



1 **Reviews and syntheses: Bacterial bioluminescence – ecology and** 2 **impact in the biological carbon pump**

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6 **Abstract.** Around thirty species of marine bacteria can emit light, a critical characteristic in the oceanic environment where
7 the major part is deprived of sunlight. In this article, we first review current knowledge on bioluminescent bacteria symbiosis
8 in light organs. Then, focusing on gut-associated bacteria, we highlight that recent works, based on omics methods, confirm
9 previous claims about the prominence of bioluminescent bacterial species in fish guts. Such host-symbiont relationships are
10 relatively well established and represent important knowledge in the bioluminescence field. However, the consequences of
11 bioluminescent bacteria continuously released from light organ and through the digestive tracts to the seawater have been
12 barely taken into account at the ecological and biogeochemical level. For too long neglected, we propose to consider the role
13 of bioluminescent bacteria, and to reconsider the biological carbon pump taking into account the bioluminescence effect
14 (“bioluminescence shunt hypothesis”). Indeed, it has been shown that marine snow and fecal pellets are often luminous due
15 to microbial colonization, which makes them a visual target. These luminous particles seem preferentially consumed by
16 organisms of higher trophic levels in comparison to non-luminous ones. As a consequence, the sinking rate of consumed
17 particles could be either increased (due to repackaging) or reduced (due to sloppy feeding or coprophagy/coprorhexy) which
18 can imply a major impact on global biological carbon fluxes. Finally, we propose a strategy, at a worldwide scale, relying on
19 recently developed instrumentation and methodological tools to quantify the impact of bioluminescent bacteria in the
20 biological carbon pump.

21

22 **1 Introduction**

23 Darkness constitutes the main feature of the Ocean. Indeed, the dark ocean represents more than 94 % of the Earth’s
24 habitable volume (Haddock et al., 2017). Moreover, the surface waters are also in dim light or darkness during nighttime.
25 Organisms living in the dark ocean biome are disconnected from the planet primary source of light. They must adapt to a
26 continuous decrease in sunlight reaching total darkness beyond a few hundred meters. Hence, it is not surprising that 76 % of
27 marine pelagic meso- and macro-organisms are bioluminescent from the surface to the deep sea, without variability over



28 depth and that bioluminescence is a major ecological function in interactions (Martini and Haddock, 2017). Bioluminescent
29 species are found in most phyla from fish to bacteria (Haddock et al., 2010; Widder, 2010). Amongst marine light-emitting
30 organisms, luminous bacteria are the most abundant and are widely distributed. Most of the 30 currently known bacterial
31 luminous species are heterotrophic, copiotrophic and facultatively anaerobic. Endowed with important motility and
32 chemotactic abilities, luminous bacteria are able to colonize a large variety of habitats (as symbionts in light organs and guts,
33 free-living in seawater or attached to particles) (e.g. (Dunlap and Kita-tsukamoto, 2006) and references therein). Bacterial
34 bioluminescence is energetically costly, and its benefices are understood in its symbiotic form. On another note, bacterial
35 bioluminescence in its free or attached forms is still to be explained. A barely investigated pathway is the bioluminescence
36 contribution into the biological carbon pump.

37 The biological and physical (solubility) carbon pumps are the main drivers of the downward transfer of carbon and play a
38 central role in the sequestration of carbon dioxide (Boyd et al., 2019; Buesseler and Lampitt, 2008; Dall'Olmo et al., 2016).
39 The biological carbon pump is defined as the process through which photosynthetic organisms convert CO₂ to organic
40 carbon, as well as the export and fate of the organic carbon sinking from the surface layer to the dark ocean by different
41 pathways (Siegel et al., 2016). Sinking particles (greater than 0.5 mm of diameter) known as marine snow are a combination
42 of phytodetritus, living and dead organisms, fecal pellets (from zooplankton and fish). Marine snow, rich in carbon and
43 nutrients, and their surrounding solute plumes are hotspots of microbial activity in aquatic systems (Alldredge et al., 1990;
44 Alldredge and Silver, 1988; DeLong et al., 1993). Marine snow is also consumed by zooplankton, and fecal pellets are a
45 food source through coprophagy. When leaving the epipelagic zone and sinking to depth, organic particles would be utilized
46 by microbial decomposition and fish/zooplankton consumption, both considered as responsible for a large part of the
47 variation in the efficiency of the biological carbon pump (De La Rocha and Passow, 2007). Recently, fragmentation
48 (potentially due to biological processes in the mesopelagic waters) has also been shown to be the primary process controlling
49 the sequestration of sinking organic carbon, accounting for $49 \pm 22\%$ of the observed flux loss (Briggs et al., 2020).

50 In this review, we will summarize the current knowledge on bioluminescent bacteria based on former and recent literature.
51 First, we describe symbiotic bioluminescent bacteria in light organs of fish or squids, its importance and controls. Then, we
52 present enteric-association occurrences and their potential role for the host. One of the consequences of these symbioses, in
53 both light organs and guts, is a massive quantity of bioluminescent bacteria daily dispersed in the ocean. Based on this
54 statement, we claim and demonstrate that bioluminescent bacteria have an ecological and a biogeochemical importance in
55 the biological carbon pump, catalyzing and amplifying the involved processes. We propose a synthetic representation of the
56 bioluminescence shunt of the biological carbon pump and a future strategy to establish and quantify the impact of
57 bioluminescence (**Figure 1**).



58 **2 Symbiotic bioluminescent bacteria in light organs**

59 In Eukaryotes, light emission has two distinct origins: intrinsic or symbiotic (Haddock et al., 2010; Neelson, 1979). Intrinsic
60 luminescence is caused by chemicals produced by the organism itself. Most bioluminescent organisms are self-luminescent
61 and have specialized luminous cells called photophores (Herring, 1977). Some animals, however, are capable of
62 luminescence using symbiotic luminous bacteria housed in elaborate and specialized organs.

63
64

65 **2.1 Discovery, importance, distribution and functions of light-organ symbiosis**

66 In the late 1880s, Raphaël Dubois was among the first to suggest bacteria to be responsible for the light emitted by some
67 animals (Harvey, 1957). In the beginning of the twentieth century, Balthazar Osorio (1912) provided clear and convincing
68 evidences of such symbiosis, when luminescent bacteria were described in high density within dedicated fish gland, called
69 the light organ (Hickling, 1926). Since then, luminous bacterial symbiosis has been the subject of interest among the
70 scientific community working on bioluminescence, to such an extent that, by the mid-twentieth century, luminescence of
71 many organisms was thought to have bacterial origin. However, some of these assessments have been refuted later (Herring,
72 1977).

73 From a species level perspective, bioluminescence ability is shared by about 8 % of all known fishes (Paitio et al., 2016).
74 Amongst luminous fishes, bacterial luminescence is the rule for almost half of them (48 %) (Davis et al., 2016). To date,
75 symbiotic bacteria are recognized as responsible for the luminescence of ray-finned fishes and some squids (Davis et al.,
76 2016; Haygood, 1993; Lindgren et al., 2012). Although forms of symbiotic luminescence have been suggested for some
77 shark species or pyrosomes (Dunlap and Urbanczyk, 2013; Leisman et al., 1980), no evidence of luminous bacteria have
78 been found so far (Claes and Mallefet, 2009; Renwart et al., 2014; Widder, 2002) and a recent study has definitely rejected a
79 bacterial origin in the velvet belly lanternshark (Duchatelet et al., 2019). Concerning luminous squids, intrinsic
80 bioluminescence is more common, and symbiotic light organs are known in two families (Sepiolidae and Loliginidae)
81 (Lindgren et al., 2012; Nishiguchi et al., 2004).

82 Symbiotic luminescence seems more common in benthic or coastal environments for fish and squid as well (Haygood, 1993;
83 Lindgren et al., 2012; Paitio et al., 2016). Shallow-water fishes with luminous bacterial symbionts include flashlight fishes
84 (Anomalopidae), ponyfishes (Leiognathidae) and pinecone fishes (Monocentridae) (Davis et al., 2016; Morin, 1983). For
85 deep-sea fishes, anglerfishes (Ceratiodei) and cods (Moridae) are among the common examples of luminous-bacteria hosts.
86 In general, the origin of light production, intrinsic or symbiotic, is the same within a host clade. However, while all other
87 Apogonidae exhibit intrinsic light, the *Siphamia* species host luminous bacteria (Paitio et al., 2016). Another exception
88 concerns a genus of anglerfishes, *Lynophryne*, which possesses both systems of light production, having intrinsic
89 luminescent barbel in addition to a symbiotic luminous esca (Hansen and Herring, 1977). To date, presence of this dual



90 system in an organism is unique among all known luminous animals (Pietsch et al., 2007). Bacterial and intrinsic light
91 organs are predominantly intern and in ventral location (Paitio et al., 2016; Wilson and Hastings, 2013). Due to the position
92 of some internal light organs, localized within the coelomic cavity, therefore away from the taxonomic examination process,
93 the luminescence ability of some fishes has remained unrecognized for a long time (Haneda and Johnson, 1962).
94 Fish and squid with bacterial light organs likely use the emitted light to conceal themselves by counterillumination,
95 obliterating their silhouette, therefore avoiding dusk-active piscivorous predators (Jones and Nishiguchi, 2004; McFall-Ngai
96 and Morin, 1991). Less common but more striking, some organisms found in the families Monocentridae, Anomalopidae and
97 numerous deep-sea anglerfishes belonging to the suborder Ceratoidei, exhibit light organs colonized by bacteria (Haygood,
98 1993). These light organs are thought to be predominantly used to illuminate nearby environment or attract prey or mates.
99

