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

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14 Abstract

15 The life expectancy (i.e., an average life span in a population) of Tripneustes gratilla has 16 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 17 18 6.85 years in the field, according to previous reports. Until present, the maximum longevity that 19 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 20 21 investigate its longevity. We especially focused on whether the maximum longevity among T. 22 gratilla individuals exceeds a decade, as in the case of most sea urchin species. At the end of the 23 rearing period, eight T. gratilla individuals were still alive. In last 9.5 years of the rearing period, 24 during which dead individuals were counted, the mortality was 41% (7 out of 17 individuals). 25 During growth, the body weight was related to the transverse test diameter to a power of 2.84. 26 The asymptotic transverse test diameter and body weight, determined by fitting to the von 27 Bertalanffy growth function, were 95.9 mm and 344 g, respectively. The results of the present 28 study suggest that T. gratilla has the maximum longevity of more than a decade under rearing 29 conditions, and the short-lived characteristics of this species in natural environments are mainly 30 attributed to ecological factors.

32 Introduction

33	Tripneustes gratilla (Linnaeus, 1758) is a sea urchin that belongs to the Toxopneustidae
34	family and is distributed in the tropical Indo-Pacific region (Rowe and Gates 1995). This species
35	is commercially valuable and is targeted for both fishery and aquaculture (Andrew et al. 2002;
36	McBride 2005). However, T. gratilla resources have been overexploited such as in Japan and the
37	Philippines (Juinio-Meñez et al. 1998; Ohta et al. 2017), and attempts have been made to restock
38	them using hatchery-produced T. gratilla (e.g., Shimabukuro 1991; Juinio-Meñez et al. 2008).
39	Despite these efforts, restocking remains challenging due to low survival of hatchery-produced
40	T. gratilla juveniles released into natural environments (Ohta et al. 2017). Lifespan is an
41	important factor to consider when restoring or conserving T. gratilla populations, as it affects
42	population stability and variability. Lifespan data are also important for aging studies that use sea
43	urchins as model organisms (e.g., Bodnar 2009).
44	Previously, T. gratilla has been regarded as a short-lived species among sea urchins
45	(Toha et al. 2017; Lawrence and Agatsuma 2020). Its average life expectancy at birth (hereafter,
46	'life expectancy'), which is based on statistical data of a population, has been estimated to be
47	from one year (Ebert 1982; Bacolod and Dy 1986; Dafni and Tobol 1986) to two years
48	(Shimabukuro 1991) in natural environments. However, Pan (2012) showed that some T. gratilla
49	individuals survived for 6.85 years in natural environments in Hawaii based on tagging and
50	recapture. Additionally, Cyrus (2013) reported that T. gratilla lived for five years under rearing
51	conditions, although details about the growth pattern and rearing conditions were not provided.
52	These latter two studies imply that some T. gratilla individuals can live much longer than their
53	life expectancy estimated as one or two years. In general, sea urchins have variable longevity
54	(defined as the lifespan that a certain individual can live), ranging from a few years to nearly 10^2
55	years, with most species having a longevity of around 10^1 years, based on growth zones in
56	skeletal ossicles (Ebert and Southon 2003). However, it is still unclear whether T. gratilla has the
57	potential longevity for over a decade like many other sea urchins or if it is physiologically
58	destined to have a short lifespan of only a few years. Elucidating this point could be a clue to
59	understanding why <i>T. gratilla</i> has such short life expectancy in natural environments.

60 The present study conducted a long-term rearing trial of hatchery-produced *T. gratilla* to
61 investigate the maximum longevity of this species. The period was about twelve years, chosen

62 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 63 64 monitored during this period to determine if the reared individuals had similar or unique growth 65 potential compared to those in previous studies. As a study design, this paper only focuses on the 66 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 67 68 is mainly because of the practical difficulty to maintain rearing conditions for a long term 69 without occurrence of mass mortality such as by diseases, which can easily affect the result of 70 estimation of life expectancy.

