

# AGE, GROWTH, AND MORTALITY OF THE NEW ZEALAND GEODUCK CLAM, *PANOPEA ZELANDICA* (BIVALVIA: HIATELLIDAE) IN TWO NORTH ISLAND POPULATIONS

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## ABSTRACT

There is increasing interest in developing fisheries and aquaculture industries for the New Zealand geoduck clam, *Panopea zelandica* (Quoy and Gaimard, 1835). However, little is known about the age structure, growth rates, and mortality of different populations of *P. zelandica*. Annual bands in polished shell sections were used to obtain estimates of age, growth rates, and mortality of *P. zelandica* at two sites in northern New Zealand. *Panopea zelandica* in Kennedy Bay ranged in age from 2 to 34 yrs whilst those in Shelly Bay ranged from 3 to 85 yrs. There was a significant difference ( $P < 0.001$ ) in growth rates (shell length-at-age) between the populations (estimated asymptotes were 111.5 mm and 103.6 mm for Kennedy Bay and Shelly Bay, respectively). However, the growth characteristics (i.e., rapid growth for the first 10–12 yrs and minimal thereafter) were similar for both populations. Drained wet weight-at-age followed a similar pattern to shell length-at-age, although growth in terms of weight was rapid until 12–13 yrs of age. The estimated maximum drained wet weight of *P. zelandica* was higher in Kennedy Bay (275.5 g) than in Shelly Bay (223.1 g). There was also a significant difference ( $P = 0.02$ ) in the relationship between total shell length and drained wet weight for the two populations. The width between the siphons visible at the sediment surface was a reasonable predictor of the shell length ( $r^2 = 0.57$ ) of *P. zelandica* in Kennedy Bay. Estimates of natural mortality using catch curve analysis, estimates of maximum age, and the Chapman-Robson estimator were very low (0.02–0.12 proportion yr<sup>-1</sup>). This study is the first to confirm that the shell bands in *P. zelandica* are deposited annually and can be successfully used to age this species. Given the low estimated rates of mortality and longevity of *P. zelandica*, fisheries managers will need to carefully consider the feasibility of commercially harvesting this species.

Bivalves are an important part of the global shellfish market. In 1999, bivalves accounted for almost 13% of total world fisheries production (126 million t), with clams, cockles, and ark-shells (3.6 million t) second only to oysters (3.9 million t) in terms of world bivalve production (FAO, 2001). New Zealand's bivalve industries are worth in excess of NZ\$180 million in export earnings annually (NZ Seafood Industry Council, 2002). The principal species exported is the Greenshell™ mussel, *Perna canaliculus* (Gmelin, 1791), which is worth NZ\$150 million annually (NZ Seafood Industry Council, 2002). Despite having species very similar to those currently available on world markets, the commercial exploitation of clams in New Zealand has been at low levels. Annual landings of commercially harvested clam species in New Zealand consist mainly of the cockle, *Austrovenus stutchburyi* (Wood, 1828), for which total landings in 2000/1 were 1859 t (G. MacGregor, NZ Ministry of Fisheries, pers. comm.). There are also small fisheries for several other clams (e.g., *Paphies australis* Gmelin 1790, *Paphies donacina* Spengler, 1793, and *Paphies subtriangulata* Wood, 1828) (McLachlan et al., 1996).

Commercial harvesting of the Pacific geoduck clam, *Panopea* (formerly *Panope*) *abrupta* (Conrad, 1849), forms the most important clam fishery on the Pacific coast of North America (Campbell et al., 1998) and is worth in excess of US\$35 million

annually (Harbo, 1998; Hoffman et al., 2000). The major fisheries are found in Washington State, British Columbia, and Alaska. A small experimental fishery (ca. 100 t annually) for the native New Zealand geoduck clam, *Panopea zelandica* (Quoy and Guimard, 1835), began in 1988 (Breen et al., 1991). The fishery was closed in the early 1990s pending its introduction into the quota management system (Breen, 1994). Recently, there has been renewed interest in developing commercial fisheries and aquaculture for *P. zelandica* because of its similarity to *P. abrupta*.

Although there is a wealth of ecological information available on infaunal bivalves, especially those of commercial importance [e.g., the ocean quahog, *Arctica islandica* (Linnaeus, 1767); the hard-shell clam, *Mercenaria mercenaria* (Linnaeus, 1758); the Pacific geoduck clam, *P. abrupta* (Conrad, 1849); Jones, 1981; Mann, 1982; Murawski et al., 1982; Ropes, 1984; Rowell et al., 1990; Kraus et al., 1992; Kennish et al., 1994; Bradbury and Tagart, 2000; Curtis et al., 2000; Hoffman et al., 2000; Kraeuter and Castagna, 2001], many of these studies have been undertaken only in response to the continued expansion of existing fisheries, and the fear that harvest rates are unsustainable. Rarely in the study of infaunal bivalve populations is a broad enough range of ecological data available prior to the inception of harvesting or culture activities to provide direction for further research, comment on the possible consequences of harvesting regimes on the sustainability of populations, or assess the possible obstacles to the development of aquaculture industries. Study of the New Zealand geoduck provides a unique opportunity to provide this information for an as yet undeveloped fishery, as well as to provide preliminary data on the feasibility of developing aquaculture industries for *P. zelandica*.

Apart from the preliminary work of Breen et al. (1991) and more recent studies on its distribution and abundance (Gribben et al., 2004b), reproductive development (Gribben and Creese, 2003; Gribben et al., 2004a), and larval development (Gribben and Hay, 2003), little basic ecological information exists for *P. zelandica*. Breen et al. (1991) provided estimates of growth and mortality for a single population of *P. zelandica* in Golden Bay, Nelson, under the assumption that counted internal growth bands were annual. However, this assumption was not validated. Accurate age, growth, and mortality data are vital for determining sustainable harvesting strategies and for realistic yield modeling (King, 1995; Bradbury and Tagart, 2000; Haddon, 2001; Zhang and Campbell, 2002). This study investigated the periodicity of internal growth bands of *P. zelandica* and whether they could justifiably be used to age geoduck clams in New Zealand. Growth rates, in terms of both weight and length, and estimates of natural mortality were then determined for two populations. This study also investigated whether the size of *P. zelandica* could be estimated from the width between paired siphon holes visible at the sediment surface.

