

Does visual or mechanosensory disruption influence risk assessment in coral reef fishes: a preliminary study

Riley Bowers | Nicholas Burgos | Ryan Meshanko | Sapna Thaker | Allison Yan | Sean O'Fallon | Daniel T. Blumstein 

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

Correspondence

Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, 621 Young Drive South, University of California, Los Angeles, CA 90095-1606, USA.
Email: marmots@ucla.edu

Funding information

UCLA Dept. EEB; UCLA Department of Ecology and Evolutionary Biology

Abstract

Interpreting and responding to environmental cues from different modalities has survival value. In fish, the role of multimodal perception has been studied in regard to both foraging and risk assessment, with modalities including vision, olfaction, and mechanoreception via lateral lines. We studied reef fish boldness by placing novel objects that obstructed vision, lateral line use, or both into a coral reef environment with native algal samples inside, and then quantifying exploration as a function of obstruction type and as a function of functional diet groups (herbivores, omnivores, carnivores). Fish were more neophobic with more sensory obstructions, displaying longer latencies to visitation across all novel objects. Fish were also less likely to pass by objects that blocked multiple perceptual modalities. Across diets, there is early evidence that different functional groups respond differently to novelty. However, this conclusion requires further study. Overall, our findings provide key insights into perceptual ecology. In turn, this knowledge can be applied to understanding the effects of novel anthropogenic modifications in the marine environment. Such modifications may include positive activities like the construction of substrates to restore coral reefs, coral transplantation to restore reefs, as well as the negative consequences of construction and pollution.

KEYWORDS

behavior, boldness, fish, multimodal perception, novelty

1 | INTRODUCTION

Animals perceive the world through a variety of sensory systems. Multimodal perception provides an animal with more information about its environment, influencing necessary behaviors such as predation risk assessment (Lombardo et al., 2008), foraging (Kulahci et al., 2008), and social behavior (Butler & Maruska, 2016; Narins

et al., 2005). When multimodal perception occurs, there can be equivalent, enhanced, or antagonistic responses to being exposed to different modalities (Munoz & Blumstein, 2012). For instance, in Western mosquitofish (*Gambusia affinis*), chemical signaling associated with predators increases inspection distances, but the addition of a visual cue indicating predator movement increases inspection distances even further (Smith & Belk, 2001).

Fish use visual, olfactory, and lateral line systems to assess risk and identify food (Bleckmann, 1986; Guthrie, 1986; Kelley, 2008). Some species of teleost, such as zebrafish (*Danio rerio*), rely primarily

Allison Yan, Riley Bowers, Ryan Meshanko, Sapna Thaker and Nicholas Burgos are equal contributors, listed alphabetically.

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on vision when engaging in foraging behavior (Howe et al., 2018), but there is high variation in the morphology and sensitivity of coral reef visual systems based on ecological niche (Collin & Pettigrew, 1988a, 1988b; Cortesi et al., 2020). Despite this, studies have confirmed the ability to discriminate between colors in multiple reef species, and both herbivores and carnivores use their vision to forage and find palatable foods (Cheney et al., 2013; Miller & Pawlik, 2013; Siebeck et al., 2008). Many marine species also use visual cues in predator risk assessment, and they are often paired with olfactory or acoustic cues (Davidson et al., 2024; McCormick & Manassa, 2008).

While vision is a key sensory input for many behaviors, lateral line mechanoreception is also essential for foraging, especially when other sensory cues are absent (Hanke & Bleckmann, 2004; Schwalbe et al., 2016). Research on the omnivorous red drum (*Sciaenops ocellatus*) showed that while juveniles could hunt in complete darkness or with their olfactory systems inhibited, interfering with their lateral line system completely stopped prey-seeking behavior suggesting that foraging was most strongly influenced by lateral line mechanoreception (Liao & Chang, 2003). The lateral line also plays a major role in predator avoidance. Zebrafish larvae primarily used lateral lines to escape predators, while adult fish relied more on vision (McHenry et al., 2009). Given the importance of vision and lateral line perception for fish behavior, we conducted a multimodal study of these perceptual modalities to understand their combined effects.

