# Effects of habitat on predation of ecologically important sea urchin species on east coast Australian temperate reefs in tethering experiments

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ABSTRACT: The expansion and persistence of urchin-dominated habitats at the expense of macroalgal cover has long been of interest in marine ecology. Macroalgal habitats are considered to harbor a high abundance of urchin predators that protect these habitats from grazing. We tested this concept using tethering experiments in south-eastern Australia to investigate whether predation on urchins is higher and faster within macroalgal habitats (dense seaweed) than in barrens-mosaic habitats (primarily bare rock with the presence of turfing algae, ascidians and macroalgae). We also assessed whether the sympatric species, the diadematoid *Centrostephanus rodgersii* and the echinometrid *Heliocidaris erythrogramma* differ in the rates at which they are preyed upon. As smaller urchins are generally considered to be easier prey, we also investigated the influence of urchin size on predation risk. We tethered a total of 96 urchins (48 *C. rodgersii* and 48 *H. erythrogramma*) in macroalgal and barrens-mosaic habitats at 4 locations (n = 24 of each species per habitat) and revisited the tethers to record mortality. A damage index assigned to urchin remains was used to infer likely sources of predation (lobster or fish), and we recorded predators in the area. We found no difference in predation between habitat types. Urchins persisted significantly longer at one location where we recorded a less diverse predator guild. Overall, we found no evidence that habitat, urchin species or size play a role in predicting rates of predation on urchins. Our observations suggest that the local predator guild plays an important role in determining predation rates on urchins.

KEY WORDS: *Centrostephanus rodgersii* · *Heliocidaris erythrogramma* · Diadematoid · Echinometrid · Echinoidea · Macroalgae · Urchin barrens · New South Wales

## 1. INTRODUCTION

Sea urchins are ecologically important herbivores that exert a strong influence on the community structure of reef ecosystems (Filbee-Dexter & Scheibling 2014, Ling et al. 2019, Glasby & Gibson 2020, Steneck 2020). Predation is thought to be a key driver that regulates urchin populations, with a broad predator guild observed or assumed to play a significant role in controlling urchin populations (Fagerli et al. 2014, Ling et al. 2019, Trowbridge et al. 2019, Glasby & Gibson 2020) and thereby preventing overgrazing of macroalgae (Bologna & Steneck 1993, Sheppard-Brennand et al. 2017, Layton et al. 2020, Kawamata & Taino 2021). Macroalgal habitats reportedly support a broad suite of associated predators that contribute to significant levels of predation on urchins compared with areas where macroalgae is reduced

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or absent (Bologna & Steneck 1993, Byrnes et al. 2006, Ling et al. 2009, Sheppard-Brennand et al. 2017, Layton et al. 2020). Determining whether this pattern is general across reefs will inform and improve the management of these habitats, particularly the expansion and persistence of urchin-dominated habitats at the expense of macroalgal cover. Loss of macroalgae associated with overgrazing by urchins is a topic of concern, as seen in the poleward range extension of urchins in eastern Australia, increases in urchin populations following disease-driven mass mortality of their predators in western North America and overfishing of predators in Japan (Ling & Johnson 2009, Byrne & Andrew 2020, Layton et al. 2020, Kawamata & Taino 2021, Ling & Keane 2021, Smith et al. 2022a).

Overfishing of urchin predators is often implicated when urchin numbers increase followed by a decrease in macroalgae (Filbee-Dexter & Scheibling 2014, Ling & Keane 2021, Cresswell et al. 2022). Lobsters are considered to be important urchin predators on reefs in both the Northern and Southern Hemisphere (Wharton & Mann 1981, Tegner & Levin 1983, Scheibling 1996, Kawamata & Taino 2021, Ling & Keane 2021). Overfishing of lobster populations has been implicated in the increased density of urchins in California (Lafferty 2004, Stephens et al. 2006), eastern Canada (Mann 1977, Johnson & Mann 1988, Scheibling 1996), New Zealand (Babcock et al. 1999, Shears & Babcock 2002), Tasmania (Pederson & Johnson 2006, Barrett et al. 2009, Ling et al. 2015) and Japan (Kawamata & Taino 2021). Temporal reductions in lobster abundance associated with annual migrations (Jeffs et al. 2013) may also affect urchin density. However, despite the keystone paradigm-like contention that lobster predation regulates urchin populations, the evidence is equivocal (Elner & Vadas 1990, Scheibling 1996). In Atlantic North America, fluctuations in urchin abundance on decadal time scales appear to be regulated by disease, warm temperature anomalies and other factors (Elner & Vadas 1990, Scheibling 1996, Gendron et al. 2001, Smith et al. 2022b). Along the Pacific coast of North America, the prevalence of urchins is most recently attributed to climate-related phenomena and mass mortality of predators (e.g. sea stars) (Rogers-Bennett & Catton 2019, Rogers-Bennett et al. 2022). Large fishes such as wrasse and snapper also prey on urchins and have been suggested to play a role in controlling urchins in Canada (Mann 1977, 1982), California (Cowen 1983, Stephens et al. 2006, Foster & Schiel 2010), New Zealand (Andrew & MacDiarmid 1991, Shears & Babcock 2002) and Norway (Norderhaug et al. 2021).

Where predators are considered insufficient to control urchin populations, management actions to control urchin grazing have been trialled, including divers removing them by hand or killing them *in situ*, with limited effectiveness (Tracey et al. 2015, Sanderson et al. 2016, Miller et al. 2022). While this approach is not feasible in the long term (Sanderson et al. 2016, Miller et al. 2022), it has seen some success at small spatial scales when culls are performed consistently and repeatedly over time (Tracey et al. 2015, Guarnieri et al. 2020, Miller et al. 2022, Miller & Shears 2023), but may have unintended consequences (Kingsford & Byrne 2023). Hence, it is important to understand the dynamics and importance of urchin predation before management action is taken, and a logical starting point is to investigate whether urchin control might be affected by predators currently present in the ecosystem.

Many studies report that predators including lobsters and large fishes (Hughes et al. 1994, Mayfield et al. 2001, Pederson & Johnson 2006) are unable or unwilling (Ling & Johnson 2009, Day et al. 2021, Smith et al. 2022a) to eat urchins once an urchin body-size-threshold has been reached (Pederson & Johnson 2006, Ling & Johnson 2009). Small urchins are more easily handled by predators (Tegner & Levin 1983, Sala 1997, Andrew 1999, Pederson & Johnson 2006, Ling & Johnson 2012, Selden et al. 2017). This makes larger urchins more energetically expensive to eat, which may discourage predation (Irons et al. 1986, Snellen et al. 2007). Thus, urchin size demographics, which can differ appreciably between locations (Ebert et al. 1999, Ebert 2010, Ouréns et al. 2011) are important in determining the predation risk of urchins between locations and habitats (Eurich et al. 2014, Day et al. 2021, Smith et al. 2022a). If urchins are relatively small with respect to predator size, they are more easily removed from crevices (Pederson & Johnson 2006, Andrew & Byrne 2007, Powter et al. 2010, Ling & Johnson 2012, Byrne & Andrew 2020) and may be engulfed whole (Tegner & Levin 1983, Day et al. 2021). In contrast, larger urchins require more physical manipulation by predators. For example, larger lobsters have a greater capacity to feed on large urchins by using their front appendages to flip the urchins oral-side up (Tegner & Levin 1983). Some large fishes use a ramming jaw-action to dislodge and flip urchins oral-side up to feed on them (Tegner & Dayton 1981, Andrew 1999, Foster & Schiel 2010, Clemente et al. 2013, Day et al. 2021). Non-crustacean invertebrates including cephalopods (Ambrose 1986) and sea stars (Gianguzza et al. 2016,

Rogers-Bennett & Catton 2019, Rogers-Bennett et al. 2022) also prey on urchins.

