ICES Journal of Marine Science, 2022, **79**, 1353–1362
DOI: 10.1093/icesjms/fsac058
Advance access publication date: 8 April 2022
Original Article

Spiny lobsters prefer native prey over range-extending invasive urchins

Jennifer E. Smith [1,*], John Keane [1], Craig Mundy [1], Caleb Gardner[1] and Michael Oellermann [1,2]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7053, Australia
[2]TUM School of Life Sciences, Aquatic Systems Biology Unit, Technical University of Munich, Mühlenweg 22, D-85354 Freising, Germany
*Corresponding author: tel: +61 3 6226 8277; e-mail: je.smith@utas.edu.au.

Climate change increases the need to control range-extending species, which adversely impact their recipient ecosystem. Increasing populations of resident predators may be effective to counter such range-extension, but only if they consume the novel invaders at sufficient rates. In South-East Australia, poleward range-extending Longspined Sea Urchins (*Centrostephanus rodgersii*) are causing catastrophic ecological habitat transition to extensive urchin barrens. Tasmanian native Southern Rock Lobster (*Jasus edwardsii*) is a potential predator that could control further urchin expansion. Experimental feeding trials showed that range-extending Longspined Sea Urchins are the least preferred prey choice for Southern Rock Lobsters (3.8% predation events), when compared to three local species: abalone, urchins, and snails (36.6, 32.6, and 27%). Interestingly, habitat origin and naivete of lobsters to urchins affected urchin consumption with 85% being consumed by lobsters originating from urchin barrens. Low predation rates on Longspined Sea Urchin suggest that resident lobsters are unlikely to control further barren expansion unless a behavioural shift occurs. Results imply that potential control of Longspined Sea Urchins by Southern Rock Lobsters has previously been overestimated. Additional control methods are needed to safeguard ecological communities and important commercial stocks from this climate change-induced, range-extending pest species.

Keywords: naive predator, non-native prey, predator–prey, range shift, rock lobster, species redistribution, Tasmania, urchin barrens.

Introduction

Globally, climate change is causing shifts in species distribution, with novel species in new areas damaging native ecosystems, often with negative consequences for the human livelihoods that depend upon them (Pecl *et al.*, 2017; Pinsky *et al.*, 2020). An example is the Longspined Sea Urchin (*Centrostephanus rodgersii*), extending its distributional range poleward from the east coast of mainland Australia to Tasmania. The movement of these urchins into Tasmanian waters dramatically threatens the marine ecosystem by transforming large areas of biodiverse kelp forests into over-grazed, unproductive urchin barrens unsuitable to support up to 150 native species including commercially important species such as the Southern Rock Lobster (*Jasus edwardsii*) and the Blacklip Abalone (*Haliotis rubra*; Johnson *et al.*, 2005; Ling, 2008). Conversion of reef to barren on the east coast of Tasmania is estimated to be increasing at a rate of ~10.5% a year, (Ling and Keane, 2018), it is critical that potential control measures are identified and their efficacy assessed.

The destructive transformation from kelp forest to urchin barrens by sea urchins is often attributed to a loss of their natural predators [e.g. by over-fishing or disease (Sheppard-Brennand *et al.*, 2017; Burt *et al.*, 2018)]. For example, in their native coastal habitat in New South Wales (NSW), Longspined Sea Urchins (*C. rodgersii*) are able to create and maintain extensive barrens in areas of low population levels of their natural predators. The Eastern Rock Lobster (*Sagmariasus verreauxi*) and Eastern Blue Grouper (*Achoerodus viridis*) both prey on *C. rodgersii* in NSW, but overfishing of these predatory species has allowed increased urchin barren formation (Byrne and Andrew, 2013). However, in this case, *C. rodgersii* have invaded Tasmanian waters due to ocean warming, leaving many of their native sub-tropical predators behind. An equivalent predator in Tasmania, the Southern Rock Lobster (*J. edwardsii*), is known to be an opportunistic, generalist predator, consuming a broad range of prey including Shortspined Sea Urchins (*Heliocidaris erythrogramma*), Blacklip Abalone (*H. rubra*), and other invertebrates as part of their natural diet (Guest *et al.*, 2009). *J. edwardsii* have also been observed to consume the invasive Longspined Sea Urchins (*C. rodgersii*; Ling *et al.*, 2009a; Ling and Johnson, 2012), which has led to various studies considering lobster predation in Tasmania and its potential to halt urchin invasions (Johnson *et al.*, 2005; Ling *et al.*, 2009a). However, recent research suggests that in the wild, the predicted rate at which lobsters prey on Longspined Sea Urchins is insufficient to stem increasing urchin populations (Ling and Keane, 2021), yet the reasons for this discrepancy remain unclear. Day *et al.* (2021) recently showed that Longspined Sea Urchins (*C. rodgersii*) were not as popular as Shortspined Sea Urchins (*H. erythrogramma*) in the diet of Eastern Rock Lobsters (*S. verreauxi*) in NSW. This concept of prey preference leads into the motivation for this study.

There is an evolutionary advantage for native predators to learn to prey on non-native prey species (Carlsson *et al.*, 2009), however, differences in the behaviour, size, and sex of individual predators can lead to different responses to novel, non-native species (Pintor and Byers, 2015). In

Received: December 21, 2021. **Revised:** March 1, 2022. **Accepted:** March 8, 2022

Tasmania, South-East Australia, Southern Rock Lobsters have been shown to have the capacity to prey on Longspined Sea Urchins in the wild in caged experiments and wild diet studies (Ling *et al.*, 2009a; Redd *et al.*, 2014), but how different-sized lobsters from different habitats (e.g. extensive urchin barren habitat vs. kelp-dominated reef) with varying degrees of urchin-naivete (i.e. awareness of urchins in the wild) will respond to the range-extending species is yet to be investigated.

The abundance of Southern Rock Lobster on Tasmania's East Coast is currently extremely low due to overfishing (the current stock is at a level between 8.5 and 16% of the unfished biomass), and causing local Tasmanian government to implement population rebuilding strategies for both fishery stock enhancement and increased predatory pressure on Longspined Sea Urchins [see report: DPIPWE (2018)]. The rebuild objectives provide rationale to assess predatory impact and predatory efficacy of rock lobsters on range-extending Longspined Sea Urchins in comparison to other local invertebrates. If we are to rely on the Southern Rock Lobster to decrease the threat of urchin barren formation, we must first understand its natural predation behaviour before we can estimate its effectiveness in combating invasive urchins.

