TECHNICAL RESPONSE

CAMOUFLAGE

Response to Comment on "Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments"

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Cronin *et al*. take issue with our evidence for polarocryptic carangid fish based on concerns of pseudoreplication, our contrast metric, and habitat. We clarify (i) the importance of camouflage in near-surface open ocean environments and (ii) the use of a Stokes contrast metric and further (iii) conduct individual-based statistics on our data set to confirm the reported polarocrypsis patterns.

In Brady *et al*. (*1*), we comprehensively measured the camouflage performance of live fish in one of the most dynamic optical environments on our planet (the near-surface epipelagic zone) by collecting polarization and intensity (or more appropriately, radiance) measurements from an unprecedented number of biologically relevant viewing angles. Cronin *et al*. have raised concerns about these inaugural field measures regarding the choice of habitat, employment of our Stokes contrast measure, and the possibility of pseudoreplication (*2*). We welcome the opportunity to answer these queries and hope that we provide greater clarification in the process.

First, we conducted our measurements at near surface depths (<4 m) because this represents an important ecological zone for predation in the ocean (*3*) and a region where camouflage for predators and prey is extremely challenging, given the dynamic variation in light polarization (*1*, *4*) and radiance (*5*). In deeper environments, the light field is more homogenous and the background polarization is much lower, making the physics of crypsis simpler. Our interests were in identifying camouflage processes in more complicated background light environments (e.g., with asymmetric background light fields), and our unprecedented approach provided the ability to evaluate crypsis performance in a comprehensive predator viewing space.

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Reflective camouflage strategies had been previously proposed for ocean regions with homogenous light [mirrors (*6*)] or randomly scattering backgrounds [diffuse reflectors (*7*)], yet no reflective strategy had yet been formulated for the complex and dynamic optical fields of the near-surface pelagic environment. Using a specular mirror and silvery diffuse reflector as references, we found that fish matched the background light field better than either of these reflective surfaces. Using our automated platform, we collected measurements from a variety of viewing angles to evaluate whether fish minimize their contrast from viewing angles associated with predation more than other viewing angles. We found that in this heavy-predation zone, native open-ocean fish showed significantly lower contrast to the background at ecologically relevant predator pursuit viewing angles. We further identified the physiological mechanisms that afforded the enhancement in camouflage via microscopy and histology in the laboratory.

Second, we used a measure of camouflage that accounted for the visual sensitivities of many fish living in near-surface environments. Polarization sensitivity has been documented in six different families of fish, so we selected a measure of contrast that included both polarization and intensity components of the light field. Although behavior (*8*) and laboratory (*9*) studies have documented behavioral responses to polarization, the exact weighting of this sensory information relative to intensity components is not yet known in any vertebrate. Hence, we employed a conservative approach to evaluating the light field using Stokes contrast that includes both polarization and intensity, an approach that is similar to using Euclidian distance to evaluate conspicuousness with color and brightness quantities (*10*). In addition, we also report results for each component of the Stokes vector [*I*, *Q*, and *U*; for definitions, see (*1*)]. We found that fish

