary greatly in amphipods. Indeed, there is a factor of 100 in PI of *Scina crassicornis* at 1.70×10^{9} photons/s (mechanical stimulation through stirring) and *Cyphocaris anonyx* at 3.60×10^{11} photons/s (mechanical stimulation through gentle manipulation), although relative

stimulation intensities are unclear, as emission intensity for many organisms is positively correlated with intensity of mechanical stimulation (see Section 2.1) (Herring, 1981; Bowlby et al., 1991). More research is needed to describe emission kinetics of species of the genus *Cyphocaris* and *Scina* to have a better understanding of that clade's bioluminescence, especially considering how well bioluminescence is represented in this clade.

2.2.3 Ostracoda

Ostracods, commonly referred to as seafleas, are crustacean zooplankters found in both marine and freshwater systems, although only marine species are bioluminescent. Ostracods have a reduced number of feeding and swimming appendages, and their bodies, generally up to 2 mm in length, are encased in two valves (Brusca et al., 2016). Most of the bioluminescent species are part of the families Cypridininae and Halocypridae (Herring, 1985). More than 100 species are known to bioluminesce, but the majority of them remain undescribed, both in their morphology and in their bioluminescent emissions (Cohen and Morin, 2003). They can be planktonic to great depths (Heger et al., 2007) or benthic burrowers, as is the case for the well-studied bioluminescent cypridinid *Vargula hilgendorfii*. Harvey (1917) provides a complete review of the chemical aspect of this species' bioluminescence. This particular ostracod burrows in sandy beaches and emerges at night to feed, where waves provide mechanical stimulation inducing bioluminescence. While this organism is a burrower, its abundance—thus the overall MSL potentially produced by the population—is highly linked to the tidal cycle (Ratheesh Kumar et al., 2016). A light-reflecting organ that can redirect the bioluminescent flash of the organism has been described by Abe et al. (2000). This biological mirror is thought to help in intraspecific directional signaling to announce foraging behavior to others. Tsuji et al. (1970) also observed mechanically induced bioluminescence in *Cypridina serrata*.

Bioluminescent emissions of ostracods originate from the labral glands located near the mouth, although they are only present on the valves' margins in the family Halocypridae (Angel, 1968; Herring, 1985). Bioluminescence in ostracods can be seen as milky clouds secreted out of their valves or as a series of precisely timed flashes, and is always extracellular for the family Cypridininae (Morin, 1986). Ostracod bioluminescence can serve as a predator deterrent similarly to copepods, i.e., burglar alarm, but the complexity of their bioluminescence emissions as mating signals is likely unmatched in crustaceans (Rivers and Morin, 2009). When looking for a mate, males will begin producing quick flashes while swimming in a straight line or in tight spirals (Ellis et al., 2023). As they advance, the flashes will become shorter and the space between flashes will be reduced (Rivers and Morin, 2008; Morin, 2019). Since this behavior is under strong sexual selection, the quantity, spacing, and length of the flashes is unique to each species (Morin, 1986; Gerrish and Morin, 2016). On average, the FF-MSL of a defense flash is 50 times higher than a courting signal (Rivers and Morin, 2012). Although flashes produced as mating signals are voluntary and not mechanically induced, their species-specific patterns could prove useful in identification when observed *in situ*.

Angel (1968) observed bioluminescence in 11 halocyprid species when applying gentle pressure on the valves, but more work is needed to determine if bioluminescent emissions for these species can be induced by shear flows. The MSL of 16 halocyprid species was measured through stirring in a tube by Batchelder and Swift (1988), who discovered a range of PI of 1.00×10^{9}photons/s to 3.08×10^{11}photons/s per individual on average, suggesting that there is great variation in bioluminescence intensity among ostracods. Other flash kinetics, however, such as RT and FD, remain unknown to our knowledge. Peak wavelengths of bioluminescent flashes of *V. hilgendorfii* and *V. tsujii* were measured at 465 and 466 nm, respectively (Widder et al., 1983). With the recent progress on ostracod culturing in laboratory conditions (Goodheart et al., 2020), first flash kinetics induced by mechanical stimulation could be a tractable problem in the near future.

2.2.4 Euphausiacea

With very large biomass throughout global oceans, krill populations contribute significantly to the carbon pump and can feed entire ecosystems, from cephalopods to whales (Nicol, 2003; Cavan et al., 2019). In fact, aggregates of krill are so dense that acoustic instruments can track their vertical position in the water column throughout the day (Green et al., 1992). All 10 genera from the Euphausiidae family include species with light-producing photophores (Herring, 1985). All of these bioluminescent species produce light internally using 10 photophores located on the eyestalks and the ventral underside (Krönström et al., 2009) with no excreted luminescent mucus like ostracods or copepods. Herring (2007) noted a difference in the number and size of photophores between male and female *Nematobrachion flexipes*, though it is unclear if this translates into a difference in FF-MSL. The northern krill *Meganyctiphanes norvegica* emits 1.2×10^{10} photons/s at peak intensity from mechanical stimulation by UBAT with a 468-nm wavelength maxima (Johnsen et al., 2014). Peak emissions of studied species vary from 453 to 540 nm (Herring, 1983; Santhanam, 2022) (Table 2). While some species can bioluminesce for extended periods of time, i.e., up to 35 min (Herring, 1985), the flashes are on average 800 ms in duration for *M. norvegica* and 440 ms for *Thysanoessa inermis* (Cronin et al., 2016).

Bioluminescence in krill might also serve to startle potential predators, since Green et al. (1992) observed individuals would not flash, unless mechanically disturbed. In addition, since these organisms undergo vertical migration (Tarling et al., 2010), they are more often than not living in light-deprived environments, where bioluminescence may be used for intraspecific signaling.

Activation of the photophores of *M. norvegica* can be achieved via injections of serotonin, electrical stimulation, reducing ambient light, and water displacement by oscillating a sphere in front of the organism (Fregin and Wiese, 2002). Since krill can sense flow and increase their bioluminescence emissions when sensing water movement, it would be relevant to study their shear stress threshold and range for flash activation and resultant emission kinetics. Fregin and Wiese (2002) noted water vibrations created by acoustic pressure waves between 5 and 40 Hz increased light

production. Measurements of the diel BP-MSL of these populations may allow for vertical tracking, giving us insight into the spatiotemporal aspect of densely aggregated zooplankton. Given the flash intensity of a single organism and the large size of krill patches, Cram and Malan (1971) noted *Euphausia dana* bioluminescence could be used as a proxy for biomass using autonomous sensing approaches.

2.3 Annelida

Bioluminescence has been documented in several polychaete species, both benthic and planktonic (Verdes and Gruber, 2017). Bioluminescent species are part of eight families, i.e., Acrocirridae, Chaetopteridae, Cirratulidae, Flabelligeridae, Polynoidae, Syllidae, Terebellidae, and Tomopteridae. Since this review focuses on MSL, only Acrocirridae, Tomopteridae, and Flabelligeridae species will be discussed.

Perhaps the most well-known bioluminescent worms are the planktonic *Tomopteris* spp., which can produce yellow to blue-green light from MSL (Gouveneaux et al., 2017a). Indeed, while the peak emissions of *T. planktonis* are at 450 nm, *T. nisseni* and *T. septentrionalis* produce yellow bioluminescence that peaks respectively at 565 and 557 nm (Latz et al., 1988; Gouveneaux et al., 2017a). There is great diversity of the light emitted among a single genus. For this holoplanktonic and highly transparent genus, the emitted light is constrained to the parapodia (Dales, 1971; Gouveneaux et al., 2017b). To date, 12 species of bioluminescent *Tomopteris* spp. have been identified (Santhanam, 2022).

For the Acrocirridae, species of the deep-sea living genus *Swima* can autotomize branchial segments when disturbed that will emit green light (Osborn et al., 2011). These discarded segments are used to distract predators while the worm escapes (Osborn et al., 2009). It is thought that bioluminescence in pelagic polychaetes is mainly used as a predator deterrent, with the exception of Syllid and Tomopterid worms, which also use bioluminescence for mating and intraspecific signaling (Fischer and Fischer, 1995; Gouveneaux et al., 2018).

Francis et al. (2016) studied the bioluminescence of two planktonic Flabelligeridae species, *Flota flabelligera* and *Poeobius meseres*. Bioluminescence could be produced through mechanical stimulation for both species. For *F. flabelligera*, light was produced at the parapodia, similar to *Tomopteris* spp., with peak emission at 497 nm. For *P. meseres*, however, light was produced all across the body and peaked at 495 nm.

2.4 Cnidaria

Planktonic cnidarians are composed of scyphozoans, hydromedusae, and siphonophores. These gelatinous clades are widespread in every ocean and present throughout the water column. Martini and Haddock (2017) reported the vast majority of sampled scyphozoans and planktonic hydrozoans were bioluminescent, with most of the biomass in the first 1,000 m of the water column. Their high tolerance range for salinity, temperature, hypoxia, and water quality allow them to bloom at incredible speeds, quickly dominating the planktonic biomass (Condon et al., 2013). With climate change and ocean acidification, gelatinous blooms are getting larger and more frequent (Siddique et al., 2022). Like copepods, gelatinous plankton are an important part of the oceanic carbon pump (Lebrato et al., 2013; Lebrato et al., 2019). Owing to their biomass and the ubiquity of bioluminescence across the phylum, they are a strong contributor to the bioluminescence of a given marine environment.

In scyphozoans, bioluminescence has been observed and described in the classes Coronatae and Semaeostomeae. Species of Coronatae have bells that are a few centimeters in diameter, whereas the Semaeostomeae have the largest species of jellyfish with bells that can reach 2 m in diameter and tentacles several meters in length (Brusca et al., 2016). Santhanam (2022) reported 12 species of bioluminescent scyphozoans. Emission maxima range from 442 to 491 nm. Most of the species can produce light after mechanical stimulation, starting from the point of contact of high shear and propagating to the rest of the bell (Herring, 1990; Herring and Widder, 2004). In the red-pigmented *Periphylla*, MSB can be triggered in all life stages, from the eggs to the adults (Jarms et al., 2002). Bioluminescent displays in scyphozoans are thought to be for defense from visual predators.

Most hydromedusae are bioluminescent (Martini and Haddock, 2017). Apart from siphonophores, planktonic individuals are generally up to a few centimeters in bell diameter. Like scyphozoans, they can be mechanically stimulated and will tend to produce blue-green light (Haddock and Case, 1999). Once stimulated, the signal can propagate from the disturbance's origin to the rest of the organism (Mackie, 1991). The bioluminescence of the hydrozoan *Aequorea victoria* has been extensively studied, since it is in this organism that the green fluorescent protein (GFP) was discovered. GFP has two excitation peaks at 395 and 475 nm, and an emission peak at 509 nm. It is used in laboratories worldwide for fluorescence microscopy and molecular biology. Since this discovery, several more photoproteins have been discovered and described (see Haddock et al. (2010) for a review of the chemical mechanisms of bioluminescence). Bioluminescence in *A. victoria*, and most probably other hydromedusae, is semi-intrinsic, as the luciferin component, coelenterazine, must be acquired through their diet (Haddock et al., 2001). The mean wavelength maxima of hydrozoan emissions range from 443 to 680 nm, the highest of all reviewed clades. Among the Hydrozoa is the colonial class Siphonophora. While the organisms themselves are quite small, the colonies they form can be several meters in length. These chain-like colonies are composed of highly specialized zooids with specific functions, e.g., gastrozoids for feeding, nectophores for propulsion, gonophores for reproduction, and bracts and pneumatophores for floatability. Haddock et al. (2010) noted that 91% of siphonophores are bioluminescent, with at least 175 described species. Martini and Haddock (2017) observed that 99% of siphonophores sampled off the California coast were bioluminescent with a relatively consistent abundance from the surface to 3,900 m deep.

While all siphonophore species of the genus *Erenna* bioluminesce, *E. sirena* produce red light, an uncommon region

of the spectrum for marine luminescence (Pugh and Haddock, 2016). In early development, the luminescent lures are milky white in color and progressively shift toward red as the organism ages. In some species, the larva will not emit light in the first few days, and older nectophores and bracts will eventually stop luminescing (Freeman, 1987). This study is one of the few instances where bioluminescence was studied with ontogenic variation in mind [see Nikolaevich and Vladimirovna (2016) for a similar study on ctenophores]. This orange-red luminescence is produced by a tri-modal emission centered at 583, 620, and 680 nm (Haddock et al., 2005). It is thought that this red fluorescence is excited by the blue light emitted by ambient bioluminescence from prey. With 25 species tested, Haddock and Case (1999) reported a bi-modal mean of 450 and 486 nm for the emitted light of siphonophores. Bassot et al. (1978) and Pagès and Madin (2010) reported MSB for *Hippopodius* sp. and *Hallistemma cupulifera*.

Although we know the emission spectrum of several cnidarian species (Table 2, Figure 3C), only a dozen species have had their flash kinetics characterized, mainly through mechanical stimulation in an integrating sphere (Table 3) (Widder, 1991). Most of the described species have a flash duration of several seconds and rise times in the order of hundreds of milliseconds.

