

## ARTICLE

## Coastal and Marine Ecology

# The sunflower sea star reduces grazing rates of purple sea urchins dependent upon urchin starvation state

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**Abstract**

Ecosystem function is maintained in part by direct species interactions, but indirect interactions and non-consumptive effects may be of equal ecological importance. Along the west coast of North America, the recent population collapse of the predatory sunflower sea star *Pycnopodia helianthoides* has been implicated in the proliferation of the purple sea urchin *Strongylocentrotus purpuratus*, and a concurrent decline in kelp canopy cover in several locales. Recent work began to quantify the predation rates effects (i.e., direct consumptive effects) of *Pycnopodia* on sea urchins that may lead to density-mediated indirect effects on kelp. However, the importance of non-consumptive effects on urchin behavior and the possible trait-mediated indirect effects of *Pycnopodia* on kelp are not well understood. This leaves a critical gap in our knowledge about how these predators may be controlling grazer populations and, indirectly, primary production by macroalgae in nearshore habitats. We measured the non-consumptive behavioral effects of *Pycnopodia* on *S. purpuratus* in the laboratory including grazing rates, feeding behavior, and movement of starved versus fed urchins, the latter simulating urchin metabolic conditions within urchin barrens. We found that the presence of a waterborne *Pycnopodia* cue reduced the grazing rate of fed urchins by 50% over short (~24 h) time scales. In contrast, starved urchins consumed kelp and did not exhibit an escape response in the presence of a *Pycnopodia* cue. This study highlights a trait-mediated indirect interaction between *Pycnopodia*, *S. purpuratus*, and kelp, showing how the urchin response to a predator cue may differ based on urchin metabolic conditions or ecosystem state, and helps clarify the positive role of *Pycnopodia* on kelp forest health.

**KEYWORDS**

antipredator response, grazers, kelp forest, landscape of fear, *Pycnopodia helianthoides*, *Strongylocentrotus purpuratus*, trait-mediated indirect interaction, trophic ecology

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## INTRODUCTION

In marine ecosystems, non-consumptive effects (NCEs) have been implicated in a range of predator–prey interactions (Werner & Peacor, 2003). Predatory cues propagate through these systems via various pathways such as visual, auditory, or chemosensory pathways. Chemosensory cues proliferate as water flow carries the “cue” of the predator through the water and can change the behavior of organisms across the seafloor as they encounter it (Kats & Dill, 1998). As such, a single predator may have a “larger” effect (i.e., multiple prey species responding) via this non-consumptive interaction than with consumption of a single prey item. Chemosensory cues can act as NCEs and may trigger various physiological and behavioral responses in the prey. Physiological responses may include metabolic changes (Hawlena & Schmitz, 2010), reduced fecundity (Bourdeau et al., 2016), and impaired growth (Werner & Peacor, 2003), while behavioral changes can include reduced foraging time (Werner & Peacor, 2003), increased crypsis (Scheibling & Hamm, 1991), and more frequent escape response (Freeman, 2006). All these effects can be experienced individually, or simultaneously, and can have serious consequences for the prey species. The frequency of encounters with a predator cue may also produce various responses in the potential prey. Continuous exposure to a predator cue could result in a prolonged high-stress state on the one hand, or gradual habituation on the other (Dehaudt et al., 2019; Van Dievel et al., 2016). In addition, the preexisting physiological state of an organism can modulate the specific response to a predator. This is seen, for example, when a hungry prey species is more willing than a fed one to risk predation in order to obtain food (Vadas et al., 1994).

NCEs of predators can scale up to the ecosystem level as an analog to the classic trophic cascade based on consumptive predation pressure (e.g., Ripple et al., 2016). Frequently, trait-mediated indirect interactions (TMIIs) act via NCEs through the modification of a grazing prey species’ feeding behavior, relieving the grazers’ food source from grazing pressure (Gravem & Morgan, 2019; Haggerty et al., 2018). The so-called “ecology of fear” can have dramatic effects on ecosystem productivity, changing foraging times and grazing rates of important consumers in a suite of habitats (Brown et al., 1999).

The recent population collapse of the generalist invertebrate mesopredator *Pycnopodia helianthoides* (hereafter *Pycnopodia*) due to sea star wasting disease has been implicated as a contributing factor to the proliferation of the grazing purple urchin, *Strongylocentrotus purpuratus*, after its release from *Pycnopodia* predation across much of the west coast of North America (Burt et al., 2018; Galloway et al., 2023; Hamilton et al., 2021;

Harvell et al., 2019). This effect has been most pronounced along the central and southern end of the range of both *Pycnopodia* and *S. purpuratus* along the Oregon and California coasts, although similar patterns have been observed between *Pycnopodia* and red urchins (*Mesocentrotus franciscanus*) and green urchins (*Strongylocentrotus droebachiensis*) farther northward into British Columbia (Burt et al., 2018; Rogers-Bennett & Catton, 2019; Schultz et al., 2016).

*Pycnopodia* preys upon a variety of sea urchins, including *S. purpuratus* (Herrlinger, 1983; Mauzey et al., 1968; Shivji et al., 1983). *S. purpuratus* employ a less effective defense strategy against *Pycnopodia* predation compared to other sympatric urchin species (esp. *M. franciscanus*), typically relying on their pedicellaria and fleeing response to deter a predator rather than using their spines, which may make them more prone to predation (Moitza & Phillips, 1979). NCEs from *Pycnopodia* chemical cues may add to the response of urchins in addition to removal via direct consumption (Freeman, 2006). *Pycnopodia* is only one among a suite of potential predators of *S. purpuratus*, although the geographic extent and identity of urchin predators change across their range. The spiny lobster (*Panulirus interruptus*) and California sheepshead (*Semicossyphus pulcher*) are constrained to the southern end of *S. purpuratus*’s range (Tegner & Dayton, 1981), while the wolf eel (*Anarrhichthys ocellatus*; Marliave, 1987) and sea otter (*Enhydra lutris*; Smith et al., 2021) are found in low densities or are not uniformly distributed across the seascape. As such, the coincident population decline of *Pycnopodia* has been implicated in the concurrent increase in urchin populations in the North American west coast, though additional factors including warming water and increased urchin recruitment are also implicated in the recent urchin population surge (Burt et al., 2018; Rogers-Bennett & Catton, 2019).

