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POPULATION ABUNDANCE ESTIMATES OF THE NEW ZEALAND GEODUCK CLAM, *PANOPEA ZELANDICA*, USING NORTH AMERICAN METHODOLOGY: IS THE TECHNOLOGY TRANSFERABLE?

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ABSTRACT This study investigates the applicability of methods used to describe patterns of distribution, and estimates of density and biomass of the Pacific geoduck clam, *Panopea abrupta*, from western North America for populations of the New Zealand geoduck, *Panopea zelandica* in Kennedy Bay, on the Coromandel Peninsula, and in Wellington Harbour. Central to this is the use of line transect surveys and estimations of the detection rate of geoduck (show-factor) using counts of siphon holes. Studies were restricted to less than 17 m water depth. Geoduck in Kennedy Bay were found from 4–8 m water depth, whereas geoduck in Wellington Harbour occurred in several separate beds from 4–16 m. In Wellington Harbour, there was a pattern of increasing numbers with depth up to ~15 m. Numbers seemed to decrease thereafter. Analysis of sediment samples indicated that *P. zelandica* was more prevalent in fine sand to fine silty sand substrates. *P. abrupta* is found in similar habitats. There was no significant difference in the show-factor (the proportion of geoduck detectable by sight or touch vs. the actual number of geoduck present) of geoduck with respect to season (summer and winter), region (Wellington Harbour and Kennedy Bay), or tidal height (low, mid, and high tide). Hence, a mean show-factor of 0.914 was used to adjust density estimates from all surveyed populations. Estimates of the mean population density (±SE) of *P. zelandica* were much lower than those reported for *P. abrupta* ranging from 0.058 (±0.01) geoduck/m^2 in Kennedy Bay to 0.489 (±0.08) geoduck/m^2 in Shelly Bay, Wellington Harbour. Survey densities, abundance, and biomass estimates were reasonably well determined with coefficients of variation (CVs) generally less than 20%. The results suggest that the methods used to provide population estimates for *P. abrupta* are readily transferable to *P. zelandica*. However, further research needs to be conducted on the diver variability on counts of geoduck, the role that geoduck occurring in water depths >17 m play in the population dynamics of local populations, and the density dependence of fertilization success of *P. zelandica*. Given the low estimates of density in this study, fisheries managers will have to carefully consider the feasibility of sustainably harvesting this species.

KEY WORDS: abundance, biomass, density, detectability, habitat, hiatellidae, mollusca, *Panopea zelandica*, show-factor

INTRODUCTION

Geoduck are one of the largest and longest-lived clams in the world (Beattie & Blake 1999). The Pacific geoduck clam, *Panopea abrupta* (Conrad 1989) (=*generosa*), from western North America can reach ages in excess 100 years (Goodwin & Shaul 1984, Sloan & Robinson 1984) and individuals as large as 3.25 kg have been recorded (Goodwin & Pease 1991). The only other species for which detailed biological information is available is the New Zealand geoduck, *Panopea zelandica* (Quoy & Gaimard 1835). Although not as large as *P. abrupta*, individual *P. zelandica* can reach 600 g and 80 years of age (Gribben & Creese, in press).

Commercial harvesting of *P. abrupta* forms the most important clam fishery on the Pacific Coast of North America. Large numbers are found in Puget Sound, Washington, and British Columbia, where subtidal stocks have been exploited since the 1970s. The combined Washington and British Columbian fisheries are worth US$35 million annually (Harbo 1998, Hoffman et al. 2000). A small fishery established in 1988 for *P. zelandica* was closed in the early 1990s pending its introduction into the quota management system (QMS) (Breen 1994). Recently, there has been renewed interest in establishing commercial fisheries and aquaculture industries because of the similarity of *P. zelandica* to *P. abrupta*.

Fisheries for *P. abrupta* are based on detailed habitat descriptions and established methods for providing accurate density and biomass estimates (Hand & Dovey 1999, 2000). Geoduck density is estimated by counting the number of siphon holes visible at the sediment surface. However, this can lead to an underestimation of the number of geoduck present as not all geoduck show at the same time (Goodwin 1977, Hand & Dovey 1999). Central to obtaining accurate density estimates is the use of show-factors. The show-factor is the proportion of geoduck that is visible or can be felt below the sediment surface versus the total number present in control plots. Any estimates of geoduck density obtained using diver transects are then adjusted by the appropriate show-factor. These have been shown to vary seasonally (Goodwin 1977), tidally (Hand & Dovey 1999) and with storms (Campbell et al. 1996a).

Most of the current literature available for *P. zelandica* concerns estimates of age, growth and mortality (e.g., Breen et al. 1991, Gribben & Creese, in press), as well as descriptions of larval (Gribben & Hay 2003) and sexual development (Gribben & Creese 2003, Gribben et al. 2004). *Panopea zelandica* is known to occur throughout New Zealand's three main islands in subtidal sand and mud habitats (Morton & Miller 1973, Powell 1979). However, the distribution and general habitat preference of local populations' remains poorly described. Moreover, the applicability of methods used to provide reliable density and biomass estimates for *P. abrupta* is also yet to be investigated. Understanding the environmental requirements and providing realistic estimates of the density for local populations will be the first step in developing sustainable management policies and for assessing the suitability of *P. zelandica* for culture (Malouf & Bricelj 1989, Murawski & Serchuk 1989).

This study describes the distribution and general habitat preference (i.e., sediment type and water depth) of populations occurring in Kennedy Bay, on the Coromandel Peninsula, and Welling-

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ton Harbour, and also investigates the show-factors of *P. zelandica* occurring in these same populations. It also determines whether established methods of providing density estimates for *P. abrupta* (i.e., counts of siphon holes using diver transect surveys) are readily transferable to *P. zelandica*, and whether they can be used reliably to provide further population abundance/biomass estimates.

METHODS

The harvestable biomass of *P. abrupta* is considered to be only that part of the population that occurs in waters shallower than 17 m below chart datum. This is due to the risks posed to divers spending considerable lengths of time underwater at depths greater than this. Thus all research in this study was conducted in waters no deeper than 17 m.

Relationship Between Gross Environmental Characteristics and Distribution

Transect surveys were used to determine the distribution and sediment characteristics of local *P. zelandica* populations occurring in Kennedy Bay, on the Coromandel Peninsula, and Shelly Bay, in Wellington Harbour (Fig. 1A to C). Similar methodologies were used for describing the distribution of local *P. abrupta* populations in North American (Hand & Dovey 1999, 2000).