## METHODS

**GROWTH.**—The growth rates of *P. zelandica* were investigated using analysis of the age structure of the populations and tag and recapture methods in Kennedy Bay and Shelly Bay in the North Island of New Zealand (Fig. 1). Kennedy Bay is a shallow, moderately sheltered bay approximately 1.5 km in diameter, which gently slopes to a maximum water depth of ca. 11 m at its entrance. Subtidal sediments are relatively homogenous throughout the bay, mainly consisting of clean fine sediment with a little silt present (Gribben et al., 2004b). Shelly Bay is a small sheltered embayment with depths in excess of 20 m within 200 m of the shoreline. The sediments found in this bay are more variable, ranging from coarse to very silty with in-

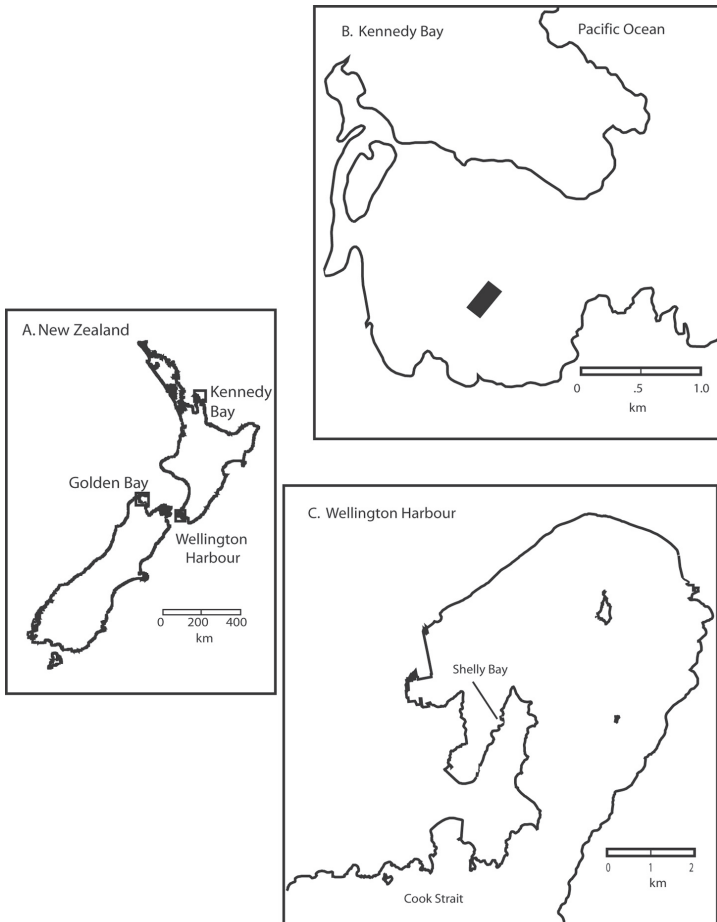


Figure 1. The location of the populations where *Panopea zelandica* were studied in (A) New Zealand: (B) Kennedy Bay and Shelly Bay, (C) Wellington Harbour. An additional population for which data are available is located in (A) Golden Bay, Nelson. Black box in (B) indicates area where geoducks were collected from Kennedy Bay.

creasing water depth, although the densest areas of geoducks are found in fine sand sediments (Gribben et al., 2004b).

**COLLECTION OF ANIMALS.**—Between 19 and 39 *P. zelandica* were collected monthly from March 2000 to August 2001 in Kennedy Bay and from March 2000 to September 2001 in Shelly Bay. However, *P. zelandica* could not be sampled in all months due to poor weather conditions. Additional samples were collected from Shelly Bay in February 2002 and from Kennedy Bay in April 2002. Geoducks were collected haphazardly by SCUBA in order to obtain samples representative of the size structure of each population. Geoducks were only collected when water visibility was good, with all *P. zelandica* collected by a single diver experienced in collecting this species. Once removed from the sediment, shell length (maximum anterior-posterior length of the right valve) was measured to the nearest mm using vernier callipers, and whole wet weight was obtained to the nearest 0.1 g using a Mettler electronic balance. The shells were then removed from the animal, labeled, and stored until they could be sectioned (see below).

**AGE VALIDATION.**—In order to create growth curves from length-at-age data, methods for ageing *P. zelandica* must first be validated. If the age of animals is not known prior to the sectioning of their shells, the periodicity and timing of the deposition of shell growth bands

can be determined by regular sampling of individual cohorts through time. If one band is laid down per year then it could be reasonably assumed that they are annual. This can be validated by following a single cohort for a number of years (Breen, 1991). Fortunately, unusually high recruitment of *P. zelandica* in Kennedy Bay just prior to the initiation of our study resulted in an unambiguous cohort of young individuals making validation possible (Gribben, 2003).

In total, 154 *P. zelandica* shells (right valve only) from Kennedy Bay and 112 from Shelly Bay were sectioned. The Kennedy Bay sample consisted of all geoducks collected in March 2000, June 2000, September 2000, October 2000, February 2001, and March 2002. For Shelly Bay, only those shells collected in July 2000, September 2000, November 2000, December 2000, and February 2001 were sectioned. All shells were sectioned through the umbo, and polished on a grinding wheel using a series of 120, 220, 500, 1200, and 4000 grit silicon-carbide paper. Sections were then polished with 3- $\mu\text{m}$  diamond abrasive and the surface etched for 30 min with 0.1 M EDTA. The sections were then dried and viewed under a reflecting light microscope at 5 $\times$ , 10 $\times$ , and 20 $\times$  magnification. Further manipulation of the sections, such as the preparation of acetate peels, was not necessary as the internal bands were clearly visible and could be easily counted.

