ORIGINAL ARTICLE

WILEY marine ecology

Scales of predator detection behavior and escape in *Fissurella limbata*: A field and laboratory assessment

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Abstract

The consumptive effects of predators are widely acknowledged, but predation can also impact prey populations through non-consumptive effects (NCEs) such as costly antipredator behavioral responses. The magnitude of antipredator behavioral responses by prey is determined by an assessment of risk using sensory cues, which in turn is modulated by the environmental context. We studied the detection behavior and escape response of the keyhole limpet *Fissurella limbata* from the predatory sea star *Heliaster helianthus*. Through laboratory and field experimental trials, we quantified the distance and time of predator detection behavior by the prey, and measured their active escape responses when elicited. We found that predator detection by the limpet was chiefly mediated by distance, with experimental individuals capable of detecting predator presence effectively up to distances of at least 50 cm in the field and 70 cm under laboratory conditions. Our results indicate that this prey species is able to evaluate the proximity of its predator and use it as an indication of predation risk; therefore, predator–prey distance appears to be a primary predictor of the magnitude of the antipredator response. Given the tight relationship between predator distance and prey movement and the important role herbivores can play, particularly in this ecosystem, we expect that NCEs will cascade to the patterns of abundance and composition of rocky shore communities through changes in prey foraging behavior under risk.

KEYWORDS
antipredator behavior, escape, non-consumptive effects, predator detection behavior, predator–prey interactions, rocky inter-tidal, spatial scale

1 | INTRODUCTION

Non-consumptive effects (NCEs) of predators are defined as changes in prey traits induced by predation risk that directly affect prey population dynamics (Lima, 1998a; Schmitz, Ovadia, & Krivan, 2004). NCEs can cascade through food webs impacting multiple trophic levels by altering community composition (Suraci, Clinchy, Dill, Roberts, & Zanette, 2016; Werner & Peacor, 2003) and ecosystem function (Schmitz et al., 2008). Behavioral predator-induced responses have a cost on prey fitness, for example through diminished recruitment, survival or reproduction (Ellrich & Scrosati, 2016; Gosnell & Gaines, 2012; Lima & Dill, 1990; Lima, 1998b), and cascading community-level effects through prey behavioral responses (Schmitz, Beckerman, & O'Brien, 1997).

As proposed by Helfman (1989), the threat-sensitive predator avoidance hypothesis predicts that prey will trade off predator avoidance against other activities depending on the magnitude of the predatory threat. Several studies have shown that prey can accurately assess the level of predation risk and respond commensurately (Ferrari, Messier, & Chivers, 2006; Turner & Montgomery,

2003; Van Buskirk & Arioli, 2002), with the induction of antipredator behavior depending on the spatial and temporal proximity between predators and prey (Turner & Montgomery, 2003). Thus, the ecological importance of NCEs in a given ecosystem is critically dependent on the scales over which they trigger costly antipredator responses.

The spatial and temporal scales over which predators induce prey trait shifts and how these behavioral changes generate impacts at the landscape level have received scant attention (Basille et al., 2015; Kimbro, Grabowski, Hughes, Piehler, & White, 2017; Turner & Montgomery, 2003; Weissburg, Smee, & Ferner, 2014). Prey use several sensory modalities or combinations of them to perceive risk from environmental information, such as visual, chemical, mechanical and electrical cues, among others (Weissburg et al., 2014). The physical environment can enhance or attenuate perception, affecting the ability of prey to assess risk and react and respond to predators in an effective manner. In marine ecosystems, predation threat can be detected visually and/or chemically; in both cases the environment modulates the intensity of perceived cues. For example, the strength of a chemical signal will decay with distance from the source (Turner & Montgomery, 2003) and water hydrodynamics can affect chemical signal detection, affecting antipredator behavior (Wisenden, Binstock, Knoll, Linke, & Demuth, 2010). Turner and Montogomery (2003) empirically demonstrated that refuge use by the snail *Physa acuta* held at varying distances from a caged pumpkinseed sunfish *Lepomis gibbosus* was highest near the fish and that this antipredator behavior gradually decayed with distance, with a characteristic response range of 1.0 m. Studies with other marine species such as clams and dogwhelks have demonstrated that flow-induced mixing and dilution of chemical cues diminishes the probability of predator detection by prey (Smee, Ferner, & Weissburg, 2008; Large, Smee, & Trussell, 2011).

The keyhole limpet *Fissurella limbata* is one of the most abundant herbivores on the low rocky inter-tidal zone of the Chilean coast (Oliva & Castilla, 1992), particularly in wave-exposed areas under kelp stands of *Lessonia* spp., which mark the limits between the inter-tidal and subtidal zones (Santelices, Castilla, Cancino, & Schmiede, 1980). Together with other herbivores such as chitons and sea urchins, *F. limbata* plays an important role in structuring algal assemblages (Aguilera & Navarrete, 2012; Oliva & Castilla, 1986). In turn, this limpet is consumed by one of the most important invertebrate predators of the rocky inter-tidal zone of Central Chile, the sun star *Heliaster helianthus* (Castilla, Navarrete, Manzur, & Barahona, 2013; Navarrete & Manzur, 2008), and other large predators such as seagulls and sea otters. Prior field studies have shown that *F. limbata* exhibits a strong behavioral response when mechanically stimulated by *H. helianthus*, recognizing the signal as a threat and engaging in an active escape behavior (Escobar & Navarrete, 2011). Laboratory experiments showed that the sole presence of *H. helianthus* led to an increase in movement activity, distance traveled and feeding rates, together with an increased metabolic rate as part of the induced stress response (Manzur, Vidal, Pantoja, Fernández, & Navarrete, 2014). Better understanding of the ecological impact of the non-consumptive predator–prey interaction requires the establishment of the scales over which the limpet can perceive predation risk. Thus, measuring the functional dependence of predator detection behavior and escape on the spatial separation between predator and prey is key to determining the importance of NCEs in these rocky shore ecosystems. Therefore the main goal of this study was to characterize the spatial scale of the detection behavior of the predator *H. helianthus* by its herbivore prey *F. limbata*, performing experimental trials in a controlled system in the laboratory and under field conditions in the benthic environment.

