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Letter to the Editor

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Sponge larvae do not swim that fast: a reply to Montgomery *et al.* (2019)

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Montgomery *et al.* (2019) demonstrated through a meta-analysis that the current idea that planktotrophic larvae of marine invertebrates swim faster than their non-feeding counterparts should be challenged. They demonstrated using quantitative analysis that the ciliated lecithotrophic larvae of sessile organisms (especially sponges) swim faster than those of non-sessile animals (polychaetes and echinoderms). The amount of data collected by the authors is impressive and the outcomes of this dataset are also noteworthy. However, the fact that the ciliated larvae of sponges swim faster than the other phyla caught our attention. We have studied larvae of several species of sponges in the Mediterranean Sea and the Western Atlantic Ocean and the results shown in the work are very discordant to our own experiences and to the majority of literature about sponge larval behaviour. We, therefore, decided to write this reply to expand a little the discussion about the speed of the larvae of sponges based on Montgomery *et al.*'s (2019) findings.

Montgomery *et al.* (2019) provided a supplementary table with the dataset used for their analysis. In the first step, we checked the original publications indicated by Montgomery *et al.* (2019) for the phylum Porifera to compile their dataset, because we found the values too high. Our review indicated three inconsistencies. The speed of *Tedania ignis* presented in their supplementary table (9 mm s^{-1}) was converted incorrectly (the original speed was an average of 0.098 cm s^{-1} in Maldonado & Young, 1996). A similar situation was observed for *Coscinoderma mattewsi*: they report that the speed of the larvae of the species is 45 mm s^{-1}, while the original data presented is 0.45 cm s^{-1} (Wahab *et al.*, 2011). Finally, the speed of the larvae of *Haliclona tubifera* was indicated as 2.8 mm s^{-1}, while the original speed reported by Woollacott (1990) is 3.6 mm s^{-1}. We did not check the original data for the other phyla, though, as we focused only in Porifera.

These three different entries in the original dataset reduced the average ± SD of the swimming speed in Porifera from 11.01 ± 14.43 mm s^{-1} to 6.68 ± 9.21 mm s^{-1} (Figure 1A). Nonetheless, the result of a one-way ANOVA taking in consideration only the speed of the larvae among the phyla with this corrected dataset still indicated that sponges presented the fastest larvae ($P < 0.0001$; Figure 1A), although a reduction in the difference among the means of the phyla could be observed (Figure 1C,D). In addition to these mistakes when converting the values of the speed of the sponge larvae, we also added five entries to the original dataset: *Haliclona* cf. *permolis* (speed = 0.4 mm s^{-1}; Elliot *et al.*, 2004); *Sigmadocia caerulea* (speed = 4 mm s^{-1}; Maldonado *et al.*, 1997); *Halichondria melanodocia* (speed = 2.2 mm s^{-1}; Woollacott, 1990); *Haliclona tubifera* (speed = 1.7 mm s^{-1}; Maldonado & Young, 1996) [Demospongiae] and *Sycon coactum* (speed = 0.09 mm s^{-1}; Elliot *et al.*, 2004) [Calcarea]. This complemented dataset decreased even further the average of Porifera larvae speed to 5.11 ± 9.21 mm s^{-1} (Figure 1B), but it still was significantly different than the other phyla ($P = 0.0004$). However, with the complemented dataset, Porifera is no longer different than cnidarian and bryozoan larvae (Figure 1E).

Secondly and maybe more important, is related to the swimming behaviour of the sponge larvae. It is clear in the work how the authors obtained the speed of the larvae used in their meta-analysis ('All speeds used in the analysis were absolute speeds and were not standardized to body size. Wherever possible, horizontal swimming speeds (mm s^{-1}) were used, but these data were not always reported in the literature. When multiple swimming directions were reported, the fastest reported speed was used (e.g. among upward and downward swimming speeds)'). However, it is well known that sponge larvae do not swim constantly and the reported speeds are likely bursts of the larvae that cease soon after it starts. For instance, Uriz *et al.* (2008) reported that '[larvae of *Scopalina lophyropoda*] swam erratically and alternated very short periods of relatively fast (up to 15 mm s^{-1}) directional swimming with other periods of slow (1–3 mm s^{-1}) erratic swimming' and Wahab *et al.* (2011) observed that the highest speed of the larvae of *C. mattewsi* (4.5 mm s^{-1}) was observed only after larval release, subsequently slowing down. The most comprehensive investigation of sponge larvae behaviour, comprising more than 20 taxa, did not measure quantitatively the speed of these propagules. Nonetheless, almost all larvae in that study were considered to swim weakly, even under light stimuli (Mariani *et al.*, 2005). Montgomery *et al.*'s (2019) data suggest that sponges have the fastest ciliated propagules among the investigated group, and such strong swimming behaviour should have not passed unattended by Mariani *et al.* (2005). In addition, it is important to note that most swimming speeds for sponge larvae were recorded under