Here, using single- and multi-choice feeding experiments, we assess the effectiveness of lobsters as a predatory control of Longspined Sea Urchin in Tasmania and estimate the potential rate of urchin removal from the ecosystem. Specifically, we examine (1) whether predatory Southern Rock Lobsters show a preference for the range-extending Longspined Sea Urchins in comparison to three local invertebrate prey species. (2) We investigate whether predator size plays a role in the rate of predation of different prey species, with larger lobsters expected to prey on Longspined Sea Urchins and local prey species more frequently than smaller lobsters as they are better able to physically "handle" the urchin's wider spine canopy (Andrew and MacDiarmid, 1991; Pederson and Johnson, 2006; Ling *et al.*, 2009a). (3) Finally, we hypothesize that habitat, and therefore urchin-naivete, influences the likelihood of resident lobsters predating on Longspined Sea Urchins, with lobsters from urchin barrens expected to be more accustomed to prey on Longspined Sea Urchins.

Methods

In situ observations of predation are limited by time availability for underwater observations of natural events, and become increasing challenging when the behaviour of both predator and prey is nocturnal. In order to accurately quantify prey-preference and rate of consumption, we conducted tank-based experiments at the Institute for Marine and Antarctic Studies (IMAS) Taroona laboratory.

Experimental design

Captive feeding experiments were designed to test differences in feeding rate with regards to four factors: "prey species" (four levels), "lobster size class" (three levels), "lobster habitat" (two levels), and "trial type" (two levels). Initial experimental trial design was based on Dumas *et al.* (2013) and modified for species and factors of interest in Tasmania. Replicate lobsters were taken across sizes (10 per size class) and habitat (total 30 per habitat).

Sample size

To ensure enough replicates for statistical significance, we conducted a power analysis [sample size of six, to reach 86% power at $p = 0.05$ error, using effect size of 0.8 from Dumas *et al.* (2013)]. To further increase confidence we rounded up to 10 replicates per size class, per site.

Lobsters were split into three size classes: small [carapace length (CL) < 110 mm], medium (CL 110–140 mm), and large (CL > 140 mm). This was to represent likely important Longspined Sea Urchin predators (large; Ling *et al.*, 2009a); lobsters accessible to the fishery but less effective predators (medium); and those not accessible to the fishery (legally undersize) and assumed less effective predators of Longspined Sea Urchins (small). We aimed for a 50:50 ratio of both sexes, but this was not always achieved within a size class—it was particularly difficult to obtain sufficient large females at the time of collection. However, post-experimental analysis confirmed sex did not influence likelihood of predation events (see results).

Lobster collection and sites

A total of 42 lobsters were collected during two potting events in the Elephant Rock Research Reserve (St Helens, North-East Tasmania) during December 2020 and the Crayfish Point Research Reserve (Taroona, South-East Tasmania) during January 2021. Potting was conducted by methods similar to Redd *et al.* (2014). Additional lobsters ($n = 18$) were collected by SCUBA divers around the same time to complete size class requirements. An interrupted trial meant one lobster was removed from analysis. Elephant Rock is an extensive urchin barren, which has been completely grazed by Longspined Sea Urchins such that no kelp is present, hence in this study, lobsters from "urchin barren" habitat represent lobsters that have been exposed to Longspined Sea Urchins in the wild for several decades. Crayfish Point is an ungrazed, rocky reef habitat, with no *C. rodgersii*, hence in this study, lobsters from "kelp habitat" represent lobsters totally naive to Longspined Sea Urchins. Both sites are scientific no-take research areas.

Tank setup

Lobsters were transported in damp hessian sacks to semi-outdoor, flow-through tanks with untreated sea water in aquaria facilities at IMAS Taroona, with each individual put into its own tank covered by mesh to prevent escape. Large lobsters were kept in 212-l tanks (40 cm × 82 cm diameter), while small and medium lobster were held in 78-l tanks ($38 \times 32 \times 64$ cm^2). All tanks had concrete floor and plastic walls, no shelter was provided for lobsters or prey. Although all prey species were able to climb the walls of the tanks, the water level and mesh ensured they were always within reach of the lobsters. Following expert advice and pilot trial result, lobsters were acclimated in their trial tank for 4 d before beginning feeding trials. Pilot acclimation trials were run in the weeks preceding with an individual subjected to the same collection and transportation process. Video recording was used to assess when the new arrival first started feeding (< 48 h after arrival).

Prey collection

Longspined Sea Urchins (*C. rodgersii*), and local invertebrates: Shortspined Sea Urchins (*H. erythrogramma*), Wavy Periwinkles (*Lunella undulata*) and Blacklip Abalone (*H. rubra*) were collected on SCUBA from local reef sites on the Tasman Peninsula when required for trials. We chose prey species, which matched the described diet of *J. edwardsii* (Edmunds, 1996), and which have commercial importance for fisheries in Tasmania. Prey were collected from both incipient barrens (where *C. rodgersii* exist but have not yet formed extensive barrens) and reef to avoid differences in prey preference associated with habitat-specific prey quality (Eurich *et al.*, 2014). Prey were collected across a range of sizes (see Supplementary file 1) to satisfy lobster:urchin size ratio limits, described in Ling *et al.* (2009a), to ensure variation in the size of individual prey did not impact its vulnerability to predation by lobsters. Prey were kept in holding tanks prior to being introduced to lobsters during feeding trials.

Throughout this paper, we use common names for these urchin species to emphasise the morphological differences between Longspined Sea Urchins (*C. rodgersii*) and Shortspined Sea Urchins (*H. erythrogramma*), which are critical to the objectives of the study.

Trials

Two types of feeding trials were used:

(1) No Choice trials—lobsters offered only *one prey species* throughout the trial to determine rate of consumption when no other species are available.
(2) Choice trials—lobsters offered *all four prey species simultaneously* to determine rates of consumption when other prey options are available.

Feeding trials were conducted over a 5-week schedule. Every lobster completed four No Choice trials (one for each prey type) and one Choice trial. These trials happened in a random order for each individual lobster, constrained by fieldwork opportunities to collect more prey. A post-experiment test of randomness confirmed no effect of previous trial species on feeding rate in subsequent trial ($p = 0.07$, df = 3258, and F = 2.3647, see Supplementary file 2). All trials took place between December 2020 and April 2021.

Trials ran over four consecutive days, with a 3-d starvation period prior to and between each trial. On the first day of the trial period, prey items were measured, counted, and weighed, with the size of prey items given dependent on the size class of each lobster and number of prey dependant on the prey size. Prey animals would always be supplied in excess of one and would fill approximately 20% of tank area to control for "chance of discovery" (Dumas *et al.*, 2013).

During subsequent trial days, lobsters would be checked once in the morning and once in the evening to avoid excessive disturbance, but allow for relatively constant replacement of consumed prey items. For any prey items that had been killed, remains would be removed from the tank, weighed, measured, and discarded. Anything consumed was replaced with a similar sized individual of the same species. On the final day of the trial, surviving prey items would be removed from lobster tanks, counted, and weighed. Lobsters would then enter the 3-d starvation period before the next trial.

