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# Variability in low tide populations of tuatua, *Paphies donacina*, in Pegasus Bay, Canterbury, New Zealand

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Abstract Paphies donacina (Spengler, 1793) populations were surveyed at 11 low tide sites on surf beaches along Pegasus Bay, Canterbury, New Zealand, during summer 1998. Random sampling was not feasible. At the non-random sites chosen the average number of tuatua per 5 m of shoreline ranged between 0.1 and 62. Total wet weight biomass  $m^{-2}$  was highest at the southern sites in the Bay. There were site-related differences in length frequency distributions of tuatua populations. Northern populations included a wide length range and southern populations were dominated by larger bivalves. Average shell length increased significantly with distance south, being close to 40 mm at Waikuku and 80 mm at Taylors Mistake. The shell length : width and weight relationships were similar for tuatua collected over the whole geographic range. Average dry weight condition index varied significantly between sites (ANOVA F = 23.3, d.f. = 10, 329) depending on the length distribution of the contributing population. Where populations included a wide length range the condition index was positively correlated with shell length but in populations dominated by larger bivalves there was either no relationship or a negative relationship with shell length. Juvenile tuatua were found at average densities between 81 and 1200 m<sup>-2</sup> at all sites except Taylors Mistake. The mean length of recruits

M98031 Received 19 June 1998; accepted 7 October 1999 ranged from 2.2 to 3.1 mm and shell length was independent of both juvenile and adult density. These results are discussed in relation to the environmental and other factors thought to influence population structure and recruitment of tuatua in Pegasus Bay.

Keywords *Paphies donacina*; tuatua; population structure; condition index; Pegasus Bay, Canterbury

# INTRODUCTION

The Pegasus Bay, Canterbury, New Zealand, coastline consists of dynamic, meso-tidal high energy exposed surf beaches which are classified within the range intermediate to dissipative on a worldwide scale (Short & Wright 1983; Short 1990). Typically they result from high wave action and well-sorted fine sand which produce a low beach and surf zone gradient and a breaker zone, 200–500 m offshore (Blake 1968). This habitat is dominated by mobile crustaceans and burrowing surf clams which avoid extremes of physical stresses (Brown & McLachlan 1990; McLachlan & Jaramillo 1995).

In New Zealand, intertidal surf clam species include the toheroa (Paphies ventricosa) and two species of tuatua. P. subtriangulata occurs in the North Island and north coast of the South Island, and P. donacina is distributed mainly around the South Island (Beu & DeRooij-Schuling 1982: Cranfield et al. 1994b). Although tuatua represent an important cultural and recreational resource, interest in them has increased recently because of the potential for commercial harvesting (Smith et al. 1989; Cranfield et al. 1993; Haddon et al. 1996). To manage shellfish resources, information is needed on population densities, reproductive biology, and recruitment patterns. As tuatua occur mainly at the low tide to depths of 4 m on exposed sand beaches there have been relatively few studies on their biology. Dawson (1954) studied intertidal populations of P. donacina in Pegasus Bay and Cranfield et al. (1993, 1994, 1996), Michael et al. (1994), and Haddon et al. (1996) have studied subtidal P. donacina.

The aims of the present study were to evaluate the tuatua resource available to low-tide recreational shellfish gatherers along Pegasus Bay and to determine the population structure and potential for recruitment. Sampling sites were chosen close to surf clubs or areas traditionally used for recreational harvesting. The study describes the population structure, shell morphometrics and physiological condition of southern tuatua, *P. donacina*, from 11 sites and attempts to relate these to environmental factors including geomorphological changes known to occur within Pegasus Bay.

## MATERIALS AND METHODS

Eleven sites were sampled along the northern Canterbury Coast, from Waikuku in the north to Taylors Mistake in the south (Fig. 1, Table 1) between 2 January and 2 March 1998. Some of the sites were close to areas sampled by Dawson (1954) and Site 9 has been the subject of a 3-year seasonal tuatua study. Each site was visited once during low spring tide periods when the tidal heights from the New Zealand Nautical Almanac tables were between 0.0 and 0.2 m above chart datum. Seawater temperatures at the time of collection were all close to 18.5°C. Tuatua populations were not always accessible and tidal conditions varied considerably on a daily basis. In calm conditions tuatua could be hand collected from a band at the low-tide level over a period of 1-1.5 h.

