

# Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb $^{14}$ carbon

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Red sea urchins (*Strongylocentrotus franciscanus*) along the west coast of North America, like most large sea urchins in temperate waters worldwide, are the focus of a commercially important fishery. In a review of biological data for purposes of fishery management, the life span of red sea urchins was suggested to be 7–10 years (Sloan, 1986) and they have been included with much shorter-lived species for illustrating complex population dynamics (Hastings and Higgins, 1994). Recent work with tetracycline and calcein tagging (Ebert, 1998; Ebert et al., 1999), however, has shown that individuals continue to grow throughout life, although at a very slow rate, and large individuals are estimated to be in excess of 100 years old. A potential problem with the studies using tetracycline and calcein is that one-year time intervals were used between tagging and recapture and therefore it is possible that occasionally there may have been very good years for growth that were missed. If occasional growth spurts occurred, largest sizes would have been attained in much less than 100 years. The potential problem of missed good years for growth could be resolved with a marker that captures a longer period of time. The accuracy of age estimates has consequences for resource management where size limits may need adjustment in order to protect older individuals (Hilborn and

Walters, 1992; Congdon et al., 1994; Ebert, 1998). There is also the need to understand the evolution of life histories of species where long life tends to be an indicator of uncertainty in individual reproductive success (Murphy, 1968; Roff, 1992; Stearns, 1992).

Enhanced radiocarbon in the oceans due to atmospheric testing of nuclear weapons that began in the 1950s (Nydal and Lovseth, 1983; Broecker et al., 1985; Duffy et al., 1995) provides a permanent marker in carbonate-based skeletal elements that are not reworked by resorption and deposition during growth and hence has a long time period between mark and recovery. The enhanced radiocarbon marker has been used in various studies to validate the periodic (usually annual) nature of growth zones in fish (Kalish, 1993, 1995; Campana, 1997; Campana et al., 2002) and invertebrates (Turekian et al., 1982; Witbaard et al., 1994; Peck and Brey, 1996) where validation by chemical tags such as tetracycline has been impractical. Red sea urchins lack interpretable growth zones (Breen and Adkins, 1976) and therefore there is no natural feature to serve as a cross check for studies using chemical tags. In the present study we present a test and confirmation of age in red sea urchins estimated from tetracycline tagging using an enhanced  $^{14}$ C signal in the ocean from nuclear weapons testing.

## Materials and methods

Red sea urchins were tagged with tetracycline from 1989 to 1992 in northern California, Oregon, and Washington and collected after time intervals of approximately one year (details presented in Ebert et al., 1999). It is not possible to determine whether a live sea urchin has a tetracycline mark and therefore large collections had to be made. Skeletal elements were cleaned with sodium hypochlorite bleach to remove all organic material not bound in the calcite of the skeleton, and then skeletal ossicles were examined by using UV illumination to detect the tetracycline marks, which fluoresce yellow. Growth increments were measured in jaws of Aristotle's lantern of 1582 tagged-recovered red sea urchins and used to estimate growth parameters. Jaw ossicles, the demipyramids of Aristotle's lantern, are internal skeletal elements that grow around all surfaces but not equally in all directions so that a change in jaw length,  $\Delta J$ , is mostly at the end closest to the esophagus and there is little growth closest to the mouth, the labial end, where the teeth extend from the jaw.

The Tanaka function (Eq. 1) was used to describe growth (Tanaka, 1982, 1988) because it can model data that show an initial lag, an exponential phase with a maximum, and can include continuing growth throughout life. This function is described in greater detail elsewhere (Tanaka, 1982, 1988; Ebert et al., 1999). The usual formulation of the Tanaka model is  $\Delta \text{size}$  as a function of size at time  $t$  and  $\Delta t$  is assumed to be fixed for all individuals in the sample, usually at  $\Delta t = 1$  year (Tanaka, 1982, 1988; Ebert, 1998; Ebert et al., 1999) and not included explicitly in the equation. In the present study we estimated the amount of jaw that would have to be removed to represent the time span from the time of collection in the 1990s with relatively high  $^{14}$ C levels to the time before atmospheric testing of atomic bombs (relatively low  $^{14}$ C) and

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therefore the Tanaka model was modified from previous uses to make  $\Delta J$  a function of  $J_{t+\Delta t}$ , the size on the date of recapture rather than the date of marking, which is the usual way of estimating growth parameters. Also,  $\Delta t$  was explicitly included as a variable (Eq. 2),

$$\Delta J = J_{t+\Delta t} - \frac{1}{\sqrt{f}} \ln \left[ 2G + 2\sqrt{G^2 + fa} \right] - d \quad (1)$$

where

$$G = E/4 - fa/E - f\Delta t \quad (2)$$

and

$$E = \exp \left( \sqrt{f} (J_{t+\Delta t} - d) \right). \quad (3)$$

The three parameters of the Tanaka function,  $a$ ,  $d$ , and  $f$ , have biological meaning: " $a$ " is related to maximum growth rate, which is approximately  $1/\sqrt{a}$ ; " $d$ " shifts the size at which growth is maximum; and " $f$ " is a measure of the rate of change of the growth rate. A graphical presentation of how changes in these parameters change the growth curve is given in Ebert et al. (1999).

