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Primary Research Paper

Testing for the effects of seasonal and lunar periodicity on the reproduction of the edible sea urchin Tripneustes gratilla (L) in Kenyan coral reef lagoons

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Key words: continuous reproduction, coral reef lagoons, Kenyan coast, lunar periodicity, Tripneustes gratilla

Abstract

The annual and lunar reproductive cycle of the widely distributed edible sea urchin Tripneustes gratilla (L) was examined through measurements of gonad index, histological examination of gametogenesis, and induction of spawning with KCl injections. The population density and morphological characteristics of urchins at Diani, Kanamai, and Vipingo reef lagoons were also studied as well as the effects of seawater temperature and light on reproduction. Gonad growth started early during the northeast monsoon and reached a peak in June at the beginning of the southeast monsoon followed by a sharp decrease in gonad size of 50% in July and August towards the end of the southeast monsoons. Histological examination of gonads, revealed many different stages of gametogenesis with gametes present throughout the year, indicating continuous reproduction. There was a significant relationship between gonad index and lunar day with spawning occurring between lunar day 7 and 21, but spawning was not in perfect synchrony in the population. The population density of urchins at each reef is variable from year to year and was highest on average at Vipingo. Urchins at Kanamai had the lowest gonad indices, the largest jaws and smallest individuals an indication of food limitation. The gonads (roe) of T , gratilla at all three sites, were perpetually 'runny' an attribute that is not suitable for urchin fisheries. Studies to develop techniques to improve roe quality are recommended.

Introduction

Coral reef fisheries provide an important source of income for coastal communities in Kenya (Glaesel, 1997; King, 2000). However, the increasing need for fish and other marine products is putting pressure on Kenyan coral reef ecosystems, leading to overexploitation and reef degradation (Samoilys, 1988; McClanahan & Shafir, 1990; McClanahan, 1995; Watson et al., 1996). Due to the decline in the finfish fishery, interest has developed in alternative fisheries in Kenya, such as sea urchins, in order to divert fishing pressure away from traditional fisheries (Fisheries dept, pers. comm.).

Sea urchins are mainly harvested for their gonads (roe) and although the high demand has resulted in over-exploitation in the main producing nations (Sloan, 1985) there remains a high demand for this product worldwide, leading to expansion into new fishing grounds (Keesing & Hall, 1998). Of the 19 genera of sea urchins that are exploited for subsistence or commercial use worldwide (Lawrence, 2001), Echinometra, Diadema, Tripneustes, and Toxopneustes are commonly found along the east coast of Africa (Clark & Rowe, 1971). Only one species of Tripneustes, T. gratilla occurs in the region. This species would make a suitable target species for a potential fishery due to the fact that it is commonly

used by local fishers as bait (in Kenya), food (in Mozambique), it is relatively easy to handle (Diadema and Toxopneutes have poisonous spines and pedicellarie and Echinometra has a hard test and spines) and it is commonly traded in the SE Asian market (Sloan, 1985). Tripneustes gratilla inhabits a wide range of intertidal and subtidal habitats throughout the Indo-West Pacific (Clark $&$ Rowe, 1971; Lawrence, 2001) and is a dominant species in coral reef lagoons throughout the Kenyan coast (McClanahan & Shafir, 1990; McClanahan, 1998). However, few studies have been carried out on the ecology of this species in the region. Recently T. gratilla population increases have been the subject of some concern due to their grazing effects on seagrass beds in the Watamu and Diani marine reserves (Kenya Wildlife Service, pers. comm.). The causes of this population explosion are not clear although a reduction in the predators of urchins has been implicated in several studies in Kenya (McClanahan & Shafir, 1990; McClanahan, 1998).

Studies on the reproduction of T. gratilla indicate seasonal reproductive patterns in the northern hemisphere between 13° N and 35° N (Tuason & Gomez, 1979; Pearse, 1974; Chang-Po & Kun- Hsiung, 1981) and in the southern hemisphere between 16° S and 29° S (Pearse & Cameron, 1991). Continuous gametogenic activity was reported in Madagascar (Maharavo, 1993). The lack of a relationship between latitude and spawning however, led Pearse (1974) to the conclusion that reproduction in T . gratilla has no relationship to temperature. No studies have been carried out on the reproductive biology of T. gratilla on the east African coast, information that is essential to developing a sea urchin fishery.

