



## Modelling somatic growth in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinometridae)

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### Abstract

Somatic growth was examined in two populations of the sea urchin *Evechinus chloroticus* (Valenciennes). Growth was quantified for smaller urchins (< 10 mm test diameter (TD)) through laboratory rearing and in situ airlift sampling of newly settled juvenile cohorts, and for larger individuals (> 10 mm TD) by calcein tagging and recapture. Newly settled urchins grew to a mean size at 1 year of 8.05 mm TD in the laboratory and an estimated 10.5 mm TD in the field. Growth of newly settled urchins appeared to be biphasic with a period of slow growth (0–200 days post-settlement), followed by accelerated growth. Larger, calcein tagged individuals were recaptured 1 year after tagging and their growth modelled using three asymptotic growth functions (Brody-Bertalanffy, Richards and Jolicoeur) and one non-asymptotic function (Tanaka). A second sample of tagged urchins was recovered from one of the sites 3.9 years after the initial tagging. Evaluation of each growth model was made using (1) sum of the squares residual values of the difference equation regressions for each growth function (2) an examination of the regression residuals (3) a comparison of the predicted versus observed size at age at 1 year for *E. chloroticus* sampled in Doubtful Sound, and (4) a comparison of the predicted growth of urchins over 3.9 years, with the observed growth in the urchins recovered 3.9 years post-tagging. The sample taken 3.9 years after tagging also allowed us to examine whether growth is asymptotic in the larger size classes. While growth does not appear to be asymptotic, we found the Richards function best described growth in *E. chloroticus* overall. Using this model, the test diameters of individuals at ages 1 to 6 years are about 10, 25, 40, 55, 65 and 72 mm TD, respectively. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Growth; Sea urchin; Echinoid; *Evechinus chloroticus*

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## 1. Introduction

Growth rate is a critical parameter of the population dynamics of a species. For many populations of marine invertebrate species, however, accurate estimates of growth rate are lacking. This is due, in part, to the difficulties associated with sampling, monitoring and tagging individuals in marine populations. A further problem is the application of a suitable growth model to marine invertebrate populations (Ebert and Russell, 1993).

These problems apply to investigations into the growth of sea urchin species (Echinodermata: Echinoidea). Gage and Tyler (1985) highlighted this fact when analysing growth ring counts in the deep water sea urchin, *Echinus affinis*. Using five different growth models, they found differences in predicted juvenile growth and asymptotic size depending on the growth model applied. A similar result was found by Ebert and Russell (1993) when analysing growth of *Strongylocentrotus franciscanus* using three growth models. These latter workers noted that asymptotic growth functions may not be appropriate when modelling sea urchin species if they continue to grow throughout their lifetime. Furthermore, of the S-shaped growth models used to describe sea urchin growth, all but one are symmetrical. For this reason, the first limb (early growth) and second limb (later growth) of the curve are not independent and, hence, growth of juveniles and adults is linked (Gage and Tyler, 1985; Ebert and Russell, 1993).

In this study, we examine growth of the New Zealand sea urchin, *E. chloroticus*, in two populations. Growth in very small sea urchins (< 1 year old) was measured by in vitro rearing and the analysis of size frequency distributions of newly settled urchins in the field. Older sea urchins (> 1 year old) were tagged in situ using a fluorescent dye, and growth after 1 year modelled using four growth models. Three of the models are asymptotic growth functions, the Brody-Bertalanffy growth model (von Bertalanffy, 1938; Brody, 1945)

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

the Richards growth model (Richards, 1959)

$$S_t = S_\infty(1 - be^{-Kt})^{-n} \quad (2)$$

and the Jolicoeur model (Jolicoeur, 1985)

$$S_t = S_\infty(1 - bt^{-K})^{-1} \quad (3)$$

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. The fourth model applied was the Tanaka growth model (Tanaka, 1982, 1988)

$$S_t = \left( \frac{1}{\sqrt{f}} \right) \ln(|2ft(t-c) + 2\sqrt{f^2(t-c)^2 + fa}|) + d \quad (4)$$

where  $S_t$  = size at time  $t$ , and  $f$ ,  $c$ ,  $a$  and  $d$  are growth parameters. In contrast to the three asymptotic growth models, the Tanaka model incorporates an initial period of slow growth, a period of exponential growth followed by an indefinite period of slow growth.

To ascertain whether growth in *E. chloroticus* is asymptotic, we resampled one of the populations 3.9 years after the initial tagging. These data also allowed us to compare observed growth rates over the 3.9 years with predicted growth over the same period for each growth model. We use these comparisons to assess growth estimates for *E. chloroticus* in each of the studied populations, and discuss the appropriateness of using asymptotic and non-asymptotic growth functions for modelling growth in this species.

## 2. Materials and methods

### 2.1. Study sites

One of the populations of *Evechinus chloroticus* occurs at Espinosa Point (166° 58' 45" E, 45° 18' 00" S) within the Doubtful-Thompson-Bradshaw Sound complex (Fig. 1a), which is approximately 110 km long in total, and 2 km wide with a 40 km main channel and five secondary arms. The other population occurs in Titi Bay (174° 11' 40" E, 41° 14' 15" S) within Tory Channel, Marlborough Sounds (Fig. 1b), an open waterway 20 km long and an average of 2 km wide, with a maximum depth of 50 m.

### 2.2. Growth estimates

#### 2.2.1. Early *Evechinus chloroticus* growth (<1 year)

Newly settled *E. chloroticus* juveniles were obtained from stocks of larvae reared in the laboratory. Competent larvae were pipetted into small plastic containers containing 400 ml of 15°C, 45 µm millipore filtered seawater and a number of small coralline algae encrusted pebbles. Twenty-four hours after the transfer of larvae, the pebbles were examined under a dissecting microscope, and the test diameters (TD) of the newly metamorphosed sea urchins were measured to the nearest 0.01 mm. Subsequent measurements of test diameters were made at 2-week to 2-monthly intervals for 1 year. The measurements of any individuals that died within the year were excluded from all growth estimates. Water temperature was kept at 15°C, and 50% of the water was replaced with filtered seawater every 2 weeks. At this time, all pebbles free of sea urchins were replaced with freshly collected coralline encrusted pebbles.

Growth rates of juveniles (<10 mm TD) in the field were calculated from changes in the size-frequency distribution of newly settled urchins in Doubtful Sound and Tory Channel (Fig. 1) between 27 January 1993 and 23 July 1993. On each sampling date, eight randomly placed 1-m<sup>2</sup> quadrats were sampled, four each at 6 and 10 m depths using an underwater airlift sampler. The area within the quadrat was intensively sampled using the airlift, with collection efficiency improved by agitation of the substratum with a paint brush. The samples containing the small urchins were retained in a 300-µm mesh bag located at the top of the airlift, and frozen within 3 h of collection. Samples were later sorted through a 10-mm sieve, with the sea urchins retained on a second 300 µm sieve. These samples were preserved in 70% ethanol for further sorting under a dissecting microscope.

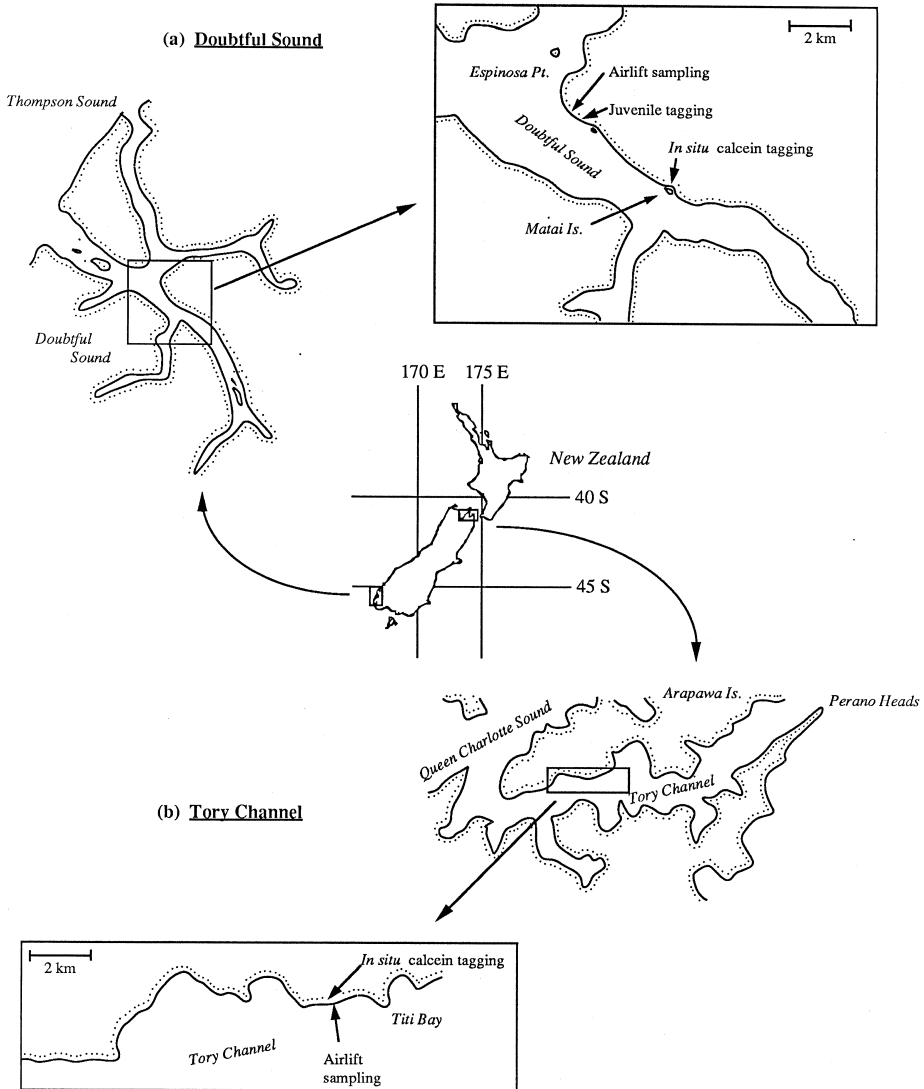


Fig. 1. Map showing the location of airlift sampling, juvenile calcein tagging and in situ calcein tagging of *E. chloroticus* in Doubtful Sound (a) and Tory Channel (b).

