

# Predation cues rather than resource availability promote cryptic behaviour in a habitat-forming sea urchin

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**Abstract** It is well known that predators often influence the foraging behaviour of prey through the so-called “fear effect”. However, it is also possible that predators could change prey behaviour indirectly by altering the prey’s food supply through a trophic cascade. The predator–sea urchin–kelp trophic cascade is widely assumed to be driven by the removal of sea urchins by predators, but changes in sea urchin behaviour in response to predators or increased food availability could also play an important role. We tested whether increased crevice occupancy by herbivorous sea urchins in the presence of abundant predatory fishes and lobsters is a response to the increased risk of predation, or an indirect response to higher kelp abundances. Inside two New Zealand marine reserves with abundant predators and kelp, individuals of the sea urchin *Evechinus chloroticus* were rarer and remained cryptic (i.e. found in crevices) to larger sizes than on adjacent fished coasts where predators and kelp are rare. In a mesocosm experiment, cryptic behaviour was induced by simulated predation (the addition of crushed conspecifics), but the addition of food in the form of drift kelp did not induce cryptic behaviour. These findings demonstrate that the ‘fear’ of predators is more important than food availability in promoting sea urchin cryptic behaviour and suggest that both density- and

behaviourally mediated interactions are important in the predator–sea urchin–kelp trophic cascade.

**Keywords** Behaviourally mediated indirect interaction · Density-mediated indirect interaction · Fear effect · Kelp forest · Trophic cascades

## Introduction

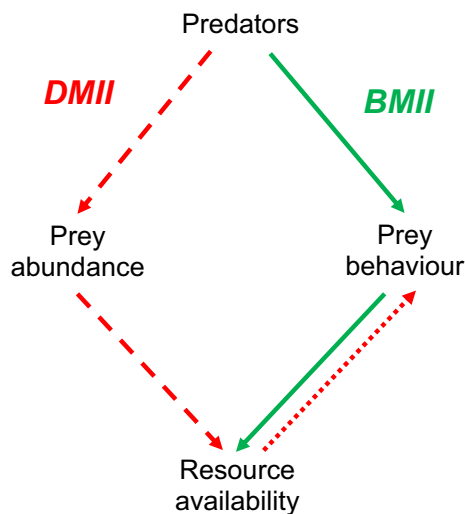
Trophic cascades have traditionally been viewed as density-mediated indirect interactions (DMIIs), in which predators reduce the abundance of their prey, leading to an increase in the abundance of the prey’s primary food resource (Carpenter et al. 1985; Pace et al. 1999). It is now clear that predators can further reduce the impact of prey on their food resource (and thus strengthen the trophic cascade) by constraining the foraging behaviour of surviving prey individuals, i.e. a behaviourally mediated indirect interaction (BMII) (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005; Trussell et al. 2006). For example, in Yellowstone National Park the mere presence of wolves deters elk from risky habitats and facilitates plant regrowth (Ripple et al. 2001). However, predators could also alter the foraging behaviour of their prey by affecting the prey’s food supply. Predators could boost the amount of available food per prey individual by increasing the total amount of food in the system through a trophic cascade or by reducing intraspecific competition for the same amount of food through the removal of prey individuals. When food is plentiful, individuals of many species become more sedentary to save energy and reduce the risk of being preyed upon (Higginson and Ruxton 2015). This appears to be an overlooked pathway in which changes in prey behaviour could be mistakenly attributed to the direct threat of predation (Fig. 1).

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**Fig. 1** Density-mediated (DMII; *dashed line*) and behaviourally mediated (BMII; *solid line*) trophic cascades and the alternative pathway (*dotted line*) via which predators may indirectly influence prey behaviour by altering resource availability. Predators may influence prey behaviour directly when increased predation risk causes prey to alter their behaviour (BMII), whereas prey may also change their behaviour in response to increased resource availability, which can occur as an indirect effect of predators (DMII)

The predator–sea urchin–kelp interaction is perhaps the best known example of a marine trophic cascade (Estes and Duggins 1995; Shears and Babcock 2002; Byrnes et al. 2006; Blamey and Branch 2012). In many regions, the destruction of kelp forests by sea urchins has been attributed to the overharvesting of sea urchin predators such as sea otters, fishes or lobsters (Steneck et al. 2002). Predators are generally thought to increase kelp biomass by removing sea urchins, i.e. a DMII (Estes and Duggins 1995; Blamey and Branch 2012). Less attention has been paid to the potential role that predators play in altering sea urchin behaviour and driving changes in kelp biomass through BMII, although it has been shown that the mere presence of predators can initiate predator avoidance, escape responses or defensive behaviours in sea urchins (Hagen et al. 2002; Vadas and Elner 2003; Manzur and Navarrete 2011), which can create sea urchin-free patches of reef (Watson and Estes 2011). Furthermore, predation-related cues can reduce grazing rates of sea urchins (Byrnes et al. 2006; Matassa 2010). Consequently, the presence of predators could lead to shifts in sea urchin behaviour and contribute to the maintenance and persistence of kelp forests.