Studies have been conducted on multimodal perception in fish, revealing how fish with different diets use multiple senses in combination. Multiple species of freshwater predatory fish rely primarily on vision to find prey, with lateral line mechanoreception aiding visual cues to inform striking distance or orientation (Abboud & Coombs, 2000; New, 2002). Studies on zooplanktivorous fish, including the marine piper (*Hyporhamphus ihi*), have shown that lateral line information complements visual information when detecting prey, especially in low light conditions (Montgomery, 1989; Saunders & Montgomery, 1985). Regarding risk assessment, the omnivorous orange clownfish (*Amphiprion percula*) uses mechanosensory cues in addition to visual and chemical cues to socially learn predator recognition from conspecifics, and this learning still occurs when visual and chemical cues are absent (Manassa et al., 2013). There is evidence supporting that multimodality is equally as important for herbivores, such as the Ambon damselfish (*Pomacentrus amboinensis*), which uses multimodal signaling to communicate with conspecific competitors and reduces these cues when predators are present (Davidson et al., 2024). Integrating sources of multimodal information has significant effects on fishes' boldness around new habitats or objects, especially when various sensory cues are available.

Boldness has been defined as the willingness to explore a novel environment or object (Wilson et al., 1994; Wright et al., 2006). This in turn impacts the survival of animals and their ability to carry out essential functions such as feeding (Dingemans et al., 2004). Prior research on the response to novel stimuli and risk assessment in fish has examined several modalities such as visual (Hamilton, 2018; Wallace & Hofmann, 2021), olfactory (Valentinčič, 2004), and acoustic (Huijbers et al., 2012; Leis et al., 2002). While some novelty studies

test mechanosensory stimuli (Dunlop & Laming, 2005), we are not aware of prior multimodal novelty experiments building this into their design.

The structure of novel objects can inherently obstruct both visual and mechanosensory input in fish, influencing their willingness to explore a novel object. We therefore conducted a novelty experiment examining how interference with multimodal perception affects reef fish boldness in Mo'orea, French Polynesia. We used a community level approach, looking at the main effects of our treatments on different fish functional groups defined by diet. Based on the importance of visual and lateral line modalities for both foraging (Coombs & Patton, 2009; Montgomery, 1989; New, 2002; Newport et al., 2021) and predator avoidance (Manassa et al., 2013; Stewart et al., 2014), we predicted that fish across functional groups would be most neophobic around objects that obstructed both modalities, followed by objects that obstructed one modality. Multimodal cues provide information to make more accurate decisions and enhanced responses that aid survival, which is relevant to fish behaviors among all trophic levels.

Understanding the effects of novel objects on multimodal perception is important to assess the impact of anthropogenic changes to a marine environment, such as the construction of offshore wind turbines (Gill et al., 2020) and restorative artificial reefs (Koeck et al., 2013). The nature of these objects can obstruct different sensory modalities under water, and understanding how such obstructions impact fish behavior can help guide the construction of them to maximize recruitment and retention of all functional groups.

2 | METHODS

2.1 | Ethics statement

The care and use of experimental animals complied with French Polynesian and United States of America animal welfare laws, guidelines, and policies as approved by Convention d'accueil number 130005820 issued on November 24, 2023, as well as the UCLA IACUC protocol number 2000-147 approved on November 28, 2023.

2.2 | Study location

We conducted our study on the fringing reef of the north shore in Maharepa off Mo'orea, French Polynesia (17°29'7"S, 149°47'56"W) between January 25, 2024 and February 4, 2024 (we planned additional work, but a series of cyclone warnings and storms formally closed the waters for all activities, including research, for 2 weeks).

2.3 | Experimental methods

Inspired by Bednekoff and Blumstein (2009), we constructed 30 × 30 × 30 cm boxes made with PVC pipes. The walls consisted of

either black opaque plastic to multimodally block cues of both sight and lateral line mechanosensation, or clear acrylic to unimodally block only lateral lines (Figure 1a,b). Three of the sides in the black and clear treatments were “walled,” leaving one possible entrance on the planar axis. While entry into a box from above was a possibility, this was not observed during our study. A box with only the PVC frame and no walls was also deployed to control for box effects, as well as a no-stimulus control (Figure 1c,d). Since this was originally conceived as a foraging experiment intended for herbivorous fish, each box and our no-stimulus control contained 10 g (wet weight; see Keeley et al., 2015 for methods) of *Padina boryana*, a highly favored macroalgae (Keeley et al., 2015; Mantyka & Bellwood, 2007). *P. boryana* was collected from the waters off the Gump Research Station, where it was common, about 1.5 km from our study site, where it was rare. Olfactory responses to algae were not factored into this experiment, but no treatments were watertight or prevented diffusion, so there should not be any difference between them in that regard. Boxes were weighted with dive weights to keep them submerged (all were deployed in 1–2.5 m water) and prevent their movement. The four treatments were deployed in alternating order, approximately 10 m from each other in a line across the reef flat. Exact placement sites were selected haphazardly on a day-to-day basis based on accessibility given the water conditions and distance from other sites because we believed distribution of species was relatively even across our site.