### 2.2.2. *Evechinus chloroticus* tagging and recapture

*Evechinus chloroticus* were tagged with the fluorescent dye, calcein, using a working solution of 500 ppm calcein in filtered seawater (45  $\mu\text{m}$  pore size) buffered to pH 8 with NaOH. For sea urchins <20 mm TD, incorporation of the dye was done by soaking the animals in a bath of the calcein solution for between 5 and 12 h. Larger urchins (>20 mm TD) had 1.0 ml of the calcein solution injected into the coelom through the

peristomeal membrane. Administration of the dye was done in situ by SCUBA divers using an adjustable dose, automatic refilling syringe, fitted with a 16-gauge hypodermic needle. Tagging of 250–300 *E. chloroticus* was done on 2 December 1993 in Doubtful Sound, and for 800–900 individuals on 19 and 20 April 1994 in Tory Channel.

Doubtful Sound was first revisited on 1 December 1994 (365 days post-tagging) when 167 *E. chloroticus* ranging in size from 43 to 116 mm TD were collected from the tagging site. Tagged sea urchins were removed from the Tory Channel site on 12 April 1995 (358 days post-tagging), with 196 urchins ranging in size from 28 to 95 mm TD collected. On these days, sea urchins were collected by SCUBA, bagged and returned to the field station for processing. For each animal, the TD was measured to the nearest millimetre using knife-edged vernier calipers, and the Aristotle's lantern dissected out. Later, each Aristotle's lantern was cleaned and disassembled by soaking in 5% sodium hypochlorite. The samples were air dried for 3–4 days and the size (to the nearest 0.1 mm) of one of the demi-pyramids measured from the oral tip to the epiphysis junction (Fig. 2). Each lantern was then inspected under a dissecting microscope that was illuminated by an external ultraviolet light source. If a fluorescent tag was detected (Fig. 2), then the distance between the oral tip and the point where the calcein tag met the external edge of the demi-pyramid ( $J_t$ ) was measured (Fig. 2). Measurements were made to the nearest 0.01 mm using an ocular micrometer. To assess growth over a longer time period (3.9 years post-tagging), a second sample of 83 *E. chloroticus* ranging in size

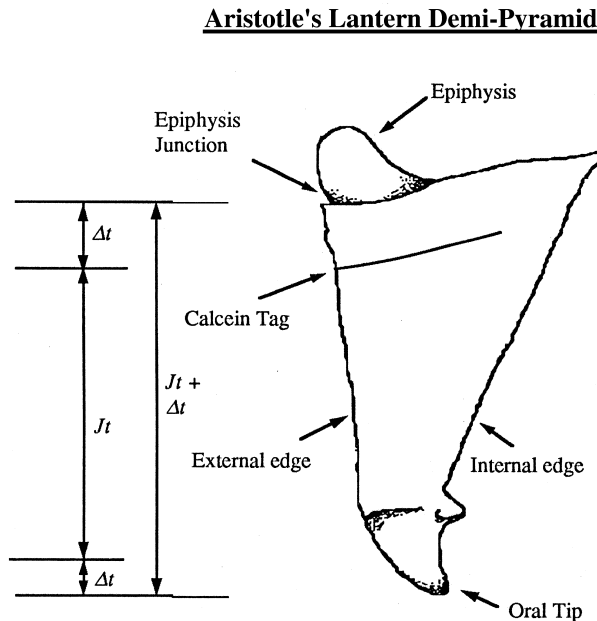


Fig. 2. Measurements made on the Aristotle's lantern demi-pyramid to estimate change in lantern size in *E. chloroticus* following calcein tagging. The previous position of the epiphysis junction ( $J_t$ ) is represented by the location of the calcein tag, and is used to calculate the change in demi-pyramid size over time ( $J_t + \Delta t$ ).

from 46 to 103 mm TD were collected from the Doubtful Sound site on 17 November 1997. Logistical constraints did not allow a second sample to be taken from the Tory Channel site.

As calcein is incorporated into the sites of active calcium deposition (Fig. 2), the position of the tag represents the size of the lantern at the time of the tagging,  $Jt$ . The size of the lantern at the time of the measurement represents size at  $Jt + \Delta t$ , in this case  $\Delta t$  being 1 year for the first samples, and 3.9 years for the second of the Doubtful Sound samples. In order to convert these data on changes in lantern size to changes in sea urchin size, the relationship between the demi-pyramid length and test diameter was established over the range of *E. chloroticus* sampled. For each population, demi-pyramid length ( $J$ ) was converted to test diameter (TD) using the non-linear, logarithmic equation

$$\text{TD} = c + m \ln J \quad (5)$$

with the homogeneity of slopes between both sites tested using ANCOVA. Thus  $Jt$  was converted to test diameter at the time of tagging (TD $t$ ) and harvest (TD $t + \Delta t$ ).

### 2.3. Estimating growth model parameters

For each site, the paired measurements of initial (TD $t$ ) and final (TD $t + \Delta t$ ) test diameters were analysed using Walford plots (Walford, 1946). The relationship between the initial and final sizes can be established for each of the four growth models using the appropriate linear or non-linear difference (or regression) equation.

#### 2.3.1. Brody-Bertalanffy growth function

Parameters for the Brody-Bertalanffy function;

$$S_t = S_\infty (1 - be^{-Kt}) \quad (6)$$

were estimated using the linear regression model,  $y = c + mx$  of initial and final sizes (Walford, 1946), where  $y$  = final size (TD $t + \Delta t$ ) and  $x$  = initial size (TD $t$ ), and the slope of the regression,  $m = e^{-Kt}$ . Therefore

$$\text{Maximum size } S_\infty = \frac{c}{(1 - m)} \quad (7)$$

$$\text{Growth constant } K = \frac{-\ln m}{t} \quad (8)$$

where  $t$  = time between initial and final measurements and

$$b = 1 - \frac{S_0}{S_\infty} \quad (9)$$

where  $S_0$  = size at settlement. Newly settled urchins reared in the laboratory were found to have a test diameter of 0.4 mm. Therefore,  $S_0$  was replaced by 0.4 mm when estimating growth of the test diameter and the difference model only estimated  $S_\infty$  and  $K$ .

Instantaneous growth rates ( $I$ ) were calculated using the equation

$$I = S_{\infty} K b e^{-Kt} \quad (10)$$

### 2.3.2. Richards growth function

Parameters for the Richards function,

$$S_t = S_{\infty} (1 - b e^{-Kt})^{-n} \quad (11)$$

were estimated using a non-linear regression model for the difference equation

$$y = [c + m x^{(-1/n)}]^{-n} \quad (12)$$

where  $y$  = final size (TDt +  $\Delta t$ ) and  $x$  = initial size (TDt) and

$$\text{Maximum size } S_{\infty} = \left[ \frac{c}{(1-m)} \right]^{-n} \quad (13)$$

$$\text{Growth constant } K = \frac{-\ln m}{t} \quad (14)$$

and

$$b = \frac{\left[ S_{\infty}^{\left(\frac{-1}{n}\right)} - S_0^{\left(\frac{-1}{n}\right)} \right]}{S_{\infty}^{\left(\frac{-1}{n}\right)}} \quad (15)$$

Parameters for the difference equation were estimated by the simplex method using the SYSTAT statistical package (Wilkinson, 1989), with a model

$$Y = (C + (V * (X^{(-1/N)})))^{-N} \quad (16)$$

where  $v = m$ ,  $c = c$ ,  $N = n$ , and  $X$  and  $Y$  are the initial and final test diameters, respectively.

Instantaneous growth rates ( $I$ ) were calculated using the equation

$$I = -S_{\infty} n b K e^{-Kt} (1 - b e^{-Kt})^{-n-1} \quad (17)$$

### 2.3.3. Jolicoeur growth function

Parameters for the Jolicoeur growth function

$$S_t = S_{\infty} (1 - b t^{-K})^{-1} \quad (18)$$

were estimated using a non-linear regression model for the difference equation

$$y = \frac{S_{\infty}}{1 - b \left[ \left( \frac{(x - S_{\infty})}{bx} \right)^{\left(\frac{-1}{K}\right)} + t \right]^{-K}} \quad (19)$$

where  $y = \text{TDt} + \Delta t$  and  $x = \text{TDt}$  and

$$b = \frac{S_0 - S_{\infty}}{S_0} \quad (20)$$

Parameters of the difference equation were estimated by the simplex method using the SYSTAT statistical package (Wilkinson, 1989) with a model

$$Y = SM / (1 - (((SO - SM) / SO) \cdot (((X - SM) / ((SO - SM) / SO) \cdot X)))^{(-1/K)} + 1)^{-K} \quad (21)$$

where  $Y$  = final size ( $TDt + \Delta t$ ),  $X$  = initial size ( $TDt$ ),  $SM = S_{\infty}$ ,  $SO = S_0$  and  $K = K$  (Ebert and Russell, 1993).

