

## Growth and morphometrics in the New Zealand sea urchin *Pseudechinus huttoni* (Echinoidea: Temnopleuridae)

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**Abstract** We examined somatic growth in the New Zealand sea urchin, *Pseudechinus huttoni*. This species normally inhabits the continental shelf, but in the New Zealand fiords can be found at shallower depths. These shallower populations provided an opportunity to quantify growth of these deep water sea urchins using chemical tag recapture techniques. Growth was modelled in three Doubtful Sound populations and varied spatially, with maximum test diameter (TD) and maximum growth rates ranging from 33.8 to 42.7 mm TD and 2.9 mm yr<sup>-1</sup> to 23.9 mm yr<sup>-1</sup>, respectively. Size-at-age modelling suggests that *P. huttoni* is c. 5–15 mm TD at 1 year, 20–30 mm TD at 4 years, and adults approach a maximum size of 30–40 mm TD after 6 to 11 years. Growth in continental shelf populations was inferred from measured growth in the fiord population by comparing population statistics (size structures, mean size), morphometrics, and nutritional status among both habitats. Our results indicate that growth of *P. huttoni* populations on continental shelves varies spatially (with depth), but is within the range of growth measured in the Doubtful Sound populations. A generalised growth model for *P. huttoni* based on the three Doubtful Sound populations is described by the Brody-Bertalanffy equation  $S_t = 42.17(1 - 0.99e^{(-0.229t)})$ .

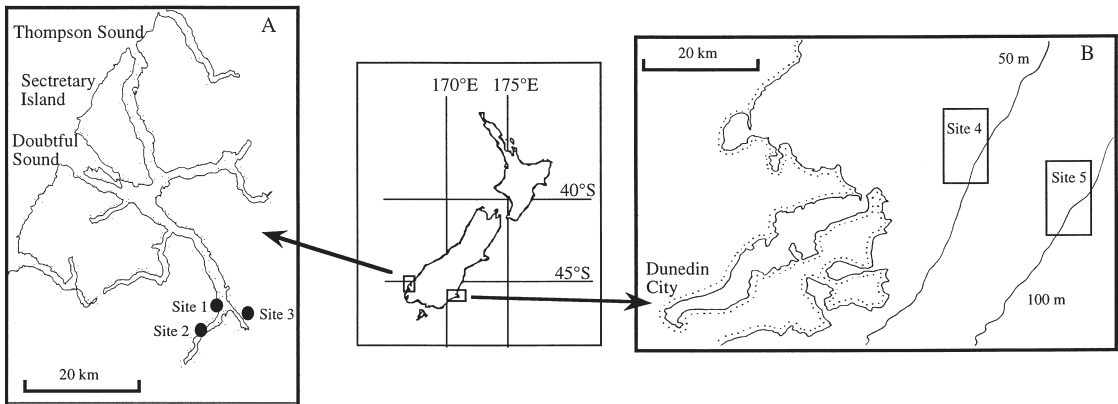
**Keywords** sea urchin; echinoid; growth; *Pseudechinus huttoni*; Brody-Bertalanffy equation; Doubtful Sound; Otago Shelf

### INTRODUCTION

Basic quantitative information on the biology of offshore and deep-water invertebrates is limited compared with shallow water counterparts, primarily owing to the logistical constraints of working in deeper habitats. Ecological characteristics such as growth of deeper water invertebrates are not well described but are essential to understanding many aspects of their biology and ecology. In this paper we examine growth in the sea urchin, *Pseudechinus huttoni*, a continental shelf inhabitant found off the coast of New Zealand, and in shallower waters within the New Zealand fiords (McClary & Sewell 2003).

Quantitative measurements of growth are common for many shallow water invertebrates, but are rare in less accessible deeper habitats. Sea urchins are a good example of the lack of quantitative information on growth of deeper water counterparts. Measurements of growth in shallow water species are now routinely obtained using a variety of methods such as growth rings, modal progression, or tag/recapture (see review by Ebert 2001). However, somatic growth rates have only been reported in two deep water genera of echinoids (*Sterechinus* and *Echinus*) (Gage & Tyler 1985; Gage et al. 1986; Brey 1991; Brey et al. 1995) despite the importance of this group in deep sea communities (Herring 2002). Growth estimates in these deeper water species were made from growth rings in test plates, and no direct measurements of *in situ* growth exist. This lack of data reflects the difficulty of re-sampling deep water populations required for direct measures of growth.

One way to examine growth in deeper water is to quantify growth in populations of deeper water species that occur at unusually accessible shallow depths to infer growth in the species as a whole. An obvious drawback of this method is that growth often



**Fig. 1** Location of three populations of *Pseudechinus huttoni* examined in Doubtful Sound, Sites 1 to 3; and two populations off the Otago coast, New Zealand, Sites 4 and 5.

varies spatially within a species (i.e., Turon et al. 1995; Ebert et al. 1999; Wing et al. 2003), and this could be accentuated in a study of a population living at the extreme of a species distribution (such as in shallow water). Therefore, if growth is inferred, the degree that the ecology (nutritional status, population structure, density, morphometrics) of the shallow water individuals differ from that of the deeper populations needs to be quantified.

We examined growth in the deeper water sea urchin species *Pseudechinus huttoni* (Echinoidea: Temnopleuridae) by quantifying growth in shallow populations found in a fiord, Doubtful Sound. The *Pseudechinus* genus comprises 11 species, all restricted to the Southern Hemisphere. Six of the 11 species, including *P. huttoni*, are endemic to New Zealand (McKnight 1969). *Pseudechinus huttoni* inhabits the New Zealand continental shelf from 30 to 550 m (McClary & Sewell 2003) and also occurs in New Zealand's southern fiords where it can be accessed in depths as shallow as 9 m (M. D. Lamare pers. obs.). Deep-water emergence is common in these fiords, and is seen in a number of other species including black coral, *Antipathes fiordensis*, and red coral *Errina novaezelandiae* (Grange et al. 1981). This emergence is thought to reflect the deep-water-like environments of the New Zealand fiords, where low light, low water motion, and low sedimentation environments exist at relatively shallow depths (<40 m).

In this study, we quantified growth of *P. huttoni* in the Doubtful Sound fiord population using standard chemical tag/recapture methods (Ebert 2001), and assessed the degree to which the fiord populations differ from deep-water populations by

comparing population statistics (size structures, mean size), morphometrics, and nutritional status. This comparison included gonad production and Aristotle's lantern indices, which are particularly useful in echinoid studies as they are often used as an indicator of historical nutritional status of individuals (i.e., Edwards & Ebert 1981; Black et al. 1982).

Data were used in two ways. First, within the fiord population, we compared growth rates with population statistics and morphometrics to quantify the extent to which growth varies spatially, and the degree to which differences in growth rates are reflected in spatial differences in population statistics and morphometrics. Second, we compared population statistics and morphometrics among fiord and deeper-water shelf populations to assess the degree of homogeneity. With these measurements we inferred growth rates of *P. huttoni* in deeper water from growth rates measured in Doubtful Sound.

## MATERIALS AND METHODS

### Study sites and sampling

*Pseudechinus huttoni* was examined at two locations (Fig. 1), Doubtful Sound, Fiordland (45°25'S, 167°06'E) and on the continental shelf off the Otago Peninsula (45°45'S, 170°56'E). Sampling off the Otago coast was conducted at two sites that were 8–12 km offshore. The two sites were c. 4 km apart and differed in depth of 60 and 80 m. Each site was visited on four occasions in 2003, 18 March (late summer), 10 June (winter), 18 August (late winter) and 11 November (late spring). Samples were collected from 60 and 80 m depth using a 1.8 m

beam trawl deployed off the vessel RV *Munida*. The duration and number of dredges conducted during each trip varied, dependent on numbers of *P. huttoni* collected in each trawl. Samples were immediately placed in bins continually supplied with fresh sea water, before dissection the following day. In Doubtful Sound three sites were sampled by SCUBA diving, with collections of *P. huttoni* between 9 and 15 m depth conducted on 29 April, 22 July, 2 December, and 27 April 2004. Samples were kept moist in insulated bins for transportation to the field station where they were dissected within 12 hr of collection.