Our experiment was conducted every other day for a total of six experimental days. A “session” was defined as a series of deployments with all experimental conditions set out together within the same hour. A session contained either eight or 12 experiments depending on water conditions, with equal numbers of deployments per treatment. All but 1 day had a single session per day. The single day with two sessions had a 6-h gap between deployments. Thus, we had a total of seven sessions. All deployments occurred when Beaufort wind scale readings were ≤ 3 . A Vemont or Crosstour CT 1080P action

camera was positioned 0.7 m (Sura et al., 2021) from the front wall of each box to observe and quantify fish behavior. Between 45 min and 1.5 h of footage was recorded per deployment, during which time observers were not present around the boxes so as not to impact fish activity. Following the deployment period, observers collected the boxes and cameras.

2.4 | Video scoring

We counted the number of passes ($N = 1953$) and rare visitations inside the box. Passes were defined as a fish swimming within 25 cm on any side (front, back, left, or right) of the centrally-placed algae across all treatments. However, despite the added *P. boryana*, we observed minimal foraging. Visits were scored as repeats and not counted if a fish left the camera frame for less than 5 s before entering the field of view again. If a fish left for more than 5 s, a subsequent pass was scored again, since fish abundance at our site was high enough to infer that separate individuals were being observed. Observers ($N = 5$) were trained to accurately identify the fish to ensure consistency across observations. Treatments were done in the same general area throughout the course of the experiment. While habituation over time was a possibility, this was accounted for in our analysis by including session number as a covariate.

Each time we observed a pass, we identified the species and recorded the time of the pass. From this we calculated two variables: the latency to first pass and the pass rate (N passes/total time recorded). Passes near a frame are a measure of boldness because the boxes were a novel object within the fishes' habitat (Andersson et al., 2014; Michelena et al., 2008). While a larger sample size may allow data to be analyzed on a species-specific basis, our data were suitable only to focus functional groups.

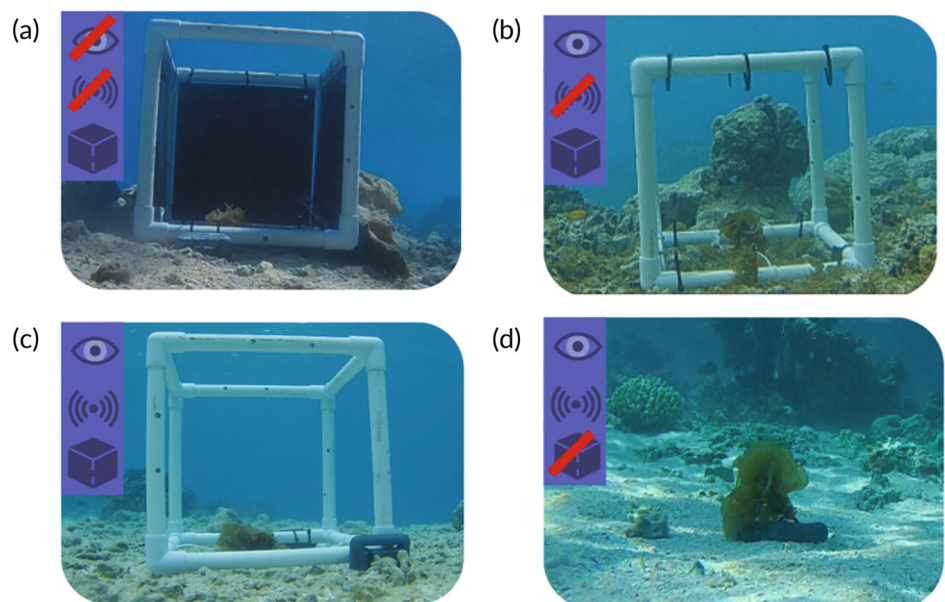


FIGURE 1 Images of treatments with decreasing levels of obstruction: (a) box with opaque walls to obstruct vision and lateral lines; (b) box with clear walls to obstruct lateral lines; (c) frame only to control for box effects; (d) algae only (control).

We used FishBase to categorize the dietary habits of each fish species as herbivorous, omnivorous, carnivorous, or corallivorous (Froese & Pauly, 2023). These functional groups were selected based on the observations of fish species which visited our boxes. We excluded corallivores from subsequent analysis due to limited observations.

Finally, we noted whether each video had a full unobstructed view of the box, whether it was partially obstructed, or whether because of box movement or camera displacement it was mostly obstructed (Figure S1). We removed videos where the view of the box was mostly or fully obstructed from analysis. If a box moved during the video so that the view became mostly or fully obstructed, analysis was stopped at the point where the box was no longer in view and the video length was reduced to reflect only the scorable video time.

