

Predation domes: In-situ field assays to measure predatory behaviours by fish

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Abstract

1. Biotic interactions such as predation are difficult ecological processes to quantify in the wild. This is especially the case in the marine environment due to logistical difficulties in capturing animal behaviour. Common approaches use aquarium-based experiments, live-tethering, or assays with bait as proxies for quantifying predation pressure. However, these methods often fail to account for natural interactions between species in the wild and may raise ethical and animal welfare concerns.
2. We designed a novel field-based method to quantify predator–prey interactions for marine fishes. The “predation dome” is a clear acrylic aquarium that contains a live fish. The dome is filmed and, in contrast to other methods, it allows for natural olfactory and visual cues, and the prey fish is returned to the wild after the assay. Here, we provide a step-by-step guide on building and deploying the predation dome in the wild. To demonstrate its use, we quantified predation pressure using the domes in two tropical and two temperate locations.
3. Piscivores were attracted to the domes and displayed predatory behaviours such as circling or striking. Although the overall number of predatory attacks did not differ among locations, predation domes revealed higher predation pressure by piscivores at the tropical locations in comparison to temperate reefs.
4. Our results show that predation domes represent an ethical and complementary approach to measure predation that may better represent piscivory as compared to other behaviours. Predation domes can be also used to measure other biotic interactions such as territorial defence or courtship.

KEYWORDS

biotic interactions, field experiments, fish, marine ecosystems, predation

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1 | INTRODUCTION

Predation is a key biotic interaction that can impact ecosystem functions and community structure (Chesson, 2013; Hixon, 1991). Predators can influence entire communities via trophic cascades (Estes et al., 1998), and their absence can alter ecosystem function and services (Atwood et al., 2015; Estes et al., 2011). Overfishing and climate change are altering predator–prey interactions in marine ecosystems in multiple ways (Coni et al., 2022; Munday et al., 2008). For example, as prey species expand their ranges because of ocean warming, they are escaping native predators but also encountering new predatory species against which they may have no defences (Carthey & Blumstein, 2018; Coni et al., 2022). Understanding changes in the intensity and identity of predator–prey interactions can help discern further impacts on the rest of the ecosystem (Blois et al., 2013).

Predation events are difficult to quantify in marine ecosystems due to logistical challenges. Activities requiring SCUBA diving are limited by the amount of time and the depth at which divers can operate, and importantly, the presence of divers can alter fish behaviour (Dickens et al., 2011). To overcome these challenges, different experimental techniques have been developed to measure predation. For example, aquarium-based studies provide experimental settings that include visual and chemical cues from prey and light control over other environmental variables (Beck et al., 2016; Palacios et al., 2016). However, running aquarium experiments can be expensive, requires the manipulation of both predator and prey, and lacks the environmental context and sequence of stimuli that would characterize predation events in the wild.

In situ tethering experiments are often used as a proxy for predation pressure in the field, whereby live prey is restrained for a certain period and then recorded as predated or not predated (e.g. Chittaro et al., 2005; Dorenbosch et al., 2009). Tethering has the advantage of not including the presence of divers. The addition of cameras recording consumption events can also help to register specific behaviours otherwise biased by diver presence (Branconi et al., 2019). However, tethering of prey can alter their behaviour, and the result of death raises ethical issues (Aronson & Heck, 1995; Baker & Waltham, 2020). An alternative is to use non-living baits, such as squidpops, a stick tethered with a small piece of dried squid (Duffy et al., 2015), whereby scavenging events are measured as the proportion of baits taken by predators. An advantage of squidpops is the use of standardized bait, which has enabled global comparisons of relative consumption rates (Whalen et al., 2020). A potential disadvantage of squidpops is that they do not incorporate all the cues of natural prey that may attract predators (movement, smell, and colour), and may therefore only measure the feeding intensity of generalist predators or scavengers (Duffy et al., 2015).

Here, we design a new predation assay that incorporates the natural behaviour of both prey and predator and avoids death of prey. We designed the predation domes as a non-lethal underwater fish “aquarium”, where a live fish is placed inside the dome to attract predators. These assays are filmed to document predation

behaviours without the presence of a diver. To test our method, we trialled the predation domes in temperate and tropical locations, which are characterized by differences in predation pressure (Freestone et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Predation dome: Building and materials

The predation dome was constructed from transparent acrylic that was 6 mm thick and 300 mm in diameter (Figure S1a). A non-slippery rubber mesh mat was attached to the open bottom of the dome using bolts and wingnuts through eight holes evenly distributed around the flange (Figure S1b). When immersed in seawater the clear acrylic allows for the predator to visually target the prey. The mesh mat sits ~2 cm above the seafloor, which allows for water exchange with ambient seawater for the prey to survive and allows for the transfer of olfactory prey cues, although the extent of the chemical plume was not measured in this study (Text S1).