Data analysis and statistical methods

In total, two approaches were taken for data analysis to address specific questions of interest. First, we followed the protocol outlined by Fletcher *et al.* (2005), splitting the results into binomial presence–absence of predation events (Figure 1 and Table 1), which allowed calculation of factors influencing the likelihood of a predation event occurring. Second, to determine the likelihood of a predation event and the presence of any preferences towards prey species, we applied a multinomial modelling approach described by Venables and Ripley (2002), which included the number of predation events as an additional factor (Table 2).

All analysis was executed in R (R Core Team, 2021) and RMarkdown file is available in the supplementary files. A generalized linear mixed effect model (GLMER) was fit as follows using the "lme4" package (Bates *et al.*, 2015): glmer(formula = Eaten ∼ Trial Species ∗ Habitat + Trial Type + (1 | Lobster ID) + (1 | Trial Week), family = binomial). Lobster ID and trial week were included as random effects in the model to account for inherent differences in lobster behaviour and as randomised trial order was not controlled. Lobster habitat, trial species, and trial type were included as categorical fixed effects. Lobster size class, sex, and all factor interactions except species∗habitat were removed from the model following model parsimony improvement using the dropterm function in package "MASSextra" (Venables, 2021). *Post hoc t*-tests were used to visualize comparisons between levels within factors (Table 1).

Results

We conducted 295 feeding trials with 59 lobsters over 5 months and found that Longspined Sea Urchins were the least preferred prey by Southern Rock Lobsters, relative to three local prey species.

Higher preference for local prey

A total of 29 lobsters from kelp habitat and 30 from urchin barren habitat consumed 703 prey individuals, of which 36.6% were Blacklip Abalone, 32.6% were Shortspined Sea Urchin, 27% were Wavy Periwinkle, and only 3.8% were Longspined Sea Urchin.

Analysis of the presence–absence data showed a significant effect of prey species, habitat, and trial type on the likelihood of a predation event occurring (Table 1). Abalone was the most popular prey of choice, followed by Shortspined Sea Urchin then periwinkle, all of which were consumed nearly an order of magnitude more frequently then Longspined Sea Urchins (Figure 1 and Table 1). Predation events were significantly more common during No Choice trials compared to Choice trials across all prey species ($p < 0.001$; Table 1). There was no significant effect of lobster habitat overall, but predation events of Longspined Sea Urchins were significantly more common in lobsters from urchin barren habitat than lobsters from kelp habitat (Figure 1 and Table 1; $p < 0.05$). Sex and size class did not explain likelihood of predation occurring. Results show that predation events were primarily on local species and not the Longspined Sea Urchin (Figure 1). A total of 65% of predation events occurred at night, compared to only 35% during the day.

In most cases, lobsters would catch abalone off the tank wall and fully consume their soft body parts, leaving an intact shell behind, occasionally chips were found around the edges of the shell. Periwinkle shells were often left, mostly intact, but with chips around the entrance and operculums were not consumed. Shortspined Sea Urchin tests were found with a hole in the position of the Aristotle's lantern. Longspined Sea Urchin

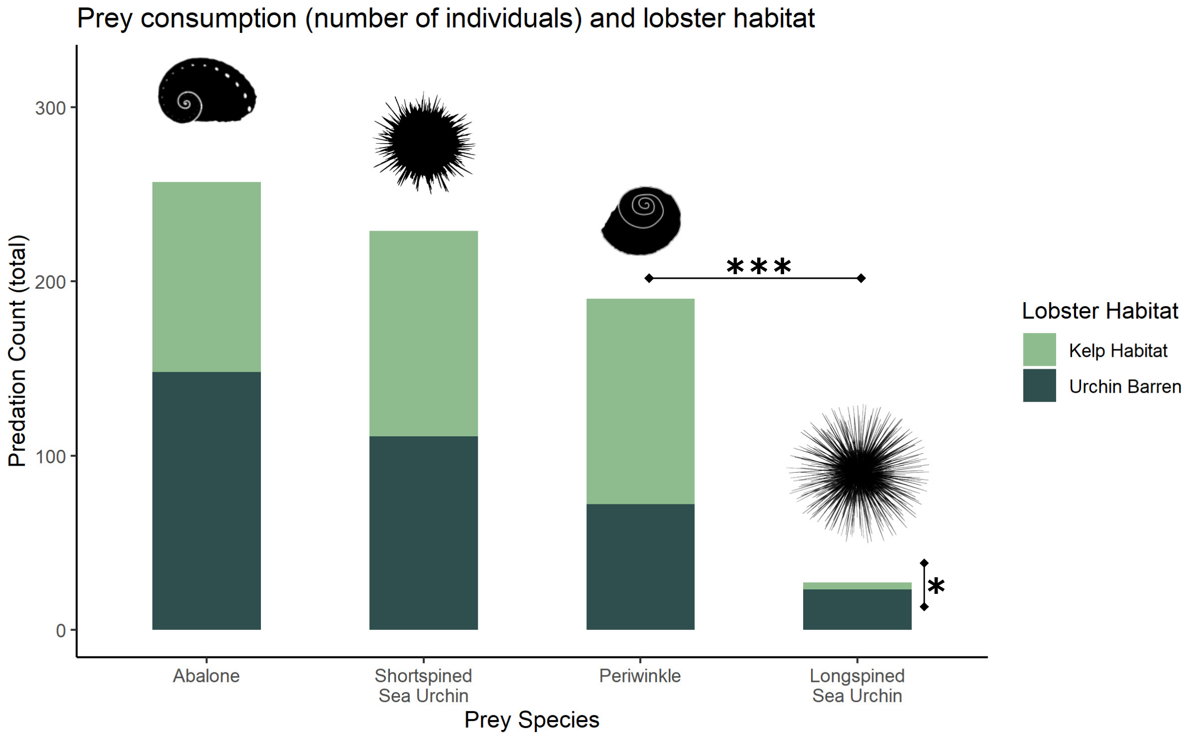

Figure 1. Number of total predation events for each prey type by all 59 Southern Rock Lobsters across all 295 experimental trials. Lobster habitat is shown in colour: "Kelp Habitat" lobsters are naive to Longspined Sea Urchins, "Urchin Barren" lobsters are accustomed to Longspined Sea Urchins in the wild. Significance bars show evidence of differences between prey species (horizontal) and between habitat (vertical) (p-values: *** < 0.001, ** < 0.01, and * < 0.05) determined by GLMER in Table 1. Silhouettes indicate prey species [not to scale, Hawkey (2008); Kraeer and Van Essen-Fishman (2008)].

Table 1. Generalized Linear Mixed Effect Model (GLMER) results on predation data (i.e. likelihood of predation event occurring). "Longspined" and "Shortspined" refer to respective urchin species. *Post hoc t*-tests were used to visualize comparisons between levels within factors (linear hypotheses). Asterisks indicate p-values values: *** < 0.001, ** < 0.01, and * < 0.05.