2.5 | Statistical analysis

To explain variation in both latency to first pass and pass rate, we fitted generalized linear models with a negative binomial distribution as a function of diet, treatment, observation session (to account for changes in tolerance over time), degree of box obstruction, video length (to account for the opportunity for longer latencies, all videos were ca. 1 h long), and interaction between diet and treatment. We checked that residuals were normally distributed with the use of the `check_model` function in the “performance” package in R, as well as visually analyzing Q-Q plots. For both models, observation session and the interaction between diet and treatment were not significant, so we removed them from the following analysis. For significant variables, we compared groups with Bonferroni contrasts and visualized these with box plots. All statistical analyses were conducted in R 4.3.2 (R Core Team, 2023) and R studio (RStudio Team, 2023), using the packages `dplyr` (Wickham et al., 2023), `readr` (Wickham, Hester, & Bryan, 2024), `performance` (Lüdtke et al., 2021), `multcomp` (Hothorn et al., 2023), and `ggplot2` (Wickham, 2024). In all cases, we set our alpha to 0.05.

3 | RESULTS

Our final dataset consisted of 1948 passes recorded over 62 scorable deployments, which created 80 h of scorable video: 855 of these were by carnivores, 346 were by omnivores, and 736 were by herbivores. In total we observed 46 different species pass close to our novel objects (Table 1). We also calculated an accumulation curve, which allowed us to be confident that we were surveying a representative sample of the typical fish species residing in the area (Figure S2).

3.1 | Latency to pass

After controlling for significant variation explained by video length and the level of box obstruction, we found significant differences in

the latency to first pass as a function of treatment, but not diet functional group (Table 2a). All of our experimental treatments (frame, clear, and black) had significantly different latencies compared to our control, but they did not differ from each other. Specifically, all of these treatments had longer latencies when compared to the control (Table 3a and Figure 2a).

3.2 | Pass rate

As with the latency to first visit, we found different responses in pass rate as a function of treatment after video length and level of box obstruction were controlled for. However, pass rate also differed as a function of diet functional group (Table 2b). Across treatments, the black treatment had a significantly lower pass rate than the control (Table 3b, Figure 2b). Also, the pass rate of omnivores was significantly different from both carnivores and herbivores. Carnivores and herbivores had higher pass rates than omnivores, but were not significantly different from each other (Table 3c and Figure 2c). Although diet and treatment had significant effects on pass rate, these main effects were independent of each other as the interaction between diet and treatment was not significant.

4 | DISCUSSION

The presence of any novel object resulted in longer latency to visit, regardless of sensory obstruction. All treatments, including the frame treatment, which we assumed obstructed no modalities and controlled for a novel structure, had significantly longer latencies, suggesting that novel objects in general are associated with greater neophobia in fish. Still, only the black treatment, which blocked both visual and mechanosensory stimuli, had a significantly different pass rate from the control. This lower pass rate for the black treatment suggests that multimodal obstructions in particular are associated with greater neophobia. This is consistent with our hypothesis and existing literature because visual and mechanosensory cues are essential to behaviors such as hunting, predator avoidance, and social interactions (Montgomery, 1989; Stewart et al., 2013). Access to multimodal cues facilitates accuracy and learning in these behaviors (Ålund et al., 2022; Manassa et al., 2013; Ward & Mehner, 2010), and we found that the obstruction of these cues in combination influenced the boldness to investigate novel objects. Although we have this evidence that multimodality is important, we are unable to conclude which modality (vision or mechanoreception) is more important in explaining variation in boldness. In regard to predator evasion, some literature supports that fish are predisposed towards using visual cues versus other stimuli (Utne-Palm, 2001). Other studies, however, have found that mechanosensory stimuli allow for faster evasion in response to close encounters with predators (Stewart et al., 2013) and are therefore just as essential. Our study had one test for the unimodal mechanosensory obstruction, but there were no treatments testing for a unimodal visual obstruction. Future studies should evaluate different modalities

TABLE 1 Fish species and families observed passing our novel objects.