Along the east coast of temperate Australia, the large diadematoid urchin *Centrostephanus rodgersii* is an ecologically important herbivorous grazer that is responsible for forming barrens patches amongst macroalgae at low densities and vast extensive barrens habitats when at high densities (Andrew & O'Neill 2000, Flukes et al. 2012, Byrne & Andrew 2020). The sympatric smaller echinometrid species *Heliocidaris erythrogramma* can also create barrens (Wright et al. 2005, Pederson & Johnson 2008, Keesing 2020). Lack of predation on these urchins is argued to be a key driver enabling them to reach densities that result in overgrazing of macroalgae (Pederson & Johnson 2006, Ling et al. 2015, Ling & Keane 2021). With respect to predators, options for management being considered include augmentation of the predator guild (Layton et al. 2020, Day et al. 2021) by transplanting lobsters into urchin-affected areas (Redd et al. 2014, Ling & Keane 2021, Smith et al. 2022a) and increasing urchin predator densities through the implementation of no-take marine reserves or fisheries closures (Tegner & Dayton 2000, Shears & Babcock 2002, Spyksma et al. 2017, Kawamata & Taino 2021). For eastern Australia, it is unknown which species are the main urchin predators (Day et al. 2021). In New South Wales (NSW), Australia, known urchin predators include fishes, such as *Achoerodus viridis* (eastern blue groper) and *Chrysophyrus auratus* (pink snapper) (Lee et al. 2015, Rees et al. 2018, Knott et al. 2021), and the lobsters *Jasus edwardsii* (southern rock lobster) and *Sagmarisus verreauxi* (eastern rock lobster) (Jeffs et al. 2013, Linnane et al. 2015, Woodings et al. 2018). Here, we contribute to the understanding of potential predators in experiments where urchins were tethered away from shelter in habitats along the south coast of NSW, following similar studies in New Zealand, Tasmania and Japan (Pederson & Johnson 2006, Ling et al. 2015, Kawamata & Taino 2021).

The predation risk that different urchin species experience may differ for a range of reasons. For example, *H. erythrogramma* is suggested to experience a higher risk of predation than *C. rodgersii* due to differences in urchin body size, with *H. erythrogramma* being the smaller species (Ling et al. 2015, Sanderson et al. 2016, Sheppard-Brennand et al. 2017, Day et al. 2021, Smith et al. 2022a). Lobsters may also have a feeding preference for *H. erythrogramma* over *C. rodgersii* (Day et al. 2021, Smith et al. 2022a). The difficulty involved with dislodg-

ing urchins from the substratum or crevices may also influence predation risk (Ling & Johnson 2009, Clemente et al. 2013, Sanderson et al. 2016).

We tethered *C. rodgersii* and *H. erythrogramma* in and outside of dense macroalgal habitat at 4 rocky reefs along the NSW coast to assess potential predation pressure and to test the hypotheses that predation would be greater for (1) urchins tethered in macroalgal habitats, (2) *H. erythrogramma* than *C. rodgersii* and (3) smaller than larger urchins. We revisited tethers at set time periods to record survival, assigning a damage index to describe urchin remains left on tethers and infer potential sources of predation (lobster, fish or other).

## 2. MATERIALS AND METHODS

### 2.1. Study locations

Our study was conducted at 4 locations along the NSW south coast: Wollongong (34.42488° S, 150.8931° E), Bass Point (34.5973° S, 150.8874° E), Jervis Bay (35.0481° S, 150.7447° E) and Bendalong (35.2280° S, 150.4892° E) (Fig. 1A) from June to November 2019. Urchins were tethered in 2 habitat types at 3 sites within each location (see below) to produce an estimate of the rates of urchin predation between habitats and species and across a range of urchin sizes (Fig. 1B). Each tethering experiment lasted a maximum of 14 d, depending on urchin survival. We also undertook direct observations of predators whilst in the field to record the potential predator guilds present at each location, where we recorded the presence of fish, shark and ray predators as well as lobsters and other invertebrates. This work was undertaken under a permit from the NSW Department of Primary Industries (permit number P13/0037-2.0). All experimental apparatus were collected at the end of fieldwork.