2.5 Ctenophora

The vast majority of planktonic ctenophores have the ability to bioluminesce (Haddock and Case, 1999; Martini and Haddock, 2017). The difficulty of identifying some species and mistaking a cydippid larva for an adult has sometimes attributed bioluminescent capabilities to non-bioluminescent ctenophores, i.e., the genus *Pleurobrachia* (Haddock and Case, 1995). Bioluminescence has been reported in five of the seven orders of ctenophores, i.e., Beroida, Cestida, Cydippida, Lobata, and Thalassocalycida (Herring, 1987; Haddock and Case, 1999; Brusca et al., 2016). For *M. leidyi*, emissions can occur as soon as they are released as gametes from the adults. Bioluminescence occurs along a line of cells within the eight divisions and meridional canals of the ctenophore. On the molecular level, the photons that excite the photosensitive opsins are halted when in the dark and allow for the calcium-regulated luciferin-luciferase reaction to take place (Anctil and Shimomura, 1984). Haddock and Case (1999) reported emission maxima peaking on average at 486 nm and ranging from 458 to 501 nm for the 41 sampled species, with no statistical difference between different orders. Their bioluminescence response can be provoked via mechanical, electrical, and chemical stimulation. Nikolaevich and Vladimirovna (2016) showed they are brightest when they are about to reproduce. *Mnemiopsis leidyi* and *Ocyropsis maculata immaculata* have bioluminescent abilities that are photoinhibited by light, making the energetically expensive action of bioluminescence only happen in dark environments when it can be seen (Haddock and Case, 1999). As with several other clades, bioluminescence is most likely emitted by ctenophores to startle potential predators.

Because of their high abundance in shallow and coastal waters, several studies have assessed the drivers of ctenophore bioluminescence. Results showed the bioluminescence capacities of these organisms to be highly varied based on abiotic factors and intrinsic characteristics of the individual. Light emitted by *M. leidyi* and *Beroe ovata*, for example, can vary based on their diet (Mashukova and Tokarev, 2013), their developmental stage and size (Tokarev et al., 2012), the metabolism of the individual, environmental parameters such as temperature (Nikolaevich and Vladimirovna, 2016), and whether or not they are in the process of regeneration (Mashukova and Tokarev, 2016). It is not known if those parameters affect the flash kinetics of other phyla in the same manner, warranting further research.

The flash kinetics of ctenophores are relatively well studied, and vary with the strength and duration of mechanical stimulation. Widder (1991) measured PI, FF-MSL, RT, and FD for several species; when mechanically stimulated in an integrating sphere, ctenophores can reach very high peak intensities, i.e., *Beroe cuvata* will peak at $3.40{\times}10^{12}$ photons/s/ind, and will flash for a few seconds, similarly to cnidarians (Table 3).

2.6 Chaetognatha

Chaetognaths, or arrow worms, are planktonic carnivores and are up to 15 cm in length (Pechenik, 2006). They use grasping spines near their mouth to capture prey such as copepods and fish larvae. Martini and Haddock (2017) found approximately 10% of the sampled chaetognath individuals are capable of bioluminescence. Bioluminescent species were found at depths varying from 500 to 3,500 m (Martini et al., 2019). Only two species, *Caecosagitta macrocephala* and *Eukrohnia fowleri*, are known to be bioluminescent (Haddock and Case, 1994; Thuesen et al., 2010). Both these species will release clouds of luminous material upon mechanical stimulation, most likely for defense and escape purposes. Like other deep-sea organisms, their gut lining is bright orange, which would hide the subsequent flashes of ingested copepods or other bioluminescent preys (Thuesen et al., 2010; Thuesen and Haddock, 2013). Little is known on their flash kinetics, other than *C. macrocephala* emissions peaking at 467 nm. The hexagonal shape of the chambers containing the luciferins and luciferases is unique among bioluminescent organisms (Thuesen et al., 2010).

2.7 Chordata

There are two classes of bioluminescent planktonic nonvertebrate chordates: the gelatinous house-building appendicularians (Larvacea) and the thaliaceans (salps, doliolids, and pyrosomes).

Larvaceans are tadpole-like organisms that secrete a mucus house around them several times every day. This house is used for filtering food particles pushed by the current created by the larval-like tail of the organism. The house is then ingested with the captured particles or discarded into the water column (Brusca et al., 2016). Owing to their rapid growth rates and the quick turnover of the house, recent studies have shown that the contribution of larvaceans to the carbon pump has been underestimated, further increasing the importance of gelatinous

plankton in marine pelagic ecosystems (Jaspers et al., 2023). Unlike other groups of chordates, MSB is widespread in appendicularians. Both the individuals and the secreted houses can bioluminesce when mechanically stimulated (Widder et al., 1989). Galt (1978) observed houses can bioluminesce up to 4 h after being discarded, although captured particles like dinoflagellates can also bioluminesce, thus making accurate measurements of their bioluminescence quite variable and complex (Galt and Sykes, 1983). The mechanically stimulated bioluminescence of the *Oikopleura* genus has been measured and studied using a bathyphotometer pumping at 15 L/min, with peak emissions of 1.7×10^{11} photons/s at 483 nm (Widder et al., 1983; Swift et al., 1985). An interesting observation by Galt and Sykes (1983) is that the kinetics of the organism itself and its house are very different from each other, i.e., the RT of the organism is about half of the house's (see Galt et al. (1985) for a detailed list of larvacean flash kinetics). In these experiments, larvaceans and their houses were mechanically stimulated by injecting a volume of seawater into the sample vial, creating flow within. At least in *Oikopleura rufescens*, *Megalocercus huxleyi*, and two species of *Vexillaria* sp., light is produced in micrometer-sized granules located on the house rudiment and the secreted house (Galt et al., 1985). Both Martini and Haddock (2017) and Galt et al. (1985) agree appendicularians species, when present, are usually bioluminescent and occupy a significant proportion of the water column's planktonic biomass. Alldredge (1972) measured densities of discarded houses of *Oikopleura* spp. at up to 623 houses/m^3. Considering the enormous planktonic biomass these houses represent, coupled with their bioluminescence capabilities, these gelatinous structures could contribute a significant fraction of extrinsic MSB for upper trophic levels (Gorsky and Fenaux, 1998; Purcell et al., 2005). Most of the species of larvaceans with described flash kinetics are from the *Oikopleura* genus, although most appendicularians are known to be bioluminescent.

Salps are mainly colonial and can form chains of organisms several meters in length. Doliolids are small solitary organisms, i.e., less than 1 cm, but some species can be seen forming planktonic colonies (Brusca et al., 2016). Most of the described species of salps and doliolids are not bioluminescent. Little is known on the bioluminescence across these two groups, and even less on their flash kinetics and the function of their bioluminescence. However, one would expect development in this field with recent advances in deep sea *in situ* measurements and gelatinous plankton sampling methods (Robison et al., 2005).

Pyrosomes are cylindrical colonies made of millimeter-sized individuals found in every ocean, in the top layers of the water column (De Carvalho and Bonecker, 2008). Pyrosomes can be significant contributors to carbon export and can rapidly form blooms, changing water column diversity and bioluminescence profiles (Lilly et al., 2023). The bioluminescence of the *Pyrosoma* genus has been well documented. Their bioluminescence is interesting in the sense that flash duration is extremely long, i.e., up to 1 min. The response can also be provoked by mechanical, photic, and electrical stimulation. Bowlby et al. (1990) and Nicol (1958a) estimated the FF-MSL of *Pyrosoma atlanticum* to be up to 2.30×10^{13} photons/ind through mechanical stimulation in an integrating sphere, possibly due to the significant size of the colony. The spectral properties of this species are unique due to a bimodal spectrum with a main and secondary peak at 493 and 471 nm, respectively (Latz et al., 1988). The emission spectra of *P. spinosum* was measured at 485 nm (Swift et al., 1977). However, pyrosomes being colonial species, the number of individuals and the total area of the colony are highly variable, thus introducing variance in the BP-MSL of the species (Bowlby et al., 1990). In *P. atlanticum*, bioluminescence is caused by the microbial symbiont *Photobacterium Pa-1* (Berger et al., 2021). Further studies are needed to assess the bioluminescence mechanisms of other pyrosomes. Bowlby et al. (1990) noted mechanical stimulation produced the strongest bioluminescence with a flash duration of 59 s on average. Their mean RT is also one the longest observed with 20 s before reaching maximum intensity. With such flash kinetics, pyrosomes have one of the longest MSL flashes ever described among marine plankton.

2.8 Radiolaria

Radiolarians are small protists, with both solitary and colonial species, that are exclusively marine, planktonic, and can have an internal siliceous skeleton (Brusca et al., 2016). They are mostly found in tropical, warmer waters. MSL has been confirmed in at least six taxa (Latz et al., 1987b). Bioluminescence in radiolarians most likely serves as a predator deterrent, similar to dinoflagellate species (Herring, 1979). Latz et al. (1987b) identified radiolarians as important contributors to surface bioluminescence in the Sargasso Sea. However, their small size and difficulties associated with collecting and preserving these species might contribute to underestimating their contribution to planktonic MSL. In colonial species like *Acrosphaera murrayana*, *Siphonosphaera tenera*, or *Collosphaera* spp., bioluminescence is emitted from multiple points within the colony. Radiolarians have long flash durations varying from 1 to 5 s (Latz et al., 1987b; Latz et al., 1991), which is much longer than most other planktonic bioluminescent species and other unicellular organisms, i.e., dinoflagellates (Table 3). Measured PIs are within the lowest order of magnitude observed for dinoflagellates, with 6.70×10^{8} photons/s for *Thalassicolla nucleata* (Latz et al., 1991).

2.9 Summarizing diversity of MSB emission spectra and flash kinetics

Published mean emitted wavelength maxima are compiled for each phyla with described planktonic bioluminescent emissions (Table 2, Figure 4). These maxima are 528.9 ± 41.0 nm for annelids, 467.0± 12.5 nm for arthropods, 467.0 nm for chaetognaths, 488.7 ± 9.80 nm for chordates, 470.4 ± 55.7 nm for cnidarians, 486.9 ± 10.1 nm for ctenophores, 476.6 ± 3.20 nm for dinoflagellates, and 450 ± 5.00 nm for radiolarians (Figure 4). Only one of the two bioluminescent species of chaetognath has its spectral properties described (Thuesen et al., 2010). Owing to several species—mainly from the genus *Tomopteris*—producing yellow bioluminescence,

the phylum Annelida has the highest mean emitted wavelength maxima of all compiled phyla. The bandwidths at which emissions reach half of the maxima's intensity (FWHM) are also listed for several species in Table 2. These FWHM are typically broadly ranging from 50 to 100 nm except for the dinoflagellates, where this bandwidth ranges from 35 to 38 nm for the four species with available data.

Haddock and Case (1999) have found for gelatinous plankton, i.e. ctenophores, cnidarians, and non-vertebrate chordates, wavelength maxima can be correlated to the depth at which the species are found, with deeper species having maxima that are increasingly blue-shifted (Reynolds and Lutz, 2001). This presumably is due to deeper waters having peak transmissions increasingly blue-shifted with increasing water clarity, likely an adaptation to optimize signaling. Matching peak emission with peak transmission through water has a lower energetic cost per emission than other wavelengths, assuming the photon flux is identical. This would also explain why most phyla have their mean emitted wavelength maxima for clear ocean water in the 450–500 nm range (Table 2), and why phyla with wider water column distributions such as cnidarians have broader wavelength ranges than organisms such as dinoflagellates. Bioluminescence spectra also vary based on habitat. Coastal species will tend to have emission maxima between 490 and 520 nm, whereas maxima of clear open ocean species are often between 450 and 490 nm, most likely due to higher turbidity and dissolved organic matter in coastal waters (Hastings, 1996). These ranges include benthic and sessile species, in addition to planktonic and nektonic organisms, presumably because all of these species are using bioluminescence to signal through the water column.

Out of all the phyla compiled, cnidarians show the largest range in mean emitted wavelength (Figure 3). This is because most species of cnidarians emit in the green-blue range, although *Erenna sirena* has distinctive red bioluminescent lures. Relatively high absorption by water in the red would suggest that these emissions have evolved to be impactful over relatively small distances. The distribution among cnidarians does not follow a normal distribution curve of mean emitted wavelength maxima (Figure 3). This might be because cnidarians are found in almost every marine system and throughout the water column. This allows for very different water clarity conditions, water composition, and prey–predator relations, which can all be evolutionary drivers for spectral bioluminescent emissions.

Figure 3A shows the distribution of mean emitted wavelength maxima for all species from Table 2; Figures 3B–D show the three phyla with most described species that have mechanically stimulated bioluminescence (Arthropoda, Cnidaria, and Ctenophora). The mean emitted wavelength maxima distribution for dinoflagellate species is not shown in Figure 3 since its low sample size did not allow for a representative histogram. Shapiro–Wilk tests were made for all wavelength data and for phyla in Figure 3. *p*-values for the Arthropoda and Ctenophora distributions were 0.246 and 0.193, respectively, thus accepting the hypothesis of normal distribution at a significance level of 5%. This was not the case for the phylum Cnidaria and for all wavelength data combined. A non-parametric one-way ANOVA was applied to identify any significant differences in wavelength maxima distributions. Following an *ad hoc* Dunn test, it was identified that Arthropoda's distribution is statistically different from the phyla Annelida, Chordata, Cnidaria, and Ctenophora ($p < 0.05$). The differences in distributions for Ctenophora and Cnidaria, in addition to Annelida and Cnidaria, were also significant. All other comparisons of phyla were inconclusive.

Since arthropods, cnidarians, and ctenophores all use coelenterazine for bioluminescent emissions, it is interesting that their spectral properties are all statistically different (Haddock et al., 2010; Widder, 2010a). However, the small sample sizes for annelids, chordates, and dinoflagellates may not allow for accurate representation of the phyla and sufficient statistical outputs.