The microhabitat occupied by sea urchins can be categorised as “exposed”, where the sea urchin is on an open reef surface, or “cryptic”, where it occupies a refuge such as a crevice (Sala and Zabala 1996). Refuge occupancy has often been considered an anti-predator behaviour (Bernstein et al. 1981; Tegner and Levin 1983). However, cryptic

behaviour in sea urchins could also be a response to plentiful food, particularly in the form of detrital (“drift”) kelp (Harrold and Reed 1985; Vanderklift and Wernberg 2008). Detritus is constantly produced by kelps and subsidises consumers within the forest and in adjacent habitats (Krumhansl and Scheibling 2012), so when drift kelp is readily available sea urchins can adopt a cryptic ‘sit and wait’ feeding strategy, whereas when food is scarce they leave refugia and forage in the open (Harrold and Reed 1985). Predators could, therefore, lead to a more cryptic population of sea urchins through two mechanisms: (1) as a direct response to predation risk, or (2) indirectly via a trophic cascade that increases food availability for sea urchins.

In north-eastern New Zealand, the recovery of kelp forests within well-established marine reserves has been attributed to the recovery of previously harvested predators and subsequent declines in sea urchin densities (Babcock et al. 1999; Shears and Babcock 2002). While this trophic cascade has largely been assumed to be density-driven, sea urchins within marine reserves are typically more cryptic (Cole and Keuskamp 1998; Shears et al. 2008) and it has been suggested that predator-induced changes in sea urchin behaviour may facilitate the recovery of kelp (Shears and Ross 2010). However, it remains unknown whether the increased crypticity at reserve sites is due to the higher abundance of predators or a greater availability of the sea urchins’ preferred food (kelp). In the present study, we examine whether the cascading effects of predators on kelp are augmented by a BMII, whereby sea urchins increase their occupancy of crevices due to increased predation risk, or whether increased crypticity is an indirect response to predators (i.e. through increased food availability). We compare sea urchin densities, size-specific rates of crevice occupancy of sea urchins, and kelp densities between two well-established marine reserves and adjacent fished areas. We then use a mesocosm experiment to determine the relative effects of predation cues and food supply on sea urchin behaviour.

## Methods

### Field survey

We used two well-established marine reserves located on moderately exposed rocky coasts and adjacent fished areas in north-eastern New Zealand as a natural experiment (Fig. S1). The Cape Rodney to Okakari Point Marine Reserve (hereafter the Leigh Marine Reserve LMR) is 549 ha and was established in 1977, while the Tawharanui Marine Reserve (TMR) is 350 ha and was established in 1982. All marine life is fully protected within both reserves, while on the surrounding coast the sea urchin predators *Pagrus*

*auratus* (“snapper”) and *Jasus edwardsii* (“red rock lobster”) are heavily targeted by commercial and recreational fishers. The sea urchin *Evechinus chloroticus* is lightly harvested at sites that are readily accessible from shore. We surveyed sea urchins and kelp at four sites within each marine reserve and at four sites within each of two adjacent fished areas (Fig. S1). These had similar topographic relief and exposure to wave action to the marine reserves (Cole and Keuskamp 1998; Shears et al. 2008).

Field surveys of sea urchins and kelp were carried out in August 2013 for the Leigh area and October–November 2013 for the Tawharanui area. Sea urchin densities, sea urchin crevice occupancy, and kelp densities were quantified at each site within five 1-m<sup>2</sup> quadrats haphazardly placed within the 4–6 m depth zone. This depth range is within the depth zone where *E. chloroticus* is most abundant on moderately exposed reefs in north-eastern New Zealand (Shears et al. 2008). The test diameter of each sea urchin was measured using calipers ( $\pm 5$  mm), and its position recorded as either “cryptic” (at least partially hidden or wedged under/between rocks below the surface of the reef) or “exposed” (on open surfaces of reef). All *Ecklonia radiata* (kelp) individuals, including new recruits, were measured (stipe and primary lamina length  $\pm 5$  mm) and recorded. No other macroalgae were present in significant numbers.

