

# Impacts of the New Zealand screwshell *Maoricolpus roseus* on growth and condition of juvenile commercial scallops *Pecten fumatus*

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**ABSTRACT:** The invasion of SE Australia by the exotic New Zealand screwshell *Maoricolpus roseus* has sparked concern over its potential impact on native soft-sediment assemblages and, in particular, on commercially harvested molluscs. Here we quantify the impact of both live and dead and empty *M. roseus* shells on the growth, condition and survival of juvenile commercial scallops *Pecten fumatus*. In a manipulative experiment, *P. fumatus* juveniles exhibited up to 27% slower linear shell growth, 5% lighter shells (dry weight), 12% less somatic tissue (ash-free dry weight) and 17% poorer condition when caged with live *M. roseus*. Dead and empty screwshells also reduced scallop growth and condition relative to controls but only at low scallop densities. Scallop mortality did not differ between treatments. The level of impact observed was also dependent on the density of *P. fumatus*. At low scallop densities, the effects of the invasive *M. roseus* are largely due to competition for space, as the results from treatments containing live screwshells and those containing dead and empty screwshells were comparable. However, at higher scallop densities, the significant difference between the treatments indicates competition for both space and food. Moreover, comparison between the different scallop densities provides evidence of a combination of both inter- and intraspecific effects. Given the widespread distribution of *M. roseus* and its occurrence at high densities across large areas of seafloor in SE Australia, impacts on scallop growth and condition have the potential to greatly affect both commercial and recreational scallop fisheries in SE Australia.

**KEY WORDS:** Mollusc · Invasive species · Competition · Marine · Soft-sediment

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## INTRODUCTION

The accelerated introduction of non-indigenous species (NIS) is regarded as a major threat to the integrity and function of natural marine ecosystems worldwide (Carlton et al. 1990, Carlton & Geller 1993, Ruiz et al. 2000). While some NIS expand to significantly impact commercial and recreational fisheries and aquaculture, often with substantial economic repercussions (Hall & Mills 2000), the great majority of introduced species do not invoke major

changes to native assemblages. Given this, and because resources for management of NIS are typically limited (Ross et al. 2002, 2003a), it becomes imperative to prioritize management responses to NIS based, at least in part, on their immediate and potential threat to native assemblages (Byers 2002, Ross et al. 2002, 2003a). Molluscs in particular have been highly successful invaders of marine environments, as illustrated by species such as the Asian clam *Corbula amurensis* (Carlton et al. 1990, Nichols et al. 1990) and European clam *C. gibba* (Currie &

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Parry 1999, Talman & Keough 2001), among several others.

The New Zealand screwshell *Maoricolpus roseus* (Quoy & Gaimard, 1834), a large, solid turrnellid gastropod that grows up to 87 mm in length, was first identified in Australian waters in 1963, although anecdotal evidence suggests that *M. roseus* may have arrived in Tasmania as early as the 1920s, accompanying shipments of live oysters from New Zealand (Bax et al. 2003). The oyster species *Tiostrea chilensis* and/or *Crassostrea glomerata* were sporadically imported to Tasmania from the late 1800s to bolster a failing local oyster industry (Bax et al. 2003). The imported oysters were sold at local markets and were kept fresh by being suspended in crates in the local estuary. In the ca. 100 yr since its arrival, *M. roseus* has become one of Australia's most widespread marine NIS, expanding northwards along Australia's eastern coast as far as northern New South Wales, with the majority of high-density aggregations occurring in Victoria, Bass Strait and southeastern Tasmania (Allmon et al. 1994, Gunasekera et al. 2005). More recently, the species has been detected in South Australia, which indicates a possible westward expansion in the species' invasive range (Wiltshire et al. 2010). Throughout its introduced range, *M. roseus* occupies a variety of habitats from muddy silts to rocky reefs and regularly attains densities of 200 to 1200 m<sup>-2</sup> (Allmon et al. 1994) and up to 2500 m<sup>-2</sup> (Reid 2003), although it is most common on shelly substrata and coarse sands (Bax et al. 2003, Reid 2003) over a depth range of 0 to 200 m. Despite the wide distribution and high densities attained by *M. roseus*, its impacts on native soft-sediment assemblages are largely unknown (but see Nicastro et al. 2009). Although Nicastro et al. (2009) examined the impacts of *M. roseus* shells in a dynamic coastal lagoon and found negligible effects on infauna and the foraging efficiency of the generalist predator *Carcinus maenas*, the authors noted that the impacts of *M. roseus* in more stable coastal environments, where shells are likely to persist for longer and live populations reach high densities, remain unclear.

*M. roseus* is a primarily sedentary ciliary suspension feeder (Scott 1997, Bax et al. 2003) relying on water currents to provide a mechanism for food particle and seston delivery and waste removal. While ciliary suspension feeding is the most common feeding mode among turrnellids (Scott 1997), some species such as *Gazameda gunnii* are capable of switching to alternate modes (i.e. deposit feeding), particularly in times when the abundance of pelagic

sources of nutrition is limiting (Allmon 1988). There is some evidence that *M. roseus* may also be capable of switching to a deposit-feeding mode, but the possibility requires further investigation (Davenport & Bax 2002).

Despite occupying the soft-sediment benthos at extreme densities, *M. roseus* exhibits rapid growth rates, particularly when conditions are favorable, but like all turrnellids, growth rates and abundances have been shown to depend on environmental conditions such as the degree of exposure, phytoplankton concentration, substratum type and complexity, population density, predation and temperature (Allmon et al. 1994, Scott 1997). *M. roseus* tends to exhibit a logarithmic growth pattern, growing faster and laying down significantly greater amounts of shell while young. The growth and development of the shell at later ages is slower, which is suspected to reflect an ontogenic decline as more energy is invested into reproduction. Growth is seasonal, with the most rapid seasonal growth during the warmest months, particularly in the first year of life (Scott 1997, Bax et al. 2003).