The sampling program was a stratified block design to investigate spatial variation of the tuatua



Fig. 1 Map of the Canterbury Coast, New Zealand, showing sampling sites. (Names are shown in Table 1.)

**Table 1** Site information for Pegasus Bay, New Zealand, tuatua (*Paphies donacina*) survey. (N = site number; date = sampling date; day = from first sample; T Ht = tidal height (m); Dist. = distance from Waikuku (km); W = width of the low-tide tuatua zone (m); and deg S = min south of 43°.)

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Site name	N	Date	Day	T ht	Dist.	W	deg S
Waikuku	1	4 Jan	3	0.2	0	10	17
Woodend	2	31 Jan	30	0.1	6	10	20
Pines beach	3	1 Mar	59	0.0	9	5	22.5
Spencer park	4	2 Jan	1	0.2	14.5	5	25.2
Waimari	5	2 Feb	32	0.1	21.3	10	31
North Brighton	6	28 Feb	58	0.0	23	5	30
New Brighton	7	1 Feb	31	0.1	24.5	11	29.5
South Brighton	8	1 Feb	31	0.1	27.5	10	32
End of Spit	9	2 Mar	60	0.0	29.5	15	33
Sumner	10	3 Jan	2	0.2	32.5	5	34.5
Taylors Mistake	11	3 Feb	33	0.1	34.3	5	35

population and recently settled juveniles. Sites were grouped into three blocks from north to south with one site chosen randomly from each block during each spring-tide sampling period. The morphology of the surf beach is quite variable, characterised by gently sloping areas separated by sandbars, rips, holes, and channels (Blake 1968). These latter microhabitats, with their variable sediment and water movements, are often unstable, changing on a daily basis. The random samples were therefore taken only within more stable areas with a regularly sloping beach, so that the sampling scheme, taken overall, contains substantive non-random aspects within sites. During summer these are the areas traditionally used for swimming, surfing, and harvesting tuatua.

Although Dawson (1954) and Grant (1994) evaluated population densities of tuatua from random quadrats, this method was unsuccessful in the present study. During preliminary sampling at two sites, the majority of random quadrats contained no shellfish. The only samples to include tuatua were those where tufts of hydroids were seen on the sand surface. As a result of these trials tuatua were collected by detecting the hydroid tuft that attaches to the ridged surface on the posterior of the shell. This technique, which is used to collect the Pismo clam along the Pacific Coast of North America (Fitch 1950), did not uncover dead clams or empty shells. However, during sampling two individuals of the wedge shell, Spisula aequilateralis, were also detected.

At each site tuatua density was estimated indirectly from the number of hydroid tufts in 10

random 5-m sections of shoreline located at least 10 m apart, working from north to south within 200 m of shoreline. At northern sites, where there was low population density, it was necessary to sample 10 m of shoreline. At two southern sites 1 m shoreline was sampled because of sea conditions. Apart from Taylors Mistake, the slope of the beaches and the particle size distribution were similar at all sites and the length of low-tide beach available for sampling ranged between 5 and 15 m (Table 1). At each site 30 random tuatua were hand collected by the tuft detection method and the surrounding  $25 \times$ 25 cm area was hand searched for hidden individuals. A larger area could not be searched because of time constraints for the sampling, and thus it is not possible to accurately assess biomass without bias, except in relative terms between sites. The hidden individuals were counted and at each site the average number of individuals collected from each hydroid tuft was used as a correction factor for tuatua density.

If tidal conditions remained favourable, the shell length and width of additional tuatua were measured for estimates of the population structure and these were immediately replaced in the sand. This resulted in sample size of between 30 and 70 individuals from each site. Bivalves were returned to the laboratory in buckets of sea water for measuring and processing.

