LONGEVITY, LIFE HISTORY, AND RELATIVE BODY WALL SIZE IN SEA URCHINS[1]

Thomas A. Ebert

Department of Biology, San Diego State University,
San Diego, California 92182 USA

Abstract. Annual survival rates in 38 populations of 17 sea urchin species in the Indo-West Pacific were related to relative size of the body wall and exposure to the surf. The urchin species are: *Heterocentrotus trigonarius*, *H. mammillatus*, *Colobocentrotus atratus*, *Echinometra mathaei*, *E. oblonga*, and *Heliocidaris erythrogramma* in the family Echinometridae; *Prionocidaris baculosa* in the Cidaridae; *Stomopneustes variolaris* in the Stomopneustidae; *Echinothrix calamaris*, *E. diadema*, *Centrostephanus rodgersi*, *Diadema paucispinum*, and *D. setosum* in the Diadematidae; *Tripneustes gratilla*, another *Tripneustes* sp. (possibly the same as *T. gratilla*), and *Toxopneustes pileolus* in the Toxopneustidae; and *Salmacis belli* in the Temnopleuridae. Populations were studied at Hawaii, Enewetak Atoll, Queensland, New South Wales and Western Australia, Sri Lanka, Seychelles, Kenya, Zanzibar, and Israel (Eilat).

Live animals were dissected to determine the size of body components. The relative size (mass) of the body wall for a species is expressed by the constant α in the equation $B = \alpha T^\beta$, where B is wet mass of the body wall and T is total wet mass. A common β value of 0.976 ± 0.004 (SE) was used for all species, so α values can be used to compare relative body wall sizes among species. Values of α ranged from 0.966 for *Heterocentrotus trigonarius* (Enewetak Atoll) to 0.360 for *Salmacis belli* (Moreton Bay, Queensland, Australia).

Parameters of the Richards growth function were determined from animals tagged with tetracycline. Tagged animals were collected after they had been in the field for 1 yr. Growth parameters were used with parameters from size-frequency distributions to estimate Z, the mortality coefficient. Annual survival probability p is e^{-Z}.

Stepwise multiple regression was used to examine the relationship between annual survival probability (p) and two independent variables, α and E, where E is a subjective measure of exposure to surf (1 = most exposed). The function is $p = 1.206\alpha + 0.061E - 0.350$. Survivorship increases with increased relative size of the body wall and with increased protection from the surf. The positive relationship between survival probability and relative body wall size supports the hypothesis that survival is related to allocation of resources to maintenance.

The significance of longevity in urchins probably is that it is related to the predictability of survival of prereproductive individuals. The greater the unpredictability, the longer life must be. Long life requires a greater investment in maintenance mechanisms and hence, among other adaptations, a more massive body wall.

Key words: allometry; Australia; echinoid; Enewetak; growth; Hawaii; Israel; Kenya; life history; mortality; Richards function; Seychelles; Sri Lanka; tetracycline; Zanzibar.

INTRODUCTION

Factors that drive selection of life history features are existing adaptations of indiuduals and the way in which variation in these adaptations contributes to variation in fitness in the environments in which the individuals live. Stearns (1976, 1977) has explored this statement and presented two opposing theories for life history evolution: one deterministic and the other stochastic, commonly called the theories of r- and K-selection and bet hedging, respectively. The theory of r- and K-selection, derived by Mac Arthur and Wilson (1967) from the ideas of Dobzhansky (1950), emphasizes the importance of biotic interactions with associated density-dependent effects and environmental stability in favoring development of long-lived organisms, the K-selected forms. Bet-hedging theory provides an alternative view of the factors that shape development of longevity. The theory as presented by Holgate (1967), Murphy (1968) and Schaffer (1974) emphasizes the unpredictability of recruitment success in determining length of life. Factors that cause unpredictability could be biotic or abiotic, density dependent or independent. Environments perceived by individuals of a species as very predictable with respect to prereproductive survival would favor evolution of short life, which is directly opposite to expectation based on the theory of r- and K-selection.

Underlying both points of view is the belief that selection can be linked to energy budgets. Resource allocation within an individual is considered to "make sense" in terms of length of life and scheduling of births (Gadgil and Bossert 1970, Calow 1977, 1979, Sacher 1978, Kirkwood and Holliday 1979, Law 1979, Lynch 1980).

There are several important questions that can be directed toward any group of organisms that show different life histories:

ENERGY AND MATERIALS

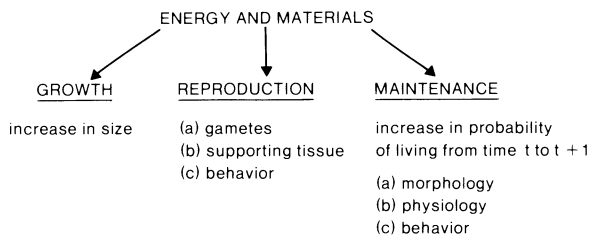| GROWTH	REPRODUCTION	MAINTENANCE
increase in size	(a) gametes (b) supporting tissue (c) behavior	increase in probability of living from time t to t +1 (a) morphology (b) physiology (c) behavior

FIG. 1. Allocation of resources, energy, and materials to three compartments. Model is adapted from Gadgil and Bossert (1970).

1) Are life histories related to resource allocation?
2) Are life histories related to variation in age-specific survivorship?
3) Are life histories related to the intensity of biotic interactions (i.e., competition and predation in a density-dependent manner)?

Any general theory of life history evolution must generate hypotheses that are testable with data related to these three questions. The purpose of the work presented in this paper is to examine aspects of question 1, in particular the relationship between life span and resource allocation, using data on 17 species of sea urchins, most of them from the tropical Indo-Pacific. As such, this study does not address directly the problem of discriminating between r- and K-selection vs. bet hedging (questions 2 and 3) but does attempt to form a basis for examining these alternative theories, using sea urchin species.

The allocation model

As presented by Gadgil and Bossert (1970), organisms have limited resources with which to operate. This statement seems to be true whether or not an organism lives in an environment where resources are in short supply (Law 1979). Even with superabundant resources, an animal or plant can assimilate only a finite amount each day, and this finite amount must be allocated to various structures, processes, or activities.

Fig. 1 is a representation of the Gadgil-Bossert model. Energy or materials are allocated to growth, reproduction, or maintenance. Allocation to growth means allocation to increase the size of body parts, with attendant complications of allometry and constraints on how parts can change in relative proportion and still follow basic rules of being, for example, a toad, a toadflax, or a toadstool (the constraint rules of Stearns [1977] or Gould and Lewontin [1979]).

Allocation to reproduction includes not only gametes but supporting somatic tissues of the gonad plus reproductive behavior. In urchins, reproductive behavior is present in brooding species such as certain polar cidaroids (Hyman 1955) and possibly in species that form aggregations prior to spawning (reviewed by

Reese 1966). Most urchin species appear not to have resource requirements associated with reproductive behavior.

Maintenance allocation includes all those morphological features, physiological processes, and behavioral characteristics that increase the probability of survival, i.e., solutions to the problems of getting to the age of first reproduction, getting from there to the next reproductive period, and so on. In urchins these solutions include such morphological features as sharp spines or toxic pedicellariae; physiological processes such as systems for temperature tolerance (Lawrence 1973) or immune responses (Johnson 1969, Johnson and Chapman 1970); and behavioral adaptations such as excavation of cavities (Otter 1932, 1937), the "shadow response" (Millott 1954, Millott and Yoshida 1957), and aggregating (Pearse and Arch 1969, Snyder and Snyder 1970) for possible protection from predators, covering reactions (Lees and Carter 1972), or agonistic behavior (Grünbaum et al. 1978).

Although heuristically the Gadgil-Bossert model is very useful, it possesses a fundamental problem: the various categories in Fig. 1 are not all measurable, nor are they mutually exclusive. For example, the probability of survival may be related to growing rapidly to a size that can escape predation, as suggested for cladocerans (Lynch 1980) and shown for the urchin *Paracentrotus lividus*, in which large individuals are safe from crab predators (Muntz et al. 1965). Furthermore, maintenance, as such, is not measurable, though rate and amount of DNA repair is an index at the cellular level (e.g., Hart and Setlow 1974). Respiration rate is not maintenance because it includes metabolism associated with growth and reproduction.

An alternative approach to using the Gadgil-Bossert model as shown in Fig. 1 is to turn the model around and use features that are measurable and attempt to assign functions to these features. This approach suffers from a loss of generality (it is difficult, though not impossible, to transfer insights about urchins to studies of cacti), and measurable items do not necessarily have single functions. However, measurable features are the focus of study in this approach, and therefore it is the one I use in this paper.

Table 1 shows body parts that can be measured following dissection of an urchin, together with what seem to be primary and secondary functions. All components grow, so all body parts compete for resources that are allocated to the category called "growth" in Fig. 1. "Maintenance" functions are provided by the body wall by virtue of thickness and presence of spines, together with qualitative differences in spines, pedicellariae, and in a few cases such as in *Asthenosoma*, poison sacs on the spines. Other body parts also contribute to maintenance. Aristotle's lantern, with associated teeth, is an important structure for excavating cavities; the gonad and gut are storage organs (Lasker and Giese 1954, Lawrence et al. 1966), and the peri-

TABLE 1. Body components of sea urchins with suggested functions. My view of "primary" function is listed first. The body wall includes both test and spines as well as other structures on the test such as pedicellariae, tubefeet, and the ampullae of the water vascular system.

Body wall	Aristotle's lantern	Gut	Gonad	Perivisceral fluid (PVF)
Maintenance	Food gathering	Food processing	Reproduction	Space adjustment
Food gathering	Maintenance (hole excavation)	Maintenance (energy storage)	Maintenance (energy storage)	Maintenance (clotting, immune response)

visceral fluid (PVF) contains cells that form clots following a break in the test as well as cells that attack foreign bodies (Endean 1966).

In this paper I will concentrate on the relationship between morphology and lifespan, and so stated, the work is an attempt to link allocation to body parts with longevity. It is the approach that has been used to relate longevity to brain size (Sacher 1976, 1978) and to total mass (Blueweiss et al. 1978, Western 1979).

I wish to argue that the body wall of an urchin, with its calcareous skeleton, spines, pedicellariae and associated soft tissue, together with the tube feet, is a morphological structure of importance in maintaining life. Consequently, there should be a positive correlation between relative size of the body wall and the probability of survival. The details of allocation cannot be examined in this paper because annual energy budgets for the species do not exist. It will be assumed that the relative size of a body component (Table 1) is an index of annual allocation to the component, which is an assumption that probably is reasonable for parts other than the gonad.

The outline for presentation will be to establish relative size of the body wall for 22 species of sea urchins, present survivorship information for 38 populations of urchins comprising 17 species, and then relate survivorship to relative body size. The analysis is complicated by having study sites that range from high-energy benches to protected bays. Some species are found in a wide range of surf conditions, and it would not be surprising to discover that survivorship would change under different surf conditions. Consequently, analysis includes two independent variables: relative size of the body wall and exposure. The question that is asked is: under similar conditions of exposure, is there a significant relationship between survivorship and relative body size? The test for significance of the multiple regression coefficients is a partial test of whether allocation is related to survivorship.

METHODS

Determination of body wall size

Live animals were drained on absorbent paper for ≈1 min, and their mass was determined. They were then dissected into component parts: body wall, lantern, gut, gonad, perivisceral fluid (PVF), and gut contents, and the masses of the components were determined. The selection of parts was based on ease of separation of components. I selected the same components (other than gut contents) as those used by Giese and some of his students (e.g., Giese 1966, Lawrence 1967). The body wall includes surface structures of the test (spines and pedicellariae), tube feet, and the ampullae of the water vascular system and the peristomal membrane. A range of sizes of urchins was used, so allometry of the body wall could be examined.

Determination of survival probability

Estimation of survival probability was not done directly, but by making use of the fact that a size-frequency distribution is the result of interaction of a growth function and a survivorship function, together with variation in recruitment within a year (seasonal recruitment) and between years (strength of year-classes). By assuming that a population is stable and has a stationary structure, it is possible to estimate survival using a size distribution and growth parameters (Ebert 1973, 1981, Van Sickle 1977). The assumption of a stable population with $r = 0$ is probably violated by many, if not most, of the populations I examined. My solution to this problem has been to try to sample a large number of populations and accept an unknown error in my estimates. For a large number of populations, the average value of r should be 0, and I should tend to overestimate mortality rate as frequently as I underestimate it.

Size distributions were obtained at each sampling site by collecting all individuals within an area and measuring test diameter (or test length in the Family Echinometridae) with vernier calipers. Caliper jaws were worked down among the spines, so a measurement estimates size of the test. Numbers of individuals in a sample varied depending upon available animals, local conditions of tide and surf, and numbers of assistants, but an effort was made to have no fewer than 200 individuals in each sample.

Growth was determined from individuals tagged with tetracycline (Kobayashi and Taki 1969, Pearse and Pearse 1975, Ebert 1977, 1980a). Two grams of tetracycline-HCl were dissolved in 100 mL of seawater,

and ≈ 0.2 mL was injected into each urchin through the peristomal membrane. An automatically filling syringe (Clay Adams "Aupette") was used to decrease handling time of individual urchins. After tagging, animals were returned to the area where they were collected. At least one assistant helped with collecting and tagging at each location, and after 1 yr the assistant(s) returned to the given area, collected urchins, dried them in the sun, and boxed and shipped them to me for further processing.

Organic matter was removed from urchins with a 5% sodium hypochlorite solution (household bleach). Parts were washed in tap water several times and left overnight in water after spending a day in bleach, and then the parts were air dried. Test diameter or length of each individual was measured, and half-pyramids of Aristotle's lantern were examined using longwave ultraviolet (UV) light (Mineralight® UVSL-25, Ultraviolet Products, San Gabriel, California, USA). Tetracycline fluoresces under UV, and tagged animals could usually be recognized easily. However in some cases lines were faint, and in some samples there were what appeared to be natural fluorescing lines that severely complicated selection of the tetracycline tags. I used jaws rather than plates of the test to determine growth because the jaws were much easier to measure. The jaw does not require grinding to reveal the tetracycline marks, and both initial and final sizes can be measured on a single jaw. In the test, the initial ambital plate may become part of the oral surface as the urchin grows, and to determine initial and final size it is necessary to scan a number of plates to find the largest glowing image to use as initial size. Test plates have been used previously to determine growth with tetracylcine tagging (Ebert 1977).