*M. roseus* may affect native soft-sediment species in several ways including modifying habitat, providing a substratum for settlement of other species, pre-ating on planktonic larvae, and competing for food and space. Competition with native species is of particular interest, as several commercially important species occupy similar habitats and, like *M. roseus*, are benthic filter feeders. One such species is the commercial scallop *Pecten fumatus* (Reeve 1852). *P. fumatus* and *M. roseus* are both common in eastern Tasmania and, in another study spanning the whole length of the D'Entrecasteaux Channel, were found to co-occur at all 20 sites, both occupying a range of substratum types from mud to coarse sand (A. P. Reid et al. unpubl.).

Like *M. roseus*, *P. fumatus* occupies soft-sediment benthos over a similar depth range, although it is more common in water <20 m, and the commercial fishery for the species predominately operates in water shallower than 100 m. *P. fumatus* is a functional hermaphrodite, which normally reaches sexual maturity in 2 yr (Ovenden et al. 2016). Larval scallop spat remain in the water column for up to 6 wk before first settling, attaching to a hard substratum such as shell grit, and remain attached until 6 mm long. The small scallops then detach and settle into the soft sediment. Growth rates vary depending on location, but on average, spat grow quickly and reach 70 to 75 mm shell length within 18 mo of settlement. The species has been known to reach up to

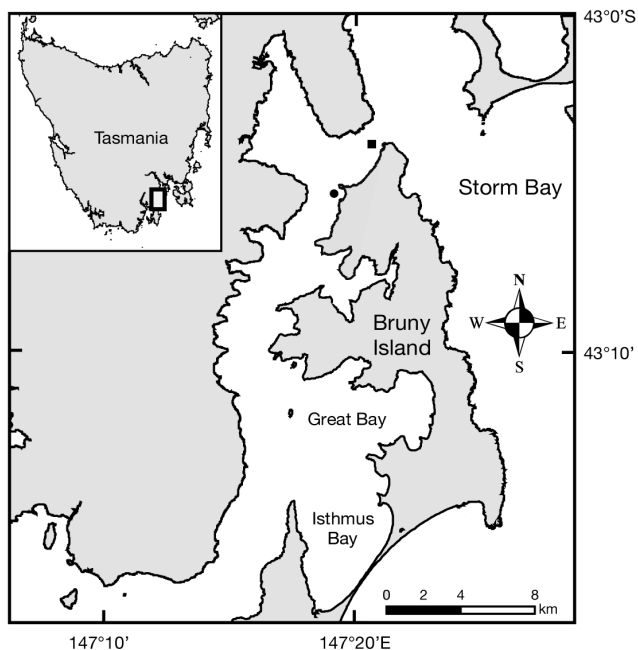


Fig. 1. D'Entrecasteaux Channel, Tasmania, showing the location of the study site at Bligh Point (●) and the screwshell collection site at Dennes Point (■)

145 mm in shell length, and the commercial fishery targets beds where 80% of the scallops are >85 mm (AFMA 2016).

Like *M. roseus*, *P. fumatus* is also a ciliary suspension feeder, and commercial beds of the species correlate with locations where water currents deliver food resources (Ovenden et al. 2016). Given the remarkably similar ecophysiology between *M. roseus* and *P. fumatus* and the distributional overlap between the 2 species, the potential for competitive interactions, including possible impacts to the commercial fishery, is high.

Additionally, *M. roseus* shells can occupy the sea floor at densities of  $\sim 1200 \text{ m}^{-2}$  when they form an unbroken mat over the sediment, and at densities of over  $2000 \text{ m}^{-2}$ , they are amassed as a layer  $\sim 100$  mm deep. Since *P. fumatus* typically recesses into the sediment, remaining partially buried for much of the time, reduced access to soft-sediment habitat, and competition for space in areas where screwshells form dense mats, may also impact the growth and condition of *P. fumatus* individuals.

Despite extensive research on NIS in freshwater and terrestrial systems, quantitative experimental data on potential impacts of non-indigenous marine species are typically less comprehensive (Ruiz et al. 1999, Talman & Keough 2001). Moreover, studies addressing impacts of NIS in marine habitats have

typically focused more on qualitative observational data obtained through surveys than on quantitative examination of the mechanisms of impact through the use of controlled experiments (Brenchley & Carlton 1983, Grosholz & Ruiz 1995, Ross et al. 2002, 2003b). In this paper, we use a manipulative experiment to quantify the impact of *M. roseus* on the growth, condition and survivorship of *P. fumatus* juveniles. We compare impacts associated with live and dead *M. roseus* shells and quantify differences in interspecific and intraspecific competition. This study provides one of the first quantitative assessments of the impact of *M. roseus* on a native species in Australia.

## MATERIALS AND METHODS

### Experimental site, scallop tagging and screwshell collection

The D'Entrecasteaux Channel is a narrow inlet of the Tasman Sea, extending for  $\sim 55$  km between Bruny Island and the southeastern coast of mainland Tasmania. The experiment was conducted *in situ* at Bligh Point on Bruny Island (Fig. 1), which consists of a shallow rocky reef that descends quickly into a gently sloping soft-sediment bottom dominated by fine sands and shell grit. The experiment was carried out at 12 m depth, where both commercial scallops ( $\sim 2 \text{ m}^{-2}$ ) and screwshells ( $\sim 200 \text{ m}^{-2}$ ) co-occurred at low densities.

Juvenile *Pecten fumatus* were obtained from Jolly Roger Holdings, Tasmania, and held in laboratory aquaria with unfiltered flow-through seawater prior to deployment onsite. Scallops were individually tagged with a small cylindrical plastic fish tag, cemented into the central groove of the upper valve using Loctite® 454 cyanoacrylate. Initial measurements of shell length and width, measured to the nearest 0.1 mm using Vernier calipers, were taken at the same time as tagging. A digital photograph was also taken of the flat right valve of each scallop prior to deployment and was used in both growth analysis and as a back-up identification in the case any individuals were retrieved without identification tags during the study.