Tethered *C. rodgersii* and *H. erythrogramma* urchins were placed in (1) macroalgal habitats consisting of *Ecklonia radiata* (golden kelp), *Phyllospora comosa* (cray weed) and *Sargassum* spp. (gulf weed) forming a canopy and in (2) barrens mosaic habitat which consisted mostly of bare rock but also had coralline turfing algae, Cunjevoi *Pyura praeputalis* and macroalgae, forming a mosaic. These habitats are characteristic of the near-shore benthos in the area (Underwood et al. 1991, Curley et al. 2002, Glasby & Gibson 2020, Kingsford & Byrne 2023). Predatory fishes in the region are known to use the mosaic of habitats across macroalgae and barrens as
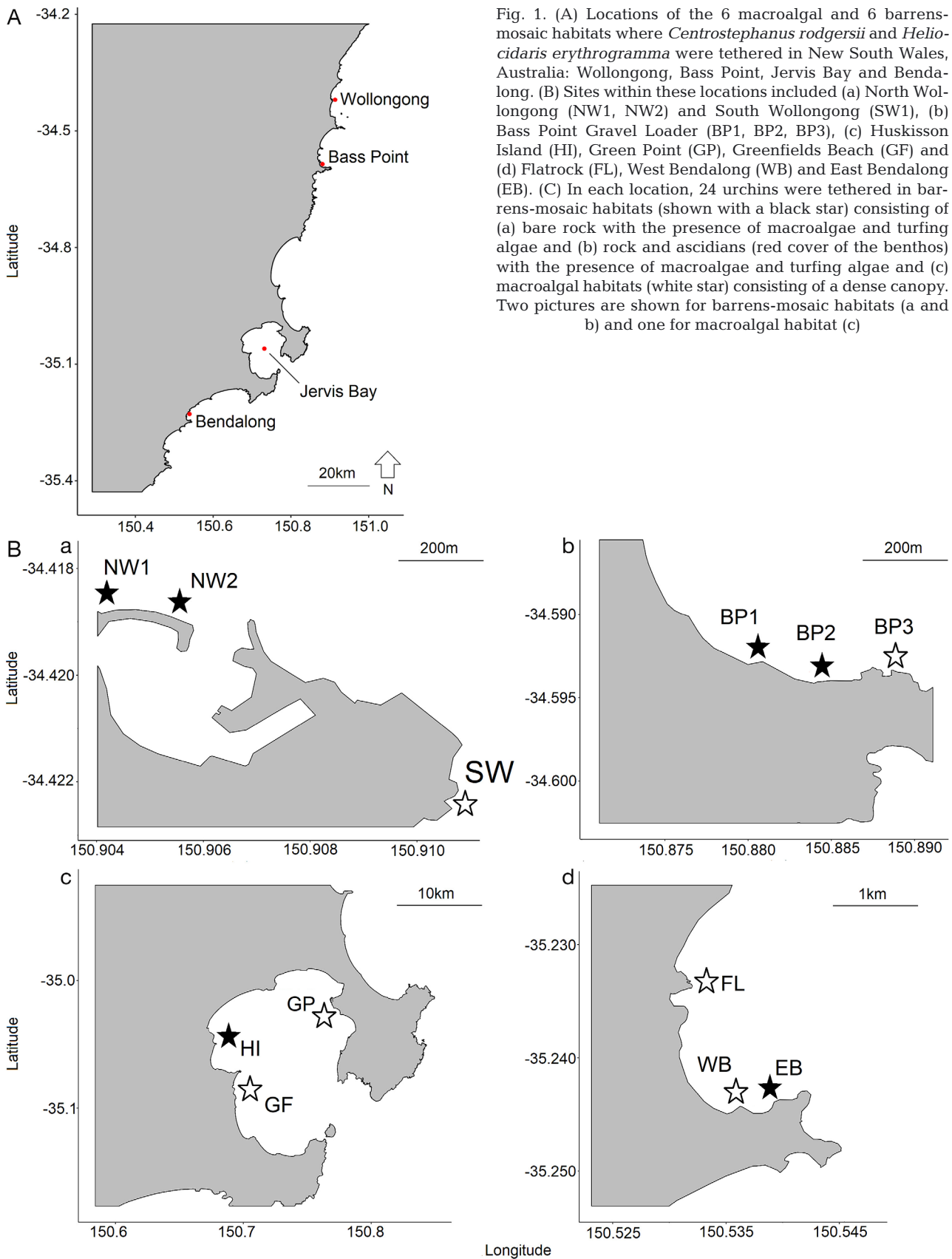
Fig. 1. (A) Locations of the 6 macroalgal and 6 barrens-mosaic habitats where *Centrostephanus rodgersii* and *Helio-cidaris erythrogramma* were tethered in New South Wales, Australia: Wollongong, Bass Point, Jervis Bay and Benda-long. (B) Sites within these locations included (a) North Wol-longong (NW1, NW2) and South Wollongong (SW1), (b) Bass Point Gravel Loader (BP1, BP2, BP3), (c) Huskisson Island (HI), Green Point (GP), Greenfields Beach (GF) and (d) Flatrock (FL), West Bendalong (WB) and East Bendalong (EB). (C) In each location, 24 urchins were tethered in bar-rens-mosaic habitats (shown with a black star) consisting of (a) bare rock with the presence of macroalgae and turfing algae and (b) rock and ascidians (red cover of the benthos) with the presence of macroalgae and turfing algae and (c) macroalgal habitats (white star) consisting of a dense canopy. Two pictures are shown for barrens-mosaic habitats (a and b) and one for macroalgal habitat (c)
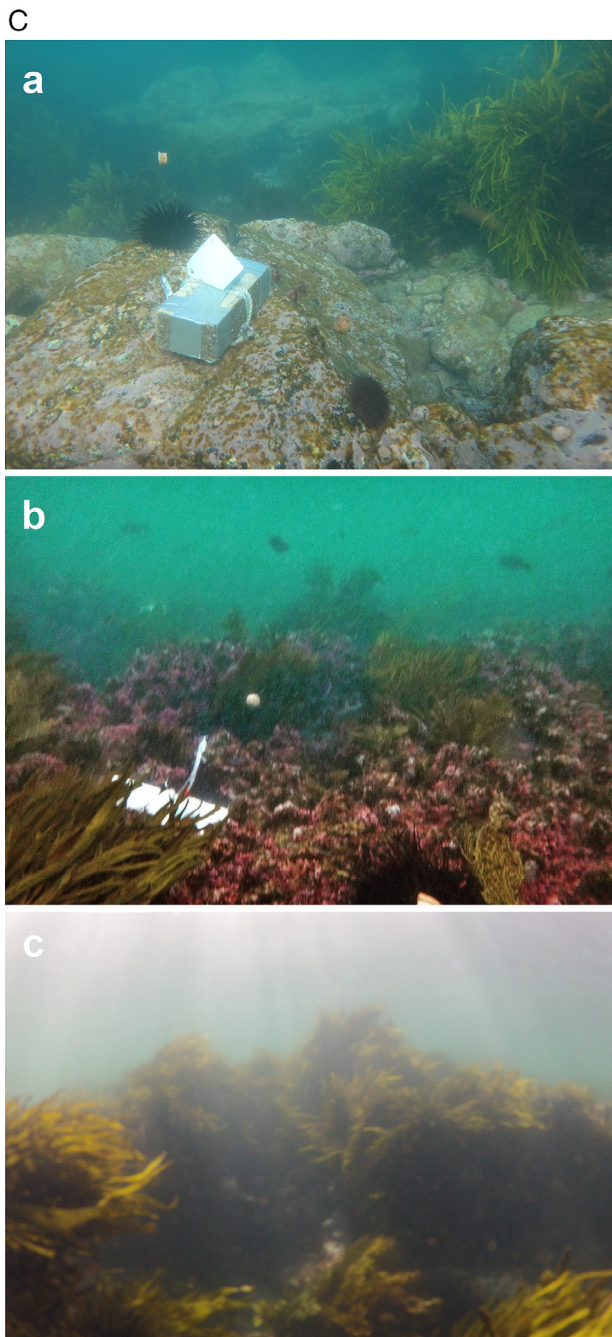
C



Fig. 1 (continued)

their hunting grounds (Curley et al. 2002). To enable independent treatments and avoid edge effects, we were careful to place brick tethers on the benthos approximately in the centre of macroalgal habitats at least 5 m from any habitat 'edge'. Thus, the urchins in this habitat were well within the algal canopy. In the barrens-mosaic habitat, the tethered urchins were placed on bare rock or Cunjevoi, ~2–3m from macroalgae or other cover (Fig. 1C).

To ensure that the urchins used were representative of the size range in each area, we determined the size range of *C. rodgersii* and *H. erythrogramma* within the 4 locations. Urchins were measured with vernier callipers to the nearest 1 mm at 9 sites of differing habitat (macroalgae or barrens-mosaic) within 4 locations (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m714p071_supp.pdf). This work was done on snorkel, with 100 urchins haphazardly collected and measured at each site. To determine the size distribution for each site, we plotted a cumulative curve (Table S1, Fig. S1). These data were used to inform the sizes of urchins used for tethering. In the statistical analysis, however, urchin size was treated as a continuous variable (see below).

