Reply to referee #1 on bg-2020-64

Interactive comment on "Reviews and syntheses: Bacterial bioluminescence – ecology and impact in the biological carbon pump" by Lisa Tanet et al.

Anonymous Referee #1

This manuscript presents a very thorough review of the ecology of luminous marine bacteria in a variety of habitats (symbiosis, free-living, enteric). The paper is quite ambitious in scope and the authors have synthesized a lot of literature. Furthermore, the authors present a hypothesis that interactions of luminous bacteria with animal hosts may have important consequences for marine ecosystem level processes such as the biological carbon pump. It's hard to find this argument convincing because there is little known about luminous bacteria in many parts of this particular cycle, but I find the ideas presented very interesting and the authors have done an impressive job supporting their ideas with published literature and suggesting ideas for future research.
The manuscript is generally well written, the figures are lovely, and I enjoyed reading it. The ambitious nature of the review makes it very long and sometimes hard to follow.
Because the authors are trying to review everything, some points seem out of place. I have made suggestions below for potential ways to shorten, focus and structure the manuscript to make it a bit easier to follow. My additional major comment is that in trying to provide a very broad review of all bioluminescent symbioses, the authors have sometimes given the impression that patterns found in one well studied symbiosis (E. scolopes - A. fischeri) are true of all bioluminescent symbioses. At points the authors fail to clarify when less (or nothing) is known from other systems, but we should not make the assumption that what is true for squid is generally true for other species. At other points, some data is available for fish systems, but it is sometimes missing from the manuscript or presented unevenly compared to squid work, as an add on or exception.
I've made suggestions below for some additional references to consider and places to change wording to more evenly cover various luminous symbiotic systems.

Answer: We thank Referee #1 for perceptive and helpful comments and will work to improve our manuscript. Indeed, in addition to a comprehensive review of the ecology of marine bioluminescent bacteria, our main goal is to present the link between bioluminescence and its potential impact on the biological carbon pump. Below, in blue, we highlight the modifications to our manuscript and discuss our responses to its suggestions. Along the text some parts that were not essential to our approach will be removed in order to lighten the text.

General comments:

Lines 30-31 - I'd like references for the statements "luminous bacteria are the most abundant and are widely distributed" and "Most of the 30 currently known bacterial luminous species." What metrics are you using to say that luminous bacteria are more abundant and widespread than other luminous organisms? Abundant by biomass or prevalence? This seems like an unnecessary comparison in either case, since the ecology of bacteria is so different than luminous eukaryotes and they are likely using light in different ways. Maybe change this statement to something more general about the diversity and prevalence of luminous bacteria? Also, with the statement of a specific number of luminous species, citations need to be provided for these, such as a review with additional newer papers. Does this statement include terrestrial bacteria?
I counted up the marine species I was aware of and didn't get 30, so the references would be useful for researchers in the field.
Answer: We agree with the reviewer that the notion of "abundance" is inappropriate in this context, and we will change the sentence for a more general statement talking about the prevalence of luminous bacteria: "Amongst marine light-emitting organisms, luminous bacteria

are the most widely distributed in oceans". Regarding the number of 30 bacterial luminous species, we referred to a synthesis on bacterial bioluminescence written by Dunlap (2014)*, in which the author talks about "Thirty or more species" and provides a table of species names.
We will rephrase as follows: "Most of the currently known bacterial luminous species (about thirty) are heterotrophic, copiotrophic and facultatively anaerobic (Dunlap, 2014)."

*Dunlap, P. (2014). Biochemistry and genetics of bacterial bioluminescence. In Bioluminescence: Fundamentals and Applications in Biotechnology-Volume 1 (pp. 37-64). Springer, Berlin, Heidelberg.

Lines 34 - 35- benefices change to benefits? I think these sentences could be clarified.
What are the benefits of symbiosis to luminous bacteria? What are hypothesized benefits of luminescence to free-living bacteria? Why do you think that the carbon pump may be important to this? Maybe a more general statement about the effects of bacterial luminescence on ecosystem level processes, such as the carbon pump, are understudied? The abstract does a good job walking the reader through how these very different ideas (luminescence, symbiosis and carbon cycling) are connected, but this is currently less well explained in the introduction and the transition to explain the carbon pump is awkward. In order to understand your arguments the reader has to understand that luminous bacteria are being released into the ocean from symbiosis of growth in guts and not all readers will be familiar with these facts. I think some of the ideas need to be stated earlier in the intro, which some examples and citations.
Answer: As suggested, we will revise this part of the introduction section to elaborate a better connection between the different ideas that will be developed in the following sections.
We will rephrase as follows:
"[...] Bioluminescent species are found in most phyla from fish to bacteria (Haddock et al., 2010; Widder, 2010). Amongst marine light-emitting organisms, luminous bacteria are widely distributed in oceans. Most of the currently known bacterial luminous species (about thirty) are heterotrophic, copiotrophic and facultatively anaerobic (Dunlap, 2014). Endowed with important motility and chemotactic abilities, luminous bacteria are able to colonize a large variety of habitats (as symbionts with macro-organisms, free-living in seawater or attached to particles) (e.g. (Dunlap and Kita-tsukamoto, 2006) and references therein). In their symbiotic forms, bioluminescent bacteria are mostly known to colonize light organs and guts, in which they find better growing conditions than in the open ocean. These symbioses lead to a continuous release of luminous bacteria from light organs and digestive tracts, directly into the seawater or through fecal pellets (Ramesh et al., 1990). Bacterial bioluminescence in its free or attached forms is much less studied but is worth reconsidering, in its prevalence as well as its ecological implications. Indeed, some studies pointed out the well-adapted vision of fish or crustacean to the detection of point-source bioluminescence (Busserolles and Marshall, 2017; Frank et al., 2012; Warrant and Locket, 2004). The compiled data, from all forms of marine bacterial bioluminescence, presented and discussed in this review bring out the uninvestigated pathway of the bioluminescence contribution into the biological carbon pump, through the visual attraction of consumers for luminous particles.."

Lines 37-41 - The end point of the biological carbon pump is sequestration of carbon in ocean sediment, correct? I think this needs to be clearly stated here to explain that any marine snow that doesn't sink is being taken out of the pump.
Answer: We agree with the reviewer's comment and the sentence will be modified as follows:
"The biological carbon pump is defined as the process through which photosynthetic organisms convert CO_2 to organic carbon, as well as the export and fate of the organic carbon sinking from the surface layer to the dark ocean and its sediments by different pathways."

Lines 94 - 98 - This should be restated that fish and squid with ventral light organs likely use them for counter illumination. As far as I'm aware, this has only been demonstrated for bobtailed squid, but is hypothesized in other cases where the light organ illuminates the animal's ventral surface. This is distinct from other fish which have light organs located externally and near the face. Also, some references on anomalopid behavior which might be useful: Morin et al., 1975, A light for all reasons, versatility in the behavioral repertoire of the flashlight fish; Hellinger et al., 2017, The Flashlight Fish Anomalops katoptron Uses Bioluminescent Light to Detect Prey in the Dark.

Answer: We understand the comment and will reword this paragraph for clarity. It is true that there are studies demonstrating the counterillumination strategy for many species other than the bobtail squid (remaining the most commonly studied). These studies include non-bacterial bioluminescence.

Some references hereafter:

- Paitio, et al (2020). Reflector of the body photophore in lanternfish is mechanistically tuned to project the biochemical emission in photocytes for counterillumination.
- Claes et al (2010). Phantom hunter of the fjords: camouflage by counterillumination in a shark (Etmopterus spinax).
- Johnsen et al (2004). Propagation and perception of bioluminescence: factors affecting counterillumination as a cryptic strategy.
- Warner et al (1979). Cryptic bioluminescence in a midwater shrimp.

If we consider only luminous organisms in symbiosis with bacteria, the counterillumination strategy has been demonstrated for the bobtail squid and leiognathids fish, and hypothesized for others.

- Jones, B. W. and Nishiguchi, M. K.: Counterillumination in the Hawaiian bobtail squid, Euprymna scolopes Berry (Mollusca: Cephalopoda), Mar. Biol., 144(6), 1151–1155, https://doi.org/10.1007/s00227-003-1285-3, 2004.
- McFall-Ngai, M. J. and Morin, J. G.: Camouflage by disruptive illumination in Leiognathids, a family of shallow-water, bioluminescent fishes, J. Exp. Biol., 156(1), 119–137, 1991
- Dunlap, P. V., Kojima, Y., Nakamura, S. and Nakamura, M.: Inception of formation and early morphogenesis of the bacterial light organ of the sea urchin cardinalfish, Siphamia versicolor, Mar. Biol., 156(10), 2011–2020, https://doi.org/10.1007/s00227-009-1232-z, 2009.
- McAllister, D. E.: The significance of ventral bioluminescence in fishes, J. Fish. Res. Board Canada, 24(3), 537–554, https://doi.org/10.1139/f67-047, 1967.

This has been clarified in the text. Moreover, additional references have been added for other possible uses of bacterial bioluminescence in symbioses.

We will rephrase as follows: "Symbiotic luminescence seems more common in benthic or coastal environments for fish and squid as well (Haygood, 1993; Lindgren et al., 2012; Paitio et al., 2016). Shallow-water fishes with luminous bacterial symbionts include flashlight fishes (Anomalopidae), ponyfishes (Leiognathidae) and pinecone fishes (Monocentridae) (Davis et al., 2016; Morin, 1983). For deep-sea fishes, anglerfishes (Ceratiodei) and cods (Moridae) are among the common examples of luminous-bacteria hosts.

Bacterial and intrinsic light organs are predominantly internal, ventrally located (Paitio et al., 2016). Many luminous organisms with ventral light organs likely use the emitted light to conceal themselves by counterillumination. This defensive strategy allows luminous species to match with the intensity, spectrum, and angular distribution of the downwelling light, thus obliterating their silhouette and therefore avoiding dusk-active piscivorous predators (Claes et al., 2010; Johnsen et al., 2004; Warner et al., 1979). Amongst bacterial light symbioses, counterillumination has been demonstrated for the bobtail squid Euprymna scolopes (Jones and Nishiguchi, 2004), some leiognathids fish (McFall-Ngai and Morin, 1991), and hypothesized for other bioluminescent fishes (Dunlap et al., 2009; McAllister, 1967). Less common but more

striking, some organisms found in the families Monocentridae, Anomalopidae and numerous deep-sea anglerfishes belonging to the suborder Ceratoidei, exhibit externally-located light organs colonized by bacteria (Haygood, 1993). The external light organs of flashlight fish have been demonstrated to be used to illuminate nearby environment and detect prey (Hellinger et al., 2017), or schooling behavior (Gruber et al., 2019), while the lure of female anglerfish is generally believed to be used for mate-finding purposes and prey attraction (Herring, 2007)."

Lines 103 - 109 - Move the statement about the best studied symbiosis being that between Aliivibrio fischeri and E. scolopes to proceed these references and state that we don't understand how symbioses are established in most other systems. All of the references on light organ morphogenesis are on bobtailed squid and we don't know if similar mechanisms exist in most fish, so it's misleading to say that these things are common. For some references on light organ development and potential specificity factors in fishes see: Dunlap et al, 2013, Inception of bioluminescent symbiosis in early developmental stages of the deep-sea fish, Coelorinchus kishinouyei (Gadi- formes: Macrouridae); Dunlap et al., 2012, Symbiosis initiation in the bacterially luminous sea urchin cardinal fish Siphamia versicolor; Gould and Dunlap, 2019, Shedding Light on Specificity: Population Genomic Structure of a Symbiosis Between a Coral Reef Fish and Luminous Bacterium

Answer: As suggested, the statement about the squid-*Vibrio* symbiosis constituting the major source of information for luminous symbiosis has been moved at the beginning of paragraph 2.2. The paragraph will be lightened to improve clarity. A sentence will be added to answer the reviewer's comment as follows:

"While the bobtail-squid model provides a window to understand the establishment of such symbioses, this system cannot be systematically transferred to other bacterial luminous symbioses. Although less well known, the other associations are no less important and many questions remain unresolved since they might be harder to study."

