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Growth, morphometrics and size structure of the Diadematidae sea urchin *Centrostephanus rodgersii* in northern New Zealand

Danilo Pecorino[A,B], *Miles D. Lamare*[A] *and Mike F. Barker*[A]

[A]Department of Marine Science, University of Otago, Dunedin, New Zealand.
[B]Corresponding author. Email: danilo.pecorino@gmail.com

Abstract. The sea urchin *Centrostephanus rodgersii* has increased its range in Eastern Australia resulting in important ecological changes. *C. rodgersii* may also have expanded its distribution range to northern New Zealand in the last five to six decades, although little is known about this process and of the biology of the species in New Zealand. We investigated morphometrics as well as growth using two techniques (growth line count in genital plates and tag–recapture using the fluorescent marker tetracycline). These methods allowed modelling of size at age of *C. rodgersii* in New Zealand, which we compared with populations recently established in Tasmania. The modelled growth rate was only slightly higher in the New Zealand population, and no differences in morphometrics were observed. The New Zealand population structure suggests that annual recruitment occurs regularly, with the population including a range of ages (3 to 10+ years).

Additional keywords: climate change, competition, growth lines, range expansion, tag–recapture.

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Introduction

Centrostephanus rodgersii (Agassiz, 1863) is a large Diadematidae sea urchin that occurs intertidally and subtidally (0 to 30 m depth) along the eastern coast of mainland Australia, Tasmania, Norfolk and Lord Howe Islands, and northern New Zealand (Andrew 1993; Andrew 1994; Andrew and Byrne 2007). It is associated with hard corals in the north of its distribution and kelp communities in the south, where it is capable of forming and maintaining extensive patches of *barrens* habitat (Andrew and Underwood 1989, 1993; Andrew 1991, 1993; Hill *et al.* 2003; Andrew and Byrne 2007; Connell and Irving 2008; Ling *et al.* 2009*a*).

In the last 5–6 decades, *C. rodgersii* has expanded its range from south-eastern mainland Australia to Tasmania, where it was first recorded in 1978 (Johnson *et al.* 2005). In the subsequent years the southern range expansion continued, and by 2005 the species had reached the south-western tip of Tasmania (Ling *et al.* 2008). There is anecdotal evidence that suggests *C. rodgersii* increased in range into New Zealand at about the same time. It was noted to be present in New Zealand at the Poor Knights Islands in 1967 (Barker pers. obs.) and later on nearby off-shore islands immediately south, namely the Mokohinau and Great Barrier Islands (Choat and Schiel 1982).

The southward range expansion of *C. rodgersii* has been attributed to a strengthening of the Eastern Australian Current (EAC) and its increased southerly extension (Ridgway 2007; Ling *et al.* 2009*b*). This has, in turn, increased winter sea surface temperatures above 12°C, a temperature that allows larvae of *C. rodgersii* to develop (Ling *et al.* 2008). For this reason, the establishment of a population around the Tasmanian coastline is closely linked to increases in winter sea surface temperatures above the 12°C winter threshold (Ling *et al.* 2009*b*). The potential for changes in population size and ranges of *C. rodgersii* in New Zealand as a result of changes in the EAC and increases in sea surface temperatures is unknown.

To gain a better understanding of the processes that may affect *C. rodgersii* populations in New Zealand, information on the biology of this species, including growth, morphometrics and population structure is required. In the present paper we examine growth in a New Zealand population and compare estimates of size-at-age of *C. rodgersii* with those in Tasmania. *C. rodgersii* is a moderately fast growing sea urchin, reaching 50 mm test diameter (*TD*) at an age of 4–5 years, and approaching a maximum size of ~114 mm after ~25 to 35 years, after which, growth slows considerably (Ling *et al.* 2009*b*). The species shows a degree of spatial variation in growth between environments, with higher growth rates in macroalgal boundaries compared with *barren* grounds (Ling and Johnson 2009). Rates of growth of the New Zealand population are unknown, although they may differ from the Tasmanian population, given the plasticity of growth rates that are known in sea urchin species based on differences in temperature and food availability (Ebert *et al.* 1999).

Quantifying growth in sea urchins requires changes in size at age to be established and that an appropriate model of growth is utilised. Growth in sea urchins has been examined using several methods including annual growth ring counts (Gage 1992; Brey *et al.* 1995), tag–recapture (Ebert and Russell 1992; Lamare and

Mladenov 2000; Kirby *et al.* 2006; Ling *et al.* 2009*b*), laboratory rearing (Lamare and Mladenov 2000), and cohort analysis (Swan 1958; Ebert 1968; Raymond and Scheibling 1987). Similarly, a range of growth models have been applied to sea urchins including those that assume asymptotic growth such as the Brody–Bertalanffy (von Bertalanffy 1938; Brody 1945) and Richards functions (Richards 1959) to more complex models that allow for continued growth through the life of the animal, such as the Tanaka function (Tanaka 1982). The advantages of the different approaches and details of the methods have already been widely discussed (Dix 1970; Pearse and Pearse 1975; Nelson and Vance 1979; Olson and Newton 1979; Ebert 1988; Gage 1992; Ebert and Russell 1993; Bureau 1996; Robinson and MacIntyre 1997; Ebert *et al.* 1999; Lamare and Mladenov 2000; Russell and Meredith 2000; Duggan and Miller 2001; Rogers-Bennett *et al.* 2003; Kirby *et al.* 2006; Pederson and Johnson 2008; Ellers and Johnson 2009; Ling and Johnson 2009; Ling *et al.* 2009*b*).

We use both tag–recapture and growth line counts to estimate growth in *C. rodgersii* in a population in northern New Zealand, and apply three growth models to our data. At the same time we examine morphometrics and size at age distributions in the same population. These data allow for the first estimates of growth of the species in New Zealand, and increase our understanding of its population biology at this location. Given the significant changes in the Tasmanian coastal ecosystems that have been attributed to the expansion of *C. rodgersii*, the implications of our findings for the species in terms of its establishment in New Zealand and future ecological interactions are discussed.

