

## Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve

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### Abstract

Responses of benthic macrofauna and epibenthic predators/sediment disturbers to controlled density (0, 12, 120, 600 and 1200 individuals  $\text{m}^{-2}$ ) and patch size (0.25, 1.0 and 9.0  $\text{m}^2$ ) manipulations of the venerid bivalve *Austrovenus stutchburyi* (Gray) were examined on an intertidal sandflat. Bivalve density manipulations greater than 600  $\text{m}^{-2}$  had a mixed influence on macrofauna colonisation; two species were reduced, three enhanced and three were unaffected. There was no clear functional group-related pattern as to which species were affected by *Austrovenus*. The most pronounced influence of high bivalve densities was the reduction in the abundance and alteration of the size-structure of post-set (ca. 250–360 mm) tellinid bivalves, *Macomona liliana* Iredale. Patch size manipulations of *Austrovenus* had no measurable effect on macrofauna colonisation, probably because patch density (120 bivalve  $\text{m}^{-2}$ ) was too low. While a variety of epibenthic predators were present at the study site, *Austrovenus stutchburyi* mortality estimates in both experiments were relatively low (0.01–0.03% individuals lost  $\text{day}^{-1}$ ) and were independent of both density and patch size. In contrast, the proportion of nipped bivalve siphons was relatively high (11–37%) in both experiments. While proportions of nipped siphons were similar across the range of manipulated densities, siphon browsing was more than 2 times higher in 9.0  $\text{m}^2$  plots than 0.25  $\text{m}^2$  plots. Scale-dependent foraging of sub-lethal marine benthic predators is previously unreported and our results illustrate the necessity for conducting studies on predator–prey dynamics at ecologically meaningful spatial scales for both the predator and prey species. © 1997 Elsevier Science B.V.

**Keywords:** Sandflat; Colonisation; Adult–juvenile interaction; Patch dynamics

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## 1. Introduction

Considerable attention has been directed to studying the role resident adult infaunal invertebrates have determining the structure of assemblages in soft sediment habitats. Apart from potential taxonomic biases and density-dependent variations in adult–juvenile interactions, Ólafsson et al. (1994) recently concluded that deposit-feeding and predatory infaunal invertebrates typically act to reduce recruitment, whereas suspension-feeding molluscs generally exert much less effect on the recruitment dynamics of infaunal organisms. Others, however, have shown that suspension-feeders can have strong interactions of benthic–pelagic coupling in shallow water (Dame, 1993, for a recent review) and may affect infaunal community structure by removing small planktonic larvae before they reach the sediment surface (e.g., Kristensen, 1957; Woodin, 1976; André et al., 1993). In addition, modification of local boundary flow patterns by physical structures (e.g., Eckman, 1985) and siphonal currents (e.g., Monismith et al., 1990; O’Riordan et al., 1993) may also influence larval settlement. Suspension-feeding bivalves also may interact with deposit-feeding populations by removing phytoplankton and/or by deposition of faeces or pseudofaeces (e.g., Cloern, 1982; Officer et al., 1982; Lin and Hines, 1994). Large infaunal bivalves that live near the sediment surface can also affect other species by providing refugia from predation (e.g., Luckenbach, 1987; Peterson and Black, 1993). Lastly, several authors have noted the spatial scale at which many experimental studies of benthic suspension feeders have been conducted may limit the generality of conclusions as well as explain the apparent inconsistencies of the interactions of resident suspension-feeding bivalves and other benthic invertebrates (e.g., Black and Peterson, 1988; André and Rosenberg, 1991; André et al., 1993).

Since most benthic organisms are patchily distributed over a range of spatial scales (e.g., Thrush, 1991), it is important to study the major variables characterising these spatial arrangements: organism density and three components of scale (grain or patch size, lag or distance between patches and extent or area occupied (Thrush et al., 1997a). These components of the spatial arrangement of density can be independently manipulated in experiments, at least up to the 10’s m scale, to identify their role in affecting ecological processes. The goal of this study was to assess benthic fauna responses to manipulations of patch size (grain) and density of a common suspension-feeding bivalve, *Austrovenus stutchburyi* (Gray) inhabiting an intertidal sandflat habitat.

The focus of our study was to assess how macroinfaunal recruitment and epibenthic bivalve predators/sediment disturbers responded to controlled manipulations of *Austrovenus stutchburyi* density and patch size. Experimental density manipulations were restricted to naturally meaningful levels (e.g., Ólafsson et al., 1994; Thrush et al., 1996) and similarly, variations in spatial arrangement reflected natural patterns of the shellfish at the study site. For example, Hewitt et al. (1996) found an average *Austrovenus* density (mean  $\pm$  SD) of  $740 \pm 458 \text{ m}^{-2}$  in a  $50 \text{ m}^2$  area of study site with high bivalve densities. They also found spatial structure of *Austrovenus* at 1.3 and 3 to 3.7 m and also indicated smaller-scale variations at about 30 cm.

Our experiments were designed to test several hypotheses. Those related to the effects of altering *Austrovenus stutchburyi* density were: (a) macrofauna recruitment will be

reduced at high bivalve densities due to shellfish filtration and space limitation (e.g., Woodin, 1976; Cloern, 1982; Lin and Hines, 1994; André et al., 1993), (b) macroinfauna recruitment and/or immigration responses will be dependent upon functional group (e.g., tube-building species will be negatively affected by dense populations of suspension feeders while burrowing species will remain unaffected (Woodin, 1976; Jensen, 1984; Flach, 1992)), (c) at intermediate bivalve densities, macrofauna recruitment will be enhanced due to sediment stabilisation by shell structure and possible enrichment by production of pseudofaeces for surface deposit feeders (e.g., Commito and Boncavage, 1989) and (d) due to predator aggregation foraging behavior, both lethal and sublethal predation will increase with bivalve density (e.g., Hassell and May, 1985; “prey taxis”: Kareiva and Odell, 1987). Hypotheses related to manipulation of grain were: (a) larger patches of suspension feeders will result in lower macrofauna recruitment for species with low flux rates or small scales of movement due to a reduced ratio of perimeter to area (e.g., Smith and Brumsickle, 1989; Thrush et al., in press) and (b) lethal and sublethal predation on the bivalves should be most pronounced on largest patches of prey due to aggregative predator responses (e.g., Wilson, 1990; Colwell and Landrum, 1993; Horne and Schneider, 1995). These hypotheses were tested by manipulating either patch size with a constant density of *Austrovenus* or bivalve density in a patch of constant grain.

