NOTE

Australian scallops do not recognise the introduced predatory seastar *Asterias amurensis*

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ABSTRACT: Escape responses of Australian scallops (*Pecten fumatus* and *Chlamys asperrima*) to native and introduced predatory seastars were compared in laboratory and field trials. The native seastar *Coscinasterias muricata* elicited an almost immediate escape response by scallops in all trials. In contrast, there was a low frequency of escape response exhibited by scallops when held in contact with the introduced seastar *Asterias amurensis*. These results are consistent with the hypothesis that escape response in invertebrates has evolved relative to predation risk. The absence of predator recognition in marine invertebrates may have serious implications for wild and farmed populations in southern Australia where introduced predators are prevalent.

KEY WORDS: Predator recognition · Escape response · Introduced species · Northern Pacific seastar

INTRODUCTION

Human-mediated introductions in the marine environment are recognised as a major threat to native biodiversity (Carlton 1989, Steneck & Carlton 2001). The coastal waters of Australia are no exception, with over 100 introduced and cryptogenic species in Port Phillip Bay alone (Hewitt et al. 2004). One of the more conspicuous introduced species in southern Australian waters is the northern Pacific seastar *Asterias amurensis*, first recorded in the Derwent Estuary in southeast Tasmania in 1986 (Turner 1992, Buttermore et al. 1994). The seastar is thought to have been introduced to Tasmania in ballast water or as a hull-fouling organism on ships from Japan, although the discovery of an adult in the water intake of a vessel indicates that other methods of transfer are possible (Thresher et al. 2000). The seastar was first discovered on mainland Australia in Port Phillip Bay in 1995, where its population has increased to an estimated 75 (±15 SE) million in 2000

(Parry & Cohen 2001). Genetic data indicate that *A. amurensis* in Port Phillip Bay is the result of translocation from Tasmania (Murphy & Evans 1998).

Introduced predators are likely to have large impacts on native communities (Elton 1958, Lodge 1993, Lafferty & Kuris 1994). Members of Asteriodea are among the most important predators in marine benthic systems (Menge 1982). Seastars of the genus *Asterias* are well known predators of bivalves, causing considerable damage to commercial shellfishes such as oysters, mussels, cockles, scallops and other bivalves (Galtsoff & Loosanoff 1939, Hancock 1958, Hatanaka & Kosaka 1958, Nojima et al. 1986). In Japan, outbreaks of *Asterias amurensis* have caused considerable damage to the shellfish industry (Hatanaka & Kosaka 1958). Recent work in its introduced range has also shown that while *A. amurensis* is a generalist predator able to consume a wide variety of prey, it has clear food preferences for bivalves (including several commercial species) that live on or just below the sediment surface

(Ross et al. 2002). This is of particular concern to the small but growing number of Australian commercial operations harvesting wild populations of bivalves that live near the sediment surface. Furthermore, losses of commercial scallop spat over a settlement season due to *A. amurensis* predation are reported to be as high as 50% in Tasmania (S. Crawford pers. comm.).

Many prey species have evolved adaptations to reduce the risk of being eaten (Legault & Himmelman 1993). Vermeij (1987) described 2 primary anti-predator adaptations by bivalve prey to predation: (1) armour and (2) locomotion. Bivalve prey place differential emphasis on these, by either increasing predator handling time, via armour, or reducing predator encounter rate, via avoidance (Seitz et al. 2001). Locomotive escape behaviours have been described for numerous marine invertebrates, including seastar-mediated escape responses in bivalve molluscs (Bullock 1953, Feder 1972). The escape response of bivalves when encountering a seastar include jumping and swimming by clapping of the valves of the shell in rapid succession as seen in scallops, or thrusting out the foot and leaping into the water by pushing against the substrate as seen in cockles (Feder 1972).

A number of possible mechanisms may elicit these escape responses (Thomas & Gruffydd 1971). Scallops, for instance, have non-cephalic image-forming eyes, which can detect shadows and movements at distance, and extensible tentacles on the mantle edge, which have chemo- and mechanoreceptors (Wilkens 1991). In addition, Mackie (1970) and Phillips (1978) demonstrated that prey can detect the steroid glycosides excreted from the tube feet of seastars.

The present study grew out of an aquarium observation in which contact with the introduced seastar *Asterias amurensis* did not elicit characteristic escape behaviour in the native commercial scallop *Pecten fumatus*, which is seen when contact occurs with native seastars such as *Coscinasterias muricata*. This raises the possibility that prey species, in this case scallops, may not recognise the recently introduced seastar *A. amurensis* as a predator. We expected that predator and prey response would not be independent, and that this would be reflected in a higher frequency of scallop escape responses to native seastars than to introduced seastars.