## 2.2. Urchin tethering

To tether urchins, we modified previous methods to reduce potential impacts on the urchins (Fig. S2). Rather than using a chain attached to benthos (Shears & Babcock 2002), we attached the urchins to bricks with spliced synthetic rope and monofilament fishing line. In our methodology, a very small hole was first made in the test using a titanium drill bit (1.25 mm diameter), through which we passed a curved mattress needle (1 mm diameter) threaded with monofilament (15 kg tensile strength). We then tied a bowline in the standing end of the monofilament and used shark clips and swivels to attach urchins to the 2 available eyes of spliced rope on either side of the bricks.

To ensure that the urchins were not unduly harmed by our tethering method, we undertook a pilot study during which we monitored tethered urchins (4 *C. rodgersii* and 4 *H. erythrogramma*) in aquaria for 10 d (Fig. S3A,B). These urchins had 100% survival with no indication of deleterious effects. Further, to test if the tethering process might attract predators, we undertook a second pilot study in aquaria where we exposed 1 and 2 tethered *C. rodgersii* to medium-sized *S. verreauxi* (122 and 125 mm carapace length [CL], respectively), which are known to be capable urchin predators on the basis of body size (Day et al. 2021), for a period of 1 wk (Fig. S3C,D). We did not observe any predation and there were also no deleterious effects of tethering evident on these 3 urchins.

To assist in keeping track of the tethered urchins, we also tagged them with a 20 mm piece of cork attached to a size 2/0 (39 mm) fishing hook for large urchins and a size 1/0 (34 mm) fishing hook for smaller urchins attached to the aboral surface (Tuya

et al. 2003). The efficacy of this tagging method was tested in a pilot study with 20 *C. rodgersii* and 20 *H. erythrogramma* tagged in an enclosed rockpool. These urchins were checked daily and showed 100% tag retention over 1 wk with no deleterious effects (Fig. S3E,F).

At each of the 3 sites across 4 locations, 8 urchins were tethered to a brick weight (4 locations, 3 sites, 8 urchins per site; 96 total). Each brick had one *C. rodgersii* and one *H. erythrogramma* attached (Fig. 1). To standardize the potential attractiveness of urchins as prey, we only used urchins collected locally from macroalgal habitat, as past work has suggested that urchins taken from barrens habitat are less attractive prey (Eurich et al. 2014). We tethered 48 *C. rodgersii* (30–125 mm test diameter [TD]) and 48 *H. erythrogramma* (30–101 mm TD) (Table S2). For *C. rodgersii*, the TD of the small and large individuals tethered at Wollongong, Bass Point, Jervis Bay and Bendalong were 45–80 and 81–122 mm (Wollongong), 47–65 and 66–90 mm (Bass Point), 71–95 and 96–125 mm (Jervis Bay) and 30–60 and 61–95 mm (Bendalong), respectively. For *H. erythrogramma* at these 4 locations, the small and large urchins had a TD of 32–50 and 51–83 mm (Wollongong), 30–60 and 61–85 mm (Bass Point), 35–65 and 66–101 mm (Jervis Bay) and 32–63 and 64–98 mm (Bendalong), respectively. At each site, random combinations of urchin sizes were deployed to the 4 bricks, with each of the 4 combinations present at each site (Table S2).

## 2.3. Inferring causes of mortality

Causes of urchin mortality with respect to potential predators can be inferred from the remains left on tethers (Scheibling 1996, Pederson & Johnson 2006, Cook & Vanderklift 2011, Ling & Johnson 2012, Day et al. 2021, Delgado & Sharp 2021, Kawamata & Taino 2021). Predation by lobsters (*S. verreauxi* and

*J. edwardsii*) on *C. rodgersii* and *H. erythrogramma* is indicated by the presence of an intact test on the tether with the Aristotle's lantern absent and an empty test (Andrew & MacDiarmid 1991, Shears & Babcock 2002, Pederson & Johnson 2008, Ling & Johnson 2009, Day et al. 2021). Cephalopod predators can leave urchin remains similar to those left by lobsters (Ambrose 1986, Day et al. 2021). Predatory fishes can leave characteristic remains including cracked urchin tests or may leave no remains, since the urchin tests may either be cracked *in situ*, engulfed completely or carried elsewhere (Andrew 1999, Aronson et al.2001, Cook & Vanderklift 2011, Delgado & Sharp 2021). We only used urchins >30 mm TD, as smaller ones are completely engulfed by predators (Pederson & Johnson 2006, Day et al. 2021). Lobsters preying on *C. rodgersii* and *H. erythrogramma* >30 mm TD in past feeding trials left characteristic feeding remains with no test-cracking and did not engulf whole urchins (Day et al. 2021). As in a past tethering study (Cook & Vanderklift 2011), an empty urchin test was taken to indicate predation on urchins *in situ*, absent urchin remains where the tethering loop was still intact was taken to indicate an urchin that was eaten whole and a snapped tether without the tethering loop intact was taken to indicate an urchin that was either eaten whole or carried off elsewhere.

Tethered urchins were inspected to record predation events at 3 time points until Day 14. Tethers were assessed on Day 3–4, Day 5–7 and Day 12–14, depending on weather conditions and safely gaining access to the experimental areas. When inspected, any remains of the urchin test were photographed and assigned a damage index (DI) to infer the likely feeding predator. This index was assigned to the urchin remains as follows: DI-1: snapped tether, tether wire with no visible urchin remains; DI-2: broken test, test remains still attached to tethers; and DI-3: urchin eaten with the test intact (Fig. 2). Where we found snapped tethers and no urchin remains (i.e. DI-1), we



Fig. 2. Damage index (DI) of urchin remains. (A) DI-3, intact test of *Heliocidaris erythrogramma*; (B) DI-3, intact test of *Centrostephanus rodgersii*; (C) DI-2, broken test of *C. rodgersii*; and (D) DI-2, broken test of *H. erythrogramma*

searched the immediate area for tagged urchins for 5 min to confirm that these individuals had not escaped. During each inspection, we monitored the urchins to check that they were effectively attached to the bottom by their tube-feet (Fagerli et al. 2014, Boada et al. 2015). Over the 14 d (maximum) deployment, all remaining urchins were attached to the substratum with their tube feet. We inferred predation events and the likely predator responsible (invertebrate or fish) based on the remains found (see above) (Aronson et al. 2001, Pederson & Johnson 2006, Cook & Vanderklift 2011, Delgado & Sharp 2021). During all visits, the experimental area was searched on snorkel within a 20 m radius for 10 min to visually record the presence of potential urchin predators.