## 2. Methods

### 2.1. Study species

*Austrovenus stutchburyi* is widely distributed throughout the estuaries and harbours of New Zealand (Morton and Miller, 1973) and is often a dominant member of macrofauna communities (Paul, 1966; Cassie and Michael, 1968; Blackwell, 1984; Pridmore et al., 1990; Turner et al., 1995). This venerid bivalve is an obligate suspension feeder with short siphons that restrict it to the upper 1–3 cm of the sediment column. Predators of *Austrovenus* in the nearshore zone include wading shore birds (South Island Pied Oystercatcher *Haematopus ostralegus finschii* Martens, Red Knot *Calidris canutus rogersi* (Mathews), Eastern Bar-Tailed Godwit *Limosa lapponica baueri* Naumann) and gulls (Southern Black-backed Gull *Larus dominicanus* Lichtenstein, Red-billed Gull *Larus novaehollandiae scopulinus* Foster), as well as eagle rays (*Myliobatis tenuicaudatus* (Hector), crabs and gastropods (e.g., Knox, 1980; Thrush et al., 1991, 1994; Cummings et al., 1997). Several species of flounder (*Rhombosolea leporina* Gunter and *R. plebeia* Richardson) found at the study site are reported to inflict considerable siphon-nipping on *Austrovenus* (Webb, 1973; Kilner, 1974).

### 2.2. Study area

This study was conducted in the mid-intertidal zone of a sandflat located adjacent to Wiroa Island in Manukau Harbour, New Zealand (37°02' S, 174°41' E). Sediments in this area are composed of predominantly (>90%) well-sorted fine sand, and the

sediment surface is relatively homogeneous with the main physical features being sand ripples (0–2 cm high) and small drainage runnels. Biogenic structures common throughout the intertidal zone are primarily feeding pits created by eagle rays, siphon traces of *Macomona liliana* (Ireland) and small (< 10 m<sup>2</sup>) patches of eelgrass (*Zostera* sp.). Further descriptions of the biological and physical features of the Wiroa Island tidal flat habitat are presented in Thrush et al. (1997a).

### 2.3. General experimental procedures

We conducted two experiments that manipulated either grain (patch size) at a constant density or patch density at a constant grain of *Austrovenus stutchburyi* (Fig. 1(A–C)). The two experiments were established in adjacent areas of the mid-intertidal zone in a region selected for its very low ambient density of *Austrovenus* (e.g., < 4 individuals m<sup>-2</sup>) and absence of eelgrass patches. Approximately 11 500 adult *Austrovenus* (15–30

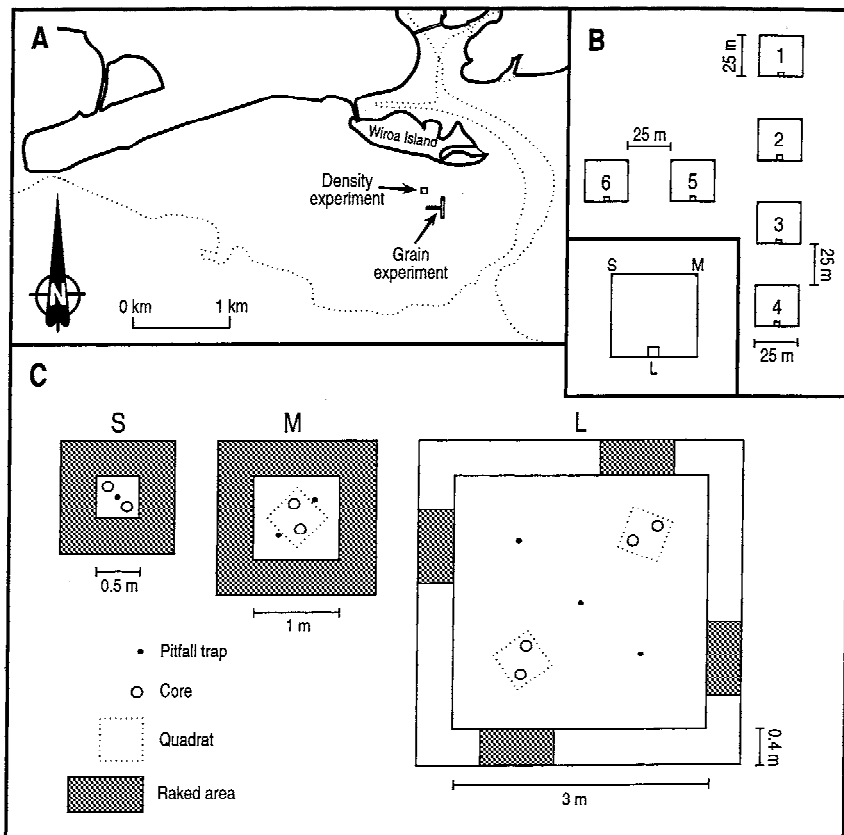


Fig. 1. Map of study site. (A) Locations of the *Austrovenus stutchburyi* density and grain experiments. (B) Layout of experimental blocks (1–6) of the grain experiment ( $S = 0.25 \text{ m}^2$ ;  $M = 1.0 \text{ m}^2$ ;  $L = 9.0 \text{ m}^2$  plots). (C) Details related to sampling associated with both experiments.

mm shell length) were collected about 200 m from the experimental plots by raking the upper 4–6 cm of the sediment. Collections were made on 4 days during January and February 1994 to provide shellfish as needed within 1–3 h of establishing experimental plots. Live, undamaged bivalves were placed in a cooler and transported for addition to the replicated experimental plots during low tide. Before the bivalves were added, each experimental plot was marked at 4 corners with metal pegs and core sample(s) (13 cm diameter, 15 cm deep) were taken. The number of cores collected increased with plot size to reduce possible increases in variability in density estimates with increasing plot size: 1 core was taken from each 0.25 m<sup>2</sup> (grain experiment only); 2 cores were taken from 1.0 m<sup>2</sup> plots (grain and density experiments); and 4 placed in 2 pairs were taken from 9.0 m<sup>2</sup> plots (grain experiment only). Surface sediment obtained adjacent to each plot was used to fill in the holes created by the cores.