**SHELL LENGTH-AT-AGE.**—Average von Bertalanffy growth curves were constructed for both the Kennedy Bay and Shelly Bay populations using the shell length-at-age data from *P. zelandica* sectioned in the age validation study using the following equation (Haddon, 2001):

$$L_t = L_\infty \left( 1 - e^{-k(t-t_0)} \right)$$

where  $t$  = age in years,  $L_t$  = shell length at  $t$ ,  $L_\infty$  = theoretical maximum length,  $k$  = exponential rate at which shell length approaches the asymptote, and  $t_0$  = hypothetical age at which the organism would have been at zero length. The parameters  $L_\infty$ ,  $k$  and  $t_0$  were estimated using non-linear least squares method (PROC NLIN, SAS Institute, 1988).

A maximum likelihood test was used to assess whether growth curves were equivalent between the Kennedy Bay and Shelly Bay populations (Haddon, 2001). The test compares the individual curves with a curve fitted to the combined data (i.e., pooled data from both populations) and is based on the following chi-squared test statistic:

$$\chi_k^2 = -N \times \text{Ln} \left( \frac{RRS_\Omega}{RRS_\omega} \right)$$

where  $k$  is the degrees of freedom (df) (equals the number of constraints placed upon the fit),  $N$  is the total number of observations from the combined data,  $RRS_\Omega$  is the total sum of the squared residuals derived from fitting both curves separately, and  $RRS_\omega$  is the total sum of squared residuals derived from fitting the curve to the combined data.

**DRAINED WET WEIGHT-AT-AGE.**—Drained weight of aged *P. zelandica* was estimated from the regression equation for whole wet weight and drained weight for separate samples collected from Kennedy Bay ( $n = 200$ ) and Shelly Bay ( $n = 178$ ), as information on the drained weight of the aged geoducks was not available. Whole wet weight was obtained by immediately blotting the external surface of the *P. zelandica* once they were extracted and weighing them on a Mettler Balance. Drained weight was obtained by slitting the body and allowing excess water to drain out prior to weighing. Drained weight-at-age ( $W_a$ ), was estimated from length-at-age ( $L_a$ ) as derived from the von Bertalanffy growth equation above (Breen et al., 1991; Bradbury and Tagart, 2000), for geoducks from Kennedy Bay and Shelly Bay using the power function (Haddon, 2001):

$$W_a = xL_a^y$$

where  $y$  is the allometric growth parameter and  $x$  is a scaling constant determined by fitting a linear regression to log-transformed length versus drained weight data (PROC GLM, SAS Institute, 1988). An F-test was used to determine whether there were allometric differences between populations.

**TAG AND RECAPTURE.**—Tag and recapture methods were also employed to describe growth rates in Shelly Bay because of the low number of small geoducks occurring in this region. A total of 130 clams (66–115 mm shell length) was collected by SCUBA from Shelly Bay in October 1999. Geoducks were transported to the Island Bay Marine Laboratory where their shell lengths were recorded and they were individually tagged with numbered plastic mollusc tags (Hallprint Pty, Adelaide, South Australia). The tags were fixed to the shells using a small amount of cyanoacrylate-based glue. The geoducks were placed back into the sediment in a 15 × 15 m grid the following day. Tagged *P. zelandica* were recovered and measured at the end of the experiment in March 2002.

**WIDTH BETWEEN PAIRED SIPHON HOLES AND DEPRESSION HOLES AS A PREDICTOR OF SHELL LENGTH.**—Removing geoducks from the sediment is generally considered the only reliable method for obtaining measurements of geoduck size, as researchers have found that for *P. abrupta* siphon hole size is a poor predictor of shell length (e.g., Andersen, 1971). However, general field observations suggested that this was worth investigating in *P. zelandica*. If feasible, measuring siphon holes would be quicker than removing *P. zelandica* from the sediment for measurement and would avoid having to sacrifice the animals, as geoducks experience very high mortality when removed and then placed back into the sediment (Gribben, 2003). The appropriateness of using widths between paired siphon holes as a predictor of shell length was only investigated in Kennedy Bay as most *P. zelandica* in Shelly Bay were found by probing the sediment and not by locating siphon holes (see Gribben et al., 2004b). Two experiments were conducted during September 2001. In the first experiment, the maximum distance between the paired siphons (i.e., outside the inhalant siphon to outside the exhalant siphon) of 51 geoducks was measured when the siphons were visible and the geoducks actively feeding. After the width between siphons was measured, the geoduck was removed from the sediment and shell length was recorded as above. The same method was employed for the second experiment except that when a geoduck was located the siphon was touched, stimulating its retraction and allowing the width of the depression remaining on the sediment surface to be measured. In total, 45 *P. zelandica* were measured in this experiment. Results were analyzed with linear regression.

**MORTALITY.**—Natural mortality ( $M$ ; proportion yr<sup>-1</sup>) of *P. zelandica* in Kennedy Bay and Shelly Bay was estimated using catch curve analysis (Breen, 1994), estimates of longevity (Breen, 1994; Annala et al., 2001), and the Chapman-Robson (CR) estimator (Chapman and Robson, 1960). The first method estimates  $M$  from the regression of ln(abundance) vs estimated age, with the slope of the regression line giving estimated  $M$ . Natural mortality was estimated using the raw data, and also by grouping geoducks into 3 and 5 yr size-classes. In Shelly Bay, the initial size class from the 3 and 5 yr groupings was excluded from the analysis because of the very low numbers occurring in this size class.

In the second method,  $M$  was estimated directly from the longevity estimate using the equation:

$$M = \frac{\log_e(p)}{A}$$

where the longevity of a stock is defined as the maximum age,  $A$ , which only a proportion,  $p$ , of the population is assumed to reach (Cranfield et al., 1993). A value of  $p = 0.01$  has often been used in studies investigating the mortality of bivalves (e.g., Hoenig, 1983; Cranfield et al., 1993; Breen, 1994; Annala et al., 2001) and was also used in this study.