The decline of kelp forests by up to >90% across the central North American west coast, particularly in Northern California, has been attributed, in part, to predation release on grazing urchins, and has been suggested to be a trophic cascade (Rogers-Bennett & Catton, 2019; Schultz et al., 2016). The resulting mosaic of kelp forests and urchin barrens is marked by decreased primary productivity, low food web complexity, and a reduction in abundances of economically important species such as abalone (Filbee-Dexter & Scheibling, 2014; Rogers-Bennett & Catton, 2019; Schultz et al., 2016). Urchins within these barrens can maintain this alternate stable state when the reduced kelp biomass leads to starvation, and constant grazing inhibits the regrowth of kelp and other macroalgae (Dolar & Edwards, 2021; Estes & Duggins, 1995; Filbee-Dexter & Scheibling, 2014; Spindel et al., 2021).

Although the direct consumptive effect of *Pycnopodia* on urchins is an important pathway of grazer control (Bonaviri et al., 2017; Galloway et al., 2023), behavioral responses by urchins to predation cues suggest that NCEs may also play a key role in suppressing sea urchin grazing behavior (Bernstein et al., 1981; Duggins, 1983; Lee et al., 2016; Moitza & Phillips, 1979). In addition, higher concentrations of urchins in urchin barrens can increase their hunger state and their response to food and predator cues, resulting in potentially complex behaviors (Parnell et al., 2017). However, the potential for *Pycnopodia* to have NCEs on sea urchin behavior and grazing rates has not been quantified. Understanding how and to what degree *Pycnopodia* may alter sea urchin grazing can provide important insights into their role in maintaining healthy kelp forest ecosystems through TMII. To address these knowledge gaps, we asked the questions: (1) Do NCEs between *Pycnopodia* and *S. purpuratus* alter the feeding rates of the urchins (*feeding experiment*)? (2) Does the hunger state of *S. purpuratus* change their response to food in the presence of a predator cue (*starvation experiment*)?

## MATERIALS AND METHODS

### Feeding experiment organism collections

Purple sea urchins (*S. purpuratus*) were collected at Lopez Island (48.4558, -122.9383) in the San Juan Archipelago of Washington State on September 11, 2020 (71 urchins) through a permitting arrangement between the Friday Harbor Labs and Washington State (Washington State House Bill 68, R.C.W.28.77.230, 1969 Revision R.C.W. 28B.20.320). Collections were made by hand on SCUBA between 3 and 8 m below mean lower low water (MLLW) in bull kelp (*Nereocystis luetkeana*) stands on bedrock. Urchins were then held for two days in flow-through sea water tanks (60 × 90 × 30 cm width × height × depth) before experimentation beginning on September 13, 2020. Urchins were shaded from direct sunlight and fed *N. luetkeana* blade tissue ad libitum while in holding.

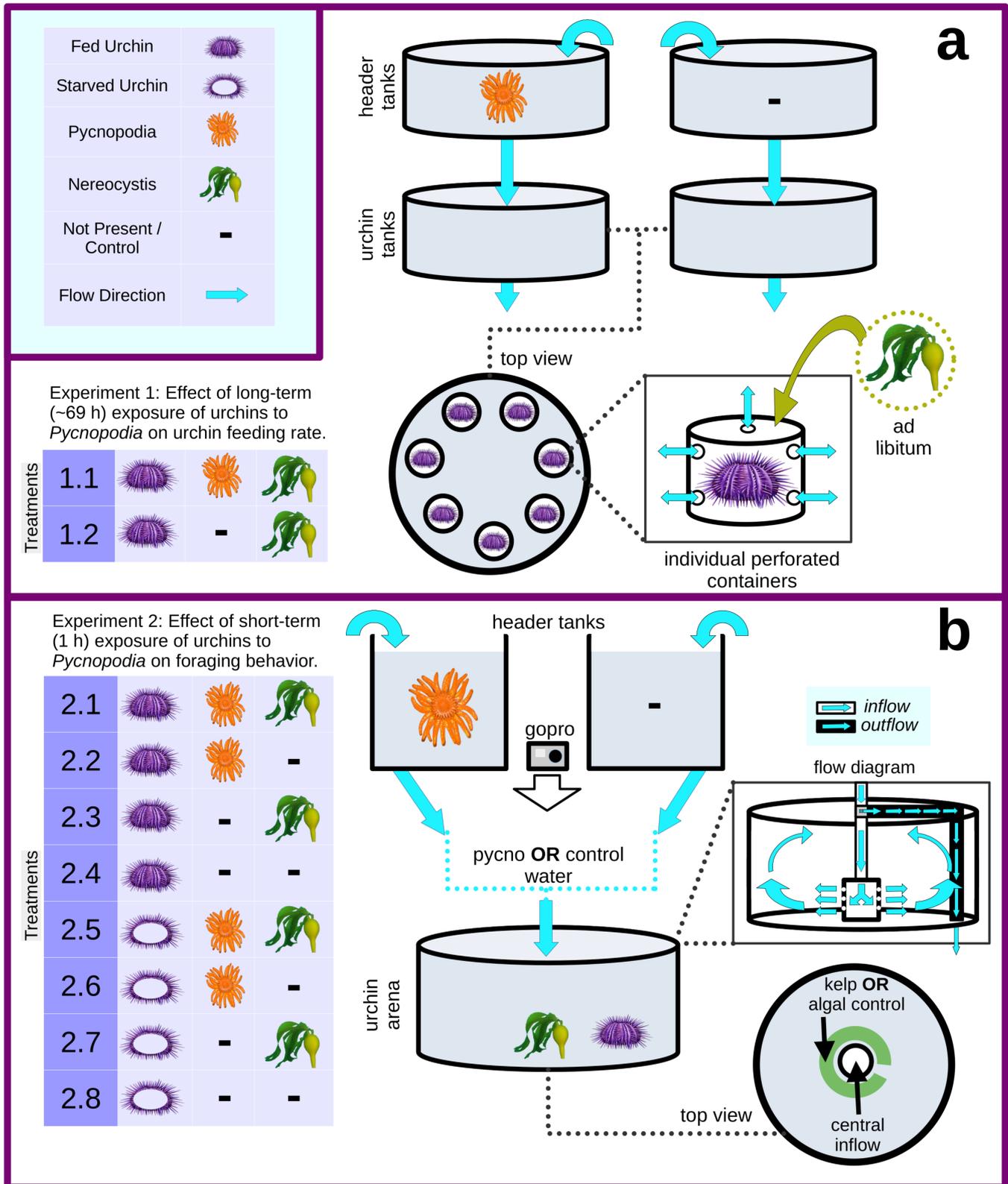
*Pycnopodia* were collected at Goose Island in the San Juan Archipelago (48.4575°, -122.9544°) on July 29, 2020 at a depth of 6 m below MLLW through the same permitting as above. It was important to minimize collection of *Pycnopodia* due to the very low abundance of this species after the sea star wasting decline and to minimize possible local, ecological effects of removing what is now a threatened species per the IUCN (Gravem et al., 2021). *Pycnopodia* were transported following lab and handling protocols described in Hodin et al. (2021) in covered 5-gallon buckets filled with seawater and placed in shaded flow-through seawater tanks for 6 weeks (120 × 40 × 45 cm width × height × depth) prior to