Before *Austrovenus stutchburyi* were added, pitfall traps consisting of a 5 cm diameter by 30 cm long PVC pipe (with a capped bottom) were buried vertically with the tops flush with the sediment surface of each plot, with the number of traps depending on the size of the plot: 1 in the middle of each 0.25 m<sup>2</sup> plots; 2 in 1.0 m<sup>2</sup> plots; and 3 in 9.0 m<sup>2</sup> plots. The pitfall traps were capped and pushed 1–3 cm below the sediment surface except when operated for specific periods (see below). *Austrovenus* were then added to experimental plots at specified densities by distributing them haphazardly over the entire plot area and then gently pushing the posterior edge of the shell about half way into the sediment. Nearly all (>95%) of the bivalves completely burrowed into the sediment within 3 h after being planted and before the tide re-covered the plots.

Predator responses to the experimental treatments were assessed in several ways during the experimental periods. Each plot was checked 2–3 times per week, and all articulated dead *Austrovenus stutchburyi* shells were recorded and removed. During these checks, we also recorded and removed hammered shells characteristic of predation by oystercatchers, the most abundant wading birds preying on adult *Austrovenus* observed on the tidal flat (Cummings et al., 1997). We also noted the occurrence of eagle ray feeding pits within the experimental plots. To estimate the activity of small mobile predators and surface sediment disturbers (e.g., crabs, gastropods), the pitfall traps were opened in each plot during a 24 h period on 9 February 1994 in the middle of the experimental period, and all organisms collected in the traps were identified to species and counted. Siphon-nipping activity of demersal fish (especially 50–235 mm long flounders (*Rhombosolea* spp.) found on the tidal flat) was estimated by haphazardly collecting 10–50 cockles (depending on treatment) subsampled from each plot at the end of the two experiments. The bivalves were opened by cutting the adductor muscle and examined under a dissecting microscope. The siphon of each individual was scored as intact (full-length tentacular fringe and black pigment on distal end), nipped (tentacles and pigment missing), or regenerating (pigment and tentacular rudiments becoming apparent) (e.g., Peterson and Quammen, 1982; Coen and Heck, 1991; Irlandi, 1994).

At the end of the experiments, a 0.25 m<sup>2</sup> quadrant was placed on the surface of each experimental plot and two cores (13 cm diameter, 15 cm deep) were taken (Fig. 1(C)). To estimate abundances of larger bivalves, the remaining sediment was excavated to a depth of 20 cm and sieved on a 4 mm mesh. All retained bivalves were identified and counted. To estimate abundances of other macrofauna species, the cores were sieved on

nested sieves of 180 and 500 mm mesh, and all retained organisms in each fraction were preserved (10% formalin with rose bengal) and later identified and counted. Shell lengths of all bivalve found in the samples were measured, either with vernier callipers (individuals  $> 1$  mm shell length) or under a dissecting microscope fitted with an ocular micrometer (individuals  $< 1$  mm shell length).

To estimate *Austrovenus stutchburyi* ( $> 4$  mm shell length) emigration from the plots, a 40 cm wide band around the perimeter of the plots was raked and searched by hand to a depth of ca. 5 cm (Fig. 1(C)). In preliminary tests, a second 40 cm wide band was raked around the outside of the first band. However, no additional bivalves were recovered (indicating that emigration *Austrovenus* ( $> 4$  mm shell length) did not extend beyond 40 cm from the edges of the plots), so this was discontinued. For 0.25 and 1.0 m<sup>2</sup> plots the entire perimeter was sampled; but for 9.0 m<sup>2</sup> plots, only 25% of each side was subsampled (Fig. 1(C)). Samples were sieved on a 4 mm mesh and all retained living *Austrovenus* were recorded.

#### 2.4. Grain experiment design

Grain treatments were established using a complete randomized block design consisting of six, 25 m  $\times$  25 m, blocks separated by 25 m (Fig. 1(B)). Each block contained one replicate of each of the 3 patch sizes: small (0.25 m<sup>2</sup>), medium (1.0 m<sup>2</sup>) and large (9.0 m<sup>2</sup>). In all treatments a constant density of 120 *Austrovenus stutchburyi* m<sup>-2</sup> was used. The large patch was located midway along the seaward side of each block, and the medium and small patches were located at the corners of the opposite side. The blocks were arranged in a T-shaped pattern of four blocks in a row perpendicular to shore and two blocks positioned parallel to shore from the middle of the row, which oriented the blocks normal to the prevailing currents delivering larvae, recruits and potential predators (Fig. 1(B)). To consider interactive effects of spatial position with treatment effects, adjacent blocks were paired into three big blocks (termed “location effect”) to provide sufficient degrees of freedom for statistical tests of interaction between location and treatment. The grain experiment patches were sampled on 17 February 1994, 20–21 days after initiating the treatments.

#### 2.5. Patch density experimental design

A randomized design was also used for the 5 treatments used in this experiment: 0 (no addition), 12, 120, 600, and 1200 *Austrovenus stutchburyi* m<sup>-2</sup>. The plot size used in this experiment was 1.0 m<sup>2</sup>, with an inter-plot distance of  $> 5$  m. Each treatment had 5 replicate plots that were assigned haphazardly, with interspersions (sensu Hurlbert, 1984), across an area of ca. 2500 m<sup>2</sup> with care to avoid eelgrass patches and eagle ray pits (Fig. 1(A)). *Austrovenus* were added to plots, in the same manner as described for the grain experiment, on 1–2 February, and sampled on 17 February 1994, 15–16 days later.

#### 2.6. Analysis

Abundance data of macrofauna were normalized with a log<sub>e</sub>-transformation and

analyzed with General Linear Models (SAS, 1992). For the grain experiment, macrofauna abundances at the start and at the finish of the experiment were tested with two-factor ANOVA for grain size, a fixed factor, location effect, a random factor, and interaction effects. In addition, differences in macroinfauna densities were tested with paired *t*-tests to determine if abundance changed during the experimental period. For the density experiment, macroinfauna abundance at the start and at the finish of the trial period were tested with one-factor ANOVA for density treatment effects. Numbers and proportion of dead and hammered *Austrovenus stutchburyi* shells in the plots were tested for treatment effects using *G*-tests with a Chi-square statistic. Frequencies of organisms caught in the pitfall traps were also compared for independence among treatments using *G*-tests. Proportions of *Austrovenus* with nipped siphons were tested for independence among treatments using ANOVA on arcsin-transformed data and *G*-tests were used to assess the significance of differences in proportion between treatments. Proportions of bivalves which emigrated from experimental plots were compared among treatments using ANOVA on arcsin-transformed data (Sokal and Rohlf, 1995). A significance level of  $p < 0.05$  was used for all statistical tests.