The final method, the CR estimator, is calculated from catch-at-age data and is defined as:

$$CR = \log_e \left( \frac{1 + \bar{a} - 1/n}{\bar{a}} \right)$$

where  $\bar{a}$  is the mean age and  $n$  the sample size (Chapman and Robson, 1960). The CR method has been shown to be more accurate (in terms of lower root mean square error) and have lower bias than regression estimators (Dunn et al., 2002). All estimates of  $M$  were based on geoducks sectioned for the age validation study described earlier.

## RESULTS

**AGE VALIDATION.**—Photographs of polished shell sections of *P. zelandica* obtained in our study clearly indicated distinct growth bands, as illustrated in Breen et al. (1991). The number of growth bands occurring in shell sections ranged from 2 to 38 for geoducks collected in Kennedy Bay and from 3 to 85 for geoducks collected from Shelly Bay (Fig. 2). The mean number ( $\pm$  SE) of growth rings per shell for geoducks from Kennedy Bay was 8.5 ( $\pm$  0.7) and from Shelly Bay was 19.7 ( $\pm$  1.6). The large difference in the mean number of growth bands was attributed to the presence of a large cohort of small geoducks ( $< 5$  yrs old) in Kennedy Bay. The mean number of growth bands in geoducks from Kennedy Bay with more than five growth rings (i.e., in the larger of the two cohorts) was 15.3 ( $\pm$  0.9). Very few geoducks with  $< 5$  growth rings were present in Shelly Bay.

Growth band frequency histograms from Kennedy Bay identified a strong cohort of small geoducks with two growth bands in March 2000 (Fig. 2). Three rings were present a year later in February 2001 and four in March 2002, providing solid evidence that growth bands are deposited annually. Analysis of the samples sectioned during 2000 indicated that the growth ring is deposited during winter (between June and September) when growth is minimal.

**SHELL LENGTH AND DRAINED WEIGHT-AT-AGE.**—Given the annual periodicity of growth rings, *P. zelandica* from the small cohort in Kennedy Bay collected by Gribben (2003) for length frequency analysis in June 1999 would have had one growth band. Hence, these animals were included in the calculation of the von Bertalanffy growth curve for Kennedy Bay (Fig. 3).

Sectioned geoducks ranged from 33 to 127 mm shell length in Kennedy Bay and from 75 to 120 mm shell length in Shelly Bay. The growth profiles of geoducks were similar for both populations until the age of 8 or 9 (Table 1; Fig. 3). Thereafter, growth in geoducks from Shelly Bay appeared to proceed more slowly than in those from Kennedy Bay. Growth in both populations was minimal beyond about 10–12 yrs of age (Fig. 3). The growth rates between the populations were significantly different ( $\chi^2 = 22.7$ ,  $P < 0.001$ ) with geoducks from Kennedy Bay attaining a larger theoretical maximum length compared with geoducks from Shelly Bay: 111.5 vs 103.6 mm, respectively. Geoducks in Shelly Bay were longer lived than those from Kennedy Bay. No geoducks older than 38 yrs were found in Kennedy Bay, but approximately 10% of the individuals sectioned from Shelly Bay were more than 40 yrs old. The oldest geoduck shell sectioned from Shelly Bay was estimated to be 85 yrs old.

Geoducks ranged from 51 to 627 g whole wet weight and from 27 to 343 g estimated drained weight in Kennedy Bay, and from 118 to 632 g whole wet weight and

