

# Spatial and temporal variation in growth of the green sea urchin, *Strongylocentrotus droebachiensis*, in the Gulf of Maine, USA

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**ABSTRACT:** The green sea urchin, *Strongylocentrotus droebachiensis*, is found primarily in subtidal habitats but also occurs in low intertidal pools in the Gulf of Maine. Previous studies of low intertidal populations on Swans Island, Maine, USA, found that this species is slow growing and long lived. However, these population parameter estimates may not be representative because low intertidal pools are at one extreme of the bathymetric range. To test whether these growth and age estimates are characteristic of the species across its bathymetric range and between habitats I compared growth from intertidal and subtidal habitats. Tanaka function growth parameter estimates indicate that temporal and spatial variation in growth exceeds variation associated with the intertidal versus subtidal habitat gradient. For green sea urchins in the Gulf of Maine, low intertidal pools are not different from shallow subtidal areas with respect to growth and age estimates. These results confirm that *S. droebachiensis* is a long-lived (> 30 years) and slow growing echinoderm.

## 1 INTRODUCTION

Quantifying growth and accurately estimating age are quintessential to understanding the life history and population dynamics of any organism. Rigorously evaluating these population parameters has economic significance as well when the organism in question is the target of an intensive fishery. The recent boom and bust trend of the green sea urchin fishery in the Gulf of Maine (Harris et al. in rev.) highlights the need for more information on basic population parameters of *Strongylocentrotus droebachiensis*. Furthermore, recent studies of the green sea urchin in the northwestern Atlantic report radically different estimates of growth rates and longevity for this ecologically and economically important species.

Using mark and recapture methods of fluorescently tagged individuals, Russell et al. (1998, p.148) reported that these sea urchins are long lived, slow growing, and that "it may be more appropriate to measure age in decades rather than years" for the largest individuals in their samples. In contrast, Meidel & Scheibling (1998) and Robinson & MacIntyre (1997) counted natural growth lines in the skeletal elements to estimate age and reported faster growth rates and lower estimates of maximum age (9 years and 23 years respectively). Besides the methods used to measure growth these studies also differed in the habitat source of the sea urchins sampled. Russell et al. (1998) studied sea urchins

occurring in low intertidal pools whereas the other two studies focused on shallow subtidal populations. The estimates of all three studies can be questioned, but for different reasons. It is necessary to validate growth lines and demonstrate that a complete cycle of opaque and translucent lines (Pearse & Pearse 1975) are added each year for all sizes of sea urchins before these data can be used to measure growth reliably. Ebert (1988) showed that complete cycles are not added annually in the congener, *S. purpuratus*, and more recently Russell & Meredith (in press) demonstrated that skeletal growth lines underestimate age in green sea urchins because larger individuals do not add a complete cycle. A legitimate criticism of the Russell et al. (1998) study is the degree to which their growth data are representative of the species. Tidepool habitats are at one end of the bathymetric range of green sea urchins and it is possible that the slow growth they reported is specific to these habitats. To test whether tidepool population estimates are characteristic of the species I compared growth from intertidal and subtidal habitats using the methods of mark and recapture of fluorescently tagged individuals. Tanaka function growth parameter estimates indicate that there is both temporal and spatial variation in growth but this variation is not associated with differences in intertidal and subtidal habitats. For green sea urchins in the Gulf of Maine, low intertidal pools are not different from shallow subtidal areas with respect to growth and age estimates.

## 2 MATERIALS AND METHODS

Experiments were set up at two intertidal and two subtidal sites on Swans Island, Maine, USA (see Petraitis 1987, p.119, for a map of the island). I used four of the seven tidepools Russell et al. (1998) sampled (pools 1, 3, 4, and 5 from their study). Pool 1 is at Hockamock Head (44°8'2"N 68°26'53"W) and pools 3, 4, and 5 are within 2 m of each other at Hero Beach (44°8'1"N 68°24'30"W) on the other side of the island. I chose these pools because they yielded the highest percentage of recovered individuals tagged in the Russell et al. (1998) study. The two subtidal sites (depth ~ 7 m) were 10 m from each other, along a kelp dominated rock ledge that borders a sandy bottom (44°7'34"N 68°25'32"W). I chose this subtidal area because sea urchin divers had "fished it out" the previous season; the area produced sea urchins with exceptionally high quality roe (L. Ranquist, sea urchin buyer, pers. comm.). These observations indicated that sea urchin growth would be faster and be resource (or habitat) limited in this subtidal area.

