

TECHNICAL COMMENT

CAMOUFLAGE

Comment on “Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments”

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Brady *et al.* (Reports, 20 November 2015, p. 965) claimed that the silvery sides of certain fish are cryptic when viewed by animals with polarization sensitivity, which they termed “polarocrypsis.” After examining their evidence, we find this claim to be unsupported due to (i) pseudoreplication, (ii) confounding polarization contrast with intensity contrast, and (iii) measurements taken at very shallow depths.

It has long been hypothesized that a major function of polarization vision is to heighten the visibility of objects in scattering media, such as water. A Report by Brady *et al.* (*I*) concludes that marine silvery fish have evolved to reduce their visibility to such vision, an adaptation the authors call “polarocrypsis.” We have a number of concerns about this study but focus here on three equally important critical ones.

First, the statistics throughout much of (*I*) are confounded by high levels of pseudoreplication. As one example, figure 2A in (*I*) reports an N of 1183 for bigeye scad (*Selar crumenophthalmus*), but the supplementary materials show that these are 1183 photos taken of only five individual fish (leading to P values as low as 10^{-24}). By using an N value of 1183, the authors are not testing whether the bigeye scad, or even a population of it, shows “polarocrypsis” but whether this group of five individual fish do (2, 3). Although these few fish may possibly be representative of the species, multiple measurements on a single animal are not statistically independent and cannot be treated as such. The situation is similar or worse for the other examined species. The 200 photos of the look-down (*Selene vomer*) were from six fish, the 77 photos of the ballyhoo were from two fish, and the 42 and 33 photos of the bar jack, and almaco jack were from one fish each. To support the conclusions of the Report, we argue that the correct values of N for each species should be 5, 6, 2, 1, and 1. Following this argument, few if any of the results would prove significant if the correct number of degrees of freedom were used, because the effect

sizes in figures 2 and 3 in (*I*) are typically quite small relative to the variances.

Second, the metric W_s used to assess contrast, termed “Stokes contrast” in (*I*), includes intensity information as well as polarization information and is thus inappropriate for judging the contrast of the polarization component of the signal. From the supplementary materials for (*I*)

$$W_s = \frac{\sqrt{(I_o - I_b)^2 + \frac{1}{2}(Q_o - Q_b)^2 + \frac{1}{2}(U_o - U_b)^2}}{I_b}$$

where I , Q , and U are the first three Stokes parameters, I being the intensity, and Q and U comprising the linear polarization information.

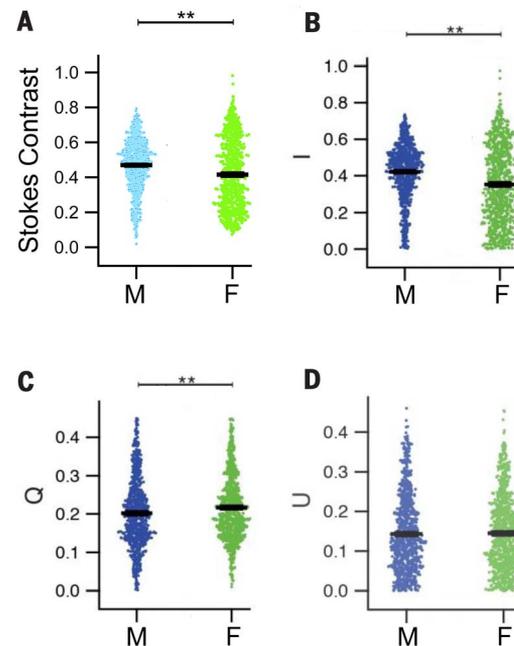


Fig. 1. A compilation of figures adapted from Brady *et al.* We do not include the diffuse mirror results for clarity. (A) Figure 2A from (*I*), which shows that the Stokes contrast W_s is less for the bigeye scad (F) than for the mirror (M). (B) Figure S4A from (*I*), which shows that the intensity contrast of the bigeye scad is also less than that of the mirror. (C and D) Figures S5A and S6A, which show that contrasts based on Q and U , the actual polarization parameters, are greater for the bigeye scad than for the mirror (7% and 2% greater based on tables S4 and S5). Together, (B) to (D) suggest that the pattern shown in figure 2A of Brady *et al.* is driven by intensity contrast rather than polarization contrast. $**P \ll 0.01$, based on the statistics used in (*I*).

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Although polarization-sensitive animals do likely combine intensity and polarization information in their visual processing (4), including intensity information in the contrast metric makes it difficult to assess whether the results are driven by the presence of “polarocrypsis,” as the authors state, or by intensity contrast. Critically, the data shown in figures S4 to S6 in (*I*) paint a more complex and revealing picture than what is shown in (*I*) (see our Fig. 1). Again using bigeye scad as an example, figure S4A from (*I*), which considers only intensity, shows the pattern seen in the main text’s figure 2 that displays Stokes contrast, where the fish have a lower contrast than the mirror. However, figures S5A and S6A from (*I*), which examine the purely polarization measures Q and U respectively, show the opposite pattern: The fish have a greater contrast than the mirror. Because Q and U are the actual polarization parameters, this suggests that the pattern seen in figure 2A of the main text is driven by intensity contrast, not polarization contrast. So, even if the results were significant, which we argue against in the above text, they show that bigeye scad are actually more visible to polarization vision than the mirror, rather than less visible. In addition, the effect sizes using any of the forms of contrast are small, and the average intensity contrast of the bigeye scad is high—0.352 (table S3 from Brady *et al.*). The minimum contrast threshold of aquatic species in bright-light conditions is typically ~ 0.02 (4). Therefore, based on well-established equations of contrast attenuation (5) and the clarity of oceanic water, the scad would be visible at distances on the order of 20 m. Thus, crypsis relative to polarization vision, if it existed, would be irrelevant because the fish are already highly visible due to their brightness contrast alone.

Third, although the silvery species examined were marine fishes that occupy a range of depths,

the work in (7) was done at depths of only two to four meters below the surface. Denton's pioneering work showed that the silvery sides of fish could indeed serve as excellent camouflage (6), but only in a simple and vertically symmetric light field. The light field in near-surface oceanic waters is anything but simple, being heavily influenced by the lensing of direct sunlight by waves, and thus varying rapidly over small temporal and spatial scales (7, 8). In addition, unless the sun is near the zenith, the light field near the surface is far from symmetric, even under windless and waveless conditions (9). All this may explain why the intensity contrasts of the measured fish and mirrors were relatively high (10), as well as why the data have a very large range. Again, as mentioned above, any sort of crypsis

relative to polarization vision is irrelevant in situations where the animals are easily seen using visual systems lacking any polarization sensitivity.

Thus, in conclusion, although we recognize that there may be circumstances where open-ocean fish face evolutionary pressures due to exposure to predation enhanced by polarization vision, we feel that the evidence presented by Brady *et al.* does not support the conclusion that open-ocean fish have evolved to become cryptic to animals with polarization sensitivity.

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