

Impact of an exotic clam, *Corbula gibba*, on the commercial scallop *Pecten fumatus* in Port Phillip Bay, south-east Australia: evidence of resource-restricted growth in a subtidal environment

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ABSTRACT: *Corbula gibba* (Olivi, 1792) a small exotic bivalve from the eastern Atlantic and the Mediterranean has been present in Port Phillip Bay, Victoria, Australia, from as early as 1987. *C. gibba* is widespread, abundant, and possesses characteristics such as fast growth which may confer a competitive advantage over endemic species like the commercial scallop *Pecten fumatus* Reeve, 1855. Experimental manipulations in the field showed that ambient densities of *C. gibba* significantly affected the size and growth of juvenile *P. fumatus*. This effect was greater than the effect of an equivalent number of conspecific scallops. *C. gibba* did not, however, affect scallop condition or survival in the short term, although the power of the test to detect a 50% decrease in survival was low. The percentage of experimental scallops lost to different sources of mortality was also unaffected by the presence of *C. gibba*, as was the density of predators found in experimental enclosures. This study is the first to experimentally demonstrate the impact of an introduced marine mollusc on an endemic species in Australia. A possible mechanism underlying this impact is competition for food, as both species are suspension feeders which live in an environment where resource limitation may occur.

KEY WORDS: Bivalve molluscs · Exotic/introduced/non-indigenous species · Density manipulation · Resource limitation

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INTRODUCTION

The introduction of non-indigenous aquatic species is a serious environmental problem globally. Accidentally or deliberately introduced species may threaten human health, fishing and aquaculture industries, and natural ecosystems of recipient environments (e.g. Nichols et al. 1990, Strayer et al. 1999). Bivalve molluscs include some particularly successful invaders of aquatic environments, as exemplified by the spread

and explosive population growth of the zebra mussel *Dreissena polymorpha*, in the Great Lakes system of North America (Griffiths et al. 1991) and the invasion of San Francisco Bay by the Asian clam *Potamocorbula amurensis* (Carlton et al. 1990). These invasions are reported to have had major ecological and, in the case of *D. polymorpha*, economic impacts (Nichols et al. 1990, Strayer et al. 1999).

Corbula gibba (Olivi, 1792), a small bivalve mollusc native to the eastern Atlantic and the Mediterranean, was first identified in Port Phillip Bay, Australia, in 1991 (Currie & Parry 1996) and subsequently identified in archived samples taken in 1987 (N. Coleman pers. comm.). Its occurrence in Port Phillip Bay is the first

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documented record of the species outside its area of natural distribution. Members of the family Corbulidae are cosmopolitan in distribution and occur in large numbers in their preferred habitat (Lamprell et al. 1998), characteristics that predispose them to successful establishment after introduction (e.g. Simberloff 1989).

Corbula gibba is now widespread and highly abundant in Port Phillip Bay (Talman 1998), so the natural ecosystem may be affected by its introduction. In some areas of the bay, *C. gibba* has been recorded in densities of 2600 m⁻² (Currie & Parry 1996), but it has the potential to reach densities of 53 000 m⁻² (Jensen 1990). *C. gibba* also possesses a number of characteristics that may give it a competitive advantage over endemic species, such as the capacity for fast growth (Jensen 1990) and the ability to tolerate a wide range of environmental conditions including partial anoxia (Christensen 1970), extreme eutrophication (Crema et al. 1991), and levels of turbidity that preclude other species (Bonvicini Pagliai et al. 1985).

Speculation on the impacts of exotic species is often based on long-term survey and observational data (Wilson et al. 1998, Currie & Parry 1999). While such information is undoubtedly important, experimental manipulation and quantitative data are required to dis-

tinguish the impact of an invasion from natural variability. Despite the huge numbers of exotic species documented in marine environments worldwide, such experimental data are surprisingly scarce (Ruiz et al. 1999). Of the 196 exotic marine species recorded in Australia (C. Hewitt pers. comm.), experimental impact data exist only for the fanworm *Sabella spallanzanii* (Holloway 1999), the seastar *Asterias amurensis* (J. Ross unpubl. data) and the shore crab *Carcinus maenas* (Sinclair 1997). No such data exist for *Corbula gibba*.