Jaws grow on all surfaces but appear to add very little calcite on the flat, ridged surface where interpyramidal or comminator muscles attach, and it was this flat surface that was examined for fluorescing lines. Growth of the jaw is at both the oral tip and the aboral end, so it was necessary to examine both ends of the jaw to determine original size. Growth at the oral tip of the jaw was always much less than at the aboral edge and in large animals there frequently was no measurable growth at the oral tip. Length of the jaws (in centimetres) was measured from the oral tip to the flat shoulder at the aboral end, which is the articulating surface between the jaw or half-pyramid and its epiphysis. A photograph of the jaws showing points of measurement is given elsewhere (Ebert 1980b).

A graph of size of the jaw after 1 yr (S_{t+1}) vs. original size (S_t) was used to estimate growth parameters. If the regression is a straight line, it is possible to estimate parameters of the Brody-Bertalanffy growth equation (Walford 1946). The regressions for jaw sizes were not straight lines, so a more flexbile growth equation, the Richards function, was used (Richards 1959, Ebert 1980a).

The Richards function can be written:

$$S_t = S_\infty[(1 - be^{-Kt})^{-n}], \tag{1}$$

in which S_t is size of an individual at time t, S_∞ is asymptotic size, b is a scaling parameter equal to $(S_\infty^{-1/n} - S_0^{-1/n})/S_\infty^{-1/n}$ with S_0 equal to size at settlement, K (yr^{-1}) is a growth rate constant, and n is a shape parameter. When $n = -1$ the equation is the Brody-Bertalanffy equation; when $n = +1$, the function is the logistic, and as $|n| \to \infty$ the function approaches the Gompertz eqauation. The procedure for estimating parameters of the Richards function, given initial and final sizes and a fixed time interval, is discussed elsewhere (Ebert 1980a).

Because the growth parameters in the Richards function were for jaws and the urchin size distributions were in test lengths, it was necessary to establish the relationship between jaw size and test size. This was done using $\log_e$ transformations of jaw and test lengths and by determining constants using a geometric mean (GM) functional regression (Ricker 1973). The relationship is:

$$J = \alpha S^\beta. \tag{2}$$

Asymptotic size of the jaw (J_∞) was obtained as one of the parameters in the Richards function, and Eq. 2 was used to estimate both asymptotic size of the test (S_∞) and a shape parameter n for the test:

$$S_\infty = (J_\infty/\alpha)^{1/\beta}; \tag{3}$$

$$n = n_j/\beta, \tag{4}$$

where n_j is the shape parameter for growth of jaws.

Using the shape parameter n, individual size measurements in a size distribution were transformed to $S^{-1/n}$, and a mean of these values for the entire size distribution, $\bar{X}$, was calculated. It has been shown elsewhere (Ebert 1981) that if a constant mortality rate is assumed, then

$$\bar{X}/S_\infty^{-1/n} = 1 - \frac{b[e^Z - 1][e^{K(1-t)}]}{e^{K+Z} - 1}, \tag{5}$$

and if a value C is established that accumulates terms that do not include Z:

$$C = \frac{S_\infty^{-1/n} - \bar{X}}{S_\infty^{-1/n}be^{K(1-t)}}, \tag{6}$$

then the instantaneous mortality coefficient Z(yr^{-1}) is

$$Z = \ln\left[\frac{1 - C}{1 - Ce^K}\right]. \tag{7}$$

The value of t is the time since recruitment of animals size S_R, which can be any arbitrary value and can be the mean value of the first component in the size frequency distribution, i.e., the average size of animals of age-class 0 on the day the size distribution was measured. The probability of surviving 1 yr for an individual that has entered the population being

studied (i.e., after settlement and large enough to be taken when all animals are collected in an area) is e^{-Z}. Expectation for further life of an individual of any age is $1/Z$, and l_x, the probability of living to age x following recruitment, is e^{-Zx}. It is obvious that Z does not include mortality in the plankton or immediately following settlement.

If the size distribution contains an obvious age-class 0, then an alternative procedure can be used to estimate annual survival probability e^{-Z} (Caughley 1967, Ebert 1981). Assuming a stable and stationary age distribution, it is possible to estimate Z from the fraction of the population in age-class 0. The terms of the stable age distribution, C_x, are:

$$C_x = \frac{l_x e^{-rx}}{\Sigma l_x e^{-rx}}, \qquad (8)$$

which simplifies to $C_x = l_x / \Sigma l_x$ when $r = 0$.

The fraction of the population in age-class 0 is C_0, and l_0 can be taken as equal to 1. Therefore, the fraction of the population in C_0 is:

$$C_0 = \frac{1}{\Sigma l_x}. \qquad (9)$$

With constant mortality, e^{-Zx} can be substituted for l_x, and so, making use of the limit of a sum of terms with negative exponents,

$$C_0 = 1 - 1/e^Z. \qquad (10)$$

The survival probability e^{-Z} is:

$$e^{-Z} = 1 - C_0. \qquad (11)$$

In words, this equation means that, given a stable age distribution with stationary structure and a constant mortality rate, the probability that an individual will live for 1 yr is equal to the fraction of the population that is greater than age 0. Another way of viewing Eq. 10 is that when $r = 0$ the number of births equals the numbers of deaths.

Both methods of estimating survival probability will be used. Which method is selected will depend upon whether or not an obvious age-0 mode is present in the size distribution and whether good estimates of growth parameters are available. The results of tagging are used in either case. For the second method, tagging results are used to establish whether a mode can be considered as being age 0. When Eq. 11 is used to estimate the instantaneous mortality rate per individual, the subscript π will be added to Z, i.e., Z_π. The symbol π is used by Macdonald and Pitcher (1979) for "proportion" in describing components of size distributions.

Areas and organisms

Work was done in the Indo-Pacific from Hawaii to Israel. Except for the samples at Enewetak Atoll, all size distributions were measured, and urchins were tagged with tetracycline during 1975–1976. At Enewe-

tak urchins were tagged during 1977–1978. Table 2 shows the areas where urchins were studied, together with the species for which growth and size data were obtained. The purpose of theis section on areas and organisms is to introduce the environmental setting for the species. Information will include exposure, water depth, and associated organisms, particularly other echinoids. A subjective ranking was established to evaluate surf exposure (E) and was based on my perceptions of the area rather than the presence of particular species (1 = most exposed; 11 = most protected). Factors considered in the ranking were whether an area was directly exposed to the open sea or was protected, my direct experience at the site, information from assistants and others at each location, and descriptions in the literature, if any.

Hawaii.—Kapapa Island is at the edge of the barrier reef across Kaneohe Bay on the northeast shore of the island of Oahu, Hawaii. The surf breaks on the outside, and secondary waves break around the island. A strong current flows around the island from the east. *Echinometra mathaei* and *E. oblonga* were tagged on the reef flat to the west of Kapapa that is exposed to the open sea ($E = 3.0$). The two species are common and live in cavities, crevices, or under rocks; however, *E. mathaei* is more abundant than *E. oblonga*. A total of 235 *Echinometra* was collected in a depression in the reef, of which 207 were *E. mathaei*. Both species also are present in the lee of Kapapa; this portion of the population has been described by Kelso (1970).

Echinothrix diadema and *Tripneustes gratilla* were tagged in the lee of Kapapa toward the eastern end of the island, ≈ 50 m offshore and at a depth of ≈ 2–3 m. The area is somewhat more protected than the area where *Echinometra* was tagged, and so I have given it an exposure value of 4.0. The bottom in this region is eroded reef derived from lithified sand dune (Stearns 1939). Some ledges and large boulders are present, and sand accumulates in large depressions by the ledges. The bottom is covered by $\approx 10\%$ living coral (Smith et al. 1973). *Echinothrix diadema* tends to live under ledges or in depressions, whereas *Tripneustes* is on more flat and exposed areas. *Echinothrix calamaris* was collected less frequently than *E. diadema*; of 292 *Echinothrix* collected, only 2 were *E. calamaris*. *Heterocentrotus mammillatus*, a slate-pencil urchin, is present but rare. Single specimens of *Echinostrephus aciculatus*, a rock-boring urchin, and *Eucidaris metularia*, a cidarid, were collected during the course of the study.

Kaneohe Bay has been studied by a team of researchers at the University of Hawaii, and physical, chemical, and biological data have been obtained. Studies include those by Smith et al. (1973), Caperon et al. (1971), and Hanson and Gundersen (1976, 1977).

Colobocentrotus atratus, a limpet-like urchin restricted to high-energy rock beaches, was tagged at Ulupau to the southeast of Kaneohe Bay and directly

TABLE 2. Species for which size data are available at one or more geographic locations. Urchins were tagged and collected 1 yr after tagging. g = growth determined, s = only size data gathered, and p = species present but not studied. Exposure rank is 1 for most exposed to surf and 11 for most protected. When two different exposure values are given for the same site, superscript letters a and b indicate which species were subject to each exposure.

Location (latitude, longitude)	Exposure rank	Family Cidaridae	*Prionocidaris baculosa* (Lamarck)	Family Diadematidae	*Centrostephanus rodgersi* (A. Agassiz)	*Diadema setosum* (Leske)	*Diadema paucispinum* A. Agassiz	*Echinothrix calamaris* (Pallas)	*Echinothrix diadema* (Linnaeus)	Family Stomopneustidae	*Stomopneustes variolaris* (Lamarck)	Family Temnopleuridae	*Salmacis belli* Döderlin	Family Toxopneustidae	*Toxopneustes pileolus* (Lamarck)	*Tripneustes gratilla* (Linnaeus)	*Tripneustes* sp.	Family Echinometridae	*Colobocentrotus atratus* (Linnaeus)	*Echinometra mathaei* (de Blainville)	*Echinometra oblonga* (de Blainville)	*Heliocidaris erythrogramma* (Valenciennes)	*Heterocentrotus mammillatus* (Linnaeus)	*Heterocetrotus trigonarius* (Lamarck)
Hawaii																								
Kapapa Island (21°29'N., 157°48'W.)	3.0[a], 4.0[b]							p[b]	g[b]							g[b]				g[a]	g[a]		p[b]	
Ulupau (21°27'N., 157°44'W.)	1.0																		g	p	s			
Makua (21°32'N., 158°14'W.)	2.0								s							s			ꞇ	g	p			
Pupukea (21°41'N., 158°3'W.)	4.0					s	p									s				s	p			
Honaunau (19°26'N., 155°55'W.)	4.0					p	p	p								p			p	p	p		g	
Enewetak Atoll																								
Ananij Reef (11°28'N., 162°24'E.)	1.5								p															g
Sand Island Channel (11°22'N., 162°21'E.)	5.0								p											s				
Australia																								
Hastings Point, New South Wales (28°22'S., 153°36'E.)	5.0																			p			s	
Moreton Bay, Queensland (27°23'S., 153°16'E.)	10.0						p						g											
Port Jackson, New South Wales (33°50'S., 151°15'E.)	8.0[a], 9.0[b]				g[a]																	g[b]		
Rottnest Island, Western Australia (32°00'S., 115°30'E.)	4.0										p									g				
Cape Peron, Western Australia (32°17'S., 115°42'E.)	5.0																					g		
Sri Lanka																								
Negombo (7°12'N., 79°53'E.)	6.0										g													
Seychelles																								
Round Island (4°38'S., 55°30'E.)	11.0		s			s		s	p		p				s	s								
Anse à la Mouche (4°44'S., 55°29'E.)	5.0		p			p		p	p		s				p	p				s				
Kenya																								
Ras Iwatine (4°4'S., 39°40'E.)	5.0							p			p				s					g				
Zanzibar																								
Yange Sand Bank (6°S., 39°E.)	6.0					s			p											p				
EAMFRO* (6°9'S., 39°11'E.)	6.0					g										p								
Israel																								
Eilat (29°27'N., 34°57'E.)	6.0					g		p									g			g				

* East Africa Marine Fisheries Research Organization.

below and to the east of the Naval Ocean Systems Center (NOSC) laboratory (Henderson and Smith 1978). Ulupau has an exposed lava solution bench 16–20 m wide that is undercut and possesses numerous "blowholes." This was the most-exposed site and was given an exposure value of 1.0. *C. atratus* was collected intertidally at the seaward edge of the bench where it occurs in small patches.

Two species of *Echinometra* were present at Ulupau. In a sample of 90 *Echinometra*, 3 were *E. mathaei*. Several small *Heterocentrotus mammillatus* and *Tripneustes gratilla* were observed on the bench.

Makua is on the southwestern shore of Oahu and has a lava bench with a large pool that flushes at high tide. The pool has a maximum depth of ≈1 m and is given an exposure value of 2.0. In 1975, *Echinometra mathaei* was more abundant than *E. oblonga*; in a sample of 629 animals only 14 were *E. oblonga*. Other urchins present in the pool in 1975 were *Tripneustes gratilla* and *Echinothrix diadema*, which were represented by 54 and 6 individuals, respectively, *Eucidaris metularis* (uncommon), and *Cyrtechinus verruculatus* (rare). *T. gratilla* and *E. diadema* occurred in the open areas of the pool that were relatively free of cobbles; other species lived around or under lava boulders and cobbles.

Pupukea Beach Park, on the north shore of Oahu, has a large pool protected by a high lava ridge. Maximum depth of the pool is ≈2 m, and because of the protecting ridge, the pool is given an exposure value of 4.0. *Echinometra* was tagged near a notch in the lava ridge where the surf enters the pool. Out of a sample of 352 animals only 2 were *E. oblonga*. Other species in the pool that were tagged were *Tripneustes gratilla* (common) and *Diadema paucispinum* (infrequent); also present were *Echinothrix calamaris* (infrequent), *Cyrtechinus verruculatus* (rare), *Eucidaris metularia* (rare), and *Echinostrephus aciculatus* (rare).