### 3. Results

Observations of the sediment surface the day following *Austrovenus stutchburyi* additions indicated that all bivalves had apparently successfully burrowed and established themselves in all treatment plots of both experiments.

#### 3.1. Grain experiment

##### 3.1.1. *Austrovenus* responses

At the experimental density of 120 *Austrovenus stutchburyi* m<sup>-2</sup>, no obvious differences in the surface texture or elevation of the sediment surface were apparent between the three sizes of test plots and surrounding substrate. Ambient densities of *Austrovenus* did not differ significantly among treatments but did differ significantly among experimental location effects. In one block (Block 1) background densities of *Austrovenus* averaged 72 bivalves m<sup>-2</sup>, whereas ambient shellfish densities in all other blocks were <4 bivalves m<sup>-2</sup>. After adjusting for background densities of shellfish in each block, the density of *Austrovenus* (>4 mm) did not differ significantly among patch sizes and averaged 104 bivalves m<sup>-2</sup>, which is 87% of the nominal experimental density. Emigration of *Austrovenus* (>4 mm) from the plots (estimated from cockles raked around the periphery of the experimental patches as a proportion of the total number added to the plot) averaged 2.1–3.6% and did not differ significantly among patch sizes (Table 1).

##### 3.1.2. Epibenthic predator/sediment disturber responses

Predator responses to variations in *Austrovenus stutchburyi* patch size depended on predator type. The proportion of articulated dead shells recovered from each density

Table 1

Estimates of mortality, siphon cropping (nipped and regenerating combined) and emigration of *Austrovenus stutchburyi* (> 4 mm shell length) in the grain treatment plots (see text for details and assumptions)

Treatment	Articulated Dead Shells		Articulated Cracked Shells		Nipped <i>Austrovenus</i> Siphons	Emigration	
Plot size	Avg. no. per plot	Avg. % mortality	Avg. no. per plot	Avg. % mortality	Avg. %	Avg. no. per plot	Avg. %
0.25 m <sup>2</sup>	1.0	3.3	0.3	1.1	11.5	0.6	2.1
1.0 m <sup>2</sup>	4.5	3.8	0.7	0.6	20.0	3.4	2.8
9.0 m <sup>2</sup>	26.8	2.5	3.8	0.4	26.9	38.7	3.6

treatment averaged 2.5–3.8% during the trial period and did not differ significantly among treatments (Table 1). Similarly, the average proportion of *Austrovenus* with hammered shells was very low (0.4–1.1%) across all treatments and was unrelated to plot size (Table 1). Pitfall traps captured 3 species of small mobile epibenthic invertebrates (the crab *Halicarcinus whitei* (Miers) and the gastropods *Zeacumantus lutulentus* (Kiener) and *Cominella glandiformis* (Reeve)), but these were not abundant (14 of 32 traps had no organisms, and the mean total catch was 0.8 organisms per trap, range = 0–4 organisms per trap). Frequencies did not differ significantly among *Austrovenus* patch size treatments (Chi-square = 0.513, df = 2,  $p > 0.6$ ). Although eagle ray feeding pits were observed in the experimental site, only 2 pits were recorded within the plots (1 on the edge of a 1.0 m<sup>2</sup> plot and 1 in a 9.0 m<sup>2</sup> plot). Thus, estimated mortality indicated by empty, articulated and hammered shells combined was low (3.8–4.4%), and the combined estimates of emigration and mortality (ca. 7%) accounted for approximately half of the observed (ca. 13%) decline in bivalve densities of the experimental plots during the test period. In contrast to these indexes of lethal predation, sublethal browsing indicated the proportion of *Austrovenus* with nipped siphons was comparatively high (11–27%) and differed significantly among grain treatments, with large patches having the highest proportion of nipped siphons (Table 1).

### 3.1.3. Macrofauna responses

Core samples collected 27 taxa: 6 bivalves, 13 polychaetes, 5 crustaceans, 2 gastropods and 1 nemertine. Densities of 16 species increased, 1 decreased and 10 did not change significantly during the experimental period. Nine species comprised > 95% of all individuals sampled and included: the bivalves *Austrovenus stutchburyi*, *Macomona liliana* and *Cyclomactra ovata* (Gray), the polychaetes *Travisia olens* Ehlers, *Magelona?dakini* (Jones), *Microspio maori* Blake., *Aonides oxycephala* (Sars) and an unidentified nereid, and the crustaceans *Exosphaeroma* spp. and *Colurostylis lemurum* Calman (Table 2). Prior to the addition of *Austrovenus* to the plots, densities of each of the dominant species did not differ among the grain size treatments, and only densities of *Austrovenus* > 10 mm and 4 < 10 mm in length and *Microspio* differed significantly among location effects (Table 2). At the termination of the experiment, only densities of *Cyclomactra* differed among patch size treatments, with treatment means: 0.25 m<sup>2</sup> = 10.2 per core, 1.0 m<sup>2</sup> plots = 6.00 per core, and 9.0 m<sup>2</sup> plots = 8.22 per core (Table 2).



Table 2

Results of two-way ANOVA for the *Austrovenus stutchburyi* grain experiment

	Day 0			Day 20–21			Change
	Grain	Location effect	Interaction	Grain	Location effect	Interaction	
<i>Cyclomactra ovata</i>	0.191	0.622	0.737	<b>0.034</b>	<b>0.003</b>	0.183	<b>0.001</b>
<i>Aonides oxycephala</i>	0.852	0.594	0.411	0.427	<b>0.011</b>	0.097	<b>0.001</b>
<i>Colurostylis lemurum</i>	0.536	0.243	0.630	0.464	0.412	0.210	<b>0.001</b>
<i>Exosphaeroma</i> spp.	0.405	0.405	0.456	0.170	<b>0.050</b>	0.791	<b>0.001</b>
<i>Microspio maori</i>	0.121	<b>0.021</b>	0.342	0.175	0.762	0.345	0.193
Nemertines	0.405	0.405	0.456	0.352	0.828	0.706	<b>0.001</b>
Nereid sp.	0.598	0.203	0.708	0.400	<b>0.015</b>	0.322	<b>0.001</b>
<i>Travisia olens</i>	0.414	0.850	0.403	0.756	0.227	0.702	0.731
<i>Magelona?dakini</i>	0.280	0.134	0.320	0.056	0.140	0.138	0.260
<i>Austrovenus stutchburyi</i>							
> 10 mm	0.266	<b>0.026</b>	0.600	0.642	0.442	0.842	0.286
4–10 mm	0.484	0.354	0.613	0.988	0.853	0.896	0.187
1–4 mm	0.766	0.666	0.832	0.368	0.816	0.800	0.101
0.5–1 mm	0.543	0.119	0.786	0.987	0.833	0.903	<b>0.008</b>
0.2–0.5 mm	0.443	0.455	0.444	0.284	0.225	0.982	<b>0.006</b>
<i>Macomona liliana</i>							
> 15 mm	0.056	0.301	0.855	0.403	0.140	0.287	0.809
4–15 mm	0.926	0.366	0.482	0.726	0.245	0.157	0.177
1–4 mm	0.267	0.776	0.854	0.419	0.429	0.787	0.203
0.5–1 mm	0.345	0.622	0.585	0.873	0.259	0.202	<b>0.003</b>
0.2–0.5 mm	0.783	0.405	0.455	0.130	0.100	0.008	0.002