Materials and methods

Study site and collection

Populations of *C. rodgersii* were examined at two sites located in the Mokohinau Islands, a cluster of small islands situated north-east of the northern part of the North Island, New Zealand (Fig. 1). Site 1 is at North-East Bay of Fanal Island (35°56.146′S, 175°08.922′E), and site 2 is on the eastern side of Burgess Island (35°54.117′S, 175°7.143′E). The habitat at both sites is characterised by large rock boulders (1 to 2 m) and dense macroalgal coverage, dominated by the canopy forming brown seaweed *Ecklonia radiata*. The sea urchin *C. rodgersii* is patchily distributed and occurs sympatrically with the more numerous New Zealand endemic echinoid *Evechinus chloroticus* (Echinometridae). Sea urchins were chemically tagged *in situ* by SCUBA divers on 24 January 2010 and were sampled one year later, on 31 January 2011 for the tag–recapture study (see '*Tetracycline tagging and recapture*' for details). Between January 2010 and November 2010, sea urchins were sampled on 7 occasions to provide age estimates obtained from growth lines (see '*Growth lines*' paragraph for details). Samples were collected from a depth of 5 to 15 m, with between 10 and 20 sea urchins collected on each sampling date. The sea urchins that were collected included both tagged and untagged individuals because tags were not visible externally.

Morphometrics

The *TD* of each individual collected between January 2010 and November 2010 ($n = 84$) was measured (to the nearest 0.1 mm) with digital callipers, then they were drained of water and coelomic fluid, weighed (0.01 g precision) and dissected. Major body components (Aristotle's lantern and test) were weighed and the genital plates and Aristotle's lantern were bleached in 10% NaClO overnight to remove organic matter. Following this, the lantern was disassembled and the average length of each demi-pyramid (referred to hereafter as 'jaws') measured from the oral tip to the epiphysis. Jaw length was plotted against *TD* to check for its size relatively to the diameter. An average lantern index (LI) for the population, defined as the ratio between jaw length and test diameter and expressed as a percentage, was then calculated as the average of the LI of each individual.

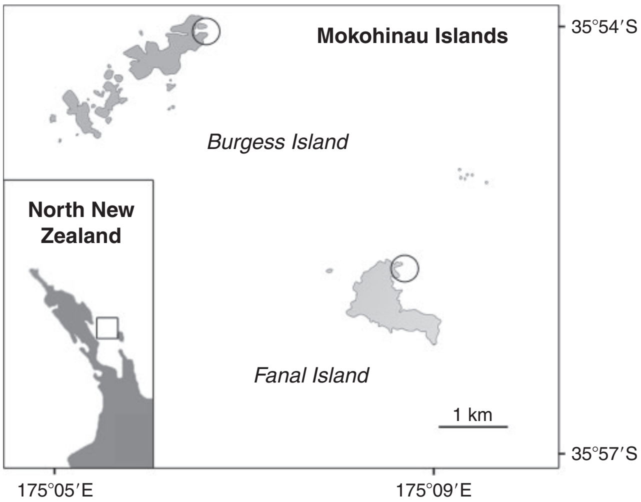

Fig. 1. Location of the Mokohinau Islands in New Zealand. The position of *Centrostephanus rodgersii* sampling and tagging sites at Fanal Island and Burgess Island is indicated by the circles.

Growth estimates

Growth lines

Age lines were counted on the same individuals used for morphometric measurements. Bleached genital plates were dried at 60°C for 1 day and subsequently placed into a muffle furnace at 500°C for 15 min to make growth lines more visible. At that point, each genital plate had the external surface gently sanded with fine sandpaper (P240 grade), rinsed in 96% ethanol and air-dried, before being submerged in xylene. To estimate age, the number of lines was counted under a dissecting microscope, with one translucent and one opaque growth line assumed to represent a 1-year time period.

Marginal increment analysis was used to validate annual growth lines deposition in the genital plates (Schuhbauer *et al.* 2010). For this, one randomly selected genital plate from each aged individual was examined under a dissecting microscope, and whether the outermost growth region was translucent or opaque was noted. Periodicity of opaque and translucent line deposition was determined from the proportion of individuals that exhibited a translucent line at the margin of the genital plates on each sampling time. Periodicity of deposition of growth lines was also validated by using the genital plates of tagged individuals recollected one year after tagging ($n = 24$ individuals that exhibited a fluorescent mark on the genital plates, see '*Tetracycline tagging and recapture*' for the marking and reading method) by counting the number of lines visible after the tag and assuming that no more than two growth lines, one opaque and one translucent, can be deposited each year, assuming line deposition follows an annual pattern.

Tetracycline tagging and recapture

On 24 January 2010, 80 *C. rodgersii* were chemically tagged with an injection of 2–4 mL of a 1% tetracycline solution through the peristomial membrane into the coelomic cavity. SCUBA divers performed the task using a syringe that automatically refills, with the gauge set to deliver 2 mL. One or two injections were administered to each animal according to its estimated size (approximately 2 mL of tetracycline if $TD < 70$ mm, and approximately 4 mL of tetracycline if $TD > 70$ mm). On 31 January 2011, the tagging site was revisited and 91 sea urchins were collected, returned to the mainland and their *TD* measured. Each urchin was dissected and Aristotle's lantern and test weighed. The lanterns were cleaned in 10% NaClO overnight and the jaws separated and inspected for fluorescent tags under a dissecting microscope equipped with an external UV light source. Tetracycline that has been incorporated into the skeleton is fluorescent under UV light. The location of the fluorescent tag in the jaw represents the length of the jaw at the time of tagging J_t. If a tag was found, the total length of the jaw J_{t+1} and increment ΔJ at the aboral end (i.e. the length of the portion of jaw that was deposited at the aboral end during the 1-year time interval before tagging and recapture) were measured and the length of the jaw at the time of tagging J_t was obtained (Fig. 2). No measurable growth was present at the oral end of the jaws. Twenty-four tagged specimens (and jaws) were recovered.