2 | MATERIAL AND METHODS

Laboratory trials were carried out in experimental facilities in the Universidad Católica del Norte (UCN), Coquimbo, North-central Chile, during the first half of 2015. *Fissurella limbata* and *Heliaster helianthus* individuals were collected from the low inter-tidal zone at Guanaqueros (11 71°28′48.15″W), a site located 30 km south of Coquimbo. Both species inhabit the mid to low inter-tidal zone, with sun star densities in Guanaqueros of 1.5 individuals/m^2, and limpets of 0.8 individuals/m^2, at the high and low end of densities along North-central Chile, respectively (Broitman, Navarrete, Smith, & Gaines, 2001). Body size of sun stars ranged between 2 and 22 cm (mean 14 cm) and for limpets between 2 and 9 cm (mean 5 cm). Limpets and sun stars were maintained in separate running seawater tanks without food for 24–48 hr before trials.

To quantify the distance at which limpets reacted to sun star presence in the laboratory we ran trials placing limpets (4.4–8.7 cm length) at different distances (10, 40 and 70 cm) from sun stars (13 to 22 cm diameter). The exact distances between the sun star and limpet at which the limpet reacted to sun star presence were later binned into distance ranges (0–10, 10–40 and 40–70 cm) to allow comparisons with field data (see below). Experiments were carried out in an experimental arena (0.20 × 1.40 × 0.12 m; 33 L), under low (1 L/min) and high (4 L/min) water velocities (i.e., 5 and 21 cm/s). We used flowing filtered seawater from the UCN aquaculture system, at 14–16°C, which was poured into the experimental arena through a pipe fitted with a valve to regulate flow. Water flowed in one direction and exited through an outlet located at the rear end of the arena 10 cm above the bottom, so animals stayed submerged over the course of the experiment in an environment akin to a tide pool. The experimental arenas were made of transparent acrylic and were devoid of foreign objects. The size of the experimental arena was selected based on the escape distances of *F. limbata* upon contact with *H. helianthus*, which can be up to 40 cm in the field (Escobar & Navarrete, 2011). Therefore, we expected that detection should take place at comparable distances. The water velocities in our laboratory experiments were not chosen to mimic the extreme flow environments reported under field conditions (i.e., 16–20 m/s; Denny, Miller, Stokes, Hunt, & Helmuth, 2003), but to evaluate limpet behavior under controlled conditions and compare it with behavioral responses we observed in the field. A treatment without

H. helianthus was included as a control of limpet behavior in the absence of a predator for both water velocity conditions. Each limpet was tested individually in only one trial and in each one a different sun star individual was positioned upstream of the limpet; we performed replicate trials (*n* = 7) for each distance and water velocity treatment. Limpets were placed 20 cm before the water outlet of the experimental arena for a 6-min acclimation period before sun star entry to the tank. Individuals that did not show 'resting' behavior (animal still, occasional and slow movement of cephalic tentacles, shell down, slightly more lifted frontally) within this acclimation period were not used. Behavioral responses of limpets were evaluated for a 10-min period after the addition of the sun star to the tank. Sun stars were tethered to the tank wall with a thin nylon string, which allowed predator movement but prevented lethal attacks on limpets.

We quantified the number of limpets reacting as those that displayed a behavioral response departing from a standard resting behavior (see above), which signals the detection of the predator. These responses were characterized by the lifting of the mantle, lateral movement of the shell, lifting and rapid movement of cephalic tentacles and in some cases rapid displacement (Escobar & Navarrete, 2011). We also quantified the time limpets took to respond (detection time), the exact distance between prey and predator when detection behavior occurred, and the displacement, defined as the distance travelled by a limpet engaged in an escape response. Between trials, the experimental arena was washed with ethanol (70%), thoroughly scrubbed and rinsed with fresh water and then with filtered seawater.

Field trials to assess the distance for detection behavior and escape of *F. limbata* when exposed to *H. helianthus* presence were performed in the low inter-tidal zone at Guanaqueros using flat and positive sloping rock benches (≤10°; T. Manzur, personal observations). Trials were conducted with limpets found resting and without manipulating or perturbing them before the trial. *Heliaster helianthus* individuals were collected in situ. Five trials were conducted for each predator and prey distance treatment (10, 20, 40 and 50 cm), using different individuals for each trial, with limpets ranging between 3.9 and 7.8 cm in length and sun stars between 15.5 and 18.2 cm length. Limpets were used in trials only when they were observed to be resting (see above for resting behavior details) for 1 min prior to exposure to sun star presence. Following this period, one *H. helianthus* was located upstream from the limpet's position at a randomly assigned distance so the water from the receding swash flowed down from the predator to the prey; limpet behavior was observed for the next 5 min. We began recording time as soon as the sun star was placed on the rock. Additionally, a control treatment without *H. helianthus* was included, where limpet behavior was recorded for the same 1 + 5-min period of observation. The shorter observation period was due to the faster response times in the field and the logistic constraints posed by waves in the inter-tidal zone. All experiments were carried out during diurnal low tide periods during austral spring, 2015.

