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OPTIMIZING THE SUCCESS OF *AUSTROVENUS STUTCHBURYI* RESTORATION: PRELIMINARY INVESTIGATIONS IN A NEW ZEALAND ESTUARY

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ABSTRACT Degradation of coastal habitats can result in loss or depletion of valued vegetation, fish, and shellfish stocks. Consequently, there are many initiatives to protect and restore these areas or populations to their previous state. Here we describe a study designed to provide necessary information on dispersal, mortality and growth rates of transplanted adult (25–32-mm shell length) cockles, *Austrovenus stutchburyi* (Gray) with which to evaluate the density of transplants and need for predation protection that should be used in larger-scale projects. Marked *Austrovenus* were transplanted at high (75 ind) and low (20 ind) densities, at two sites on an intertidal sandflat. To distinguish between epibenthic predator-associated mortality, other mortality and natural dispersal, caged and uncaged plots (30 × 30 cm) were used. Around 30% of the adult *Austrovenus* transplanted remained in the plots 12 mo later, and abundances were enhanced relative to pretransplant ambient densities. Death rates increased in later months and were significantly higher for *Austrovenus* kept at high densities in cages. There was no effect of caging on plot sediment characteristics, no obvious targeting of the plots by predators and no size-dependency of the deaths. However, being caged at high densities appeared to act as a stressor that rendered *Austrovenus* less able to cope with the extreme environmental conditions that occurred in later months. Growth rates were low over the 12-mo trial (<0.2 cm mo^{-1}), did not differ significantly with site, transplant density, or the presence/absence of cages. Results indicate adult *Austrovenus* should be transplanted at densities intermediate between those used here and that caging is unnecessary. Our observations of dispersal of cockles out of the uncaged plots suggest that future trials should investigate transplanting cockles in patches within larger areas than the plots used here.

KEY WORDS: *Austrovenus stutchburyi*, restoration, transplants, soft sediment, intertidal, dispersal, cockle

INTRODUCTION

There is global concern over the degradation of coastal habitats caused by land development, and over harvesting (e.g., Towns & Ballantine 1993). Habitat changes resulting from these practices can result in loss or depletion of valued vegetation, fish, and shellfish stocks (for example). Consequently, there are many initiatives to protect and restore these areas or populations to their previous state. These directives have come from individuals concerned with their local environment, or from management organizations (e.g., local or regional government agencies). In some cases, cooperative, often large-scale, coordinated efforts involving managers, community groups, and scientists to restore specific species have resulted (e.g., Rice et al. 2000). Increasingly, the long-term goal is ecosystem-level recovery and restoration of ecosystem function (e.g., French McCay et al. 2003, Peterson et al. 2003).

Successful restoration and/or enhancement of particular populations require a detailed knowledge of the species' ecology, over a range of spatial and temporal scales. Their growth and survival is affected by a variety of factors, from the physical environment (e.g., waves and substrate), to water quality, pollution, and the biological environment (e.g., predation, competition and food). Once the cause(s) of depletion have been removed, and provided the habitat is suitable, the likelihood of organisms colonizing the area *via* dispersal from unaffected areas elsewhere will determine whether restoration is likely to occur naturally, or whether intervention is required. Where natural recovery of stocks is unlikely, or expected to be slow, differences in availability and mobility of different life stages of a particular species will often influence the decision as to whether to transplant adults, juveniles or seed/larvae (Arnold 2001). For shellfish species in soft sediment habitats, the mobility/dispersal of the transplanted individuals is a key factor to be considered, and it is particularly important when evaluating the success or failure of the restoration/enhancement effort.

In the United States, there have been many studies to determine the ecological requirements of important shellfishery species and the best techniques for seeding, on growing and predator protection methods, aimed at maintaining a viable fishery (e.g., Arnold 2001). However, for many species, knowledge of information required to conduct successful transplants is limited. Together with the inherent variation in environmental characteristics and conditions between habitats and locations, this means there is no one "recipe" for a successful restoration effort, and to a large extent these projects require trial and error.

Different life history stages of the same species may have different requirements for optimum growth and survival (e.g., shore height; Dobbinson et al. 1989, Stewart & Creese 2002). Survivorship of transplants may increase with increasing size (Peterson et al. 1995, McFarlane 1998, Stewart & Creese 2002) and both survivorship and growth may vary with season (Peterson et al. 1995, McFarlane, 1998, Stewart & Creese 2002). Density-dependence of growth rates and survival has also been recorded. For example, growth of the hardclam *Mercenaria mercenaria* (Linnaeus) was slower when transplanted at higher densities, with those transplanted at 1,159 m^{-2} taking 12 mo longer to attain the same size as seed transplanted at 290 m^{-2} (Eldridge et al. 1979); however, survival was significantly lower at the low densities. Predation also varies

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with life stage and density of transplanted individuals: smaller sized seed of *Mercenaria* require multiple protection methods to enhance their survival (e.g., Kraeuter & Castagna 1985, and references therein), compared with individuals >25–30 mm, which have a reduced suite of predators (Kraeuter 2001). In addition, McFarlane (1998) noted that higher densities of *Mercenaria* attracted predators.

Here we describe a small-scale study, conducted in advance of large-scale transplants, to help assess the likely success of transplantation of adults of the suspension feeding bivalve *Austrovenus stutchburyi* (Gray). Generally, *Austrovenus* is common on intertidal sand and mudflats throughout New Zealand; however, habitat change and over harvesting has resulted in declines in its abundance in some areas. We concentrate on adults as seed of *Austrovenus* is not yet commercially produced (and thus is not readily available for enhancement practices) in New Zealand. The study provides the necessary information on dispersal of transplanted individuals and on predation, mortality, and growth rates at varying times of the year, with which to evaluate the density of transplants and the need for predation protection that should be used in larger-scale projects. *Austrovenus* has proven very robust to transplantation in numerous previous studies (Dobbinson et al. 1989, Stewart & Creese 2002, Hewitt & Norkko 2007).

Marked *Austrovenus* were transplanted at high and low densities, at two midshore level locations on an intertidal sandflat in northern New Zealand. To minimize predation, large (25–32 mm shell length) individuals were transplanted. To enable us to distinguish epibenthic predator-associated mortality, other mortality, and natural dispersal, net caged and uncaged plots were used. Whereas netted cages can result in increased sedimentation rates inside the caged area (Kaiser et al. 1996, Spencer et al. 1996), this was not the case for these cages in previous tests (Hewitt & Norkko 2007). To better determine dispersal of individuals and an optimal transplant density, we also extended our sampling beyond the perimeter of the uncaged plots. Survival, growth, and dispersal were monitored regularly over a one-year period.