Considering the dominance of bioluminescent traits across zooplankton clades and the number of known bioluminescent species, only a handful have had their emissions measured quantitatively, and even less have had their flash kinetics described (Haddock et al., 2010). For example, Herring (1988) lists 58 species of confirmed bioluminescent copepods, with an additional 26 with unconfirmed bioluminescence (i.e., misidentified species, anecdotal observations, and observations from non-monospecific cultures), while only 12 species have partially described flash kinetics (Table 3). Similarly, Marcinko et al. (2013b) lists 68 species of dinoflagellates with confirmed bioluminescence, while the only metric that is widely available is total mechanically stimulated light for most measured species. The genera *Gonyaulax* and *Protoperidinium* have the best coverage for TMSL data, but other dinoflagellate clades have poor taxonomic coverage.

3 Measuring mechanically stimulated bioluminescence

A wide variety of methods have been used in controlled laboratory environments for applying shear in MSL measurements, including Couette flow, pipe flow, microfluidic constriction, microfluidic obstruction, Svet, orbital shaker, various stirring apparatuses, acoustic pressure, applying a vacuum, and using a needle probe. The Svet is a photometer system using water flow to stimulate bioluminescence within a cuvette, differing in sizes based on the organisms being tested (Tokarev et al., 2012; Mashukova et al., 2016; Nikolaevich and Vladimirovna, 2016). Light is collected via a photomultiplier tube (PMT) that sits 1 cm away from the cuvette (Mashukova et al., 2023). Samples are maintained in constant stimulation in view of this PMT until the bioluminescent response has ended. The magnitude and duration of shear stress applied is often not considered, however. Since emission intensity and other kinetic parameters are usually dependent on the magnitude of shear stress imposed by a given approach (Latz and Rohr, 2013), interpreting and comparing results can be difficult. Some aspects of emission such as flash duration and the rate of decay from peak emission, i.e., e-folding, are less dependent on the intensity of incident shear and, thus, are more comparable between techniques and organisms. Important exceptions in using quantifiable shear in experimental work are the simple Couette flow and pipe flow approaches (Rohr et al., 1999; Latz et al., 2004a; Jing et al., 2011), where repeatable, well-characterized fluid shear stress levels can be used to characterize MSB dynamics.

TABLE 2 Mean emitted wavelength maxima and spectrum width at half maxima for bioluminescent zooplankton and dinoflagellate species.

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Annelida			
Polychaeta Terebellida			
Flota flabelligera	497		Francis et al. (2016)
Polychaeta Phyllodocida			
Odontosyllis enopla	503		Shimomura et al. (1963)
Odontosyllis phosphorea	494–504		Deheyn and Latz (2009)
Poeobius meseres	495		Francis et al. (2016)
Tomopteris carpenteri	564		Gouveneaux (2016)
Tomopteris helgolandica	576		Gouveneaux and Mallefet (2013)
Tomopteris nationalis	565		Francis et al. (2014)
Tomopteris nisseni	565	55	Latz et al. (1988)
Tomopteris planktonis	450		Gouveneaux (2016)
Tomopteris septentrionalis	557		Dales (1971)
Arthropoda			
Copepoda Calanoida			
Euaugaptilus magnus	480	76	Herring (1983)
Gaussia princeps	483	75	Widder et al. (1983)
Lucicutia flavicornis	483	79	Herring (1983)
Metridia lucens	482		Herring (1983)
Metridia okhotensis	493		Takenaka et al. (2012)
Metridia pacifica	489	79	Herring (1983)
Pleuromamma abdominalis	486	77	Latz et al. (1987a); Latz et al. (1988)
Pleuromamma borealis	480	84	Herring (1983)
Pleuromamma xiphias	492	77	Latz et al. (1988)
Copepoda Cyclopoida			
Oncaea conifera	469	90	Herring (1983)
Ostracoda Halocyprida			
Conchoecia imbricata	474	94	Latz et al. (1988)
Conchoecia secernenda	481	95	Latz et al. (1988)
Ostracoda Myodocopida			
Vargula antarctica	475		Herring (1983)
Vargula hilgendorfii	465	83	Widder et al. (1983)
Vargula tsujii	466	87	Widder et al. (1983)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Malacostraca Amphipoda			
Cyphocaris faurei	475–595	83–78	Bowlby et al. (1991)
Parapronoe crustulum	475	90	Herring (1983)
Scina sp.	444	89	Latz et al. (1988)
Scina marginata	435	64	Herring (1983)
Scina rattrayi	439	70	Widder et al. (1983)
Malacostraca Decapoda			
Acanthephyra brevirostris	455	69	Herring (1983)
Acanthephyra curtirostris	460	70	Herring (1983)
Acanthephyra eximia	450	77	Herring (1983)
Acanthephyra gracilipes	460	71	Herring (1983)
Acanthephyra microphtalma	455	71	Herring (1983)
Acanthephyra stylorostratis	455	67	Herring (1983)
Ephyrina benedicti	465	75	Herring (1983)
Ephyrina bifida	455	69	Herring (1983)
Ephyrina figuerai	455	63	Herring (1983)
Ephyrina hoskynii	465	78	Herring (1983)
Ephyrina ombango	460	69	Herring (1983)
Glyphus marsupialis	455	66	Herring (1983)
Heterocarpus grimaldii	460	70	Herring (1983)
Hymenodora sp.	456	70	Widder et al. (1983)
Hymenodora sp.	450	70	Herring (1983)
Meningodora mollis	460	64	Herring (1983)
Meningodora vesca	460	73	Herring (1983)
Notostomus auriculatus	460	68	Herring (1983)
Oplophorus spinosus	465	73	Herring (1983)
Sergestes similis	472	58	Widder et al. (1983)
Sergia phorcus	472	97	Widder et al. (1983)
Systellaspis braueri	455	69	Herring (1983)
Systellaspis cristata	460	68	Herring (1983)
Systellaspis debilis	460	65	Latz et al. (1988)
Systellaspis pellucida	450	66	Herring (1983)
Malacostraca Euphausiacea			
Euphausia americana	470	49	Herring (1983)
Euphausia brevis	462	43	Latz et al. (1988)
Euphausia frigida	470	53	Herring (1983)
Euphausia gibboides	467	53	Latz et al. (1988)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Euphausia hemigibba	470	48	Herring (1983)
Euphausia krohnii	475	46	Herring (1983)
Euphausia superba	475	53	Herring (1983)
Euphausia tenera	468	38	Swift et al. (1977)
Euphausia triacantha	475	50	Herring (1983)
Euphausia pacifica	470	46	Widder et al. (1983)
Meganyctiphanes norvegica	475–520:540	51	Herring (1983)
Nematobrachion flexipes	453	32	Latz et al. (1988)
Nematoscelis difficilis	483	81	Widder et al. (1983)
Nematoscelis megalops	470	46	Herring (1983)
Nematoscelis microps	463	43	Latz et al. (1988)
Nyctiphanes couchii	470	48	Herring (1983)
Nyctiphanes simplex	467	44	Widder et al. (1983)
Stylocheiron abbreviatum	470	53	Herring (1983)
Thysanoessa gregaria	470	54	Herring (1983)
Thysanoessa macrura	470	54	Herring (1983)
Thysanoessa raschii	476–520:540		Herring (1983)
Thysanoessa monocantha	465	42	Herring (1983)
Thysanoessa tricuspidata	465	49	Herring (1983)
Malacostraca Lophogastrida			
Gnathophausia ingens	484	83	Widder et al. (1983)
Neognathophausia ingens	481		Frank et al. (1984)
Chaetognatha			
Caecosagitta macrocephala	467		Thuesen et al. (2010)
Chordata			
Appendicularia Copelata			
Oikopleura dioica	483	95	Widder et al. (1983)
Appendicularia Thaliacea			
Pyrosoma sp.	490	103	Herring (1983)
Pyrosoma atlanticum	471–493	93	Latz et al. (1988)
Pyrosoma spinosa	485	102	Swift et al. (1977)
Pyrosoma verticillata	483	96	Widder et al. (1983)
Cnidaria			
Hydrozoa Anthothecata			
Bougainvillia earolinensis	452	74	Latz et al. (1988)
Bythotiara depressa	488	80	Haddock and Case (1999)
Euphysora valdiviae	464	93	Haddock and Case (1999)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Pandea sp.	466	80	Latz et al. (1988)
Pandea conica	470	98	Haddock and Case (1999)
Hydrozoa Leptothecata			
Aequorea forskalea	503		Haddock and Case (1999)
Clytia hemishpaericum	504	37	Haddock and Case (1999)
Halopsis ocellata	458	99	Haddock and Case (1999)
Mitrocoma cellularia	505	55	Haddock and Case (1999)
Microcomella sp.	500	62	Haddock and Case (1999)
Obelia sp.	502		Haddock and Case (1999)
Obelia lucifera	509		Poupin et al. (1999)
Octophialucium funerarium	487	72	Haddock and Case (1999)
Hydrozoa Narcomedusae			
Aegina citrea	459	73	Latz et al. (1988)
Aeginura grimaldii	464	88	Haddock and Case (1999)
Cunina globosa	462	76	Haddock and Case (1999)
Pegantha laevis	460	75	Haddock and Case (1999)
Solmissus albescens	478	76	Haddock and Case (1999)
Solmissus marshalli	477	75	Haddock and Case (1999)
Solmundella bitentaculata	477	83	Haddock and Case (1999)
Hydrozoa Siphonophorae			
Abylopsis eschscholtzii	517		Hunt et al. (2012)
Abylopsis tetragona	489	61	Haddock and Case (1999)
Agalma okeni	444	70	Latz et al. (1988)
Amphicaryon acaula	487	65	Latz et al. (1988)
Amphicaryon ernesti	487	47	Latz et al. (1988)
Chuniphyes multidentata	481	61	Haddock and Case (1999)
Craseoa lathetica	489	90	Haddock and Case (1999)
Diphyes dispar	464	92	Latz et al. (1988)
Erenna sp.	455	109	Haddock and Case (1999)
Erenna sirena	583–620–680		Haddock et al. (2005)
Frillagalma vityazi	455	91	Haddock and Case (1999)
Halistemma sp.	446	81	Haddock and Case (1999)
Halistemma amphytridis	451	88	Haddock and Case (1999)
Hippopodius hippopus	450	83	Haddock and Case (1999)
Maresearsia praeclara	473	64	Widder et al. (1983)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Mugiaea sp.	500	76	Haddock and Case (1999)
Nanomia bijuga	457	87	Haddock and Case (1999)
Nanomia cara	454	92	Haddock and Case (1999)
Nectadamas diomedeae	443	83	Haddock and Case (1999)
Nectopyramis natans	447	81	Haddock and Case (1999)
Praya dubia	447	86	Haddock and Case (1999)
Rosacea larva	488	55	Latz et al. (1988)
Rosacea plicata	491	77	Haddock and Case (1999)
Vogtia glabra	448	79	Haddock and Case (1999)
Vogtia serrata	451	86	Haddock and Case (1999)
Hydrozoa Trachymedusae			
Colobonema sericeum	494		Widder et al. (1989)
Halicreas minimum	469	88	Haddock and Case (1999)
Haliscera conica	451	85	Haddock and Case (1999)
Halitrephes maasi	458	125	Haddock and Case (1999)
Halitrephes valdiviae	443	80	Haddock and Case (1999)
Pegantha clara	460	71	Latz et al. (1988)
Scyphozoa Coronatae			
Atolla parva	468	89	Haddock and Case (1999)
Atolla vanhoeffeni	469	84	Haddock and Case (1999)
Atolla wyvillei	470	98	Haddock and Case (1999)
Nausithoe atlantica	480	88	Haddock and Case (1999)
Nausithoe globifera	494	85	Haddock and Case (1999)
Paraphyllina ransoni	465	85	Haddock and Case (1999)
Periphylla	470	89	Herring (1983)
Periphyllopsis braueri	473	85	Haddock and Case (1999)
Scyphozoa Semaestomea			
Chrysaora hysosceles	478	95	Latz et al. (1988)
Pelagia noctiluca	469	94	Latz et al. (1988)
Phacellophora camtschatica	491	107	Haddock and Case (1999)
Poralia rufescens	468	84	Haddock and Case (1999)
Ctenophora			
Nuda Beroida			
Beroe sp.	484	80	Widder et al. (1983)
Beroe abyssicola	491	88	Haddock and Case (1999)
Beroe cucumis	489	88	Haddock and Case (1999)
Beroe forskalii	491	89	Haddock and Case (1999)
Beroe gracilis	495	89	Haddock and Case (1999)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Beroe ovata	493	89	Haddock and Case (1999)
Tentaculata Cestida			
Cestum veneris	493	89	Haddock and Case (1999)
Velamen parallelum	501	90	Haddock and Case (1999)
Tentaculata Cydippida			
Aulacoctena acuminata	458	90	Haddock and Case (1999)
Charistephane fugiens	468	84	Haddock and Case (1999)
Euplokamis sp.	483	85	Haddock and Case (1999)
Euplokamis stationis	467	82	Haddock and Case (1999)
Haeckelia beehleri	500	88	Haddock and Case (1999)
Haeckelia bimaculata	490	98	Haddock and Case (1999)
Haeckelia rubra	489	98	Haddock and Case (1999)
Lampea lactea	469	85	Haddock and Case (1999)
Lampea pancerina	473	81	Haddock and Case (1999)
Tinerfe lactea	486	85	Latz et al. (1988)
Tentaculata Lobata			
Bathocyroe fosteri	459–492	102	Haddock and Case (1999)
Bolinopsis sp.	488	80	Latz et al. (1988)
Bolinopsis infudibulum	488	88	Haddock and Case (1999)
Bolinospis vitrea	490	90	Haddock and Case (1999)
Deiopea kaloktenota	489	95	Haddock and Case (1999)
Eurhamphaea vexilligera	496	94	Haddock and Case (1999)
Kiyohimea aurita	491	103	Haddock and Case (1999)
Leucothea multicornis	488	93	Haddock and Case (1999)
Leucothea pulchra	488	92	Haddock and Case (1999)
Mnemiopsis sp.	480	83	Widder et al. (1983)
Mnemiopsis leidyi	480–485		Herring (1983)
Ocyropsis sp.	480	78	Herring (1983)
Ocyropsis maculata immaculata	489	90	Haddock and Case (1999)
Tentaculata Thalassocalycida			
Thalassocalyce inconstans	491	92	Haddock and Case (1999)
Myzozoa Dinoflagellata			
Tripos fusus	474		Latz et al. (2004b)
Ceratocorys horrida	474		Latz et al. (2004b)
Dissodinium pseudolunula	475		Poupin et al. (1999)
Lingulodinium polyedra	474	35	Widder et al. (1983)

