

GROWTH AND NATURAL MORTALITY RATES OF RED SEA URCHIN (*STRONGYLOCENTROTUS FRANCISCANUS*) IN BRITISH COLUMBIA

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ABSTRACT Growth and natural mortality rates (M) of the red sea urchin (RSU), *Strongylocentrotus franciscanus*, were estimated based on tetracycline tagging studies and abundance surveys in Queen Charlotte Islands (QCI), Price Island (PI), Alert Bay (AB), and Tofino, British Columbia. Growth was modeled using the Tanaka function and logistic dose-response function and was variable between locations. The growth rate of the RSU remained constant or even increased in the first few years, before declining with test diameter or age. The RSU appeared to be a slow growing and long lived species. Growth for the RSU to recruit into the fishery, at a test diameter of 90 mm, took about 10 and 14 y in QCI and AB respectively, and about 18.5 y in PI and Tofino. Growth rates seemed to be correlated with population density. RSU density was the lowest in QCI, and lower in AB than in PI or Tofino. M was estimated by comparing the survey-derived density of the RSU with the expected density calculated using the growth function and the densities in the previous survey years. The estimated mean M was about 0.08 y^{-1} in PI and Tofino, 0.12 y^{-1} in QCI, and 0.21 y^{-1} in AB.

KEY WORDS: red sea urchin, growth, mortality, tagging, Tanaka, logistic, *Strongylocentrotus*

INTRODUCTION

The red sea urchin (RSU) (*Strongylocentrotus franciscanus*) is distributed along the west coast of North America from Baja California to Alaska, usually on rocky substrates, typically from the intertidal zones to depths of 50 m. The RSU is the largest and most abundant species of sea urchin in British Columbia (BC) (Bernard & Miller 1973). They mature at about 50 mm test diameter (TD) (Bernard & Miller 1973), and spawning usually occurs during May and June in BC (Kramer & Nordin 1975).

The RSU has been commercially harvested by divers in BC since the 1970s. The fishery has been managed by a minimum size limit of 90 mm TD, a conservative fixed exploitation rate of about 2% of estimated biomass, limited license entry; and an individual quota program in which the total quota is divided equally among licences (Campbell et al. 2004, 2008). The fishery management scheme may be improved if we obtain a good understanding of the population biology of the RSU. Among the most fundamental biological parameters are the growth and natural mortality, which, together with a stock-recruitment function, can substantially affect the dynamics of a population.

A growth curve, which expresses the mean size of a population as a function of age, may be formulated based on direct observation of animal sizes at ages, which are usually obtained through the analysis of hard parts of individual animals (Francis & Mulligan 1998, Fablet 2006). However, age determination of individual animals is difficult for some species, including RSU. In these cases, tag-recapture studies are useful for providing information on individuals' growth (Ricker 1975). The RSU is usually tagged by injection of tetracycline or soaking in a calcein solution, which leaves a fluorescent mark at the time of tagging in the skeleton, such as demi-pyramids of the Aristotle's Lantern (jaw) of the RSU (Ebert & Russell 1992). Due to a high correlation between jaw length and TD (Ebert & Russell 1992), TD could be estimated from jaw length.

The growth of tag-recaptured animals is modeled using a growth function, most commonly the von Bertalanffy model. However, this model is not appropriate for the RSU, as a scatter plot of size at recapture *versus* size at tagging does not seem to be linear (Ebert et al. 1999). A generalization of the von Bertalanffy model known as the Richards function (Richards 1959) has been used to model the growth of urchin populations (Ebert 1980, Russell 1987, Ebert & Russell 1992, Kenner 1992, Rogers-Bennett et al. 2003). Ebert et al. (1999) found, however, that the Tanaka function (Tanaka 1982, 1988) is a better function to model the growth of the RSU than the Richards function. Rogers-Bennett et al. (2003), however, demonstrated that the logistic dose-response function (termed as Logistic function thereafter) fitted the tag-recaptured growth data of the RSU better than the Tanaka function.

A constructed growth curve would enable us to examine some biological features important to the fishery management. We may use the growth curve to estimate the number of years to grow and the number of years to spawn before recruiting to the fishery. We may also use the growth curve to investigate how the population biomass would change as a function of growth. The growth function is also useful in the estimation of the natural mortality rate, another essential biological parameter. Ebert & Russell (1993) and Ebert et al. (1999) showed that the mean TD of a population is a function of growth and survival rate. With the growth parameters estimated, the survival rate could be estimated based on the mean TD of the samples (Ebert & Russell 1993, Ebert et al. 1999). However, this method relies on two restrictive assumptions: the population is neither growing nor decreasing and the annual recruitment has been sufficiently constant across the studied years (Ebert & Russell 1993). These two assumptions are likely to be violated, as recruitment of an urchin population can be highly variable (Ebert 1983, Ebert et al. 1994).

In this paper, we used the Tanaka and Logistic functions to model the growth of the RSU in BC, based on tag-recapture studies conducted in the mid 1990s. Taking advantage of density estimations from the abundance surveys, we were able

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to use the growth functions to estimate the natural mortality rate, and the estimation would not be affected by variable recruitment. Growth parameters and mortality rates were estimated using the Bayesian approach.