GLMER (binomial) Linear hypotheses	Estimate	Std. Error	z value	Pr(> |z|)		Interpretation
Species:						
Longspined—Abalone == 0	−4.5196	0.7041	−6.419	8.23E-10	***	Longspined < Ab
Shortspined—Abalone == 0	−0.4321	0.4626	−0.934	0.35		Shortspined = Ab
Periwinkle—Abalone == 0	−1.2595	0.4584	−2.747	0.018	*	Periwinkle < Ab
Shortspined—Longspined == 0	4.0875	0.6824	5.99	1.05E-08	***	Shortspined > Longspined
Periwinkle—Longspined == 0	3.2601	0.6559	4.97	2.67E-06	***	Periwinkle > Longspined
Periwinkle—Shortspined == 0	−0.8274	0.4398	−1.881	0.12		Periwinkle = Shortspined
Trial type:						
Choice—No Choice == 0	−0.9213	0.2579	−3.572	0.000354	***	Choice < No Choice
Habitat:						
Longspined:Barren	1.825276	0.821324	2.222358	0.026259	*	Longspined Sea Urchin predations were more often by barren lobsters

test remains were often in multiple pieces as if the lobster had to crack them open.

Average number of prey consumed per day

During No Choice trials, lobsters consumed the local prey species at a far greater rate than the range-extending Longspined Sea Urchin. However, when given a choice of prey, barren lobsters showed a slight trend in preference for the local prey options (Figure 2, dark bars), with abalone the prey of choice, followed by Shortspined Sea Urchin and finally periwinkle. This difference in local prey species consumption rates was not significant in either trial type and the interaction was removed from the model (see Table 1).

The maximum consumption rate of Longspined Sea Urchins seen in our trials was by lobsters collected from urchin barrens during No Choice trials, where urchins were consumed at a rate of 0.175 (± SE 0.12) per day (Figure 2), which translates to approximately 64 (± SE 44) Longspined Sea Urchins per year per lobster (this is an extrapolation of multiplying by 365). Comparatively, only nine Longspined Sea Urchins per year would be predated on by barren

Table 2. A multinomial model was fitted to the count data. This table gives estimated probabilities of predation events of each prey species for lobsters in each habitat, size class, and trial type based on our trials.

Habitat	Size class	No Choice trials				Choice trials			
		Abalone	Longspined Sea Urchin	Shortspined Sea Urchin	Periwinkle	Abalone	Longspined Sea Urchin	Shortspined Sea Urchin	Periwinkle
Kelp Habitat	Large	0.12	0.02	0.4	0.46	0.19	0	0.45	0.35
	Medium	0.23	0.02	0.32	0.44	0.34	0	0.34	0.31
	Small	0.5	0.01	0.28	0.21	0.62	0	0.25	0.13
Urchin Barren	Large	0.22	0.1	0.39	0.28	0.34	0.03	0.43	0.21
	Medium	0.38	0.09	0.28	0.24	0.53	0.02	0.29	0.16
	Small	0.65	0.06	0.2	0.09	0.77	0.01	0.17	0.05

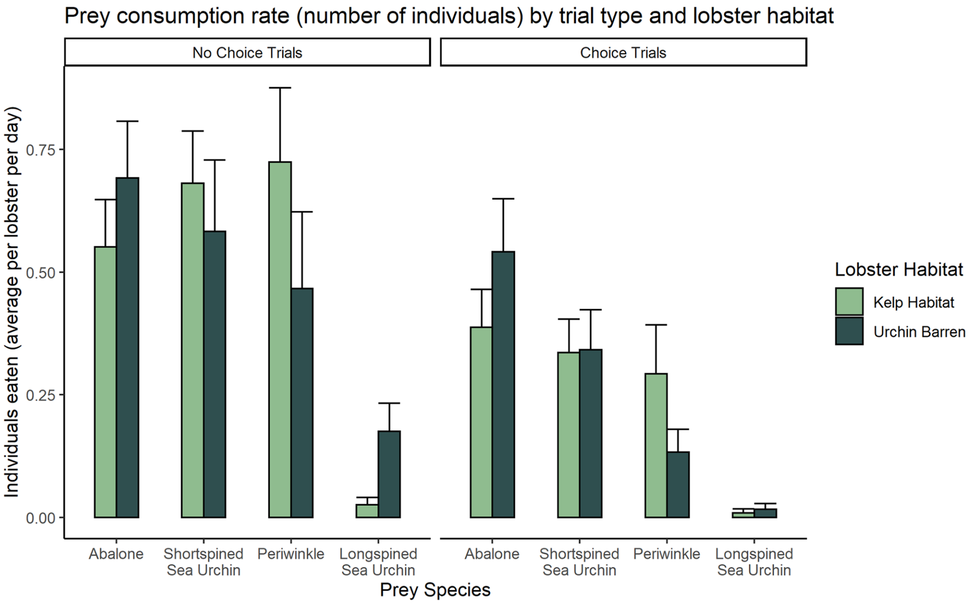

Figure 2. Average number of total predation events per lobster per day during experimental trials for each prey type, in No Choice Trials and Choice Trials. Lobster habitat is shown in colour: "Kelp Habitat" lobsters are naive to Longspined Sea Urchins, "Urchin Barren" lobsters are accustomed to Longspined Sea Urchins in the wild. Bars represent standard error.

lobsters when given a choice of other prey, representing a 90% decrease in Longspined Sea Urchin predation events when lobsters have alternative prey options (Figure 2). In reef lobsters naive to Longspined Sea Urchins, only 14 Longspined Sea Urchins would be predated per lobster per year during No Choice situations—an 85% decrease in predation events compared to barren lobsters, and only four urchins would be consumed per year by a reef lobster with a choice of prey.

Comparatively, barren lobsters during No Choice trials ate abalone at a rate of 0.69 (± SE 0.24) per day (Figure 2). At this rate, approximately 252 (± SE 87) abalone would be predated upon per year per lobster. During Choice trials, however, this reduces to 198 (± SE 80) abalone per year. In reef lobsters, the rate during Choice trials was 144 (± SE 58) abalone per lobster per year.

Shortspined Sea Urchin predation rates were very similar across lobsters from both habitats during Choice Trials: reef lobsters ate Shortspined Sea Urchins at a rate of 0.34 (± SE 0.14) per day and barren lobsters at 0.34 (± SE 0.17) per day. For periwinkles during Choice Trials, reef lobsters ate at a rate of 0.29 (± SE 0.2) per day and barren lobsters at 0.13 (± SE 0.09) per day. Data on predation rates can be found in Supplementary file 3.

Probability of lobster predation on different prey species

A multinomial model was fitted according to Venables and Ripley (2002) to calculate the expected predation values according to the raw count data (Table 2). Results are similar to the binomial fit (Table 1), in that the three native species are predated on at substantially higher rates compared to Longspined Sea Urchins across all groupings of lobsters. Lobster size had the greatest effect on prey species consumption, with trial type and habitat having a minor effect on the probability of prey species being consumed (Table 2). Smaller lobsters were more likely to eat abalone than medium or larger lobsters, while the inverse was observed for periwinkles. There was a fivefold increase in the probability of a lobster from a barren consuming Longspined Sea Urchins compared to lobsters from kelp habitat. Small lobsters from barrens were half as likely to consume Longspined Sea Urchins than medium or large lobsters (Table 2).