(Continued)

TABLE 2 Continued

Taxonomy	Parameters		References
	Emitted wavelength maxima (nm)	Bandwidth at half maxima (nm)	
Noctiluca scintillans	470		Nicol (1958a)
Peridinielle catenata	480		Poupin et al. (1999)
Polykrikos schwartzii	480		Poupin et al. (1999)
Protoperidinium divergens	480		Poupin et al. (1999)
Protoperidinium ovatum	480		Poupin et al. (1999)
Protoperidinium pallidum	480		Poupin et al. (1999)
Protoperidinium steinii	480		Poupin et al. (1999)
Protoperidinium depressum	480		Poupin et al. (1999)
Pyrocystis acuta	474		Poupin et al. (1999)
Pyrocystis fusiformis	471	35	Widder et al. (1983)
Pyrocystis lunula	472	38	Widder et al. (1983)
Pyrocystis noctiluca	472	35	Widder et al. (1983)
Pyrodinium bahamense	479		Herring (1983)
Radiolaria			
Acrosphaera murrayana	443	80	Latz et al. (1987b)
Collosphaera huxleyi	456	79	Latz et al. (1991)
Collosphaera sp.	453	76	Latz et al. (1987b)
Collosphaera sp.	445	84	Latz et al. (1987b)
Collosphaera sp.	444	70	Latz et al. (1987b)
Myxosphaera coerulea	453	84	Latz et al. (1987b)
Rhaphidozoum acuferum	458	87	Latz et al. (1987b)
Siphonosphaera tenera	450	78	Latz et al. (1987b)
Thalassicolla sp.	450	80	Herring (1983)

Measuring bioluminescence *in situ* is a challenging problem from both engineering and biological perspectives. Bioluminescence occurs throughout all ocean depths and organisms can be patchy and elusive with various sampling approaches. From micron-sized bacteria to colonial gelatinous plankton reaching meters in length, PIs of flashes span at least nine orders of magnitude (Widder, 2010a) and resolving full kinetics requires sensitive low-light detector(s). With kinetic parameters being dependent on incident shear levels, an understanding of the associated small-scale fluid dynamics for a given approach can be vital in interpretation. In fact, to fully describe and interpret MSL, one must also understand the effect abiotic and biotic factors can have on the bioluminescent manifestations of an organism, including recent history of exposure to light and other potential sources of shear (Valiadi and Iglesias-Rodriguez, 2013). Moreover, every measurement approach has advantages and disadvantages and assumptions in interpretation must practically be made. Furthermore, no one approach will work for all organisms.

Discussed below are three general approaches in measuring bioluminescence *in situ*: (1) the flow-through bathyphotometer, (2) imaging a mesh net, and (3) passive detection.

3.1 Flow-through bathyphotometers

Bathyphotomers use flow agitation within an enclosed chamber to mechanically stimulate bioluminescence (Herren et al., 2005; Latz and Rohr, 2013). The Seliger bathyphotometer from 1968 was the first system measuring bioluminescence to quantify the abundance of source organisms (Seliger and McElroy, 1968). This bathyphotometer was equipped with an impeller facing a PMT, ensuring water flow would be directed toward the PMT and emissions would be captured. In the next iteration of this bathyphotometer, mechanical stimulation of organisms was achieved through flow constriction into a 1.5-inch-diameter hole facing the PMT. It was used in the bioluminescent bays of Jamaica

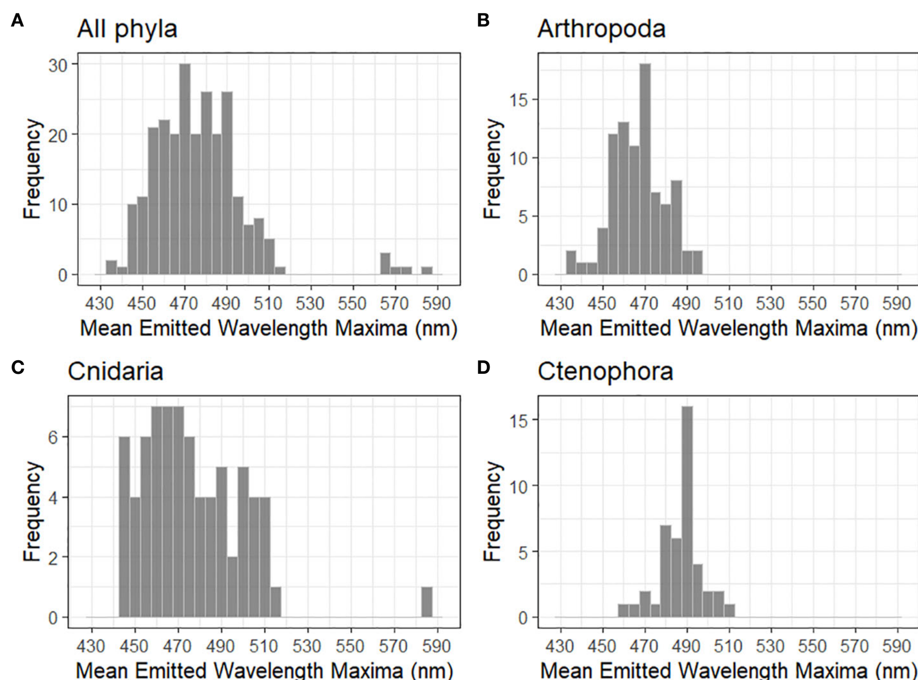

FIGURE 3
Distribution of mean emitted wavelength maxima for **(A)** all planktonic phyla with reported mechanically stimulated bioluminescence (n = 247), **(B)** Arthropoda (n = 87), **(C)** Cnidaria (n = 73), and **(D)** Ctenophora (n = 43). The highest intensity wavelength was used when a species showed multi-modal spectral maxima. All bins are 5 nm.

TABLE 3 Flash kinetics of mechanically stimulated bioluminescent zooplankton and dinoflagellate species.

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Arthropoda					
Copepoda Calanoida					
Centropages furcatus		8×10^{7} per flash			Herring (1988)
Gaussia princeps		4.3×10^{11}			Latz et al. (1990)
Heterorhabdus norvegicus		1.60×10^{11}			Batchelder and Swift (1989)
Heterorhabdus spinifrons		1.60×10^{11}			Batchelder and Swift (1989)
Lucicutia flavicornis		1.06×10^{10}			Latz et al. (1990)
Metridia sp.	6.47×10^{9}		130	400	Cronin et al. (2016)
Metridia longa	2.05×10^{9}	2×10^{11} per flash		560	Lapota et al. (1989); Johnsen et al. (2014)
Metridia lucens		3.30×10^{12} per flash			Clarke et al. (1962)
Paracalanus indicus		3×10^{7} per flash			Herring (1988)
Pleuromamma robusta		7.10×10^{10}			Swift et al. (1995)
Pleuromamma xiphias (single fast flash)	2.3×10^{11}		63.9	378.8	Latz et al. (1990)
Pleuromamma xiphias (single slow fash)	1.21×10^{11}		283.5	1.60×10^{3}	Latz et al. (1990)

(Continued)

TABLE 3 Continued

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Pleuromamma xiphias (double flash)	3.32×10^{11}		80.3	1.60×10^{3}	Latz et al. (1990)
Copepoda Cyclopoida					
Corycaeus latus		1×10^{8} per flash			Herring (1988)
Corycaeus speciosus		5×10^{7} per flash			Herring (1988)
Oncaea sp.	6.10×10^{8}	9.40×10^{7}	33	120	Widder (1991)
Oncaea conifera (Mediterranean)			26.2	88.5	Herring et al. (1993)
Oncaea conifera (North Atlantic)			64.9	213.9	Herring et al. (1993)
Malacostraca Amphipoda					
Cyphocaris anonyx	3.60×10^{11}				Herring (1981)
Cyphocaris challengeri	3.60×10^{11}				Herring (1981)
Cyphocaris faurei	2.20×10^{10}	5.7×10^{10} per flash		9.3×10^{3}	Bowlby et al. (1991)
Cyphocaris richardi	3.60×10^{11}	2.6×10^{9} per flash			Bowlby et al. (1991); Herring (1981)
Scina crassicornis	1.70×10^{9}	1.50×10^{9} per flash	1.60×10^{3}	3.0×10^{3}	Bowlby et al. (1991)
Malacostraca Euphausiacea					
Meganyctiphanes norvegica	1.20×10^{10}		150	800	Cronin et al. (2016); Johnsen et al. (2014)
Thysanoessa furcilia		5×10^{9} per flash			Lapota et al. (1989)
Thysanoessa inermis	2.50×10^{10}		220	440	Cronin et al. (2016)
Thysanoessa longicauda		1.10×10^{11}			Swift et al. (1995)
Malacostraca Decapoda					
Acanthephyra purpurea		3.9×10^{9} per flash		2.37×10^{3}	Nicol (1958a)
Ostracoda Halocyprida					
Boroecia sp.	7.67×10^{10}		340		Cronin et al. (2016)
Conchoecia atlantica		2.00×10^{9}			Batchelder and Swift (1988)
Conchoecia bispinosa		3.80×10^{10}			Batchelder and Swift (1988)
Conchoecia curta		7.20×10^{10}			Batchelder and Swift (1988)
Conchoecia daphnoides		1.60×10^{10}			Batchelder and Swift (1988)
Conchoecia elegans		1.00×10^{10} per flash			Lapota et al. (1989)
Conchoecia imbricata		1.60×10^{10}			Batchelder and Swift (1988)
Conchoecia magna		5.00×10^{9}			Batchelder and Swift (1988)
Conchoecia oblonga		9.00×10^{9}			Batchelder and Swift (1988)
Conchoecia parthenoda		7.00×10^{9}			Batchelder and Swift (1988)
Conchoecia procera		6.00×10^{9}			Batchelder and Swift (1988)
Conchoecia spinifera		2.00×10^{9}			Batchelder and Swift (1988)

(Continued)

TABLE 3 Continued

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Conchoecia spinirostris		1.00×10^{9}			Batchelder and Swift (1988)
Conchoecia subarcuata		1.60×10^{10}			Batchelder and Swift (1988)
Halocypris brevirostris		3.08×10^{11}			Batchelder and Swift (1988)
Chordata					
Appendicularia Copelata					
Oikopleura sp.		1.70×10^{11}			Swift et al. (1985)
Oikopleura dioica	2×10^{9}		24	278	Galt (1978); Galt and Sykes (1983)
Oikopleura dioica (House)			41		Galt and Sykes (1983)
Oikopleura fusiformis (House)			11	150	Galt et al. (1985)
Oikopleura labradoriensis		4.3×10^{11}	22	278	Buskey (1992); Galt and Sykes (1983)
Oikopleura labradoriensis (House)			58		Galt and Sykes (1983)
Oikopleura rufescens			10	108	Galt et al. (1985)
Oikopleura rufescens (House)			44	200	Galt et al. (1985)
Oikopleura vanhoeffeni		6.8×10^{11}			Buskey (1992)
Stegosoma magnum			9	56	Galt et al. (1985)
Stegosoma magnum (House)			8	40	Galt et al. (1985)
Appendicularia Thaliacea					
Pyrosoma atlanticum	3.3×10^{12}	2.30×10^{13} per flash	2.00×10^{5}	5.92×10^{5}	Bowlby et al. (1990)
Pyrosoma verticillata	7.5×10^{11}	8×10^{12}	4.3×10^{3}	1.16×10^{5}	Bowlby et al. (1990)
Cnidaria					
Hydrozoa Leptothecata					
Octophialucium sp.	1.80×10^{10}	3.40×10^{10}	193	7.08×10^{3}	Widder (1991)
Phialidium sp.	2.40×10^{10}	2.70×10^{10}	280	3.51×10^{3}	Widder (1991)
Hydrozoa Narcomedusae					
Aeginura grimaldii		4.4×10^{11} per flash		3.7×10^{3}	Nicol (1958b)
Solmaris sp.	1.70×10^{10}	2.80×10^{9}	118	573	Widder (1991)
Solmissus marshalli	6.90×10^{10}	3.20×10^{10}	585	1.67×10^{3}	Widder (1991)
Hydrozoa Trachymedusae					
Crossata alba		4.9×10^{7} per flash		3.8×10^{3}	Nicol (1958b)
Haliscera conica	1.5×10^{10}	4.3×10^{9}	332	976	Widder (1991)
Hydrozoa Siphonophorae					
Vogtia glabra		1.4×10^{11} per flash		3.5×10^{3}	Nicol (1958b)
Vogtia spinosa		2.3×10^{11} per flash		4.43×10^{3}	Nicol (1958b)
Scyphozoa Coronatae					
Atolla wyvillei		1.4×10^{11} per flash		5.79×10^{3}	Nicol (1958b)
Paraphyllina sp.	1.70×10^{10}	1.30×10^{10}	232	3.51×10^{3}	Widder (1991)