The size : weight relationships for *P. donacina* were determined from measurements of wet weight, shell length, width, and shell and tissue dry weight. Ten bivalves from each sample were used to determine the dry weight condition index (Lucas &

**Table 2** Mean tuatua (*Paphies donacina*) density and wet weight biomass at non-random low tide sites in Pegasus Bay, New Zealand. (Hydroids, average number of hydroid tufts per 5 m shoreline; H SE = standard error of hydroids; sk = skewness of hydroids; ratio = the average number of tuatua per hydroid tuft; tuatua/5 m = average tuatua number from 5 m shoreline; T/1 m = average number of tuatua per m shoreline; B/1 m = estimated total wet weight biomass (g) including shell and wet weight of tissue per m shoreline; T/m<sup>2</sup> = average tuatua density per m<sup>2</sup>; and B/m<sup>2</sup> = average biomass per m<sup>2</sup>.)

Site	Hydroids	H SE	H sk	ratio	Tuatua/5 m	T/1 m	B/1 m	T/m <sup>2</sup>	B/m <sup>2</sup>
1	0.9	0.35	0.86	1.1	0.99	0.20	3.2	0.02	0.32
2	1.0	0.33	0.71	1.2	1.20	0.24	9.4	0.02	0.94
3	0.1	0.10	3.16	1.2	0.12	0.02	0.3	0.01	0.07
4	3.3	0.60	1.81	1.0	3.30	0.66	11.5	0.13	2.30
5	3.6	0.98	1.06	1.0	3.60	0.72	33.0	0.07	3.29
6	0.3	0.21	2.28	1.0	0.30	0.06	2.6	0.01	0.52
7	51.5	5.32	-0.26	1.2	61.80	12.36	663.6	1.11	53.95
8	14.3	3.40	0.82	1.1	15.73	3.15	215.2	0.32	21.52
9	10.1	3.75	2.13	3.6	36.36	7.27	449.7	0.49	29.99
10	11.7	2.22	0.47	1.6	18.74	3.75	294.2	0.74	58.83
11	3.5	1.34	0.92	2.2	7.70	1.54	116.4	0.31	23.44



Beninger 1985), dry weight of tissue/shell dry weight  $\times$  100. In addition, the tissue dry weight : wet weight ratio was calculated for each clam. Using the average ratio for each site, the dry weight condition index was estimated for a further 20 tuatua which were preserved for histological examination of the gonad. Possibly biased total biomass estimates were derived for each site from the wet weight values of shell and body tissue.

At each site, the density of newly settled tuatua was estimated from six random samples collected within the zone occupied by the adult tuatua. A 105 mm diameter corer  $(0.0087 \text{ m}^{-2})$  was pushed into the sediment to a depth of 10 cm, below which juveniles are not found. Sand samples were sieved through a 0.5 mm mesh in the laboratory. At all sites, with the exception of Taylors Mistake (Site 11), the majority of the sand particles passed through the sieve allowing juveniles to be easily separated. Sand from Taylors Mistake on Banks Peninsula is of volcanic origin, the particle size is larger and the sediments are less well sorted.

#### RESULTS

#### Tuatua density and biomass

At low tide on north Canterbury surf beaches, hydroid tufts appearing on the sand surface were attached to buried tuatua. Average number of hydroid tufts varied between 0.1 and 51.5 per 5 m shoreline (Table 2). Highest values were found close to New Brighton (Site 7) and lowest values at the more northern sites. At most sites the hydroid tufts were aggregated as shown by the skewness values (Table 2). Although each hydroid tuft generally identified a single tuatua within the substratum, at the end of the Brighton Spit, Sumner, and at Taylors Mistake (Sites 9-11), additional individuals were present below the sand surface. Using the hydroid ratio, the adjusted values (Table 2) suggest a region of moderately high tuatua density extending over a distance of 8 km in the southern part of Pegasus Bay. Relative tuatua population densities were highly variable between sites (1-way ANOVA, F = 16.03, d.f. = 10, 109, P = <0.001).

Total wet weight biomass  $m^{-2}$  calculated from mean length/wet weight relationships and average density  $m^{-2}$  for each site suggest lower yields  $m^{-2}$ in the six northern sites (0.07–3.29 g) and higher values for the five southern sites (21.52–58.8 g). The average wet weight biomass value (±SE) for the southern Pegasus Bay sites was 17.74 ± 6.61 m<sup>-2</sup>.



**Fig. 3** Mean length  $(\pm SE)$  of tuatua (*Paphies donacina*) along the Pegasus Bay, New Zealand from Waikuku in the north to Taylors Mistake in the south. Based on the non-random sampling detailed in Materials and Methods.