*Maoricolpus roseus* were collected at Dennes Point (Fig. 1) in 12 m of water using a dredge (opening =  $630 \times 350$  mm, depth = 320 mm) and held in laboratory aquaria prior to deployment. Live *M. roseus* were separated from dead and empty shells and shells containing hermit crabs. Additional dead and

empty *M. roseus* were obtained from Blackman's Bay beach (43° 00.085' S, 147° 19.577' E).

Juvenile scallops approximately 40 mm in width were used in the experiments. They were reproductively immature, which allows any observed impacts on scallop growth and condition (to both soft tissue and the shell) to be interpreted independently of processes associated with directing energy to gametogenesis or to biomass loss from spawning.

### Experimental design

The experiment was carried out in circular cages consisting of a rigid 60 mm high PVC ring (1 m<sup>2</sup>) attached to a ring of oyster mesh (600 mm high and mesh size of 20 × 20 mm). Cages had no roofs or floors, and a small curtain of soft mesh supported by buoys attached to the top of the cages prevented sea stars from entering. Cage walls were sufficiently high to prevent scallops from swimming over the top. Cages were pushed into the sediment to a depth of 80 mm and pinned into place to prevent the escape of scallops and the incursion of predators under the cages. Cages were cleared of any fouling every 2 wk.

Screwshells were added to the experimental cages 1 wk before the introduction of scallops to minimise impact to the natural sediment structure. Screwshells were allocated randomly to 2 treatments: cages with live screwshells added at 1000 m<sup>-2</sup> and cages with dead and empty screwshells added at 1000 m<sup>-2</sup>. The densities of screwshells used in the experiment were similar to those from random quadrat samples undertaken during a pilot survey and represented natural densities of screwshells commonly observed in SE Tasmania.

A control cage, which did not contain any screwshells, was also deployed. Each treatment was applied to 6 individual cages, and each of the 6 cages in each treatment was then randomly allocated 5, 10, 15, 20, 25 or 30 *P. fumatus* juveniles (total n = 18 cages). This design allowed both inter- and intraspecific competition to be quantified and allowed definitive separation of impacts of live screwshells (competition for food and space) from impacts related to the physical presence of screwshells alone (competition for space). Natural densities of adult commercial scallops (shell width >80 mm) in the D'Entrecasteaux Channel have been reported as high as 8 m<sup>-2</sup> (Mendo et al. 2014), although no data are available for juveniles or spat. We note, however, that densities of juveniles and spat are likely to be higher than adults, and it is not uncommon for

scallop spat and juveniles to exceed 100 m<sup>-2</sup> (or 100% cover) under aquaculture conditions, with minimal mortality. Moreover, the densities of scallops used in our experiment are comparable to other manipulative experiments using the species (Talman & Keough 2001).

The experiment commenced on 21 May 2005 and ran for 85 d. On completion, all surviving scallops were measured for the following parameters: shell width (mm), shell length (mm), right valve growth (mm), dry weight of shell and soft tissue (g) and ash-free dry weight of somatic tissue (g). Right valve growth was calculated as the distance between a clearly visible stress ring, laid down at the time of relocation of the scallops, and the edge of the shell. Dry weights were calculated by carefully removing somatic tissue from the shell and drying each component separately to a constant weight, which was achieved at 60°C for 48 h. Ash-free dry weight of somatic tissue was determined after burning off organic matter for 7 h at 500°C in a blast furnace. A measure of condition was calculated by dividing the ash-free dry weight of soft tissue by the dry weight of the shell for each individual scallop (Lucas & Beninger 1985).

Mortality was assessed weekly, with dead shells removed from their respective cages. Shells that were chipped or broken indicated predation from crabs or octopus as a source of mortality and were recorded accordingly. Because entry of the cages by sea stars was prevented successfully by the design of the cage, dead scallops with intact undamaged shells, often with residual somatic tissue remaining attached to the shell, were assumed as lost to other sources of mortality. Remaining scallops, fully intact but dead, were presumed as lost to starvation. Zero mortality was observed during the first 67 d of the 85 d experiment.

### Statistical analyses

Comparisons of shell dry weight, soft tissue dry weight and soft tissue ash-free dry weight among treatments were analysed using a single-factor ANCOVA with screwshell type and density as the fixed treatment factor and scallop density as the covariate. Because measurements of individual scallops within the same cage were not independent, the analysis was conducted on the means for each cage. Regressions fitted to each treatment were initially tested for homogeneity of slopes before proceeding with comparison of the intercepts. All data were

examined using box plots and normal probability plots to ensure the assumptions of normality and homogeneity of variances were satisfied. No transformation was necessary for any parameters. The parameters of shell dry weight, somatic tissue dry weight and somatic tissue ash-free dry weight were standardised by shell width to avoid confounding with variation in scallop size. Weights were only standardised after ensuring that both the relationship between shell weight and shell width and the relationship between somatic tissue weight and shell width were linear.

Non-linear trends were identified in the treatment with live screwshells for the parameters of shell width, shell length and right valve growth. As such, ANCOVA was not considered appropriate for these parameters, because non-homogeneous slopes precluded the ability to compare between treatments. Therefore, a 2-parameter scaled logistic model was fitted to the data for the treatment containing live screwshells and linear regressions for the control and treatment containing dead screwshells. This was undertaken for all the parameters where a non-linear relationship was identified, namely shell width, shell length and right valve growth.

Level of significance for all analyses was  $p \leq 0.05$ .

### Caveats

Maintenance of treatment densities of both *M. roseus* and *P. fumatus* required the use of artificial cages. A potential problem in using cages is that they potentially create artifacts that do not arise under natural conditions. In particular, altered current flows and development of a fouling community on the mesh walls of cages have been shown to slow growth of some bivalves by reducing the supply of seston (Claereboudt et al. 1994, Harrison et al. 1996). However, the large mesh size used in this experiment would have minimized alteration to current flows and turbulence, and fortnightly cleaning of the cages prohibited development of a macroscopic fouling community on the cage walls.