The fluorescent tagging method employed in this study has been used successfully in other sea urchin growth studies (e.g., Lamare & Mladenov 2000, Ebert & Russell 1993, Ebert & Russell 1992, Russell 1987, Pearse & Pearse 1975, Kobayashi & Taki 1969). Briefly, sea urchins were tagged internally with either tetracycline or calcein, which marked the skeletal structures and indicated the size at the time of tagging. Larger sea urchins ( $\geq 20$  mm test diameter) were injected through the peristomal membrane with tetracycline (between 0.1 ml and 1 ml of a solution of 1g tetracycline in 100 ml of sea water) and smaller sea urchins were held for 24 hours in a bath of calcein (0.625 g calcein and 0.5 g sodium bicarbonate dissolved in 100 ml of tap water used for ~ 30 liters of seawater). The sea urchins were released in the field and then one year later all the individuals in the area of release were collected and processed. The test diameters were recorded and the soft tissue was removed with 5% sodium hypochlorite. The demipyramid of Aristotle's lantern (jaw) was examined with UV light for the fluorescent mark and both the original and final size of the element was determined (yielding size specific growth). Finally, an allometric regression of test and jaw size was used to transform the jaw growth parameters to test growth.

I thoroughly searched and removed any resident sea urchins before releasing tagged individuals at all four sites. Between June 3 – 6, 1996, sea urchins were collected from Duck Cove (44°7'50"N 68°25'43"W), tagged, and transplanted to pool 1 and subtidal site 1. Duck Cove is an area ignored by sea urchin divers because of poor quality roe (it lacks large brown kelps). On September 27, 1996, I accompanied sea urchin divers to Great Duck Island (44°9'30"N 68°15'0"W) to observe harvesting tech-

niques. I collected the "cull" – smaller sea urchins ( $< 50$  mm) usually returned after harvesting – to tag and transplant to the two other sites: Hero Beach on September 28, 1996, and subtidal site 2 on September 30, 1996. One year after tagging (June and September, 1997) all the sea urchins at the four sites were collected, processed, and examined for the fluorescent tag.

Figure 1 summarizes the design of this study. Sea urchins were tagged and released at two times to encompass two summer seasons, the time of maximal somatic growth. At each tagging sea urchins were released at both subtidal and intertidal sites. The subtidal samples were released on the same rock reef (10 m apart) but were separated in time (subtidal site 1 for growth during summer 1996 and subtidal site 2 for summer 1997, Fig. 1). For the intertidal sites Russell et al. (1998) reported growth data between 1994 and 1995 so the results presented here for 1996 – 1997 provide the first estimate of site-specific inter-annual growth variation for this species.

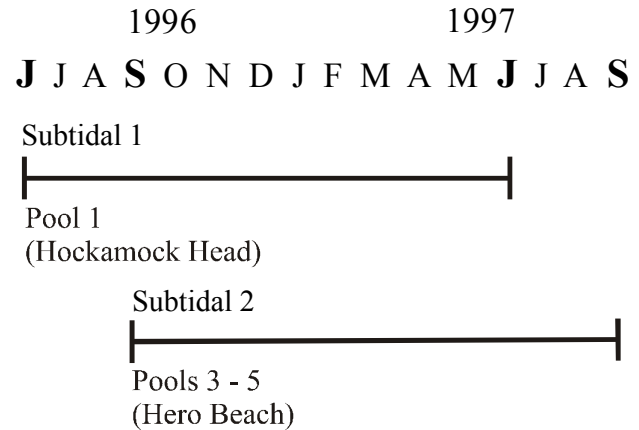


Figure 1. Sampling design. The letters represent months in 1996 and 1997. Sea urchins were marked and recaptured in June and September.

The Tanaka function was used to fit the jaw growth data (Tanaka 1982, Tanaka 1988).

