Accepted paper, please cite as: Barrett LT, Swearer SE, Dempster T (In Press) Native predator limits the capacity of an invasive seastar to exploit a food-rich habitat. Marine Environmental Research.

Native predator limits the capacity of an invasive seastar to exploit a food-rich habitat

Luke T Barrett[12]*, Stephen E Swearer[2] and Tim Dempster[1]

[1] Sustainable Aquaculture Laboratory – Temperate and Tropical (SALTT), School of BioSciences, University of Melbourne, Parkville 3010 Victoria, Australia
[2] National Centre for Coasts and Climate (NCCC), University of Melbourne, Parkville 3010 Victoria, Australia

*Corresponding author: luke.barrett@unimelb.edu.au

ABSTRACT

Biodiverse ecosystems are sometimes inherently resistant to invasion, but environmental change can facilitate invasion by disturbing natural communities and providing resources that are underutilised by native species. In such cases, sufficiently abundant native predators may help to limit invasive population growth. We studied native and invasive seastars feeding under two mussel aquaculture sites in south-east Australia, to determine whether food-rich farm habitats are likely to be reproductive hotspots for the invasive seastar (*Asterias amurensis*) and whether the larger native seastar (*Coscinasterias muricata*) reduces the value of the farms for the invader. We found that invaders were not significantly more abundant inside the farms, despite individuals residing within the farms having higher body condition metrics and reproductive investment than those outside. By contrast, the native seastar was 25× more abundant inside the two farms than outside. We observed several intraguild predation events and an absence of small invaders at the farms despite reports of high larval recruitment to these environments, consistent with some level of biotic control by the native predator. A laboratory choice experiment showed that invaders were strongly attracted to mussels except when the native predator was present. Together, these findings indicate that a combination of predation and predator evasion may play a role in reducing the value of food-rich anthropogenic habitats for this invasive species.

Keywords: invasion biology, biotic control, bivalve aquaculture, benthic invertebrates, *Coscinasterias muricata*, *Asterias amurensis*

INTRODUCTION

Invasive species are economically costly, and an important contributor to biodiversity loss worldwide (Pimentel et al. 2001, Clavero & García-Berthou 2005). Species introductions are increasing in frequency as a result of human transport, but the likelihood of a newly-introduced species establishing and becoming invasive depends on multiple interacting factors, including environmental conditions, ecosystem characteristics and species traits (Carlton 1996, Keane & Crawley 2002, Kennedy et al. 2002, Kimbro et al. 2013, Papacostas et al. 2017).

Intact biodiverse ecosystems have inherent biotic invasion resistance (Elton 1958), conferred by low niche vacancy rates and strong competition for resources (Kennedy et al. 2002), as well as a higher likelihood of the new arrival encountering predators or other enemy species (Keane & Crawley 2002, Kimbro et al. 2013). However, ecosystem-level invasion resistance is being eroded by large-scale habitat disturbance and loss of biodiversity associated with human-induced rapid environmental change (HIREC: Vitousek et al. 1997, Sanderson et al. 2002, Halpern et al. 2008, Vörösmarty et al. 2010, Sih et al. 2011). Non-native species can benefit from the impacts of HIREC by taking advantage of man-made or degraded habitats that are low in biodiversity and have resources that are underutilised by native competitors or predators (Mack et al. 2000, Didham et al. 2005, MacDougall & Turkington 2005), and in the early stages of invasion, or at range limits, these refuge habitats may become invasion hubs: satellite populations that facilitate persistence and expansion (Carlton 1996, Suarez et al. 2001, With 2002, Russell et al. 2011, Letnic et al. 2014). Later, they may function as reproductive hotspots for the invader, for example by permitting high local population densities that overcome Allee effects (Inglis & Gust 2003, Ling et al. 2012).

A single abundant predator can exert considerable top-down control and play an important role in limiting the eventual population size and distribution of an invader, essentially providing invasion resilience when invasion resistance has failed (DeRivera et al. 2005, Kimbro et al. 2013, Papacostas et al. 2017). Predator-mediated biotic control may be particularly effective in cases where the invader does not recognise or respond appropriately to the native predator, a scenario that is most likely to occur when the invader has no evolutionary history with the native predator or its relatives (Cox & Lima 2006, Sih et al. 2010). Such conditions favour the formation of an ‘evolutionary trap’ in which individuals choose a habitat or exhibit behavioural responses that lead to poor fitness outcomes (Robertson et al. 2013). These traps usually arise as a result of environmental change outpacing the evolution of behaviour, and account for some of the disastrous effects of invasive predators on naïve native prey (e.g. juvenile fish avoid reefs with a resident native predator but not those with a resident invasive predator: Benkwitt 2017). Most work has focused on mitigating traps that affect native species, but evolutionary traps also have potential as tools in the management of non-native species (Robertson et al. 2017). One potential approach is to increase mortality rates at attractive sites to create attractive sinks (this type of evolutionary trap, arising from maladaptive habitat selection, is termed an ‘ecological trap’: Robertson & Hutto 2006, Hale & Swearer 2016, Robertson et al. 2017). For example, the installation of inexpensive barriers around artificial water sources in the Australian arid zone converted them from stepping stones for invading cane toads into ecological traps, as the toads were still attracted to the water but could not access it (Letnic et al. 2014, 2015). Native predators may also contribute to the formation of ecological traps for non-native species, but such traps have not yet been empirically demonstrated.

Here, we studied interactions between native and invasive seastars at shellfish farms in southern Australia. Shellfish farms are an excellent model for a range of anthropogenic marine habitats worldwide that are simultaneously highly disturbed and enriched in food for benthic predators (especially in the form of shellfish that fall from farm structure: Inglis & Gust 2003, D’Amours et al. 2008, McKindsey et al. 2011). This combination of traits makes such habitats highly vulnerable to exploitation by invasive species (e.g. Ling et al. 2012). The invasive seastar *Asterias amurensis* was introduced to Tasmania during the 1980s (Grannum et al. 1996), and mainland Australia in 1995

(Parry & Cohen 2001), with the mainland population reaching 75 million by 2000 (Parry & Cohen 2001). The invader has decimated naïve bivalve populations (Ross et al. 2003, Hutson et al. 2005), and has few predators in its new environment, but there have been reports of intraguild predation by a larger native predator, the eleven-arm seastar *Coscinasterias muricata* (Byrne et al. 2013, Parry 2017). The trophic subsidy provided by shellfish farms may be attractive to both species, but the ability of the invader to benefit from the high food availability will depend on competition and predation risk from the native predator (Fig. 1). If the native predator does not impede the ability of the invader to access the food resource, then such habitats are likely to act as reproductive hotspots (Ling et al. 2012, Letnic et al. 2014). Alternatively, if the invader enters the farms but then suffers high predation rates or competitive exclusion, there is potential for an ecological trap to occur (i.e. the preferred habitat does not confer high fitness: Robertson & Hutto 2006, Hale & Swearer 2016).

We combine data on population distribution, individual body condition, reproductive investment and foraging behaviour to provide evidence that an abundant native predator (i) limits the ability of an established invader to exploit an anthropogenic food-rich habitat, and (ii) may create an age-dependent ecological trap for the invader.

METHODS

Study locations

Port Phillip Bay is a 1930 km^2 semi-enclosed marine water body in south-eastern Australia, subject to multiple impacts from invasive species and urbanisation (Hewitt et al. 2004, Sampson et al. 2014). We studied native and invasive seastar populations at 2 shellfish farms 12 km apart in the south-western part of the bay: Clifton Springs and Grassy Point. These farms primarily produce blue mussels (likely a genetic mix of native *Mytilus planulatus* with contributions from the closely related non-native species *M. galloprovincialis*: Popovic et al. 2020) grown on suspended longlines. The Clifton Springs and Grassy Point reserves contain approximately 81 and 42 ha of shellfish farms, respectively. Both reserves are located on soft sediment between 8-14 m depth, with constant mixing and exchange of water by tidal cycling and wind-generated currents. Clifton Springs is the more sheltered of the two locations and is dominated by silty substrate, while Grassy Point is characterised by sandy substrate and lower turbidity. The natural benthos at both locations is dominated by exposed sediment and *Halophila australis* seagrass beds, with paper mussels (*Electroma georgiana*) attached to available seagrass or macroalgae. *Caulerpa* spp. beds are common at Grassy Point. Seastars are the predominant benthic predators within and around both farms.