MATERIALS AND METHODS

Tag-recapture studies and abundance surveys were conducted in four study areas in BC. RSU were tagged using tetracycline or calcein solution, which left in the jaw (see below) a fluorescent mark visible under UV light. The TD of recaptured individuals at tagging was back-calculated from the lengths of the jaw at tagging and recapture, and the TD of the individual at recapture. The growth of the RSU was modeled using the Tanaka and Logistic functions. Natural mortality rates were estimated by comparing the survey-derived density with the expected density calculated using the estimated densities in the previous survey years and the growth functions.

Tag-recapture Studies

Tagging and abundance surveys were conducted in four study areas: Queen Charlotte Islands (QCI), Price Island (PI), Alert Bay (AB), and Tofino (Fig. 1), which have been closed to fishing since 1994–1995. The four areas had nine experimental plots (sites) each, three of which served as controls (with no harvesting) and the other six sustained different intensities of harvesting. To exclude the impact of harvesting on the estimation of growth and natural mortality rate (M), we only used the data from the three control sites of each area in this study. Abundance surveys started in 1994–1995, and proceeded mostly on an annual basis for a number of years (Table 1). In each survey, RSU density and size frequency distributions were measured on dive transects.

Approximately 1,000 RSU were tagged at each of the nine experimental sites at QCI (1996), PI (1996) and Tofino (1995 and 1996), and at the three control sites at AB (1996). Urchins >25 mm TD were tagged *in-situ* by divers by injecting tetracy-

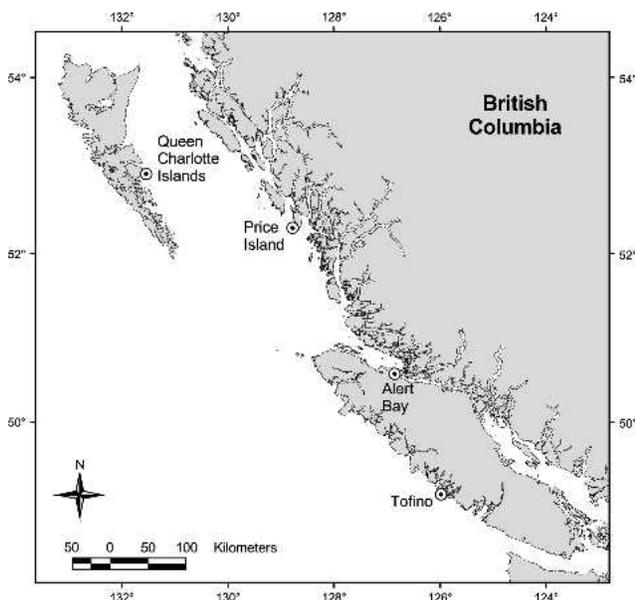


Figure 1. Geographic locations of the four study areas in British Columbia.

TABLE 1.

Number of control sites surveyed, by year, in each area during the study period.

Year	Queen Charlotte			
	Islands	Price Island	Alert Bay	Tofino
1994	0	0	3	3
1995	1	3	3	3
1996	3	3	3	3
1997	3	3	3	3
1998	3	3	0	3
1999	3	0	0	0
2000	0	3	0	0
2001	3	3	0	3
2002	3	3	0	0
2003	0	0	0	3
2004	3	3	0	2
2005	0	0	0	3

cline (20g/L sea water) with a syringe. Urchins ≤ 25 mm TD were collected by divers and soaked in a calcein solution (125 mg/L seawater) overnight before being released on the tag site the next day. A calcein bath was used to tag small urchins because they are difficult to tag with the use of a syringe. Tetracycline and calcein are chemical tags that bind to calcium in growing portions of the skeleton and therefore provide a fluorescent mark, visible under a UV light, indicating the size of the bony structure at the time of tagging.

One year after tagging, approximately 1,000 urchins were harvested from each tag site. Test diameter of each urchin was measured with callipers and the Aristotle's lantern (mouth parts) removed and checked for tags. Tagged Aristotle's lanterns were kept for further processing at the laboratory. These Aristotle's lanterns were then soaked in 12.5% bleach overnight to dissolve soft tissues. The demi-pyramids of the Aristotle's lantern (jaw) were kept for measurements. In 1997 (1996 and 1997 for Tofino), one year after tagging for each site, 478, 672, 540, and 553 tagged urchins were recaptured from the control sites of QCI, PI, AB, and Tofino respectively.

Jaw length of recaptured urchins was measured with callipers. Growth of the demi-pyramids was measured, under a microscope equipped with a UV light, as the distance between the top of the demi-pyramid and the tetracycline (or calcein) tag. Jaw length at the time of tagging was calculated as the jaw length at tag-recovery minus jaw growth.

Back-calculation of Test Diameter at Tagging

We used a power model to describe the relationship between the expected test diameter (\hat{D}) and jaw length (L) at the time of recapture for each of the four areas:

$$\hat{D} = aL^b \quad (1)$$

where a and b are the model parameters, which were estimated by the least squares. The data were well fitted by the power model with coefficients of determination lying between 0.95 and 0.98.