METHODS

Study Area

Reseeding trials were established on the Takahiwai sandflat, Whangarei Harbour, on July 2–4, 2004. The sandflat has no known contaminants, and recreational harvesting of shellfish in the study area is infrequent because of low numbers of edible-size shellfish. Two sites, separated by approximately 250 m, were established at midtide level on the sandflat. Each site was approximately 37 × 22 m in area. The East site was situated at 35°49.462′S, 174°25.628′E, and the West site at 35°49.452′S, 174°25.461′E.

Experimental Set Up

At each site, the locations of all *Austrovenus* transplant plots (0.3 × 0.3 m) were marked using small metal pegs. Two sediment cores (each 2 cm diam., 1 cm deep) were collected from each plot to determine organic and chlorophyll *a* content, and grain size. The plot was then excavated to a depth of approximately 5 cm, and the sediment sieved (1-mm mesh). Any *Austrovenus* retained on the sieve were counted and measured, and all other fauna were identified. The sieved sediment, minus the fauna, was then returned to the plot. For plots with cages (30 × 30 × 10 cm high, 4-mm mesh), a cage was inserted to a depth of 5 cm before the sieved sediment was returned. Twenty or 75 *Austrovenus* were then added to each plot, dependent on the treatment. *Austrovenus* used in the transplants were collected from a dense *Austrovenus* bed (Snake Bank, Whangarei Harbour, 4.5 km from the transplant site), measured using electronic calipers (widest point), and the shells marked with paper correction fluid. The transplanted *Austrovenus* were adults, ranging in size from 25–32 mm.

Two densities were used: high density plots contained 75 *Austrovenus*, and low density plots contained 20 *Austrovenus*. Typical average densities of *Austrovenus* on New Zealand sandflats range from 0–600 (Pridmore et al. 1990) and 740 ± 458 m^{-2} (Hewitt et al. 1996). The densities chosen for this experiment encompass these values, equating to 222 and 832 m^{-2} for the low- and high-density treatments, respectively. Caged and uncaged plots were established for each density treatment, the former to control for the presence of predators or movement of *Austrovenus* away from the plots. Four replicate plots of each density/cage combination were established at each site. Plots were arranged in four rows, orientated parallel with the shore, with each row containing one replicate plot of each treatment. Plots within a row were separated by 10 m, and rows were separated by 5 m.

Monitoring

Assessments of growth and survival of the transplanted *Austrovenus* were carried out at 5–9 wk intervals over the 12 mo following setup. *Austrovenus* has been the subject of much study in New Zealand and has never shown a marked response to handling. Further, at the end of a recent yearlong transplant experiment on the same sandflat, the physiological condition of cockles that were monitored routinely over this time was not significantly different from those left undisturbed until the end of the experiment (authors unpublished data). Nevertheless, to minimize the frequency of disturbance, only two of the four replicate plots of each treatment were monitored on each occasion (Table 1).

Two small sediment cores were collected from each plot to determine sediment characteristics (as described earlier). *Austrovenus* were then recovered by carefully hand sifting the

TABLE 1.

***Austrovenus stutchburyi* transplant sampling dates, and the replicate plots monitored on each occasion.**

Sampling Date	Days (weeks) After Setup	Replicate Plots Sampled
August 14, 2004	41 (5.8)	1, 3
September 25, 2004	83 (11.8)	2, 4
October 30, 2004	118 (16.8)	1, 3
December 11, 2004	149 (21.3)	2, 4
January 22, 2005	204 (29.1)	1, 3
March 7, 2005	246 (35.1)	2, 4
May 12, 2005	312 (44.6)	1, 3
June 22, 2005	353 (50.4)	2, 4

sediment. Marked *Austrovenus* (alive and dead) were counted and measured; unmarked *Austrovenus* from the uncaged plots were also counted. To provide information on potential predators that may have been targeting the plots, the presence of gastropods, crabs and eagle ray feeding pits was also noted, and the dead marked cockle shells were examined to determine whether they had been prized open (i.e., evidence of bird [oystercatcher] predation).

To assess movement of the *Austrovenus* out of the uncaged plots, the number of marked *Austrovenus* found in a 0–15 cm and 15–30 cm perimeter area was recorded and, from October 2004, numbers of unmarked *Austrovenus* found in these areas were also counted. All *Austrovenus* were returned to the area from which they had been recovered.

Assessing Austrovenus *Growth and Survival*

Austrovenus sizes over the monitored period were used to calculate growth per month (GR):

$$GR = (Size_{end} - Size_{initial})/no.\,mo$$

where $Size_{initial}$ is average size of marked *Austrovenus* when initially transplanted (in July 2004), and $Size_{end}$ is the average size of marked *Austrovenus* on the last monitoring date. Both were calculated separately for each plot. Because only two of the four replicate plots were sampled on each occasion, the $Size_{end}$ averages were calculated separately for replicate plots 1 and 3 (i.e., May 2005 – July 2004) and plots 2 and 4 (June 2005 – July 2004). Sizes of live and dead *Austrovenus* were used in these calculations.

Survival of the transplanted *Austrovenus* was assessed by examining the number of dead marked *Austrovenus* found on each sampling date. A death rate per month (DR) was calculated for each replicate plot:

$$DR = D_{cum}/no.\,mo$$

where D_{cum} is the cumulative sum of the number of dead *Austrovenus* over the whole monitored period. Because a large increase in the abundance of dead *Austrovenus* was noted late in the monitored period, we also calculated a death rate per month for these two time periods separately:

$$DR_{early} = D_{early}/no.\,mo$$
$$DR_{late} = D_{late}/no.\,mo$$

where D_{early} is the cumulative sum of the number of deaths up to and including January/March 2005, and D_{late} is the cumulative sum of the number of deaths between January/March and May/June 2005.

Assessing Austrovenus *Dispersal*

Diffusion coefficients (D) were calculated for plots sampled 6 and 29 wk after transplanting (i.e., plots 1 and 3, August 2004 and January 2005; Table 1). *Austrovenus* were assumed to follow a random walk, such that the probability that an individual is at distance x at time t follows a normal distribution with a mean of zero and a variance of $2\,Dt$ (Pielou 1969).