Throughout the text, we have been cautious to specify when our point was to specifically discuss the bobtail squid symbiosis. As examples:

"One of the best-documented symbioses is the association of *Aliivibrio fischeri* with the bobtail squid *Euprymna scolopes* [...]."

"Knowledge of the mechanisms involved in the selection and the establishment of bacterial symbionts in the squid-*Vibrio* symbiosis have considerably improved over the last few decades."

Lines 122 - 130 - I think this section is worded in a way that may be misleading. Light organs are generally monospecific, but not necessarily monoclonal, which is what the comparison to pure culture suggests to me. It's pretty well established that E. scolopes can be colonized by multiple strains (I think this is different from the wording here, "have been reported for some", which implies that multi strain colonization might happen but isn't common) (See several Bongrand and Ruby references such as https://www.nature.com/articles/s41396-018-0305-8) and similar levels of diversity seem to exist for some fish (I think some Dunlap references show multiple strains from a light organ, the Gould reference mentioned above discusses diversity with Siphamia light organs). Some fish do seem to have monoclonal light organs (Anomalopids and Ceratioids, Hendry et al, 2016, Genome Evolution in the Obligate but Environmentally Active Luminous Symbionts of Flashlight Fish, GBE; Baker et al., 2019). The wording for the Keading reference is also misleading, because not all of the fish studied in there had both symbionts. Please rephrase this section to more clearly state what is known for which species.

Answer: The paragraph will be removed since it was not essential in our approach. It allows lightening the text.

Line 169 - “Variation of light emission is closely linked to the concentration of one component involved in the bacterial light reaction, which could be host controlled” I’m not sure what the component being referred to here is, please explain and provide a reference.

Answer: The component was referring to molecules like oxygen, iron or phosphate which concentrations can be regulated inside the light organ leading to extremely favorable conditions as explained at the end of the paragraph. However, we agree that this sentence was confusing and it will be removed from the new version.

Lines 166-173 - After this discussion of quorum sensing control in A. fischeri, it would be good to add mentions that it is not known if other species have similar control mechanisms, or the extent to which other host species control their symbionts. This review is very ambitious and I think trying to be very thorough, but as a consequence any missing information stands out. Be careful throughout to clarify what is known from only the squid-vibrio system and what might be a common feature across host species. For instance, anomalopid symbionts have lost quorum sensing genes so that luminescence appears to be constitutively expressed in the bacteria (Hendry et al 2014; Hendry et al., 2016, GBE), and anglerfish symbionts don’t have quorum sensing genes (Hendry et al 2016, mBio).

Answer: A sentence will be added to specify that quorum-sensing is not a common feature, as follows: “Here again, while the control mechanisms of the squid-Vibrio symbiosis are well understood, these of the other symbioses remain enigmatic and there are indications that they may vary. For example, the absence of the quorum-sensing-gene detection in anglerfish and flashlight fish symbionts suggests a constitutive light emission by the bacteria (Hendry et al. 2016, 2018).”.

Lines 178 - 183. Again, these sentences are written as though they describe growth in light organs broadly but really describe what we know about the squid symbiosis. Please clarify that this may not be the situation for other host species. For instance, the Haygood 1984 reference that you use in the paragraph shows that monocentrids and anomalopids regularly release bacteria, rather than expelling them once a day.

There are a number of differences between these systems which might account for this. These light organs are external, so bacteria can be pushed directly out of the tubules into sea water. Anomalopids are also strictly nocturnal and photophobic, they don’t experience the same diurnal cycle that Euprymna does because they avoid light, so the same strategy of emptying the light organ and regrowing the bacteria may not be appropriate. Although much of the information in this review necessarily comes from the Euprymna system, in order to make it inclusive of bioluminescent symbiosis broadly, please be sure to compare and contrast what is known in other systems, or at

the very least clarify when data from diverse systems is missing. It may be the case that in most symbiotic systems (fish), symbionts are released regularly and that the squid system is actually the exception, where there is one release per day. Currently, you mention these differences in a short paragraph (lines 193-195), but this feels like an add on, not an integrated part of the review that really tells us what is known and what is unknown.

Answer: Thanks for this very important comment. We will modify the paragraph and reorganize it as follows:

”For all symbioses, luminous symbionts, within the light organ, reach a very high density which reduces the oxygen availability, essential for the light reaction. Such oxygen limitation leads to a decrease in the specific luminescence activity (Boettcher et al., 1996). Bacterial population inside the light organ is regulated by the host, by coupling the restriction of the growth rate and the expulsion of symbionts. Growth repression is thought to reduce the energetic cost of the symbiosis to the host (Haygood et al., 1984; Ruby and Asato, 1993; Tebo et al., 1979). Additionally, since luminous bacteria are densely packed inside tubules communicating with

the exterior of the light organ (Haygood, 1993), the cell number of symbionts is regulated by the regular expulsion of most of the bacterial population, followed by a period of regrowth of the remaining symbionts. Concerning the well-known squid-*Vibrio* symbiosis, its daily release is highly correlated with the diel pattern of the host behavior. Indeed, the bobtail squid expels 95 % of the luminous symbionts in the surrounding environment at dawn, the beginning of its inactive phase. The remaining 5 % of *A. fischeri* grow through the day and the highest concentration is reached at the end of afternoon, at the nocturnal active phase of the squid (Nyholm and McFall-Ngai, 2004; Ruby, 1996). Currently, with the exception of the squid-*Vibrio* symbiosis, accurate data on the symbiont release are still largely unknown. Indeed, the frequency of release may vary and occur more than once a day as it has been shown for some flashlight and pinecone fishes (Haygood, 1984)."

Lines 213-215 - This discussion of P. leiognathi vs. V. harveyi seems unnecessary for the story, the point is just that fish guts have bioluminescent bacteria. The review is already fairly long and dense, I think this bit could be cut. Additionally, identification at the time would be difficult without the molecular sequencing abilities that we have now to determine bacterial species.

Answer: Part of the paragraph will be removed since it was not essential in our approach. It allows lightening the text. The sentence will be as follows:

"Most hosts with internal light organ release luminous bacteria into the digestive tract (Haygood, 1993; Nealson and Hastings, 1979), and thus may largely contribute to their abundance in luminous fish intestines. However, many fishes without light organ also harbor luminescent bacteria in their gut (Makemson and Hermosa, 1999), which clearly demonstrates the existence of other sources for enteric luminous bacteria."

Lines 228 - 265 - Similarly, I would suggest cutting some of these points about luminous bacteria in fish guts if they are not needed to support your points. The point you are trying to make, that fish gut content contribute to introducing luminous bacteria into sea water, is relatively straight forward and I'm not sure that the additional detail is needed. This whole section feels long to me. Note also that they Freed et al, 2019 reference includes discussion of ceratioid microbiome, including gut samples, which might be relevant.

Answer: We agree that some of our explanations were straight forward for the microbiologist community. We will remove some sentences that were redundant. However, this article is dedicated to a pluridisciplinary audience and we decided to keep some parts that, we believe, will be helpful for non specialists. We will also add the reference of Freed et al (2019) relevant in this paragraph.

Section 3.2 - It's not clear to me what role this section plays in the manuscript. As I said above, the review is aiming to be impressively thorough, but is becoming a little diffuse at points and a bit long. It's not really possible to include everything in a manuscript while keeping it manageable for the reader, so maybe consider if this is important information that the reader needs to know? This section is coming 8 pages into the text, out of an 18 page document, and we haven't yet gotten to the meat of the argument on the carbon pump, which is supposed to be a main focus of the paper. I think keeping
the review a bit more focused with help the reader and highlight the new and interesting contributions of this paper.

The references that are just in Table 1 don't seem to be in the reference list. For example, Baker et al., 2019; Hendry and Dunlap, 2014; Hendry and Dunlap, 2011

Answer: This section will be deleted to reduce the length of the manuscript. The missing references will be added.

Specific comments:

Line 57 - Fig 1 is really nice, but I think it's too complicated to ask the reader to look at this early in the manuscript, it seems like it would be referenced for the first time after some of these ideas have been introduced, in section 4.4.
Answer: We discussed while writing the interest of putting the figure 1 at the end of the introduction. We thought that it would be easier for the reader to be able to use it as a guideline throughout the review and modified our text to say so.
We will add the following sentence: "Figure 1 represents, throughout the text, the guideline of the bioluminescence shunt hypothesis of the biological carbon pump."

Line 91 - internal, ventrally located
Answer: We will rephrase as follow: "Bacterial and intrinsic light organs are predominantly internal, ventrally located (Paitio et al., 2016)"

Lines 92-93 - this sentence is hard to follow, please rephrase
Answer: The sentence has been removed since it was not essential in our approach. It allows lightening the text.

Lines 119 - 121 - This sentence is poorly worded, please revise.
Answer: The sentence will be removed.

Lines 121 - clarify that you mean bacterial species
Answer: "Bacterial" will be added.

Lines 131 - 134 - Some wording changes for clarity - "appears consistent at the host species level" to clarify host species tend to have one symbiont species, but symbiont species can colonize multiple host species. I don't understand this statement: "These symbiont strains present no clear phylogenetic divergence between themselves." Do you mean that host and symbiont phylogenies are not congruent?
Answer: The paragraph will be removed since it was not essential in our approach. It allows lightening the text.

Line 145 - Hendry et al., 2016 (GBE) is the genome description for the second anomalopid symbiont.
Answer: The reference Hendry et al., 2016 (GBE) will be added.

Line 149 - obligately dependent, not obligatory
Answer: It will be changed

Line 153 - I'm not sure what the sentence "The light organ is a separate and highly evolved entity" is referring to.
Answer: The sentence will be removed.

Line 154 - I don't think you want "communicate" here, maybe connect to? Or provide access to? Communicate implies that the bacteria are getting information from the light organ surface through the tubules, and I'm not sure that is known.
Answer: As suggested, "communicate to" will be replaced by "connect to".

Line 156 - What is mechanical stimulation?
Answer: This part will be removed in this section since unappropriated here. However, we think that it is important to specify the kinetic differences between luminous bacteria and other organisms, since we use this fundamental feature in section 5.2.1 of our manuscript. The mechanical stimulation notion is commonly used in the litterature. As an example, dinoflagellates emit light due to wave motion (a mechanical stimulation). So, we will add in the introduction section the following sentence:
"Luminescent bacteria can glow continuously under specific growth conditions (Nealson and Hastings, 1979), while, in contrast, eukaryotic bioluminescent organisms require mechanical stimulation to emit light (Haddock et al., 2010)."

Line 339 - reword "the copiotrophic type"
Answer: We reworded this sentence to 'the copiotrophic trait' which is more appropriated.

Line 342 - "all : : : Vibrio and Photobacterium" I think this statement could be changed to something like "all luminous Vibrionaceae, except reduced genome symbionts, possess.." and still be accurate? I'm not aware of any Vibrionaceae species shown to just have 1 chromosome and the only examples of low rRNA operon copies that I know of are anomalopid and ceratioid symbionts. Not sure about Salinivibrio off the top of my head though…
Answer: We agree with this suggestion and the sentence will be changed as suggested: "All luminous *Vibrionaceae*, except reduced genome symbionts, possess two chromosomes in their genome [...]"

Line 351 - Henceforth means "from now on," I think you want "therefore" or "hence"
Answer: As suggested, "Henceforth" will be replaced by "Hence".