experimentation. They were fed a maintenance diet of two mussels (*Mytilus* spp.) every other day prior to experimentation, and in-between trials during experimentation following lab and handling protocols described in Hodin et al. (2021).

### Feeding experiment setup

To determine whether there are NCEs of *Pycnopodia* on *S. purpuratus* feeding rates, five replicate feeding trials were run between September 13 and October 2, 2020, each lasting from 51 to 69 h in shaded outdoor tanks. Across all trials, two different individual *Pycnopodia* were used to generate the chemical cue for the *Pycnopodia* water treatments (both *Pycnopodia* were approximately the same size, ~42 cm in diameter). All urchins ( $n = 71$ ) were used in the experiment only once to ensure independence of replicates. *S. purpuratus* test diameters were measured with hand calipers to the nearest millimeter, and urchins were assigned to two experimental groups (*Pycnopodia* exposure or control). The experimental setup, including organism arrangement, tanks, and plumbing, was modified after the initial Trial 1 to reduce stress on the *Pycnopodia*, but the effective predator cue treatments remained consistent between trials, so they were analyzed as replicate experiments. For Trial 1, five urchins were placed in each of three tanks (circular: 50 cm depth × 104 cm diameter); one of these tanks contained a caged *Pycnopodia* so that chemical cues were released into the tank but no physical interaction with the urchins was possible. The other two tanks served as controls (one a “cage control” with an empty predator enclosure, the other without an enclosure) without a *Pycnopodia*. For Trials 2–5, 14 urchins were evenly distributed into two tanks (seven urchins per tank; circular: 30 cm depth × 104 cm diameter). One of these tanks received a predator cue via effluent from a header tank containing *Pycnopodia* (Figure 1a) to the urchin tank while the other served as a control and received plain seawater (no cue). Urchins within a tank in all treatments were individually contained within buckets perforated with multiple small holes on the sides and top of each container (<1 cm diameter each) to maintain water flow within each, while preventing interactions among urchins in the tank (Figure 1a). Water flow rate into experimental tanks was  $3.89 \pm 0.46$  L min<sup>-1</sup>, water temperature during the experiment was  $10.0 \pm 0.16$ °C, salinity  $30.54 \pm 0.81$  ppt, as measured by the Friday Harbor Labs Ocean Observatory, and ambient light was an 11:13 h light:dark cycle.

Each urchin in the individual tank buckets was fed 12 standardized circular pieces of kelp “confetti” (21 mm diameter) created by using a cork punch on



**FIGURE 1** Setup for (a) urchin feeding and (b) urchin movement experiments. All treatment combinations are shown for each experiment in tables. The urchin grazing behavior setup depicts the “fed urchin with algae” treatment, and the flow diagram shows general flow created by water inflow located at the center-bottom of the arena, and outflow at the center-top. Two identical “urchin arenas” were used for the grazing behavior experiment to allow for tank cleaning between trials, but only one is shown here for clarity.

vegetative *N. luetkeana* (hereafter kelp) blade tissue. A subsample of kelp confetti was weighed at the beginning and end of the experiment to estimate the biomass of kelp consumed, and a subset of trials ( $n = 4$ ) contained additional control confetti held separately from urchins that were weighed before and after each trial to detect changes in confetti weights that were not related to urchin feeding. Urchins in each experimental unit were fed kelp confetti ad libitum and their consumption rates tracked by counting the number of intact confetti pieces and estimating proportion of partially consumed pieces present at three time points per day (08:00, 14:00, 20:00) for up to 3 days. Kelp confetti had a mean biomass of  $0.341 \pm 0.030$  g per disk ( $n = 49$ ), and control confetti weights were not statistically different before and after trials (linear mixed-effects model [lme], denominator  $df = 92$ ,  $t = 0.45$ ,  $p = 0.65$ ) and so were not used as a correction factor when considering biomass loss. Any consumed confetti were replaced with fresh confetti to maintain a total of ~12 pieces per urchin. Trial 1 had to be stopped after 51 h as the experimental conditions induced a stress response in the *Pycnopodia*, while all remaining trials were run for 69 h.

## Starvation experiment organism collections

*S. purpuratus* were collected at Lopez Island ( $48.4558^\circ$ ,  $-122.9383^\circ$ ) in the San Juan Archipelago of Washington State on June 11, 2021 (49 urchins) under Friday Harbor Laboratories (FHL) permitting (see above). Collections were made by hand using the same protocols as above, and urchins were then held in flow-through seawater tanks (circular: 30 cm depth  $\times$  104 cm diameter) before being moved into the experimental tanks (rectangular: 60  $\times$  90  $\times$  30 cm WHD).