To check whether habitat complexity influenced spatial patterns of crevice occupancy by sea urchins, we quantified rugosity and crevice volume within five 1-m<sup>2</sup> quadrats. Three measurements of rugosity were made along straight lines crossing each quadrat (along two edges and through the middle). A 1-m length of chain (28-mm link length) was moulded to the rock surface, and rugosity calculated as the inverse of the linear distance spanned by the chain (Risk 1972). Crevice availability was estimated by counting and measuring all crevices  $\geq 125$  cm<sup>3</sup> (i.e.  $5 \times 5 \times 5$  cm). It was not practical to measure smaller crevices and this minimum size was used as it would accommodate an urchin of ~40 mm test diameter, which is the size where urchins typically emerge from a cryptic to exposed lifestyle at fished sites (Shears and Babcock 2002). This approach, therefore, provides a measure of crevice availability for urchins  $\geq 40$  mm. Based on these measurements, the total volume of available crevices was calculated in each quadrat as well as the number of crevices inside each quadrat that fitted into two broad size classes: “Small”  $< 1$  L and “Large”  $> 1$  L. Small crevices were considered large enough to house urchins up to ~100 mm test diameter, whereas larger crevices could house multiple urchins.

Surveys of sea urchin predators were carried out in 2014 around the Leigh and Tawharanui coastlines by J. Richardson (snapper, *P. auratus*) and T. Haggitt (lobster, *J. edwardsii*). Relative abundances of *P. auratus* were estimated

using 30-min baited underwater video drops (BUV; Willis and Babcock 2000), following the survey design of Willis et al. (2003). Eighteen replicate deployments were made inside the LMR with a further 18 carried out along the adjacent fished coast. Twelve replicate deployments were made inside the TMR, with a further 12 along the adjacent fished coast. Footage was analysed to obtain the maximum number of legal-sized individuals ( $> 270$  mm fork length) in the field of view within a single frame during each recording (Willis and Babcock 2000). *J. edwardsii* densities were quantified using  $50 \times 10$  m (500 m<sup>2</sup>) visual transects. Five replicate transects were carried out at six sites within each marine reserve and a total of six sites across the two fished areas (two Leigh and four Tawharanui sites). The size of each observed individual was estimated visually (following Kelly et al. 2000) and the number of legal-sized lobsters ( $\geq 100$  mm carapace length) per transect was analysed. Legal-sized lobsters and snapper are known to be effective predators of sea urchins (Andrew and MacDiarmid 1991; Shears and Babcock 2002).

## Experiment

To determine the effects of predation cues and food availability on behaviour of *E. chloroticus*, a mesocosm experiment was run at the Leigh Marine Laboratory, adjacent to the Cape Rodney to Okakari Point Marine Reserve, between September and October 2013. Eight 1500 L outdoor tanks were set up. Tanks were 1.8 m diameter and contained a 1-m<sup>2</sup> rock-covered area in the centre, allowing sea urchins access to shelter. Small rocks and boulders were collected from a nearby reef, and were 15–30 cm diameter, free of erect macroalgae and predominantly covered in crustose coralline algae. These were arranged in a way in the centre of each tank that provided shelter availability that was analogous to the survey sites. The 1-m<sup>2</sup> area was enclosed by a 15-mm mesh cage to prevent sea urchins moving off the reef. To mimic the natural subtidal environment, each tank was fitted with a 60-L dump bucket to provide turbulence, fed with flow-through seawater from the adjacent coast at a rate of 1500 L h<sup>-1</sup>, and was covered by shade cloth that excluded 80% of the natural light. *E. chloroticus* of 50–79 mm test diameter were collected from a nearby fished reef (36°18′12.54″S, 174°48′02.58″E) and transferred (fully submerged) into a 1500-L seawater tank to settle for three days before the experiment began. Ten individuals were added to each tank.

Sea urchins were subjected to two treatments in a fully crossed design. For the predation cue treatment, one large sea urchin was cracked open and placed inside the tank between ~5–6 pm three times per week (with the old sea urchin being removed each time) to simulate a nearby conspecific being eaten (“+predation cue”). Control tanks

were not subjected to this simulated predation (“–predation cue”). In the food availability treatment (“+food”), ten *E. radiata* fragments (~20 cm length pieces of secondary lamina) were added to each tank three times per week (at ~5–6 pm) to simulate the regular provision of drift kelp, while control tanks received no additional food (“–food”). Uneaten *E. radiata* fragments were not removed.

Observations were made at 12 am, 8 am, 12 pm and 8 pm in four day blocks, over a three-week period. At each time, the position of each sea urchin was recorded as either “exposed” (visible on the outside of the reef) or “cryptic” (at least partially hidden under rocks or wedged between rocks and the cage). Due to the limited number of tanks available (two per treatment/level combination), the experiment was run twice using a new set of sea urchins on the second occasion to give a total of four replicates for each treatment/level combination.