MATERIALS AND METHODS

Laboratory trials. The seastars *Asterias amurensis* and *Coscinasterias muricata*, and the scallops *Pecten fumatus* and *Chlamys asperrima*, were collected by divers in Port Phillip Bay during February 2003 and held in a filtered, closed-circuit aquarium system.

A. amurensis was not common at the location where the experimental scallops were collected. All species were maintained in separate tanks at a constant temperature of 16°C. The maximum diameter of seastars ranged from 11.5 to 25.0 cm for *A. amurensis* and from 16.0 to 33.4 cm for *C. muricata*. The shell length of scallops ranged from 5.0 to 9.3 cm for *P. fumatus* and from 3.3 to 5.7 cm for *C. asperrima*.

Escape behaviour was studied in 60 l glass tanks (30 cm × 60 cm × 36 cm) with a gravel filter to allow aeration of a 5 cm deep layer of sediment lining the bottom of the tank. The reaction of the scallops to physical contact with the tube feet at the tip of an arm of a seastar was quantified for each predator prey species combination (n = 15). Different individual prey and predators were used in each trial. Each scallop was placed in the aquarium for at least 15 min before trials to allow it to resume normal behaviour. For *Pecten fumatus*, individuals were placed flush with the sediment surface as this is their natural resting and feeding position. In contrast, *Chlamys asperrima* were placed on top of the sediment because they attach to surfaces using byssal threads in the natural environment. We attempted to cause a prey response by moving a predator (seastar) into contact with the mantle of a scallop. A prey response was recorded when the mantle of the scallop was touched with seastar tube feet for a maximum of 60 s. Responses were classed as positive or negative. A positive escape response was recorded if the scallop propelled itself away from the seastar, while a negative response was recorded if the scallop did not behave in a way that propelled it away from the seastar. The time taken to respond was recorded.

Field trials. To test whether differences in escape response between the introduced and native seastars observed in the laboratory extended to field conditions, the trials were repeated *in situ* in April 2003. The size range of predators and prey were within the same limits as those used in laboratory trials. We used SCUBA to run the trials at a depth of ~12 m, directly offshore from Mornington in Port Phillip Bay where *Pecten fumatus* is abundant. Divers swam between scallops carefully so as to minimise disturbance to the sediment and scallops. A diver then touched the mantle of *P. fumatus* with a seastar's tube feet for a maximum of 60 s (n = 24). As described for the laboratory trials, different individual prey and predators were used in each trial, and a positive or negative escape response was recorded on underwater data sheets. A waterproof stopwatch was used to determine the time taken to respond.

The data were cast into 2-way contingency tables of the predictor variable (predator species) by the prey response variable (response/no response) for each scallop trial. Expected frequencies were calculated

assuming the null hypothesis was true and there was no association between variables. Differences between observed and expected frequencies were tested using the chi-square test (Quinn & Keough 2002).

RESULTS

Pecten fumatus and *Chlamys asperrima* displayed similar escape responses, involving initial extension of the tentacles, opening of the valves and enlargement of the inner fold of the velum (or pallial curtain), allowing water to enter the mantle cavity. This was followed by repetitive and rapid shell closure or 'clapping', resulting in jet-like propulsion of water from the mantle and a swimming movement that lifted the scallop into the water column and away from the predator. Alternatively, a 'jump' response was displayed when water jetted out of the mantle caused a change in the rotation of the shell, but did not lift the scallop into the water.

The responses of *Pecten fumatus* and *Chlamys asperrima* differed between the native seastar *Coscinasterias muricata*, and the introduced seastar *Asterias amurensis* (Table 1). Contact with *C. muricata* always elicited a swimming escape response in *P. fumatus* in laboratory and field trials, with a mean response time of 4.5 s (±0.7 SE) and 7.2 s (±2.9 SE), respectively. *C. muricata* elicited a swimming escape response in C*hlamys asperrima* in 13 trials and a jump response in 2 trials. The mean response time was 10.9 s (±2.9 SE).

In contrast, *Asterias amurensis* elicited a swimming escape response in *Pecten fumatus* in 4 of the 15 trials in the laboratory, and in 8 of the 24 trials conducted in the field. In the remaining observations, *P. fumatus* showed varying degrees o f tentacle extension, opening of the valves, and enlargement of the inner fold of the velum, but did not swim. One *P. fumatus* in the laboratory appeared to jet water towards *A. amurensis*, but did not move. In the encounters where *A. amurensis* elicited a swimming escape response, the mean response time was 17.3 s (±5.3 SE) in the laboratory and 26.1 s (±6.5 SE) in the field. *Chlamys asperrima* did not respond to *A. amurensis*; however, this species behaved similarly to *P. fumatus* when touched by the seastar, i.e. tentacle extension, opening of the valves, and enlargement of the velum occurred.

