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Integrating Diel Vertical Migrations of Bioluminescent Deep Scattering Layers Into Monitoring Programs

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The deep sea (i.e., >200 m depth) is a highly dynamic environment where benthic ecosystems are functionally and ecologically connected with the overlying water column and the surface. In the aphotic deep sea, organisms rely on external signals to synchronize their biological clocks. Apart from responding to cyclic hydrodynamic patterns and periodic fluctuations of variables such as temperature, salinity, phytopigments, and oxygen concentration, the arrival of migrators at depth on a 24-h basis (described as Diel Vertical Migrations; DVMs), and from well-lit surface and shallower waters, could represent a major response to a solar-based synchronization between the photic and aphotic realms. In addition to triggering the rhythmic behavioral responses of benthic species, DVMs supply food to deep seafloor communities through the active downward transport of carbon and nutrients. Bioluminescent species of the migrating deep scattering layers play a not yet quantified (but likely important) role in the benthopelagic coupling, raising the need to integrate the efficient detection and quantification of bioluminescence into large-scale monitoring programs. Here, we provide evidence in support of the benefits for quantifying and continuously monitoring bioluminescence in the deep sea. In particular, we recommend the integration of bioluminescence studies into long-term monitoring programs facilitated by deep-sea neutrino telescopes, which offer photon counting capability. Their Photo-Multiplier Tubes and other advanced optical sensors installed in neutrino telescope infrastructures can boost the study of bioluminescent DVMs in concert with acoustic backscatter and video imagery from ultra-low-light cameras. Such integration will enhance our ability to monitor proxies for the mass and energy transfer from the upper ocean into the deep-sea Benthic Boundary Layer (BBL), a key feature of the ocean biological pump and crucial for monitoring the effects of climate-change. In addition, it will allow for investigating the role of deep scattering DVMs in the behavioral responses, abundance and structure of deep-sea benthic communities. The proposed approach may represent a new frontier for the

study and discovery of new, taxon-specific bioluminescence capabilities. It will thus help to expand our knowledge of poorly described deep-sea biodiversity inventories and further elucidate the connectivity between pelagic and benthic compartments in the deep-sea.

Keywords: bioluminescence, deep scattering layer, diel vertical migrations, activity rhythms, monitoring technologies, neutrino telescopes

INTRODUCTION

The deep sea (i.e., >200 m depth) is the largest biome of the planet. It represents the 65% of the whole planet's surface and contains more than 95% of the biosphere, with more than three quarters of the ocean's surface projecting to depths below 3,000 m (Costello et al., 2010; Haddock et al., 2017; Sweetman et al., 2017). Unfortunately, only a minimal percentage of the deep sea has been explored in terms of its biological components, and therefore most of marine biodiversity remains uncensused (Mora et al., 2011; Snelgrove, 2016). Species accumulation curves obtained from a range of deep-sea studies to date do not reach an asymptotic plateau, indicating that the cataloged number of species does not come close to the true species richness (Danovaro et al., 2010; Webb et al., 2010; Costello et al., 2012). In fact, on Earth, of all classified species only 16% are marine (Costello and Chaudhary, 2017). During the second half of the previous century, the prevalent perception of an isolated benthic environment, with relative stability in terms of hydrodynamism and associated oceanographic conditions, was overturned (Hessler and Sanders, 1967; Levin et al., 2010; Ramirez-Llodra et al., 2010; Levin and Sibuet, 2012; Smith et al., 2017). Additionally, it was considered oligotrophic and sustaining low biomass and biodiversity, which in turn was causing underestimations of global species abundance and biomass (reviewed in Rex et al., 2006; Thurber et al., 2014).

Nowadays this perception has changed drastically and, although population densities are low and clustered, and while depth-related decreasing trends exist globally, this biome musters higher than expected biodiversity (Danovaro et al., 2010; Costello and Chaudhary, 2017) and carbon turnover rates through biological mechanisms (Snelgrove et al., 2017). Moreover, new knowledge has been gathered on the tight linkages between benthic ecosystems in continental margins or abyssal oceanic plains and the pelagic zone above. Such linkages are either expressed as the settling of food falls and pulses of organic matter (Davies et al., 2006; Aguzzi et al., 2012b, 2018; Thomsen et al., 2017), resuspension due to wind-driven upwelling (Allen and Durrieu de Madron, 2009), or are actively mediated by animal behavior, with vertical displacements taking place throughout the water column (Steinberg et al., 2008; Schmidt et al., 2011; Drazen and Sutton, 2017; Griffiths et al., 2017). These movements, when occurring on a diel (i.e., 24-h) basis, are known as Diel Vertical Migrations (DVMs; Brierley, 2014). DVMs are primarily driven by trade-off strategies balancing the elevated risk of visual predation vs. the benefit of using light in the search for prey, as animals utilize background light for their feeding strategies (Hays et al., 2010). A depth- and light-related niche partitioning

may generate a series of synchronized vertical movements of predators and preys within the adjacent depth strata (i.e., staged migrations) or those movements could even occur in a single run (Naylor, 2005; Aguzzi and Company, 2010; Brierley, 2014). Along continental margins on the middle and lower slopes, as well as at abyssal depths, animals could approach or even enter the ecotone between the water column and the benthic ecosystems (i.e., the benthic boundary layer; BBL) at a certain time of the day, acting as predators or prey, hence being vectors of carbon and energy.