## Data analysis

Field data on predators, sea urchins, kelp and crevice availability were analysed using PERMANOVA in PRIMER v6 to account for the non-normality associated with count data. The PERMANOVA design consisted of two fixed factors: Area (Leigh or Tawharanui) and Status (Reserve or Fished) and a random factor; Site nested within Area  $\times$  Status. Count data were log-transformed prior to analysis to correct for heterogeneity of variance and analyses were based on Euclidean distance matrices. Chi-squared tests were used to compare the differences in the proportion of cryptic sea urchins in each size class between reserve and fished populations.

To examine how sheltering behaviour (cryptic or exposed) changed in relation to predation cues and food availability in the mesocosm experiment a generalised linear model (family = binomial) was conducted in R v.3.0.2. The model had three fixed factors: Predation cue ( $\pm$ ), Food ( $\pm$ ) and Week (1, 2 and 3). An optimal model was fitted using backwards elimination of non-significant interaction terms. This resulted in the final model only having one significant interaction term—predation cue  $\times$  week.

## Results

### Field survey

Densities of legal-sized *P. auratus* and *J. edwardsii* were significantly higher within both marine reserves than on adjacent fished coasts (Fig. 2a, b; Table 1). The maximum number of legal-sized *P. auratus* averaged  $6.6 \pm 1.9$  (SE) individuals BUV drop<sup>-1</sup> inside the LMR,  $4.3 \pm 1.6$  inside the TMR, and only  $0.1 \pm 0.1$  and  $0.7 \pm 0.7$  in the

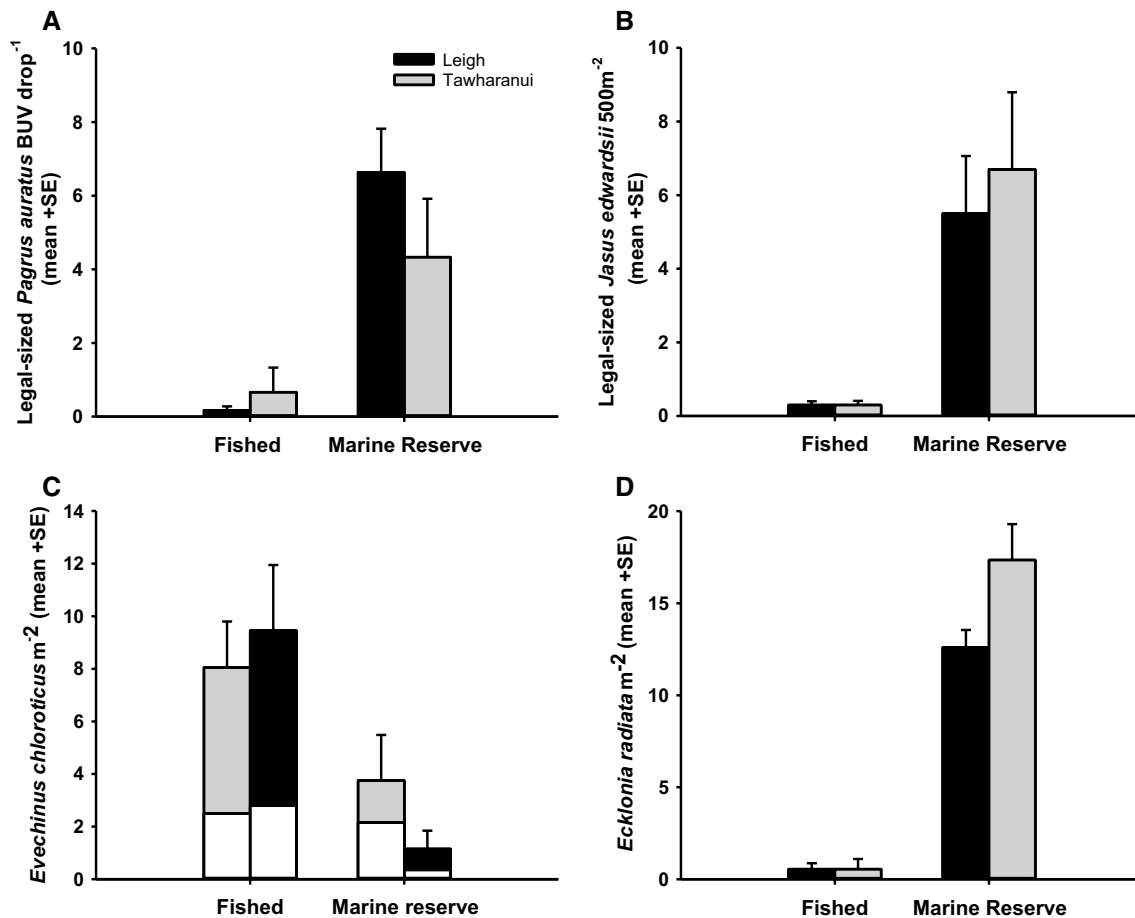
respective fished areas. The average density of legal-sized *J. edwardsii* was  $5.5 \pm 1.6$  individuals 500 m<sup>-2</sup> inside the LMR and  $6.7 \pm 2.1$  within the TMR, and only  $0.3 \pm 0.1$  within both fished areas.