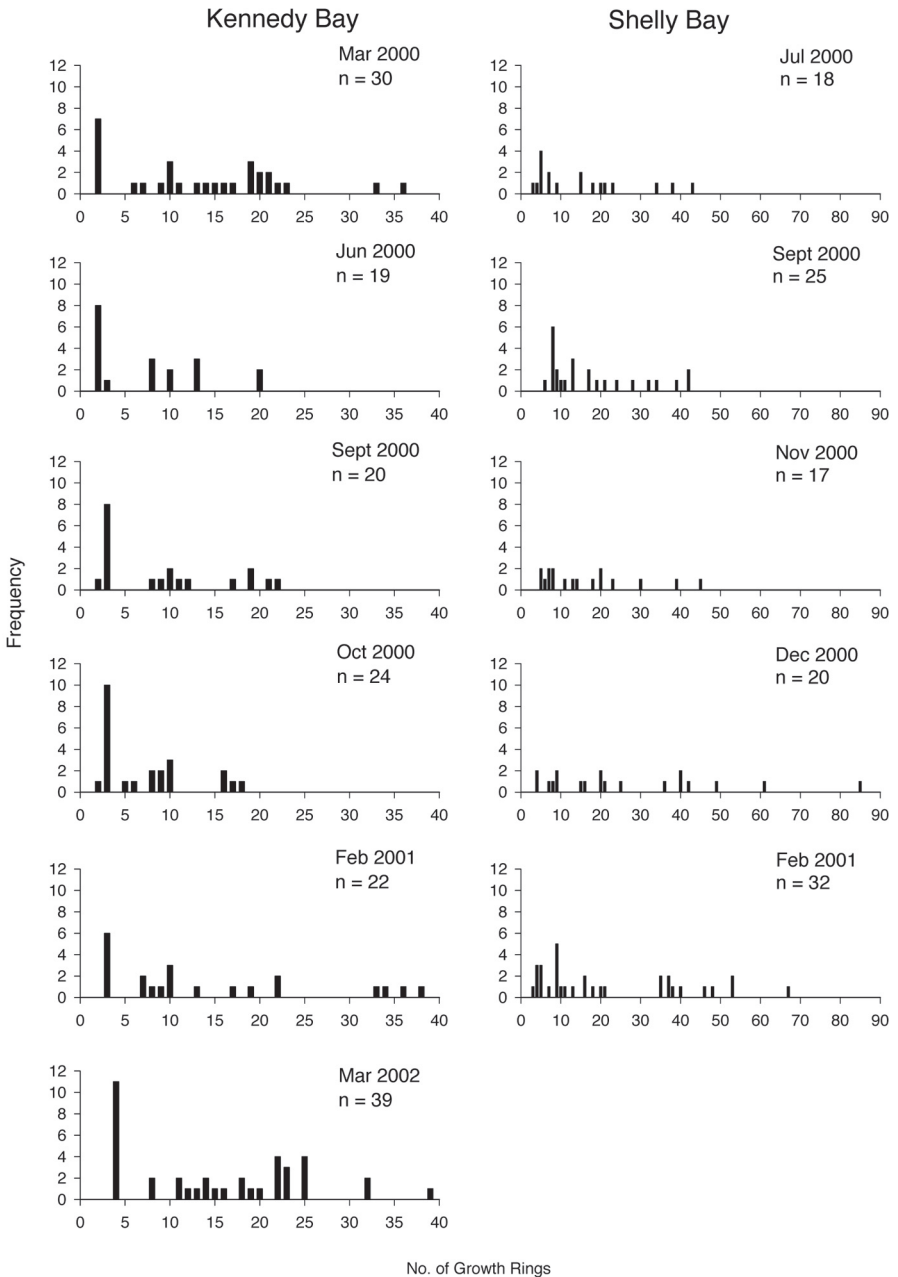


Figure 2. Frequency of growth rings in selected monthly samples for *Panopea zelandica* collected from Kennedy Bay (March 2000–2002) and Shelly Bay (July 2000–February 2001) for length frequency analysis. Note differences in X-axis.

from 54 to 303 g estimated drained weight in Shelly Bay. The regression equations for Kennedy Bay ( $y = 0.622x + 8.89$ ) and Shelly Bay ( $y = 0.5176x + 30.469$ ) were good predictors of drained weight given wet whole wet weight ( $r^2 = 0.92$  and  $0.79$  for Kennedy Bay and Shelly Bay, respectively). A significant difference (F-test:  $P = 0.02$ ) was

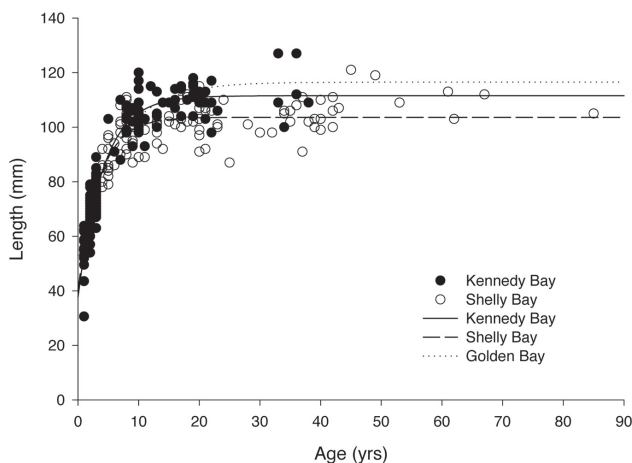


Figure 3. Von Bertalanffy length-at-age growth curves for *Panopea zelandica* from Kennedy Bay ( $n = 182$ ), Shelly Bay ( $n = 112$ ), and Golden Bay (data from Breen et al., 1991). Parameter values of the fitted lines are estimated from log-transformed data.

detected in the shell length vs estimated drained weight relationship between Kennedy Bay and Shelly Bay.

Growth in weight with respect to age was similar to that for shell length, in that growth was rapid for approximately the first 13 yrs and minimal thereafter (Fig. 4). The estimated asymptote was higher in Kennedy Bay (275.5 g) than in Shelly Bay (223.1 g) (Table 1). As was the case with length-at-age, there was large variability in weight-at-age for both populations, especially in older *P. zelandica*.

**TAG AND RECAPTURE.**—Of the 130 geoducks initially tagged only ten were recovered. Little growth was apparent in those geoducks recaptured. Three tagged shells were recovered on the sediment surface indicating that the poor recapture rate may primarily have been a result of mortality.

**WIDTH BETWEEN SIPHON HOLES AND DEPRESSION HOLES AS A PREDICTOR OF SHELL LENGTH.**—The width of siphon holes was an adequate predictor of shell length ( $r^2 = 0.57$ ) (Fig. 5). Although the width between siphon holes in the mid size range (30–40 mm) were associated with variable shell lengths, geoducks with the smallest and largest distances across the siphons generally had the smallest and largest shell lengths, respectively. The width of the depression left by the retracted siphon was a poor predictor of shell length ( $r^2 = 0.29$ ).

Table 1. Parameter estimates for length-at-age ( $L_\infty$ ,  $k$ , and  $t_0$ ) from the Von Bertalanffy model fitted to *Panopea zelandica* collected from Kennedy Bay (KB) and Shelly Bay (SB), and estimates of  $x$ ,  $y$ , and  $W_\infty$  used in the power curve to model weight-at-age. Parameter estimates for Golden Bay (GB) are from Breen et al. (1991).

| Area | Length-at-age |      |       | Weight-at-age         |       |            |
|------|---------------|------|-------|-----------------------|-------|------------|
|      | $L_\infty$    | $K$  | $t_0$ | $x$                   | $y$   | $W_\infty$ |
| KB   | 115.5         | 0.25 | -1.67 | $2.40 \times 10^{-4}$ | 2.960 | 275.5      |
| SB   | 103.6         | 0.29 | -1.69 | $6.46 \times 10^{-3}$ | 2.252 | 223.1      |
| GB   | 116.5         | 0.16 | -3.80 | $3.45 \times 10^{-3}$ | 2.422 | 348.8      |



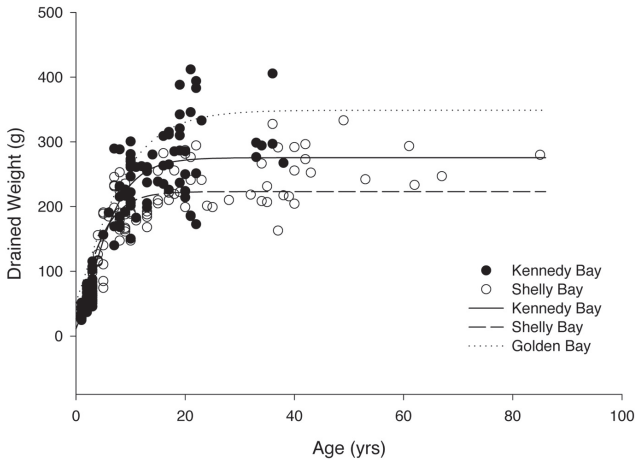


Figure 4. Drained weight-at-age of *Panopea zelandica* in Kennedy Bay ( $n = 182$ ), Shelly Bay ( $n=112$ ), and Golden Bay determined using the power curve  $W_a = xL_a^y$  where  $W_a$  (weight-at-age) is fitted from  $L_a$  as determined from the Von Bertalanffy curve for length-at-age. Parameter values for the fitted lines for each population were estimated from log-transformed data. Golden Bay data from Breen et al. (1991).