Corbula gibba might affect endemic species via habitat modification, predation on planktonic larvae, and competition, and 1 species of concern is the commercial scallop *Pecten fumatus* Reeve, 1852. The fishery for this species closed in 1996, partly as a result of depleted stocks. *C. gibba* and *P. fumatus* overlap in distribution. A bay-wide survey conducted in 1998 showed that they co-occurred at 15 of the 28 sites sampled, in sandy-muddy sediments at depths of 7 to 22 m (Talman 1998, Cohen et al. 2000). Also, as suspension feeders, they presumably utilize similar food resources. *C. gibba* and *P. fumatus* may therefore compete for space and/or food, especially in the deeper regions of Port Phillip Bay where *C. gibba* is highly abundant (Talman 1998).

Our study aimed to (1) experimentally determine the impacts of *Corbula gibba* and conspecific scallops on the size, growth, condition, and survival of juvenile native scallops in the field, as well as to (2) assess the effects of *C. gibba* and conspecific scallops on factors of scallop mortality such as starvation and crab predation. The experiment was conducted at 2 sites in Port Phillip Bay to assess the generality of the results.

MATERIALS AND METHODS

Port Phillip Bay is a semi-enclosed, predominantly tidal embayment (surface area of 1.95 × 10⁹ m²) that is linked to Bass Strait by a narrow entrance. The experiment was done at 2 sites within the Geelong arm of Port Phillip Bay, where scallops are known to occur. One site was located inshore, in 8 m of water, while the other was located further north, in 15 m of water (Fig. 1).

Pecten fumatus were obtained from Shellfish Culture Ltd., Tasmania, on 29 March 1999, and *Corbula gibba* were collected by divers in Port Phillip Bay during January 1999. All animals were held in laboratory aquaria with flow-through filtered (30 µm) seawater and occasionally fed powdered algae until 30 March 1999.

Immature scallops were used in this experiment because they are more likely to interact with *Corbula gibba* than adults: they are similar in size (approx. 10 to

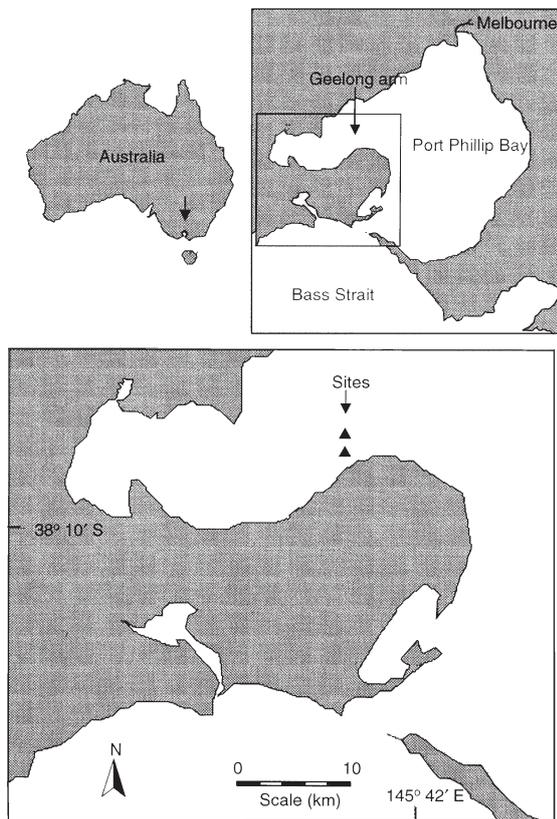


Fig. 1. Location of sites in Geelong arm of Port Phillip Bay, south-eastern Australia

15 mm in length compared to 7 to 10 mm for *C. gibba*), use the same microhabitat, and, perhaps, similar food resources. Immature scallops are also fast-growing, with few energy reserves, so the effects of competition on size and growth would be detected more readily than for adults. Using reproductively immature scallops also avoided the confounding effect of gametogenesis on soft tissue weight (Martinez & Mettifogo 1998).

Densities of both species were manipulated within experimental cages. Cages consisted of a steel frame (330×330 mm = 0.1 m², 200 mm height) covered with steel mesh (5 mm square). The mesh on the top of the cage was removable. To a base density of 30 juvenile *Pecten fumatus* per 0.1 m² (control), either 40 adult *Corbula gibba* (Treatment 1) or 40 extra juvenile scallops (Treatment 2) were added. This design allowed for the separation of intra- and interspecific effects on scallops, since Treatments 1 and 2 contained equal numbers of bivalves, although biomass was probably slightly greater in Treatment 2 because native scallops were initially larger than *C. gibba* individuals.