Experiment 1: Effect of shellfish farming on population density of native and invasive seastars

We surveyed *Asterias* and *Coscinasterias* population densities along diver transects inside and outside the two farms: Clifton Springs on 6 occasions between July 2014 and June 2016, and Grassy Point on 7 occasions between July 2014 and June 2015. On each sampling occasion, we surveyed 3 replicate 2×25 m transects (extended to 2×50 m where <10 seastars were recorded) both inside and outside the farm boundaries (totalling 6 transects farm^{-1} occasion^{-1}). 'Inside' transects were haphazardly placed (>50 m apart) within active shellfish aquaculture plots (primarily mussels) on each occasion. 'Outside' transects were placed on each occasion by selecting a random point within a ~100 ha area of natural soft sediment habitat at a distance of 1-2 km around the farm. Around this point, the 3 replicate transects were laid out 50-100 m apart, each on a random heading. The renewed placement of transects on each occasion was intended to accumulate spatial replication at the level of transects across multiple sampling occasions. Transects were surveyed by laying a centreline and counting all seastars that had their central point within 1 m of the transect centreline. Individuals down to 4-5 cm are readily detectable at distances relevant to this survey method, while smaller sizes are also detectable but more likely to be obscured by benthic structure (especially *Coscinasterias*, which are more cryptic than *Asterias*).

This is a natural experiment in the sense that we compare seastar populations within pre-existing farms to seastar populations in surrounding areas, rather than applying the manipulation ourselves in a randomised and spatially interspersed manner. Results should be interpreted with this in mind. Inside and Outside transects were comparable in terms of depth (10-14 m) and water flow, and superficial evidence of sediment enrichment (e.g. shell debris, density of benthic growth, sediment colour) appeared strongest under mussel longlines, indicating that differences between the areas inside and outside the farms are likely due to aquaculture activities.

To test for differences in seastar population density inside and outside the farms, we fitted negative binomial generalised linear mixed models for each of the 2 species and each of the 2 locations (4 models total) using the *glmmTMB* package for R version 3.6.0 (Brooks et al. 2017, R Core Team 2019). 'Habitat' was included as a fixed effect (the term 'habitat' is used throughout the text to denote the comparison of populations inside and outside each of the two farms). Because transects were moved between sampling occasions, all transects are treated as spatial rather than temporal replicates. The date of each sampling occasion was included as a random intercept term to account for temporal effects that apply across all transects surveyed on the same day, whether inside or outside the farms. Each model contained 1 fixed effect (Habitat) and 1 random effect (Date) (Table A1). We tested the significance of the Habitat term using an analysis of deviance with type II SS (*Anova* function, *car* package: Fox and Weisberg 2011). Suitable model fit was verified by visual inspection of residual plots.

Experiment 2: Effect of shellfish farming on size and condition of native and invasive seastars

To evaluate size differences inside and outside the farms, we measured the armspan of all seastars encountered on each transect (or the first 30 of each species), by summing the length of the two longest arms (starting from the centre of the central disc). Because individuals on the same transect might be considered statistically non-independent, we computed the mean armspan species^{-1} transect^{-1} and used that value for the analysis.

We compared condition metrics inside and outside the farms by collecting up to 20 individuals of each species farm^{-1} occasion^{-1}. When fewer than 20 individuals were available in either habitat type on a given day, we limited our sample size in the other habitat to avoid temporal bias caused by seasonal dynamics in condition metrics. Drained and gutted carcass weight provided a measure of size that was expected to be largely independent of body condition, as seastars store nutrients (especially lipids) primarily in the coelomic fluid, pyloric caeca and digestive organs (e.g. Oudejans & van der Sluis 1979). The relative size of the pyloric caeca (digestive organs that increase in size with feeding activity) provided a measure of body condition and an indirect measure of food availability inside and outside the farms. We calculated the pyloric caeca index relative to somatic weight: PCI = PCW/CW, where PCW = pyloric caeca wet weight and CW = gutted carcass weight drained of coelomic fluid. We considered reproductive condition both in terms of relative reproductive investment (gonadosomatic index: GSI = GW/CW, where GW = gonad weight) and potential fecundity (gonad size). A study of 23 *Coscinasterias* and 20 *Asterias* individuals demonstrated that PCI and GSI can be accurately estimated from a single limb (linear R^2: *Asterias* PCI = 0.79, GSI = 0.90; *Coscinasterias* PCI = 0.88, GSI = 0.78) (Fig. A1). This permitted the release of the native *Coscinasterias* after the removal of a single limb. As *Asterias* is a declared noxious aquatic species, entire *Asterias* individuals were taken, but only a single limb dissected. *Asterias* are sufficiently abundant and mobile that the removal of <20 individuals farm^{-1} occasion^{-1} likely had a negligible effect on numbers in later surveys (Andrews et al. 1996). Limbs were cut open longitudinally, drained of coelomic fluid and weighed. The pyloric caeca and gonads were then removed and weighed separately. Individuals were sexed based on the colour of the gonads, a method that was validated by microscopy during a pilot study (n = 20, 100 % accuracy).

To test for differences in size and condition inside and outside the farms, we fitted linear mixed models with Habitat and Sex as fixed terms and Date as a random intercept term. We tested the Habitat term as per *Experiment 1*. Responses were transformed as necessary to approximate normality based on visual inspection of histograms and residual plots; a $\log_{10}$ transformation for *Asterias* armspan and 4th root transformation for PCI and GSI gave the best fit.

Experiment 3: Interactions between native and invasive seastars

Any fitness benefits of high food availability may be offset if there is an elevated predation risk. We recorded evidence of predation during population surveys for *Experiment 1*, including predation events in progress and sublethal damage that is unlikely to be explained by asexual reproduction (e.g. damage to arms consistent with crab or fish predation: Ling & Johnson 2013). We also compared the size distributions of *Asterias* inside and outside farms for evidence of size-dependent predation or avoidance of the farm environment.

Given evidence that the native seastar does prey on the invasive seastar, we devised a laboratory-based choice experiment to test the strength of the invader's attraction to fallen mussels, and whether this attraction is moderated by the presence of either conspecifics or native predators in a laboratory setting. We conducted the experiment in a 72 L flume tank (120×30×20 cm), housed within a recirculating seawater facility containing ca. 12000 L of continuously filtered and UV-treated seawater. A flow rate of 4 L min^{-1} was divided between the two chambers at the head of the tank, with both chambers opening into an undivided downstream portion of the tank containing the *Asterias* subject (Fig. A2).

We compared rates of attraction to 4 treatments (n = 40 replicates per treatment, total 160 replicates): a seawater control with no predatory nor prey cues (‘SW’), 5 thawed mussels placed in a perforated compartment at the upstream end of the chamber (‘M’), 5 thawed mussels with 3 conspecifics in the chamber immediately downstream of the perforated compartment (‘AM’), and 5 thawed mussels with a large *Coscinasterias* individual arranged as for AM (‘CM’) (Fig. A2). Freezing and thawing mussels will alter chemosensory cues relative to fresh mussels (including an increase in the concentration of some chemical cues in the flume). As a result, the strength of responses here may differ from those in the field, although we expect that the qualitative effects of conspecifics and potential predators on foraging behaviour will remain. We applied treatments singly, with the cue randomly assigned to one of the two chambers. We left the subjects overnight (16 hrs), and considered them to be attracted to a cue if they were present inside the corresponding chamber at the completion of the trial, providing a binary outcome (attracted or non-attracted). The flume tank was cleaned and flushed between trials. Subjects were randomly selected from a large captive population (>200) collected from the wild within 2 months of the trial, fasted for at least 48 hours prior to the trial, and randomly assigned to a treatment. The size range of subjects was 4-17 cm in every treatment group (mean 11 ± 0.2 cm).