Only one site on the island of Hawaii (the Big Island) was selected: Honaunau, a semiprotected bay with a large lava bench to the north of the City of Refuge Historical Monument on the Kona Coast ($E = 4.0$). At the edge of the bench, the water is ≈3–4 m deep, and it was at this vertical drop that *Heterocentrotus mammillatus* was tagged. The bottom slopes very gradually to a depth of ≈10 m after the initial drop at the shore and is covered primarily by living coral. A large number of urchin species are present in addition to *H. mammillatus*. Small individuals of *Colobocentrotus atratus* were present at the water's edge followed by the two species of *Echinometra*. *Tripneustes gratilla* and *Echinothrix* sp. were abundant. *Diadema paucispinum* was common, and *Eucidaris metularia* and *Echinostrephus aciculatus* were present, though rare. Density data for the urchins of Honaunau have been published by Kelso (1969, 1970), and a size distribution for *Heterocentrotus mammillatus* has also been published (Ebert 1971). The survey in 1968 (Kelso 1969) found that *Diadema* and *Tripneustes* were not abundant or common. Both of these species appear to have increased in abundance from 1968 to 1975.

Enewetak Atoll.—Two locations were selected at Enewetak Atoll: the reef at Ananij Island ($E = 1.5$) and the channel between Enewetak Island and Sand Island ($E = 5.0$). There has been confusion in the literature concerning the naming of the islands of Enewetak Atoll. Ananij was called Japtan by Johannes et al. (1972) and Aniyaani by Bakus (1973). The United States military named the island Bruce.

Heterocentrotus trigonarius is very abundant at Ananij. Individuals live in cavities at the reef edge in what Wells (1954:385–486) calls the algal ridge and Odum and Odum (1955) call the coral-algal ridge. *H. trigonarius* is the only urchin that is abundant in this zone; however, a few *Echinothrix diadema* were observed living under coral tables on the reef flat just shoreward from the algal ridge. Odum and Odum (1955) reported that *H. trigonarius* was abundant at the reef edge. Their transect was run to the north of Japtan Island, which is on the windward reef just south of Ananij. The location of their transect relative to the reef where I studied *H. trigonarius* is shown on a map published by Johannes et al. (1972), who call Japtan Island Muti. The reef at Ananij has a gutter on the seaward side where the sea cucumber *Holothuria* (*Halodiema*) *atra* has been studied (Bakus 1973, Ebert 1978).

H. trigonarius is rare on the reef off Enewetak Island at the southeast corner of the atoll and is uncommon at Enjebi reef at the north end of the atoll. I did not see any *H. trigonarius* at Biken Island (Leroy), an isolated island on the leeward (west) reef, although there were *Heterocentrotus* spines on the beach.

Echinometra mathaei was tagged in the Sand Island channel, which is a shallow reef flat covered by ≈1 m of water at high tide. *Echinometra* lives under boulders and in cavities in piles of coral rubble that are held together by sponges. The common living coral in this area is *Porites lutea*. *Echinothrix diadema* is present in similar habitats in the channel nearer to Sand Island, and *Echinostrephus aciculatus* is abundant on the reef flat toward the sea. The location where *E. mathaei* was tagged was in the general area where Russo (1980) studied bioerosion by *E. mathaei* and *E. aciculatus*.

Australia.—Five locations in Australia were selected for tagging urchins, three on the east coast and two on the west coast. *Salmacis belli* was tagged at the Myora Banks off North Stradbroke Island in Moreton Bay, Queensland, at a depth of ≈0.5–1.5 m on sand ($E = 10.0$). This region is termed the Eastern Bank by Stephenson et al. (1970) and Community Type 4 by Young and Kirkman (1975). The site where *S. belli* was tagged was to the west of Rainbow Channel (Stephenson et al. 1970), where there is a series of sand flats covered with sea grasses (*Zostera capircorni* and *Halodule ovalis*). There was a steep drop at the edge of the grass-covered region down to a depth of ≈1.5 m, a sand bottom without sea grasses. *Salmacis* appeared to be concentrated at the edge of the grass bed at the edge of the steep drop. In addition to *Salmacis belli*, *Echinothrix calamaris* and *Temnopleurus toreumaticus* were collected at Myora Banks, but these two species were rare. Endean (1961) reports *Toxopneustes pileolus* and *Echinostrephus aciculatus* to be at Myora, the latter species obviously on hard surfaces.

Heliocidaris erythrogramma is a common urchin of the low rocky intertidal and subtidal from southern Queensland around southern Australia to Western Australia. An ancient lava flow at Hastings Point, New South Wales, formed an offshore reef and hence a protected region near shore ($E = 5.0$). *H. erythrogramma* was tagged and returned to this semiprotected area at a depth of 1–1.5 m. The area of Hastings Point is similar to the rocks at Currumbin in southern Queensland that have been described by Endean et al. (1956). Other urchin species were present, but other than *Heliocidaris*, none was common. Out of 878 urchins collected, 869 were *H. erythrogramma*, 2 were *H. tuberculata*, 5 were *Phyllacanthus parvispinus*, and 2 were *Echinometra mathaei*.

Balmoral Beach is ≈4 km inside the entrance to Port Jackson, the harbor of Sydney, New South Wales. *Heliocidaris erythrogramma* was collected at a depth of 2–3 m ($E = 9.0$). Other urchins tagged in Port Jackson were *Centrostephanus rodgersi* and *Pseudoboletia indiana* at Camp Cove in the lee of the Inner South Head at the entrance to the port. Camp Cove has an estimated exposure of 8.0.

In Western Australia urchins were tagged at Cape Peron and Rottnest Island near Perth. *Heliocidaris erythrogramma* was tagged at Cape Peron at a depth of 1–2 m and placed along an underwater ledge in holes or crevices. The exposure value was estimated to be 5.0. No other urchin species were seen, but two starfish species were present though neither was common: *Coscinasterias calamaria* and *Pentogonaster deubeni*. The rocks supported a luxuriant growth of algae, including *Eklonia*.

A large limestone platform ($E = 4.0$) exists at Rottnest Island at about low tide level. *Echinometra mathaei* has been abundant on these flats for many years, and work on this species has been reported by Pearse and Phillips (1968). *E. mathaei* was tagged at Radar Reef near the mountings of one of E. P. Hodgkin's tide gauges. The littoral environment of Rottnest has been descirbed by Hodgkin et al. (1959). The only other urchin seen at Rottnest besides *E. mathaei* was *Stomopneustes variolaris*, which was rare.

Sri Lanka.—*Stomopneustes variolaris* was tagged at Duwa Reef, Negombo, Sri Lanka. A sandstone reef runs off at an angle from the shore, providing a protected pool that opens at one end ($E = 6.0$). *S. variolaris* was very abundant in the shallow areas (<0.5 m) of this pool and was the only species that was observed.

Seychelles.—Urchins were tagged at two sites in Seychelles, one in the National Marine Park in Victoria Harbor ($E = 11.0$) and the other on the west coast of Mahé on the north side of Anse à la Mouche ($E = 5.0$). In the marine park, *Tripneustes gratilla*, *Toxopneustes pileolus*, *Diadema setosum*, and *Echinothrix calamaris* were tagged and released in the lee (western side) of Round Island in ≈3 m of water on a rubble

bottom with some large coral boulders separated by sandy areas with sea grasses and *Sargassum*. The general habitat has been described by Taylor and Lewis (1970). The common sea grass was *Thalassia hemprichii*, but *Syringodium isoetifolium* also was present.

Prionocidaris baculosa was released in shallow water ≈1 m deep and closer to the shore of Round Island. Round Island is not labeled on the map given by Taylor and Lewis. It is, however, shown on their map and is the small island to the southwest of L'ile Moyenne and northwest of L'ile Longue, and is part of the reef system that includes the islands of Cerf, Long, and Moyenne. In addition to *Thalassia hemprichii*, *Halophile ovata* was common in the shallow water near Round Island.

Echinoderms were very abundant in the sea grass beds near Round Island. In addition to the species that were tagged, the following echinoids were present: *Echinothrix diadema* (common), *Astropyga radiata* (infrequent), *Stomopneustes variolaris* (single specimen seen), *Phyllacanthus imperialis* (rare), and *Echinostrephus molaris* (uncommon). The sea cucumber *Holothuria* (*Halodeima*) *atra* was very abundant in the shallow sea grass beds to the south of Round Island. The starfish *Protoreaster lincki* and *Pentacer-aster horridus* were common to the south and southeast of the island (Ebert 1976).

Anse à la Mouche is a sheltered bay with a barrier reef. *Echinometra mathaei* and *Stomopneustes variolaris* were tagged and released inside the reef near the north shore at ≈1-m depth. Other urchins present were *Tripneustes gratilla*, *Toxopneustes pileolus* (both of which were common), *Echinostrephus molaris* (uncommon), *Prionocidaris baculosa* (rare), and outside the reef, *Echinothrix diadema*, *E. calamaris*, and *Diadema setosum* (all abundant). The crown-of-thorns starfish, *Acanthaster planci*, was present outside the reef.

I was unable to obtain any animals from Seychelles 1 yr after they were tagged, so no growth information can be presented for these urchins. Survival estimates must be based just on population size structure data.

Kenya.—Ras Iwatine is north of Mombasa, Kenya, and south of Bamburi Beach. It is an eroded rocky headland with a reef bench that I have assigned an exposure value of 5.0. The edge of the bench drops to a depth of 1–3 m, where the bottom is eroded reef with many ledges and large rock slabs. *Echinometra mathaei*, *Tripneustes gratilla*, and *Stomopneustes variolaris* were abundant enough to tag, but four additional species were present: *Echinothrix diadema* (uncommon), *Diadema setosum* (uncommon), *Toxopneustes pileolus* (uncommon), and *Salmacis bicolor* (rare). The area of Ras Iwatine has greater topographic relief than Diani Beach, south of Mombasa, which has been described by Khamala (1971) in his study of *Echinometra* distribution.

Tanzania.—*Diadema setosum* was tagged and re-

leased at the seawater intake of the East African Marine Fisheries Research Organization (EAMFRO) laboratory in Zanzibar. The intake is a concrete rubble pile in ≈2–3 m of water and is surrounded by sand with sea grass. Some *D. setosum* were present at the intake, but most animals were brought to the site from Yange Sand Bank, a reef ≈5 km offshore with an exposure value of 6.0. *Tripneustes gratilla* was common on the sea grass surrounding the water intake. At Yange Sand Bank, *Diadema setosum* was exceedingly abundant. Animals were so dense that it seemed unlikely that I could ever hope to recover any tagged individuals without tagging many thousands. It was for this reason that urchins were moved to the rubble pile in front of the laboratory. Size structure of the *D. setosum* population, however, was determined at a region of Yange Sand Bank. Other species present were *Echinometra mathaei* (abundant) in very shallow water, *Echinothrix* sp. (common), *Phyllacanthus imperialis* (rare), *Echinostrephus molaris* (rare), and *Eucidaris metularia* (single specimen). Herring (1972) worked at Mazizini Reef in Zanzibar, and in addition to abundant *D. setosum*, *Echinometra mathaei*, and *Echinothrix calamaris*, he found *Stomopneustes variolaris*, *Astropyga radiata*, and *Microcyphus rousseaui*.

Israel.—The bottom slopes away very rapidly in front of the Heinz-Steinitz Marine Laboratory at Eilat, so there is only a narrow subtidal region that is less than several metres deep. I tagged animals to the south of the laboratory at the edge of an area of beach that has been altered with massive rocks and which I have given an exposure value of 6.0. The bottom in this area is rubble with some ledges and coral heads. Three species were tagged with tetracycline. *Echinometra mathaei* and a *Tripneustes* sp. were in the rubble, and *Diadema setosum* was associated with the ledges and coral heads. Other species present were *Echinothrix calamaris* (frequent), *Nudechinus* sp. (uncommon), which possibly is *N. ambonensis* or may be a new species (A. Clark, *personal communication*), *Eucidaris metularia* (rare), and *Heterocentrotus mammillatus* (rare).

The *Tripneustes* species deserves comment. It has been called *T. gratilla* by biologists working with urchins from the Gulf of Eilat (Aqaba) such as James and Pearse (1969), Lawrence (1971, 1973), and Clark and Rowe (1971), but it does not appear to be typical of *T. gratilla* for several reasons. First, the color is very different from that of typical *T. gratilla*; animals at Eilat are red or white or brown, and so were like the *Tripneustes* described by James and Pearse (1969) in the northern Red Sea south of the Gulf of Suez. None was seen at Eilat with the color patterns of *T. gratilla* from Hawaii, Enewetak, Seychelles, Kenya, or Zanzibar. From Hawaii to Zanzibar, *T. gratilla* has virtually the same color: a dark body with spines with white tips. Some specimens may have more or less tan coloration, and some have irridescent blue regions,

but never white or red bodies. The *Tripneustes* at Eilat is flatter than other *Tripneustes* I have seen, and the gill slits appear to be not as deep. I choose to call the *Tripneustes* from Eilat *Tripneustes* sp. in this paper. Its systematic position is being investigated by J. Dafni from Hebrew University (*personal communication*).

The fauna of the northern Gulf of Eilat has been described by a variety of workers including Loya (1972), Fishelson (1971, 1973), Mergner and Schumacher (1974), and Mergner and Svoboda (1977). Mergner and Schumacher (1974), working south of Aqaba, report finding several additional echinoid species that I did not see at Eilat: *Microcyphus rousseaui*, *Phyllacanthus imperialis*, and *Prionocidaris baculosa*.