Instantaneous growth rates ( $I$ ) were calculated using the equation

$$I = -S_{\infty} b K t^{-K-1} (1 - b t^{-K})^{-2} \quad (22)$$

#### 2.3.4. Tanaka growth function

Parameters for the Tanaka growth function

$$S_t = \left( \frac{1}{\sqrt{f}} \right) \ln \left( |2ft - c + 2\sqrt{f^2(t-c)^2 + fa}| \right) + d \quad (23)$$

where  $c$  (age of maximum growth) =  $a/E$  and

$$E = \exp(\sqrt{f(S_0 - d)}) \quad (24)$$

were estimated from a non-linear regression for the difference equation

$$y = \left( \frac{1}{\sqrt{f}} \right) \ln \left( |2G + 2\sqrt{G^2 + fa}| \right) + d \quad (25)$$

where

$$G = \frac{E}{4} - f \frac{a}{E} + f \quad (26)$$

and

$$E = \exp(\sqrt{f(x - d)}) \quad (27)$$

where  $y$  = final size ( $TDt + \Delta t$ ) and  $x$  = initial size ( $TDt$ ).

Parameters for the difference equation were estimated by the Quasi-Newton method using the SYSTAT statistical package (Wilkinson, 1989) with a model

$$Y = 1 / \text{SQR}(F) \cdot \text{LOG}(2 \cdot \text{ABS}((\text{EXP}(\text{SQR}(F) \cdot (X - D)))) / 4 - F \cdot A / \text{EXP}(\text{SQR}(F) \cdot (X - D))) + F + \text{SQR}(((\text{EXP}(\text{SQR}(F) \cdot (X - D)))) / 4 - F \cdot A / \text{EXP}(\text{SQR}(F) \cdot (X - D))) + F)^2 + F \cdot A)) + D \quad (28)$$

where  $Y$  = final size ( $TDt + \Delta t$ ),  $X$  = initial size ( $TDt$ ),  $D = d$ ,  $F = f$ , and  $A = a$  (Ebert and Russell, 1993).

Instantaneous growth rates ( $I$ ) were calculated using the equation

$$I = \frac{1}{\sqrt{f(t-c)^2 + a}} \quad (29)$$

and  $1/\sqrt{a}$  is the maximum growth rate.

#### 2.4. Comparison of growth functions

Evaluation of each growth model was made using (1) standard sum of the squares error residual (SSE) of the difference equation regressions, (2) an examination of the regression residuals, (3) a comparison of the predicted versus observed size at age 1 year for *E. chloroticus* sampled in Doubtful Sound, and (4) a comparison of the predicted growth of urchins over 3.9 years, with the observed growth in the urchins recovered 3.9 years post-tagging.

The comparison of observed growth over 3.9 years in Doubtful Sound with the models' prediction of growth over the same period was made by converting the size of the lantern at the time of tagging to the test diameter at that time. Predicted growth of these tagged urchins for the 3.9 years after tagging was calculated using each of the four growth models. As an example, one recovered urchin was 82.2 mm TD at the time of tagging, which according to the Brody-Bertalanffy ( $B_B$ ), Richards ( $R_D$ ), Jolicœur ( $J_L$ ) and Tanaka ( $T_K$ ) growth models would have an age of  $B_B = 5.9$  years,  $R_D = 6.9$  years,  $J_L = 7.7$  years and  $T_K = 8.9$  years. This urchin was predicted to grow  $B_B = 15.6$  mm,  $R_D = 15.4$  mm,  $J_L = 12.6$ , and  $T_K = 11.7$  mm over the 3.9-year period. The individual actually grew 12.5 mm over the 3.9 years.

The relationship between the predicted and observed growth of the tagged urchins over the 3.9 years was examined using linear regression analysis. Assessment of each growth model was made by comparing the co-efficient of variation, standard sum of the squares error residual, the distribution of residuals, and the slope of the regression.

#### 2.5. Mathematical and statistical calculations

All statistical analysis was carried out using the SYSTAT statistical package (Wilkinson, 1989).

### 3. Results

#### 3.1. Early *Evechinus chloroticus* growth (<1 year)

Five *E. chloroticus* individuals were kept alive for the entire year and their growth calculated from changes in test diameter over that period (Fig. 3a). The mean sea urchin TD ( $\pm$ SD) after 1 year was  $8.05 \pm 0.61$  mm, with growth rates averaging  $0.16$  mm week<sup>-1</sup>. A maximum average growth rate of  $0.24$  mm week<sup>-1</sup> was recorded between days 56 and 120. The rate of growth increased in the first 150 days, followed by a period of slower, linear growth.

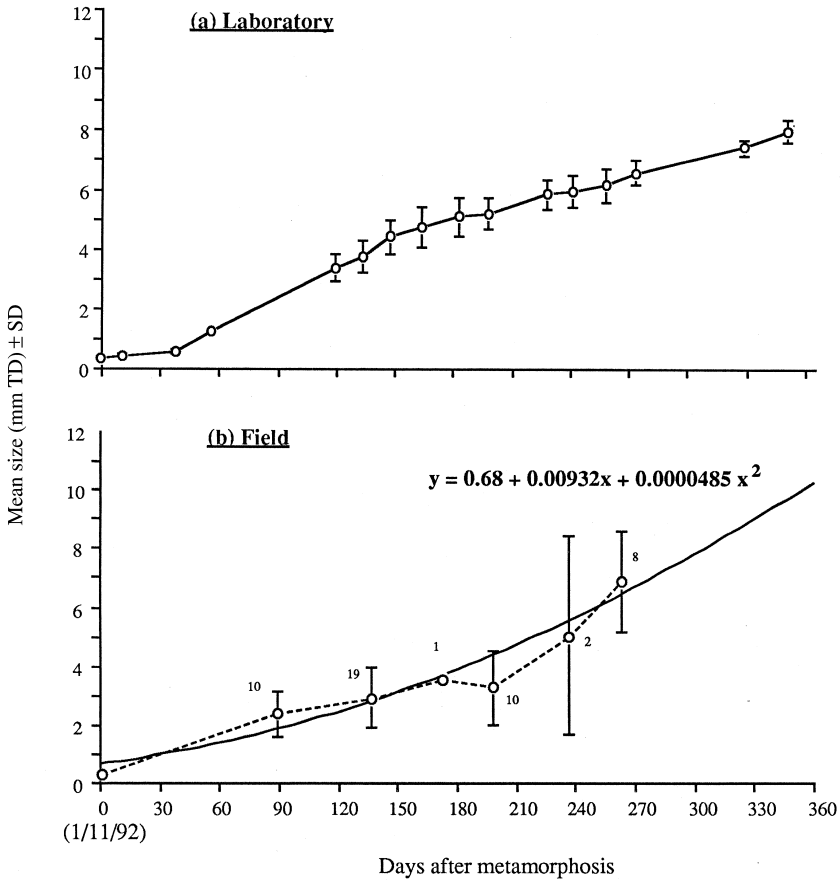


Fig. 3. Change in the mean test diameter of newly settled *E. chloroticus* ( $\pm$ SD) reared in the laboratory (a) at 15°C ( $n=5$ ), and sampled from Doubtful Sound (b). The number of individuals sampled on each date is indicated for the field samples. Sea temperatures in the field ranged from 10.9 to 14.0°C during sampling.

Only one early post-settlement sea urchin (1.48 mm TD) was recovered from airlift samples taken in Tory Channel, while a total of 50 early post-settlement sea urchins ranging in size from 0.96 to 9.50 mm TD were recovered from Doubtful Sound over the sampling period. Size-frequency distributions were generated for each of the Doubtful Sound samples (Fig. 4) and the mean size ( $\pm$ SD) of the juvenile cohort calculated for each sampling date. To calculate growth rate, the mean size ( $\pm$ SD) of the juvenile cohort on each sampling date was plotted against the time since the estimated day of juvenile settlement of the cohort, estimated from settlement samplers (Lamare (1997), as 1 November 1992 (Fig. 3B). The mean growth rate in the field over the sampling period was 0.19 mm week<sup>-1</sup>, with a maximum growth rate of 0.51 mm week<sup>-1</sup> estimated between 27 June and 23 July 1993. Growth of the juveniles in the field appears to be non-linear, with slow growth for the first  $\approx$ 197 days (0.12 mm week<sup>-1</sup>) followed by a period of accelerating growth when individuals grew 1.70 mm month<sup>-1</sup> during the

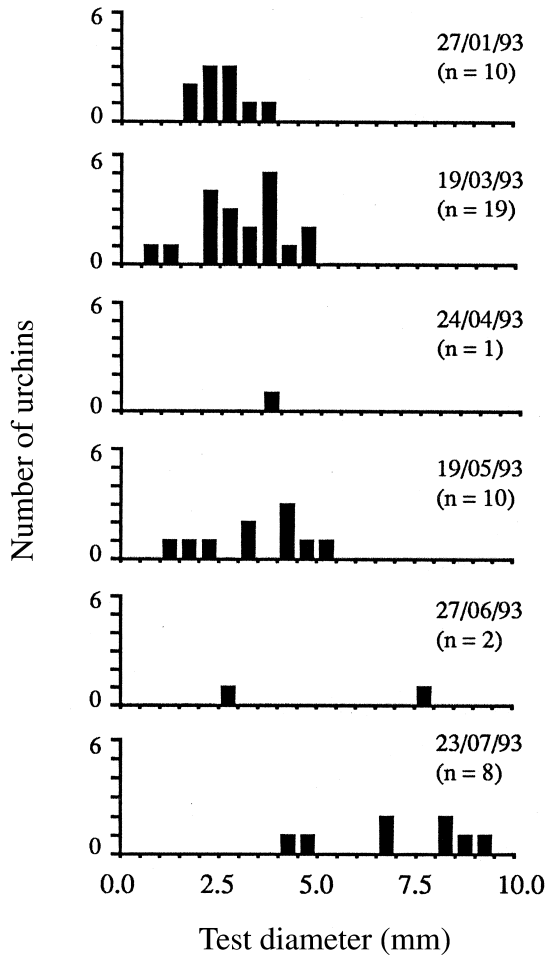


Fig. 4. Size distribution (0.5 mm TD size classes) of juvenile *E. chloroticus* collected from airlift samples taken in Doubtful Sound between 27 January 1993 and 23 July 1993. Total area sampled on each sampling date = 8 m<sup>2</sup>, *n* = number collected on each sampling date.

following 65 days. The average size of 1-year-old urchins in the field was estimated from the non-linear curve, size (mm) =  $0.68 + 0.00932x + 0.0000485x^2$ , where  $x$  = days after settlement. An extrapolation of this curve gave an estimated average size of 10.5 mm test diameter for 1-year-old individuals.