The density of *Corbula gibba* in Treatment 1 corresponded to local density, as determined from 20 random Eckman grab (0.025 m²) samples taken near the deeper site in February 1999. This density therefore dictated the density of extra scallops in Treatment 2. The base of *Pecten fumatus* was set at 30 individuals per 0.1 m² to allow for a sufficient number of individuals to be recovered for analysis. This meant the density in Treatment 2 was 70 juvenile scallops per 0.1 m². It is not known how this density relates to local densities of juvenile *P. fumatus* because such data are unavailable because of the cryptic nature of small scallops (Heasman et al. 1998) and their exclusion from stock-assessment surveys (Coleman 1998). However, according to data for juvenile *P. maximus* in Ireland, a density of 70 per 0.1 m² is possible (although exceptional) in the wild (Minchin 1992).

At each of the 2 sites, 9 cages were deployed (3 replicates of each treatment) in a Latin-square design. Cages were separated from each other by 1 m and pushed into the sediment to a depth of approximately 50 mm. The animals would not be in contact with the cage bottom at this depth because both species live close to the sediment-water interface (Yonge 1946, Coleman 1998). The use of cages and a large mesh size allowed the experimental bivalves to be exposed to the natural sediment and fauna of the site while preventing loss through emigration. The experiment commenced on 30 March 1999 and was recovered approximately 2 mo later, on 1 June 1999. Cages were cleared of accumulating algae and fouling organisms after 1 mo in the field to reduce the impact of these organisms on scallop growth.

Ten live scallops were randomly selected from each replicate at each site and 5 parameters were measured for each: shell area (mm²), shell growth (mm²), dry weight of shell and soft tissue, and ash-free dry weight of soft tissue (all weights in mg). To determine shell area, the surface area of the right valve was measured using BioScan Optimate 6.5 (Media Cybernetics, L.P., Silver Spring, MD), an image-analysis software package. To determine shell growth, the area of the shell at the time of deployment was measured and subtracted from the final shell area. It was possible to distinguish initial area because a single, highly visible disturbance ring was present on each shell. As these rings had not been present at the time of deployment, it was assumed that they represented the stress of relocation from the hatchery to the field. Such disturbance rings are readily formed on shells of young scallops (Minchin 1992). To determine shell and soft-body weights, the soft tissue was carefully removed from the shell and each component dried to a constant weight (60°C for 48 h). The ash content of the soft tissue was then determined by burning off organic matter in a muffle furnace (500°C for 7 h).

The condition index (ash-free dry soft tissue weight:dry shell weight) of these scallops was also determined (Lucas & Beninger 1985). Low values indicate that energy reserves have been depleted, either for maintenance under poor environmental conditions or for gametogenesis (Martinez & Mettifogo 1998). In this study, scallops were reproductively immature, so low index values would indicate an expenditure of energy for maintenance.

Animals in each cage were counted to obtain a value for percentage survival. The percentage of the original number of scallops that were lost to crabs (shells crushed and chipped), gastropods (shells with tubular boreholes), other agents such as starfish predation and starvation (shells undamaged) and unknown factors (shells missing) were determined. Potential predators found within each cage were identified and counted.

Comparisons of parameters were made with 2-factor (site and treatment) ANOVA. Cages were the unit for experimental replication, so mean values for individuals within each cage were used. If the effect of treatment was significant, planned comparisons were made between the control and each treatment. If the effect of treatment was non-significant, the power to detect a 50% decrease from the average control value was calculated. Before conducting an ANOVA, data were examined using boxplots to assess normality and homogeneity of variances. To satisfy these assumptions, it was necessary to log₁₀-transform shell area, shell growth, dry weight of shell and soft tissue, and ash-free dry weight of soft tissue and to arcsine square-root transform percentage data. Condition index and predator density did not require transformation.