Kennedy Bay is a large circular, sheltered bay 1.5 km in diameter, which is shallow and gently sloping with a maximum depth of 11 m at the bay entrance. Kennedy Bay is generally only exposed to winds from the north-northeast. Shelly Bay, a small sheltered embayment located within Wellington Harbour, is more sheltered, although steeper in slope, than Kennedy Bay and can reach depths of 20 m within 60 m of the sea shore.

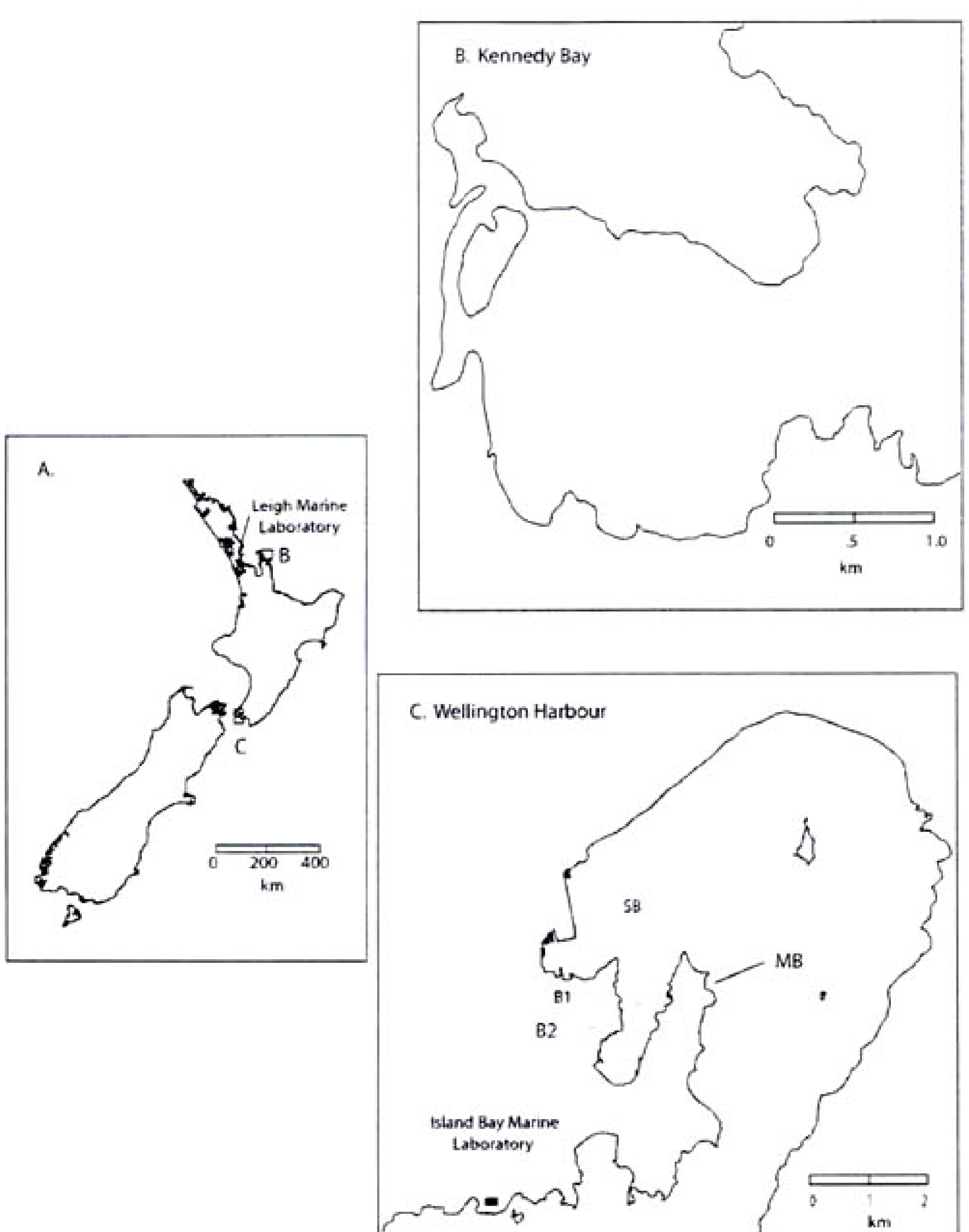

Figure 1. Map of New Zealand (A) indicating the position of study sites in Kennedy Bay (B), and Wellington Harbour (C), including Shelly Bay (SB), Mahunga Bay (MB), Bay 1 (B1) and Bay 2 (B2).

In Kennedy Bay, five transects 1400 m long and 250 m apart (designed to encompass the majority of the subtidal area of the bay) were sampled from Sept 29 to Oct 1, 1999. Eight stations 200 m apart (as determined by DGPS prior to the beginning of the survey) were sampled along each transect. The number of geoduck in 16 × 1-m2 quadrats was determined at each sample station. The large number of quadrats searched reflected the low density of geoduck found in this bay observed from previous exploratory studies (Gribben unpubl. data). Sediment samples were collected at all stations using a hand held corer. Approximately 600 g of sediment was extracted for analysis at each station using a corer 5 cm in diameter pushed a depth of 100 mm into the sediment. In Shelly Bay, five transects 50 m apart (determined by running a tape measure parallel to the shoreline) were sampled from Oct 26 to 28, 1999. Transects started at the 5 m depth contour, except for the first transect which began at the 2.5 m depth contour. Sediment samples were collected every 15 m along a tape measure run perpendicular to the shore. Transects ranged in length from 75–120 m, with 4 × 1-m2 quadrats searched for geoduck at each station. Lower numbers of quadrats were used in this survey because geoduck were much more abundant in this area (Gribben unpubl. data). Each transect ended between the 13–16-m depth contours depending on when the sediment became too silty, making it difficult to effectively search quadrats for geoduck. All sediment samples collected from Kennedy Bay and Shelly Bay were put in labeled plastic bags and transported back to the Leigh Marine Laboratory where they were dried in an oven at 60 °C for 3 days. Samples were sieved using a vibrating shaker through a graded series of seven sieves: mesh sizes <125 μm, 125 μm, 250 μm, 500μm, 1mm, 2 mm, and 4mm (Wentworth grade classification) (Ingham 1971). Median phi size was calculated for each sample as per the methods outlined in Buchanan (1984). The results are displayed as bubble plots of geoduck density versus water depth and median phi size for both populations (Sigma Plot, SPSS 2000).