(Continued)

TABLE 3 Continued

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Periphylla	1.90×10^{11}	5.50×10^{11}	426	1.14×10^{4}	Widder (1991)
Ctenophora					
Nuda Beroida					
Beroe cucumis	1.04×10^{10}	5.40×10^{10}	1.12×10^{3}	1.38×10^{3}	Cronin et al. (2016); Johnsen et al. (2014); Widder (1991)
Beroe cuvata	3.40×10^{12}	9.30×10^{11}	151	514	Widder (1991)
Beroe forskalii	1.50×10^{12}	4.10×10^{11}	204	644	Widder (1991)
Tentaculata Cydippida					
Euplokamis sp	8.10×10^{12}	8.20×10^{11}	79	355	Widder (1991)
Haeckelia beehleri	2.70×10^{10}	1.60×10^{10}	225	1.19×10^{3}	Widder (1991)
Lampea pancerina	1.90×10^{10}	9.40×10^{10}	824	1.08×10^{5}	Widder (1991)
Mertensia ovum	6.50×10^{9}		340	260	Cronin et al. (2016); Johnsen et al. (2014)
Tentaculata Lobata					
Bolinopsis sp.	9.70×10^{11}	2.00×10^{11}	157	621	Widder (1991)
Leucothea multicornis	2.00×10^{10}	7.40×10^{9}	221	1.28×10^{3}	Widder (1991)
Ocyropsis fusca	2.00×10^{12}	6.40×10^{11}	298	2.24×10^{3}	Widder (1991)
Myzozoa Dinoflagellata					
Tripos fusus	3.41×10^{9}	5.30×10^{8}		239	Buskey and Swift (1990); Latz et al. (2004b)
Tripos horridum		5.30×10^{8}			Buskey and Swift (1990)
Ceratocorys horrida	9.20×10^{9}		41	184	Latz and Lee (1995)
Gonyaulax digitale		2.10×10^{7}			Esaias and Curl (1972)
Gonyaulax grindleyi		1.00×10^{8}			Swift et al. (1995)
Gonyaulax monacantha		6.60×10^{8}			Buskey and Swift (1990)
Gonyaulax parva		9.70×10^{7}			Swift et al. (1995)
Gonyaulax polygramma		1.60×10^{9}			Buskey and Swift (1990)
Gonyaulax scrippsae		3.60×10^{8}			Buskey and Swift (1990)
Gonyaulax spinifera		3.00×10^{8}			Esaias and Curl (1972)
Lingulodinium polyedra	2.70×10^{9}	1.17×10^{8}	34	148	Biggley et al. (1969); Latz and Lee (1995); Latz et al. (2004b)
Noctiluca scintillans	9.00×10^{10}	2.50×10^{11}	44	568	Buskey et al. (1992); Widder (1991)
Protoperidinium brevipes		2.00×10^{8}			Swift et al. (1995)
Protoperidinium ceraseus		4.80×10^{8}			Esaias and Curl (1972)
Protoperidinium concoides		2.00×10^{9}			Swift et al. (1995)
Protoperidinium conicum		3.40×10^{9}			Esaias and Curl (1972)

(Continued)

TABLE 3 Continued

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Protoperidinium crassipes		1.90×10^{9}			Buskey and Swift (1990)
Protoperidinium curtipes		3.00×10^{9} per flash			Lapota et al. (1989)
Protoperidinium depressum		2.00×10^{9} per flash			Lapota et al. (1989)
Protoperidinium divergens		1.6×10^{10}			Buskey et al. (1992)
Protoperidinium excentricum		1.5×10^{10}			Buskey et al. (1992)
Protoperidinium exiquipes		8.00×10^{9}			Buskey et al. (1992)
Protoperidinium globulus		1.10×10^{9}			Buskey and Swift (1990)
Protoperidinium granii		8.10×10^{8}			Esaias and Curl (1972)
Protoperidinium leonis		1.40×10^{9}			Buskey and Swift (1990)
Protoperidinium minutum		2.00×10^{9}			Swift et al. (1995)
Protoperidinium oceanicum		7.10×10^{9}			Buskey and Swift (1990)
Protoperidinium ovatum		1.60×10^{9}			Buskey and Swift (1990)
Protoperidinium palladium		2.80×10^{9}			Buskey and Swift (1990)
Protoperidinium pellucidum		2.00×10^{8}			Esaias and Curl (1972)
Protoperidinium pentagonum		8.00×10^{9}			Buskey et al. (1992)
Protoperidinium pyriforme		1.00×10^{8}			Swift et al. (1995)
Protoperidinium steinii		1.10×10^{9}			Buskey and Swift (1990)
Protoperidinium saltans		2.00×10^{8}			Swift et al. (1995)
Protoperidinium sinaicum		2.00×10^{8}			Swift et al. (1995)
Protoperidinium sournia		2.00×10^{8}			Swift et al. (1995)
Protoperidinium steinii		1.40×10^{8}			Esaias and Curl (1972)
Protoperidinium subinerme		1.50×10^{9}			Esaias and Curl (1972)
Protoperidinium tubum		2.00×10^{9}			Swift et al. (1995)
Pyrocystis fusiformis	4.79×10^{10}		10	200	Latz et al. (2004b); Widder and Case (1981)
Pyrocystis lunula		3.89×10^{9}			Biggley et al. (1969)
Pyrodinium bahamense		3.35×10^{8}			Biggley et al. (1969)
Radiolaria					
Collosphaera huxleyi			289	700	Latz et al. (1987b)
Collosphaera sp.			205	1.1×10^{3}	Latz et al. (1987b)

(Continued)

TABLE 3 Continued

Taxonomy	Flash kinetics				References
	Peak intensity (photon/s)	MSL (photons)	Rise time (ms)	Flash duration (ms)	
Raphodozoum acuferum			375	2.4×10^3	Latz et al. (1987b)
Sphaerozoum punctatum			280	900	Latz et al. (1987b)
Sphaerozoum verticillatum			449	1×10^3	Latz et al. (1987b)
Thalassicolla nucleata	6.70×10^8	9.20×10^8	923	5×10^3	Latz et al. (1991)

and Puerto Rico to measure the abundance of the dinoflagellate *Pyrodinium bahamense* (Seliger and McElroy, 1968; Seliger et al., 1969), contributing to an understanding of the mechanisms that contributed to their high abundance in the bays (Seliger et al., 1971).

The most commonly implemented approach for measuring MSL *in situ* has been the mixing chamber bathyphotometer, which is also the design employed for the only commercial off-the-shelf embodiment, the Underwater Bioluminescence Assessment Tool (UBAT; Seabird Scientific, www.seabird.com, Bellevue, WA). These sensors have relatively slow flow rates, typically ranging from 0.2 to 1 L/min, and a single, small mixing chamber, and thus can be compact and practical in deployment. Besides UBAT, examples of past iterations of this design include the MBBP models from Dr. Jim Case's laboratory at UCSB (Herren et al., 2005) that served as predecessors of the UBAT, a bathyphotometer developed at URI in the 1980s (Swift et al., 1985), the Over-The-Side (OTiS) bathyphotometer (Bivens et al., 2001), NOSC (Latz and Rohr, 2013), and BIOLITE (Latz and Rohr, 2013). Organisms are mechanically stimulated before the flow enters the mixing chamber using means including an impeller pump, flow constriction, or flow obstruction. A sensitive detector such as a PMT is positioned in close proximity to the mixing chamber. Advantages of this approach include compact size and ease of deployment. The 60-Hz sampling rate of the UBAT is capable of resolving flash kinetics for individual organisms. This makes the identification of source organisms possible based on their flash properties (Johnsen et al., 2014; Cronin et al., 2016; Messié et al., 2019; Chen et al., 2023).

Both the URI bathyphotometer and the NOSC used a pump downstream, creating turbulence in the mixing chamber to mechanically stimulate organisms (Latz and Rohr, 2013). Measurements by the URI bathyphotometer, as well as those by

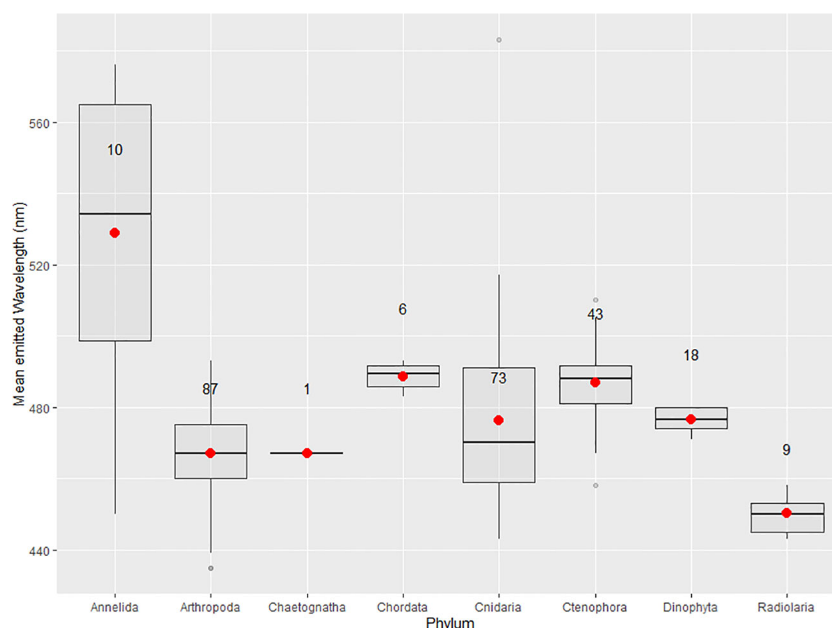

FIGURE 4
Boxplots of the mean emitted wavelength maxima for phyla with described bioluminescent planktonic species. Red dots indicate the mean of the distribution and sample size is displayed on every boxplot. Maximal wavelengths 2 standard deviations above or below the phyla's mean are displayed as outliers.

the NOSC bathyphotometer, were coupled with abundance data obtained from net tows to calculate light budgets that determined the contribution of source organisms to the bioluminescence field (Swift et al., 1983; Lapota et al., 1989; Lapota et al., 1992a; Lapota et al., 1992b; Swift et al., 1995).

The only other commercialized bathyphotometer is the GlowTracka (Chelsea Technologies, UK), a small low power, low flow rate instrument that uses a photodiode as a light detector. Despite limited sensitivity, it is still suitable for coastal areas with high levels of dinoflagellate bioluminescence (Kim et al., 2006; Le Tortorec et al., 2014; Parvathi et al., 2021).

Drawbacks of mixing chamber bathyphotometers such as UBAT include (1) poorly defined levels of shear in most iterations, (2) low flow rates creating a likely severe underrepresentation bias for mobile zooplankton able to avoid entrainment, and (3) potential prestimulation in entrance tube configurations transporting the water to the agitator. There is also the inherent property of a mixing chamber being fully turbulent, resulting in ambiguity in (1) the number of secondary stimulations occurring within the chamber, and (2) the residence time of an organism in the chamber, ultimately defined by a probability distribution function. Consequently, measured MSL in photons/L from different mixing chamber bathyphotometers are not directly comparable but may be correlated (Latz and Rohr, 2013), especially considering there are idiosyncratic time dependencies that are not typically characterized.

In the 1990s, the HIgh flow rate Defined EXcitation (HIDEX) bathyphotometer and associated variants were developed (Widder, 1991; Bivens et al., 2001; Widder et al., 2003) to address some of the ambiguities related to mixing chamber bathyphotometers. Organisms were mechanically stimulated as they flowed through a circular grid with a square hole pattern with 1-cm spacing; this form of excitation has readily modeled hydrodynamic and shear stress properties (McKenna and McGillis, 2004; Lacassagne et al., 2020). First flash MSL kinetics were then resolved by an array of PMT detectors lining a 1.6-m tube, removing residence time ambiguity and potential secondary flashes as laminar pipe flow quickly develops after initial grid stimulation (Widder et al., 1993). An integrated measurement of total intensity was also measured via an array of optical fibers surrounding the tube, all coupled to a single PMT. Flow rates could be varied and were typically kept between 18 and 22 L/s in field measurements. This relatively rapid flow rate was essential when trying to entrain mobile zooplankton as small as copepods with the ability to instantaneously leap up to 1 m when threatened, although some behavior avoidance was still likely. Varying flow rate also had the advantage of varying maximal shear rates experienced via grid stimulation. The bathyphotometer tube was opaque and had a helical, rotating baffle upstream of the stimulation grid to minimize ambient light from entering the tube; the baffle shape was designed to minimize prestimulation of organisms. HIDEX instruments were deployed by the US Naval Oceanographic, the Naval Ocean Research and Development Activity (NORDA), the Naval Oceanographic and Atmospheric Laboratory (NOARL), and the Naval Research Laboratory (NRL) until the mid-2000s but were never commercialized for general use.