Centrostephanus-specific predation events

A total of 27 Longspined Sea Urchin predation events were recorded during all 295 trials (Figure 3). Of those 27 events, 85% of the Longspined Sea Urchins were consumed by

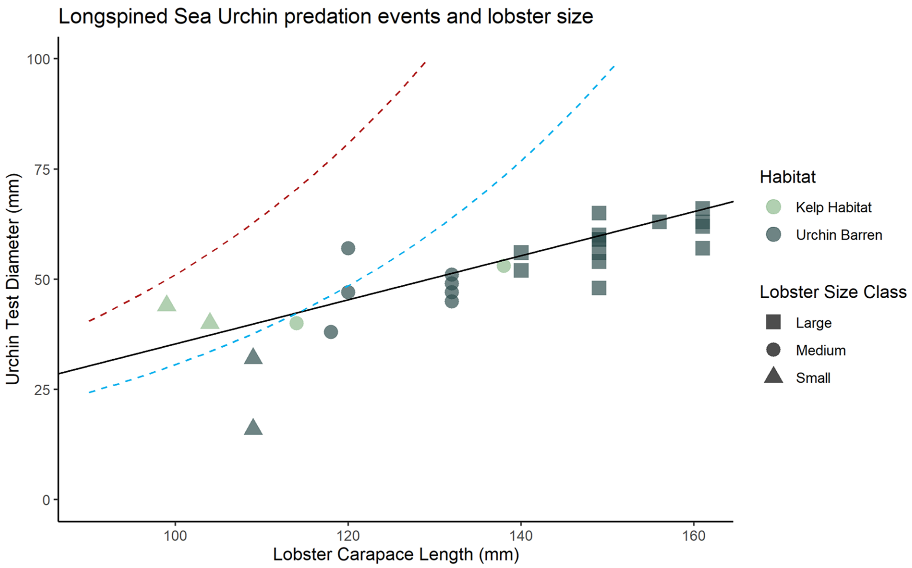

Figure 3. All Longspined Sea Urchin predation events observed in this study (27 observations). Size of urchin and size of lobster are shown on *y*- and *x*-axes, respectively. Lobster habitat is shown in colour: "Kelp Habitat" lobsters are naive to Longspined Sea Urchins, "Urchin Barren" lobsters are accustomed to Longspined Sea Urchins in the wild. Black solid line shows linear regression of this data. Red dashed line shows previous study lobster:urchin theoretical physical limit of predation (Ling *et al.*, 2009a). Blue dashed line shows 60% of this limit defined previously as the upper limit of observed predation events *in situ* (Ling *et al.*, 2009a).

lobsters from barren habitat compared to only 15% by reef lobsters. Furthermore, 91% of those urchins killed by barren lobsters were predated during No Choice trials. Our observations fitted well within theoretical physical limits defined by Ling *et al.* (2009a), and follow a similar trend of larger lobsters eating larger urchins (Figure 3). It must be noted that all lobsters were offered urchins and other prey within these physical limits (red line) so as to not reduce the chance of predation by limited accessibility. We found that small lobsters (CL < 110 mm) can and do prey on small Longspined Sea Urchins in aquaria. We understand that we observed the smallest lobster (99 mm CL) predation of Longspined Sea Urchin (40 mm test diameter) on record, with the previous smallest lobster being 110 mm CL (Ling *et al.*, 2009b).

Individual lobsters

Only 14 of 59 lobsters were responsible for the 27 Longspined Sea Urchin predation events across all trials. Predation events were recorded for 33% of barren lobsters and 14% of reef lobsters. A total of five large lobsters were responsible for half ($n = 14$) of all predation events, while six medium lobsters and three small lobsters accounted for the remaining nine and four predation events, respectively. In 63% of the trials in which a lobster predated on Longspined Sea Urchins ($n = 16$), only one urchin was eaten, in 25% two were eaten. Only two lobsters ate more than two Longspined Sea Urchins, both were large barren lobsters in No Choice trials—one ate four urchins and one ate five. Only 7% of barren lobsters predated on Longspined Sea Urchins during Choice trials, compared to one reef lobster out of 29 (3%). Comparatively, for local prey species: 87% of all barren lobsters ate abalone, 66% ate Shortspined Sea Urchin, and 47% ate periwinkle. For reef lobsters 90% ate abalone, 86% ate Shortspined Sea Urchin, and 66% ate periwinkle.

Discussion

Southern Rock Lobsters are known to be opportunistic, generalist predators but little work has been done to quantify their diet proportions. Guest *et al.* (2009) found that urchins, periwinkles, and ascidians accounted for much of their diet along with other invertebrates, but that importance of food items varied spatially. In this study, we advance the knowledge on the prey preference of spiny lobsters on commercial species of interest in South-East Australia and address their importance as a predator of invasive Longspined Sea Urchins. Our laboratory-based prey preference experiments demonstrate that the range-extending Longspined Sea Urchins are not the prey of choice for Tasmanian Southern Rock Lobsters. Predation rates on local prey species were much higher for all sizes of lobster from both habitats during Choice and No Choice trials. Predation of Longspined Sea Urchin by lobsters from kelp habitat where Longspined Sea Urchins are not present was negligible, suggesting a potential effect of naivete in these lobsters. Therefore, despite the assumption that large lobsters are the primary predators of Longspined Sea Urchins (Ling *et al.*, 2009a), control of urchins by rebuilding local lobster populations in reef environments is unlikely to stop the formation of new urchin barrens and other control methods will be required. Further to this, lobsters prey on local species at substantially higher rates and as lobster biomass increases, decreases in abundance of these native species is expected before an impact on Longspined Sea Urchin populations is observed. A slight trend in preference during the Choice trials was seen, where lobsters appear to prey on abalone at a higher rate than other species when offered a choice of all the prey species. On healthy reefs with greater prey options, increased lobster densities could, therefore, prove more of a threat to local invertebrate species, such as the abalone and Shortspined Sea Urchin, than an effective control of the Longspined Sea Urchin (Barrett *et al.*, 2009).