As in the laboratory trials, during the field experiment we quantified the number of reacting limpets, the detection time and the number of limpets that engaged in an active escape as well as the distance traveled. The low inter-tidal of wave-exposed zones is compressed and structurally complex; these field conditions limited the distance between predator and prey at which predator detection behavior could be observed to 50 cm instead of the 70 cm of laboratory trials. Also, unlike the laboratory trials where sun stars were tethered in the experimental arena, which allowed them to move over a limited range, sun stars in the field were fixed in their original position during the whole trial by hand to avoid dislodgment by waves or their escape from the trial area. Hence laboratory trials could be analysed both by continuous distance and by distance range classes, whereas field trials could be analysed only by the distance treatment between predator and prey.

An institutional bioethics committee reviewed and approved all the animal care procedures for the field and experimental trials.

2.1 | Statistical analysis

2.1.1 | Laboratory trials

Changes in predator detection behavior with distance were evaluated by comparing the frequencies of responding limpets among different predator–prey distance ranges and between low and high water velocity using a nominal logistic model (Agresti, 1996). The same analysis was carried out to compare the proportion of limpets that initiated active escape after detecting predator presence among different predator–prey distance ranges and between low and high water velocities.

The probability of predator detection behavior in the laboratory was estimated with a nominal logistic model between the binary response variable, reaction or no reaction, and the actual measured predator–prey distance and then the relationship between the probability of predator detection behavior and distance was estimated with a logistic regression. This analysis was performed with data from high and low water velocity trials pooled to increase the degrees of freedom, following the absence of differences in the frequency of predator detection response by the limpets between seawater velocities (see Results). A z-score test did not detect any outliers in the probability of predator detection behavior with distance ($p < .05$) so all observations were included in the logistic regression.

Differences in detection time between distance ranges and between seawater velocities were evaluated with a two-way factorial analysis of variance (ANOVA), with distance ranges and high/low seawater velocity as fixed factors. Displacement distance by escaping limpets was standardized by units of body length to minimize variability due to different individual sizes. Differences in standardized displacement were also evaluated with a two-way factorial ANOVA, with distance ranges and high/low water velocity as fixed factors. Detection time and displacement were log-transformed to improve normality and homoscedasticity, which were evaluated with Shapiro–Wilk and Levene tests, respectively.

As no limpets showed any behavioral change during the laboratory trials in the control treatment (without *Heliaster helianthus*, see Results), we dropped this treatment from statistical comparisons of detection time and displacement.

In the case of significance in ANOVA tests, post hoc comparisons were made with Student's *t* tests and reported in the figures.

2.1.2 | Field trials

The frequency of movements indicating detection, and escape frequency were compared between distance treatments with a nominal logistic model (Agresti, 1996). Detection time was log-transformed to improve homoscedasticity and normality. Differences among predator–prey distance treatments both in detection time and standardized displacement (traveled distance/limpet body length) were analysed separately with one-way ANOVA. In the case of significance, post hoc comparisons were made with Student's *t* tests and reported in the figures.

All statistical analyses were performed in the statistical package JMP® 7.0.1.