At a flow rate of 18 L/s, the residence time of an organism traversing the HIDEX bathyphotometer tube was approximately 1 s. All the emission kinetic parameters discussed in Section 2.8 could be resolved. For organisms with flashes longer than 1 s (see Table 3), all kinetic parameters were still generally resolvable except for flash duration, which may still be inferred in typical cases. Zooplankton with minimum length scales greater than 1 cm could not be resolved, and rapid flows impacting a grid can also disintegrate delicate organisms such as some gelatinous plankton, with associated emissions being more consistent with a "death glow" than typical MSL. Durations of death glows of gelatinous plankton are typically much longer than natural MSL, often lasting tens of seconds (Bowlby et al., 1990; Widder, 1991). Despite these drawbacks, to which we can add the HIDEX system was about the size of a small car and challenging to deploy, measurements of MSL with HIDEX may be considered the most precise ever made *in situ*.

Bathyphotometers have been profiled from a ship, towed by a ship, deployed as an expendable probe (Case et al., 1993; Fucile et al., 1999), configured in flow-through mode on a ship (Bivens et al., 2002; Latz and Rohr, 2013), autonomously moored (Berge et al., 2012), and mounted on AUVs (Thomas et al., 2003; Moline et al., 2009; Johnsen et al., 2014) mounted on a Slocum glider (Shulman et al., 2020). Any particular deployment approach may have advantages based on a specific research application.

3.2 *In situ* stimulation by a mesh grid

Another *in situ* MSB approach is imaging a mesh grid producing mechanical contact of fluid shear by moving through water, either by vertical profiling from a ship (Priede et al., 2006; Craig et al., 2009; Craig et al., 2010) or by horizontal transects from a moving submersible (Widder et al., 1989; Widder, 2002; Malkiel et al., 2006). Termed the Spatial PLankton Analysis Technique CAMera (SPLATCAM), a low-light camera (ISIT in this case) is focused on a mesh grid approximately 1 m away (Widder and Johnsen, 2000). Shear stress is produced as the grid moves through the water and flashes from dinoflagellates, copepods, euphausiids, and gelatinous organisms were differentiable. When capturing bioluminescent emissions with a single camera, there is a trade-off between imaging the organism, which requires illumination, and seeing the bioluminescence under low-light conditions. To counter this problem, Widder (1992) developed a dual camera system, where an infrared camera captured the organism and an ISIT camera captured the emission. Since the two cameras capture in different spectral regions, the organism and its emissions can be distinguished at the same time. This can be a valuable tool when studying small-scale interactions like predatory events involving dinoflagellates and fast swimming copepods, i.e., displays of the burglar alarm hypothesis.

3.3 Passive detection

With passive detection approaches, stimulation occurs naturally from biological activity and from physical instabilities such as breaking of surface and internal waves (Stokes et al., 2004), boundary layer currents, bubbles (Deane et al., 2016), swimming dolphins (Rohr et al., 1998), deep-sea infrastructures (Tamburini

et al., 2013; Holzapfel et al., 2023), etc. Emissions are resolved with a sensitive detector or imaging system (Roithmayr, 1970; Nealson et al., 1984; Buskey and Swift, 1990). With this approach, the relative placement of a detector can significantly impact bioluminescence estimates. Nealson et al. (1984) measured 10 to 25 times more bioluminescence when a passive detector was positioned over the side of a boat looking down in the water column compared to another passive detector moored at 40 m looking up through the same water column. Presumably, there were more bioluminescent organisms and more shear in surface waters from higher biological activity and potentially from physical instabilities. However, attenuation of emitted light through the water column will have a significant but unknown impact on passive measurements, as the distances of individual emissions to the detector and the optical properties of the water are ostensibly unknowns. For example, passive emissions in the Nealson et al. study could have been similar throughout the water column but water clarity could have been poorer near 40 m than near the surface. While detection of naturally induced bioluminescence may thus be difficult to interpret, it can still be important for assessing impacts on ambient light fields, which is the property being directly measured (Craig et al., 2011). Tamburini et al. (2013) observed mechanically stimulated bioluminescence at the ANTARES neutrino telescope in the deep Mediterranean Sea using low-light cameras. Deep currents passing next to moored infrastructure would create shear stress and bioluminescence events. Temporal kinetic patterns in passive detection may also be valuable in assessing what organisms are present. While intensity of emissions would be difficult to interpret due to unknown attenuation as light propagates to the detector, aspects such as flash patterns, flash durations, rise times, e-folding times, and spectral quality of flashes are all aspects that may have potential diagnostic value if the emissions are sufficiently proximal to the detector. Spatial distributions through remote imaging instead of only using a single sensitive light detector could also be valuable in interpretation, as emissions from colonies, or exuded clouds, secreted extracellular structures, or autotomized limbs could be diagnostic of the specific emitting organism(s). Such imagery may be particularly useful for zooplankton that are too large for an MSL measurement with a particular bathyphotometer and/or for zooplankton able to avoid entrainment in the flow of such sensors. Patterns of emission in imagery may also be used to identify the natural source of shear, e.g., a swimming organism or breaking wave. For emissions imaged from above water (Roithmayr, 1970; Altinağaç et al., 2010), special considerations should be made for filtering of emissions as the light propagates through the water column, which can spectrally shift the peak in radiance (Moline et al., 2007).

4 Distributions of bioluminescent organisms

Zooplankton and dinoflagellates account for almost the totality of the bioluminescence observed at the oceanic's surface waters (Swift et al., 1983). However, the relative importance of both groups to the water column's MSL is highly variable. Indeed, Swift et al. (1983) reported the majority of bioluminescence in the Sargasso Sea can be attributed to zooplankton. Batchelder and Swift (1989) provide a comprehensive description of bioluminescent zooplankton of that region, while also providing relative contributions to MSL of the water column. However, the mesh size of their plankton net did not allow for representative sampling of dinoflagellate species. This study was one of the first efforts to develop a light budget for primary bioluminescent groups.

In many cases, zooplankton are not the main contributor to water column bioluminescence. Lapota et al. (1989) estimated the bioluminescence of zooplankton in the first 100 m of Vestfjord, Norway was approximately 4% of the total bioluminescence measured, although bioluminescent zooplankton biomass was also low during the sampling period. With these differences in mind, it is clear that a multitude of variables can affect the bioluminescence of a given system, e.g., timing, location, primary production, diversity, and community composition (Neilson et al., 1995; Craig et al., 2010; Haddock et al., 2010; Wimalasiri et al., 2020). For example, recent increases in temperature in Antarctic waters have changed the planktonic community from dominant krill swarms to salp colonies, reducing the bioluminescence of the water column by half (Melnik et al., 2021). The depth of maximum bioluminescence also varies throughout the day, following the diel vertical migration of zooplankton (Berge et al., 2012; Shulman et al., 2012), although some studies attribute the diel variation of bioluminescence mainly to the circadian photoinhibition of dinoflagellates and select zooplankton (Batchelder et al., 1992; Mashukova, 2009). Lapota et al. (1992a) observed a significant difference in the contribution to total bioluminescence of dinoflagellates and zooplankton, depending on if they were sampling under the sea–ice interface or in the marginal ice zone (MIZ). In the first 10 m of the MIZ, the dinoflagellates *Protoperidinium* spp. represented 90% of total bioluminescence, whereas in the open ocean, that same percentage was attributed to the copepod *Metridia longa*. Although Buskey (1992) did not observe significant differences in the epipelagic bioluminescence between the MIZ and open waters of the Greenland Sea, the relative contribution of copepods, larvaceans, ostracods, and krill varied considerably over time, and dinoflagellates accounted for a very small percentage. Approximately 60%–80% of species are bioluminescent in the open ocean, compared to 1%–2% in coastal environments (Morin, 1983). However, these very few bioluminescent coastal species often dominate the water column in biomass.

When measuring bioluminescence throughout the water column, peak MSL usually occurs in the mixed layer or near the thermocline (Wimalasiri et al., 2020). Indeed, this is typically a region of higher phytoplankton productivity, on which bioluminescent zooplankton can thrive. The pycnocline is also a relatively discrete region of the water column, often with high shear (Basterretxea et al., 2020). Considering most bioluminescent zooplankton can produce light when mechanically stimulated and that total emission is correlated with shear levels, the pycnocline typically is a region of high MSL (McManus et al., 2003; Polonsky et al., 2020). On a global oceanic scale, bioluminescence in Atlantic surface waters has been linked to coastal upwelling currents, with an

easterly decreasing gradient (Piontkovski et al., 1997). Staples (1966) provides an extensive review of bioluminescence events and their seasonal variation in most major oceanic basins. Peaks and variations in bioluminescence have also been linked to internal waves in the tropical Atlantic (Kushnir et al., 1997). High bioluminescence has been measured in thin sound scattering layers in the Gulf of Maine, for which the euphausiid *Meganypctiphanes norvegica* and the ctenophore *Euplokamis* sp. were thought to be the main species responsible (Widder et al., 1992). Acoustic instruments able to map patchy zooplankton in the water column on fine scales suggest that previous estimates of zooplankton MSB may be significantly underestimated (Benoit-Bird et al., 2010b; Moline et al., 2010; Sullivan et al., 2010). Indeed, MSL is as much as 200 times greater in thin sound scattering layers than background bioluminescence outside them (Widder et al., 1992). This is further complicated by the vertical migration of these sound scattering layers, effectively moving bioluminescence hot spots through the water column with isolumes (Clarke and Backus, 1964; Clarke, 1971). Ancillary acoustic measurements can therefore provide vital fine-scale spatiotemporal information when trying to study zooplankton bioluminescence, considering the inherent patchiness and their diel vertical migrations sometimes spanning hundreds of meters (Boden, 1970).

Discriminating assemblages of bioluminescent organisms typically requires relatively laborious net tow collections followed by microscopic identification of individual organisms on a ship by a taxonomist. There are, however, submersible microscopic imaging systems that may now be employed to image organisms *in situ* and quantitatively assess their distributions through automated machine learning algorithms (Sosik and Olson, 2007; Guo et al., 2021; Le et al., 2022). Higher organism counts can usually be obtained using these approaches and the imaging system can be collocated with a bathyphotometer during deployments. Submersible imaging microscopes developed over the last 15 years include (1) holographic imagers such as the custom HOLOCAM and AUTOHOLO developed at Harbor Branch Oceanographic Institute (Florida Atlantic University) (Nayak et al., 2016; Nayak et al., 2019; Barua et al., 2023) and the LISST-HOLO commercialized by Sequoia Scientific (www.sequoiasci.com; Bellevue, WA), (2) designs based on conventional microscope and cytometer approaches like the FlowCytobot (IFCB) (Olson and Sosik, 2007; Orenstein et al., 2020), and (3) shadowgraph imagers such as those commercialized by Bellamare (www.bellamare-us.com; Miami, FL). Since these instruments could be used to image organisms in close proximity to the bathyphotometer, it may be possible to verify organism diversity in separate net and bottle sampling *in situ*.

5 Applications for studying and measuring bioluminescent emissions

Biological oceanographers can consider light emissions in the water column as a proxy for the abundance and diversity of bioluminescent organisms when studying marine systems. Bioluminescence can also serve as a proxy for biomass (Squire and Krumboltz, 1981), primary and secondary production, remote identification and monitoring (Johnsen et al., 2014), and long-term climate change impacts (Piontkovski and Serikova, 2022). The following section describes applications for measuring bioluminescence and flash kinetics in marine ecosystems.

The patchiness of zooplankton populations in the water column is a subject of interest in remote sensing and acoustics studies (Jaffe, 1999; Holliday et al., 2003; Taylor et al., 2005; Sullivan et al., 2010; Basedow et al., 2019). In systems where zooplankton bioluminescence is dominant, vertical profiles of the BP-MSL can offer insight into the distribution of the zooplankton in the water column (Gitelson and Levin, 1989). In addition to net tows at depth and acoustic profiling, bioluminescence profiles can be an additional tool in these studies trying to resolve zooplankton spatial composition. Cram and Malan (1971) proposed the bioluminescence of krill, a very important functional group to both fisheries and marine ecosystems, may be their best characteristic for remote sensing. In Widder et al. (1999), bioluminescence was used to precisely pinpoint thin layers half a meter thick of high biomass of the copepod *Metridia lucens*, instead of sampling zooplankton with conventional net methods every meter and potentially missing aggregations.

5.1 Bioluminescence as a tool for flow visualization

Bioluminescence can be used to study biological hydrodynamics, which are often very complex systems to model. Knowing the shear stress threshold to trigger a flash response can provide rapid insight into the state of the system, essentially using dinoflagellates as flow markers (Latz et al., 1995), and offers opportunities to model their flash response (Deane and Stokes, 2005). Bioluminescent flashes of dinoflagellates were studied by Rohr et al. (1998) to resolve the flow around a swimming dolphin. It was concluded that levels of shear stress greater than threshold were achieved over most of the dolphin's body, except for the head, rostrum, and fins. Bioluminescence emissions were correlated with boundary layer thickness and identified regions where separation of the flow from the body occurred. A similar study was done a decade prior with harbor seals, essentially identifying three zones of high shear through bioluminescent emissions, i.e., whiskers, shoulders, and hind flippers (Williams and Kooyman, 1985). Hobson (1966) suggested this same species might use bioluminescence around swimming prey as a hunting strategy at night. This is of interest to biological oceanographers, functional morphologists, and fluid mechanics experts by providing an unusual approach to identifying high shear zones, quantifying drag around a moving object in water. Researchers studying ocean currents may benefit from dinoflagellate bioluminescence, as Rohr et al. (2002) suggested they be used to identify high-energy zones with prominent stratification.