2.2 | Deployment and in situ testing of the domes

Predation domes were deployed in shallow reefs (4 to 6 m deep) at two regions on the east coast of Australia. Assays were conducted in Lizard Island during March–April 2021, and in Sydney during May–June 2021 (Figure 1). Predation dome procedures



FIGURE 1 (a) Site locations (Lizard Island and Sydney) where predation domes were used (b).

were approved by the UNSW Animal Care & Ethics Committee #20/122B. All experiments were carried out under NSW Fisheries permit P13/0007-2.0, QLD Fisheries permit 209716 and Great Barrier Reef Marine Park Authority permit G20/43969. The tidal range is ~1.23 m for Lizard Island and ~0.93 m for Sydney. All deployments were made under calm conditions, with wave height <1.5 m. In each region, we conducted the assays between 12:00–16:00 at two sites separated by ~1 km, with all treatments run concurrently. These assays were repeated twice. For each assay, the experiment included three domes containing a juvenile fish (<10 cm, *Acanthurus triostegus*) previously collected from rock-pools nearby to the test site, and three control domes with no fish ($n=6$ per site, Figure S2). *A. triostegus* is a range-expanding tropical herbivore that is seasonally abundant as a juvenile in temperate reefs (Basford et al., 2015). We used this species as prey because it is present in both regions, allowing contrasts without any prey-type biases. Although we lack specific information on the species that typically predate on *A. triostegus*, we expect any piscivorous fish would be able to predate on juvenile surgeonfish of the size used in our assays. Weighted domes were deployed on the seafloor by two SCUBA divers and were separated by ~10 m (Figure 2a). Domes were filmed by a Hero 4+ GoPro camera placed 80 cm in front of the domes for approximately 1 h (Figure 2b–d). Cameras and domes were collected after this time, and fishes were released back into the original catch site (Text S2).

2.3 | Video analysis

Video footage from domes was reviewed using EventMeasure software (SeaGIS, version 5.74) to identify predator species and their behaviours. Predators were assigned into one of the following trophic groups: herbivores, invertivores, omnivores, piscivores or planktivores, using information from FishBase (Froese & Pauly, 2022) and general literature (Table S1). The different behaviours of fish approaching the dome ("bait") were grouped into two categories: (1) Attack—striking at the bait, burst swimming towards the bait and/or touching the bait; and (2) inspection—approach and movement near the area of the bait.

2.4 | Data analysis

To compare the predation pressure among the tropical and temperate regions using predation domes, we used generalized linear mixed Models (GLMM) with *glmmTMB* (Brooks et al., 2017). Behaviour was the response variable (attacks or inspections), with region (Sydney vs. Lizard Island) as a fixed effect, site as a random effect, and log (video duration) as an offset to account for variation in the observation period. Poisson (attacks) and negative binomial (interactions) distributions were assumed for each model. In addition, we ran models at the trophic group level for each type of behaviour, where an individual trophic group (i.e. piscivores' attacks) was the response