3 | RESULTS

Limpets in control treatments (without a predator) under laboratory conditions did not show signs suggesting predator detection behavior (Figure 1a). Conversely, in the different distance range treatments in the presence of *Heliaster helianthus*, over 66% of limpets showed predator detection behavior. The distance between predator and prey affected the proportion of responding limpets. Nearly 100% of the limpets responded to the predator's presence up to a distance of 40 cm from the predator, but decreased over longer distances (Figure 1a, nominal logistic for distance range, L-R $X^2_{(3)}$ (likelihood-ratio Chi-square test statistic) = 49.083, $p =$ (likelihood-ratio Chi-square test statistic) .0001). The probability of detection behavior decreased with predator–prey distance. Probability was high
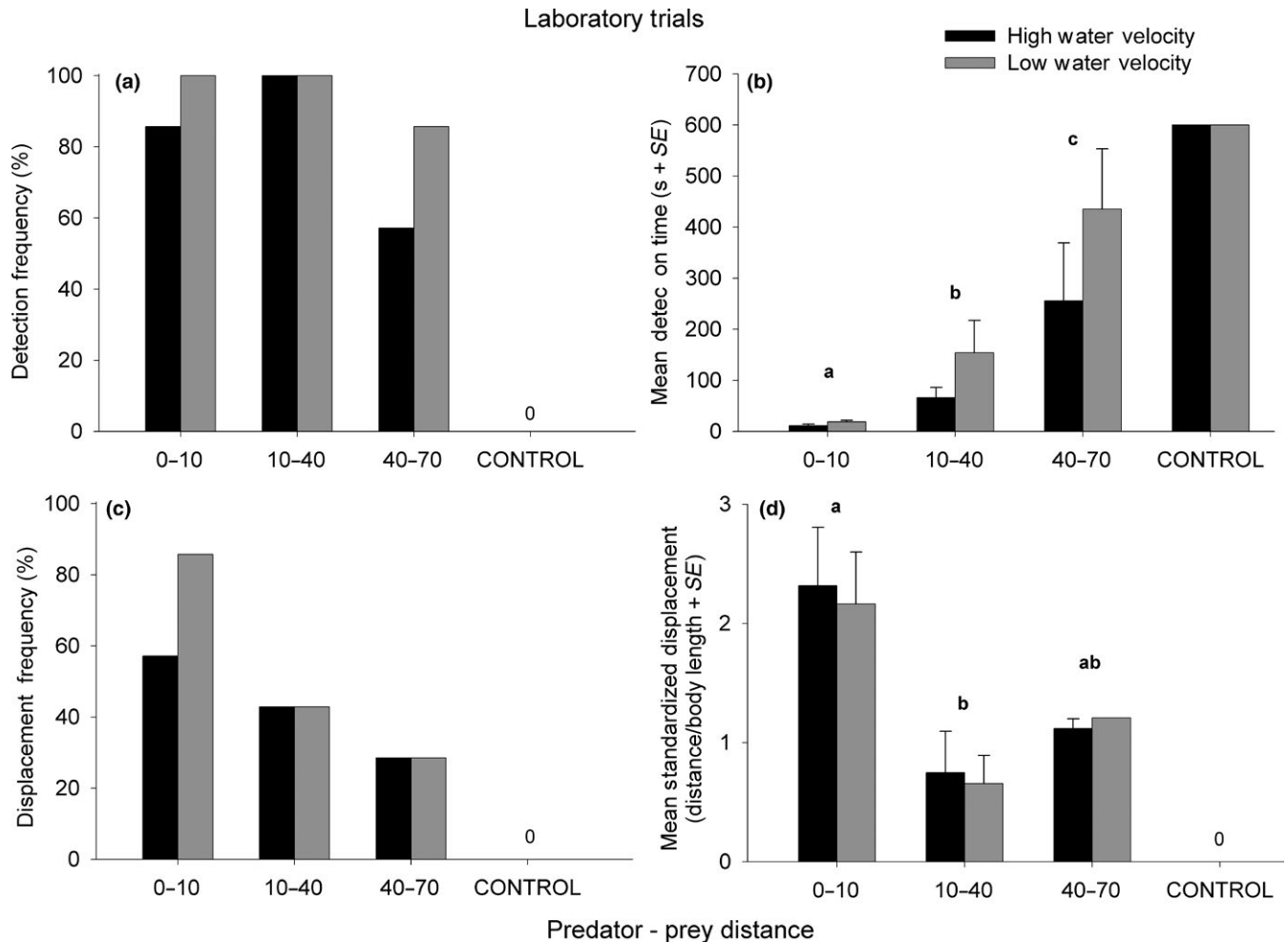
FIGURE 1 Detection frequency (a), time until detection (mean, *SE*; b), displacement frequency (c) and standardized displacement (mean, *SE*; d) for the different predator and prey distance treatments and control without predator for *Fissurella limbata* under low (gray bars) and high (black bars) water velocity in laboratory trials. Student's *t* post hoc comparisons for distance range on detection time: 0–10 ≠ 10–40 ≠ 40–70, *t* = 2,040, *p* < .05; and for distance range on mean standardized displacement: 40–70 = 0–10 ≠ 10–40 = 40–70, *t* = 2.160, *p* < .05, bars not connected by lower-case letters are significantly differents, *p* < .05
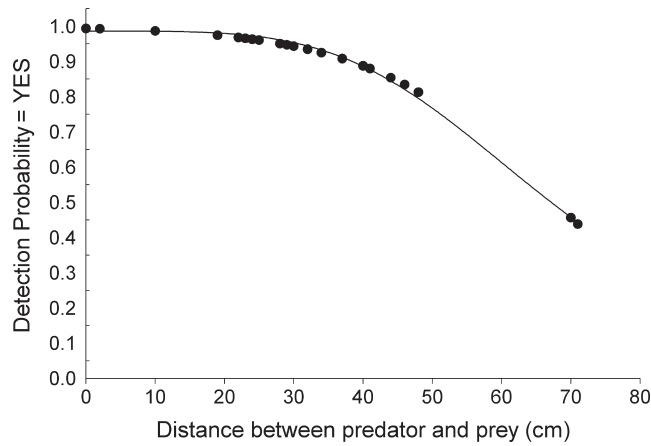
(between 1 and 0.8) at distances shorter than 50 cm and tailed off

FIGURE 2 Logistic regression for the probability of detection at different distances between predator and prey for *Fissurella limbata* under laboratory conditions

to less than chance (0.43) at distances longer than 70 cm (Figure 2, $R^2 = 0.9981$, $p = .008$).