The relationship between jaw length (*J*) and test diameter (*TD*) was assessed using the following equation:

$$TD = 61.821 \times \ln J - 101.61,$$

with jaw length converted to *TD* at the time of tagging (TD_t) and at the time of recapture one year later (TD_{t+1}).

Growth model

Three growth equations were used to model growth of *C. rodgersii*. The equations used for size (TD_t) at age (*t*) were: Brody–Bertalanffy (von Bertalanffy 1938; Brody 1945)

$$TD_t = TD_\infty (1 - be^{-kt}) \qquad (1)$$

Richards (Richards 1959)

$$TD_t = TD_\infty (1 - be^{-kt})^{-n} \qquad (2)$$

and Jolicoeur (Jolicoeur 1985)

$$TD_t = TD_\infty (1 - bt^{-k})^{-1} \qquad (3)$$

where TD_t is size at time *t*, TD_∞ is the asymptotic size, *b* is the scaling parameter to adjust for size $t \neq 0$ at time 0, *K* is the growth constant and *n* is the shape parameter for the Richards model.

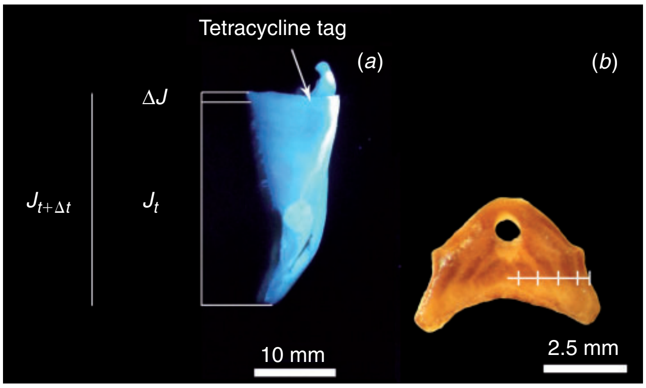

Fig. 2. From left to right (*a*) a demi-pyramid with measurements for growth modelling indicated and (*b*) a genital plate of a 5 year old individual with growth lines visible. Tetracycline tags appear much brighter to the naked eye than we could obtain by photography.

The three growth models were applied to both tetracycline tagged animals and animals aged from growth lines. To apply the models to growth-line aged animals, the size versus age (i.e. the number of growth lines) for each individual was plotted and the parameters of each growth curve estimated by performing a non-linear regression using the Newton method.

To estimate growth rates from the tetracycline tagged animals, the relationship between test diameter at time of tagging (TD_t) and test diameter at time of recapture, one year after marking (TD_{t+1}), was plotted using a Walford plot (Walford 1946) and either a linear or non-linear regression of the difference equation for each model used to estimate parameters for each growth equation (Ebert and Russell 1992; Lamare and Mladenov 2000). The difference equations for each growth model are as follows:
Brody–Bertalanffy

$$TD_{t+1} = c + mTD_t \qquad (4)$$

Richards

$$TD_{t+1} = \left(c + mTD_t^{-\frac{1}{n}}\right)^{-n} \qquad (5)$$

and Jolicoeur

$$TD_{t+1} = \frac{TD_\infty}{1 - b\left[\left(\frac{TD_t - TD_\infty}{bTD_t}\right)^{-\frac{1}{k}} + \Delta t\right]^{-k}} \qquad (6)$$

Details on parameter fitting can be found in Ebert and Russell (1992) and Lamare and Mladenov (2000).

Instantaneous growth rates

After fitting curves to the data, the derivative of each growth equation with respect to time, together with the fitted parameters, were used to plot the instantaneous growth rate

(IGR, mm year^{-1}) and the age of maximum growth and maximum growth rate (MGR, mm year^{-1}) for each curve.

Model comparisons

Growth model fits obtained from growth lines and tag–recapture data were assessed considering residuals standard sum of squares error (SSE), distribution of residuals and second order Akaike Information Criterion (AICc) paired with the Δ_i statistic to compensate for differences in the number of parameters in each model (Akaike 1974; Burnham and Anderson 1998).

Sea surface temperatures

Changes in sea surface temperature (SST) at the Mokohinau Islands over the study period were obtained from the SST probe of the satellite Terra MODIS (http://oceancolor.gsfc.nasa.gov/, data can be accessed through the 'Level 3 browser' by selecting the appropriate time frame). The SST for the Mokohinau Islands at each time were calculated from the average SST for a 9 pixels reticulum (16 km^2 each) centred on the coordinates of the sampling site.

Statistical analyses

All statistical analyses and non-linear modelling were performed using JMP7 (SAS Institute Inc., Cary, NC).

Results

Morphometrics

A significant relationship existed between demi-pyramid length and test diameter ($R^2 = 0.882$, d.f. = 90, $P < 0.001$, Fig. 3*a*) and between test wet weight and test diameter ($R^2 = 0.898$, d.f. = 90, $P < 0.001$, Fig. 3*b*). Using jaw length and test diameter for each individual, we calculated a mean ± s.e. lantern index for *C. rodgersii* of LI% = 26.2 ± 2.2 mm, with the lantern index found to be independent of test diameter (Fig. 3*c*).

Marginal increment analysis

An example of a genital plate with alternating opaque and translucent annular lines can be seen in Fig. 2*b*. A plot of the proportion of genital plates with a translucent margin in each sampling month (Fig. 4*a*) indicated a peak in the occurrence of individuals with a translucent margin in September (91.7%). By November no individuals had translucent marginal bands. The maximum proportion of individuals with translucent margins corresponded with the minimum sea surface temperature (14.8 ± 0.1°C, mean ± s.d.) during the year (Fig. 4*b*).