Explicit use of  $\Delta t$  and making  $\Delta J$  a function of  $J_{t+\Delta t}$  required a modification of the usual presentation of the Tanaka function. In Ebert et al. (1999) Equation 2 was written as

$$G = E/4 - fa/E + f \quad (4)$$

with no  $\Delta t$  and with " $+f$ ". Equation 3 was written as

$$E = \exp \left( \sqrt{f} (J_t - d) \right). \quad (5)$$

with  $J_t$ , rather than  $J_{t+\Delta t}$ . Tetracycline tagging for a period of one year,  $\Delta t = 1$ , provides the Tanaka parameter estimates and these parameters were used to estimate a  $\Delta J_{\text{jaw}}$  size that would cover the time from the date of collection to a time,  $\Delta t$ , before A-bomb testing;  $\Delta t$  is time run backwards from the date of collection, which is the reason for the sign change from Equation 4 to Equation 2.

The samples of red sea urchins that were selected for radiocarbon analysis were part of the tagging study at Halftide Rocks off San Juan Island, Washington (Ebert et al., 1999). Individuals were tagged with tetracycline on 26 October 1991 and collected again on 21 October 1992. The recaptured tagged individuals ( $n=365$ ) are part of the 1582 tagged sea urchins from northern California, Oregon, and Washington that were used to estimate Tanaka parameters. For  $^{14}\text{C}$  analysis, specimens were selected from the Halftide Rocks collection that did not show fluorescence in the skeleton and therefore probably had not been handled in 1991. The use of untagged individuals for radiocarbon analyses avoids any possible contamination from handling and tagging in 1991.

Cleaned jaws for  $^{14}\text{C}$  analysis were cemented to aluminum blocks with a two-part epoxy cement and aligned so that the esophageal margin was approximately parallel with the block base. The block was held on the stage of a small milling machine and the stage tilted so that the jaw

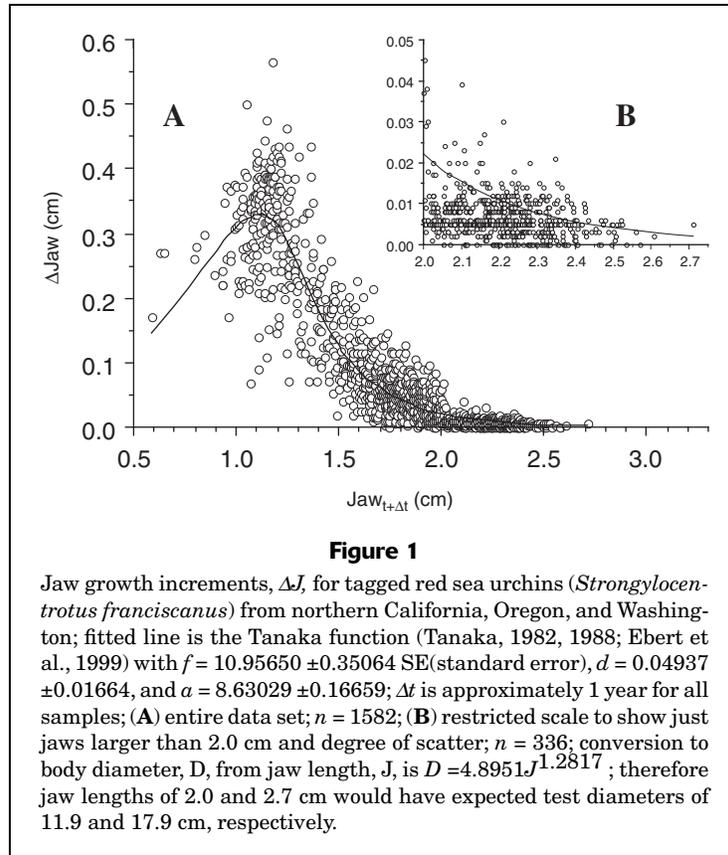
was as parallel as possible with the milling bit. Approximately 0.5 mm of the jaw surface was removed and sides were milled to remove recently deposited calcite and to expose the underlying older skeleton. The jaw was measured and successive samples were milled from the esophageal edge to a depth of 0.5 mm, which produced samples larger than 1 mg of carbonate in most cases. Samples were placed in individual reaction chambers, evacuated, acidified with orthophosphoric acid, and heated. The evolved  $\text{CO}_2$  was converted to graphite by reduction with an excess of hydrogen in individual reactors with iron powder as a catalyst (Vogel et al., 1987). Analysis of  $^{14}\text{C}$  in the graphite targets was done at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, and reported as  $\Delta^{14}\text{C}\%$  (Stuiver and Polach, 1977), which includes a correction for a  $\delta^{13}\text{C}$  of  $-3$  based on stable isotope analyses. Mean precision (1 standard deviation) of radiocarbon measurements was 4.2‰ (range: 3.0–7.9).