TDs of the individuals at the time of tagging were back-calculated. We assumed that if the TD of an individual was larger or smaller by a percentage than the mean (expected) TD for the RSU with the same jaw lengths as this individual at the

time of recapture, the TD of this individual was also larger or smaller by the same percentage than the mean TD for the RSU with the same jaw lengths as this individual at the time of tagging a year earlier. The TD of this individual at the time of tagging was, therefore, estimated using the following equation:

$$D_t = D_{t+1} \left(\frac{L_t}{L_{t+1}} \right)^b \tag{2}$$

where D_t and D_{t+1} are the TDs at the time of tagging and recapture respectively, and L_t and L_{t+1} are the jaw lengths at the time of tagging and recapture respectively.

Growth Models

Plots of annual growth showed that the growth rate practically remained the same or even increased slightly with TD for small urchins and decreased with TD for large ones (Fig. 2). To determine if there was a statistical significance in the increase of the growth rate with TDs in the early years, we conducted an analysis of variance test on the simple linear regression of the annual growths versus TDs, for RSUs <30 mm TD. Scatter plots of TDs at recapture against TDs at tagging over the entire size range were obviously nonlinear (not shown). The growth of the RSU was modeled using the Tanaka (Tanaka 1988, Ebert & Russell 1993) and Logistic (Rogers-Bennett et al. 2003) functions. Both functions have three parameters to be estimated from the tag-recapture data.

Using the differential form of the Tanaka function, the expected TD at time $t + 1$ was modeled as:

$$\hat{D}_{t+1} = \frac{1}{\sqrt{f}} \log \left| 2f \left(\frac{E}{4f} - \frac{a}{E} + 1 \right) + 2 \sqrt{f^2 \left(\frac{E}{4f} - \frac{a}{E} + 1 \right)^2 + f \times a} \right| + d \tag{3}$$

where f , a , and d are the model parameters, and E was calculated as:

$$E = \exp(\sqrt{f}(\hat{D}_t - d)) \tag{4}$$

Using the Logistic function, the expected TD at time $t + 1$ was modeled as:

$$\hat{D}_{t+1} = \frac{a}{1 + (\hat{D}_t/b)^c} + \hat{D}_t \tag{5}$$

We assumed that the errors between the observed TD (D) and expected TD (\hat{D}) at the time of tagging and recapture were normally distributed:

$$D = \hat{D} + \varepsilon \tag{6}$$

where ε is a normal variate $\varepsilon \sim N(0, \sigma^2)$. The Bayesian approach was applied to estimate the growth parameters, and uninformative priors were assigned to the parameters. The prior distributions for the parameters of the Tanaka function were: $f \sim N(0.5, 100^2) I(0,)$ where $I(0,)$ indicates that the distribution lies above 0; $a \sim N(0.5, 100^2)$; $b \sim N(100, 100^2)$. The prior distributions for the Logistic function were: $a \sim N(10, 100^2) I(0,)$; $b \sim N(20, 100^2) I(0,)$; $c \sim N(10, 100^2) I(0,)$. For both functions, σ^2 was assigned an informative inverse gamma distribution: $1/\sigma^2 \sim \text{Gamma}(0.001, 100^2)$ where 0.001 and 0.0001 represent the parameters of shape and rate of the gamma distribution.

The WinBUGS software program (Spiegelhalter et al. 2003) was used for the Bayesian analyses. The first 10,000 samples were treated as a burn-in period, and the next 10,000 samples were saved. Two chains were used with different initial values. Evidence of convergence was warranted by the Gelman-Rubin diagnostics test. The goodness of fit by the two functions was judged by Deviance Information Criterion (DIC). A smaller DIC would indicate a better fit to the data.

To produce a growth curve in terms of TD versus age, a small TD of 0.5 mm (Rowley 1990, Ebert & Russell 1992) was assumed for the RSU at settlement, and TDs at later years were obtained by a recursive calculation.