### 3.2. Recovery of calcein tagged *Evechinus chloroticus*

The rate of recovery of tagged *E. chloroticus* was higher in Doubtful Sound (37.7 and 30.12%) than in Tory Channel (23.5%) (Table 1). For Doubtful Sound, tagged individuals were found throughout the size range of sea urchins collected. In the Tory

Table 1

Summary of the tagging and recovery of *Evechinus chloroticus* in Doubtful Sound and Tory Channel using the fluorescent dye, calcein

	Doubtful Sound		Tory Channel
No. of sea urchins tagged (date)	250–300 (2/12/93)		800–900 (19/04/94)
Size range tagged (TD) (mm)	20–120		20–110
No. of sea urchins collected (date)	167 (1/12/94)	83 (17/11/97)	196 (12/04/95)
No. with calcein tags	63	25	46
% tagged	37.70	30.12	23.50
Size range collected (TD) (mm)	43–116	46–103	28–95
Size range of tagged urchins (TD) (mm)	48–112	66–103	45–89

Channel sample, smaller sea urchins were collected (down to 28 mm TD), but no urchins <45 mm TD carried calcein tags.

### 3.3. Transforming demi-pyramid length to test diameter

The relationship between test diameter and demi-pyramid length differed between sites (Fig. 5). Analysis of covariance of test diameter vs.  $\ln(\text{demi-pyramid length})$  between sites showed that the slopes were heterogeneous ( $P < 0.001$ , Table 2) and the samples could not be pooled. Two separate regression equations were therefore used to transform demi-pyramid length to test diameter: for Doubtful Sound (Fig. 6a)

$$\text{Test diameter} = -113.29 + 171.19 \cdot \ln(\text{demi-pyramid})$$

and for Tory Channel (Fig. 6b)

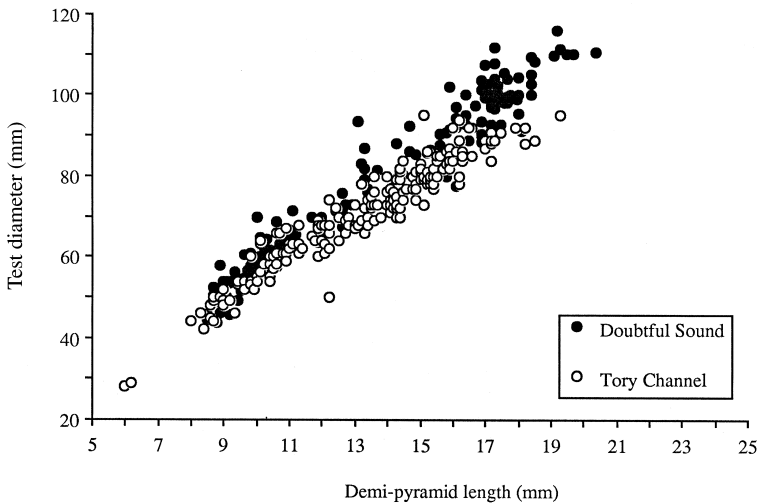


Fig. 5. Relationship between test diameter and demi-pyramid length for *E. chloroticus* from Doubtful Sound ( $n = 167$ ) and Tory Channel ( $n = 196$ ).

Table 2

Analysis of covariance of test diameter vs. ln (demi-pyramid length) for *Evechinus chloroticus* from Doubtful Sound ( $n=167$ ) and Tory Channel ( $n=196$ ); the dependent variable is ln (demi-pyramid length) and the covariant is test diameter

Homogeneity of slopes					
Analysis of variance	SS	df	MS	F-ratio	P
Location	0.080	1	0.080	86.828	0.000
Test diameter	18.896	1	18.896	20621.651	0.000
Location · test diameter	0.109	1	0.109	119.287	0.000
Error	0.329	359			

$$\text{Test diameter} = -80.761 + 136.29 \cdot \ln(\text{demi-pyramid})$$

### 3.4. Growth models

#### 3.4.1. Comparison of growth function parameters

Demi-pyramid length was converted to test diameter, and *E. chloroticus* test diameter growth was modelled using Walford Plots of the initial and final size of tagged sea urchins from each site (Fig. 7). The parameters for each of the growth models were calculated from the regression analysis (Table 3), and growth rate at age (Fig. 8) and size at age estimated (Fig. 9).

##### 3.4.1.1. Tory channel

Comparison of the growth models in Tory Channel (Table 3a, Fig. 8a) showed the maximum predicted growth rate was highest for the Brody-Bertalanffy model (33.1 mm year<sup>-1</sup>), intermediate in the Tanaka model (22.36 mm year<sup>-1</sup>) and lowest in the Jolicoeur (16.86 mm year<sup>-1</sup>) and Richards (16.03 mm year<sup>-1</sup>) models. Age of maximum growth was also found to differ, from time 0 in the Brody-Bertalanffy model,

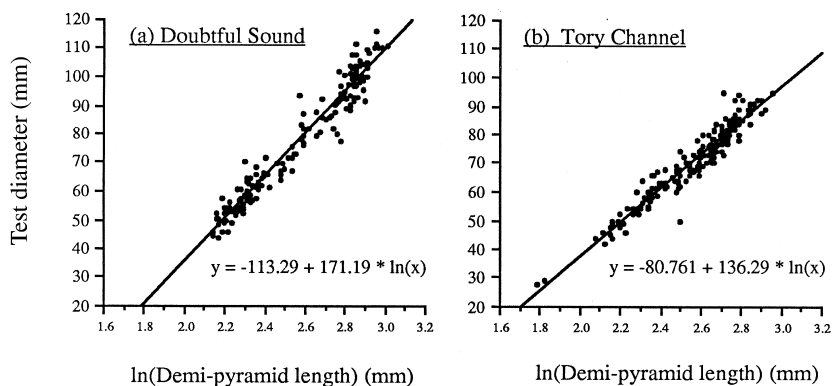


Fig. 6. Regression of test diameter versus ln(demi-pyramid length) for *E. chloroticus* from Doubtful Sound (a) and Tory Channel (b).