## Results

Of the 1582 tag recoveries from all sites, 739 jaws showed a growth increment,  $\Delta J$ , of  $\leq 0.02$  cm and of these only 13 had a labial measurement  $>0$ , which is at the end of the jaw at the mouth opening. The smallest nonzero measurements were 0.001 cm and therefore growth less than this was recorded as 0; 54 sea urchins in the sample had clear tetracycline marks but 0 measurable growth. For large jaws, the measured labial component was too small to be measured and therefore all of the calculated  $\Delta J$  since the late 1950s was milled from the esophageal end of the jaw only.

Tetracycline tagging indicated that annual jaw growth (Fig. 1) was very slow for large sea urchins and many individuals showed annual increments of less than 0.01 cm. The resulting growth curve of jaw length as a function of age (Fig. 2A) showed that at least some large individuals would be expected to have ages in excess of 100 years. If this age estimate is correct, a drop in  $^{14}\text{C}$  should be found in successive small slices removed from large jaws, which would first show current  $^{14}\text{C}$  levels and then drop to pre-bomb levels. Because the Halftide Rocks samples were collected in 1992 we used  $\Delta t = 35$  years, which would go back to 1957. Using Equations 1–3, growth parameters given in Fig. 1, and  $\Delta t = 35$  years, we estimated the increment to be between 1 and 2 mm for jaws between 2.5 and 2.6 cm (Fig. 2B).

Successive milled samples from the esophageal ends of large jaws (Fig. 3, A–D) showed a precipitous drop in radiocarbon to prebomb levels over 1–2 millimeters, in agreement with predictions. Variations across replicates and samples probably are the result of differences in the width of milled samples and an inability to remove all recently deposited calcite or to follow the exact growing edge of the jaw with the milling machine. Smaller jaws (Fig. 3, E–G) were not expected to show a prebomb signature, and indeed they did not. They do, however, indicate the  $^{14}\text{C}$  level to be expected in recent skeletal material and emphasize the rapid change in radiocarbon shown in large jaws. Changes in  $^{14}\text{C}$  in successive milled samples in jaws



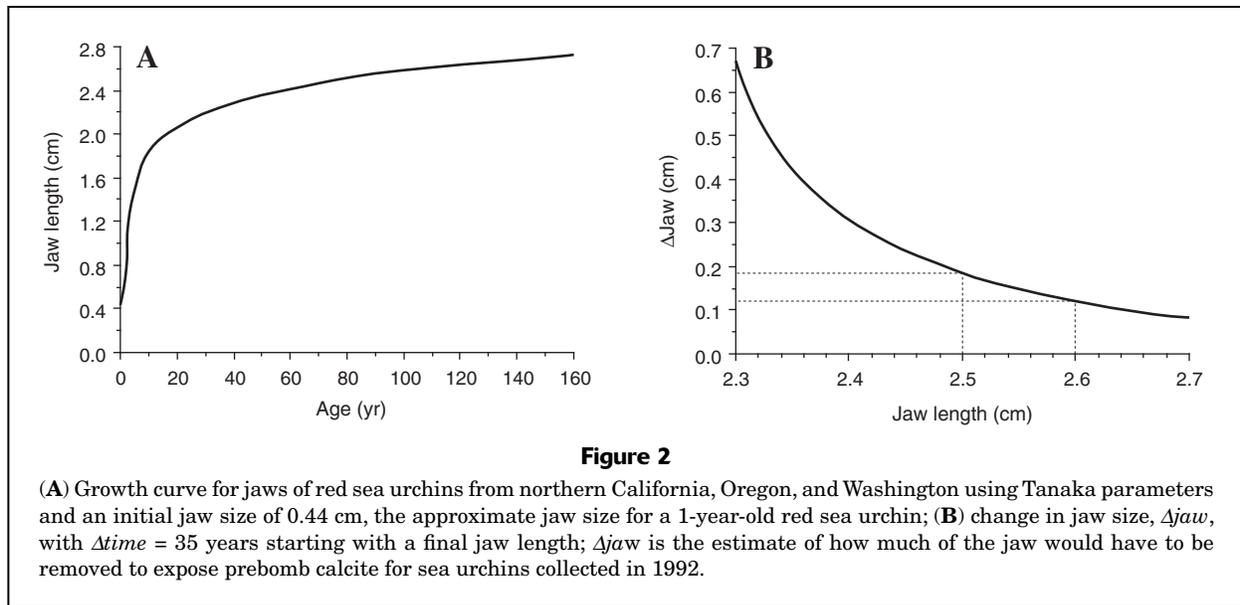
E–G are similar to changes shown in coral samples from the Galápagos (Guilderson and Schrag, 1998) and may indicate that <sup>14</sup>C levels in surface waters in regions of strong upwelling were still rising when sea urchin were collected in 1992. The conclusion is that <sup>14</sup>C analysis supports the age estimates based on tetracycline tagging and use of the Tanaka function: large red sea urchins are old and may have ages of 100 years or more