One important agent for the transfer of carbon and energy between benthic and pelagic ecosystems is the formation of deep scattering layers, i.e., aggregations of invertebrates and vertebrates driven by ecological needs, including food acquisition, reproduction or avoiding predators (Dietz, 1962). Since physical and chemical gradients in the ocean are generally stronger in the vertical rather than in the horizontal axis over comparable spatial scales, they result in these horizontal large layers of organisms (Benoit-Bird et al., 2017; Sato and Benoit-Bird, 2017). Through the exchange of energy across adjacent oceanic layers at rates faster than the ones dictated by passive sinking and hydrodynamically-induced vertical mixing, the migrating animals enhance the efficiency of the biological pump, sustain food webs, and provide temporal triggers for deep-sea communities, ultimately contributing to the vertical connectivity in the marine environment (Bianchi et al., 2013; Davison et al., 2013; Ochoa et al., 2013; Irigoien et al., 2014; Kelly et al., 2019). As such, for the majority of benthic ecosystems (i.e., apart from the occasional spots of chemosynthetic primary productivity; e.g., Tunnicliffe et al., 2003), benthopelagic coupling remains the principal—if not sole—path that provides the energy to sustain their functions, as well as the structure and biomass of their communities. A re-evaluation of the mechanism of the biological pump is therefore required, with carbon transfer models including passive sinking, diffusion and advection of dissolved organic matter, alongside the active transport by the vertical migration of animals (Vereshchaka et al., 2019).

A major part of marine organisms produce and emit their own light (a process named bioluminescence). In the water column, more than 75% of all organisms larger than 1 cm, from the surface down to 4,000 m depth, are known from the literature to be bioluminescent (Martini and Haddock, 2017). At the seafloor on the other hand, benthic bioluminescent organisms include between 30 and 40% of all animal taxa (Johnsen et al., 2012; Martini et al., 2019). Bioluminescence is an ecological trait with an important role in relationships between organisms, as it impacts their efficiency of resource acquisition, reproduction, as well as survival (Haddock et al., 2010; Martini et al., 2020a). Since light emission is an ubiquitous

functional trait in the ocean, recording and quantifying it *in situ* has been used as a bio-optical measurement to describe the fine-scale distribution of secondary producers such as dinoflagellates, copepods, euphausiids or gelatinous zooplankton (Nealson et al., 1986; Widder et al., 1999; Cronin et al., 2016; Messié et al., 2019), especially in the less observed zones of the ocean such as mesopelagic depths (St. John et al., 2016).

At meso- and disphotic depths (from 200 to 1,000 m), small-sized mesopelagic fishes, gelatinous zooplankton and crustaceans dominate the deep scattering layer, with the exact taxonomic composition of the migrating layers, however, yet to be determined in most oceanic areas (Kaltenberg et al., 2007; Irigoien et al., 2014; Gjørseter et al., 2017; Proud et al., 2017; Seki and Polovina, 2019). Industrial fisheries at near-global scales are expected to target the mesopelagic deep scattering layers in years to come, as an exploitable source for aquaculture (e.g., fish and crustaceans' meal), nutritional supplements and pharmaceutical products (Hidalgo and Browman, 2019; Wright et al., 2020). Apart from the impact of this direct pressure, climate-driven changes in oceanographic conditions (Levin and Le Bris, 2015), as well as extreme physico-chemical conditions and energy pollution associated with deep-sea mining (e.g., turbidity and toxic metals in the form of sediment plumes that are discharged during mining activities and the noise generated by operations; Gillard et al., 2019; Drazen et al., 2020; Smith et al., 2020), are also expected to harm the mesopelagic communities associated with the areas where mining might potentially take place, with the potential additive effects on resident communities and their environments still unpredicted to date.

The intensive exploitation of a more or less pristine system such as the twilight zone (Martin et al., 2020), is bound to have repercussions on the active, vertical transfer of carbon and nutrients to the deep seafloor-benthic areas of the planet by DVMs, through the alteration of the complex trophic relationships which can extend down to the BBL (Longhurst and Harrison, 1988; Davison et al., 2013; Klevjer et al., 2016; Aumont et al., 2018). Moreover, a potential weakening of the synchronization that this displacement exerts on the behavioral activity of predators and preys in the deeper benthic realms, both in terms of the onset, offset and total duration of activity phases, should be evaluated in relation to the overall ecosystem functioning (Ochoa et al., 2013; Aguzzi et al., 2015). Indeed, the rhythmic behavior (see section "Biological Rhythms in the Deep Sea" below) of the species constituting any community over the diel and the seasonal basis strongly affects what we perceive as local richness, and therefore our understanding of the food web structure (Bahamon et al., 2009; Hart et al., 2010; Naylor, 2010; Sardà and Aguzzi, 2012; Mat, 2019), an estimation which is mostly based on temporally scattered (non-continuous or of inadequate frequency and/or duration) sampling and monitoring routines (e.g., cruise-based surveys).

Here, we reviewed the available literature to provide the state of the art of deep-sea bioluminescence and propose the integration of its measurements into a strategy for the continuous, long-term *in situ* monitoring of DVMs. In

doing so, the role of bioluminescent species as agents of temporal variability of the depth of the deep scattering layers (which in turn, by interacting with deep benthos, could synchronize the latter's behavioral rhythms worldwide) can be better understood. As the carbon interchange between the water column and the seabed is an ecosystem function which should be measured at temporal frequencies corresponding to the DVMs and the temporal responses of benthic species within and above the BBL, we provided a conceptual overview of technologies and protocols for the monitoring of bioluminescence. In doing so, we focused on neutrino telescope assets as promising, temporally intensive monitoring sites, increasing their societal value through potential contributions toward fishery management, and merging the interest of two very broad communities: marine and astrophysical scientists.