00 2.2 Symbiont selection and colonization of the light organ

01 Like most symbiotic bacterial associations with animals, luminous bacteria are acquired from the surrounding environment
02 by individuals, independently of their ancestry (i.e. horizontally transmitted) (McFall-Ngai, 2014).
03 Knowledge of the mechanisms involved in the selection and the establishment of bacterial symbionts have considerably
04 improved in last decades. Harvest of the luminous symbionts from the bacterioplankton is driven by microbial recognition
05 and molecular dialog (Kremer et al., 2013; Nyholm et al., 2000; Nyholm and McFall-Ngai, 2004; Pankey et al., 2017;
06 Schwartzman and Ruby, 2016; Visick and Ruby, 2006). Bacterial colonization of host tissues induces the morphogenesis
07 process of the light organ and appears to signal its further development and maturation (McFall-Ngai and Ruby, 1991;
08 Montgomery and McFall-Ngai, 1998). The luminescence feature is essential for a correct morphogenesis process of the light
09 organ and symbiont persistence inside (McFall-Ngai et al., 2012; Visick et al., 2000). One of the best-documented symbioses
10 is the association of *Aliivibrio fischeri* with the bobtail squid *Euprymna scolopes* (Nyholm and McFall-Ngai, 2004; Ruby,
11 1996). Through the easy independently cultivation of both partners in laboratory, this symbiosis has become a perfect model
12 for studying the process of bacterial colonization into the light organ, and understanding bacteria–animal interactions,
13 broadly speaking (Mandel and Dunn, 2016; McFall-Ngai, 2014). *E. scolopes* squid is able to reject non-luminous strains of
14 *A. fischeri* (Bose et al., 2008; Koch et al., 2014), suggesting that the host possesses the capability of detecting (at a molecular
15 or physiological level) if its symbiont is bioluminescent or not (Miyashiro and Ruby, 2012; Peyer et al., 2014; Tong et al.,
16 2009). Additionally, a genetic distinction between strains of the same bacterial species, such as the presence of two operons
17 containing the light-emission-involved genes (Ast et al., 2007), is sufficient to avoid a successful colonization of the light
18 organ in a given host (Urbanczyk et al., 2012).
19 Although it was previously reported that symbionts from light organs were all members of the genus *Photobacterium*
20 (Nealson and Hastings, 1979), we now know through taxonomic reclassifications and the rise of acquired knowledge, that
21 they are not restricted to this clade. To date, 11 species are known to be involved in light-organ symbioses (**Table 1**). In a
22 light organ, the bacterial population is most of the time monospecific (Dunlap and Urbanczyk, 2013; Ruby, 1996). Thus,



23 organisms with light organ perform bioluminescent-bacteria batch culture as microbiologists try to do. Interestingly enough,
24 it is one of the rare bacterial cultures done *in situ* by marine organisms. Although light organs are generally colonized by a
25 unique species, existence of genetically distinct strains have been reported for some *E. scolopes* (Wollenberg and Ruby,
26 2009). Moreover, in the light organ of certain squid and fish, two species of luminous bacteria can co-occur. Indeed, light
27 organ of some *Sepiolo* spp. are colonized by a mixed population of *A. fischeri* and *A. logei* (Fidopiastis et al., 1998). The *P.*
28 *mandapamensis* and *P. leiognathi* species are also co-symbionts of some Perciformes fish (Kaeding et al., 2007). In the same
29 vein, some loliginid squids have been found to harbor a consortium of several luminous species in their light organ,
30 including at least *P. angustum*, *P. leiognathi* and *V. harveyi* (Guerrero-Ferreira et al., 2013).

31 The host-symbiont specificity appears consistent at the species level (see Table 1). However, this is not true at the host
32 family taxonomic level (Dunlap et al., 2007). Moreover, multiple unrelated host species are colonized by the same symbiont
33 species. These symbiont strains present no clear phylogenetic divergence between themselves, revealing no evidence of
34 codivergence between symbiont and host. Such a lack of strict symbiont/host specificity and codivergence in luminescence
35 symbiosis may be due to the environmental acquisition of luminous bacteria at each new generation rather than a parental
36 transmission which could favor higher genetic speciation (Dunlap et al., 2007).

37 Considering that fish and squid housing luminous bacteria are never found without symbionts in nature, the symbiosis
38 appears obligatory for hosts (Haygood, 1993). In contrast, most symbiotic bacteria are viable outside the light organ, and
39 thus are considered as facultatively symbiotic. These facultative symbiotic bacteria are readily culturable under laboratory
40 conditions, outside the host light organ. Exceptions have been highlighted for the luminous symbionts of two groups of fish,
41 the flashlight fish (family Anomalopidae) and the deep-sea anglerfish (suborder Ceratiodei) (Dunlap and Kita-tsukamoto,
42 2006; Haygood and Distel, 1993). Indeed, despite the fact that the bacterial origin of the light was proved by microscopic
43 observation and that genes from luminous bacteria were amplified (Haygood and Distel, 1993), bacterial cultivation has been
44 yet unsuccessful. Thanks to the emergence of genome sequencing, complete genome of these symbionts has been reported in
45 the last years. Analyses revealed a genome reduction in size by about 50 % and 80 % for anglerfish and flashlight-fish
46 symbionts respectively, compared to facultative luminous symbionts or free-living relatives (Hendry et al., 2014, 2018).
47 Genome reduction is a common trait shared by bacteria involved in obligatory symbiosis (Moran et al., 2009) and explains
48 the inability of these symbionts to grow in laboratory cultures. Flashlight-fish and anglerfish symbionts appear to be
49 obligatory dependent on their hosts for growth, as some metabolic capacities (e.g. genes necessary for amino acid synthesis)
50 are absent in the genome.

51 2.3 Light organs are under well-established controls

52 Although light organs can differ in form, size or location according to the host (see Table 1), some structural and functional
53 features are common for all of them. The light organ is a separate and highly evolved entity. Luminous bacteria are densely
54 packed within tubules which communicate to the exterior of the light organ (Haygood, 1993; Nealson, 1979). The host
55 provides nutrients and oxygen to the tubules through a highly vascularized system (Tebo et al., 1979). Bioluminescent



56 bacteria, which are not directly affected by mechanical stimulation, emit light continuously in the light organ, as they do in
57 laboratory cultures (Nealson and Hastings, 1979). However, the light intensity varies over time. As for self-luminescent fish,
58 bacterial light organs have evolved with multitude of adaptations of tissue, to serve as reflectors, diffusers, screens, and light-
59 conducting channels (Haygood, 1993; Munk et al., 1998). Such anatomical features assist in directing and enhancing light
60 output (Sparks et al., 2005). In addition, the host can control the light diffusion through different mechanisms, which may be
61 external lids, chromatophores, organ rotation, filters, occlusion with a shutter, or muscle contraction (Hansen and Herring,
62 1977; Herring, 1977; Johnson and Rosenblatt, 1988). As example, for counterillumination, controlling the intensity of light
63 output gives the host a better camouflage, adapting its silhouette to environmental changes in light (Jones and Nishiguchi,
64 2004; McFall-Ngai and Morin, 1991). For intra-species communication, it permits to produce sudden flashes or specific
65 signal/rhythm of light (e.g. schooling behavior (Gruber et al., 2019)).

66 In squid-*vibrio* symbiosis, bacterial luminescence genes are regulated with quorum-sensing system, a cell-density-dependent
67 process. When the cell density reaches a certain level, autoinducers responsible for triggering the synthesis of the genes
68 involved in light emission are accumulated in sufficient amount, and light is emitted (Nealson et al., 1970; Verma and
69 Miyashiro, 2013). Variation of light emission is closely linked to the concentration of one component involved in the
70 bacterial light reaction, which could be host controlled. Interestingly, *A. fischeri* produces a higher level of luminescence
71 within the light organ than in laboratory cultures, despite a similarly-high cell density (Boettcher and Ruby, 1990). Hence,
72 Verma and Miyashiro (2013), suggested that the light organ environment offers specific conditions such as the levels of
73 oxygen, iron, or phosphate, to enhance bacterial light emission.