The purpose of this study is to examine (1) the reproductive patterns of T. gratilla populations along the Kenyan coast in order to establish the temporal and spatial availability of gonads (roe) (2) the relationship between reproduction and seawater temperature, light, and lunar periodicity, in order to establish the factors that control reproduction in this species and (3) the population dynamics of T. gratilla in different locations along the Kenyan coast in order to determine the effects of population density on reproductive output.

Materials and methods

The reproductive rhythm of Tripneustes gratilla was investigated by haphazardly, collecting monthly samples of 20 individuals or more at Kanamai (3° 55' S; 39° 47' E) inner reef lagoon (described in McClanahan & Shafir, 1990) from September 1987 to October 1988 for the investigations of the annual periodicity. Individual urchins were weighed; the test diameter measured across the longest axes at the ambitus and dissected. The gonads, guts (plus contents), and jaws were removed and weighed and Organ Indices were calculated (Organ Index $=$ wet organ weight/wet body weight \times 100). The mean monthly gonad index was calculated and plotted against the month.

In addition, histological samples were prepared of the aboral tip of one lobe per urchin in a sample (Pearse, 1969). Slides were examined under the microscope and the gametogenic stage was categorized using characteristics of Fuji (1960). The proportion of ripe individuals in each sample was also calculated from the percentage of individuals in a sample with gametes filling over 50% of gonadal tubule lumens (Pearse & Phillips, 1968). Observations were also made on the firmness of the gonads.

Lunar periodicity was investigated at Kanamai for two complete lunar cycles between the months of April–May and June–July 1992 when gonadal development was at its peak. Ten to twenty urchins were collected every 2–5 days, for each lunar period, and dissected for gonad index measurements. The mean gonad index for each sample was calculated and plotted against the Lunar day, where New moon $=$ Lunar day 0. Regressions of gonad weight on urchin size for the four quarters of the moon were also calculated to extrapolate the weight of gonads of different sized urchins throughout the month. In addition, the proportion of urchins spawning was calculated for each lunar day by inducing 10–20 haphazardly sampled urchins to spawn with $1-1.5$ ml of 0.5 M KCl injections into the coelom. In order to distinguish individuals that had partially spawned from those that were ripe but had not spawned, the percentage of individuals that responded to KCL injections by releasing less than 0.2 ml of gametes and those that released more than 0.2 ml of gametes was calculated.

The effects of seawater temperature on the reproductive pattern of T. gratilla were studied by correlating mean monthly gonad indices with mean monthly seawater temperatures collected at Kanamai reef lagoon from 1990 to 1994 (Muthiga, 1996). In addition, the effects of light were investigated by correlating gonad indices with solar radiation measurements compiled for the period 1992–1994 (Muthiga, 1996) from data collected by the Kenya Meteorological Department Mombasa station (the closest weather station to Kanamai).

The population density of T. gratilla was compiled from data collected by the Coral Reef Conservation Project from 1987 to 2003 at Kanamai, Diani (4° 21' S; 39 $^{\circ}$ 34' E), and Vipingo $(3^{\circ}$ 47' S; 39° 50' E) reef lagoons. The density of T. *gratilla* was estimated in 10 $m²$ quadrats haphazardly placed in the inner reef lagoons of Vipingo, Diani, and Kanamai. In addition, morphometric characteristics including urchin size and organ indices were calculated from samples at Diani and Vipingo for comparison with urchins collected at Kanamai. The density of urchins of different sizes at Kanamai was calculated by plotting the cumulative frequency of urchins of different test diameters of T. gratilla.

The cumulative frequency was then used to estimate the density of different sizes using the average density of T. gratilla at Kanamai (6.2/ 10 m^2) and a regression of test diameter on population density was performed.

Results

The sex ratios of urchins collected at Diani, Kanamai, and Vipingo were 0.67:1, 0.69:1 and 1:1,

Figure 1. The relationship between test diameter (mm) and gonad weight (wet weight, gm) of Tripneustes gratilla from Kanamai reef lagoon ($n = 163$).

females to males, respectively and did not differ significantly from a ratio of 1:1 (Table 1). A regression of gonad index on test diameter of individual urchins collected from Kanamai showed no significant relationship $(r = 0.08, n = 116)$. However, a regression of gonad weight on test diameter showed a highly significant relationship $(r = 0.53, n = 163, p < 0.000)$ with a tendency for larger individuals to have heavier gonads (Fig. 1).