Individuals are free to remain in the downstream portion of the tank rather than entering either of the upstream chambers, and the non-attracted outcome includes individuals that remained downstream as well as those that entered the non-cue chamber. We therefore do not define the null hypothesis as an equal frequency of attraction and non-attraction. Instead, the null hypothesis is that there is no difference in attraction rates between the 4 treatments (SW, M, AM, CM). We tested for differential attraction to cues by fitting a series of binomial generalised linear models (with logit link function) to the binary data using the glm function in R. Appropriate model fit was verified based on deviance scores and residual plots. The first model tested for differential responses according to the cue (treatment as the fixed effect), with a post-hoc pair-wise X^2 tests of proportions conducted using the prop.test function in R. We then tested whether smaller *Asterias* individuals were more likely to avoid other seastars, by fitting separate models to CM and AM subsets of the trial data, with subject armspan as the fixed effect in each model. Finally, because the size of conspecifics used as cues in the AM replicates varied considerably, we also tested the effect of subject size relative to the size of the conspecifics used as cues. Relative size was calculated using the formula $\ln\left(\frac{Size_S}{Size_C}\right)$, where $Size_S$ and $Size_C$ are the armspan of the subject and mean armspan of the 3 conspecifics, respectively).

RESULTS

Experiment 1: Effect of shellfish farming on population density of native and invasive seastars

The invasive seastar *Asterias* was common on silty substrate and mussel shell debris both inside and outside the farm at Clifton Springs (Fig. 2A). *Asterias* was most abundant on some inside farm transects, but densities were highly variable and there was no overall difference inside and outside the farm during 2014-2016 (mean 1.8× higher, p = 0.18: Table 1, Table A1). *Asterias* was nearly absent from the Grassy Point area, only recorded on a single transect inside the Grassy Point farm in winter 2014 (Fig. 2B).

The native seastar *Coscinasterias* had a contrasting distribution (Fig. 2). At Grassy Point, *Coscinasterias* occurred both inside and outside the farm (Fig. 2D), with a 14× higher population density inside ($p < 0.0001$: Table 1, Table A2). They were also common inside the Clifton Springs farm, but were absent on transects outside the farm (Fig. 2C). Pooling data across both locations indicated that *Coscinasterias* were 25× more abundant inside than outside ($p < 0.0001$: Table 1, Table A2).

Experiment 2: Effect of shellfish farming on size and condition of native and invasive seastars

Due to the rarity of *Asterias* outside Grassy Point and the rarity of *Coscinasterias* outside Clifton Springs, we compared the size distribution of each species inside and outside a single farm (*Asterias* at Clifton Springs, *Coscinasterias* at Grassy Point). Both seastar species were larger on average inside the farm where the comparison was made compared to the area outside the farm.

Asterias inside Clifton Springs had on average a 25 % wider armspan than their counterparts outside ($p < 0.0001$), corresponding to a 92 % increase in gutted weight ($p < 0.0001$) (Table 1; Fig. 3A,B). This effect occurred at all but one sampling occasion. All body and reproductive condition metrics that we assessed in *Asterias* were higher inside the farm than outside (Table 1). Specifically, drained weight was 77 % higher ($p < 0.0001$, Fig. 4A), gonad weight 57 % higher ($p = 0.0009$, Fig. 4B), PCI 26 % higher ($p < 0.0001$, Fig. 4C) and GSI 57 % higher ($p < 0.0001$, Fig. 4D).

Likewise, *Coscinasterias* inside the Grassy Point farm had a 7 % wider armspan ($p = 0.001$) and 42 % heavier gutted weight ($p = 0.0002$) than those outside (Table 1; Fig. A3). Individuals inside the farm also had 11 % higher body condition (PCI: $p = 0.022$) but there was no difference in either gonad weight ($p = 0.96$) or GSI ($p = 0.75$) (Table 1; Fig. A4).

Experiment 3: Interactions between native and invasive seastars

The difference in mean armspan of *Asterias* in Experiment 2 was driven by a truncation at the lower end of the size-frequency distribution inside the Clifton Springs farm, more so than the presence of larger individuals (Fig. 5). The truncation was such that there were twice as many 14-15 cm individuals as 12-13 cm individuals, while individuals <12 cm were almost absent. We recorded 3 native-on-invasive seastar predation events on transects inside the Clifton Springs farm, with none observed on transects outside. We also noted a further 10 predation events off-transect, as well as 5 skeletons of recently consumed *Asterias*, all inside the farm boundary. Large *Asterias* individuals may also pose a threat to smaller conspecifics; we observed a single cannibalism event, also on a transect inside the Clifton Springs farm.

We found strong effects of prey and predator cues on foraging behaviour by the invasive *Asterias* in the laboratory ($n = 40$ per treatment, $p < 0.0001$) (Fig. 6). The mussel cue (M) attracted *Asterias* subjects at a significantly higher rate than the seawater control (SW) (93 vs. 28 % respectively, $X^2 = 32$, $p < 0.0001$). Mussels remained more attractive than seawater when 3 *Asterias* conspecifics were present feeding on the mussels (AM) (88 %, $X^2 = 27$, p <0.0001), and there was no difference between rates of attraction to M or AM cues (93 % vs. 88 % respectively, $X^2 = 0.1$, p = 0.7). By contrast, the presence of a single *Coscinasterias* individual feeding on the mussels (CM) resulted in a dramatic decline in attraction rates relative to both the M (28 vs. 93 % respectively, $X^2 = 32$, p <0.0001) and AM cues (28 vs. 88 % respectively, $X^2 = 27$, p <0.0001). Of the 11 individuals that selected the chamber with the CM cue, 2 were predated by the *Coscinasterias* (1 fully, 1 partially consumed overnight). *Asterias* individuals that avoided the chamber with the CM cue exhibited a variety of behaviours, such as moving immediately to the cue-free (seawater control) chamber and remaining there for the duration of the study, circling the downstream portion of the tank, or attempting to reach the mussels before evading a predation attempt by *Coscinasterias*. We found no evidence that the size of the subject influenced their response to the presence of conspecifics ($z_{38} = 1.1$, p = 0.3) or *Coscinasterias* ($z_{38} = 1.0$, p = 0.3). The size differential between the subject and the 3 conspecifics in the AM treatment also did not influence the likelihood of attraction to the mussels ($z_{38} = 0.6$, p = 0.5).

If both species were distributed according to availability of a common food source, we may expect a positive correlation between the abundance of the two species. Instead, the population density data indicate that at the level of transects, *Asterias* density is strongly negatively predicted by *Coscinasterias* density overall (Kendall's rank correlation: $\tau = -0.21$, p = 0.02). A negative binomial mixed effects model with *Coscinasterias* density and Location as fixed effects, including an interaction term, also found a negative effect of *Coscinasterias* on *Asterias* density ($X^2 = 7.2$, p = 0.007) and no interaction between the *Coscinasterias* and location effects ($X^2 = 0.1$, p = 0.91), indicating that this result is not strongly dependent on location. However, the rarity of *Asterias* at Grassy Point is notable, and may or may not be affected by abundance of *Coscinasterias* at that location. We therefore also tested the correlation with the data restricted to Clifton Springs, and found no significant correlation between *Coscinasterias* and *Asterias* density at the transect level with this reduced sample size ($\tau = -0.04$, p = 0.72)

DISCUSSION

In highly disturbed ecosystems, any predators that are able to persist may be the last line of defence against invaders, limiting the probability of establishment and subsequent population growth. Here, the large native seastar *Coscinasterias muricata* occurred at 25× higher abundance inside 2 shellfish farms relative to adjacent reference habitats, with the shellfish farm accounting for almost the entire population in an area with non-preferred silty substrate (Clifton Springs). In contrast, we did not find evidence that the invasive seastar *Asterias amurensis* was reliably more abundant inside the farms. Invaders residing inside the Clifton Springs farm possessed higher body condition and reproductive condition metrics than did conspecifics outside, consistent with the hypothesis that shellfish farms have the food availability to be potential reproductive hotspots for the invader (albeit evidence from a single farm). When contrasted with the lack of a clear difference in population density in the field, this suggests an inability to take full advantage of a valuable food resource. Accordingly, we found evidence of elevated predation risk for the invasive species inside the shellfish farm, and found that in the laboratory, the invader recognises and avoids the native predator even if it means forgoing a favoured prey item. Taken together, these findings suggest that the native predator may limit the ability of the invader to exploit this disturbed food-rich habitat via a combination of avoidance behaviour and occasional predation events.