*P*-values are shown for each factor and interaction, with significant *P* values indicated in bold. “Change” indicates results of paired *t*-tests for differences in density between Day 0 and Day 20–21 of the experiment.

Five species (*Austrovenus*, *Cyclomactra*, *Aonides*, *Exosphaeroma* spp., and the unidentified nereid) differed significantly among location effects at the end of the experiment, but none of the species exhibited significant treatment–location effect interactions (Table 2). None of the small size classes (< 2.0 mm shell length) of *Austrovenus* and *Macomona* differed significantly in density among treatments, location effects or interactions (Table 2).

### 3.2. Density experiment

#### 3.2.1. *Austrovenus* responses

Over the two-week period of the experiment, the sediment surface of 600 and 1200 *Austrovenus stutchburyi* m<sup>-2</sup> plots became slightly elevated (0.5–2 cm) compared to the surrounding sediment. At the end of the experiment, the three high *Austrovenus* density treatments (120, 600 and 1200 bivalves m<sup>-2</sup>) differed significantly from each other while the lowest density treatment (12 bivalves m<sup>-2</sup>) did not differ from ambient density

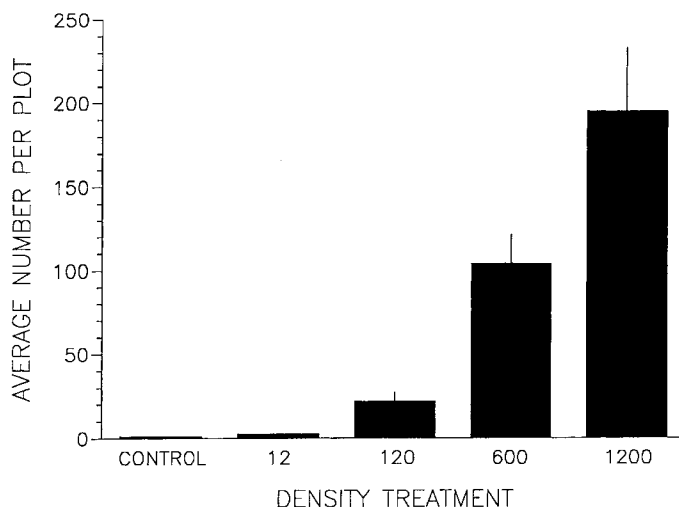


Fig. 2. Densities of *Austrovenus stutchburyi* in treatment plots at end of the patch density experiment. Bonferroni a posteriori tests used to test significant differences between means.

plots (Fig. 2). *Austrovenus* ( $>4$  mm) ambient densities were very low and averaged 1.25 individuals  $0.25 \text{ m}^{-2}$  in the experiment area. The proportion of *Austrovenus* recovered in each density treatment did not differ significantly among treatments ( $F_{3,16} = 3.014$ ,  $P > 0.06$ ) and averaged 70–87% (after correcting for an average ambient density).

Density estimates of *Austrovenus stutchburyi* recovered from the 40 cm-wide bands surrounding the plots indicated that much of the reduction of bivalves in the plots was likely due to migration (Table 1). Correcting for ambient density, and assuming that all of the bivalves found in the 40 cm wide bands resulted from *Austrovenus* ( $>4$  mm) emigration from the plots, 1.2–13% of the reduction in planted *Austrovenus* density could be ascribed to bivalve emigration from the plots. The proportion of cockles recovered outside the experimental plots was independent of treatment density (Table 3).

Table 3

Estimates of mortality, siphon cropping (nipped and regenerating combined) and emigration of *Austrovenus stutchburyi* ( $>4$  mm shell length) in the density treatment plots (see text for details and assumptions)

Density treatment	Articulated dead shells		Articulated cracked shells		Nipped <i>Austrovenus</i> siphons	Emigration	
	Avg. no. per plot	Avg. % mortality	Avg. no. per plot	Avg. % mortality	Avg. %	Avg. no. per plot	Avg. %
0	0.0	0.0					
12	0.2	1.7	0.2	1.7	26.2	1.4	13.3
120	5.2	4.3	0.2	0.2	17.3	1.6	1.2
600	14.8	2.5	0.8	0.1	21.4	56.4	9.4
1200	22.2	1.9	5.8	0.5	31.6	71.4	6.0

### 3.2.2. Epibenthic predator/sediment disturber responses

Although predation on *Austrovenus stutchburyi* was highest at intermediate densities, there was no significant differences in the proportion of dead shells collected in the different treatments (Table 3). The number of articulated dead shells recovered from each density treatment indicated that mortality estimates among the various treatments averaged 1.5–4.3% during the experiment. Average *Austrovenus* mortality attributable to bird predation (i.e. hammered shells) was also very low across all treatments (0.1–1.7%), and was unrelated to treatment density (Table 3). Pitfall traps captured 4 epibenthic species (the crab *Haliscarcinus whitei* and the gastropods *Zeacumantus lutulentus*, *Cominella glandiformis* and *Diloma subrostrata* (Gray)), but these were not abundant (13 of 25 traps had no organisms, and the mean total catch was 0.6 organisms per trap, range = 0–2 organisms per trap) and their frequencies did not differ significantly among *Austrovenus* patch size treatments (Chi-square = 2.43, df = 5,  $P > 0.6$ ). Although eagle ray pits were observed in the vicinity of and among the plots, no pits were recorded within any of them. The proportion of *Austrovenus* with nipped siphons ranged from 17–31% but did not differ significantly among treatments (Table 3).