When calculated as a wet weight of biomass per m shoreline, the yield values ranged between 0.28 g at Site 3 (Pines Beach) to 663.6 g at Site 7 (New Brighton). Although these biomass estimates may be biased as a result of the sampling scheme, within the sampled zone conclusions on relative density differences between sites remain well founded.

#### **Population structure**

Population structure of *P. donacina* along the Canterbury coast (Fig. 2) consisted of a wide length range in the northern regions and was dominated by larger length groups at the southern sites. There were significant differences in tuatua length between sites (1-way ANOVA F = 88.7, d.f. = 10, 531, P = <0.001). Average length of tuatuas (Fig. 3) increased significantly with distance south (correlation coefficient = 0.9, P = 0.01). The predicted mean length was close to 40 mm at Waikuku compared with 80 mm at Taylors Mistake.

#### Weight relationships

At all sites, the shell width of *P. donacina* increased linearly with shell length and shell weight increased logarithmically with shell length (Regression analysis, Table 3). Comparison of these regression lines revealed significant heterogeneity between the data sets (Bartletts tests, followed by Chi-square analysis) because of differences in the length distributions between sites. As would be expected from a single species that does not have major morphological shape changes with maturity, the slopes and intercepts of the regression lines did not show consistent trends with location and Sites 4 and 10 displayed minimum and maximum slope values. When these two data sets were excluded, both the slopes and elevations of the remaining regression lines relating shell weight to shell length were similar (Analysis of covariance (ANCOVA), Snedecor & Cochran (1976), F slope = 2.26, d.f. = 8, 252, Felevation = 3.09, d.f. = 8, 260).

Dry weight condition index for *P. donacina* ranged from 6.4 for a 30 mm length individual from Waikuku to 14.9 for a 48 mm tuatua from Spencer Park. The mean condition index was significantly different between sites (Table 4; 1-way ANOVA,

F = 23.3, d.f. = 10, 329, P < 0.001) and also increased with distance south (y = 0.086x + 7.927, where y is the condition index and x is the distance from 43° south; r = 0.44, d.f. = 329, P = 0.01).

The condition index for individual *P. donacina*, plotted against shell length (Fig. 4 and Table 4) show trends consistent with the length distribution of the sample. In sites dominated by smaller tuatua the population showed a significant increase in physiological condition with increasing body length, whereas the condition index from populations containing larger individuals showed either no size effect or a negative relationship. Site 2 included a combination of both of these trends with maximal condition for 60 mm length individuals. The condition index of larger tuatua collected from

**Table 3** Regression analyses and equations relating shell height H (mm) to shell length (mm) and shell dry weight Wt (g) to shell length (mm) for tuatua (*Paphies donacina*) along the Canterbury Coast, New Zealand. (N = 30 in all instances, x = shell length, b = regression coefficient, c<sub>1</sub> and c<sub>2</sub> = constants,  $r^2 =$  coefficient of determination, P = probability level.)

			$H = bx + c_1$			$Wt = c_2 x^b$				
Site		b	c <sub>1</sub>	r <sup>2</sup>	P	b	c <sub>2</sub>	$r^2$	P	
1	Waikuku	0.62	2.22	0.90	0.01	2.48	0.00071	0.88	0.01	
2	Woodend	0.65	1.45	0.96	0.01	2.57	0.00046	0.98	0.01	
3	Pines Beach	0.61	2.65	0.90	0.01	2.43	0.00081	0.96	0.01	
4	Spencer Park	0.46	10.46	0.82	0.01	1.76	0.0114	0.79	0.01	
5	Ŵaimari	0.59	3.89	0.94	0.01	2.67	0.00032	0.96	0.01	
6	North Brighton	0.61	3.038	0.90	0.01	2.68	0.00032	0.96	0.01	
7	New Brighton	0.53	8.62	0.84	0.01	3.06	0.00006	0.88	0.01	
8	South Brighton	0.63	2.16	0.84	0.01	2.40	0.00103	0.86	0.01	
9	End of Spit	0.64	1.08	0.90	0.01	3.25	0.00003	0.92	0.01	
10	Sumner	0.59	4.37	0.86	0.01	3.50	0.00001	0.92	0.01	
11	Taylors Mistake	0.62	2.48	0.88	0.01	2.82	0.00018	0.92	0.01	

**Table 4** Mean condition values for tuatua (*Paphies donacina*) from each site. (SE = standard error, together with linear regression analysis, y = bx + c, where y = CI (condition index), x = shell length (mm), c = constant, b = slope of the regression line,  $r^2 =$  coefficient of determination, P = probability level, and NS = not significant.)