71 Materials and Methods

72 Hatchery-produced juveniles of T. gratilla were supplied by the Sea Farming Center of 73 the Okinawa Prefectural Government located in Motobu, Okinawa, Japan, on 11 April 2011 (five 74 months after larval settlement). These juveniles were reared in cages (55 cm \times 55 cm \times 40 cm in 75 height) made of high-density polyethylene net with 10 mm × 10 mm mesh (N-24, C.I. 76 Takironcivil Corporation, Osaka, Japan). The cages were suspended in seawater-flowing tanks at 77 the Japan Fisheries Research and Education Agency facilities in Ishigaki, Okinawa, Japan. The 78 following tanks were used for rearing: a 4800-L fiber-reinforced plastics (FRP) raceway tank 79 (with an inside size of 5 m \times 1.5 m \times 0.7 m in height, ERT-4.8, Nihon Sacas Co., Ltd., 80 Hiroshima, Japan) at the Ishigaki Field Station (abolished in 2016) until 2016, and a 2000-L FRP 81 round tank (with an inside size of 1.94 m in diameter × 0.8 m in height, MF-2000S, Nihon Sacas 82 Co., Ltd., Hiroshima, Japan) and a 400-L FRP square tank (with an inside size of $1.4 \text{ m} \times 0.6 \text{ m}$ 83 × 0.49 m in height, KF-400S, Nihon Sacas Co., Ltd., Hiroshima, Japan) after 2016 at the 84 neighboring Yaeyama Field Station. Seawater (with a temperature range of 19–31°C and a 85 salinity of 34–35) filtered through silica sand was supplied to the tanks at a rate above 4 L min⁻¹. 86 The types and amount of feed were not uniform throughout the rearing period. The types of feed 87 mainly included Sargassaceae, Ulva spp., Padina spp., and leaves of mulberry tree (Morus alba), 88 but also included other seaweeds and land plants.

89 The transverse test diameter and body weight of *T. gratilla* individuals were continually
90 measured. The total number of *T. gratilla* reared at the start of sampling (14 May 2012) was 436

91 individuals. The sampling design varied between the early (May 2012 to January 2013) and late
92 (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.

99 During the late period of rearing after March 2014, the remaining 14 individuals were 100 continuously reared. At every sampling time, sizes of all reared individuals were measured and 101 then returned to the cages for continuously rearing until the next measurement. In addition to 102 natural death during rearing, two individuals were mistakenly killed by human error between 22 103 July 2016 and 6 November 2017.

104 The relationship between test diameter (*L*) and body weight (*W*) was determined using105 the following equation:

106 $W = b \times L^a,$

107 where *a* and *b* are the constants. The growth curve of *T. gratilla* based on test diameter was108 fitted to the von Bertalanffy growth function (VBGF):

109 $L = L_{\infty}(1 - \exp(-Kt)),$

110 where L_{∞} , *K*, and *t* denote asymptotic test diameter, growth coefficient, and age, respectively. 111 The age of *T. gratilla* individuals was defined as the time after settlement, calculated as being 30 112 days from the spawning date (24 September 2010), assuming a typical planktonic larval period 113 for this species (Shimabukuro 1991). In contrast, the growth curve of *T. gratilla* based on body 114 weight was fitted to another form of VBGF:

115
$$W = W_{\infty}(1 - \exp(-K_{sp}t))^a$$

116 where W_{∞} and *a* are the asymptotic body weight and a constant, respectively. The constant *a*

117 was determined from the diameter–weight relationship using the first equation. All these fittings

118 were performed by the least-squares method using the "curve_fit" function of the "optimize" 119 module in the "scipy" library in Python 3.10 (https://www.python.org/).

120 **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.

128 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 $L_{\infty} =$ 129 130 95.9 ± 0.9 (mm) and $K = 0.660 \pm 0.014$ (Fig. 1b), whereas those based on the body weight 131 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 132 larger than previously reported values (82-114 mm, Bacolod and Dy 1986; Juinio-Meñez et al. 133 2008; Regalado et al. 2010), regardless of the longer-term rearing, supporting the view that this 134 size represents the biological maximum size of T. gratilla. The K value was lower than those 135 previously reported as 1.08–1.8 (Bacolod and Dy 1986; Juinio-Meñez et al. 2008; Regalado et al. 136 2010), probably because of the non-satiated feeding condition. Partly due to this slow growth 137 rate, increase in test diameter and body weight was recognizable until around 5-7 years old. That 138 is, T. gratilla still possessed growth capability even at ages much older than its common life 139 expectancy in the wild (1-2 years, Ebert 1982; Bacolod and Dy 1986; Dafni and Tobol 1986; 140 Shimabukuro 1991), which seems to be related to the fact that senescence is negligible in sea 141 urchins (Ebert 2008; Bodnar 2015).