## Discussion

The largest reported red sea urchins, with body diameters over 19 cm, are from British Columbia, Canada, (Bureau, 1996) and with estimated jaw lengths of about 2.8 cm would be expected to be around 200 years old (Fig. 2A). Age estimates of 100+ years far exceed estimates of life span for other sea urchins (Table 1) based on growth lines in ossicles. Natural growth lines, however, tend to underestimate ages of old individuals because very small increments will have alternations of dark and light areas that are difficult or impossible to resolve and hence counts underestimate age (Ebert, 1988). For example, the maximum age estimate for *Strongylocentrotus droebachiensis*, the commercial species of the U.S. east coast, is 25 years by counts of growth lines (Robinson and MacIntyre, 1997) but at least twice this if tagging and size structure (Russell et al., 1998) are used. Similarly, tagging and size structure

of *Evechinus chloroticus* (Lamare and Mladenov, 2000) have indicated survival rates similar to *S. franciscanus* but the maximum number of growth lines reported was only 10 (Dix, 1972). Survival rate, however, is not a fixed parameter for a species and there is local variation, as well as geographic patterns, evident in the survival rate for *S. franciscanus* (Ebert et al. 1999).

Estimates of annual survival rates based on growth parameters and mean size for red sea urchins from southern California to Alaska (Ebert et al., 1999) indicate that very old individuals would not be expected in southern California where few individuals attain ages of 50 years. At more northern locations, the probability of long life increases (Fig. 4) and ages of 100+ are expected, particularly in Washington and Alaska. The mechanism causing the latitudinal pattern are unclear. Latitudinal differences in survival may be due to increased disease outbreaks associated with higher temperatures in the south (Ebert et al. 1999) or the presence of more predator species in the south (Tegner, 2001). Physiological senescence related to temperature is unlikely because there is no pattern to growth differences associated with latitude (Ebert et al., 1999) and no evidence for physiological decline in relative gonad size in the south (Tegner and Levin, 1983) or north (Kramer and Nordin, 1975). The largest individuals continue to develop gonad masses in accord with the same allometric relationships as smaller individuals. It is reasonable to conclude that senescence does not occur in red sea urchins.