Sediment Analyses

One core sample from each plot was homogenized and subsampled to determine sediment grain size and organic content, whereas the other was used to determine chlorophyll *a* content. Grain size was determined by digesting sediments in 6% hydrogen peroxide to remove organic matter, followed by wet sieving and pipette analysis (Gatehouse 1971). Results are presented as percentage dry weight composition of gravel/shell hash (>2,000 μm), coarse sand (500–2,000 μm), medium sand (250–500 μm), fine sand (62.5–500 μm), silt (3.9–62.5 μm), and clay (<3.9 μm). Sediment organic content (% dry weight) was determined by drying homogenized sediment at 60°C to constant weight, and combusting it for 5.5 h at 400°C. Chlorophyll *a* (μg g^{-1} sediment) was extracted from freeze-dried sediment by boiling in 90% ethanol, and the extract processed using a spectrophotometer. An acidification step was used to separate degradation products from chlorophyll *a* (Sartory 1982).

Climate

Information on local climatic conditions was obtained from the weather station at Whangarei Airport, situated 5 km across the harbor from our study sites. Hourly data on wind speed, direction, temperature, and rainfall was summarized to describe conditions for each day over the monitored period. These included average, maximum, and minimum daily temperature (T_{ave}, T_{max}, and T_{min} respectively), temperature range ($T_{max} - T_{min}$), total daily rainfall, and wind exposure (% time from a particular direction × fetch from that direction). The average climate conditions were then calculated, for each variable, over each of the time periods between monitoring dates for replicate plots 1 and 3 and plots 2 and 4, respectively (see Table 1 for details of dates). For rainfall, T_{max}, T_{ave} and T_{min}, minimum and maximum values, as well as averages were calculated.

Statistical Analyses

Statistical tests were carried out to determine whether the sediment characteristics, *Austrovenus* size, DR or GR differed between sites or treatments. Initial analyses included row (block) as a factor but because this was found to be insignificant it was removed from the models and is not reported here.

Data were tested for normality and homogeneity of variances and transformed where needed to meet assumptions. The significance of differences between treatments and sites in sediment characteristics immediately prior to the transplants (i.e., July 2004) was tested using a 2-way ANOVA with site and treatments as fixed factors (PROC GLM). Differences between means were assessed using Duncan or Bonferroni tests, for rank transformed and untransformed data, respectively. If a significant interaction term was detected, contrasts between treatment means were conducted for each site. On the last sampling date, differences between treatments, sites and time (i.e., May and June 2005) were assessed in a similar manner.

Paired *t*-tests were used to investigate whether there were differences between the sizes of the live and dead *Austrovenus* found in the treatments over time.

To determine whether *Austrovenus* dispersal followed a simple diffusion model (e.g., Okubo 1980), where movement is solely determined by Brownian motion, the relationship between calculated diffusion coefficients, ambient density, and transplant density was examined. An ANCOVA was conducted for both times, using transplant density as the fixed categorical factor and ambient density as a continuous factor. For the 6 wk

sampling occasion, the ambient densities used were the number of *Austrovenus* sized >15 mm found in the 30 × 30 cm transplant area when the transplants were set up. For the 29 wk sampling occasion, ambient densities were taken to be the number of unmarked >15 mm individuals found in the 15–30 cm perimeter area.

A number of variables that potentially influence *Austrovenus* survival were included in a generalized linear model to determine the most important factors correlated with *Austrovenus* death over the monitored period. These variables were summarized over the time period between each sampling occasion for replicates 1 and 3, and replicates 2 and 4, separately. Climate variables included in the model were: wind exposure, average daily temperature range, maximum T_{max}, minimum T_{max}, average T_{max}, maximum T_{min}, minimum T_{min}, average T_{min}, maximum T_{ave}, minimum $T_{ave,}$ average T_{ave}, maximum daily rainfall, and average daily rainfall. Other, nonclimatic variables included in the model were: the sediment characteristics that showed significant differences between sites or treatments (i.e., sediment silt, clay, chlorophyll *a*, and organic content), total number of live *Austrovenus* (marked and unmarked) inside the plots, the number of dead marked *Austrovenus*, treatment (i.e., caged and uncaged), and site (i.e., East and West).

RESULTS

Background Density

Considerably more *Austrovenus* were excavated from the East site plots than at the West site prior to the transplants (i.e., <1–4 cf. 12–16 individuals on average; Table 2). They ranged in size from an average of 18–22 mm at the East site to 20–28 mm at the West site (Table 2).

Sediment Characteristics

The sediments at the East and West sites were comprised predominantly of fine sand (>90%), with low organic content (i.e., ≤2.11%). Prior to the establishment of the trial in July 2004, the only significant differences noted were between the East and West sites: the East site sediments contained a higher proportion of fine sand and had less organics, coarse sand, medium sand, and clay than the West site (Table 3A). The between-site differences in the organic content and the proportions of medium sand and fine sand were still apparent in May and June 2005 (Table 3B). These differences are small (i.e., 0.3% to 4%) and likely to be because of different hydrodynamic conditions affecting sediment sorting at the two sites. The chlorophyll *a* content ranged from 1.8–14.6 μg g^{-1} sediment over the monitored period, and it was not significantly different between sites or treatments, either immediately prior to their establishment in July 2004 (Table 3A) or on the most recent sampling dates (May and June 2005; Table 3B). There were no significant differences between treatments in any of the sediment characteristics at either site in May/June 2005, indicating that neither *Austrovenus* density nor the presence/absence of cages was influencing sediment composition or food content (Table 3B). Although there were some differences in sediment characteristics between the May and June 2005 sampling dates (i.e., % organic content, silt and clay were higher in May; Table 3B), these differences were very small (< 0.5%) and unlikely to affect adult *Austrovenus*.

TABLE 2.

Average total abundance (N) and size of *Austrovenus stutchburyi* excavated from the 30 × 30 cm plots in July 2004. SE = standard error.

Site	Density	Caged (Y/N)	N ± SE	Size (mm) ± SE
East	Low	N	12 ± 2.00	22.31 ± 0.89
	Low	Y	15.5 ± 5.09	19.91 ± 0.87
	High	N	13.25 ± 5.48	19.32 ± 0.93
	High	Y	15.25 ± 4.07	17.86 ± 0.77
West	Low	N	2.75 ± 0.29	21.07 ± 2.18
	Low	Y	4.25 ± 2.42	21.31 ± 1.98
	High	N	3.25 ± 1.96	20.38 ± 2.00
	High	Y	0.75 ± 0.55	27.87 ± 3.34

Initial Size of Transplanted Austrovenus

The *Austrovenus* transplanted to the East site in July 2004 were slightly larger than those transplanted to the West site (i.e., average size at the East site = 29.01 cm; West site = 27.69 cm; site $P = 0.0053$, treatment $P = 0.0230$, site × treatment $P = 0.0388$). At the East site, the high caged plots contained larger individuals than the other plots, by 2 mm on average ($P = 0.0050$). At the West site, *Austrovenus* were similar sized in all treatments and replicate plots ($P = 0.2023$). These differences in initial size were taken into consideration when calculating *Austrovenus* growth rates over the entire monitored period (see Methods).