Low predation rates on novel, range-extending species in the wild may arise due to a lack of prey familiarity, with native predators required first to recognize novel prey and then to learn "how to handle" the novel food sources (Carlsson *et al.*, 2009). This naivete and lack of "handling skills" may explain why lobsters in our trials preferred local species over Longspined Sea Urchin [see Pintor and Byers (2015)], and why the majority of observed Longspined Sea Urchin predation events were by lobsters collected from an established (multidecadal) Longspined Sea Urchin barren, i.e. lobsters that were accustomed to urchins in the wild. A total of two large barren lobsters in No Choice trials consumed Longspined Sea Urchins at a higher rate than all other lobsters (four and five urchins each during the trial period), which could imply a learned behaviour in these particular individuals compared to others, which may be yet to master the predatory "skills" required to consume the Longspined Sea Urchins. Lobsters from kelp habitat, which had never encountered Longspined Sea Urchins in the wild were responsible for only four predation events, suggesting lobsters have the ability to learn to prey on novel species, but the timescale on which this behaviour is learned is uncertain (Carlsson *et al.*, 2009). Further to this, the predation of Longspined Sea Urchins by lobsters from urchin barrens were often only during No Choice trials, suggesting an "only when desperate" or exploratory response. A recent study by Day *et al.* (2021), however, found Eastern Rock Lobsters (*S. verreauxi*) in New South Wales preferred Shortspined Sea Urchins over Longspined Sea Urchins despite long-term exposure to both species on local barrens, suggesting naivete of Longspined Sea Urchins may not be solely responsible for driving the preference for local prey species we found in this study.

The Optimal Foraging Theory suggests that predators will target prey with the most reward and least energetic cost (Pyke, 2019). Optimal foraging may also limit the feeding capacity of Southern Rock Lobsters [and their eastern relatives (Day *et al.*, 2021)] on Longspined Sea Urchins, potentially explaining the observed preference in this study. Energetic gain provided by an accessible Longspined Sea Urchin may not be worth the energetic output needed to capture, handle, and digest the individual urchins. Given their morphological differences, handling of Longspined Sea Urchins is likely to be more energetically expensive and less time efficient compared to Shortspined Sea Urchins, thus increasing the risk of predation for the predator itself and ultimately decreasing the energetic worth of the urchin (Tegner and Levin, 1983; Selden *et al.*, 2017). Further, the energetic value gained through consumption of a Longspined Sea Urchin could be less than that of individuals of other species when compared to the energetic demand of predation. Longspined Sea Urchins mature at a test diameter of ∼40–60 mm (King *et al.*, 1994), thus the lack of nutritionally rich gonad in immature urchins may limit the attractiveness of these smaller, more accessible individuals. Alternatively, abalone, the most popular prey species in our trials, may provide more nutritional and digestible content than other species, may be more easily accessible, or both. Further research into the nutritional energetics of these prey species would allow the factors driving prey preferences in barren and reef lobsters to be identified. Differences associated with habitat-specific prey qualities, which have been previously observed in spiny lobsters (Eurich *et al.*, 2014), are unlikely to be an important factor driving the prey preferences observed in this study as all prey species were collected from similar habitats.

Energetics and optimal foraging is likely to interact with predator size and the accessibility of prey to predators. For example, large lobsters are expected to predate at a higher rate than smaller lobsters due to higher energetic demands and enhanced predation ability (Andrew and MacDiarmid, 1991; Pederson and Johnson, 2006). This held true for predation of Longspined Sea Urchins, Shortspined Sea Urchins, and periwinkles, which was positively correlated with lobster size, but in this study we found the opposite for abalone, which had a higher predation rate in small lobsters. This unexpected result may be due to differences in the accessibility (i.e. ease of predation) of each prey species across size classes. For example, smaller periwinkles appear to have stronger shells relative to larger periwinkles, which may make predation more energetically expensive for smaller lobsters (J. Smith, pers. obs.). Further, the abductor muscle in abalone that provides a means of holding onto the substrate is much stronger in larger abalone, and shell thickness of larger abalone is greater, thus the energetics associated with extracting larger abalone from the substrate are likely to be higher than for smaller abalone. This could indicate a cost-benefit interaction between lobster size and type of prey species.

Although we observed trends with lobster size and amount of prey eaten, size class of lobster did not greatly affect the likelihood of a consumption event occurring for any species in our trials. Lack of competition in isolated experimental tanks meant all lobsters had equal opportunity to predate; in the wild, larger lobsters would likely out-compete smaller ones during predatory conflict. Lobsters were also only provided with prey of sizes they could physically attack (Andrew and MacDiarmid, 1991; Ling *et al.*, 2009a), ruling out the possibility that prey animals were inaccessible to the lobsters due to size or spine length. In the wild, it is likely that smaller individuals of all prey species would be cryptic and less available to lobster predators, meaning smaller lobsters cannot find as many accessible prey items as easily as the larger lobsters, which are able to prey on larger, emergent animals (Ling *et al.*, 2009a). However, both Longspined Sea Urchins and Southern Rock Lobsters are nocturnally active, which may provide a window of opportunity for small lobsters to prey on small urchins in the wild (Byrne and Andrew, 2013).

Despite being the least popular prey species, Longspined Sea Urchins were predated on by all size classes of lobster. Until now, it was thought that primarily large lobsters (CL > 140 mm) actively prey on emergent Longspined Sea Urchins, with the presence of Longspined Sea Urchin in small lobster faecal samples assumed to be acquired through scavenging of other predation events (Redd *et al.*, 2014). Biomass estimates for lobster control in Tasmania exclude smaller predators for this reason, but our results suggest lobsters of size 99–140 mm can contribute to predation of Longspined Sea Urchins, albeit at a lower rate. Lobsters of all size classes should, therefore, be included in total biomass counts when assessing stock rebuilding targets for urchin control.

Predatory control of Longspined Sea Urchin barrens in Tasmania

Southern Rock Lobsters were first shown to be capable of predating on Longspined Sea Urchins in the early 2000s, and subsequently a long-term management plan to rebuild lobster numbers for urchin control and fisheries production was established (Ling and Johnson, 2012; DPIPWE, 2018). This management plan suggests that reduced fishing pressure would allow lobster densities to recover, in turn increasing urchin predation and limiting the habitat shift from kelp habitat to overgrazed urchin barrens. Yet, a recent study showed the rate of urchin barren expansion inside a 30-year-old marine reserve was the same as that on adjacent unprotected reefs (Perkins *et al.*, 2020), despite discrete and unsanctioned urchin culling by recreational divers and commercial operators within the reserve (J. Keane, pers. obs.). Lobsters have, however, been shown to limit barren expansion inside a closed-fishery area where urchin densities were low and into which large lobsters were translocated to increase predator density (Ling and Keane, 2021). While our results confirm that lobsters will and do prey on Longspined Sea Urchins, predatory behaviour varies between lobster habitat and size classes, and therefore, rebuilding predator numbers may not be universally effective for minimizing urchin barren expansion.