**Table 1**

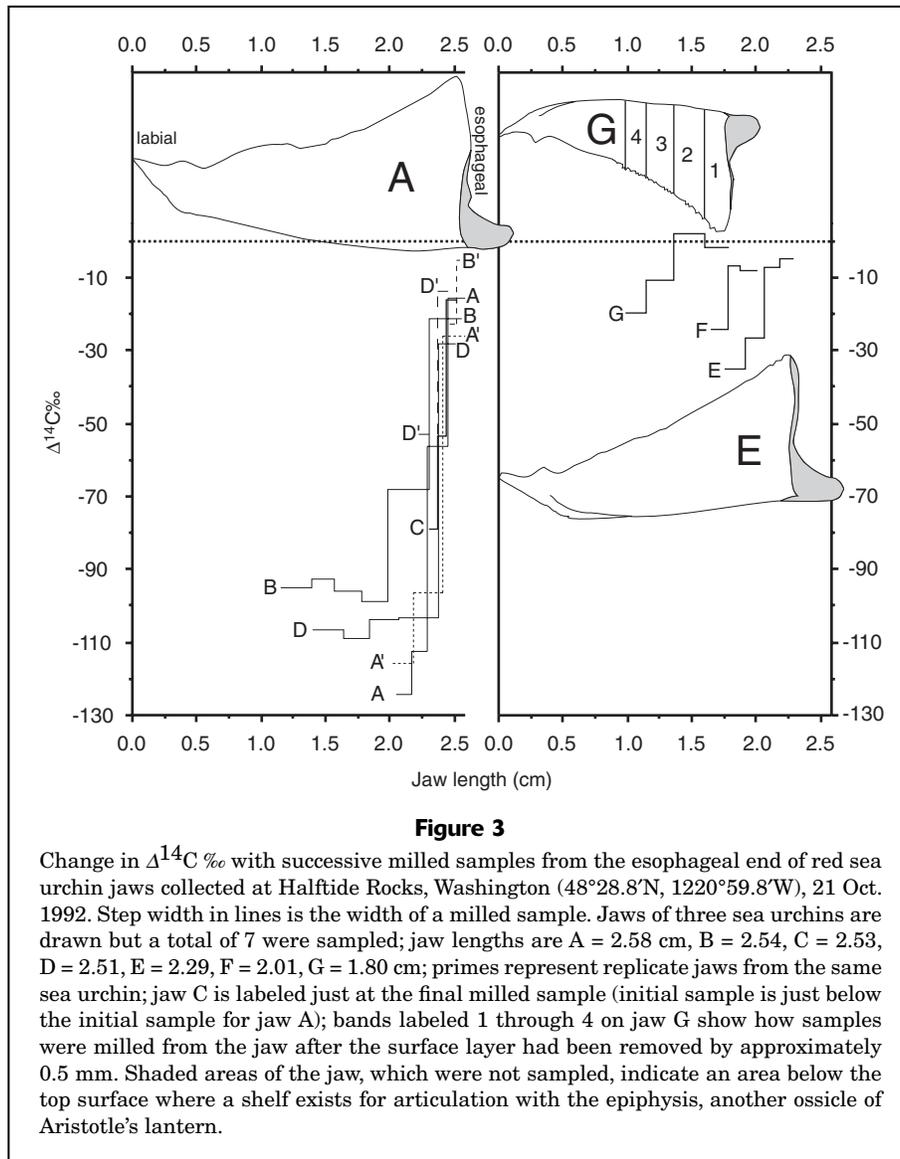
Maximum age estimates for sea urchins based on growth zones in skeletal ossicles.

| Species                                      | Years | Reference                          |
|--|-------|------------------------------------|
| <i>Lytechinus variegatus</i>                 | 4     | Beddingfield and McClintock (2000) |
| <i>Strongylocentrotus nudus</i>              | 6     | Kawamura (1966)                    |
| <i>Psammechinus miliaris</i>                 | 7     | Jensen (1969)                      |
| <i>Paracentrotus lividus</i>                 | 8     | Crapp and Willis (1975)            |
| <i>Sphaerechinus granularis</i>              | 9     | Lumingas and Guillou (1994)        |
| <i>Evechinus chloroticus</i>                 | 10    | Dix (1972)                         |
| <i>Psammechinus miliaris</i>                 | 10    | Gage (1991)                        |
| <i>Strongylocentrotus intermedius</i>        | 10    | Agatsuma (2001)                    |
| <i>Echinus acutus</i> var. <i>norvegicus</i> | 11    | Gage et al. (1986)                 |
| <i>Loxechinus albus</i>                      | 11    | Gebauer and Moreno (1995)          |
| <i>Echinus esculentus</i>                    | 12    | Nichols et al. (1985)              |
| <i>Allocentrotus fragilis</i>                | 15    | Sumich and McCauley (1973)         |
| <i>Echinus elegans</i>                       | 21    | Gage et al. (1986)                 |
| <i>Strongylocentrotus droebachiensis</i>     | 24    | Robinson and MacIntyre (1997)      |
| <i>Echinus affinis</i>                       | 28    | Gage and Tyler (1985)              |
| <i>Sterechinus neumayeri</i>                 | 40    | Brey et al. (1995)                 |
| <i>Sterechinus antarcticus</i>               | 75    | Brey (1991)                        |

Red sea urchins larvae spend at least two months in the plankton (Strathmann, 1978) during which time they can be carried far along the coast or out to sea. There is year-to-year variation in settlement and recruitment and years of zero success and greater variation at northern sites (Bernard and Miller, 1973, Low, 1975, Tegner and Dayton, 1981, Duggins, 1983, Pearse and Hines, 1987, Sloan et al., 1987, Ebert et al., 1994). An important point, however, is that these authors reported some recruitment at study sites and so extreme longevity would at first seem unnecessary for species survival. The important issue for evolution of life histories, however, is not whether some individuals

recruit to the population but how successful an individual is each year in leaving offspring. The long life of adult red sea urchins emphasizes the difficulties individuals have in successfully having offspring that settle in suitable habitat and survive to reproductive age. Many annual reproductive episodes appear to be required to succeed and therefore red sea urchins are classic bet hedgers that use resources to promote annual survival of adults as well as to reproduce (Stearns, 1992).