Growth parameters estimates from growth lines

The estimated parameters of the three growth models obtained from fits to the annular lines are summarised in Table 1. Maximum test diameter estimates were similar among the three models, ranging from 119.1 mm for the Richards model to 126.4 mm for the Jolicoeur function (Table 1a). The rate of change in growth was slightly higher for the Jolicoeur curve ($k = 1.698$) and similar for the Brody–Bertalanffy and the Richards curve ($k = 0.235$ and $k = 0.305$ respectively, Table 1).

In terms of model goodness-of-fit, all three models have a similar residual SSE when fitted to the annual data (Table 1), the lowest being the Jolicoeur curve (SSE = 6162.6). The Δ_i also indicated that the Jolicoeur model had the highest support ($\Delta_i = 0$), followed by the Brody–Bertalanffy function ($\Delta_i = 1$), and Richards function ($\Delta_i = 3$), which were also well supported. Using the Jolicoeur model, instantaneous growth in *C. rodgersii*

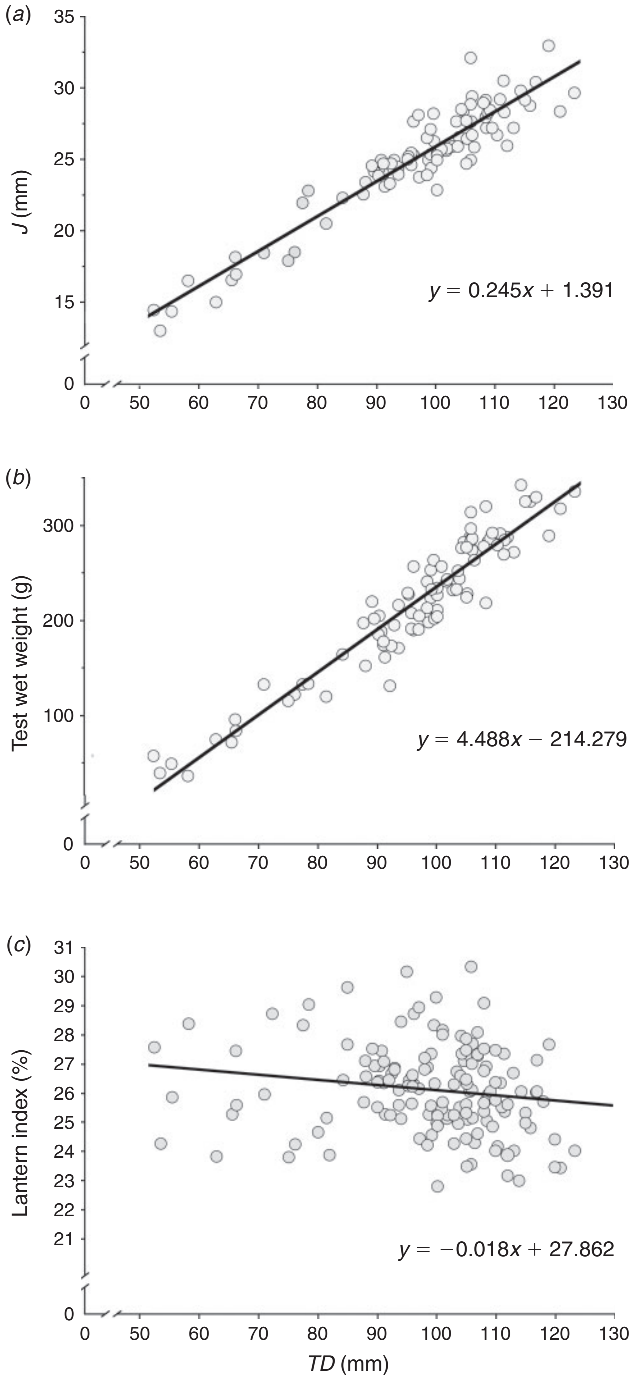

Fig. 3. Relationship between (*a*) jaw length (*J*) and test diameter (*TD*), and (*b*) test wet weight and test diameter and (*c*) Lantern index (%) and test diameter for *Centrostephanus rodgersii* from the Mokohinau Islands, $n = 84$.

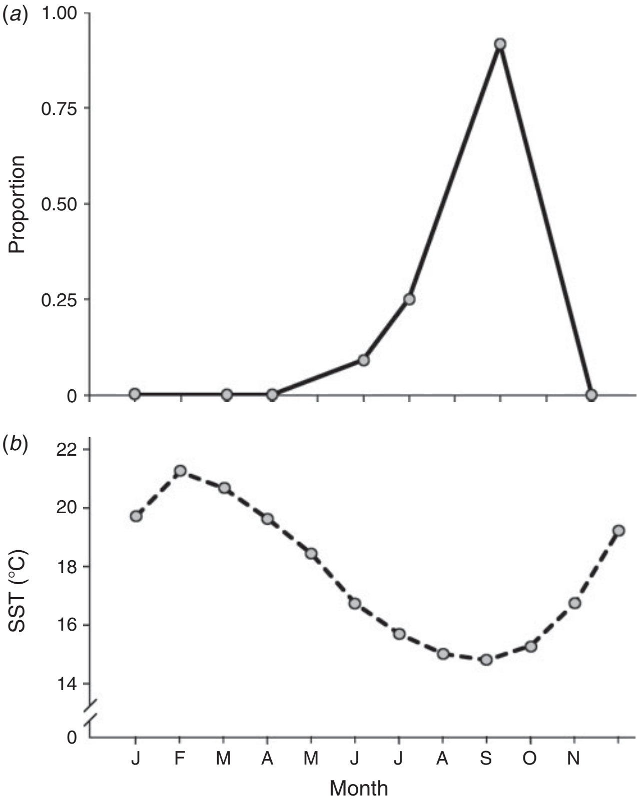

Fig. 4. (*a*) Proportion of translucent margins at the edges of the genital plates and (*b*) mean sea surface temperature at the Mokohinau Islands during 2010.

was found to reach a maximum rate of 23.8 mm year^{-1} at an age of 1.4 years, with growth decreasing to ~10 mm year^{-1} by age 5 (Fig. 5). Animals reach a size of ~85 mm *TD* by age 5 (Fig. 6*a*), and approach an asymptotic size of 126 mm *TD* between 15 and 20 years (Fig. 6*a*).