THE DEEP-SEA ECOSYSTEMS: A SYMPHONY OF CYCLES AND RHYTHMS

Environmental Cycles and Episodic Signals

Deep-sea hydrodynamic flows are modulated by periodic (e.g., tides) and episodic (e.g., atmospheric patterns) events that drive surface circulation. Surface tides supply much of the mechanical energy required to generate internal tides, as they move stratified water up and down mid-ocean ridges and seamounts, thus producing waves in the ocean's interior. Internal waves, produced at a tidal frequency, are primary drivers of deep-sea mixing processes (Vic et al., 2019) that modulate the behavior of deep-sea organisms (Aguzzi et al., 2010; Couvelier et al., 2017).

Surface-generated mesoscale eddies, i.e., circular, ~100 km wide currents, may be responsible for the creation of deep-sea inertial currents, leading to the transfer of energy from mesoscale to small-scale motions. In the China Sea for example, surface mesoscale eddies have been found to be related to deep-sea current velocities of 0.1 m s^{-1} , with periods of 1–2 months and a 10-fold increase in kinetic energy (i.e., the energy of water due to its motion) (Zhang et al., 2015). In the Eastern Mediterranean Sea, deep-sea cyclonic and anticyclonic events of shorter period (i.e., from quasi inertial to between 5 and 11 days; Rubino et al., 2012; Meccia et al., 2015), derived from bathymetric constraints of abyssal circulation patterns, have been detected, showing energetic episodes with current intensities that may reach up to 0.15 m s^{-1} , effectively contributing to deep-sea mixing processes (Meccia et al., 2015).

Episodic events such as benthic storms, increasing bottom-water turbidity in the deep ocean, are primarily created by deep cyclones and can take place at different temporal and spatial scales. These storms may last from a few hours to a few weeks, covering distances from several hundred meters to several hundred kilometers, when related to internal, slow-moving Rossby waves (Gross and Williams, 1991) produced by the effect of Earth's rotation on ocean circulation. The

storms, generally linked to current speeds exceeding 0.2 m s^{-1} (Hollister and McCave, 1984), are able to move and resuspend vast quantities of sediments from the seabed, leading to the formation of benthic nepheloid (turbid) layers (Gross and Williams, 1991; Gardner et al., 2017). These nepheloid layers are absent or weak in deep-sea areas subject to relatively low eddy kinetic energy events (Gardner et al., 2017). Benthic storms have been detected in areas with high sea-surface eddy kinetic energy, frequently occurring beneath the meandering, e.g., the Argentine Basin (S Atlantic) and the Gulf Stream (N Atlantic) with its associated rings. There, they generate deep cyclones, anticyclones, and topographic waves that in turn create currents with sufficient bed-shear stress to erode and resuspend sediment, thus initiating or enhancing benthic storms (Gardner et al., 2017). Volcanic eruptions and earthquakes can also generate submarine slides and turbidity currents (Aguzzi et al., 2012a; Gardner et al., 2017). The effect of the storms on the benthic environment depends on the stress for deposition and erosion of fine sediments, in turn related to both large-scale topographic effects (100 km) and small-scale bottom roughness (1 cm) caused by benthic infauna (Gross and Williams, 1991).

Winter convective mixing may produce semi-periodic deep-sea storms. In the western Mediterranean, the cooling of surface water in winter eventually increases water density enough to cause cascading down canyons, the continental slope (Canals et al., 2006; Palanques et al., 2009; Puig et al., 2013a), or even in the open sea (Houpert et al., 2016), transporting large amounts of sediment down to depths of 2,400 m, and creating nepheloid layers as thick as 1,500 m. The convection currents may reach speeds $>0.6 \text{ m s}^{-1}$ (Canals et al., 2006), exporting large amounts of organic matter toward the sea bottom, unlike the relatively smooth flux of organic matter taking place during winter and spring seasons in years of shallower and discontinuous convective mixing (Bernardello et al., 2012). Similar cooling and cascading phenomena have been measured at high latitudes in the NE and NW Atlantic (Koeve et al., 2002; Puig et al., 2013b). In the subtropics off southern Taiwan (W Pacific), torrential rainfall may also create sufficiently high sediment concentrations to generate turbid hyperpycnal down-canyon flows (Kao et al., 2010).

Finally, moving onto multiannual scales, an increasing frequency of extreme winter conditions linked to climate change may lead toward more often deep-sea convection events (Schroeder et al., 2016), while the spatiotemporal shifting of semi-periodic climate change indicators (Zhang et al., 2011; Srivastava et al., 2020) such as El Niño and the Southern Oscillation (ENSO), the Pacific-North American teleconnection pattern (PNA), the North Atlantic Oscillation (NAO) and the Mediterranean Oscillation (MO), may also alter the known patterns of episodic deep-sea events and the fluxes of sediments and organic matter.