The pattern of reproduction for T. gratilla at Kanamai displays a defined annual cycle, with mean monthly gonad indices ranging from 2.35% to a high of 4.90% (Fig. 2). Gonad indices were generally low from the months of August $(2.4 \pm 0.23\%)$ to October $(2.3 \pm 0.31\%)$. The gonad index then showed a gradual increase to peak in June (4.9 \pm 0.64%) with a large decrease of 50% by August. Histological examination of the gonads revealed individuals at different stages of development in each sample. No individuals in the recovery stage (gonadal lobes filled with nutritive phagocytes) were observed in any of the samples and most individuals had 'runny' gonads

Table 1. Morphometric characteristics of Tripneustes gratilla calculated as means $(\pm$ sem) at Diani, Kanamai and Vipingo, Kenya (sample sizes in brackets). Gonad and jaw indices are calculated relative to wet weights of individual urchins. Sex ratio are tested using chi-squared test ($ns = not$ significant).

Characteristic	Diani	Kanamai	Vipingo
Body weight (g)	192.78 ± 9.63 (20)	119.97 ± 2.33 (208)	$160.34 \pm 6.02(40)$
Test diameter (mm)	77.36 ± 1.26 (20)	$65.91 \pm 0.44(74)$	$74.14 \pm 1.75(20)$
Gonad weight (g)	$9.82 \pm 0.97(20)$	4.54 ± 0.24 (208)	$9.02 \pm 0.75(40)$
Gonad index $(\%)$	5.28 ± 0.60 (20)	3.72 ± 0.18 (208)	$5.82 \pm 0.53(40)$
Jaw index $(\%)$	$1.64 \pm 0.07(20)$	1.97 ± 0.04 (91)	1.90 ± 0.08 (40)
Sex Ratio, F:M	$0.67:1$ (ns)	$0.69:1$ (ns)	$1:1$ (ns)
Density (urchins/10 m ²)	3.47 ± 0.64 (27)	$6.07 \pm 0.95(30)$	6.11 ± 3.22 (29)

Figure 2. The pattern of reproduction of Tripneustes gratilla at Kanamai measured as the mean monthly gonad index (\pm sem).

Figure 3. The mean gonad index (\pm sem) of Tripneustes gratilla for two complete lunar periods April–May and June–July (New moon = day 0).

Figure 4. The proportion of urchins releasing gametes upon injection with KCl on different lunar days. Ten to twenty individual urchins were induced to spawn on each lunar day and scored as individuals that responded by releasing less than 0.2 ml (open symbol) and individuals who spawned by releasing more than 0.2 ml of gametes (closed symbol).

that easily released gametes upon handling. The proportion of individuals with ripe gonads in monthly samples showed a variable pattern throughout the year, ranging from 0% to 75% of a sample, and a correlation between the mean monthly gonad index and the proportion of ripe individuals in a sample showed no significant relationship ($r = 0.19$, $n = 12$).

The relationship between mean gonad index and lunar day (Fig. 3) was statistically significant $(r = 0.79, p < 0.05, n = 16)$ with gonad indices increasing from the new moon and peaking a day after the first quarter, reaching the lowest values in the last quarter of the lunar cycle. Regressions of gonad weight on urchin size (test diameter) of urchins collected during the four quarters of the moon also indicated urchins on average having larger gonads for the same size urchin in the period between lunar day 8 and 14. However, the frequency of individuals that responded to KCl injections by releasing gametes either in small or copious amounts showed no relationship with lunar day (Fig. 4). In general a high proportion of individuals (>80%) released gametes regardless of lunar day and more than 50% released copious amounts on any lunar day (Fig. 4). The percentage of urchins spawning only copious amounts of gametes also showed no relationship with lunar day ($r = 0.55$, $n = 9$).

The mean monthly seawater temperature displays a defined seasonal annual pattern with a peak in February–March $(31.6 \degree C)$ during the northeast monsoons declining and with the lowest temperatures occurring in July (26.3 °C) during the southeast monsoon period (Muthiga, 1996). A comparison between mean monthly gonad index and mean monthly seawater temperature showed no significant relationship ($r = 0.08$, $n = 12$). A regression of gonad index on temperature timelagged by 1 month $(t-1)$ also showed no significant relationship ($r = 0.41$, $n = 11$).

Light measurements also exhibited a seasonal pattern ranging from a high of 23 $MJ/m^2/day$ between February and March to a low of 15.5 MJ/ m2 /day in July (Muthiga, 1996). There was a poor relationship ($r = 0.38$, $n = 12$), between mean monthly light and mean monthly gonad indices. However, a regression of gonad index on light time lagged by one month $(t-1)$ was statistically significant ($r = 0.63$, $p = 0.04$, $n = 11$).