## 2.4. Statistical analysis

We tested the hypotheses that predation on tethered urchins would be greater (1) in macroalgae than in barrens-mosaic areas, (2) for *H. erythrogramma* than *C. rodgersii* and (3) for smaller than larger urchins, and that these responses would be general across locations. We used generalised linear mixed models (GLMMs) and ranked the models using Akaike's information criterion corrected for small sample sizes to test these hypotheses and compare the statistical significance of predictors. We predicted that these effects would be general but that there may also be interactions among the factors of size, species, habitat and location (Ling & Johnson 2009, 2012, Pinna et al. 2012), and therefore we assessed all possible interactions in the analysis. Assumption testing was undertaken using the 'DHARMa' package v.0.4.6 (Hartig 2022) in RStudio, which showed significant dispersion at an α-level of 0.05 (dispersion test, p = 0.04), indicating that data showed mildly significant deviation from a Gaussian distribution; this was confirmed by *Q–Q* plot residuals showing a linear relationship between the observed and expected variables. We expected that this difference was due to outliers in the data. Accordingly, non-parametric dispersion and outlier testing returned a normal distribution in both cases and showed minor outliers at the lower end of the scale (outlier test, p = 0.54). Since collinearity testing also showed no collinearity between predictors (Pearson's correlation, p > 0.05) and that urchin size data were generally normally distributed (Shapiro-Wilks test, p > 0.05), we decided to use the GLMM approach. It is important to note that our study is large and used

an orthogonal design to allow statistical power and efficiency to be maximised. At the site level, averaged values provided a strong estimate, and the design also enabled various interactions to be assessed with reasonable statistical power. In our analysis, urchin size was treated as a continuous variable, and random effects of site were included in the modelling. We chose to use random effects GLMM models because they are better able to account for site-level replication compared to other methods (Quené & Van den Bergh 2008, Yu et al. 2022). To provide a complete picture, comparisons for random effects at the site level were also tested where all models showed only moderate influences (see Table 1). No effect of tethering brick was observed (Table S3); therefore, 'brick' was removed from the analyses. In our analysis, we used the binomial distribution and the associated logit-link function since urchin mortality was recorded in binomial format (1: urchin eaten; 0: urchin not eaten). We wanted to know whether the patterns we report would be general, so we tested locations (Soininen et al. 2007, Crase et al. 2012). All statistical analyses and plots were done using the statistical program R v.3.6.3 (R Core Team 2021) and the associated packages 'lme4' v.1.1.23 (Bates et al. 2015), 'MuMIn' v.1.43.17 (Barton 2020), 'ggplot2' v.3.3.0 (Wickham 2016), 'dplyr' v.0.8.5 (Wickham et al. 2023) and 'emmeans' v.1.6.2-1 (Lenth 2023).

## 3. RESULTS

### 3.1. Urchin tethering

In our analyses, location was the only significant factor affecting whether urchins had been preyed upon by the first inspection, and we did not record any of the expected effects of urchin size or habitat (Fig. 3, Table 1). Urchins tethered in Wollongong showed far lower predation rates (28.1%) than elsewhere (Fig. 3A, Table 1), which ranged between 96.9 and 100% mortality at the first inspection. While a significant difference in urchin mortality is predicted at the level of location, no similar trend was found based on urchin species or habitat (Fig. 3B, Table 1). Overall, differences in tethered urchin mortality between the 2 species (Fig. 3A) or between habitats (Fig. 3B) were negligible. For *C. rodgersii*, all urchins were preyed on first in Bendalong (100% mortality by Day 3–4), then Jervis Bay and Bass Point (100% mortality by Day 5–7) and Wollongong (100% mortality by Day 12–14) (Fig. 3). Tethered urchins experienced the lowest predation in Wollongong (Day

Fig. 3. Percentage of urchin survival at each inspection period by (A) urchin species *Centrostephanus rodgersii* or *Heliocidaris erythrogramma* and (B) habitat (barrens-mosaic or macroalgae)

3–4, 37.5 % [barrens-mosaic], 25 % [macroalgae]; Day 5–7, 37.5 % [barrens-mosaic], 50 % [macroalgae]; Day 12–14, 100 % [barrens-mosaic and macroalgae]). Apart from one urchin tethered in Jervis Bay which was sighted alive at the first inspection (Day 3–4, 100 % [barrens-mosaic], 87.5 % [macroalgae]), all other *C. rodgersii* were killed (Fig. 3, Table S3). Overall, *C. rodgersii* was sighted alive on tethers on 17 occasions (18.1 % urchins sighted alive from 96 inspections) in Wollongong on Days 3–4, 5–7 and 12–14 and in Jervis Bay on Day 3–4.

For *H. erythrogramma*, a similar pattern was observed, with all urchins preyed on first in Bendalong (100 % mortality by Day 3–4) then Jervis Bay (100 % mortality by Day 5–7) and Bass Point and Wollongong (100 % mortality by Day 12–14). At Bass Point, one urchin was sighted alive during the first and second inspections (Day 3–4, 87.5 % [barrens-mosaic], 100 % [macroalgae]; Day 5–7, 87.5 % [barrens-mosaic], 100 % [macroalgae]), while all other *H. erythrogramma* had been killed (Fig. 3, Table S3). Overall, *H. erythrogramma* was sighted alive on tethers on 18 occasions (18.8 % urchins sighted alive from 96 inspections) in Bass Point and Wollongong on Days 3–4 and 5–7 and at Jervis Bay and Bendalong on Day 3–4.

### 3.2. Potential urchin predators

Observations of the DI (species and habitat type combined) on tethered urchins showed DI-1 (snapped tether) 36 times in barrens-mosaic habitat and 37 times in macroalgal habitat, DI-2 (broken urchin test)

Table 1. Results of model selection within a generalized linear mixed model using Akaike's information criterion corrected for reduced sample sizes (AICc). Outcomes are shown for urchin mortality recorded at the first inspection interval only (Day 3–4). Model weights (Weight), logarithmic likelihoods (Log. Lik) and contributions of fixed ($R^2m$) and fixed plus random effects ($R^2c$) are shown. Models are ranked from the lowest AICc to the highest, with the lowest model shown in **bold.** All possible interactions were tested and here the top 10 highest-weight models are shown. Models within ±2 AICc of the lowest AICc model are significant

| Model | df | AICc | ΔAICc | Weight | Log. Lik | $R^2m$ | $R^2c$ |
|---|---|---|---|---|---|---|---|
| **Mortality ~ Location + (1\|Site)** | **6** | **39.7** | **0.00** | **0.806** | **−13.36** | **0.52** | **0.64** |
| Mortality ~ (1\|Site) (NULL) | 3 | 44.6 | 4.92 | 0.069 | −19.16 | 0 | 0.64 |
| Mortality ~ Location + Habitat + (1\|Site) | 7 | 44.6 | 4.98 | 0.067 | −14.69 | 0.51 | 0.65 |
| Mortality ~ Location + Species + (1\|Site) | 7 | 46.0 | 6.29 | 0.035 | −15.34 | 0.52 | 0.64 |
| Mortality ~ Habitat + (1\|Site) | 4 | 47.9 | 8.21 | 0.013 | −19.72 | 0.02 | 0.66 |
| Mortality ~ Species + (1\|Site) | 4 | 50.7 | 11.06 | 0.003 | −21.14 | 0.05 | 0.85 |
| Mortality ~ Location + Habitat + Species + (1\|Site) | 8 | 51.0 | 11.33 | 0.003 | −16.67 | 0.51 | 0.64 |
| Mortality ~ Location + Size + (1\|Site) | 7 | 51.6 | 11.94 | 0.002 | −18.16 | 0.53 | 0.65 |
| Mortality ~ Location + Habitat + Location * Habitat + (1\|Site) | 10 | 53.4 | 13.70 | 0.001 | −15.38 | 0.46 | 0.69 |
| Mortality ~ Habitat + Species + (1\|Site) | 5 | 54.1 | 14.40 | 0.001 | −21.70 | 0.16 | 0.66 |

