Occurrence of the collector sea urchin Tripneustes gratilla with over-a-decade longevity under rearing

Occurrence of the collector sea urchin *Tripneustes gratilla* with over-a-decade longevity under rearing

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A short running title: Longevity of *Tripneustes gratilla*

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Abstract

The life expectancy (i.e., an average life span in a population) of *Tripneustes gratilla* has been reported as short as 1 or 2 years in natural environments, which is relatively short among sea urchins. However, some *T. gratilla* individuals can live for up to 5 years under rearing and 6.85 years in the field, according to previous reports. Until present, the maximum longevity that a certain individual of *T. gratilla* can physiologically live remains unknown. The present study conducted long-term rearing during 12.2 years of hatchery-produced *T. gratilla* in tanks to investigate its longevity. We especially focused on whether the maximum longevity among *T. gratilla* individuals exceeds a decade, as in the case of most sea urchin species. At the end of the rearing period, eight *T. gratilla* individuals were still alive. In last 9.5 years of the rearing period, during which dead individuals were counted, the mortality was 41% (7 out of 17 individuals). During growth, the body weight was related to the transverse test diameter to a power of 2.84. The asymptotic transverse test diameter and body weight, determined by fitting to the von Bertalanffy growth function, were 95.9 mm and 344 g, respectively. The results of the present study suggest that *T. gratilla* has the maximum longevity of more than a decade under rearing conditions, and the short-lived characteristics of this species in natural environments are mainly attributed to ecological factors.

Introduction

Tripneustes gratilla (Linnaeus, 1758) is a sea urchin that belongs to the Toxopneustidae family and is distributed in the tropical Indo-Pacific region (Rowe and Gates 1995). This species is commercially valuable and is targeted for both fishery and aquaculture (Andrew et al. 2002; McBride 2005). However, *T. gratilla* resources have been overexploited such as in Japan and the Philippines (Juinio-Meñez et al. 1998; Ohta et al. 2017), and attempts have been made to restock them using hatchery-produced *T. gratilla* (e.g., Shimabukuro 1991; Juinio-Meñez et al. 2008). Despite these efforts, restocking remains challenging due to low survival of hatchery-produced *T. gratilla* juveniles released into natural environments (Ohta et al. 2017). Lifespan is an important factor to consider when restoring or conserving *T. gratilla* populations, as it affects population stability and variability. Lifespan data are also important for aging studies that use sea urchins as model organisms (e.g., Bodnar 2009).

Previously, *T. gratilla* has been regarded as a short-lived species among sea urchins (Toha et al. 2017; Lawrence and Agatsuma 2020). Its average life expectancy at birth (hereafter, 'life expectancy'), which is based on statistical data of a population, has been estimated to be from one year (Ebert 1982; Bacolod and Dy 1986; Dafni and Tobol 1986) to two years (Shimabukuro 1991) in natural environments. However, Pan (2012) showed that some *T. gratilla* individuals survived for 6.85 years in natural environments in Hawaii based on tagging and recapture. Additionally, Cyrus (2013) reported that *T. gratilla* lived for five years under rearing conditions, although details about the growth pattern and rearing conditions were not provided. These latter two studies imply that some *T. gratilla* individuals can live much longer than their life expectancy estimated as one or two years. In general, sea urchins have variable longevity (defined as the lifespan that a certain individual can live), ranging from a few years to nearly 10^2 years, with most species having a longevity of around 10^1 years, based on growth zones in skeletal ossicles (Ebert and Southon 2003). However, it is still unclear whether *T. gratilla* has the potential longevity for over a decade like many other sea urchins or if it is physiologically destined to have a short lifespan of only a few years. Elucidating this point could be a clue to understanding why *T. gratilla* has such short life expectancy in natural environments.

The present study conducted a long-term rearing trial of hatchery-produced *T. gratilla* to investigate the maximum longevity of this species. The period was about twelve years, chosen not only for its practicality as a rearing period but also to confirm if *T. gratilla* has potential longevity over a decade, like the majority of other sea urchins. The growth pattern was also monitored during this period to determine if the reared individuals had similar or unique growth potential compared to those in previous studies. As a study design, this paper only focuses on the potential longevity of *T. gratilla* at an individual level and does not address its life expectancy at a population level, which needs to be estimated by continuously monitoring the mortality rate. It is mainly because of the practical difficulty to maintain rearing conditions for a long term without occurrence of mass mortality such as by diseases, which can easily affect the result of estimation of life expectancy.