Use of circular cages in this experiment alleviated effects of cage corners, and scallops appeared to utilize the full area provided with no obvious association with cage walls. Further, the lack of a cage floor and roof enabled scallops and screwshells to recess into the sediment and allowed motile fauna (other than sea stars, which were excluded by a curtain of soft mesh) to enter through the top of the cages without interference.

## RESULTS

### Intraspecific competition in scallops

There were clear intraspecific effects on the growth of *Pecten fumatus*, evidenced by a decline in all of the scallop growth and condition parameters assessed with increasing scallop density in both the control and live screwshell treatments (Fig. 2). For the parameters of shell width, shell length and right valve growth, this relationship was non-linear in the live screwshell treatment, which was best described as a scaled logistic decline in the aforementioned parameters. Notably, however, this was not the case in the treatment with dead screwshells, in which the various parameters remained uniformly low with increasing scallop density, at a level similar to that in the highest scallop density in the control (Fig. 2). This was reflected in the ANCOVA for somatic tissue dry weight; the significant covariate  $\times$  treatment interaction indicated that slopes were non-homogeneous across treatments (Table 1).

Given a similar, albeit not significant, pattern observed for the other parameters, the ANCOVAs were repeated using data from the control and live screwshell treatments only (Table 2), and individual regressions were fitted to data for the dead screwshell treatment (Table 3). As previously discussed, the nonlinear trend for the treatment with live screwshells for the parameters of shell width, shell length and right valve growth were described using a scaled logistic model, and this precluded the use of ANCOVA for these parameters (Fig. 2, Table 4).

### Interspecific competition between screwshells and scallops

The presence of live *Maoricolpus roseus* had a significant negative effect on scallop growth, measured as change in the width and length of the shell and right valve growth, and on absolute yield, expressed as dry shell weight, somatic tissue dry weight and somatic tissue ash-free dry weight (Fig. 2). On average, scallops housed with live screwshells exhibited significantly less growth in shell width and shell length and in the lower right valve (Fig. 2). At the lowest scallop densities (5–10 scallops cage<sup>-1</sup>), scallops housed with live screwshells exhibited 14 to 22% lower shell width, 15 to 21% lower shell length and 20 to 22% lower right valve growth than scallops in control cages. This impact was even more prevalent at the highest initial scallop density (30 scallops

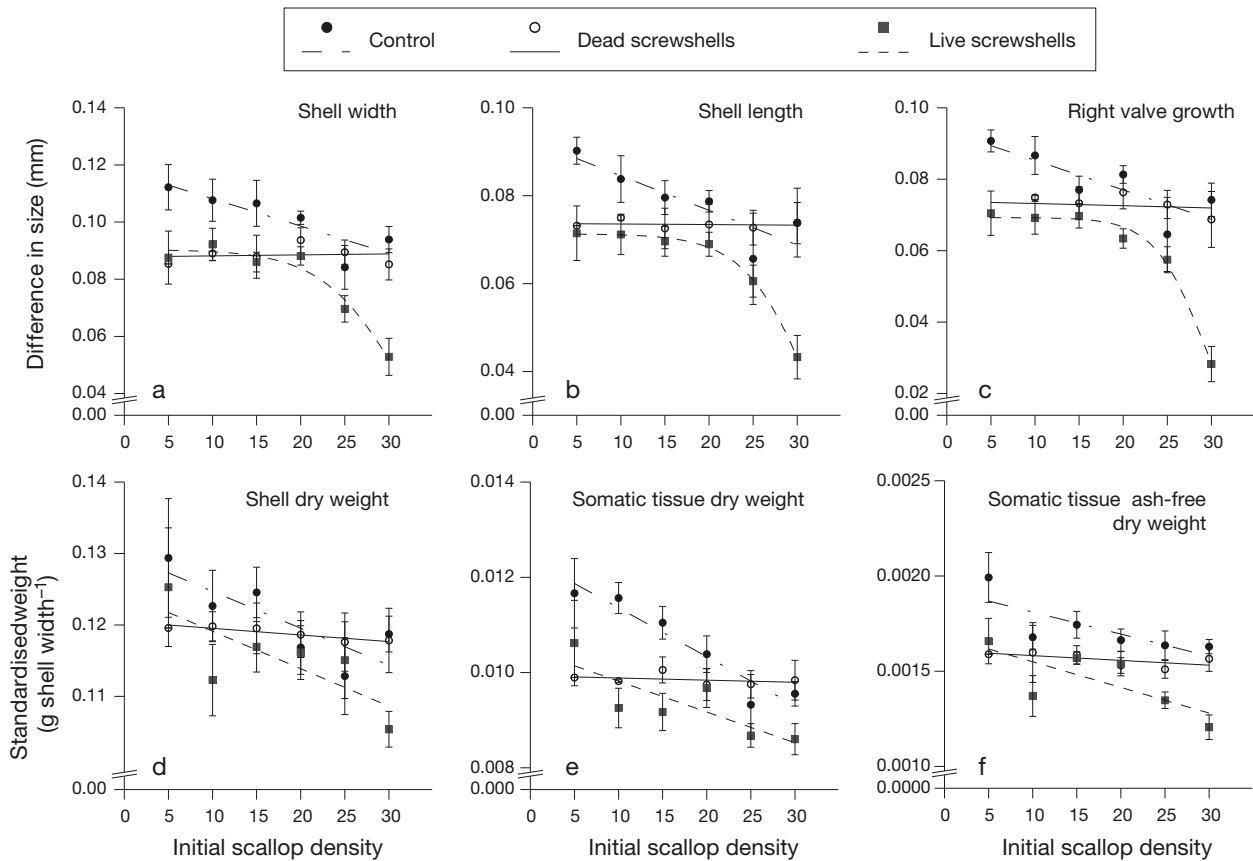


Fig. 2. Differences in *Pecten fumatus* juveniles under the different treatment conditions and across all initial scallop densities at the conclusion of the experiment. Shell width (a) and shell length (b) were calculated as the difference in scallop size between the start and end of the experiment, and right valve growth (c) was calculated by measuring the distance of the right valve from the shell edge to the stress line laid down during deployment. Dry shell weight (d), dry somatic tissue weight (e) and ash-free dry somatic tissue weight (f) were standardised by shell width. All measurements displayed as means  $\pm$  SE for individual cages. Linear trends were identified for shell dry weight, somatic tissue dry weight and somatic tissue ash-free dry weight between the live screwshell treatment and the control; therefore, ANCOVA was used for comparison. The dead screwshell treatment across all parameters yielded a slope not significantly different from zero and was assessed using regression analysis. For the parameters of shell width, shell length and right valve growth, this relationship was non-linear in the live screwshell treatment; consequently, a scaled logistic model was fitted to describe the curve