Growth parameters estimates from tag–recaptures

The estimated parameters of the three growth models obtained from tag–recapture data are summarised in Table 1. Maximum growth rate ranged from 14.3 mm year^{-1} for the Richards function to 20.3 mm year^{-1} for the Brody–Bertalanffy model. Age of maximum growth rate ranged from 2.8 years in the Jolicoeur model to 2.5 years in the Richards model and at settlement (age 0) for the Brody–Bertalanffy model, with the rate of change in growth rate greatest for the Jolicoeur model ($k = 2.322$) and least for the Brody–Bertalanffy model ($k = 0.189$) (Table 1). Maximum test diameter was estimated at $TD_\infty = 108.0$ mm for Brody–Bertalanffy, $TD_\infty = 106.6$ mm for Richards and $TD_\infty = 106.2$ mm for Jolicoeur (Table 1).

In terms of model goodness-of-fit, the residual SSE for curves fitted to the tagged individuals was lowest for the Jolicoeur model (SEE = 10.574) and highest for the Richards model (SEE = 30.387) (Table 1). The AICc gave similar results, with the lowest Δ_i found in the Jolicoeur model ($\Delta_i = 0$) and the highest value in the Richards model ($\Delta_i = 25$). All the models, aside from Jolicoeur, receive essentially no support from the data when comparing AIC (i.e. $\Delta_i > 10$; Burnham and Anderson 1998). Using the Jolicoeur model of growth of the tagged sea urchins, instantaneous growth in *C. rodgersii* was found to reach a maximum rate of 17.7 mm year^{-1} at an age of 2.8 years (Table 1, Fig. 5), with growth decreasing to ~13 mm year^{-1} by age 5 (Fig. 5). Animals reach a size of ~63 mm *TD* by age 5, and approach an asymptotic size of 106 mm *TD* between 10 and 15 years (Fig. 6*b*).

For the Jolicoeur model, the residuals move from negative to positive with increasing size, indicating that growth continues even after the asymptotic size has been reached. This was also apparent for the Brody–Bertalanffy and Richards models, suggesting that growth is continuous in the largest animals.

Discussion

During the past 50 years, the sea urchin *C. rodgersii* has greatly expanded its southern distributional range along the south-eastern Australian and Tasmanian coastlines. This has been attributed to an increase in the southward and eastward flow of the East Australian Current and a corresponding increase in sea surface temperatures along the SE Australian and Tasmanian coasts (Ridgway 2007; Ling *et al.* 2009*b*) that has enhanced *C. rodgersii* larval survival and recruitment (Ling *et al.* 2008). Anecdotal evidence suggests that the changes in the East Australian Current may also have allowed for the establishment of this species in northern New Zealand. Determining if its occurrence in New Zealand is recent is difficult because very little is known on the biology of the species in New Zealand, including aspects of its population biology such as growth, morphometrics and recruitment. So as to gather information on the population biology of the species in a new environment, growth in a New Zealand population of *Centrostephanus rodgersii* from the Mokohinau Islands was studied.

Growth was estimated using two methods, the first by estimating the age of individuals by counting annular lines in the genital plate and assuming that they are related to differences in the deposition of the stereom over an annual cycle (Pearse and Pearse 1975). Aging by this method has been applied to several echinoderm species (Pearse and Pearse 1975; Gage and Tyler 1985; Nichols *et al.* 1985; Brey *et al.* 1985; Gebauer and Moreno 1995; Robinson and MacIntyre 1997; Schuhbauer *et al.* 2010). The validity of such a method, however, requires knowing at what periodicity the growth lines are added because it has been shown that patterns of calcium deposition rates are not always correlated with seasonality, but merely to periods of different abundance of food regardless of season (Ebert 1988). Indeed, in the case of sea urchins, growth lines have been shown to be unreliable for some species (Ebert 1988; Russell and Meredith 2000) and therefore validation is essential.

We validated our aging data by marginal increment analysis (Schuhbauer *et al.* 2010) to quantify the proportion of individuals in each sample of genital plates with opaque lines at their margin. Most of the marginal transluscent bands occurred in September samples (91.3%), which decreased to 0% in November. This indicates that the deposition of the translucent band is rapid, probably lasting only 1–2 months, and is followed by the slow deposition of the opaque band that occurs over the remainder of the year. This is consistent with a pattern of one

Table 1. Estimates of *Centrostephanus rodgersii* growth parameters for the Brody–Bertalanffy, Richards and Jolicoeur curve by both growth lines and tag–recapture methods