Materials and Methods

Hatchery-produced juveniles of *T. gratilla* were supplied by the Sea Farming Center of the Okinawa Prefectural Government located in Motobu, Okinawa, Japan, on 11 April 2011 (five months after larval settlement). These juveniles were reared in cages (55 cm × 55 cm × 40 cm in height) made of high-density polyethylene net with 10 mm × 10 mm mesh (N-24, C.I. Takironcivil Corporation, Osaka, Japan). The cages were suspended in seawater-flowing tanks at the Japan Fisheries Research and Education Agency facilities in Ishigaki, Okinawa, Japan. The following tanks were used for rearing: a 4800-L fiber-reinforced plastics (FRP) raceway tank (with an inside size of 5 m × 1.5 m × 0.7 m in height, ERT-4.8, Nihon Sacas Co., Ltd., Hiroshima, Japan) at the Ishigaki Field Station (abolished in 2016) until 2016, and a 2000-L FRP round tank (with an inside size of 1.94 m in diameter × 0.8 m in height, MF-2000S, Nihon Sacas Co., Ltd., Hiroshima, Japan) and a 400-L FRP square tank (with an inside size of 1.4 m × 0.6 m × 0.49 m in height, KF-400S, Nihon Sacas Co., Ltd., Hiroshima, Japan) after 2016 at the neighboring Yaeyama Field Station. Seawater (with a temperature range of 19–31°C and a salinity of 34–35) filtered through silica sand was supplied to the tanks at a rate above 4 L min^{-1}. The types and amount of feed were not uniform throughout the rearing period. The types of feed mainly included Sargassaceae, *Ulva* spp., *Padina* spp., and leaves of mulberry tree (*Morus alba*), but also included other seaweeds and land plants.

The transverse test diameter and body weight of *T. gratilla* individuals were continually measured. The total number of *T. gratilla* reared at the start of sampling (14 May 2012) was 436 individuals. The sampling design varied between the early (May 2012 to January 2013) and late (March 2014 to January 2023) periods of rearing.

During the early period, a total of 403 individuals were sampled for size measurement. These individuals were not returned to the rearing cages and served for another study (Y. Machiguchi unpublished data). The number of replicates at each timing of size measurement ranged from 9 to 60 individuals. Individuals that died naturally during rearing were not recorded before July 2013 but were recorded from that time until the end of the rearing. The size of these dead individuals was also used for growth analysis along with data from live individuals.

During the late period of rearing after March 2014, the remaining 14 individuals were continuously reared. At every sampling time, sizes of all reared individuals were measured and then returned to the cages for continuously rearing until the next measurement. In addition to natural death during rearing, two individuals were mistakenly killed by human error between 22 July 2016 and 6 November 2017.

The relationship between test diameter (L) and body weight (W) was determined using the following equation:

$$W = b \times L^a,$$

where a and b are the constants. The growth curve of *T. gratilla* based on test diameter was fitted to the von Bertalanffy growth function (VBGF):

$$L = L_\infty(1 - \exp(-Kt)),$$

where L_∞, K, and t denote asymptotic test diameter, growth coefficient, and age, respectively. The age of *T. gratilla* individuals was defined as the time after settlement, calculated as being 30 days from the spawning date (24 September 2010), assuming a typical planktonic larval period for this species (Shimabukuro 1991). In contrast, the growth curve of *T. gratilla* based on body weight was fitted to another form of VBGF:

$$W = W_\infty(1 - \exp(-K_{sp}t))^a,$$

where W_∞ and a are the asymptotic body weight and a constant, respectively. The constant a was determined from the diameter–weight relationship using the first equation. All these fittings were performed by the least-squares method using the "curve_fit" function of the "optimize" module in the "scipy" library in Python 3.10 (https://www.python.org/).