74 Within the light organ, luminous symbionts reach a very high density which reduced the oxygen availability, essential for the
75 light reaction. Such oxygen limitation leads to a decrease in the specific luminescence activity (Boettcher et al., 1996).
76 Bacterial population inside the light organ is regulated by the host, by coupling the restriction of the growth rate and the
77 expulsion of symbionts. Growth repression is thought to reduce the energetic cost of the symbiosis to the host (Haygood et
78 al., 1984; Ruby and Asato, 1993; Tebo et al., 1979). Additionally, the cell number of symbionts is regulated by the daily
79 expulsion of most of the bacterial population, followed by a period of regrowth of the remaining symbionts. This periodical
80 released is highly correlated with the diel pattern of the host behavior. For example, in squid-*vibrio* symbiosis, the host
81 expels 95 % of the luminous symbionts in the surrounding environment at dawn, the beginning of its inactive phase. The
82 remaining 5 % of *A. fischeri* grow through the day and the highest concentration is reached at the end of afternoon, at the
83 nocturnal active phase of the squid (Nyholm and McFall-Ngai, 2004; Ruby, 1996). For all symbioses, luminous bacteria in
84 excess, densely packed inside tubules communicating with the exterior of the light organ, are regularly expelled (Haygood,
85 1993). Regular expulsion of symbionts maintains favorable conditions in the light organ for the bacterial population, but it
86 also seeds the environment with luminous symbionts for colonization of the next host generation. The consequence is a
87 release of a huge quantity of bioluminescent bacteria in the seawater inducing a major contribution to the ocean microbiome.
88 To make it more concrete and provide an order of magnitude, two examples are proposed thereafter. Using laboratory
89 experiments on different fishes (Monocentridae, Anomalopidae), Haygood et al. (1984) estimated a release between 10^7 to



90 10^9 bioluminescent bacterial cells per day and per individual. Another study on the Hawaiian bobtail squid (*E. scolopes*) has
91 estimated that the squid expels about 5×10^8 bioluminescent bacterial cells per day and per individual (Lee and Ruby, 1994).
92 These discharges lead to a regular luminous-bacteria enrichment of the areas inhabited by this organism.
93 Depending on the anatomical location of the light organ (see **Table 1**), luminous symbionts are released directly into the
94 surrounding seawater or through the digestive tract (Haygood, 1993; Nealson and Hastings, 1979). An enteric lifestyle has
95 indeed been suggested for the luminous bacteria (Ruby and Morin, 1979; Nealson, 1979).

96

97 **3 Enteric associations**

98 The gastrointestinal (GI) tract of an animal is a very complex and dynamic microbial ecosystem (Nayak, 2010). Current
99 knowledge and concepts on GI microbiota derive from studies on humans or other terrestrial mammals. In contrast, GI
:00 ecosystems of marine inhabitants have yet received little attention, and studies focused on farmed fish or commercially
:01 important species of fish. Whether aerobes or anaerobes are the main group in the microbiota in fish intestines is still
:02 discussed (Romero et al., 2014). For marine fish, the dominant members seem to be facultative anaerobes (Wang et al.,
:03 2018). Considering that most of the bioluminescent bacteria are facultatively anaerobes (Ramesh et al., 1990; Reichelt and
:04 Baumann, 1973), it is not surprising to find them in gut niches.

:05

:06 **3.1 Occurrence in marine-fish guts**

:07 Although luminescence of dead fish was a well-known phenomenon, one of the first mentions of the presence of luminescent
:08 bacteria in fish slime and intestinal contents is only from the beginning of the 1930's (Stewart, 1932). Since then, the high
:09 occurrence of luminous bacteria in fish intestines has been reported in many studies (Baguet and Marechal, 1976; Barak and
:10 Ulitzur, 1980; Liston, 1957; Makemson and Hermosa, 1999; O'Brien and Sizemore, 1979; Ramesh and Venugopalan, 1988;
:11 Reichelt and Baumann, 1973; Ruby and Morin, 1979). Most of hosts with internal light organ release luminous bacteria into
:12 the digestive tract (Haygood, 1993; Nealson and Hastings, 1979), and thus may largely contribute to their abundance in
:13 luminous fish intestines. However, one interesting case concerns a leiognathid fish, which internal light organ is colonized
:14 by *P. leiognathi*. Although its light organ is directly connected to its digestive tract (Dunlap, 1984), the luminous enteric
:15 population was not dominated by *P. leiognathi* (33 %), but by *V. harveyi* (67 %) (Ramesh et al., 1990). Actually, many
:16 fishes without light organ also harbor luminescent bacteria in their gut (Makemson and Hermosa, 1999), which clearly
:17 demonstrates existence of other sources for enteric luminous bacteria.

:18 Through the gut-content analysis of 109 fish species from the Gulf of Oman, Makemson and Hermosa (1999) showed that
:19 the relative proportion of the occurring culturable luminous bacteria was strongly variable. While some fish guts harbor more
:20 than 80 % of luminous bacteria, some others have between 20-50 %, and a minority have none detected, with a substantial



21 intra and inter-species fish variability. As other authors, Makemson and Hermosa (1999) highlighted *V. harveyi* and *P.*
22 *phosphoreum* as the dominant luminous species found in fish guts (Reichelt and Baumann, 1973; O'Brien and Sizemore,
23 1979; Ramesh and Venugopalan, 1988). Interestingly, a high proportion of luminescent bacteria (>70 %) has been found in
24 the gut of an Atlantic halibut recently fed, while an individual male in spawning condition, that had not been eating recently,
25 had a flora dominated by non-luminescent microorganisms (Verner-Jeffreys et al., 2003). This result underlines the link
26 between food ingestion and abundance of luminous bacteria and suggests that they do not persist within the halibut gut once
27 the feces are eliminated. This also suggests that luminous bacteria are then released with the feces in the water column.

28 Seasonal variations have been observed in both luminous bacterial density (Liston, 1957; Ramesh and Venugopalan, 1988),
29 and predominant species (Bazhenov et al., 2019). Such variability is not surprising since it is inferred to the structure and
30 composition of the gut microbiota of fish which is influenced by a series of factors, including (i) host factors (e. g genetics,
31 gender, weight, age, immunity, trophic level), (ii) environmental factors such as water, diet, and surrounding environment,
32 (iii) microbial factors (e.g. adhesion capacity, enzymes and metabolic capacity), (iv) and individual variations and day-to-
33 day fluctuations (Nayak, 2010; Sullam et al., 2012; Wang et al., 2018). Hence, contrasting results can be found in the
34 literature: for example, a dominance of the *Clostridium* (a non-luminous clade) is commonly associated with herbivorous
35 fishes (Clements et al., 2009), while *Vibrio* and *Photobacterium* (which are clades with luminous representatives) are the
36 dominant genera in carnivorous fish diet (Egerton et al., 2018). In contrast, Makemson and Hermosa (1999) have reported a
37 slightly higher proportion of culturable luminous bacteria in herbivore fish compared to carnivore. They also emphasized the
38 higher incidence of luminescent bacteria in pelagic than in reef-associated fish, as well as filter-feeder-fish guts contain more
39 luminous bacteria compared to other feeding type (e.g. predator). For bigger fishes, a potential introduction source of
40 luminous bacteria into gut could be the ingestion of smaller preys bearing bacterial light organ. For all organisms, enteric
41 luminous bacteria may be transferred to the gut bacterial community of their predators.

42 It should be emphasized that investigations on microbial communities of fish have long been limited by the use of culture-
43 dependent methods (Austin, 2006; Romero et al., 2014). We now know that only a small proportion of microorganisms can
44 be cultivated under laboratory conditions (Amann et al., 1995). Moreover, the fish-gut microbiota has been reported to be
45 particularly of low cultivability, with less than 0.1 % of the total microbial community cultivable (Zhou et al., 2014),
46 although the level of cultivability may be taxon dependent (Ward et al., 2009). Today, advanced molecular techniques offer a
47 wide variety of culture-independent methods, such as Next-Generation Sequencing (NGS), for analyzing fish microbiota
48 (Tarnecki et al., 2017). As a consequence, it is appropriate to investigate if luminous microbiota constitute a significant
49 portion of the total gut microbiota of fish as it has been suggested in previous works mentioned above, or if this trend was
50 distorted by the use of culture-dependent methods.

51 Several studies using gene sequencing based on 16S rRNA to characterize the gut microbiome of fish have reported the
52 genus *Photobacterium* as the most abundant in the guts of salmon and trout (Bagi et al., 2018; Givens et al., 2015; Michl et
53 al., 2019; Riiser et al., 2018), shark (Michl et al., 2019) and Atlantic cod (Bagi et al., 2018; Givens et al., 2015; Michl et al.,
54 2019; Riiser et al., 2018). Other studies reported the presence of *Photobacterium* spp. in the gut of hydrothermal shrimp



:55 (Durand et al., 2009), and, seasonally variable, in the gut of Norway lobster (Meziti et al., 2010). However, because not all
:56 *Photobacterium* spp. have luminescence ability, it is important to be able to resolve dominant OTU at the species level,
:57 which, most of the time, is not possible with a 16S rRNA barcoding sequencing approach. The emergence of multi-gene
:58 approaches offers more detailed insights into the taxonomic diversity of these communities (i.e. species level). Thus, using
:59 metagenomic shotgun sequencing, two independent and recent works on wild Atlantic cods also concluded of the
:60 *Photobacterium* spp. domination and have been able to go deeper into the taxonomic identification. Le Doujet et al. (2019)
:61 demonstrated that *Photobacterium* genus represents 78 % of all present genera and identified the *P. phosphoreum* clade as
:62 the most abundant *Photobacterium* lineage. According to Riiser et al. (2019), the luminous species *P. kishitanii* constitutes
:63 over 26 % of the Vibrionales community, which is the dominant clade, and the authors underlined the presence of the
:64 functional *lux* genes. Therefore, recent metagenomic studies seem to confirm the trend of a high occurrence of luminous
:65 bacteria in fish intestines.