Summary of areas and urchins

Overall, the habitats that were selected can be described as intertidal to shallow subtidal, as none was deeper than ≈3–4 m. The exposure ranged from high-energy benches such as Ulupau, Hawaii, to protected bays such as the region surrounding Round Island in Victoria Harbor, Seychelles. With the exceptions of *Heliocidaris erythrogramma* and *Centrostephanus rodgersii*, the animals all are tropical. Most of the species are widely distributed, and some are abundant in many locations (e.g., *Echinometra mathaei* and *Diadema setosum*). Different habitats were included at the various locations, and an attempt was made to tag certain species at many locations. It was possible to do this with *Echinometra mathaei* and to a lesser extent with *Tripneustes gratilla*. What was gained by great diversity of species and locations was naturally lost in terms of the detail of local variations. Such variation is probably present in all of the species studied so that growth characteristics probably vary over small distances similar to variation reported for *Strongylocentrotus purpuratus* in Oregon (Ebert 1968, 1982).

A final note on taxonomy must be added. I refer to all *Diadema* outside of Hawaii as *D. setosum*. Field characters given by Pearse and Arch (1969) are that *D. setosum* can be distinguished from *D. savignyi* by: (1) longer spines, (2) blue spots rather than blue lines, (3) an orange ring around the anal cone, and (4) five interradial white spots. In Seychelles, most animals had blue lines and no spots, although one individual was found south of Round Island that had a blue ring around the anus, no other blue lines, and white spots. In general, the animals could be called *D. savignyi* other than the urchin with white spots, which might be called *D. setosum*, except that it lacked the orange anal ring. In Zanzibar the animals had white spots and sometimes white lines from the genital plates extending down to the white spots. Usually there were blue spots below the white spots, and there was an orange ring around the anus. These urchins would be *D. setosum*. The urchins at Eilat, Israel, had white spots (as does *D. setosum*) and blue lines (as does *D. savignyi*). Pearse and Arch (1969) and James and Pearse

TABLE 3. Urchin species that were dissected and analysed for allometry between body wall mass and total wet mass. All individuals of a species were combined for analysis. Arrangement of species in the table is based on relative size (mass) of the body wall, starting with the greatest relative size.

Species	Source of animals	Exposure rank	N	Date dissected
Heterocentrotus trigonarius	Enewetak Atoll	1.5	7	September 1977
			4	September 1977
Heterocentrotus mammillatus	Honaunau, Hawaii	4.0	20	September 1975
Colobocentrotus atratus	Ulupau, Hawaii	1.0	8	July 1975
Echinometra oblonga	Kapapa Island, Hawaii	3.0	8	September 1975
Echinometra mathaei	Punaluu, Hawaii	5.0	3	September 1975
	Kapapa Island, Hawaii	3.0	2	September 1975
			2	October 1975
	Pupukea, Hawaii	4.0	3	September 1975
	Enewetak Atoll	5.0	4	September 1977
Echinostrephus aciculatus	Enewetak Atoll	6.0	5	September 1977
Echinothrix diadema	Kapapa Island, Hawaii	4.0	9	July 1975
			2	October 1975
	Enewetak Atoll	6.0	3	September 1977
Strongylocentrotus purpuratus	San Diego, California	7.0	13	July 1978
Heliocidaris erythrogramma	Hastings Point, New South Wales, Australia	5.0	2	December 1975
			9	January 1976
			5	January 1976
Strongylocentrotus franciscanus	San Diego, California	7.0	13	July 1978
Lytechinus anamesus (=*pictus*)	San Diego, California	8.0	14	August 1978
Diadema setosum	Zanzibar	6.0	7	June 1976
Echinothrix calamaris	Eilat, Israel	6.0	5	July 1976
Tripneustes gratilla	Kapapa Island, Hawaii	4.0	4	August 1975
			7	September 1975
	Pupukea, Hawaii	4.0	3	September 1975
Tripneustes sp.	Eilat, Israel	6.0	13	June 1975

(1969) note that the characteristics were not very constant in the Gulf of Suez. Clark and Owen (1965) express doubt concerning the distinctness of the two species. I choose to call all of them *D. setosum*.

RESULTS

Dissections

To determine the relationship between total wet mass (x) and wet mass of the body wall (y), data were transformed using natural logarithms. Analysis of covariance was used to test for significant differences among species with respect to slope and intercept. Some additional data on dissections of southern California urchins are added to the information of the Indo-West Pacific echinoids. The point of doing this is to include animals that are more familiar to United States mainland investigators and so, I hope, make comparisons of tropical species somewhat more meaningful. Table 3 provides the names of the urchins, their locations, and dates of collection. Species were included in this portion of the analysis only if a range of sizes had been dissected that spanned at least several centimetres and included small animals. This restriction excluded *Prionocidaris baculosa*, *Salmacis belli*, *Toxopneustes*

pileolus, and *Diadema paucispinum* from the analysis of allometric coefficients.

The tests for significant differences among slopes and elevations for 15 species are presented in Table 4. The F value for testing the hypothesis that all slopes are equal is 4.43 (df = 14 149). $F_{.05(1)} = 1.76$, so H_0 could be rejected. I choose not to reject H_0 for the following reasons: first, residual mean squares appear not to be homogeneous based on a Bartlett's test ($B = 41.3$, df = 14; $B_{.05} = 23.7$). I recognize the difficulties of applying Bartlett's test (Zar 1974); nonetheless, the B value is more than just barely significant, and so suggests heteroscedasticity. Second, species with the relatively largest and smallest body walls are not different with respect to slope (*Heterocentrotus trigonarius* vs. *Tripneustes* sp. from Eilat). A multiple comparison test (Student-Newman-Keuls) showed that *Tripneustes gratilla* from Hawaii was the sample that had the significantly different slope; it was the only species with a slope greater than one. Other samples were not significantly different with respect to slope, and there is no trend of change in slope from urchins with large body walls to urchins with small body walls. Because only one sample was different, the sample

TABLE 4.   Calculations for testing for significant differences between slopes and elevations of regressions of ln body wall wet mass vs. ln total wet mass for 15 urchin species. Analysis follows Zar (1974: sections 17.3–17.6). Arrangement of species in the table is in order of decreasing values of α (Eq. 2).

Species	Sums of squares			Slope	Residual ss	Residual df
	SS_x	SS_{xy}	SS_y			
Heterocentrotus trigonarius	16.393	15.997	15.619	0.976	0.00743	9
Heterocentrotus mammillatus	32.654	32.415	32.194	0.993	0.01692	18
Colobocentrotus atratus	18.800	18.300	17.826	0.973	0.01329	6
Echinometra oblonga	14.148	13.749	13.384	0.972	0.02260	6
Echinometra mathaei	30.310	28.819	27.480	0.951	0.07791	16
Echinostrephus aciculatus	3.124	3.065	3.009	0.981	0.00203	3
Echinothrix diadema	36.032	35.474	34.998	0.984	0.07328	12
Strongylocentrotus purpuratus	16.640	15.625	14.711	0.939	0.03851	11
Heliocidaris erythrogramma	29.102	28.129	27.264	0.967	0.07460	14
Strongylocentrotus franciscanus	5.535	5.157	4.846	0.932	0.04183	11
Lytechinus anamesus	8.107	7.487	6.926	0.924	0.01184	12
Diadema setosum	9.921	9.363	8.891	0.944	0.05345	5
Echinothrix calamaris	9.029	8.352	7.734	0.925	0.00766	3
Tripneustes gratilla	25.631	26.877	28.284	1.049	0.10136	12
Tripneustes sp. (Eilat)	28.299	27.743	27.257	0.980	0.07804	11
"Pooled" regression					0.62075	149
"Common" regression	283.724	276.542	270.422		0.87927	163
"Total" regression	433.204	434.017	450.412		15.5798	177

F value for common slope = 4.432 $F_{.05(1),\ 14\ 149}$ = 1.76
F value for common elevation = 194.7 $F_{.05(1),\ 14\ 163}$ = 1.75

was not at one of the extremes of body wall size, and because the residual mean squares appear not to be homogeneous, it seems to make better biological sense not to reject H_0 at this time. The samples are small for all species, and additional dissections may indeed show that a common slope is inappropriate. Accepting a common slope moves the analysis to testing of a common elevation, which must be rejected because of the large F value (F = 194.66, df = 14 163). It is clear that the regression lines have different intercepts.

The allometric equation is $B = \alpha T^\beta$, where B is the body wall wet mass and T is total wet mass. The slope of the ln-ln regression β is 0.975; however, a better estimate is obtained by using the geometric mean functional regression (Ricker 1973) because both x and y are subject to error in measurement, and the error is about the same for both. The GM functional slope is β = 0.976 ± 0.004 (SE). The standard error is calculated using section 8 and Eq. 6 of Ricker (1973). The value of α is the antilog$_e$ of the intercept for each species, using the GM slope of 0.976.

Values for *Prionocidaris baculosa*, *Salmacis belli*, *Toxopneustes pileolus*, and *Diadema paucispinum* were obtained by calculating means for x and y of the log$_e$-transformed data, solving for the intercept C in $C = \bar{y} - \beta\bar{x}$, and taking the antilog$_e$ of C.

Stomopneustes variolaris and *Centrostephanus rodgersii* were not dissected; however, it is still possible to estimate the values of α for these two species. Giese et al. (1964) studied *S. variolaris* in Madras Harbor. They dissected 319 animals with an average mass of 454 g. Giese (1966) provides body index values for *Stomopneustes variolaris* based on these animals. His

Table 30-1 gives the percent body wall as 56.0%. Consequently, for an average animal of 454 g, the body wall weighed 254.2 g. Using the allometric equation gives 254.2 = $\alpha 454^{0.976}$, from which α = .647.

No body wall information exists for *Centrostephanus rodgersii* or any other species of *Centrostephanus*. I base my estimate of body wall size on an examination of the relationship between total body wall calcite mass and test diameter, which is information available from the dried animals shipped to me from Australia. The general appearance of *Centrostephanus* is somewhat like *Echinothrix diadema* and somewhat like *Strongylocentrotus franciscanus*; Fig. 2 shows the relationship between body wall calcite and test diameter for these three species. *Centrostephanus* falls between *Echinothrix diadema* (α = .57) and *Strongylocentrotus franciscanus* (α = .53) but is closer to *E. diadema*, so a reasonable value of α for *Centrostephanus* is .56.

Table 5 shows all species considered in this paper together with their α values, which are the intercepts from the regression analysis of Table 4 when a common functional slope of 0.976 is used. For a first approximation, the α values can be read as the percent body wall in an animal with a mass of 1 g. Because the common functional slope, 0.976, is <1.0, the relative size of body wall decreases as an animal grows. For example, in *Heterocentrotus trigonarius*, with α = .966, a 1-g animal would be 96.6% body wall, a 100-g individual would be only 89.7% body wall, and a 1000-g urchin would be 84.9% body wall. The mass of the body wall of a 1000-g animal would be 849 g: 849 g = (0.966)(1000)$^{0.976}$ and (849/1000) × 100% = 84.9%.

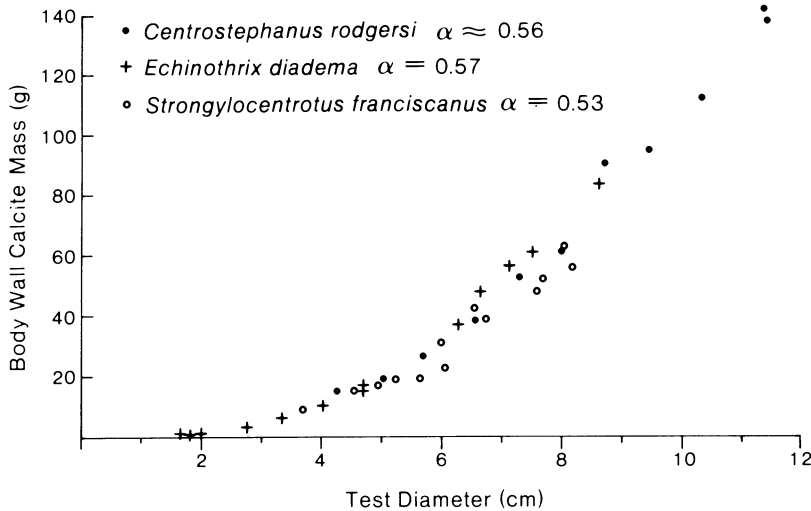FIG. 2. Total body wall calcite mass as a function of test diameter. Relationship used to estimate α for *Centrostephanus rodgersi*; α values for *Echinothrix diadema* and *Strongylocentrotus franciscanus* determined from dissections of live animals.

The three species from southern California have α values from .50 to .56 and are in the middle of the range of values that were found for Indo-West Pacific urchins. These α values are in general agreement with the index values for *Strongylocentrotus* sp. reported by Giese (1966): a body wall index of 48.5 ± 6.3% for *S. purpuratus* and 43.2 ± 5.5% for *S. franciscanus*. The α values are .559 and .530, respectively, for these two species. For a 100-g individual, the percent body wall would be 50% for *S. purpuratus* and 47% for *S. franciscanus*, which is within less than one standard deviation of the values reported by Giese.

The central question concerning allocation and survival probability now can be focused on the data presented in Table 5. If allocation is related to survival, then one would expect that at any particular location the α values should be predictors of longevity: at Honaunau Bay ($E = 4.0$), *Heterocentrotus* should be longer lived than *Echinothrix diadema*, which should be longer lived than *Tripneustes gratilla*. The following section will show the estimates of survival probability for some of the species shown in Table 5. The approach will be to present the data needed to obtain parameters in the Richards function so growth can be described and then to combine these parameters with size distributions to estimate the instantaneous mortality coefficient Z and the annual survival rate or probability, p.