Results and Discussion

At the end of the rearing period of 12.2 years, eight individuals of *T. gratilla* were still alive. This result clearly showed that *T. gratilla* can have a longevity of over a decade at least at an individual level, which is comparable to the longevity of many other sea urchins (Ebert and Southon 2003). Unfortunately, the mortality was not recorded throughout the entire rearing period. However, from July 2013 to January 2023, during which dead individuals were counted, the mortality was 41% (7 out of 17 individuals), excluding two individuals who were mistakenly killed. No *T. gratilla* individuals died during the last five years of the rearing after 2017.

During growth, the body weight of *T. gratilla* was related to the test diameter with a power of $a = 2.84$ (Fig. 1a). The growth parameters of VBGF based on test diameter were $L_\infty = 95.9 \pm 0.9$ (mm) and $K = 0.660 \pm 0.014$ (Fig. 1b), whereas those based on the body weight were $W_\infty = 344 \pm 5$ (g) and $K_{sp} = 0.643 \pm 0.009$ (Fig. 1c). The L_∞ in the present study was no larger than previously reported values (82–114 mm, Bacolod and Dy 1986; Juinio-Meñez et al. 2008; Regalado et al. 2010), regardless of the longer-term rearing, supporting the view that this size represents the biological maximum size of *T. gratilla*. The K value was lower than those previously reported as 1.08–1.8 (Bacolod and Dy 1986; Juinio-Meñez et al. 2008; Regalado et al. 2010), probably because of the non-satiated feeding condition. Partly due to this slow growth rate, increase in test diameter and body weight was recognizable until around 5–7 years old. That is, *T. gratilla* still possessed growth capability even at ages much older than its common life expectancy in the wild (1–2 years, Ebert 1982; Bacolod and Dy 1986; Dafni and Tobol 1986; Shimabukuro 1991), which seems to be related to the fact that senescence is negligible in sea urchins (Ebert 2008; Bodnar 2015).

The short life expectancy of 1–2 years for *T. gratilla* in natural environments (Ebert 1982; Bacolod and Dy 1986; Dafni and Tobol 1986; Shimabukuro 1991), compared to its maximum longevity under rearing conditions, is probably due to ecological factors rather than senescence. In fact, several mortality factors have been reported for *T. gratilla* in the environment. For example, stormy waves caused mortality scaled of an entire population of *T. gratilla* in the northern Red Sea, although such mortality occurred seasonally and not every year and occurred only in wave-exposed sites and not in reef-protected sites (Dafni and Tobol 1986). Heavy rain (41 mm / 2 h) during low tide is also known to cause mass mortality of juvenile *T. gratilla* (35.7% of the total individuals) due to low salinity in Okinawa, Japan (Shimabukuro 1991). This mortality occurred in the habitat of juveniles in shallow near-shore areas but not in more offshore areas at the inner reef. Such physical mortality factors are also recognized as significant for hatchery-produced juveniles of *T. gratilla* after released into natural environments, in restocking programs from 1995 to 2013 in Okinawa, Japan (Ohta et al. 2017). Compared to other sea urchins, *T. gratilla* has relatively thin body wall and mainly inhabits environments with low exposure to surf, which is interpreted as that *T. gratilla* allocates more resources to growth and reproductive ability than "maintenance" of the body (i.e., morphological features, physiological processes, and behavioral characteristics that increase the probability of survival), and thus, susceptible to various stresses including physical disturbances and predation etc. (Ebert 1982).

Predation is another major mortality factor for *T. gratilla* and can change its density and population structure (Dafni and Tobol 1986; McClanahan 1998; Eklöf et al. 2009). Especially small (< 40 mm) individuals of *T. gratilla* are heavily predated (Dafni and Tobol 1986). Its major predators are Balistidae and Labridae (e.g., *Coris aygula*) fishes (but potentially a more diverse species, Keller 1983; Parker and Shulman 1986), sea stars (e.g., *Protoreaster lincki*, *Culcita schmideliana*, and *Pentaceraster mammillatus*) and gastropods (typically of the genus *Cassis*, Hughes and Hughes 1971; Keller 1983) (Dafni and Tobol 1986; McClanahan 1998; Eklöf et al. 2009). Predation on *T. gratilla* is apparently high in open sandy areas (Dafni and Tobol 1986) and is ameliorated by the presence of shelters such as seagrass canopies (e.g., 700 shoots m^{-2} of *Thalassodendron ciliatum*, Eklöf et al. 2009). Small rock crevices (~5–20 cm) that fit sea urchin bodies can also be shelters, but available crevices are usually limited in environments and competed among sea urchins (McClanahan 1988). McClanahan (1998) reported that the degree of predation pressure changes the partitioning of those shelters between several sea urchin species, and *T. gratilla* adapts to environments at a relatively low level of predation. Predation on sea urchins is also reduced by removal of predators by overfishing (McClanahan and Shafir 1990).