:66

:67 **3.2 Are enteric luminous bacteria playing a specific role for the host?**

:68 From their presence in GI tract, the enteric bacteria may gain rich-nutrient accessibility. In reply, GI microbial communities
:69 may play critical roles on host health, development and nutrition (Romero et al., 2014; Wang et al., 2018). A clear
:70 understanding of the role that the specific gut microbiota plays is still lacking. It has been highlighted that components of the
:71 bacterial microflora are associated with several functions, such as epithelial renewal, amino-acid production, complex-
:72 molecule degradation, or inhibitory-compound secretion, that protect host against bacterial pathogen colonization (Austin,
:73 2006; Wang et al., 2018). However, little is known about a possible role of enteric luminous bacteria on the host physiology.
:74 A rare item is that some luminous bacteria, and particularly *Photobacterium* spp., may contribute to the digestion of complex
:75 molecules, like for example, being involved in chitin degradation (Ramesh and Venugopalan, 1989; Spencer, 1961).

:76 Pathogen processes related to bioluminescent bacteria are regularly investigated and reviewed (Austin and Zhang, 2006;
:77 Dunlap and Urbanczyk, 2013; Fidopiastis et al., 1999; Nelson et al., 2007; Ramesh and Mohanraju, 2019; Wang et al.,
:78 2015). Many luminous bacteria can act as opportunistic pathogens, and particularly on marine crustaceans, by entering the
:79 body of animals through lesions on its surface. However, such opportunistic pathogen behavior is not specific to luminous
:80 bacteria, but their presence is probably highlighted due to the visible light emitted (Dunlap and Urbanczyk, 2013).

:81 Based on the increase in light emission observed on dead marine animals, Wada et al. (1995) argue that, at the death of the
:82 host, enteric luminous bacteria may have an important saprophytic lifestyle. On dead organisms, luminous bacteria present in
:83 the gut of the host could initiate rapid propagation and decomposition of the host body, and result in the formation of
:84 luminous debris in the marine environment. For marine vertebrates, luminous strains of *Photobacterium* spp.,
:85 psychrotolerant and histamine producing, are regularly described as the major spoilage organisms on fish caught and stored
:86 (Barak and Ulitzur, 1980; Bjornsdottir-Butler et al., 2016; Dalgaard et al., 1997; Figge et al., 2014; Macé et al., 2013). In



.87 contrast to dead organisms, on living vertebrate specimens, infection by luminous bacteria rarely occurs (Dunlap and
.88 Urbanczyk, 2013).

.89

.90 **4 Luminous bacteria and the biological carbon pump**

.91 As previously discussed, light organs and guts act as a source for luminous-bacteria persistence in the oceans. Therefore,
.92 luminous bacteria are widespread in the ocean. They can be found as free-living forms or attached to particles (Nealson and
.93 Hastings, 1979; Ramesh and Mohanraju, 2019; Ruby et al., 1980).

.94

.95 **4.1 Bioluminescent bacteria in the water column**

.96 Qualitative and quantitative studies showed that the luminous bacteria are dynamic over time and space. Seasonal variations
.97 have been identified, both in abundance and predominant species (O'Brien and Sizemore, 1979; Ruby and Nealson, 1978;
.98 Yetinson and Shilo, 1979). A wide variability has been observed in species repartition over depth and between geographic
.99 areas (DeLuca, 2006; Gentile et al., 2009; Nealson and Hastings, 1979; Ramaiah and Chandramohan, 1992; Ruby et al.,
.00 1980). Horizontal, vertical and seasonal variations were most of the time presumed to reflect physiological preference, and
.01 particularly temperature or salinity sensitivity (Orndorff and Colwell, 1980; Ramesh et al., 1990; Ruby and Nealson, 1978;
.02 Shilo and Yetinson, 1979; Yetinson and Shilo, 1979). Some works mentioned that symbiotic niches, such as light organs and
.03 enteric tracts, may serve to inoculate the planktonic population (Nealson et al., 1984; Nealson and Hastings, 1979; Ramesh et
.04 al., 1990; Ruby et al., 1980). To our knowledge, very few studies focused intensively on the contribution of species-specific
.05 symbiotic associations on the occurrence and distribution of luminous bacteria in the surrounding water. Amongst these rare
.06 studies, Lee and Ruby (1994) reported that the abundance of *A. fisheri*, the luminous symbiont of the Hawaiian squid *E.*
.07 *scolopes* was 24 to 30 times higher, in both water column and sediments, in areas inhabited by the squids than in similar
.08 locations where squids were not observed.

.09 Bioluminescent bacteria also seem to be the cause of the spectacular and still largely unexplained events, so-called milky
.10 seas (Lapota et al., 1988; Nealson and Hastings, 2006). Milky seas are characterized by an unusual brightness on the ocean
.11 surface and extend over such a large area that the light emitted is detectable from space (Miller et al., 2005). The light-
.12 emission pattern of milky seas is continuous and homogeneous, which is consistent with light emission from bacteria and
.13 easily distinguished from blooms of dinoflagellates.

.14 **4.2 Bioluminescent bacteria attached to particles**

.15 Outside of spatially restricted niches, as light organ or gut environments, role of the dispersed luminous cells in marine
.16 environment was matter of debate and it was thus mentioned that non-symbiotic bacteria may have no ecological



17 significance (Hastings and Greenberg, 1999; Nealson and Hastings, 1979). However, Herren et al. (2004) suggested that
18 luminous bacteria are more attached to particles than free-living, which was confirmed by Al Ali et al. (2010). Many
19 bacteria, including bioluminescent bacteria (Ruby and Asato, 1993; Zhang et al., 2016), can develop swimming behavior to
20 colonize the sinking organic material, therefore reaching a cell density 100 to 10,000 times higher than in the water column
21 (up to 10^8 to 10^9 cells mL^{-1}) (e.g. Ploug and Grossart, 2000).

22 Bacteria that glow on particles can attract macro-organisms. After being ingested, they will find a more favorable
23 environment to live and grow in their gut (Andrews et al., 1984; Ruby and Morin, 1979). Actually, this is the preferred
24 current hypothesis that supports a positive selection related to the dispersion and propagation of the bacteria. Indeed,
25 luminous bacteria growing on particulate matter could produce enough light to be visible by other organisms. For bacterial
26 species with light production under cell-density control (i.e. under quorum-sensing regulation), the high cell concentration
27 reached on particles can allow the sufficient accumulation of the autoinducers, and thus the emission of light for attracting
28 predators. For species which light production is not subject to cell-density control (i.e. not under quorum-sensing regulation)
29 (Tanet et al., 2019), to be able to produce light at very low cell concentration could give them an advantage for being prior
30 eaten. Continuously glowing bioluminescent emissions are thought to attract predators (Nealson and Hastings, 1979). In the
31 water column, the glowing bacteria aggregated on particles would lead to the detection, attraction, ingestion and
32 decomposition of particles by larger organisms. Grazers would consume luminous matter at a higher rate than invisible
33 particles. Being consumed and ending up into the gut, bacteria would benefit of a more suitable environment regarding the
34 growth conditions and the nutrient accessibility. In open ocean, and particularly in deep regions, where sparse nutrient
35 supply prevails, rich-nutrient gut niches of the surrounding animals could appear as an oasis of life for bacteria. This
36 dispersion hypothesis has also been strongly consolidated by field data where bacterial bioluminescence was observed in
37 freshly excreted fecal pellets and in materials collected from sediment traps (Andrews et al., 1984), as well as by laboratory
38 experiments where glowing zooplankton were preferentially ingested by fishes (Zarubin et al., 2012).

39 The copiotrophic type of luminous bacteria is another point supporting their particle-attached lifestyle. Bacterial population
40 colonizing nutrient-rich environments (e.g. floating carcass, marine snow, fecal pellets or the gut tract of a marine eukaryote)
41 are defined as copiotrophs, by opposition to the oligotrophs which are members of free-living microbial populations (Lauro
42 et al., 2009). All luminous marine bacteria from *Vibrio* and *Photobacterium* spp. possess two chromosomes in their genome
43 (Boyd et al., 2015; Zhang et al., 2016), with a high copy number of rRNA operons. Such genomic features, as a large
44 genome size and multiple rRNA operons, are considered as an adaptation for a copiotrophic lifestyle (Klappenbach et al.,
45 2000; Lauro et al., 2009). Copiotrophs are thought to have strong adaptability skills, permitting them to survive long enough
46 between two nutrient-rich environments (Yooseph et al., 2010).

47 Fish guts could also act as an enrichment vessel for the growth of luminous bacteria, and thus enhance their propagation
48 (Nealson and Hastings, 1979; Ramesh and Venugopalan, 1988). When expelled with feces, enteric luminous bacteria can be
49 easily isolated from the fresh fecal material. This fecal luminescence increased in intensity over a matter of hours, proving
50 that luminous bacteria survived the digestive process and can proliferate on such organic material (Ruby and Morin, 1979).



51 Henceforth, fish feces appear to be an important source of viable luminous bacteria in the marine environment and could
52 affect both the distribution and the species composition of luminous populations. The luminescence of fecal particles has
53 been reported numerous times and was always associated to luminous bacteria, due to the observation of continuous light
54 emission or direct isolation (Andrews et al., 1984; Ramesh et al., 1990; Raymond and DeVries, 1976; Ruby and Morin,
55 1979; Zarubin et al., 2012).

56 In comparison with free-living luminous bacteria, few studies have focused on bioluminescence of marine snow and fecal
57 pellets. Yet, observations on materials collected from sediment traps revealed light emission in 70 % of all samples, with two
58 distinct patterns of light kinetics, probably due to the presence of different luminescent organisms (Andrews et al., 1984).
59 Surface-sample (above 60 m depth) analyses reported that more than 90 % of the luminous-aggregate samples exhibited
60 bacterial luminescence (Orzech and Nealson, 1984). Another study (between 2 and 17 m depth) also reported a large part of
61 luminous marine snow, but more likely due to dinoflagellates (Herren et al., 2004).