| Fish species (common name) | Family | Diet functional group | Observations |
|---|----------------|--------------------------|--------------|
| <i>Abudefduf septemfasciatus</i> (banded sergeant) | Pomacentridae | Omnivore | 1 |
| <i>Abudefduf sexfasciatus</i> (scissortail sergeant) | Pomacentridae | Omnivore | 5 |
| <i>Arothron meleagris</i> (guineafowl puffer) | Tetraodontidae | Omnivore | 2 |
| <i>Balistapus undulatus</i> (orange-lined triggerfish) | Balistidae | Omnivore | 95 |
| <i>Canthigaster bennetti</i> (Bennett's puffer) | Tetraodontidae | Omnivore | 2 |
| <i>Canthigaster solandri</i> (spotted sharpnose puffer) | Tetraodontidae | Omnivore | 2 |
| <i>Caranx melampygus</i> (bluefin trevally) | Carangidae | Carnivore | 19 |
| <i>Centropyge bispinosus</i> (dusky angelfish) | Pomacanthidae | Herbivore | 5 |
| <i>Centropyge flavissima</i> (lemonpeel angelfish) | Pomacanthidae | Herbivore | 22 |
| <i>Chaetodon auriga</i> (threadfin butterflyfish) | Chaetodontidae | Omnivore | 10 |
| <i>Chaetodon citrinellus</i> (speckled butterflyfish) | Chaetodontidae | Omnivore | 31 |
| <i>Chaetodon ephippium</i> (saddle butterflyfish) | Chaetodontidae | Omnivore | 1 |
| <i>Chaetodon lunula</i> (raccoon butterflyfish) | Chaetodontidae | Omnivore | 50 |
| <i>Chaetodon lunulatus</i> (redfin butterflyfish) ^a | Chaetodontidae | Corallivore ^a | 9 |
| <i>Chaetodon ornatissimus</i> (ornate butterflyfish) ^a | Chaetodontidae | Corallivore ^a | 1 |
| <i>Chaetodon reticulatus</i> (mailed butterflyfish) ^a | Chaetodontidae | Corallivore ^a | 1 |
| <i>Chaetodon ulietensis</i> (Pacific double-saddle butterflyfish) | Chaetodontidae | Omnivore | 1 |
| <i>Chaetodon vagabundus</i> (vagabond butterflyfish) | Chaetodontidae | Omnivore | 18 |
| <i>Chlorurus sordidus</i> (bullethead parrotfish) | Scaridae | Herbivore | 60 |
| <i>Coris centralis</i> (Central Pacific coris) | Labridae | Carnivore | 1 |
| <i>Ctenochaetus striatus</i> (striated surgeonfish) | Acanthuridae | Omnivore | 126 |
| <i>Epinephelus merra</i> | Serranidae | Carnivore | 1 |
| <i>Fistularia commersonii</i> (bluespotted cornetfish) | Fistulariidae | Carnivore | 9 |
| <i>Gomphosus varius</i> (bird wrasse) | Labridae | Carnivore | 5 |
| <i>Halichoeres hortulanus</i> (checkerboard wrasse) | Labridae | Carnivore | 11 |
| <i>Halichoeres trimaculatus</i> (threespot wrasse) | Labridae | Carnivore | 347 |
| Juvenile parrotfish ^b | Scaridae | Herbivore | 571 |
| <i>Mulloidichthys flavolineatus</i> (yellowstripe goatfish) | Mullidae | Carnivore | 83 |
| <i>Parapercis millepunctata</i> (black-dotted sand perch) | Pinguipedidae | Carnivore | 1 |
| <i>Parupeneus barberinus</i> (dash-and-dot goatfish) | Mullidae | Carnivore | 1 |
| <i>Parupeneus cyclostomus</i> (gold-saddle goatfish) | Mullidae | Carnivore | 6 |
| <i>Parupeneus multifasciatus</i> (manybar goatfish) | Mullidae | Carnivore | 118 |
| <i>Pygoplites diacanthus</i> (royal angelfish) | Pomacanthidae | Carnivore | 37 |
| <i>Scarus forsteni</i> (whitespot parrotfish) | Scaridae | Herbivore | 5 |
| <i>Scarus ghobban</i> | Scaridae | Herbivore | 1 |
| <i>Scarus oviceps</i> (dark-capped parrotfish) | Scaridae | Herbivore | 5 |
| <i>Scarus psittacus</i> (common parrotfish) | Scaridae | Herbivore | 3 |
| <i>Scarus rubroviolaceus</i> (ember parrotfish) | Scaridae | Herbivore | 1 |
| <i>Scorpaenopsis papuensis</i> (Papuan scorpionfish) | Scorpaenidae | Carnivore | 1 |
| <i>Stegastes nigricans</i> (dusky farmerfish) | Pomacentridae | Omnivore | 2 |
| <i>Stethojulis bandanensis</i> (red shoulder wrasse) | Labridae | Carnivore | 103 |
| <i>Synodus variegatus</i> (variegated lizardfish) | Synodontidae | Carnivore | 1 |
| <i>Thalassoma hardwicke</i> (sixbar wrasse) | Labriade | Carnivore | 16 |
| <i>Zanclus cornutus</i> (Moorish idol) | Zanclidae | Carnivore | 95 |
| <i>Zebbrasoma scopas</i> (twotone tang) | Acanthuridae | Herbivore | 63 |

Note: We classified diet functional groups by using Fish Base (Froese & Pauly, 2023). Observations were quantified as a sum total of all passes recorded across all videos.