5.2 Bioluminescence to locate fish populations

Fish schools swimming through the water column will also trigger bioluminescent displays. These emissions can be monitored

from boats or aircraft to detect fish populations at night. Squire and Krumboltz (1981) describe such a technique using a low-light video system capturing the bioluminescence created by anchovies triggering planktonic bioluminescence. Other fish species of considerable economic value, i.e., mackerel, sardine, herring, and yellowfin tuna, have also been detected by fishing vessels at night using water column bioluminescence (Roithmayr, 1970). Experienced fishermen can evaluate school biomass based on the size of the bioluminescent cloud and identify fish species based on patterns of bioluminescence propagation (Altinağaç et al., 2010). On the other hand, it has been suggested that water column bioluminescence created by fishing nets may trigger either avoidance or attraction behavior by fish (Jamieson et al., 2006). Monitoring bioluminescence above the water surface could prove a useful technique and asset for fish school sighting and biomass estimation by fisheries and population monitoring programs.

5.3 Correlation of bioluminescence with ocean parameters

The same can be said for the planktonic biomass itself. Considering that a considerable fraction of zooplankton species have bioluminescent capabilities, one can use bioluminescence measurements to infer the primary and secondary production of the water column (Craig et al., 2010). Other variables also covary with water column bioluminescence. In the Mediterranean Sea, surface chlorophyll *a* correlated with MSL and could be used to predict bioluminescent zooplankton abundance in the mesopelagic zone (Craig et al., 2010). Lapota et al. (1989) observed that the same approach could be used to approximate dinoflagellate abundance in a Norwegian fjord. Ondercin et al. (1995) developed a model of North Atlantic water column bioluminescence based on bio-optical properties such as temperature, chlorophyll *a*, irradiance, mixed layer depth, and nitrate concentration. To understand the variability of bioluminescence in the context of ecology and hydrology, it is important to measure other abiotic parameters simultaneously, such as dissolved oxygen, turbidity, and temperature using instruments such as a CTD/rosette or multiparameter sondes simultaneously (Bivens et al., 2002).

5.4 Identifying luminescent organisms based on flash characteristics

One of the most promising applications for MSB is identifying the presence of specific species without needing to collect organisms (Cronin et al., 2016; Messié et al., 2019). Indeed, since many species have different first flash kinetics, it may often be possible to discriminate between different bioluminescent planktonic clades *in situ* using a bathyphotometer providing well-resolved levels of shear stress stimulation. This type of autonomous sampling can be of great help in detecting fragile organisms like gelatinous plankton, species living at great depths that would otherwise not be present in net tows, species with very low abundance that would most likely not be sampled over a discrete time period and organisms difficult to culture and maintain in laboratory conditions such as heterotrophic dinoflagellates, larvaceans, and salps. Not only could bathyphotometers detect the presence of specific species with flash kinetics, but the biomass could also be estimated if the integrated bioluminescence of an individual flash is known. Using relative bioluminescent intensities over two wavelengths and first flash kinetics, Nealson et al. (1986) were able to correctly identify 10 species of dinoflagellates, krill, copepods, and corals, with 100% accuracy for some species. More recently, a similar experiment took place in the Arctic where Johnsen et al. (2014) described the variation of bioluminescence over a diurnal cycle and partitioned the total bioluminescence over key clades using the spectral properties and kinetics of bioluminescent flashes. Certain clades can also be identified from images of the bioluminescent flashes. Kocak et al. (1999) developed a model capable of tracking and identifying organisms based on flash size and duration. Bioluminescent emissions observed with the SPLAT CAM have been used to calculate nearest-neighbor distances for dinoflagellate and copepod layers in the Gulf of Maine (Widder and Johnsen, 2000), and to identify thin layers and aggregations of copepods, euphausiids, dinoflagellates, and ctenophores (Widder et al., 1999). Once a species has had its first flash kinetics and spectral properties described, a bathyphotometer could supplement the time-intensive processes of zooplankton fixation and identification in future sampling efforts by providing presence/absence information on finer scales over a much larger area. Messié et al. (2019) used bioluminescence measurements to identify dominant species of dinoflagellates and zooplankton in Monterey Bay, California. Background bioluminescence was associated with dinoflagellates and peaks were assumed to be caused by zooplankton flashes. The simultaneous use of a fluorometer allowed distinction between auto and heterotrophic dinoflagellate species. Based on glider observations of bioluminescence, fluorescence, and optical backscattering, Shulman et al. (2020) demonstrated a shift from an autotrophic and mixotrophic bioluminescent community toward a more heterotrophic one in the Delaware Bay area, DE.

5.5 Bioluminescence assays for toxicology

Bioluminescence measurements using MSL can be useful as sensitive non-lethal proxies for toxic compounds, complementing expensive and time intensive bioassays (Lapota et al., 2007; Widder and Falls, 2013; Perin et al., 2022). Half of the known dinoflagellate clades with bioluminescent capabilities are toxic (Haddock et al., 2010). The proposed method could augment expensive and time-intensive bioassays. Not only could bioluminescence help assess the presence of dinoflagellate toxins in water, but it can also be used to detect blooms at their inception, which is not possible with most alternative methods (Haddock et al., 2010; Le Tortorec et al., 2014; Le Tortorec 2017). Dinoflagellates can bloom rapidly and create health hazards to humans and marine life in coastal environments. Constant sampling and cell counting to monitor populations can be labor intensive. An autonomous underwater bathyphotometer providing real-time *in situ* BP-MSL of an area prone to harmful algal blooms could detect increases in dinoflagellate populations

without the need for constant sampling (Kim et al., 2006). Species like *P. bahamense*, *L. polyedra*, and *A. monilatum* are all bioluminescent and are often responsible for HABs events in coastal Florida or California. Bioluminescence monitoring could also be applied to other invasive species prone to rapid blooming, like the ctenophore *M. leidyi* in the Black and Caspian Sea (Kideys, 2002). This species is a threat to local fisheries as it decimates zooplankton and ichthyoplankton populations. Melnik et al. (2020) noted that an increase in *M. leidyi* biomass resulted in a decrease of dinoflagellate bioluminescence in the Black Sea. Since emissions of these two groups are distinct (Table 3), the relative contribution of both to water column bioluminescence may be a good indicator of the ecosystem's state, and could be measured remotely without intensive field deployments (Widder, 2010b). This could include ballast water monitoring. With over 90% of planktonic cnidarians potentially having bioluminescent capabilities (Martini and Haddock, 2017), their bioluminescence could be monitored to detect gelatinous blooms in the early stages.

5.6 Climate change and bioluminescence

Climate change and ocean acidification are causing rapid changes and shifts in marine communities worldwide (Doney et al., 2012; Beaugrand et al., 2014; Johnsen et al., 2014). Since most marine phyla possess bioluminescent species, climate change is expected to have significant impacts on the MSL of marine systems as well. However, very few studies have looked at the effects of climate change on bioluminescence and oceanic distributions of responsible organisms.

Dinoflagellates of the genus *Tripos* have many bioluminescent species and have extended their habitable range into warmer waters in the last few decades (Hays et al., 2005). Heating of surface layers in the Gulf of Alaska and Northeast Pacific in 2013 deprived the water column of silica, resulting in a dramatic shift in phytoplankton assemblage from diatoms to dinoflagellates (Arteaga and Rousseaux, 2023). As diatoms are not bioluminescent, a shift to a dinoflagellate-dominated system is expected to significantly increase the bioluminescence of these waters. On the other hand, Hinder et al. (2012) have noted a long-term shift in relative abundance from dinoflagellate to diatoms in the North Sea and Northern Atlantic, which would be expected to result in an overall decrease in coastal bioluminescence.

A particularly important bioluminescent zooplankton group globally is gelatinous plankton, whose blooms are getting larger and more frequent (Siddique et al., 2022). Considering these groups have many bioluminescent species, a concomitant increase in the MSL in diverse oceanic waters may be expected. Brodeur et al. (1999) noted a significant increase in gelatinous plankton biomass in the Bering Sea, mostly from scyphozoan and hydrozoan jellyfish, that was attributed to warming waters. Gelatinous plankton are very tolerant to a wide range of nutrient levels and environmental parameters, and thus can bloom rapidly and cause community changes in surface waters in virtually all of the Earth's oceans (Condon et al., 2013). Since the mean emitted wavelength maxima of cnidarian species can be statistically distinguished from most other phyla, the spectral properties of bioluminescent emissions could be used to monitor increases in gelatinous biomass and study the effects of climate change on community shifts.

There is now growing evidence that other bioluminescent zooplankton are both migrating in their distributions and shifting in importance in global oceanic ecosystems on time scales relevant for climate change; however, again, our assessment of associated impacts on MSL can only be implied. For example, copepods, main contributors to the ocean's carbon pump (SampeiH et al., 2009; Pinti et al., 2023), have been found to be migrating hundreds of kilometers northward in the northern hemisphere every decade (Ratnarajah et al., 2023). On the other hand, Edwards et al. (2021) observed a decrease in krill biomass over decade-long observations in the North Atlantic. *Euphausia superba*, the bioluminescent krill serving as the keystone species of Antarctic food webs with an estimated global biomass of 215 million tons (Cavan et al., 2019), has been found migrating toward the South Pole. Zooplankton body size, which often correlates to bioluminescence intensity (Biggley et al., 1969; Herring, 2007; Tokarev et al., 2012), has been found to decrease with increasing water temperature (Ratnarajah et al., 2023). This will most likely impact the FF-MSL of large bioluminescent organisms, e.g., scyphozoans, siphonophores, ctenophores, and planktonic annelids. Piontkovski and Serikova (2022) noted a significant decrease in the integrated water column MSL of the tropical Atlantic Ocean over a 40-year period, for which zooplankton species are the main contributors, which correlated with increased water temperatures. Another study in Antarctic waters observed a community shift over 20 years, with salp colonies increasing in importance relative to krill with associated bioluminescence decreasing by 50%, which they hypothesized was caused by climate change, specifically warming waters (Melnik et al., 2021). Rigorously testing such hypotheses is difficult, as modeling of zooplankton community composition is a very complex problem requiring robust time series abundance data for all trophic levels on which to base the model (Ratnarajah et al., 2023). A further complication is rapid changes in environmental parameters driven by climate change create conditions that may not be reflected in previous data (Villarino et al., 2015). We note these studies that suggest monitoring zooplankton communities through species-specific flash kinetics in key locations could give valuable insight into species migration and community shifts.

Other effects of climate change have received scarce attention with respect to bioluminescence but likely have significant impacts on the global ocean bioluminescent potential. Global warming is particularly intense in polar regions, which, in turn, will promote the melting of the arctic ice coverage, resulting in increasing global sea level and decreasing seawater salinity [models predict an increase of the sea level between 3.0 and 3.3 mm/year based on current hydrocarbon emissions (Cazenave et al., 2014; Dieng et al., 2017)]. Changes in sea level will change coastal landscapes and are sure to modify their ecosystems and species interactions. Decreasing salinity will select for more generalist-type organisms that can withstand wide environmental ranges. Many such species are bioluminescent, e.g., gelatinous plankton. Additionally, hydrocarbon emissions are responsible for the acidification of our oceans. Models predict acidification of −0.2 pH for the coast of

California by 2040 (Marshall et al., 2017). For dinoflagellates, the scintillons, or the cellular organelles responsible for harboring the bioluminescence reaction are activated through a local drop in pH in the cell (Fogel and Hastings, 1972). It is still unclear how environmental changes in the water column's pH will affect bioluminescent emissions of organisms. With these important and rapid environmental changes in mind, climate change will undoubtedly drive changes in coastal and pelagic bioluminescence through community shifts and changes in the physiology of bioluminescent organisms. Research is needed to better understand how environmental shifts driven by climate change may affect organism bioluminescence kinetics and the role of bioluminescent species in marine systems.

6 Research perspectives, gaps, and biases

Measuring and interpreting bioluminescent emissions and their temporal variation *in situ* is not a trivial task. In Sections 3 and 5, we discussed the potential challenges and biases one can encounter when measuring the mechanically stimulated bioluminescence of organisms in the laboratory and *in situ*. Here, we elaborate on research and technology gaps, suggest approaches to standardize measurements, and consider possible broader roles for bioluminescence measurements and first flash characterization in studies of diversity, ecology, functional morphology, and small-scale fluid mechanics.

6.1 Organism emissions

Widder et al. (1999) described a key challenge at the time of publication as the absence of good taxonomic coverage of flash kinetics and spectral properties for most planktonic groups. Unfortunately, few species have had their bioluminescence described since then. As discussed in Section 2.9, it is clear that a minority of the known bioluminescent plankton have described flash kinetics and spectral properties. Studied species also rarely possess a full set of measured kinetics. For example, Widder et al. (1989) observed 30 species of mostly gelatinous plankton with bioluminescent capabilities in the Monterey Canyon. The spectral properties and flash kinetics of some of these species remain undescribed today. Most of the dinoflagellate species with described kinetics are part of the *Gonyaulax* and *Protoperidinium* genera (Table 3), while bioluminescence is present in several others, i.e., *Alexandrium*, *Tripos*, *Pyrodinium*, and *Pyrocystis* (Marcinko et al., 2013b). At least 100 species of ostracods are known, while in 2019, only 31 were described (Cohen and Morin, 2003), and fewer even had their flash kinetics characterized. Though several bioluminescent copepod species have been observed and documented, few have had their bioluminescence response and flash kinetics measured with quantifiable mechanical stimuli (Herring, 1983; Lapota and Losee, 1984; Herring et al., 1993; Widder et al., 1997). In fact, the clades Copepoda, Amphipoda, and Ostracoda, which are all well represented with bioluminescent planktonic species, are identified as among the groups with the most undiscovered species (Appeltans et al., 2012).