Table 1. *Pecten fumatus*. Analysis of variance of body parameters (\log_{10} -transformed). Bold-face values: $p < 0.05$

| Source of variation | df | Mean square | F | p |
|---|----|-------------|-------|--------------|
| Shell area (mm²) | | | | |
| Site | 1 | 0.031 | 6.853 | 0.022 |
| Treatment | 2 | 0.020 | 4.518 | 0.034 |
| Site × Treatment | 2 | 0.000 | 0.072 | 0.931 |
| Residual | 12 | 0.005 | | |
| Shell growth (mm²) | | | | |
| Site | 1 | 0.205 | 6.236 | 0.028 |
| Treatment | 2 | 0.142 | 4.327 | 0.038 |
| Site × Treatment | 2 | 0.002 | 0.068 | 0.935 |
| Residual | 12 | 0.033 | | |
| Shell dry wt (mg) | | | | |
| Site | 1 | 0.052 | 5.374 | 0.039 |
| Treatment | 2 | 0.046 | 4.714 | 0.031 |
| Site × Treatment | 2 | 0.001 | 0.092 | 0.913 |
| Residual | 12 | 0.010 | | |
| Soft tissue dry wt (mg) | | | | |
| Site | 1 | 0.072 | 5.651 | 0.035 |
| Treatment | 2 | 0.069 | 5.452 | 0.021 |
| Site × Treatment | 2 | 0.006 | 0/481 | 0.630 |
| Residual | 12 | 0.013 | | |
| Soft tissue ash-free dry wt (mg) | | | | |
| Site | 1 | 0.028 | 1.742 | 0.212 |
| Treatment | 2 | 0.064 | 3.974 | 0.047 |
| Site × Treatment | 2 | 0.000 | 0.006 | 0.994 |
| Residual | 12 | 0.016 | | |

Table 2. *Pecten fumatus*. Planned comparisons between treatments for body parameters (\log_{10} -transformed). Bold-face values: $p < 0.05$

| Source of variation | Comparison |
|---|---|
| Shell area (mm²) | |
| Control vs Treatment 1 | $F_{1,12} = 8.900, p = \mathbf{0.011}$ |
| Control vs Treatment 2 | $F_{1,12} = 1.373, p = 0.264$ |
| Shell growth (mm²) | |
| Control vs Treatment 1 | $F_{1,12} = 8.629, p = \mathbf{0.012}$ |
| Control vs Treatment 2 | $F_{1,12} = 1.769, p = 0.208$ |
| Shell dry wt (mg) | |
| Control vs Treatment 1 | $F_{1,12} = 9.418, p = \mathbf{0.010}$ |
| Control vs Treatment 2 | $F_{1,12} = 2.087, p = 0.174$ |
| Soft tissue dry wt (mg) | |
| Control vs Treatment 1 | $F_{1,12} = 10.652, p = \mathbf{0.007}$ |
| Control vs Treatment 2 | $F_{1,12} = 4.274, p = 0.061$ |
| Soft tissue ash-free dry wt (mg) | |
| Control vs Treatment 1 | $F_{1,12} = 7.905, p = \mathbf{0.016}$ |
| Control vs Treatment 2 | $F_{1,12} = 1.504, p = 0.244$ |

RESULTS

Corbula gibba had a significant impact on the terminal size and growth of the shell, on the dry weight of shell and soft tissue, and on the ash-free dry weight of

Table 3. *Pecten fumatus*. Analysis of variance for condition index

| Source of variation | df | Mean square | F | p |
|---------------------|----|-------------|-------|-------|
| Site | 1 | 0.000 | 0.904 | 0.360 |
| Treatment | 2 | 0.000 | 0.333 | 0.723 |
| Site × Treatment | 2 | 0.000 | 0.185 | 0.833 |
| Residual | 12 | 0.000 | | |

Table 4. *Pecten fumatus*. Analysis of variance of survival (%) (arcsine square-root transformed)

| Source of variation | df | Mean square | F | p |
|---------------------|----|-------------|-------|-------|
| Site | 1 | 0.005 | 0.049 | 0.829 |
| Treatment | 2 | 0.050 | 0.480 | 0.630 |
| Site × Treatment | 2 | 0.087 | 0.828 | 0.460 |
| Residual | 12 | 0.105 | | |

soft tissue of juvenile *Pecten fumatus* (Table 1, Fig. 2). Compared to scallops in the control treatment, scallops in the presence of *C. gibba* had shells that were, on average, 35 % lighter, 24 % smaller, and exhibited 54 % less growth (Table 2, Fig. 2). Similarly, individual soft tissue weight was, on average, 40 % less than that obtained for control scallops (Table 2, Fig. 2). While *C. gibba* had a significant impact on the size and growth of scallops compared to controls, an equivalent number of extra scallops did not (Table 2, Fig. 2). The patterns were similar between sites, with no significant site-treatment interaction for any of the parameters measured (Table 1).