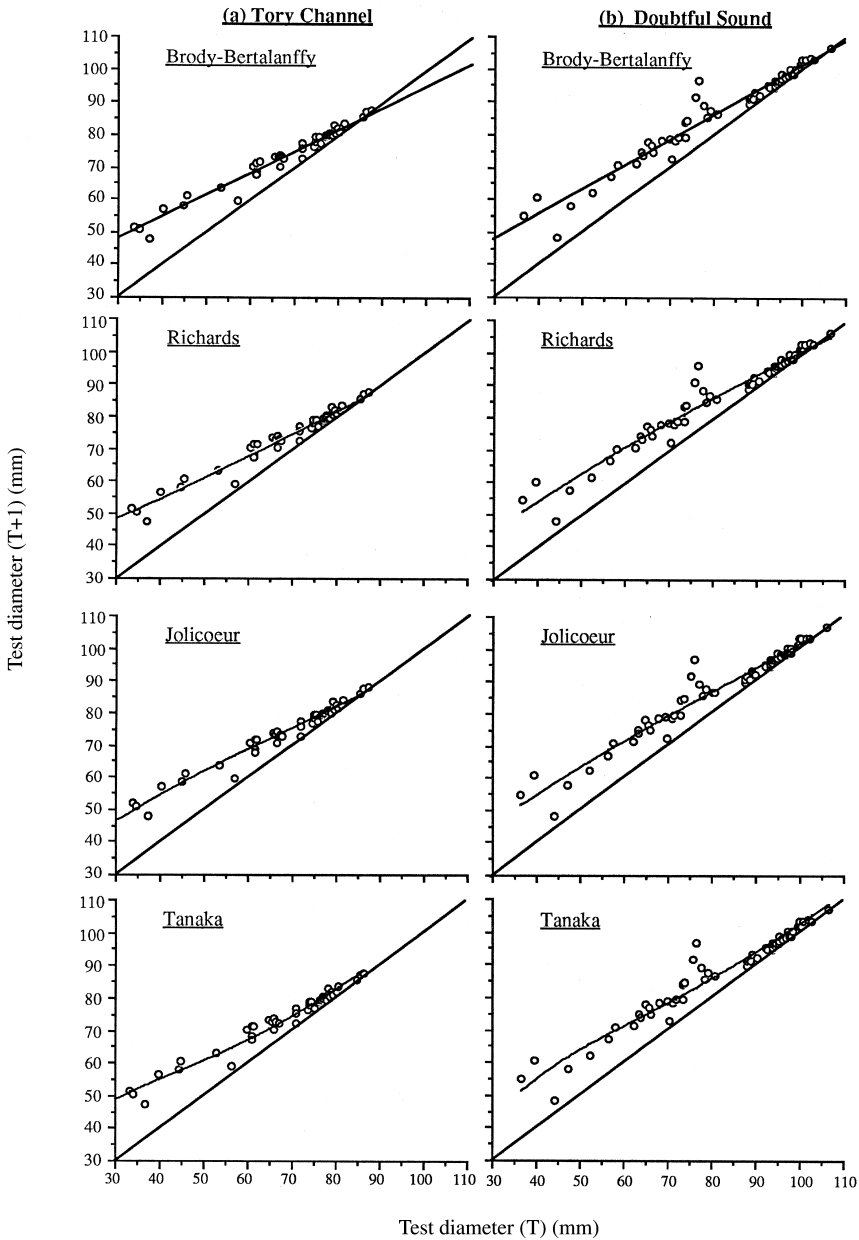


Fig. 7. Walford plots of test diameter changes over a 1-year period for calcein tagged *E. chloroticus* from Tory Channel (a) and Doubtful Sound (b). Regression lines for Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models are superimposed. The 45° line indicates zero growth;  $n=46$  for Tory Channel and  $n=63$  for Doubtful Sound.

Table 3

Estimated parameters for the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models for test diameter growth in tagged *Evechinus chloroticus* from Tory Channel (a) and Doubtful Sound (b)<sup>a</sup>

Brody-Bertalanffy		Richards		Jolicoeur		Tanaka	
(a) Tory Channel							
<i>m</i>	0.678	<i>m</i>	0.682			<i>f</i>	0.003±0.001
<i>c</i>	27.438	<i>c</i>	2.544			<i>d</i>	121.460±6.609
<i>S<sub>∞</sub></i> (mm)	85.07	<i>S<sub>∞</sub></i> (mm)	85.806	<i>S<sub>∞</sub></i> (mm)	86.937	<i>a</i>	0.002±0.001
<i>S<sub>0</sub></i> (mm)	0.4	<i>S<sub>0</sub></i> (mm)	0.4	<i>S<sub>0</sub></i> (mm)	0.4		
<i>K</i>	0.389	<i>K</i> and <i>n</i>	0.383 and -2.141	<i>K</i>	3.422		
<i>b</i>	0.995	<i>b</i>	0.919	<i>b</i>	-216.408		
Age of MGR	0	Age of MGR	1.776	Age of MGR	4.032	Age of MGR	1.516
MGR (mm year <sup>-1</sup> )	33.1	MGR (mm year <sup>-1</sup> )	16.026	MGR (mm year <sup>-1</sup> )	16.857	MGR (mm year <sup>-1</sup> )	22.361
SSE	181.006	SSE	175.006	SSE	174.063	SSE	172.787
(b) Doubtful Sound							
<i>m</i>	0.759	<i>m</i>	0.72			<i>f</i>	0.002±0.001
<i>c</i>	25.234	<i>c</i>	1.991			<i>d</i>	151.812±19.526
<i>S<sub>∞</sub></i> (mm)	104.897	<i>S<sub>∞</sub></i> (mm)	103.867	<i>S<sub>∞</sub></i> (mm)	106.785	<i>a</i>	0.004±0.001
<i>S<sub>0</sub></i> (mm)	0.4	<i>S<sub>0</sub></i> (mm)	0.4	<i>S<sub>0</sub></i> (mm)	0.4		
<i>K</i>	0.275	<i>K</i> and <i>n</i>	0.329 and -2.367	<i>K</i>	3.099		
<i>b</i>	0.996	<i>b</i>	0.905	<i>b</i>	-265.785		
Age of MGR	0	Age of MGR	2.313	Age of MGR	4.881	Age of MGR	3.541
MGR (mm year <sup>-1</sup> )	28.5	MGR (mm year <sup>-1</sup> )	16.134	MGR (mm year <sup>-1</sup> )	15.183	MGR (mm year <sup>-1</sup> )	15.811
SSE	571.308	SSE	561.167	SSE	562.151	SSE	661.581

<sup>a</sup> *m* = slope, *c* = y-intercept, *S<sub>∞</sub>* = maximum size, *S<sub>0</sub>* = size at settlement, *K* = growth constant, *b* = scaling parameter to adjust for *s* ≠ 0 at settlement, MGR = maximum growth rate, *n* = shape parameter for the Richards model and *f*, *d*, *a* = Tanaka growth parameters (±SE).

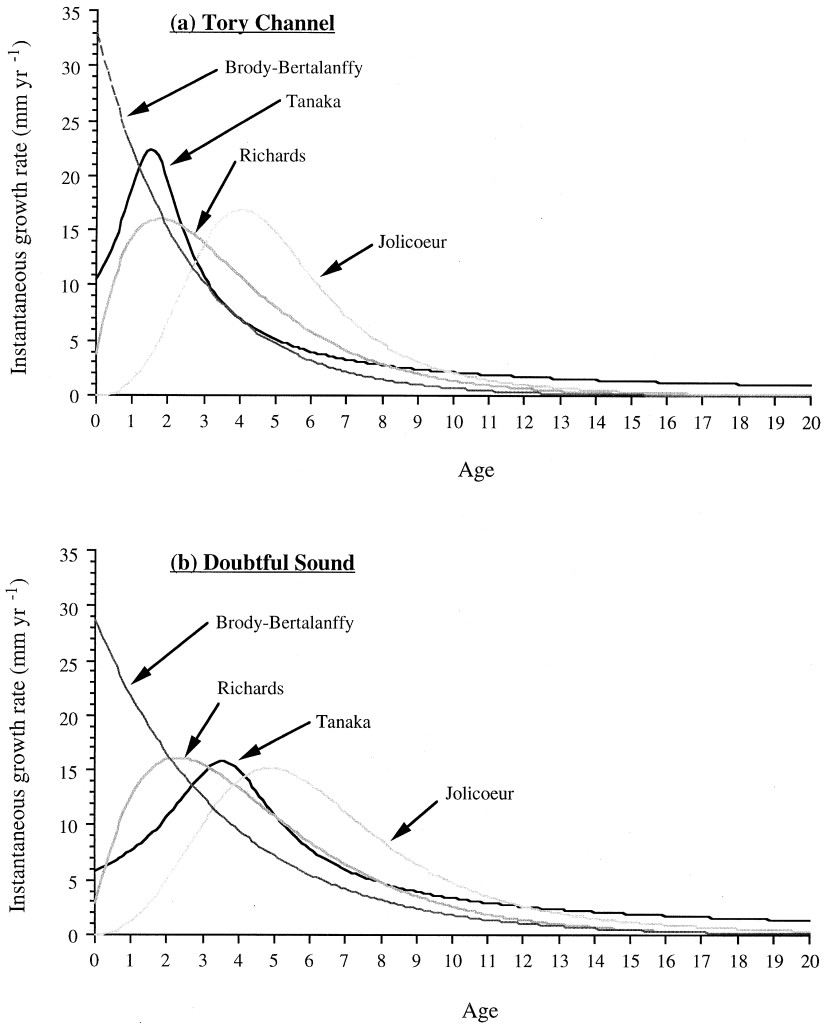


Fig. 8. Predicted changes in the instantaneous growth rate with age for *E. chloroticus* in Tory Channel (a) and Doubtful Sound (b) using the Tanaka, Richards, Jolicoeur and Brody-Bertalanffy growth models.

up to 4.03-years-old in the Jolicoeur model. For the three asymptotic growth functions, estimates of maximum test diameter were similar, ranging from 85.07 to 86.94 mm (Table 3a).

#### 3.4.1.2. Doubtful sound

Maximum growth rates of urchins from Doubtful Sound (Table 3b, Fig. 8b) were highest in the Brody-Bertalanffy model (28.5 mm year<sup>-1</sup>), but varied little between the remaining growth models (15.18 to 16.13 mm year<sup>-1</sup>). The age of maximum growth ranged from 0 years in the Brody-Bertalanffy model, up to 4.88 years old for the

Jolicoeur model. Maximum test diameter estimates were also found to vary little between the three asymptotic growth functions, ranging from 103.87 mm in the Richards model, to 106.79 mm for the Jolicoeur model (Table 3b).

A comparison of growth parameters between the two populations (Table 3) showed that the age of maximum growth was younger in Tory Channel, with maximum growth rates higher for Tory Channel for all but the Richards model. The rate of change in growth rate with time for Brody-Bertalanffy ( $K_{VB}$ ), Richards ( $K_{RD}$ ), Jolicoeur ( $K_{JK}$ ) and the Tanaka function ( $f$ ), were consistently higher in Tory Channel urchins ( $K_{BB}=0.389$ ,  $K_{RD}=0.383$ ,  $K_{JK}=3.422$ ,  $f=0.003$ ) compared with Doubtful Sound ( $K_{BB}=0.275$ ,  $K_{RD}=0.329$ ,  $K_{JK}=3.099$ ,  $f=0.002$ ). Estimates of maximum test diameter for each of the asymptotic growth functions were consistently greater for *E. chloroticus* from Doubtful Sound compared with Tory Channel.

