ISRAEL JOURNAL OF ZOOLOGY, Vol. 34, 1986/87, pp. 191–204

POPULATION STRUCTURE PATTERNS OF A COMMON RED SEA ECHINOID *(TRIPNEUSTES GRATILLA ELATENSIS)*

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ABSTRACT

Recruitment and size distribution patterns of *Tripneustes gratilla elatensis* were studied between 1979-1984 in the northern Gulf of Elat (= Gulf of 'Aqaba, Red Sea). Annual settlement of postlarval echinoids in the subtidal zone of a wave-exposed shore occurs at late spring and the recruits grow rapidly, emerging from their understone shelters and moving offshore. In the first winter they attain adult size (>35mm) before being eliminated by destructive late-winter wave storms. The recruitment in a nearby wave-protected coral reef area is less predictable, and the subtidal juveniles retain a cryptic behaviour for >1 yr. These juveniles are apparently subject to predation by wrasses (*Coris aygula*, Labridae) when crossing the sandy lagoon to the reef. Consequently, the entire 35-50 mm size-group was absent from this site. The reef-flat adults, on the other hand, exhibited stable size distribution patterns for several consecutive years, indicative of high survival. Following an unusual multi-recruitment event, in 1984, both sites became densely populated with postlarvae, and numerous growing urchins crossed the lagoon, recruiting the reef-flat sub-population. These recruitment and life-history patterns generally agree with Ebert's (1982) model that emphasizes the role of recruitment variability and pre-reproductive survival on the determination of longevity, demonstrating the role of predators and surf conditions in shaping the population structure of this echinoid.

INTRODUCTION

Being the main grazers of many marine shallow water environments, fluctuations in sea-urchin populations may have a strong impact on the entire community (see review by Lawrence & Sammarco, 1982). Various factors affect echinoid growth and population structures: variation in postlarval recruitment (Ebert, 1983); adult facilitation (Tegner & Dayton, 1977); migration (Bak & Nojima, 1980; Engstrom, 1982); food availability (Lilly, 1975); predation (Fricke, 1971, 1974; Hendler, 1976; Tegner & Dayton, 1981); wave action (Ebert, 1975, 1982); competition (Williams, 1981); natural catastrophies (Glynn, 1968) or disease (Pearse & Hines, 1979; Lessios et al., 1984). Several factors may combine to produce stable alternative states in nearby populations, characterized by different echinoid size, density or morphology (Lawrence, 1983).

While populations of long-lived echinoids may remain stable for extended periods, short-lived species' populations frequently show extreme temporal fluctuation (Ebert, 1982, 1983). Ebert (1982) proposed that longevity, obtained in

Received 21 March 1986 and in revised form 30 September 1986

more sheltered environments, is linked with variable recruitment of postlarvae and with unpredictable survival of the pre-reproductive individuals, whereas according to MacArthur & Wilson's (1967) model it is mainly affected by post-recruitment interactions (competition or predation). Ebert (1982) found that although the size structure patterns of many species conform with his model, other species' patterns are difficult to interpret. They exhibit temporally stable patterns in one location, indicative of high annual survival, whereas other populations show rapid growth and low survival. He suggested that these populations may differ in their recruitment patterns, owing to local environmental conditions.

Among these variable species, Ebert (1982) listed the common Indo-Pacific echinoid *Tripneustes gratilla* (L.), the subject of the present study. Known from various soft-bottom habitats in the Indo-Pacific (Mortensen, 1943; Macnae & Kalk, 1958; Herring, 1972), its northern Red Sea populations (recognized as a distinct subspecies, *T. g. elatensis* Dafni, 1983) almost exclusively inhabit hard substrates (Mastaller, 1979). Observations revealed exceedingly high individual growth rates in this subspecies (Lawrence, 1975; Ebert, 1982), as well as strong fluctuations in its abundance in the Gulf of Elat (Gulf of 'Aqaba) (Benayahu & Loya, 1977; Mastaller, 1979). Some populations had stable population structures for several consecutive years (J. Dafni & Y. Kalgard, unpubl. obs.).

This paper attempts to elucidate the environmental effects that dominate the *T. g. elatensis* life-cycle, presenting the results of a five-year study of the population dynamics of this subspecies. These results are evaluated in reference to Ebert's (1982) model.