Investigation of Show-Factors

The show-factor of *P. zelandica* was investigated in Shelly Bay and Mahunga Bay, Wellington Harbour, and in Kennedy Bay (Fig. 1). The general methods are as follows. Depending on the experiment (see below), a number of semipermanent quadrats were placed in each population in areas of known high density (as determined from the survey above) to increase precision. Each quadrat was visited for 5 consecutive days. The first time a quadrat was visited the geoduck present (those whose siphons could be felt or seen) were recorded and staked. On subsequent visits any geoduck not previously recorded were also counted and staked. Estimation of show-factor proportions follows the methods outlined in Hand and Dovey (1999). The proportion showing on any day, SP_i, in any given quadrat is calculated as

$$SP_i = X_i \Big/ \sum_i T \qquad (1)$$

where X_i is the number of geoduck showing on day i and T is the total number of geoduck observed, assuming that no geoduck remained hidden for more than 5 consecutive days (justification for this is given in the discussion). The standard error of the estimate ($se(SP_i)$) is approximated by

$$se(SP_i) = \sqrt{\frac{(SP_i(1 - SP_{i1}))}{\sum T}} \quad (2)$$

because SP_i is binomially distributed.

Two studies were conducted in Mahunga Bay and Shelly Bay, in Wellington Harbour. The first study investigated the show-factor of geoduck at different tidal heights (slack low tide and slack high tide), seasons (summer and winter) and sites (Mahunga Bay and Shelly Bay). The winter survey was conducted from June 26 to July 1, 1999, and the summer survey from Jan 29 to Feb 4, 2000. Five replicate 4 m^2 quadrats per treatment were placed in areas of high density within each population. The second study, conducted from Oct 17 to 21, 2000, investigated whether the show-factors at the two sites differed between slack tide or mid tide: there was no seasonal component to this experiment. However, the quadrats used in the first study were too large to search efficiently because disturbed sediment obscured the search for geoduck before the quadrat was completely searched. Instead, 10 × 1-m2 quadrats were used for each treatment combination at each site.

In Kennedy Bay, studies one and two, described above, were combined. The effect of tidal flow (slack low, slack high, and mid tide) and season on show-factors was investigated in summer from Jan 19 to 23, 2001 and in winter from July 23 to 27, 2001. Thirteen replicate 1 m^2 quadrats were used for each treatment combination. The show-factors were modeled as binomial proportions using logistic regression (PROC Logit, SAS 1988) to investigate whether they were influenced by tidal flow, season or location.

Population Estimates

Estimates of area, density, abundance, and biomass of geoduck populations in Kennedy Bay, Shelly Bay, and Mahunga Bay were provided once the initial distribution surveys had been conducted. Surveys of population estimates in Wellington Harbour were extended to include 2 bays immediately to the south of Shelly Bay, hereafter referred to as Bay 1 and Bay 2 (Fig. 1A to C).

In the Wellington Harbour sites, transects (20 m apart) of a known length and width (1 m) were placed in each population to provide area and density estimates. Although the transects were spaced at regular intervals, the first transect was placed randomly at the either northern or southern perimeter of the bay. This effectively renders all transects random. All transects began at 6 m below chart datum and ran to 15 m. The length of each transect was recorded with a tape measure. All geoduck encountered along the tape measure within the bounds of a 1-m stick centered on tape measure were recorded. A total of 11 transects were run in Mahunga Bay, 10 transects in Shelly Bay, 6 transects in Bay 1, and 10 transects in Bay 2. In Kennedy Bay, a total of 14 transects, 600 m long and ~60 m apart were run through the population as defined in the initial survey. The starting point for each transect was determined by DGPS prior to the beginning of the survey. Again, although the transects were regularly spaced, the accuracy with which this could be done effectively renders the transects random (Hand et al. 1998a).

Area Estimates

Estimates of area follow the methods outlined in Hand and Dovey (1999). The surveyable area in each bay was defined to be the sum of the area of all the possible transects. Because transect length was only known for those sampled, the length of transects not sampled was assumed to be equal to the length of the nearest sampled transect (Hand & Dovey 1999). Thus, the surveyable area A (m^2) is

$$A_j = \sum_{i=1}^{n} L_i(W1_i + W2_i) \quad (3)$$

where n is the number of transects sampled in bed j, L_i is the length (m) of the i^{th} transect, and $W1_i$ and $W2_i$ are the distances (m) on either side of the transect i, equidistant to its adjacent transect. That is, as transects are 20 m apart in Wellington Harbour and 60 m in Kennedy Bay, both $W1_i$ and $W2_i$ are 10 m in Wellington Harbour and 30 m in Kennedy Bay.

Density Estimates

A common show-factor was assumed for all transects within a bed. Estimates of mean geoduck densities were obtained by estimating the mean density of observed geoduck over a bed, and then adjusting for the show-factor. The mean density of geoduck observed in a bed, o_j, was estimated using the ratio estimator method because it reduces the variance of the estimate arising due to unequal transect lengths by weighting the transect counts according to the transect length (Hand & Dovey 1999). This gives

$$o_j = \frac{\sum_{i=1}^{n} b_i}{\sum_{i=1}^{n} a_i} \quad (4)$$

where b_i is number of geoduck found along a transect and a_i is the total area of transect i in square meters. The standard error of o_j is given by

$$se(o_j) = \sqrt{\frac{\sum_{i=1}^{n}(b_i - o_j a_i)^2}{n(n-1)\bar{a}^2}} \quad (5)$$

where

$$\bar{a} = \frac{1}{n}\sum_{i=1}^{n} a_i$$

is the average area of the transects (Campbell et al. 1998a, Hand & Dovey 1999).

Adjusting for the show-factor gives the estimate of mean adjusted geoduck density (d_j) is

$$d_j = o_j/SP \quad (6)$$

where SP is the estimated show-factor (Campbell et al. 1998a, Hand & Dovey 1999). The estimation variability of SP needs to be considered when calculating the standard error of d_j. This is done using the formula

$$se(d_j) = \quad (7)$$

after Thompson (1992).

Population Density and Biomass Estimates

Estimates of total numbers (±1 SE) of geoduck in each bed were calculated from the estimates of mean density (m^{-2}) and total surveyed area of each population. Total biomass (±1 SE) of geoduck in each population was determined from estimates of total abundance and mean whole wet weight (±1 SE).

Estimates of mean whole wet weight (g) (±1 SE) of geoduck in Kennedy Bay and Wellington Harbour were determined by haphazardly collecting geoduck by SCUBA Kennedy Bay (n = 153) during January 1999 and from Shelly Bay (n = 113) during June 1999. Whole wet weight was measured to the nearest 0.1 g, using a Mettler electronic balance for all individuals. All clams were processed within 15 minutes of capture. The mean whole wet weight from Shelly Bay was assumed to be representative of all bays in Wellington Harbour. The standard error of the product of mean weight (W) and total abundance (N) was estimated by the equation

$$S.E.(NW) = \sqrt{W^2 s_N^2 + N^2 s_w^2} \quad (8)$$

as given in Topping (1962).