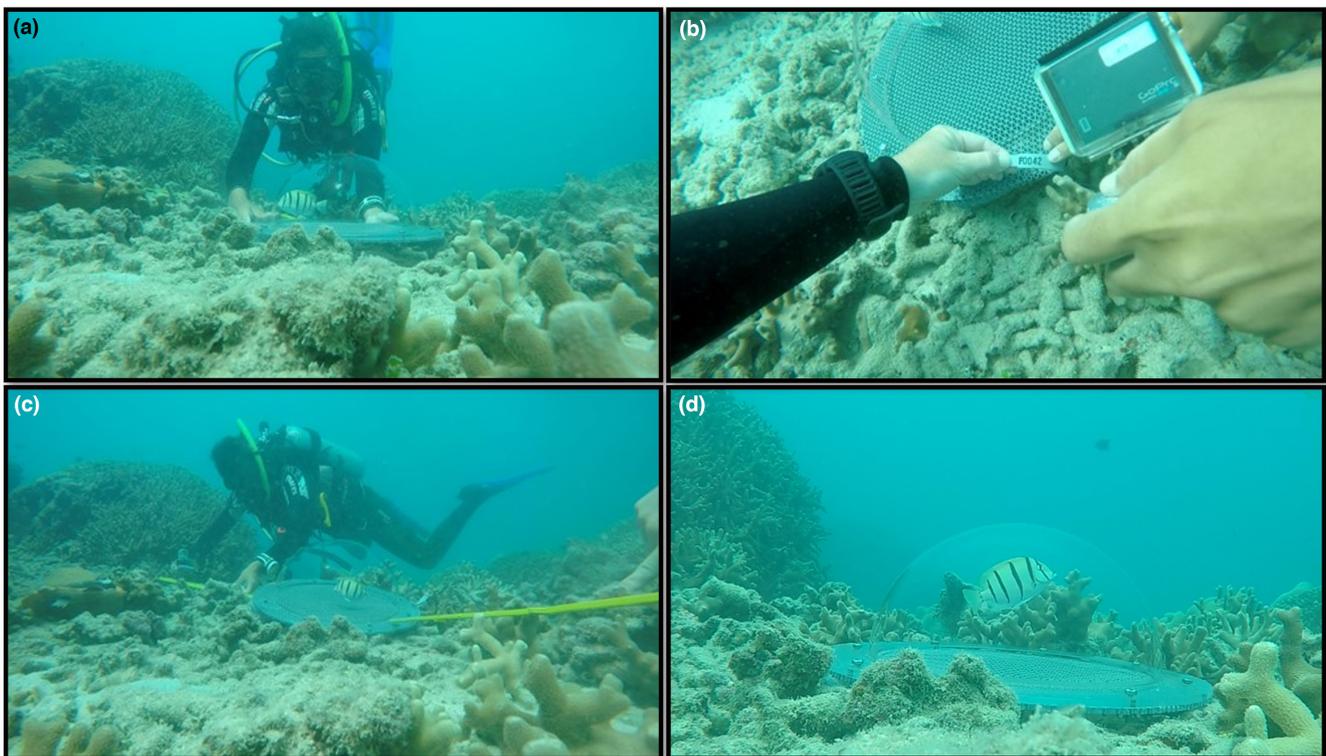


FIGURE 2 Steps of the experiment using a predation dome. (a) placing the dome; (b) filming the tag to identify the dome; (c) measuring the distance between the dome and the GoPro; and (d) fish being filmed. Photos from Lizard Island.

variable, region (Sydney vs. Lizard Island) was a fixed effect, site was a random effect, and log (video duration) was an offset. We only ran these models for the trophic groups that included data in both regions (e.g. no model was run for herbivores when comparing attacks between regions as these were none recorded in Sydney). Poisson (piscivores' attacks and inspections) and negative binomial (planktivores' inspections) distributions were assumed for each model. Distribution, normality and homoscedasticity were checked using DHARMA to ensure model assumptions were met (Hartig, 2022). All analyses were run using R version 4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Predation dome field test

The dome predation events filmed in tropical and temperate sites revealed no differences in the number of attacks between regions (GLMM, effect of region, $p=0.28$, Table S2), however, we found that attacks by piscivores were significantly higher in the tropical sites (GLMM, effect of region, $p=0.03$; Figure 3a; Figure S3a,b). Omnivores (*Nelusetta ayraud*) attacked domes only in temperate sites (Figure S3c), while herbivores performed few attacks in tropical sites. Different species of piscivores (i.e. blacktip reef shark and coral trout) were observed at the same time around the domes in tropical sites.

Four trophic groups inspected the domes in tropical ecosystems, while three trophic groups inspected temperate reefs (Figure 3b), although these were not different between regions (GLMM, effect of region, $p=0.19$, Table S2). Only two trophic groups inspected the domes in both regions: piscivores, which were more often inspected by predators in tropical compared to temperate sites (GLMM, effect of region, $p<0.01$), and planktivores, inspections by which did not differ between regions (GLMM, effect of region, $p=0.82$). In temperate sites, omnivores inspected the domes the most. We found no

species attacking or investigating the domes with no fish inside in either tropical or temperate reefs.

4 | DISCUSSION

The natural processes leading to marine predation events are difficult to observe due to the logistical challenges of underwater fieldwork. We designed the "predation domes" to have a better understanding of marine predation, where death is not an endpoint. Our method successfully isolates piscivorous behaviours from other forms of predation, as demonstrated by piscivores and omnivores dominating attacks on domes.

Our field test using predation domes shows that piscivores are attracted to the experiment and displayed predatory behaviours such as circling or striking, with twice the number of attacks at the tropical sites. This higher number of piscivorous attacks in tropical sites is consistent with the hypothesis that predation pressure is highest in lower latitudes (Freestone et al., 2021; Schemske et al., 2009). However, high predation rates have been also reported in higher latitudes (Roesti et al., 2020; Whalen et al., 2020). These studies revealed predation by species from multiple trophic groups, and the lack of standardized methods used between studies is a potential reason for the mixed evidence, which our novel method seeks to address.