MATERIAL AND METHODS

Study Sites

Two sites, 300 m apart and differing in physiographical characteristics, were selected in the northernmost part of the Gulf (Fig. 1). The natural conditions and the impact of recent pollution in this area have been discussed by various authors (Fishelson, 1971, 1973; Mergner & Schuhmacher, 1974; Mergner, 1981; Walker & Ormond, 1982). Although under the prevailing northern wind the water in the gulf is calm, throughout the winter season (Jan.-Apr.) southern winds cause sudden wave storms, which strongly influence the shore (Friedman, 1968).

The selected sites differed, among other features, in the degree of shelter they provide against the southern waves. Site A, a 100 m stretch of shore in the front of the H. Steinitz Marine Laboratory at Elat, runs in a northeasterly direction and is fully exposed to the waves. The 3-4 m wide intertidal zone is strewn with pebbles and larger boulders, whereas the subtidal (0-1 m below low tide mark) abounds with algal turf-covered flat stones. During the late winter in some years, ephemeral seaweeds (*Ulva, Enteromorpha* and *Sargassum*) dominate the subtidal zone. Offshore, slopes are rubble-covered with scattered coral patches. Site B, a typical reef area at the Elat Nature Reserve, is wave-protected by a continuous fringing reef and by the westward curving shoreline. A 20-40 m wide and <2 m

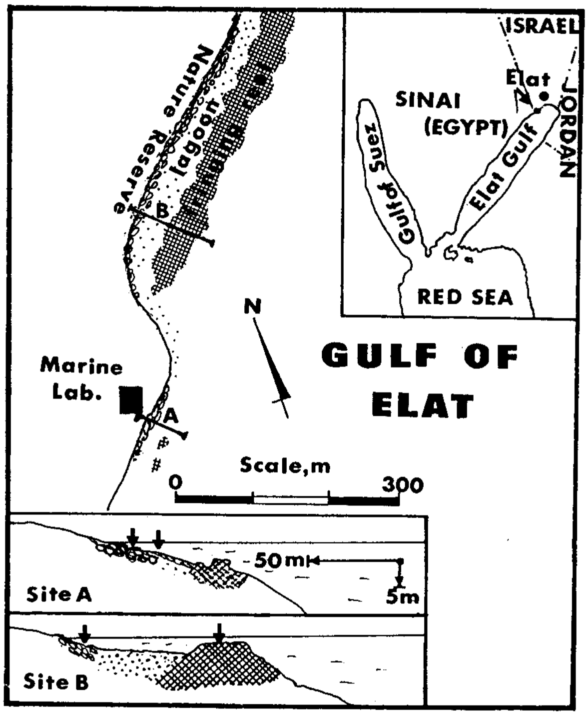


Fig. 1. Map of the northern Gulf of Elat and the study area. Lower left inset — longitudinal sections of the shore at both sites, with arrows marking the approximate position of the transects (circles = flat boulders; crossed lines = reef formation; dots = native rock or sand).

deep sandy lagoon, partly covered with seagrass (*Halophila stipulacea* Forskål), separates the rocky subtidal from the reef-flat. The 5 m wide tidal zone is composed of beach-rock, covered with stones and coral debris.

Subtidally, *T. g. elatensis* shares the habitat with the echinoids *Echinometra mathaei* (de Blainville) and *Diadema setosum* (Leske). In site B offshore reef-flats, *Heterocentrotus mammillatus* (L.) and *Echinothrix calamaris* (Pallas) were also present. A gravel-covered sloping area between the sites was populated mainly by *D. setosum* and *E. calamaris.*

Population Structure Study

Counts and measurements were taken from 30-100 m long transects, parallel to the shore. A shallow transect, 0.5 m deep and 1 m wide, 3-5 m from the high water mark, was examined at both sites. A second transect was examined in site A, parallel to the first, at a depth of 1-1.5 m, whereas site B's second transect stretched along the reef-flat, parallel to the shore (Fig. 1). Since the length of the examined transects varied as to the abundance of urchins, the number of urchins collected per unit of searching time served as an arbitrary, semi-quantitative measure of abundance. Search was equally divided between the exposed rock surface and the underpart of stones and crevices.

Site A was studied for five consecutive years (1979-1984), divided into three periods: (1) IV.1979-III.1980, when mainly observations were made with sporadic sampling, (2) IV.1980-XII.1982, the main sampling period, when monthly transect samples were analysed, and (3) occasional observations throughout 1983 and half of 1984, with a final transect sampling in VII.1984.