Rebuilding lobster density by reduced lobster fishing will only be effective in halting urchin barren expansion if lobsters actively prey on the Longspined Sea Urchins in non-barren environments. Extrapolated estimates of lobster predation on Longspined Sea Urchins in no-take, closed fishery sites (Ling *et al.*, 2009a; Johnson *et al.*, 2013), suggests a rate of ∼43–108 urchins killed a year per lobster (see Supplementary Table S1). Although these extrapolations contain uncertainty, they suggest that lobsters from urchin barrens, with no other prey choice could consume Longspined Sea Urchins at a rate of up to ∼64 (± SE 44) urchins a year, fitting within the previous calculated range (Ling *et al.*, 2009a; Johnson *et al.*, 2013; Supplementary Table S1). However, we found a decrease of 90% in predation of these urchins by barren lobsters when offered a choice of alternative prey species. Furthermore, our results from reef lobsters show a much lower predation rate, ∼3 Longspined Sea Urchins per lobster per year. Wild predation rates are likely to be lower again as diversity of prey choice increases. These results imply lobsters may be much less effective at controlling urchins than previously thought, which is in line with a recent study that found experimental increases in lobster densities had no impact on urchin populations or barrens cover on extensive urchin barrens (Ling and Keane, 2021).

To assess the potential for lobster control of urchin barrens in the ecosystem, we extrapolated our predation rates further. With Tasmanian east coast Southern Rock Lobster populations predicted to have reached 1066 tonnes by 2018 (commercial legal size) and at an average weight of 1 kg per lobster, we predict that there are approximately 1 million individual lobsters capable of predating on urchins on the east coast of Tasmania (DPIPWE, 2018). To stem the invasion of urchins into kelp habitat, and therefore, reduce the spread of urchin barrens, lobsters in reef environments would need to prey on Longspined Sea Urchins at a sufficient rate. Based on the consumption rate of Longspined Sea Urchins by reef lobsters during Choice Trials in this study (0–3 Longspined Sea Urchins lobster^{-1} year^{-1}), we would expect a predator population size of 1 million lobsters to consume Longspined Sea Urchins at between 0 and 3 million individuals per year. Despite this predation potential, the current annual increase in populations of emergent Longspined Sea Urchins in eastern Tasmania is predicted to be ∼0.5 million individuals (Ling and Keane, 2018). Based on this, urchin recruitment may be up to 3.5 million individuals year^{-1}, or alternatively, both urchin recruitment and lobster predation are substantially lower. Considering the presence of other available prey choices, no enforced starvation periods and the spatial/density distribution of predators and prey in the wild, three Longspined Sea Urchins per lobster per year is likely a substantial over-estimate and predation rates are actually closer to lower end of the 0–3 urchins lobster^{-1} year^{-1} range. Therefore, we consider that the potential control of Longspined Sea Urchins by Southern Rock Lobster predation is overestimated in the literature.

The variation around our estimated predation potential implies that predation trials in a captive environment did not capture all factors impacting lobster predation on Longspined Sea Urchins in the wild. Even in very densely populated areas, lobsters are not reducing Longspined Sea Urchin numbers as we would expect from these rates (Perkins *et al.*, 2020; Ling and Keane, 2021). These extrapolations do not consider spatial arrangement and density of lobster populations. Further, once Longspined Sea Urchins grow larger than lobsters can physically handle [∼120 mm test diameter, Ling *et al.* (2009a)]—they are no longer vulnerable to lobster predation. Other nutritional sources (e.g. other available prey species), density and spatial distribution of the lobsters and prey and large size of emergent urchins could be influencing predation impact and reducing the efficacy of lobsters as a control of urchins in Tasmania.

Our findings highlight the need to reassess the current effectiveness of Southern Rock Lobsters as a control mechanism of Longspined Sea Urchins on the East Coast of Tasmania. Consideration of alternate non-predatory methods, such as diver harvesting/culling or chemical control (Ling and Keane, 2018; Keane *et al.*, 2019), is advised with rigorous assessment of their feasibility. As rock lobster biomass continues to increase under current harvest strategies, we can expect far greater impact on the abundance of local, commercially important, prey species than on Longspined Sea Urchins [see Johnson *et al.* (2013); Ling and Keane (2018); and Ling and Keane (2021)].

Despite our general conclusions that Southern Rock Lobster predation is unlikely to be an overall effective control measure for the range-extending Longspined Sea Urchin, areas with low abundance of native prey species and low density of Longspined Sea Urchins may be susceptible to enough predatory pressure for lobster control to be influential. In deeper waters (> 25 m), low density of urchins are capable of forming extensive barrens due to decreased productivity (kelp growth) at this depth (Ling and Keane, 2018), while low abundances of known important lobster prey items also occur. Lobster population rebuilding strategies focusing on enhancing lobster abundance in this depth range [e.g. by translocation; DPIPWE (2018)] may be effective.

Experimental tank studies are primarily limited by the influence of captivity on animal behaviour (predator and prey), and such behaviour may differ to behaviour in the wild. For example, lack of shelter and interference between prey species could account for behavioural abnormalities. Diet analysis in wild lobsters, between sizes and habitat type and further studies on nutritional content and energetic demands during predation events would be sensible next steps for this research.

Species on the move are having ecological and societal consequences worldwide and species redistributions are expected to continue for the foreseeable future (Pecl *et al.*, 2017). Here, we have focused on the role of a local predator in controlling a novel, range-extending prey species. Human-driven declines in local predatory populations (e.g. exploitation by fishing) can increase invasion success of range-extending pest species (Carlsson *et al.*, 2009), but here, we show that native predators will not always actively prey upon a novel range-extending species. This is especially true if the predator is completely naive to the novel prey species, as is the case in non-invaded areas. We have shown the importance of investigating the effectiveness of native predatory control vs. other control methods for range-extending pest species, with a particular focus on the planning and management of commercially important marine environments.

Funding

This project was partly funded by the Holsworth Wildlife Research Endowment—Equity Trustees Charitable Foundation and the Ecological Society of Australia and by the Tasmanian Government *via* the Abalone Industry Reinvestment Fund. MO was supported by the German Research Foundation (DFG) fellowships OE 658/1 and OE 658/2.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Authors' contributions

JS led the project design, conducted the trials, and wrote the manuscript. JS, MO, JK, and CG worked on the project design and funding applications. JS and JK carried out the fieldwork. JS, CM, and MO worked on the analysis. All authors contributed to the writing of the manuscript.

Data availability statement

The data underlying this article are available from the IMAS data repository: ["Lobster predation trials"], at https://metadata.imas.utas.edu.au/geonetwork/srv/eng/catalog.search.

Acknowledgements

We acknowledge the palawa, traditional custodians of lutruwita, who have extensive knowledge of nubeena. JS would like to thank Shenae Willis, Ella Clausius, and Aidan Dudgeon for their invaluable help during the experimental feeding trials.

References

Andrew, N., and MacDiarmid, A. 1991. Interrelations between sea urchins and spiny lobsters in Northeastern New Zealand. Marine Ecology Progress Series, 70: 211–222.

Barrett, N. S., Buxton, C. D., and Edgar, G. J. 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. Journal of Experimental Marine Biology and Ecology, 370: 104–119.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67: 1–48.

