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Marine holobiont in the high throughput sequencing era

[Sophie Arnaud-Haond](#) and [Corinne Vacher](#) based on reviews by Sophie Arnaud-Haond and Aurélie Tasiemski

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A recommendation of:

Simon M. Dittami, Enrique Arboleda, Jean-Christophe Auguet, Arite Bigalke, Enora Briand, Paco Cárdenas, Ulisse Cardini, Johan Decelle, Aschwin Engelen, Damien Eveillard, Claire M.M. Gachon, Sarah Griffiths, Tilmann Harder, Ehsan Kayal, Elena Kazamia, Francois H. Lallier, Mónica Medina, Ezequiel M. Marzinelli, Teresa Morganti, Laura Núñez Pons, Soizic Pardo, José Pintado Valverde, Mahasweta Saha, Marc-André Selosse, Derek Skillings, Willem Stock, Shinichi Sunagawa, Eve Toulza, Alexey Vorobev, Catherine Leblanc, and Fabrice Not. **A community perspective on the concept of marine holobionts: current status, challenges, and future directions (2020)**, Zenodo, 3696771, ver. 4 peer-reviewed by Peer Community in Ecology. [10.5281/zenodo.3696771](https://doi.org/10.5281/zenodo.3696771)

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The concept of holobiont dates back to more than thirty years, it was primarily coined to hypothesize the importance of symbiotic associations to generate significant evolutionary novelties. Quickly adopted to describe the now well-studied system formed by

zooxanthella associated corals, this concept expanded much further after the emergence of High-Throughput Sequencing and associated progresses in metabarcoding and metagenomics. Holobionts – defined as the association between an individual host and its microbiota - are now increasingly described at sea and on land. The opinion article by Dittami et al. [1] provides a synthetic overview of marine holobionts. It retraces the history of the holobiont concept, recalls the main mechanisms underlying the association between hosts and microbial communities, highlights the influence of these symbioses on marine ecosystem functioning, and outlines current tools and future lines of research. In particular, the article discusses some particularities of marine systems, such as the strong connectivity allowing an exchange of microorganisms and chemical signals between and within holobionts. The authors advocate the need to bridge the gap between large scale exploration studies and smaller scale mechanistic studies, by conducting interdisciplinary research (combining physiology, biochemistry, ecology, experimentation and computational modeling) on some keystone holobionts. Finally, one strength of the paper by Dittami et al. [1] is that it places the concept of the holobiont in an applied research framework. Several possible applications of knowledge on host-microbiota interactions are suggested, both in the field of aquaculture and that of monitoring the health of marine ecosystems. This article contains all the necessary elements for someone who would like to jump into the study of the holobionths in the marine world.

References [1] Dittami SM, Arboleda E, Auguet J, Bigalke A, Briand E, Cardenas P, Cardini U, Decelle J, Engelen AH, Eveillard D, Gachon CMM, Griffiths SM, Harder T, Kayal E, Kazamia E, Lallier FH, Medina M, Marzinelli E, Morganti T, Núñez Pons L, Prado S, Pintado J, Saha M, Selosse M, Skillings D, Stock W, Sunagawa S, Toulza E, Vorobev A, Leblanc C, Not F. (2020). A community perspective on the concept of marine holobionts: current status, challenges, and future directions. Zenodo, ver. 4 peer-reviewed and recommended by PCI Ecology. doi: 10.5281/zenodo.3696771

Revision round #3

2020-01-09

Dear Dr. Dittami, We thank you for this revised version. Please receive our sincere apologies for the long delay in revising it. We feel the article is substantially improved with this new revision. We believe there is room for a more significant contribution, would the consortium take side on the realistic and operational scale of boundaries to apply to the holobionts concept (lines 246->253) the way they discuss it in the rest of the paper. Would the consortium advocate its extension to extremely large scale of ecosystem, would they consider it pragmatic and useful considering the research and application axis they forecast ? We also feel there is a need to clarify the fundamental questions raised considering the holobionts concept (lines 255->268). We attach a version including comments and suggestions for editing. We still feel more detailed recommendations would be needed in the last section on new methods, to enhance the interest and the future use. We however appreciate the long time now since first submission, and are willing to recommend your manuscript on receipt of the next version.