The condition of the scallops was variable and showed no significant relationship with either site or treatment (Table 3, Fig. 3). The power to detect a 50 % decrease in condition index from the average value in the control treatment was >0.99 ($\alpha = 0.05$). Scallop survival was also highly variable and did not differ between sites or treatments (Table 4, Fig. 3), although the power to detect a 50 % decrease in survival from the average control value was low (0.29, $\alpha = 0.05$). The percentage of scallops lost to different sources of mortality did not differ between sites or treatments (Table 5). Approximately 40 % of the scallops were lost to unknown factors, as the shells were missing from the cages (although this indicates predation of a sort that breaks up the shell), and another 10 % were lost to agents of mortality that do not damage the shell, such as starfish predation, starvation and disease (Fig. 4). Crabs killed about 3 % of the original number while no shells were found with the characteristic boreholes of predatory gastropods (Fig. 4). The only potential predators to be recovered from experimental cages were the crab species *Litocheira bispinosa*, *Paguristes*

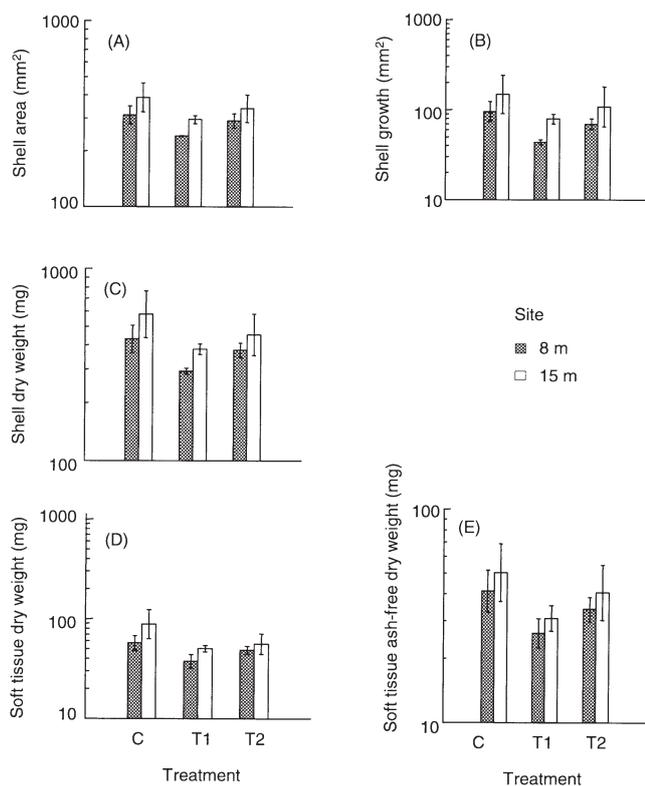


Fig. 2. *Pecten fumatus*. Area (A), growth (B) and dry wt (C) of juvenile shell and dry wt (D) and ash-free dry wt (E) of soft tissue (mean \pm SE) amongst treatments and sites at conclusion of the experiment. C: control, 30 *Pecten fumatus*; T1: Treatment 1, 30 *P. fumatus* + 40 *Corbula gibba*; T2: Treatment 2, 70 *P. fumatus*. Note differences in scale

pugil, *Ebalia (Phlyxia) intermedia* and *Pilumnopus serratifrons*, which were significantly more abundant at the shallow site (Table 6, Fig. 5).

The terminal size and growth of the shell and the dry weight of shell and soft tissue of juvenile *Pecten fumatus* were significantly greater at the 15 m-deep site than at the 8 m deep site for all treatments (Table 1, Fig. 2).