Sea urchin densities were lower within the marine reserves than on adjacent fished reefs (Fig. 2c; Table 1). This pattern was consistent across both areas, but total average density was lower in the TMR ( $1.2 \pm 0.7$  m<sup>-2</sup>) than in the LMR ( $3.8 \pm 1.7$  m<sup>-2</sup>). There was no overall difference in the density of cryptic sea urchins between reserve and fished areas, but the density of exposed sea urchins was much lower at reserve sites than at fished sites (Table 1).

The kelp *E. radiata* was abundant at 4–6 m depth in the marine reserves and rare in both fished areas (Fig. 2d; Table 1). *E. radiata* formed canopies at all reserve sites and other brown macroalgae were rare. The density of individuals averaged  $12.6 \pm 1.0$  m<sup>-2</sup> inside LMR and  $17.4 \pm 2.0$  m<sup>-2</sup> inside the TMR. On adjacent fished reefs, densities were significantly lower at  $0.6 \pm 0.4$  m<sup>-2</sup>.

Crevice occupancy varied with sea urchin size and reserve status (Fig. 3; Table 2). Regardless of location, all sea urchins <40 mm test diameter were cryptic, and the proportion of cryptic individuals generally declined with increasing size to the point where most individuals  $\geq 80$  mm were exposed. However, individuals within the marine reserves remained cryptic to a larger size than did individuals in fished areas. In the marine reserves, 94–100% of 60–79 mm individuals were cryptic, whereas in fished areas 6–28% of similar sized urchins were cryptic (Table 2).

Rugosity, the number of large crevices and overall crevice volume did not differ significantly between reserve and fished sites (Fig. S2; Table 1). All reefs were moderately complex, with average rugosity values ranging from  $1.35 \pm 0.14$  to  $1.60 \pm 0.18$  (Fig. S2a) and 2–3 large crevices (i.e. >1 L) m<sup>-2</sup> at both fished and protected areas (Fig. S2c). The total crevice volume available in each quadrat was on average 8–9 L, therefore, capable of accommodating several *E. chloroticus* of any size. TMR had a substantially higher average crevice volume (~15 L m<sup>-2</sup>) but this was largely driven by two sites (Comet Rocks and North Cove), which had the highest crevice volumes of all the sites sampled. There were significantly more small crevices at fished sites compared to the reserve sites (Table 1); however, small crevices were still relatively abundant at all sites (Fig. S2b). At the fished sites (Leigh Fished LF, and Tawharanui Fished TF), the average volume of large crevices (>1 L) was  $6.2 \pm 1.2$  L m<sup>-2</sup> at LF and  $6.0 \pm 1.3$  L m<sup>-2</sup> at TF. Densities of sea urchins >40 mm test diameter averaged  $6.2 \pm 0.7$  ind. m<sup>-2</sup> at LF sites and  $7.8 \pm 2.3$  ind. m<sup>-2</sup> at TF sites, so there was sufficient crevice space to accommodate those individuals (even allowing for the spines) if they had chosen to remain cryptic.



**Fig. 2** Relative densities of the sea urchin predators **a** legal-sized *Pagrus auratus* (snapper) ( $n = 18$  BUV drops for each of LMR and LF, and  $n = 12$  BUV drops for each of TMR and TF) and **b** legal-sized *Jasus edwardsii* (lobster) ( $n = 30$  transects for each of LMR and TMR,  $n = 10$  transects for LF and 20 for TF), **c** sea urchins

*Evechinus chloroticus* ( $n = 5$  quadrats at each of four sites) and **d** kelp *Ecklonia radiata* ( $n = 5$  quadrats at each of four sites) on fished versus protected reefs at Leigh and Tawharanui, north-eastern New Zealand. In panel **c**, the white areas of each bar represent cryptic *E. chloroticus* and shaded areas represent exposed individuals