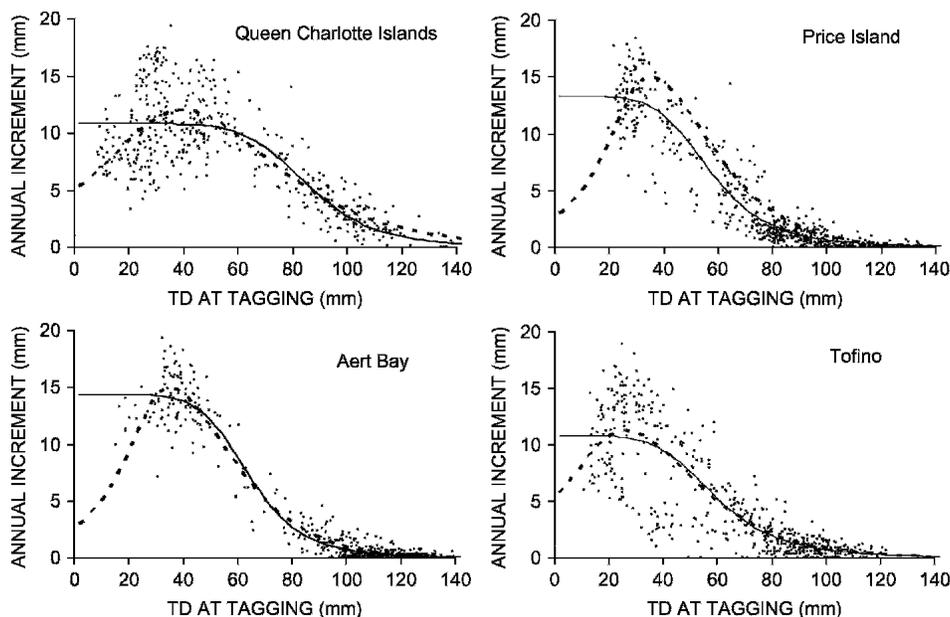


Figure 2. Comparisons of observed annual growth (dots) and predicted annual growth by the Tanaka function (broken lines) and the logistic dose-response function (solid line) as a function of test diameters (TD) at the time of tagging for red sea urchins in the four studied areas.

Estimation of Natural Mortality Rates

M was estimated by comparing survey-derived urchin density with the expected density at each site and in each survey year. Survey-derived densities and associated standard deviations were estimated for each control site and year based on the survey data. Mean survey-derived densities varied between 1.6 and 8.0/m² in QCI, between 7.6 and 43.2/m² in PI, between 3.8 and 9.6/m² in AB, and between 3.7 and 32.8/m² in Tofino. Using a state-space approach, the expected density in a survey year was calculated based on the expected density rather than the observed density in the previous survey year. The size frequency distributions were used to account for the impact of growth on M estimation.

To eliminate the effect of likely variable settlement on the estimation of M , the RSU measurements were divided into a large sized group (≥ 60 mm TD) and a small sized group (< 60 mm TD). We chose the delimiting size to be 60 mm TD, so that very small RSU, hardly observed in a survey, were unlikely to grow into the large sized group based on our estimated growth rates.

We did not consider possible migration of RSU into or out of each site in the M estimation. Therefore, a change in the density of large sized RSU from one survey year to the next one was assumed to be caused by the interaction between natural mortality and recruitment because of growing of small sized RSU into the large sized group. We estimated the amount of recruitment through Monte Carlo simulations.

A small sized RSU of test diameter, D_t , at one survey would grow to a test diameter of D_{t+1} in the next year according to the Tanaka function:

$$D_{t+1} = \frac{1}{\sqrt{f}} \log \left| 2\bar{f} \left(\frac{E}{4\bar{f}} - \frac{\bar{a}}{E} + 1 \right) + 2\sqrt{\bar{f}^2 \left(\frac{E}{4\bar{f}} - \frac{\bar{a}}{E} + 1 \right)^2 + \bar{f} \times \bar{a}} \right| + \bar{d} + \bar{\varepsilon} \tag{7}$$

and to the Logistic function:

$$D_{t+1} = \frac{\bar{a}}{1 + (D_t/\bar{b})^{\bar{c}}} + D_t + \bar{\varepsilon} \tag{8}$$

where \bar{a} , \bar{d} , \bar{f} and $\bar{\varepsilon}$ in Eq. 7, and \bar{a} , \bar{b} , \bar{c} and $\bar{\varepsilon}$ in Eq. 8 were randomly generated values based on the estimated means and variances of the Tanaka and Logistic function parameters respectively. If the two consecutive surveys were 2 or 3 y apart, Eq. 7 or 8 was recursively used. All together 5,000 such simulations were conducted, and the proportion of these simulations, where resultant D_{t+1} was ≥ 60 mm TD, indicated the percentage of small sized RSU of this size, which would grow into the large sized group by the subsequent survey time.

Densities of different sized RSU were estimated as the product of the survey-derived density of all sized RSU and the proportion of size-specific RSU obtained from the size frequency distributions. Leaving out the natural mortality, the density of recruits (R) because of growth of small urchins into the large group was estimated as:

$$R = \sum_{d=1}^{60} P_d \times N_d \tag{9}$$

where N_d is the estimated density of small urchin with a TD of d in one survey, and P_d is the estimated proportion of small

urchins of this TD, which would have grown into the large sized group by the time of the subsequent survey.

We assumed that M was the same for RSU in all sites of an area, but may vary in different areas. The expected density of large sized RSU in Site j of Area i at survey time $t + \Delta t$ ($\hat{D}_{i,j,t+\Delta t}$) was estimated based on the expected density of large sized RSU in the same location at the previous survey time ($\hat{D}_{i,j,t}$) and the amount of potential recruitment ($R_{i,j,t}$):

$$\hat{D}_{i,j,t+\Delta t} = (\hat{D}_{i,j,t} + R_{i,j,t}) \exp(-M_i \Delta t) \tag{10}$$

where M_i is the natural mortality rate for Area i , Δt is the time interval in years between the two consecutive surveys. The expected density of large sized RSU at the 1st survey, however, could not be calculated using Eq. 10. The errors between survey-derived and expected densities of large sized RSU at the 1st survey as well as the subsequent survey times were assumed to be normally distributed:

$$D_{i,j,t} = \hat{D}_{i,j,t} + \varepsilon_{i,j,t} \tag{11}$$

where $\varepsilon_{i,j,t}$ is a normal variate $N(0, \sigma^2_{i,j,t})$, where the variance $\sigma^2_{i,j,t}$ was estimated based on the survey data in Site j of Area i at survey time t (unpublished data).