Section 5.2.2 - This header is long and hard to follow, change to: quantification and diversity of luminous bacteria and their variability between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments)
Answer: We have followed the reviewer's suggestion and we will modify the header as proposed. Moreover, in the next section (5.2.4), we will follow the same advice and will reduce both headers. The headers will be as follows:

5.2.2 Quantification and diversity of luminous bacteria and their variability between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments)

5.2.4 Quantification of the particles consumption rate and fate of the organic matter between glowing and non-glowing particles

Section 5.2.4 - What is lock in this context?
Answer: We will modify the beginning of this subsection to clarify our goals.
This sentence will be removed:

“One main lock to evaluate the importance of bioluminescence in the biological carbon pump is to quantify the transfer rate of organic carbon between trophic levels.”

And we will add a more detailed description as follow:
“One current challenge to evaluate the importance of bioluminescence in the biological carbon pump is that, in the literature, there is no quantification of organic carbon transfer rates due to glowing bacteria attached to particles to higher trophic levels. Comparisons between glowing particles and non-glowing ones and the fate of the organic matter (i.e. decomposition, and particles sinking rate and fluxes) in both cases are necessary.”

Reply to referee #2 on bg-2020-64

Interactive comment on "Reviews and syntheses: Bacterial bioluminescence – ecology and impact in the biological carbon pump" by Lisa Tanet et al.

Anonymous Referee #2

General comments:

This is a fascinating subject for a review and I read it with much interest. It is extremely thorough, and in some places even a bit too detailed and requires a step back for the non-expert (see specific comments below). It is well organized and generally well written, although requires a thorough editing for grammar (some examples below).

The one figure and Table are well done, but in a review of this detail and length a few more figures to help illustrate some of the concepts would be helpful. One example that comes to mind is a diagram showing the mechanisms of expulsion.

The discussion on impacts on the biological C pump need to be qualified more. Luminescent bacteria are not always a catalyst for sequestration. If bioluminescence leads to disaggregation and "slowing down the sinking rate of particles and consequently increasing their degradation and the remineralization rate" and this happens in the mixed layer, that will decrease carbon export and sequestration.

Answer: We thank referee#2 for his favorable comments. We will have the manuscript proofread by a language specialist. We agree that a review such as ours would benefit from a little more illustration. However, we chose not to add the illustration suggested by the referee because the mechanisms of expulsion are little known and, as far as we know, differ from one organism to another. Indeed, there are numerous types of light organs, with a large diversity of both structure and location. Only a few of them have been described in detail. The most studied is that of the squid but, in accordance with the comments of referee #1, we have chosen to avoid systematically focusing our interest on this organism so as not to make its functioning a generality. However, in order to integrate additional information on the localisation of the ejections of bioluminescent bacteria, either directly into the surrounding seawater or indirectly through the gut, we will complete Table 1 (see at the end of this document). The Table caption will be changed as followed:

Table 1: List of luminous bacterial species found in light organ symbiosis in fishes and squids. The diagrammatic fish, from Nealson and Hastings (1979), was used to indicate, in blue, the approximate locations of the light organ of the different families of symbiotically-luminous fishes. E: indicates an external expulsion of the bioluminescent bacteria, directly into the seawater. I: indicates an internal expulsion of the bioluminescent bacteria, in the digestive tract. (E) or (I) indicate a putative localisation of the expulsion.

Moreover, we propose the addition of another illustration, that will explain in more detail the importance of bioluminescence in the accessibility of organic matter for marine organisms, in section 4.4.

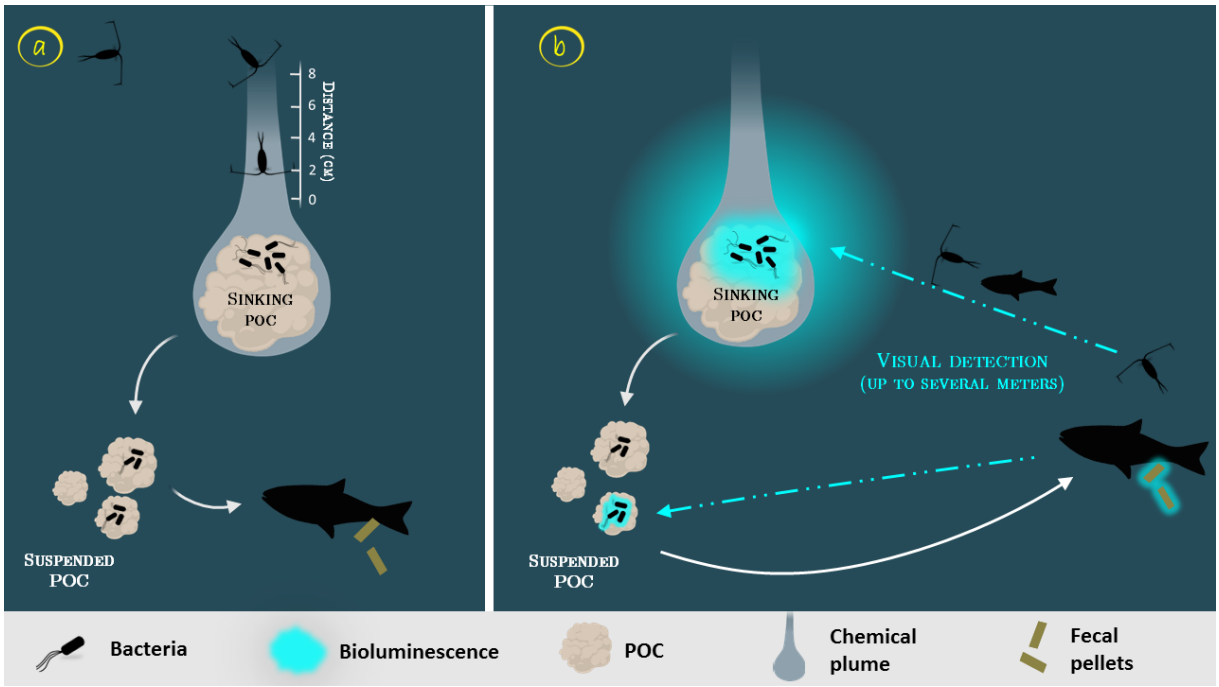


Figure 2: Zoom on the carbon fluxes at the level of a gravitational sinking particle (inspired by Azam and Long 2001). The sinking POC is moving downward followed by the chemical plume (Kiørboe 2011). The plain white arrows represent the carbon flow. Panel (a) represents the classical view of a non-bioluminescent particle. The length of the plume is identified by the scale on the side (Kiørboe and Jackson 2001). Panel (b) represents the case of a glowing particle in the bioluminescence shunt hypothesis. Bioluminescent bacteria are represented aggregated onto the particle. Their light emission is shown as a bluish cloud around it. Blue dotted arrows represent the visual detection and the movement toward the particle of the consumer organisms. Increasing the visual detection allows a better detection by upper trophic levels, potentially leading to the fragmentation of sinking POC into suspended POC due to sloppy feeding. The consumption of the bioluminescent POC by fish can lead to the emission of bioluminescent fecal pellets (repackaging), which can also be produced with non-bioluminescent POC if the fish gut is already charged with bioluminescent bacteria.

Specific comments:

Paper uses ‘bacteria’ throughout. Are Archaea bioluminescent too? (This should be mentioned somewhere).
Answer: No archaea has been characterized as bioluminescent. The sentence “To our knowledge, no archaea has been characterized as bioluminescent” will be added in the introduction section.

p. 2, L 34 beneficies (should this be benefits?)
Answer: Done

p. 3, L 68 spelling- evidence
Answer: Done

p. 3, L 77 pyrosomes are not fishes (they are pelagic tunicates)
Answer: We will modify the paragraph to clarify. In this paragraph, we will discuss the symbioses with luminous bacteria in general and not only with fishes.

p. 3, L 87 Anglerfishes- would be more clear if you give the rule first then the exception (isn't it that nearly all the esca in Angler fishes are symbiotic luminous bacteria and not intrinsic light organs?
Answer: This part will be removed subsequently to the referee #1 comments in order to lighten the text.

p. 4, L 91 spelling- internal
Answer: Done

Section 2.2; p. 4, L 101-118 This section gives examples, but does not actually explain how symbiont selection or colonization occurs. What is 'microbial recognition and molecular dialog' and how does it work? How colonization occurs is not described at all.
Answer: This review is already very thorough as both referees commented. We would rather not add more information regarding subjects that are not directly related to the BCP since many authors have already extremely well reviewed information on symbiont selection or colonization and the more described are the squid's ones. These publications are indicated in the text. As suggested by referee #1, we don't want to talk systematically about the squid so that it doesn't become the general case. Moreover, the text will slightly be modified at some points in order to clarify what is known only for the squid symbiosis and what is valid for all symbioses. These changes are indicated in the reply to referee#1.

p. 6, L 174- spelling- reduces
Answer: Done

p. 6, L 176- The bacterial ...
Answer: Done

p. 7, L 193- More detail needed here. How does the expulsion actually take place? How do the bacteria get from the tubules into the digestive tract (are all light organs directly connected to the digestive tract, and through what)? Or from tubules into the surrounding water, for that matter- do all tubules have an opening on the animal surface- seawater interface, or only some ? For example, I have always wondered in an Anglerfish esca, how are the bacteria expulsed? A figure would be helpful to illustrate.
Answer: As mentioned above, there is an important diversity in the structure and location of the light organs, and actually, with the squid exception, many points of the other symbioses (symbiont selection, population regulation, frequency of the symbiont expulsion...) remain unclear. That's why it is not possible to have a simple description of the process. Since this is not the topic of our review and as explained in the 2.2 answer, we chose not to add a figure. However, this comment prompted us to add, in the Table 1, an information related to the expulsion pathway of the luminous bacteria (directly connected to the environment if the light organ has pores or ducts opening into the surrounding sea, or indirectly if the light organ has ducts connected to the gut). We think it is an interesting piece of information and thank the referee#2 for that.

p. 7, L 193- "Most hosts with internal light organs…"
Answer: Done.

p.8, L237- "in an herbivorous fish compared to a carnivore." p.8, L240- prey

Answer: Done

p. 9, L273- what is meant by 'A rare item'? Do you mean that one rare piece of information we do have is that luminescent bacteria are known to help in chitin digestion, or that in rare cases luminescent bacteria are known to help in chitin digestion.
Answer: The former suggestion is the right one. However, this section will be deleted to reduce the length of the manuscript according to referee #1 comments.

p.11 , L329-330 'prior eaten' is awkward
Answer: This part will be removed since this idea is already discussed all along the paragraph and the turn of phrase was not ideal.

p.12 , L353 'and is always associated with luminous bacteria'
Answer: Done

p.13, L387- replace the word 'unbelievable'
Answer: 'unbelievable' will be replaced by "huge".
The sentence will be as follows: "As indicated previously, the release of bioluminescent bacteria from light organs and fecal pellets could represent a huge quantity of bioluminescent bacteria in the water column."

p.13, L394 - 'amphipods were attracted'
Answer: Done

p.13, L398- do you mean 'the attraction of luminous bacteria to zooplankton'?
Answer: No, we mean the contrary. Since the sentence was confusing, the two last sentences of the paragraph will be modified as follows : "To our knowledge, the only one known is from Zarubin et al. (2012), who demonstrated that zooplankton is attracted to luminous particles and feeds on the luminous bacteria-rich organic matter. Because of the ingestion of the luminous bacteria, the zooplankton itself starts to glow. Then, they experimentally measured 8-times-higher ingestion rate of glowing (due to ingestion of bioluminescent bacteria) zooplankton by fishes, compared to non-luminous zooplankton."