All the best, Sophie Arnaud-Haond and Corinne Vacher

Preprint DOI: <https://peerj.com/preprints/27519/>

Author's reply:

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Revision round #2

2019-07-26

Dear Dr. Dittami, Thank you for your detailed response to the comments of the two reviewers. I have read the revised version of your article carefully and I think the revisions have improved the article. However, there is still room for improvement. For your paper to become a reference in the field of holobiont research, I think you should list the priority research questions and indicate the biological models and the techniques that are appropriate to answer them. The glossary and the figures should also be strengthened. My detailed comments are

in the attached pdf. I hope that you will find these comments useful and invite you to re-submit your article to PCI Ecology after this second round of revisions.
Yours sincerely, Corinne Vacher.

Additional requirements of the managing board: As indicated in the 'How does it work?' section and in the code of conduct, please make sure that:

- Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad (to pay) or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.
- Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.
- Details on experimental procedures are available to readers in the text or as appendices.
- Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

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Author's reply:

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Revision round #1

2019-04-12

Dear Dr. Dittami, Thank you for submitting your article to PCI Ecology. I have now received two reviews of your manuscript, which you will find below. Both reviewers greatly appreciated your work, which is an extremely comprehensive and well-written review. I invite you to take into account all their comments and

submit a revised version to PCI Ecology. In particular, the two reviewers suggest that the section on the evolution of holobionts be strengthened and better integrated with the rest of the study. I also suggest that throughout the manuscript, what distinguishes marine holobionts from terrestrial holobionts in terms of functioning, study methods and challenges, should be better highlighted. Future lines of research could also be more clearly stated in the summary and conclusion, with an emphasis on those specific to marine holobionts. I hope that these comments will allow you to further improve the manuscript and look forward to receiving the revised version. Yours sincerely, Corinne Vacher

Preprint DOI: <https://peerj.com/preprints/27519/>

Reviewed by [Aurélie Tasiemski](#), 2019-04-03 15:33

The review well written by Simon M. Dittami et al gives a very interesting state of the art as well as the methods and perspectives about the concept of holobionts transposed to marine organisms. This review emerged from the brainstorming of the main participants of a workshop recently organized on this topic. This work also underlines the major limits which make the holobiont concept still puzzling and challenging to decipher even more for uncultivable species with numerous genes/molecules with still unknown functions. I think that some point of discussion should be addressed: do the authors think that unicellular and pluricellular organisms can be considered the same way in terms of plasticity/evolution and also in terms of methodologies? Also the authors do not mention the differences in between ecto and endosymbiosis and their respective impact on the genome evolution and adaptation, plasticity of both partners. The definition of endosymbiosis should be better detailed (intra, extracellular, strict...with some examples) and the ectosymbiosis should be defined. Do the authors think that the term “long lasting interactions” is finally well adapted to the holobiont concept if we take into consideration that along the life cycle of an individual (and its varying environment) the symbiotic community changes?

Reviewed by [Sophie Arnaud-Haond](#), 2019-03-21 17:48

This manuscript, “the community perspective on the concept of marine holobionths: state-of-the-art, challenges, and future directions”, has been written by a working group created during the workshop on marine holobionths in March 2018. The manuscript builds on the evolution of the holobionth concept in the research landscape where new generation sequencing allowed unravelling the extent of long-term relationships between hosts and their diverse microbiota across the tree of life. The authors aimed at discussing the way concepts in research and marine holobionths evolved those last years to highlight the need of a better understanding of those complex systems, and detail the roadmap they forecast considering the technological and conceptual challenges this represents. To that extent, this is a very timely and interesting topic. The main objectives appear to be the promotion of an increased a focus/scale up of research at the level of the holobionts, and in fine of a better integration of manipulative experiments on models with large-scale inventories and analysis of interactions/co-occurrence. I found this perspective and opinion manuscript very interesting, but also very dense. I make several comments here below that I hope can be useful.