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

The Tanaka function can be expressed as a difference equation (Ebert 1998, Ebert & Russell 1993) where size of the jaw at one year ( $J_{t+1}$ ) is a function of original jaw size ( $J_t$ ):

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

$$\text{where } G = \frac{E}{4} - f \frac{a}{E} + f \quad (3)$$

$$\text{and } E = e^{\sqrt{f}(J_t - d)} \quad (4)$$

A nonlinear regression (SAS) analysis of the difference equation was used to estimate the growth pa-

rameters,  $a$ ,  $d$ , and  $f$ . Parameter  $c$  of the Tanaka function was calculated from equation 5.

$$c = \frac{a}{E} \quad (5)$$

To convert the jaw growth parameters into test diameter growth, the relationship between test diameter,  $D$ , and jaw length,  $J$ , was established using the allometric relationship:

$$D = \alpha J^\beta \quad (6)$$

The parameters  $\alpha$  and  $\beta$  were calculated from Model II linear regressions of  $\ln$  transformed measurements of both tagged and untagged sea urchins (Ebert & Russell 1994).

To generate test diameter – age relationships from the size specific growth curves one simply assigns an age for any particular test size (e.g., Russell et al. 1998). At metamorphosis green sea urchin test size is  $\leq 0.5$  mm (Harris et al. 1993) so 0.5 mm is assigned age-zero.

### 3 RESULTS

Table 1 lists sample sizes of sea urchins tagged in 1996 and recovered in 1997.

Table 1. Numbers of sea urchins tagged and transplanted (Planted) to sites in 1996, recovered one year later (Collected), showing the fluorescent mark (Marked), and percentage (%) of recovered individuals marked.

| Site                           | Planted | Collected | Marked | %  |
|--------------------------------|---------|-----------|--------|----|
| Subtidal 1                     | 400     | 173       | 125    | 72 |
| Pool 1<br>(Hockamock Head)     | 174     | 87        | 44     | 51 |
| Subtidal 2                     | 292     | 175       | 100    | 57 |
| Pools 3, 4 & 5<br>(Hero Beach) | 169     | 54        | 30     | 56 |
| Totals                         | 1035    | 489       | 299    | 61 |

Figure 2 plots the residuals from a common set of Tanaka function parameters fit to all the growth data combined and indicates that the four samples are not evenly distributed around zero and that there is more variation for small than for large sizes. The sum of the residuals for Hockamock Head, subtidal site 1, and Hero Beach are all positive (0.24, 3.54, and 0.61 respectively); whereas the sum of the residuals for subtidal site 2 is negative (-6.30). An ANOVA of the residuals from this regression confirms that a common set of Tanaka function parameters is not the best fit for these data and that subtidal site 2 is significantly different from the other three sites ( $P < .02$ ,  $SSE = 0.1761$ ,  $F_{3,295} = 3.71$ ). Therefore, two sets of growth parameters were calculated, one set for sub-

tidal site 2, and one set for the other three sites combined (Table 2). An ANOVA of the residuals of the growth parameters for both intertidal sites and subtidal site 1 combined indicates a common set of growth parameters describes these three samples ( $P > .09$ ,  $SSE = 0.1117$ ,  $F_{2,196} = 2.38$ ). Therefore, the subsequent analyses of the growth data are for two groups: subtidal site 1 plus both intertidal sites; and subtidal site 2. Figure 3 displays Walford plots (Walford 1946) of jaw growth for these two groups. The Tanaka function growth curves in each plot were generated with the parameters in Table 2.

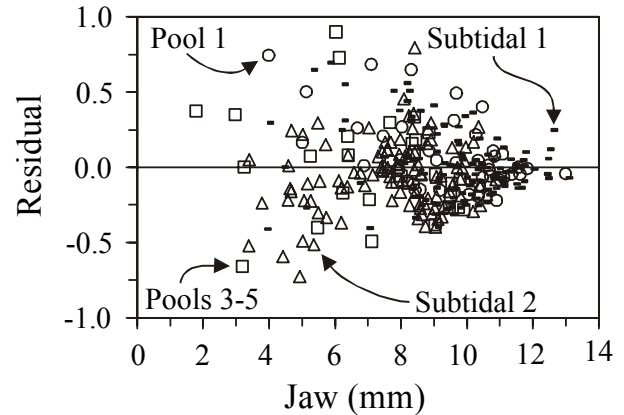


Figure 2. Residuals from a common set of Tanaka function parameters (equation 2) for all four samples.