RESULTS

Environmental Characteristics

The mean density of geoduck ranged from 0 to 3.5 geoduck/m^2 at stations sampled in Shelly Bay, and from 0 to 0.44 geoduck/m^2 for stations sampled in Kennedy Bay (Fig. 2). Geoduck in Shelly Bay were found between 4–16 m below sea level, although few geoduck were found in water shallower than 6 m and deeper than 15 m. It is noted that few stations deeper than 15 m were sampled. Geoduck were not evenly distributed throughout their depth range and appeared to be clumped into 2 main areas, one between 6–8 m below sea level and another between 10–15 m. The low number of geoduck from 8–10 m corresponds with an area that has larger amounts of shell on the surface of the sediment, which runs through this bay at these depths (Gribben pers. obs.). The distribution of geoduck in Kennedy Bay was mostly confined to an area approximately 1000 × 600 m (Fig. 3). The depth range (~3.5 to 8 m) of geoduck in Kennedy Bay was more restricted than that in Shelly Bay (Fig. 2).

Median phi size in Shelly Bay was variable, ranging from minus 3 to 2.8 (large stones to sand-silt sediments). The narrower range of phi sizes in Kennedy Bay, 1.0 to 2.9 (sand to fine sand sediments) reflected the more homogenous nature of sediments in this area (Fig. 2). Geoduck in Shelly Bay were only found in sediments with a median phi size between 1.8 and 2.5 (fine sand to silty fine sand sediments) (Fig. 2). No geoduck were found in sediments coarser than <1.8. Geoduck in Kennedy Bay were not found in sediments coarser then 2.5, although few stations were of that type. This study ignored any patterns of abundance that may have existed for geoduck in Shelly Bay occurring in waters deeper than 16 m.

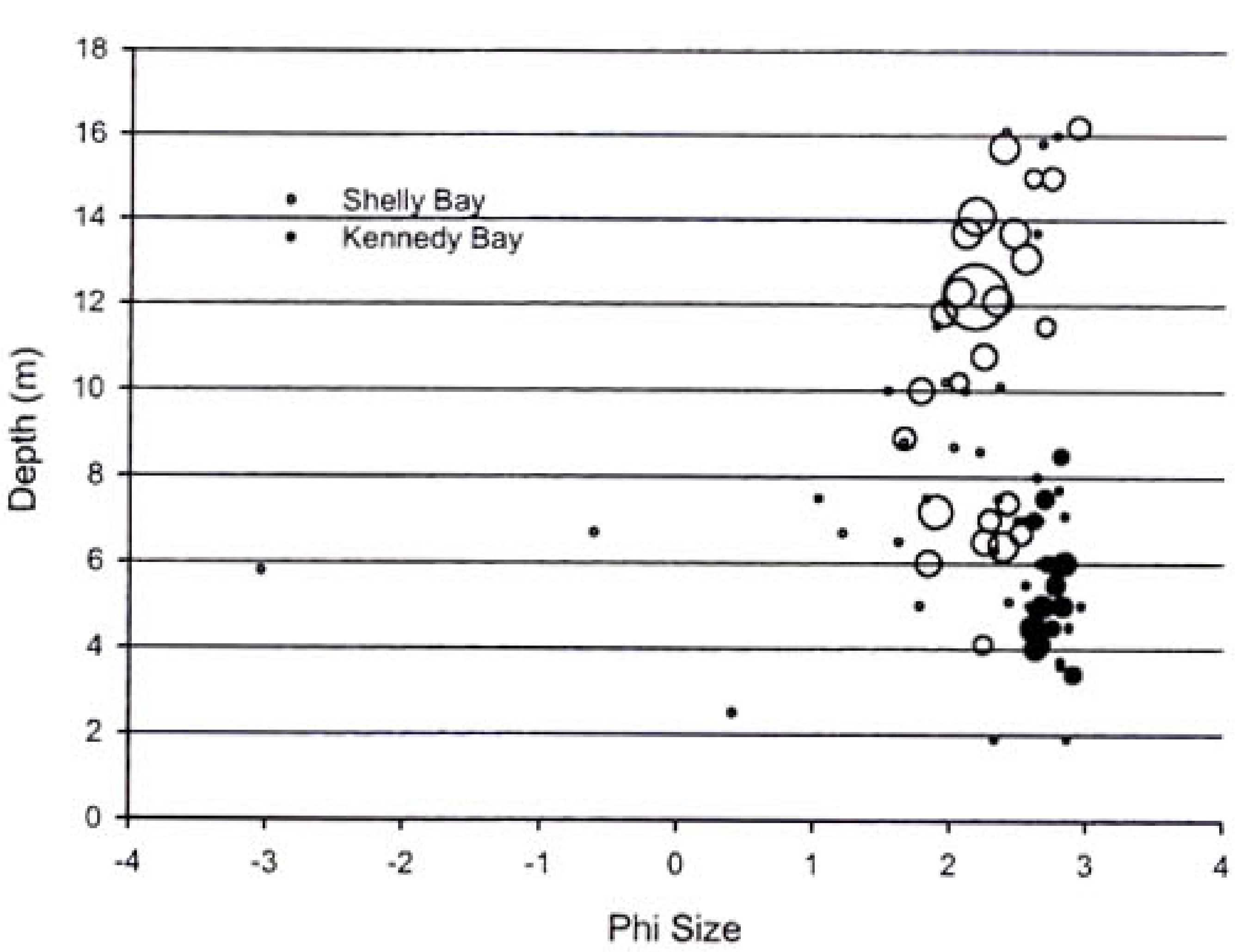

Figure 2. Plot of geoduck density (m^{-2}) in relation to Phi size and water depth in Kennedy Bay (black circles) and Shelly Bay (clear circles). Circles are mean density of geoduck sampled at each station. Smallest circles = no geoduck, median circles = 1.75 m^{-2} and largest circles = 3.5 m^{-2}.

Show-factors

The mean proportions (±SE) of geoduck showing in Wellington Harbour and Kennedy Bay are summarized in Figures 4 and 5 respectively. In Wellington Harbour, few new geoduck were observed after day 3 in experiment 1 (Fig. 4A,B), whereas no new geoduck were found after day 2 in experiment 2 (Fig. 4C). The change of experimental design seems justified because the proportions of geoduck found on the first visit were significantly higher ($P < 0.005$) in experiment 2 compared with experiment 1. No new geoduck were found in Kennedy Bay after day 2 (Fig. 5).