Main comments The team chose a “short” format that, because rather well documented, is also rather dense. Some of the sections may gain in being structured in subsections, or rephrased for the reader to follow better the lines of thoughts and connection among sentences and examples. This is particularly true for the sections on models and emerging methodologies. Section on “marine holobionts models” may be easier to follow, and possibly more accurate with a clear distinction between works on symbiosis (i.e. the observation and study of bilateral associations), versus their extension to the analysis of the complexity and function of a holobiont system as a unit (in a similar way Margulis is approaching this in its 1990 article). The detailed descriptions of symbiotic models may this way naturally reflect the reasoning that led to the development and increasing used of the holobionts concept. The part on evolution of holobionts seemed to me slightly disconnected from the rest of the MS mostly dealing with ecological approaches and consequences of the holobionts structure and function. As it stands, it is too short to render justice to the many aspects to consider and change in our approaches, to integrate the holobionts concept to evolutionary

theories and studies (compared to subsequent sections mostly dealing with ecological studies). If remaining in the MS, this section may gain in being better integrated with the following ones (meaning those should also be expanded). Another option would be to keep the focus of the MS on ecology and skip that part. The part on marine holobionts functioning relates much more to the determinants and mechanisms of association and dislocation of partners, than to their respective functions in an ecosystem, maybe another title would be more appropriate? The way the two main axes of research are presented in figure 3 and discussed pages 9 and 10 is very interesting and offers a very clear view of the extent of the gap that needs to be bridged. Would it be interesting to consider the use of large-scale studies describing complex systems over large spatial and temporal scales to identify new models for experimental approaches in order to help bridging that gap? How could this be done on the basis of large networks describing complex systems of “Russian dolls” in nature? This may interestingly link to the section on emerging methodologies and the use of “-omics” techniques? In relation to this, the figure 3 is interesting but may be more complete and offer a better global view of the scope and conclusions of this article if completed to illustrate the way new technologies will help bridging the identified gap. It may also include the illustration of the way such changes in paradigm and approaches can have a cascade of consequences on the applications detailed in the last section. Line 427 to 429, and later: A significant amount of literature has been published those last years on marine systems including not only corals or sponges but also macrophytes, showing the importance of taking into account the microbial compartment to understand the ecology and evolution of the host. How could management plans to fight against some invasive species, or conserve of declining ones similarly take into account and manipulate microbiota, reform cautions wisely discussed in the end of that section? Finally, this manuscript is mostly written on an ecological (rather than evolutionary) perspective. Following that line, it seems to me that an interesting add to this opinion article would be a discussion on the accuracy of the now exploding amount of habitat models and forecasts for habitat shifts (particularly under global change scenario) most often only taking into account the abiotic compartment and ignoring the biotic one.

Minor comments and suggestions: Line 120 As opposed to vertical transmission, I may suggest that the arisen transmission is just the acquisition of the associated microbiom from the environment (which process can be continuous and independent of the emergence of new generation?).

Line 159-161 and on: the authors offer brief and interesting history of the research lines that led to coin the term holobionts. This article from Margulis should be cited as 673-670 (not just 673). Despite the term holobionts is introduced in the legend of 2 figures, most discussion in this particular article relate to the difference between symbiosis and mutualism, analogy between symbiosis and sex, and symbiosis as a main source of novelty (compared to gradual changes; in the sense of Mereschkovsky). May be this is a semantic distinction, yet the way this is phrased in the 1990 article relates symbiosis to evolutionary novelty rather than describing it as the way “evolution mainly work...”. Is it possible that the description of the proposition of Margulis (lines 159-161) in the present manuscript would be more related to its book “Symbiosis as a Source of Evolutionary Innovation” (1991) that is most often cited as the origin of this term? Line 156: Is widespread (I is missing) Line 210-213: sentence difficult to understand Line 328 to 332 the sentence is unclear. Line 352 biology is a rather vague term here, and it may be worth here to detail the need for physiology and biochemistry?

Author's reply:

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