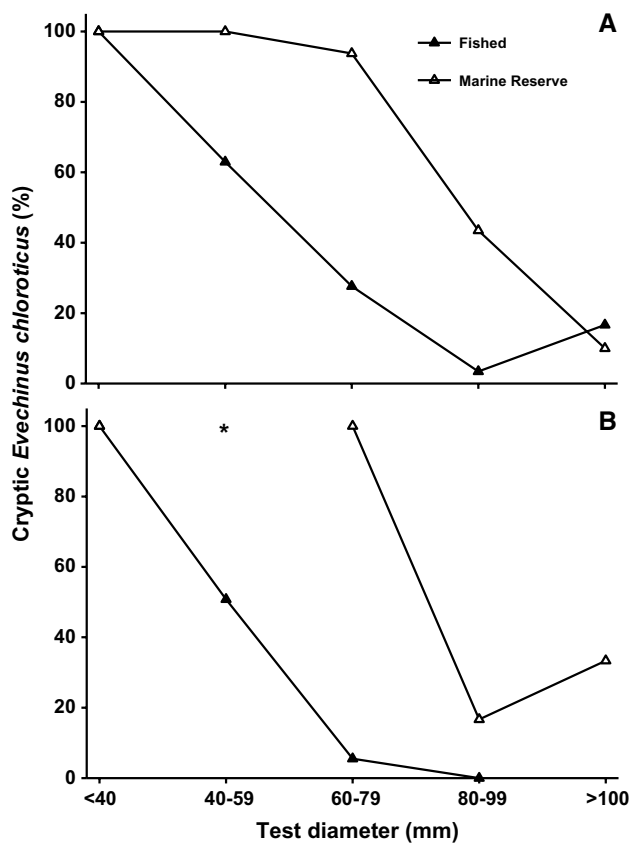
**Table 1** Results from PERMANOVA assessing the effects of area, reserve, area  $\times$  reserve and site (area  $\times$  reserve) on (A) densities of legal-sized snapper (*Pagrus auratus*), legal-sized lobster (*Jasus edwardsii*), sea urchins (*Evechinus chloroticus*) and the kelp *Ecklonia radiata*, and (B) crevice availability metrics including rugosity, the number of small ( $<1$  L) and large ( $>1$  L) crevices, and total crevice volume

Variable	Area		Reserve		Area $\times$ reserve		Site (area $\times$ reserve)	
	MS	F	MS	F	MS	F	MS	F
(A) Densities								
Legal-sized <i>Pagrus auratus</i>	0.21	0.4	120.2	232.94***	0.45	0.88	0.51	3.13**
Legal-sized <i>Jasus edwardsii</i>	0.24	0.22	44.44	40.95***	0.3	0.28	1.09	3.60***
All <i>Evechinus chloroticus</i>	1.94	1.7	1.94	1.70**	1.37	1.2	1.14	1.94*
Exposed <i>E. chloroticus</i>	0.18	0.19	26.79	28.72***	0.46	0.49	0.93	1.75
Cryptic <i>E. chloroticus</i>	0.31	0.29	2.92	2.75	4.55	4.29	1.06	2.13*
<i>Ecklonia radiata</i>	0.12	0.34	16.54	48.01***	0.59	1.71	0.34	1.11
(B) Crevice availability								
Rugosity	5.66	3.4	0.00	0.00	1.45	0.87	1.67	2.05*
Number of crevices $<1$ L $^{-1}$	3.31	1.52	9.49	4.36*	2.32	1.07	2.18	3.69**
Number of crevices $>1$ L $^{-1}$	1.28	0.72	0.53	0.30	3.2	1.79	1.79	2.17*
Total crevice volume	3.24	2.56	4.64	3.66	2.88	2.27	1.27	1.53

Asterisk represents significant  $P$  values

\*  $0.05 > P > 0.01$ , \*\*  $0.01 > P > 0.001$ , \*\*\*  $P < 0.001$





**Fig. 3** Proportion of sea urchin *Evechinus chloroticus* individuals occupying crevices or under rocks (“cryptic”) on fished versus protected rocky reefs at **a** Leigh ( $n$  for LF = 160,  $n$  for LMR = 160) and **b** Tawharanui ( $n$  for TF = 189,  $n$  for TMR = 23), north-eastern New Zealand. \*No 40–59 mm sea urchins were recorded inside TMR

Sea urchin size-frequency distributions (Fig. S3) within both fished areas were unimodal and left-skewed, with a relatively high proportion of juvenile sea urchins present. Sea urchins inside the LMR had a bimodal size distribution with a small trough at 45–55 mm, while sea urchins in the TMR had a unimodal distribution dominated by large individuals and very few small individuals (only 23 sea urchins were recorded within this reserve and 90% were larger than 75 mm).