No differences in the frequency of limpet detection behavior were observed at high or low water velocities (Figure 1a, nominal logistic for water velocity, L-R $X^2_{(3)} = 0.00001715$, $p = .9967$, water velocity × distance range, L-R $X^2_{(1)} = 0.39344767$, $p = .9416$).
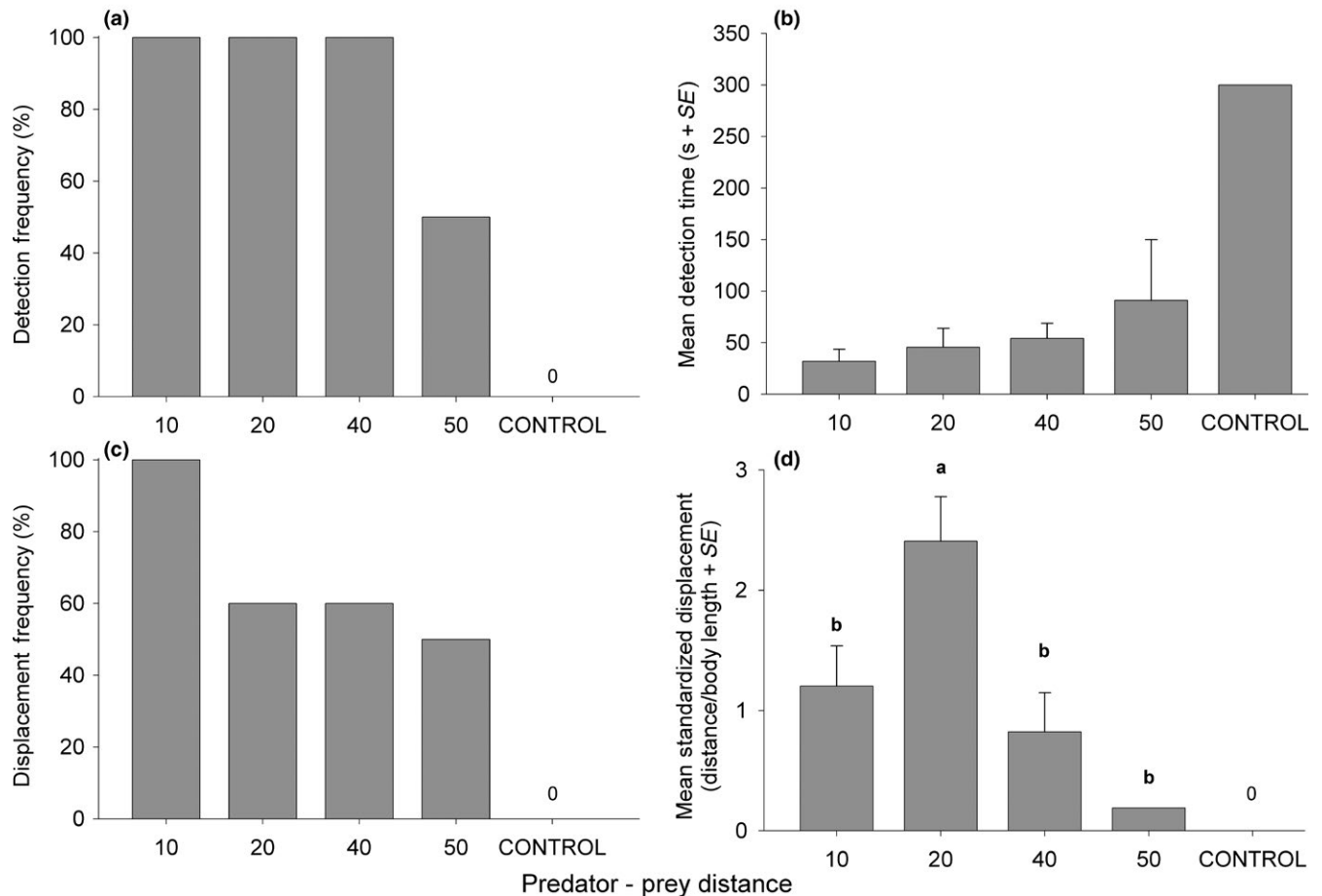
Similarly, detection time increased with distance between predator and prey, approaching 5 min at distances greater than 40 cm and declining to roughly 155 and 19 s for 10–40 and 0–10 cm distances, respectively (Figure 1b, two-way ANOVA for distance range, $F_{(2,31)} = 40.0906$, $p = .0001$). Water velocity had effects on predator detection time. Predator presence was perceived more quickly under high than under low water velocity conditions (Figure 1b, two-way ANOVA for water velocity, $F_{(1,31)} = 6.581$, $p = .0154$).

Among the limpets that responded to predator presence under the different water velocities, c. 40% initiated an active escape. Escapes were less frequent at longer distances, decreasing from 70% at distances of 0 to 10 cm to less than 35% when predators were 40 to 70 cm away (Figure 1c, nominal logistic for distance range, L-R $X^2_{(3)} = 20.3721$, $p = .0001$).

FIGURE 3 Detection frequency (a), time until detection (mean, *SE*; b), displacement frequency (c) and standardized displacement (mean, *SE*; d) for the different predator and prey distance treatments and control without predator for *Fissurella limbata* in field trials. Student's *t* post hoc comparisons for distance treatment on mean standardized displacement: 10 = 40 = 50 ≠ 20, *t* = 2.306, *p* < .05, bars not connected by lower-case letters are significantly differents, *p* < .05

Escape distances were rather short, with limpets separating themselves from the predator an average of 13.3 ± 3.6 cm at all distances or 1.6 ± 0.2 limpet body length, a small distance considering the longer distances at which they detected their predator. In agreement with this dampened response, displacement was reduced when predator–prey distances were greater than 10 cm (Figure 1d, two-way ANOVA for distance range, $F_{(2,13)}$ = 8.1957, p = .005). There were no significant effects of water velocity on displacement (two-way ANOVA for water velocity: $F_{(1,13)}$ = 0.0098, p = .9226; water velocity × distance range, $F_{(2,13)}$ = 0.0261, p = .9743).