62

63 **4.3 Bioluminescent bacteria in the sediments**

64 Information relative to luminous bacteria in sediment is also limited. It is known that bioluminescent bacteria can be isolated
65 from sediment samples (Ramesh et al., 1990), but rare data exist about their distribution or abundance. In some sediment
66 samples, occurrence of luminous bacteria among total heterotrophic bacteria could reach up to 70 %, with seasonal
67 variations (Ramesh et al., 1989), although less pronounced than in water column (O'Brien and Sizemore, 1979). Main
68 sources of luminous bacteria in sediments are likely the glowing sinking marine snow, and benthic or demersal host
69 harboring symbiotic light organ with regular discharges.

70 More recently, sediment resuspension events (Durrieu de Madron et al., 2017) were correlated with newly formed deep-
71 water events and deep-sea bioluminescent events recorded in the NW Mediterranean Sea (Martini et al., 2014; Tamburini et
72 al., 2013a). Since the presence of active luminous bacteria has been demonstrated on the site (Martini et al., 2016), it has
73 been hypothesized that resuspended luminescent bacteria present in sediment can be part of these luminescence events
74 (Durrieu de Madron et al., 2017). Additionally, dense water formation, conveying particulate organic matter, could further
75 increase luminous bacteria proliferation and activity (Tamburini et al., 2013a).

76

77 **4.4 How do bioluminescent bacteria impact the biological carbon pump?**

78 Based on the ecological versatility of the bacterial bioluminescence reviewed above, we propose to reconsider the classical
79 view of the fate of organic matter in the oceans. **Figure 1** represents the guideline of the bioluminescence shunt hypothesis
80 of the biological carbon pump.

81 Bioluminescent bacterial emissions are continuous over time and such characteristic is thought to attract predators. Indeed,
82 the light color from bioluminescence contrasts well against the dim or dark background of the ocean depths. In the



83 bathypelagic zone (1000–4000 m), where no daylight remains, bioluminescent emissions are considered as the major visual
84 stimulus (Warrant and Locket, 2004; Widder, 2002). For such reason, symbiotic associations have been selected as an
85 advantage for hosts (fish or squid) in light organs. Luminous bacterial symbionts are successively acquired by juveniles and
86 released into the seawater to control population concentration (**Figure 1, step 1**). As indicated previously, the released of
87 bioluminescent bacteria from light organs and fecal pellets can represent an unbelievable quantity of bioluminescent bacteria
88 in the water column.

89 Recent studies underlined the very-well-adapted fish vision to the detection and location of point-source bioluminescence
90 (Busserolles and Marshall, 2017; Mark et al., 2018; Musilova et al., 2019; Paitio et al., 2016; Warrant and Locket, 2004).
91 Although less intensively documented than fishes, crustacean (copepods, amphipods, isopods...) visual system is also
92 reported to have sensitivity shift to bluer wavelength, which aids their bioluminescence detection (Cohen and Forward, 2002;
93 Frank et al., 2012; Marshall et al., 1999; Nishida et al., 2002). In laboratory experiments, Land et al. (1995) demonstrated
94 that amphipods were attracted to a blue-light-emitting diode. Unfortunately, and despite these statements, rare studies have
95 investigated the effect of bioluminescence on the ingestion rates of predators (**Figure 1, step 2**). To our knowledge, the only
96 one known is from Zarubin et al. (2012), who experimentally measured 8-times-higher ingestion rate of glowing (due to
97 ingestion of bioluminescent bacteria) zooplankton by fishes, compared to non-luminous zooplankton. Moreover, they
98 demonstrated the attraction of zooplankton by luminous bacteria.

99 Glowing bacteria have been observed attached to particles of organic matter, marine snow and fecal pellets (**Figure 1**, from
100 symbionts in guts in **step 1** and through predation in **step 2**) sinking into the deep ocean. Thus, while sinking into the deep,
101 these glowing bacteria living on organic carbon particles (marine snow, fecal pellets...) would lead to the detection,
102 attraction, ingestion and decomposition of particles by larger organisms. Consumers would ingest luminous matter at a
103 higher rate than invisible particles and consequently will augment luminous-microorganism dispersion by fecal-pellet
104 excretion. Bioluminescent sinking material should accelerate the consumption of organic matter by attracting grazing
105 organisms. Interestingly, bacteria associated with animal guts are thought to be particularly adapted to high-hydrostatic
106 pressure (Deming et al., 1981; Ohwada et al., 1980; ZoBell and Morita, 1957). Indeed, certain bioluminescent bacteria resist
107 to high hydrostatic pressure (Brown et al., 1942), and some of them have a higher growth rate and emit more light than at
108 atmospheric pressure (Martini et al., 2013). Such piezotolerance, or piezophile lifestyle, is undoubtedly an advantage for
109 luminous bacteria attached to particles that are exposed to pressure variations during the sinking-particles fluxes (Tamburini
110 et al., 2013b). The addition of these bioluminescent tags on particles has two indirect impacts (**Figure 1, steps 2 & 3**). First,
111 due to aggregate fragmentation by sloppy feeding and coprorhexy, fast-sinking particles are transformed into slow-sinking or
112 suspended particles. Fragmentation has been shown to be the primary process controlling the sequestration of sinking
113 organic carbon (Briggs et al., 2020). The second possibility is that organic matter ingestion leads to aggregation by
114 repackaging, and the excreted pellets of higher density, are fast-sinking particles. Filter-feeder plankton, without visual
115 detection and food selection by light, will also passively contribute to such aggregation or fragmentation of particles. For
116 these organisms, bioluminescence can even have a negative effect since they can be identified by the luminous material



17 filtered. Additionally, the consumption of organic material colonized by bioluminescent bacteria increases their dispersal rate
18 provided by migrating zooplankton, and even more so by actively swimming fish, following the conveyor-belt hypothesis
19 (Grossart et al., 2010) (**Figure 1, step 4**). This dispersion due to the expelling of luminous feces is several orders of
20 magnitude greater than that of water-borne free bacteria.

21 Sediment resuspension is another process implying the consumption of luminous bacteria by higher trophic levels (**Figure 1,**
22 **step 5**). This potentially re-inseminates bacteria into the bioluminescence loop through the consumption by epi-benthic
23 organisms.

24 Considering this bioluminescence shunt hypothesis, all the processes described above show that bioluminescence can be
25 view as a catalyst in the biological gravitational carbon pump (Boyd et al., 2019), by either increasing the carbon
26 sequestration into the deep ocean, or by slowing down the sinking rate of particles and consequently increasing their
27 degradation and the remineralization rate. Bioluminescence and especially luminous bacteria may therefore influence the
28 export and sequestration of biogenic carbon in the deep oceans. A better quantification of these processes and impacts in the
29 biological carbon pump are a requirement in future studies.
30

31 **5 Past and future instrumentation for bioluminescence assays**

32 **5.1 Previous sampling methods to describe diversity and abundance of luminous bacteria**

33 In the existing literature, to estimate the diversity and the distribution of bioluminescent bacteria, studies were based on a
34 restricted number of sampling methods and instruments. These methods focused either on environmental samplings where
35 bacteria are present, or on organisms with associated bacteria.

36 First, vertical samplings in the water column were performed using sterile-bag samplers (Ruby et al., 1980), or later, using
37 Niskin bottles (mounted on rosette profilers) (Al Ali et al., 2010; Gentile et al., 2009; Kita-Tsukamoto et al., 2006; Martini et
38 al., 2016; Yetinson and Shilo, 1979). This approach is commonly set up in oceanography but rely on relatively small
39 volumes of water (up to 20L). Furthermore, it does not fully capture the heterogeneity of the ecosystem since it provides one
40 discreet sample over restricted time and space. Other instruments dedicated to the acquisition of sediment sampling are
41 the multiple-core samplers, deployed onto the seafloor (Kita-Tsukamoto et al., 2006). For particulate organic carbon and
42 fecal pellets, in order to describe the diversity of associated luminous bacteria, sediment traps have been occasionally
43 deployed from the surface down to the deep ocean (Andrews et al., 1984). Using them, fresh luminous material has been
44 collected between 30 to 1900 m depth down.

45 To study the presence of luminous symbionts in guts and light organs larger organisms are caught. The most common way to
46 catch deep-sea animals is the deployment of trawls and more generally nets. They are well adapted to sample squid
47 (Zamborsky and Nishiguchi, 2011) or fishes, like the anglerfish (Freed et al., 2019). One particularity of these methods is
48 that the sampling covers a large section of the water column and pulled everything into one catch with a limited precision



49 about depth layers. SCUBA diving is another method to gently select these large animals (Zamborsky and Nishiguchi, 2011).
50 It has also been used to catch fecal pellets and sinking particles (Orzech and Neelson, 1984). Obviously, SCUBA diving has
51 a strong depth limitation (generally above 50 m depth). It can be more efficient at night for some migrating species and has a
52 restricted sampling size of organisms and number of samples carried back to the ship.