Site B was studied irregularly between early 1979 and IV.1981. Between IV.1981 and XII.1982 regular samples were taken at 2-4 month intervals, followed by occasional observations throughout 1983-1984, and one final sampling in VII.1984.

The horizontal diameter (HD) of all urchins was measured with a sliding caliper (precison of 0.5 mm) and the animals were released in their original location.

Predation

The possibility that the wrasse *Coris aygula* (Lacepede) (= *C. angulata*), a predator of echinoids (Fricke, 1971; Randall, 1983), is controlling *T. g. elatensis* populations was studied by observing its feeding behaviour in both sampling sites. The activity of individuals and groups were observed in calm sea by swimming at the surface, from a distance of 3-5 m, and from a board-walk 3 m above the sea.

In an *in situ* feeding experiment, carried out at site B, adult *C. aygula* were offered live *T. g. elatensis* (previously measured), exposed on a 30 x 50 cm metal tray, and their predation response was recorded (number of ingested or rejected specimens according to their size). In a second experiment, *T. g. elatensis* were exposed simultaneously with *E. mathaei*, and the wrasse feeding preference noted. In a third experiment, the wrasses could choose between *T. g. elatensis* and a brittle-star (*Ophiocoma* sp.).

RESULTS

Recruitment and Population Structure

In the first sampling, summer 1979, the site A population consisted of two size groups: small-sized urchins, apparently new recruits (age 0), in the lower intertidal zone exposed in extreme low-tides; and adults, mainly in the offshore deeper transect (Fig. 2A). At site B, only larger individuals were found, the majority on the reef-flat (Fig. 2B). Non-quantitative observations during the summer of 1979 showed that site A, age 0, cohorts grew rapidly, and their apparent numbers increased due to their emergence to the open from the subtidal hideouts. Most of the site A population disappeared in the following winter after a series of wave storms. In spring 1980, site A was re-populated by new recruits (Fig. 3). In site, B, the *T. g. elatensis* population structure was stable between VII.1979 and VI.1981: juveniles were not recruiting to the reef-flat or subtidal sub-populations, and the reef-flat sub-population was not affected by the storms. Quantitative assessment of the reef-flat urchin density or abundance was unsuccessful since urchins

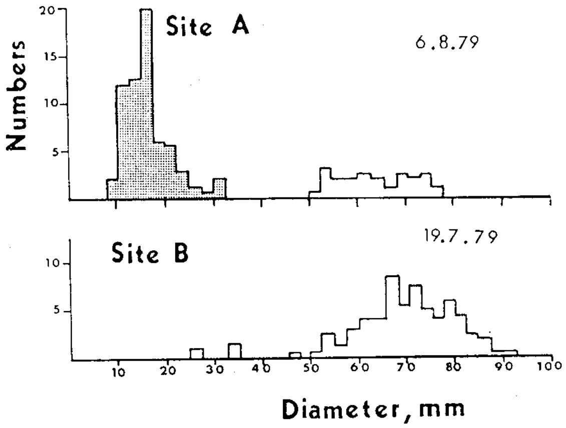


Fig. 2. Size distribution pattern of site A and B populations in the summer of 1979. Dark columns = subtidal juveniles, white columns = offshore and reef-flat sub-population.

