

Habitat complexity mediates predation of juvenile abalone by starfish

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ABSTRACT: Predation strongly influences the abundance and distribution of prey populations due to its disproportionately large effects on survival during the early life-history stages. However, the intensity of predation can vary dramatically among habitats. The habitat can directly affect the interaction between predator and prey; but also, by determining the distributions of predators and prey, the habitat can mediate the likelihood of a predatory encounter. Here, we used laboratory experiments to identify the likely predators of juvenile abalone *Haliotis iris* on temperate reefs in central New Zealand. Predator performance in the laboratory was assessed in conditions without prey refuge, in simulated juvenile habitat as well as in the presence of alternate prey. We then used surveys to compare the abundance of predators and juvenile abalone to explore if negative associations between predator and prey in the laboratory manifest in the field. Last, we manipulated algal habitat complexity at 2 depths and quantified the effect of predator exclusion on juvenile abalone survival in the field. We found that starfish were the likely predators of juvenile *H. iris* in our study system. Furthermore, predation of juvenile abalone by starfish was lowest in habitats with the greatest structural complexity, and there is evidence that predation by starfish in cobble habitats was size-dependent. Overall, we found that habitat variability mediates predation on juvenile abalone by determining the likelihood of an encounter between predator and prey.

KEY WORDS: Barrens · Macroalgae · Urchin · *Haliotis* · New Zealand

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INTRODUCTION

The demographics of populations are conditional on variability in the intensity of predation (Connell 1961, Paine 1966), and in many cases, habitat plays a central role in mediating the conflict between predators and prey (Werner et al. 1983, Gaines & Roughgarden 1987). Habitat variation determines the contexts in which predators and prey interact, and by favouring the success of either predator or prey, differences among habitats can shape the strength of predator–prey interactions and thereby the demographics of populations. Consequently, habitat mediated differences in the intensity of predation,

feature prominently in our understanding of the ecological processes structuring populations and communities (Chase et al. 2002, Agrawal et al. 2007).

Reduced habitat complexity is generally linked with an increase in predation risk (Werner et al. 1983, Lima 1990, Caley & St John 1996). Moreover, the increase in predation risk is often most pronounced for juveniles, which commonly lack the mechanisms of predator avoidance possessed by more mature individuals (Werner et al. 1983, Gosselin & Qian 1997). Hence, for many species, the early juvenile stages are concentrated in habitats where the structural complexity of the habitat provides protec-

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tion from predators (Werner et al. 1983, Tupper & Boutilier 1997, Hovel & Lipcius 2001).

In temperate reef communities, widespread transitions from structurally-complex macroalgal habitats to structurally-simplified barren habitats have received much attention in recent years (Sala et al. 1998, Tegner & Dayton 2000). Barrens communities are typically associated with human induced declines in top-down trophic control of urchins (Estes & Duggins 1995, Tegner & Dayton 2000, Shears & Babcock 2003). Consequently, direct and indirect interactions between urchins and other temperate reef organisms are common on temperate reefs. Urchins and abalone are known to compete for food and shelter (Lowry & Pearse 1973, Andrew & Underwood 1992), and while in some cases abalone and urchins coexist (Underwood et al. 1991, Schiel et al. 1995, Day & Branch 2002), in locations where barren habitats are maintained, abalone often become locally extinct (Shepherd 1973, Andrew 1993). The most common explanation for the local extinction of abalone following a transition from macroalgal to barren habitats is starvation (Andrew 1989, Karpov et al. 2001). However, alternative mechanisms (i.e. predation) have received less attention, and the factors mediating declines in juvenile abalone abundance following transitions to barren habitats remain unclear.

Like many marine organisms, recruitment severely limits the abundance and distribution of abalone populations; however, the drivers of recruitment variability in abalone are poorly understood, and habitat-mediated interactions remain largely undescribed (McShane 1996). Predation by fish (Tegner & Butler 1989, Shepherd & Clarkson 2001), crabs (Shepherd 1973, Schiel & Welden 1987, Tegner & Butler 1989, Shepherd & Clarkson 2001, Stotz et al. 2006, Griffiths & Gosselin 2008, Won et al. 2013), lobsters (Schiel & Welden 1987, Tegner & Butler 1989, Van Zyl et al. 2003, Pederson et al. 2008), octopus (Tegner & Butler 1989) and starfish (Schiel & Welden 1987, Day et al. 1995, Stotz et al. 2006, Griffiths & Gosselin 2008, Won et al. 2013) on larger juvenile abalone has been shown in both laboratory and field experiments (Shepherd & Turner 1985, Day et al. 1995, Shepherd & Clarkson 2001). Nonetheless, few studies have explored the effects of predation during the early juvenile stages when we might expect predation to be the strongest.

Here, we used laboratory experiments to identify the likely predators of juvenile (4–10 mm shell length [SL]) black-foot abalone *Haliotis iris* in central New Zealand. We also examined the relationship between

predator and prey abundance in the field. Finally, to examine if transitions from barren to macroalgal habitats could influence predation on juvenile abalone, we used a manipulative field experiment to quantify predation of juvenile abalone in barren and macroalgal habitats.