Table 1. ANCOVA results for shell dry weight, somatic tissue dry weight and soft tissue ash-free dry weight of *Pecten fumatus* in all treatments. Scallops refers to scallop density. **Bold** values indicate significance at  $p \leq 0.05$

Source of variation	df	Mean square	F	p
<b>Shell dry weight (g)</b>				
Treatment	2	$2.85 \times 10^{-5}$	2.09	0.1662
Scallops	1	$1.88 \times 10^{-4}$	15.21	<b>0.0021</b>
Treatment $\times$ Scallops	2	$2.67 \times 10^{-5}$	2.16	0.1575
<b>Somatic tissue dry weight (g)</b>				
Treatment	2	$1.92 \times 10^{-6}$	16.12	<b>0.0004</b>
Scallops	1	$4.30 \times 10^{-6}$	36.07	<b>&lt;0.0001</b>
Treatment $\times$ Scallops	2	$1.07 \times 10^{-6}$	8.97	<b>0.0041</b>
<b>Somatic tissue ash-free dry weight (g)</b>				
Treatment	2	$3.20 \times 10^{-8}$	3.75	0.0544
Scallops	1	$1.12 \times 10^{-7}$	12.95	<b>0.0037</b>
Treatment $\times$ Scallops	2	$1.50 \times 10^{-8}$	1.75	0.2147

age<sup>-1</sup>), where scallops housed with live screwshells exhibited 43% lower shell width, 41% lower shell length and 62% lower right valve growth than scallops in control cages. Similarly, these scallops also showed an average 5% loss in shell mass and 12% loss of somatic tissue mass and carried 18% less ash-free somatic tissue than scallops grown in otherwise identical conditions without screwshells, across all levels of initial scallop densities (Fig. 2).

Significant differences in the condition of *P. fumatus* juveniles were also detected between the live screwshell treatment and the controls. Independent of the decline in condition of scallops with

Table 2. ANCOVA results for shell dry weight, somatic tissue dry weight and soft tissue ash-free dry weight of *Pecten fumatus* in control and live screwshell treatments. Scallops refers to scallop density. **Bold** values indicate significance at  $p \leq 0.05$ 

Source of variation	df	Test for homogeneous slopes			df	Test for intercepts		
		Mean square	F	p		Mean square	F	p
Shell dry weight (g)								
Treatment	1	$1.74 \times 10^{-5}$	0.95	0.3593	1	$9.56 \times 10^{-5}$	5.84	<b>0.0389</b>
Scallops	1	$2.37 \times 10^{-4}$	12.89	<b>0.0071</b>	1	$2.37 \times 10^{-4}$	14.5	<b>0.0042</b>
Treatment $\times$ Scallops	1	$2.00 \times 10^{-8}$	0.01	0.9771				
Somatic tissue dry weight (g)								
Treatment	1	$2.12 \times 10^{-6}$	12.37	<b>0.0079</b>	1	$4.74 \times 10^{-6}$	16.12	<b>0.0007</b>
Scallops	1	$6.11 \times 10^{-6}$	35.61	<b>0.0003</b>	1	$6.11 \times 10^{-6}$	32.63	<b>0.0003</b>
Treatment $\times$ Scallops	1	$3.13 \times 10^{-6}$	1.82	0.2141				
Somatic tissue ash-free dry weight (g)								
Treatment	1	$3.38 \times 10^{-8}$	2.74	0.1366	1	$2.27 \times 10^{-7}$	20.53	<b>0.0014</b>
Scallops	1	$1.37 \times 10^{-7}$	11.08	<b>0.0104</b>	1	$1.37 \times 10^{-7}$	12.37	<b>0.0065</b>
Treatment $\times$ Scallops	1	$7.85 \times 10^{-10}$	0.06	0.8075				

Table 3. Regression results of all growth parameters of *Pecten fumatus* in the treatments with dead screwshells. Note that none of the parameters varied significantly with scallop density. SD refers to scallop density

Parameter measured	Regression	r <sup>2</sup>	t	p
Shell width (SW, mm d <sup>-1</sup> )	SW = $-3.57 \times 10^{-5}$ (SD) + 0.088	0.0113	0.21	0.841
Shell length (SL, mm d <sup>-1</sup> )	SL = $-1.30 \times 10^{-5}$ (SD) + 0.074	0.0187	-0.28	0.7961
Right valve growth (RVG, mm d <sup>-1</sup> )	RVG = $-6.17 \times 10^{-5}$ (SD) + 0.074	0.0421	-0.42	0.6965
Shell dry weight (SDW, g)	SDW = $-5.86 \times 10^{-5}$ (SD) + 0.120	0.5095	-2.04	0.1111
Somatic tissue dry weight (STDW, g)	STDW = $-4.49 \times 10^{-6}$ (SD) + 0.010	0.1355	-0.79	0.4729
Somatic tissue ash-free dry weight (STAFDW, g)	STAFDW = $-2.51 \times 10^{-6}$ (SD) + 0.006	0.4343	-1.75	0.1546

Table 4. Results of scaled logistic models fitted for the parameters of shell width, shell length and right valve growth of *Pecten fumatus* in the treatments with live screwshells. Calculations made using the following formula:  $y = k - (k \times e^{a+b \times x}) / (1 + e^{a+b \times x})$ . **Bold** values indicate significance at  $p \leq 0.05$ 