Biological Rhythms in the Deep Sea

Behavioral rhythms of benthic fauna are regularly evident in the form of depth-related, vertical (benthopelagic) or horizontal

(nektobenthic) migrations, or stationary emergence/retraction (endobenthic) patterns from/into the seabed (Aguzzi and Company, 2010; Aguzzi et al., 2015; Benoit-Bird et al., 2017). For example, the burrowing habits of the deep-sea Norway lobster (*Nephops norvegicus*) drive massive population emergence peaks, phased at an optimum light intensity threshold (Chiesa et al., 2010; Sardà and Aguzzi, 2012). At disphotic depths (i.e., $>400 \text{ m}$), animals receive different temporal cues substituting sunlight, and utilize them in order to time these populational movements through a synchronization of their biological clocks. For crustacean decapods and fishes, this syncing can either be a result of direct environmental signals such as periodic hydrodynamism (i.e., internal tides and inertial currents; Wagner et al., 2007; Aguzzi et al., 2010; Doya et al., 2014), changes in water temperature and salinity (Matabos et al., 2014) and phytopigment and oxygen concentrations (Chatzievangelou et al., 2016), or can be indirectly induced by the intermittent presence of massive numbers of predators and prey from a vertically migrating deep scattering layer, which rhythmically come in contact with the BBL (Ochoa et al., 2013; Aguzzi et al., 2018). In the case of the latter, this behaviorally-sustained benthopelagic coupling is to date poorly studied, due to the lack of a sufficient volume of continuous, long-term and high frequency time-series at reference locations in the deep sea. For example, Vereshchaka et al. (2019) reported that vertical migrations are nearly absent from the lower bathypelagic Atlantic zone due to a sharp decrease in the concentration of planktonic food. Aguzzi et al. (2017), however, reported the presence of bioluminescent migrating deep-scattering layers at depths $>3 \text{ km}$ in the oligotrophic Central Mediterranean (see also section “Monitoring Diel Biological Rhythms in Along the Continental Margin and at Abyssal Areas” below).

Moving toward lower geophysical frequencies, lunar tidal cues (i.e., alternation of spring and neap tide cycles; Talley et al., 2011) are indirectly transferred to the deep sea, with tidally controlled particle fluxes and current regimes (Mercier et al., 2011). Marine organisms adapt to these lunar and semi-lunar cycles mainly by synchronizing their spawning and general reproductive activity (Tessmar-Raible et al., 2011). On the other hand, seasonality may occur with internal time-keeping mechanisms (Helm et al., 2013), calibrated by variations in multiple factors such as environmental variables, the availability of food and energy transfer (e.g., seasonal variations in food falls of primary productivity such as the settling of spring and summer blooms, as well as rapid transfer of detritus in winter) and predator-prey dynamics, or by ontogenetic cycles related to growth and reproduction (Sardà et al., 1994; McClain and Barry, 2010; Lambert et al., 2017a,b; Thomsen et al., 2017; Chauvet et al., 2018). Accordingly, the strength of the rhythmic movements of the deep scattering layer can also follow a seasonal pattern, due to the tuning of reproduction and growth upon photoperiodic (i.e., day-length) changes in photic and disphotic areas, as well as upon variations in carbon-inputs by primary productivity in the deep-sea (Gage and Tyler, 1991). Finally, the intensity of those effects on animal activity and behavior can be latitude-dependent, following the respective clines of tidal phases and solar photoperiod, thus highlighting the multifaceted nature of biological rhythms and

the fundamental role of habitat as they were shaped throughout the evolutionary process (Gerkema et al., 2013; Helm et al., 2013; Hut et al., 2013).

MONITORING DIEL BIOLOGICAL RHYTHMS ALONG THE CONTINENTAL MARGIN AND AT ABYSSAL AREAS

Background

Early artisanal fisheries in areas of narrow continental slope were our first point of observational access to the deep-sea fauna (Gordon et al., 2003), providing the first indications of the existence of deep-sea rhythms and resulting in a day/night fishing schedule. Following these empirical observations, scientific tools to obtain field results consisted of classical technologies such as direct sampling by trawling, and were then gradually replaced by more advanced (but still vessel-assisted) imaging tools like towed cameras (Bicknell et al., 2016; Clark et al., 2016) and short-term deployments of camera modules by submersibles (e.g., up to 4 weeks; Tunnicliffe et al., 1990). Indicatively, Aguzzi et al. (2015) depicted benthopelagic coupling with temporally scheduled trawling on the western Mediterranean slope (~400 m), where synchronized day-night rhythms were detected between benthopelagic and benthic predators and preys. Previously, analysis of melatonin extracted from hauled demersal fishes showed the occurrence of tidally-modulated rhythms (Wagner et al., 2007), while towed surveys showed varying patterns in the activity of two crustacean species (Trenkel et al., 2007). The aforementioned results apply over many crustacean decapods across deep continental margins on a global scale (see Aguzzi and Company, 2010; Aguzzi et al., 2011), and are also corroborated by laboratory experiments, where crustacean locomotion was assessed under conditions of constant darkness and varying hydrodynamic flows (Aguzzi et al., 2007, 2009; Aguzzi and Sardà, 2008; Sbragaglia et al., 2015, 2017; Nuñez et al., 2016).