MATERIALS AND METHODS

General laboratory methods

To determine the predators of juvenile *Haliotis iris* in our study system, we selected 14 potential predators based on their observation in cobble habitats in the field (see Appendix 1, Table A1). Based on the results of our pilot experiments, the 4 predator species included in the first laboratory experiment (predation in the absence of refuge) were 3 starfish species (*Astrostele scabra*, *Coscinasterias calamaria*, *Pateriella regularis*) and the triplefin fish *Fosterygion varium*. In the second (predator preference in the absence of refuge) and third (predation in cobble habitat) laboratory experiments, we focused on only the starfish *A. scabra* and *C. calamaria*. In the first and second laboratory experiments, we randomly arranged 2 l aquaria (170 × 170 × 90 mm) that were filled with unfiltered, flowing seawater in a large water bath. In the first and second laboratory experiments, we provided no refuge for juvenile abalone. In the third laboratory experiment we provided refuge for juvenile abalone by filling plastic trays with small cobbles (50–100 mm diameter) that were cleared of all macroalgae except crustose coralline algae. Cobble size was restricted to standardize the number of cobbles per tray. The trays were then placed in a large aquarium (>200 l) filled with unfiltered, flowing seawater. To prevent juvenile abalone from escaping, the sides and base of the trays were lined with a fine mesh (1 mm). Furthermore, to prevent predators from moving between replicates, we attached a section of 3.5 mm square, plastic mesh to the top of trays with cable ties. Control (no-predator) treatments were used to estimate mortality due to handling, and consisted of only the prey species.

Predators and prey were collected from the field 1 and 2 d prior to the experiment, respectively. To allow prey to attach and acclimate, we placed prey in aquaria 1 h before predators were introduced. The size of predators varied within and between species; however, sizes were indicative of those observed in the field. Similar sized prey were used in all experiments. Predators were starved for 1 d prior to use in

experiments. For each experimental replicate, we recorded whether the prey was alive or dead at each census interval. The juvenile abalone in our laboratory experiments remained attached to the aquaria, and were able to reattach if accidentally dislodged. Hence, there was no indication of ill-health among juvenile abalone used in our laboratory experiments. If the prey was consumed, the condition of the shell was inspected for any damage that may be indicative of predation by the different predator species (Schiel & Welden 1987, Tegner & Butler 1989).

Predation in the absence of refuge

In the first laboratory experiment, we quantified juvenile abalone survival in the presence of the 3 most likely predators identified in our pilot experiments (Appendix 1, Table A1). The predators considered were *Astrostole scabra* (16–53 mm radius), *Coscinasterias calamaria* (7–52 mm radius), and *Fosterygion varium* (55–126 mm total length). Because *A. scabra* and *C. calamaria* are benthic predators, it is possible that their movement along the benthos could smother and kill juvenile abalone. Consequently, to partition the effects of predation and smothering on juvenile abalone survival, we included the herbivorous starfish *Pateriella regularis* (14–43 mm radius) in our experiment (Naylor & McShane 2001). Each predator treatment consisted of one juvenile *Haliotis iris* (5.8–9.9 mm SL) and one predator. There were 19 replicate aquaria for each predator species and 19 control aquaria. We inspected aquaria every 3 h for 12 h during the day and allowed the experiment to continue overnight. A replicate ended when the prey was consumed. Predators were allowed a maximum of 3 d to consume prey. Juvenile *H. iris* survival in the different predator treatments was analysed using logistic regression. The response was binary (1 indicated the juvenile abalone survived, 0 indicated the juvenile abalone died during the course of the experiment), and predator was considered a fixed effect with 4 levels: *C. calamaria*, *F. varium*, *P. regularis* and no-predator. Because predation by *A. scabra* was 100% (see Fig. 1a), we excluded this species from formal statistical analysis. Differences in search efficiency (i.e. the time until capture) for *A. scabra* and *C. calamaria* were analysed using one-way ANOVA. Search efficiency was not investigated for *F. varium* or *P. regularis* because juvenile abalone survival in *F. varium* and *P. regularis* treatments was not significantly different to no-predator treatments (see 'Results').

Predator preference in the absence of refuge

Starfish predation had a strong effect on juvenile abalone survival in our first laboratory experiment (see 'Results'). Hence, in our second laboratory experiment we examined preference for juvenile abalone by starfish. Each predator treatment (*Astrostole scabra* [16–37 mm radius] and *Coscinasterias calamaria* [14–42 mm radius]) contained 1 juvenile *Haliotis iris* (5.5–9.5 mm SL), 1 juvenile mussel *Mytilus galloprovincialis* (7.1–14.1 mm SL) and 1 predator. There were 22 replicate aquaria for each predator species and 22 control aquaria. We inspected aquaria every 3 h for 12 h during the day and allowed the experiment to continue overnight. A replicate ended when the first prey species was consumed. In all replicates, predators consumed at least one prey within 3 d. We assumed a null-hypothesis of no choice (i.e. an odds ratio = 1) and analysed deviations from the null for each predator species with Fisher's exact χ^2 test.