Survival

Figure 1 shows the average total numbers of live and dead marked *Austrovenus* recovered from each treatment on each monitoring date at the two sites. Survival of *Austrovenus* was high in all treatments for the first 35 wks of the trials, and there was no difference in DR_{early} between treatments or sites (Table 4). There was a notable increase in the number of dead marked *Austrovenus* recovered in the period from March to June 2005 (Fig. 1), with DR_{late} significantly higher at the East site than the West site (Table 4). In addition, significantly more of these deaths occurred in the high-density caged plots at both sites (Table 4).

Austrovenus deaths were strongly correlated with weather conditions, with more deaths occurring in the last few months of the monitored period when there was lower rainfall and larger temperature ranges. Modeling results showed that higher wind exposure, total numbers of live *Austrovenus*, average T_{ave}, a larger temperature range and caged treatments were all correlated with higher *Austrovenus* deaths, whereas high maximum T_{max} and maximum rainfall had the opposite effect (see Table 5).

We examined the sizes of the dead *Austrovenus* on each monitoring date, to determine whether there was some size-dependency in the deaths (e.g., larger, older *Austrovenus* may have been dying at a higher rate). Significant differences between the sizes of live and dead *Austrovenus* were noted on only two occasions (East site: high uncaged plot 3, May 2005,

TABLE 3.

Results of ANOVA to investigate differences between sites and treatments in sediment characteristics. MS = mean square; SS = sum of squares; df = degrees of freedom. Chl *a* = chlorophyll *a* (μg g^{-1} sediment), Med sand = medium sand. Site = East or West, trt (treatment) = plot type.

	Pr > F	F-value	MS	SS	df	Multiple Comparisons
A. July 2004.						
Chl *a*						
site	0.0948	3.02	5.87	5.87	1	
trt	0.4777	0.86	1.66	4.97	3	
site*trt	0.1927	1.70	3.31	9.92	3	
% Organics						
site	**<0.0001**	53.81	0.86	0.86	1	West > East
trt	0.6257	0.59	0.01	0.03	3	
site*trt	0.3356	1.19	0.02	0.06	3	
% Gravel						
site	0.1267	2.50	0.09	0.09	1	
trt	0.3061	1.27	0.05	0.14	3	
site*trt	0.2030	1.66	0.61	0.18	3	
% Coarse sand						
site	**0.0363**	4.92	0.12	0.12	1	West > East
trt	0.5047	0.80	0.02	0.06	3	
site*trt	0.7100	0.46	0.01	0.03	3	
% Med sand						
site	**<0.0001**	22.42	98.91	98.91	1	West > East
trt	0.8389	0.28	1.24	3.71	3	
site*trt	0.9144	0.17	0.76	2.27	3	
% Fine sand						
site	**<0.0001**	30.68	161.37	161.37	1	East > West
trt	0.8853	0.21	1.13	3.39	3	
site*trt	0.7087	0.47	2.45	7.35	3	
% Silt						
site	0.1273	2.49	0.52	0.52	1	
trt	0.8948	0.20	0.04	0.12	3	
site*trt	0.8753	0.23	0.05	0.14	3	
% Clay						
site	**0.0258**	5.65	1.50	1.50	1	West > East
trt	0.0847	2.49	0.66	1.98	3	
site*trt	0.1282	2.09	0.55	1.66	3	
B. May/June 2005.						
Chl *a*						
site	0.2153	1.66	5.52	5.52	1	
trt	0.662	0.54	1.79	5.37	3	
site*trt	0.2023	1.72	5.72	17.15	3	
time	0.2088	1.72	5.69	5.69	1	
site*time	0.3735	0.84	2.78	2.78	1	
trt*time	0.1266	2.21	7.33	21.98	3	
site*trt*time	0.5363	0.75	2.50	7.49	3	
% Organics						
site	**0.0466**	4.65	0.12	0.12	1	West > East
trt	0.3611	1.15	0.03	0.09	3	
site*trt	0.7799	0.36	0.01	0.03	3	
time	**<0.0001**	60.71	1.62	1.62	1	May 05 > Jun 05
site*time	0.9575	0.00	0.00	0.00	1	
trt*time	0.0620	2.99	0.08	0.24	3	
site*trt*time	0.8361	0.28	0.01	0.02	3	
% Gravel						
site	0.2753	1.28	0.04	0.04	1	
trt	0.2362	1.57	0.04	0.13	3	
site*trt	0.4500	0.93	0.03	0.08	3	

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TABLE 3.
continued

	Pr > F	F-value	MS	SS	df	Multiple Comparisons
time	0.3517	0.92	0.03	0.03	1	
site*time	0.7692	0.09	0.00	0.00	1	
trt*time	0.1111	2.35	0.06	0.19	3	
site*trt*time	0.9816	0.06	0.00	0.00	3	
% Coarse sand						
site	0.069	3.8	1.84	1.84	1	
trt	0.709	0.47	0.23	0.68	3	
site*trt	0.6021	0.64	0.31	0.93	3	
time	0.2978	1.16	0.56	0.56	1	
site*time	0.3274	1.02	0.50	0.50	1	
trt*time	0.4105	1.02	0.49	1.48	3	
site*trt*time	0.4401	0.95	0.46	1.38	3	
% Med sand						
site	**0.0008**	17.6	106.20	106.20	1	West > East
trt	0.4089	1.03	6.19	18.58	3	
site*trt	0.4432	0.95	5.71	17.13	3	
time	0.7479	0.11	0.65	0.65	1	
site*time	0.4979	0.48	2.91	2.91	1	
trt*time	0.4961	0.83	5.03	15.09	3	
site*trt*time	0.7577	0.4	2.39	7.17	3	
% Fine sand						
site	**0.0015**	14.96	140.72	140.72	1	East > West
trt	0.6714	0.53	4.94	14.83	3	
site*trt	0.6802	0.51	4.81	14.44	3	
time	0.6821	0.17	1.64	1.64	1	
site*time	0.7283	0.13	1.18	1.18	1	
trt*time	0.532	0.76	7.18	21.55	3	
site*trt*time	0.7757	0.37	3.48	10.44	3	
% Silt						
site	0.67	0.19	0.00	0.00	1	
trt	0.6672	0.53	0.01	0.02	3	
site*trt	0.189	1.79	0.02	0.06	3	
time	0.1361	2.46	0.03	0.03	1	
site*time	**0.0287**	5.78	0.06	0.06	1	(Sig for West only) May 05 > June 05
trt*time	0.5095	0.8	0.01	0.03	3	
site*trt*time	0.6391	0.58	0.01	0.02	3	
% Clay						
site	0.9112	0.01	0.00	0.00	1	
trt	0.6365	0.58	0.02	0.07	3	
site*trt	0.6207	0.61	0.02	0.07	3	
time	**0.0011**	15.73	0.65	0.65	1	May 05 > Jun 05
site*time	0.6022	0.28	0.01	0.01	1	
trt*time	0.9542	0.11	0.00	0.01	3	
site*trt*time	0.5083	0.81	0.03	0.10	3	

dead > live, $P > |t| = 0.0038$; West site: low caged plot 1, May 2005, live > dead, $P > |t| = 0.0038$).