### Morphometrics

Before dissection, the test diameter of each individual was measured (the average of two measurements) to the nearest 0.1 mm using digital callipers. Each urchin was blotted dry on a paper towel for 10 to 20 s to remove surface water but to minimise any loss of coelomic fluid. Wet weight (g) was recorded as the entire urchin blotted dry and weighed to the nearest 0.01 g. Urchins were dissected and gonads were removed and blotted dry on a paper towel. Gonad and gut weight (g) were measured to the nearest 0.01 g. Aristotle's lanterns were removed from the test and placed in sodium hypochlorite until all organic material had been dissolved. Demi-pyramids were then rinsed with freshwater and left to air dry. Demi-pyramid length (to the nearest 0.1 mm) was measured from the oral tip to the epiphysis junction as in previous studies (Ebert & Russell 1993; Ebert et al. 1999). Length of at least two demi-pyramids per individual were measured and an average calculated.

Gonad and lantern index were calculated for each individual using the following equations:

$$\text{Gonad index (\%)} = \frac{\text{Gonad weight (g)}}{\text{Total wet weight (g)}} \times 100\% \quad (1)$$

$$\text{Lantern index (\%)} = \frac{\text{Lantern length (mm)}}{\text{Test diameter (mm)}} \times 100\% \quad (2)$$

### Growth measurement

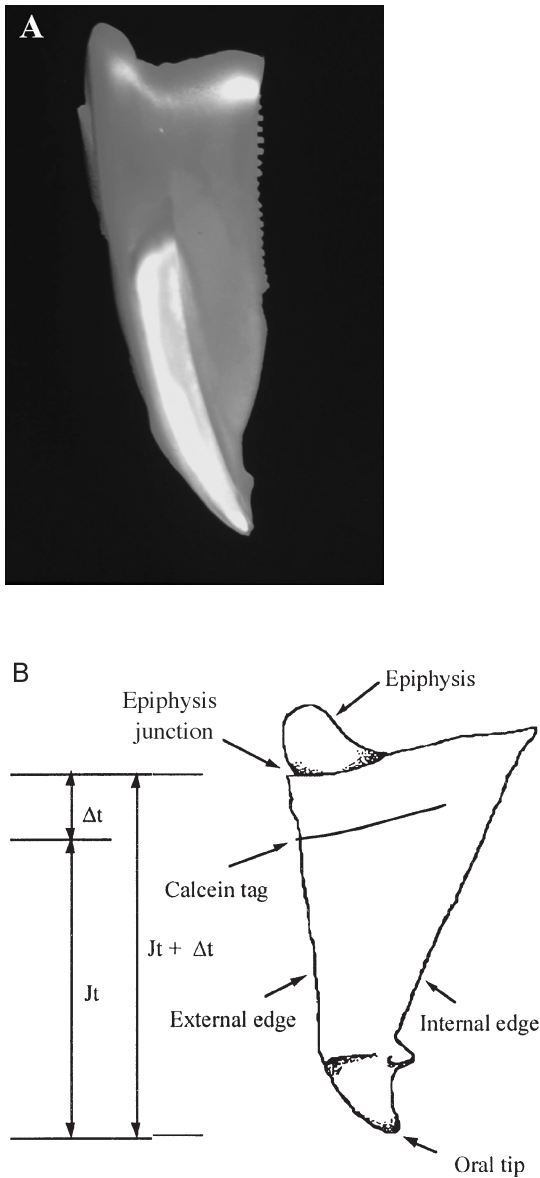
Chemical tagging of *P. huttoni* using the florescent dye, calcein, was carried out between 29 April and 2 May 2003 at the three Doubtful Sound sites. Individuals were tagged either *in situ* by SCUBA divers or collected and carefully tagged on a boat deck. Those urchins tagged on the boat deck were out of the water for c. 30 min but were kept cool and shaded. SCUBA divers carefully returned urchins to

the substrate from which they were collected. For tagging, we used a solution of 500 ppm calcein in filtered sea water (45  $\mu\text{m}$  pore size) buffered to pH8 with NaOH (Lamare & Mladenov 2000).

Individual urchins were given an intercoelomic injection of 1 ml of calcein solution using an adjustable dose, automatic refilling syringes (sheep inoculation gun) fitted with a 22 gauge sterile hypodermic needle. The gun was connected by plastic tubing to a 250 ml plastic bottle containing calcein, thus allowing 250 urchins to be injected at one time. After each tagging dive, the remaining calcein was removed from the bottles and measured with a graduated cylinder to determine the total amount used. This amount (in ml) was used to gain an estimate of the number of individuals tagged per dive (Table 1). To assess if tagging was successful, we collected 20 individuals from each site three months after tagging.

Urchins were re-sampled between 26 and 29 April 2004, approximately 1 year (362 to 365 days) from the time of initial tagging. Collections were made between 10 and 15 m in depth. Following re-sampling, urchins were dissected and test diameter and height (to the nearest 0.1 mm), wet weight (to the nearest 0.01 g), and Aristotle's Lantern demi-pyramid length (to the nearest 0.01 mm) were recorded. Demi-pyramids were cleaned with sodium hypochlorite, rinsed with fresh water, air dried and examined under UV light to determine the presence of a calcein tag. If a clearly defined tag was visible (Fig. 2), demi-pyramids were placed in plastic bags and labelled for later growth measurements.

Growth was recorded as the change in the Aristotle's Lantern demi-pyramid length (mm) over the 1-year period. Tagged demi-pyramids were illuminated by UV light and examined under a dissecting microscope equipped with a Wild 1.25 $\times$  drawing tube. The location of the calcein tag represented the original position of the epiphysis junction at time of tagging. Demi-pyramid length at time of tagging ( $t = 0$ ) was measured as the distance between the oral tip and the calcein tag (Jt) (Fig. 2). Growth of the demi-pyramid (Jt +  $\Delta t$ ) was measured as the distance from the calcein tag to the new epiphysis junction (Ebert & Russell 1993; Lamare & Mladenov 2000). Measurement of growth at the oral tip was not possible, as a calcein tag was either not visible (in most specimens) or greatly diffused in those specimens where it was detected. Any growth at the labial end likely represents only a small amount of the total growth (TA Ebert pers. comm.) and, therefore, our methods are unlikely to greatly underestimate growth.



**Fig. 2** A, Calcein tagged lantern demi-pyramid of *Pseudochinus huttoni* under UV light. Calcein tag is visible as an intense glow near the epiphysis junction. Lantern pictured is 9 mm in length. B, Measurements of the change in Aristotle's lantern size following calcein tagging. Previous position of the epiphysis junction ( $J_t$ ) is represented by the calcein tag and is used to calculate the change in demi-pyramid size over 1 year ( $J_t + \Delta t$ ).

The relationship between test diameter (TD) and demi-pyramid length (J) was established to determine the change in test diameter over time (Ebert & Russell 1993; Lamare & Mladenov 2000). For each site, the change in size (TD) was determined from demi-pyramid length (J) using non-linear regression of TD and J that fitted the allometric equation:

$$TD = aJ^b \quad (3)$$

Parameters  $a$  and  $b$  were estimated by non-linear regression and a test diameter at the time of tagging ( $TD_t$ ) and time of collection ( $TD_t + \Delta t$ ) was calculated. Modelling test diameter growth from changes in demi-pyramid size has been used in a number of sea urchin growth studies (Ebert & Russell 1993), and the assumptions associated with this approach have been outlined by Ebert (2001).