p.13, L404- replace 'excreted' with 'egested'
Answer: Done

p.13, L414- replace 'excreted' with 'egested'
Answer: Done

p. 14, L424-429. As mentioned in general comments, need to be careful here- it is not always a catalyst for sequestration: if bioluminescence leads to disaggregation and slowing down the sinking rate of particles and consequently increasing their degradation and the remineralization rate, and this happens in the mixed layer, that will decrease carbon flux and sequestration.
Answer: We agree with the comment. Bioluminescence can impact the BCP in both ways and we clearly indicate these two hypotheses several times through the text. We realize that the term catalyst can be misinterpreted. We will modify the specific paragraph to clarify as follows :

"Considering this bioluminescence shunt hypothesis, all the processes described above show that bioluminescence affects the biological gravitational carbon pump (Boyd et al., 2019), by either increasing the carbon sequestration into the deep ocean, or by slowing down the sinking rate of particles and consequently increasing their degradation and the remineralization rate. Bioluminescence and especially luminous bacteria may therefore influence the export and

sequestration of biogenic carbon in the deep oceans (either positively or negatively). A better quantification of these processes and impacts in the biological carbon pump are a requirement in future studies."

p. 14, L438- relies
Answer: Done

p. 14, L448- replace 'pulled' with 'combines'
Answer: Done

p. 15, L467- 'role of bioluminescence bacteria..."
Answer: In this subpart, we not only propose to investigate bioluminescent bacteria but more generally to quantify bioluminescence globally (as indicated for exemple in "1) the assessment of the global importance of bioluminescence in the oceans"). This justifies the use of a more general title.

p. 15, L473- 'pursuit' of investigations
Answer: Done

p. 15, L475-476- be specific- vertical migration of what ? (diel vertical migration zooplankton and fish?)
Answer:We will define the vertical migration more precisely as suggested.

p.16, L486-487; suggest make this more broad/ global statement than just European initiatives (mention of ARGO is good, and Bioargo should be mentioned too).
Answer: We agree with the comment. We will modify the text as follows :
'For temporal scales, in the last decades, the multiplication of long-term observatories such as Ocean Network Canada (ONC), the Ocean Observatories Initiative (OOI), the station ALOHA, the European Multidisciplinary Seafloor and water column Observatory (EMSO-ERIC), or the Biogeochemical Argo International Program have increased global-ocean observations at long time scales (more than 10 years) and high sampling frequency.'

p. 17, L518- The 'pursuit' of investigations
Answer: The section title will be changed according to the referee #1.

p. 17, L528- what about use of acrylamide gels in sediment traps, which preserve the integrity of the particle, and presumably the attached bacteria? Fecal pellets should be mentioned in this section
Answer: Acrylamide gel is efficient for the conservation of the pellets. It might be worth trying for cell conservation but will certainly alter the bioluminescence. For that reason, we decided not to add this methodology into the subsection.

p. 17, section 5.2.3- I found this section unfocused (too much of 'catch all'), and it also does not discuss vertical migration, which is mentioned in the section heading. Fecal pellets should be mentioned in this section

Answer: We will follow reviewer #2's comment and will remove this section. Two sentences will be moved into the next subsection 5.2.4, since we believe that this information, based on already existing literature, is of major importance for future investigations.

"As an example, Vibrio are important contributors to particulate organic carbon fluxes that have been observed at abyssal depths in the Pacific Ocean (Preston et al., 2019, Boeuf et al., 2019).

A better characterization at species or functional level should highlight the luminous potential related to the presence of such organisms, even at low abundance."

The description of the effects of vertical migration of zooplankton and fish on luminous bacteria dispersal will be added in part 4.4 (Figure 1, step 4), we will include the following details:

"Additionally, the consumption of organic material colonized by bioluminescent bacteria increases their dispersal rate provided by migrating zooplankton, and even more so by actively swimming fish, following the conveyor-belt hypothesis (Grossart et al., 2010) (Figure 1, step 4). After being ingested, bacteria (including luminous ones), attached to the particles consumed by zooplankton and fish, stay in their digestive tract. At night, these organisms migrate in the upper part of the water column and release feces in niches and at depth that, eventually, would not have been otherwise colonized by luminous bacteria. This dispersion, due to the expelling of luminous feces, is several orders of magnitude greater than that of water-borne free bacteria."

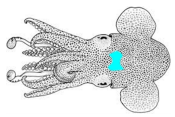
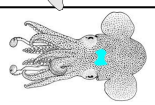
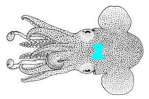
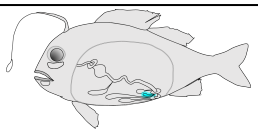
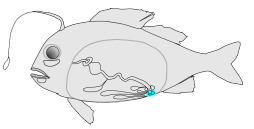
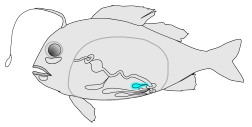
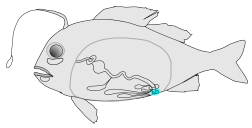
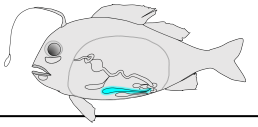
p. 18, section 5.2.4 L554- the word 'lock' needs to be replaced whole section- I thought bioluminescence in zooplankton was used mainly to startle or confuse a predator. Also, bacteria in fecal pellets should be mentioned in this section.

Answer: We will remove the word 'lock' and use "One current challenge". In this subsection we mainly described future actions to quantify the attraction rate of particles (including fecal pellets), glowing due to bioluminescent bacteria, by higher trophic levels. As the reviewer says, it is commonly admitted that bioluminescence from bacteria attracts, while flashes of light in most zooplankton deters. Here we describe the attraction of bacteria on zooplankton. We will add the sentence as follows to avoid misunderstanding and take into account the comment of the reviewer:

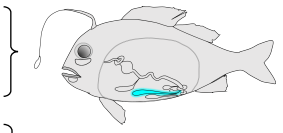
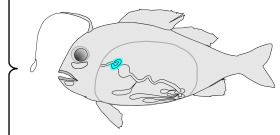
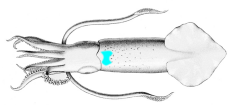
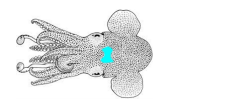
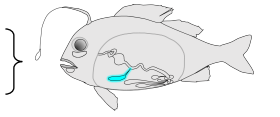
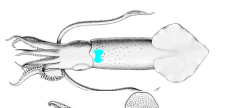
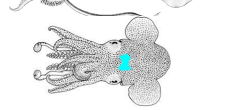
"Few studies related the preferential consumption of luminous bacteria by zooplankton (copepods in Nishida et al., 2002) or fish (Zarubin et al., 2012). It is well-known that marine snow is intensively colonized by bacteria (about 10^9 bacteria per millilitre) (Azam & Long, 2001). Amongst them, luminous bacteria attract zooplankton by emitting light continuously (while flashes of light emitted by zooplankton deter, as mentioned earlier)."

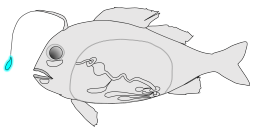
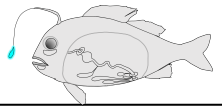
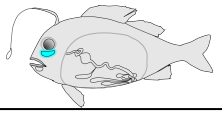
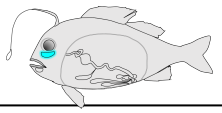
Figure 1- not clear to me why the arrow in 4 denotes slow sinking (why are particles released from vertical migrators slower than those repackaged or from sloppy feeding?)
Answer: We agree with the remark and the arrow will be corrected from dotted arrow to solid arrow.

Table 1.- Caption should specify 'in fishes and squids' (as there are also luminescent bacteria in zooplankton, which are not shown here). "List of luminous bacterial species found in light organ symbiosis in fishes and squids"
Answer: We will add 'fishes and squids' to Table 1 caption as suggested.

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

* firstly identified as *Vibrio logei* by Fidopiastis et al., 1998

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

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

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

Lisa Tanet[1], Séverine Martini[1], Laurie Casalot[1], Christian Tamburini[1]

[1]Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille, France

Correspondence: Christian Tamburini (christian.tamburini@mio.osupytheas.fr)

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

1 Introduction

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

depth and that bioluminescence is a major ecological function in interactions (Martini and Haddock, 2017). Bioluminescent species are found in most phyla from fish to bacteria (Haddock et al., 2010; Widder, 2010). Amongst marine light-emitting organisms, luminous bacteria are widely distributed in oceans. Luminescent bacteria can glow continuously under specific growth conditions (Nealson and Hastings, 1979), while, in contrast, eukaryotic bioluminescent organisms require mechanical stimulation to emit light (Haddock et al., 2010). Most of the currently known bacterial luminous species (about thirty) are heterotrophic, copiotrophic and facultatively anaerobic (Dunlap, 2014). Endowed with important motility and chemotactic abilities, luminous bacteria are able to colonize a large variety of habitats (as symbionts with macro-organisms, free-living in seawater or attached to particles) (e.g. (Dunlap and Kita-tsukamoto, 2006) and references therein). In their symbiotic forms, bioluminescent bacteria are mostly known to colonize light organs and guts, in which they find better growing conditions than in the open ocean. These symbioses lead to a continuous release of luminous bacteria from light organs and digestive tracts, directly to the seawater or through fecal pellets (Ramesh et al., 1990). Bacterial bioluminescence in its free or attached forms is much less studied but is worth reconsidering, in its prevalence as well as its ecological implications. To our knowledge, no archaea has been characterized as bioluminescent.

The biological and physical (solubility) carbon pumps are the main drivers of the downward transfer of carbon and play a central role in the sequestration of carbon dioxide (Boyd et al., 2019; Buesseler and Lampitt, 2008; Dall'Olmo et al., 2016). The biological carbon pump is defined as the process through which photosynthetic organisms convert CO_2 to organic carbon, as well as the export and fate of the organic carbon sinking from the surface layer to the dark ocean and its sediments by different pathways (Siegel et al., 2016 and references therein). Sinking particles (bigger than 0.5 mm of diameter) known as marine snow are a combination of phytodetritus, living and dead organisms, fecal pellets (from zooplankton and fish). Marine snow, rich in carbon and nutrients, and their surrounding solute plumes are hotspots of microbial activity in aquatic systems (Alldredge et al., 1990; Alldredge and Silver, 1988; DeLong et al., 1993). Marine snow is also consumed by zooplankton, and fecal pellets are a food source through coprophagy. When leaving the epipelagic zone and sinking to depth, organic particles would be utilized by microbial decomposition and fish/zooplankton consumption, both considered as responsible for a large part of the variation in the efficiency of the biological carbon pump (De La Rocha and Passow, 2007). Recently, fragmentation (potentially due to biological processes in the mesopelagic waters) has also been shown to be the primary process controlling the sequestration of sinking organic carbon, accounting for 49 ± 22 % of the observed flux loss (Briggs et al., 2020). Moreover, some studies pointed out the well-adapted vision of fish or crustacean to the detection of point-source bioluminescence (Busserolles and Marshall, 2017; Frank et al., 2012; Warrant and Locket, 2004). The compiled data, from all forms of marine bacterial bioluminescence, presented and discussed in this review bring out the uninvestigated pathway of the bioluminescence contribution into the biological carbon pump, through the visual attraction of consumers for luminous particles.

In this review, we will summarize the current knowledge on bioluminescent bacteria based on former and recent literature. First, we describe symbiotic bioluminescent bacteria in light organs of fish or squid, its importance and controls. Then, we present enteric-association occurrences. One of the consequences of these symbioses, in both light organs and guts, is a

massive quantity of bioluminescent bacteria daily dispersed in the ocean. Based on this statement, we claim and demonstrate that bioluminescent bacteria have an ecological and a biogeochemical importance in the biological carbon pump. They catalyze and amplify the involved processes, either by aggregating or fragmenting organic matter. We propose a synthetic representation of the bioluminescence shunt of the biological carbon pump and a future strategy to establish and quantify the impact of bioluminescence **(Figure 1)**. **Figure 1** represents, throughout the text, the guideline of the bioluminescence shunt hypothesis of the biological carbon pump.