Brody–Bertalanffy		Richards		Jolicoeur	
Growth lines					
TD_{∞} (mm)	122.9	TD_{∞} (mm)	119.1	TD_{∞} (mm)	126.4
TD_0 (mm)	−1.4	TD_0 (mm)	0	TD_0 (mm)	0
k	0.235	k	0.305	k	1.698
b	1.011	b	1.012	b	−7.431
		n	−1.415		
Age of MGR	0	Age of MGR	1.1	Age of MGR	1.4
MGR (mm year^{-1})	29.1	MGR (mm year^{-1})	21.8	MGR (mm year^{-1})	23.8
SSE	6212.062	SSE	6210.701	SSE	6162.653
AICc	368	AICc	370	AICc	367
Δ_i	1	Δ_i	3	Δ_i	0
Tag–recapture					
m	0.827	m	0.757		
c	18.69	c	2.029		
TD_{∞} (mm)	108.0	TD_{∞} (mm)	106.6	TD_{∞} (mm)	106.2
TD_0 (mm)	0.5	TD_0 (mm)	0.5	TD_0 (mm)	0
k	0.189	k	0.278	k	2.322
b	0.996	b	0.921	b	−28.134
		n	−2.199		
Age of MGR	0	Age of MGR	2.5	Age of MGR	2.8
MGR (mm year^{-1})	20.3	MGR (mm year^{-1})	14.3	MGR (mm year^{-1})	17.7
SSE	22.122	SSE	30.387	SSE	10.574
AICc	3	AICc	13	AICc	−12
Δ_i	15	Δ_i	25	Δ_i	0

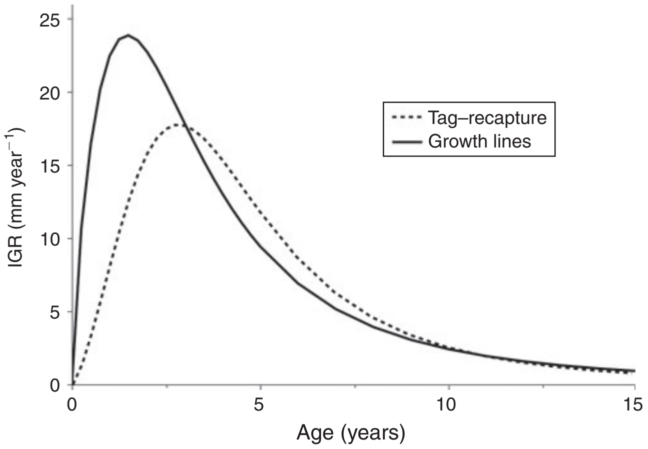

Fig. 5. Estimated change in instantaneous growth rate (IGR) with age for *Centrostephanus rodgersii* for growth line counts and tag–recapture methods.

translucent and one opaque line deposited annually in *C. rodgersii*, and with growth occurring during or after minimum temperatures, which has also been demonstrated for the sea urchin *Loxechinus albus* (Schuhbauer *et al.* 2010).

We also validated the annual nature of growth lines by examining the number of opaque and translucent lines in genital plates deposited in the year following tetracycline tagging. In all urchins examined, we observed that no more than one pair of lines (an opaque and a translucent one) was deposited beyond the fluorescent tag, although in two very large individuals (113.1 and 111.1 mm) there were no lines apparent. This clear deposition pattern was most evident in the skeletal elements of smaller specimens in which growth is faster compared with larger individuals. It also implies that age estimates conducted using this method are more reliable for young individuals in which lines are clear and well spaced, than for older individuals, in which the lines corresponding to the latest deposition of calcium carbonate tend to overlap. In this case, the age of older animals will be underestimated.

The second method of estimating growth was through tag–recapture of tetracycline marked individuals, which, together with the use of other fluorescent tags, has become widely used to measure growth in sea urchins (Ebert 1988; Gage 1992; Ebert and Russell 1993; Bureau 1996; Ebert *et al.* 1999; Lamare and Mladenov 2000; Rogers-Bennett *et al.* 2003; Kirby *et al.* 2006; Pederson and Johnson 2008; Ellers and Johnson 2009; Ling and Johnson 2009; Ling *et al.* 2009*b*). The advantage of tagging individuals is that growth is measured directly without making assumptions on the growth pattern of the population as a whole (as done using modal progressions for example).

For both methods of estimating growth, selecting the appropriate growth model to describe size at age is equally important. Our conclusion, on the basis of the analysis of the residuals of the models and the values of Δ_i, is that the Jolicoeur function fitted using growth line data may provide the best current model of growth for *C. rodgersii* in New Zealand. The Jolicoeur model assumes an asymptotic size, which may underestimate growth in older individuals, but has been applied to

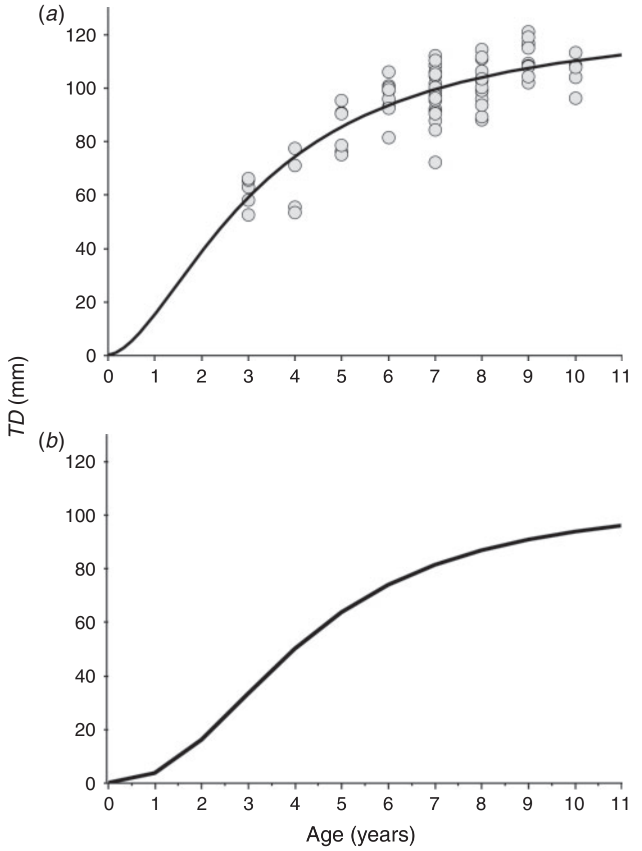

Fig. 6. Growth curves of *Centrostephanus rodgersii* using data from (*a*) growth lines counts ($n = 84$) and (*b*) tag–recapture jaw growth estimates ($n = 24$).