In studies using squidpops, predation is typically driven by multiple trophic groups including planktivorous and omnivorous fish as well as invertebrates (i.e. Duncan et al., 2019; Musri et al., 2019), and may not be capturing what we would consider as predatory interactions/piscivory. In contrast, our results showed that both omnivores and piscivores attacked the dome, suggesting it provides a more reliable proxy of piscivory. Squidpops may be better suited to quantify consumption intensity across several trophic groups (Lefcheck et al., 2021; Ritter et al., 2021) and have the added convenience that allows global comparisons (Duffy et al., 2015; Whalen

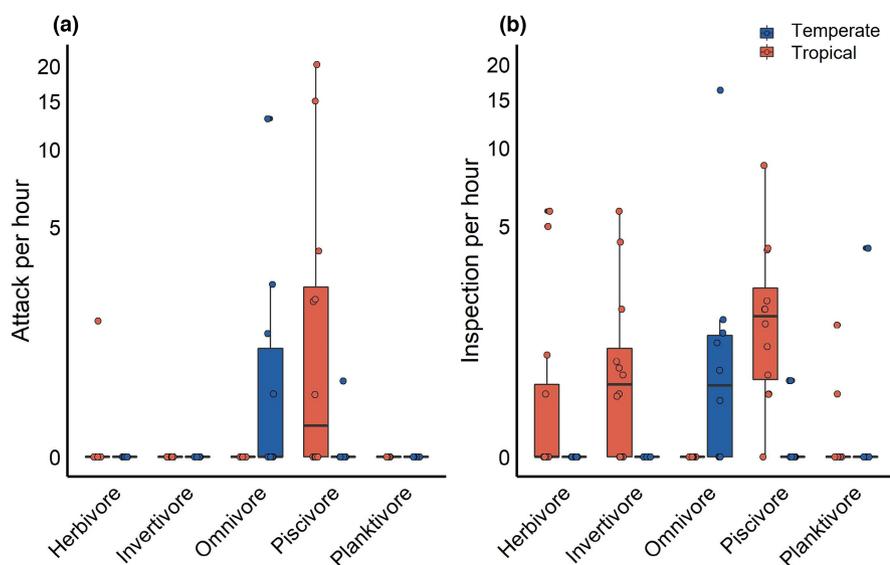


FIGURE 3 Fish species behaviour using the predation domes in tropical (Lizard Island) and temperate (Sydney) regions: (a) attack per hour and (b) inspection per hour. Each dot represents the individual dome-level value. Note that y-axes are on log scale. [Corrections added on 24 June 2023, after first online publication: Figure 3 has been updated to include a colour key.]

et al., 2020). Our results show that predation domes may represent an ethical and complementary approach to measure predation to better represent piscivory.

Filming the predation assays using the domes allows observations of piscivory events in the wild while also providing a record of the environmental context (e.g. presence of other species) and eliminating disturbance from divers (Dickens et al., 2011). The video footage recorded shows different prey and predator behaviours that may be difficult to observe otherwise. For example, we observed a blacktip reef shark attacking the dome on Lizard Island for more than 3 min, which appeared to prevent the approach of a coral trout (also a predator). These observations provide opportunities to better understand interactions between predators, as has been explored in terrestrial species. For example, foxes can be attracted to the odour of their competitors and help in food localization (Banks et al., 2016). On the other hand, competitors' odour can result in a decrease in predation by foxes (Leo et al., 2015).

We also observed herbivores approaching the domes and displaying different behaviours, such as touching the dome several times and raising their spines. While this may look like an attack, it is more likely to be a territorial defence, as most fishes displaying this behaviour belong to the Pomacentridae family within which aggressive territorial behaviour is common (Figure S4; Osório et al., 2006). While this type of behaviour may be possible to see in other filmed assays, our predation dome experiment shows a complementary way to observe multiple competitive interactions.

5 | CONCLUSIONS AND CAVEATS

Our predation domes provide a new approach to measure predatory behaviour. Further assays with greater replication would allow formal testing of differences in piscivory among regions and in contrast to other methods. One of the caveats of this methodology is the lack of ability for the prey to escape (Aronson et al., 2001), potentially leading to an overestimation of predation (Aronson & Heck, 1995). While this is a limitation, the presence of olfactory and visual cues and recording behaviours while swimming within the dome are nevertheless improvements when compared to tethered assays. Future experiments that provide shelter within the domes could be a way to measure prey escape and present more natural visual cues to potential predators. The method we describe here is intended as a starting point to better understand biotic interactions.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed methodology; M. Paula Sgarlatta collected the data; M. Paula Sgarlatta and Alistair G. B. Poore analysed the data. M. Paula Sgarlatta led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest to the content, authorship and/or publication of this article.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code are publicly available in Zenodo <https://doi.org/10.5281/zenodo.8022081> (Sgarlatta et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Different parts of the dome.

Figure S2. Experimental design of the predation assay.

Figure S3. Different predator species around the dome.

Figure S4. *Dischistodus prosopotaenia* (Honey-head damselfish) raises its spines probably to defend its territory.

Table S1. List of species interacting with predation domes.

Table S2. Analysis of deviance table (type II Wald chi-square tests) for the Generalized Linear Mixed Models.

Text S1. Predation dome construction.

Text S2. Essential equipment needed and step-by-step for using the dome in the field.

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