## Experiment

In the mesocosm experiment, sea urchins responded to the presence of crushed conspecifics by becoming increasingly cryptic through time, regardless of food availability (Fig. 4; Table 3). When predation cues were not present, sea urchins became less cryptic over time, again regardless of food availability. In “+predation cue” tanks, an average of 38–48% of sea urchins was cryptic during the final week (day 15–17), while in “–predation cue” tanks only 3–4% of

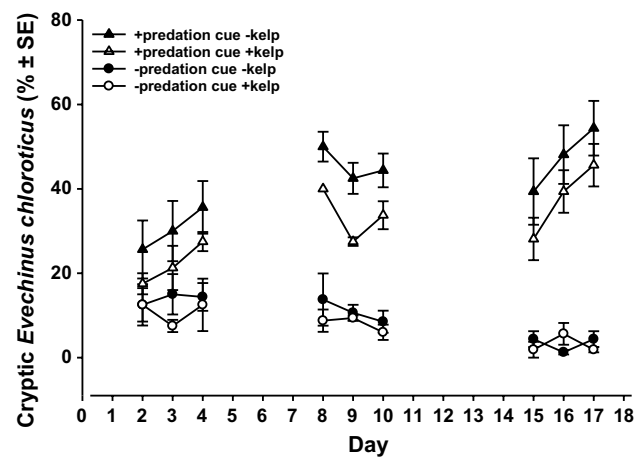
**Table 2** Results from Chi-squared tests assessing for differences in the proportions of cryptic sea urchins between fished and reserve sites at (A) Leigh and (B) Tawharanui

Size classes (test diameter)	<i>df</i>	$\chi^2$	<i>P</i>
(A) Leigh			
<40 mm		N/A <sup>a</sup>	
40–59 mm	1	2.11	0.15
60–79 mm	1	18.52	<0.001
80–100 mm	1	17.86	<0.001
>100 mm	1	2.55	0.11
(B) Tawharanui			
<40 mm		N/A <sup>a</sup>	
40–59 mm		N/A <sup>b</sup>	
60–79 mm	1	13.37	<0.001
80–100 mm	1	1.09	0.30
>100 mm		N/A <sup>b</sup>	

Chi-squared tests were run on  $2 \times 2$  contingency tables

<sup>a</sup> 100% of observed sea urchins were cryptic

<sup>b</sup> Chi-squared test could not be performed due to lack of data



**Fig. 4** Proportion of sea urchin *Evechinus chloroticus* individuals ( $n = 10$  individuals in each of four tanks per treatment) occupying crevices or under rocks (“cryptic”) in a mesocosm experiment in which predation cues and food availability were manipulated

sea urchins were cryptic. Food availability did not have a significant effect on sheltering behaviour. There was also a clear diurnal pattern in crevice occupancy across all four of the treatment combinations, with a higher proportion of sea urchins being cryptic during daytime hours (Fig. S4).

## Discussion

In north-eastern New Zealand marine reserves, where predators are abundant, sea urchin densities were lower and kelp

**Table 3** Results from generalised linear model (family = binomial) assessing the effects of food ( $\pm$ ), predation cue ( $\pm$ ) and week on the proportion of sea urchins sheltering in the mesocosm experiment

Source of variation	Coefficient	SE	Z value	P value	Odds ratio
Intercept	−0.93	0.59	−1.57	0.12	NA
Food	−0.42	0.24	−1.77	0.076	0.65
Predation cue	−0.18	0.69	−0.27	0.79	0.83
Week	−0.74	0.34	−2.26	0.024	0.48
Predation cue $\times$ week	1.10	0.37	2.99	0.003	2.51

Non-significant interaction terms were removed by backward elimination (see “Methods” for details)

densities considerably higher than on adjacent coasts where predators are fished. These findings are consistent with the predator–sea urchin–kelp trophic cascade previously documented for these reserves (Babcock et al. 1999; Shears and Babcock 2002). Sea urchins within marine reserves were more cryptic than those outside, with only the largest individuals ( $\geq 80$  mm test diameter) in both reserves regularly found in the open (“exposed”). While this pattern may be a direct behavioural response to predation cues, an alternative explanation is that cryptic behaviour is indirectly induced by predators via cascading trophic interactions or reduced competition that increases the availability of detrital kelp within marine reserves (Fig. 1). A mesocosm experiment was run to distinguish between these contrasting mechanisms, and showed that medium-sized sea urchins from a fished reef (which were mostly exposed in the field) became more cryptic when exposed to predation cues, but not when food availability was increased. This predator-induced cryptic behaviour is likely to contribute to the predator–sea urchin–kelp trophic cascade and also allow sea urchin populations to persist where predators are abundant.

Several studies have shown that sea urchins flee from predation-related cues (Vadas and Elner 2003; Manzur and Navarrete 2011), but we provide the first evidence that crevice-dwelling is promoted by predation risk. Addition of crushed conspecifics in the mesocosm experiment elicited a clear response with urchins seeking shelter. This response is consistent with the patterns of crypticity seen inside both marine reserves, where predator densities are higher than on fished reefs. Despite similar levels of reef complexity and available shelter at reserve and fished reefs, most urchins at fished sites were exposed, with only small urchins typically occupying shelter, while at reserve sites most urchins were cryptic and only the largest urchins ( $>80$  mm test diameter) were exposed. Though large lobsters are capable of consuming *E. chloroticus* larger than 80 mm (Andrew and MacDiarmid 1991), predation rates are considerably higher on the smaller size classes of