For the starvation experiment, a different *Pycnopodia* individual (approximately 40 cm diameter) was collected under the FHL docks ( $48.54532$ ,  $-123.01192$ ) on July 3, 2021 via SCUBA at a depth of 4 m below MLLW under the FHL permit. This single *Pycnopodia* was used to generate the predator-cue treatment water for this experiment to minimize effects of collection on wild populations of this endangered species. The sea star was transported in a shaded 5-gallon bucket filled with seawater and then held in a partially shaded flow-through seawater tank (120  $\times$  40  $\times$  45 cm WHD) before experimentation.

## Starvation experiment setup

The diameters of all *S. purpuratus* ( $n = 49$ ) were measured using calipers and then separated haphazardly into

two groups: “fed” and “starved.” “Fed” urchins were fed kelp, ad libitum, and starved urchins were not fed for seven weeks while in holding. This time frame has been previously documented to result in different gonadal conditions among urchin feeding groups (Galloway et al., 2023). At the end of the starvation period, all urchins were used in individual trials, placing starved ( $n = 25$ ) and fed urchins ( $n = 24$ ) separately into one of two identical circular aquaria “arenas” (30 cm depth  $\times$  104 cm diameter), respectively, in which individual urchin movement and behavior was tracked over 1 h. The 1-h time frame was selected to capture the short-term (i.e., in minutes) response of the urchins to the cue. There were a total of eight treatments in a factorial design crossing urchin treatment (fed vs. starved), *Pycnopodia* cue (cue vs. no cue), and kelp treatment (kelp vs. kelp replica; Figure 1b). The *Pycnopodia* cue was delivered as effluent from a header tank containing one *Pycnopodia* (120  $\times$  40  $\times$  45 cm WHD) and “control” no-cue water from a header tank with no *Pycnopodia* (same dimensions). In kelp-present trials, a 55  $\times$  4 cm kelp strip was wrapped around an inverted perforated sampling cup through which the header source water flowed into the experimental arena. In no-kelp control treatments a kelp replica (55  $\times$  4 cm plastic sheeting material) was wrapped around the entry point of the header water source. In all cases, the centrally placed header *Pycnopodia* cue inflow and kelp/replica location is referred to as the “cue source.”

All inflow of water during each 1-h trial came from the header tank. Water temperature ( $12.9 \pm 1.19^\circ\text{C}$ ), and light flux ( $1922 \pm 1166$  lx) were measured using a HOBO Tidbit v2 Data Logger (Onset, Bourne, MA, USA), and salinity ( $31.1 \pm 1.46$ ) was measured using a hand refractometer. Experimental flow rates were standardized to  $2.5 \text{ L min}^{-1}$ . Patterns of flow diffusion within each experimental unit were visualized intermittently between trials using fluorescein dye injected at the outflow of the header tank to confirm constant flow and even distribution of the cue. Each treatment was run at least six times with naive urchins for all eight possible combinations, and one trial was rerun due to a malfunctioning camera, for a total of 49 individual trials. Urchins were observed in 1-min intervals for each 1-h trial for the following target behaviors: movement (not moving or moving); interacting with central cue (interacting, not interacting); where interacting was defined as at least one tube foot touching the cue source (kelp or kelp replica) and is used as proxy for food-seeking behavior. Quantity of kelp consumed (in trials with kelp) was calculated as the reduction in surface area of experimental kelp strip from known dimensions after the trial was concluded using photos taken with a scale bar and processed in ImageJ

(Schneider et al., 2012). Experimental arenas were drained, rinsed with fresh water, and scrubbed by hand between all trials to eliminate cross-contamination of chemosensory cues.

Trials were also recorded with GoPro cameras (HERO4 Silver; San Mateo, CA, USA) with a medium FOV setting. Videos of each trial were processed in the video analysis software Tracker (Brown et al., 2020) using the AutoTracking function. The path of each urchin was extracted as  $x$  and  $y$  coordinates in 3.3-s increments and calibrated to a bullseye of known dimensions centered underneath the urchin via a center of mass function in Tracker to maximize accuracy. Total distance traveled was calculated for each urchin using the R package *adehabitatLT* (Calenge, 2006).

## Statistical analysis

Data were summarized, quality controlled to detect any data entry errors or erroneous values, and visualized using R (R Core Team, 2022) in RStudio (RStudio Team, 2022) with the *tidyverse*, *adehabitatLT*, and *viridis* packages (Calenge, 2006; Garnier et al., 2021; Wickham et al., 2019). Statistical analyses were performed in R with the *lme4* package (Bates et al., 2015) and in JMP v17.0.0 (SAS Institute Inc., Cary, NC, USA). Both experiments used a restricted number of *Pycnopodia* to generate the treatment with a chemical cue. It was very difficult and prohibitively time-consuming to find *Pycnopodia* at the time of this experiment. It should also be noted that we did not wish to introduce replicate “treatments” of predator signals when at all possible as *Pycnopodia* were scarce, and it would be difficult to collect enough for robust statistical power differentiating between individual *Pycnopodia* signals.

## Feeding experiments

Differences in mean amount of kelp consumed per urchin per hour between treatments over the course of each trial were tested with a linear mixed-effects model. The response variable of mean kelp consumed per hour was  $\log(x + 1)$  transformed to address variance heteroscedasticity. Fixed effects included: treatment, hour since beginning of the trial, and their interactions. Random effects included: urchin identity nested within treatment and trial tank, and trial tank nested within treatment, to account for any variation not attributed to the fixed effects.