The absence of any significant differences in show-factors within either region allowed investigation of possible differences that may have existed between Kennedy Bay and Wellington Harbour. The Kennedy Bay pooled data set was tested against a Wellington data set containing only the pooled data (including both Mahunga Bay and Shelly Bay) from experiment 2, as it followed the same methodology as that in Kennedy Bay. There was no significant difference in the show-factor between the two data sets ($P = 0.99$). As a consequence, a show-factor of 0.914 (±0.019), estimated from the combined Wellington Harbour and Kennedy Bay data sets, was used to adjust total geoduck found and density, abundance, and biomass estimates from both regions (see below). The standard error of the total number of geoduck encountered for each transect was provided by equation 7 (see earlier).

Population Estimates

Mean transect density of geoduck in Kennedy Bay ranged from 0.01 to 0.13 geoduck/m^2, and in Wellington Harbour ranged from 0.04 to 1.14 geoduck/m^2 (Table 1). Geoduck were found on all transects sampled in all populations except for transects 5 to 10 in Bay 2. Thus, estimates of area, abundance, density, and biomass for this bay were determined for the first four transects only. Also, because of the very low number of geoduck found along transects 12 to 14 in Kennedy Bay, they were considered to be outside the bounds of the main population and were excluded from further analyses.

The population of geoduck in Kennedy Bay occupied the largest area (39.6 ha) of all of the five bays sampled (Table 2). Mean geoduck density was highest in Shelly Bay and lowest in Mahunga Bay. Kennedy Bay had the highest estimated abundance and biomass of geoduck and B1 the lowest, mainly due to the size of the area surveyed. Although Kennedy Bay was over an order of magnitude larger in terms of area than Shelly Bay, the overall biomass was only approximately 60% larger. This was a result of the lower mean density and smaller estimated weight found in Kennedy Bay.

DISCUSSION

There is considerable interest in developing fisheries and aquaculture industries for geoduck species throughout Asia and the

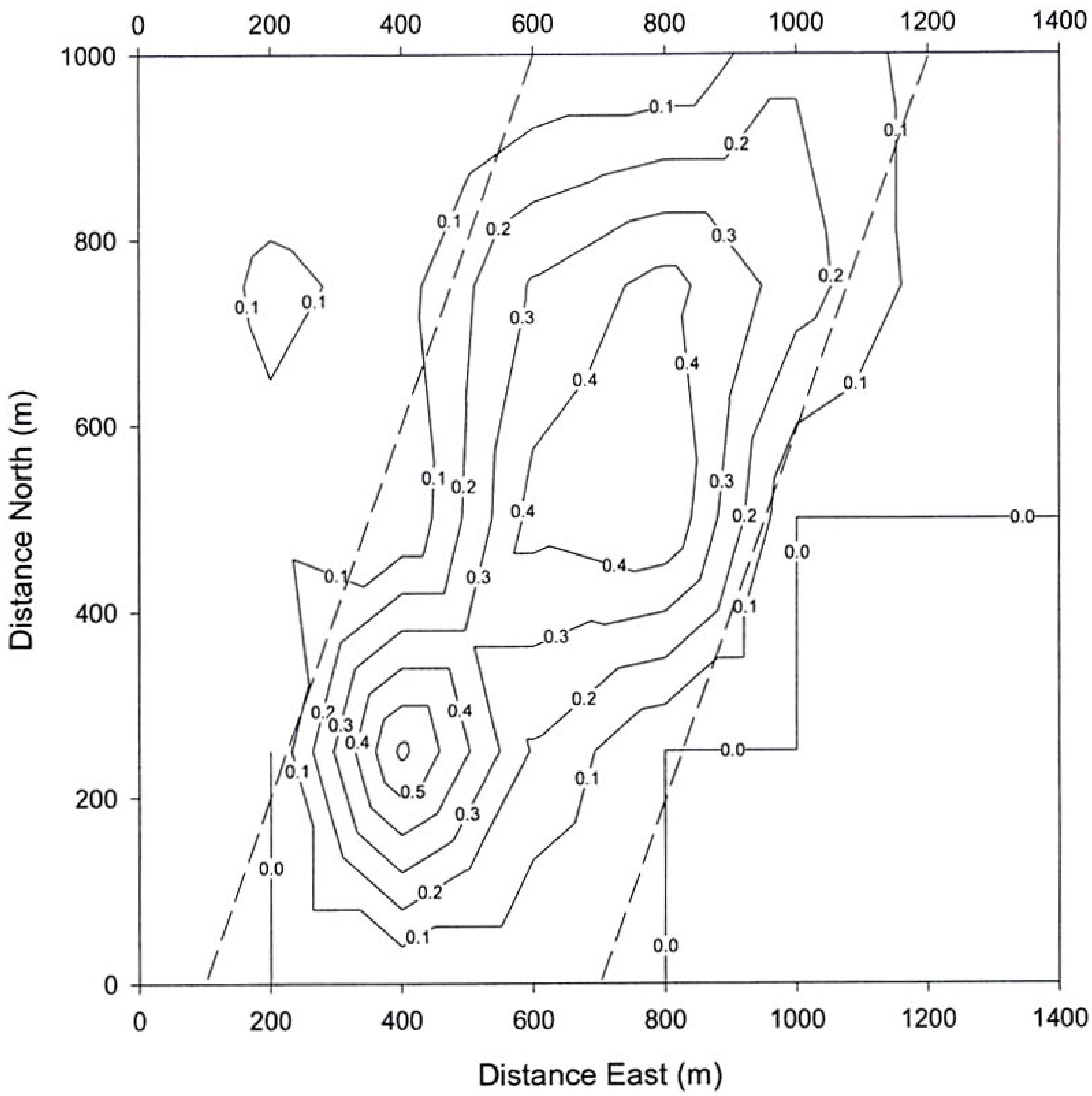

Figure 3. Contour plot of the distribution and density (not adjusted for show-factors) of geoduck (number m^{-2}) in Kennedy Bay. Dashed lines indicate the main area of the bed used in subsequent analyses.

Pacific. Therefore, studies investigating the transferability of existing methodologies for determining population size and structure for *P. abrupta* from North America are both timely and necessary. This is the first study to describe the distribution, density and biomass of local populations of the New Zealand geoduck, *Panopea zelandica,* although this study was restricted to the harvestable population at <17 m water depth.

Morton and Miller (1973) and Powell (1979) described *P. zelandica* as an ocean beach mollusk found in sand and mud habitats throughout New Zealand. This study indicated that *P. zelandica* habitat range was more diverse than previously described. All the populations of *P. zelandica* investigated in this study occurred in sheltered bays indicative of more benign conditions, a habitat similar to that described for *P. abrupta* (Goodwin & Pease 1989). Other populations not investigated in this study occur at similar depths and environments (e.g., Golden Bay, Nelson, Gribben unpubl. data).