We assumed that M_i is exchangeable and comes from a normal distribution, $M_i \sim N(U_M, \sigma^2_M)$, where the hyperparameters U_M and σ^2_M denote, respectively, the mean and variance across different areas. Bayesian hierarchical approach was used in the estimation. Uninformative priors were assigned to the hyperparameters and the expected density of large sized RSU at the 1st survey in each location: $U_M \sim N(0.8, 100^2) I(0,); 1/\sigma_M \sim \text{gamma}(0,001, 0,0001); \hat{D}_{i,j,1} \sim \text{unif}(0, 50)$ a uniform distribution between 0 and 50. The first 50,000 samples were treated as a burn-in period, and the next 10,000 samples were saved. Two chains were used with different initial values. Evidence of convergence was warranted by the Gelman-Rubin diagnostics test.

RESULTS

Estimated growth parameters and associated variances for the Tanaka and Logistic functions were presented in Table 2. The Tanaka and Logistic functions fitted the data well (Fig. 2). Both functions predicted similar growth rates within the range of available data in QCI, AB, and Tofino. The Tanaka function, however, predicted somewhat higher growth rates than the Logistic function in PI (Fig. 2). The growth rate remained high for the RSU ≤ 30 –40 mm TD. The growth rate then declined with TD, asymptotically approaching to zero. The analysis of variance test showed that the growth rate increased significantly ($P < 0.001$) for small RSU (< 30 mm TD) in QCI and Tofino, but not significantly in PI and AB ($P > 0.20$) although the growth rate for these small RSU also increased, on average, with TD.

The main difference between the two functions was the growth rates extrapolated beyond the available data range for small RSU. According to the Tanaka function, the growth rate of the RSU was initially small and increased with TDs until the maximum growth rate was reached. Thereafter, the RSU's growth declined with TD. According to the Logistic function, the growth rate was comparatively high initially and remained practically the same for the first few years, and then decreased with increasing TD.

TABLE 2.

Estimated means, standard deviations (sd), and 95% confidence intervals (95% CI) for the parameters of the Tanaka and Logistic dose-response functions (see text for explanation of parameters).

Model	Parameter	Area	Mean	sd	95% CI Lower - Upper
Tanaka	<i>a</i>	Queen Charlotte Island	0.00681	0.00023	0.00636–0.00726
		Price Island	0.00539	0.00015	0.00510–0.00568
		Alert Bay	0.00420	0.00009	0.00403–0.00437
		Tofino	0.00767	0.00035	0.00701–0.00838
	<i>d</i>	Queen Charlotte Island	190.3	5.5	180.4–201.3
		Price Island	118.2	2.1	113.9–122.4
		Alert Bay	125.4	1.8	122.1–128.9
		Tofino	131.1	4.9	122.6–142.0
	<i>f</i>	Queen Charlotte Island	0.00126	0.00009	0.00110–0.00144
		Price Island	0.00342	0.00019	0.00307–0.00381
		Alert Bay	0.00348	0.00014	0.00321–0.00376
		Tofino	0.00232	0.00022	0.00188–0.00275
	σ	Queen Charlotte Island	1.80	0.06	1.69–1.92
		Price Island	1.21	0.03	1.14–1.27
		Alert Bay	0.87	0.03	0.82–0.93
		Tofino	1.88	0.06	1.78–2.00
Logistic	<i>a</i>	Queen Charlotte Island	10.83	0.1656	10.51–11.15
		Price Island	13.28	0.1992	12.89–13.67
		Alert Bay	14.38	0.1488	14.09–14.67
		Tofino	11.26	0.2852	10.71–11.83
	<i>b</i>	Queen Charlotte Island	85.76	1.397	82.95–88.52
		Price Island	57.29	0.8051	55.7–58.86
		Alert Bay	64.42	0.6934	63.08–65.8
		Tofino	55.93	1.512	52.97–58.84
	<i>c</i>	Queen Charlotte Island	7.07	0.6819	5.858–8.521
		Price Island	5.371	0.2332	4.93–5.85
		Alert Bay	6.707	0.2373	6.263–7.193
		Tofino	4.465	0.3306	3.862–5.161
	σ	Queen Charlotte Island	2.716	0.0876	2.551–2.897
		Price Island	1.612	0.04473	1.526–1.704
		Alert Bay	1.181	0.03594	1.112–1.254
		Tofino	2.572	0.0777	2.424–2.729

Estimated growth curves in terms of TD as a function of age were comparable for the RSU in PI, AB, and Tofino (Fig. 3). The growth curve for young RSU in QCI was also similar to those in the other three areas. However, the growth curve for older RSU (≥ 8 y) in QCI was substantially elevated because of higher growth rates in comparison with the growth curves in the other three areas (Fig. 3). For 100-y-old RSU, the mean TD was approximately 33% and 20% larger in QCI according, respectively, to the Tanaka and Logistic functions.