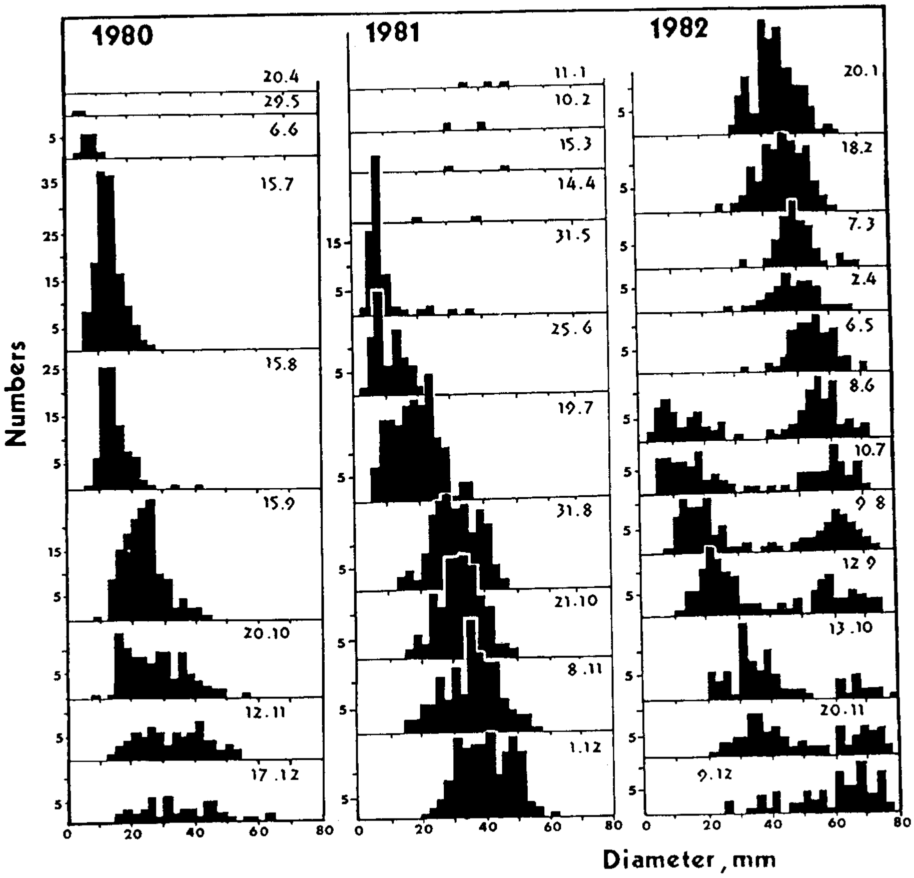
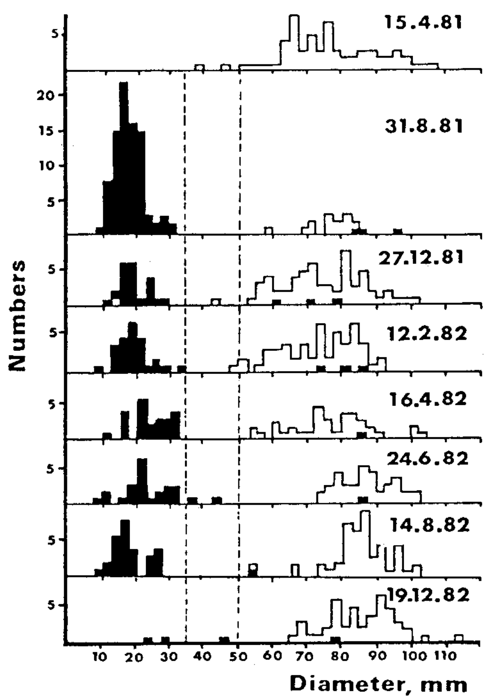


Fig. 3. Size frequency distribution of site A population, 1980-1982.

constantly foraged across the reef-flat in large aggregations, often migrating outside the sampled area.

Figures 3 and 4 present the size distribution histograms for site A and B populations, for 2-3 recruitment seasons. Figure 3 demonstrates the prevailing annual pattern shown in site A: the 1980-cohort, first discovered on 29.V.1980, reached by XII.1980 an average HD of 34 mm, with some individuals attaining >60 mm. On 9.I.1981 an unusually destructive storm, with waves >3 m, hit the site A shore (C. Porter, pers. commun.), destroying the entire *T. g. elatensis* population. Numerous echinoid tests were found on the beach, and broken tests were scattered in shallow water. Observations during a milder phase of the storm showed that most adult urchins sought refuge in crevices. Once detached from their solid substrate, they were washed away and perished. Late winter sampling in site A yielded only several 30-50 mm urchins. A 21 mm individual found there probably represents early winter recruitment.

The site B population survived the above-mentioned storm. Samples taken on 15.IV.1981 showed that the reef-flat population structure (Fig. 4) was essentially the same as previously recorded (Fig. 2B). A survey of ca. 25 km along the NW shores of the Gulf was conducted to assess the influence of this particular storm on *T. g. elatensis* populations. It showed that all wave-exposed populations were



N	$\bar{X}_1$	$\bar{X}_2$
62	--	76.2
102	20.3	74.4
85	26.2	73.6
79	25.0	72.9
60	25.8	76.5
63	25.6	85.9
79	18.9	85.3
50	--	86.3

Fig. 4. Size frequency distribution of site B population, 1981-1982. N — sample size; $\bar{X}_1$ — mean HD of the subtidal sub-population (dark columns); $\bar{X}_2$ — mean HD of the reef-flat sub-population (white columns). Broken vertical lines mark the 35-50 mm size group, almost absent from the samples.

destroyed, whereas populations inhabiting sheltered coves and reef-protected shores were almost unaffected.