5 times in barrens-mosaic habitats and 6 times in macroalgae habitats, and DI-3 (intact, empty urchin test) 6 times in barrens-mosaic habitats and 5 times in macroalgal habitats. At the site level, we found snapped tethers (DI-1) 22, 19, 19 and 15 times in Wollongong, Bass Point, Jervis Bay and Bendalong, respectively, broken tests (DI-2) 2, 4, 1 and 4 times and snapped tethers (DI-3) 1, 1, 4 and 5 times at these sites, respectively (Fig. 4).

We observed 8 potential predators of the urchins: *Sagmarisus verreauxi*, *Achoerodus viridis* and *Chrysophyrus auratus* (which were expected) and *Heterodontus portusjacksonii* (Port Jackson shark), *Bathytoshia brevicaudata* (smooth stingray), *Octopus tetricus* (Sydney octopus), *Sepia apama* (giant cuttlefish) and *Gymnothorax prasinus* (moray eel), which were unexpected (Fig. 4). At the location level, all predators were present except for *G. prasinus*, which was only encountered in macroalgal habitat, and *S. apama*, which was only encountered in barrens-mosaic habitat. We recorded *S. verreauxi*, *A. viridis* and *S. apama* in Wollongong, *S. verreauxi*, *A. viridis*, *O. tetricus*, *B. brevicaudata*, *G. prasinus* in Bass Point, *A. viridis*, *B. brevicaudata*, *H. portusjacksonii*, *O. tetricus* and *G. prasinus* in Bendalong and *A. viridis*, *C. auratus* and *H. portusjacksonii* in Jervis Bay. At Wollongong and Bass Point, the presence of *S. verreauxi* was inferred from the presence of moulted lobster carapaces on some checkups. Tethered and tagged urchins were observed being attacked by small pomacentrid fish and the cephalopods *S. apama* and *O. tetricus* in Wollongong, *H. portusjacksonii* in Jervis Bay and *G. prasinus* in Bendalong. We were able to obtain photographic records of *H. portusjacksonii* and *Parma unifasciata* (girdled scalyfin) attacking the urchins (Fig. 5).

## 4. DISCUSSION

Our findings from *in situ* tethering of *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* at 4 locations along the NSW coast indicate that they are preyed upon rapidly when removed from their crevice-shelter and physically restricted from returning to refugia. In most locations, the urchins were eaten by Day 3–4, except for Wollongong and Bass Point, where urchins persisted until Day 12–14. The DI and our qualitative observations in the field indicated that the tethered urchins were attacked by a broad predator guild. Counter to expectations, there was no effect of urchin TD or habitat type on predation of the 2 species. Predation was similar in dense macroalgae and barrens-mosaic habitats. Location was the only significant factor affecting whether urchins were preyed upon. Our results suggest that predation of tethered *C. rodgersii* and *H. erythrogramma* along the south coast of NSW occurs rapidly but varied spatially and potentially in relation to the local predator guild.

The urchins were eaten within a few days of being tethered, irrespective of TD, species or habitat type. This finding differs from previous tethering studies done in Tasmania (Ling & Johnson 2009) and Japan (Kawamata & Taino 2021), where tethered urchins in macroalgal habitats were preyed upon at a significantly higher rate than those tethered in habitats with sparse macroalgae. In contrast to the rapid predation of *C. rodgersii* in our study (3–14 d), survival of tethered *C. rodgersii* in Tasmania was much higher, with the urchins remaining alive for longer (5–90 d) (Ling & Johnson 2012). In addition, small urchins were eaten first and some large urchins
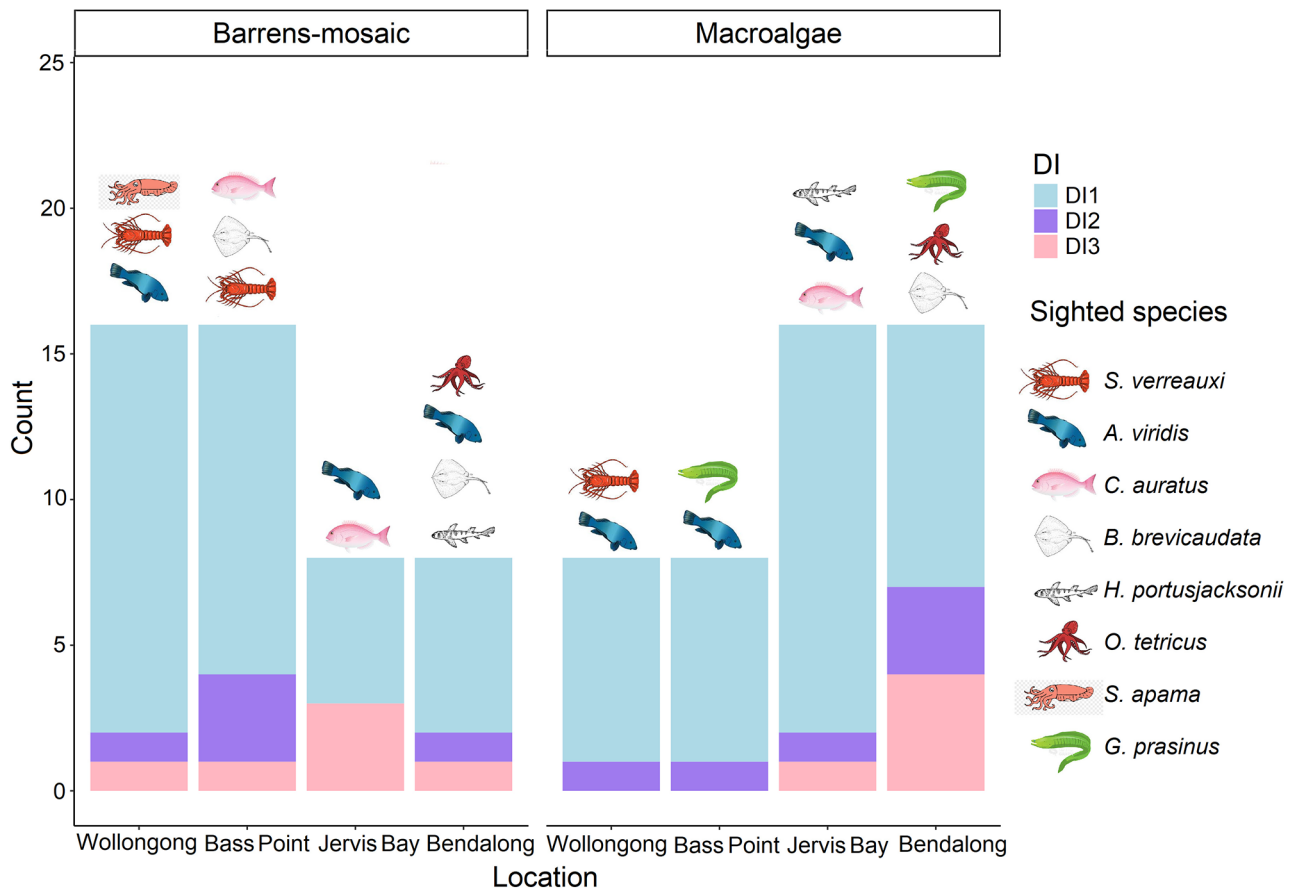
Fig. 4. Damage index (DI) counts: DI-1 (snapped tether), DI-2 (test broken) and DI-3 (test intact) at each habitat nested within sites. Images of putative urchin predators observed at each location are overlaid to show predator diversity. These included *Sagmariasus verreauxi* (eastern rock lobster), *Achoerodus viridis* (eastern blue groper) and *Chrysophyrus auratus* (pink snapper), *Bathytoshia brevicaudata* (smooth stingray) and *Heterodontus portusjacksonii* (Port Jackson shark), *Gymnothorax prasinus* (green moray), *Sepia apama* (giant cuttlefish) and *Octopus tetricus* (Sydney octopus). Images from https://publicdomainvectors.org/