The TDs of young RSU predicted by the Tanaka function were smaller than those predicted by the Logistic function. The mean TD of age 1 RSU was 1.8–4.5 times larger, based on the Logistic function (Table 3). However, the difference in the ages of recruitment to the fishery (90 mm TD) was not so great because of accelerating growth rates in the first few years according to the Tanaka function. The recruitment ages were approximately 9–19 y and 11–19 y based on the Tanaka and Logistic functions respectively (Table 3). The data were slightly better fitted using the Tanaka function than using the Logistic function based on the DIC values (Table 3).

Natural mortality rates (M) estimated using the Tanaka function or the Logistic function were about the same (Table 4). The mean natural mortality rate (U_M) for the RSU pop-

ulation across the areas was estimated to be around 0.13 y^{-1} . M was relatively low ($< 0.1 \text{ y}^{-1}$) in PI and Tofino, intermediate (0.12 y^{-1}) in QCI, and the highest (0.21 y^{-1}) in AB (Table 4). The high estimated M in AB was because of the dramatic declines in the densities in all the three control sites in AB in 1996. Survey-derived densities of all sized RSU decreased by 41% to 49% in 1996 relative to the densities in 1995. M would be well below 0.1 y^{-1} , if this drastic decline in the population densities were not considered in the estimation. Also, the estimated M in AB was associated with the highest amount of variation, because there were only four years of survey data available for AB, considerably less than for the other three areas.

DISCUSSION

The RSU grew in a different fashion than many aquatic invertebrate species. The RSU exhibited a sigmoidal growth, which could not be adequately modeled by the most frequently used von Bertalanffy function (Ebert & Russell 1993, Rogers-Bennett et al. 2003). The less commonly used Tanaka and Logistic functions were found to be more adequate for describing RSU growth (also see Ebert & Russell 1993, Rogers-Bennett et al. 2003).

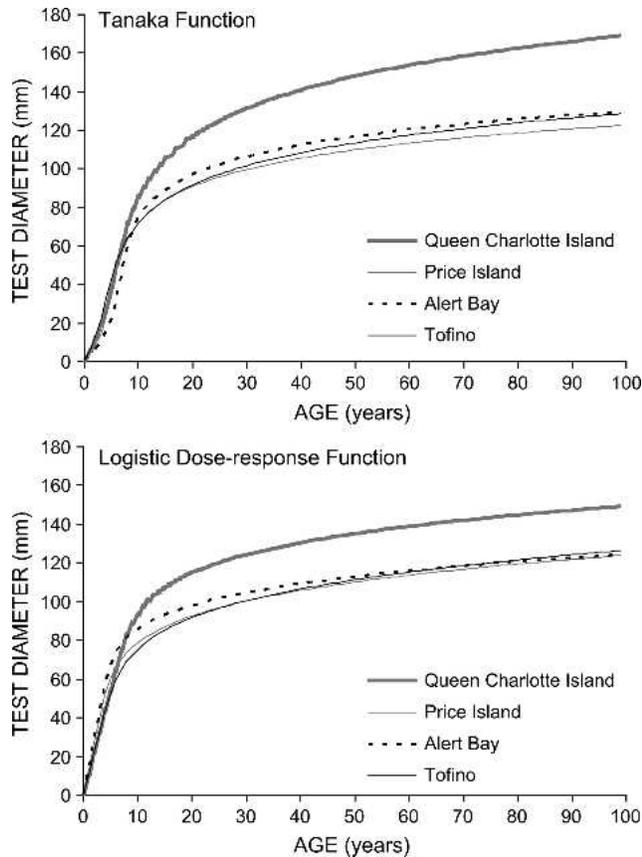


Figure 3. Estimated growth curves for the red sea urchin using the Tanaka and Logistic functions.

The Tanaka function was designed to accommodate a growth curve with a general sigmoid shape (Tanaka 1988). This function demands an increasing growth rate in the initial period of growth and a decreasing growth in the remaining period. There is a major difference between the Tanaka function and other sigmoidal functions such as the Gompertz growth function (Quinn & Deriso 1999). The Tanaka function lacks an asymptotic size and allows the animals to continue to grow as long as they live, although the growth rate asymptotically approaches to zero. The Gompertz growth function sets an asymptotic size for the animal population. The Gompertz growth function was rejected after being tried because of a poor fit of the RSU growth data.

The Logistic function was found to fit the growth data of the RSU in California better than the Tanaka function (Rogers-Bennett et al. 2003). The Logistic function dictates an approximately equal growth rate in the initial growth period and decreasing growth rate in the remaining period. Like the Tanaka function, the Logistic function does not impose an asymptotic size on the animal population, and also allows the animals to grow as long as they live with the growth rate asymptotically approaching to zero.