Studies have shown that the density of *P. abrupta* in Puget Sound, Washington, was higher in sand or mud-sand habitats than in mud, pea-gravel, or gravel substrates (Goodwin & Pease 1989). Other research has shown that density was positively correlated with water depth from 0–25 m, decreasing thereafter (Goodwin & Pease 1989, 1991; Campbell et al. 1996b). Similar results were obtained for *P. zelandica* in this study. Although, our research only considered that part of the population that was harvestable, searches for geoduck at in silty sediments at depths greater >17 m indicated they were scarce (Gribben unpubl. data). However, the level to which geoduck found at greater depths contribute to the population dynamics of local populations is unknown and requires further investigation (Hand & Dovey 1999). Potentially, these harvest refugia could be an important source of larval recruits to the shallower fished stocks.

Although not quantified, observations suggested that geoduck in all bays appeared to be more abundant in areas that were covered in a film of benthic algae during spring and summer (Gribben unpubl. data). In Kennedy Bay, this region was in 5–6 m water depth and in the Wellington Harbour populations this occurred around 10–12 m. This may explain why geoduck in Kennedy Bay were mainly restricted to depths of 4–6 m when most of the bay appeared to have relatively homogenous sediments. The biofilms may provide a settlement cue for competent larvae as has been shown other marine bivalves (reviewed in Wieczorek & Todd 1998). Populations of *P. zelandica* spawn from spring to late summer so larvae would be in the water column and competent to settle during this period (Gribben et al. 2004). In a laboratory study, *P. zelandica* were shown to have a larval development

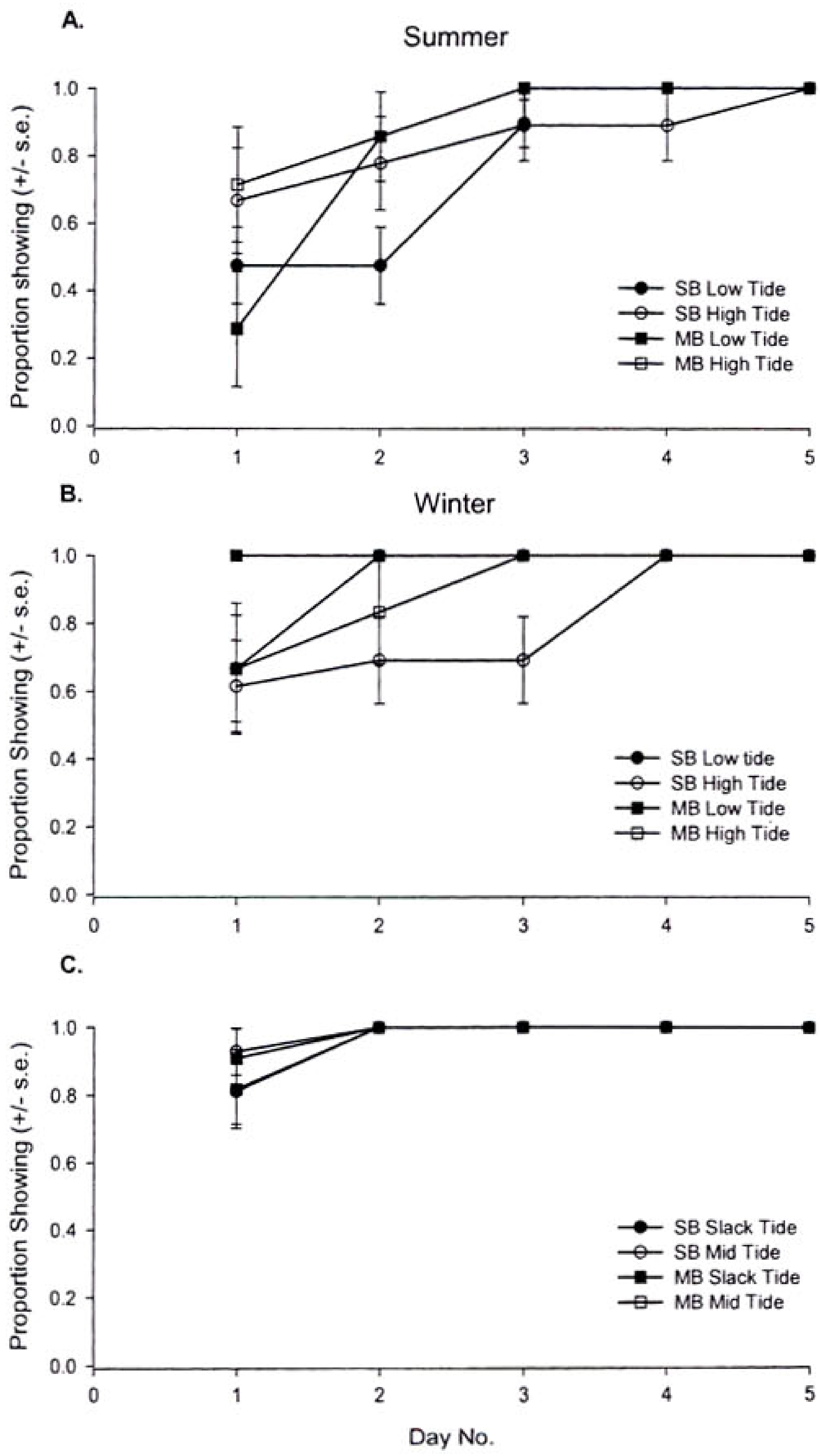

Figure 4. Cumulative proportion (±SE) of geoduck showing in show-factor plots in Shelly Bay (SB) and Mahunga Bay (MB), Wellington, during experiment one conducted during summer (A) from 29/01/2000 to 4/02/2000, winter (B) from 26/06/1999 to 1/07/1999, and experiment two (C) from 17-21/10/2000. Means are dots and vertical lines are ±1SE.

period of 16 days when maintained in water of 17 °C (Gribben & Hay 2003). Further to this, in studies on the feeding ontogeny of newly settled geoduck, *P. abrupta* were found to have incomplete siphons and used their palps to pass sediment surface material into their mouths (King 1986). Thus benthic algal mats may also provide a potential food source newly settled geoduck.