Predation in cobble habitat

In our first and second laboratory experiments, we examined predation in the absence of a refuge. In the field, juvenile *Haliotis iris* commonly occupy cobble habitats (Aguirre & McNaught 2012); therefore, in our third laboratory experiment we examined starfish predation on juvenile abalone in cobble habitat. Each predator (*Astrostole scabra* [16–36 mm radius] and *Coscinasterias calamaria* [16–30 mm radius]) treatment consisted of 5 juvenile *H. iris* (4.5–10.4 mm SL) and 1 predator. There were 6 replicate trays for each predator species and 6 control trays. Because searching for juvenile abalone required that every cobble be overturned, we inspected trays every 2 d to minimise disturbance. The experiment was allowed to continue for 7 d. The effects of starfish on juvenile abalone survival in cobble habitat were analysed using a generalized linear mixed model (GLMM) with binomial error distribution and a logit link function. The response was the proportion of juvenile abalone alive at the end of the experimental period. Predator was a fixed effect with 3 levels: *A. scabra*, *C. calamaria* and no-predator; tray was included as an observation level random effect. In analyses for the effects of starfish size on juvenile *H. iris* survival, predator was a fixed effect with 2 levels (i.e. *A. scabra*, *C. calamaria*) and starfish size a covariate.

Distribution of predators and prey in the field

Our laboratory experiments indicated that starfish are the likely predators of juvenile *Haliotis iris* in our 'study system' (see 'Results'). Hence, to calibrate the results of our laboratory experiments, we surveyed starfish (*Coscinasterias calamaria* and *Astrostele scabra*) and juvenile *Haliotis iris* (<10 mm SL) abundance at 6 sites on the Wellington South Coast, New Zealand: Red Rocks (RR); Yunghe Penn (YP); West Taputeranga Island (WTI); Te Raekaihau (TR); Tarekena Bay (TB); and Reef Bay (RB). A more detailed description of the survey protocol, as well as analysis of the habitat associations of *H. iris* at these study sites is presented in Aguirre & McNaught (2012). Surveys were conducted using haphazardly-placed 0.25 m² quadrats on cobble reef habitats. We used a relatively small quadrat as we were most interested in capturing small-scale associations between abalone and starfish (Strain & Johnson 2010). For each quadrat, we counted the number of juvenile *H. iris* and the number of starfish. To analyse the relationship between predator and prey abundance, we used a GLMM with a Poisson error distribution and a log link function. The response was the number of juvenile *H. iris* per quadrat. Quadrats where no abalone or starfish were present were removed from the data set. The final data set consisted of 285 quadrats (59 from RR; 99 from YP; 20 from WTI; 17 from TR; 56 from TB; and 34 from RB). Predator abundance was a fixed continuous predictor. Site and quadrat were categorical random factors. We used nested log-likelihood ratio tests (LRTs) to examine predator abundance × site interactions.

Effects of habitat complexity on juvenile abalone survival in the field

Our laboratory experiments and field survey suggest that starfish play an important role in determining the abundance of juvenile *Haliotis iris* in our study system (see 'Results'). Therefore, we aimed to quantify starfish predation on juvenile abalone in the field using a manipulative field experiment. The experiment was a balanced, factorial design with 3 fixed factors — caging, depth, and algal habitat — each considered at 2 levels. For caging, the 2 levels were caged (predator exclusion) and partially caged (accessible to predators); for depth, the levels were deep (5–6 m) and shallow (2–3 m); and for algal habitat the levels were macroalgal (undisturbed macroalgal communities) and barren (areas cleared of all macroalgae except

crustose coralline algae). We used 2 field sites for this experiment: Reef Bay (RB) and West Taputeranga Island (WTI). At each site, we haphazardly arranged 5 replicates of each predation treatment (caged or partially caged) at each depth (shallow and deep) and algal habitat (barren and macroalgal) treatment combination. Because these sites had been used in a previous experiment (Aguirre & McNaught 2011), barren and macroalgal treatments had been maintained for 7 mo prior to the start of this experiment. The abundance of juvenile abalone and predators varies with depth (Aguirre & McNaught 2012, Cole et al. 2012); hence, in our experiment we considered the main effects of algal habitat and depth (as well as their interaction) to better identify the drivers of predation on juvenile abalone. Finding and tagging enough wild juvenile *H. iris* prevented us from doing the experiment at both sites simultaneously, so we conducted one run of the field experiment in January 2006 at RB and a second run in March 2006 at WTI.