Recovery and Dispersal of Live Austrovenus

Numbers of marked *Austrovenus* found inside both the low and high density uncaged plots declined over the monitored period, with 15% to 36% of them recovered alive almost a year after they were transplanted (Fig. 2).

On all sampling occasions marked individuals were observed 30 cm from the initial transplant location. Six weeks after transplanting (August 2004), the majority of marked bivalves were found in the 30 × 30 cm transplant area (Table 6, Fig. 2); with an exponential decrease to the area 15 and 30 cm outside the transplant area. At this time, movement away from the sampled area seemed related to transplant density and ambient density, with more movement away from high density plots in low ambient density areas (Table 6, Fig. 3). Diffusion coefficients exhibited a significant interaction between transplant and ambient density ($P = 0.0877$, $df_{model} = 3$, $df_{error} = 7$), with a stronger negative effect of ambient density at the high transplant density (estimate = –1.42, $P = 0.0450$) than at the low transplant density (estimate = –0.47, $P = 0.1455$).

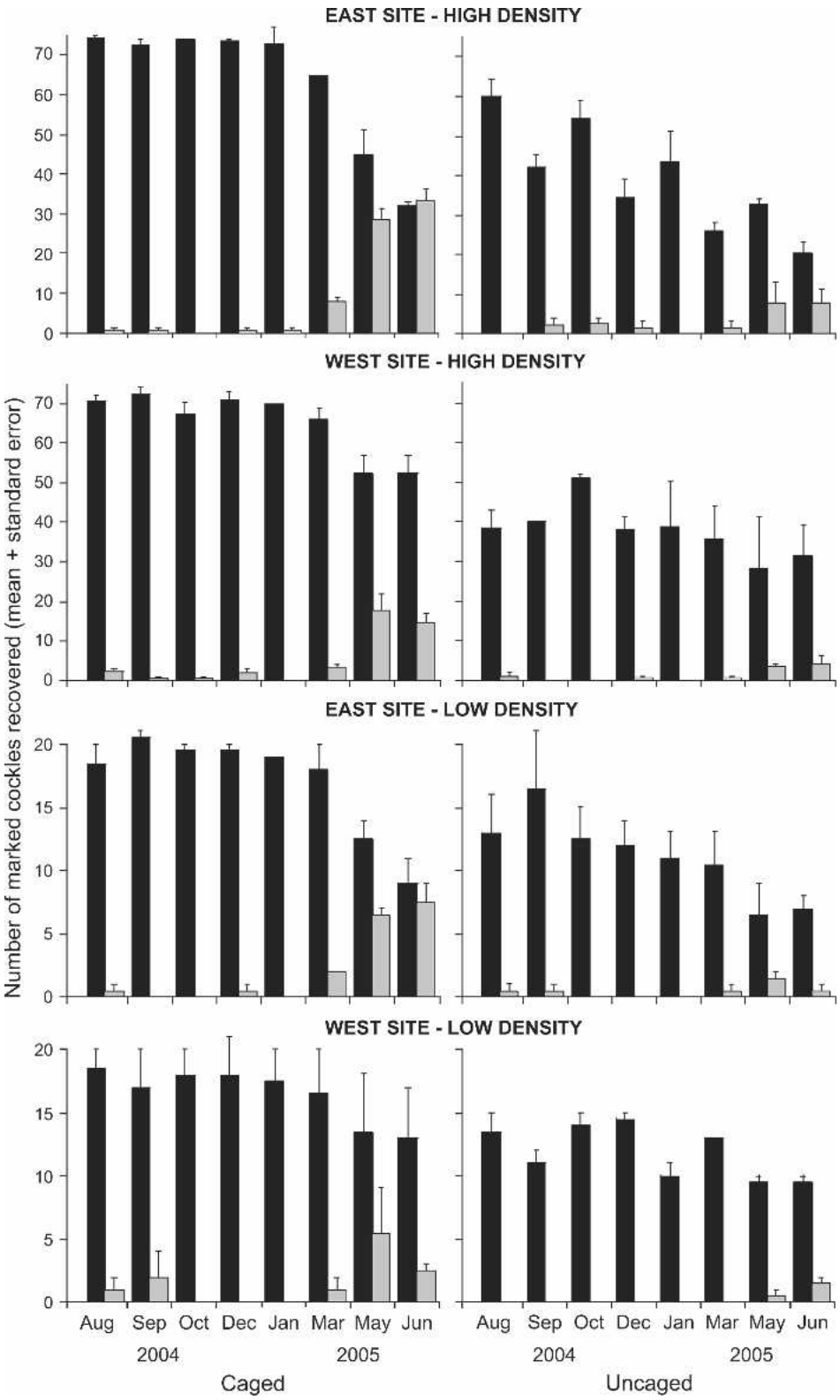

Figure 1. Average numbers of live (black bars) and dead (grey bars) marked *Austrovenus stutchburyi* recovered from each treatment on each monitoring date. For the uncaged plots, numbers include *Austrovenus* recovered from inside and up to 30 cm outside of the plots. Initial transplant densities were 75 individuals in the high plots, and 20 individuals in the low-density plots.

TABLE 4.

Results of ANOVA to investigate differences between sites and treatments in *Austrovenus stutchburyi* death rate. DR_{cum} = cumulative number of deaths from July 2004 to May/June 2005, DR_{early} = cumulative number of deaths from July 2004 to January/March 2005, DR_{late} = cumulative number of deaths from January/March 2005 to May/June 2005. LC = low density caged plots, L = low density uncaged plots, HC = high density caged plots and H = high density uncaged plots.