2 Symbiotic bioluminescent bacteria in light organs

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

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

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

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

Symbiotic luminescence seems more common in benthic or coastal environments for fish and squid as well (Haygood, 1993; Lindgren et al., 2012; Paitio et al., 2016). Shallow-water fishes with luminous bacterial symbionts include flashlight fishes (Anomalopidae), ponyfishes (Leiognathidae) and pinecone fishes (Monocentridae) (Davis et al., 2016; Morin, 1983). For deep-sea fishes, anglerfishes (Ceratiodei) and cods (Moridae) are among the common examples of luminous-bacteria hosts. Bacterial and intrinsic light organs are predominantly internal, ventrally located (Paitio et al., 2016). Many luminous organisms with ventral light organs likely use the emitted light to conceal themselves by counterillumination. This defensive strategy allows luminous species to match with the intensity, spectrum, and angular distribution of the downwelling light, thus obliterating their silhouette and therefore avoiding dusk-active piscivorous predators (Claes et al., 2010; Johnsen et al., 2004; Warner et al., 1979). Amongst bacterial light symbioses, counterillumination has been demonstrated for the bobtail squid *Euprymna scolopes* (Jones and Nishiguchi, 2004), some leiognathids fish (McFall-Ngai and Morin, 1991), and hypothesized for other bioluminescent fishes (Dunlap et al., 2009; McAllister, 1967). Less common but more striking, some organisms found in the families Monocentridae, Anomalopidae and numerous deep-sea anglerfishes belonging to the suborder Ceratoidei, exhibit externally-located light organs colonized by bacteria (Haygood, 1993). The external light organs of flashlight fish have been demonstrated to be used to illuminate nearby environment and detect prey (Hellinger et al., 2017), or schooling behavior (Gruber et al., 2019), while the lure of female anglerfish is generally believed to be used for mate-finding purposes and prey attraction (Herring, 2007).

2.2 Symbiont selection and colonization of the light organ

Like most symbiotic bacterial associations with animals, luminous bacteria are acquired from the surrounding environment by individuals, independently of their ancestry (i.e. horizontally transmitted) (Baker et al., 2019; Haygood, 1993; McFall-Ngai, 2014). One of the best-documented symbioses is the association of *Aliivibrio fischeri* with the bobtail squid *Euprymna scolopes* (Nyholm and McFall-Ngai, 2004; Ruby, 1996). Through the easy independent cultivation of both partners in the laboratory, this symbiosis has become a perfect model for studying the process of bacterial colonization into the light organ, and understanding bacteria–animal interactions, broadly-speaking (Mandel and Dunn, 2016; McFall-Ngai, 2014).

Knowledge of the mechanisms involved in the selection and the establishment of bacterial symbionts in the squid-*Vibrio* symbiosis have considerably improved over the last few decades. Harvest of the luminous symbionts from the bacterioplankton is driven by microbial recognition and molecular dialog (Kremer et al., 2013; Nyholm et al., 2000; Nyholm and McFall-Ngai, 2004; Pankey et al., 2017; Schwartzman and Ruby, 2016; Visick and Ruby, 2006). Moreover, bacterial colonization of host tissues induces the morphogenesis process of the light organ and appears to signal its further development and maturation (McFall-Ngai and Ruby, 1991; Montgomery and McFall-Ngai, 1998). The luminescence feature is essential for a correct morphogenesis process of the light organ and symbiont persistence inside (McFall-Ngai et al., 2012; Visick et al., 2000).

While the bobtail-squid model provides a window to understand the establishment of such symbioses, this system cannot be systematically transferred to other bacterial luminous symbioses. Although less well-known, the other associations are no less important and many questions remain unsolved since they might be harder to study.

To date, 11 bacterial species are known to be involved in light-organ symbioses **(Table 1)**. In a light organ, the bacterial population is most of the time monospecific (Dunlap and Urbanczyk, 2013; Ruby, 1996).

Considering that fish and squid housing luminous bacteria are never found without symbionts in nature, the symbiosis appears obligatory for hosts (Haygood, 1993). In contrast, most symbiotic bacteria are viable outside the light organ, and thus are considered as facultatively symbiotic. These facultative symbiotic bacteria are readily culturable under laboratory conditions, outside the host light organ. Exceptions have been highlighted for the luminous symbionts of two groups of fish, the flashlight fish and the deep-sea anglerfish (Dunlap and Kita-tsukamoto, 2006; Haygood and Distel, 1993). Indeed, despite the fact that the bacterial origin of the light was proved by microscopic observation and that genes from luminous bacteria were amplified (Haygood and Distel, 1993), bacterial cultivation has not been yet successful. Thanks to the emergence of genome sequencing, complete genome of these symbionts has been reported in the last years. Analyses revealed a genome reduction in size by about 50 % and 80 % for anglerfish and flashlight fish symbionts respectively, compared to facultative luminous symbionts or free-living relatives (Hendry et al., 2014, 2016, 2018). Genome reduction is a common trait shared by bacteria involved in obligatory symbiosis (Moran et al., 2009) and explains the inability of these symbionts to grow in laboratory cultures. Flashlight fish and anglerfish symbionts appear to be obligately dependent on their hosts for growth, as some metabolic capacities (e.g. genes necessary for amino acid synthesis) are absent in the genome.

2.3 Light organs are under well-established controls

Although light organs can differ in form, size or location according to the host **(see Table 1)**, some structural and functional features are common for all of them. Luminous bacteria are densely packed within tubules which connect to the exterior of the light organ (Haygood, 1993; Nealson, 1979). The host provides nutrients and oxygen to the tubules through a highly vascularized system (Tebo et al., 1979). Bioluminescent bacteria emit light continuously in the light organ, as they do in laboratory cultures (Nealson and Hastings, 1979). However, the light intensity varies over time. As for self-luminescent fish, bacterial light organs have evolved with multitude of adaptations of tissue, to serve as reflectors, diffusers, screens, and light-conducting channels (Haygood, 1993; Munk et al., 1998). Such anatomical features assist in directing and enhancing light output (Sparks et al., 2005). In addition, the host can control the light diffusion through different mechanisms, which may be external lids, chromatophores, organ rotation, filters, occlusion with a shutter, or muscle contraction (Hansen and Herring, 1977; Herring, 1977; Johnson and Rosenblatt, 1988). As an example, for counterillumination, controlling the intensity of light output gives the host a better camouflage, adapting its silhouette to environmental changes in light (Jones and Nishiguchi, 2004; McFall-Ngai and Morin, 1991). For intra-species communication, it permits to produce sudden flashes or specific signal/rhythm of light (e.g. schooling behavior (Gruber et al., 2019)).

In squid-*Vibrio* symbiosis, bacterial luminescence genes are regulated with quorum-sensing system, a cell-density-dependent process. When the cell density reaches a certain level, autoinducers responsible for triggering the synthesis of the genes involved in light emission are accumulated in sufficient amounts, and light is emitted (Nealson et al., 1970; Verma and Miyashiro, 2013). Interestingly, *A. fischeri* produces a higher level of luminescence within the light organ than in laboratory cultures, despite a similarly-high cell density (Boettcher and Ruby, 1990). Hence, Verma and Miyashiro (2013), suggested that the light organ environment offers specific conditions such as the levels of oxygen, iron, or phosphate, to enhance bacterial light emission. Here again, while the control mechanisms of the squid-*Vibrio* symbiosis are well understood, these of the other symbioses remain enigmatic and there are indications that they may vary. For example, the absence of the quorum-sensing-gene detection in anglerfish and flashlight fish symbionts suggests a constitutive light emission by the bacteria (Hendry et al. 2016, 2018).

For all symbioses, luminous symbionts, within the light organ, reach a very high density which reduces the oxygen availability, essential for the light reaction. Such oxygen limitation leads to a decrease in the specific luminescence activity (Boettcher et al., 1996). The bacterial population inside the light organ is regulated by the host, by coupling the restriction of the growth rate and the expulsion of symbionts. Growth repression is thought to reduce the energetic cost of the symbiosis to the host (Haygood et al., 1984; Ruby and Asato, 1993; Tebo et al., 1979). Additionally, since luminous bacteria are densely packed inside tubules communicating with the exterior of the light organ (Haygood, 1993), the cell number of symbionts is regulated by the regular expulsion of most of the bacterial population, followed by a period of regrowth of the remaining symbionts. Concerning the well-known squid-*Vibrio* symbiosis, its daily release is highly correlated with the diel pattern of the host behavior. Indeed, the bobtail squid expels 95 % of the luminous symbionts in the surrounding environment at dawn, the beginning of its inactive phase. The remaining 5 % of *A. fischeri* grow through the day and the highest concentration is reached at the end of afternoon, at the nocturnal active phase of the squid (Nyholm and McFall-Ngai, 2004; Ruby, 1996). Currently, with the exception of the squid-*Vibrio* symbiosis, accurate data on the symbiont release are still largely unknown. Indeed, the frequency of release may vary and occur more than once a day as it has been shown for some flashlight and pinecone fishes (Haygood et al., 1984).

Regular expulsion of symbionts maintains favorable conditions in the light organ for the bacterial population, but it also seeds the environment with luminous symbionts for colonization of the next host generation. The consequence is a release of a huge quantity of bioluminescent bacteria in the seawater inducing a major contribution to the ocean microbiome. To make it more concrete and provide an order of magnitude, two examples are proposed thereafter. Using laboratory experiments on different fishes (Monocentridae, Anomalopidae), Haygood et al. (1984) estimated a release between 10^7 to 10^9 bioluminescent bacterial cells per day and per individual. Another study on the Hawaiian bobtail squid (*E. scolopes*) has estimated that the squid expels about 5×10^8 bioluminescent bacterial cells per day and per individual (Lee and Ruby, 1994). These discharges lead to a regular luminous-bacteria enrichment of the areas inhabited by these organisms.

Depending on the anatomical location of the light organ **(see Table 1)**, luminous symbionts are released through pores or ducts into the surrounding seawater or into the digestive tract (Haygood, 1993; Nealson and Hastings, 1979). An enteric lifestyle has indeed been suggested for the luminous bacteria (Ruby and Morin, 1979; Nealson, 1979).

3 Enteric associations in marine-fish guts

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

Although luminescence of dead fish was a well-known phenomenon, one of the first mentions of the presence of luminescent bacteria in fish slime and intestinal contents is only from the beginning of the 1930's (Stewart, 1932). Since then, the high occurrence of luminous bacteria in fish intestines has been reported in many studies (Baguet and Marechal, 1976; Barak and Ulitzur, 1980; Liston, 1957; Makemson and Hermosa, 1999; O'Brien and Sizemore, 1979; Ramesh and Venugopalan, 1988; Reichelt and Baumann, 1973; Ruby and Morin, 1979). Most hosts with internal light organ release luminous bacteria into the digestive tract *via* ducts (Haygood, 1993; Nealson and Hastings, 1979), and thus may largely contribute to their abundance in luminous fish intestines. However, many fishes without light organ also harbor luminescent bacteria in their gut (Makemson and Hermosa, 1999), which clearly demonstrates the existence of other sources for enteric luminous bacteria. Through the gut-content analysis of 109 fish species from the Gulf of Oman, Makemson and Hermosa (1999) showed that the relative proportion of the occurring culturable luminous bacteria was strongly variable. While some fish guts harbor more than 80 % of luminous bacteria, some others have between 20-50 %, and a minority have none detected, with a substantial intra- and inter-species fish variability. As other authors, Makemson and Hermosa (1999) highlighted *V. harveyi* and *P. phosphoreum* as the dominant luminous species found in fish guts (O'Brien and Sizemore, 1979; Reichelt and Baumann, 1973; Ramesh and Venugopalan, 1988).