To simulate juvenile *Haliotis iris* habitat (Aguirre & McNaught 2012), we filled plastic trays (310 × 240 × 90 mm) with small cobbles as in the third laboratory experiment described above. To exclude predators from caged treatments, we attached a section of 3.5 mm square, plastic mesh to the top of trays with cable ties. For partially caged treatments, we covered half the tray with the same mesh, and we fixed a 3 mm steel bar half way across the open section of the tray. The partial cage and steel bar were used to minimize experimental artefacts of caging (e.g. differences in water flow and algal disturbance between caged and partially caged treatments). Replicate trays were placed a minimum of 1 m apart and a minimum of 1 m from the edge of each algal habitat treatment. In the field, trays were attached to large sandbags (50 kg) with cable ties (Aguirre & McNaught 2011). To allow access by predators, cobbles and boulders from the surrounding area were piled alongside each tray so that the top of the tray was level with the surrounding reef.

For each run of the experiment, we collected approximately 300 wild *Haliotis iris* juveniles (4.2–10.1 mm SL) from an independent site (YP). After collection, juveniles were placed in laboratory aquaria that were filled with unfiltered, flowing sea water and left there to acclimate for 2 d. Numbered tags (2 mm diameter bee tags, The Bee Works) were then attached to the top of the juveniles' shells using cyanoacrylate glue. After tagging, juveniles were maintained in laboratory aquaria for 1 additional day before being transplanted to the field. On the day we transplanted juveniles to the field, we randomly

assigned tagged juveniles to numbered vials (7 ind. vial⁻¹ at RB and 6 ind. vial⁻¹ at WTI) filled with fresh seawater, and transported the vials to the field site in a large insulated aquarium.

At the field site, divers carefully placed one vial of tagged juveniles into each tray. After 7 d in the field, divers searched the trays *in situ* and recorded the number of tagged juveniles that were alive, dead (tagged empty-shells) or missing. There was no indication of ill-health among the tagged juveniles prior to introducing them to the trays. Furthermore, natural mortality in caged treatments was low (3%) suggesting minimal deleterious effects of transplant stress and handling. No untagged immigrants were recorded. Recovery of tagged juveniles or empty shells was extremely high (99%) indicating minimal emigration; hence, the single missing individual was excluded from our analysis. The number of starfish found in each tray was also recorded. Patterns of survival were analysed using a GLMM with binomial error distribution and a logit link function. Sites were analysed separately, to reflect slight differences in the date of each experimental run and the number of juvenile abalone in each experiment. The response was the proportion of tagged juvenile abalone alive at the end of the experimental period. In analyses for each site, algal habitat, depth and caging were considered fixed factors. Tray was included as an observation level random effect. The significance of the main effects, as well as their interactions were examined using nested LRTs. At WTI, some of the caged trays (5 in total) were invaded by *Coscinasterias calamaria*—these trays were removed from the data set. All analyses were done using the stats and lme4 packages in R v. 2.10.1 (R Development Core Team 2013).

RESULTS

Predation in the absence of refuge

Predation of juvenile *Haliotis iris* by the starfish *Astrostole scabra* and *Coscinasterias calamaria* in the absence of refuge was 100% and 90%, respectively (Fig. 1a). Predation by *C. calamaria* was significantly greater than no-predator (i.e. control) treatments ($Z_{3,73} = -3.910$, $p < 0.001$) (Fig. 1a). *Fosterygion varium* had a marginally non-significant effect on juvenile abalone survival ($Z_{3,73} = -1.744$, $p = 0.081$) (Fig. 1a) and survival in *Pateriella regularis* treatments was not significantly different from no-predator treatments ($Z_{3,73} = -0.501$, $p = 0.620$) (Fig. 1a). *A. scabra* was faster ($F_{1,36} = 4.954$, $p = 0.032$) at capturing juve-

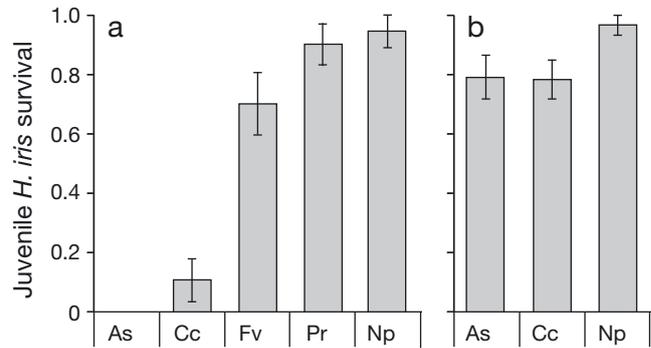


Fig. 1. Survival of juvenile *Haliotis iris* (mean \pm SE) in the laboratory when exposed to the presence of *Astrostole scabra* (As), *Coscinasterias calamaria* (Cc), *Fosterygion varium* (Fv), *Pateriella regularis* (Pr) and no-predator (Np) in (a) the absence of refuge and (b) cobble habitats

nile *H. iris* than *C. calamaria* (mean search efficiencies \pm SE were 8 ± 3.6 h and 17 ± 4.5 h for *A. scabra* and *C. calamaria*, respectively). The shells of juvenile abalone consumed by starfish were undamaged (see also McShane & Naylor 1997).