urchins (Shears and Babcock 2002). Therefore, while it is unlikely that these larger urchins reach a size escape from predation, the predation risk is considerably lower at these larger sizes. The lower density of mid-sized (40–79 mm) urchins in the reserves is consistent with higher predation as they emerge from a cryptic to exposed lifestyle (Cole and Keuskamp 1998; Shears and Babcock 2002). However, the particularly low number of juvenile sea urchins in the TMR contrasts patterns from the LMR, and also previous data from the TMR where juveniles are common (Shears and Babcock 2002; Shears et al. 2008). Consequently, the low density of juveniles in the TMR likely reflects low recruitment in recent years rather than possible indirect effects of predators or marine protection.

Food availability was hypothesised as a likely driver of cryptic behaviour (Fig. 1, Harrold and Reed 1985), but provision of additional food in the form of drift kelp did not affect shelter use by sea urchins in our 17-day long experiment. While the lack of a short-term response to food addition may be due to the artificial conditions in the tanks, all possible measures were taken to replicate field conditions, with similar sized boulders and crevice availability, and turbulence added to help disperse kelp fragments. Consequently, all urchins in the kelp addition treatments had ready access to pieces of kelp and shelter. However, when predation cues were absent, the urchins did not switch their behaviour to occupying crevices, as seen when predation cues were added. Although not measured, the amount of kelp remaining in both treatments at the end of the experiment was similar (AJPS pers. obs.), indicating that food was not limiting in either treatment and, interestingly, that both exposed and cryptic urchins were eating similar amounts of drift kelp. While further tests are needed to investigate this, preferably in the field, these results suggest that provision of drift kelp alone is not enough for urchins to switch to occupying crevices. Kelp may, however, cause urchins to seek shelter through other mechanisms such as the physical action of living kelp (“whiplash” effect) (Konar and Estes 2003) or potentially due to other changes in physical conditions under kelp canopies (e.g. by altering water flow and sedimentation). It is, therefore, likely that in some systems both the presence of living kelp and predators act to increase urchin shelter occupancy and allow kelp forests to persist in the presence of sea urchins.

Lethal predation on sea urchins clearly reduces the impact of sea urchin populations on kelp (Estes and Duggins 1995; Blamey and Branch 2012), and in our study total sea urchin densities were lower in marine reserves where predators and kelp were abundant. While previous studies have shown that predation rates on exposed sea urchins are higher in reserves than at fished sites (Shears and Babcock 2002), our findings suggest that the effect of predators extends beyond removal of individuals to the behaviour

of survivors. The predator-induced sheltering behaviour observed in this study is, therefore, likely to contribute to the predator–sea urchin–kelp forest trophic cascade documented in this system. Such behaviourally mediated effects are potentially as important as density modifications (Beckerman et al. 1997; Schmitz et al. 2004; Trussell et al. 2006) but can also occur simultaneously with density-mediated effects on herbivores (Preisser et al. 2005). Our findings are consistent with this and suggest that the previously reported recovery of kelp forests in north-eastern New Zealand marine reserves is due to both direct predation on sea urchins and predator-induced changes in behaviour of sea urchins. These changes in behaviour also have population level consequences for prey species, as refuge use can allow prey to persist in the face of intense predation pressure (Magalhães et al. 2007), albeit at lower densities than when predators are absent (Hines and Pearse 1982; Micheli et al. 2008). Clumping of individuals in refugia may incidentally boost fertilisation success, reducing predator-driven Allee effects and lowering the risk of localised extinction (Gascoigne and Lipcius 2004).

Our results highlight the need for future research to simultaneously investigate the relative strengths of density- and behaviourally mediated effects so we can gain a clearer understanding of the effects of predators on ecosystem structure. We also suggest an alternate pathway whereby predators could affect the behaviour of prey by altering the prey's food supply through a trophic cascade or the removal of competitors, and that this could complement or potentially supplant behavioural changes resulting from the more direct threat of predation risk. While we found no evidence for this alternative mechanism in our study on sea urchins, many other small consumers (mostly predators) switch between sit-and-wait and free-ranging foraging modes depending on food availability and are themselves subject to predation (Higginson and Ruxton 2015). It is, therefore, possible that in such systems foraging behaviour is potentially affected both directly and indirectly by predators. We suggest that further research on BMIs should consider the potential effect of predator-induced changes to prey resources on prey behaviour, rather than assuming that behavioural changes in the presence of predators are a response to predation risk alone.

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**Author contribution statement** AJPS, RBT and NTS conceived and designed the experiments. AJPS and NTS performed the experiments.

AJPS, RBT and NTS analysed the data. AJPS, RBT and NTS wrote the manuscript.

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