142 The short life expectancy of 1–2 years for *T. gratilla* in natural environments (Ebert 143 1982; Bacolod and Dy 1986; Dafni and Tobol 1986; Shimabukuro 1991), compared to its 144 maximum longevity under rearing conditions, is probably due to ecological factors rather than 145 senescence. In fact, several mortality factors have been reported for *T. gratilla* in the 146 environment. For example, stormy waves caused mortality scaled of an entire population of T. 147 gratilla in the northern Red Sea, although such mortality occurred seasonally and not every year 148 and occurred only in wave-exposed sites and not in reef-protected sites (Dafni and Tobol 1986). 149 Heavy rain (41 mm / 2 h) during low tide is also known to cause mass mortality of juvenile T. 150 gratilla (35.7% of the total individuals) due to low salinity in Okinawa, Japan (Shimabukuro 151 1991). This mortality occurred in the habitat of juveniles in shallow near-shore areas but not in 152 more offshore areas at the inner reef. Such physical mortality factors are also recognized as 153 significant for hatchery-produced juveniles of T. gratilla after released into natural 154 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 155 156 environments with low exposure to surf, which is interpreted as that T. gratilla allocates more 157 resources to growth and reproductive ability than "maintenance" of the body (i.e., morphological 158 features, physiological processes, and behavioral characteristics that increase the probability of 159 survival), and thus, susceptible to various stresses including physical disturbances and predation 160 etc. (Ebert 1982).

161 Predation is another major mortality factor for T. gratilla and can change its density and 162 population structure (Dafni and Tobol 1986; McClanahan 1998; Eklöf et al. 2009). Especially 163 small (< 40 mm) individuals of T. gratilla are heavily predated (Dafni and Tobol 1986). Its 164 major predators are Balistidae and Labridae (e.g., Coris aygula) fishes (but potentially a more 165 diverse species, Keller 1983; Parker and Shulman 1986), sea stars (e.g., Protoreaster lincki, 166 *Culcita schmideliana*, and *Pentaceraster mammillatus*) and gastropods (typically of the genus 167 Cassis, Hughes and Hughes 1971; Keller 1983) (Dafni and Tobol 1986; McClanahan 1998; 168 Eklöf et al. 2009). Predation on T. gratilla is apparently high in open sandy areas (Dafni and 169 Tobol 1986) and is ameliorated by the presence of shelters such as seagrass canopies (e.g., 700 170 shoots m⁻² of *Thalassodendron ciliatum*, Eklöf et al. 2009). Small rock crevices (~5–20 cm) that 171 fit sea urchin bodies can also be shelters, but available crevices are usually limited in 172 environments and competed among sea urchins (McClanahan 1988). McClanahan (1998) 173 reported that the degree of predation pressure changes the partitioning of those shelters between 174 several sea urchin species, and T. gratilla adapts to environments at a relatively low level of 175 predation. Predation on sea urchins is also reduced by removal of predators by overfishing 176 (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).

181 In summary, there are many known mortality factors, and the life expectancy of T. 182 gratilla, which is much shorter than its maximum longevity under rearing conditions, can be 183 probably explained by them. On the other hand, mortality can be considerably variable among 184 environments as described above. In general, populations in habitats with high adult mortality 185 (i.e., "marginal" habitats) are sustained by high recruitment and mainly composed of young 186 individuals, whereas populations in habitats with low adult mortality (i.e., "superior" habitats) 187 are mainly composed of high-age individuals but have low recruitment (Ebert 1982). Ebert 188 (1982) and Dafni and Tobol (1986) consistently reported that the life expectancy of T. gratilla 189 was annual at "marginal" habitats but perennial at "superior" habitats. However, accurate length 190 of the "perennial" life was not evaluated in these studies due to methodological limitation. 191 Namely, their analyses based on body size composition have difficulty resolving cohorts at high 192 ages, as T. gratilla, for example, attains 95% of the maximum size in 1.66 years when K = 1.8193 (Bacolod and Dy 1986) and shows minimal growth beyond this age. Therefore, it should be 194 noted that the recognition of the life expectancy of this species as one or two years (e.g., Toha et 195 al. 2017) contains rather ambiguity about its upper limit.

196 Knowledge has been limited about the longevity of T. gratilla in such "superior" habitats, 197 except for Pan (2012) who reported the 6.85-year longevity of T. gratilla in the wild. The 198 longevity of T. gratilla over 12.2 years in the present study indicates the life history potential of 199 this species to adapt to such "superior" habitats. Further research is required to evaluate the 200 variability of the longevity of this species among different habitats, for example, using 201 techniques for more precise age estimation such as chemical tags and radiocarbon markers (e.g., 202 Ebert and Southon 2003), or by surveys in unexplored habitats (e.g., deep habitats up to 75 m, 203 Rowe and Gates 1995).

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273 **Figure legends**

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

278 Figures