Predator preference in the absence of refuge

When presented with an alternate food source (juvenile *Mytilus galloprovincialis*), *Astrostole scabra* consumed juvenile *Haliotis iris* first (Odds ratio [\pm 95% CI] = 0.112 [0.669, 0.010], $p = 0.006$), whereas *Coscinasterias calamaria* showed no preference for either prey species (Odds ratio [\pm 95% CI] = 0.547 [2.273, 0.125], $p = 0.520$).

Predation in simulated juvenile habitat

In cobble habitats, survival of juvenile abalone was lower in treatments where *Astrostole scabra* and *Coscinasterias calamaria* were present than in treatments where no predator was present; however, this trend was marginally non-significant ($Z_{2,15} = -1.814$, $p = 0.069$ for both predator species) (Fig. 1b). Nevertheless, in cobble habitats, smaller starfish consumed significantly more juvenile abalone than larger starfish [juvenile survival] = $\text{logit}^{-1}(-2.790 + 0.1799 \times \text{starfish radius})$, $Z_{1,9} = 2.333$, $p = 0.020$).

Distribution of predators and prey in the wild

On the Wellington South Coast, the abundance of juvenile *Haliotis iris* was negatively associated with

the abundance of starfish (*Astrostole scabra* and *Coscinasterias calamaria*), but the relationship varied among sites (Fig. 2, Table 1). The relationship was negative and significant for 5 of the 6 sites (RB, TB, WTI, YP and RR; Fig. 2, Table 1), but marginally non-significant for the remaining site (TR; Fig. 2, Table 1). We then explored the relationship between the abundance of juvenile *H. iris* and each starfish species separately. For each starfish species, we found juvenile abalone abundance declined with increasing starfish abundance, but the significance of this relationship varied among sites (Table 1). For *C. cala-*

maria, the negative relationship between starfish abundance and juvenile abalone abundance was significant in 5 of 6 sites (RB, TB, YP, WTI and RR; Table 1), and marginally non-significant for the remaining site (TR; Table 1). Conversely, for *A. scabra*, the relationship was significant for only 3 of the 6 sites (TB, YP and WTI; Table 1) and non-significant at the remaining 3 sites (RB, TR and RR; Table 1).

Effects of habitat complexity on juvenile abalone survival in the field

At RB and WTI, juveniles in caged treatments had significantly greater survival than juveniles in partially caged treatments (caging LRT: $\chi^2_1 = 4.475$, $p = 0.034$; and $\chi^2_1 = 15.249$, $p < 0.001$, for RB and WTI, respectively) (Fig. 3). However, survival was lower at WTI than RB (78 % and 97 % survival, respectively). For both sites, there were no significant interactions among factors (caging, algal habitat and depth). At WTI, survival in macroalgal treatments was significantly higher than survival in barren treatments (algal habitat LRT: $\chi^2_1 = 4.084$, $p = 0.043$) (Fig. 3). Algal habitat had no effect on juvenile survival at RB (algal habitat LRT: $\chi^2_1 = 0.185$, $p = 0.667$) (Fig. 3) and depth had no significant effect on juvenile survival at RB or WTI (depth LRT: $\chi^2_1 = 0.024$, $p = 0.877$ and $\chi^2_1 = 0.840$, $p = 0.359$, respectively) (Fig. 3). *Coscinasterias calamaria* and *Astrostole scabra* were present in 30 % of partially caged trays at the time we measured juvenile abalone survival; thus, we hesitate to provide formal statistical analysis of habitat effects on starfish abundance in our field experiments. However, we note that carnivorous starfish abundance was 1200 % greater at WTI than RB as well as 300 % and 100 % greater in barren than macroalgal treatments at WTI and RB, respectively. In addition, we

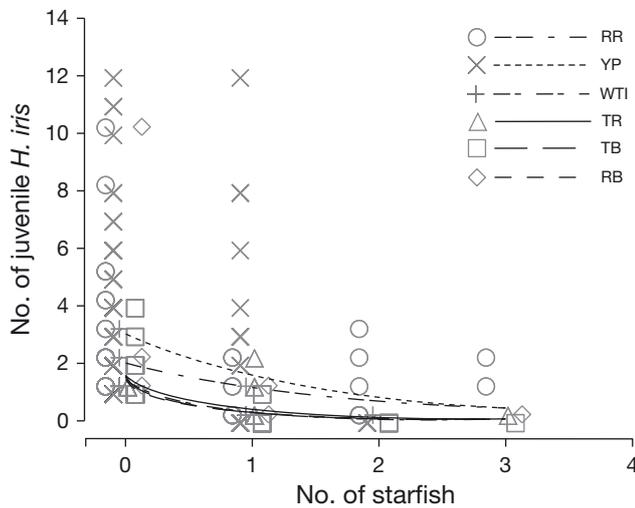


Fig. 2. The relationship between starfish (*Astrostole scabra* and *Coscinasterias calamaria*) abundance and the abundance of juvenile *Haliotis iris* (<10 mm shell length) at 6 sites (Red Rocks [RR]; Yung Penn [YP]; West Taputeranga Island [WTI]; Te Raekaihau [TR]; Tarekena Bay [TB]; and Reef Bay [RB]) on the Wellington South Coast, New Zealand. There was a significant negative relationship between starfish abundance and juvenile abalone abundance at RB, TB, WTI, YP and RR. Points are offset on both the x and y-axis to improve clarity