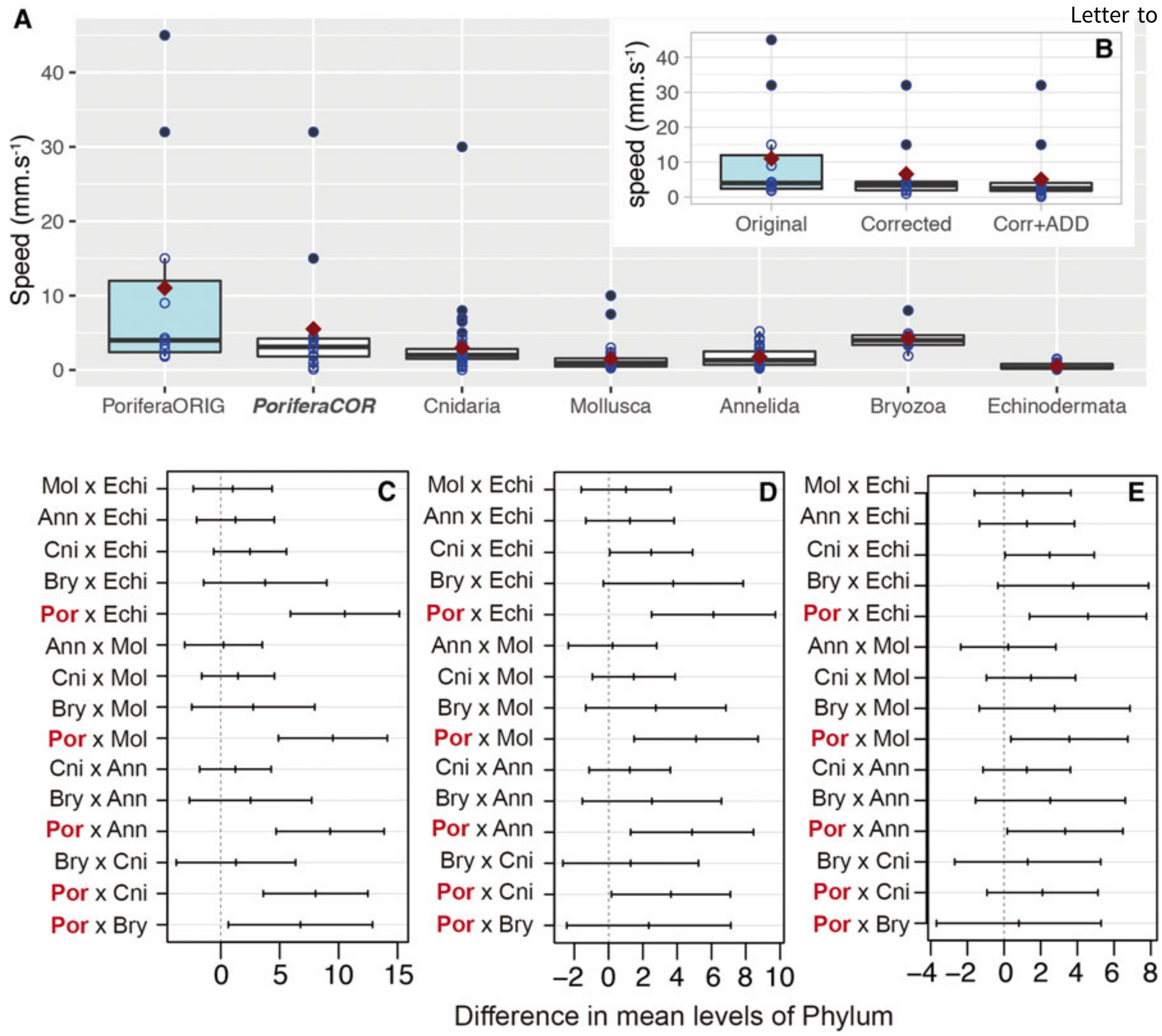

Fig. 1. Effects of the changes of the data about the speed of the larvae of Porifera on the dataset of Montgomery *et al*. (2019). (A) Box-plot showing the variation on the speed of the ciliated larvae of the different phyla. Each open blue dot indicates a single entry (mostly species), the box indicates upper and lower quartiles, horizontal line indicates the median. Outliers are represented as filled blue dots. The red diamond indicates the average in each phylum. Note that the correction of three values in the original dataset reduced the average of the speed of Porifera (*PoriferaMOD*). (B) Box-plot (as in A) comparing the data related to Porifera from the original, corrected and corrected + 5 new data of larval speed of sponges (see text). (C–E) 95% family-wise confidence level of the Tukey post-hoc test (the difference is significant when the lines do not cross zero): (C) Original dataset; (D) Corrected dataset; (E) Corrected dataset with the additional data (see text).