The population density of T , gratilla at all three sites fluctuated from year to year (Fig. 5) with densities being lowest on average at Diani reef lagoon (Table 1). Urchin density at Vipingo showed a large increase in 1994 from an average of 5 urchins/ 10 m^2 to more than 20 urchins/ 10 m^2 , however the population decreased back to less than 5 urchins/ 10 m^2 by 1996. Urchins at Kanamai had statistically smaller body sizes and gonads compared to urchins at Diani or Vipingo (Table 1). The urchins at Kanamai also had statistically larger jaws relative to body size than urchins at Diani but not Vipingo (Table 1). There was no statistical difference between the test diameter or gonad index of urchins at Diani and Vipingo (Table 1). The cumulative frequency of urchins of different test diameters at Kanamai showed a significant relationship $(r = 0.97, p < 0.000, n = 163)$. Eighty percent of the population of T. gratilla at Kanamai were less than 70 mm test diameter (Fig. 6). A regression of test diameter on urchin density showed a highly significant inverse relationship $(r = 0.95,$ $p \le 0.000, n = 163$.

Discussion

Tripneustes gratilla has been reported to have restricted spawning periods (Pearse & Cameron, 1991) except in Madagascar where continuous reproduction occurs (Maharavo, 1993). In this study, T. gratilla shows an annual cycle with a period of gonad growth during the northeast monsoon and a decrease towards the end of the

Figure 5. The population density of Tripneustes gratilla at Diani, Kanamai and Vipingo reef lagoons between 1987 and 2003 compiled from annual monitoring data collected by the Coral Reef Conservation Project, Mombasa.

Figure 6. The cumulative frequency of Tripneustes gratilla of different sizes (test diameter) at Kanamai reef lagoon.

southeast monsoons. Monthly gonad samples revealed different stages of gametogenic development with little synchrony amongst individuals, indicating that individuals are reaching maturity and spawning at different times throughout the year. This suggests that T , gratilla populations on the Kenyan coast have a reproductive pattern that is continuous throughout the year superimposed on an annual cycle of gonad growth. A similar pattern of continuous reproduction with a seasonal cycle of gonad growth has been reported for Diadema savignyi in Kenya (Muthiga, 2003).

The factors that control the reproduction of T. gratilla are not well understood. Pearse (1974) concluded that seawater temperature and light are probably not important factors, which was collaborated by Fouda & Hellal (1990) in a study of T. gratilla in the Gulf of Aqaba and the northern Red Sea. Chang-Po & Kun-Hsiung (1981) however, showed that gonad growth and spawning of T. gratilla tracked seawater temperatures in Taiwan. Seawater temperature and light have been linked to reproduction in the echinoid E. mathaei (Muthiga, 1996; Muthiga & Jaccarini, 2005) and D. savignyi (Muthiga, 2003) inhabiting the same sites along the Kenyan coast and D. savignyi on the east coast of South Africa (Drummond, 1995). Results from this study show that there is no relationship between gonad growth and seawater temperature, a factor that exhibits seasonal patterns on the East Coast of Africa (McClanahan, 1988). This fact coupled with the lack of synchrony amongst individual urchins suggests that light and temperature do not control reproduction of T. gratilla directly. These factors however, may indirectly influence reproduction

through their effects on benthic productivity; hence the large decline in the gonad index in August through October could be a reflection of food limitation and not synchronous spawning.

Food scarcity has been shown to cause reduced gonad growth in many studies on urchins (Ebert, 1982; Thompson, 1982; Andrew, 1989; Muthiga, 2003). Although food availability was not measured in this study, T. gratilla feeds on macrophytes (Herring, 1972; Maharavo, 1993) whose biomass is reported to decrease during the southeast monsoons due to increased water turbulence on the Kenyan coast (McClanahan et al., 2002). Food scarcity is therefore expected to influence gonad development in T. gratilla during this period. In addition, the significant response of T. gratilla gonad indices to light time-lagged by 1 month indicates a delayed reaction of gonad growth to light related to the time it takes for benthic productivity to influence gonad growth. The findings of this study support the suggestion by Pearse (1974) that factors other than seawater temperature and light control the reproduction of T. gratilla hence further experimentation on the response of these and additional factors such as food availability are required.