Limpet responses to predator presence in the field were similar to the responses under laboratory conditions. Although we were not able to measure limpet response at longer distances in the field (see Material and Methods for details), the number of reacting limpets diminished with predators at distances of 50 cm, with 100% response at shorter distances (Figure 3a, nominal logistic for distance range, L-R $X^2_{(4)}$ = 23.4294, p = .0001). All limpets in no-predator control trials maintained their original resting condition (Figure 3a). Detection time in the field was almost invariant up to distances of 50 cm (Figure 3b, one-way ANOVA for distance range, $F_{(3,13)}$ = 1.1477, p = .3667), and occurred in less than 1 min.

The proportion of reacting limpets that initiated an escape in field trials was higher than in the laboratory trials across all distance classes pooled (70% versus 40% on average, respectively), but followed the same decreasing trend with increasing predator–prey distance (Figure 3c, nominal logistic for distance range, L-R $X^2_{(4)}$ = 15.312, p = .0041). The distance traveled by limpets that escaped from their predator in the field was short (less than 10 cm on average or 1.3 ± 0.3 limpet body length) and did not change much at different predator–prey distances, except at 20 cm where displacement was greatest (Figure 3d, one-way ANOVA for distance treatment, $F_{(3,8)}$ = 4.070, p = .0499).

4 | DISCUSSION

Strong ecological interactions shape the inter-tidal landscape of rocky shores (Shurin et al., 2002); thus, NCEs hold great potential as modifiers of the community-level impacts of predators in this system (Schmitz et al., 2004) as a consequence of the compromises that prey incur through costly antipredator responses (Kats & Dill, 1998). The transmission of NCEs will depend on predator detection, avoidance behavior and environmental conditions, which interact with specific predator and prey traits. These traits include characteristics such as sensory modality of information acquisition, the type of prey response to risk, predator hunting mode, body size and mobility, among others (Hill & Weissburg, 2013; Preisser, Orrock, & Schmitz, 2007; Weissburg et al., 2014). NCEs will also depend on conditions that change prey risk perception, such as physical space and predator proximity through density or encounter rate (Turner & Montgomery, 2003). *Fissurella limbata* in our experiments assessed risk magnitude as a function of its separation from the predator. Over half of the limpets reacted to the presence of *Heliaster helianthus*

up to the maximum distances we assessed, both under laboratory and natural conditions, and the magnitude of prey responses was independent of water velocity in the laboratory, despite differences in detection time (Figures 1 and 3). The contrasting conditions of the field and laboratory setting in our experiments did not produce significant changes in the reactive distance or escape response. Limpets responded rapidly and engaged in active escapes more frequently at shorter predator–prey distances (Figures 1 and 3). This indicates that our study prey species responds to a threat with an intensity that matches its level of risk (Helfman, 1989), as shown for other prey species (Ferrari et al., 2006; Hartman & Abrahams, 2000; Wahle, 1992) in the distance they travel after perceiving its predator.

Differences in water velocity and experimental setting affected the time needed for limpets to detect the predator. More rapid detection as water velocity increased was observed in the laboratory, while response behavior observed under field conditions was faster than in the lab (Figure 1b and 3b). Although we were not able to experimentally control the flow environment, our results suggest that, for *F. limbata*, the process of cue sensing and risk evaluation can occurs over the spatial scales and the potential range of water velocities considered in our study (e.g., ~50 cm, from 0.05 to 20 m/s). Ferner and Weissburg (2005) studied the tracking of prey by the marine whelk *Busycon carica* and found that fast and turbulent water flow facilitated cue tracking and reduced prey searching time. They proposed that slow-moving animals, such as whelks or limpets, which have a limited capacity for spatial sampling, may collect a temporal average of chemical cues and integrate between samples to facilitate detection of dilute odors or to estimate the concentration of a rapidly fluctuating signal. The temporal integration of cues could be a strategy used by our study species to gather information from the environment to detect predators. As *F. limbata* has a relatively large body size, is a slow-moving species inhabiting an energetic hydrodynamic environment and has to cope with predator-induced costs driven by stress (Manzur et al., 2014), it may trade the cost of spatial sampling for the temporal integration of cues, as is the case for whelks. However, effects of flow environment (i.e., water velocity and turbulence) on predator avoidance responses are complex as extreme flow, either low or high, may hinder predator detection, which is at a maximum over intermediate flow velocities (Large et al., 2011).

In a field study with the same predator–prey system, Escobar and Navarrete (2011) found that detection time and escape distance were 10 s and ~ 35 cm, respectively. This contrasts with our results of field trials, which showed that detection time was twice as slow (19 s) and escapes were shorter by half (~20 cm across treatments). These differences may be reconciled by the perceived level of risk. Prey responses in our trials were quantified prior to contact with the predator, while Escobar and Navarrete (2011) initiated their trials after *H. helianthus* made direct contact with the limpet. Therefore the escape response, twice as intense as our results, followed the highest possible level of risk and translated into faster detection times and longer escape distances. Despite this interpretation, there are other factors that may account for the contrast between our results and those of Escobar and Navarrete (2011), such as the

geographic range of field sites employed or other uncontrolled features such as bench slope or benthic community composition.