	Pr > F	F-value	MS	SS	df	Multiple Comparisons
DR_{early}						
site	0.4118	0.70	0.03	0.03	1	
trt	0.0640	2.76	0.12	0.37	3	
site*trt	0.9683	0.08	0.00	0.01	3	
DR_{late}						
site	0.0008	14.79	24.85	24.85	1	East > West
trt	<0.0001	39.49	66.37	199.12	3	
site*trt	0.0143	4.32	7.27	21.80	3	
East	<0.0001	22.02	58.51	175.52	3	HC > H LC L
West	<0.0001	21.49	15.1	45.41	3	HC > H LC L

Although the numbers of marked individuals remaining in the 30 × 30 cm transplanted areas were low and declined over time, numbers retained in the 90 × 90 cm sampled area were higher and more consistent. Twenty-nine weeks after transplanting (i.e., January 2005), the numbers of marked individuals remaining within the 90 × 90 cm area averaged 46 and 40 for the East and West site high-density transplants, respectively, and 14 for low density transplants at both sites. Reflecting this, diffusion coefficients calculated over the 29-wk period exhibited no relationship with ambient density (interaction term $P = 0.9620$). Interestingly, at this time, diffusion coefficients observed in the low-density transplant plots were 1.5 × higher than those observed in the high-density transplants (41.3 cf. 25.9, $P = 0.0003$).

Growth

Growth rates of *Austrovenus* over the monitored period were low (i.e., <0.2 cm mo^{-1} on average; Fig. 4). GR was not significantly different between sites (i.e., East *vs.* West), and was not affected by *Austrovenus* density (i.e., high *vs.* low), or the presence/absence of cages (Table 7). As expected, initial size of *Austrovenus* was the only factor that affected GR, with smaller *Austrovenus* growing faster than larger ones (Table 7).

TABLE 5.

Results of a generalized linear model to investigate potential variables influencing *Austrovenus stutchburyi* deaths over the monitored period. Live = total live *Austrovenus*, Wind exp = wind exposure, Max = maximum, Ave = average, T = temperature, Cage effect = caging increased deaths.

Source	Pr > F	F-value	MS	SS	df	Parameter Estimate
Model	<0.0001	23.13	89.71	627.96	7	
Error	.	.	3.89	457.61	118	
Live	0.0059	7.87	30.51	30.51	1	0.7336
Wind exp	0.0058	7.90	30.62	30.62	1	0.0527
Max T_{max}	<0.0001	67.03	259.93	259.93	1	–1.6654
Ave T_{ave}	<0.0001	58.87	228.31	228.31	1	1.5418
Max rainfall	<0.0001	33.56	130.16	130.16	1	–0.2096
T range	<0.0001	51.52	199.79	199.79	1	2.4061
Cage effect	0.0235	5.26	20.41	20.41	1	0.8354

Predation

Small crabs (e.g., *Helice crassa* [Dana], *Hemigrapsus crenulatus* [Milne-Edwards]) and gastropods (*Xymene plebius* [Hutton]), *Cominella adspersa* (Bruguiere), *C. glandiformis* [Reeve], *Diloma* sp. Phillipi, and *Zeacumantus lutulentus* [Kiener]) were found in the plots over the monitored period. Only two of these species are known *Austrovenus* predators: *Xymene* and *C. adspersa*. *C. adspersa* is known to prefer smaller *Austrovenus* (size preferences of *X. plebius* are unknown). Neither species, however, was noted in very high abundances in any of the plots (maximum of 2 *C. adspersa* and 1 *Xymene* $plot^{-1}$) and we did not notice any evidence of drilling on the *Austrovenus* shells. The cockles used in this experiment are likely to be too large to be predated by eagle rays; very few ray-feeding pits were noted in the experimental area during our visits, and none of these occurred inside our experimental plots. Large (25–37 mm) *Austrovenus* are predated by South Island pied oystercatchers (*Haematopus ostralegus finschi* Martens), but we found no evidence of prising on the dead marked shells.

Pre Versus Post Transplant Austrovenus *Densities on the Takahiwai Sandflat*

Despite the decrease in numbers noted over the year after the transplants, average abundances on the last monitoring occasion were still higher than the pretransplant densities (Table 2), indicating the potential success of this approach to *Austrovenus* restoration.

DISCUSSION

This study was designed to provide necessary information on dispersal, mortality, and growth rates of transplanted adult cockles with which to evaluate the density of transplants, and need for predation protection, that should be used in larger-scale projects to restore populations of *Austrovenus* on intertidal flats in New Zealand. On average, around 30% of the adult *Austrovenus* transplanted remained in the 30 × 30 cm plots 12 mo later, irrespective of the density at which they were initially transplanted; and abundances in the plot area were enhanced relative to pretransplant ambient densities. Survival was high in the first 29 wks (July 2004 to January 2005), and death rates over this time period were similar irrespective of site, transplant density, or the presence/absence of cages.

Austrovenus death rates increased in later months (March and June 2005), and were significantly higher at the East site than the West site, and for *Austrovenus* transplanted at high densities in cages. There was no size-dependency of the deaths, no effect of the cages on plot sediment characteristics (grain size composition, or organic or chlorophyll *a* content), and no obvious targeting of the plots by predators that might explain these relatively high death rates in the later monitoring months. Modeling results showed that higher wind exposure, average daily mean temperature, and a larger temperature range were