Growth and survivorship analysis

In analyzing some of the growth data, it was necessary to combine several populations because of the distributions of data points. Combining was done for similar species where one or more samples were represented by few recaptures or by a poor spread of data points. By "similar" I mean sea urchins in the same

genus or, in a few cases, in the same family. In cases where populations were combined, a shape parameter for transforming data was selected that was based on the population with the greatest spread and the most

TABLE 5. Allometric relationship between body wall wet mass (y) and total wet mass (x). A common allometric coefficient was used. $\beta = 0.976 \pm 0.004$ (SE), to determine α. Only those species shown in Table 3 were included in determining β; α for other species was calculated by using the common β; N = number of individuals that were dissected. The estimate for *Stomopneustes variolaris* was derived from Giese et al. (1964) and Giese (1966); the estimate for *Centrostephanus* was determined from Fig. 3. * = species for which survival probabilities will be calculated.

| Species	N	α
*Heterocentrotus trigonarius**	11	.966
*Heterocentrotus mammillatus**	20	.919
*Colobocentrotus atratus**	8	.788
*Prionocidaris baculosa**	4	.727
*Echinometra oblonga**	8	.687
*Echinometra mathaei** (Hawaii, Enewetak)	18	.672
*Stomopneustes variolaris**	0	.647
*Echinometra mathaei** (Eilat)	2	.604
Echinostrephus aciculatus	5	.577
*Echinothrix diadema**	14	.570
*Centrostephanus rodgersi**	0	.560
Strongylocentrotus purpuratus	13	.559
*Heliocidaris erythrogramma**	16	.537
*Diadema paucispinum**	1	.532
Strongylocentrotus franciscanus	13	.530
Pseudoboletia indiana	2	.517
Lytechinus anamesus	14	.502
*Toxopneustes pileolus**	5	.439
*Diadema setosum**	7	.422
*Echinothrix calamaris**	5	.411
*Tripneustes gratilla**	14	.398
Tripneustes sp.*	13	.367
*Salmacis belli**	12	.360
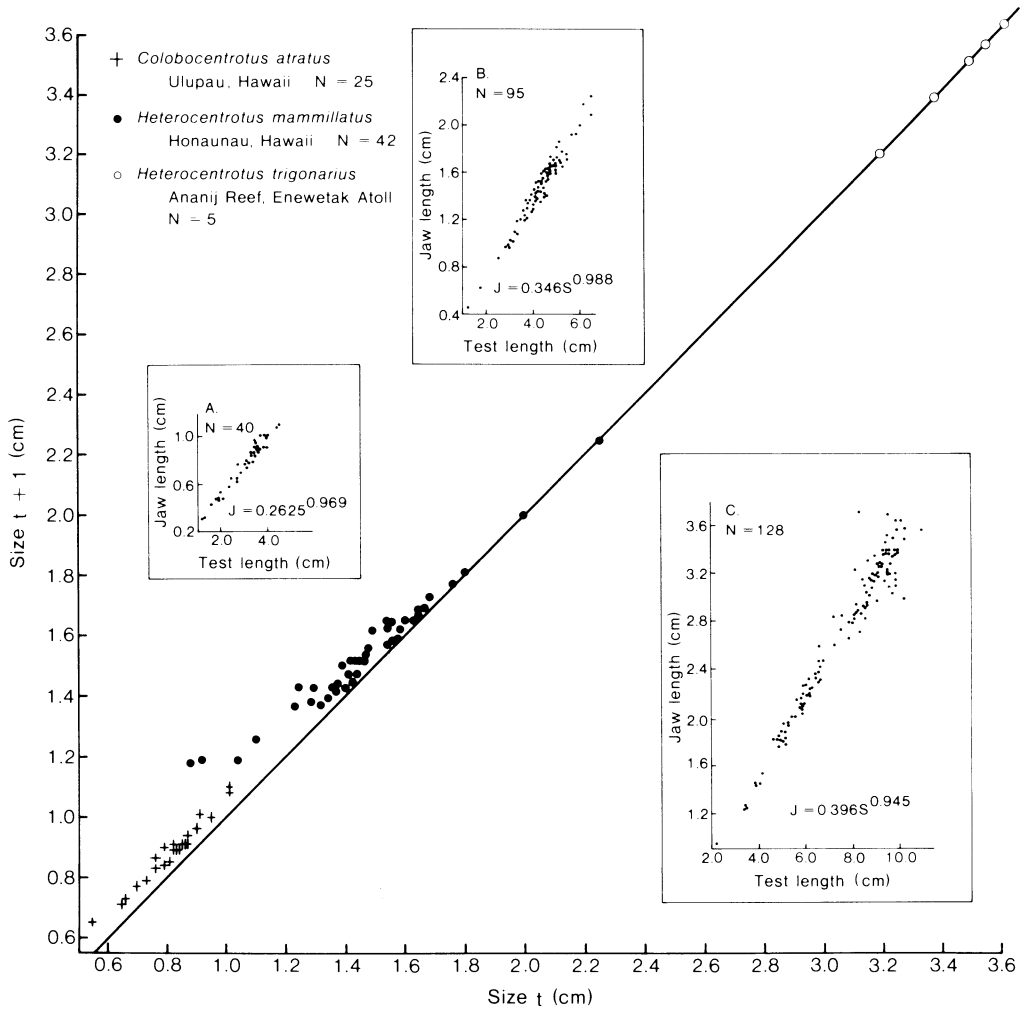
FIG. 3. Walford plot for growth of jaws. Original size S_t is the size of the glowing image in jaws of individuals tagged with tetracycline. S_{t+1} is jaw size after 1 yr, i.e., the size of the jaw when the urchin was collected 1 yr after tagging. Inset graphs A–C are used to convert growth parameters for jaws into growth parameters for the test. A is *Colobocentrotus atratus*, B is *Heterocentrotus mammillatus*, and C is *H. trigonarius*. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$.

points. Data pairs S_{t+1} and S_t were transformed to $S_{t+1}^{-1/n}$ and $S_t^{-1/n}$ for all of the samples being analyzed together. The transformed data pairs were subjected to analysis of covariance to select the best values for slope(s) and intercept(s), which are used to estimate the parameters K and S_∞. The scaling parameter b in Eqs. 1, 5, and 6 requires an estimate of size at settlement. I will use a test size of 0.05 cm as S_0 for all species.

Heterocentrotus *sp. plus* Colobocentrotus atratus

Results from tagging *Heterocentrotus mammillatus* at Honaunau Bay, Hawaii, on 21–22 August 1975 were good with respect to number of recaptures, 42 out of 80 collected in August 1976. The span of sizes also was acceptable in that original jaw sizes ranged from

0.8 to 2.2 cm. Returns of *Heterocentrotus trigonarius* tagged at Enewetak Atoll on 15–16 September 1977, in contrast, were disappointing. After 1 yr, only 5 tagged individuals were recovered out of a sample of 136; furthermore, all of the tagged individuals were large. *Colobocentrotus atratus*, tagged at Ulupau, Hawaii, on 6 and 8 July 1975 showed a reasonable return of 25 tagged individuals out of a sample of 41 1 yr later. However, the spread of sizes of the tagged individuals was restricted.

Fig. 3 shows the growth data for jaws of the three species. When analyzed separately, *H. mammillatus* data yielded a shape parameter n of -0.213, and because these data were best in terms of numbers and spread, this shape parameter was used for *H. trigonarius* and *Colobocentrotus atratus*. Original and final jaw sizes for the three species were transformed using
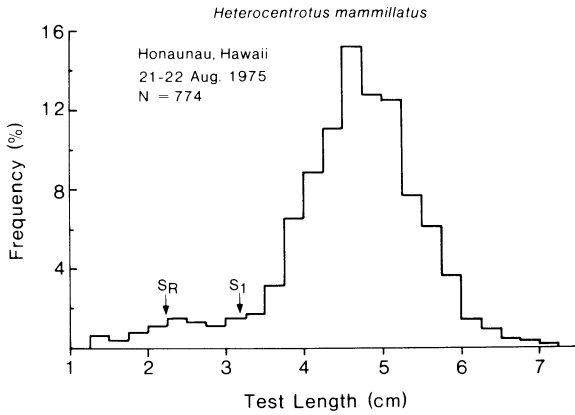
FIG. 4. Size structure of the slate-pencil urchin, *Heterocentrotus mammillatus*. S_R (estimated size at recruitment) is position of the mode of the first component of the size distribution determined using the program of Macdonald and Pitcher (1979). S_1 is estimated size of a 1-yr-old urchin, using the Richards function parameters derived from Fig. 3 and shown in Table 6. Exposure value for Honaunau is 4.0.
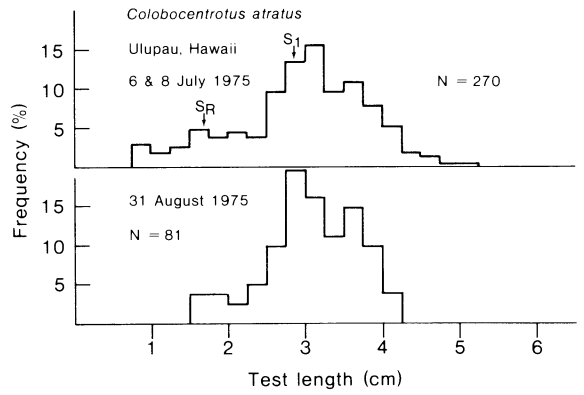

FIG. 6. Size structure of the *Colobocentrotus atratus* population at Ulupau, Hawaii (exposure value 1.0). S_R and S_1 are as in Fig. 4.

$n = -0.213$, and regressions of $S_{t+1}^{-1/n}$ vs. $S_t^{-1/n}$, with a common functional slope of 0.969 (determined for *H. mammillatus*), were used to estimate intercepts for each species. The intercepts determine the value of J_∞, the asymptotic size of the jaws,

$$J_\infty = (C/(1 - m))^{-n}, \qquad (12)$$

with C = the intercept, m = the slope, and n = the shape parameter. The values for asymptotic size of the jaws for *H. mammillatus*, *H. trigonarius*, and *C. atratus* are 2.29, 3.57, and 1.51 cm, respectively. Eq. 3 is used to determine asymptotic size of the test for each species: 6.77, 10.24, and 6.05 cm, respectively.

The shape parameter n must be changed for test growth to reflect the allometry between jaw and test (Eq. 4), and these values are $n = -0.217, -0.226,$ and -0.219, respectively, for the three species. The common growth rate constant K is equal to 0.032/yr.

Size distributions for the three species are shown in Figs. 4–6 and were analyzed using the program developed by Macdonald and Pitcher (1979) for separating distributions into normal components. The particular component of greatest interest is the first, π_1 which would be the young-of-the-year. Average size of individuals in this first component is an estimate of the size at recruitment, S_R, to the population on the day of sampling, so the time since recruitment, t, can be assigned the value of 0.0 in Eqs. 6 and 7. The values of S_R, shown in Figs. 4–6, are 2.22, 4.79, and 1.75 cm for *H. mammillatus*, *H. trigonarius*, and *C. atratus*, respectively. The estimates of Z, using Eqs. 5–7, are 0.11, 0.03, and 0.40/yr for the three species and, using $p = e^{-Z}$, these values translate to annual survival probabilities (p) of 0.89, 0.97, and 0.67 for *H. mammillatus*, *H. trigonarius*, and *C. atratus*, respectively.

A summary of the data and calculated values is presented in Table 6, which also shows the number of animals entering each calculation. N_4 is the number of animals in the size distribution used to estimate $\bar{X}$ in Eqs. 5 and 6 and the number dissected according to
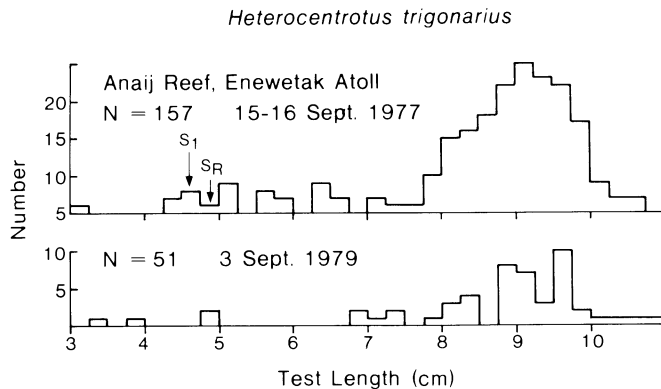

FIG. 5. Size-frequency distribution of test lengths of the slate-pencil urchin *Heterocentrotus trigonarius* at Enewetak Atoll, Marshall Islands (exposure value 1.5). S_R and S_1 are as in Fig. 4.

TABLE 6. Analysis of growth and survivorship of *Heterocentrotus trigonarius*, *H. mammillatus*, and *Colobocentrotus atratus*. A common shape parameter for growth of the jaws was used as determined from *H. mammillatus*, $n_j = -0.213$, as well as a common growth rate constant $K = 0.032/yr$ (Fig. 3). Numbers in parentheses are standard errors of the estimated parameters. C is the intercept of the Walford plot, J_∞ and S_∞ are the asymptotic sizes of jaws and test as used in the Richards function, S_R is the test size of a new recruit, N_1 is the number of animals used to determine the allometric constants for jaw vs. test, N_2 is the number of tagged individuals recovered after 1 yr in the field and used to determine growth parameters, N_3 is the total number of animals collected after 1 yr, N_4 is the number of individuals in the size distribution used to calculate Z, N_5 is the total number of animals tagged and released, $p = e^{-Z}$ is the probability that an individual size S_R or larger will live for 1 yr, S_1 is size after 1 yr, starting with a settlement size of 0.05 cm and determined using Eq. 1, π_1 is the proportion of the size distribution in the first mode, and Z_π is estimated from Eq. 11.

| | $J = \alpha S^\beta$ | | | Walford plot | | | | | | Survivorship | | | | | | |
Species and location	N_1	α	β	N_2	N_3	C	J_∞	S_∞	n_t	S_1	S_R	Z (yr^{-1})	p	N_4	N_5	π_1	Z_π (yr^{-1})
H. trigonarius, Enewetak Atoll	128	.396	0.945 (0.014)	5	136	12.081	3.570	10.243	−0.226	4.7	4.791 (0.096)	0.029	0.97	157	182	0.006 (0.006)	0.006
H. mammillatus, Honaunau, Hawaii	95	.346	0.988 (0.018)	42	80	1.500	2.291	6.768	−0.217	3.2	2.221 (3.636)	0.111	0.89	752	774	0.056 (0.329)	0.058
C. atratus, Ulupau, Hawaii	40	.262	0.969 (0.012)	25	41	0.215	1.511	6.052	−0.219	2.8	1.745 (0.327)	0.398	0.67	270	245	0.237 (0.094)	0.270

Macdonald and Pitcher's (1979) method to determine S_R and π_1, the proportion of the distribution in the first mode. For *H. mammillatus*, N_4 is 752 and is the same as is shown in Fig. 4. N_5 is greater than N_4 for the two *Heterocentrotus* species because in addition to the animals used to construct the size distribution, additional small urchins were collected and tagged in hope of recovering growth information on young animals. For *C. atratus*, N_5 is smaller than N_4 because some urchins were saved for dissection. S_1 is an estimate of size for a 1-yr-old urchin, based on the Richards function parameters and assuming that individuals are 0.05 cm at settlement. It is provided for comparison with S_R, the average size of age-0 individuals on the day of tagging. S_R always would be smaller than S_1 if I could find individuals as small as 0.05 cm in proportion to their true abundance. Because I can't do this, it is possible that S_1 could be slightly smaller than S_R, which is the case for *H. trigonarius*.