### Growth modelling

Size at tagging ( $T$ ) and recapture ( $T + 1\text{yr}$ ) was analysed using Walford Plots (Walford 1946), with two growth models fitted to the data. These were the Brody-Bertalanffy growth model (von Bertalanffy 1938; Brody 1945)

$$S_t = S_\infty (1 - be^{-Kt}) \quad (4)$$

and the Richards growth model (Richards 1959)

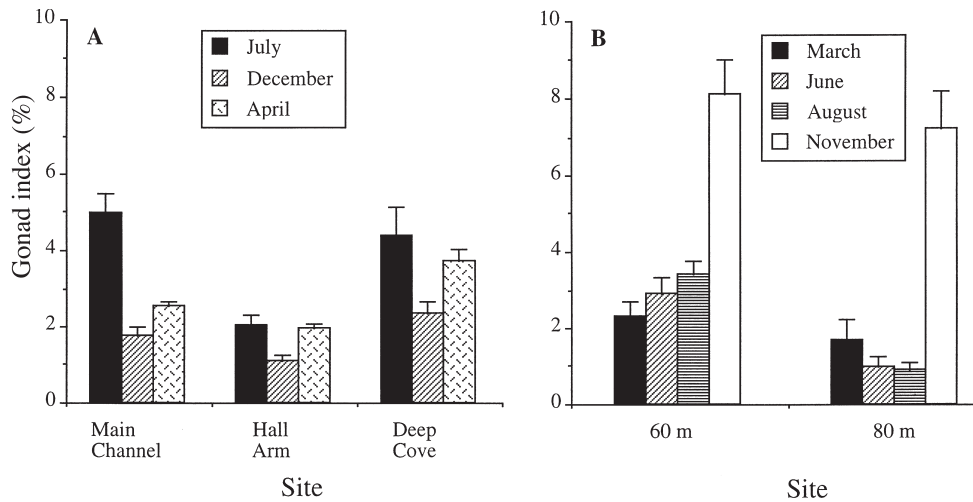
$$S_t = S_\infty (1 - be^{-Kt})^n \quad (5)$$

where  $S_t$  = size at time  $t$ ,  $S_\infty$  = asymptotic size,  $b$  = scaling parameter to adjust for size  $\neq 0$  at time 0,  $K$  = growth constant, and  $n$  = shape parameter for the Richards model. Details on the application of these models to sea urchin test diameter growth, including their limitations, have been outlined in Ebert & Russell (1993) and Lamare & Mladenov (2000).

For comparison of growth among the three *P. huttoni* populations, and with growth rates reported in the literature for other sea urchin species, we estimated an overall growth performance index ( $\theta$ ) for each population. The index describes the relationship between asymptotic size ( $S_\infty$ ) and the growth constant ( $K$ ) using the equation

$$\theta = 1n(K) + 21n(S_\infty) \quad (6)$$

The index was used by Munro & Pauly (1983) for finfish, and has recently been applied to comparisons among limpets over a latitudinal gradient (Clarke et al. 2004). Similar growth performance indices were developed for examining growth among populations of the sea urchin *Echinocardium cordata* (Duineveld & Jenness 1984) and the bivalve *Mya arenaria* (Appeldoorn 1983).



**Fig. 3** Mean gonad indices ( $\pm$ SD) for *Pseudechinus huttoni* measured seasonally at: **A**, three sites in Doubtful Sound; and **B**, two sites on the Otago continental shelf, New Zealand. Number of samples each time was 20 for each site.

### Statistical analysis

Statistically significant differences in gonad index among sites and sampling times were identified using a two-way ANOVA including interactions, whereas differences among sites in lantern index and mean test diameter size were identified using one-way ANOVA (Underwood 1999). Normality of data was examined visually, and homogeneity of variances tested using Cochran's C-statistics (Underwood 1999). Subsequently, percentage measurements (lantern and gonad indices) were transformed using arcsine square-root, whereas test diameter measurements were log-transformed ( $\ln$ , natural logarithm). Post-hoc pair-wise comparisons were made using Tukey's honest significance-differences (HSD) test ( $P > 0.05$ ). The relationship between demi-pyramid length and test diameter was tested using analysis of covariance (ANCOVA) of  $\ln(\text{test diameter})$  versus  $\ln(\text{demi-pyramid length})$ .

## RESULTS

### Morphometrics

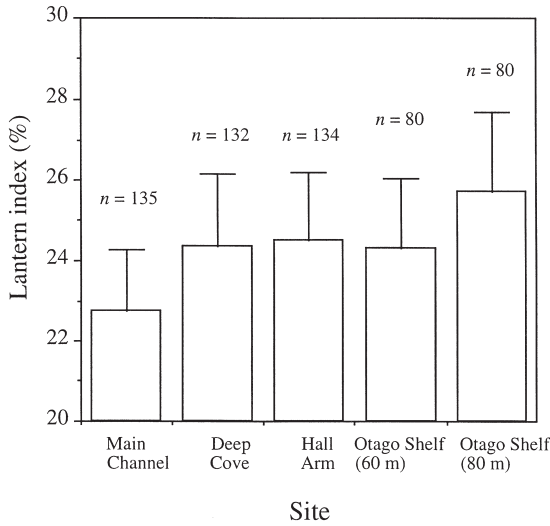
Spatial and temporal differences in Gonad Index (GI) were evident for the Otago Shelf and Doubtful Sound populations (Fig. 3). Mean gonad indices in urchins from Doubtful Sound were highest during July for all sites (2.02 to 4.99%), with urchins from Deep Cove and Main Channel sites exhibiting greater increases in gonad indices during this time compared

with urchins from Hall Arm (Fig. 3A). For the Otago population maximum GI occurred in November, measured at 8.15% for urchins at 60 m and 7.22% for those at 80 m depth (Fig. 3B). Gonad indices remained relatively low during March, June, and August for the Otago Shelf population (Fig. 3B).

For Doubtful Sound urchins, mean GI was significantly different among sites ( $F_{(2, 410)} = 18.51$ ,  $P < 0.0001$ ), and months ( $F_{(2, 410)} = 23.126$ ,  $P < 0.0001$ ). Changes in GI were asynchronous between sites (month  $\times$  site:  $F_{(4, 410)} = 3.412$ ,  $P = 0.0009$ ). Maximum gonad indices in Doubtful Sound populations (2.02 to 4.99%) were lower than the observed maximum for the Otago Shelf populations (7.22 to 8.15%). For the Otago Shelf population, mean GI was significantly different between depths ( $F_{(3, 152)} = 46.535$ ,  $P < 0.0001$ ) and between months ( $F_{(1, 152)} = 26.907$ ,  $P < 0.0001$ ). A significant interaction between month and site ( $F_{(3, 152)} = 3.068$ ,  $P < 0.03$ ) indicated changes in GI were asynchronous between depths.

The mean lantern index at each site ranged from 22.74% to 25.71% (Fig. 4). One-way ANOVA indicated lantern indices varied significantly among sites ( $F_{(4, 556)} = 41.554$ ,  $P < 0.001$ ). A Tukey's HSD test indicated that the Otago Shelf 80 m population had significantly larger indices than the other sites ( $P < 0.001$ ), whereas the Main Channel population in Doubtful Sound had significantly smaller lantern indices than the other four sites ( $P < 0.001$ ).