#### 3.4.2. Size at age

When translating the differences in the growth model parameters in terms of size at age of *E. chloroticus* (Fig. 9), all four growth models predict individuals in Tory Channel will initially grow at higher rates, resulting in larger initial size at age compared with Doubtful Sound individuals. According to the models, growth rates will then decrease at both sites, with the decrease being more rapid in Tory Channel (larger  $K$  and  $f$  values). The net result will be a transition, with Doubtful Sound individuals attaining a larger size at age compared with Tory Channel individuals.

### 3.5. Evaluation of growth models

#### 3.5.1. Residual standard sum of the squares error (SSE)

For Tory Channel, the residual SSE of the growth model regressions (Table 3a) was found to be highest for the Brody-Bertalanffy model (181.006). The SSE of the remaining growth models were all higher, but very similar in magnitude (172.787 to 175.006). For Doubtful Sound (Table 3b), SSE was lowest for the Richards (561.167), Jolicoeur (562.151) and Brody-Bertalanffy (571.308) models, and considerably higher in the Tanaka model (661.581).

#### 3.5.2. Examination of residuals

The distribution of the residuals for each model (Fig. 10) is similar within each site. A significant difference, however, is the behaviour of the residuals in the larger size classes, particularly in Doubtful Sound. For all three asymptotic growth functions, the residuals of the larger sizes move from negative to positive, indicating growth is continuing beyond the maximum predicted size. In contrast, the residuals in the Tanaka model remain negative, the model allowing for continued growth of the larger size classes (although over-estimating growth of larger size classes).

#### 3.5.3. Comparison of the predicted versus observed size at age 1

The behaviour of the residuals in the smaller size classes could not be determined due to lack of data points. This is unfortunate, as the growth functions differ in their modelling of early sea urchin growth. For instance, estimates of test diameter at 1 year at

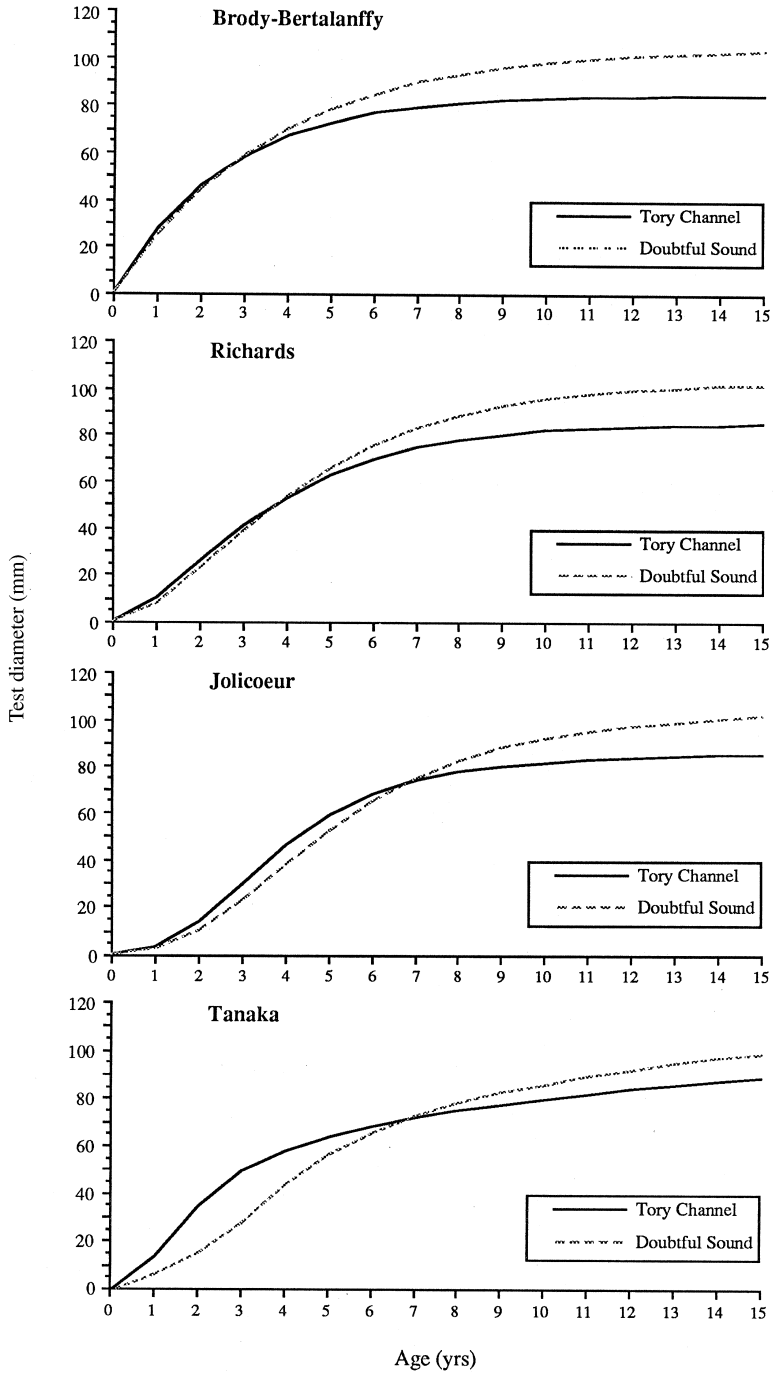


Fig. 9. Predicted size at age for *E. chloroticus* in Tory Channel and Doubtful Sound using the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models.

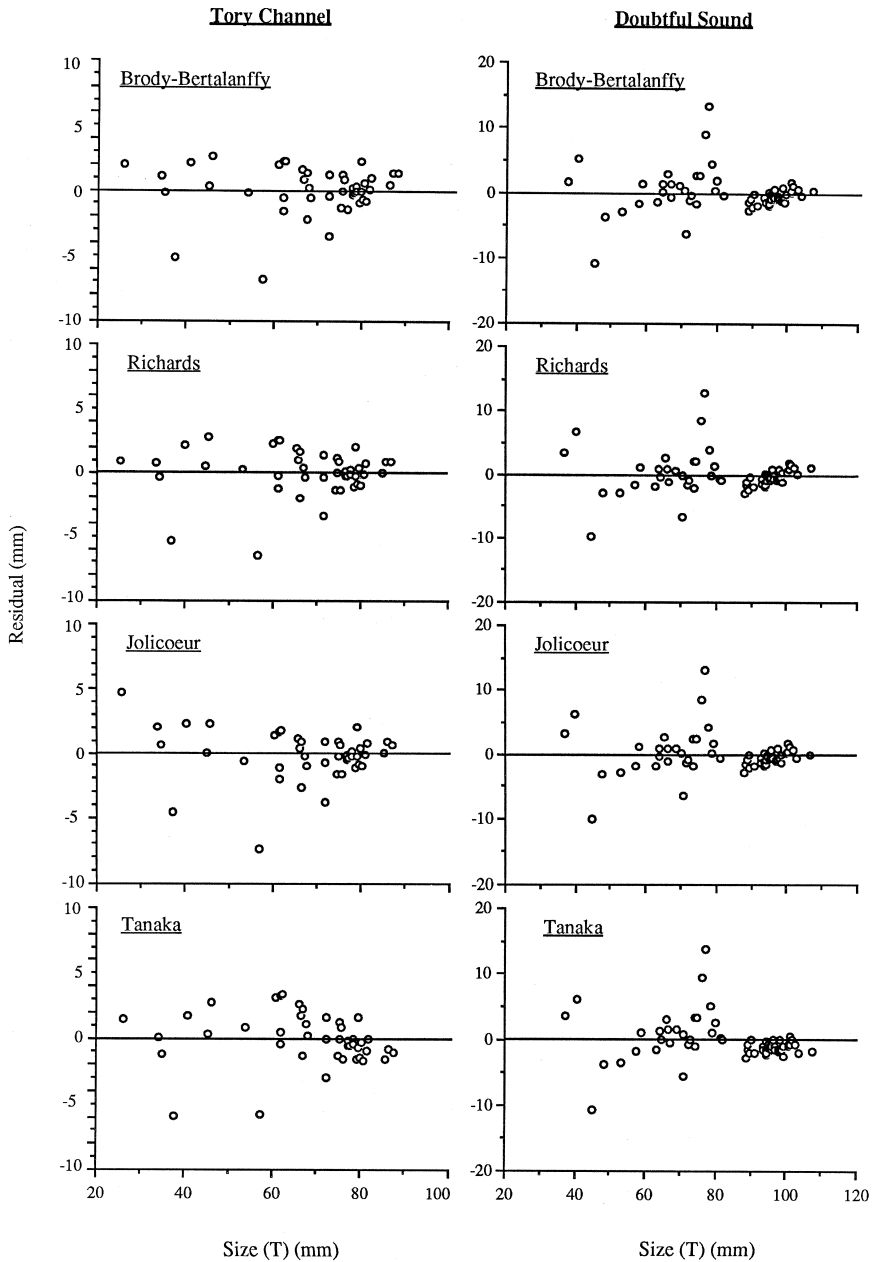


Fig. 10. Distribution of residuals of test diameter ( $T + 1$ ) as a function of test diameter ( $T$ ) for *E. chloroticus* from Tory Channel ( $n = 46$ ) and Doubtful Sound ( $n = 63$ ). Residuals were calculated from the regression of the difference equations for the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models using Walford plots.

both sites (Table 4) range from 4.1 to 27.7 mm in Tory Channel and from 3.3 to 25.5 mm in Doubtful Sound, depending on the model. An alternative assessment was made by comparing the growth models' predictions of growth in the first year in Doubtful Sound, with the independent measurements of early *E. chloroticus* growth made in the laboratory and from airlift samples (Table 4). A comparison of size at age 1 year shows the Richards growth model provided the closest fit to the observed growth rates. The Richards model estimates of size at 1 year of 8.58 mm TD (Doubtful Sound) and 10.42 mm TD (Tory Channel) are comparable to the 8.05 and 10.5 mm TD estimated from the laboratory and airlift samples, respectively. Both the Jolicoeur and Tanaka models underestimated the size at age 1, while the size predicted by the Brody-Bertalanffy model greatly exceeded that observed. Further comparison shows that the increase in growth rate over the first year indicated from the airlift samples was predicted in the Richards, Jolicoeur and Tanaka models, while the Brody-Bertalanffy model predicted growth would decrease over the first year.