No comparative data exist for *Heterocentrotus trigonarius* other than a second size distribution that I obtained in September 1979 (Fig. 5). The shape of the 1979 distribution is about the same as the distribution of September 1977, and hence the estimate of Z for this species is probably fairly representative of the population at Ananij Island. It is unfortunate that no comparative data for growth are available to check the accuracy of the parameters used in estimating Z. In 1977, the fraction of the population in the first mode, π_1 or age-0 individuals, is $\approx 7\%$. By Eq. 11, the estimate of Z_π is 0.073/yr, and so $p = 0.93/yr$. Small individuals in 1979, π_1, also comprised $\approx 7\%$ of the population, so the estimate of Z_π again is $\approx 0.07/yr$.

Comparative size data are available for *Heterocentrotus mammillatus* from 1968 (Table 7). One of these size distributions (8 August 1968) has been published

previously (Ebert 1971). The April 1968 distribution is significantly different from the August 1968 and August 1975 distributions by a Kolomogorov-Smirnov two-sample test (Tate and Clelland 1957). Animals in the April 1968 sample were larger than in either of the two other distributions, as indicated at the interval with the largest difference, 4.51–4.75 cm. The April distribution showed only 23.46% of the sample to be 4.75 cm or smaller, whereas in the August 1968 distribution 69.74% were equal to 4.75 cm or less. In August 1975, 54.53% of the urchins were 4.75 cm or smaller. The August 1968 and 1975 distributions are not significantly different at $\alpha = .05$. My impression is that the differences shown in Table 7 probably are due to very local variation in size structure, a phenomenon previously reported for *Strongylocentrotus purpuratus* (Ebert 1968). The large sample of 1975 ($N = 774$), in part, may average such local variation, but in so doing also may be masking local differences of biological importance. For purposes of this paper, however, such averaging is tolerable because the focus is on between- rather than within-population comparisons.

A significant feature of the two 1968 distributions is that neither shows many small individuals, and so both are similar to the 1975 distribution in having few young animals. The fraction of age-0 individuals in the April 1968 sample is $\approx 2.2\%$, and in August the estimate is $\approx 2.6\%$. Using Eq. 11, the estimates of Z_π are 0.023 and 0.027/yr, respectively, which are somewhat lower than the estimate based on Eqs. 6 and 7, but all estimates give annual survival probabilities >0.9.

An estimate of the mortality coefficient for *Colobocentrotus atratus* has been published for a population at the Lani Overlook, Oahu, Hawaii (Ebert 1975) based on two size distributions separated by a period

of 8 mo and assuming Brody-Bertalanffy growth (Ebert 1973). The estimated value of Z was 0.33/yr, which is close to the estimate of 0.40/yr for *C. atratus* at Ulupau. Both data sets yield estimates of the annual survival probability of ≈ 0.7. A third estimate of Z is obtained from the fraction of the population in the first mode of the 1975 size distributions: π_1 is 0.237, and so Z_π is 0.270/yr and p is 0.76/yr, which is a value that agrees very well with the other two estimates of p.

Echinometra mathaei *and* Echinometra oblonga

Echinometra mathaei was tagged at three locations in Hawaii: Kapapa Island, Makua, and Pupukea; in the Sand Island Channel at Enewetak Atoll; Rottnest Island, Western Australia; Anse à la Mouche, Seychelles; Ras Iwatine, Kenya; and Eilat, Israel. *Echinometra oblonga* was tagged at Kapapa Island and at Ulupau, Hawaii.

Recovery success of tagged individuals was highly variable. Problems with animals from Seychelles have already been indicated. For other locations (Table 8), frequency of tagged animals in the samples ranged from highs of 39% (18/46) and 35% (166/480) for Kapapa Island and Rottnest Island, respectively, to 5% (16/292) and 1% (3/287) for Ras Iwatine and Eilat, respectively, and 0% (0/44 and 0/142) for both Pupukea and Enewetak Atoll. The two locations with high recovery rates are reef benches where *Echinometra* lives in cavities.

Fig. 7 shows the growth of jaws for *Echinometra mathaei* and *E. oblonga*. A common shape parameter ($n_j = -0.552$) was used for the jaws and was determined from the Rottnest Island sample, which had the largest number of marked individuals. All six samples had a common slope of 0.725 ± 0.009 (SE) and hence a common growth rate constant, $K = 0.322/yr$.

The relationship between test length and jaw length is shown in Fig. 8. The allometric coefficients are given in Table 8, together with the summary of the growth and survival analysis. Size distributions for all areas are given in Figs. 9–11.

The estimates of Z_π based on using the fraction of age-0 individuals (Eq. 11) are in most cases quite different from the estimates of Z that use both growth and size data (Eqs. 6 and 7). A striking example is provided by the two samples from Rottnest Island (Fig. 9). In 1976 the fraction in the first mode, π_1, is 0.244 ± 0.020 (SE), but in 1977 π_1 is 0.014 ± 0.005 (SE). The estimates of Z_π based on these two values are 0.28 and 0.014, respectively. Combining the two size distributions (as was done in Table 8) and using Eqs. 6 and 7 gives a Z of 0.145/yr, which is based on conditions over a 2-yr period, but probably is too high. Recruitment, obviously, is highly variable, and estimates based on Eq. 11 would be highly sensitive to this variation.

The sample from Makua (Fig. 9) also may reflect the

TABLE 7. Size distributions of *Heterocentrotus mammillatus*, Honaunau Bay, Hawaii.

A. Size range (cm)	16 April 1968		8 August 1968		21–22 August 1975	
	Number	Cumulative %	Number	Cumulative %	Number	Cumulative %
1.01–1.25	1	0.56				
1.26–1.50		0.56			5	0.65
1.51–1.75		0.56			4	1.17
1.76–2.00		0.56			6	1.95
2.01–2.25	1	1.12			8	2.98
2.26–2.50	1	1.68			12	4.53
2.51–2.75		1.68			10	5.82
2.76–3.00	1	2.24			10	7.11
3.01–3.25		2.24	2	2.63	12	8.66
3.26–3.50		2.24		2.63	13	10.34
3.51–3.75	1	2.80	8	13.16	24	13.44
3.76–4.00	4	5.03	3	17.11	49	19.77
4.01–4.25	9	10.06	14	35.53	68	28.56
4.26–4.50	12	16.76	12	51.32	85	39.54
4.51–4.75	12	23.46	14	69.74	116	54.53
4.76–5.00	24	36.87	7	78.95	99	67.32
5.01–5.25	22	49.16	10	92.11	96	79.72
5.26–5.50	19	59.77	3	96.06	61	87.60
5.51–5.75	21	71.50	2	98.69	46	93.54
5.76–6.00	18	81.56		98.69	26	96.90
6.01–6.25	12	88.26		98.69	11	98.32
6.26–6.50	9	93.29	1	100.00	7	99.22
6.51–6.75	6	96.64			3	99.61
6.76–7.00	2	97.76			2	99.87
7.01–7.25	2	98.88			1	100.00
7.26–7.50	1	99.44				
7.51–7.75		99.44				
7.76–8.00	1	100.00				
Total	179		76		774	

B.
Komogorov-Smirnov two-sample test: critical difference in cumulative % at $\alpha = .05$ is $136 \sqrt{(N_1 + N_2)/(N_1 N_2)}$; * = significantly different with respect to position of mode or shape at $\alpha = .05$.

Comparison	Maximum difference (%)	Interval (cm)	Critical difference (%)
April 1968 vs. August 1975	31.07*	4.51–4.75	11.28
August 1968 vs. August 1975	15.21	4.51–4.75	16.35
April 1968 vs. August 1968	46.28*	4.51–4.75	18.62

high degree of year-to-year variation in recruitment with a particularly poor recruitment shown in the 1975 sample with $\pi_1 = 0.081$ and estimated $Z_\pi = 0.085/yr$, whereas using Eqs. 6 and 7, Z is estimated to be about five times greater ($Z = 0.431/yr$).

The population at Ras Iwatine, Kenya, shows a Z based on Eq. 11, Z_π, which is $>Z$ based on Eqs. 6 and 7. Like the 1976 population at Rottnest, the Ras Iwatine sample has too many age-0 individuals based on the Z calculated by Eqs. 6 and 7. The Anse à la Mouche size distribution (Fig. 10) is shaped much like the Makua distribution (Fig. 9). Based on the observed growth rates at other locations, it seems reasonable to say that the major mode at Anse à la Mouche was not com-

TABLE 8. Analysis of growth and survivorship of *Echinometra mathaei* and *E. oblonga*. A common shape parameter, $n = -0.552$, determined for *E. mathaei* from Rottnest Island, Western Australia, was used to describe growth for all samples. A regression of transformed values of S_{t+1} vs. S_t had a common slope of 0.725 ± 0.009 (SE), which yields a common growth rate constant $K = 0.322/\text{yr}$. Additional explanation of columns is provided in Table 6. Samples from the Lani Overlook, Hawaii, are a reanalysis of data presented in Ebert (1975).

Species and location	$J = \alpha S^\beta$			Walford plot						Survivorship							
	N_1	α	β	N_2	N_3	C	J_∞	S_∞	n_t	S_R	S_1	Z	p	N_4	N_5	π_1	Z_π
Echinometra mathaei, Kapapa Island, Hawaii	52	.271	1.017 (0.030)	18	46	0.598	1.534	5.499	−0.543	1.919 (0.494)	2.7	0.185	0.83	207	204	0.079 (0.049)	0.082
Makua, Hawaii	85	.250	1.108 (0.037)	16	80	0.409	1.244	4.254	−0.498	1.309 (0.040)	2.2	0.431	0.65	615	613	0.081 (0.012)	0.085
Pupukea, Hawaii				0	44					1.193 (0.077)				354	350	0.120 (0.028)	0.127
Rottnest Island, Western Australia	385	.251	1.082 (0.014)	166	480	0.522	1.424	4.978	−0.510	1.184 (0.019)	2.6	0.145	0.87	944	612	(See text)	
Ras Iwatine, Kenya	277	.285	0.985 (0.019)	16	292	0.483	1.363	4.894	−0.561	2.550 (0.050)	2.4	0.157	0.85	822	797	0.351 (0.026)	0.432
Eilat, Israel	262	.289	1.062 (0.017)	3	287	0.523	1.425	4.496	−0.520	1.582 (0.016)	2.3	2.473	0.08	713	709	0.715 (0.057)	1.257
Anse à la Mouche, Seychelles										2.074 (0.146)				335	330	0.033 (0.013)	0.034
Enewetak Atoll 1978										1.694 (0.110)				227		0.715 (0.177)	1.255
Enewetak Atoll 1979										1.585 (0.110)				281		0.382 (0.072)	0.481
Echinometra oblonga, Kapapa Island, Hawaii	21	.338	0.915 (0.046)	6	15	0.392	1.215	4.049	−0.603	1.50	1.9	0.142	0.87	28	25		
Ulupau, Hawaii										1.275 (0.123)				87		0.351 (0.109)	0.432
Echinometra mathaei, Lani Overlook Hawaii				77	$K = 0.292$			4.095	−0.543	2.007 (0.213)	1.9	0.504	0.60	143		0.490 (0.216)	0.673
Echinometra oblonga, Lani Overlook, Hawaii				35	$K = 0.358$			3.087	−0.603	1.620 (0.249)	1.5	0.377	0.69	81		0.373 (0.256)	0.467

posed of age-0 individuals and that the young-of-the-year were represented by the small mode to the left with a mean of ≈ 2.07 cm (Table 8). The fraction of the population in this small mode is only ≈ 0.033, so the estimate of Z_π is 0.034/yr, a value that seems very low and, as with the 1976 Rottnest sample, probably reflects unusually poor recruitment.

The two size distributions from Enewetak Atoll (Fig. 10) have a shape that is quite different from that seen at other locations. Because of growth characteristics at other sites, it seemed unreasonable to suggest that there were only two modes in 1978. Three modes seemed like a minimum in 1979 and so three components were separated from the 1978 distribution. In 1978, the three means were 1.69, 2.77, and 3.38 cm, and the fraction of the distribution in each component was 0.71, 0.17, and 0.12. In 1979, the three means were estimated to be 1.59, 2.59, and 2.65. Using Eq. 11, the estimates for Z_π for the 2 yr are $Z_\pi = 1.26$ and 0.48/yr. Once again, a high degree of year-to-year variation is evident.

Only 25 *Echinometra oblonga* were tagged at Ka-

papa, and 6 tagged individuals were recovered. The primary site for *E. oblonga* was to have been Ulupau, but a severe winter storm removed many urchins, and none was recovered after 1 yr. Consequently, the results in Table 8 show estimates of Z based on Eqs. 6 and 7 for Kapapa, but the sample size is too small to attempt to separate components. The size frequency distribution is analyzed for Ulupau (Fig. 11), and Z_π is estimated from Eq. 11. The two estimates of Z are 0.14 and 0.43/yr, respectively.

