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GROWTH RATE OF THE SEA URCHIN *TRIPNEUSTES GRATILLA ELATENSIS*

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ABSTRACT

Growth rates of the sea urchin *Tripneustes gratilla elatensis* were recorded from two sources: a natural population and in culture, under various diets. *T. g. elatensis* recruited in the spring, reached an average size of 35 mm horizontal diameter (HD) and a maximum size of 60 mm HD in 150 days. The annual growth rate coefficient, k, of both the Brody-Bertalanffy and Johnson's growth equations for a field population, was 0.87. The fastest-growing individuals, in both equations, showed a growth rate coefficient of 1.46 and 2.89, respectively. The mean growth rate of sea urchins fed the green macroalga *Ulva lactuca* in culture was higher than that obtained in three other groups: the field population (k = 2.14 and 2.92, respectively for both equations) those in culture fed algal turf (k = 1.46 for the Brody-Bertalanffy equation and 2.05 for Johnson's) and those fed the seagrass *Halophila stipulacea* (k = 1.40 and 2.05, respectively).

INTRODUCTION

Tripneustes gratilla elatensis is a Red Sea subspecies of the Indo-Pacific *T. gratilla* (Dafni, 1983). It forms unstable populations (Dotan, 1990) that may reach densities of over 8 adult urchins per m^2 (Mastaller, 1979). Densities may increase in polluted habitats (Mergner, 1981). This subspecies also occurs in inland salt-ponds, tolerating salinity >45‰ and winter temperatures below 15 °C (Dafni, unpublished observations). Its diet consists mainly of macroalgae and small amounts of seagrass, diatoms and coral tissue scraped from the rock (Mastaller, 1979).

Echinoid growth studies involve repeated measurement of individual sea urchins, tagged or untagged (Ebert, 1982; Crapp & Willis, 1975; Fenaux & Nouguier, 1976; Lawrence, 1975). Most commonly, growth rates are derived from samples drawn from field populations at regular intervals (Lewis, 1958; McPherson, 1965; Fuji, 1967; Ebert, 1968, 1982; Nichols et al., 1985; Bacolod & Dy, 1986).

Ebert (1975) reviewed previous papers dealing with echinoid growth and calculated growth parameters from the data, using the Brody-Bertalanffy growth model. Others (Kaufmann, 1981; Nichols et al., 1985) have questioned the use of growth curves based on this model for most organisms, pointing out its asymptotic nature when predicting maximal growth of the smallest juveniles, which is seldom the case in reality. They

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proposed, instead, the use of sigmoid growth curves, which consist of an initial exponential phase, followed by an asymptotic one. Ricker (1979) evaluated several sigmoid growth curves, such as Gompertz', the logistic and Johnson's equations, setting criteria for the use of growth curves. He also expressed his opinion that whichever curve is used, the resultant growth parameters, k, S_∞ and t_0, based on this model should correspond to the biology of the organism. Other criteria for choosing a growth curve are goodness of fit and convenience.

The aim of this paper is to establish the growth rate of *Tripneustes gratilla*, known as one of the fastest-growing tropical echinoids (Ebert, 1975; Bacolod & Dy, 1986) in the western area of the northernmost limit of its geographical range.

MATERIAL AND METHODS

Samples were drawn from a small natural population of *Tripneustes gratilla elatensis*, located off a relatively isolated rocky shore in front of the H. Steinitz Marine Biology Laboratory, Elat (Gulf of Aqaba). Seawater monthly temperatures in this area range between 20.7°C and 26.7°C, and salinity averages 40.6‰ (Paldor & Anati, 1979). The diet available to *T. g. elatensis* at this site is turf algae (*Sphacelaria*, *Chaetomorpha* and *Ceramium*) with seasonal appearance of the ephemeral chlorophytes *Ulva lactuca* and *Enteromorpha* spp.

Samples of 20–150 individuals were collected each month for almost 3 years (May 1980–December 1982) while snorkeling along a stretch 100 m long and 15 m wide, to a depth of 1.5 m. These samples comprised a significant part of the entire population. The HD (horizontal diameter) of each individual was measured with a caliper to the nearest 0.5 mm, and the individual immediately replaced.