In the absence of abundant native predators, man-made habitats such as shellfish farms, fish farms and mussel-fouled infrastructure can be reproductive hotspots for invasive *Asterias amurensis* populations, simultaneously supporting orders-of-magnitude higher population density and elevated individual reproductive potential (Ling et al. 2012). Within their native range, *Asterias* species also have highly elevated population densities at shellfish farms; they do not appear to be exposed to high densities of potential predators at such sites (e.g. Olaso Toca 1979, Saranchova & Kulakovskii 1982 cited in McKindsey et al. 2011, D'Amours et al. 2008).

Effective top-down control of non-native animals by native predators has been reported in numerous marine, freshwater and terrestrial systems (e.g. DeRivera et al. 2005, Cheng & Hovel 2010, Tetzlaff et al. 2011, Freed & Leisnham 2014). *Asterias* is thought to be primarily food limited in its new range: growth rates declined during the first 3 years following its introduction to mainland Australia, coinciding with increasing population densities and large declines in prey abundance (Parry & Cohen 2001). Body condition and reproductive investment data in this study show elevated condition inside the Clifton Springs farm, perhaps indicating that food limitation still exists outside. If this is the case more broadly, then the native predator could exert indirect biotic control on the invasive population in some inshore areas simply by restricting access to the trophic subsidy at farms and other food-rich habitats, although the invasive population will remain abundant in other areas.

The data also suggest that the invaders may be vulnerable to a predation-mediated ecological trap at the Clifton Springs farm. In Australia, *Asterias* recruit in large numbers directly to mussel lines (Dommisse & Hough 2004). This creates the conditions for an ecological trap affecting juvenile *Asterias*, as individuals that settle on mussel lines are (a) unlikely to reach sexual maturity before the mussel lines are harvested, and (b) likely to experience high predation risk if they fall to a benthic environment populated by >2000 *Coscinasterias* ha^{-1}. The truncated size-frequency distribution for *Asterias* inside the Clifton Springs farm is consistent with these explanations, as are our observations of predation events in progress. Other (non-mutually-exclusive) explanations are conceivable, such as avoidance of the farm environment for reasons unrelated to predation, or faster growth rates in the farm due to the higher benthic productivity, coupled with extended recruitment failure, leading to a rarity of small individuals inside the farm. However, the threat of predation is the more parsimonious mechanism in our view. The severity of a predation-mediated ecological trap would likely be increased if juveniles do not have sufficiently strong predator avoidance behaviour (Cox & Lima 2006, Sih et al. 2010). In our foraging behaviour trial, small and large individuals were equally likely to avoid the native predator. This may place smaller individuals at a relatively higher risk of predation (Parry 2017). As adults, the potential for an ecological trap at shellfish farms will depend on the degree to which individuals are attracted to the farm (i.e. the strength of their preference for bivalve prey versus their avoidance response to the native predator) and the net fitness effects of any preference for the farm (i.e. food availability versus predation risk). The choice experiment found that *Asterias* were strongly attracted to bivalves, but only in the absence of the native predators, and while predation rates are likely higher inside farms than outside (this study, Parry

2017), so is reproductive output (this study, Ling et al. 2012). Further work is needed to calculate the net effect of these opposing factors, but we consider it unlikely that adult *Asterias* would encounter an ecological trap here – it seems more likely that individuals residing within farms are able to obtain abundant food while mostly evading predation.

Invading *Asterias* benefitted from the naivety of Australian bivalves (Ross et al. 2003, Hutson et al. 2005), but to date there has been little evidence that *Asterias* responds naïvely to novel predators, despite theoretical expectations arising from a lack of shared evolutionary history (Cox & Lima 2006, Sih et al. 2010). Behavioural data on predator-prey interactions in the early days of invasion are not available, but it is possible that the establishment and expansion of *Asterias* in Australia was assisted by pre-existing predator cues evolved in response to functionally similar predators in its native range (Sih et al. 2010). Specifically, the only two species in southern Australia that have been observed to predate *Asterias* with any regularity—*Coscinasterias muricata* and the giant spider crab *Leptomithrax gaimardii* (Byrne et al. 2013, Ling & Johnson 2013)—are phylogenetically related and functionally analogous to the major predators of *Asterias* in the northern Pacific: the sun star *Solaster paxillatus* and king crab *Paralithodes camtschaticus*, respectively (Byrne et al. 2013).

Little is known about how the *Asterias* invasion affected native predators. A meta-analysis by Pintor & Byers (2015) found that simultaneous access to native and non-native prey was associated with increased native predator abundance, but exceptions are common where native and non-native species compete for a shared food resource or where abundant non-native species drive severe ecological change (e.g. Pothoven et al. 2001, Suarez & Case 2002). Here, the invader competes with the native species for prey where their habitat usage overlaps, but localised high densities of mussels, such as those on rocky reefs, shellfish farms and marine infrastructure may suit the native species by improving their ability to exclude *Asterias* from the food resource, as well as supplementing their main diet with intraguild predation on the invader. Where an intraguild predator is also the stronger competitor (as may be the case here if *Asterias* do indeed forego resources occupied by *Coscinasterias*), some theory predicts that the intraguild prey should decline in the shared habitat (e.g. Holt & Polis 1997). However, there are a variety of scenarios in which both may persist (Holt & Polis 1997, Janssen et al. 2007, Abrams & Fung 2010). More work is needed to fully understand the competitive and predatory interactions in this system.

Eradication of this invader is not feasible, but any top-down pressure may have local ecological benefits by partially releasing vulnerable prey populations from predation and reducing the likelihood of new populations establishing (Mack et al. 2000, DeRivera et al. 2005, Letnic et al. 2009). A range of harvesting methods have been employed to control seastars globally, but none are yet cost-effective (Barkhouse et al. 2007). In particular, a lack of spatial population structure on homogeneous landscapes limits the efficiency of control methods, but attractive habitats such as shellfish farms and other marine infrastructure add spatial structure and may leave invasive populations more vulnerable if mortality can be induced at such sites, whether through natural predation or human intervention (Bascompte et al. 2002, Russell et al. 2011, Letnic et al. 2015). Here, evidence from one shellfish farm, together with behaviour in captivity, indicates that a combination of predation and predator-avoidance behaviour may limit the ability of the invader to exploit a food-rich resource. Future work may consider the feasibility of augmenting native predator populations in strategic areas such as sites of new introductions (Atalah et al. 2013, Atalah et al. 2016, Parry 2017).

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could appear to have influenced the work reported in this paper.

ACKNOWLEDGMENTS

This work was funded by a Holsworth Wildlife Research Endowment awarded to LB. Lance Wiffen kindly provided access to aquaculture leases, while Chris Taylor, Simon Reeves, Emily Fobert, Dean Chamberlain, Jack O'Connor, Ben Cleveland, Kevin Jensen, Kevin Menzies, Oliver Thomas and Rod Watson assisted with fieldwork. The manuscript benefitted from discussions with colleagues in the SALTT and REEF labs at the University of Melbourne, Greg Parry, and 3 anonymous reviewers. Collections were conducted with relevant permits from the Victorian Fisheries Authority.

SUPPLEMENTARY MATERIAL

Supplementary material to this article can be found online at *Marine Environmental Research*. Data will be made available online at: https://doi.org/10.6084/m9.figshare.11626194

REFERENCES

Abrams PA, Fung SR (2010) Prey persistence and abundance in systems with intraguild predation and type-2 functional responses. J Theor Biol 264:1033–1042. doi: 10.1016/j.jtbi.2010.02.045

Andrews D, Whayman G, Edgar G (1996) Assessment of optimal trapping techniques to control densities north Pacific seastars on marine farm leases. Tasmanian Department of Primary Industries and Fisheries, Australia.