Some comparative data are available for *Echinometra* sp. in Hawaii. Animals were tagged with nylon monofilament (Ebert 1965) at Lani Overlook, Oahu, in 1968 and measured several times for nearly 1 yr. The data were analyzed assuming the Brody-Bertalanffy model (Ebert 1975). Growth data for *E. mathaei* and *E. oblonga* from the Lani Overlook were reanalyzed using the shape parameters for these species at Kapapa Island: −0.543 and −0.603, respectively. Size measurements were transformed using these shape parameters. Because different time intervals were involved, Fabens' (1965) program was used to estimate
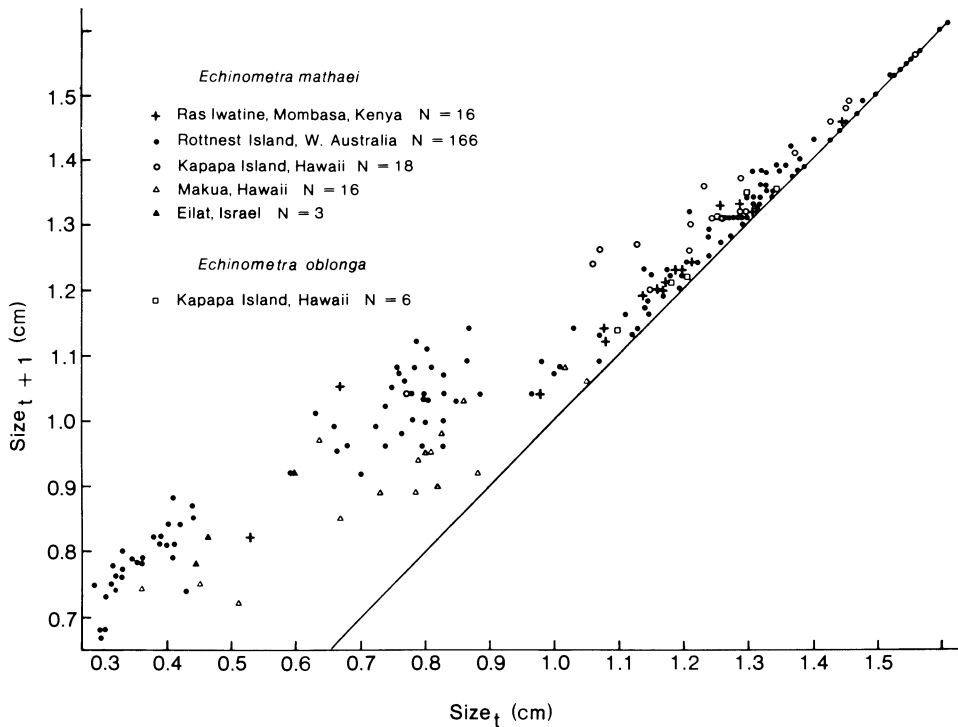
FIG. 7. Growth of jaws of *Echinometra mathaei* and *E. oblonga*. S_t and S_{t+1} are separated by 1 yr, and original size was determined by tetracycline tagging. Summary of growth parameters is given in Table 8. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$.

K and S_∞; Eqs. 6 and 7 were used to estimate Z. The resulting estimates of survival probability are similar to those from Makua: 0.60 vs. 0.65 for *E. mathaei* and 0.69 for *E. oblonga*. The environments are similar, exposed pools on a bench, though the pools at the Lani Overlook lack the protective barrier present at Makua and are not as large or as deep.

Heliocidaris erythrogramma

The population of *Heliocidaris erythrogramma* at Hastings Point was destroyed during 1976 when it was covered by sand during a storm (Richard Martin, *personal communication*). Only a few animals were collected in 1977, and none was tagged. Tagged urchins were present in samples from Port Jackson and Cape Peron.

Size distributions (Fig. 13) for all three areas differ with respect to the position of the major mode; it is at ≈5.5 cm at Hastings Point, 5.75 cm at Balmoral Beach, and at ≈7.25 cm at Cape Peron. The largest individuals in the samples reflect this same trend, which may mean that asymptotic size is smaller at Hastings Point.

Fig. 12 shows growth of the jaws for urchins at Balmoral Beach, Port Jackson, and Cape Peron. It is apparent that use of a common shape parameter probably is not warranted because small animals in Port Jackson seemed to grow slower than somewhat larger

individuals, displaying an exponential phase in growth, whereas small individuals at Cape Peron showed rapid growth with no exponential phase.

The shape parameter n is +0.154 for test growth of *H. erythrogramma* at Balmoral Beach. I suspect that this value is not reasonable for the entire growth curve, although it would be adequate for describing the growth of animals larger than ≈4.0 cm (the smallest tagged urchin that was recaptured at Balmoral Beach). Extrapolation back to settlement provides an estimate of S_1, test diameter at 1 yr (Table 9), of 0.05 cm, which is about the size at settlement. The growth parameters are for a curve that has a very slow rise and so, if accepted at face value, individuals in the first mode of the size distribution (Fig. 13) at 2.41 cm (S_R) would be 71 yr old, which seems extremely unreasonable.

The growth parameters estimated for the urchins at Cape Peron ($n = -0.360$) give S_1 equal to 4.0 cm. If this value is even roughly correct for *H. erythrogramma* at Balmoral Beach, then the mode at 2.41 cm is composed of the young-of-the-year. This interpretation seems more reasonable than using $S_1 = 0.05$ cm.

If 2.41 cm is used for S_R at Balmoral Beach and other parameters are as shown in Table 9 ($n = +0.154$, $S_\infty = 7.193$ cm, and $K = 0.356/yr$), then Z is 0.07/yr, and p is 0.93/yr. The estimate of annual survival probability p at Cape Peron is 0.91/yr.
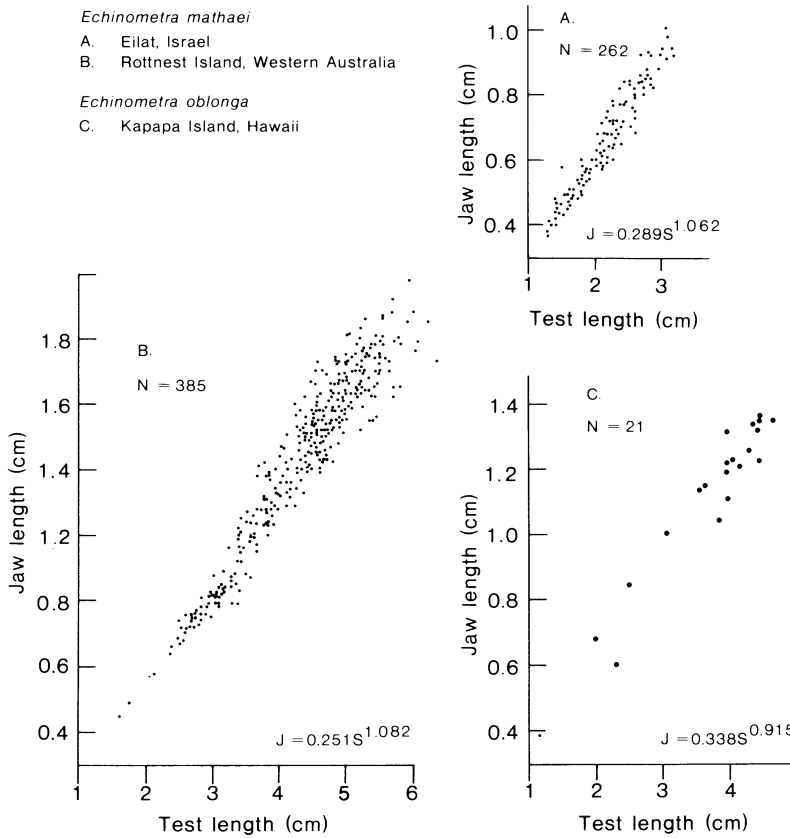
FIG. 8. Representative scatter diagrams relating jaw length to test length, which were used to change growth parameters for jaws to appropriate parameters for test growth.

No growth parameters are available for the urchins at Hastings Point, so I used π_1, the fraction of the population in the first mode, together with Eq. 11 to estimate Z_π and p: Z_π is equal to 0.04/yr, and so p is 0.96/yr. Overall, *Heliocidaris erythrogramma* seems to be a species in which individuals are long lived.

Echinothrix diadema, E. calamaris, Centrostephanus rodgersi, Diadema setosum, *and* D. paucispinum

Growth information on three species and survivorship estimates for five species in the Family Diadematidae were obtained. Growth parameters were determined for *Echinothrix diadema* at Kapapa Island, Hawaii; *Centrostephanus rodgersi* at Camp Cove in Port Jackson, New South Wales; and *Diadema setosum* at Zanzibar and Eilat, Israel. Survivorship was estimated for these three species plus *Echinothrix calamaris* at Kealakekua Bay, Hawaii, and Round Island, Seychelles and *Diadema paucispinum* at Kealakekua Bay and Pupukea, Hawaii.

Jaw growth for *E. diadema* and *C. rodgersi* is shown in Fig. 14, along with graphs illustrating the relationship between jaw length and test diameter. Jaw growth

and the relationship between the sizes of jaw and test for *Diadema setosum* are presented in Fig. 15. The size distributions for the species are in Figs. 16–19, and the summary of size, growth, and survival is given in Table 10.

No growth information is available for *Echinothrix calamaris* at Round Island in the Marine Park of Victoria Harbor, Seychelles; however, the size distribution (Fig. 17) is sufficient for a preliminary estimate of survivorship. Based on the growth of *E. diadema* at Kapapa Island, the first mode in Fig. 17 can reasonably be assigned to age 0. The mean size of individuals in the first mode is 3.64 cm, which is ≈ 1 cm less than the predicted size of a 1-yr-old *E. diadema*. The fraction of the population in the first mode is 0.159, so Z_π is equal to 0.173/yr (Eq. 11) and p is 0.841/yr.

A size distribution of *E. calamaris* in Kealakekua Bay, Hawaii, has been published previously (Ebert 1971) and can be used to provide an additional estimate of *E. calamaris* survivorship. The mean size of individuals in the first mode is 7.25 ± 2.919 (SE) cm, and the fraction of the population in this first mode is 0.430, which gives $Z_\pi = 0.563$/yr. The average size seems large for a 1-yr-old animal, but the size distri-
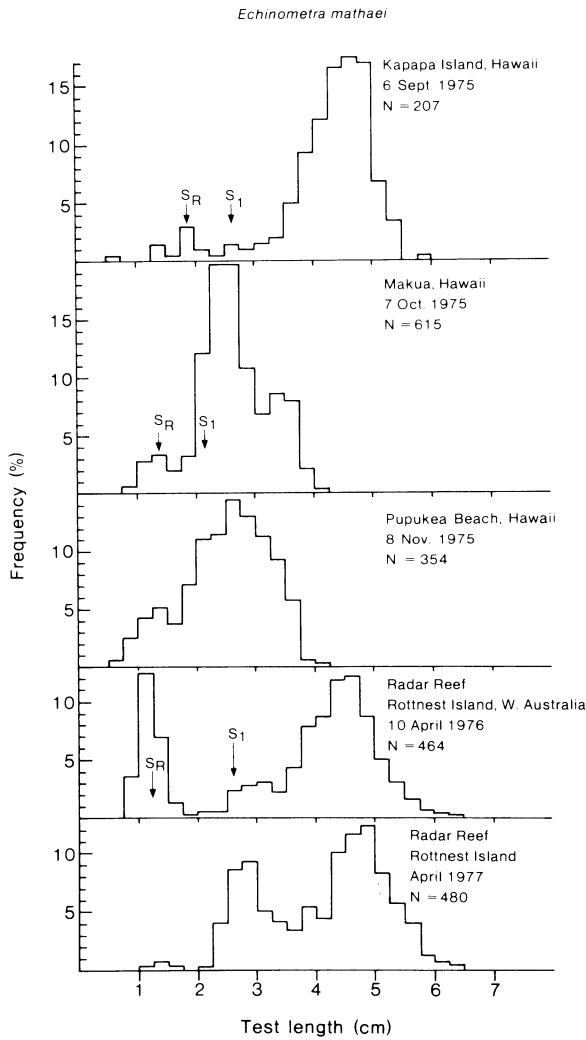
FIG. 9. Size-frequency distributions for *Echinometra mathaei* from Hawaii and Australia. Exposure values are 3.0 for Kapapa, 2.0 for Makua, 4.0 for Pupukea, and 4.0 for Rottnest Island. S_R and S_1 are as in Fig. 4.
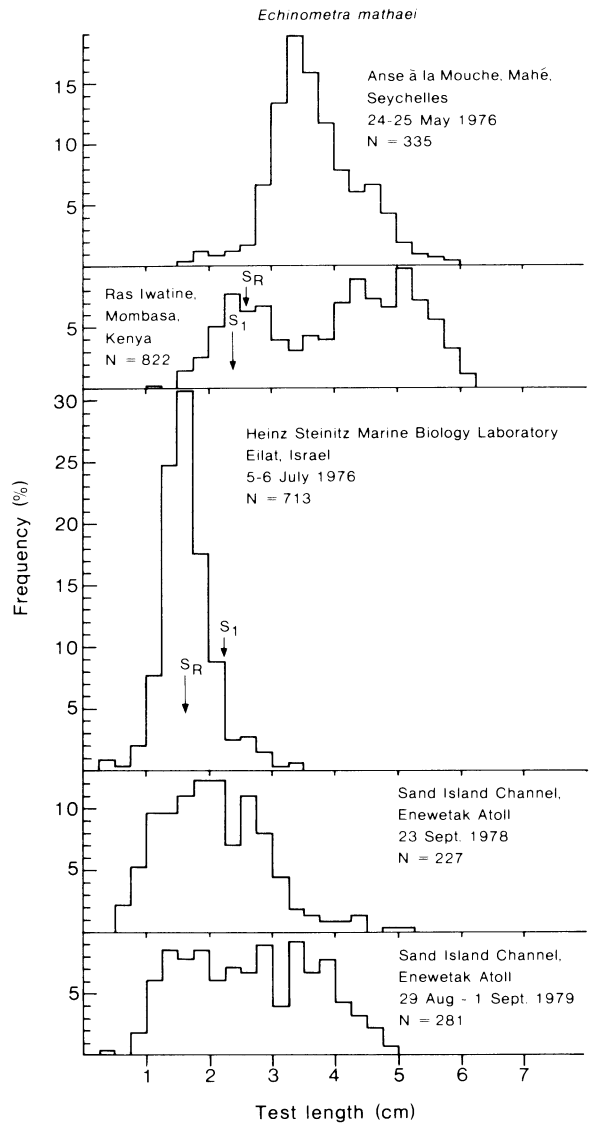

FIG. 10. Size structure of *Echinometra mathaei* populations (continued). Exposure values are 5.0 for Anse à la Mouche, 5.0 for Ras Iwatine, 6.0 for Eilat, and 5.0 for Sand Island Channel.

bution is bimodal and one possible interpretation is that there was no recruitment of *E. calamaris* in 1968 in Kealakekua Bay, in which case the 7.25-cm individuals are the youngest animals in the population but would be older than a maximum of 1 yr.