As more advanced technologies emerged, cabled observatories and landers were used to increase the potential for either higher frequency and/or longer duration for *in situ* monitoring of activity rhythms in the deep sea. The fauna of a hydrocarbon seep in Sagami Bay, Japan (~1,100 m) displayed tidally-controlled rhythmicity, with animal responses varying in orders of magnitude (Aguzzi et al., 2010) based on footage of a permanent observatory. At shallower depths in the same area (~500 m), continuous monitoring of a whale carcass with landers revealed the presence of mostly day-night and occasionally tidal-based rhythms for the majority of the benthic species during the early succession stages (Aguzzi et al., 2018). Various fixed and mobile platforms (i.e., benthic crawler) of the NEPTUNE Cabled Observatory operated by Ocean Networks Canada¹ have been used for similar studies, with faunal behavior in a range of aphotic depths being connected to the local tidal regimes and to periodic fluctuations of oceanographic and atmospheric conditions (e.g., Doya et al., 2014; Matabos et al.,

2014; Chatzievangelou et al., 2016; Lelièvre et al., 2017). Day-night and tidal-related rhythms have been recently found at the Lofoten-Vesterålen (LoVe) deep-sea observatory in Norway for sessile and motile megafauna such as the bubblegum coral (*Paragorgia arborea*; Zuazo et al., 2020), a deep, cold-water coral (*Lophelia pertusa*; Osterloff et al., 2019), shrimps (Osterloff et al., 2016), rockfish (*Sebastes* sp.; described in Aguzzi et al., 2020b but not formally analyzed yet by chronobiological statistics), and other fauna (Purser, 2015). Moreover, a cabled monitoring module (i.e., TempoMini) evidenced inertial and tidal rhythms in communities of deep hydrothermal vents in both the NE Pacific and Mid-Atlantic (Cuvelier et al., 2014, 2017; Lelièvre et al., 2017). Finally, electronic tags have been applied to migrating deep-water predators (i.e., sablefish *Anoplopoma fimbria* individuals reported between the upper subsurface layer and depths down to 1,250 m, with mean depth differences between day and night reaching 250 m; Goetz et al., 2018; Sigler and Echave, 2019), showing distinct patterns that potentially depend on prey availability (i.e., both night ascending and, inversely, night descending). A more comprehensive review of similar case-studies and advances in applications of telemetry technologies in marine ecology was provided by Hussey et al. (2015).

Capturing the Rhythmic Movements of the Deep Scattering Layer

DVMs of the deep scattering layer, comprised mainly of zooplankton and mesopelagic fish, have been extensively reported at a global scale (Hays, 2003; Klevjer et al., 2016). Such rhythmic displacement patterns produce a ubiquitous acoustic signature in the pelagic realm, although their total biomass, upper and lower limits vary across oceanic fronts, depending on climate trends, surface productivity, light penetration, oxygen levels, temperature and water mixing (Aksnes et al., 2017; Proud et al., 2017, 2019; Behrenfeld et al., 2019). Even though they are most commonly limited to depths down to the lower mesopelagic zone (~1,000 m), DVMs can reportedly extend to several km into abyssal waters (e.g., Natantian decapods in the Mediterranean; Aguzzi and Company, 2010). Traditionally, they are captured as anomalies in the acoustic backscatter signal (due to different reflective properties attributed to the physical differences of animal tissue and seawater and the presence of the swim bladder in the case of fish; Marshall, 1951) by either upward- or downward-facing Acoustic Doppler Current Profilers–ADCPs (Flagg and Smith, 1989; Plueddemann and Pinkel, 1989; Heywood et al., 1991; Ochoa et al., 2013; Bozzano et al., 2014; De Leo et al., 2018) or sonars/echosounders (Barham, 1966; Opdal et al., 2008; Benoit-Bird et al., 2017; Giorli et al., 2018; Van Engeland et al., 2019), as well as with trawl and plankton net surveys (Roe, 1984; Fock et al., 2002; Steinberg et al., 2002; Drazen et al., 2011; Darnis and Fortier, 2014). Remarkably, trawl avoidance behavior has been reported for some mesopelagic fish species which adapted their vertical migrating patterns (Kaartvedt et al., 2012), while there is a practically inevitable sampling bias favoring size and robustness in the deep pelagic zone (Craig et al., 2015). This, in addition to

¹www.oceannetworks.ca

net selectivity, may lead to underestimations of biomass if *in situ* sampling is not accompanied by remote monitoring methods (which can have their own selectivity limitations nonetheless; Kloser et al., 2016).

Bioluminescence is an ecological trait widely distributed amongst marine organisms (Widder, 2010), from shallow to deep-sea environments (Martini and Haddock, 2017), with massive surface aggregations of bioluminescent organisms even visible from space by satellites (Miller et al., 2005). Biomass dominant taxa found in deep scattering layers such as copepods, euphausiids, gelatinous zooplankton (Herring, 1987) and mesopelagic fishes such as the conspicuous myctophids (Paitio et al., 2016), are known to be bioluminescent. Thus, when mass migrating into deeper layers of the ocean, these species can potentially affect the background intensity of ambient light. Indeed, variability of light intensities has already been recorded over multiannual time-series in the deep ocean using sensors, originally installed with the purpose to study neutrino emissions in the ocean's interior (Tamburini et al., 2013; Martini et al., 2014; Aguzzi et al., 2017). In general, the presence of bioluminescent organisms at aphotic depths, where there are minimal—if any at all—detectable traces of sunlight, can modify the local ambient light regime by being the strongest (or sole) light source (Cronin et al., 2016), consequently shaping local communities and important functions of the respective ecosystems. For example, bioluminescent organisms and their predators are hypothesized to play a major role in the biological carbon pump, through preferential consumption of luminous particles by high-level consumers. This can affect the sinking rates of the former, their remineralization and their availability in the deeper waters (Tanet et al., 2020) or lead to higher success rates of visual predation for macro-organisms (Vacquié-Garcia et al., 2012).