Small groups, 5–11 individuals each, of different sizes (5–72 mm HD) were kept in separate tanks in the laboratory, with running seawater at ambient temperature, and offered one of the following three plants ad libitum: (1) algal turf, which the sea urchins scraped from algae covered stones brought from the adjacent beach; (2) *Halophila stipulacea*, a seagrass collected from a neighboring shallow seagrass meadow; and (3) *Ulva lactuca*, cultivated in an artificial pond. Size measurements were taken at the beginning of each experiment and after 60 days. Urchins chosen for each batch varied both in coloration and size, which enabled individual recognition throughout the experiment. These experiments were repeated during different seasons, but since no significant seasonal differences were observed, the results for each diet were pooled.

Growth curves were fit to the data, using a practical method proposed by Ricker (1979) based on the following equations:

The Brody-Bertalanffy equation (Ebert, 1975): $$S_t = S_\infty(1-be^{-kt}) \tag{1}$$

and Johnson's growth equation (Ricker, 1979): $$S_t = S_\infty be^{-1/kt} \tag{2}$$

where S_t is the size on day t; t = number of days since the first new recruited urchins were spotted each year; b is a scaling factor, equal to $(S_\infty - S_0)/S_\infty$; k is the instantaneous growth rate coefficient; S_∞ is the asymptotic size; and t_0, in extrapolation, the time when $S_t = 0$ (Ebert, 1975).

For the indoors feeding experiments, I applied Chapman's (1961) differential modification to the Brody-Bertalanffy curve:

$$dS = S_{\infty}(1-e^{-kT} - S_t(1-e^{-kT}) \qquad (3)$$

and a differential form of Johnson's equation (Ricker, 1979; Kaufmann, 1981):

$$dS = kS_t dT(\ln S_{\infty} - \ln S_t)^2 \qquad (4)$$

RESULTS

FIELD POPULATION

Annual recruitment during the study took place in May–June, when 4–5 mm HD (horizontal diameter) juveniles appeared beneath stones in the subtidal zone. Several months before the study began, the entire population of *Tripneustes gratilla elatensis* was eliminated by a succession of wave-storms. Consequently, in May 1980 the population consisted entirely of newly arrived recruits. Strong wave-storms killed most of the sea urchins also in the following winter, and recruitment occurred in the spring. Thus, throughout most of the time the population consisted of only one cohort. In the third winter wave-storms were mild and both cohorts survived, with no size overlap between them. At the end of the third winter, individuals recruited in the second year reached an age of about 570 days. The monthly size distribution histograms based on these data have been published (Dafni & Tobol, 1986), whereas Fig. 1 presents the monthly mean and maximal diameters by time since day 0 (on which new recruited *T. g. elatensis* were recorded in a given year).

Figure 1A shows the monthly mean HD's, while Fig. 1B shows the size of the single largest individual in each measurement. An assumption is made (based on the homogeneity of the population, which most of the time consisted of one cohort only) that a growth curve based on maximal monthly sizes can be used as a measure of maximal observed growth potential of the subspecies in this habitat.

The Brody-Bertalanffy and Johnson's models (equations 1 and 2) were applied to the data. The calculated asymptotic values for both models differed considerably. The Brody-Bertalanffy curve reached an asymptotic size of HD = 95 mm while Johnson's curve maximal size was 130 mm. The slopes, represented by k, (the growth constant) were identical for both curves ($k = 0.87$). Johnson's curve showed an inflection point between the exponential and asymptotic growth phases at approximately 20 mm, whereas the Brody-Bertalanffy curve was entirely asymptotic. The extrapolated origins of the curve (t_0, days before recruitment) were –34 days for Brody-Bertalanffy's and –162 days for Johnson's curve.

A more pronounced difference between these models was shown for the maximal size curves (Fig. 1B). The exponential growth slope of Johnson's curve was steeper ($k = 2.89$) than the Brody-Bertalanffy slope ($k = 1.46$). Moreover, t_0 also differed (–109 and –75 days). The asymptotic sizes (S_{∞}) however, did not differ considerably (95 and 85 mm, respectively).