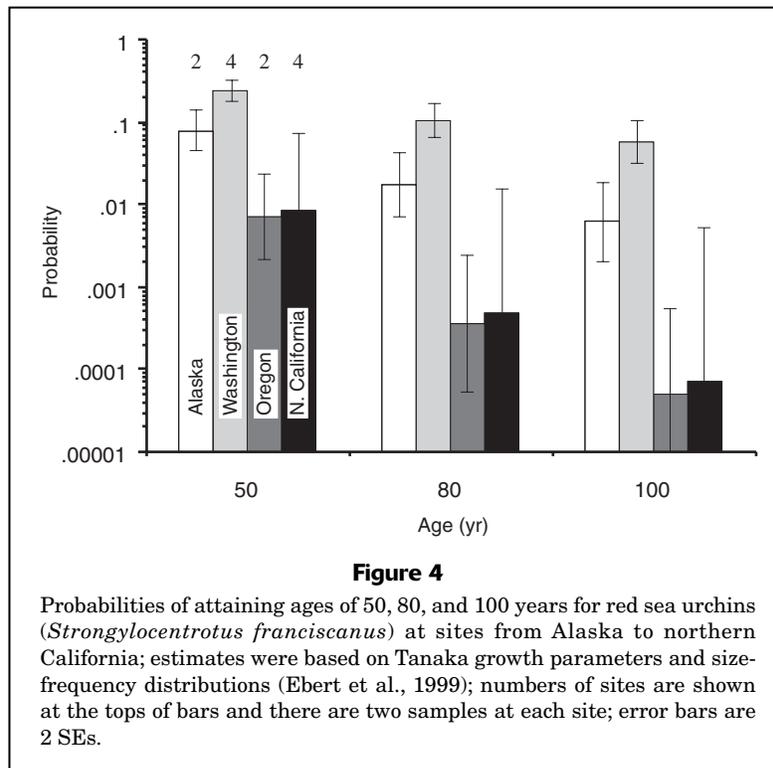
Attributes of a long life span have consequences for resource management. The implications for management of the red sea urchin resource have been explored by us-



ing elasticity analysis (de Kroon et al., 1986) of a matrix model and have shown that small changes in survival of individuals larger than 9 cm would have a greater effect on population maintenance than survival of smaller sea urchins (Ebert, 1998). The conclusion from matrix analysis, which is supported by the  $^{14}\text{C}$  test of growth and age of *Strongylocentrotus franciscanus* we present in our study, is that the preservation of large individuals must be included in long-term management plans for this species as well as for other long-lived sea urchins in developing fisheries such as that for *Evechinus chloroticus* (Barker, 2001). Finally, our work strongly suggests that life spans of other exploited sea urchin species should be explored in greater detail in developing management plans because preservation of large and old individuals may be very important for the long-term viability of these fisheries.

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## Literature cited

- Agatsuma, Y.  
2001. Ecology of *Strongylocentrotus intermedius*. In Edible sea urchins: biology and ecology (J. M. Lawrence, ed.), p. 333–346. Developments in aquaculture and fisheries science, no. 32. Elsevier Science B. V., Amsterdam, Netherlands.
- Barker, M. F.  
2001. The ecology of *Evechinus chloroticus*. In Edible sea urchins: biology and ecology (J. M. Lawrence, ed.), p. 245–260. Developments in aquaculture and fisheries science, no. 32. Elsevier Science B. V., Amsterdam, Netherlands.
- Beddingfield, S. D., and J. B. McClintock.  
2000. Demographic characteristics of *Lytechinus variegatus* (Echinoidea: Echinoidea) from three habitats in a north Florida bay, Gulf of Mexico. *Mar. Ecol.* 21:17–40.
- Bernard, F. R., and D. C. Miller.  
1973. Preliminary investigation on the red sea urchin resources of British Columbia [*Strongylocentrotus franciscanus* (Agassiz)]. *Fish. Res. Board Can. Tech. Rep.* 400: 1–37.
- Breen, P. A., and B. E. Adkins.  
1976. Growth rings and age in the red sea urchin, *Strongylocentrotus franciscanus*. *Fish. Res. Board Can. Manusc. Rep. Ser.* 1413.
- Brey, T.  
1991. Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea shelf and slope, Antarct. *Antarctic Sci.* 3:251–256.
- Brey, T., J. Pearse, L. Basch, J. McClintock, and M. Slattery.  
1995. Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarct. *Mar. Biol.* 124:279–292.
- Broecker, W. S., T.-H. Peng, G. Ostlund, and M. Stuiver.  
1985. The distribution of bomb radiocarbon in the ocean. *J. Geophys. Res.* 90:6953–6970.
- Bureau, D.  
1996. Relationship between feeding, reproductive condition, jaw size and density in the red sea urchin, *Strongylocentrotus franciscanus*. M.S. thesis, 90 p. Simon Fraser Univ., Burnaby, Canada.
- Campana, S. E.  
1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock *Melanogrammus aeglefinus*. *Mar. Ecol. Prog. Ser.* 150:49–56.
- Campana, S. E., L. J. Natanson, and S. Myklevoll.  
2002. Bomb dating and age determination of large pelagic sharks. *Can. J. Fish. Aquat. Sci.* 59:450–455.
- Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels.  
1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Am. Zool.* 34:397–408.
- Crapp, G. B., and M. E. Willis.  
1975. Age determination in the sea urchin *Paracentrotus lividus* (Lamarck), with notes on the reproductive cycle. *J. Exp. Mar. Biol. Ecol.* 20:157–178.
- de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell.  
1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.
- Dix, T. G.  
1972. Biology of *Evechinus chloroticus* (Echinoidea: Echinometridae) from different localities. 4. Age, growth, and size. *N. Z. J. Mar. Freshw. Res.* 6:48–68.
- Duffy, P. B., D. E. Eliason, A. J. Bourgeois, and C. C. Covey.  
1995. Simulation of bomb radiocarbon in two global ocean general circulation models. *J. Geophys. Res.* 100:22545–22563.