**MORTALITY.**—Estimates of instantaneous natural mortality (proportion  $\text{yr}^{-1}$ ) of *P. zelandica* provided by catch curve analyses ranged from 0.05 to 0.07 for Kennedy Bay and from 0.02 to 0.04 for Shelly Bay (Figs. 6,7; Table 2). Estimated mortality using all methods was higher in geoducks collected from Kennedy Bay compared to those collected from Shelly Bay. Estimates of mortality based on maximum age were higher than those for catch curve analyses for both Kennedy Bay (0.12) and Shelly Bay (0.05). CR estimates were almost identical to longevity estimates. There was little difference in estimates of mortality from Kennedy Bay using raw or grouped data (range 0.05–0.07). Estimates of mortality from Shelly Bay were extremely low, although estimated mortality for data grouped into 5 yr size classes (0.04) was twice that estimated using the raw data (0.02). This was because of the low numbers of *P. zelandica* < 10 yrs old in the raw data set for Shelly Bay.

## DISCUSSION

In studies of the length-frequency of individuals within a population, modes in length-frequency histograms are generally assumed to represent a single age class and associated variation. In another study of *P. zelandica* from the Kennedy Bay and Shelly Bay, length-frequency analysis indicated the presence of only two cohorts in Kennedy Bay and one distinct cohort of large geoducks in Shelly Bay (Gribben, 2003). Although the smaller cohort in Kennedy Bay did indeed contain geoducks of the same age (the same cohort was used to validate growth rings in this study), the larger cohort contained animals from > 15 age classes. Thus, true cohorts (especially in larger size classes) are not often readily discernable and in populations that are dominated by a single large cohort, length-frequency analyses contribute little to our understanding of population dynamics.

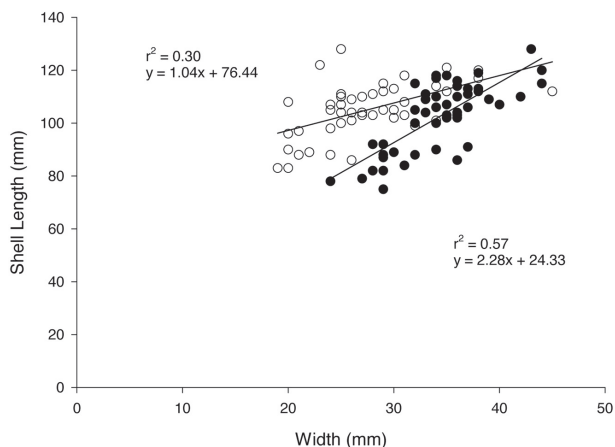


Figure 5. Relationship between shell length and width between siphon holes (solid circles), and shell length and width of depressions in the sediment (open circles) for *Panopea zelandica* from Kennedy Bay.

Annual bands can be deposited in response to spawning events (e.g., *Spisula solidissima* (Dillwyn, 1817) see Jones et al., 1978; *Phacosoma japonicum* (Reeve, 1850) see Sato, 1995) or during periods of minimal growth, such as the suppression of growth due to high (e.g., *Chamelea gallina* (Linnaeus, 1758), see Ramón and Richardson, 1992) or low winter water temperatures (e.g., *Mercenaria mercenaria*, Grizzle and Lutz, 1988; and *Saxidomus gigantea* (Deshayes, 1839) see Paul et al., 1976). *Panopea zelandica* mature in their third year, thus the cohort used to determine the periodicity of growth rings was sampled initially when this cohort contained only immature individuals (i.e., age 2), and then as mature geoducks (i.e., as 3- and 4-yr olds). Given that only one ring is deposited by both immature and mature geoducks, and spawn-

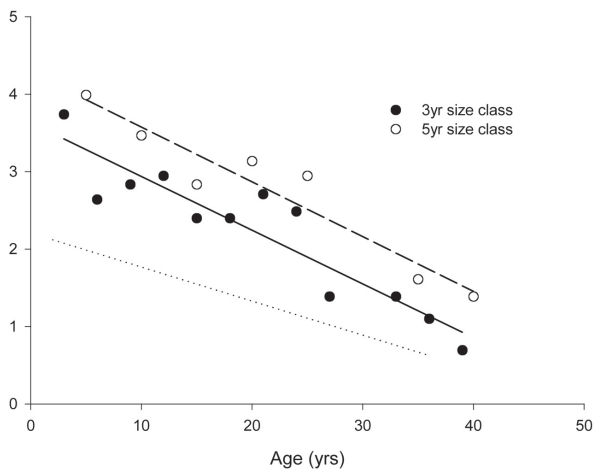


Figure 6. Relationship between abundance and estimated age of *Panopea zelandica* sectioned from Kennedy Bay grouped into 3 yr size classes (solid line), 5 yr size classes (dashed line), and raw data (dotted line; only regression line shown).