laboratory conditions, while in the wild, larvae when seen are reported to act merely as passive particles drifting with the current until they reach proximity to their settlement surfaces and start actively swimming (Maldonado, 2006).

We understand the challenges that come with analysing such a diverse literature and some generalizations have to be made to obtain the big picture, compromising the idiosyncrasies of each system. However, we think that a discussion about the behaviour of these larvae is still necessary, mostly because of the implications this could have for larval dispersal modelling in the future. As mentioned before, most of the sponge larvae swim intermittently, and the majority of their movements are rotating around their own axis and describing small circles clock or counter-clockwise (Maldonado, 2006). A constant and strong swimming would be highly energetically costly, which is not in accordance with the energetic reservoir of the sponge larvae. Due to their reduced size, the sponge larva depends entirely on its ciliary movements to swim and at the same time when the cilia stop, the larva is stuck in the water (Maldonado, 2006). Although Montgomery *et al*. (2019) state that the shape of the larvae of Porifera is mostly 'spheroid' (generating less 'drag') and that sponge larvae lack mineralized parts, the truth is that the majority of sponge larvae are bullet-shaped and, especially in Demospongiae, many have spicules made of silica. Therefore, the main characteristics used by Montgomery *et al*. (2019) to explain this unexpected result do not seem to be actual and widespread characteristics of Porifera larvae.

Finally, Montgomery *et al*. (2019) state 'Clearly there is something unique about the swimming mechanics of sponge larvae that deserves further attention'. Although we agree with the need for further investigations on the swimming mechanics of sponge larvae, we believe that the discussion presented in their work is misleading, as the large differences pointed out by them are likely artefacts of the data obtained for the study. The number of entries for the phylum Porifera is limited (only 11 entries) if compared to the other phyla (except Bryozoa) and it might be that the results obtained are not the real average speed of sponges (as showed above).

As models to predict the dispersal of marine larvae usually consider the propagule speed, hydrographic conditions and planktonic duration, it is necessary to have in mind the different types of behaviour (Mariani *et al*., 2005). The absence of such a concern in their study compromises the results and the discussion of Montgomery *et al*. (2019) and we fear that their conclusions might be propagated without proper discussion. The objective of meta-analysis studies is always to provoke discussions and to point further research topics aiming to refine the knowledge in a given field. The work of Montgomery *et al*. (2019) indicates that more data about sponge larval speed are necessary and, in addition, new ways to 'normalize' the speed of larvae in the investigated phyla against their behaviour will be important to make this comparison more sound.

References

Elliot GRD, MacDonald TA and Leys SP (2004) Sponge larval phototaxis: a comparative study. *Bolletino dei Musei e degli Istituti Biologici dell'Universitá di Genova* **68**, 291–300.

Maldonado M (2006) The ecology of the sponge larva. *Canadian Journal of Zoology* **84**, 175–194.

Maldonado M and Young CM (1996) Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series* **138**, 169–180.

Maldonado M, George SB, Young CM and Vaquerizo I (1997) Depth regulation in parenchymella larvae of a demosponge: relative roles of skeletogenesis, biochemical changes and behavior. *Marine Ecology Progress Series* **148**, 115–124.

Mariani S, Uriz MJ and Turon X (2005) The dynamics of sponge larvae assemblages from northwestern Mediterranean nearshore bottoms. *Journal of Plankton Research* **27**, 249–262.

Montgomery EM, Hamel JF and Mercier A (2019) Larval nutritional mode and swimming behaviour in ciliated marine larvae. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1027–1032.

Uriz MJ, Turon X and Mariani S (2008) Ultrastructure and dispersal potential of sponge larvae: tufted versus evenly ciliated parenchymellae. *Marine Ecology* **29**, 280–297.

Wahab MA, de Nys R and Whalan S (2011) Larval behaviour and settlement cues of a brooding coral reef sponge. *Coral Reefs* **30**, 451–460.

Woollacott RM (1990) Structure and swimming behavior of the larva of *Halichondria melanadocia* (Porifera: Demospongiae). *Journal of Morphology* **205**, 135–145.