53 Once environmental samples or material from organism's light organs have been acquired, the objective is either to describe
54 the taxonomy and diversity of luminous bacteria, or to quantify them. To do so, earlier studies have filtered seawater samples
55 through a polycarbonate filter with a pore size of 0.2 μm to retain bacteria. The filter is then placed with the bacterial side up
56 on growth medium in petri dishes (Kita-Tsukamoto et al., 2006; Ruby et al., 1980). For symbiotic bacteria, light organ or
57 guts are aseptically dissected shortly after death, and the content is homogenized before culture or microscopic observations
58 (Dunlap, 1984). After hours of incubation, the total colony forming units is observed; the luminous colonies can, then, be
59 enumerated and selected for taxonomic investigation.

60 Further investigations of symbiotic associations, in relation to surrounding environment, would require a reliable taxonomy
61 of luminous bacteria and robust knowledge on species-specific symbiotic associations. As an example, *Photobacterium*
62 *phosphoreum* was thought to be the specific symbiont of light organ of numerous deep-sea fish (Hendrie et al., 1970; Ruby
63 et al., 1980; Ruby and Morin, 1978), before a phylogenetic analysis showed distinct evolutionary lineages in the *P.*
64 *phosphoreum* clade according to the colonized habitat. This resolution revealed that all the *P. phosphoreum* symbionts
65 isolated from light organ should actually be identified as *P. kishitanii* (Ast and Dunlap, 2005).
66

67 **5.2 Future strategy to quantify the role of bioluminescence in the biological carbon cycle**

68 Since these first investigations on luminous bacteria in symbioses or in the environment, there has been a huge improvement
69 in technology and molecular-biology techniques. To better evaluate the role of bioluminescence and luminous bacteria in the
70 biological carbon pump further studies have to follow an efficient strategy. Such strategy will focus on quantifying this
71 functional trait and how it impacts the transfer of organic carbon between trophic levels, as well as its sequestration into the
72 deep ocean. This approach can be divided into several key points 1) the assessment of the global importance of
73 bioluminescence in the oceans, 2) the pursue of investigations about the quantification and diversity of luminous bacteria and
74 their variability between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments),
75 3) the quantification of luminous bacterial release into the surrounding environment and the potential impact of vertical
76 migration, and 4) the quantification of the transfer rate of bacteria attached on glowing particles into zooplankton and the
77 quantification of the effects on organic matter decomposition, sinking rate and fluxes, in comparison to non-glowing
78 particles. In this review, future perspectives to allow major advances on these specific key points are proposed based on
79 technologies recently developed.
80



81 **5.2.1 The assessment of the global importance of bioluminescence in the oceans**

82 In order to establish the global importance of light emitted by organisms, which include glowing bacteria, quantitative
83 surveys are needed at large spatial scales including geographical variability and depth. Current existing fixed platforms
84 (including observatories), oceanographic vessels, remotely-operated and autonomous underwater vehicles (AUV), and
85 gliders have considerably increased our knowledge of marine ecosystems and their spatial variability. For temporal scales, in
86 the last decades, the multiplication of long-term observatories and ongoing European *in situ*-observing-infrastructure
87 initiatives, such as the Fixed-point Open-Ocean Observatories (FixO3), the European Multidisciplinary Seafloor Observatory
88 (EMSO), the European Research Infrastructure, or the ARGO International Program (EuroArgo) (Favali and Beranzoli,
89 2009; Le Reste et al., 2016) have increased global-ocean observations at long time scales (more than 10 years) and high
90 sampling frequency. To quantitatively record bioluminescence emissions, some instruments are commercially available, or
91 have been adapted from existing sensors. Bathyphotometers, a system pumping water into a closed chamber and measuring
92 the emission of light by a photomultiplier, are the most commonly used (Herren et al., 2005), and have already been
93 implemented on AUV (Berge et al., 2012; Messié et al., 2019; Moline et al., 2009) and other vertical profilers (Cronin et al.,
94 2016). Other approaches have been developed unexpectedly from astrophysics telescopes using photomultipliers with a very
95 high sensitivity to photons embedded into optical modules. These instruments have been proved to be efficient to detect
96 bioluminescence in deep-sea environments and over long-time surveys (Aguzzi et al., 2017; Martini et al., 2014; Tamburini
97 et al., 2013a). Another example of quantitative records of photon counts is the equipment of bio-samplers, such as elephant
98 seals, with a small, autonomous tag recording environmental light and bioluminescence. These tags have been shown to be a
99 great improvement in highlighting ecological functions such as predator/prey relationships and could inform on the role of
100 bioluminescent prey for seals (Vacquié-Garcia et al., 2012). The technological development of high sensitivity cameras has
101 opened another path for bioluminescence exploration. Low light cameras have been used to record *in situ* light patterns
102 (Maxmen, 2018; Phillips et al., 2016) and implemented on remotely operated vehicles for direct *in situ* observations of
103 sinking particles, or marine luminescent creatures.

104 Theoretically, both bacterial, glowing continuously, as well as eukaryotic light, emitted as flashes, could be detected. All of
105 these instruments, with the capability to record surrounding or mechanically stimulated light, have been extensively
106 developed or adapted within the last 10 years. Their future implementation on multiple observatories and vehicles will
107 definitely increase our knowledge on the global importance of bioluminescence in the oceans. Long-time surveys could
108 elucidate extreme observed events, such as, the bacterial abundance in water-mass movements and sediment resuspension
109 (Durrieu de Madron et al., 2017) or the frequency of milky seas (Lapota et al., 1988; Miller et al., 2005) due to luminous
110 bacteria. Over space, profilers will provide information about the role of bioluminescence in vertical nychthemeral
111 migrations. However, the future challenge is that the deployment of these instruments has to be done in parallel with data
112 analysis. Acquisition of quantitative signal will induce the discrimination of different groups of organisms including



13 bacteria, and, consequently, will require the development of strong statistical methods in signal analysis (Messié et al.,
14 2019).

15 To go deeper than *in situ* quantitative observations, samplings are necessary in various ecosystems including marine snow,
16 water column, sediments, as well as light organs of fishes and squids.

17

18 **5.2.2 The pursue of investigations about the quantification and diversity of luminous bacteria and their variability** 19 **between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments)**

20 Marine snow potentially glows due to luminous micro-organisms colonizing these habitats (bacteria, eukaryotes), but there
21 are only few studies, based on limited numbers of samples that have quantified luminous bacteria on marine snow in the dark
22 ocean. A first step is to establish the extent of glowing particles over depth, to assess if this is a common or marginal
23 phenomenon. This can be done either by direct observation of light or by describing the biodiversity associated to these
24 particles. Particles are difficult to sample due to their fragility. However, vehicles such as remotely operated vehicles are able
25 to collect particles of marine snow at specific depth using suction samplers and bring them back to the surface into biological
26 collectors. Sediment samplers, potentially implemented on benthic rover, are other instruments used to sample marine snow,
27 fecal pellets and particles. This is already a common tool deployed during oceanographic cruises but samples from sediment
28 traps are generally dedicated to biogeochemistry analyses which involve fixing their content using reagents. To assess the
29 activity of luminous bacteria, it will only require keeping this material fresh without fixing reagent in order to observe the
30 light emission. Glowing aggregates can be observed by using low light cameras and the light measured by photomultipliers.
31 After observations, these samples can be used for multiple biogeochemical analyses including bacterial taxonomic diversity
32 and abundance.

33 **5.2.3 The quantification of luminous bacteria in the environment and the potential impact of vertical migration**

34 The analysis of water and sediment samplings can considerably be improved by omics methods to pursue investigations of
35 bacterial taxonomic diversity and functions and assess their variability between different ecosystems (including sediments,
36 marine snow, and water column).

37 Advances in Next Generation Sequencing (NGS) methods open new opportunities to describe the structure of communities
38 and the part of luminous bacterial strains present in environmental samples. These methods are an opportunity to sequence
39 bacterial species even if it is not cultivable, which has been one major limitation of traditional methods. In order to
40 efficiently describe bioluminescent or non-bioluminescent bacteria, the description at the species level is a strong
41 requirement. As an example, *Vibrio* are important contributors to particulate organic carbon fluxes that have been observed
42 at abyssal depths in the Pacific Ocean (Preston et al., 2019, Boeuf et al., 2019). A better characterization at species or
43 functional level should highlight the luminous potential related to the presence of such organisms, even at low abundance.



44 Metabarcoding and transcriptomic could also be used on particles and fecal pellets sampled over depth to describe the
45 biogeography of luminous bacteria.

46 One track for further investigations is to take advantage of large sampling efforts to sample at a global scale made with
47 oceanographic cruises such as TARA Ocean, Tara Polar circle circumpolar expeditions (Pesant et al., 2015) or
48 MALASPINA (Duarte, 2015). These expeditions have established a protocol to provide consistent methodology on the
49 analysis of micro-organism biodiversity. The data available could give some new inputs on the variability of luminous
50 bacteria over ecosystems around the globe.

51

52 **5.2.4 The quantification of the transfer rate of bacteria attached on glowing particles to consumers and the effect on** 53 **organic matter decomposition, sinking rate and fluxes, in comparison to non-glowing particles**

54 One main lock to evaluate the importance of bioluminescence in the biological carbon pump is to quantify the transfer rate of
55 organic carbon between trophic levels. Few studies related the preferential consumption of luminous bacteria by zooplankton
56 (copepods in Nishida et al., 2002) or fish (Zarubin et al., 2012). In the laboratory, investigations on processes influencing
57 consumption rates of zooplankton on glowing particles can be performed to define the parameters inducing these higher
58 attraction rates. Future studies based on the experimental protocol described by Zarubin et al. (2012) could be improved by
59 including other zooplankton species of importance in the biological carbon pump and multiple bacterial species. In a dark
60 room, under controlled conditions (close to *in situ*) the attraction rate of glowing (fresh or infected by luminous bacteria) and
61 non-glowing aggregates can be tested on zooplankton (copepods, mysids) as well as higher trophic levels (small fish). The
62 effect of temperature, bacteria species, abundance/diversity of zooplankton communities, glowing/non-glowing particles,
63 light intensity, hydrostatic pressure and other variables can be tested on particles attraction behavior. One main improvement
64 is the capability of low-light cameras to record associated behaviors under the laboratory experiments.