- Duggins, D. O.  
1983. Starfish predation and the creation of mosaic patterns in a kelp-dominated community. *Ecology* 64:1610–1619.
- Ebert, T. A.  
1988. Calibration of natural growth lines in ossicles of two sea urchins, *Strongylocentrotus purpuratus* and *Echinometra mathaei*, using tetracycline. In *Echinoderm biology: proceedings of the sixth international echinoderm conference* (R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds.), p. 435–443. A. A. Balkema, Rotterdam, Netherlands.  
1998. An analysis of the importance of Allee effects in management of the red sea urchin *Strongylocentrotus franciscanus*. In *Echinoderms: San Francisco. Proceedings, 9th international echinoderm conference* (R. Mooi and M. Telford, eds.), p. 619–627. A. A. Balkema, Rotterdam, Netherlands.
- Ebert, T. A., J. D. Dixon, S. C. Schroeter, P. E. Kalvass, N. T. Richmond, W. A. Bradbury, and D. A. Woodby.  
1999. Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. *Mar. Ecol. Prog. Ser.* 190:189–209.
- Ebert, T. A., S. C. Schroeter, J. D. Dixon, and P. E. Kalvass.  
1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. *Mar. Ecol. Prog. Ser.* 111:41–52.
- Gage, J. D.  
1991. Skeletal growth zones as age-markers in the sea urchin *Psammechinus miliaris*. *Mar. Biol.* 110:217–228.
- Gage, J. D., and P. A. Tyler.  
1985. Growth and recruitment of the deep-sea urchin *Echinus affinis*. *Mar. Biol.* 90:41–53.
- Gage, J. D., P. A. Tyler, and D. Nichols.  
1986. Reproduction and growth of *Echinus acutus* var. *norvegicus* Duben & Kören and *E. elegans* Duben & Kören on the continental slope off Scotland. *J. Exp. Mar. Biol. Ecol.* 101:61–83.
- Gebauer, P., and C. A. Moreno.  
1995. Experimental validation of the growth rings of *Loxechinus albus* (Molina, 1782) in southern Chile (Echinodermata: Echinoidea). *Fish. Res.* 21:423–435.
- Guilderson, T. P., and D. P. Schrag.  
1998. Abrupt shift in subsurface temperatures in the tropical Pacific associated with changes in El Niño. *Science* 281:240–243.
- Hastings, A., and K. Higgins.  
1994. Persistence of transients in spatially structured ecological models. *Science* 263:1133–1136.
- Hilborn, R., and C. J. Walters.  
1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty, 570 p. Chapman & Hall, New York, NY.
- Jensen, M.  
1969. Breeding and growth of *Psammechinus miliaris* (Gmelin). *Ophelia* 7:65–78.
- Kalish, J. M.  
1993. Pre- and post-bomb radiocarbon in fish otoliths. *Earth Planet. Sci. Lett.* 114:549–554.  
1995. Radiocarbon and fish biology. In *Recent developments in fish otolith research* (D. H. Secor, J. M. Dean, and S. E. Campana, eds.), p. 637–653. Univ. South Carolina Press, Columbia, SC.
- Kawamura, K.  
1966. On the age determining character and growth of a sea urchin, *Strongylocentrotus nudus*. *Sci. Rep. Hokkaido Fish. Exp. Station* 6:56–61.
- Kramer, D. E., and D. M. A. Nordin.  
1975. Physical data from a study of size, weight and gonad quality for the red sea urchin (*Strongylocentrotus franciscanus* (Agassiz)) over a one-year period. *Fish. Res. Board Can. Manusc. Rep. Ser.* 1372:68.
- Lamare, M. D., and P. V. Mladenov.  
2000. Modelling somatic growth in the sea urchin *Evechinus chloroticus* (Echinoidea: Echinometridae). *J. Exp. Mar. Biol. Ecol.* 243:17–43.
- Low, C. J.  
1975. The effect of grouping of *Strongylocentrotus franciscanus*, the giant red sea urchin, on its population biology. Ph.D. diss., 157 p. Univ. British Columbia, Vancouver, Canada.
- Lumingas, L. J. L., and M. Guillou.  
1994. Growth zones and back-calculation for the sea urchin, *Sphaerechinus granularis*, from the Bay of Brest, France. *J. Mar. Biol. Assoc. U. K.* 74:671–686.
- Murphy, G. I.  
1968. Pattern in life history and the environment. *Am. Nat.* 102:391–411.
- Nichols, D., A. A. T. Sime, and G. M. Bishop.  
1985. Growth in populations of the sea-urchin *Echinus esculentus* L. (Echinodermata: Echinoidea) from the English Channel and Firth of Clyde. *J. Exp. Mar. Biol. Ecol.* 86:219–228.
- Nydal, R., and K. Lovseth.  
1983. Tracing bomb <sup>14</sup>C in the atmosphere 1962–1980. *J. Geophys. Res.* 88:3621–3621.
- Pearse, J. S., and A. H. Hines.  
1987. Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Mar. Ecol. Prog. Ser.* 39:275–283.
- Peck, L. S., and T. Brey.  
1996. Bomb signals in old Antarctic brachiopods. *Nature* 380:207–208.
- Robinson, S. M. C., and A. D. MacIntyre.  
1997. Aging and growth of the green sea urchin. *Bull. Aquacul. Assoc. Can.* 91:56–60.
- Roff, D. A.  
1992. The evolution of life histories, 535 p. Chapman & Hall, New York, NY.
- Russell, M. P., T. A. Ebert, and P. S. Petraitis.  
1998. Field estimates of growth and mortality of the green sea urchin, *Strongylocentrotus droebachiensis*. *Ophelia* 48:137–153.
- Sloan, N. A.  
1986. Red sea urchin. Underwater world. DFO/2322 UW/53, 4 p. Fisheries and Oceans Canada, Ottawa, Canada.
- Sloan, N. A., C. P. Lauridsen, and R. M. Harbo.  
1987. Recruitment characteristics of the commercially harvested red sea urchin *Strongylocentrotus franciscanus* in southern British Columbia, Canada. *Fish. Res.* 5:55–69.
- Stearns, S. C.  
1992. The evolution of life histories, 249 p. Oxford Univ. Press, New York, NY.
- Strathmann, R.  
1978. Length of pelagic period in echinoderms with feeding larvae from the northwest Pacific. *J. Exp. Mar. Biol. Ecol.* 34:23–27.
- Stuiver, M., and H. A. Polach  
1977. Discussion: reporting of <sup>14</sup>C data. *Radiocarbon* 19:355–363.
- Sumich, J. L., and J. E. McCauley  
1973. Growth of a sea urchin, *Alloccentrotus fragilis*, off the Oregon Coast. *Pac. Sci.* 27:156–167.