The relationship between demi-pyramid length and test diameter differed among *Pseudechinus*



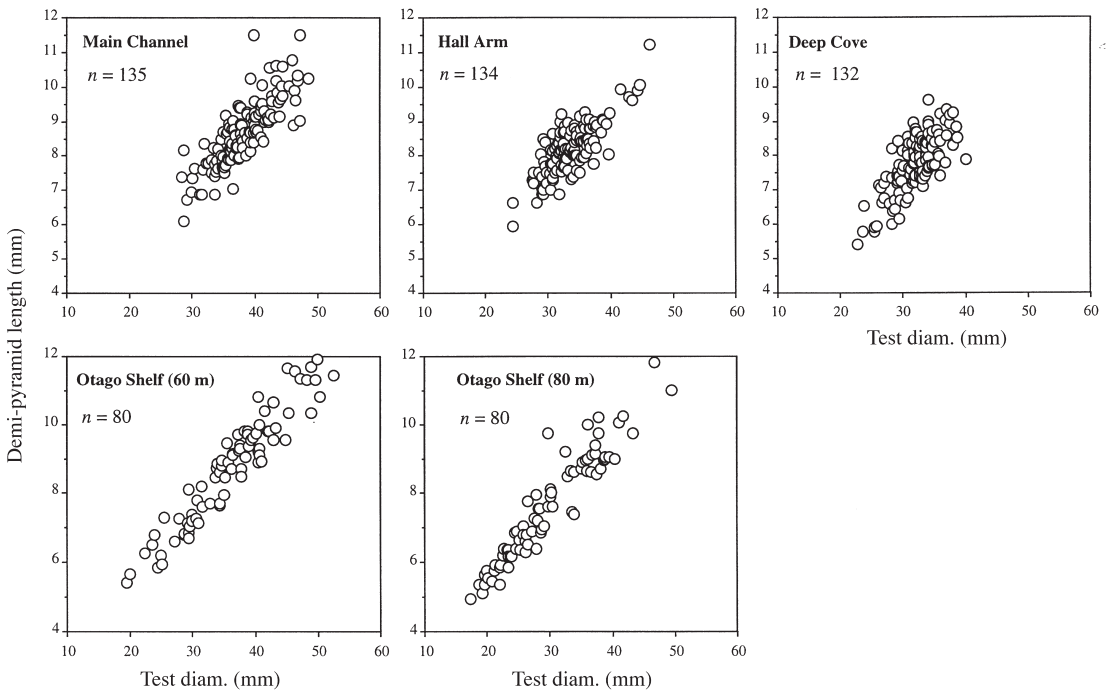
**Fig. 4** Mean lantern indices ( $\pm$ SD) for *Pseudechinus huttoni* measured at three sites in Doubtful Sound and two sites on the Otago continental shelf, New Zealand. Sample size ( $n$ ) is indicated above bars.

populations (Fig. 5). Paired comparisons among the five sites using ANCOVA (Table 2) indicated significant differences ( $P < 0.05$ ) existed between the Main Channel and 60 m, 80 m, Hall Arm and Deep Cove, and between 80 m and Hall Arm and Deep Cove.

Size distributions of *P. huttoni* populations varied between sites (Fig. 6). Mean test diameter at each site ranged from 27.3 mm (Otago Shelf, 80 m) to 37.1 mm (Main Channel, Doubtful Sound), with the range in size greatest in populations on the Otago shelf at 60 m (15 to 59 mm) and lowest at Deep Cove (18 to 47 mm). One-way ANOVA indicated significant differences among all sites in mean test diameter (ln-transformed test diameter,  $F_{(4, 2502)} = 157.609, P < 0.001$ ).

**Growth**

Chemical tagging of *Pseudechinus* was successful, with 20–25% of individuals ( $n = 20$ ) taken from each site 3 months after initial tagging showing fluorescence under UV-light. Recovery of tagged *P. huttoni* was lower after 1 year, with a recapture rate of less than 10% at each site (Table 1). The total



**Fig. 5** Relationship between lantern demi-pyramid length and test diameter for *Pseudechinus huttoni* from three sites in Doubtful Sound and two sites on the continental shelf off the Otago coast, New Zealand. ( $n$  = sample size.)

number of tagged animals recovered from each site ranged from 24 to 30, with tagged animals ranging in size from 29.4 to 46.7 mm TD. Initial and final test diameters were calculated from the initial and final demi-pyramid size using the allometric relationship

between lantern size and test diameter (Fig. 7). Initial test diameters ranged from 22.6 to 45.1 mm.

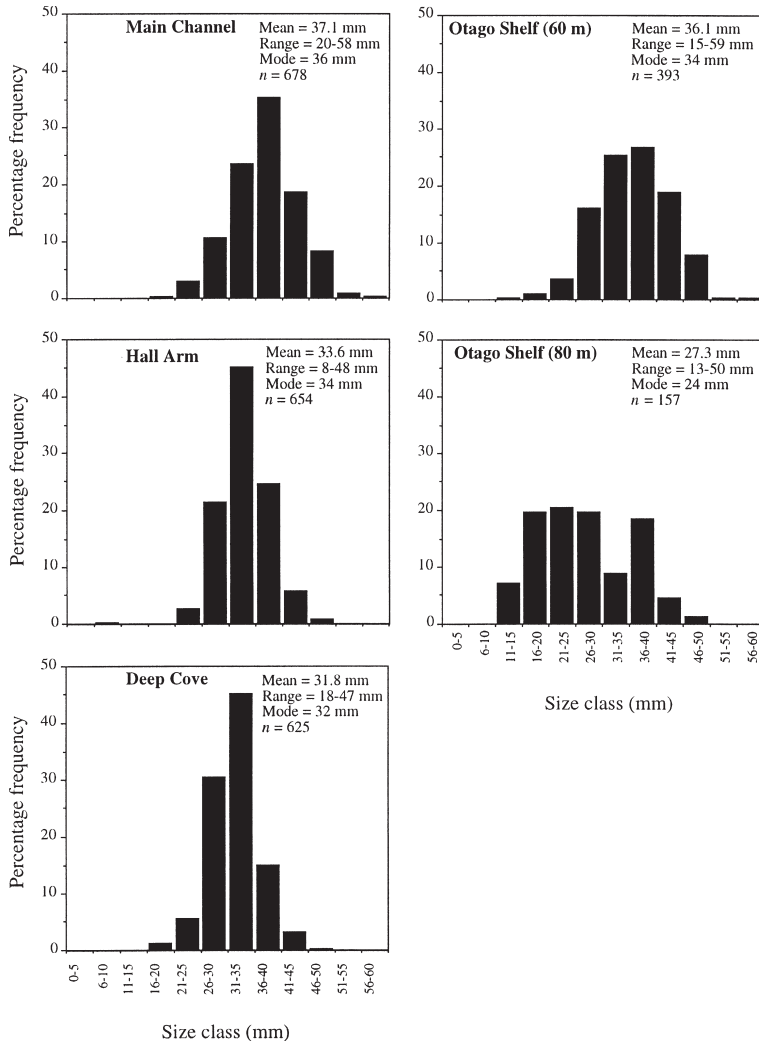
Growth rate ( $\text{mm yr}^{-1}$ ) as a function of initial test diameter (Fig. 8) indicate that *P. huttoni* from the Main Channel grew at a higher rate than those from

**Table 1** Summary of the tagging study of *Pseudechinus huttoni* using the fluorescent dye, calcein at three sites in Doubtful Sound, New Zealand between 29 April 2003 and 29 April 2004.

	Main Channel	Hall Arm	Deep Cove
No. of sea urchins tagged	485	400	506
Size range tagged (TD) (mm)	15–55	16–50	15–50
No. of sea urchins collected	305	392	340
No. with calcein tags	30	25	24
% tagged	9.8	6.3	7.1
Size range of tagged urchins (TD) (mm)	33.6–46.7	30.5–39.5	29.4–36.7

**Table 2** Analysis of covariance of test diameter versus demi-pyramid length for *Pseudechinus huttoni* from three sites in Doubtful Sound and two depths on the continental shelf off Otago, New Zealand. Dependent variable, demi-pyramid length and covariant, test diameter, both ln-transformed. (SS, sum of squares; MS, mean squares.)