^aCorallivorous fish were excluded from analysis due to limited observations.

^bAside from *Chlorurus sordidus*, specific juvenile parrotfish species were indistinguishable and were thus considered as a single taxon when analyzing functional groups.

(a) Latency to first pass

| | df | Deviance | Residual df | Residual deviation | p value |
|----------------------|----|----------|-------------|--------------------|---------|
| Null | | | 130 | 174.47 | |
| Diet | 2 | 1.915 | 128 | 172.56 | 0.418 |
| Treatment | 3 | 9.728 | 125 | 162.83 | 0.031 |
| Level of obstruction | 1 | 4.196 | 124 | 158.63 | 0.051 |
| Video length | 1 | 12.104 | 123 | 146.53 | <0.001 |
| Session | 6 | 8.061 | 117 | 138.47 | 0.291 |
| Diet:treatment | 6 | 3.413 | 111 | 135.06 | 0.795 |

(b) Pass rate

| | df | Deviance | Residual df | Residual deviation | p value |
|----------------------|----|----------|-------------|--------------------|---------|
| Null | | | 185 | 97.969 | |
| Diet | 2 | 3.201 | 183 | 94.768 | 0.002 |
| Treatment | 3 | 3.723 | 180 | 91.045 | 0.002 |
| Level of obstruction | 1 | 1.263 | 179 | 89.783 | 0.024 |
| Video length | 1 | 0.340 | 178 | 89.443 | 0.242 |
| Session | 6 | 2.757 | 172 | 86.686 | 0.085 |
| Diet:treatment | 6 | 1.237 | 166 | 85.449 | 0.546 |

TABLE 2 Results from the generalized linear models explaining variation in (a) latency to first pass, and (b) pass rate.

TABLE 3 Results of Bonferroni comparisons for significant predictors in fitted latency and pass rate models.

(a) Treatment contrasts for latency model

| | Estimate | Standard error | z value | p value |
|---------------|----------|----------------|---------|---------|
| Frame-control | 0.842 | 0.257 | 3.268 | 0.006 |
| Clear-control | 0.795 | 0.267 | 2.975 | 0.018 |
| Black-control | 1.218 | 0.291 | 4.189 | <0.001 |
| Clear-frame | -0.046 | 0.282 | -0.164 | 1.000 |
| Black-frame | 0.376 | 0.297 | 1.266 | 1.000 |
| Black-clear | 0.422 | 0.306 | 1.379 | 1.000 |

(b) Treatment contrasts for pass rate model

| | Estimate | Standard error | z value | p value |
|---------------|----------|----------------|---------|---------|
| Frame-control | -0.663 | 0.330 | -2.011 | 0.266 |
| Clear-control | -0.645 | 0.332 | -1.944 | 0.312 |
| Black-control | -1.365 | 0.403 | -3.386 | 0.004 |
| Clear-frame | 0.019 | 0.372 | 0.051 | 1.000 |
| Black-frame | -0.702 | 0.434 | -1.618 | 0.634 |
| Black-clear | -0.721 | 0.434 | -1.659 | 0.582 |

(c) Diet contrasts for pass rate model

| | Estimate | Standard error | z value | p value |
|-----------------------|----------|----------------|---------|---------|
| Omnivores-herbivores | -0.807 | 0.354 | -2.278 | 0.068 |
| Carnivores-herbivores | 0.170 | 0.278 | 0.611 | 1.000 |
| Carnivores-omnivores | 0.977 | 0.347 | 2.818 | 0.015 |

in comparison with each other because fish may prioritize certain novel habitats based on the cues available, for example evaluating a clear treatment obstructing only lateral line sensing compared to a treatment obstructing only vision, but that still allows water to flow through.