### 3.2.3. Macrofauna responses

Core samples collected 27 taxa (6 bivalves, 13 polychaetes, 5 crustaceans, 2 gastropods, and 1 nemertine). Eight species comprised >90% of all individuals sampled and included the bivalves *Austrovenus stutchburyi* and *Macomona liliana*, the polychaetes *Travisia olens*, *Magelona?dakini*, *Microspio maori* and *Aonides oxycephala*, and the crustaceans *Exosphaeroma* spp. and *Colurostylis lemurum*. Prior to the addition of *Austrovenus* to the plots, densities of each of the dominant species did not differ among the density treatment plots (Table 4).

Of the eight dominant species in the community, densities of *Travisia olens*, *Magelona?dakini*, and small (<4 mm) *Austrovenus stutchburyi* did not respond to bivalve additions. However, densities of *Aonides oxycephala*, *Microspio maori*, *Exosphaeroma*, *Colurostylis* and post-set *Macomona* (0.5–1 mm shell length) differed

Table 4

Results of one-way ANOVA ( $p$ -values) testing species density differences in each of the different density treatment plots at the beginning (Day 0) and end (Day 17) of the experiment

Species	Day 0	Day 17
<i>Austrovenus stutchburyi</i> 0.5–10 mm	0.4214	0.6182
<i>Austrovenus stutchburyi</i> <0.5 mm	0.6315	0.4023
<i>Macomona liliana</i> >15 mm	0.7077	0.6811
<i>Macomona liliana</i> 1–15 mm	0.2673	0.5338
<i>Macomona liliana</i> <1 mm	0.3162	<b>0.0018</b>
<i>Travisia olens</i>	0.1590	0.2947
<i>Magelona?dakini</i>	0.0671	0.5831
<i>Microspio maori</i>	NP	<b>0.0009</b>
<i>Aonides oxycephala</i>	0.2283	<b>0.0007</b>
<i>Exosphaeroma</i> spp.	0.3356	<b>0.0001</b>
<i>Colurostylis lemurum</i>	NP	<b>0.0014</b>

Significant  $p$ -values are indicated in bold. NP = species not present.

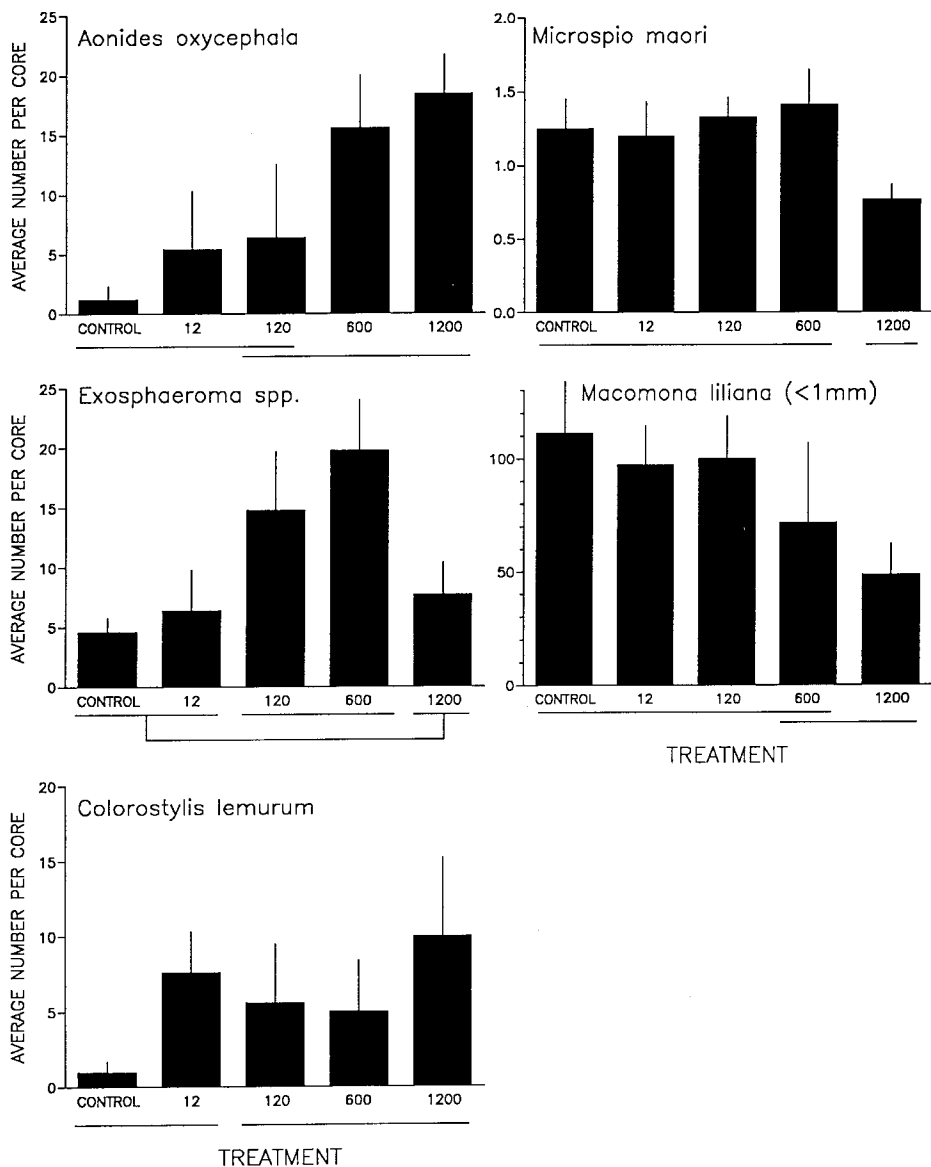


Fig. 3. Responses of 5 macroinfaunal species to variation in density of *Austrovenus stutchburyi*. Mean ( $\pm$ SD) densities per core are shown for *Aonides oxycephala*, *Microspio maori*, *Exosphaeroma* spp., *Colorostylis lemurum* and post-settlement *Macomona liliana* (0.5–1 mm shell length) in each density treatment. Bonferroni a posteriori tests used to test significant differences between means.

significantly among *Austrovenus* density treatments (Table 4). Post-set *Macomona* were significantly less abundant in the highest bivalve density treatment, with fewer than half the number of small tellinids as in the other treatments (Fig. 3). In addition, the