No	Site name	x	SE	b	с	$r^2$	Р
1	Waikuku	8.01	0.26	0.068	5.16	0.58	0.01
2	Woodend	9.77	0.27	0.009	10.40	0.01	NS
3	Pines Beach	8.73	0.19	0.072	5.32	0.36	0.01
4	Spencer Park	10.65	0.34	0.154	2.95	0.32	0.01
5	Waimari	10.71	0.21	-0.004	10.96	0.00	NS
6	North Brighton	9.01	0.18	-0.018	10.2	0.04	NS
7	New Brighton	10.64	0.18	0.007	10.14	0.00	NS
8	South Brighton	11.47	0.33	-0.137	21.67	0.25	0.01
9	End of Spit	11.97	0.27	-0.098	19.73	0.41	0.01
10	Sumner	8.61	0.30	-0.164	22.81	0.52	0.01
11	Taylors Mistake	11.31	0.40	-0.004	11.66	0.00	NS

Length (mm)



donacina) from southern Pegasus Bay, New Zealand.



Sumner (Site 10) was significantly reduced compared with adjacent populations.

# Juvenile density

The fauna separated from the sand samples was dominated by juvenile tuatua, low densities of amphipods, nereid worms, and the occasional isopod. Apart from three individuals of the wedge shell, no other juvenile bivalves were found. Densities of newly settled tuatua (Fig. 5) correspond to the range 81-1200 m<sup>-2</sup> at Site 7 (New Brighton). However, no juveniles were found at the most southern site, Taylors Mistake, where the sediment characteristics, steeper beach slope, and degree of exposure were elevated compared with the other sites. The length of juveniles was relatively similar between sites and the individuals were more uniformly distributed than adult tuatua. There was no correlation between juvenile density and distance south or sampling date (Linear regression analysis).

# DISCUSSION

Like many surf clam species worldwide (McLachlan et al. 1996) *P. donacina* exhibit considerable variability in density and spatial heterogeneity in Pegasus Bay along the north Canterbury coast. Individuals greater than 2 cm shell length were highly aggregated and recently settled juveniles more evenly distributed along the shoreline. This Fig. 5 Histogram showing mean juvenile settlement density +SE for juvenile tuatua (*Paphies donacina*) (0.0087 m<sup>-2</sup>) and mean length ( $\pm$ SE) mm of tuatua at sites in southern Pegasus Bay, New Zealand. No juveniles were found at Site 11, Taylors Mistake.

distribution pattern is typical of physically controlled sand beaches where zonation patterns are often indistinct and the low-tide grades into the subtidal surf zone (McLachlan & Jaramillo 1995). The Pegasus Bay coastline has prograded, characterised by cyclic changes in beach morphology because of accretion and erosion, markedly affected by storm events (Kirk 1980; Hall 1995). These geomorphological processes resulting in beach degradation followed rapid accretion (Kirk pers. comm.) may explain why tuatua populations during the 1950s (Dawson 1954) were entirely intertidal.

At present, adult *P. donacina* populations are restricted to the low tide and below and the beaches in the southern part of Pegasus Bay show a slow rate of accretion following disturbances in 1978 and 1979. However, since 1980, northern Pegasus Bay, which typically consists of mixed sand and gravel beaches, has seen periods of erosion extending southwards to Waikuku (Hall 1995). This pattern, typical of relatively stable coasts, is most likely leading into another period of instability (Hesp & Hilton 1996; Kirk pers. comm). These cycles initiated by major storms and resulting in offshore displacement of sand could dramatically affect recruitment and survival of southern tuatua.