65

66 **6 Conclusion**

67 Light organ and gut of marine animals act as reservoirs for the abundance and persistence of luminous bacteria in the ocean.
68 Additionally to light organs and gut niches, bioluminescent bacteria colonize particles of organic-matter, making them
69 glowing. Taking into account the powerful attraction of luminescence on fish and zooplankton consumption, luminous
70 bacteria may therefore influence, in different ways, the export and sequestration of biogenic carbon in oceans. Finally, a
71 multi-instrumented strategy will definitely increase knowledge on bioluminescence and the role of luminous bacteria in the
72 biological carbon pump. This strategy can be set up based on both traditional methods and recently developed technology
73 and is promising in the near future.

74



75 **Author contributions:**

76 LT and CT proposed the idea. LT provided the first version of the review. The following authors were in charge of the initial
77 draft of the corresponding sections: LT: luminous bacteria in light organs and guts, spatial distribution of luminous bacteria,
78 SM: role of luminous bacteria into the biological carbon pump and future strategy. LC and CT supervised the work. LT, SM,
79 LC and CT wrote, reviewed and edited the final review.

80

81 **Competing interests:**

82 The authors declare that they have no conflict of interest.

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88

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180 **Figure and Table captions.**

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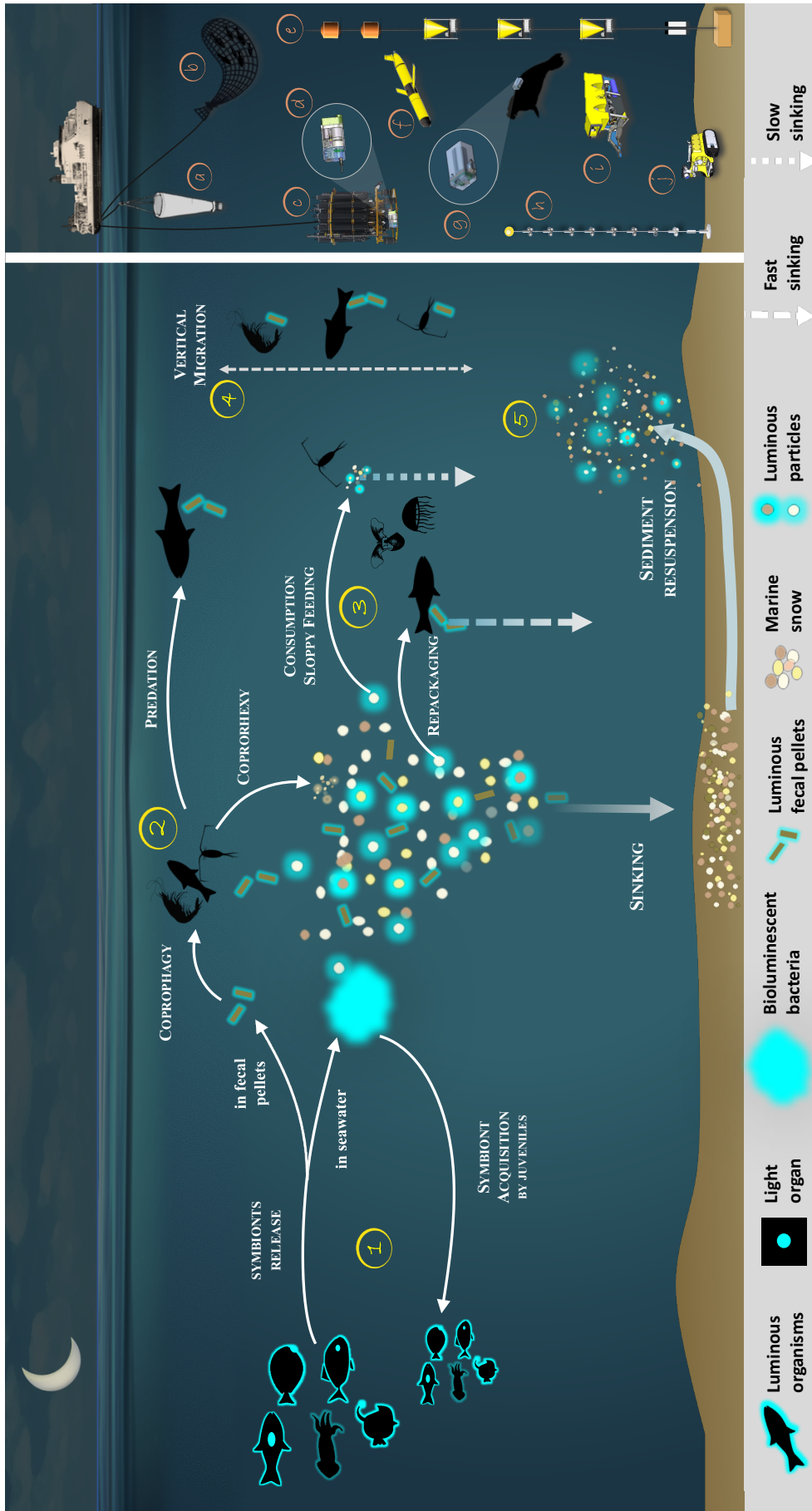
182 Figure 1: Bioluminescence shunt in the biological carbon pump in the ocean. Luminous bacteria in light-organ symbioses are successively
183 acquired by host (squid, fish) from the seawater while they are juveniles, then regularly released into the ocean. Depending on the light-
184 organ position, luminous bacteria are released from their guts into fecal pellets or directly into the seawater (step 1). Motile luminous
185 bacteria colonize organic matter sinking along the water column. Bioluminescent bacteria inseminating fecal pellets and particles influence
186 zooplankton consumption rates. Such visual markers increase detection ("bait hypothesis"), attraction and finally predation by upper
187 trophic levels (step 2). In the mesopelagic, zooplankton and their predators feed on sinking luminous particles and fecal pellets, which
188 either form aggregates (repackaging) of faster sinking rates or fragment organic matter (due to sloppy feeding) with slower sinking rates
189 (step 3). Filter feeders also aggregate sinking organic matter without particular visual detection and selection of luminous matter. Diel (and
190 seasonal) vertical migrators feeding on luminous food, metabolize and release glowing fecal pellets from the surface to the mesopelagic
191 zone (step 4). It implies bioluminescent bacteria dispersion at large spatial scales, for zooplankton or even some fish actively swimming on
192 long distances. Luminous bacteria attached on particles sink down to the seafloor, sediment can be resuspended by oceanographic physical
193 conditions (step 5) and consumed by epi-benthic organisms. Instruments area: (a) plankton net, (b) fish net, (c) Niskin water sampler, (d)
194 bathyphotometer, (e) sediment traps, (g) photomultiplier module, (f) autonomous underwater vehicles, (h) astrophysics optical modules
195 ANTARES, (i-j) remotely operated vehicles.

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197 Table 1: List of luminous bacterial species found in light organ symbiosis. In blue, the light organ position on the host body, according to
198 the schema of fish from Neelson and Hastings, 1979. * firstly identified as *Vibrio logei* by Fidopiastis et al., 1998.

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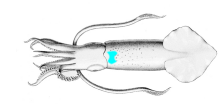
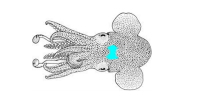
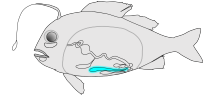


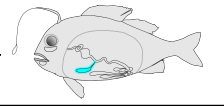
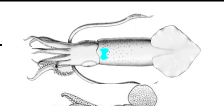
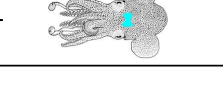
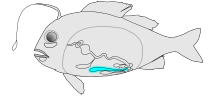


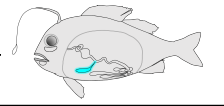
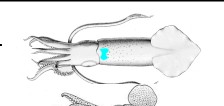
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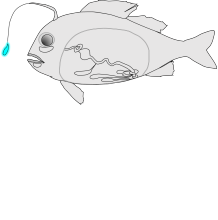