Measurement	Parameter	Estimate	SE	t	Prob (> t )
Shell width (mm)	k	0.090383	0.002913	31.026	<b><math>7 \times 10^{-5}</math></b>
	a	-7.01069	1.832594	-3.826	<b>0.0315</b>
	b	0.223709	0.062077	3.604	<b>0.0367</b>
Shell length (mm)	k	0.0713066	0.0004474	159.36	<b><math>5 \times 10^{-7}</math></b>
	a	-8.413744	0.5227047	-16.1	<b>0.0005</b>
	b	0.2660836	0.0176285	15.09	<b>0.0006</b>
Right valve growth (mm)	k	0.069261	0.001283	54.004	<b><math>1.4 \times 10^{-5}</math></b>
	a	-10.40788	1.461479	-7.121	<b>0.0057</b>
	b	0.358477	0.050267	7.131	<b>0.0057</b>

increasing initial scallop densities, scallops in cages without screwshells were consistently in better condition than those caged with live screwshells. On average, the condition of scallops cohabiting with live screwshells was 12% lower than that in the controls (Fig. 3).

The presence of dead and empty *M. roseus* shells also resulted in reduced growth of *P. fumatus* juveniles, at least at low scallop densities (Fig. 2). Scallops

cohabiting with dead screwshells showed similar growth, irrespective of initial scallop densities, with all parameters yielding a slope not significantly different from zero (Table 3). It follows that at low initial scallop densities (5–10 m<sup>-2</sup>), growth and yield of scallops in the presence of high densities of dead screwshells was markedly lower than when screwshells were absent. However, at high initial scallop densities (25–30 m<sup>-2</sup>), any effect of dead screwshells on the growth and yield of scallops was much less evident (Fig. 2). A similar pattern was evident when considering the overall condition of scallops (Fig. 3).

### Scallop mortality

There was no clear evidence of any effect of either live or dead *M. roseus* on survivorship of *P. fumatus* juveniles. Of 315 juvenile *P. fumatus* deployed initially, 266 (84.5%) were recovered by the completion of the experiment. Of those recovered, 214 were

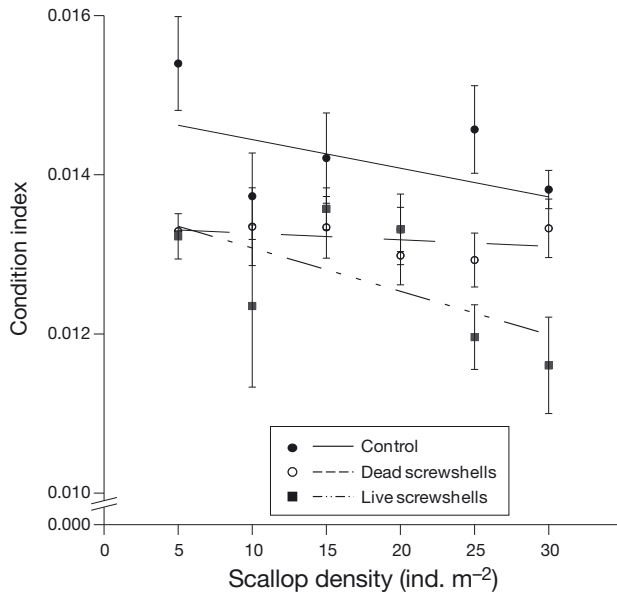


Fig. 3. Condition (mean ± SE) of *Pecten fumatus* juveniles under the control (●), dead screwshell (○) and live screwshell (■) treatments and across all scallop densities. Regression analysis on the dead screwshell treatment indicated that the slope was not significantly different from zero (regression:  $F_{1,1} = 0.09$ ,  $p = 0.779$ ). ANCOVA carried out between the control and live screwshell treatments alone indicated significant differences in intercepts between the 2 treatments (ANCOVA, test for homogeneous slopes, treatment × scallop (i.e. scallop density) interaction:  $F_{1,1} = 0.14$ ,  $p = 0.713$ , test for intercepts, treatment:  $F_{1,1} = 14.44$ ,  $p = 0.004$ , scallop density:  $F_{1,1} = 3.83$ ,  $p = 0.082$ )

alive after 85 d, and 52 were recovered over the course of the experiment having suffered some form of mortality. There was no clear effect of any treatment on the number of scallops lost to the different types of mortality, although there was a trend of higher mortality associated with predation and other sources of mortality in high scallop densities in treatments with screwshells (Fig. 4).

### DISCUSSION

The accelerated introduction of non-indigenous marine species is regarded as a major threat to the integrity and function of natural marine ecosystems worldwide (Carlton 1996a,b, Cohen & Carlton 1998, Crooks 2002, Katsanevakis et al. 2014). Because resources available to combat introduced marine species are limited, it is becoming increasingly more accepted that management must involve prioritisation of introduced species based on their immediate and potential threat to native assemblages (Byers 2002, Ross et al. 2002, 2003b). The potential impact of