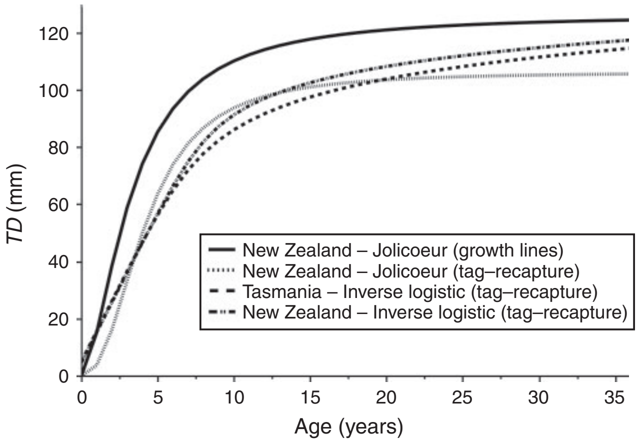

Fig. 7. Comparison of size-at-age plotted using the parameters obtained from the tag–recapture and growth lines in New Zealand *Centrostephanus rodgersii*, and from a tag–recapture study of *Centrostephanus rodgersii* in Tasmania (Ling *et al.* 2009*b*).

several temperate sea urchin species (Ebert and Russell 1993; Lamare and Mladenov 2000; Lau *et al.* 2011). Using this model, growth of *C. rodgersii* in northern New Zealand shows an initial lag phase over the first year of growth, with a maximum instantaneous growth of 23.8 mm year^{-1} at 1.4 years, when the animals have reached a size of 26.7 mm. Growth rate decreases beyond this size with an asymptotic size approached at ~10–15 years. The initial lag in growth likely reflects dietary constraints to growth on smaller cryptic individuals when they may not have access to macroalgae in their first year. Initial lags in growth followed by accelerated growth have been described for juvenile sea urchins and have been attribute to dietary shifts and movement from cryptic to open habitats (Raymond and Scheibling 1987; Rowley 1990; Lamare and Mladenov 2000). The subsequent decrease in growth after ~3 years is likely related to the onset of gametogenesis, which causes nutrients to be shifted from somatic to gonadic growth. Indeed, gonad production is only evident in New Zealand *C. rodgersii* individuals at a size of 40–50 mm *TD* (3–4 year old) (Pecorino *et al.* in press), which coincides with the size and age of decreasing somatic growth rates.

Modelled growth of *C. rodgersii* in this New Zealand population was faster than that estimated for Tasmanian populations. Comparing growth of *C. rodgersii* in this New Zealand population with the Tasmania population (Fig. 7) suggests that, for individuals older than 1 year, the species has a higher growth rate in New Zealand. Even when the same inverse logistic model used by Ling *et al.* (2009*b*) is applied to both New Zealand and Tasmanian populations, a higher growth rate in New Zealand was observed (Table 2). Estimated growth to 1 year was equivalent in both populations (Table 2). The divergence in growth rates after 1 year would be at an age when fast growth and a shift in diet to macroalgae probably occur, so it is possible that the faster growth in New Zealand is related to higher food availability in this environment. A larger jaw size (i.e. lantern index) is often used as a proxy for poorer nutritional status in sea urchins (Ebert 1980; Black *et al.* 1982, 1984; Levitan 1991; Hagen 2008; Lau *et al.* 2009) and we might, therefore, expect to see differences between the two populations if food is limiting growth. A comparison of lantern indices between the New Zealand populations with those recorded by Ling *et al.* (2009*b*) for the macroalgal habitat in Tasmania shows only a small difference, with the latter populations having smaller jaws, relative to test diameter (i.e. jaw height of ~22 mm in New Zealand and ~20 mm in Tasmania at a test diameter of 80 mm). There was no difference between the populations in other morphometric measurements such as the wet weight of the test, therefore nutritional differences between the two populations are only partially supported.

Growth rate may be related to differences in ambient water temperatures. Indeed, the faster growth rate of New Zealand populations coincides with a 3°C warmer winter sea surface temperature (15°C versus 12°C) and a ~4°C warmer summer temperature (21°C versus 16–18°C), which would be consistent with a positive effect of temperature on growth rate. Ebert *et al.* (1999) suggest that temperature does not influence growth rates within a species across a range of latitudes, whereas there are several laboratory studies that have shown a direct relationship between growth rate and optimal temperatures when other variables such as food are kept constant (Spirlet *et al.* 2000; Pearce *et al.* 2005; Watts *et al.* 2011). Similarly, a field study by Duineveld and Jenness (1984) on the echinoid *Echinocardium*

Table 2. Average estimates of size at age for *Centrostephanus rodgersii* in New Zealand and Tasmania using similar techniques
* = present study; § = Ling *et al.* 2009*b*; † = method by Ling *et al.* 2009*b* applied to the data of this study

Method	Average test diameter (mm)					
Age (years)	1	2	3	4	5	6
Growth lines (New Zealand)	15.00	38.45	58.82	74.15	85.28	93.38
Jolicoeur *						
Tag–recapture (New Zealand)						
Jolicoeur *	3.65	16.03	33.25	49.98	63.60	73.83
Inverse logistic †	15.15	25.67	36.15	46.54	56.71	66.35
Tag–recapture (Tasmania)						
Inverse logistic §	15.58	26.16	36.60	46.72	56.26	64.79

cordatum suggested higher growth rates for individuals at higher temperatures. Given that *C. rodgersii* is a warmer water species, and the Tasmanian populations are at the colder end of the species range, it is possible that these newly established populations are living in suboptimal temperatures in terms of growth.