## Starvation experiment

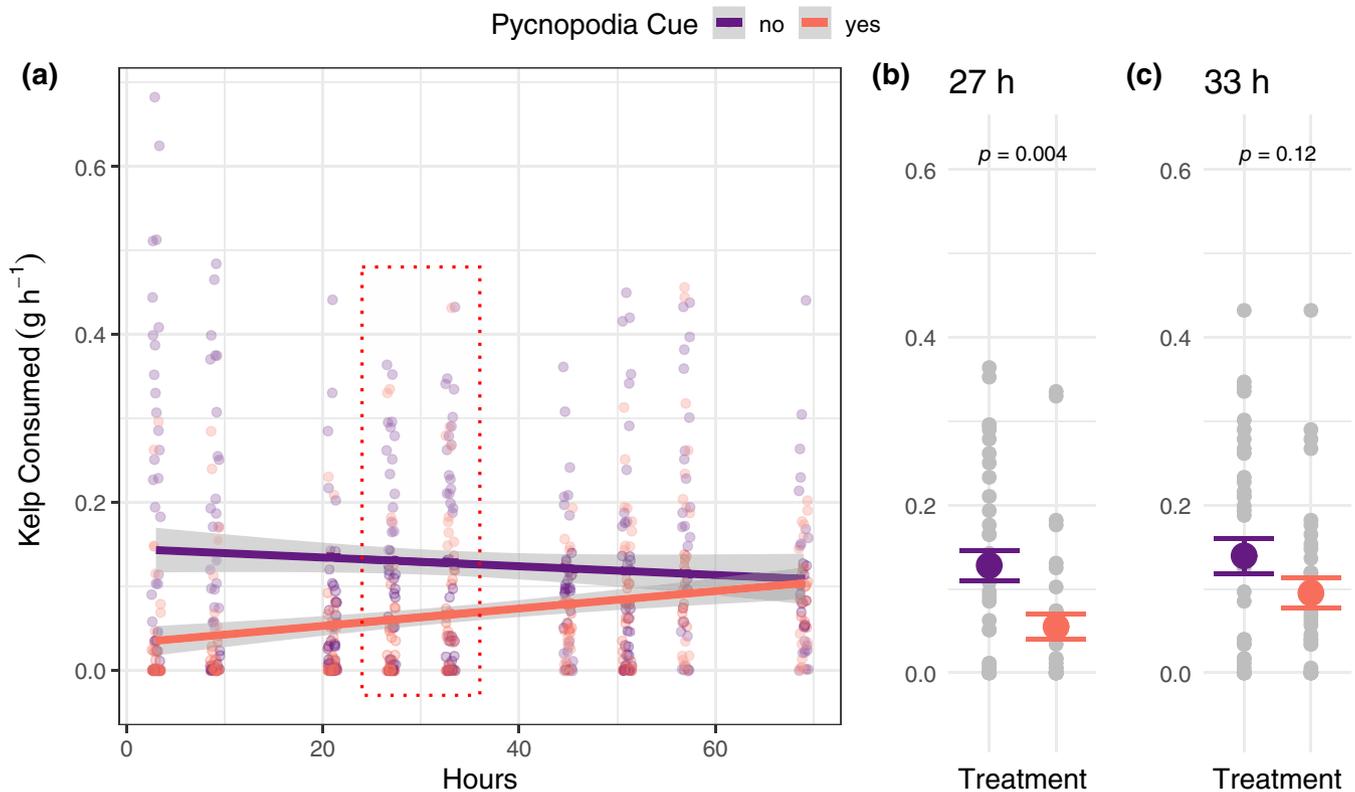
Urchin movement behaviors were averaged over 5-min increments to detect any changes in behavior over the course of each individual trial. Behaviors were assigned binary classifications for each urchin, with 0 = not moving or not interacting, and 1 = moving or interacting to give proportion of time performing each behavior within each increment. Both proportion of time moving, and proportion of time interacting were tested with a linear fixed-effects model. Fixed effects for both responses included: urchin status (fed, starved), *Pycnopodia* cue (present, absent), kelp cue (present, absent), time increment (5–60 in 5-min steps), and the full interaction of all these fixed effects. Random effects included trial arena nested within urchin status, *Pycnopodia* cue, and kelp cue, to account for any variation not attributed to the fixed effects. Feeding on kelp, when it occurred, was tested with a linear model.

Total distance traveled by urchins during each trial was tested with linear fixed-effects models. Fixed and random effects were the same as above; however, time increment was not included as the resolution of the data was only on the level of a per-trial total.

## RESULTS

### Feeding experiment

Urchins exposed to a waterborne *Pycnopodia* cue consumed 53% less kelp per hour on average ( $0.127 \pm \text{SE}$   $0.005 \text{ g h}^{-1}$ ) than urchins not exposed to a *Pycnopodia* cue ( $0.067 \pm \text{SE}$   $0.008 \text{ g h}^{-1}$ ) across all trials (lme, denominator  $df = 8.64$ ,  $t$  ratio = 2.64,  $p = 0.0279$ ; Figure 2a; Appendix S1: Table S1). There was a significant interaction between cue treatments and hours since the beginning of the trial (lme, denominator  $df = 538.9$ ,  $t$  ratio =  $-4.96$ ,  $p < 0.001$ ), reflecting differing changes in consumption rates from the beginning to the end of each trial based on treatment; however, consumption was highly variable across all treatments. Generally, urchins exposed to a *Pycnopodia* cue increased their rate of consumption over time (3 h:  $0.039 \pm 0.013 \text{ g h}^{-1}$ ; 69 h:  $0.084 \pm 0.012 \text{ g h}^{-1}$  [mean  $\pm$  SE]) while urchins not exposed to a *Pycnopodia* cue decreased their rate of consumption (3 h:  $0.191 \pm 0.032 \text{ g h}^{-1}$ ; 69 h:  $0.111 \pm 0.020 \text{ g h}^{-1}$ ). Consumption rates became indistinguishable after 27 h (Figure 2b,c). Mean hourly consumption of kelp at 27 h was  $0.055 \pm 0.015 \text{ g h}^{-1}$  (*Pycnopodia* cue) and  $0.128 \pm 0.018 \text{ g h}^{-1}$  (no *Pycnopodia* cue; lme,  $df = 69$ ,  $t$  ratio =  $-3.017$ ,  $p = 0.00357$ ), and at 33 h was  $0.095 \pm 0.018 \text{ g h}^{-1}$



**FIGURE 2** (a) Hourly consumption of kelp by urchins that were exposed (light orange) and not exposed (dark purple) to a *Pycnopodia* cue across the 69-h experimental period. Regression lines show the best fit and 95% CI for each group. Differences in hourly feeding rate (dotted red box) are shown at (b) 27 h and (c) 33 h, the time at which feeding rates become indistinguishable between the two treatments. Error bars in panels b and c represent SE.