Chi-square values were highly significant (p < 0.001) for both species of scallop tested in the laboratory and for trials conducted in the field. Consequently, the null hypothesis that predator and prey response is independent was rejected.

DISCUSSION

Escape behaviours are generally assumed to have evolved as a result of predation pressure (Feder 1972, Sih et al. 1988, Duffy & Hay 2001). An active escape response is usually evoked after recognition of a specific predator (Kohn 1961, Phillips 1976). For example, the North American whelk *Buccinum undatum* responds strongly to its main asteroid predators in laboratory trials, but not to asteroids that do not naturally attack it, suggesting that bivalves can discriminate between predatory and non-predatory asteroids (Thomas & Himmelman 1988). In our study, the native seastar *Coscinasterias muricata* elicited almost immediate escape responses by the scallops, indicating that they are aware of the potential predation threat. In contrast, the low frequency of escape responses to *Asterias amurensis* suggests that scallops do not recognise the introduced seastar as a predator that should be avoided. According to Vermeij (1994), prey response to predators depends on the frequency of interaction of the species involved. We suggest that scallops do not recognise the recently introduced predator as they have not co-evolved.

Although we are unaware of any other studies that have compared escape responses of invertebrate prey to native and introduced predators, we might expect parallel changes in the intensity of escape responses

Table 1. Frequency and mean escape response time (mean ± SE) of scallops to native and introduced seastar predators. NR: no response. All results are very highly significant at p < 0.001

Species	No. of trials	*Coscinasterias muricata*		*Asterias amurensis*		Chi-square value
		Response number (%)	Response time (s)	Response number (%)	Response time (s)	
Lab trials						
Pecten fumatus	15	15 (100)	4.5 (±0.7)	4 (27)	17.3 (± 5.3)	17.37
Chlamys asperrima	15	15 (100)	10.9 (±2.9)	0 (0)	NR	30.0
Field trials						
Pecten fumatus	24	24 (100)	7.2 (±2.9)	8 (33)	26.1 (±6.5)	24.0

among locations that vary in predator abundance and activity. This is indicated by Thomas & Himmelman's (1988) observations of escape responses of the whelk *Buccinum undatum* to the asteroid predator *Leptasterias polaris* on the Atlantic coast of Canada. Whelks from the Bay of Fundy, where *Leptasterias* is absent, did not react to contact with *Leptasterias.* Given that the population of *Asterias* in Port Phillip Bay has increased and spread dramatically in recent years, we might expect a concomitant increase in selection pressure on scallops to develop anti-*Asterias* adaptations. Sih et al. (1988) predict that anti-predator adaptations should develop rapidly when there is predation pressure, and Remy et al. (1998) showed that experience with predators can cause the development of escape responses in *B. undatum*, providing the first experimental evidence of learned anti-predator behaviour in a mollusc. Sih et al. (1988) suggest that some adaptations have evolved over many generations, whereas others are more plastic and are probably developed or lost over much shorter periods. The recent invasion of *A. amurensis* in Port Phillip Bay provides an ideal opportunity to examine whether anti-predator adaptations against *A. amurensis* predation can develop in scallops and other prey.

It is relatively easy to quantify and compare escape response frequency and intensity, but the risk of predation (i.e. the probability of mortality from predation over a given time) is more difficult to quantify (Legault & Himmelman 1993). The low escape response frequencies to *Asterias amurensis* observed in this study suggest that the risk of predation on scallops is greater for the introduced than the native seastar. Similarly, Barbeau & Scheibling (1994) found that small scallops experienced higher predation rates by *Asterias vulgaris* because they had less powerful and less frequent escape responses than larger ones.

In future studies, we plan to evaluate whether the introduced predator presents a high predatory risk. In a preliminary study, we videotaped the success of introduced and native seastar attacks on scallops in the laboratory and the field. Scallops always fled from *Coscinasterias muricata* but did not respond to *Asterias amurensis* and were consequently captured and eaten (J. J. Ahern unpubl. data). A known proclivity for surface-dwelling bivalves (Ross et al. 2002, 2003, 2004), and field observations of *Asterias* feeding on scallops in its native range (Hatanaka & Kosaka 1958, McLoughlin & Bax 1993) combined with these preliminary observations are consistent with the hypothesis that *Asterias* does present a major threat. However, before we can compare the relative risks of predation of the introduced and native seastars, the frequency and success of seastar encounters with scallops needs to be quantified in the field.

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