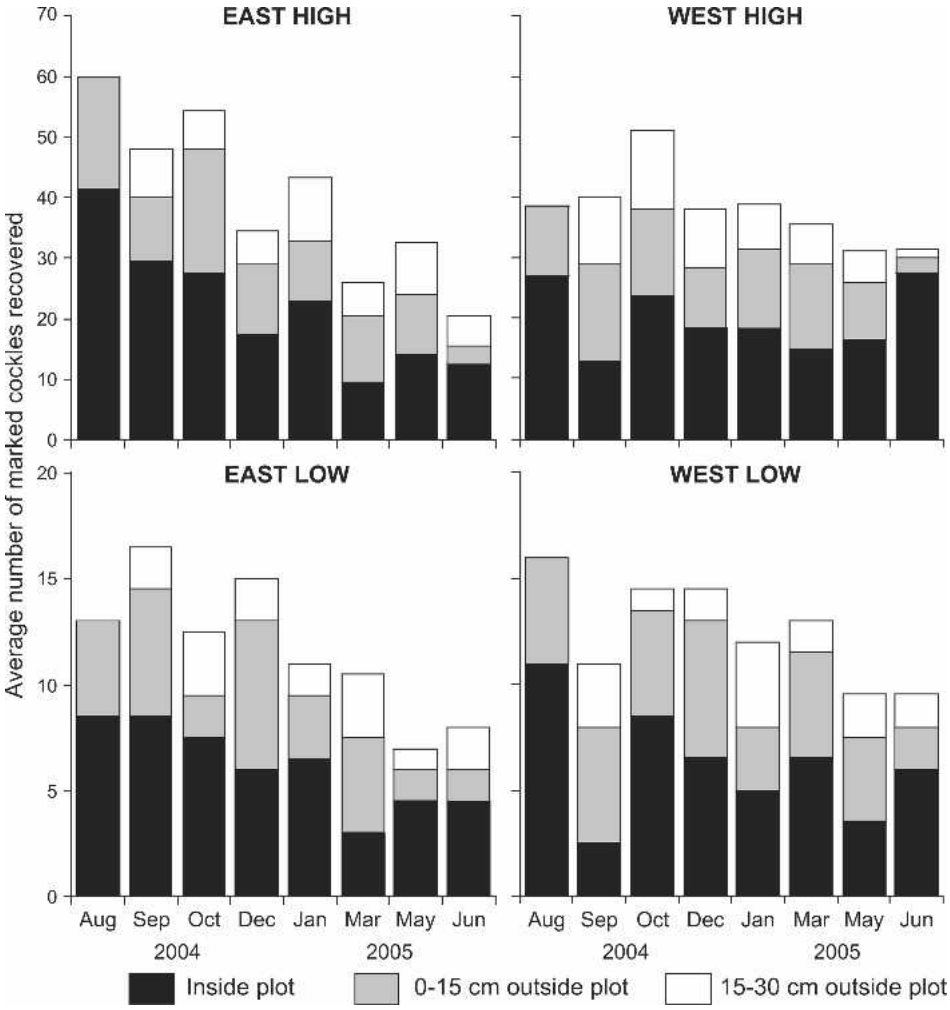

Figure 2. Average number of live *Austrovenus stutchburyi* recovered from inside, 0–15 cm and 15–30 cm outside of the 30 × 30 cm uncaged plots. Initial transplant densities were 75 individuals in the high treatments, and 20 individuals in the low treatments.

also correlated with higher *Austrovenus* deaths, whereas high maximum daily temperature and maximum rainfall had the opposite effect (see Table 5). Rainfall was considerably lower than usual in the region from January to April, with drought conditions occurring (G. MacKay, pers obs.). It is possible that being caged at high densities, whereas not causing death of the *Austrovenus per se*, may act as a stressor that renders them less able to cope with extreme environmental conditions when they occur. The fact that caged treatments with higher total numbers of live *Austrovenus* had more deaths supports this idea.

Given these results, the number of cockles transplanted into the high density plots (75 inds plot^{-1}; 832 inds m^{-2}) appears to be too high on this sandflat; consequently we believe a transplant density intermediate between the high and low (20 inds plot^{-1}; 222 inds m^{-2}) densities used here might have higher survival and recovery rates.

TABLE 6.

Location of marked individuals after six weeks. Numbers given are averages for the two replicate uncaged plots sampled. Ambient density = number of *Austrovenus stutchburyi* sized > 15 mm in July 2004; Not recovered = number of marked *Austrovenus* not found within the 90 × 90 cm area; *D* = diffusion coefficient. 75 *Austrovenus* were initially added to each high density plot, and 20 to each low density plot.

Site	Density	Ambient Density	Inside Transplant Area	Outside Transplant Area		Not Recovered	*D*
				0–15 cm	15–30 cm		
East	High	11 ± 5.6	41	19	8	7	14.0 ± 5.5
	Low	11 ± 2.8	9	5	2	4	13.3 ± 3.2
West	High	3.5 ± 2.1	27	12	11	25	28.1 ± 1.8
	Low	3.5 ± 0.7	11	5	3	3	16.2 ± 0.4

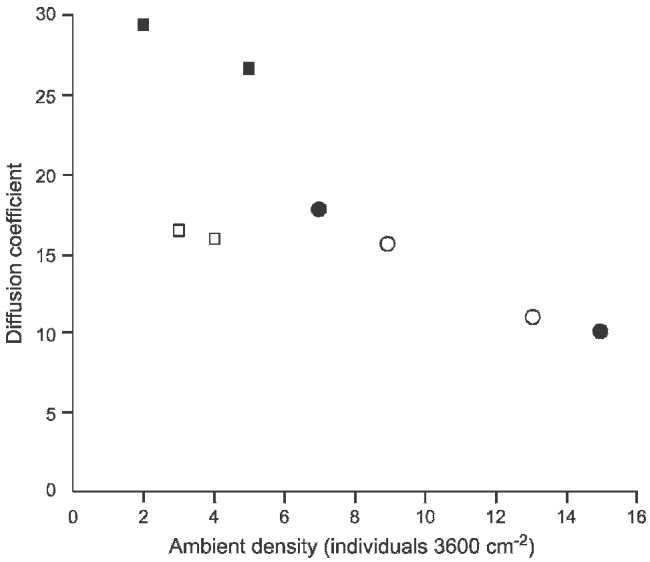

Figure 3. Diffusion coefficients, calculated after 6 wk, for high (dark-filled symbols) and low (white-filled symbols) density treatments at the East (squares) and West (circles) sites, relative to ambient densities.

Growth rates were low over the 12-mo trial (<0.2 cm mo^{-1}), did not differ significantly between sites, and were not affected by *Austrovenus* transplant density or the presence/absence of cages. Salinity dilution in combination with low phytoplankton availability has been found to reduce *Austrovenus* growth (Marsden 2004) and prolonged exposure to increased suspended sediment levels reduced *Austrovenus* biomass (Hewitt & Norkko 2007). Levels of salinity and turbidity measured at sites near our experimental plots over the 12 mo ranged from 30.7–35.6 g/l and 1–5.5 NTU, respectively. Assuming these measurements were typical, salinity and/or suspended sediment concentrations are unlikely to have affected growth and survival of the *Austrovenus* in this experiment. These growth rates are similar to those reported after 11 mo in similar sized *Austrovenus* in another northern New Zealand study (25–32 mm individuals grew only 1–2 mm; Stewart & Creese, 2002), and after 6 mo in a South Island estuary (10–30 mm individuals grew 0.17–0.35 mm mo^{-1}; Marsden 2004).