Burt, J. M., Tinker, M. T., Okamoto, D. K., Demes, K. W., Holmes, K., and Salomon, A. K. 2018. Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. Proceedings of the Royal Society B Biological Sciences, 285: 20180553.

Byrne, M., and Andrew, N. 2013. *Centrostephanus rodgersii*. *In* Developments in Aquaculture and Fisheries Science, 38, pp. 243–256. Elsevier, Amsterdam.

Carlsson, N. O., Sarnelle, O., and Strayer, D. L. 2009. Native predators and exotic prey – an acquired taste?. Frontiers in Ecology and the Environment, 7: 525–532.

Day, J. K., Knott, N. A., Swadling, D. S., and Ayre, D. J. 2021. Dietary analysis and mesocosm feeding trials confirm the eastern rock lobster (*Sagmariasus verreauxi*) as a generalist predator that can avoid ingesting urchin spines during feeding. Marine and Freshwater Research, 13: 1220–1232.

DPIPWE 2018. Tasmanian Rock Lobster fishery: east coast stock rebuilding strategy 2013-2023. Technical report, Department of Primary Industries, Water and Environment.

Dumas, J.-P., Langlois, T. J., Clarke, K. R., and Waddington, K. I. 2013. Strong preference for decapod prey by the western rock lobster *Panulirus cygnus*. Journal of Experimental Marine Biology and Ecology, 439: 25–34.

Edmunds, M. 1996. The ecology of the juvenile southern rock lobster, *Jasus edwardsii* (Hutton 1875) (Palinuridae). Ph.D. thesis, University of Tasmania, Hobart.

Eurich, J., Selden, R., and Warner, R. 2014. California spiny lobster preference for urchins from kelp forests: implications for urchin barren persistence. Marine Ecology Progress Series, 498: 217–225.

Fletcher, D., MacKenzie, D., and Villouta, E. 2005. Modelling skewed data with many zeros: a simple approach combining ordinary and logistic regression. Environmental and Ecological Statistics, 12: 45–54.

Guest, M., Frusher, S., Nichols, P., Johnson, C., and Wheatley, K. 2009. Trophic effects of fishing southern rock lobster *Jasus edwardsii* shown by combined fatty acid and stable isotope analyses. Marine Ecology Progress Series, 388: 169–184.

Hawkey, J. 2008. Longspined Sea Urchin icon. ian.umces.edu/media-library(Last accessed: 6 December 2021).

Johnson, C., Ling, S., Ross, J., Shepherd, S., and Miller, K. 2005. Establishment of the Long-spined Sea Urchin (*Centrostephanus rodgersii*) in Tasmania: first assessment of potential threats to fisheries. Technical report, Fisheries Research and Development Corporation (Australia), Canberra.

Johnson, C. R., Ling, S. D., Sanderson, J. C., Dominguez, J. G. S., Frusher, S., Gardner, C., Hartmann, K. *et al.*, 2013. Rebuilding ecosystem resilience: assessment of management options to minimise formation of 'barrens' habitat by the long- spined sea urchin (*Centrostephanus rodgersii*) in Tasmania. Technical report, Fisheries Research and Development Corporation (Australia), Canberra.

Keane, J. P., Mundy, C., Porteus, M., and Johnson, O. 2019. Can commercial harvest of long-spined sea urchins reduce the impact of urchin grazing on abalone and lobster fisheries?. FRDC Report 2013-026, Fisheries Research and Development Corporation (Australia), Canberra.

King, C. K., Hoegh-Guldberg, O., and Byrne, M. 1994. Reproductive cycle of *Centrostephanus rodgersii* (Echinoidea), with recommendations for the establishment of a sea urchin fishery in New South Wales. Marine Biology, 12: 95–106.

Kraeer, K., and Van Essen-Fishman, L. 2008. Periwinkle icon. edited. ian.umces.edu/media-library(last accessed 6 December 2021).

Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia, 156: 883–894.

Ling, S. D., and Johnson, C. R. 2012. Marine reserves reduce risk of climate-driven phase shift by reinstating size- and habitat-specific trophic interactions. Ecological Applications, 22: 1232–1245.

Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. 2009a. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences, 106: 22341–22345.

Ling, S. D., Johnson, C. R., Ridgway, K., Hobday, A. J., and Haddon, M. 2009b. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Global Change Biology, 15: 719–731.

Ling, S. D., and Keane, J. P. 2018. Resurvey of the Longspined Sea Urchin (*Centrostephanus rodgersii*) and associated barren reef in Tasmania. Technical report, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart.

Ling, S. D., and Keane, J. P. 2021. Decadal resurvey of long-term lobster experimental sites to inform *Centrostephanus* control. Technical report AIRF2019_08, Institute for Marine and Antarctic Studies. University of Tasmania, Hobart.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D. *et al*., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pederson, H. G., and Johnson, C. R. 2006. Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. Journal of Experimental Marine Biology and Ecology, 336: 120–134.

Perkins, N. R., Hosack, G. R., Foster, S. D., Monk, J., and Barrett, N. S. 2020. Monitoring the resilience of a no-take marine reserve to a range extending species using benthic imagery. PLOS ONE, 15: e0237257.

Pinsky, M. L., Selden, R. L., and Kitchel, Z. J. 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. Annual Review of Marine Science, 12: 153–179.

Pintor, L. M., and Byers, J. E. 2015. Individual variation in predator behavior and demographics affects consumption of non-native prey. Behavioral Ecology, 26: 797–804.

Pyke, G. H. 2019. Optimal foraging theory: an introduction. *In* Encyclopedia of Animal Behavior, 2nd edn. pp. 111–117. Ed. by J. C. Choe Academic Press, Oxford.

R Core Team 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Redd, K. S., Ling, S. D., Frusher, S. D., Jarman, S., and Johnson, C. R. 2014. Using molecular prey detection to quantify rock lobster predation on barrens-forming sea urchins. Molecular Ecology, 23: 3849–3869.

Selden, R. L., Gaines, S. D., Hamilton, S. L., and Warner, R. R. 2017. Protection of large predators in a marine reserve alters size-dependent prey mortality. Proceedings of the Royal Society B Biological Sciences, 284: 20161936.

Sheppard-Brennand, H., Dworjanyn, S. A., and Poore, A. G. B. 2017. Global patterns in the effects of predator declines on sea urchins. Ecography, 40: 1029–1039.

Tegner, M., and Levin, L. 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. Journal of Experimental Marine Biology and Ecology, 73: 125–150.

Venables, B. 2021. MASSExtra: Some ‘MASS’ Enhancements. https://cran.r-project.org/web/packages/MASSExtra/index.html (last accessed: 1 March 2022).

Venables, W. N., and Ripley, B. D. 2002. Modern Applied Statistics with S. 4th edn. Springer, New York, NY,

Handling Editor: Ivan Rodil