One caveat to our study was that we did not account for the effects of olfaction in our treatment design. It is known that fish use olfaction as a guide for many different behaviors (Kasumyan, 2004). For instance, salmon detect their specific breeding ground using olfactory cues (Døving et al., 1985; Hasler & Scholz, 1983; Wisby & Hasler, 1954). Olfaction could have played a role in the appeal of the bait because our boxes were open, therefore allowing for olfactory cues to spread. No treatments were watertight, however, so we hypothesize this did not have an effect on our analysis because each treatment equally allowed the diffusion of chemicals. Thus, our study design was limited because we did not have a way to measure the number of olfactory cues that were emitted by the depoloyed *P. boryana*. In turn, we were unable to determine if olfactory cues had any effect on the risk assessment and foraging behavior of different functional groups. While this was originally designed as a foraging experiment and one might expect olfactory cues to influence herbivore or omnivore behavior, we do not believe this biased our results because it did not result in herbivores foraging on the bait. In the future, studies may look into how olfaction is weighed in multimodal perceptual decisions for fishes in different dietary functional groups.

In addition to evidence that fish respond to differences in the modality of obstruction, our study also provides early evidence that different functional diet groups respond differently to the presence of novel objects. Specifically, carnivores had significantly higher pass rates when compared to omnivores, suggesting carnivores were more

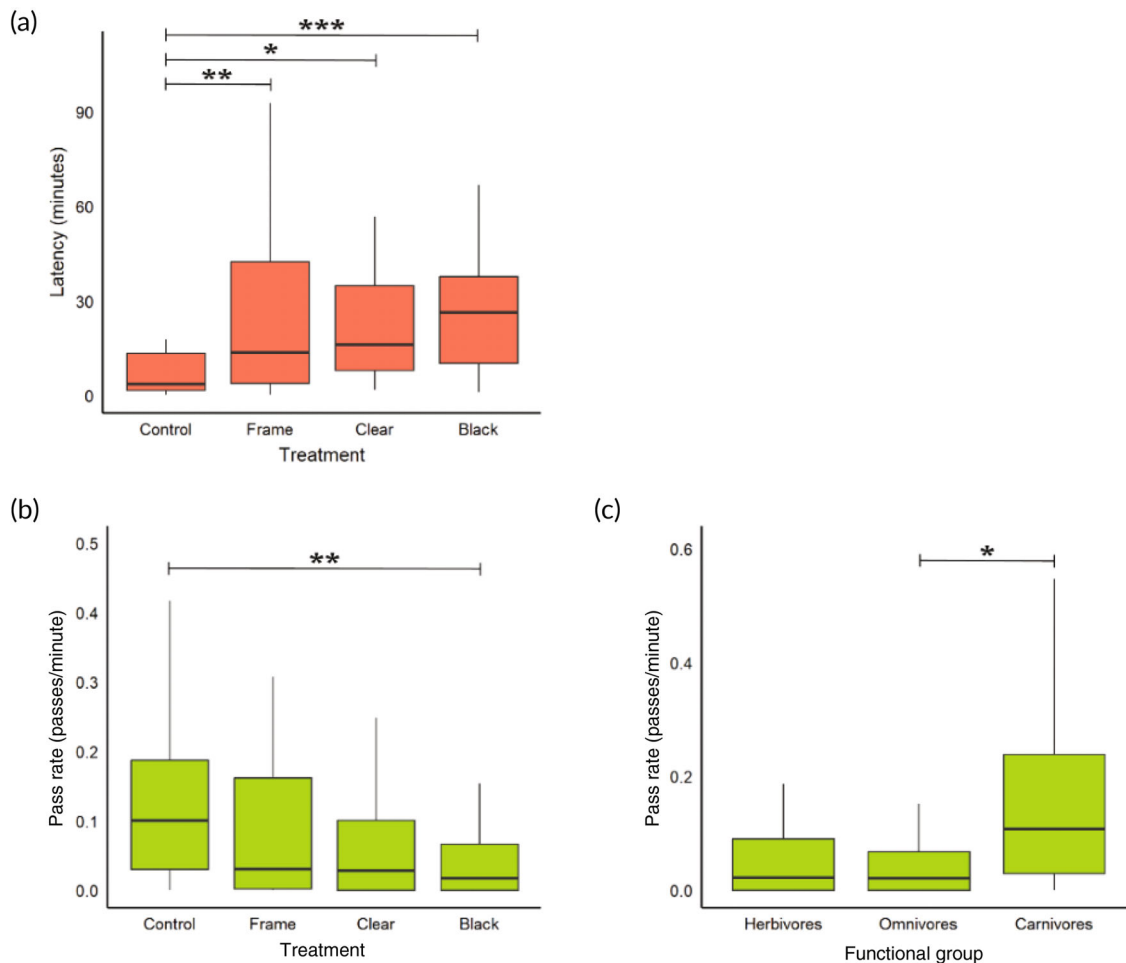


FIGURE 2 Boxplots for (a) latency by treatment, (b) pass rate by treatment, and (c) pass rate by diet. The black treatment had opaque walls, obstructing both sight and lateral line mechanosensation, the clear treatment had clear walls, obstructing only lateral line mechanosensation, the frame treatment had no walls and only PVC frames, and the control consisted of only algae. Bars indicate groups that are significantly different from each other. Levels of significant differences ($p < 0.05$, < 0.01 , and < 0.001) are denoted by *, **, and *** respectively.