During the spring and early summer of 1981 site A was re-populated with new recruits in high abundance. The number of individuals collected per min search in Aug.-Sept. was >10, compared to the previous year's record of 3.5 per min. Winter storms in 1981/2 were milder, and most 0-age individuals survived, turning into 1-age cohort in the next spring. Recruitment in 1982 was rather poor at site A. The first encounter in VI. included several individuals <20 mm, probably overlooked in the previous months.

The site B population structure pattern was very different from that of site A. New recruits were seen in spring 1981 only in the intertidal fringe and upper subtidal zone. No juveniles of <20 mm were found on the reef flat. Although recruitment did not take place after VI., cryptic juveniles were observed in the subtidal throughout the following year, their average size only slightly increasing. Consequently, two distinct sub-populations were seen here (Fig. 4): smaller, apparently 0-age, underneath the stones in the subtidal zone, and larger individuals on the reef-flat. In the following year the 0-age group's numbers decreased, and by XII.1982 almost none could be found there. Nevertheless, the size distribution pattern changed only slightly: the mean size of both sub-populations increased during the winter and spring of 1982, the smaller HD from 20 mm in VIII.1981 through 26 mm in VI.1982, while the reef-flat sub-population's mean size increased steadily from 74 mm to 86 mm in XII.1982 (Fig. 4). Spring 1982 recruitment was hardly noticed at site B, discernible only by a decrease in HD of the subtidal sub-population, from 26 mm to 19 mm in VIII.1982.

Noteworthy is the consistent absence of an intermediate size-group from site B throughout the entire sampling period. Only five out of a total of 517 urchins (<1%) had a HD of 35-50 mm (Fig. 4). An extensive search showed no evidence of emigration of this size-group to other habitats (lagoon, deeper water, etc.).

Unusual Recruitment

Shortly after the regular sampling ended, in January 1983, a large number of newly settled *T. g. elatensis* was spotted at site A, only few of which survived a subsequent wave storm. Site B was not searched during this period, but observations during the summer of 1983 failed to reveal any 0-age urchins in this site's subtidal. Another exceptional recruitment event was recorded in the following winter on both sites. Numerous juveniles of several urchin species (*T. g. elatensis, D. setosum* and *E. calamaris*) were found at site A, in February 1984, at observed densities of $>50/m^2$. These recruits also occupied areas which are normally uninhabited by *T. g. elatensis,* such as exposed gravel beds and sandy slopes. A moderately strong southern wave-storm, on 15 April 1984, failed to eliminate them.

Measurements taken at both sites three months after this winter recruitment (2 July 1984) showed unusual patterns of size frequency distribution (Fig. 5). Site A,

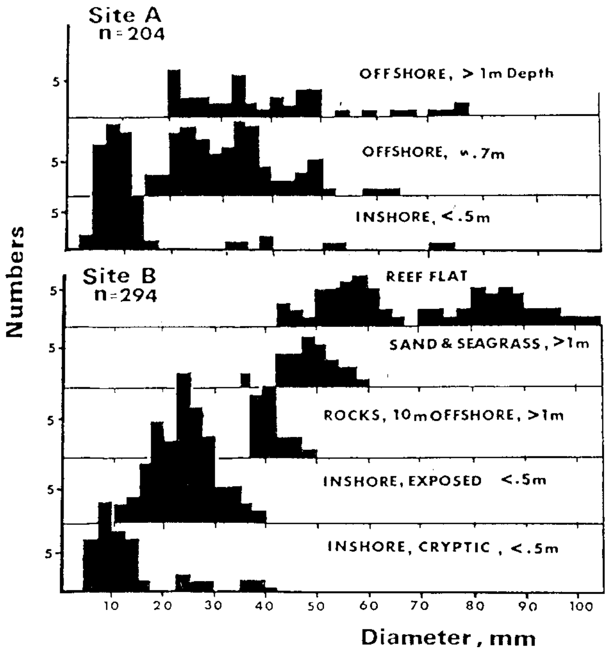


Fig. 5. Size frequency distribution of both populations on 2 July 1984, at the various transects (Fig. 1), from the intertidal offshore (lower plots are the nearest to the shore): For site **A: Lower intertidal**(<0.5 m depth); 2-5 m offshore (0.7 m); 20 m offshore (1.5 m depth). Site B sections: Underparts of stones 2 m from the lowtide mark (<0.5 m depth); Exposed urchins from the same area; Rocks and coral heads in the lagoon, 10 m offshore; Sand and *Halophila* bed, 30-40 m offshore; and shallow reef-flat.

where an additional transect, 0.7 m deep, was also examined, showed a size frequency with 3-4 distinct size groups (Fig. 5A): one with a modal size of <10mm, in the inshore under stones, and 3 peaks at 21, 34, and 48 mm, apparently representing previous recruitments, in offshore transects.