#### 3.5.4. Comparison of predicted with observed growth over a 3.9-year period

The relationship between observed and predicted growth of *E. chloroticus* (Fig. 11) was examined by linear regression analysis of observed and predicted growth over 3.9 years. A significant relationship ( $P < 0.005$ ) between the two existed for all four growth models (Table 5), with the residual standard sum of squares ranging from 335.33 for the Tanaka model to 1274.03 for the Richards model. For the three asymptotic growth models the slope of the regression did not differ significantly from a slope of 1.0 ( $t[23] \leq 0.061$ ,  $P > 0.05$ ), indicating that the mean predictions by these three models did not differ significantly from the actual growth rates. In contrast, the slope of the Tanaka model was significantly less than 1.0 ( $t[23] = -2.645$ ,  $P < 0.02$ ), over-estimating growth in the larger size classes and under-estimating growth in the smallest size classes that were resampled.

A high degree of growth variability exists between individuals of the same size (Fig. 11), and resulted in low coefficient of variation ( $R^2$ ) values. Predictions from the Tanaka model could only account for 46.1% ( $R^2 = 0.461$ ) of the observed growth (Table 5), with the remaining three models predicting 42.1% (Brody-Bertalanffy), 42.8% (Richards) and 42.8% (Jolicoeur) of the observed growth. The residuals of all four growth models were

Table 4

Estimates of size at 1 year and mean growth rate for *Evechinus chloroticus* in Tory Channel and Doubtful Sound using predictions from the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models, compared with estimates of growth from size-frequency analysis of airlifter samples, and growth of newly settled urchins in the laboratory

	Brody-Bert.	Richards	Jolicoeur	Tanaka		
Tory channel						
Size at age 1 year (mm)	27.71	10.42	4.1	13.47		
Mean growth rate (mm month <sup>-1</sup> )	2.31	0.87	0.34	1.12		
Doubtful Sound						
Size at age 1 year (mm)	25.54	8.58	3.34	5.94	Airlift	Laboratory
Mean growth rate (mm month <sup>-1</sup> )	2.13	0.72	0.28	0.5	0.88	0.67

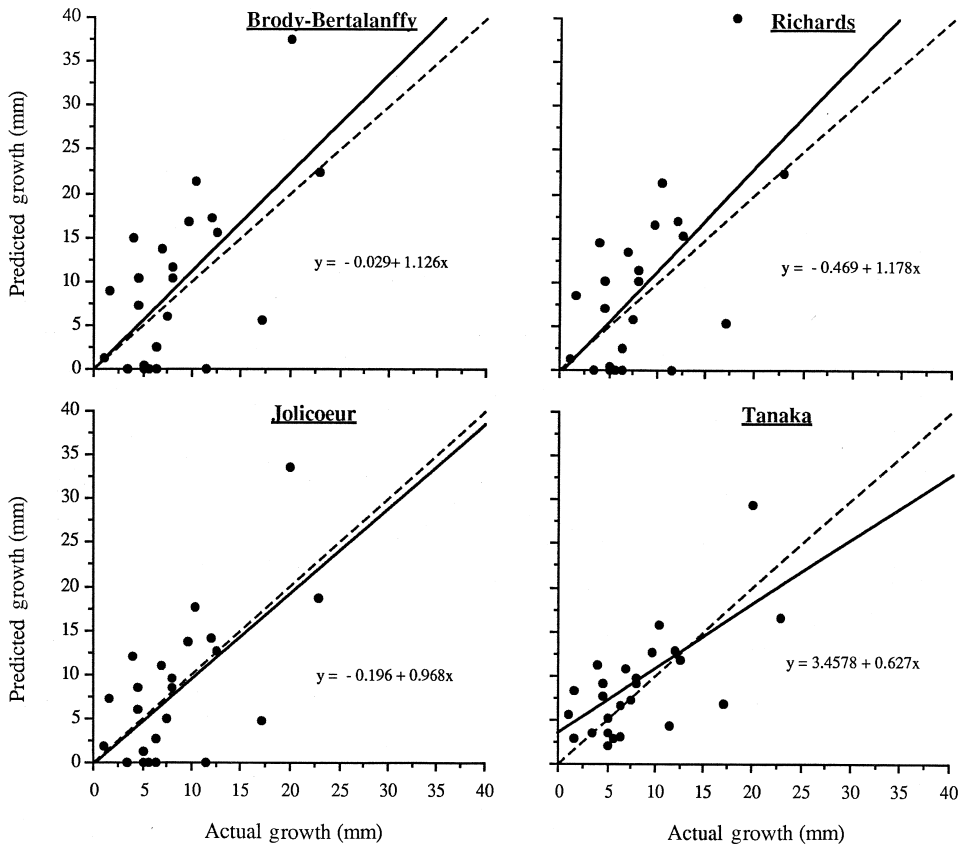


Fig. 11. Observed growth over 3.9 years of *E. chloroticus* ( $n=25$ ), versus predicted growth over the same period using the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models. The solid line is the linear relationship between the observed and predicted growth. The dashed line represents a line with a slope of 1.

Table 5

Regression analysis of observed growth over 3.9 years of *Evechinus chloroticus* ( $n=25$ ) versus predicted growth over the same period using the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models

Model	$n$	Regression equation	Residual SSE	SE of slope	SE of intercept	ANOVA (dF, $F$ , $P$ )	$R^2$
Bertalanffy	25	$y = -0.029 + 1.126x$	1197.15	0.281	2.781	24, 16.01, 0.0006	0.421
Richards	25	$y = -0.469 + 1.178x$	1274.03	0.290	2.869	24, 16.47, 0.0005	0.428
Jolicoeur	25	$y = -0.196 + 0.968x$	862.47	0.239	2.361	24, 16.43, 0.0005	0.428
Tanaka	25	$y = 3.458 + 0.627x$	335.33	0.141	1.370	24, 19.64, 0.0002	0.461

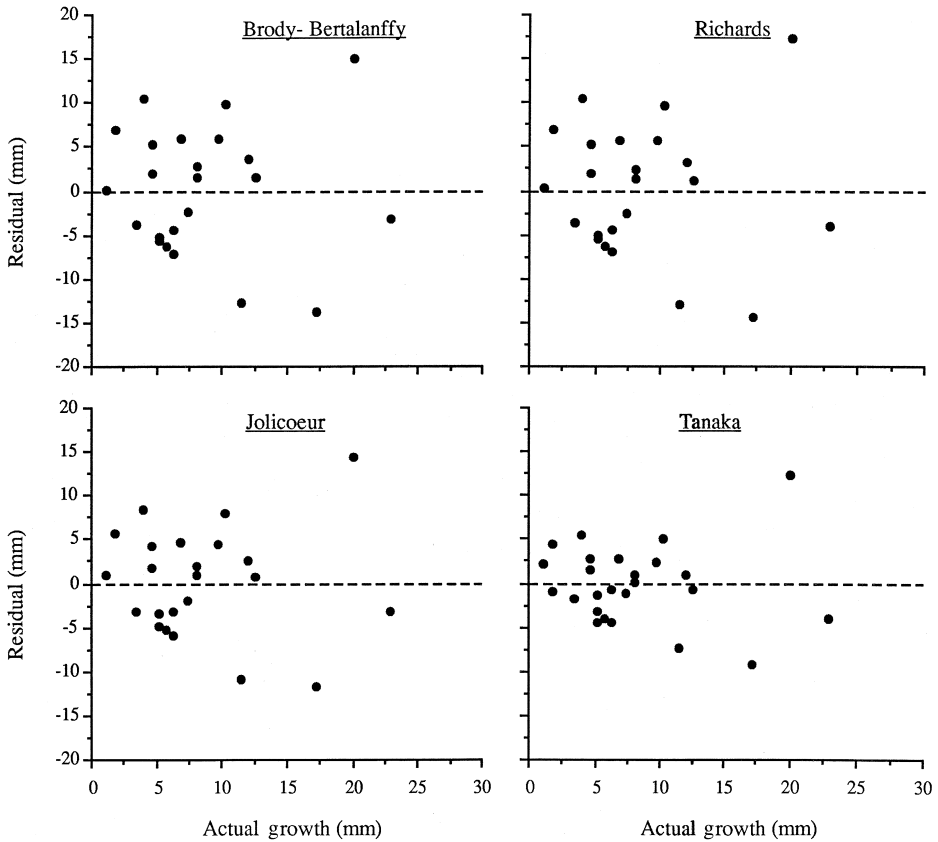


Fig. 12. Distribution of residuals from the regression of observed growth over 3.9 years of *E. chloroticus* ( $n=25$ ), versus predicted growth over the same period for the Brody-Bertalanffy, Richards, Jolicoeur and Tanaka growth models.

evenly distributed around the  $x$ -axis, but increased in dispersion with increasing growth values (Fig. 12).