likely to visit and less neophobic around novel objects compared to omnivores. Many species of fish and aquatic prey are documented to use underwater structure as a means of refuge to hide from predators (Caley & St John, 1996; Lehtiniemi, 2005; Persson, 1993). Thus, after a period of initial neophobia (latency to visit), carnivorous fish may be attracted to these possible refugia as a means of hunting prey as well as hiding from even larger predators. There were no other differences observed between functional groups so more research is needed to further evaluate the differences in neophobic behavior among diet functional groups. Importantly, the reef fish across functional groups of our study site were similar in size and habitat so these fish at similar trophic levels may be facing similar pressures regarding predation and competition, regardless of diet (Crane & Ferrari, 2017).

Considering the limited differences between functional groups, analysis on a finer scale may be required to further understand differences in neophobia. While similar studies have measured boldness on a functional group scale (Rhoades et al., 2019), others have looked at species level differences in boldness and how they influence different species' abilities to disperse and colonize new habitat

(Rehage & Sih, 2004). Furthermore, many studies have found individual variation of boldness within taxa (Ward et al., 2004; Wilson & Stevens, 2005). One study examining boldness and risk-taking behavior of juvenile bluegill sunfish (*Lepomis macrochirus*) found that individual-level differences could impact decisions to explore novel objects or take risks (Wilson & Godin, 2009). Thus, even species-level analysis itself may be inadequate to fully explain fish responses to multimodal cues from novel objects. Since our average sample size per fish species was too small to permit detailed study, we opted to focus on the functional group level instead. This was a relatively short study, limited both by the duration of our stay in the South Pacific and by inclement tropical weather during much of the expedition. Longer studies would help increase sample size and allow for analysis on smaller scales.

Our study provides new insights about the effects of novel objects on multimodal perception and provides a groundwork for future research that can integrate sensory perception to understand how novel structures influence marine environments. This knowledge will help us understand the impact of novel anthropogenic

infrastructure that includes physical objects such as breakwaters, pilings, and aquaculture poles/cages that are now changing many shallow water marine systems (Bulleri & Chapman, 2010). As noted by Gill et al. (2020), contemporary novel structures, such as offshore wind farms, change the sensory environment by producing alternative water currents, wind wake, and also emitting electromagnetic fields. Using a multimodal sensory approach to analyze response to anthropogenic structures can be important to understand the differential effects of these novel structures, and understanding the impacts at the level of functional groups can be important for understanding how physically modified environments may change fish diet and community structure.

Moreover, this form of analysis is important for predicting potential changes in community structure following the introduction of novel objects during restoration efforts. For instance, the transplant of nursery-hatched coral onto a man-made frame to create artificial reefs has been used to rebuild and revitalize habitats that have been destroyed or degraded by human activity (Ammar, 2009; Epstein et al., 2003). Prior work has shown different responses to restored reefs. Koeck et al. (2013) found that white seabream (*Diplodus sargus*) fed mainly during the day on natural reefs and mainly at night on artificial reefs. Another study conducted by Døving et al. (2006) found that five-lined cardinalfish (*Cheilodipterus quinquelineatus*) preferred the scent of artificial reef sites that had been previously occupied by conspecifics to the scent of similar reefs not occupied by conspecifics. Thus, it is important to understand how perceptual details of artificial reef construction may affect the behavior of colonizing fish, and studying the response of fishes to novel objects is a first step towards this understanding.

AUTHOR CONTRIBUTIONS

R.B.: Conceptualization, investigation, methodology, data curation, writing—original draft, writing—review and editing; N.B.: Conceptualization, investigation, methodology, data curation, writing—original draft, writing—review and editing; R.M.: Conceptualization, investigation, methodology, data curation, writing—original draft, writing—review and editing; S.T.: Conceptualization, investigation, data curation, writing—original draft, writing—review and editing; A.Y.: Conceptualization, investigation, methodology, data curation, writing—original draft, writing—review and editing; S.O.: Supervision, data curation, writing—review and editing; D.T.B.: Conceptualization, project administration, supervision, data curation, writing—original draft, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code to reproduce these analyses are available at OSF: osf.io/b2mha.

ORCID

Daniel T. Blumstein  <https://orcid.org/0000-0001-5793-9244>

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