Homogeneity of slopes Analysis of variance	SS	d.f.	MS	F	P
lnTD	5.345	1	5.345	1150.250	< 0.0001
60 m versus Main Channel	0.169	1	0.169	36.313	< 0.0001
Error	1.441	310	0.005		
lnTD	4.839	1	4.839	619.253	< 0.0001
80 m versus Main Channel	0.360	1	0.360	46.043	< 0.0001
Error	2.422	310	0.008		
lnTD	3.912	1	3.912	1052.523	< 0.0001
60 m versus Hall Arm	0.007	1	0.007	1.953	0.163
Error	1.163	313	0.004		
lnTD	3.457	1	3.457	516.897	< 0.0001
80 m versus Hall Arm	0.118	1	0.118	17.704	< 0.0001
Error	2.093	313	0.007		
lnTD	3.571	1	3.571	738.794	< 0.0001
60 m versus Deep Cove	0.005	1	0.005	1.100	0.295
Error	1.532	317	0.005		
lnTD	3.155	1	3.155	412.561	< 0.0001
80 m versus Deep Cove	0.132	1	0.132	17.234	< 0.0001
Error	2.424	317	0.008		
lnTD	4.114	1	4.114	929.529	< 0.0001
Main Channel versus Hall Arm	0.155	1	0.155	35.024	< 0.0001
Error	2.063	466	0.004		
lnTD	2.413	1	2.413	547.922	< 0.0001
Hall Arm versus Deep Cove	0.002	1	0.002	0.368	0.544
Error	2.083	473	0.004		
lnTD	3.786	1	3.786	735.422	< 0.0001
Main Channel versus Deep Cove	0.113	1	0.113	21.893	< 0.0001
Error	2.420	470	0.005		
lnTD	5.617	1	5.617	1626.420	< 0.0001
60 m versus 80 m	0.009	1	0.009	2.558	0.112
Error	0.542	157	0.003		



**Fig. 6** Size frequency distributions of *Pseudechinus huttoni* sampled from New Zealand: three populations in Doubtful Sound and two Otago Shelf populations. Mean test diameter, size range, modal size, and sample size (*n*) are indicated for each population.

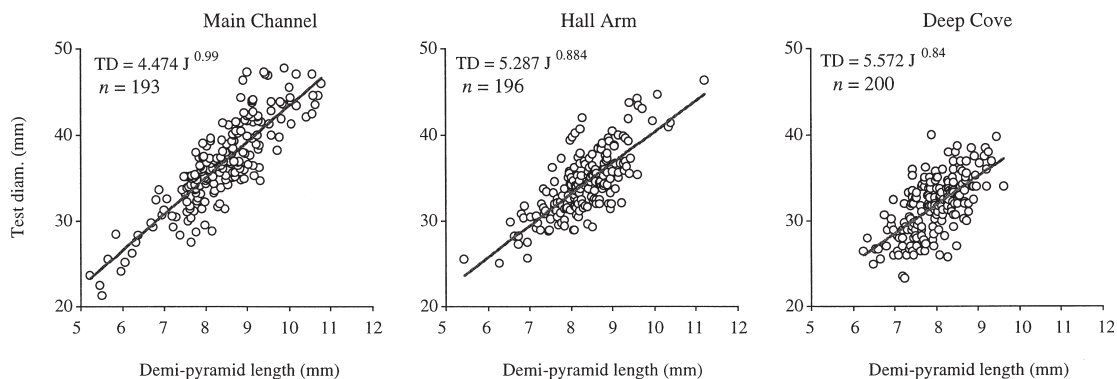
Hall Arm and Deep Cove. In the Main Channel over half of the urchins recovered grew at least 2 mm in test diameter in 1 year (Fig. 8). For Deep Cove, eight of the urchins recovered exhibited growth in test diameter that was less than 0.5 mm, whereas the remainder grew between 0.5 mm and 3.0 mm in test diameter (Fig. 8). One small individual in Deep Cove grew 7.25 mm in test diameter. The Hall Arm population was the slowest growing, exhibiting  $\leq 2.1$  mm yr<sup>-1</sup> growth for all individuals recovered.

**Growth modelling.**

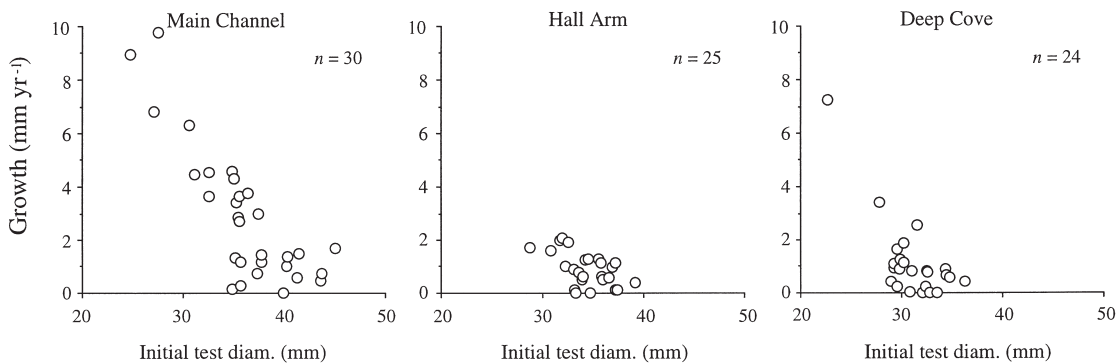
Maximum predicted urchin growth rate (MGR) for the Brody-Bertalanffy model was higher at all sites (6.21 to 23.95 mm yr<sup>-1</sup>) compared with the

Richards model (2.96 to 10.62 mm yr<sup>-1</sup>) (Table 3), with age of maximum growth rate at settlement (age = 0 yr) for the Brody-Bertalanffy models and 2.2 to 6.9 yr for the Richards model (Table 3). Predictions of asymptotic size (*S*<sub>∞</sub>) for *P. huttoni* were nearly identical between the Brody-Bertalanffy and Richards models (Table 3).

The Brody-Bertalanffy model predicts urchin growth rate to be fastest in the Main Channel (Table 3), with this site having fastest MGR (23.95 mm yr<sup>-1</sup>), largest *S*<sub>∞</sub> values (*S*<sub>∞</sub> = 42.72 mm), and the greatest rate of change in growth (*K* = 0.56). Deep Cove urchins had a smaller maximum size (*S*<sub>∞</sub> = 33.82 mm) than those at the other two sites, but maximum growth rate was intermediate (16.23 mm



**Fig. 7** Relationship between lantern demi-pyramid length and test diameter for *Pseudechinus huttoni* from three sites in Doubtful Sound, New Zealand, including modelled allometric relationship between the two measures.



**Fig. 8** Growth rate ( $\text{mm yr}^{-1}$ ) as a function of initial test diameter for *Pseudechinus huttoni* from three sites in Doubtful Sound, New Zealand. ( $n$  = sample size.)

$\text{yr}^{-1}$ ). Growth was slowest at the Hall Arm site ( $\text{MGR} = 6.21 \text{ mm yr}^{-1}$ ,  $S_{\infty} = 40.73 \text{ mm}$ ,  $K = 0.15$ ). The overall growth performance of *P. huttoni* (Table 4) based on the Brody-Bertalanffy growth model was highest in urchins from the Main Channel ( $\theta = 6.94$ ), intermediate for Deep Cove urchins ( $\theta = 6.35$ ), and lowest in Hall Arm urchins ( $\theta = 5.54$ ).