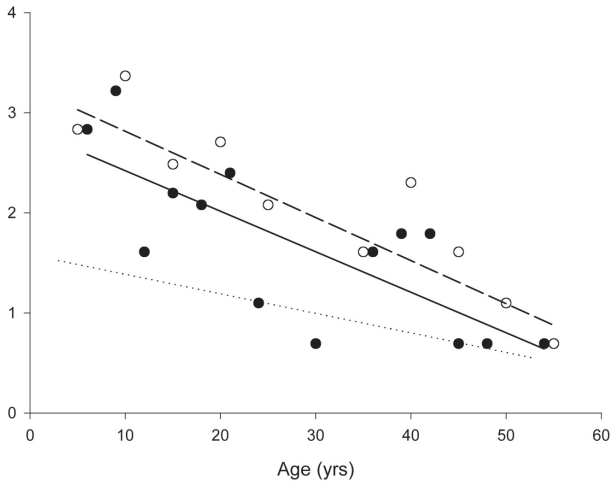


Figure 7. Relationship between abundance and estimated age of *Panopea zelandica* sectioned from Shelly Bay grouped into 3 yr size classes (solid line), 5 yr size classes (dashed line), and raw data (dotted line; only the regression line shown).

ing in Kennedy Bay occurs in spring/early summer (October/November; Gribben et al., 2004), after the growth ring is laid down during winter, it is apparent that spawning events are not responsible for the deposition of growth lines. Shaul and Goodwin (1982) found that annual growth line deposition in *P. abrupta* occurred during winter, similar to the findings of this study for *P. zelandica*.

*Panopea abrupta* is very long-lived, often reaching ages in excess of 100 yrs (Hand et al., 1998a,b). The oldest recorded *P. abrupta* individual in British Columbia was 146 yrs old (Harbo et al., 1983). The oldest recorded *P. zelandica* individual in this study was 86 yrs old. It is difficult to assess whether *P. abrupta* is longer lived than *P. zelandica* because of the somewhat low numbers of geoducks sectioned from Kennedy Bay ( $n = 155$ ) and Shelly Bay ( $n = 112$ ). Hoenig (1983) reported that an increase in sample size from 100 to 250 individuals may result in a 13% increase in maximum age observed. However, mean ages ranging from 28 to 61 yrs have been reported for populations of *P. abrupta* from British Columbia (Breen and Shields, 1983; Harbo et al., 1983; Sloan and Robinson, 1984), and from 28 to 57 yrs for 14 sites in Washington State (Goodwin and Shaul, 1984). These estimates are much higher than the mean ages estimated for *P. zelandica* by Breen et al. (1991) for a population in Golden Bay (12–13 yrs), Kennedy Bay (ca. 8.5 yrs) and Shelly Bay (ca. 19.7 yrs) in this study.

The relationship between drained weight-at-age for *P. abrupta* from Puget Sound followed similar growth patterns to that for shell length-at-age (Goodwin, 1976). That is, growth was rapid for the first 10 yrs and minimal thereafter. *Panopea zelandica* appears to follow a similar growth pattern to that of *P. abrupta* except that, in terms of weight, *P. zelandica* continued to grow rapidly until around the age of 13–15, several years after shell growth had slowed. Breen et al. (1991) presented an estimated maximum shell length of 116 mm, a maximum age of 34 yrs and an estimated drained weight of 348.8 g for a population of *P. zelandica* in Golden Bay, Nelson, the most southern of the three populations for which quantitative data are currently available. Their results are similar to ours for Kennedy Bay, the most northern of the

Table 2 Estimates of mortality from catch curve analysis, longevity and Chapman-Robson (CR) estimators for *Panopea zelandica* collected from Kennedy Bay (KB) and Shelly Bay (SB).

|             | Age class groupings | KB   | SB   |
|-------------|---------------------|------|------|
| Catch curve | Raw data            | 0.05 | 0.02 |
|             | 3 yr                | 0.07 | 0.03 |
|             | 5 yr                | 0.07 | 0.04 |
| Longevity   |                     | 0.12 | 0.05 |
| CR          |                     | 0.11 | 0.05 |

three populations. Goodwin and Pease (1989) have shown that the size of *P. abrupta* is affected by the structure of the sediment. Furthermore, Breen and Shields (1983) tentatively suggested that for *P. abrupta* shell length increases as exposure to wind and waves decreases. Although the sediment structure in which the three populations of *P. zelandica* occur appears similar (Gribben et al., 2004b), Kennedy Bay and Golden Bay occur in more exposed coastal bay environments compared to Shelly Bay, which is located in a sheltered low energy harbor with minimal current flow. This suggests that local environmental conditions may be more important in determining the growth and age characteristics of *P. zelandica* populations than any latitudinal gradients that may exist, such as those related to temperature. Regardless, the significant differences in the growth rates (in terms of both weight and shell length) and the relationship between length and drained weight between the populations sampled in Shelly Bay and Kennedy Bay, will have important implications for how individual stocks are managed and when selecting broodstock for aquaculture.

Early tag and recapture studies to measure the growth rates of *P. abrupta* in Washington indicated that growth was rapid in small geoducks and minimal in older clams (e.g., Goodwin, 1973). However, in several studies the tagging process resulted in a suppression of growth rates and a high level of mortality with few tagged geoducks being recaptured (e.g., Andersen, 1971; Goodwin, 1973, 1976). The poor recovery rate of *P. zelandica* from Shelly Bay (most likely a result of high mortality) and the lack of growth in those geoducks that were retrieved, further indicate that this is not a suitable method for assessing the growth rate of geoducks. However, an ability to determine the size of geoducks from the width between paired siphon holes would be a useful tool for assessing the size structure of geoduck populations quickly without having to sacrifice animals. Andersen (1971) found no relationship between the width between paired siphons and the size of *P. abrupta* from Hood Canal, Washington. Our study found that the width between the siphons visible at the sediment surface was a reasonable predictor of the shell length ( $r^2 = 0.57$ ) for *P. zelandica* in Kennedy Bay. However, there was a great deal of variation in the shell length of geoducks with intermediate widths between siphons (ca. 30–40 mm). While this technique will not be an entirely reliable method for estimating the size of individual *P. zelandica*, it may provide a useful indication of recruitment. If there are two or more distinct size cohorts present, as there were in Kennedy Bay during our study, then widths between siphons may be used to rapidly determine the approximate relative abundance of each cohort.

Estimates of natural mortality for many shorter-lived infaunal bivalve species (i.e., < 15 yrs) generally range from 0.2 to 0.4 (proportion  $\text{yr}^{-1}$ ; e.g., Nickerson, 1977; Cranfield et al., 1993; Urban, 1996; Annala et al., 2001). Nickerson (1977) estimated a natural mortality value of 0.1 for a population of the butter clam, *Saxidomus gigantea*.