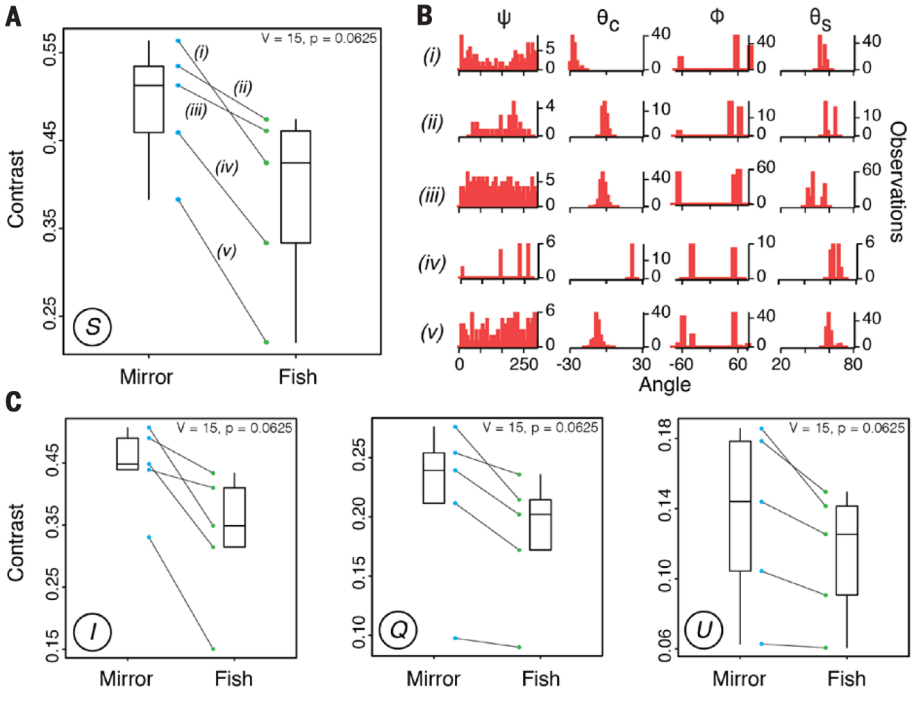

Fig. 1. Box plots of the contrast averages for five live carangid fish (from Brady *et al*.) with the largest series of measurements in chase angle conditions. (**A**) Stokes contrast averages between individual fish (labeled *i* to *v*) and mirror along with (**B**) histograms for specific angular parameters of the measurements pooled for each fish and mirror average shown in (A). We show in (**C**) the results for each linear Stokes elements *I*, *Q*, and *U*.

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minimize contrast across each of these components for predator pursuit angles. Our results suggest that fish have evolved a means to minimize contrast in this complex environment with predators that have either simple (intensity only) or complex (polarization and intensity) visual sensitivities.

Finally, we address the pseudoreplication concern of Cronin *et al*. The issue of pseudoreplication involves careful attention to relevant number of sampling units. In our study (*1*), we collected angular viewing measurement series from 11 open-ocean carangid fish [5 bigeye scad (*Selar crumenophthalmus*), 6 lookdown (*Selene vomer*)], and we extensively analyzed the data set from a number of different "sampling unit" scales—from all angles [figure 2 in (*1*)], from discrete bins of viewing angles [figure. 3 in (*1*)], and from individual viewing angles [figure 4 and figure S3 in (*1*)], with each viewing condition representing a unique optical backdrop due to the angular dependence of intensity and polarization. Inspired by Cronin *et al*., we now also evaluate the data set at the level of individual fish (see Fig. 1). When we calculate an average contrast from each of these 11 fish across all of their angular measurements, we find significant reduction in Stokes contrast relative to mirrors (Wilcoxon signed rank test at all angles: $N = 11$, $V = 55$, $P = 0.054$; chase angles: $V = 56$, $P = 0.042$). Furthermore, when we limit our examination to the five carangid fish with sufficiently large range of viewing angle measurements (ranging from 15 to 160 measurements in chase angles), we still find the same pattern of a reduction in Stokes contrast, as well as in each of the Stokes contrast elements (see Fig. 1). This individual-based analysis reveals the same pattern of improved fish crypsis (reduction in contrast) at ecologically relevant viewing angles as all of our different levels of angular comparisons from Brady *et al*. 2015 [see figures 2 to 4 and figures S3 to S6 in (*1*)], highlighting that our results are robust under a variety of statistical approaches.

Given the angular dependence of crypsis in the open ocean, we contend that it is vitally important to consider all levels of measurement sampling and direct specific attention to the unique viewing configurations that are relevant for the species of interest. Pooling all our angular measurements for each individual fish informs the reader that this is a consistent finding within these species, whereas our different angular analyses inform the reader of exactly which viewing angles carangid fish perform exceptionally well at camouflage and for which viewing angles they do not. We hope that these measurements will inspire others to investigate the complexity of any environment and incorporate angle-specific structure into their measurements to gain a more accurate picture as to how animals interact and survive within their unique optical worlds.

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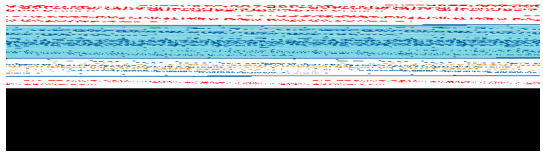

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