Unlike Tasmanian populations that have colonised regions lacking large heterospecific sea urchin populations, *C. rodgersii* in New Zealand lives sympatrically with the dominant native echinoid *E. chloroticus*, whose strong grazing activity has been shown through removal experiments (Villouta *et al.* 2001). The degree to which the two species interact in terms of competition is unknown, although, given the abundance of *E. chloroticus* (densities of up to 40 individuals per m^2 in northern New Zealand; Choat and Schiel 1982) and the ability of this species to form barrens, it could potentially limit *C. rodgersii* in New Zealand. Indeed, the slightly larger lantern indices observed in the New Zealand populations of *C. rodgersii* may reflect some food limitation exerted by a strong competitor. A similar case of interspecific competition has already been reported for *Paracentrotus lividus* and *Arbacia lixula* in the Mediterranean (Privitera *et al.* 2008), with such competition resulting in food limitation and a shift in the trophic niche of *P. lividus* (from generalist to grazer of non-encrusting macrophytes) when *A. lixula* is present at high population densities.

An important component of the interaction between *E. chloroticus* and *C. rodgersii* in New Zealand will be differences in the growth between the two species, which could, in turn, affect their survival rates through size-specific predation and their ability to dominate resources. Growth of *E. chloroticus* has been well described (McShane and Anderson 1997; Lamare and Mladenov 2000) and when compared with *C. rodgersii*, exhibits a lower maximum growth rate (15.1–16.8 mm $year^{-1}$ for *E. chloroticus* and 23.8 mm $year^{-1}$ for *C. rodgersii*) attained at an older age (4.0–4.8 years and 1.4 years respectively). This difference in size and growth rate may influence the susceptibility of the two species to predation by, for instance, the rock lobster *Jasus edwardsii*. Andrew and MacDiarmid (1991) showed that this species can predate all sizes of *E. chloroticus*, but that preference is given to smaller sea urchins (<50 mm). The same species of rock lobster also predates *C. rodgersii*, although they tend to target larger individuals. Ling *et al.* (2009*b*) found that only very large rock lobsters (carapace length >140 mm) are able to predate *C. rodgersii* in the field, and smaller sea urchins (<60 mm *TD*) are not targeted due to their cryptic nature.

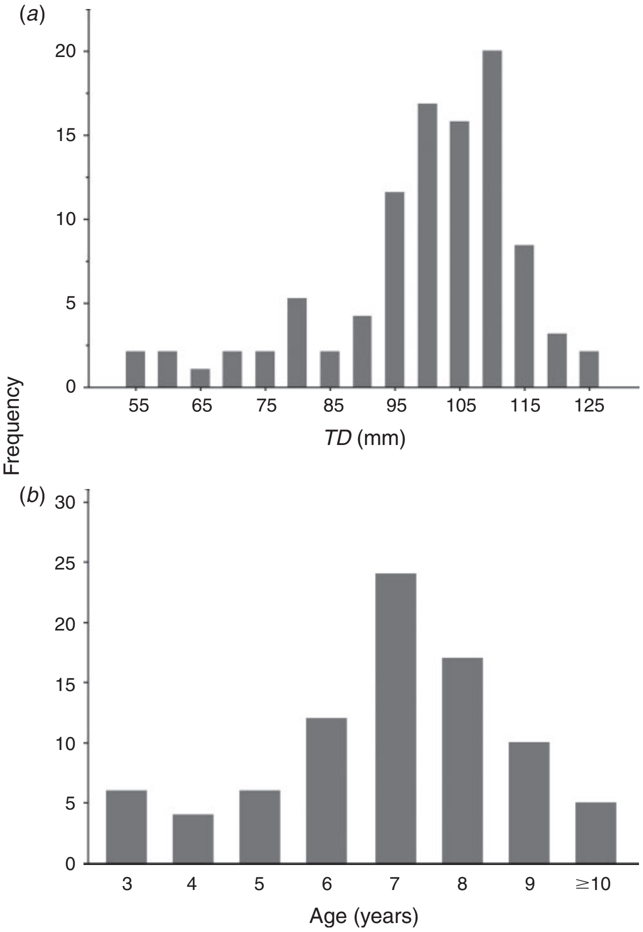

Fig. 8. (*a*) Size-frequency and (*b*) age-frequency distributions for *Centrostephanus rodgersii* collected from the Mokohinau Islands between January 2010 and December 2011 (*n* = 155).

Crucial to the understanding of future population dynamics of *C. rodgersii* is information on recruitment processes in New Zealand populations. Our data on size distributions (Fig. 8*a*, *b*) show a poly-modal distribution of sizes of *C. rodgersii* at the Mokohinau Islands characteristic of a population with ongoing recruitment and supply of settling larvae. Ling *et al.* (2008) showed that the larvae of *C. rodgersii* have a thermal threshold of 12°C, below which advanced two-arm plutei will not develop. The continuous recruitment events at the Mokohinau Islands, therefore, suggest that larval development is not prevented or hindered at sea temperatures presently experienced in the area, which are 15°C, and above the thermal threshold for their larvae. Whether the long-lived larvae (4 months; Huggett *et al.* 2005) are originating from local populations or are being transported from Australia is unknown. It is clear that the populations in New Zealand are undergoing a characteristic annual reproductive cycle and are producing viable gametes (Pecorino *et al.* in press) meaning that local recruitment is possible. Equally, genetic evidence indicates that the Australian and New Zealand populations are not genetically separate (Banks *et al.* 2007) so ongoing trans-Tasman transport of larvae can also not be discounted.

C. rodgersii may be a new arrival to New Zealand, and its ability to compete with and displace the existing species is of interest. Quantifying growth rates of this species in New Zealand is an important element of understanding how it will interact with close competitors such as *E. chloroticus*, and its wider affect on its habitat. Further research is needed to understand the population biology of the species in New Zealand, especially in relation to reproduction and recruitment under New Zealand oceanic conditions.

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