(*Pycnopodia* cue) and  $0.139 \pm 0.021 \text{ g h}^{-1}$  (no *Pycnopodia* cue; lme, df = 69,  $t$  ratio =  $-1.574$ ,  $p = 0.12$ ).

### Starvation experiment

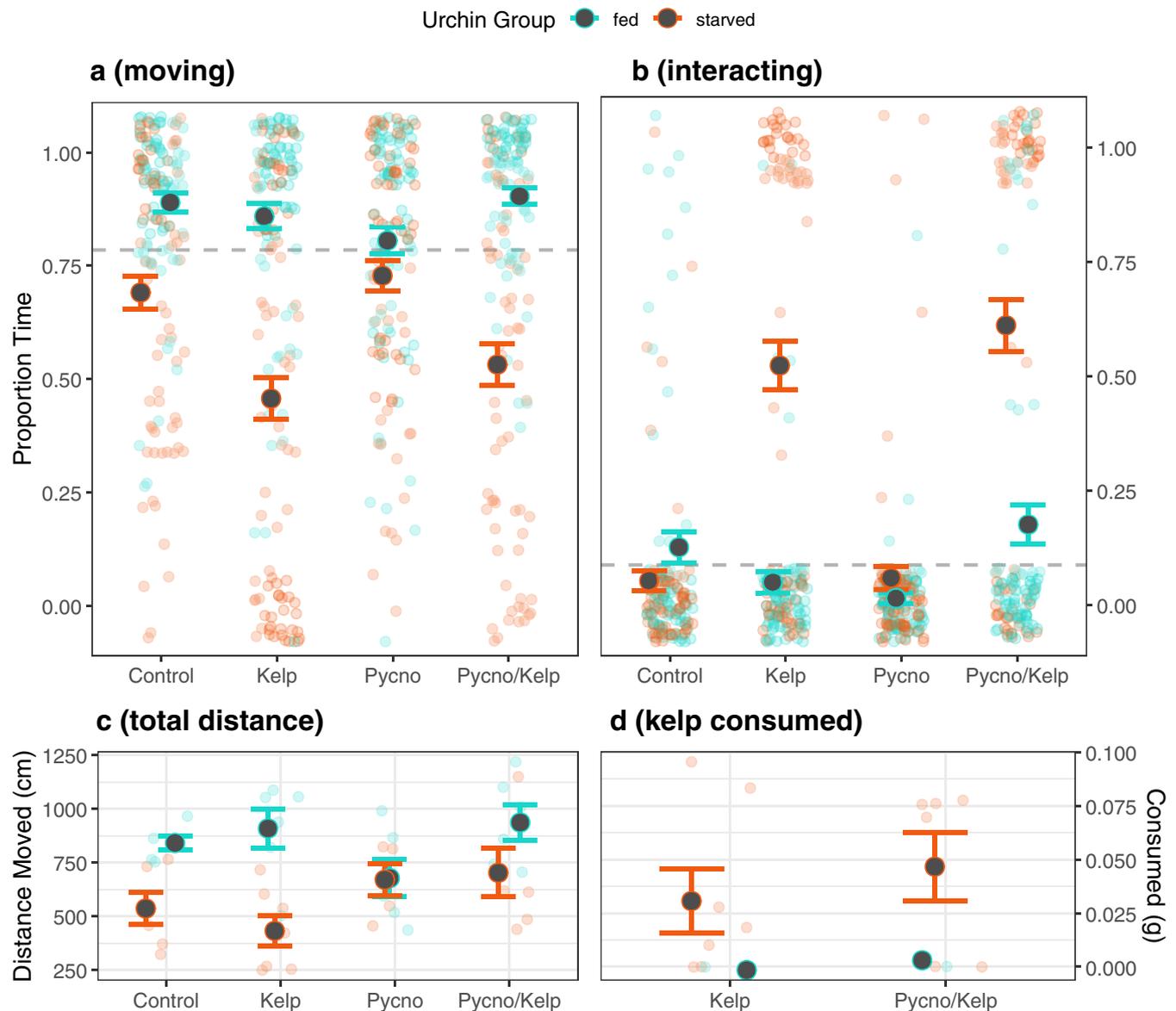
Across all treatments, starved urchins spent an average of  $59.8 \pm 5.2\%$  of the experiment moving within the arena, while fed urchins spent an average of  $86.7 \pm \text{SE } 1.8\%$  of the experiment moving (Figure 3a). Urchin status (fed, starved) was the primary single fixed factor to drive differences in time spent moving across all treatments (lme, denominator df = 41,  $t$  ratio = 4.83,  $p < 0.0001$ ; Appendix S1: Table S2). Various interactions between urchin status and other effects were also statistically important, notably urchin status and algal treatment (lme, denominator df = 41,  $t$  ratio =  $-2.20$ ,  $p = 0.0334$ ), and urchin status and time (lme, denominator df = 531,  $t$  ratio = 3.14,  $p = 0.0018$ ). *Pycnopodia* cue was only significant in an interaction with urchin status and time (lme, denominator df = 531,  $t$  ratio = 2.05,  $p = 0.0407$ ).

Time spent interacting varied widely across treatments with starved urchins spending an average of  $32.1 \pm 8.3\%$  of their time interacting, while fed urchins spent

only  $9.2 \pm 3.1\%$  of their time interacting (Figure 3b). Starved urchins in the kelp-present treatment spent much more time interacting than other groups, regardless of *Pycnopodia* cue ( $52.6 \pm 17.0\%$  cue not present;  $61.4 \pm 19.9\%$  cue present). Single fixed effects driving observed patterns of interacting included urchin status (lme, denominator df = 41,  $t$  ratio =  $-2.89$ ,  $p = 0.0062$ ), algal treatment (lme, denominator df = 41,  $t$  ratio =  $-3.67$ ,  $p = 0.0007$ ), and time (lme, denominator df = 531,  $t$  ratio =  $-2.74$ ,  $p = 0.0063$ ; Appendix S1: Table S2). Various interactions were observed between effects, though *Pycnopodia* cue was not included in any of those interactions.

