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Interactive comment on "Characterizing photosymbiosis in modern planktonic foraminifera" *by* Haruka Takagi et al.

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The authors have written one of the most comprehensive assessments of symbiosis in planktonic foraminifera that I have read in the literature. The ability of their fluorescence technique to distinguish between active symbiont photosynthesis and non-active chlorophyll in digestive vacuoles is outstanding. This paper will become a classic for researchers studying the ecology of modern planktonic foraminifera.

I recommend publication after the authors address the issues I have outlined below.

Please note that Figure 11 is not discussed at all in the manuscript text.

Howard Spero

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Line 140 – please add to this sentence that 'non functional' chlorophyll could come from phytoplankton in the guts of zooplankton prey. This caveat eliminates the potential that a reader of your paper concludes that your data indicates that all foraminifera species ingest phytoplankton prey directly which is not the case for species such as sacculifer, ruber and Orbulina.

Line 145 - The chl content of a dinoflagellate symbiont cell is » than that in a pelagophyte or chrysophyte symbiont from thermocline dwellers. How do you determine symbiont 'density', which I interpret to mean number of symbionts, from Chl a content? Certainly a single dinoflagellate cell has » chl a than a very small chrysophyte cell. Hence there is little connection between chl and symbiont 'density'. In addition, wouldn't the number of light harvesting

Line 200 – please provide a conversion for the fluorescence units you use - 10-20 m2 quanta-1 to the more generally used units - ïAmol photons m2 s-1

I am having trouble understanding the relationship between σPSII and photosynthetic saturation. For the readers, would it be possible to explain this light absorption efficiency term in a way that one can interpret it relative to the light field in the ocean. I observe that the results seem to be inverted relative to photosynthetic light saturation – a concept that many researchers understand. This should be explained better in the discussion (line 345). In this regard, on line 352 you note that this parameter indicates a higher acclimation potential to a low-light environment. How does this relate to Ik in a P/I curve for symbiont photosynthesis? Note that Jorgensen et al (1985), Spero and Parker (1985) and Rink et al. (2005; 1998) show P/I curves that could easily be related to the photosynthetic efficiency term here. Such a link would go a long way to relate previous research on symbiont photosynthesis with the new data you present here and in your other papers.

Line 190 – Does your O. universa data use pre-sphere O.universa or just spherical O. universa? Are the size measurements for Orbulina on the inner trochospiral test or the

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diameter of the sphere? If the latter, then the measurements are not that valuable as the sphere is seldom filled with cytoplasm in a plankton tow. Please indicate this in the text and tables.

Line 235. Please mention/discuss the results from Fehrenbacher et al (2018) that support a microhabitat for non-spinose species on organic aggregates. Marine snow is the primary organic particulate that transports phytoplankton cells from the surface to deep ocean. G. scitula and crassiformis may obtain chlorophyll from such material. Alternatively, many of the zooplankton prey of these foraminifera could participate in the nightly diurnal migration of the deep scattering layer where the zooplankton could feed on surface phytoplankton at night and migrate back to depth during the day where the forams could capture/ingest them.

Line 248 – contact Barbel Hoenisch at LDEO. She has unpublished observations on Sphaeroidinella dehiscens from Puerto Rico culture experiments that supports your observations on the 7 dehiscens you observed. She collected dozens of specimens using scuba and had them in culture until gametogenesis when they put on a cortex. All looked like sacculifer and contained dinoflagellate symbionts. You could ask for details and permission to provide Barbel's 'unpublished data' for the observations you describe.

Line 248 – are you 100% certain that the G. tenella and G. rubescens you claim to have collected have dinoflagellate symbionts and were not early/juvenile ruber or sacculifer? The latter look very different then the adult stages when the shells are only 100 um in size.

Line 253 – add that the relationship observed by Spero and Parker was a logarithmic relationship. Again – is the relationship in Figure 6 for Orbulina comparing sphere diameter or trochospiral shell length? You may be able to compare your chl data with the regression in Spero and Parker to generate a true chl vs symbiont density relationship for the dinoflagellate symbionts in other species.

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Section 4.2. This section discusses chlorophyll content in terms of host size, photosynthetic characteristics relative to chamber morphology or spinose vs non-spinose species. It is the opinion of this reviewer that this section fails to discuss the two most important parameters – differences in symbiont type (dinoflagellates have » more chl a per symbiont cell than does chrysophyte/pelagophyte symbionts) and depth habitat (the ambient light regime as a function of water depth controls light availability for the symbionts. Self-shading due to internal vs external symbiont distribution has little to no effect on available light as the shells are virtually transparent to light penetration given their thickness and the size of the foraminifera. Rather, the internal/external location difference will have an affect on nutrient availability or DIC supply for photosynthesis. Unlike the smaller symbionts in the deeper dwellers, the dinoflagellate symbionts in the mixed layer species would quickly exhaust their DIC supply if they were inside the foram test during the day rather than on the spines where DIC availability is only diffusion limited. This section should be modified accordingly.

Line 375 – do you see any differences in photophysiology when comparing specimens from oligotrophic environments with a deep mixed layer and clear water (deep light penetration) vs locations with a shallower chlorophyll maximum? This basic difference in light field in the water could explain some of the photophysiological differences between species and locations.

Figure 11 is very interesting, but is not discussed at all in the text of the manuscript. Nevertheless, I would like to point out that the spectrum of endosymbiosis concept drawn up in this figure does not take into consideration that the foramininfera lose their symbionts every generation and must reestablish the symbiosis every new generation. Also, I have been culturing planktic foraminifera for over 40 years and have never observed a sacculifer, Orbulina or G. ruber without symbionts. LeKieffre et al (2018) shows an amazingly tight inter relationship between symbionts and host foraminifera in Orbulina. The dinoflagellate bearing foraminifera species are incapable of surviving without their symbionts – The horizontal arrow that you have drawn in Fig. 11 does

not reflect this ‘all or nothing’ symbiotic association which must be as necessary as zooxanthellate in reef building hermatypic corals.

References

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