Table 1. Relationship between the abundance of juvenile *Haliotis iris* and the combined abundance of *Coscinasterias calamaria* and *Astrostole scabra* as well as the abundance of each predator separately. We used nested log-likelihood ratio tests to assess the significance of the model parameters (* $p < 0.05$, $^{\dagger}p < 0.1$). Sites are denoted as follows: RR = Red Rocks, YP = Yung Penn, WTI = West Taputeranga Island, TR = Te Raekaihau, TB = Tarekena Bay, RB = Reef Bay

	<i>C. calamaria</i> + <i>A. scabra</i>			<i>C. calamaria</i>			<i>A. scabra</i>		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Starfish × Site	15.547	2	<0.001*	11.399	2	0.003*	11.399	2	0.003*
RR	6.529	1	0.011*	6.235	1	0.013*	2.587	1	0.108
YP	18.434	1	<0.001*	12.962	1	<0.001*	10.019	1	0.001*
WTI	8.543	1	0.003*	5.723	1	0.017*	4.540	1	0.033*
TR	3.265	1	0.071 [†]	3.670	1	0.056 [†]	0.750	1	0.386
TB	46.390	1	<0.001*	34.930	1	<0.001*	26.829	1	<0.001*
RB	17.628	1	<0.001*	17.659	1	<0.001*	2.441	1	0.118

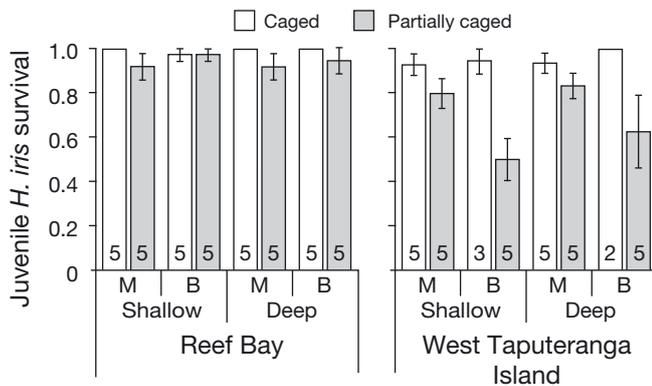


Fig. 3. Effects of depth, algal habitat and caging on survival of juvenile *Haliotis iris* (mean \pm SE) at 2 sites (Reef Bay and West Taputeranga Island) on the Wellington South Coast, New Zealand. For depth, the 2 treatments are shallow (2–3 m) and deep (5–6 m). For algal habitat, the 2 treatments are macroalgae (M) and barren (B). For caging, the 2 treatments are caged (open bars) and partially caged (shaded bars). Numbers inside bars represent the sample size for each treatment combination

found a strong negative correlation between the total number of starfish in each treatment and the mean survival of juvenile abalone ($r = -0.90$). All the empty shells recovered in the field experiment were found undamaged within the trays, consistent with our laboratory observations of predation by starfish.

DISCUSSION

Predators of juvenile *Haliotis iris*

Predation by starfish appears to be an important driver of demographic variability among abalone populations in central New Zealand. Specifically, our laboratory experiments indicated that the starfish *Astrostele scabra* and *Coscinasterias calamaria* are influential predators of juvenile *Haliotis iris* (<10 mm SL). A negative relationship between the abundance of starfish and the abundance of juvenile abalone in the field supported these laboratory results. Moreover, a manipulative field experiment confirmed that predation by starfish was the probable cause for declines in juvenile abalone survival in the field.

Of the 14 potential predators we examined in the laboratory, 5 consumed juvenile abalone, but only *Astrostele scabra* and *Coscinasterias calamaria* were considered likely predators of juvenile abalone. Of these 2 starfish species, *A. scabra* preferred juvenile abalone to mussels, whereas *C. calamaria* showed no preference for juvenile abalone or mussels. Addi-

tionally, *A. scabra* was faster at capturing juvenile abalone than *C. calamaria*. However, surveys revealed that *C. calamaria* was 177% more abundant than *A. scabra* in the field, and small-scale negative associations between *C. calamaria* and juvenile *H. iris* are more common than negative associations between *A. scabra* and juvenile *H. iris*. Hence, although *A. scabra* may be more efficient at capturing and consuming juvenile abalone, it seems that the greater abundance of *C. calamaria* increases the likelihood of an encounter between predator and prey.