In the absence of an unequivocal direct relationship between bioluminescence and acoustic backscatter signals (Berge et al., 2012), these variables should ideally be measured in tandem for the study of deep DVMs. As both methods face their own challenges in terms of resolving taxonomic identity, measuring the deep-sea light emission spectrum can be an efficient tool to complement the characterization of the species composition and abundance of the migrating organisms, in a similar way to previous shallow-water applications (Messié et al., 2019). Since the knowledge on the full spectrum of the ecological importance of bioluminescence for vertically migrating groups and for deep-sea benthos is yet to be completed (Martini et al., 2019), we propose a few overarching questions that should direct future long-term ecological monitoring, centered on the extent of deep DVMs:

- (1) How to use innovative technologies to monitor deep DVMs in the large, three-dimensional open ocean environment, in the context of benthopelagic coupling? How to couple observations from the water column dimension with now more accessible 2D and 3D video imaging of deep seafloor ecosystems?
- (2) Could bioluminescence be used, as a proxy for the extent of DVMs, as well as for large-scale environmental fluctuations linked to climate change and anthropogenic disturbance

(e.g., ocean warming, de-oxygenation, ocean acidification and overfishing)?

- (3) How to quantify the effect of the mass displacement of bioluminescent organisms, as a component of the migrating deep scattering layer, on the biodiversity and functioning of benthic ecosystems?

Tuning Ocean Monitoring to Catch the Spatiotemporal Scales of Biological Rhythms

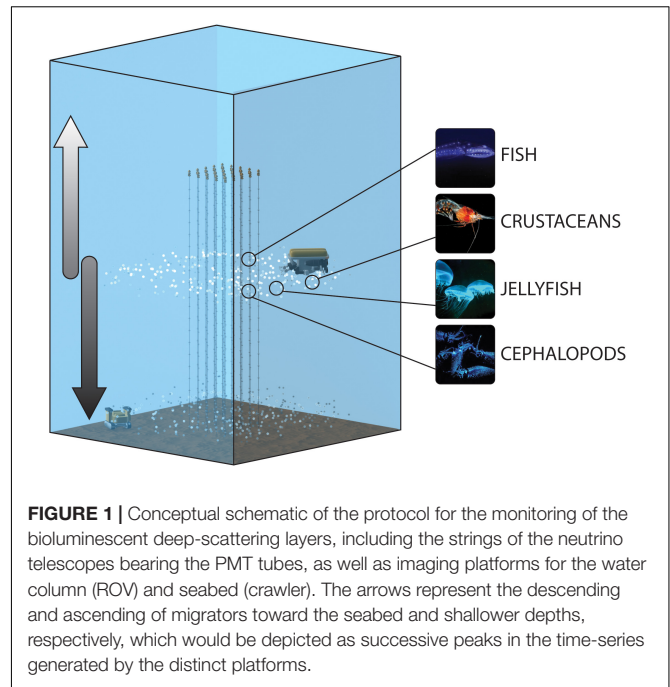
With the three-dimensional nature of the marine environment bound to become a central aspect for its conservation (Levin et al., 2018; Aspillaga et al., 2019; Totti et al., 2020), and in order to efficiently track such massive displacements occurring at all depths of the continental margins and the overlying water column volumes (Aguzzi et al., 2011; Rountree et al., 2020), the concept of the geometry of monitoring networks should follow through. New observational technologies are able to detect and quantify the movement of deep scattering layers: neutrino telescopes such as the KM3NeT neutrino telescope network², presently deployed 40 km offshore south of Toulon (Ligurian Sea) and 100 km offshore southeast of Capo Passero (Ionian Sea); Moored vertical structures equipped with Photo-Multiplier Tubes (PMTs) used as photon counters can pick up photons produced by bioluminescence, for example when animals hit the structure and emit a defensive signal (Priede et al., 2008; Ageron et al., 2011; Tamburini et al., 2013; Craig et al., 2015; Van Haren et al., 2015; Adrián-Martínez et al., 2016; Aguzzi et al., 2017). This setting acts as a relatively passive (i.e., not actively moving) observer of bioluminescence, as animals cross an area permanently occupied by the moored structures and are not reacting to the approach of a potential mobile threat (e.g., towed nets). In that way, any potential bias imposed by a reactionary behavioral control of bioluminescence is expected to be constant in time and across depths. On the other hand, the detection of bioluminescence for communication purposes among animals would be a desirable signal, of ecological significance in the deep sea (alongside sound emissions; Rountree et al., 2012). Time-series of those readings can be produced in real-time, continuously over several years, although, unfortunately, a direct identification of the light-producing organisms is not yet possible. A solution could be the deployment of imaging systems conjointly to PMTs. For example, the use of ultra-low-light imaging technology (Phillips et al., 2016) coupled with measurements from neutrino telescopes will allow cross-linking the bioluminescence light-emission bursts with emitting species at all or most of the mounted PMTs. PMT data can be used both to analyze the waveforms of light bursts, and to extract time-integrated information, such as burst rates. A proposed enhancement is the use of a subset of “*ad hoc*” PMTs equipped with wavelength filters, to allow spectral analysis of bioluminescent emissions. In that way, taxonomic richness of bioluminescent species could be obtained from imagery, to be contrasted with PMT readings. Different taxa produce different flash types

²<https://www.km3net.org/>

(e.g., signal propagation into the body of animals), which could be used as a morphological trait for their identification (Mazzei et al., 2014).