Previous and current density values for *P. donacina* vary widely depending on geographic location and zonational level. However, the average density found in this study  $(0.29 \text{ m}^{-2})$  is similar to values given by Haddon et al. (1996) for subtidal

populations along the west coast of the North Island. In contrast, densities of 17.8 m<sup>-2</sup> occur in the northern tuatua, *P. subtriangulata*, from the low tide at Dargaville (Redfearn 1974), and Dawson (1954) recorded densities between 500 and 3000 m<sup>-2</sup> of *P. donacina* at the low tide in Pegasus Bay between 1952 and 1954.

Compared with the density data, wet weight biomass m<sup>-2</sup> for P. donacina was relatively similar between adjacent sites within Pegasus Bay. Values may be generally higher than from lower in the North Island, where the average biomass was  $4.44 \text{ g m}^{-2}$ (Haddon et al. 1996), although the sampling scheme used here confounds direct comparison. In an investigation of surf clams from 16 locations around New Zealand, Cranfield et al. (1994b) concluded that maximal surf clam biomass occurs in Pegasus Bay, Canterbury with subtidal biomass estimates for P. donacina at Waikuku and Kainga being 68 and 27 g m<sup>-2</sup> respectively. The present study confirms at least concentrations of high biomass for low tide tuatua populations within Pegasus Bay, although in northern areas the values fall considerably below estimates of 38 g m<sup>-2</sup> from Clifford Bay, Marlborough (Michael et al. 1994).

Biomass estimates for low tide P. donacina within Pegasus Bay increased to the south, a feature also noted by Haddon et al. (1996) along 27.5 km of the west coast of the North Island. Many abiotic and biotic factors are thought to affect population biomass, reproduction, and growth of bivalves (Hummel 1985; Navarro et al. 1989; Smaal et al. 1997). However for surf clams, some authors believe that physical rather than biological factors are the main controlling factors (McLachlan & Jaramillo 1995), with wave height and particle size being most important. Along Pegasus Bay from the Ashley River southwards, the intertidal sediments consists of fine, well-sorted sand particles (Blake 1968; Burgess 1968) and the wave height, degree of wave action, and frequency of storms is generally similar (Kirk pers. comm.). However recent research by Hall (1995), suggests that beaches further north, including Waikuku, are eroding because of reduced inputs from the rivers. Brown & McLachlan (1990) suggest that clam biomass is related to wave energy on surf beaches with biomass increasing logarithmically with modal breaker height as a result of increased surf-zone productivity. At present it is not known if productivity increases to the south in Pegasus Bay but there is some support for this from NIWA records showing warmer surface temperatures close to Banks Peninsula during summer.



Fig. 6 Comparison of mean lengths of tuatua (*Paphies donacina*) populations 1952/53 (Dawson 1954) compared with this study (dotted line). Data are plotted against location (min south from 43°). Both regression lines are significant (P = 0.01).

Population structure for low tide *P. donacina* was generally site specific, a characteristic noted previously for tuatua populations (Dawson 1954; Haddon et al. 1996). However, unlike populations from the west coast of Wellington, where there were no juveniles below 40 mm shell length, these smallerlength groups dominated the tuatua population at Waikuku, which was the most northern site surveyed. In contrast, the more southern sites consisted of larger-length groups consisting mainly of individuals estimated to be more than 11 years old (Cranfield et al. 1996). In subtidal habitats these populations of tuatua and are thought to represent sites with poor juvenile recruitment (Haddon et al. 1996).

Of major interest in the present survey was the increase in the average length of tuatua southwards. This was also noted by Dawson in 1954 (Fig. 6) who also investigated populations at Leithfield and Amberley Beach. In his thesis, Dawson (1954) concluded that the length differences in tuatua along the coast were not because of variation in particle size and suggested they were the result of variability in recruitment and settlement. However, there may be other physical or biological factors reducing the incidence of larger tuatua in north Pegasus Bay, including increased predation pressure by gulls. Also, larger tuatua may be particularly sensitive to dislodgment during storms when they are cast up on the beach. Although P. donacina is well adapted for life in the shallow surf zone by its density and shell shape, this clam has a relatively poor digging ability and was the third slowest in a series of 12 bivalves collected from sand beaches by McLachlan et al. (1995). As burrowing time increases linearly with shell length, large tuatua might be disadvantaged if accidentally dislodged from their habitat. They could passively drift with inshore sediments and be subjected to major freshwater outflows from the Ashley and Waimakariri Rivers. Some clam species, like the yellow clam, are detrimentally affected by reduced salinities (Defoe et al. 1992) which can also decrease survival of larval stages and juvenile recruits.