Contact by starfish elicits an escape response in many abalone species (Day et al. 1995) including *Haliotis iris* (J. D. Aguirre pers. obs.), and it is probable that predator avoidance contributes to small-scale negative associations between starfish and juvenile abalone in the field. Nevertheless, because it is the presence of starfish that underlies variation in the abundance of juvenile abalone, avoidance-based mechanisms still imply that starfish play an important role in mediating the abundance and distribution of juvenile abalone (e.g. Duggins 1983). Furthermore, the strong negative correlation between abalone survival and starfish abundance in our manipulative field experiment supports the strong structuring influence of starfish on abalone populations at larger scales. A second alternative explanation for our results is that starfish abundance covaries with urchin abundance due to a shared preference for barren habitats. However, urchins were never encountered within the experimental trays, and the shells of juvenile abalone were recovered undamaged and in close proximity to the release site—consistent with predation by starfish (McShane & Naylor 1997). Thus, competitive exclusion by urchins seems improbable in our experiments.

Compared with other geographic locations, relatively little is known of the predators of juvenile abalone in New Zealand. Polychaetes have been identified as predators of larvae and post-settlers (Naylor & McShane 1997), whereas fish and starfish have been proposed as predators of late juveniles and adult (>20 mm SL) *Haliotis iris* (Schiel 1992, McShane & Naylor 1997). Our studies indicate that starfish are also important predators of early juvenile *H. iris* (<10 mm SL). Surprisingly, common abalone predators such as crustaceans (crabs and lobsters), octopi and fishes appear unlikely predators of juvenile *H. iris* in central New Zealand. *Plagusia chabrus* and *Hemigrapsus edwardsii* are 2 crab species capable of consuming juvenile abalone (Pederson et al. 2008; our Appendix 1, Table A1). However, these species were

most common near the intertidal margin or in the crevices of high relief habitats (J. D. Aguirre pers. obs. for *H. edwardsii* and *P. chabrus*, respectively), and thus rarely encountered in deeper cobble habitats where juvenile *H. iris* are most common (Aguirre & McNaught 2012). Rock lobsters *Jasus edwardsii* are commercially and recreationally harvested in central New Zealand, and were uncommon at our study sites. Small octopi such as *Pinnoctopus cordiformis* were occasionally encountered during predator surveys; however, octopi did not consume juvenile *H. iris* in the laboratory within the 3 d experimental period (Appendix 1, Table A1). Last, our results for *Fosterygion varium* and the results of Schiel (1992) also imply that fish predation may have weak effects on juvenile *H. iris* abundance in cobble habitats. Therefore, although there are a number of species capable of capturing and consuming juvenile *H. iris*, it appears that starfish are one of the most influential predators of juvenile abalone in central New Zealand.

Effects of habitat complexity on juvenile abalone survival

For many marine organisms, the structural complexity of cobble reefs habitats provides a refuge from demersal and benthic predators (Wahle & Steneck 1991, Gotceitas & Brown 1993, Dixon et al. 2006). Accordingly, the juvenile stages of most abalone species are found within the interstitial spaces of cobble reefs (Carreon-Palau et al. 2003, Pederson et al. 2008, Aguirre & McNaught 2012). Furthermore, there is evidence that smaller abalone prefer smaller cobble sizes (Tegner & Butler 1989, De Waal & Cook 2001, Carreon-Palau et al. 2003, Aguirre & McNaught 2012). Smaller cobbles decrease the size of interstitial spaces (Tegner & Butler 1989, Aguirre & McNaught 2012), and may limit the effective predator population to only the smallest size-classes (Shepherd 1973, Tegner & Butler 1989). For instance, our analyses predict that juvenile abalone survival in cobble habitats is 24% less in the presence of a 20 mm radius starfish compared with a 30 mm radius starfish. This small-scale habitat partitioning between predator and prey may explain the preference of smaller abalone for smaller cobble sizes, and highlights the importance of habitat complexity in mediating juvenile abalone survival.

The structural complexity of macroalgal habitats can also reduce predator foraging efficiency and offers an effective refuge for juvenile fish and marine invertebrates (Wahle & Steneck 1991, Tupper & Boutilier

1997). In our manipulative field experiment, the effects of algal habitat complexity on juvenile abalone survival were positive at WTI but non-significant at RB. At RB, starfish abundance was low and juvenile abalone survival was high; thus, the opportunity for algal habitat effects to manifest may have been limited. At WTI on the other hand, starfish were more common and juvenile abalone survival was lower, thereby increasing the likelihood that differences in juvenile abalone survival between barren and macroalgal habitats would manifest. Importantly, for both sites, starfish abundance was greater in barren habitats than macroalgal habitats, and we believe differences in survival among algal habitat treatments would accumulate over time at RB.