Such video monitoring could be extended to the deep seabed, for a temporally synchronous and integrated coverage of the whole deep-water column (Aguzzi et al., 2020b,c; Rountree et al., 2020). The main objective would be the detection and quantification of the temporal responses of predators and preys in relation to the rhythmic arrival of the bioluminescent species of the migrating scattering layer (Hays et al., 2010). The deployment of new prototype detectors of the KM3NeT at abyssal Mediterranean depths and covering different depth ranges of the water column (i.e., ORCA; NW basin; ~3,400 m; strings of ~150 m length and ARCA; Central basin, ~2,500 m; strings of ~650 m length³) will be a powerful tool toward that direction.

Carbon transfer by bioluminescent migrators is a three-dimensional process, as the vertical movement of animals is temporally structured across various oceanic layers, and can be combined with a horizontal displacement. The latter may vary, depending on local circulation patterns which can drag weak swimmers and contribute to plankton dispersal (Hill, 1998; Sato and Benoit-Bird, 2017). Therefore, a spatiotemporally integrated measurement protocol should be executed at appropriate geographical scales and depth ranges, in order to accurately represent this ecosystem service. Accordingly, Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUVs), and acoustic backscatter surveys also performed continuously over the 24-h for several days in the same area, should be complementing fixed cameras and benthic crawlers such as Internet Operated Vehicles (IOVs) on the seabed (Aguzzi et al., 2020a). In particular, ongoing actions are aiming to match bioluminescence signals with faunal data extracted from ROV footage obtained during maintenance operations of the telescope tower, which will also be complemented with new imaging data from the expansion of the nearby CREEP-2 cabled observatory (Aguzzi et al., 2013). At the same time, PMT data from the lower floors (i.e., closer to the seafloor) could be compared with richness records proceeding from baited lander surveys in the Central basin area, where the KM3NeT-It telescope is (Linley et al., 2018). A conceptual, minimalistic representation of the monitoring protocol is presented in **Figure 1**. A recent project focuses on implementing a benthic crawler; BathyBot (Martini et al., 2020b) with video cameras, close to the KM3NeT EMSO-LO site, off Toulon (Ageron et al., 2011; Tamburini et al., 2013). Such approach will represent a suitable asset, allowing the integration of the seabed perspective with the water-column monitoring by a nearby network of photomultipliers. The detection of the presence of animals, the quantification of their abundance and potentially the estimation of their biomass visible in our depth-related sampling windows, would allow the description of relevant behavioral interactions and hence improve our mechanistic understanding of the resulting ecosystem phenotype: the changes in the observed biodiversity on a diel and seasonal basis in the deep-sea (Aguzzi et al.,