#### 4. Discussion

Quantifying the somatic growth of *Evechinus chloroticus* requires using an appropriate model. To date, such a model probably does not exist, either for this species, or sea urchins in general (Ebert and Russell, 1993). A significant problem is the application of an asymptotic growth function to sea urchin species that may continue to grow throughout their lifetime. The current study suggests growth in *E. chloroticus* is non-asymptotic. Of the 25 tagged urchins recovered after 3.9 years, none showed any evidence of quiescence in growth. The three asymptotic models predicted no growth in five of these tagged sea urchins, while the Tanaka model predicted growth in these five

individuals to range between 2.1 and 4.2 mm ( $\bar{x}=3.264$  mm). These individuals, in fact, increased in test diameter from 3.4 to 11.4 mm ( $\bar{x}=6.2$  mm).

The comparison between predicted and observed growth over 3.9 years highlights one of the inadequacy of modelling asymptotic growth in *E. chloroticus*. Despite this, all three asymptotic growth functions modelled growth that was not statistically different from the observed growth over the 3.9 years. For these models, there was a significant regression between the observed and predicted growth rates ( $P<0.05$ ), and the slope of linear regression did not differ significantly from 1.0 ( $P>0.05$ ). For the Tanaka model, there was also a significant regression between the observed and predicted growth rates  $P=(0.0002)$ , although the slope of the line was significantly less than 1.0 ( $P<0.02$ ). This reflects an over-estimation of growth in the larger size classes and under-estimation of growth in the smaller size classes, a result also found by McShane and Anderson (1997) when applying the Tanaka model to *E. chloroticus*.

Given these findings, we suggest that of the four models presented here, the Richards model best describes growth in *E. chloroticus*. This conclusion is subjective, but based on several important considerations. Firstly, the Richards model provides the closest prediction of size at 1 year. Model predictions of 10.42 mm TD in Tory Channel and 8.58 mm TD in Doubtful Sound were similar to the size of *E. chloroticus* observed in the laboratory (8.05 mm TD), and in Doubtful Sound ( $\approx 10.5$  mm TD). In this respect, the large size at age 1 predicted by the Brody-Bertalanffy model excluded it from further consideration. Secondly, the Brody-Bertalanffy model predicted that growth in the first year decreases with age, contrary to the observations of early growth of *E. chloroticus* in the field. Thirdly, of the three remaining growth models, the sum of the squares errors was similar for all three models in Tory Channel, but considerably higher for the Tanaka model in Doubtful Sound. The Tanaka model tends to under-estimate growth in the smaller size classes and over-estimate growth in the larger size classes. Lastly, the onset of maturity is usually accompanied by a decrease in somatic growth as resources are channelled into gonad production. The Richards model predicts a decrease in somatic growth in Tory Channel after an age of 1.76 years (22 mm TD) and 2.31 years (30 mm TD) in Doubtful Sound, with growth decreasing rapidly after ages 3 to 4 years (40 to 50 mm TD). This is concordant with reported age at first reproduction in *E. chloroticus*. Macroscopic gonads were first produced at an age of 2.5 to 3 years (30–40 mm TD) (Lamare, 1997), with sexual maturity attained at 3–4 years (Dix, 1970), or a size of 40 to 50 mm TD (Dix, 1970; McShane et al., 1994). This degree of concordance was not observed at both sites using the remaining models.

The Richards model has been used to describe the growth of a number of sea urchin species (Ebert, 1980a, 1980b, 1982; Gage and Tyler, 1985; Russell, 1987; Ebert and Russell, 1992, 1993; Kenner, 1992), and the current study is the first application of the model to *E. chloroticus*. The Richards model describes a flexible S-shaped growth curve, ranging from the Brody-Bertalanffy Model (when the shape parameter,  $n = -1$ ), the logistic function (when  $n = +1$ ), to the Gompertz equation as the  $|n|$  approaches infinity (Ebert, 1980a). Reported values of  $n$  for sea urchins have ranged from  $-0.603$  to  $+0.154$  (mean  $n = -0.384$ ) in 19 tropical and subtropical species (Ebert, 1982),  $n = 106.89$  in the deep water species *Echinus affinis* (Gage and Tyler, 1985), from  $-0.390$  to  $+0.37$  (mean  $= -0.234$ ) in *Strongylocentrotus purpuratus* (Russell, 1987;

Kenner, 1992), and from  $-0.3208$  to  $-5.5636$  (mean =  $-2.062$ ) in *S. franciscanus* (Ebert and Russell, 1992, 1993). The range in  $n$  indicates that large variations in the shape of growth curves may exist for echinoids. The values of  $n$  obtained in the current study ( $-2.141$  and  $-2.367$ ) are most similar to the northern temperate species, *S. franciscanus*, and suggest growth in *E. chloroticus* has only a short initial lag phase ( $<1$  year), followed by a rapid acceleration in growth preceding a long period of slower growth.

The growth of juvenile *E. chloroticus* in the first year was found to be an average of  $8.05 \text{ mm year}^{-1}$  in the laboratory, and an estimated  $10.5 \text{ mm year}^{-1}$  in the field. Growth in the field appears to be biphasic, with an initial period of slow growth (0–200 days post-settlement), followed by a period of accelerating growth. In contrast, growth rate in the laboratory increased in the first 150 days, but remained constant after this time. Early biphasic growth has previously been observed in newly settled sea urchins (Raymond and Scheibling, 1987; Rowley, 1990) and other echinoderm species (Birkeland et al., 1971; Yamaguchi, 1973, 1974, 1975; Barker, 1979; Zann et al., 1987) and is generally associated with a major shift in diet. In sea urchins this likely involves a shift from feeding on a microbial surface film, filamentous algae epiphytes and coralline algae to a diet of fleshy kelp and algal turf (Raymond and Scheibling, 1987; Rowley, 1990). For *E. chloroticus* it is possible that for the first 150–200 days after settlement, juveniles feed on the microbial surface film, filamentous algal epiphytes and coralline algae. Growth rate over this period is between  $0.52$  and  $0.79 \text{ mm month}^{-1}$ . Between 150 and 200 days, at a size of 3–4 mm TD, juveniles commence feeding on fleshy algae and algal turf. Growth rate accelerates to  $\approx 1.70 \text{ mm month}^{-1}$ , resulting in a size of 10–11 mm TD at 1 year. Following the slow initial growth phase, growth rate increases until the sea urchin reaches a size of around 40 to 50 mm TD when the sea urchins reach maturity, after which time growth rate decreases.

Previous estimates of *E. chloroticus* growth have been made for a number of geographic locations using a variety of methods and growth models (Table 6). Estimates from ring counts, change in size distribution, and the Richards function are comparable and suggest that the test diameters of *E. chloroticus* at ages 1 to 6 years are about 10, 25, 40, 55, 65 and 75 mm TD, respectively, although considerable geographic variation in

Table 6

Average estimates of size at age for *Evechinus chloroticus* from studies employing similar growth estimate techniques

Method	Average test diameter (mm)					
	1	2	3	4	5	6
Age (years)	1	2	3	4	5	6
Ring counts <sup>a</sup>	11	26.5	41	55	66.4	75.8
Size frequency distribution <sup>b</sup>	10.5					
Tag/recapture						
Brody-Bertalanffy <sup>b,c,d</sup>	21.8	38.4	51.3	61.5	69.5	75.8
Richards <sup>b</sup>	9.5	24.6	40	53.6	64.3	72.5

<sup>a</sup> Dix, 1972.

<sup>b</sup> Current study.

<sup>c</sup> Walker, 1981.

<sup>d</sup> McShane et al., 1994.

growth is likely. Indeed, differences in the growth of *E. chloroticus* between Tory Channel and Doubtful Sound were apparent in this study. While size at age is similar in both populations in the first three years of growth, growth rates decreased more rapidly in Tory Channel. The differences in somatic growth become evident at onset of gonad production, between the ages of 3 and 4 years (40–50 mm TD).

Differences in somatic growth have been attributed to variations in food quality and quantity in a number of sea urchin species (see review by Lawrence and Lane, 1982; Klinger et al., 1983; Andrew and Choat, 1985; Raymond and Scheibling, 1987; Levitan, 1988; Rowley, 1990), and is the likely cause of the growth differences observed in this study. Indicative of this is the fact that *E. chloroticus* has relatively larger Aristotle's lanterns in Tory Channel compared to Doubtful Sound. The relative size of the Aristotle's lantern has been correlated with food availability and density of conspecifics in a number of sea urchin species (Ebert, 1980b; Black et al., 1982, 1984; Levitan, 1991b; Edwards and Ebert, 1991). It is interesting to note that the lantern indices in both populations were similar in the smaller *E. chloroticus* size classes (40–50 mm TD), but showed increasing differences with increasing age. This mirrors differences in the growth of *E. chloroticus* between the two populations, with growth diverging after 50 mm TD.

In addition to spatial differences, large differences in growth rates of individuals within the Doubtful Sound population were evident. For example, three individuals with an initial size calculated as 72, 73 and 70 mm TD grew 23, 10 and 12 mm in diameter, respectively, over 3.9 years. Individuals over 100 mm TD had growth that ranged from 1.1 to 11.4 mm over the 3.9 years. Individual variability in growth of *E. chloroticus* within a site, and the degree that differences are due either to genetic variability within a population or to other factors, such as small scale habitat variation, is of interest and warrants further study.

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