The crustose coralline algae that typify barren habitats induce abalone settlement (Morse & Morse 1984). Furthermore, barren habitats can produce a hydrodynamic environment that facilitates the transport of larvae to the substratum (Eckman et al. 1989, Eckman 1990), and thereby enhances abalone settlement (Aguirre & McNaught 2011). Barren habitats, however, appear unable to maintain abalone populations post-settlement (Andrew 1993, Karpov et al. 2001, Aguirre & McNaught 2011, Won et al. 2013). For example, Andrew (1993) monitored changes in the abundance of benthic marine invertebrates in reciprocal transplants of boulders from barren and macroalgal habitats. By the end of the experiment, no abalone remained on boulders in barren habitats, whereas abalone were always present on boulders in macroalgal habitats (Andrew 1993). Additionally, in a study examining the factors underlying a transition from deeper barren habitats to shallower macroalgal habitats, Won et al. (2013) suggest that greater predation and food limitation in barren habitats underlies ontogenetic habitat transitions in *Haliotis discus hannai*. Overall, our data indicate that starfish predation may contribute strongly to declines in abalone abundance following transitions from macroalgal to barren habitats.

Anthropogenic disturbance and predation on abalone

Fishing and hunting have caused dramatic reductions in the abundance of marine species. Alarmingly, the species commonly affected by overexploitation are species that occupy high trophic levels (Pauly et al. 1998). Hence, predators at lower trophic levels become increasingly important for maintaining community structure (Tegner & Dayton 2000,

Jackson et al. 2001). Recently, top-down control of urchins by starfish has been shown to mediate the formation of barren habitats in locations with heavily compromised or low diversity predator populations (Duggins 1983, Vasquez et al. 2006, Bonaviri et al. 2009). Starfish, although effective predators, typically occupy the lower trophic levels of subtidal communities, and the loss of starfish from these communities could trigger widespread transitions from macroalgal to barren habitats (Tegner & Dayton 2000). Thus, while we show that starfish predation has direct negative effects on abalone populations, our results also imply there may be positive indirect effects of starfish on abalone due to top-down control of a habitat modifying competitor (Chase et al. 2002). Furthermore, it is possible that if current levels of overexploitation continue, the indirect positive effects of starfish on abalone may prove more influential than direct negative effects of predation.

Changes in land use and the dumping of waste from domestic or commercial enterprises have significantly enhanced the volume of sediment entering marine ecosystems. In extreme cases, entire rocky reefs become buried under layers of sediment (Airoldi 2003). Burial is known to cause direct mortality of juvenile and adult abalone (Sainsbury 1982, Schiel 1993). Moreover, a recent study demonstrated that the accumulation of sediments within interstitial spaces of cobble reefs can induce behaviours in juvenile abalone that increase the risk of predation (Chew et al. 2013). Our results provide further evidence for negative indirect effects of sedimentation on abalone populations as a consequence of reductions in cobble habitat complexity.

The simplification of many of the world's marine ecosystems seriously threatens population persistence, and one of the major impediments to recovery is the lack of suitable juvenile habitat. Habitat heterogeneity plays a central role in determining survival during the vulnerable early juvenile stages, because in many cases it reduces the intensity of predation (Caley & St John 1996, Tupper & Boutilier 1997, Lindholm et al. 1999, Hovel & Lipcius 2001). Thus, the ecological consequences of human activities which cause direct (dredging or the removal of mangroves) or indirect (cascading effects of predator removal or land use change) habitat simplification are, and will continue to be, a central issue in ecology and species conservation.

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Appendix 1.

Table A1. Survival of *Haliotis iris* (3–10 mm shell length) in the absence of refuge for the predator species not included in the experiment presented in the manuscript. Potential predators were selected based on observations of their presence in cobble habitats in the field. For each predator species, there were more than 3 replicates. Predators were allowed a maximum of 3 d to consume prey. Although *Hemigrapsis edwardsii* was successful at capturing and consuming juvenile abalone, *H. edwardsii* was rarely observed below the intertidal margin (J. D. Aguirre pers. obs.), whereas early juvenile *H. iris* are most abundant in deeper subtidal habitats (Aguirre & McNaught 2012). Thus, we excluded *H. edwardsii* from the formal laboratory experiments, but we acknowledge that if juvenile abalone were to encounter *H. edwardsii* in the field, then predation is likely. Surprisingly, *Stichaster australis* had almost no effect on *H. iris* survival

Species	<i>Haliotis iris</i> survival
Crustaceans	
<i>Hemigrapsis edwardsii</i>	0.0
<i>Petrolisthes elongatus</i>	1.0
<i>Pilumnus novaezealandiae</i>	1.0
<i>Eurynolambrus australis</i>	1.0
Cephalopods	
<i>Pinnoctopus cordiformis</i>	1.0
Gastropods	
<i>Cominella virgata</i>	1.0
Echinoderms	
<i>Pectinura maculata</i>	1.0
<i>Stichaster australis</i>	0.95
Fish	
<i>Forsterygion lapillum</i>	1.0
Polychaetes	
<i>Nereis</i> sp.	1.0