Atalah J, Hopkins GA, Forrest BM (2013) Augmentative biocontrol in natural marine habitats: persistence, spread and non-target effects of the sea urchin *Evechinus chloroticus*. PLOS ONE 8. doi: 10.1371/journal.pone.0080365

Atalah J, Newcombe EM, Zaiko A (2016) Biocontrol of fouling pests: effect of diversity, identity and density of control agents. Mar Environ Res 115:20–27. doi: 10.1016/j.marenvres.2016.01.006

Barkhouse C, Niles M, Davidson L-A (2007) A literature review of sea star control methods for bottom and off bottom shellfish cultures. Can Ind Rep Fish Aquat Sci 279:vii + 35p.

Bascompte J, Possingham H, Roughgarden J (2002) Patchy populations in stochastic environments: critical number of patches for persistence. Am Nat 159:128–137. doi: 10.1086/324793

Benkwitt CE (2017) Predator effects on reef fish settlement depend on predator origin and recruit density. Ecology 98:896–902. doi: 10.1002/ecy.1732

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) Modeling zero-inflated count data with glmmTMB. bioRxiv 132753. doi: https://doi.org/10.1101/132753

Byrne M, O'Hara TD, Lawrence JM (2013) *Asterias amurensis*. In: Lawrence JM (ed) Starfish: Biology and Ecology of the Asteroidea. The John Hopkins University Press, Baltimore, MA, pp 174–180

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106. doi: 10.1016/0006-3207(96)00020-1

Cheng BS, Hovel KA (2010) Biotic resistance to invasion along an estuarine gradient. Oecologia 164:1049–1059. doi: 10.1007/s00442-010-1700-7

Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110. doi: 10.1016/j.tree.2005.01.003

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674–680. doi: 10.1016/j.tree.2006.07.011

D'Amours O, Archambault P, McKindsey CW, Johnson LE (2008) Local enhancement of epibenthic macrofauna by aquaculture activities. Mar Ecol Prog Ser 371:73–84. doi: 10.3354/meps07672

DeRivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86:3364–3376. doi: 10.1890/05-0479

Didham RK, Tylianakis JM, Hutchison MA, et al (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474. doi: 10.1016/j.tree.2005.07.006

Dommisse M, Hough D (2004) Controlling the northern Pacific seastar (*Asterias amurensis*) in Australia. Final report for the Australian Government Department of the Environment and Heritage, Australia.

Elton CS (1958) The ecology of invasions by animals and plants. Methuen & Co. Ltd., London.

Fox J, Weisberg S (2011) An {R} Companion to Applied Regression, 2nd edn. Sage, Thousand Oaks, California.

Freed TZ, Leisnham PT (2014) Roles of spatial partitioning, competition, and predation in the North American invasion of an exotic mosquito. Oecologia 175:601–611. doi: 10.1007/s00442-014-2909-7

Grannum RK, Murfet NB, Ritz DA, Turner E (1996) The distribution and impact of the exotic seastar, *Asterias amurensis* (Lutken) in Tasmania. Australian Nature Conservation Agency, Australia.

Hale R, Swearer SE (2016) Ecological traps: current evidence and future directions. Proc R Soc B Biol Sci 283:494–499. doi: 10.1098/rspb.2015.2647

Halpern BS, Walbridge S, Selkoe KA, et al (2008) A global map of human impact on marine ecosystems. Science 319:948–952. doi: 10.1126/science.1149345

Hewitt CL, Campbell ML, Thresher RE, et al (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. Mar Biol 144:183–202. doi: 10.1007/s00227-003-1173-x

Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. Am Nat 149:745–764. doi: 10.1086/286018

Hutson KS, Ross DJ, Day RW, Ahern JJ (2005) Australian scallops do not recognise the introduced predatory seastar *Asterias amurensis*. Mar Ecol Prog Ser 298:305–309. doi: 10.3354/meps298305

Inglis GJ, Gust N (2003) Potential indirect effects of shellfish culture on the reproductive success of benthic predators. J Appl Ecol 40:1077–1089. doi: 10.1111/j.1365-2664.2003.00860.x

Janssen A, Sabelis MW, Magalhães S, Montserrat M, Hammen T van der (2007) Habitat structure affects intraguild predation. Ecology 88:2713–2719. doi: 10.1890/06-1408.1

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170. doi: 10.1016/S0169-5347(02)02499-0

Kennedy TA, Naeem S, Howe KM, et al (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636. doi: 10.1038/nature00776

Kimbro DL, Cheng BS, Grosholz ED (2013) Biotic resistance in marine environments. Ecol Lett 16:821–833. doi: 10.1111/ele.12106

Letnic M, Crowther MS, Koch F (2009) Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? Anim Conserv 12:302–312. doi: 10.1111/j.1469-1795.2009.00250.x

Letnic M, Webb JK, Jessop TS, et al (2014) Artificial water points facilitate the spread of an invasive vertebrate in arid Australia. J Appl Ecol 51:795–803. doi: 10.1111/1365-2664.12232

Letnic M, Webb JK, Jessop TS, Dempster T (2015) Restricting access to invasion hubs enables sustained control of an invasive vertebrate. J Appl Ecol 52:341–347. doi: 10.1111/1365-2664.12390

Ling SD, Johnson CR (2013) Native spider crab causes high incidence of sub-lethal injury to the introduced seastar *Asterias amurensis*. In: Echinoderms in a Changing World: Proceedings of the 13th International Echinoderm Conference, January 5-9 2009, University of Tasmania, Hobart. p 195

Ling SD, Johnson CR, Mundy CN, et al (2012) Hotspots of exotic free-spawning sex: man-made environment facilitates success of an invasive seastar. J Appl Ecol 49:733–741. doi: 10.1111/j.1365-2664.2012.02133.x

MacDougall AS, Turkington R (2005) Are invasive species the drivers of change or passengers of change in degraded ecosystems? Ecology 86:42–55. doi: 10.1890/04-0669

Mack RN, Simberloff D, Mark Lonsdale W, et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. doi: 10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

McKindsey CW, Archambault P, Callier MD, Olivier F (2011) Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. Can J Zool 89:622–646. doi: 10.1139/z11-037

Olaso Toca I (1979) Biologia de los equinodermos de la Ría de Arosa. Bol Inst Esp Ocean 5:81–127.

Oudejans RCHM, van der Sluis I (1979) Storage and depletion of lipid components in the pyloric caeca and ovaries of the seastar *Asterias rubens* during its annual reproductive cycle. Mar Biol 53:239–247. doi: 10.1007/BF00952432

Papacostas KJ, Rielly-Carroll EW, Georgian SE, et al (2017) Biological mechanisms of marine invasions. Mar Ecol Prog Ser 565:251–268. doi: 10.3354/meps12001

Parry GD (2017) Potential for biocontrol of the exotic starfish, *Asterias amurensis*, using a native starfish. Biol Invasions 19:2185–2196. doi: 10.1007/s10530-017-1430-4

Parry GD, Cohen BF (2001) The distribution, abundance and population dynamics of the exotic seastar *Asterias amurensis* during the first three years of its invasion of Port Phillip Bay, (incorporating a Report on the Bay Pest Day, 2 April 2000). Marine and Freshwater Resources Institute, Melbourne.

Pimentel D, McNair S, Janecka J, et al (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agric Ecosyst Environ 84:1–20. doi: 10.1016/S0167-8809(00)00178-X

Pintor LM, Byers JE (2015) Do native predators benefit from non-native prey? Ecol Lett 18:1174–1180. doi: 10.1111/ele.12496

Popovic I, Matias AMA, Bierne N, Riginos C (2020) Twin introductions by independent invader mussel lineages are both associated with recent admixture with a native congener in Australia. Evol Appl 13:515–532. doi: 10.1111/eva.12857

Pothoven SA, Nalepa TF, Schneeberger PJ, Brandt SB (2001) Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North Am J Fish Manag 21:876–883. doi: 10.1577/1548-8675(2001)021<0876:CIDABC>2.0.CO;2

R Core Team (2019) R: A language and environment for statistical computing.

Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085. doi: 10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Robertson BA, Ostfeld RS, Keesing F (2017) Trojan females and Judas goats: evolutionary traps as tools in wildlife management. Bioscience 67:983–994. doi: 10.1093/biosci/bix116

Robertson BA, Rehage JS, Sih A (2013) Ecological novelty and the emergence of evolutionary traps. Trends Ecol Evol 28:552–560. doi: 10.1016/j.tree.2013.04.004

Ross DJ, Johnson CR, Hewitt CL (2003) Variability in the impact of an introduced predator (*Asterias amurensis*: Asteroidea) on soft-sediment assemblages. J Exp Mar Biol Ecol 288:257–278. doi: 10.1016/S0022-0981(03)00022-4

Russell BG, Letnic M, Fleming PJS (2011) Managing feral goat impacts by manipulating their access to water in the rangelands. Rangel J 33:143–152. doi: 10.1071/RJ10070

Sampson J, Easton A, Singh M (2014) Port Phillip Bay. In: Wolanski E (ed) Estuaries of Australia in 2050 and Beyond. Springer, pp 49–68

Sanderson EW, Jaiteh M, Levy MA, et al (2002) The human footprint and the last of the wild. Bioscience 52:891–904. doi: 10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Saranchova OL, Kulakovskii ÉE (1982) Effect of environmental salinity on different developmental stages of sea stars *Asterias rubens* and mussels *Mytilus edulis*. Sov J Mar Biol 8:32–36.

Sih A, Bolnick DI, Luttbeg B, et al (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621. doi: 10.1111/j.1600-0706.2009.18039.x

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4:367–387. doi: 10.1111/j.1752-4571.2010.00166.x

Suarez A V, Case TJ (2002) Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. Ecol Appl 12:291–298. doi: 10.1890/1051-0761(2002)012[0291:BUEOPO]2.0.CO;2

Suarez A V, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc Natl Acad Sci USA 98:1095–1100. doi: 10.1073/pnas.98.3.1095

Tetzlaff JC, Roth BM, Weidel BC, Kitchell JF (2011) Predation by native sunfishes (Centrarchidae) on the invasive crayfish *Orconectes rusticus* in four northern Wisconsin lakes. Ecol Freshw Fish 20:133–143. doi: 10.1111/j.1600-0633.2010.00469.x

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277:494–499. doi: 10.1126/science.277.5325.494

Vörösmarty CJ, McIntyre PB, Gessner MO, et al (2010) Global threats to human water security and river biodiversity. Nature 467:555–561. doi: 10.1038/nature09440

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16:1192–1203. doi: 10.1046/j.1523-1739.2002.01064.x

Accepted paper, please cite as: Barrett LT, Swearer SE, Dempster T (In Press) Native predator limits the capacity of an invasive seastar to exploit a food-rich habitat. Marine Environmental Research.

TABLES

Table 1. Population metrics for native (*Coscinasterias muricata*) and invasive (*Asterias amurensis*) seastars inside and outside 2 farms at Grassy Point and Clifton Springs aquaculture reserves. Data are missing for *Asterias* inside and outside Grassy Point and *Coscinasterias* outside Clifton Springs because too few individuals were present in these habitats.

	Clifton Springs						**Grassy Point**					
	Inside	**Outside**	**%**	**n**	**X^2**	**p**	**Inside**	**Outside**	**%**	**n**	**X^2**	**p**
Asterias amurensis												
Population density (ha^{-1})[a]	1300 ± 311	755 ± 92	72	20, 20	1.8	0.18	22 ± 22	0 ± 0	∞	18, 18	–	–
Armspan (cm)	19.5 ± 0.6	15.6 ± 0.8	25	20, 20	30	**<0.0001**	12.6 ± 12.6	–	–	1, 0	–	–
Gutted wt (g)	9.0 ± 0.5	4.7 ± 0.3	92	96, 96	79	**<0.0001**	–	–	–	0, 0	–	–
Drained wt (g)	15.2 ± 0.7	8.6 ± 0.6	77	96, 96	64	**<0.0001**	–	–	–	0, 0	–	–
PCI	0.24 ± 0.01	0.19 ± 0.01	26	96, 96	19	**<0.0001**	–	–	–	0, 0	–	–
Gonad wt (g)	3.6 ± 0.5	2.3 ± 0.5	57	96, 96	11	**0.0009**	–	–	–	0, 0	–	–
GSI	0.22 ± 0.02	0.14 ± 0.03	57	96, 96	24	**<0.0001**	–	–	–	0, 0	–	–
Coscinasterias muricata												
Population density (ha^{-1})[b]	2240 ± 460	0 ± 0	∞	20, 20	–	–	3194 ± 829	233 ± 55	14	18, 18	34	**<0.0001**
Armspan (cm)	30.1 ± 0.7	–	–	20, 0	–	–	30.7 ± 0.4	28.6 ± 0.7	7	18, 18	10	**0.001**
Gutted wt (g)	16.5 ± 0.4	–	–	0, 0	–	–	16.5 ± 0.3	15.5 ± 0.3	6	79, 79	14	**0.0004**
Drained wt (g)	23.5 ± 0.7	–	–	104, 0	–	–	21.8 ± 0.6	19.1 ± 0.8	14	79, 79	13	**0.0004**
PCI	0.21 ± 0.01	–	–	104, 0	–	–	20 ± 0.01	0.18 ± 0.01	11	79, 79	5.3	**0.022**
Gonad wt (g)	3.5 ± 0.3	–	–	104, 0	–	–	1.9 ± 0.2	1.9 ± 0.2	0	79, 79	0.0	0.96
GSI	0.20 ± 0.02	–	–	104, 0	–	–	0.11 ± 0.01	0.12 ± 0.01	-9	79, 79	0.1	0.75