Disease also caused mass mortality of *T. gratilla* in Hawai‘i (Work et al. 2023). In addition, latitudinal variation of disease and temperature-related stress likely affect mortality of sea urchins (Ebert et al. 1999). Fishery by human can also exhaust an entire population of *T. gratilla* (Juinio-Meñez et al. 1998).

In summary, there are many known mortality factors, and the life expectancy of *T. gratilla*, which is much shorter than its maximum longevity under rearing conditions, can be probably explained by them. On the other hand, mortality can be considerably variable among environments as described above. In general, populations in habitats with high adult mortality (i.e., “marginal” habitats) are sustained by high recruitment and mainly composed of young individuals, whereas populations in habitats with low adult mortality (i.e., “superior” habitats) are mainly composed of high-age individuals but have low recruitment (Ebert 1982). Ebert (1982) and Dafni and Tobol (1986) consistently reported that the life expectancy of *T. gratilla* was annual at “marginal” habitats but perennial at “superior” habitats. However, accurate length of the “perennial” life was not evaluated in these studies due to methodological limitation. Namely, their analyses based on body size composition have difficulty resolving cohorts at high ages, as *T. gratilla*, for example, attains 95% of the maximum size in 1.66 years when $K = 1.8$ (Bacolod and Dy 1986) and shows minimal growth beyond this age. Therefore, it should be noted that the recognition of the life expectancy of this species as one or two years (e.g., Toha et al. 2017) contains rather ambiguity about its upper limit.

Knowledge has been limited about the longevity of *T. gratilla* in such “superior” habitats, except for Pan (2012) who reported the 6.85-year longevity of *T. gratilla* in the wild. The longevity of *T. gratilla* over 12.2 years in the present study indicates the life history potential of this species to adapt to such “superior” habitats. Further research is required to evaluate the variability of the longevity of this species among different habitats, for example, using techniques for more precise age estimation such as chemical tags and radiocarbon markers (e.g., Ebert and Southon 2003), or by surveys in unexplored habitats (e.g., deep habitats up to 75 m, Rowe and Gates 1995).

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Figure legends

Fig. 1 (a) The diameter–weight relationship and the von Bertalanffy growth curve of *Tripneustes gratilla* based on (b) transverse test diameter and (c) body weight during 12.2 years of rearing. Solid lines, circles, and gray areas indicate model estimates, individual data, and 95% confidence intervals, respectively.

Figures

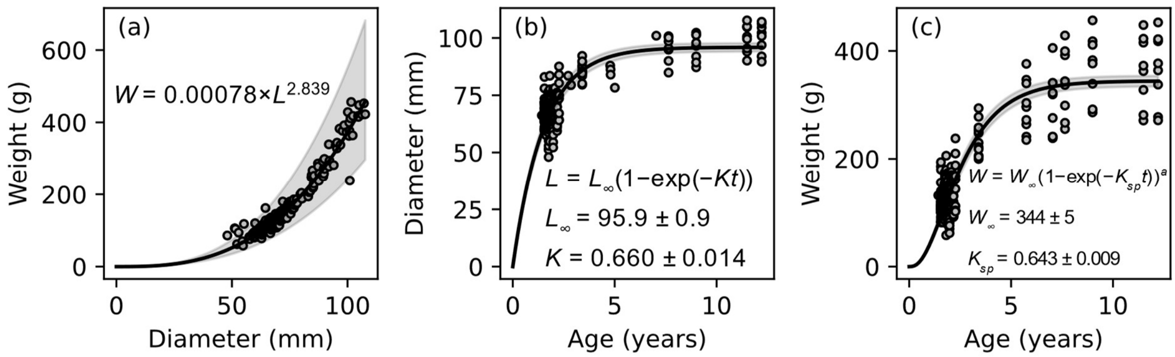

Fig. 1