remained alive for the duration of the experiment in Tasmania (Ling & Johnson 2012). Tethering studies with *H. erythrogramma* in Tasmania also report survival of large urchins for the entire experimental period (14 d), with small urchins being eaten first
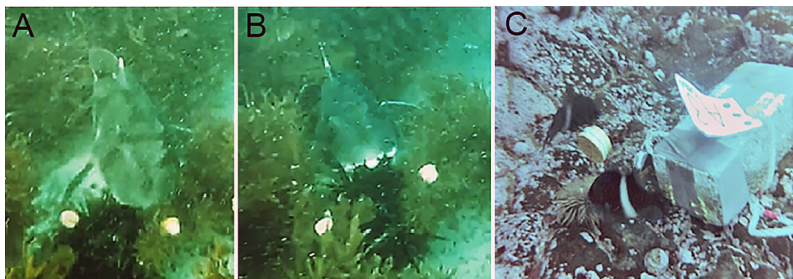


Fig. 5. Images captured on video showing (A,B) *Heterodontus portusjacksonii* (Port Jackson shark) attacking large *Centrostephanus rodgersii* in Jervis Bay, and (C) *Parma unifasciata* (girdled scalyfin) attacking a small *Heliocidaris erythrogramma.* Cork tags and brick tethers are visible

(Pederson & Johnson 2006). Predation of the 2 species in our study occurred up to 10 times faster than in Tasmania (Pederson & Johnson 2006, Ling & Johnson 2009, 2012). That we found no effect of body size on vulnerability to predation was surprising because large individuals escaped predation in Tasmania (Pederson & Johnson 2006, Ling et al. 2009) and smaller tethered *H. crassispina* and *Strongylocentrotus* spp. are more vulnerable to predation in Japan (Kawamata & Taino 2021) and California (Tegner & Levin 1983), respectively.

Urchin remains left on the tethers or snapped tethers indicated the presence of a broad range of predators. We also observed predators not previously confirmed to eat urchins, including *H. portusjacksonii* (Mc-

Laughlin & O'Gower 1971, Powter et al. 2010), *B. brevicaudata* (Michael 2006, Powter et al. 2010), *O. tetricus* (Ambrose 1986) and *G. prasinus* (Wraith 2007). Overall, tethered urchins were likely eaten primarily because they had been removed from shelter and prevented from returning (Shears & Babcock 2002, Pederson & Johnson 2006, Boada et al. 2015). We also consider the broad predator guild present at the tether locations as the reason urchins were eaten irrespective of species or body size. Varied urchin remains were left on the tethers and predation was rapid in most instances. Our finding that there was no difference in urchin predation in macroalgal compared to barrens-mosaic habitats is consistent with other studies that also did not find differences between habitats with abundant macroalgae compared to those with sparse macroalgae (Bologna & Steneck 1993, Byrnes et al. 2006, Sheppard-Brennand et al. 2017). Our approach needs to be extended to include expansive urchin barrens habitats where macroalgae is absent. While it is suggested that macroalgae is important in maintaining populations of urchin predators (Bologna & Steneck 1993, Byrnes et al. 2006, Sheppard-Brennand et al. 2017, Layton et al. 2020), in NSW, these predators avail of a range of habitats while foraging (Curley et al. 2002). Testing whether the results we report here over small spatial scales are also seen over larger spatial scales is an important area for future research.

The different results between urchin tethering experiments in NSW and Tasmanian reefs are indicative of higher predation pressure in NSW. In Tasmania, the lobster *J. edwardsii* was the main predator of tethered *C. rodgersii* and *H. erythrogramma*, with only 8% of predation attributed to fishes (Pederson & Johnson 2006, Ling et al. 2009, Ling & Johnson 2012). The survival of large urchins was suggested to be because small *J. edwardsii* (<120–140 mm CL) were unable to feed on large urchins (Pederson & Johnson 2006, Ling & Johnson 2012). In our study, we recorded little predation of tethered urchins attributable to lobsters (*S. verreauxi*), with more evidence for predation by fish (70%) and, in particular, species capable of breaking monofilament fishing line (15 kg tensile strength) or cracking urchin tests (e.g. *A. viridis* and *C. auratus*). We regularly found snapped and shortened monofilament line with no urchin remains attached, suggesting a sudden and forceful attack by a large predator (Cook & Vanderklift 2011). Large urchins may be an important food source for large fishes such as *A. viridis* (Gillanders & Kingsford 1998, Andrew 1999) and sharks such as *H. portusjacksonii* (McLaughlin & O'Gower 1971,

Powter et al. 2010). Small, locally abundant fishes such as *Notolabrus* spp. can also eat urchins (Pederson & Johnson 2006, Ling & Johnson 2012). We acknowledge the caveat that predation on tethered urchins may be higher than when they are within crevices, as seeking refugia is an important behavioural defence against predation (Colman 1972, Tegner & Dayton 1981, Tegner & Levin 1983, Gillanders 1995).