DISCUSSION

Ambient densities of *Corbula gibba* had a significant impact on the size and growth of the native juvenile *Pecten fumatus* at both sites. There is a general paucity of experimental tests of such impact worldwide (Ruiz et al. 1999), but particularly for introduced marine species in Australia. In terms of marine molluscs, experimental data only exist for species introduced into North America (e.g. Race 1982, Crooks 1998). While *C. gibba* had a significant impact on the size and growth of scallops compared to the controls, an equiv-

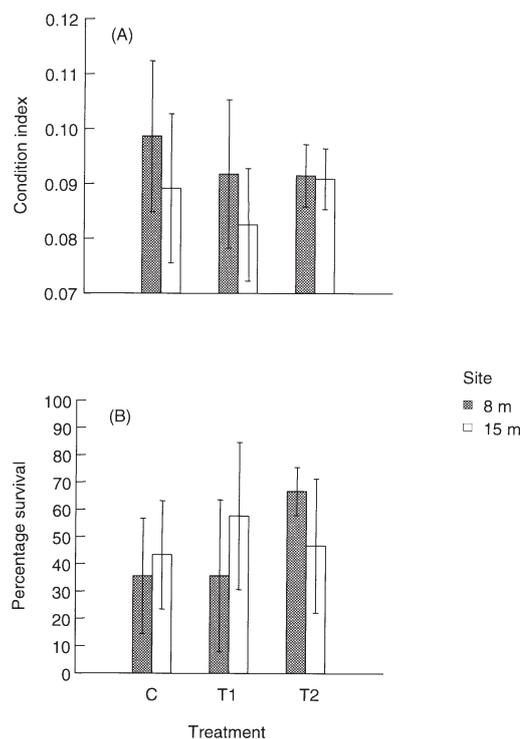


Fig. 3. *Pecten fumatus*. Condition and percentage survival of juveniles (mean \pm SE) amongst treatments and sites at the conclusion of the experiment. Treatments as in Fig. 2. Percentage survival data were arcsine square-root transformed for analysis. Note differences in scale

alent number of additional scallops did not. This indicates that at the experimental density, which is rarely attained in the wild (Minchin 1992), juvenile *Pecten fumatus* do not compete with each other. Ólafsson

Table 5. *Pecten fumatus*. Analysis of variance for percentage lost to various sources of mortality (arcsine square-root transformed)

| Source of variation | df | Mean square | F | p |
|-------------------------|----|-------------|-------|-------|
| Crab predation | | | | |
| Site | 1 | 0.001 | 0.079 | 0.784 |
| Treatment | 2 | 0.004 | 0.231 | 0.797 |
| Site \times Treatment | 2 | 0.020 | 1.217 | 0.330 |
| Residual | 12 | 0.016 | | |
| Other agents | | | | |
| Site | 1 | 0.007 | 0.175 | 0.684 |
| Treatment | 2 | 0.015 | 0.371 | 0.698 |
| Site \times Treatment | 2 | 0.005 | 0.109 | 0.898 |
| Residual | 12 | 0.042 | | |
| Unknown factors | | | | |
| Site | 1 | 0.000 | 0.005 | 0.947 |
| Treatment | 2 | 0.079 | 0.940 | 0.417 |
| Site \times Treatment | 2 | 0.045 | 0.543 | 0.595 |
| Residual | 12 | 0.084 | | |

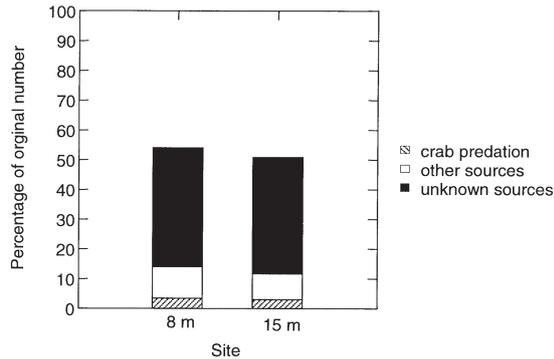


Fig. 4. *Pecten fumatus*. Mean percentage of original number of juveniles lost to crab predation (shells crushed and chipped), to other sources such as starfish predation and starvation (shells undamaged) or to unknown factors (shells missing) amongst sites. Data were arcsine square-root transformed for analysis

(1986) found that *Macoma balthica* was also unaffected by increased density, but other studies have demonstrated density-dependent growth for various bivalves (Broom 1982, Peterson 1982, Peterson & Black 1987, 1988, Peterson & Beal 1989), including *P. fumatus*, although this result was obtained at the artificially high densities used in aquaculture operations (Heasman et al. 1998). The greater importance of inter- versus intraspecific effects on the growth of juvenile *Pecten fumatus* contrasts with the results of Peterson (1982), who found that interspecific effects were usually non-significant and consistently far smaller than intraspecific effects.