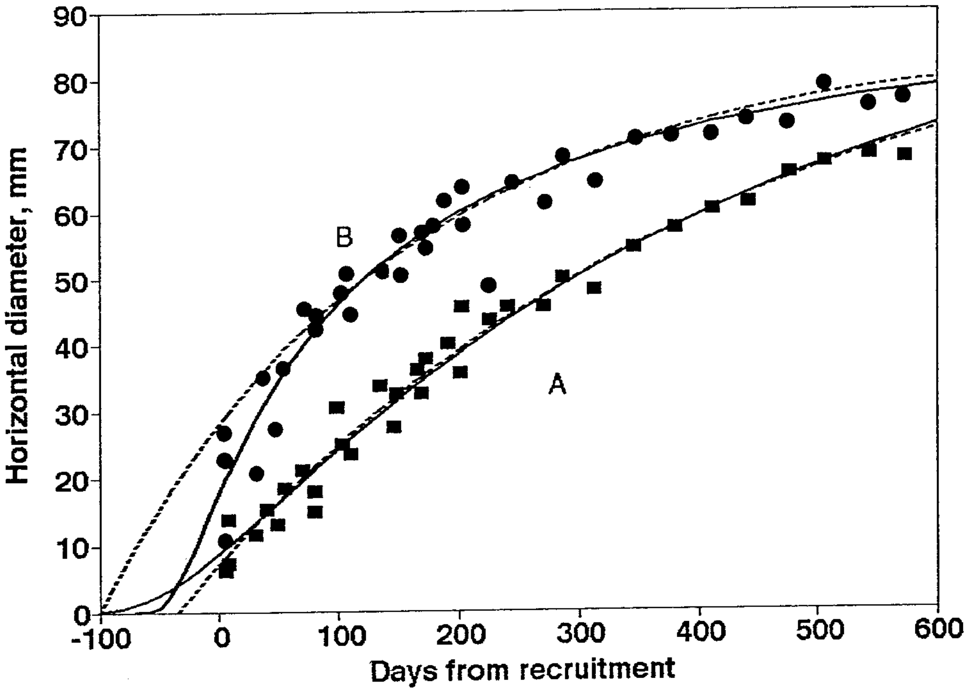

Fig. 1. Horizontal diameter (mm) of *Tripneustes gratilla elatensis* from the field population according to age (days from recruitment). A — Mean (squares) versus age. B — Monthly single largest HD's (circles), an estimate of population maxima. (Dashed lines are the Brody-Bertalanffy and solid lines are Johnson's curves.)

Both curves showed high correlation with the field data ($r > 0.99$). Gompertz' and the logistic curves were also initially fitted, but failed to provide good correlation with the field data and were therefore rejected.

EFFECT OF DIET

Figure 2 presents the different growth increments, dS, set against initial size, S_t, obtained by feeding *Tripneustes gratilla elatensis* different diets for 60 days. The slope (dS/dT) based on Brody-Bertalanffy equation was linear while Johnson's differential equation is represented by a curve. Hence the fastest growth rate, according to Johnson's curve, is shown at approximately 20 mm HD, while the Brody-Bertalanffy curve, by definition, has its maximum at 0 mm. Therefore, the latter model is not applicable for individuals smaller than 15 mm. In fact, juveniles <10 mm fed *Ulva lactuca* grew slower than predicted by Johnson's model — falling to the right of the curve (Fig. 2A). Table 1 summarizes the k and S_∞ values for all experiments.