The total distance traveled by urchins was different between starved ( $576 \pm \text{SE } 46 \text{ cm}$ ) and fed ( $842 \pm 42 \text{ cm}$ ) urchins (lme, denominator df = 4.355,  $t$  ratio = 3.86,  $p = 0.0154$ ; Figure 3c; Appendix S1: Table S2), and no other fixed effect other than urchin state contributed to those differences.

Only starved urchins were ever observed to consume the kelp in trials that contained the cue, and though they tended to consume more when the *Pycnopodia* cue was present ( $0.05 \pm 0.024 \text{ g}$ ) than when it was not ( $0.03 \pm 0.01 \text{ g}$ ), this difference was not statistically significant (Figure 3d).



**FIGURE 3** Proportional time spent by starved (light teal) and fed (dark orange) urchins across all treatment combinations in the starvation experiment for (a) the proportional time moving and (b) the proportional time interacting. Large circles are overall means per group per treatment, and transparent small circles are 5-min increment averages for individual urchins (12 points per urchin = 60-min trial). Horizontal dashed lines indicate mean proportional time spent doing each behavior for all urchins in the behavioral control treatment (no *Pycnospodia*, no kelp). (c) Total distance traveled in each of the four treatments by starved (light teal) and fed (dark orange) urchins. Large circles indicated group mean for urchin conditions (starved, fed), and smaller points indicated values for individual urchins within each treatment. (d) The total quantity of kelp consumed in kelp treatments were not different between *Pycnospodia* cue treatments between starved urchins. Fed urchins never consumed kelp in any treatment. Error bars represent SE.

## DISCUSSION

We found that waterborne cues of the sunflower sea star *Pycnospodia* decreased short-term feeding rates (~27 h) of the purple sea urchin *S. purpuratus*, and changed urchin movement patterns through NCEs. In 1-h behavior trials, urchin feeding behavior was further modified by the starvation state of the urchins, with starved urchins moving less than fed urchins, primarily to feed on kelp regardless

of predator cue presence or absence. Urchins that had been starved for 7 weeks, and were in a metabolic state similar to those in barrens, fed on kelp regardless of a *Pycnospodia* cue. This suggests that starved urchins in urchin barrens may continue to feed on kelp even as *Pycnospodia* populations begin to rebound, which may inhibit the role of NCEs on the recovery of kelp forest habitats from an urchin barren state. However, urchins that are not in a starved state (i.e., in kelp forests), may

reduce their feeding rate to engage in predator avoidance strategies such as fleeing (Moitza & Phillips, 1979), sheltering under larger conspecifics (Nishizaki & Ackerman, 2007), or crypsis (Scheibling & Hamm, 1991). The current proliferation of *S. purpuratus* across the North American west coast has coincided with kelp declines across much of the same area. Direct consumption of kelp by urchins, suppression of kelp juveniles, and stressors directly associated with climate change, including warming waters, have also been implicated in this decline (Beas-Luna et al., 2020; McPherson et al., 2021; Pfister et al., 2018; Rogers-Bennett & Catton, 2019). The amelioration of a single-origin stressor in the form of over-grazing by urchins, though only one of several multiple stressors, could lower the tipping point for alternate stable states of former kelp forests.

*Pycnopodia* is an important member of a diverse range of benthic marine ecosystems throughout the NE Pacific Ocean, and has been identified as an important mesopredator in kelp forest communities (Burt et al., 2018; Schultz et al., 2016). As *Pycnopodia* begin to recover from sea star wasting disease, they may mitigate the impact of urchins that are overpopulated in places where kelp has been extirpated via direct consumption (Galloway et al., 2023). The present study shows that there is a measurable and significant NCE of *Pycnopodia* on *S. purpuratus* feeding rates and behavior that may benefit kelp, particularly on short time-scales; these NCEs may also have important consequences for kelp ecosystems. As *Pycnopodia* population densities begin to rebound, a larger proportion of grazing sea urchins in subtidal communities will be subject to both direct consumptive and non-consumptive interactions, potentially reducing grazing rates on a population-wide and a per-capita basis. Although the single mass of the average *Nereocystis* individual is ~1200 g (Stekoll et al., 2006), well beyond the feeding capacity of even a dense aggregation of urchins, even small biomass removal, particularly from the stipe of canopy kelps, can reduce kelp resistance to waves and currents, detaching the entire kelp plant and removing it from the system (Duggins et al., 2001). The release of urchins from the direct effects of *Pycnopodia* predation is identified as one causal link leading to kelp forest decline, as *Pycnopodia* may consume up to  $0.68 \pm 0.33$  urchins per day (Galloway et al., 2023). Our work demonstrates that, in addition to this direct consumptive effect, the waterborne cues of nearby *Pycnopodia* likely exert a NCE on urchins by more than halving grazing rates when urchins are not starved. Even if *Pycnopodia* in the field do not directly consume *S. purpuratus* at rates as high as those observed in laboratory settings (Galloway et al., 2023), the NCEs documented here represent an important reduction in urchin feeding

and a potentially important TMII, in which *Pycnopodia* benefit kelp by suppressing urchin grazing.

This study provides a quantitative link between *Pycnopodia* and grazing urchins that provides insight into our knowledge of how *Pycnopodia*-urchin dynamics may play out in the field. Although few other studies have explicitly explored these linkages in natural settings, those that have found evidence that *Pycnopodia* can significantly alter both urchin behavior through elicitation of a multi-urchin “stampede” escape response (Dayton, 1973), and benthic productivity and richness through consumptive and non-consumptive interactions with urchins (Duggins, 1983). Encounter rates and *Pycnopodia* feeding preferences are an important component in these *Pycnopodia*-urchin interactions, though there is nearly no quantitative data on the former, and relatively little on the latter. What we do know of *Pycnopodia* feeding preferences suggests a preference for bivalve and urchin prey, and a tendency to switch between a role as a generalist predator and facultative scavenger (Brewer & Konar, 2005; Mauzey et al., 1968; Shivji et al., 1983). These patterns of consumption may be robust across the geographic range of *Pycnopodia* and suggest wide-scale predation of *Pycnopodia* on urchins that may elicit a community-wide response. However, there is a need to quantify these effects over meaningful scales in order to parse out correlation and causation between *Pycnopodia*-urchin interaction and kelp loss, and this study lays the groundwork for testing observed interactions on larger spatial and temporal scales.