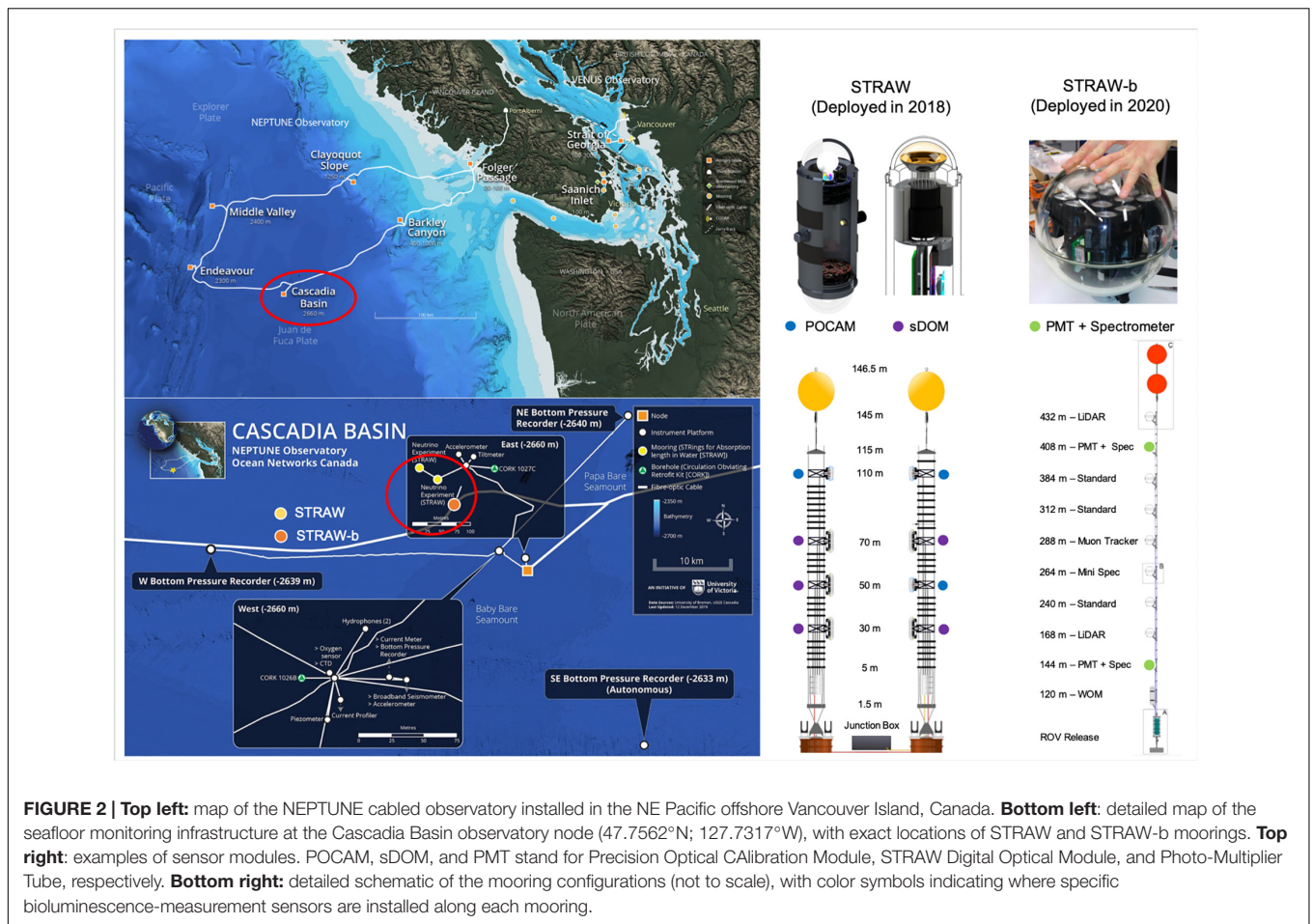


2020c), based on previous methodologies and permanent mobile platform technologies tested in shallow waters (e.g., at the Obsea cabled observatory; Condal et al., 2012; Del Rio et al., 2020).

In the NE Pacific, ~300 km offshore Canada's British Columbia, a pathfinder project envisioning the installation of a full-scale neutrino telescope is underway⁴ (Boehmer et al., 2019; Agostini et al., 2020). The first phase of the project has deployed an initial experiment, STRAW (STRings for Absorption length in Water) with the goal to establish baseline measurements of light attenuation, absorption and scattering at abyssal depths in the NE Pacific (Agostini et al., 2020). Two 150 m long mooring lines were deployed at 2,660 m depth in the Canadian abyssal plain (Cascadia Basin) and connected *via* ethernet cable with the NEPTUNE observatory (**Figure 2**). In its second iteration, STRAW-b, a single and substantially longer (450 m) mooring array is now equipped with 10 sensor modules that include a range of PMTs, spectrometers and ultra-low-light cameras that will aid a much greater capability to quantify bioluminescence and possibly assign individual taxa to specific wavelength emission signals (**Figure 2**). Ongoing data analysis already includes the quantification of temporally diffused vs. intermittent burst bioluminescence signals and their control predominantly by turbulence derived from internal tide frequencies. In addition, modeling efforts are being carried out to study bioluminescence signal response under different turbulent flow regime scenarios and using different taxa as source populations. Finally, the co-location with a standard suit of oceanographic, seismic and biological sensors, will allow for a number of multidisciplinary studies engaging particle physicists, oceanographers and marine ecologists. In particular, the NE Pacific has been subject to a range of environmental shifts in the last decade, including a few marine

³<https://www.km3net.org/research/physics/>

⁴<https://www.pacific-neutrino.org/>



heat wave anomalies (Kintisch, 2015; Peterson et al., 2017) and systemic de-oxygenation and expansion of its oxygen minimum zone (Whitney et al., 2007; Ross et al., 2020). Having a reliable long-term time-series of bioluminescence could provide another tool to monitor large-scale ecosystem changes in the NE Pacific.

Implementing such monitoring protocols on a global scale is not a viable option at present, as the cost of the infrastructure and operations would be prohibitive, which in turn could raise the need for the identification of priority regions. These cannot be defined based on purely ecological criteria, rather than being the result of open dialogue between the needs of different scientific communities, taking into account political and logistical issues together with scientific knowledge. Neutrino telescopes (existing or in development) are built in specific locations indicated by the astrophysics community, based on an optimal combination of minimal signal noise at abyssal depths and limitations such as feasibility of access and maintenance operations (e.g., distance from the shore). Similar questions were faced by the marine science community a couple of decades ago, when the first plans to install cabled observatories in the deep sea began to take shape. At present there are more cabled observatories than neutrino telescopes in the ocean, which ultimately makes the latter the limiting factor when it comes to the geographical coverage of the proposed plan. With DVMs and bioluminescence being globally ubiquitous, a combination

of such infrastructures set at any region could be utilized to answer the respective ecological questions of relevance, starting from a local level and with the potential to extrapolate to regional-scale phenomena.

CONCLUSION

- Monitoring the DVMs of shoals of bioluminescent migrators could shed light on the ecological functioning of deep-sea benthic ecosystems and biological connectivity, supporting the need for creative and innovative monitoring protocols.
- Novel infrastructure, such as neutrino telescopes, can help monitor bioluminescent DVMs down to the bathy- and abyssopelagic BBL, providing another asset toward a holistic monitoring network for benthic and water-column ecosystems, alongside current imaging and acoustic methodologies from fixed and mobile platforms.
- With interdisciplinary dialogue among astrophysicists, marine engineers and ecologists, data collection technologies and protocols can be tuned to cross-validate scans of the bioluminescence panoramas with imagery and backscatter data, to resolve the taxonomy of the light-emitting species.

AUTHOR CONTRIBUTIONS

DC: conceptualization, writing—original draft, and writing—review and editing. NB, SM, GR, and RD: writing—original draft and writing—review and editing. JR and BP: writing—original draft, writing—review and editing, and funding acquisition. MT: writing—original draft, writing—review and editing, and visualization. FD: writing—original draft, writing—review and editing, visualization, and funding acquisition. JA: conceptualization, writing—original draft, writing—review and editing, and funding acquisition. All authors contributed to the article and approved the submitted version.

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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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