Seasonal variations have been observed in both luminous bacterial density (Liston, 1957; Ramesh and Venugopalan, 1988), and predominant species (Bazhenov et al., 2019). Such variability is not surprising since it is inferred to the structure and composition of the gut microbiota of fish which is influenced by a series of factors, including (i) host factors (e. g genetics, gender, weight, age, immunity, trophic level), (ii) environmental factors such as water, diet, and surrounding environment, (iii) microbial factors (e.g. adhesion capacity, enzymes and metabolic capacity), (iv) and individual variations and day-to-day fluctuations (Nayak, 2010; Sullam et al., 2012; Wang et al., 2018). Interestingly, a high proportion of luminescent

bacteria (>70 %) has been found in the gut of an Atlantic halibut recently fed, while an individual male in spawning condition, that had not been eating recently, had a flora dominated by non-luminescent microorganisms (Verner-Jeffreys et al., 2003). This result underlines the link between food ingestion and abundance of luminous bacteria and suggests that they do not persist within the halibut gut once the feces are eliminated. This also suggests that luminous bacteria are then released with the feces in the water column. Makemson and Hermosa (1999) have reported a slightly higher proportion of culturable luminous bacteria in herbivorous fish compared to carnivorous fish. They also emphasized the higher incidence of luminescent bacteria in pelagic than in reef-associated fish, as well as filter-feeder-fish guts contain more luminous bacteria compared to other feeding types (e.g. predator). For bigger fishes, a potential introduction source of luminous bacteria into the gut could be the ingestion of smaller prey bearing bacterial light organ. For all organisms, enteric luminous bacteria may be transferred to the gut bacterial community of their predators.

It should be emphasized that investigations on microbial communities of fish have long been limited by the use of culture-dependent methods (Austin, 2006; Romero et al., 2014). The fish-gut microbiota has been reported to be particularly of low cultivability, with less than 0.1 % of the total microbial community cultivable (Zhou et al., 2014), although the level of cultivability may be taxon dependent (Ward et al., 2009). Today, advanced molecular techniques offer a wide variety of culture-independent methods, such as Next-Generation Sequencing (NGS), for analyzing fish microbiota (Tarnecki et al., 2017).

Several studies using gene sequencing based on 16S rRNA to characterize the gut microbiome of fish have reported the genus *Photobacterium* as the most abundant in the guts of salmon and trout (Bagi et al., 2018; Givens et al., 2015; Michl et 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., 2019; Riiser et al., 2018). Other studies reported the presence of *Photobacterium* spp. in the gut of hydrothermal shrimp (Durand et al., 2009), in some adult anglerfish (Freed et al. 2019) and, seasonally variable, in the gut of Norway lobster (Meziti et al., 2010). However, because not all *Photobacterium* spp. have luminescence ability, it is important to be able to resolve dominant OTU at the species level, which, most of the time, is not possible with a 16S rRNA barcoding sequencing approach. The emergence of multi-gene approaches offers more detailed insights into the taxonomic diversity of these communities (i.e. species level). Thus, using metagenomic shotgun sequencing, two independent and recent works on wild Atlantic cods also concluded of the *Photobacterium* spp. domination and have been able to go deeper into the taxonomic identification. Le Doujet et al. (2019) demonstrated that *Photobacterium* genus represents 78 % of all present genera and identified the *P. phosphoreum* clade as the most abundant *Photobacterium* lineage. According to Riiser et al. (2019), the luminous species *P. kishitanii* constitutes over 26 % of the Vibrionales community, which is the dominant clade, and the authors underlined the presence of the functional *lux* genes, the light-emission-involved genes.. Therefore, recent metagenomic studies seem to confirm the trend of a high occurrence of luminous bacteria in fish intestines.

4 Luminous bacteria and the biological carbon pump

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

4.1 Bioluminescent bacteria in the water column

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

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

4.2 Bioluminescent bacteria attached to particles

Outside of spatially restricted niches, as light organ or gut environments, role of the dispersed luminous cells in marine environment was matter of debate and it was thus mentioned that non-symbiotic bacteria may have no ecological significance (Hastings and Greenberg, 1999; Nealson and Hastings, 1979). However, Herren et al. (2004) suggested that luminous bacteria are more attached to particles than free-living, which was confirmed by Al Ali et al. (2010). Many bacteria, including bioluminescent bacteria (Ruby and Asato, 1993; Zhang et al., 2016), can develop swimming behavior to

colonize the sinking organic material, therefore reaching a cell density 100 to 10,000 times higher than in the water column (up to 10^8 to 10^9 cells mL^{-1}) (e.g. Ploug and Grossart, 2000).

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

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

Fish guts could also act as an enrichment vessel for the growth of luminous bacteria, and thus enhance their propagation (Nealson and Hastings, 1979; Ramesh and Venugopalan, 1988). When expelled with feces, enteric luminous bacteria can be easily isolated from the fresh fecal material. This fecal luminescence increased in intensity over a matter of hours, proving that luminous bacteria survived the digestive process and can proliferate on such organic material (Ruby and Morin, 1979). Hence, fish feces appear to be an important source of viable luminous bacteria in the marine environment and could affect both the distribution and the species composition of luminous populations. The luminescence of fecal particles has been reported numerous times and is always associated to luminous bacteria, due to the observation of continuous light emission

or direct isolation (Andrews et al., 1984; Ramesh et al., 1990; Raymond and DeVries, 1976; Ruby and Morin, 1979; Zarubin et al., 2012).

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

4.3 Bioluminescent bacteria in the sediments

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

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

4.4 How do bioluminescent bacteria impact the biological carbon pump?

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

Bioluminescent bacterial emissions are continuous over time and such characteristic is thought to attract predators. Indeed, the light color from bioluminescence contrasts well against the dim or dark background of the ocean depths. In the bathypelagic zone (1000-4000 m), where no daylight remains, bioluminescent emissions are considered as the major visual stimulus (Warrant and Locket, 2004; Widder, 2002). For such reasons, symbiotic associations in light organs have been selected as an advantage for hosts (fish or squid). Luminous bacterial symbionts are successively acquired by juveniles and

released into the seawater to control population concentration **(Figure 1, step 1)**. As indicated previously, the release of bioluminescent bacteria from light organs and fecal pellets could represent a huge quantity of bioluminescent bacteria in the water column. On dead organisms, luminous bacteria present in the gut of the host could initiate rapid propagation and decomposition of the host body, and result in the formation of luminous debris in the marine environment. Based on the increase in light emission observed on dead marine animals, Wada et al. (1995) argue that, at the death of the host, enteric luminous bacteria may have an important saprophytic lifestyle.

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

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

these organisms, bioluminescence can even have a negative effect since they can be identified by the luminous material filtered. Additionally, the consumption of organic material colonized by bioluminescent bacteria increases their dispersal rate provided by migrating zooplankton, and even more so by actively swimming fish, following the conveyor-belt hypothesis (Grossart et al., 2010) **(Figure 1, step 4)**. After being ingested, bacteria (including luminous ones), attached to the particles consumed by zooplankton and fish, stay in their digestive tract. At night, these organisms migrate in the upper part of the water column and release feces in niches and at depth that, eventually, would not have been otherwise colonized by luminous bacteria. This dispersion, due to the expelling of luminous feces, is several orders of magnitude greater than that of water-borne free bacteria. Zooming on the carbon fluxes at the level of a gravitational sinking particle (**Figure 2**), the bioluminescence shunt hypothesis implies that the bacterial glow of this particle increases the distance of visual detection. Such distance can be up to several tens of meters according to Warrant and Locket 2004, and probably depends on the bioluminescent bacterial concentration and the visual perception of the organisms.

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

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

5 Past and future instrumentation for bioluminescence assays

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

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

First, vertical samplings in the water column were performed using sterile-bag samplers (Ruby et al., 1980), or later, using Niskin bottles (mounted on rosette profilers, **Figure 1, item c**) (Al Ali et al., 2010; Gentile et al., 2009; Kita-Tsukamoto et al., 2006; Martini et al., 2016; Yetinson and Shilo, 1979). This approach is commonly set up in oceanography but relies on relatively small volumes of water (up to 20 L). Furthermore, it does not fully capture the heterogeneity of the ecosystem since it provides one discreet sample over restricted time and space. Other instruments dedicated to the acquisition of

sediment sampling are the multiple-core samplers, deployed onto the seafloor (Kita-Tsukamoto et al., 2006). For particulate organic carbon and fecal pellets, in order to describe the diversity of associated luminous bacteria, sediment traps (**Figure 1, item e)** have been occasionally deployed from the surface down to the deep ocean (Andrews et al., 1984). Using them, fresh luminous material has been collected between 30 to 1900 m depth down.

To study the presence of luminous symbionts in guts and light organs larger organisms are caught. The most common way to catch deep-sea animals is the deployment of trawls and more generally nets (**Figure 1, items a-b)**. They are well adapted to sample squid (Zamborsky and Nishiguchi, 2011) or fish, like the anglerfish (Freed et al., 2019). One particularity of these methods is that the sampling covers a large section of the water column and combines everything into one catch with a limited precision about depth layers. SCUBA diving is another method to gently select these large animals (Zamborsky and Nishiguchi, 2011). It has also been used to catch fecal pellets and sinking particles (Orzech and Nealson, 1984). Obviously, SCUBA diving has a strong depth limitation (generally above 50 m depth). It can be more efficient at night for some migrating species and has a restricted sampling size of organisms and number of samples carried back to the ship.

Once environmental samples or material from organism's light organs have been acquired, the objective is either to describe the taxonomy and diversity of luminous bacteria, or to quantify them. To do so, earlier studies have filtered seawater samples 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 on growth medium in Petri dishes (Kita-Tsukamoto et al., 2006; Ruby et al., 1980). For symbiotic bacteria, light organs or guts are aseptically dissected shortly after death, and the content is homogenized before culture or microscopic observations (Dunlap, 1984). After hours of incubation, the total colony forming units is observed; the luminous colonies can, then, be enumerated and selected for taxonomic investigation.

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

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

Since these first investigations on luminous bacteria in symbioses or in the environment, there has been a huge improvement in technology and molecular-biology techniques. To better evaluate the role of bioluminescence and luminous bacteria in the biological carbon pump further studies have to follow an efficient strategy. Such a strategy will focus on quantifying this functional trait and how it impacts the transfer of organic carbon between trophic levels, as well as its sequestration into the deep ocean. This approach can be divided into several key points 1) the assessment of the global importance of bioluminescence in the oceans, 2) the pursuit of investigations about the quantification and diversity of luminous bacteria

and their variability between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments), 3) the quantification of luminous bacterial release into the surrounding environment and the potential impact of diel vertical migration of zooplankton and fish, and 4) the quantification of the transfer rate of bacteria attached on glowing particles into zooplankton and the quantification of the effects on organic matter decomposition, sinking rate and fluxes, in comparison to non-glowing particles. In this review, future perspectives to allow major advances on these specific key points are proposed based on recently-developed technologies.