The main difference between the Tanaka and Logistic functions lies in the initial growth period. The growth rate for the tagged and recaptured small RSU (<30 mm TD) increased significantly with increased TD in QCI and Tofino. At PI and AB, the growth rate for these small RSU also, on average,

TABLE 3.

A comparison of test diameter at estimated age 1 (TD1), age-at-recruitment to the fishery (ARF), deviance information criterion (DIC) for the Tanaka and Logistic dose-response functions.

		Queen Charlotte Islands	Price Island	Alert Bay	Tofino
TD1 (mm)	Tanaka	5.9	4.1	3.3	6.4
	Logistic	11.3	13.8	14.9	11.3
ARF (year)	Tanaka	10.9	19.2	15.5	18.7
	Logistic	9.1	17.5	12.6	18.5
DIC	Tanaka	4,677.6	5,482.2	3,712.7	5,510.7
	Logistic	4,823.9	5,535.1	3,744.7	5,550.9

increased with increased TD albeit not significantly. We found that the growth data were fitted slightly better using the Tanaka function rather than the Logistic function contrary to that report by Rogers-Bennett et al. (2003).

The RSU's growth within the first 2–3 y after larval settlement was uncertain, because small sized RSU were not tagged in our study. For 1-y-old RSU, the Tanaka function would expect the TD to be 3.3–6.4 mm, whereas the Logistic function would predict the TD to be 11.3–14.9 mm. Our combined size frequency data for all sites and years (unpublished data) in each area showed that the first mode appeared to be in the neighborhood of 10 mm TD. Cultured RSU had an average TD of 10.7 mm at nearly 1 y of age in BC (unpublished data). Laboratory-reared purple sea urchin, *Strongylocentrotus purpuratus*, could grow by 10–30 mm TD in the 1st year (Pearse & Cameron 1991). In the natural environment, they seemed to grow slower. Purple sea urchin at 1 y of age in southern California were estimated to be 3.6 mm TD in barrens, and 17 mm TD in kelp beds based on the size-frequency analysis and mark-recapture studies (Rowley 1990). Estimated TD of green sea urchin, *Strongylocentrotus droebachiensis*, at 1 y of age in the natural environment varied from 2.6–4.3 mm in the St. Lawrence Estuary (Himmelman et al. 1983), 6–8 mm in Nova Scotia (Scheibling 1986, Raymond & Scheibling 1987), 8–10 mm in Maine (Swan 1958), 10 mm in Barents Sea, and 11–17 in

TABLE 4.

Means, standard deviations (sd), and 95% confidence intervals (95% CI) of the annual natural mortality rates (y^{-1}) estimated using the Tanaka and logistic dose-response functions.

Model	Area	Mean	sd	95% CI
Tanaka	Queen Charlotte Island	0.120	0.039	0.053–0.21
	Price Island	0.081	0.020	0.041–0.12
	Alert Bay	0.213	0.087	0.076–0.39
	Tofino	0.079	0.008	0.062–0.094
	Overall	0.128	0.063	0.040–0.28
Logistic	Queen Charlotte Island	0.115	0.038	0.048–0.198
	Price Island	0.081	0.020	0.043–0.119
	Alert Bay	0.211	0.089	0.074–0.389
	Tofino	0.077	0.008	0.062–0.093
	Overall	0.125	0.061	0.038–0.273

Nova Scotia (Miller & Mann 1973). Based on these studies, the mean TD is 8.7 mm for green sea urchin at 1 y of age. The TD for the RSU at 1 y of age is, therefore, likely to be somewhere between the two ranges predicted by the Tanaka and Logistic functions.

The Tanaka and Logistic functions suffer from a restriction on the estimation of animals' sizes at young ages. The Tanaka function imposes a symmetrical bell-shaped curve for the growth rate. This function expects that the rate of increase in growth before the point of the maximum growth is the same as the rate of decrease in growth after the point of the maximum growth. If the growth rate increases slower towards the point of the maximum growth than it decreases after the point of the maximum growth, the Tanaka function will underestimate the sizes for the small RSU. The Logistic function, however, dictates an ever decreasing growth rate, even though the rate of decrease is very small (practically unchanged) in the initial growth period. Therefore, if growth accelerates substantially in the early years, the sizes for the young RSU will be overestimated by the Logistic function.

The RSU appears to be a slow growing species. Age at recruitment to the fishery, at 90 mm TD, varied from 10 y in QCI, 14 y in AB, to 18 y in PI and Tofino. Overall, the RSU grew the fastest in QCI, and faster in AB than in PI and Tofino. The growth rate of the RSU is likely to be greatly correlated with the amount of food available to the individuals (Rowley 1990), as the growth of the RSU individuals seemed to be substantially variable especially for small sized RSU. At a low population density, reduction in the competition among individual RSU for food may increase the food supply for the individuals. The RSU density was the lowest in QCI, and lower in AB than in PI and Tofino. Correspondingly, age at recruitment to the fishery was lowest in QCI, and lower in AB than in PI and Tofino.