The spatial scale of active prey escape was in the order of a few centimeters, with 24 cm the longest escape recorded, which seems rather small compared with the maximal spatial scale of detection considered in our experiments (50 cm in the field and 70 cm in the laboratory). The spatial mismatch between perception and escape may be explained by a high cost of antipredator behavior, considering that animals should be capable of assessing risk level and responding accordingly (Ferrari, Sih, & Chivers, 2009; Weissburg et al., 2014). *Heliaster helianthus* is a relatively sedentary species (Barahona & Navarrete, 2010), so a small escape distance can reduce the level of risk perceived by the prey, which can resume escape depending on predator actions without unnecessary energy expenditure.

Our results are consistent with a predator–prey system modulated by a trade-off between energy expenditure in the antipredator response and the perceived level of risk. As proposed by Helfman (1989) in the threat-sensitive predator avoidance hypothesis, the three-spot damselfish, *Stegastes planifrons*, showed more intense antipredator responses to a model trumpetfish (*Aulostomus maculatus*) when the predator model was nearer or larger (Helfman, 1989). *Fissurella limbata* individuals were capable of perceiving the presence of *H. helianthus* at considerable distances and thus establish the level of risk as a function of predator–prey distance. The densities of limpets and sun stars that can be observed across the inter-tidal ecosystem of North-central Chile (Broitman et al., 2001, Aguilera & Navarrete, 2012; T. Manzur, personal observations) and the threshold for predator detection behavior established by our study, allow for a high probability of exposure to cues, which will require a threat-sensitive modulation of the behavioral response. Given the short spatial scale for prey behavioral response and following the strong consumptive effects that the herbivorous *Fissurella* limpets exert on the rocky inter-tidal communities (Aguilera & Navarrete, 2012), we expect that the NCEs documented by this and earlier studies (Escobar & Navarrete, 2011; Manzur et al., 2014) should translate into strong ecological impacts, for example through diminished prey recruitment (Ellrich & Scorsati, 2016). In particular, given that NCEs were manifested as modifications of limpet movement, changes in foraging behavior under risk should cascade into differential consumer-driven patterns of the inter-tidal landscape (Díaz & McQuaid, 2011; Gosnell & Gaines, 2012; Oróstica, Aguilera, Donoso, Vásquez, & Broitman, 2014).

ACKNOWLEDGEMENTS

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REFERENCES

Agresti, A. (1996). *An introduction to categorical data analysis* (p. 357). Hoboken, NJ: John Wiley and Sons Inc.

Aguilera, M. A., & Navarrete, S. A. (2012). Functional identity and functional structure change through succession in a rocky intertidal marine herbivore assemblage. *Ecology*, 93, 75–89. https://doi.org/10.1890/11-0434.1

Barahona, M., & Navarrete, S. A. (2010). Movement patterns of the sea star *Heliaster helianthus* in central Chile: Relationship with environmental conditions and prey availability. *Marine Biology*, 157, 647–661. https://doi.org/10.1007/s00227-009-1350-7

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J. P., & Courtois, R. (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96, 2622–2631. https://doi.org/10.1890/14-1706.1

Broitman, B. R., Navarrete, S. A., Smith, F., & Gaines, S. D. (2001). Geographic variation of Southeastern Pacific intertidal communities. *Marine Ecology Progress Series*, 224, 21–34. https://doi.org/10.3354/meps224021

Castilla, J. C., Navarrete, S. A., Manzur, T., & Barahona, M. (2013). The South American sun star *Heliaster helianthus*. In J. M. Lawrence (Ed.), *Asteroidea: The biology and ecology of starfish* (pp. 153–160). Baltimore, MD: The Johns Hopkins University Press.

Denny, M. W., Miller, L. P., Stokes, M. D., Hunt, L. J. H., & Helmuth, B. S. T. (2003). Extreme water velocities: Topographic amplification of wave-induced flow in the surf zone of rocky shores. *Limnology and Oceanography*, 48, 1–8.

Díaz, E. R., & MacQuaid, C. D. (2011). A spatially-explicit approach to trophic interactions and landscape formation: Patchiness in small-scale variability of grazing effects along an intertidal stress gradient. *Journal of Ecology*, 99, 416–430. https://doi.org/10.1111/j.1365-2745.2010.01779.x

Ellrich, J. A., & Scrosati, R. A. (2016). Water motion modulates predator non-consumptive limitation of prey recruitment. *Ecosphere*, 7(7), e01402. https://doi.org/10.1002/ecs2.1402.

Escobar, J. B., & Navarrete, S. A. (2011). Risk recognition and variability in escape responses among intertidal molluskan grazers to the sun star *Heliaster helianthus*. *Marine Ecology Progress Series*, 421, 151–161. https://doi.org/10.3354/meps08883.