Richards modelling of growth also predicted fastest growth at the Main Channel site (Table 3), with urchins at this site having the largest maximum size (42.43 mm) and maximum growth ( $10.62 \text{ mm yr}^{-1}$ ). The Richards shape parameter ( $n$ ) differed between sites, ranging from  $n = -8.88$  in Hall Arm to  $n = -24.35$ . The values of  $n$  suggest that growth is initially slow at all three sites, with the greatest lag in increase in growth at the Main Channel site with the highest  $n$ .

Modelled size-at-age of *P. huttoni* at each site (Fig. 9) highlights the large spatial differences in growth. Populations in the Main Channel had an asymptotic maximum size of c. 42.5 mm TD, and the age at which 50% and 90% of asymptotic size was attained was predicted at 1.2–2.8 yr and 4–5.5 yr, respectively, depending on the growth model. Although the Hall Arm site had a similar asymptotic maximum size (40.7 mm TD), the age at which 50% and 90% of asymptotic size was attained was 9.2 yr and 18.7 yr for the Richards model and 4.5 and 15.1 yr for the Brody-Bertalanffy Model, respectively. The Deep Cove population had a smaller asymptotic size, but reached 50% and 90% of maximum size at ages similar to the Main Channel site population (Table 3).

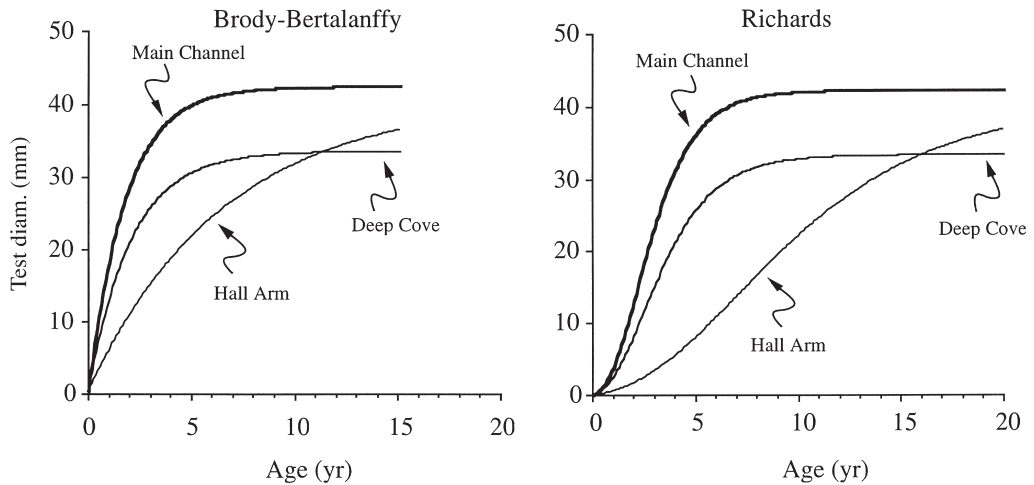
## DISCUSSION

Growth of *P. huttoni* was examined in three populations in Doubtful Sound using calcein tagging and recapture. Recovery of tagged urchins was low at each site (6.3 to 9.8%) despite the large number of sea urchins tagged ( $n = 1391$ ) and sampled after 1 year ( $n = 1037$ ). Low tag return rates are likely to be a function of migration and mortality over the year of release, and also of the frequency that the chemical tag was incorporated into the urchin skeleton. Although we cannot identify which of these factors resulted in the low tag recovery rate, the density of urchins at each site (ranging from 1.17 to 2.18 individuals  $m^{-2}$ ) did not change over

the course of the study, suggesting mortality was not the determinant. Movement of individuals may have resulted in our low recovery rates however. We took a small sample of urchins 3 months after tagging to confirm our tagging was successful and found 20–25% of individuals had fluorescent tags. In contrast, the 6.3 to 9.8% tagging rate after 1 year suggests *P. huttoni* were moving to and from the tagging area. The size range of urchins recovered with a calcein tag ranged from 29.4 to 46.7 mm TD, which equates to a size range at tagging of 22.6 to 45.1 mm TD. This means that growth rates in the smallest size classes (<20 mm TD) were not available, which places some limitations on the interpretation of the growth modelling. In particular,

**Table 3** Estimated parameters for the Brody-Bertalanffy and Richards growth models for *Pseudechinus huttoni* from three sites in Doubtful Sound, New Zealand. ( $m$ , slope;  $c$ , y-intercept;  $S_{\infty}$ , maximum size;  $S_0$ , size at settlement;  $K$ , growth constant;  $b$ , scaling parameter to adjust for  $s \neq 0$  at settlement; MGR, maximum growth rate;  $n$ , shape parameter for the Richards model.)

	Brody-Bertalanffy		Richards
<b>Main Channel</b>			
$m$	0.56	$m$	0.51
$c$	4.22	$c$	0.44
$S_{\infty}$ (mm)	42.72	$S_{\infty}$ (mm)	42.43
$S_0$ (mm)	0.4	$S_0$ (mm)	0.4
Age of $S_{\infty}$	c. 11 yr	Age of $S_{\infty}$	c. 11 yr
$K$	0.56	$K$ and $n$	0.67 and -24.35
$b$	0.99	$b$	0.17
Age of MGR	0	Age of MGR	2.2
MGR (mm yr <sup>-1</sup> )	23.95	MGR (mm yr <sup>-1</sup> )	10.62
SSE	3.17	SSE	3.52
<b>Hall Arm</b>			
$m$	0.85	$m$	0.82
$c$	1.43	$c$	0.13
$S_{\infty}$ (mm)	40.73	$S_{\infty}$ (mm)	40.81
$S_0$ (mm)	0.4	$S_0$ (mm)	0.4
Age of $S_{\infty}$	c. 50 yr	Age of $S_{\infty}$	c. 56 yr
$K$	0.15	$K$ and $n$	0.18 and -8.88
$b$	0.99	$b$	0.40
Age of MGR	0	Age of MGR	6.90
MGR (mm yr <sup>-1</sup> )	6.21	MGR (mm yr <sup>-1</sup> )	2.96
SSE	0.50	SSE	0.50
<b>Deep Cove</b>			
$m$	0.61	$m$	0.58
$c$	3.32	$c$	0.37
$S_{\infty}$ (mm)	33.82	$S_{\infty}$ (mm)	34.04
$S_0$ (mm)	0.4	$S_0$ (mm)	0.4
Age of $S_{\infty}$	c. 11 yr	Age of $S_{\infty}$	c. 11.5 yr
$K$	0.48	$K$ and $n$	0.54 and -17.22
$b$	0.98	$b$	0.23
Age of MGR	0	Age of MGR	2.50
MGR (mm yr <sup>-1</sup> )	16.23	MGR (mm yr <sup>-1</sup> )	7.02
SSE	2.18	SSE	2.44



**Fig. 9** Predicted size-at-age for *Pseudechinus huttoni* at three sites in Doubtful Sound, New Zealand, using Brody-Bertalanffy and Richards growth models.

**Table 4** Summary of population statistics, morphometrics, and growth parameters for three *Pseudechinus huttoni* populations in Doubtful Sound and two populations on the Otago Shelf, New Zealand. It was not possible to measure density or growth parameters for the Otago shelf populations. (TD, test diameter; K, growth constant.)