In addition to annual reproductive cycles, some species of sea urchins have been shown to exhibit monthly rhythms (Pearse, 1972, 1975; Bauer, 1976; Iliffe & Pearse, 1982; Lessios, 1991; Drummond, 1995; Muthiga, 2003). T. gratilla in the present study showed a reproductive rhythm that coincides closely with the changing phases of the moon with gonad indices peaking just after the end of the first quarter than decreasing to a minimum around the third quarter suggesting that spawning maybe occurring at this time. This implies that T. gratilla populations on the Kenyan coast have a lunar periodicity, the first time this is reported for T. gratilla. The fact that urchins induced to spawn with KCL injections released gametes on all days of the lunar period and that no urchins in the recovering stage were observed in histological samples indicates that gametes are continuously produced and stored for release between the second and third quarters. Storage of gametes before being spawned has been reported in other urchin species (Pearse, 1969) and has been suggested as an adaptive mechanism to ensure that individuals are spawning around the same period increasing the

chances for fertilization (Pearse & Cameron, 1991).

The value of urchin gonads in a sea urchin fishery is dependent on a number of characteristics including gonad size and firmness (Blount & Worthington, 2002). In general, gonad size is related to urchin body size where larger sized individuals generally contain larger gonads (Gonor, 1972). There was a positive relationship between T. gratilla size and the weight of the gonad in this study, with urchins that were larger than 70 mm (test diameter) having gonads ranging between 5 and 10 gm. In addition, urchins at Diani and Vipingo had on average larger gonads $({\sim}9$ gm). These relationships can be used to set harvest sizes and sites (for example, Vipingo, the reef with urchins with large gonads and a high population density). However the monthly spawning cycle of T. gratilla on the Kenyan coast results in gonads that are perpetually 'runny' resulting in low quality roe. Further experimentation will be required to determine the factors that control spawning and ways to enhance gonad quality.

Urchin size can be influenced by several factors including food availability (Ebert, 1982; McClanahan, 1988b; Levitan, 1988) and population density (Levitan, 1988; Levitan, 1991; Muthiga, 1996). In this study, the largest urchins occurred at Diani, the site with the lowest population density while the smallest urchins occurred at Kanamai a site with a higher population density. Urchins at Kanamai also produced small gonads and had the largest jaws an indication of food limitation (Ebert, 1982; Levitan, 1991). Urchins at Diani and Vipingo had large gonads despite population densities that differed by \sim 50% indicating that food may not be limited at either of these sites. Population density therefore does not appear to be an important factor in regulating T. gratilla gonadal growth. Vipingo would appear to be the most suitable site for harvest, having urchins with large gonads and relatively high population densities.

T. gratilla gonads are available during most months of the year except for a short period between August and October when gonad indices are very low $(>2.5\%)$, hence roe could be harvested at the end of the first lunar quarter of each month from February to July. However, the sizes of gonads were small, being on average less than

5 gm for urchins between 60 and 70 mm (test diameter) compared to 10–15% of wet weight for similar size ranges in other studies (Tuason & Gomez, 1979; Fouda & Hellal, 1990; Maharavo, 1993). Although the cause of these generally low gonad indices was not explored in this study the yearly pattern of gonad growth suggests that food availability is generally low for T. gratilla at Kanamai. Since reproduction is continuous throughout the year with a monthly spawning rhythm, resources are allocated to completing the gametogenic cycle and spawning, hence the gonad shows little growth from month to month. Further experimentation on the effects of food and lunar periodicity on T. gratilla gonad growth should assist in clarifying this question.

The average density of T. gratilla at the studied sites is generally within the range of other studies although much lower than densities reported in seagrass beds (Lawrence & Agatsuma, 2001). There was also temporal variability in population density, a common factor in sea urchins (Ebert, 1982). In addition, fluctuations in sea urchin abundance has the potential for causing major shifts in the structure of marine benthic communities (Lawrence, 1975; Lawrence & Sammarco, 1982; Hughes, 1994; McClanahan, 1995) due to the effects of grazing by urchins. Given that sea urchins are vulnerable to overfishing (Sloan, 1985; Pfister & Bradbury, 1996; Keesing & Hall, 1998), the development of a sea urchin fishery must take into consideration these factors to avoid a major change in community structure due to overexploitation.

This study is the first to address the biological and ecological factors that are important for the development of a T. gratilla fishery along the east coast of Africa. The study shows that although T. gratilla has gonads throughout the year, the roe is of low quality. It is suggested that further experimentation to develop techniques to improve roe quality including collection from the wild and enhancement in grow-out experiments or echinoculture should be explored.

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