Site B population, sampled in five parallel transects, demonstrated the tendency of 0-age urchins to move offshore. While urchins <20 mm were found exclusively inshore, in the upper subtidal, showing cryptic behaviour, larger urchins were fully exposed and at a high abundance. One group, with a modal size of 24 mm, was found inshore, exposed 0.5 m below low-tide level, whereas those found on rocks and coral knolls, 10 m offshore, were 37-50 mm. Still larger individuals, 40-60 mm HD, were found on bare sand and in *Halophila* meadows, next to the reef, whilst the reef-flat itself was populated with 40-105 mm individuals in two distinct size groups. It seems that all, except the 70-105 mm size group, are age-0 urchins, representing several recruitment episodes.

Predation

Coris aygula was rather common on site B. This diurnal fish emerges from its nocturnal shelters after sunrise, foraging in groups of 2-5 adults (30-50 cm total length, TL) (Tobol, 1983). Although it is known to feed on urchins (Fricke, 1971), field observations throughout 1980-1983 failed to provide unequivocal evidence of *C. aygula* preying upon *T. g. elatensis*, possibly because of the low availability of juvenile urchins. Wrasses were often observed to forage intertidally during high tide, with their dorsal fins breaking surface, but it was uncertain whether they took urchins or brittle-stars. In August 1984, when site B abounded with *T. g. elatensis* of all sizes, the results were conclusive. One foraging group, consisting of five adult wrasses, >40 cm TL, was followed for >3 hours (9 am—12.30 pm), and each fish was observed for 15 min from a distance of 3-4 m and its feeding activity recorded. Altogether there were twelve 15 min observations, during which each wrasse ingested 0-6 urchins, with an average of 2.33±1.78 (SD). The size of the ingested urchins could not be determined, but most of the urchins in the examined area were <40 mm.

A significant size dependent predation was shown in the feeding experiment (Table I): *C. aygula* ingested all *T. g. elatensis* smaller than 30 mm HD, most of them within 1 min upon offering, while only 80% of the 30-40 mm urchins were taken, mostly within 5 min. Ten out of 12 urchins >40 mm HD were totally rejected by the predator.

In another experiment, simultaneously offering one *T. g. elatensis* and one *E. mathaei*, 9 out of the 12 *T. g. elatensis* were taken first. Smaller *T. g. elatensis* were taken whole, while larger ones were often broken by smashing them into rocks (cf. Fricke, 1971). When offered together with brittle-stars, the latter were taken more readily; in 78% of the cases they were taken first ($\chi^2=50.03$, df=2, $p<0.001$).

In order to assess the predators' abundance in both sites, two eye-transects were examined by swimming from the shore into 4-5 m deep water (August-September 1982), recording *C. aygula*'s absence or presence. In only six out of 40 observations in site A subtidal area, solitary wrasses were encountered (15%), all of them in water deeper than 3m, whereas in site B they were ever-present (25 out of 25), preferably in shallow water.

TABLE I

Size-dependent predation of offered *T. g. elatensis* by adult wrasses (*C. aygula*): Urchins were exposed to the predator singly or in pairs[1].

Size mm	*Offered* (n)	*Ingested* within 1 min	1—5 min	*Rejected*
10-20	41	35	6	0
20-30	27	15	12	0
30-40	15	1	11	3
40+	12	0	2	10

[1] Chi-square test for Goodness of Fit: $\chi^2=86.47$, $p<0.0001$.

DISCUSSION

Quantitative assessment of the population density of shallow water echinoids is always problematic owing to their high temporal and spatial variation. It is particularly true for intertidal or subtidal species that occupy a relatively narrow belt parallel to the shore. An additional source of variation in *T. g. elatensis* are radical changes in the dispersion pattern during postlarval ontogeny, from extreme aggregation shortly after settlement, to a nearly random dispersion upon their emerging to superficial grazing, to the foraging aggregation of reef-dwelling adults (Mastaller, 1979).