Species	Host Collection	Hosts	Light Organ Location
<i>Aliivibrio fischeri</i> (<i>Vibrio fischeri</i>)	<i>Euprymna</i> spp. Western Pacific (Fidopiastis et al., 1998)	SEPIOLIDAE <i>Euprymna</i> spp. <i>E. morsei</i> <i>E. berryi</i> <i>E. scolopes</i> <i>E. tasmanica</i>	
	<i>Sepiolo</i> spp. Mediterranean Sea, European Atlantic coast, Japan, Philippines (Fidopiastis et al., 1998)	<i>Sepiolo</i> spp. <i>S. affinis</i> <i>S. atlantica</i> <i>S. intermedia</i> <i>S. ligulata</i> <i>S. robusta</i>	
	<i>Moconcentris japonica</i> Japan (Dunlap et al., 2007)	MONOCENTRIDAE <i>Monocentris</i> spp. <i>M. japonica</i>	
	<i>Cleidopus gloriamaris</i> East coast of Australia (Fitzgerald, 1977)	<i>Cleidopus</i> spp. <i>C. gloriamaris</i>	
	<i>Caelorinchnus</i> spp. Taiwan (<i>C. formosanus</i>) Japan (<i>C. multispinulosus</i>) (Dunlap et al., 2007)	MACROURIDAE <i>Caelorinchnus</i> spp. <i>C. formosanus</i> <i>C. multispinulosus</i>	
<i>Aliivibrio thorii</i>	<i>Sepiolo affinis</i> Mediterranean Sea (Fidopiastis et al., 1998 ; Ast et al., 2007)	SEPIOLIDAE <i>Sepiolo</i> spp. <i>S. affinis</i>	
<i>Aliivibrio wodanis</i> *	<i>Sepiolo</i> spp. Mediterranean Sea (Fidopiastis et al., 1998 ; Ast et al., 2007)	SEPIOLIDAE <i>Sepiolo</i> spp. <i>S. affinis</i> <i>S. robusta</i>	
<i>Photobacterium kishitanii</i>	<i>Opisthoproctus</i> spp. Atlantic Ocean (<i>O. grimaldii</i>) Atlantic Ocean and Indian Ocean (<i>O. soleatus</i>) (Haygood et al., 1992; Dunlap et al., 2007)	OPISTHOPROCTIDAE <i>Opisthoproctus</i> spp. <i>O. grimaldii</i> <i>O. soleatus</i>	
	<i>Chlorophthalmus</i> spp. Japan (Dunlap et al., 2007)	CHLOROPHTHALMIDAE <i>Chlorophthalmus</i> spp. <i>C. acutirostris</i> <i>C. albatrossis</i> <i>C. nigromarginatus</i>	
	<i>Caelorinchnus</i> spp. Taiwan (<i>C. kishinouyei</i>) Japan (Other species) (Dunlap et al., 2007)	MORIDAE <i>Physiculus</i> spp. <i>P. japonicus</i>	
	<i>Malacocephalus laevis</i> Indian Ocean (Dunlap et al., 2007)	MACROURIDAE <i>Caelorinchnus</i> spp. <i>C. anatrostris</i> <i>C. denticulatus</i> <i>C. fasciatus</i> <i>C. hubbsi</i> <i>C. japonicus</i> <i>C. kamoharai</i> <i>C. kishinouyei</i>	
	<i>Ventrifossa</i> spp. Japan (<i>V. garmani</i> and <i>V. longibaradata</i>) Taiwan (<i>V. rhidodorsalis</i>) (Dunlap et al., 2007)	<i>Malacocephalus</i> spp. <i>M. laevis</i> *	
	<i>Physiculus japonicus</i> Japan (Dunlap et al., 2007)	<i>Ventrifossa</i> spp. <i>V. garmani</i> <i>V. longibaradata</i> <i>V. rhidodorsalis</i>	
	<i>Aulotrachichthys prothemius</i> Japan (Ast and Dunlap, 2004)	TRACHICHTHYIDAE <i>Aulotrachichthys</i> spp. <i>A. prothemius</i>	
	<i>Acropoma hanedai</i> Taiwan (Kaeding et al., 2007; Dunlap et al., 2007)	ACROPOMATIDAE <i>Acropoma</i> spp. <i>A. hanedai</i>	



Species	Host Collection	Hosts	Light Organ Location
<i>Photobacterium leiognathi</i>	<i>Acropoma japonicum</i> Taiwan (Kaeding et al., 2007)	ACROPOMATIDAE <i>Acropoma</i> spp. <i>A. japonicum</i>	         
	<i>Gazza</i> spp. Philippines (Dunlap et al., 2004, 2007)	LEIOGNATHIDAE <i>Gazza</i> spp. <i>G. achlaniys</i> <i>G. minuta</i>	
	<i>Leiognathus</i> spp. Taiwan (<i>L. equulus</i>) Okinawa (<i>L. fasciatus</i>) Philippines (<i>L. jonesi</i> , <i>L. philippinus</i>) Japan (<i>L. nuchalis</i>) Gulf of Siam (<i>L. splendens</i>) (Dunlap et al., 2004, 2007)	<i>Leiognathus</i> spp. <i>L. equulus</i> <i>L. fasciatus</i> <i>L. jonesi</i> <i>L. nuchalis</i> <i>L. philippinus</i> <i>L. splendens</i>	
	<i>Equulites</i> spp. Japan (<i>E. elongatus</i> , <i>E. rivulatus</i>) Philippines (<i>E. leucistus</i>) (Dunlap et al., 2004, 2007)	<i>Equulites</i> spp. <i>E. elongatus</i> <i>E. leucistus</i> <i>E. rivulatus</i>	
	<i>Photopectoralis</i> spp. Japan (<i>P. bindus</i>) Philippines (<i>P. panayensis</i>) (Kaeding et al., 2007)	<i>Photopectoralis</i> spp. <i>P. bindus</i> <i>P. panayensis</i>	
	<i>Photolateralis</i> spp. Philippines (<i>P. stercorarius</i>) (Dunlap et al., 2007)	<i>Photolateralis</i> spp. <i>P. stercorarius</i>	
	<i>Secutor</i> spp. Philippines (Dunlap et al., 2007)	<i>Secutor</i> spp. <i>S. insidiator</i> <i>S. megalolepis</i>	
	<i>Uroteuthis noctilus</i> Sydney, Australia (Guerrero-Ferreira et al., 2013)	LOLIGINIDAE <i>Uroteuthis</i> spp. <i>U. noctiluca</i>	
	<i>Rondeletiola minor</i> Mediterranean Sea, France (Guerrero-Ferreira et al., 2013)	SEPIOLIDAE <i>Rondeletiola</i> spp. <i>R. minor</i>	
	<i>Sepiolina nipponensis</i> Japan (Nishiguchi and Nair, 2003)	<i>Sepiolina</i> spp. <i>S. nipponensis</i>	
<i>Photobacterium mandapamensis</i>	<i>Acropoma japonicum</i> Taiwan (Kaeding et al., 2007)	ACROPOMATIDAE <i>Acropoma</i> spp. <i>A. japonicum</i>	    
	<i>Gadella jordani</i> Taiwan (Kaeding et al., 2007)	MORIDAE <i>Gadella</i> spp. <i>G. jordani</i>	
	<i>Photopectoralis</i> spp. Japan (<i>P. bindus</i>) Philippines (<i>P. panayensis</i>) (Kaeding et al., 2007)	LEIOGNATHIDAE <i>Photopectoralis</i> spp. <i>P. bindus</i> <i>P. panayensis</i>	
	<i>Siphamia versicolor</i> Japan (Kaeding et al., 2007)	APOGONIDAE <i>Siphamia</i> spp. <i>S. versicolor</i>	
	<i>Uroteuthis chinensis</i> Thailand (Guerrero-Ferreira et al., 2013)	LOLIGINIDAE <i>Uroteuthis</i> spp. <i>U. chinensis</i>	
<i>Euprymna hyllebergi</i> Thailand (Guerrero-Ferreira et al., 2013)	SEPIOLIDAE <i>Euprymna</i> spp. <i>E. hyllebergi</i>		



Species	Host Collection	Hosts	Light Organ Location
<i>Candidatus</i> Enterovibrio escacola	<i>Ceratias</i> spp. NE Atlantic (<i>C. sp</i>) Gulf of Mexico (<i>C. uranoscopus</i>) <i>Lynophryne maderensis</i> NE Atlantic <i>Melanocetus johnsoni</i> Gulf of Mexico and NE Atlantic <i>Melanocetus murrayi</i> Gulf of Mexico <i>Chaenophryne</i> spp. NE Atlantic <i>Oncirodes</i> sp. Gulf of Mexico (Baker et al., 2019)	CERATIIDAE <i>Ceratias</i> spp. <i>C. uranoscopus</i> <i>C. sp</i> LINOPHRYNIDAE <i>Lynophryne</i> spp. <i>L. maderensis</i> MELANOCETIDAE <i>Melanocetus</i> spp. <i>M. johnsoni</i> <i>M. murrayi</i> ONEIRODIDAE <i>Chaenophryne</i> spp. <i>C. longiceps</i> <i>C. sp</i> <i>Oncirodes</i> spp. <i>O. sp</i>	
<i>Candidatus</i> Enterovibrio luxaltus	<i>Cryptosaras coesii</i> Gulf of Mexico and NE Atlantic (Baker et al., 2019)	CERATIIDAE <i>Cryptosaras</i> spp. <i>C. coesii</i>	
<i>Candidatus</i> Photodesmus blepharus	<i>Photoblepharon</i> spp. Pacific Ocean (<i>P. palpebratus</i>) Western Indian Ocean (<i>P. steinitzi</i>) (Hendry and Dunlap, 2014)	ANOMALOPIDAE <i>Photoblepharon</i> spp. <i>P. palpebratus</i> <i>P. steinitzi</i>	
<i>Candidatus</i> Photodesmus katoptron	<i>Anomalops</i> spp. Philippines (Hendry and Dunlap, 2011)	ANOMALOPIDAE <i>Anomalops</i> spp. <i>A. katoptron</i>	