There is also a lack of data on intra-specific variations of bioluminescence across different taxa, particularly for zooplankton, and associated drivers for variance in flash kinetics, e.g., ontogeny, size, diet, sex, and life history. For example, larval stages of zooplankton, most importantly crustacean zooplankton, can occupy a large portion of the planktonic biomass; since these larvae often bioluminesce, they may significantly contribute to the MSL in oceanic waters. However, there is scarce data on their kinetics. In the Norwegian Sea, Lapota et al. (1988) found the nauplii stages of the copepod *Metridia longa* were responsible for 64% of the bioluminescence at 10 m, and 97% at 25 m. Not fully understanding the variation and change of bioluminescence emissions throughout the ontogenies of species that are main contributors to water column biomass can introduce significant bias into the interpretation of results and into planktonic biomass estimations. For example, the copepod *Metridia lucens* has had its TMSL measured for most of its larval stages and as an adult (Batchelder and Swift, 1989). Mean TMSL varies from 9×10^9 photons/ind for copepodite stage 2 to 1.08×10^{11} photons/ind for female adults. Thus, significant variation exists across a developmental gradient and can likely be found in other species of bioluminescent zooplankton that are not direct developers. For the invasive ctenophore *Mnemiopsis leidyi*, bioluminescence not only varies throughout its development, from 5.00×10^8 photons/s for eggs to 5.00×10^{10} photons/s for adults (Tokarev et al., 2012), but also based on its diet and water column temperature (Mashukova and Tokarev, 2013; Nikolaevich and Vladimirovna, 2016).

Furthermore, very scarce research has been carried out to discern effects of environmental factors such as water temperature, food and nutrients availability, previous light exposure, previous shear exposure, and likely several other variables, on organism emissions. As an example, the FF-MSL of *M. longa* was not affected by starvation for up to 3 weeks (Buskey and Stearns, 1991). Since baseline flash kinetic response must first be determined for an organism, we are very far from any comprehensive understanding of abiotic factors on emissions.

The circadian timing of an organism and its light and stimulation histories have a strong impact on bioluminescence emissions (Marcinko et al., 2013a). Dinoflagellates are photoinhibited when subjected to light during their scotophase, i.e., nighttime. Sullivan and Swift (1994) measured a decrease in MSL of 90% when *Tripos fusus* received 1×10^{17} m^{-2} s^{-1} of blue light. Photoinhibition has also been measured with the heterotrophic dinofagellate *Protoperidinium depressum* (Li et al., 1996). Sullivan (2000) observed TMSL of *P. noctiluca* reached its maximum 2 h into the scotophase, as the scintillons fully migrated to the periphery of the cell. Lapota et al. (1992b) measured the bioluminescence of the dinoflagellates *Tripos fusus* and *Protoperidinium curtipes* in laboratory and found light intensities of flashes at night are orders of magnitude higher, even if dark-adapted. To counter this, samples should be grown or kept in reverse day:night light cycles for a few days before measurements are taken (Neilson et al., 1995; Latz and Rohr, 2013). To allow for representative values of flash kinetics, specifically PIs and FF-MSLs, one should avoid any prestimulation

of the organism, as subsequent flashes are typically of lesser intensity. A few hours should pass in between measurements with the same organism, allowing for complete dark adaptation and regeneration of luciferin and luciferase. Considering this, one cannot be sure flashes measured *in situ* are necessarily at full capacity, while laboratory measurements with appropriately rested organisms may be consistently indicative of full capacity flash emissions.

The above leads to an important question, namely, what is the frequency of natural stimulation and emission for an entire assemblage of bioluminescent organisms present in a given environment? Do individuals rarely need to employ a flash to help thwart predation, or on average is this needed once a night, or several times a night? Answers to these questions are ultimately a convolution of a wide range of encounter probabilities both between prey and predators as well as other sources of stimulation such as swimming nekton or a breaking wave. Such naturally occurring emissions must be studied with passive approaches using low-light detectors, which may then potentially aid in interpretation of *in situ* MSL measurements.

Some groups of gelatinous plankton may also prove to have large inherent variance in their FF-MSL, simply because they form colonies of variable sizes. Siphonophores and salps, for example, are made of hundreds of smaller individuals of different functions, and the total length of the colony can span from centimeters to several meters for the same species, depending on age and potential fragmentation. Evidently, larger colonies will produce more bioluminescence, which can pose problems when describing the bioluminescence of species or creating photon budgets of the water column. Approaches to accurately quantify emission kinetics for such colonies are a significant challenge. In addition, there is evidence that, in some instances, different parts of the colony exhibit very different kinetics (Widder et al., 1989).

When emissions are measured for a species, often only the mean wavelength maxima and peak intensities are measured, which are insufficient to adequately differentiate species *in situ* due to the intra-specific variation of peak intensity values. This lack of emission data is partly a consequence of the difficulty in culturing some of these species in the laboratory and partly due to the considerable logistics needed to study them in the field. Culturing heterotrophic dinoflagellates or zooplankton requires maintaining several other prey cultures to sustain all the trophic levels needed, which can be very challenging. In the field, sampled species must be collected, maintained onboard the research vessel, dark-adapted, and rested for optimally 24 h, and assessed individually on the ship using a benchtop bathyphotometer capable of fully resolving emission kinetics (Latz and Rohr, 2013). Moreover, this is laborious and resource-intensive. Significant research efforts are clearly needed before we may hope to use flash kinetic signatures to study organism diversity from MSL measurements alone. Establishing a robust library of flash kinetics for zooplankton species would be a powerful addition for *in situ* identification efforts and biodiversity research. The previously mentioned work of Cronin et al. (2016) and Messié et al. (2019) demonstrate this. Additionally, Davis et al. (2005) used an empirical orthogonal function analysis to not only identify dinoflagellate species, but also isolate individual flashes from mixed data sets acquired with the HIDEX. However, using biologically emitted light as an identification proxy for ecosystem monitoring only becomes useful when the majority of the community has had its kinetics described. With at least 68 bioluminescent dinoflagellate species (Marcinko et al., 2013b) and only two species with complete sets of FFKs (Table 3), additional flash characterization is needed to adequately discriminate species off their bioluminescent emissions. Moreover, considering that between one- and two-thirds of marine species have yet to be described or even discovered (Appeltans et al., 2012), much work is needed to fully describe bioluminescent processes in the marine ecosystems.

6.2 Measurements and distributions

Each type of bathyphotometer is unique in how flow agitation stimulates bioluminescence because of different agitation approaches, residence times, flow rates, and maximal shear stress values, thus typically producing different BP-MSLs for the same population (Latz and Rohr, 2013) and complicating comparisons. There may be linear correlations in BP-MSLs from different devices but the relationships are organism-dependent, so a “transfer function” to convert measurements of any particular natural assemblage from one BP to another is not straightforward, even among BPs using the same approach, e.g., mixing chamber devices. A different flow rate and mode of stimulation will create different velocity gradient environments, i.e., potential for shear stresses, resulting in different observed flash kinetics in a manner specific to each species. Additionally, a higher residency time in a turbulent mixing chamber (dependent on chamber size and flow rate) may allow some species to flash several times, assuming supra-threshold levels of shear stress are maintained. As mentioned, residence times in a mixing chamber are defined by a probability distribution function, so when multiple flashes occur, consistent results and interpretation may only be possible when a statistically significant sample size is achieved for all individual organisms in an assemblage; even for long time series at specific depths, this will not be possible given common distributions of most zooplankton. As a simple example of difficulties in comparison, the HIDEX stimulated 94% of FF-MMSL for *Lingulodinium polyedra* with a ~1-s residence time, whereas the UBAT only stimulated 17% while its residence time can be as long as 10 s (Latz and Rohr, 2013). Currently, measurements of MSL and peak intensities should always be referenced to the instrument used.

Considering the above, bathyphotometers with well-characterized, highly constrained shear stress levels are strongly preferred, where all organisms will experience similar maximal shear. For FF-MSL measurements, the sensor should have no secondary stimulation and a residence time long enough to resolve key kinetic parameters. Flow rates should be high enough to entrain small zooplankton. In fact, these were the design criteria leading to development of the HIDEX (Widder et al., 1993). However, even the grid stimulation of the HIDEX with 1-cm grid openings imposes an estimated range in potential maximal shears experienced by an organism of approximately 0.1 to 0.9 Pa at flow

rates of 18 L/s depending on their position in the flow, with organisms centered in a grid opening experiencing the least shear (Tanweer et al., unpublished data). While next-generation HIDEX-like sensors are needed, development of new grid designs providing consistent, constrained shear levels for all organisms should be considered.

Since the most important factor introducing variability between different BPs is the shear stress applied, characterization of shear stresses for BPs would seem to create the potential to report MSL in terms of shear stress, e.g., with units of photons s^{-1} L^{-1} Pa^{-1}, to help standardize measurements. There are several issues with this, however, the most important being there is a finite range of shears where emissions will be shear-dependent. Each organism has a stimulation threshold below which no emission will occur. Bioluminescence intensity then increases with increasing flow rate and presumably shear stress, until a critical flow rate is achieved, above which there is no further increase in MSL (Widder et al., 1993; Latz and Rohr, 2013). At the very least, the shear stress characteristics of a particular BP should be reported with published MSL measurements to provide some hope the measurements may be repeated in the future. This is also not straightforward, unfortunately, as the shears associated with a sensor must typically be characterized with Computational Fluid Dynamics (CFD) modeling; because there are many input variables in CFD specific to a given configuration, independent validation is highly desirable with approaches such as Particle Imaging Velocimetry (PIV) or shear probes, but this is not always feasible within the flow apparatus of a BP.

There is a lack of long-term time series of bioluminescent measurements, both at the species and ecosystem levels. Without them, bioluminescence studies are a time–space snapshot of a multitude of covarying factors that impact an organism's or the population's MSL, including the effects of physical conditions such as winds and tides, seasonal variation, population growth, cyclical change in community assemblage, longer-term climatic variability in assemblages, diel vertical migration of plankton, blooms, impacts of grazing pressure, etc. To our knowledge, the last long-term data of mechanically stimulated bioluminescence was collected in the 1990s and part of the Marine Light Mixed Layers (MLML) and Biowatt projects (Dickey et al., 1986; Marra, 1995; Marcinko et al., 2013b). These studies provided information on long-scale variations of bioluminescence in the North Atlantic over several years caused by community successions, and seasonal changes in environmental variables and optical properties of the water column (Marra, 1995). In an earlier study from the Black Sea over a 12-month period, Bityukov et al. (1967) observed coastal bioluminescence intensity varied by a factor of 4 and was dominated by a population of the dinoflagellate *Noctiluca scintillans*. The specific drivers for the variation were unknown, however. More recently, a time series on passive MSL of over 10 years was made in the deep Mediterranean Sea (Tamburini et al., 2013; Reeb et al., 2023), where deep-water currents interacting with the infrastructure of the ANTARES neutrino observatory were established as main drivers for bioluminescence.

Not taking into account how the diel space–time variability of organism patchiness contributes to bioluminescent emissions can create an enormous bias in measurements and water column profiles. Indeed, not only does total intensity vary on a temporal scale, but the bioluminescent biomass also travels up and down the water column during diel vertical migration (DMVs) (Batchelder et al., 1992). Not accounting for this migration and sampling at a constant depth could result in misinterpretation of biomass agglomerations and underestimating bioluminescence. To avoid any biases caused by the patchiness of zooplankton, bioluminescence measurements should ideally be made in tandem with high-frequency acoustic mapping to resolve spatial heterogeneity in the water column. Remote acoustic mapping may also be valuable in describing avoidance of *in situ* instruments by zooplankton (Benoit-Bird et al., 2010a). Additionally, discrete zooplankton sampling must be done with profilers using nets, bottles, etc. to assess species assemblages and densities. Moreover, the study of water column bioluminescence is a complex problem requiring multifaceted and logistically challenging approaches involving several specialized sensor systems.

Haddock et al. (2010) suggest future works on bioluminescence should focus on developing remote and autonomous methods to monitoring bioluminescence in the water column. We build on this statement in proposing that future efforts resolve the intra- and inter-specific variations of bioluminescent emissions and expand our library of bioluminescent signatures to increase the potential and relevance of autonomous monitoring of bioluminescence. Documenting the flash kinetics and spectral properties of bioluminescent species will allow for *in situ* and remote identification of organisms, which is relevant for monitoring algal blooms, biomass shifts, and ecosystem structure. Developing instruments with high flow rates and defined shear stress levels will provide less variability in measurements and will limit avoidance of zooplankton, allowing for better comparison between studies.

Author contributions

FL: Conceptualization, Data curation, Formal analysis, Investigation, Supervision, Visualization, Writing – original draft, Writing – review & editing. MT: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. AB: Writing – original draft. CP: Data curation, Formal analysis, Writing – original draft. ML: Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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