FIGURES

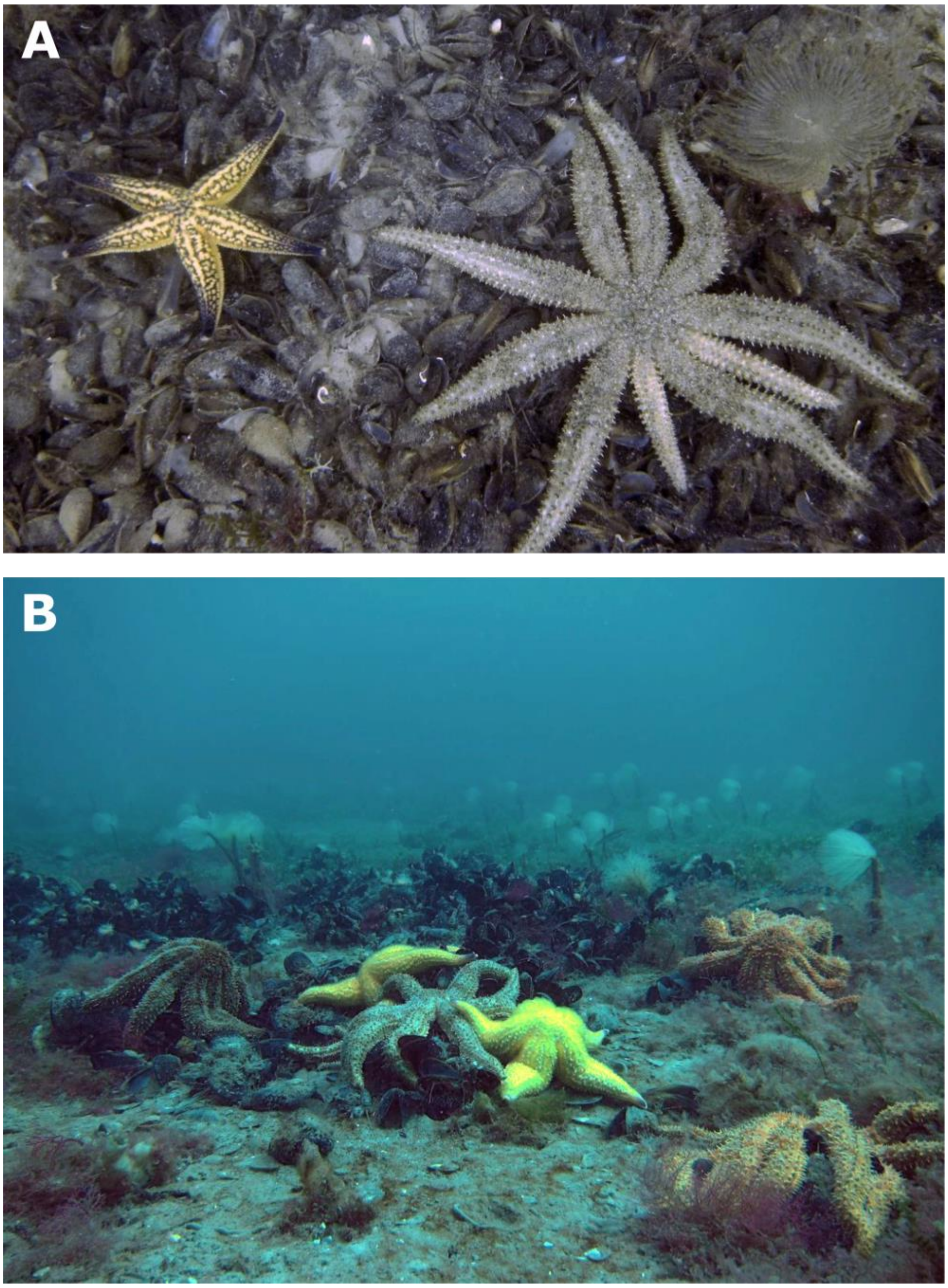

Figure 1. (A) Attempted predation of *Asterias amurensis* by *Coscinasterias muricata*. Image credit: Emily Fobert. (B) Large *Asterias amurensis* individuals (>20 cm) feeding on fallen mussel clumps alongside *Coscinasterias muricata*.

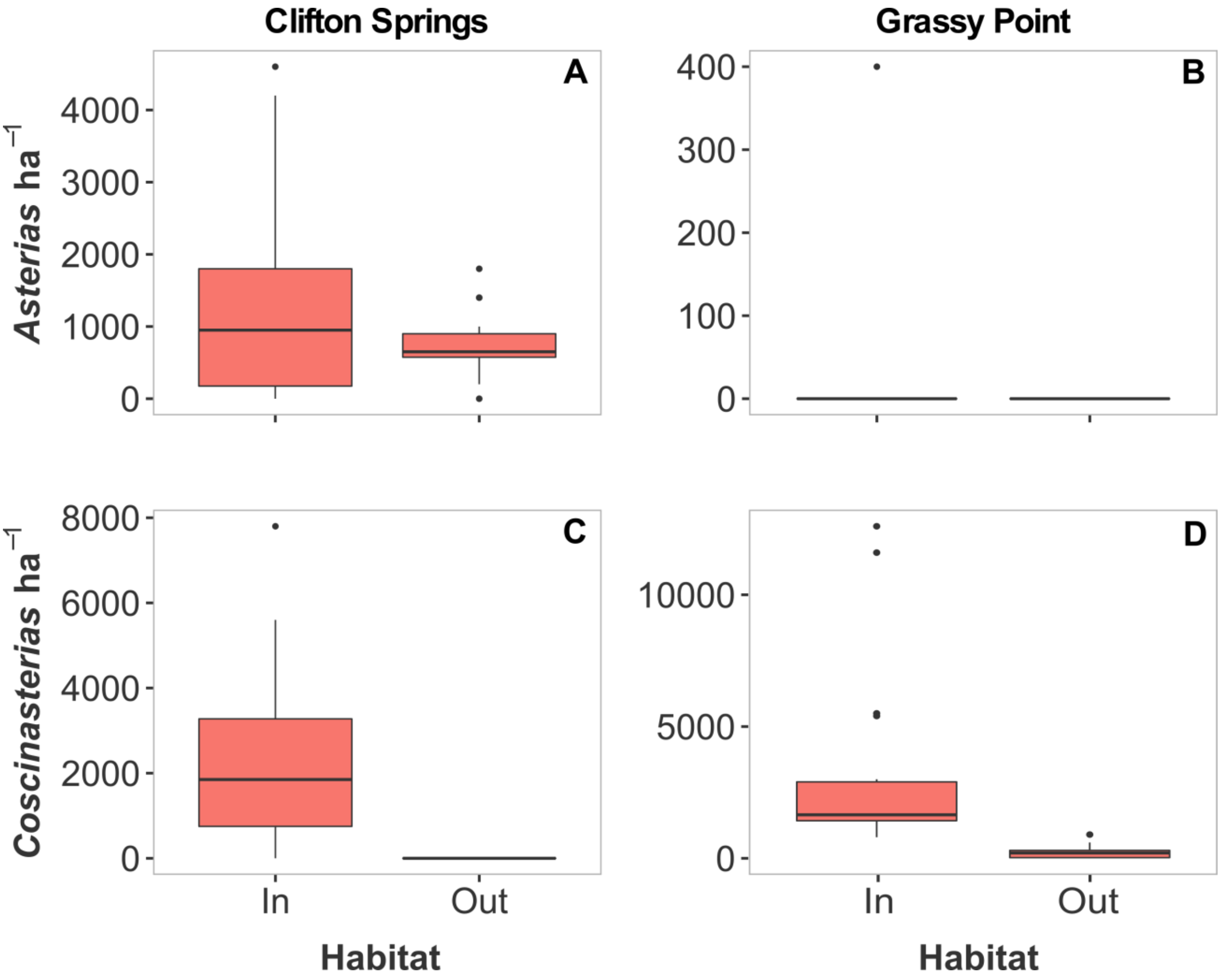

Figure 2. Population density of *Asterias amurensis* (plots A and B) and *Coscinasterias muricata* (plots C and D) inside and outside mussel farms in the Clifton Springs and Grassy Point aquaculture reserves. Boxes denote median and lower (25 %) and upper (75 %) quartiles. Whiskers denote 1.5x interquartile range.

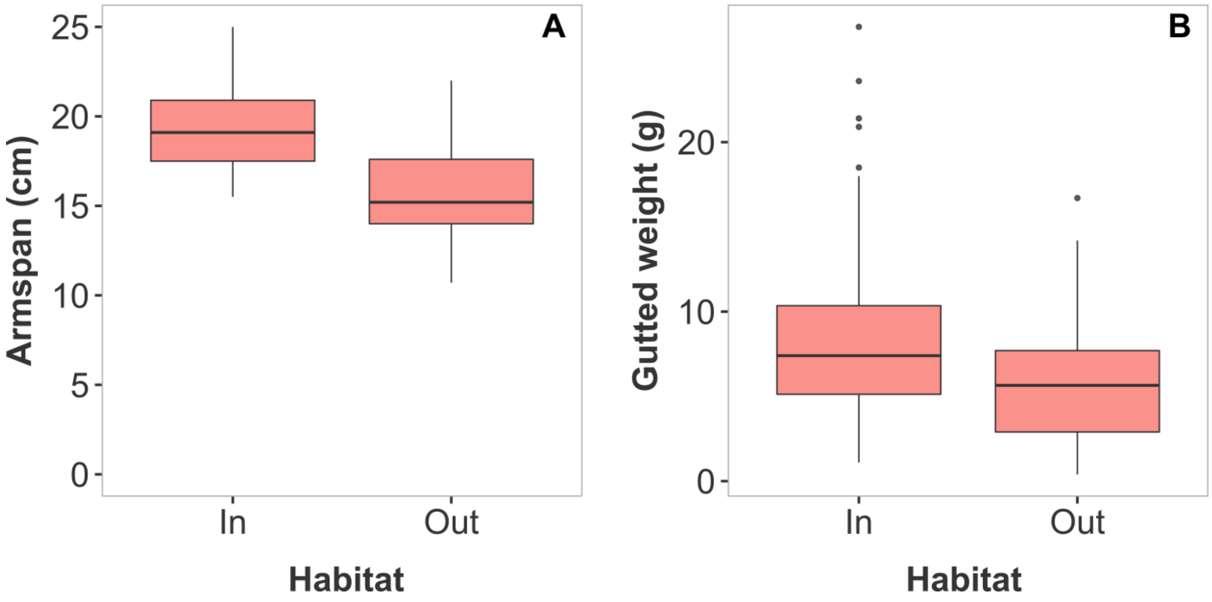

Figure 3. Armspan (A) and gutted weight (B) of *Asterias amurensis* inside and outside a mussel farm in the Clifton Springs aquaculture reserve. Boxes denote median and lower (25 %) and upper (75 %) quartiles. Whiskers denote 1.5x interquartile range.