- Tanaka, M.  
1982. A new growth curve which expresses infinite increase. Publ. Amakusa Mar. Biol. Lab. 6:167-177.  
1988. Eco-physiological meaning of parameters of ALOG growth curve. Publ. Amakusa Mar. Biol. Lab. 9:103-106.
- Tegner, M. J.  
2001. The ecology of *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In *Edible sea urchins: biology and ecology* (J. M. Lawrence, ed.), p. 307-332. Developments in aquaculture and fisheries science, no. 32. Elsevier Science B. V., Amsterdam, Netherlands.
- Tegner, M. J., and P. K. Dayton.  
1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. Mar. Ecol. Prog. Ser. 5: 255-268.
- Tegner, M. J., and L. A. Levin.  
1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. J. Exp. Mar. Biol. Ecol. 73:125-150.
- Turekian, K. K., J. K. Cochran, Y. Nozaki, I. Thompson, and D. S. Jones.  
1982. Determination of shell deposition rates of *Arctica islandica* from the New York Bight using natural  $^{228}\text{Ra}$  and  $^{228}\text{Th}$  and bomb produced  $^{14}\text{C}$ . Limnol. Oceanogr. 27: 737-741.
- Vogel, J. S., J. R. Southon, and D. E. Nelson.  
1987. Catalyst and binder effects in the use of filamentous graphite for AMS. Nucl. Instru. Methods Phys. Res. Sec. B 29:50-56.
- Witbaard, R., M. I. Jenness, K. van der Borg, and G. Ganssen.  
1994. Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes. Neth. J. Sea. Res. 33:91-101.