Since the transects were non-random and different methods were employed to locate and collect the different age-groups at the different seasons, the thus measured abundance is of limited value. Yet, being taken from the same transects (±1m) it largely compensates for the bias entered in the sampling, providing a basis for semi-quantitative comparison between different years.

As far as *T. g. elatensis* is concerned, the two sites represent two environmental extremes. The factors involved were, according to our observations, wave action and predation and to a somewhat lesser extent the fluctuations in postlarval recruitment. Substrate type played a minor role.

Surf Exposure. Tripneustes is a typical sea-urchin of sheltered habitats. This is well explained both by its fragile test and its relative absence from wave-beaten habitats (Ebert, 1982). In the normally calm northern Red Sea shores with rough sea conditions limited only to the winter season, it may extend its distribution into more exposed shores by adapting an annual life-cycle, as demonstrated by site A population.

It is suggested that, in addition to postlarval survival, larval recruitment may also be affected by the seasonal sea conditions. Considering that *T. g. elatensis* starts to spawn in October (Pearse, 1974; Dafni, 1984), and larval development to metamorphosis under controlled conditions may be accomplished within 18 days of spawning (Mortensen, 1937), one may expect settlement of new recruits in November-December. Growth from the postlarval size (<1 mm), when they settle on the substrate, to a HD of 4-5 mm, when they are first discernible in the field, may take another two months. Thus, the earliest recruits are expected to appear in January-February. Hence, the late spring (May-June) recruitment, normally occurring in both sites, probably reflects a delay in settlement owing to the rough sea conditions, whereas the observed 1983 and 1984 mid-winter recruitments were obviously non-delayed.

In sheltered bays along the NW Sinai shore, >20 mm 0-age urchins were commonly seen as early as April even in years of normal recruitment (1980, 1981 — J. Dafni, unpublished).

Ebert (1982), who sampled site A's *T. g. elatensis* population in 1976, attributed the complex size distribution pattern he found there (his fig. 24), with three modes in the <40 mm size group, to several episodes of recruitment within one season. Thus, non-delayed mid-winter recruitment may be linked with multi-recruitments.

Recruitment Variability. From 1979 to 1980 no recruitment was shown at site B. In 1981 new recruits were recorded subtidally, but it seems that only a few of these juveniles reinforced the reef-flat sub-population. From 1982 to 1983, recruitments at site B were also meagre, with no apparent influence on the reef-flat sub-population, whereas in 1984 strong recruitment had a more profound effect on this population (Fig. 5). It appears that only twice during this study, in 1981 and 1984, any significant recruitment of the reef-flat sub-population may have occurred.

Although annual fluctuations in echinoid recruitment are well documented, it is hard to differentiate between variation in settlement and survival of earlier stages (Ebert, 1983). The unusual abundance of newly recruited *T. g. elatensis* in 1984 had been recorded in other locations within and outside the Gulf. At Sharm-esh-Sheik, in the northern Red Sea, numerous >20 mm 0-age *T. g. elatensis* were encountered in June 1984 (A. Dotan, pers. commun.). Since this was by no means a calm winter, the profusion in postlarvae may suggest favourable conditions during the planktonic larval life, whereas the different observed recruitments at site A and B may be due to local conditions, such as high or lesser predation of postlarvae in their cryptic hideouts. We suggest that the prevailing late-winter single recruitment in the observed sites is largely the consequence of pre and post-settlement mortality.

Predation. Stable bi-modal size frequency patterns, as shown in Fig. 4, suggest exclusion of medium-sized individuals (Tegner & Dayton, 1981). Here the two modes also involve spatially separated sub-populations. Despite fluctuations due to their erratic foraging, site B adults' size pattern was stable (Fig. 4), whereas the juvenile sub-population's pattern was apparently controlled by the wrasses. Tobol (1983) found that *C. aygula* males (40-50 cm TL) occupied well-defined territories of about 2500 m^2 in site B, extending over reef-flat and lagoon areas, while smaller individuals (juveniles and females) moved more freely between these territories.