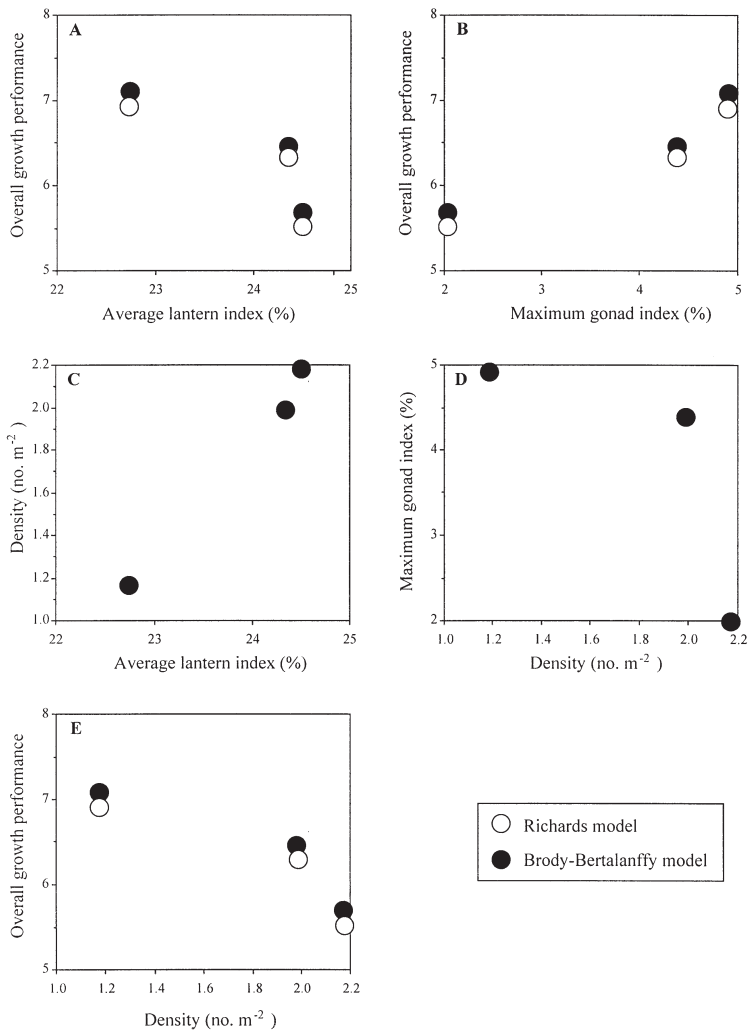
Population statistics	Doubtful Sound			Otago Shelf	
	Main Channel	Hall Arm	Deep Cove	60 m depth	80 m depth
Mean TD (mm)	37.19	33.61	31.80	36.16	27.39
Maximum size (mm)	58	48	47	59	49
Density no. per m <sup>2</sup>	1.17	2.18	1.99	—	—
Mean gonad index (%)	3.10	1.69	3.40	4.21	2.72
Maximum gonad index (%)	4.99	2.02	4.39	8.15	7.23
Maximum gut index (%)	3.87	3.52	5.03	3.67	4.99
Mean lantern index (%)	22.74	24.36	24.52	24.33	25.71
<b>Growth parameters (Richards growth model)</b>					
Maximum size ( $S_{\infty}$ )	42.43	40.81	34.04	—	—
Maximum growth rate	10.62	2.96	7.02	—	—
K	0.67	0.18	0.54	—	—
<b>Growth performance index</b>					
$\theta$ Brody-Bertalanffy model	6.94	5.54	6.35	—	—

estimates of growth in the smallest size classes based on modelling can not be validated.

Growth varied spatially in Doubtful Sound, with maximum test diameter and maximum growth rates ranging from 33.8 to 42.7 mm TD and 2.9 mm yr<sup>-1</sup> to 23.9 mm yr<sup>-1</sup>, respectively. Size-at-age modelling suggests that *P. huttoni* is c. 5–15 mm TD at 1 year, 20–30 mm TD at 4 years, with adults approaching a maximum size of 30–40 mm TD after 6 to 11 years.

Sea urchin growth can vary spatially, for example in species such as *Paracentrotus lividus* (Turon et al. 1995), *Strongylocentrotus franciscanus* (Ebert

et al. 1999), and *Evechinus chloroticus* (Lamare & Mladenov 2000; Wing et al. 2003). Therefore, inferring growth estimates from *P. huttoni* populations in Doubtful Sound (that are at the extreme distribution range of this species) to typical shelf populations requires, first, an understanding of the relationship between somatic growth and the ecology of urchins in the fiord populations (principally nutritional status). Second, it requires an understanding of the degree to which the ecology of fiord populations differs from continental shelf populations, and specifically if growth is potentially faster or slower in fiord populations.



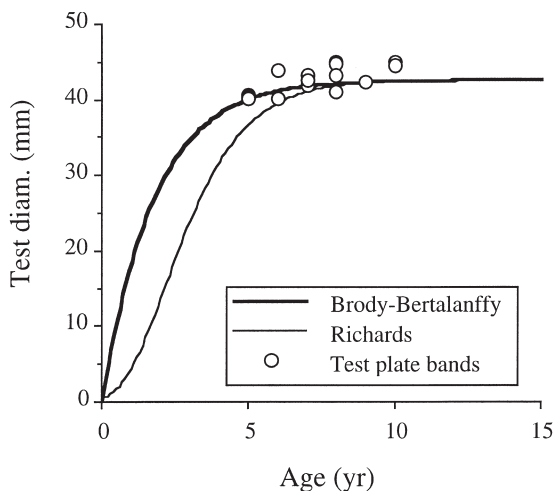
**Fig. 10** Relationships between growth, morphometrics and population density for three *Pseudoechini huttoni* populations in Doubtful Sound, New Zealand. Relationships shown are: **A**, overall growth performance versus average lantern index; **B**, overall growth performance versus maximum gonad index; **C**, average lantern index versus average population density; **D**, maximum gonad index versus average population density; **E**, overall growth performance versus average population density.

For the three fiord populations, there appeared to be a relationship between somatic growth and nutritional history. Overall growth performance ( $\theta$ ) as a single measure of growth was compared with mean lantern index and maximum gonad index (measures of nutritional history). A negative relationship exists between  $\theta$  and lantern index (Fig. 10A), whereas a positive relationship exists between  $\theta$  and maximum gonad index (Fig. 10B). These relationships are consistent with the suggestion that those populations under greater nutritional stress (larger lantern indices and lower gonad production) have a lower growth performance.

Differences in growth and nutritional history may be density-dependent. This result has been found for other echinoids such as *Echinometra mathaei*, for which lantern index increased with increasing

population density (Black & Johnson 1982). For *P. huttoni*, lantern index was greater at higher population density (Fig. 10C), whereas maximum gonad index (Fig. 10D) and overall growth performance index (Fig. 10E) were lower.

If differences in growth reflect differences in nutritional history, how does the nutritional status of the three fiord populations compare with the two shelf populations? Quantitative measurements of the Otago Shelf population at 60 m are not indicative of urchins with significantly different nutritional histories (Table 4). Lantern, gut, and gonad indices, and mean size are all comparable to the Doubtful Sound populations. The Otago Shelf population at 80 m had some features of a population under greatest nutritional stress (smaller mean size, larger mean lantern index), however gut and gonad indices



**Fig. 11** Comparison between size-at-age estimates from Brody-Bertalanffy and Richards growth modelling based on calcein tagged *Pseudechinus huttoni* in Main Channel, Doubtful Sound (this study), and test plate growth bands from *Pseudechinus* on the Otago Shelf ( $n = 15$ ). Latter estimates were made by Smith (1982) using methods described in Jensen (1969).

were comparable to or larger than those in the other populations. The Main Channel population in Doubtful Sound had the higher measured growth rates and had both the highest mean size and the smallest lantern index.

Based on these observations, we suggest that growth of *P. huttoni* populations on continental shelves likely varies spatially (at least with depth), but are within the range of growth measured in the Doubtful Sound populations. A generalised growth model for *P. huttoni* (averaged for the three Doubtful Sound populations) could be described by the Brody-Bertalanffy equation  $S_t = 42.17(1 - 0.99e^{-(0.299t)})$  and an overall growth performance  $\theta = 6.05$ .