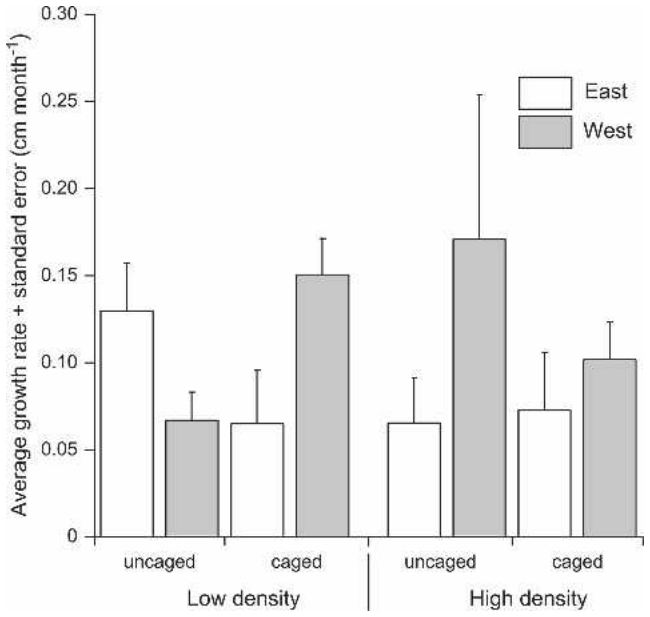

Figure 4. Average growth rates of the transplanted *Austrovenus stutchburyi* in each treatment over the monitored period.

TABLE 7.

Results of ANOVA to investigate differences between sites and treatments in *Austrovenus stutchburyi* growth rate per month (GR). MS = mean square; SS = sum of squares; df = degrees of freedom. site = East or West, trt (treatment) = plot type, rep = replicate; ave = average size of transplanted *Austrovenus* in July 2004.

	Pr > F	F-value	MS	SS	df
site	0.8804	0.02	0.00	0.00	1
trt	0.2210	1.96	0.00	0.01	3
site*trt	0.2653	1.70	0.00	0.01	3
rep	0.5346	0.43	0.00	0.00	1
ave	**0.0118**	12.75	0.01	0.01	1

Examining the dispersal of *Austrovenus* from the uncaged plots can help determine the appropriate plot size for future transplants. Previous analysis of spatial patterns of adult *Austrovenus* has suggested a daily movement range of 1.3–1.7 m (Hewitt et al. 1996). The decreased variability observed in the number of marked *Austrovenus* found in the extended 90 × 90 cm sampling areas over the 12 mo supports these daily range estimates, and suggest that transplanting into an area of this size would decrease the amount of movement of transplanted individuals away from the transplant site. Interestingly, Stewart & Creese (2002) noted a 60% to 90% recovery rate for large *Austrovenus* (i.e., 25–32 mm) transplanted at similar densities to the Takahiwai trials, after 1 y in Whangateau Harbour. Stewart & Creese (2002) used slightly larger plots (i.e., 50 × 50 cm) than our trials and their results are more comparable to the percentage of individuals recovered from our 90 × 90 cm sampled area.

Our observations suggest that *Austrovenus* dispersal does not follow a simple diffusion model. Six weeks after transplanting, dispersal was dependent on transplant density and ambient density, with higher dispersal from high-density transplants embedded in a low-density area (Fig. 3). However, after 29 wks there was no relationship between transplant and ambient density. Furthermore, rather than densities in the high and low plots tending towards similar numbers over time as the *Austrovenus* move around to attain their ''optimum'' density, considerably more *Austrovenus* were found inside high-density than low-density plots on the most recent sampling dates (May/June 2005) at each site (Fig. 2). Given that *Austrovenus* frequently appear to be attracted to groups of other *Austrovenus* (Hewitt pers obs., Whitlatch et al. 1997), a biased random walk model, allowing for aggregation of conspecifics (Gurney & Nisbet 1975) is likely a more appropriate measure of *Austrovenus* dispersal:

$$\frac{\partial u}{\partial t} = D\frac{\partial 2u}{\partial x2} + \left(ku\frac{\partial u}{\partial x}\right)$$

where D is the diffusion coefficient, u is population density, and k is the measure of attraction/repulsion varying from –1

(attraction) to +1 (repulsion). Investigations of the difference in movement observed between transplant densities after 29 wks using such a model suggests that k is close to –0.5.

For some species and/or small sized individuals, protection from predation is essential for high survival rates (e.g., Goldberg & Walker 1990, Goldberg et al. 2000). As noted earlier, we observed no obvious targeting of the plots by predators, and conclude that caging was not needed to protect the adult *Austrovenus* from predation (although it is likely to be necessary for enhancing survival of smaller *Austrovenus*; e.g., Arnold 2001). Several species of small crab and gastropod were found in the plots over the 12-mo trial, but only two are known *Austrovenus* predators: the drilling gastropods *Xymene plebius*, and *Cominella adspersa*. *C. adspersa* is known to prefer smaller *Austrovenus* than those used in this study, but the size preferences of *X. plebius* are unknown. South Island pied oystercatchers (*Haematopus ostralegus finschi* Martens) are known to prey on large (25–37 mm) *Austrovenus* (Cummings et al. 1997). Although observations of oystercatchers were not specifically made during this trial, the caged *Austrovenus* would have been protected from this type of predation. Therefore, the fact that numbers of dead shells recovered from the uncaged plots was not considerably higher than that from the caged plots suggests that predation by shorebirds did not have a large influence on the Takahiwai reseeding trials. In addition, none of the dead marked *Austrovenus* recovered showed evidence of being drilled by gastropods or prised open by shorebirds. Targeting of the plots by shorebirds was also unlikely given the small size of the experimental plots used (e.g., Cummings et al. 1997).

We have gained valuable information on the methods of reseeding *Austrovenus* that can likely be applied on other New Zealand sandflats. By definition, shellfish reseeding efforts are likely to be conducted in areas with low ambient densities. Our work suggests that abundances of *Austrovenus* transplanted to areas of low ambient density will initially decline as they disperse, but that over time higher density patches will develop as they switch to aggregative behavior. Our observations of the dispersal of transplanted cockles out of the uncaged plots suggest that future trials should investigate transplanting within larger areas than the 30 × 30 cm plots used here. Previous studies that have mapped the distribution of *Austrovenus* populations on sandflats show that they consist of a landscape of patches of relatively high density embedded within a lower density area (or *vice versa*) (e.g., Legendre et al. 1997). Thus, we also suggest that transplanting cockles in patches within these larger areas may better mimic the natural situation than transplanting at constant densities. This approach is also less likely to increase lethal and sublethal (e.g., siphon nipping) predation because the small patches will be below the detection threshold of many predators (e.g., Cummings et al. 1997, Hines et al. 1997, Whitlatch et al. 1997). Finally, we suggest transplanting adult cockles at densities intermediate between those used here, and consider uncaged plots to be a better option, because of the higher death rate of *Austrovenus* in some of the caged plots under extreme environmental conditions, and the fact that protection from predation does not appear to be a necessity for *Austrovenus* of this size.

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