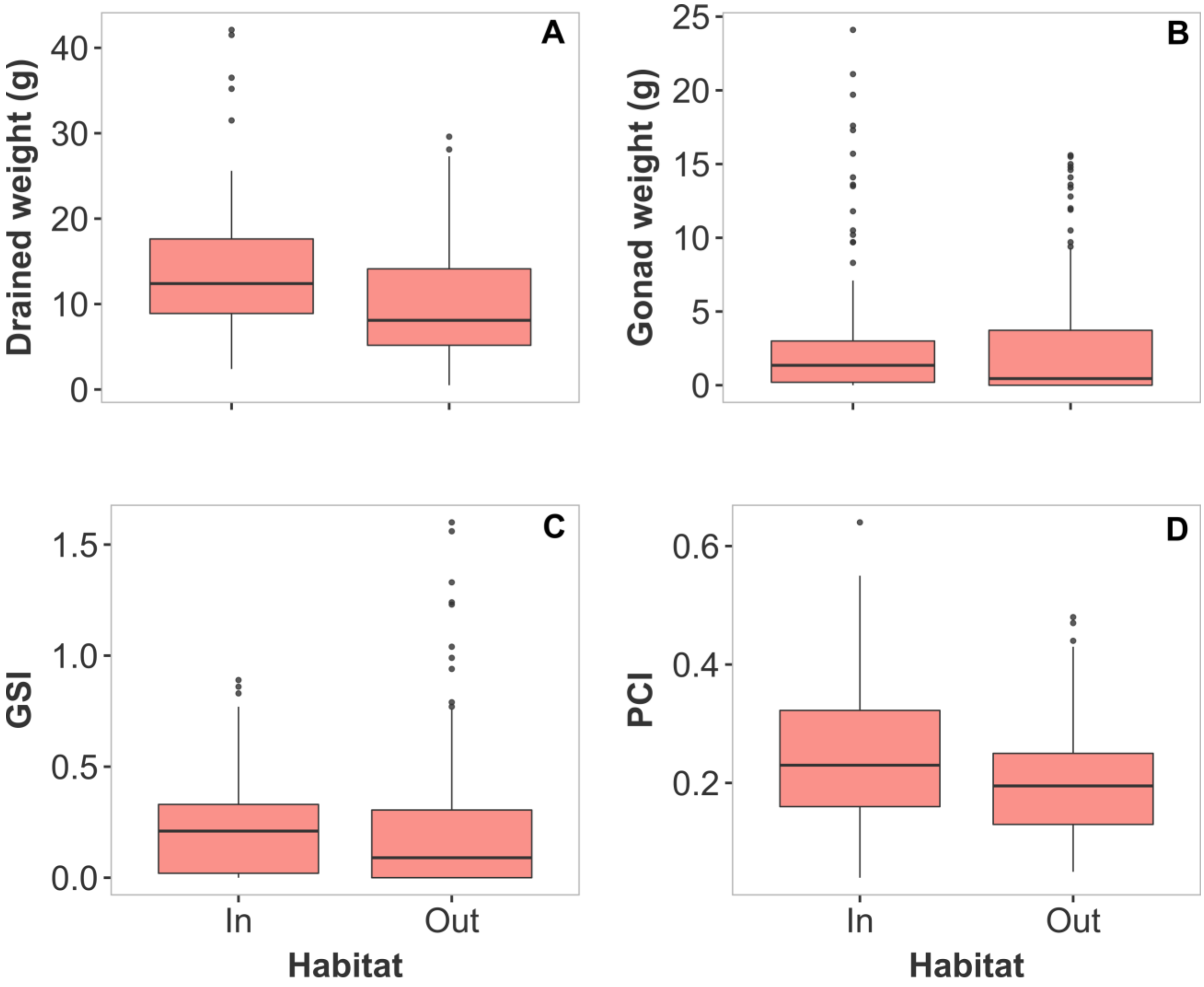

Figure 4. Condition metrics for *Asterias amurensis* inside and outside a mussel farm in the Clifton Springs aquaculture reserve: drained carcass weight (A), gonad weight (B), gonadosomatic index (C), and pyloric caeca index (D). Boxes denote median and lower (25 %) and upper (75 %) quartiles. Whiskers denote 1.5x interquartile range.

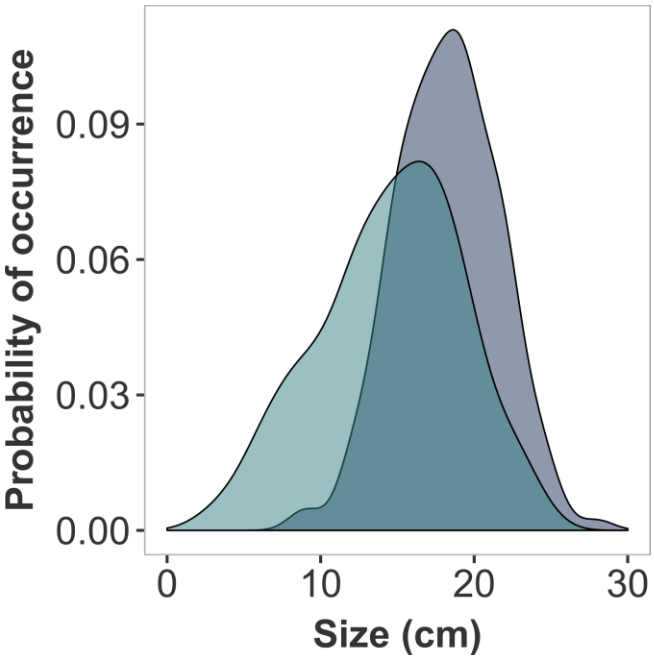

Figure 5. Density plot of *Asterias amurensis* size distribution inside (dark purple) and outside (light green) a mussel farm in the Clifton Springs aquaculture reserve. N = 165 (inside) + 107 (outside).

Accepted paper, please cite as: Barrett LT, Swearer SE, Dempster T (In Press) Native predator limits the capacity of an invasive seastar to exploit a food-rich habitat. Marine Environmental Research.

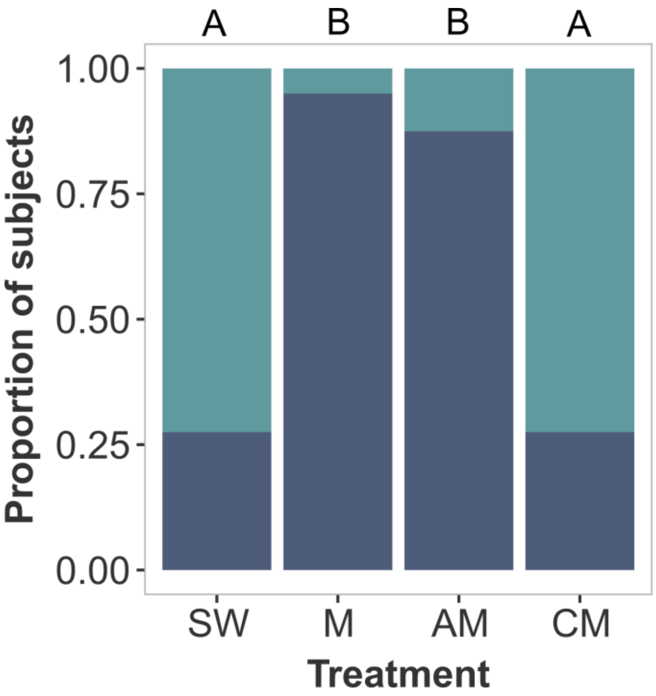

Figure 6. Effect of prey, conspecifics and predators on habitat selection decisions by the invasive seastar *Asterias amurensis* in laboratory trials. Purple bars indicate the proportion attracted, green bars indicate the proportion not attracted. Treatments: SW = seawater control, M = mussels, AM = mussels + *Asterias* conspecifics, CM = mussels + *Coscinasterias*. Bars show the proportion of subjects that are attracted to the cue chamber ('Y') or not ('N') according to the treatment. N = 160 (40 per treatment). Matching letters indicate treatment responses that do not differ statistically.