*teus* (Deshayes, 1839), estimated to live ca. 30 yrs. Estimates of natural mortality for populations of *P. abrupta* are very low, ranging from 0.01 to 0.05 (Breen and Shields, 1983; Harbo et al., 1983; Sloan and Robinson, 1984; Noakes and Campbell, 1992; Bradbury and Tagart, 2000). Although higher than those for *P. abrupta*, the estimates of natural mortality for *P. zelandica* in Shelly Bay and Kennedy Bay were also very low. In terms of establishing a fishery, low natural mortality is hardly ideal, as low turnover rates suggest sustainable yields may be a small fraction of harvestable biomass (Breen and Shields, 1983). There were, however, differences in estimated natural mortality between the various estimators employed in this study. The longevity estimate for geoducks in Kennedy Bay was twice that provided by catch curve analyses and is similar to that estimated for a population in Golden Bay (0.14 based on maximum age observed of 34 yr; Breen et al., 1991). There are two assumptions underpinning the use of catch curves to estimate mortality. Firstly, recruitment rates are approximately constant during the time that aged geoducks were recruited, and secondly, that mortality is similar for all age classes (Breen and Shields, 1983; Vetter, 1988). Breen et al. (1991) reported estimated mortality rates of between 0.14 and 0.26 depending on the minimum age included (range 6–13 yrs) for *P. zelandica* based on catch curve analyses. However, spatial and temporal variability in recruitment was so high that this estimate was later rejected (Breen, 1991). Analysis of the age-frequency histograms for geoducks from Kennedy Bay and Shelly Bay indicated an absence of many age classes and neither population yielded individuals in the 1–10 yrs age range in numbers that would be consistent with constant recruitment and mortality rates. Although sectioning more geoduck shells may have, in part, solved this problem, the difficulty with this technique is similar to that reported for *P. abrupta* (Breen and Shields, 1983; Goodwin and Shaul, 1984; Sloan and Robinson, 1984). Thus, catch-curve analyses may not be appropriate for estimating natural mortality in *P. zelandica*.

In a small study investigating in situ mortality of *P. abrupta* in Meares Island, British Columbia, Fyfe (1984) found that 18 out of 70 individuals in a plot died over the course of 1 yr. The calculated natural mortality of 0.25 was much higher than previously reported using catch-curve analyses. Given that the longevity and CR estimates of mortality yielded very similar results, in the absence of in situ results these estimators appear more appropriate than using catch-curve estimates. However, in terms of managing a fishery, estimates of sustainable yield are very sensitive to estimated natural mortality rates (Breen, 1991). It is, therefore, necessary to determine whether CR and longevity estimates provide sufficiently accurate estimates of natural mortality. This could be achieved relatively easily by following the fate of individuals within plots (e.g., Fyfe, 1984), as geoducks are immobile and easily found but not so readily removed and tagged without causing mortality.

Most studies on bivalve recruitment indicate that it is sporadic and can vary markedly within and between years (Ansell, 1961; Noshio and Chew, 1972). Recruitment in populations of *P. abrupta* is highly variable both spatially and temporally, and juveniles are rare (e.g., Goodwin, 1976; Goodwin and Shaul, 1984). As mentioned above, analysis of the age frequency distributions from Kennedy Bay and Shelly Bay (our study) and Golden Bay (Breen et al., 1991) indicated significant fluctuations in recruitment with many age classes not represented. Except for a major recruitment event in Kennedy Bay around 1998–99, there was an absence of small geoducks. There is a possibility that procedures used to collect *P. zelandica* (i.e., the location

of siphon holes) resulted in the collection of mainly larger geoducks, as their siphon holes were most obvious. However, the age frequency distribution of geoducks from Kennedy Bay indicated that animals as young as 2 yrs old could be readily found if they were present. Given that the populations were sampled for 3 yrs, the only geoducks likely to have been missed were any new settlers who did not subsequently recruit into the adult population. Furthermore, large stable populations dominated by older and larger individuals are likely to be governed by density dependent processes, which are commonly characterized by having minimal recruitment (Orensanz et al., 2000).

According to Orensanz et al. (2000) recruitment rates in populations of *P. abrupta* have been falling for several decades on a large geographic scale. *Panopea abrupta* are found aggregated in large beds and are highly fecund. Such populations are usually regulated through over-compensatory, post-dispersal density-dependence (Orensanz et al., 2000). However, due to the nature of harvesting, a reduction in abundance is accompanied by a dilution in stock (Orensanz et al., 2000). Thus, pre-dispersal depensation mechanisms, such as the density dependence of fertilization success, may have severe consequences for levels of recruitment. This may have even more important implications for the sustainability of populations of *P. zelandica*, as it occurs at much lower densities than *P. abrupta* (Gribben et al., 2004b). Additionally, Gribben and Creese (2003) have shown that individual *P. zelandica* are protandric. *Panopea zelandica* initially mature into males in their third year with individuals developing into females in subsequent years. As a result, a high proportion of female geoducks are found in largest size classes. Given that the largest siphon holes are most easily found and generally contain the largest geoducks, there is the possibility that any fishery may inadvertently target large female geoducks resulting in populations that are egg-limited. Similar data sets with males dominating the smaller size classes and females becoming more prevalent as shell length increases have also been reported for *P. abrupta* (e.g., Andersen, 1971; Campbell and Ming, 2003). This may offer an alternative explanation to the fall in levels of recruitment observed in populations of *P. abrupta*.

In summary, our study confirmed that the internal growth bands in *P. zelandica* can be used to age geoducks and also to provide valuable growth and mortality data. It also indicated that there are regional differences in growth rates (with regard to both shell length and weight) and mortality estimates. Given the unique life history (e.g., Gribben and Creese, 2003), old age obtained, low levels of estimated mortality and recruitment, and low population density estimates (Gribben et al., 2004b), fisheries managers will need to carefully consider the feasibility of commercially harvesting this species in New Zealand.

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