The counting of geoduck siphons is preferable to removing samples from the substrate because of the depth to which they bury, as removing them from the sediment and replacing them can lead to high levels of mortality (Gribben & Creese, in press). However, individual geoduck siphons are not consistently visible throughout the day, season or year (Goodwin 1973, 1977; Fyfe 1984; Campbell et al. 1998b). Consequently, area and time specific show-factors are required to correct the density counts in British Columbia and Washington State. Mean show-factors for *P. zelandica* were consistently above 90% regardless of the season, site, and time of tide, suggesting that this value may be generally applicable. However, our calculation of show-factors is based on the assumption that all geoduck do not remain hidden for more than 5 days. We believe that this is a valid assumption for the following reasons. Many studies on *P. abrupta* consistently indicated high show-factors (>90%) during summer months (Fyfe 1984, Hand & Dovey 1999, 2000). On a smaller scale, Hand and Dovey (1999, 2000) visited show-factor plots of *P. abrupta* of known abundances for 8–9 consecutive days. Show-factors were high on any given day (71% to 100%), indicating that nearly all geoduck were showing each day of the survey. In our study, once found a geoduck was visible on all subsequent days. This indicates that only reason that geoduck were not located initially was due to poor visibility or they were inadvertently missed.

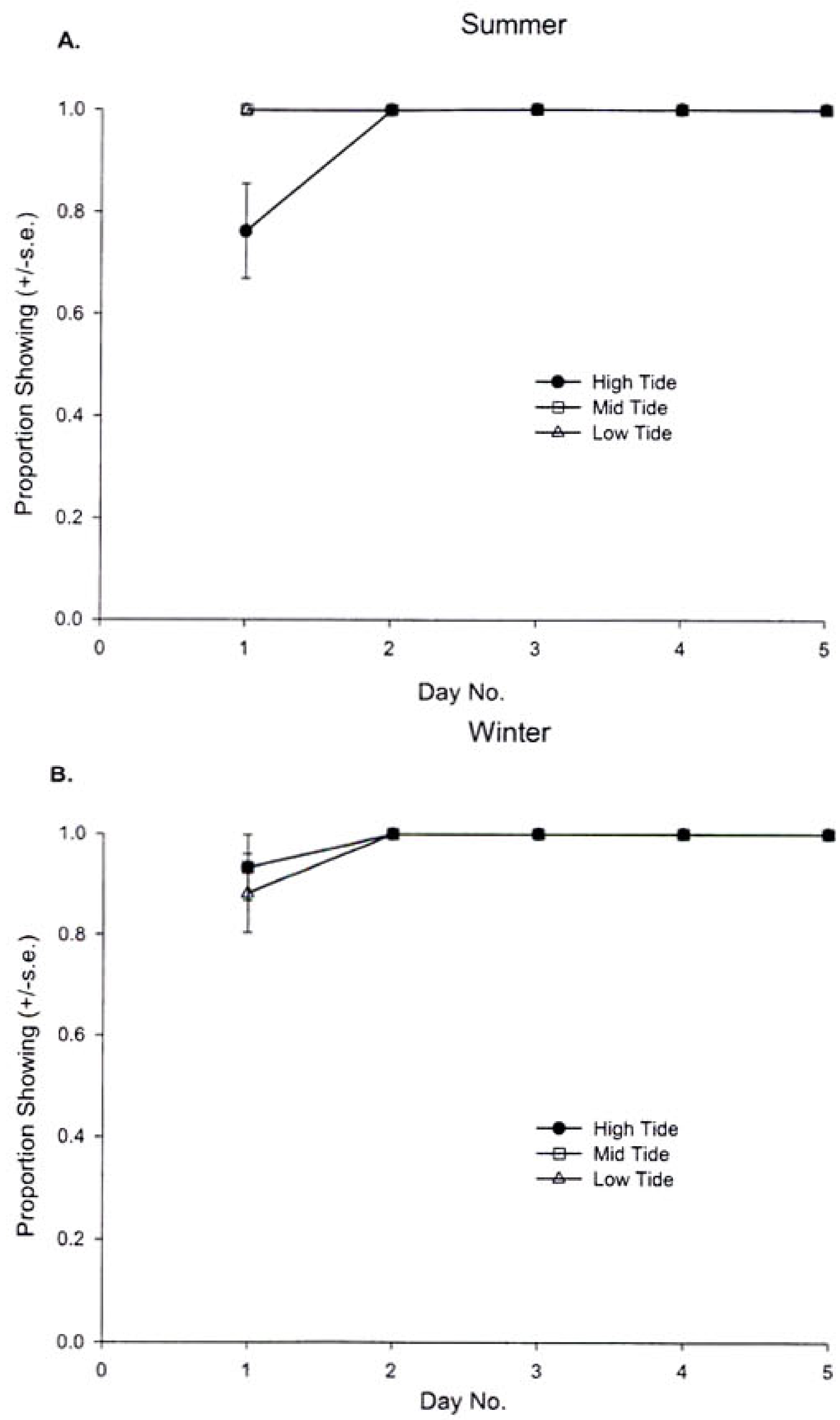

Figure 5. Cumulative proportion (±SE) of geoduck showing in show-factor plots in Kennedy Bay during summer (A) and winter (B) at high, mid, and low tides sampled from 26/6/1999 to 1/7/1999. Means are dots and vertical lines are ±1SE.

TABLE 1.

Transect no. (T), length of transect (m) (L) and number of geoduck (no.) along each transect sampled in each location.

	Population									
	Kennedy Bay		Shelley Bay		Mahunga Bay		Bay 1		Bay 2	
T	L	No.	L	No.	L	No.	L	No.	L	No.
1	600	12	100	46	170	20	45	2	105	54
2	600	44	100	32	145	16	40	6	70	38
3	600	78	100	24	60	12	40	6	60	26
4	600	36	115	34	100	10	35	18	60	4
5	600	34	100	46	100	18	35	40	60	0
6	600	36	100	46	55	8	40	12	60	0
7	600	28	80	52	85	14			80	0
8	600	16	85	86	100	4			75	0
9	600	22	80	36	105	12			85	0
10	600	28	75	16	65	8			95	0
11	600	16			100	14				
12	600	4								
13	600	4								
14	600	2								

Although several studies on *P. abrupta* have shown that show-factors are depressed during winter (Goodwin 1973, 1977; Fyfe 1984), winter is a period of active gametogenic development in populations of *P. zelandica* (Gribben et al. 2004). If *P. zelandica* were remaining inactive for extended periods of time, then it seems unlikely they could meet all metabolic needs, including gamete production during winter. Fyfe (1984), in a study of geoduck in Ritchie Bay, British Columbia, found that *P. abrupta* may lay "dormant" for periods of up to 2 months, possibly in response to low winter temperatures and food availability (Goodwin 1973, 1977; Fyfe 1984). However, the plots were only visited once a month during the winter period. Fyfe (1984) assumed that previously tagged geoduck not visible at the next sampling period had remained inactive for at least that period. This may certainly not have been the case. In fact, gametogenesis in *P. abrupta* from both Washington (Andersen 1971, Goodwin 1976, Beattie & Goodwin 1992) and British Columbia (Sloan & Robinson 1984) also progresses rapidly through autumn and winter. Hence, it would also seem unlikely that *P. abrupta* would remain inactive for extended periods.