This work also broadens our knowledge of urchin response to NCEs and how direct chemosensory detection of a sea star predator is sufficient to alter an urchin's behavior. Sea urchins are known to be sensitive to chemical cues related to predation, though their response is dose-dependent (Hagen et al., 2002). However, much work to date on the sea urchin response to predation cues has focused on their reaction to damaged conspecifics as an alarm cue, rather than the presence of a predator itself (Belleza et al., 2021; Campbell et al., 2001; Spyksma et al., 2017; but see Matassa, 2010). While this is a good proxy for actively feeding predators that may break or otherwise damage urchins such as sea otters and spiny lobsters, it does not account for the potential effects of predators that are not actively feeding. When the effect of a predator cue has been tested directly on urchins, it has been done with gastropod (*Hexaplex trunculus*) and arthropod (*Panulirus interruptus*) predators (Knight et al., 2022; Pagès et al., 2021). Similar to Knight et al. (2022), we found that starved urchins tended to consume kelp whether a predator was present or not, though their study did detect a difference in consumption between

predator treatments in the case of well-fed urchins, while in our starvation experiment fed urchins did not consume kelp in any treatment, including those without a *Pycnopodia* cue. This difference could be a result of several factors, including differential response to particular predators (*Pycnopodia* vs. lobster), an effect of urchin density cues in treatments (tested individually versus with conspecific cue), or a statistical effect ( $n = 8$  in Knight et al. (2022) vs.  $n = 71$  in this study). In other studies, urchins exposed to gastropod predator cues have been shown to exhibit a more linear and fast movement escape response than urchin movement without the cue (Pagès et al., 2021). This is in contrast with our study, where we did not detect a statistical difference in total distance traveled or proportion of time spent moving in response to a *Pycnopodia* cue between fed and starved urchins. However, starved urchins moved slightly less during the starvation experiment compared with fed ones, and there was a slight reduction in distance traveled when fed urchins were exposed to a *Pycnopodia* cue only. This raises the possibility that the response of urchins to a predator cue is highly variable or dependent upon other factors such as conspecific density, urchin size variation, or shelter availability (Green, 2012; Nishizaki & Ackerman, 2007).

Predator speed and hunting style may also affect the response of urchins to a particular predator cue. Starved urchins moved less than fed urchins regardless of *Pycnopodia* cue presence, though this difference was not significant and was most pronounced when there was no predator cue but with kelp offered. This is most likely a hunger-response by the starved urchins to the kelp cue, which suggests that the non-consumptive waterborne *Pycnopodia* cue was not sufficient to inhibit urchin feeding. This may also be a metabolic consequence of the starved urchins as they are known to divert energy from reproduction into maintenance and need access to food to quickly restore metabolic activity and replenish somatic reserves (Smith & Garcia, 2021). Both the hunger and metabolic consequences of starvation could indicate that food access despite the danger of predation is a stronger incentive than predator avoidance for starved urchins.

The fact that starved urchins increased total distance traveled in the case of a *Pycnopodia* cue compared with no predator cue could suggest predator evasion, although the overall patterns we observed were not strong enough for unequivocal conclusions. The same is not true of the fed urchins, which, while moving greater distances than starved urchins in general, had decreased movement distances in the presence of a *Pycnopodia* cue alone. This seems to be contrary to a predator flight response evident in starved urchins, and these differences highlight the need to further study indirect effects of sea star predators on urchins.

*Pycnopodia* are generalist scavengers and opportunistic predators that are highly mobile within their environment, and are known to elicit escape responses by green and red sea urchins (Freeman, 2006; Montgomery, 2014; Paul & Feder, 1975). This mobility may increase the reach of the *Pycnopodia*'s NCEs, especially where urchins are congregated in dense aggregations. Such aggregations are most common in urchin barrens (Rowley, 1989), which typically represents urchins in starved conditions (Dolarin & Edwards, 2021; Smith & Garcia, 2021). Other factors including urchin size (Freeman, 2006), water temperature (Bonaviri et al., 2017), urchin species identity (Duggins, 1983), and life stage (Nishizaki & Ackerman, 2007) can result in different feeding or escape behaviors.

This study demonstrated a non-consumptive behavioral effect of *Pycnopodia* on *S. purpuratus* in laboratory conditions, but the potential ecological impact of this effect would be dependent upon in situ conditions and the ability of urchins to detect *Pycnopodia* cues in nature, which are subject to diffusion, wave action, and currents (Chivers et al., 2013). It remains to be seen which long-term effects *Pycnopodia* may have on urchins in the field, whether that be persistent cryptic behavior (Spyksma et al., 2017), habituation (found in holothuroids; Hamel et al., 2021), or something in-between. Although we found short-term (3 h to 2 days) behavioral changes, the effects of concentration and periodicity of predator cues require more study.

This work provides key findings on the effects of NCEs between *Pycnopodia* and their *S. purpuratus* prey, and contributes new knowledge to our understanding of the indirect effects of *Pycnopodia* on kelp in controlled conditions and generates testable hypotheses for future corresponding work in natural reef settings. The results show that reestablishment of *Pycnopodia* populations could assist in maintaining healthy kelp forests in the Northeast Pacific based on indirect predator-prey interactions.

## AUTHOR CONTRIBUTIONS

The study was conceived by Ross Whippo with conceptual support from Aaron W. E. Galloway and Sarah Gravem. Ross Whippo carried out all field collections with assistance from Aaron W. E. Galloway. Lab experiments were conducted by Ross Whippo. Video data extraction was done by Ethan Porter-Hughes. Statistical analyses were developed by Ross Whippo with assistance from Sarah Gravem. Ross Whippo wrote the manuscript with editorial input from all authors.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Whippo, 2024) are available from Zenodo: <https://doi.org/10.5281/zenodo.11992332>.

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## SUPPORTING INFORMATION

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

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