The potential mechanisms underlying the impact of *Corbula gibba* on juvenile *Pecten fumatus* include competition for space and/or food. Space is unlikely to have been the limiting resource. Assuming *C. gibba* and *P. fumatus* to have the maximum sizes of 10 and

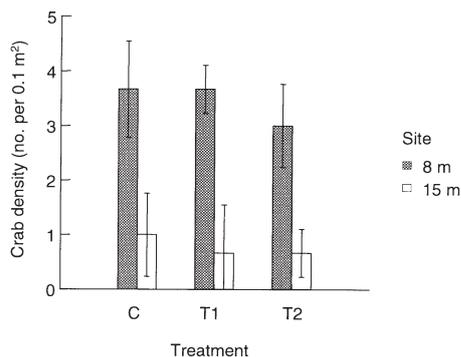


Fig. 5. Density (mean \pm SE) of crabs found in experimental cages amongst treatments and sites at the conclusion of the experiment. Treatments as in Fig. 2

Table 6. Analysis of variance of density (nos. per 0.1m²) of crabs (various species) in experimental cages. Bold-face values: $p < 0.05$

| Source of variation | df | Mean square | F | p |
|-------------------------|----|-------------|--------|--------------|
| Site | 1 | 32.000 | 36.000 | 0.000 |
| Treatment | 2 | 0.389 | 0.438 | 0.656 |
| Site \times Treatment | 2 | 0.167 | 0.187 | 0.831 |
| Residual | 12 | 0.889 | | |

15 mm respectively and to be square in shape, areal coverage by bivalves would have been approximately 10% in Treatment 1 and 14.5% in Treatment 2. In addition, *P. fumatus* is essentially epibenthic while *C. gibba* is endobenthic, reducing actual crowding. Another possible mechanism is competition for food. The quality and quantity of available food is one of the primary factors controlling growth and fecundity in pectinids (e.g. MacDonald & Thompson 1985, Pilditch & Grant 1999). Food limitation may therefore have a pronounced effect on size and growth. However, this mechanism can only account for the observed pattern if *C. gibba* and *P. fumatus* utilise some of the same food items and local food depletion by bivalves occurs. *C. gibba* and *P. fumatus* are suspension feeders that live and feed at the sediment surface and so, presumably, utilise similar food resources. Benthic food species are important for the scallop, *Placopecten magellanicus* (Shumway et al. 1987) and probably for *C. gibba*, as it ingests a large amount of sediment during feeding (Yonge 1946). However, data on the actual size and character of particles consumed by *C. gibba* and *P. fumatus* are not available.

Food (or 'seston') limitation is thought to be responsible for density-dependent effects in other bivalves (Broom 1982, Peterson 1982, Peterson & Black 1987, 1988, Peterson & Beal 1989), and there is some quantitative evidence of seston depletion by intertidal bivalves (e.g. Fréchette & Bourget 1985, Peterson & Black 1991). Similarly, benthic bivalves may have a significant impact on phytoplankton biomass in shallow estuaries (Cloern 1982, Nichols 1985, Strayer et al. 1999). This impact is, in some cases, attributed to exotic bivalves such as *Potamocorbula amurensis* in northern San Francisco Bay (Alpine & Cloern 1992) and *Corbicula fluminea* in the Potomac River estuary (Cohen et al. 1984). These studies were all conducted in intertidal areas or in estuaries with mean depths of 2 to 8 m, while our study sites were located in 8 and 15 m of water.

It is possible that seston depletion also occurs in these deeper waters because seston concentration, in the form of chlorophyll *a*, is relatively low in Port

Phillip Bay (range of 0.63 to 1.45 $\mu\text{g l}^{-1}$; Arnott et al. 1997). Similarly, in the 'inner' zone of the bay, where *Corbula gibba* and *Pecten fumatus* co-occur, vertical mixing of the water column is weak (Black et al. 1993). If vertical mixing is reduced, replenishment of the benthic boundary layer is decreased and the boundary layer may become depleted of food particles, particularly if the removal rate by suspension feeders is high (Wildish & Kristmanson 1997).