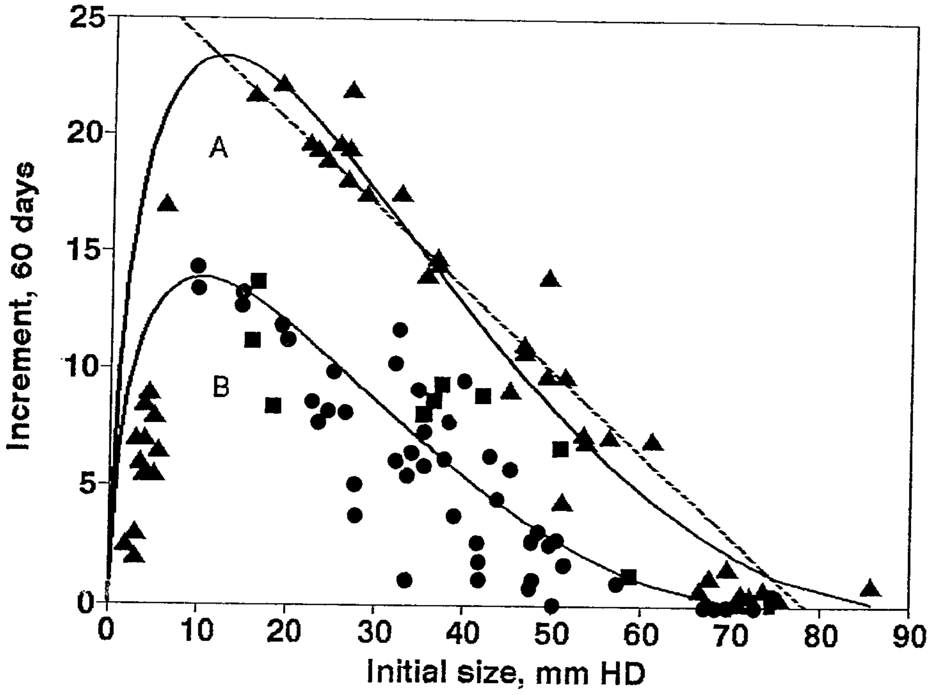

Fig. 2. Growth increments (mm HD) of *Tripneustes gratilla elatensis* vs. initial size (mm HD) under different food regimes for 60 days. A — Individuals fed *Ulva lactuca* (triangles). The upper curved line is Johnson's curve, the dashed line is the Brody-Bertalanffy curve, both for A. B — Individuals fed turf algae (circles). C — Sea urchins fed *Halophila stipulacea* (squares). The lower curved line comprises two identical Johnson's curves, for B and C. (See Table 1 for parameters.)

TABLE 1

Annual growth rates of *Tripneustes gratilla elatensis* (field population, fed *Ulva lactuca, Halophila stipulacea* and turf algae) using the Brody-Bertalanffy and Johnson's differential equations (eqs 3 and 4)

Population	N	Brody-Bertalanffy equation k	Brody-Bertalanffy equation S_∞	Brody-Bertalanffy equation t_0	Johnson's equation k	Johnson's equation S_∞	Johnson's equation t_0
Field population[1]	~88	0.87	95	–34	0.87	130	–162
Largest individuals[1]	32	1.46	85	–75	2.89	95	–109
Fed *Ulva lactuca*[2]	55	2.14	78		2.92	90	
Fed *Halophila stipulacea*	11	1.40	70		2.05	75	
Fed turf algae[2]	47	1.46	63		2.05	75	

[1] Based on monthly samples for 3 years.

[2] Pooled.

N = sample size; k = growth constant, time (days)$^{-1}$; S_∞ = a symptotic size, mm; t_0 = extrapolated origin of the curve.

DISCUSSION

GROWTH RATES

The above data confirm previous reports of rapid growth by several *Tripneustes* species (Lewis, 1958; McPherson, 1965; Ebert, 1982) and emphasize the effect of food quality on echinoid growth. The Brody-Bertalanffy and Johnson's equations yielded different growth constants, due to the different nature of the curves. The advantage of Johnson's curve is apparent in this study, which includes both adults and juveniles, and growth estimates derived from this equation are therefore more realistic than those based on the Brody-Bertalanffy curve, which is suitable in describing the growth of individuals larger than 20 mm. Although I strongly advocate the use of Johnson's model, results based on both models are presented in order to permit the comparison of growth parameters of *T. g. elatensis* with previously published data based on the other equation.

Growth rates of the *Tripneustes gratilla elatensis* field population were lower than those reported for *Tripneustes ventricosus* (k = 1.39 and 1.24) using the Brody-Bertalanffy curve (Lewis, 1958 and McPherson, 1965, calculated by Ebert, 1975) and for *T. gratilla* from the Philippines (k = 1.8, calculated by Bacolod and Dy, 1986). Having examined Lewis' and Bacolod and Dy's size-distribution plots, I suggest that the populations they studied consisted of several cohorts, which may have influenced the accuracy of their calculations. McPherson's data for *T. ventricosus* are less ambiguous, showing rapid growth in the first summer and fall, but growth almost ceased during the second year.