The health of bivalves can be assessed by measuring the physiological condition and the dry weight condition index (Lucas & Beninger 1985) varies with many factors including body size, season, and reproductive condition. Bivalves such as subtidal and intertidal mussels from close geographic areas may have similar values (Aldrich & Crowley 1986; Hickman et al. 1991; Marsden & Weatherhead 1999) but this may not be a general feature for burrowing bivalves (Harvey et al. 1993). For the cockle Austrovenus stutchburyi from the nearby Avon-Heathcote Estuary, condition index increased with nutrient availability and salinity (Marsden & Pilkington 1995). The observed increase in condition index for P. donacina with distance south may reflect increased nutrient availability or more favourable conditions for reproduction.

The size at sexual maturity for P. donacina has not been accurately determined, but Dawson (1954), observed active sperm and ova in individuals he regarded as in their fourth summer (c. 35 mm shell length). Spawning events in the tuatua P. subtriangulata, can occur, either over extended periods or shorter periods of rapid weight loss when the gonad is fully mature (Grant & Creese 1995). This weight loss, which is most dramatic in larger clams, results in a sharp decline in the condition index, as seen in P. donacina from southern sites. Some valves for the condition index recorded here for southern tuatua are close to the maximal values recorded monthly during a 3-year study of tuatua from Brighton Spit. They contrast with the northern tuatua (P. subtriangulata) and toheroa (P. ventricosa) from Dargaville (Redfearn 1974; Greenway 1981), where wet weight condition values were consistently low over the summer and high during the winter. Clearly there are considerable differences in the temperature regime between these locations which may explain differences in condition indices and reproductive periodicities.

Paphies donacina, like some other low-tide surf clams has a population distribution based on size (McLachlan et al. 1996), with adults occurring in shallow subtidal habitats and juvenile recruitment extending into the mid tide, distributed by the swash and swell of the waves. Settlement and recruitment patterns of surf clams worldwide are often irregular and for the Pismo clam (Defeo et al. 1992) detectable settlement occurs once in a decade, with major settlement events occur episodically at 18-28 years on California beaches. This results in a skewed population structure that is a feature of both subtidal P. donacina and those occurring intertidally in the southern part of Pegasus Bay. Apart from Taylors Mistake, where no juveniles were found, the densities of newly-settled southern tuatua were similar along Pegasus Bay (81–1200 m<sup>-2</sup>) and are higher than toheroa densities  $(1-5 \text{ m}^{-2})$  over a 10-30 mstrip of beach at Dargaville (Redfearn 1974). There was also no apparent effect of adult P. donacina on juvenile density at the various sites. Some studies suggest that recruitment can be reduced locally in shellfish beds with high population densities of adults. In the yellow clam (Mesodesma mactroides), a close relative of the tuatuas, few juveniles occur in localities where adult density exceeded 120 m<sup>-2</sup> (McLachlan et al. 1996). With a predicted larval lifespan of 20 days (Redfearn pers. comm.), it is suggested here that larval P. donacina could be widely distributed throughout Pegasus Bay both by inshore currents and sediment transport (Burgess 1968).

In conclusion, this study found reasonably abundant low-tide tuatua stocks close to Christchurch. This includes areas at the end of Brighton Spit where harvesting pressure is greatest. Tuatua collecting is normally restricted to a few days each lunar cycle during the low spring tides when between 3 and 20 harvesters have been observed. If each person takes their bag limit of 150 bivalves a day then this level of harvesting can be maintained in the short term. However, as these tuatua populations are dominated by larger-length groups and their longevity has not been established, the future of the fishery remains uncertain. For recruitment purposes it is important to determine the extent of intermediate-length tuatua in the offshore surf zone within southern Pegasus Bay. Also in the future it may be necessary to consider a minimum length for tuatua harvesting as is currently in place for the toheroa and similar clams from other parts of the world (Millar & Olsen 1995; McLachlan et al. 1996). The size limit for P. donacina should be based on knowledge of the growth rate, age and size at sexual maturity, length related fecundity and longevity.

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