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

Anonymous Referee #1

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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.

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.

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.

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.

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.

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

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.

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.

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).

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.

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.

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.

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;

Specific comments:

Line 57 - Fig 1 is really nice, but I think its 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.

Line 91 - internal, ventrally located

Lines 92-93 - this sentence is hard to follow, please rephrase

Lines 119 - 121 - This sentence is poorly worded, please revise.

Lines 121 - clarify that you mean bacterial species

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?

Line 145 - Hendry et al., 2016 (GBE) is the genome description for the second anomalopid symbiont.

Line 149 - obligately dependent, not obligatory

Line 153 - I’m not sure what the sentence “The light organ is a separate and highly evolved entity” is referring to.

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.

Line 156 - What is mechanical stimulation?

Line 339 - reword “the copiotrophic type”

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. . .

Line 351 - Henceforth means “from now on,” I think you want “therefore” or “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)

Section 5.2.4 - What is lock in this context?

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