Table 2. Results of nonlinear regression analysis fitting the Tanaka function parameters to the jaw growth data (equation 2).

| Subtidal site 1 plus all intertidal pools, N = 199 |          |       |                                   |
|--|----------|-------|-----------------------------------|
| Source   | SS       | df    | MS                                |
| Regression   | 196.912  | 3     | 65.637                            |
| Residual   | 0.115    | 196   | 0.001                             |
| Total  | 197.027  | 199   |                                   |
| Corrected  | 4.635    | 198   |                                   |
| Parameter  | Estimate | se    | 95% confidence interval ( $\pm$ ) |
| a  | 12.741   | 1.058 | 2.086                             |
| d  | -0.336   | 0.039 | 0.076                             |
| f  | 20.982   | 1.751 | 3.454                             |
| Subtidal site 2, N = 100,                          |          |       |                                   |
| Source   | SS       | df    | MS                                |
| Regression   | 75.330   | 3     | 25.110                            |
| Residual   | 0.053    | 97    | 0.001                             |
| Total  | 75.383   | 100   |                                   |
| Corrected  | 1.749    | 99    |                                   |
| Parameter  | Estimate | se    | 95% confidence interval ( $\pm$ ) |
| a  | 22.408   | 3.784 | 7.510                             |
| d  | -0.460   | 0.092 | 0.183                             |
| f  | 17.202   | 3.082 | 6.117                             |

The allometric relationships between test diameter and jaw size were established for the two groups to convert jaw growth parameters to test growth.

Intertidal pools and subtidal 1 ( $r^2 = 0.95$ ):

$$D = 3.34J^{1.20} \quad (7)$$

Subtidal 2 ( $r^2 = 0.97$ ):

$$D = 3.21J^{1.23} \quad (8)$$

Figure 4 shows the size – age relationships for the two groups as well as the growth curves for tide-pools 1 – 7 from 1994 - 1995.

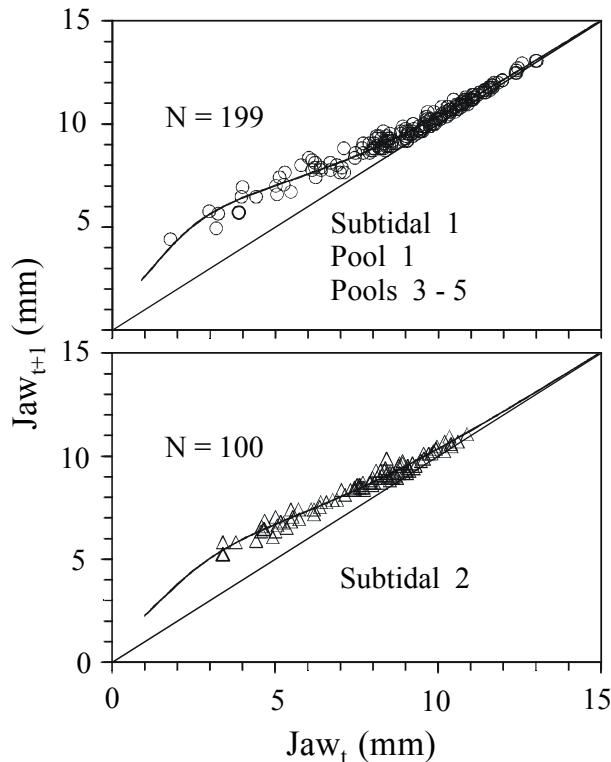


Figure 3. Walford plots of jaw growth data and Tanaka function curves. The diagonal line represents no growth (slope = 1).

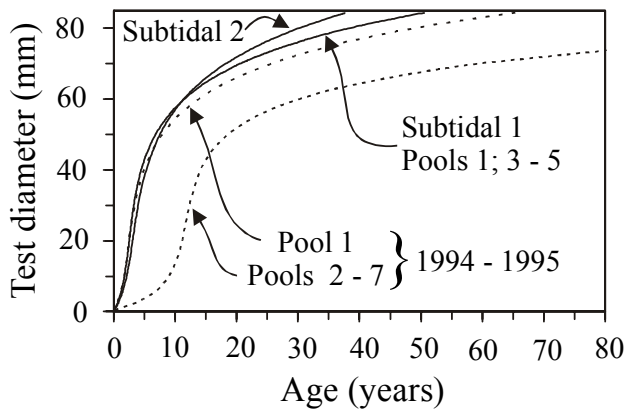


Figure 4. Test diameter – age relationships for this study (solid lines). The dashed lines are the growth curves reported in Russell et al. (1998).