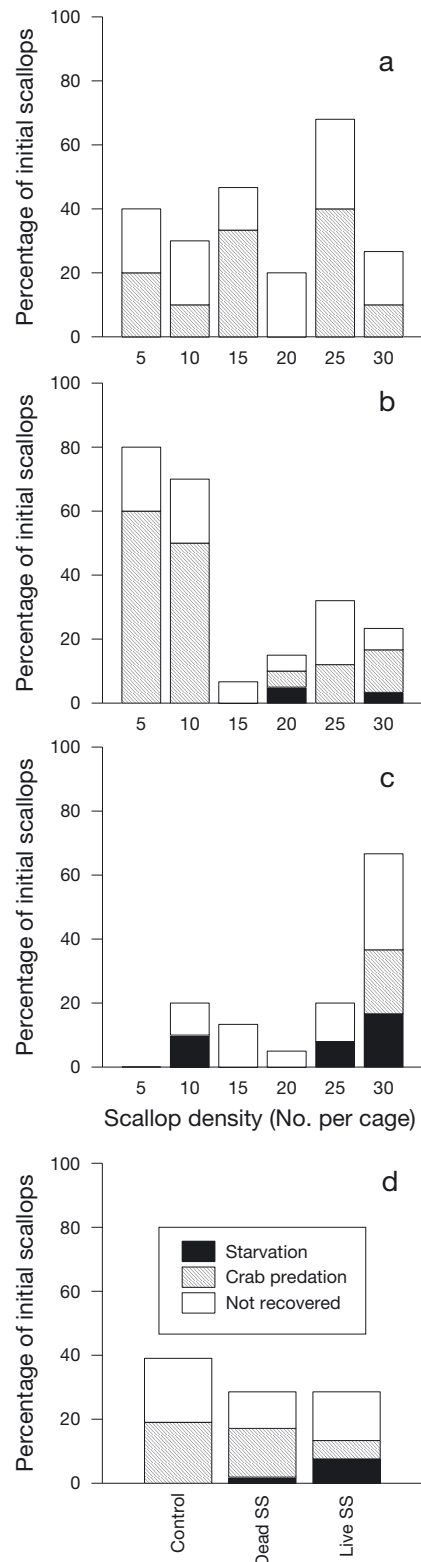


Fig. 4. Percentage of scallops lost to different sources of mortality in the (a) control, (b) dead screwshell and (c) live screwshell treatments. (d) Losses to the different sources of mortalities for all 3 treatments, pooled across all initial scallop densities. SS: screwshell



introduced species on the growth and development of commercially important species (Galimany et al. 2017) is a particular concern given the likely economic repercussions (Hall & Mills 2000). Therefore, the prioritisation of management for introduced species must include an estimate of impact to commercially important species.

### Interspecific and intraspecific competition

Intraspecific effects on growth have been well documented in bivalves (Peterson 1979, Peterson & Black 1987, 1988, Frechette & Daigle 2002) and have often been considered more important than interspecific effects in governing growth and development of individual bivalves (Peterson & Beal 1989) and whole populations (Weinberg 1985, 1998). The present work demonstrated a reduction in all scallop parameters of growth and condition, indicating an intraspecific density-dependent effect on *Pecten fumatus* growth and condition in the absence of screwshells. In fact, over the full array of scallop densities used in the experiment (5–30 m<sup>-2</sup>), intraspecific effects appeared to be greater than interspecific impacts in most, if not all, scallop parameters of growth and condition. However, considering that natural densities of juvenile *P. fumatus* are rarely likely to exceed 10 m<sup>-2</sup>, interpretation of impacts only at low densities of scallops (5–10 m<sup>-2</sup>) indicates that interspecific effects are likely to be greater than intraspecific effects.

Natural densities of live *Maoricolpus roseus* had a significant impact on the growth and condition of *P. fumatus* juveniles, thereby providing evidence of interspecific competition. The magnitude of the effect was consistent across all initial scallop densities (5–30 m<sup>-2</sup>). The presence of either live or dead and empty *M. roseus* shells greatly reduced the growth and condition of juvenile *P. fumatus*. Similar results were reported from experiments in which *P. fumatus* were caged with an exotic bivalve, *Corbula gibba* (Talman & Keough 2001), where growth rates of juvenile *P. fumatus* were markedly reduced when caged with the NIS.

### Potential mechanisms of impact

#### Reduced food quantity

The reduced growth and condition of scallops observed in the treatment with live screwshells can be partially explained by reduced food supply.

Restricted seston quantity and quality is often suggested to account for density-dependent effects observed in many bivalves (Peterson & Black 1987, 1988, Rheault & Rice 1996), including scallops (Pilditch & Grant 1999a,b). This could partially explain both the inter- and intraspecific effects observed in our experiment. Depletion of benthic and pelagic phytoplankton within the benthic boundary layer and the subsequent competition between individuals for food resources has been demonstrated in many suspension-feeding species (Wildish & Kristmanson 1984, Wildish et al. 1992, Jensen 1993, Josefson 1998) and at scales as large as whole estuaries (e.g. Nichols et al. 1990, Strayer et al. 1999).

If a reduction in seston quantity is to account for the reduced growth of scallops, this would require utilisation of similar food resources by both *P. fumatus* and *M. roseus*. *M. roseus* is capable of filtering particles 8 to 75 µm in size (T. Probst pers. comm.), although quantitative estimates of clearance rates and assimilation efficiencies of this species have only been determined for particles <10 µm (Scott 1997). Scallops, in general, are capable of retaining particles 2 to 350 µm, although 100% retention efficiency is attained only with particles exceeding 5 to 7 µm, and efficiency declines for particle sizes less than this (Shumway & Parsons 2006 and references therein). Clearance rates of screwshells range from 0.102 to 0.290 l h<sup>-1</sup> g<sup>-1</sup> dry weight (Scott 1997) dependent on particle concentration, and although quantitative estimates of clearance rates and assimilation efficiency for *P. fumatus* are unavailable, a similar scallop species, *Placopecten magellanicus*, exhibits clearance rates of 0.871 to 1.318 l h<sup>-1</sup> g<sup>-1</sup> dry weight (MacDonald & Thompson 1986). Given the strong overlap in particle size used by both species, the reduced growth in scallops cohabiting with live screwshells could be attributed, at least in part, to competition for food.

Benthic sources of phytoplankton can also be important to growth and development in scallop species (Shumway et al. 1987, Grant et al. 1997). While benthic resources in the form of detritus and benthic microalgae cannot alone sustain scallop growth and development (Cranford & Grant 1990, Grant & Cranford 1991), they are nonetheless an important source of nutrition for scallops, particularly when phytoplankton availability is low (Grant et al. 1997, Shumway & Parsons 2006). In this context, it is important to note that *M. roseus* may be capable of both suspension feeding and deposit feeding (Bax et al. 2003). The purported ability to switch feeding modes suggests that *M. roseus* might reduce growth in *P. fuma-*

*tus* by depleting both pelagic and benthic food sources. However, we note that the relative importance of the 2 feeding mechanisms employed by *M. roseus* is yet to be determined. Moreover, better quantitative estimates of site-specific consumption of pelagic and benthic particles by both *M. roseus* and *P. fumatus* are necessary to establish evidence of reduced benthic resources as a mechanism of impact.