It is suggested that *T. g. elatensis*, which emerge from their subtidal hideouts, are vulnerable to predation owing to their fragile test and short spines. Toxic pedicellaria (Alender et al., 1965), which may deter predators, are apparently less developed in the juveniles. It is believed that predation mainly takes place when the juveniles emerge from under the stones, moving offshore. Thus this offshore migration is controlled by the predator. During "population explosions" the number of offshore moving urchins is higher than the predator population can possibly handle. In site A the distribution of predator and prey does not normally overlap, and predation is a less important factor in survival.

Although lasting predation has been shown to affect echinoid behaviour (Snyder & Snyder, 1970; Fricke, 1974; Nelson & Vance, 1979; Tegner & Levin, 1983), cryptic behaviour of juvenile echinoids is, presumably, an inherited avoidance response. We suggest that since there is no record of late summer recruitment, the year-round existence of smaller individuals in site B subtidal, as well as the presumable hindered migration of these urchins towards the reef, through the sandy lagoon, mainly result from the constant prowling of the wrasses. Since cryptic behaviour may involve lesser nourishment, they possibly become stunted. In a Ca^{45} incorporation assay, in which four 20 mm HD urchins from site B were compared to equal sized urchins from site A, their calcification rates were 2.5 times lower (Dafni & Erez, unpublished data).

Environmentally controlled life histories. Data presented here suggest different life histories in the different sites. While site A population exercises an apparent annual cycle — settlement, rapid growth and mortality during stormy winters — all within 8-10 months, site B reef population exhibits a perennial pattern, characterized by variable recruitment of postlarvae, low juvenile survival, but considerably longer life expectancy for adults.

With recruitment variability, wave exposure and predation of pre-reproductive urchins as primary factors, these results agree with Ebert's (1982) model. Since it is unlikely that both populations differ genetically, it seems that the differential effect of the physical environment plays a major role in determining the population life history, rather than any density-dependent factor, as required by MacArthur & Wilson's (1967) model. In Ebert's (1982) terminology site B is a typical "superior habitat", characterized by a high annual survival. Another superior habitat, frequently visited in the course of this study, was the wide table-reef at Wadi Murach, separated from the shore by an extensive sandy area. For four consecutive years *T. g. elatensis* population there consisted only of >70 mm HD adults, inhabiting the offshore reef-edge. Only once, in spring 1981, a considerable number of 0-age urchins appeared on the shoreward side of the reef-flat, growing rapidly and moving offshore (this site was not revisited in 1984) (Dafni, pers. obs.). Site A is, according to Ebert's definition, a "marginal" habitat, where survival depends on physiological adaptation (development of protective devices or early reproduction) (Ebert, 1982). The demarcation between superior and marginal habitats is less distinct during calmer winters or consequent to exuberant recruitment.

T. g. elatensis ability to inhabit marginal habitats rests upon its rapid growth and early reproduction. Field data (Figs. 3 & 5) and captivity feeding experiments (Dafni, 1984) indicate rapid growth, that depends on food supply and feeding opportunity. As for reproduction, Mortensen (1943) found that the genital pores of Red Sea *T. gratilla* first appear at 20 mm HD, while in the Indo-Pacific conspecific they appear at >30mm. All site A individuals >25 mm, that were examined in early winter (December), had open genital pores, and those >40 mm had ripe gonads (Dafni, unpublished). Hence, approximately half of site A 0-age urchins had an opportunity to spawn before the onset of the winter storms.

Being a fast-growing species, the impact of recruitment variation on *T. g. elatensis* marginal habitats is essentially short-lived, in contrast with the long-lasting effect of "strong" recruitments, discernible for many years in the population structure of temperate zone species (Ebert, 1983).

Mergner (1981) and Walker & Ormond (1982) linked a recent increase in abundance of echinoids at 'Aqaba, Gulf of Elat, with increase of algal production and environmental deterioration. Although strong recruitments, such as those of 1983 and 1984, might have benefited from the prevailing pollution-induced eutrophication (Fishelson, 1973), fluctuations in *T. g. elatensis* were known for >20 years (F.D.Por, pers. commun.) and were also recorded from non-polluted localities (A. Dotan, pers. commun.). We suggest, therefore, that the environmental stress produced by pollution may contribute to the fluctuations, rather than cause them.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the encouragement provided by Prof. F.D. Por and Dr. J. Erez during this study. Drs. H. Fricke, J.J. Kendall, J.S. Pearse, A. Diamant, and Mr. A. Dotan read early drafts of the manuscript and offered valuable comments. The friendly help of the H. Steinitz Marine Biology Laboratory staff is highly appreciated.

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