#### 4 DISCUSSION

The spatial and temporal variation in growth rates of green sea urchins observed in this study is not correlated with differences associated with intertidal pool versus subtidal habitats. Growth in both intertidal samples (Hero Beach and Hockamock Head) grouped with subtidal sample 1 (Figs. 3-4). The

source of the sea urchins and timing of the transplant were the same for Hockamock Head (pool 1) and subtidal sample 1 and a common set of Tanaka function parameters describe growth in these samples (Table 2). Although subtidal sample 2 was immediately adjacent to subtidal sample 1, different sets of Tanaka function parameters were required to describe growth in these samples. The variability between subtidal samples could be due to the source of the sea urchins (Duck Cove and Little Duck Island), temporal differences (summer growth in 1996 for subtidal sample 1, and summer growth in 1997 for subtidal sample 2) or some combination of the temporal and spatial differences. Although the source of the sea urchins was different for the two subtidal samples, the sea urchins planted in the intertidal pools at Hero Beach – which shared the same source of sea urchins as subtidal sample 2 – grouped with subtidal sample 1 and the pool at Hockamock Head. This suggests that at least part of the variation in growth between the subtidal samples can be ascribed to temporal variation.

Comparing the results of this study to those obtained by Russell et al. (1998) emphasizes both the spatial and temporal components of growth variation. Russell et al. (1998) reported two sets of Tanaka function parameters: one set for pool 1 and another set grouping pool 2 (another site at Hockamock Head) with the pools at Hero Beach (Fig. 4). Despite being on the same side of the island, the sea urchins in pools 1 and 2 displayed different growth characteristics in 1994 – 1995. During the 1994 – 1995 period the sea urchins in pool 1 grew faster than the sea urchins from the other pools (Hero Beach and pool 2). In contrast, the 1996 – 1997 data reported here groups the Hero Beach pools with pool 1 at Hockamock Head. Therefore, growth characteristics for sea urchins varied between habitats during one year but were similar for these habitats during another year.

Given the observed temporal and spatial variation in growth observed in green sea urchins, how can growth rate best be summarized? One way is to combine the data from this study and Russell et al. (1998) to generate an overall test diameter – age relationship (Fig. 5). The Tanaka function parameters that produced this overall curve ( $a=15.793$ ,  $d=-0.417$ ,  $f=19.407$ ,  $c=2.299$ ) are remarkably similar to the parameters originally reported by Russell et al. (1998) for pool 1 ( $a=15.105$ ,  $d=-0.401$ ,  $f=19.220$ ,  $c=2.395$ ). This analysis confirms that green sea urchins are long lived and slow growing. The estimated age of a 50 mm (test diameter) sea urchin is 7.6 years and the largest tagged individual in the sample (69.85 mm – subtidal site 1) would be 30.4 years (Fig. 4).

One question that still remains is what are the growth characteristics of recently settled juveniles? The inset of the growth curve in Figure 5 suggests an

early lag phase (also see Figs. 3-4). However, of the 561 tagged sea urchins that were recovered and used to produce the growth curve in Figure 5, only four (0.7%) were less than 20 mm. Although suggestive, the extent (even existence) of this lag phase should be treated as a working hypothesis that requires testing.

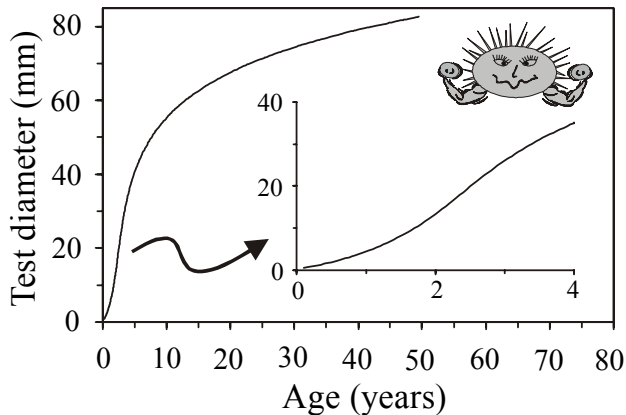


Figure 5. Summary growth curve combining the data from Russell et al. (1998) and this study. This curve is based on 561 tagged sea urchins. Inset is a magnification of early juvenile growth indicating the possibility of a lag phase in growth. More data are needed to confirm the lag phase (see text).

The analyses and interpretations of the life history of *S. droebachiensis* presented here have serious implications for managers of the green sea urchin fishery. Strategies for maintaining sustainable yields include size limits (lower and upper), closures (seasonal and geographic), quotas, and augmenting natural populations with some form of aquaculture program. Any strategy must incorporate the growth and age estimates reported here if the fishery is to be managed effectively.

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