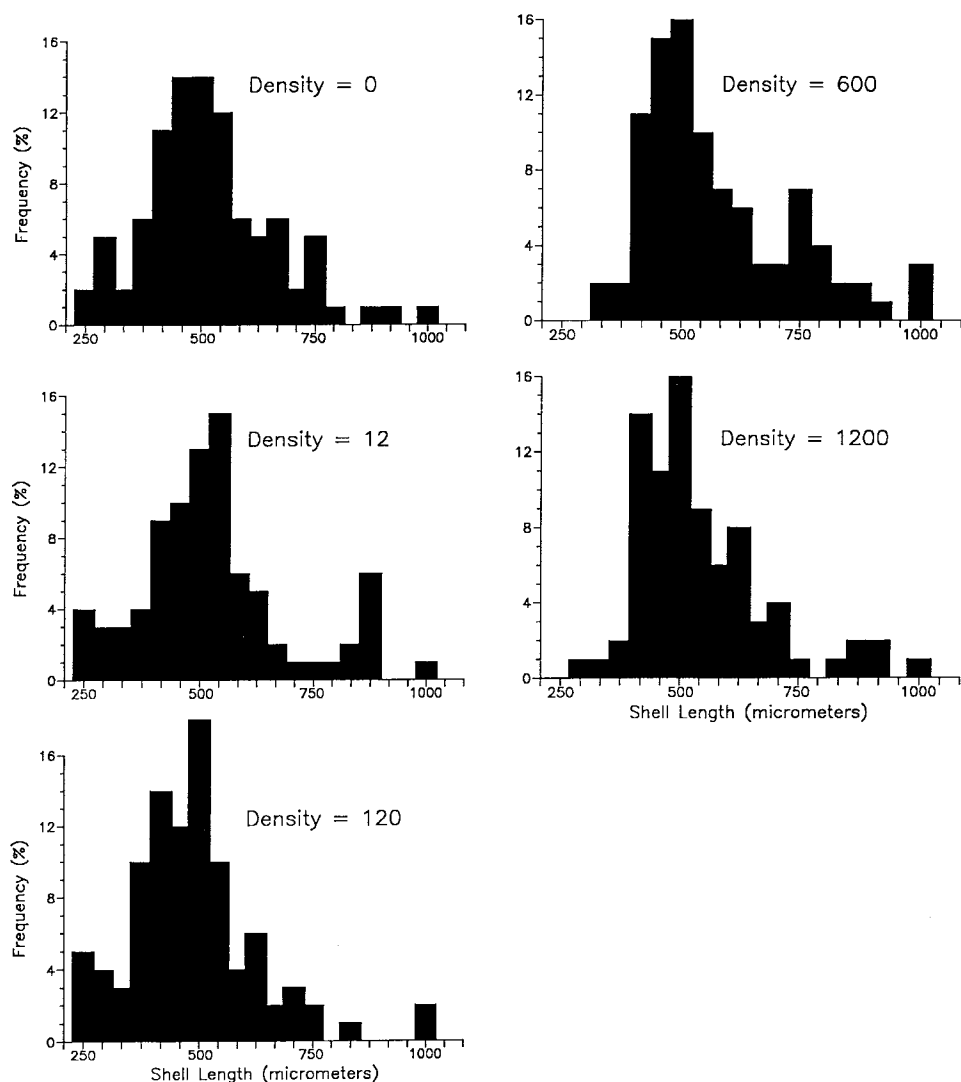


Fig. 4. Size–frequency distributions of newly settled *Macomona liliana* in different *Austrovenus stutchburyi* density treatments at the end of the experiment.

size–frequency distributions of *Macomona* less than 1 mm in shell length in the 600 and 1200 density treatments differed from the lower density treatments, with significantly fewer individuals < 380 mm in the two highest density treatments than the other treatments (Fig. 4). *Microspio* was significantly less abundant in the highest *Austrovenus* density treatment, while significantly more *Exosphaeroma* were found at the intermediate (120 and 600) density treatments (Fig. 3). Fewer *Colurostylis* were found in ambient plots and the 12-*Austrovenus* treatment compared to the other density

treatments, and *Aonides* was more abundant in the 600 and 1200 density treatments than the lower density treatments (Fig. 3). Thus, most of the significant macrofauna responses to manipulations of *Austrovenus* density occurred at densities of 600 bivalves  $\text{m}^{-2}$  or greater.

#### 4. Discussion

At the end of the two experiments 70–80% of the planted *Austrovenus stutchburyi* were recovered from the various treatments. Despite reductions in the abundance of *Austrovenus* primarily due to lateral migration, desired differences in bivalve density were maintained across treatments during the experiment. Peterson (1982) has shown that a hierarchy of responses to competition may occur in suspension-feeding bivalves and that lateral migration is the usual response to limited space conditions of the bivalves in unfenced plots. Our study does not substantiate this as *Austrovenus* migration was independent of both density and grain. Perhaps the duration of our experiment was too short for adult bivalve movements to reflect intra-specific interactions and/or small-scale physical transport processes.

Many macrofauna increased significantly in abundance during the time course of the two experiments, indicating that recruitment was an important process at the study area. However, manipulations of *Austrovenus stutchburyi* patch size had no measurable effect on macrofauna recruitment, probably because bivalve density ( $120 \text{ m}^{-2}$ ) was too low. Macrofauna recruitment was not significantly affected by *Austrovenus* until bivalve densities reached at least 600 individuals  $\text{m}^{-2}$ . While *Austrovenus* can attain high adult densities (e.g., 2000–3700 individuals  $\text{m}^{-2}$  in some locations on the North Island of New Zealand (Blackwell, 1984)), on the sandflats of Manukau Harbour densities of 0–600 *Austrovenus*  $\text{m}^{-2}$  are more typical (Pridmore et al., 1990). In fact, our experiment was specifically designed to reflect adult densities and spatial arrangements described in previous studies at the site (Hewitt et al., 1996; Thrush et al., in press). Thus, while the experiments do not reflect the maximum possible influence that adult *Austrovenus* may have on macrobenthic community structure and function, they provide realistic and relevant information on the importance of this species on the Wiroa Island sandflat.