The age at recruitment to the fishery for the RSU was variable, reflecting variable growth rates for the RSU in different locations. The age at recruitment to the fishery (89 mm TD) for the RSU in northern California was approximately 8.2 and 6.6 y using the Tanaka and Logistic functions respectively (Rogers-Bennett et al. 2003). For the RSU from various locations in California, Oregon, Washington, and Alaska, estimated ages at 90 mm TD ranged between 5 and 34 y with a mean of 14.6 y (Ebert et al. 1999). The estimated ages at recruitment to the fishery for the RSU in BC were well within the published age range. The RSU in AB grew at an average rate for the RSU on the west coast of North America, whereas the RSU from QCI grew faster than the average and the RSU from PI and Tofino grew slower. The relatively slow growth for the RSU in Tofino may be related to their dietary components. The stomach content examination revealed that drift eel grass, *Zostera marina*, was a major diet item for the RSU in Tofino (Bureau 1996). Morris & Campbell (1996) found that RSU fed with eelgrass grew almost 50% slower than those fed with bull kelp, *Nereocystis luetkeana*.

Although the RSU showed differences in growth over a substantial portion of its geographic range, the growth was found to be independent of latitude (Ebert et al. 1999). Differences in growth can be as great over very short distances as over more than 20° of latitude (Ebert et al. 1999). Despite the proximity of the two sites, Cosign Cove and Northwest Point, on San Nicolas Island, CA, the RSU exhibited very different

growth rates. It would take 6 y for a RSU to reach 70 mm TD in the Northwest Point, whereas it would take twice as long to achieve this size at Cosign Cove (Ebert & Russell 1992). Our results also showed growth variability between locations had no latitudinal gradient.

The RSU seemed to be a long-lived species. The estimated mean TD for 100-y-old RSU was smaller than 130 mm in PI, AB, and Tofino. RSU with measured TDs ≥ 130 were more likely to be older than 100 y. The growth curves estimated by Ebert et al. (1999) also showed a high longevity for the RSU, which seemed to continue to grow throughout their lives and can live up to over 100 y. Using marks induced by enhanced radiocarbons in the ocean from nuclear weapons testing, Ebert & Southon (2003) confirmed that the RSU are long-lived animals. In addition, the largest individuals continue to develop gonad masses in accord with the same allometric relationships as smaller individuals, and senescence does not appear to occur in the RSU (Ebert & Southon 2003).

A sound fishery management plan relies on accurate estimates of natural mortality rates (M) of the managed species. M has been estimated for the RSU in a number of locations using size-frequency data (SFD). Based on the SFD and growth increment under the assumption of constant recruitment, M was estimated to be 0.14 y^{-1} for the RSU in an unharvested location in southern California (Botsford et al. 1993), and to be, on average, 0.09 y^{-1} for the RSU in three unharvested locations in northern California (Morgan et al. 2000). Using a modified version of the catch-at-size analysis (Sullivan et al. 1990), Lai & Bradbury (1998) estimated M and fishing mortality rate for the harvested RSU population in the northern end of the San Juan Islands, WA. The estimated average M was 0.16 y^{-1} based on the SFD collected from surveys (Lai & Bradbury 1998).

Ebert & Russell (1992, 1993) and Ebert et al. (1999) estimated M for the RSU using the mean TD of the samples and the estimated growth function under the assumption of constant recruitment and stable population structure. Ebert et al. (1999) found that M was correlated with latitude, with higher estimates in southern California and lower estimates from northern California to Alaska (excluding BC). M varied from $0.088\text{--}0.401 \text{ y}^{-1}$ with an average of 0.242 y^{-1} in southern California, and from $0.016\text{--}0.204 \text{ y}^{-1}$ with an average of 0.066 y^{-1} from northern California to Alaska (Ebert et al. 1999). The difference in the survival rate for the RSU in the south and north was likely caused by temperature-related disease and stress (Ebert et al. 1999).

M estimates for the RSU in the north by Ebert et al. (1999) were generally lower than the estimates by other authors (Lai & Bradbury 1998, Morgan et al. 2000). Our estimated M for the RSU in BC was comparable to the estimates by the latter authors. M was estimated to be 0.08 y^{-1} in PI and Tofino, 0.12 y^{-1} in QCI, and 0.21 y^{-1} in AB. The extraordinarily high M in AB was caused by a dramatic reduction (41%–49%) in the RSU density between 1995 and 1996. We are uncertain about the cause for such a high decline in density, which may be caused by poaching or emigration. If this drastic density reduction were not considered in the M estimation, then estimated mean M for the RSU in AB would be much smaller.

In the current study, the estimated growth function, based on the tag-recapture data, was used in the estimation of M as in

the study of Ebert et al. (1999). Using their way of estimation, we estimated M to be considerably lower in BC: at 0.046 y^{-1} in QCI, 0.034 y^{-1} in PI, 0.031 y^{-1} in AB, and 0.049 y^{-1} in Tofino. However, this estimation hinged on the assumption of constant recruitment and stable population structure. This assumption was unlikely valid, because recruitment was likely to be substantially variable in different years. In our study, no such assumption was necessary, because the RSU densities were measured and the impact of variable annual recruitment could be incorporated. Our estimates should, at least theoretically, be more accurate than those by Ebert et al. (1999).

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