Despite the emphasis in many studies that lobsters are the most important urchin predators (Pederson & Johnson 2006, Ling & Johnson 2012, Kawamata & Taino 2021), this was not indicated in our study. The impact of lobsters on urchin populations might be less than previously proposed in the region of our investigation (Plagányi et al. 2018, Layton et al. 2020). Recent studies have shown that both the eastern and southern lobster species are capable urchin predators, but they may be more reluctant to eat urchins than first thought or may have wide-ranging diets; these studies show that both lobster species prefer molluscan prey to *C. rodgersii* and *H. erythrogramma* (Day et al. 2021, Smith et al. 2022a). It appears that the effect of lobsters on urchin populations in NSW (Provost et al. 2017, Day et al. 2021) is less than that reported for Tasmania (Pederson & Johnson 2008, Ling et al. 2019); although a recent study from Tasmania suggests that lobsters alone might not control urchin grazing there (Smith et al. 2022a). The results of this study (~30% predation of tethered urchins attributable to lobsters in NSW compared to ~90% in Tasmania) suggests that the potential for lobster predation to control urchin populations in NSW may be limited compared to elsewhere.

The 2 lobster species in temperate eastern Australia differ in their biology and ecology. In NSW, *S. verreauxi* undergoes seasonal migration many orders of magnitude greater in distance than that of *J. edwardsii* in Tasmania (Booth 2010, Jeffs et al. 2013, Woodings et al. 2018). The southern species *J. edwardsii* also has a much smaller home range and is resident in nearshore habitats at large sizes (Kelly 2001, Gardner et al. 2003). Comparatively, the eastern species *S. verreauxi* travels up to 1000s of km seasonally and in NSW are more abundant in deeper water than where dense *C. rodgersii* populations occur (Jeffs et al. 2013). Taken together, these aspects of lobster ecology may explain the differing outcomes for urchin tethering experiments in NSW and Tasmania. Moreover, *C. rodgersii* is newly arrived in Tasmania, having extended its range significantly poleward over the last 50 yr, and has created a novel,

dynamic and changing seascape, with increasing populations causing increasing barrens habitat (Ling & Keane 2021, Cresswell et al. 2022). As a new prey source, *C. rodgersii* does not appear to have a suite of predators in Tasmania. In contrast, in its native range the *C. rodgersii* barrens–macroalgae seascape has been stable for decades (Andrew & O'Neill 2000, Booth 2010, Glasby & Gibson 2020). This is likely associated with a predator guild that influences urchin population dynamics, as observed in California (Tegner & Dayton 1981, Stephens et al. 2006) and Japan (Kawamata & Taino 2021). The potentially 1000s of years of co-evolved urchin predator–prey dynamics along the coast of NSW contrasts with the emerging ecosystem outcomes in Tasmania.

We recorded some interactions between predators and tethered urchins, including species not expected to be urchin predators. Based on anecdotal reports and stomach contents (Gillanders & Kingsford 1998, Andrew 1999), we expected that *A. viridis* would be an important predator of the tethered urchins but did not observe this species preying on the urchins even though they were present at all our sites. We observed 4 species not previously known to eat urchins feeding on or attacking tethered urchins. These species included one chondrichthyan (*B. brevicaudata*), 2 cephalopods (*S. apama* and *O. tetricus*) and one anguilliform (*G. prasinus*) species. With respect to the shark *H. portusjacksonii*, our observations of predation on *C. rodgersii* are important, as this species has been suggested to eat urchins because it possesses sturdy biting and grinding dentition (Colman 1972, Powter et al. 2010), with just a single report of urchins in its gut contents (McLaughlin & O'Gower 1971). Our recording of previously unknown or little-known urchin predators indicates that we have a poor understanding of the breadth of the feeding guild that consumes urchins. This is also noted in Europe, where urchins are eaten by a broad range of predators and not primarily by lobsters (Trowbridge et al. 2019). This is congruent with our results, where fish played a larger role along with other invertebrate or chondrichthyan predators in eating tethered urchins compared with lobsters. It is important to note, however, that the broad urchin predator guild we report here may not be representative of predation under nonexperimental conditions since the urchins were tethered away from crevices, and this may affect vulnerability to predation (Boada et al. 2015). That said, the striking contrast between our results (urchins eaten in ~3–14 d and little predation attributable to lobsters) and those for tethered urchins in Tasmania (urchins remaining

alive at >90 d and most predation attributable to lobsters) (Ling & Johnson 2012) is an important indication that these regions differ ecologically.

Fishing of urchin predators such as lobsters and predatory fishes is considered to have a cascading ecosystem effect on reducing the vulnerability of urchin populations to predation (Ling et al. 2009, Ling & Johnson 2012, Kawamata & Taino 2021). This was reflected in our study, where location was the only significant factor with the greatest predation at Jervis Bay and Bendalong followed by Shellharbour and Wollongong. This suggests that predator guilds vary spatially. Interestingly, the level of predation reflects the proximity of the tethered urchins to nearshore human populations and the extent of activities such as fishing, with the 2 ends of the spectrum being Jervis Bay Marine Park (least exposed to anthropogenic pressures) and Wollongong (a city being most exposed). These observations highlight the need to consider the influence of adjacent human populations on rates of predation on tethered urchins, as in the gravity models used to predict *C. auratus* populations (Rees et al. 2021) and the health of coral reefs (Brewer et al. 2013, Cinner et al. 2018). Our observations suggest a north–south difference in urchin predation pressure in NSW, and since this difference also coincides with human population/fishing pressure, there is a need to consider this spatial factor in the design of predation studies.

The contrasting findings on predation of *C. rodgersii* in its native (NSW) range where the macroalgae–barrens mosaic has been stable for decades (Andrew & O'Neill 2000, Booth 2010, Glasby & Gibson 2020) and extended (Tasmania) range where barrens dynamics are increasing rapidly with negative impacts on local biodiversity (Ling et al. 2009) highlights the need for a nuanced (region-specific) approach to the management of urchin populations (Kingsford & Byrne 2023). Region-specific management strategies need to be considered and these will likely differ. For NSW, it appears that a broad range of predators feed on urchins and so it is unclear if a key urchin predator is missing due to past overfishing (Byrne & Andrew 2020). Predation on the tethered urchins was potentially influenced by the impacts of human populations on the local predator guild through fishing pressure (Cinner et al. 2018, Rees et al. 2021). Importantly, our results suggest that the role of lobsters in controlling urchins in NSW may be overstated and that many predator species are likely to influence population levels (Byrne & Andrew 2020), as reported elsewhere (Tegner & Dayton 1981). As moves to increase the *C. rodgersii* fishery and ini-

tiate culling campaigns are being considered as a means to transition barrens habitat to a more desirable kelp forest state (www.aph.gov.au/Parliamentary_ Business/Committees/Senate/Environment_and_ Communications/Invasivemarinespecies), targeted research is needed to determine whether NSW has an urchin problem to begin with. In Tasmania, it is notable that no significant decrease in barrens areas attributable to commercial harvest have been recorded in ~15 yr of fishing *C. rodgersii* at or near maximum sustainable yield (Cresswell et al. 2022). Conversely, in NSW, *C. rodgersii* is an important ecosystem engineer that maintains local biodiversity (Curley et al. 2002, Kingsford & Byrne 2023) and also presents a potentially sustainable fishery resource (Blount & Worthington 2002). Hence, any removal of this urchin across its native range will need to be managed carefully.

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