We have a limited but independent assessment of the robustness of our growth estimates. A previous study by Smith (1982) examined *P. huttoni* reproduction on the Otago shelf, including a limited examination of size-at-age using test plate growth bands in *Pseudechinus* species. Although caution is needed when interpreting test plate banding patterns (Ebert 2001), a comparison between our modelled size-at-age with size-at-age estimates by Smith (1982) indicates good agreement for urchins between 5 and 10 years old and 40–45 mm TD (Fig. 11).

If the generalised growth pattern of *P. huttoni* in Doubtful Sound is representative of growth of continental shelf inhabitants, then this study has

provided some useful estimates of growth characteristic of a deeper water sea urchin. A wider comparison of *P. huttoni* with other sea urchin species was made by comparing overall growth performance from studies that have modelled growth using a Brody-Bertalanffy growth model (Table 5). Overall growth performance (OGP) among the surveyed species ranges from  $\theta = 4.75$  to 8.53, with OGP generally decreasing with increasing latitude but not necessarily with depth of collection. Those species with the lowest OGP are those occurring in colder water (*Strongylocentrotus pallidus*, *Stereochinus antarcticus*, *Stereochinus neumayeri*) and in the *Echinus* genus that has deep-water representatives. The growth performance of *P. huttoni* is relatively low (average  $\theta = 6.05$ ), similar to these slower growing species, despite occurring in mid-latitudes. The shallow waters of the Antarctic continental shelf have also been considered to provide an opportunity to study deeper-water organisms within SCUBA depths, and the similar growth performance of the Antarctic *Stereochinus neumayeri* and *P. huttoni* is notable.

Although slow somatic growth and extended longevity are not restricted to deep-water echinoids (Ebert & Russell 1993; Ebert & Southon 2004), slower growth appears to be a characteristic of deeper-water representatives. Growth in the deep-water *Echinus* genus has been described from size-at-age estimates using growth rings. For *E. affinis* (Gage & Tyler 1985), growth rate modelled using the von Bertalanffy growth function was presented as  $Y_\infty = 47.70(1 - e^{-0.10(t-1.39)})$ , which describes relatively slow growth and extended longevity (maximum test diameter of 40 to 50 mm was reached after 25 to 28 years). For *E. acutus* var. *norvegicus* and *E. elegans* growth was modelled as  $Y_\infty = 64.75(1 - e^{-0.126(t-0.207)})$  and  $Y_\infty = 85.56(1 - e^{-0.096(t-0.272)})$ , respectively. Maximum size was reached within 10 years for *E. elegans*, and 20 to 22 years for *E. acutus* var. *norvegicus*.

The slowest growth rates reported to date have been found in the deep-water Antarctic species, *Stereochinus antarcticus*, inhabiting the continental shelf and slope of the Weddell Sea (Brey 1991). The species may have an asymptotic size of c. 80 mm TD that is reached in excess of 70 to 80 years, growing at a rate of c. 1 mm yr<sup>-1</sup>. Growth in this species is likely to be a function of its polar distribution. The closely related *Stereochinus neumayeri* growing in McMurdo Sound also exhibited slow growth (maximum size of c. 70 mm TD reached in excess of 40 years) despite its relatively shallow distribution (<20 m depth) (Brey et al. 1995).

**Table 5** Growth performance index ( $\theta$ ) estimates for sea urchin species that have had somatic growth modelled using the Brody Bertalanffy growth function  $S_t = S_\infty(1 - b \exp^{-kt})$ . Included are  $S_\infty$  and  $K$  from which the growth performance index was calculated, and latitude/longitude co-ordinates and depth of collection when reported.

Species	Location	Lat/Long	Depth (m)	$S_\infty$	$K$	$\theta$	Reference
<i>Pseudechinus huttoni</i>	Main Channel	45°25'S, 167°06'E	10 to 15	42.72	0.56	6.94	This study
	Hall Arm	45°28'S, 167°09'E	10 to 15	40.73	0.15	5.54	This study
	Deep Cove	45°27'S, 167°09'E	10 to 15	33.82	0.48	6.35	This study
<i>Evechinus chloroticus</i>	Doubtful Sound, New Zealand	166°58'E, 45°18'S	5 to 10	104.89	0.275	8.01	Lamare & Mladenov (2000)
	Tory Channel, New Zealand	174°11'E, 41°14'S	5 to 10	85.07	0.389	7.94	Lamare & Mladenov (2000)
<i>Strongylocentrotus droebachiensis</i>	Maine, United States			63.1	0.1404	6.33	Vadas (2002)
	Maine, United States			88.5	0.1263	6.90	Vadas (2002)
	Maine, United States			67	0.2315	6.95	Vadas (2002)
<i>Strongylocentrotus pallidus</i>	Maine, United States			63.4	0.3268	7.18	Vadas (2002)
	Maine, United States			80.1	0.1776	7.04	Vadas (2002)
	Maine, United States			95.2	0.1181	6.98	Vadas (2002)
<i>Sphaerechinus granularis</i>	Barents Sea	30–35°E, 79–80°N		102.3	0.011	4.75	Bluhm et al. (1998)
<i>Loxechinus albus</i>	Southern Brittany	47°45'N, 4°W	5 to 10	99	0.28	7.92	Jordana et al. (1997)
	Southern Brittany	47°45'N, 4°W	5 to 10	105	0.23	7.84	Jordana et al. (1997)
	Mehuin, south Chile	39°24'S 73° 13'W	0	152.1	0.22	8.53	Gebauer (1995)
<i>Sphaerechinus granularis</i>	Mehuin, south Chile	39°24'S 73° 13'W	0	141.2	0.13	7.86	Gebauer (1995)
	Mehuin, south Chile	39°24'S 73° 13'W	0	131.7	0.16	7.93	Gebauer (1995)
	Bay of Brest, France	48°20'N, 4°28'W		93.065	0.386	8.11	Lumingas & Guillou (1994)
<i>Tripeustes gratilla elatensis</i>	Bay of Brest, France	48°20'N, 4°28'W		92.552	0.374	8.07	Lumingas & Guillou (1994)
<i>Echinus affinis</i>	Red Sea			60	0.87	8.05	Dafni (1992)
<i>Echinus elegans</i>	Rockall Trough, west Scotland	56–57°N, 9–10°W	1632 to 2300	47.7	0.1	5.43	Gage & Tyler (1985)
<i>Echinus acutus</i> var. <i>norvegicus</i>	Hebrides-Malin Slope, west Scotland	56–59°N, 07–09°W	400 to 1075	64.75	0.126	6.27	Gage et al. (1986)
<i>Sterechinus neumayeri</i>	Hebrides-Malin Slope, west Scotland	56–59°N, 07–09°W	400 to 1075	85.56	0.096	6.56	Gage et al. (1986)
	McMurdo Station	167–166°E, 77°45'S	6 to 20	70.23	0.031	5.03	Brey et al. (1995)
<i>Sterechinus antarcticus</i>	Weddell Sea and Slope, Antarctica	70–75°S, 10–60°W	450 to 1200m	68.17	0.1	6.14	Brey et al. (1995)
				82.4	0.017	4.75	Brey (1991)

*Pseudechinus huttoni* occurs at shallower depths than *E. acutus*, *E. affinis*, and *S. antarcticus*, and has growth rates comparable, if not, faster than these species (approaching a maximum size of 30–40 mm TD after 6 to 11 years). Gage et al. (1986) suggested that growth in the *Echinus* genus is depth-dependent (both within and among species), and related to energy availability. The relatively faster growth rates in the comparatively shallow *Pseudechinus* genus are consistent with this suggestion.

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