The different t_0 values obtained by the different models may have a biological significance related to the growth rates and biology of *Tripneustes* larvae. It has been established that *T. g. elatensis* spawns in the northern Red Sea in early winter, but juveniles appear in the sublittoral only 5–6 months later (Dafni & Tobol, 1986). Hence, Johnson's model estimate of $t_0 = -162$ seems more realistic than Brody-Bertalanffy's estimate (–34 days).

Growth rates calculated from monthly average sizes naturally underestimate the growth potential of the species. The rates based on maximal observed size (k = 1.46 and 2.89, through the Brody-Bertalanffy and Johnson's equations) exceed the average growth rate of *Tripneustes ventricosus* in Florida (McPherson, 1965) but are about the same as rates exhibited by individuals fed turf algae indoors (1.46 and 2.05, respectively, present study). This may indicate that *T. g. gratilla* in the field were under sub-optimal conditions, due to over-grazing by ever-increasing numbers of sea urchins in the summer (Dafni & Tobol, 1986). Juveniles in the field, however, did not show the rapid growth both models predicted (Fig. 1). Highest growth rates were obtained in individuals kept indoors and fed *Ulva lactuca*. They by far exceed those recorded in outdoor experiments with *Tripneustes ventricosus*, both caged or penned (McPherson, 1965) but are similar to the rates obtained for *T. ventricosus* maintained in traps (Lewis, 1958, his Fig. 2) where food was abundant. Similar records were shown by individuals of *T. g. elatensis* at Elat: one growing from 8.8 mm to 37.9 mm (0.24 g to 20.5 g wet weight) in 150 days (Lawrence, 1975) and one from 15 mm to 55 mm in one year (Ebert, 1982).

FOOD REQUIREMENTS

These results agree with previous evidence that the growth rate of echinoids is associated with food availability and quality (Ebert, 1968; Fuji, 1967) and is influenced by its energetic value and the efficiency of foraging and absorption (Lilly, 1975; Lawrence & Lane, 1982). In the field, where turf algae, the preferred diet of subtidal *T. g. elatensis*, are short and widely scattered and foraging is less efficient, the growth rate was suboptimal. On the other hand, in the laboratory, where the same food was abundant and feeding optimal, higher rates were obtained. The contribution of lush stands of *Ulva lactuca*, supporting record growth rates in the laboratory ($k = 2.92$) (2.14 for Brody-Bertalanffy) is limited in nature, due to seasonality. The contribution of *Halophila stipulacea*, shown here to support substantial growth rates, was minimal due to a notable absence of *T. g. elatensis* from its stands in the northern Gulf of Aqaba (Mastaller, 1979; Dafni, 1983, 1984).

AQUACULTURE POTENTIAL

Sea urchins are harvested in many coastal areas. Many natural populations have declined considerably. (Scheibling and Mladenov, 1987) and ever-increasing market demands (Sloan, 1985) suggest echinoid aquaculture as a possible source.

Being a fast-growing tropical species collected extensively for food throughout the Indo-Pacific tropical region, *Tripneustes gratilla* was already proposed for aquaculture (O'Connor et al., 1976; Bacolod and Dy, 1986). According to a definition set by Lawrence (1990) it is a ruderal species, affected by disturbances (r-strategist) but given the opportunity it completes its entire life-cycle within one year. *T. g. elatensis* matures early, and all individuals over 40 mm have ripe gonads (Dafni & Tobol, 1986). Yet, low gonadal index (wet gonad weight/total wet weight) was found in *Ulva*-fed urchins (< 3%, up to 2.3 g gonad weight for a 60 mm HD individual — Dafni, unpublished observations). This could be corrected by changing their food to a diet that supports gonadal growth. It has been demonstrated by Jafari and Mahasneh (1987) that *T. gratilla* fed *Halophila stipulacea* had a nitrogen content twice that of those fed *Ulva lactuca*, and a five-fold gonadal index (5% vs. 1%), which comes close to the desired value (10%) (Matsui, 1968).

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