5.2.1 Assessment of the global importance of bioluminescence in the oceans

In order to establish the global importance of light emitted by organisms, which include glowing bacteria, quantitative surveys are needed at large spatial scales including geographical variability and depth. Current existing fixed platforms (including observatories), oceanographic vessels, remotely-operated and autonomous underwater vehicles (AUV), and gliders (**Figure 1, items f,i)** have considerably increased our knowledge of marine ecosystems and their spatial variability. For temporal scales, in the last decades, the multiplication of long-term observatories such as Ocean Network Canada (ONC), the Ocean Observatories Initiative (OOI), the station ALOHA, the European Multidisciplinary Seafloor and water column Observatory (EMSO-ERIC), or the Biogeochemical Argo International Program have increased global-ocean observations at long time scales (more than 10 years) and high sampling frequency. To quantitatively record bioluminescence emissions, some instruments are commercially available, or have been adapted from existing sensors. Bathyphotometers (**Figure 1, item d)**, a system pumping water into a closed chamber and measuring the emission of light by a photomultiplier, are the most commonly used (Herren et al., 2005), and have already been implemented on AUV (Berge et al., 2012; Messié et al., 2019; Moline et al., 2009) and other vertical profilers (Cronin et al., 2016). Other approaches have been developed unexpectedly from astrophysics telescopes (**Figure 1, item h)** using photomultipliers with a very high sensitivity to photons embedded into optical modules. These instruments have been proved to be efficient to detect bioluminescence in deep-sea environments and over long-time surveys (Aguzzi et al., 2017; Martini et al., 2014; Tamburini et al., 2013a). Another example of quantitative records of photon counts is the equipment of bio-samplers, such as elephant seals, with a small, autonomous tag recording environmental light and bioluminescence (**Figure 1, item g)**. These tags have been shown to be a great improvement in highlighting ecological functions such as predator/prey relationships and could inform on the role of bioluminescent prey for seals (Goulet et al., 2020; Vacquié-Garcia et al., 2012). The technological development of high sensitivity cameras has opened another path for bioluminescence exploration. Low light cameras have been used to record *in situ* light patterns (Maxmen, 2018; Phillips et al., 2016) and implemented on remotely operated vehicles for direct *in situ* observations of sinking particles, or marine luminescent creatures (**Figure 1, items i-j**).

Theoretically, both bacterial, glowing continuously, as well as eukaryotic light, emitted as flashes, could be detected. All of these instruments, with the capability to record surrounding or mechanically stimulated light, have been extensively developed or adapted within the last 10 years. Their future implementation on multiple observatories and vehicles will

definitely increase our knowledge on the global importance of bioluminescence in the oceans. Long-time surveys could elucidate observed extreme events, such as, the bacterial abundance in water-mass movements and sediment resuspension (Durrieu de Madron et al., 2017) or the frequency of milky seas (Lapota et al., 1988; Miller et al., 2005) due to luminous bacteria. Over space, profilers will provide information about the role of bioluminescence in diel vertical migrations of zooplankton and fish. However, the future challenge is that the deployment of these instruments has to be done in parallel with data analysis. Acquisition of quantitative signal will induce the discrimination of different groups of organisms including bacteria, and, consequently, will require the development of strong statistical methods in signal analysis (Messié et al., 2019).

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

5.2.2 Quantification and diversity of luminous bacteria and their variability between ecosystems (free-living in the water column, on sinking particles and fecal pellets, or in sediments)

Marine snow potentially glows due to luminous microorganisms colonizing these habitats (bacteria, eukaryotes), but there are only few studies, based on limited numbers of samples that have quantified luminous bacteria on marine snow in the dark ocean (Andrews et al, 1984; Orzech and Nealson, 1984). A first step is to establish the extent of glowing particles over depth, to assess if this is a common or marginal phenomenon. This can be done either by direct observation of light or by describing the biodiversity associated with these particles. Particles are difficult to sample due to their fragility. However, vehicles such as remotely operated vehicles are able to collect particles of marine snow at specific depth using suction samplers and bring them back to the surface into biological collectors. Sediment samplers, potentially implemented on benthic rovers, are other instruments used to sample marine snow, fecal pellets and particles. This is already a common tool deployed during oceanographic cruises but samples from sediment traps are generally dedicated to biogeochemistry analyses which involve fixing their content. To assess the activity of luminous bacteria, it will only require keeping this material fresh without fixing reagent in order to observe the light emission. Glowing aggregates can be observed by using low light cameras and the light measured by photomultipliers. After observations, these samples can be used for multiple biogeochemical analyses including bacterial taxonomic diversity and abundance.

5.2.3 Quantification of the particles consumption rate and fate of the organic matter between glowing and non-glowing particles

One current challenge to evaluate the importance of bioluminescence in the biological carbon pump is that, in the literature, there is no quantification of organic-carbon-transfer rates due to glowing bacteria attached to marine snow and fecal pellets to higher trophic levels. Comparisons between glowing particles and non-glowing ones and the fate of the organic matter (i.e. decomposition, and particles sinking rate and fluxes), in both cases, are necessary. Few studies related the preferential

consumption of luminous bacteria by zooplankton (copepods in Nishida et al., 2002) or fish (Zarubin et al., 2012). It is well-known that marine snow is intensively colonized by bacteria (about 10^9 bacteria per millilitre) (Azam and Long, 2001). Amongst them, luminous bacteria attract zooplankton by emitting light continuously (while flashes of light emitted by zooplankton deter, as mentioned earlier). As an example, Vibrio are important contributors to particulate organic carbon fluxes that have been observed at abyssal depths in the Pacific Ocean (Preston et al., 2019, Boeuf et al., 2019). A better characterization at species or functional level should highlight the luminous potential related to the presence of such organisms, even at low abundance. In the laboratory, investigations on processes influencing consumption rates of zooplankton on glowing particles can be performed to define the parameters inducing these higher attraction rates. Future studies based on the experimental protocol described by Zarubin et al. (2012) could be improved by including other zooplankton species of importance in the biological carbon pump and multiple bacterial species. In a dark room, under controlled conditions (close to *in situ*) the attraction rate of glowing (fresh or infected by luminous bacteria) and non-glowing aggregates can be tested on zooplankton (copepods, mysids) as well as higher trophic levels (small fish). The effect of temperature, bacteria species, abundance/diversity of zooplankton communities, glowing/non-glowing particles, light intensity, hydrostatic pressure and other variables can be tested on particles attraction behavior. One main improvement is the capability of low-light cameras to record associated behaviors under the laboratory experiments.

6 Conclusion

Light organ and gut of marine animals act as reservoirs for the abundance and persistence of luminous bacteria in the ocean. Additionally to light organs and gut niches, bioluminescent bacteria colonize particles of organic-matter, making them glow. Taking into account the powerful attraction of luminescence on fish and zooplankton consumption, luminous bacteria may therefore influence, in different ways, the export and sequestration of biogenic carbon in oceans. In this review, we essentially focused on luminous bacteria. Bioluminescence, although neglected, is known to be one major trait of marine organisms. Therefore, further studies should take into account bioluminescence in other trophic levels and their impact in the biological carbon pump. Finally, a multi-instrumented strategy will definitely increase knowledge on bioluminescence in the biological carbon pump. This strategy can be set up based on both traditional methods and recently-developed technology, and is promising in the near future.

Author contributions:

LT and CT proposed the idea. LT provided the first version of the review. The following authors were in charge of the initial draft of the corresponding sections: LT: luminous bacteria in light organs and guts, spatial distribution of luminous bacteria,

SM: role of luminous bacteria into the biological carbon pump and future strategy. LC and CT supervised the work. LT, SM, LC and CT wrote, reviewed and edited the final review.

Competing interests:

The authors declare that they have no conflict of interest.

Acknowledgements

LT was supported by a doctoral grant "Région Sud" and TANGRAM Architectes agency. We gratefully acknowledge support from CNRS (Project EC2CO "HEMERA"). The project leading to this publication has received funding from European FEDER Fund under project 1166-39417. We thank H.P Grossart and J. Mallefet for providing helpful comments on an earlier version of this review.

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Figure and Table captions.

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

Figure 2: Zoom on the carbon fluxes at the level of a gravitational sinking particle (inspired by Azam & Long, 2001). The sinking POC is moving downward followed by the chemical plume (Kiørboe 2011). The plain white arrows represent the carbon flow. Panel (a) represents the classical view of a non-bioluminescent particle. The length of the plume is identified by the scale on the side (Kiørboe and Jackson 2001). Panel (b) represents the case of a glowing particle in the bioluminescence shunt hypothesis. Bioluminescent bacteria are represented aggregated onto the particle. Their light emission is shown as a bluish cloud around it. Blue dotted arrows represent the visual detection and the movement toward the particle of the consumer organisms. Increasing the visual detection allows a better detection by upper trophic levels, potentially leading to the fragmentation of sinking POC into suspended POC due to sloppy feeding. The consumption of the bioluminescent POC by fish can lead to the emission of bioluminescent fecal pellets (repackaging), which can also be produced with non-bioluminescent POC if the fish gut is already charged with bioluminescent bacteria.

Table 1: List of luminous bacterial species found in light organ symbiosis in fishes and squids. The diagrammatic fish, from Nealson and Hastings (1979), was used to indicate, in blue, the approximate locations of the light organ of the different families of symbiotically-luminous fishes. E: indicates an external expulsion of the bioluminescent bacteria, directly into the seawater. I: indicates an internal expulsion of the bioluminescent bacteria, in the digestive tract. (E) or (I) indicate a putative localisation of the expulsion.

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

Lisa Tanet[1], Séverine Martini[1], Laurie Casalot[1], Christian Tamburini[1]

[1]Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille, France

Correspondence: Christian Tamburini (christian.tamburini@mio.osupytheas.fr)

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

1 Introduction

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

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

The biological and physical (solubility) carbon pumps are the main drivers of the downward transfer of carbon and play a central role in the sequestration of carbon dioxide (Boyd et al., 2019; Buesseler and Lampitt, 2008; Dall'Olmo et al., 2016). The biological carbon pump is defined as the process through which photosynthetic organisms convert CO_2 to organic carbon, as well as the export and fate of the organic carbon sinking from the surface layer to the dark ocean by different pathways (Siegel et al., 2016). Sinking particles (greater than 0.5 mm of diameter) known as marine snow are a combination of phytodetritus, living and dead organisms, fecal pellets (from zooplankton and fish). Marine snow, rich in carbon and nutrients, and their surrounding solute plumes are hotspots of microbial activity in aquatic systems (Alldredge et al., 1990; Alldredge and Silver, 1988; DeLong et al., 1993). Marine snow is also consumed by zooplankton, and fecal pellets are a food source through coprophagy. When leaving the epipelagic zone and sinking to depth, organic particles would be utilized by microbial decomposition and fish/zooplankton consumption, both considered as responsible for a large part of the variation in the efficiency of the biological carbon pump (De La Rocha and Passow, 2007). Recently, fragmentation (potentially due to biological processes in the mesopelagic waters) has also been shown to be the primary process controlling the sequestration of sinking organic carbon, accounting for 49 ± 22% of the observed flux loss (Briggs et al., 2020).

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

2 Symbiotic bioluminescent bacteria in light organs

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

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

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

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

Symbiotic luminescence seems more common in benthic or coastal environments for fish and squid as well (Haygood, 1993; Lindgren et al., 2012; Paitio et al., 2016). Shallow-water fishes with luminous bacterial symbionts include flashlight fishes (Anomalopidae), ponyfishes (Leiognathidae) and pinecone fishes (Monocentridae) (Davis et al., 2016; Morin, 1983). For deep-sea fishes, anglerfishes (Ceratiodei) and cods (Moridae) are among the common examples of luminous-bacteria hosts.

In general, the origin of light production, intrinsic or symbiotic, is the same within a host clade. However, while all other Apogonidae exhibit intrinsic light, the *Siphamia* species host luminous bacteria (Paitio et al., 2016). Another exception concerns a genus of anglerfishes, *Lynophryne*, which possesses both systems of light production, having intrinsic luminescent barbel in addition to a symbiotic luminous esca (Hansen and Herring, 1977). To date, presence of this dual

system in an organism is unique among all known luminous animals (Pietsch et al., 2007). Bacterial and intrinsic light organs are predominantly intern and in ventral location (Paitio et al., 2016; Wilson and Hastings, 2013). Due to the position of some internal light organs, localized within the coelomic cavity, therefore away from the taxonomic examination process, the luminescence ability of some fishes has remained unrecognized for a long time (Haneda and Johnson, 1962).