#### Reduced food quality

High densities of *M. roseus* may also affect *P. fumatus* growth by reducing the quality of food resources or interfering with the scallop feeding and respiratory apparatus (Grant & Thorpe 1991). Both could arise as a secondary impact of the expulsion of large quantities of pseudo-faeces by the screwshell. This effect has been suggested for other bivalve species (Talman & Keough 2001). If pseudo-faecal exudates are not easily resuspended, the contents are simply removed from the available pool (Grant et al. 1997), directly reducing the quantity of resources available for consumption. Even if they are readily resuspended, plankton exudates in resuspended pseudo-faeces are likely to have highly altered nutritional value and chemical composition.

#### Competition for space

Competition for space is also likely to contribute to reduced growth rates of *P. fumatus* as evident by clear reductions in scallop growth and condition of *P. fumatus* juveniles caged with high densities of dead and empty screwshells. The effect of screwshells was more evident at low densities of scallops (5–10 ind. m<sup>-2</sup>). Conversely, at high initial scallop densities (25–30 ind. m<sup>-2</sup>), there was no evidence of restricted growth and development of scallops in the presence of dead screwshells. This suggests that at low scallop densities competition with screwshells for space reduces scallop growth and condition, while at high scallop densities intraspecific competition between juvenile scallops associated with food acquisition outweighs any effect of interspecific competition for space.

The reduced growth and condition observed in the dead and empty screwshell treatment suggests the possibility of a higher energy expenditure of these scallops. *P. fumatus* is a species that recesses or partially buries into the sediment, possibly to optimise feeding currents (Wildish et al. 1987, Wildish &

Saulnier 1992, 1993, Pilditch & Grant 1999b), minimize predation (Shumway & Parsons 2006) and/or assist in expulsion of pseudo-faeces. In areas where screwshells mat the surface, it is probable that scallops will continue to swim to attain a clear area of benthos in which to recess. This will increase energy use, and other studies have noted that it may take bivalves several hours to recover from swimming (Thompson et al. 1980, Brokordt et al. 2000a,b). This, compounded by less time spent filter feeding because of increased swimming, may ultimately reduce scallop growth rates and condition. Further, scallops unable to recess or positioned on top of screwshell mats may have to deal with sub-optimal current speeds and turbulence (Kirby-Smith 1972, Wildish & Kristmanson 1988, Pilditch & Grant 1999b), atypical boundary layer conditions (Wildish & Kristmanson 1984) and a higher exposure to predators (Shumway & Parsons 2006), all of which could inflict negative impacts on growth and condition.

#### Evidence of multiple mechanisms of impact

Identifying the mechanisms by which *M. roseus* impacts scallop growth and condition is aided by comparing responses to the treatment containing live screwshells with that of dead and empty screwshells. More specifically, effects in the treatment with live screwshells are likely to reflect a combination of interspecific competition for food and space, whereas the treatment with dead and empty shells is likely to reflect effects solely associated with interspecific competition for space.

While competition for space is more prevalently documented in intertidal sedentary species (Leppäkoski et al. 2002, McQuaid et al. 2015 and references therein), it is not unreasonable to conclude that the presence of dense screwshell mats that preclude access to the sediment by *P. fumatus* has resulted in a significant reduction in growth rate of the juvenile scallops.

Moreover, any observed effects in control cages can only result from intraspecific interactions. Given evidence of significant effects in all experimental treatments (including the control), there is clear evidence that intraspecific competition for food between *P. fumatus* individuals, interspecific competition for food between *P. fumatus* and *M. roseus* and interspecific competition for space all contribute, at least in part, to explaining the observed treatment effects. Previous evidence has indicated that the type and level of NIS impacts on native species is a function of

both the similarities in trophic level and the respective species (Thomsen et al. 2014). Given the trophic and functional similarities between *M. roseus* and *P. fumatus*, it is perhaps not surprising to see the level of impact observed in this study.

#### Scallop mortality

The experiment failed to detect differences between the treatments with respect to the rate and types of mortality experienced by juvenile *P. fumatus*. However, given that cages were designed to restrict access of potential scallop predators, it is not surprising only ~15% of *P. fumatus* juveniles were recovered having suffered some form of mortality. The result may be an artifact of predator exclusion; if there is differential predation in the presence and absence of screwshells, then the current design will not detect this. Regarding sources of mortality not related to predation, some studies have described starvation of bivalves in high densities, although death via resource limitation appears to be very uncommon (Peterson 1982, Talman & Keough 2001).

#### CONCLUSIONS

Many concerns have been raised regarding the establishment of *Maoricolpus roseus* in SE Australia and its potential impact on native soft-sediment assemblages. This experiment yields strong evidence that the growth, development and condition of the commercially important scallop species *Pecten fumatus* is significantly reduced by the presence of both dead and live *M. roseus* shells. The most likely mechanism is via interspecific competition for food; however, there is also clear evidence that the physical presence of *M. roseus* independent of their feeding also resulted in reduced growth and condition of scallops. The latter may result from higher metabolic costs associated with scallops swimming in an attempt to find clear sediment patches in which to recess. *P. fumatus* shows obvious preferences for bare sediment over benthos dominated by screwshells (A. P. Reid et al. unpubl.). It seems certain that the impact of *M. roseus* on scallop growth and condition extends beyond areas occupied by live *M. roseus* and includes accumulations of dead screwshells. Further, dead screwshell accumulations may persist for lengthy periods of time, and as a result, impacts associated directly with the physical presence of *M. roseus* shells may continue well past the lifespan of

screwshells. Furthermore, given the vast distribution of high densities of *M. roseus* in SE Australia, a vast area of seafloor is now sub-optimal habitat for *P. fumatus*. This indicates that the effect of the screwshell on scallop growth and condition and, by extension, the fishery in SE Australia has already been significant.

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