The surprisingly greater strength of interspecific effects of *Corbula gibba* on juvenile scallops may be due to faster and/or more efficient filtration by *C. gibba*. Standardised filtration rates (volume per unit time per unit weight) are unavailable, but Kiørboe & Møhlenberg (1981) found that *C. gibba* was more efficient at removing food from inhalant water than another scallop species, *Aequipecten opercularis*. Most of the overlap in the distribution of *C. gibba* and *Pecten fumatus* occurs in soft-sediment areas, where above-bottom turbidity is higher than in sandy habitats (e.g. Young & Rhoads 1971), so an enhanced ability to select organic from inorganic material is an obvious advantage.

Corbula gibba also has adaptations for disposing of large quantities of pseudo-faeces (Yonge 1946), which is another advantage in turbid environments. Part of the negative impact of *C. gibba* on juvenile scallops may be due to these biodeposits, which can interfere with the feeding and subsequent growth of *Pecten fumatus* by clogging its feeding mechanisms (Riisgård & Møhlenberg 1979). The effects of *Corbula gibba* did not extend to the condition index, and the power to detect a difference in scallop condition between treatments was high, so although scallops were smaller and grew less in the presence of *C. gibba*, they were not more physiologically 'stressed' than scallops in the control treatment. Rather than depleting energy reserves to maintain growth, scallops with *C. gibba* grew more slowly.

Similarly, juvenile scallop survival did not differ between treatments and sites, but the power to detect a 50% decrease in survival was low, so this result needs to be viewed with caution. Other studies that have demonstrated density-dependent growth in bivalves have found survival to be density-independent (Peterson 1982, Peterson & Black 1987, Heasman et al. 1998). Peterson (1982) suggested that mortality is the last response to competitive stress, following emigration and effects on growth and reproduction. So, although *Corbula gibba* does not reduce the survival of *Pecten fumatus* over 2 mo, it may do so in the long term or it may increase the susceptibility of scallops to other factors (Peterson & Black 1988). Only 48% of juvenile scallops survived the experimental period. This value is very low compared to survival of juveniles protected

by mesh in Jervis Bay, New South Wales (Heasman et al. 1998), but similar to estimates for unprotected adult populations in Port Phillip Bay (Gwyther & McShane 1988). Even though the removable mesh on top of the cages was tied down, small gaps probably allowed access to predators. This high rate of mortality may mean that the survivors who were analysed for their size and growth may have been initially larger or better able to escape predation. *C. gibba* may therefore have an even greater impact on the less 'fit' juveniles in a population.

The percentage of scallops lost to different sources of mortality did not differ between sites and treatments, despite a larger number of crabs being found in cages at the shallow site. A high percentage was missing from the cages so this source of mortality could not be determined, although it is likely that crab predation was responsible, given that complete shells could not pass through the mesh. Of the crab species found within the cages, *Pilumnopus serratifrons* and *Litochceira bispinosa* would be capable of crushing juvenile scallop shells. Crabs as well as starfish are significant predators of *Pecten fumatus* elsewhere in Australia (Heasman et al. 1998).

Experimental cages were necessary to maintain treatment densities and to enable retrieval of cryptic juvenile scallops in conditions of poor visibility. However, cages introduce artifacts. For example, the importance of predation as a source of mortality is probably under-estimated, given that cages exclude large predators. Similarly, the cage and its associated fouling community alter water flow, which in turn affects food availability, and the sedimentary and physicochemical environment within the cage (Hulberg & Oliver 1980). Peterson & Beal (1989) found that *Mercenaria mercenaria* growth was enhanced by up to 21% inside enclosures, indicating increased food supply. This does not affect the test, as identical cages were used for all treatments, but it is possible that the experiments underestimate the impacts that may occur in more food-limited situations. Cages also prevent emigration, which may be the first response to resource limitation (Peterson 1982). However, even if juveniles were able to move, *Corbula gibba* is so widespread and abundant, that they may have difficulty finding low-density patches within swimming distance.

Our study provides experimental evidence of resource-restricted growth of bivalves in deep subtidal environments, in contrast to previous work in this area, which has only focussed on bivalves in shallow-water systems. The study is also unique in experimentally demonstrating the impact of an introduced mollusc on an endemic species in Australia, although a better understanding of the impact may be obtained by using a range of natural densities of both species in further

experiments. Experimental data such as these are important for assessing the true nature of invasion impacts around the world.

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