Fish and squid with bacterial light organs likely use the emitted light to conceal themselves by counterillumination, obliterating their silhouette, therefore avoiding dusk-active piscivorous predators (Jones and Nishiguchi, 2004; McFall-Ngai and Morin, 1991). Less common but more striking, some organisms found in the families Monocentridae, Anomalopidae and numerous deep-sea anglerfishes belonging to the suborder Ceratoidei, exhibit light organs colonized by bacteria (Haygood, 1993). These light organs are thought to be predominantly used to illuminate nearby environment or attract prey or mates.

2.2 Symbiont selection and colonization of the light organ

Like most symbiotic bacterial associations with animals, luminous bacteria are acquired from the surrounding environment by individuals, independently of their ancestry (i.e. horizontally transmitted) (McFall-Ngai, 2014).

Knowledge of the mechanisms involved in the selection and the establishment of bacterial symbionts have considerably improved in last decades. Harvest of the luminous symbionts from the bacterioplankton is driven by microbial recognition and molecular dialog (Kremer et al., 2013; Nyholm et al., 2000; Nyholm and McFall-Ngai, 2004; Pankey et al., 2017; Schwartzman and Ruby, 2016; Visick and Ruby, 2006). Bacterial colonization of host tissues induces the morphogenesis process of the light organ and appears to signal its further development and maturation (McFall-Ngai and Ruby, 1991; Montgomery and McFall-Ngai, 1998). The luminescence feature is essential for a correct morphogenesis process of the light organ and symbiont persistence inside (McFall-Ngai et al., 2012; Visick et al., 2000). One of the best-documented symbioses is the association of *Aliivibrio fischeri* with the bobtail squid *Euprymna scolopes* (Nyholm and McFall-Ngai, 2004; Ruby, 1996). Through the easy independently cultivation of both partners in laboratory, this symbiosis has become a perfect model for studying the process of bacterial colonization into the light organ, and understanding bacteria–animal interactions, broadly speaking (Mandel and Dunn, 2016; McFall-Ngai, 2014). *E. scolopes* squid is able to reject non-luminous strains of *A. fischeri* (Bose et al., 2008; Koch et al., 2014), suggesting that the host possesses the capability of detecting (at a molecular or physiological level) if its symbiont is bioluminescent or not (Miyashiro and Ruby, 2012; Peyer et al., 2014; Tong et al., 2009). Additionally, a genetic distinction between strains of the same bacterial species, such as the presence of two operons containing the light-emission-involved genes (Ast et al., 2007), is sufficient to avoid a successful colonization of the light organ in a given host (Urbanczyk et al., 2012).

Although it was previously reported that symbionts from light organs were all members of the genus *Photobacterium* (Nealson and Hastings, 1979), we now know through taxonomic reclassifications and the rise of acquired knowledge, that they are not restricted to this clade. To date, 11 species are known to be involved in light-organ symbioses **(Table 1)**. In a light organ, the bacterial population is most of the time monospecific (Dunlap and Urbanczyk, 2013; Ruby, 1996). Thus,

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

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

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

2.3 Light organs are under well-established controls

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

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

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

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

10^9 bioluminescent bacterial cells per day and per individual. Another study on the Hawaiian bobtail squid (*E. scolopes*) has estimated that the squid expels about 5 x 10^8 bioluminescent bacterial cells per day and per individual (Lee and Ruby, 1994). These discharges lead to a regular luminous-bacteria enrichment of the areas inhabited by this organism.

Depending on the anatomical location of the light organ **(see Table 1)**, luminous symbionts are released directly into the surrounding seawater or through the digestive tract (Haygood, 1993; Nealson and Hastings, 1979). An enteric lifestyle has indeed been suggested for the luminous bacteria (Ruby and Morin, 1979; Nealson, 1979).

3 Enteric associations

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

3.1 Occurrence in marine-fish guts

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

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

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

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

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

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

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

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

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

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

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

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

4 Luminous bacteria and the biological carbon pump

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

4.1 Bioluminescent bacteria in the water column

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

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

4.2 Bioluminescent bacteria attached to particles

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

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

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

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

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

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

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

4.3 Bioluminescent bacteria in the sediments

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

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

4.4 How do bioluminescent bacteria impact the biological carbon pump?

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

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

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

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

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

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

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

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

5 Past and future instrumentation for bioluminescence assays

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

6 Conclusion

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

Author contributions:

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

Competing interests:

The authors declare that they have no conflict of interest.

Acknowledgements

LT was supported by a doctoral grant "Région Sud" and TANGRAM Architectes agency. We gratefully acknowledge support from CNRS (Project EC2CO "HEMERA"). The project leading to this publication has received funding from European FEDER Fund under project 1166-39417. We thank H.P Grossart and J. Mallefet for providing helpful comments on an earlier version of this review.

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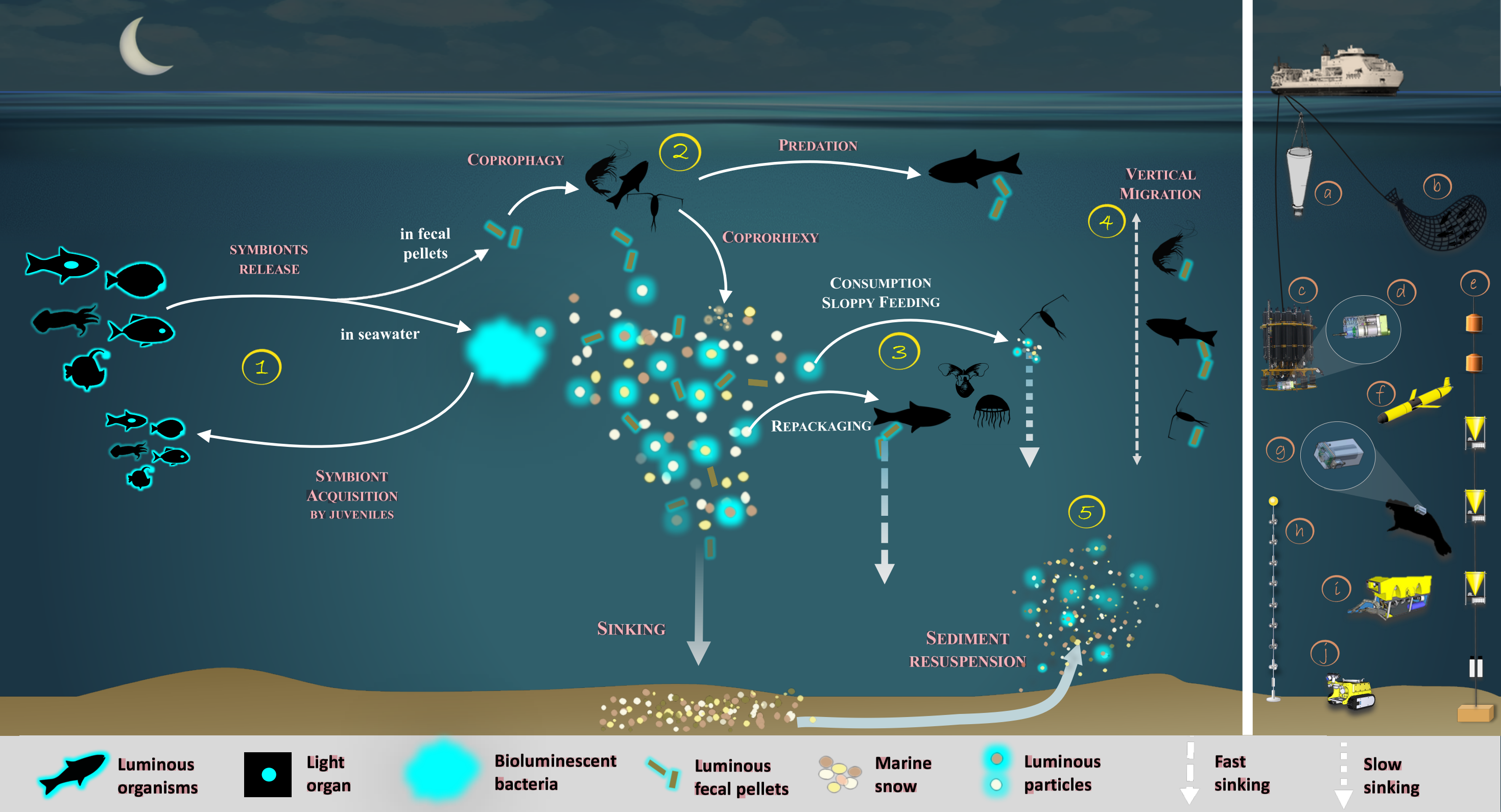
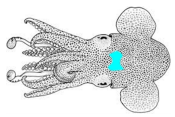
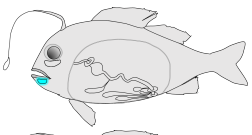
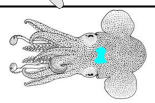
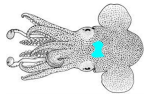
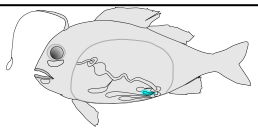
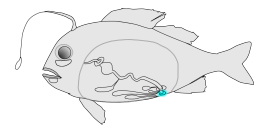
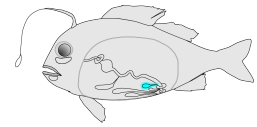
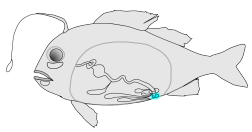
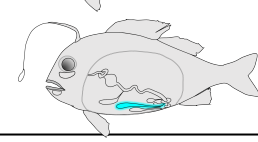
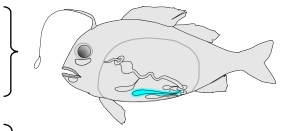
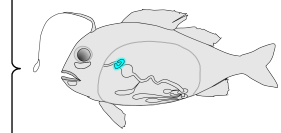
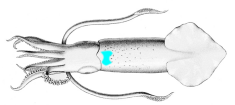
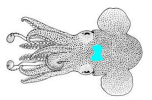
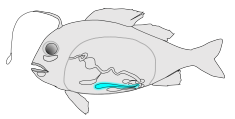
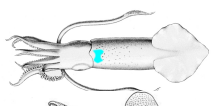
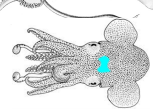
Figure and Table captions.

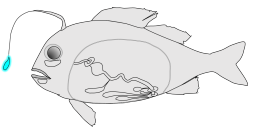
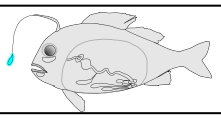
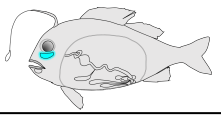
Figure 1: Bioluminescence shunt in the biological carbon pump in the ocean. Luminous bacteria in light-organ symbioses are successively acquired by host (squid, fish) from the seawater while they are juveniles, then regularly released into the ocean. Depending on the light-organ position, luminous bacteria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

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


SYMBIONTS RELEASE
in fecal pellets
in seawater
1
SYMBIONT ACQUISITION BY JUVENILES
COPROPHAGY
2
PREDATION
COPRORHEXY
CONSUMPTION SLOPPY FEEDING
3
REPACKAGING
VERTICAL MIGRATION
4
5
SINKING
SEDIMENT RESUSPENSION
a
b
c
d
e
f
g
h
i
j
Luminous organisms
Light organ
Bioluminescent bacteria
Luminous fecal pellets
Marine snow
Luminous particles
Fast sinking
Slow sinking

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

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

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