Ferner, M. C., & Weissburg, M. J. (2005). Slow-moving predatory gastropods track prey odors in fast and turbulent flow. *Journal of Experimental Biology*, 208, 809–819. https://doi.org/10.1242/jeb.01438

Ferrari, M. C., Messier, F., & Chivers, D. P. (2006). The nose knows: Minnows determine predator proximity and density through detection of predator odours. *Animal Behaviour*, 72, 927–932. https://doi.org/10.1016/j.anbehav.2006.03.001

Ferrari, M. C., Sih, A., & Chivers, D. P. (2009). The paradox of risk allocation: A review and prospectus. *Animal Behaviour*, 78, 579–585. https://doi.org/10.1016/j.anbehav.2009.05.034

Gosnell, J. S., & Gaines, S. D. (2012). Keystone intimidators in the intertidal: Non-consumptive effects of a keystone sea star regulate feeding and growth in whelks. *Marine Ecology Progress Series*, 450, 107–114. https://doi.org/10.3354/meps09567

Hartman, E. J., & Abrahams, M. V. (2000). Sensory compensation and the detection of predators: The interaction between chemical and visual information. *Proceedings of the Royal Society of London Series B*, 267, 571–575. https://doi.org/10.1098/rspb.2000.1039

Helfman, G. S. (1989). Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology*, 24, 47–58. https://doi.org/10.1007/BF00300117

Hill, J. M., & Weissburg, M. J. (2013). Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia*, *172*, 79–91. https://doi.org/10.1007/s00442-012-2488-4

Kats, L. B., & Dill, L. M. (1998). The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience*, *5*, 361–394. https://doi.org/10.1080/11956860.1998.11682468

Kimbro, D. L., Grabowski, J. H., Hughes, A. R., Piehler, M. F., & White, J. W. (2017). Non-consumptive effects of a predator weaken then rebound over time. *Ecology*, *98*, 656–667. https://doi.org/10.1002/ecy.1702

Large, S. I., Smee, D. L., & Trussell, G. C. (2011). Environmental conditions influence the frequency of prey responses to predation risk. *Marine Ecology Progress Series*, *422*, 41–49. https://doi.org/10.3354/meps08930

Lima, S. L. (1998a). Non-lethal effects in the ecology of predator–prey interactions. *BioScience*, *48*, 25–34.

Lima, S. L. (1998b). Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, *28*, 215–290.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

Manzur, T., Vidal, F., Pantoja, J. F., Fernández, M., & Navarrete, S. A. (2014). Behavioural and physiological responses of limpet prey to a sea star predator and their transmission to basal trophic levels. *Journal of Animal Ecology*, *83*, 923–933. https://doi.org/10.1111/1365-2656.12199

Navarrete, S. A., & Manzur, T. (2008). Individual- and population-level responses of a keystone predator to geographic variation in prey. *Ecology*, *89*, 2005–2018. https://doi.org/10.1890/07-1231.1

Oliva, D., & Castilla, J. C. (1986). The effects of human exclusion on the population structure of keyhole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *Marine Ecology*, *7*, 201–217.

Oliva, D., & Castilla, J. C. (1992). Guía para el reconocimiento y morfometría de diez especies del género *Fissurella* Bruguiére 1789 (Mollusca Gastropoda) comunes en las pesquerías y conchales indígenas de Chile Central y Sur. *Gayana Zoología*, *56*, 77–108.

Oróstica, M. H., Aguilera, M. A., Donoso, G. A., Vásquez, J. A., & Broitman, B. R. (2014). Effect of grazing on distribution and recovery of harvested stands of *Lessonia berteroana* kelp in northern Chile. *Marine Ecology Progress Series*, *511*, 71–82. https://doi.org/10.3354/meps10931

Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter non-consumptive effects in predator- prey interactions. *Ecology*, *88*, 2744–2751. https://doi.org/10.1890/07-0260.1

Santelices, B. S., Castilla, J. C., Cancino, J., & Schmiede, P. (1980). Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. *Marine Biology*, *59*, 119–132. https://doi.org/10.1007/BF00405461

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology*, *78*, 1388–1399. https://doi.org/10.1890/0012-9658(1997)078

Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., & Vonesh, J. R. (2008). From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. *Ecology*, *89*, 2436–2445. https://doi.org/10.1890/07-1030.1

Schmitz, O. J., Ovadia, O., & Krivan, V. (2004). Trophic cascades: The primacy of trait-mediated interactions. *Ecology Letters*, *7*, 153–163.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., ... Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, *5*, 785–791. https://doi.org/10.1046/j.1461-0248.2002.00381.x

Smee, D. L., Ferner, C., & Weissburg, M. (2008). Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. *Oecologia*, *156*, 399–409. https://doi.org/10.1007/s00442-008-0995-0

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*, 10698. https://doi.org/10.1038/ncomms10698

Turner, A. M., & Montgomery, S. L. (2003). Spatial and temporal scales of predator avoidance: Experiments with fish and snails. *Ecology*, *84*, 616–622. https://doi.org/10.1890/0012

Van Buskirk, J., & Arioli, M. (2002). Dosage response of an induced defense: How sensitive are tadpoles to predation risk? *Ecology*, *83*, 1580–1585. https://doi.org/10.1890/0012-9658(2002)083

Wahle, R. A. (1992). Body-size dependent anti-predator mechanisms of the American lobster. *Oikos*, *65*, 52–60. https://doi.org/10.2307/3544887

Weissburg, M., Smee, D. L., & Ferner, M. C. (2014). The sensory ecology of non-consumptive predator effects. *The American Naturalist*, *184*(2), 141–157. https://doi.org/10.1086/676644

Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, *84*, 1083–1100. https://doi.org/10.1890/0012-9658(2003)084

Wisenden, B. D., Binstock, C. L., Knoll, K. E., Linke, A. J., & Demuth, B. S. (2010). Risk-sensitive information gathering by cyprinids following release of chemical alarm cues. *Animal Behaviour*, *79*(5), 1101–1107. https://doi.org/10.1016/j.anbehav.2010.02.004