Adult *Austrovenus stutchburyi* densities of at least  $600 \text{ m}^{-2}$  had a mixed effect on macrofauna colonisation. Of the eight most abundant species, the tellinid *Macomona liliana* and the spionid *Microspio maori* were reduced, while the densities of three species (the spionid *Aonides oxycephala*, the isopod *Exosphaeroma* spp. and the cumacean *Colurostylis lemurum*) were enhanced, the ophelid *Travisia olens* and the magelonid *Magelona?dakini*, and smaller size classes of *Austrovenus* were not significantly affected by the density manipulations. Thus, our experiment did not support the hypothesis suggesting only negative effects of the suspension feeders on macrofauna recruitment. Moreover, since effects on macrofauna were only apparent at high *Austrovenus* densities, our experiment also does not support the hypothesis of enhanced recruitment at intermediate suspension feeder densities. While macrofauna community composition can be affected in areas of high adult *Austrovenus* density, our experiment

provides no support for hypotheses relating colonisation of plots to functional groupings based on taxonomy, feeding strategy, location within the sediment or organism mobility. There was no clear functional group-related pattern (e.g., Woodin, 1976) as to which species were reduced, enhanced or unaffected by the presence of *Austrovenus*. There are other examples which demonstrate that the elevation of adult suspension feeder densities have no effect on recruit density (Commito and Boncavage, 1989; Ólafsson, 1989). In fact, in at least one year of their study, Peterson and Black (1993) reported facilitation of recruitment around high densities of two venerid suspension feeding bivalves (*Katelysia scalarina* and *K. rhytiphora*). While earlier research tended to focus on the inhibitory role of resident adults upon recruitment success of larvae (e.g., Thorson, 1966; Rhoads and Young, 1970), it is now recognized that resident adults can have a wide variety of effects on recruiting macrofauna (e.g., Gallagher et al., 1983; Whitlatch and Zajac, 1985; Hines et al., 1989; Thrush et al., 1992, 1996). It is important to cautiously interpret generalities based on functional group aggregations because of species-specific differences in animal biology (Weinberg, 1984; Ólafsson, 1989; Hines et al., 1989; Posey, 1990; Ahn et al., 1993).

One of the more pronounced interactions seen in this study was the reduction in the abundance and alteration of the size-structure of post-set *Macomona liliana* in the presence of high densities of *Austrovenus stutchburyi*. In an earlier study on the effects of adult *Austrovenus* on bivalve recruits (Thrush et al., 1996), no significant effects were demonstrated in a sandy habitat, while in a muddy-sand habitat a non-linear response to variations in adult *Austrovenus* was found. The Thrush et al. (1996) experiments were conducted using density manipulations of 12 and 48 bivalves enclosed in 0.04 m<sup>2</sup> containers (i.e. 289 and 1157 individuals m<sup>-2</sup>). Differences in experimental outcomes may be related to scales of manipulation as Hewitt et al. (1997) have shown that the intensity and direction of adult–juvenile bivalve associations on the Wiroa Island tidal flat vary according to spatial scale. Further studies are required which more effectively assess the importance of adult–juvenile interactions at ecologically relevant spatial scales (e.g., Thrush et al., 1997b).

Reduction in the abundance of small *Macomona liliana* recruits (ca. 250–360 mm shell length) most likely reflects ingestion of larvae or small settling bivalves (*Macomona* settle out of the water column at about 200 mm and grow to 500 mm in about 3 months (M. Taylor, per. comm.)) by *Austrovenus stutchburyi*. André and Rosenberg (1991) demonstrated that the density of recruits of a suspension feeding bivalve (*Cerastoderma edule*) decreased with increasing adult density. However, this effect was only significant in the first five days of their study; one week later there was no significant effect of their density manipulations. Flume experiments and field observations of Ertman and Jumars (1988) indicate that siphonal currents generated by suspension feeding bivalves can actually increase flux of larvae to the bed. Similarly, flume studies of André et al. (1993) show that while adult suspension feeding bivalves (*Cerastoderma edule*) can ingest large numbers of bivalve larvae, uningested larvae were able to settle near adults indicating that ingestion effects were not important in the immediate locality of adults.

Adult *Austrovenus stutchburyi* mortality estimates in both experiments were relatively low (range: 0.1–4.4%) and independent of density and patch size. Bird predators,

notably the South Island Pied Oystercatcher, appeared to be the principal mortality agent. Oystercatchers have previously been shown to be an important predator of *Austrovenus*, where estimates of consumption of 261–368 bivalves day<sup>-1</sup> predator<sup>-1</sup> have been reported (Knox, 1980). While there are abundant populations of bird predators on the Wiroa Island tidal flats (Cummings et al., 1997), our results are consistent with a previous experiment at this site which failed to identify significant effects of excluding shorebirds on the density of adult *Austrovenus* (Thrush et al., 1994).

The proportion of *Austrovenus stutchburyi* exhibiting nipped siphons was relatively high (range: 11–27%) in both experiments but was similar to values reported for other venerid bivalves (e.g., Peterson and Quammen, 1982; Coen and Heck, 1991). While the proportion of bivalves exhibiting nipped siphons was similar across the range of manipulated *Austrovenus* densities, the percentage of sub-lethal browsing was related to patch size. The 9.0 m<sup>2</sup> plots, for instance, had more than twice the proportion of nipped siphons than the 0.25 m<sup>2</sup> plots. While this apparently is the first reported case of a scale-dependent foraging response of a sub-lethal marine benthic predator, aggregative responses have been reported for marine birds (e.g., Goss-Custard et al., 1977; Schneider and Platt, 1986; Wilson, 1990) and fish (e.g., Horne and Schneider, 1995; Hines et al., 1997) predators. The foraging behaviour of benthic predators often depends on prey density and characteristics of prey patches (e.g., Lipcius and Hines, 1986; Colwell and Landrum, 1993) and our results illustrate the need for conducting experimental studies on benthic predator–prey dynamics at ecologically relevant spatial scales of both the predator and prey. A number of studies have documented the prevalence of siphon-nipping in soft-sediment habitats by conducting small-scale (1–2 m<sup>2</sup>) field experiments (e.g., Peterson and Quammen, 1982; Coen and Heck, 1991; Skilleter and Peterson, 1994); however, these may have underestimated the intensity of siphon-cropping if the predators display aggregative foraging responses similar to those found in the present study.

## Acknowledgements

We thank Paul Dayton, Sarah Lawrie and Michelle Wilkinson for help in the field and laboratory, other members of the workshop for stimulating discussions and companionship, two anonymous reviewers for their thoughtful reviews, and the Auckland Airport Security for access to the study site. This research was made possible by support from NIWA-NSOF and FRST-CO1517.

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