This study indicated the benefit of using smaller sized quadrats when assessing show factors, as shown by the significant increase in show-factors between experiments 1 and 2 in Wellington Harbour. The smaller quadrats used in experiment 2 were easier and quicker to search. The poor show-factor and large confidence intervals in experiment 1 were due to the large size (2 m × 2 m) of the quadrats and the silty nature of the sediment. The time needed to search the quadrats increased the disturbance of the sediment making geoduck difficult to find. However, the 1-m^2 quadrats used in subsequent experiments could be further refined into narrow strip transects (approx. 1 m × 10 m), similar to those used in the North American surveys (e.g., Hand & Dovey 1999, 2000) that would allow increased numbers and a larger area to be surveyed.

In Puget Sound, a show-factor of 0.75 is currently used to adjust density estimates on all beds for refishing surveys unless a show plot is established (Bradbury et al. 2000). This is strictly a management decision assumed to give a conservative estimate of harvestable biomass. The common 0.914 show-factor presented here suggests that this adjustment may be applicable to other populations of *P. zelandica*. However, more research needs to be conducted on the applicability of a general show-factor to other populations, especially those found in cooler waters. All geoduck counts in this study were conducted by a single experienced geoduck diver.

Density and Biomass Estimates

The setting of annual quotas for *P. abrupta* is reliant on reliable estimates of density and area, which vary geographically (Sloan 1985). Every parameter used in calculating virgin density, abundance, and biomass is estimated with varying uncertainty (Hand & Dovey 1999). Survey densities, abundance, and biomass estimates were reasonably well determined with coefficients of variation (CVs) of less than 20% except for the two smallest bays for which the CVs were approximately 30%. This may have been due to the small number of transects surveyed within the bounds of the populations. Increasing sample sizes (i.e., running more transects within the bays) may have helped reduce the CVs.

Estimates of the average densities of geoduck populations in British Columbia have ranged from 0.2 to 5.0 geoduck/m^2 (Breen & Shields 1983, Hand et al. 1998a, Hand et al. 1998b). Densities as high as 30 m^{-2} have been recorded in Griffith Harbour, British Columbia (Hand & Dovey 2000). Average density based on 8589 transects in Puget Sound was 1.7 m^{-2} and ranged from 0–22.5 geoduck/m^2 (Goodwin & Pease 1991). The mean population density estimates provided for *P. zelandica* in this study are lower than those estimated for the *P. abrupta* (Table 2). Although large in area, the low estimated density in Kennedy Bay would appear to make harvesting in this bay unsustainable. In Wellington Harbour, the mean density was much higher although the combined area of geoduck occupied in the regions surveyed was only ~5.5 ha. However, this is likely to be only a portion of the total population in the harbor, as many other bays with similar habitats to those surveyed were not explored. Geoduck will probably not be harvested from this harbor for reasons of pollution. Other larger populations are known to occur in the Marlborough Sounds, and Golden Bay, Nelson. Studies investigating the density, abundance and biomass of geoduck in this area are yet to be conducted.

Fisheries managers will have to be particularly careful in determining whether populations of *P. zelandica* can be harvested sustainably. Harvesting geoduck results in a thinning of the population, with the densest areas the most heavily fished. Evidence suggests that recruitment into North American geoduck populations has been falling for the past 20 years (Orensanz et al. 2000), although some several recruitment events have occurred in British Columbia in the last decade (Bureau et al. 2002). Because *P. zelandica* already occurs at low densities, harvesting may have a large effect on the potential fertilization success of geoduck. However, little is known of the density dependence of fertilization success for geoduck species and this warrants further investigation. Further to this, *P. zelandica* is protandric with females dominating the large size classes (Gribben & Creese 2003). Given that harvesting geoduck involves searching for siphon holes and the largest siphon holes generally contain the largest geoduck, harvesting may also target female geoduck resulting in populations that are egg-limited (Gribben & Creese 2003). This may have severe repercussions for future recruitment success.

TABLE 2.

Estimates of total area, show-factor (SF) adjusted total, mean density, total abundance, mean individual weight and biomass of geoduck found in all transects in each location.

	Area (ha)	SF Adj. Total (±SE)	Density (m^{-2}) (±SE)	Abundance (±SE)	Mean Weight (g) (±SE)	Biomass (t) (±SE)
KB	39.60	382.9 (131.5)	0.06 (0.01)	22976.0 (4007.3)	242.2 (8.6)	5.56 (0.99)
SB	1.87	457.3 (131.5)	0.49 (0.08)	9146.6 (1421.2)	358.8 (7.5)	3.28 (0.51)
MB	2.17	148.8 (34.3)	0.14 (0.01)	2975.9 (282.1)	358.8 (7.5)	1.07 (0.10)
B1	0.47	91.9 (63.57)	0.39 (0.17)	1838.1 (803.7)	358.8 (7.5)	0.66 (0.29)
B2	0.59	224.4 (181.9)	0.45 (0.11)	2669.6 (637.2)	358.8 (7.5)	0.96 (0.23)

KB, Kennedy Bay, SB, Shelly Bay; MB, Mahunga Bay; B1, Bay 1, and B2, Bay 2.
Standard error (±SE) given in parentheses.

The large differences in mean density and size of geoduck between the Kennedy Bay and Wellington populations may, in part, be due to large storm events that occurred in the Coromandel region in the mid 1990s, which saw large numbers of geoduck stranded on the beaches surrounding Kennedy Bay (George Potae, Kennedy Bay Mussel Company Ltd, pers. comm.). Since then, a large recruitment event occurred during 1997/1998 resulting in the population being dominated by two cohorts (Gribben et al. 2004). Geoduck in Shelly Bay were mainly large individuals with very few small geoduck present. Thus mean size and biomass in Kennedy Bay are unlikely to be static and will increase as the cohort develops. The future contribution that this smaller cohort will make to later biomass estimates is unknown because no reliable estimates of mortality are currently available for *P. zelandica* (Breen 1991, Gribben 2003).

The results presented in this study indicate that the methods used for describing the distribution, density, and biomass of populations of *P. abrupta* could be readily adopted for *P. zelandica*. However, less experienced searchers may have more difficulty in finding geoduck, especially when visibility is poor and during winter months. During this period, geoduck were usually found by searching potential siphon holes, which is more time consuming. We recommend that abundance and biomass estimates not be conducted during winter or periods of poor visibility because less experienced divers may miss many geoduck leading to biomass underestimates, and that the variability in diver counts be investigated. Finally, before the sustainability of harvesting geoduck can be assessed further, work on the density dependence of fertilization success, recruitment, and natural mortality of *P. zelandica* must be conducted.

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