Additional size data gathered during 1968–1969 are available for *Echinothrix diadema* from Kapapa Island (Ebert 1975) and used to estimate a mortality coefficient of $Z = 0.64/yr$, compared with the present estimate of $Z = 0.32/yr$. The probabilities of surviving 1 yr are 0.53 and 0.73, respectively. The analysis published in 1975 (Ebert 1975) assumed Brody-Bertalanffy growth and simultaneously estimated K and Z from two size distributions. Based on the present work, the mortality estimate published in 1975 probably is too high and can be accounted for by the use of the Brody-

Bertalanffy model. The effect can be demonstrated by using the Richards function parameters in Table 10 and applying them to the analysis of the 1968–1969 size distributions (Ebert 1975: Table 4). The four size distributions for *Echinothrix* taken in 1968–1969 provide four estimates of Z with a mean value of $0.173/yr \pm 0.066$ (SE).

Echinothrix diadema at Kapapa Island is not uniformly distributed in the lee of the island. Although the pattern was not documented, there appeared to be a change in density and size structure from directly in the lee around the island to the east. Density appeared to increase toward the east, and average size seemed

to become smaller, although size structure also was patchy. The sample from 4 November 1975 (Fig. 16) was taken about even with the eastern end of the island and in ≈3 m of water. The sample from 10 and 15 July was more in the lee of the island.

There are no comparative data available for *Centrostephanus rodgersi* or any other member of this genus, although some information is available that provides an insight into how typical the Camp Cove site might be. The largest individual (Fig. 18) that was measured was 11.7 cm; 6% of the population was >10.0 cm and ≈10% was >9.25 cm. O'Connor (1975) presents size data on *C. rodgersii* for two sites in New South Wales: the Solitary Islands (29.5°S.), a region of coral reefs, and Port Stephens (32.5°S.), a coastal area. O'Connor measured samples of 25 of the larger animals every 3 mo during 1973–1974. At the Solitary Islands the means of large animals were between 8.0 and 9.5 cm at a depth of 6 m and from 7.0 to 7.5 cm at a depth of 18 m. Animals were larger at Port Stephens during 1975. The average size of large animals ranged from ≈8.0 to 10.0 cm at a depth of 6 m. The animals at Camp Cove certainly appear to be larger than the urchins at the Solitary Islands and may be larger than individuals at Port Stephens. It is unfortunate that no size distributions are available for comparison to decide whether the differences are related to survivorship or growth.

The preferred habitat of *Centrostephanus* cannot be deduced from available literature. O'Conner (1975) shows highest densities at 6 m with high values of ≈11 individuals/m² at the Solitary Islands in summer 1973. At 18 m, densities of 3 urchins/m² were about maximum. At Port Stephens, densities of 3.5 individuals/m² were measured at 6 m. The general impression given by O'Connor is that 6-m depths have greater densities than do 18-m depths. Shepherd (1973), on the other hand, shows highest densities at ≈20 m at Gabo Island lighthouse, Victoria, an exposed site with "rough conditions" and also at 10–15 m at a protected site on the south side of Gabo Island. Densities at the exposed site were ≈0.5 and ≈10 individuals/m² at the protected site. Based on O'Connor's and Shepherd's work, it would seem that Camp Cove could be considered a protected area for *Centrostephanus*, and the small Z value that was calculated, $Z = 0.064$/yr, is consistent with this interpretation.

Analysis of data on *Diadema setosum* at Zanzibar has been published as parts of two papers that deal with techniques for estimating parameters of the Richards function (Ebert 1980a) and estimating the mortality coefficient Z from growth parameters and a size distribution (Ebert 1981). The differences between the published values and those in Table 10 are due to the inclusion of seven tagged *D. setosum* from Eilat, Israel, to estimate common parameters of K and J_∞ for jaw growth. The differences, however, are not great. In Table 10, K is 0.008/yr, and J_∞ is 2.835 cm for the combined data, compared with 0.019/yr for K and 2.328
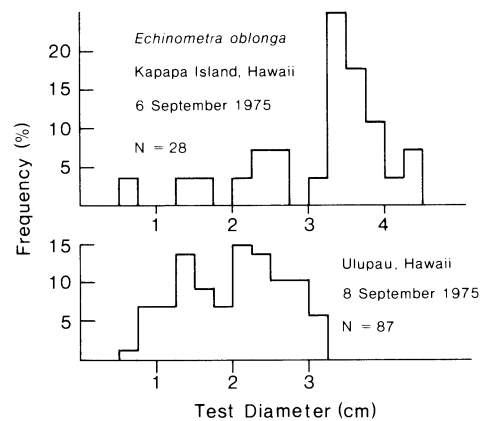

FIG. 11. Size structure of *Echinometra oblonga* at two sites in Hawaii. Exposure value is 3.0 for Kapapa reef and 1.0 for Ulupau.

cm for J_∞ for the Zanzibar population analyzed separately (Ebert 1980a). The compensatory nature of lowering K and increasing J_∞ is shown by comparing estimates of jaw sizes, using the two sets of parameters. Size of jaws of a 1-yr-old urchin would be 1.01 cm using the parameters in Table 10 and 1.00 cm using the parameters in Ebert (1980a). At 5 yr the comparison is 1.42 vs. 1.40 cm, and at 10 yr the comparison is 1.64 vs. 1.60 cm.

The comparison of size distributions from Zanzibar and Eilat (Fig. 19) suggests that either recruitment patterns are different at the two locations or more microhabitats were sampled at Eilat. The obvious gap in the distribution at Yange Sand Bank is missing in the sample at Eilat. Growth characteristics are the same (Fig. 15), and my impression was that the area at Eilat was reasonably homogeneous, so either differences in length of the recruitment period or more than one recruitment episode during a year seem to be the most reasonable explanation for the missing hiatus at Eilat. The survival rate also is much lower at Eilat (Table 10).

Only 17 individuals of *Diadema paucispinum* were collected at Pupukea, Hawaii. The average size was 3.85 ± 0.15 cm, which is reasonable for age-0 animals. The distribution was unimodal, and the maximum size observed was 4.94 cm. It seems best to assign all animals to age 0; so the fraction of the population in the first mode is 1.00, and the probability of annual survival is 0.00.

A size distribution for *D. paucispinum* has been published for Kealakekua Bay, Hawaii (Ebert 1971). The distribution is bimodal, with an average size of individuals in the first mode being 4.38 ± 0.08 (SE) cm. The fraction of the population in the first mode is 0.848, so $Z_\pi = 1.883$ and $p = 0.152$.

Species of *Diadema* are common in tropical waters of all oceans. Frequently they are sufficiently abun-
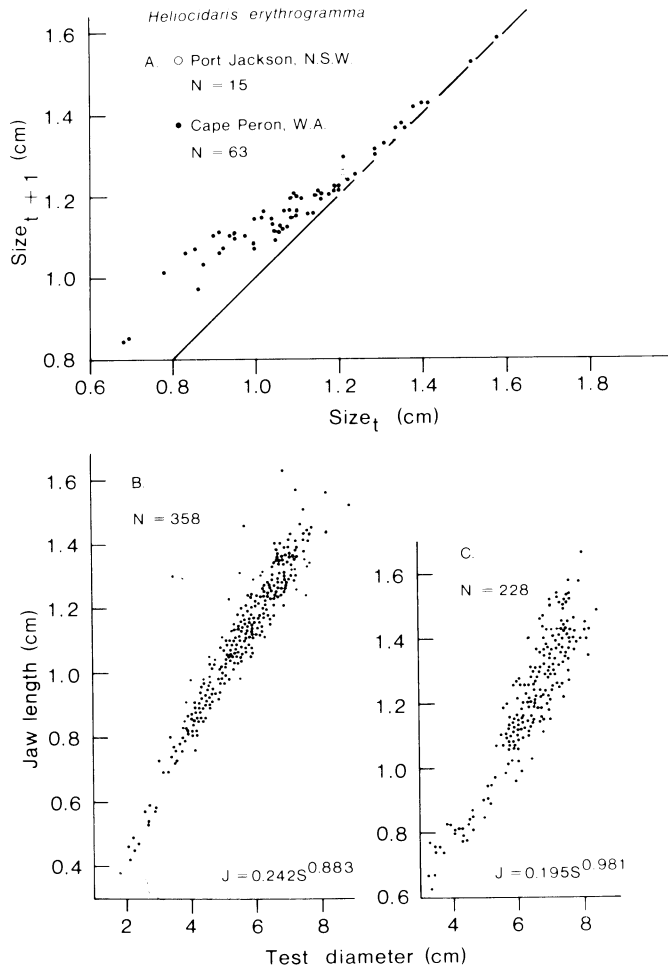
THOMAS A. EBERT

FIG. 12. (A) Jaw growth of *Heliocidaris erythrogramma* in Australia. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$. (B) Relationship between jaw length and test diameter for animals from Cape Peron. (C) Relationship for urchins from Port Jackson. Summary of growth parameters is given in Table 9.

dant to provide the major visual impression of a reef. Published size distributions of *Diadema antillarum* (Bauer 1976) suggest rapid growth with high annual recruitment. The estimates of Z based on work done by Randall et al. (1964) and Lewis (1966) and assuming Brody-Bertalanffy growth were $Z = 1.3/yr$ and $Z = 1.4/yr$, respectively (Ebert 1975). These values would be too high if *D. antillarum* grows in a manner similar to *D. setosum* and has rapid initial growth followed by slow growth for an extended period of time. The estimates for *D. setosum* at Zanzibar and Eilat, Israel, of $Z = 0.29/yr$ and $Z = 0.65/yr$, respectively, may be

TABLE 9. Analysis of growth and survivorship of *Heliocidaris erythrogramma*. Shape parameter n_j is for growth of the jaws, and n_t is for growth of the test; K is the growth rate constant of the Richards function; other headings are as in Table 6.

Study area	$J = \alpha S^\beta$			Walford plot							Survivorship							
	N_1	α	β	N_2	N_3	n_j	K	J_∞	S_∞	n_t	S_R	S_1	Z	p	N_4	N_5	π_1	Z_π
Port Jackson, New South Wales	358	.242	0.883 (0.011)	15	358	+0.136	0.356	1.379	7.193	+0.154	2.412 (0.096)	0.053	0.073	0.93	325	441	0.071 (0.015)	0.074
Cape Peron, Western Australia	228	.195	0.981 (0.024)	63	301	−0.360	0.191	1.429	7.619	−0.367	2.500 (1.637)	4.0	0.098	0.91	354	348	0.021 (0.039)	0.021
Hastings Point, New South Wales											2.273 (0.320)				869	858	0.036 (0.012)	0.037

more reasonable. The estimate of $Z = 1.9$/yr for *D. paucispinum* at Kealakekua Bay, however, is as high as the estimates for *D. antillarum*.

Stomopneustes variolaris

Stomopneustes variolaris was tagged at Duwa Reef at Negombo, Sri Lanka; Anse à la Mouche, Island of Mahé, Seychelles; and at Ras Iwatine, north of Mombasa, Kenya. Tagged individuals were recovered only from Sri Lanka.

Out of 358 individuals shipped from Sri Lanka, 101 had a tetracycline mark. Growth of the jaws based on these individuals is shown in Fig. 20, together with the scatter diagram for the relationship between jaw length and test diameter. Size distributions for *S. variolaris* from the three sites are shown in Fig. 21, and results are summarized in Table 11.

The estimates of Z for the population at Duwa Reef, Sri Lanka, are $Z = 0.187$/yr using Eqs. 6 and 7, and 0.265/yr based on Eq. 11. The two values are reasonably close together, and annual survival probabilities are 0.83 and 0.77 for the two estimates.

The estimate of Z_π for the population of *S. variolaris* at Ras Iwatine is similar to the Duwa Reef population; Z_π is equal to 0.305/yr, with an associated p of 0.74/yr, but the estimate for Anse à la Mouche is much higher with $Z_\pi = 1.561$/yr and $p = 0.21$/yr. The presence of relatively more large urchins at Ras Iwatine and Anse à la Mouche, compared with Duwa Reef (Fig. 21) may indicate more rapid growth or larger maximum size (or both). The mortality rate for animals at Anse à la Mouche is based on the assumption that the first mode at 3.98 cm (Table 11) is for age-0 individuals, which is not unreasonable considering that S_1 for Duwa Reef is 3.9 cm; the presence of large individuals at Anse à la Mouche may indicate more rapid growth. The shape of the distribution, with a positive skew, also suggests high mortality. The shape of the distribution from Ras Iwatine is similar to the shape of the distribution from Duwa Reef, except that the major mode is translated to the right, i.e., larger size. The small number of urchins larger than 6 cm at Duwa Reef may be associated with food scarcity. Urchin densities at Duwa Reef were high, and the substrate was primarily bare rock. Densities were lower at the other two sites, and macroalgae and aquatic angiosperms were abundant.

Tripneustes sp. and Toxopneustes pileolus

Populations of *Tripneustes gratilla* were tagged at three locations in Hawaii: Kapapa Island, Makua, and Pupukea; at Ras Iwatine, Kenya, and at Round Island in Victoria Harbor on Mahé, Seychelles. A *Tripneustes* sp. also was tagged at Eilat, Israel, and a *Toxopneustes pileolus* population was studied at Round Island, Seychelles.

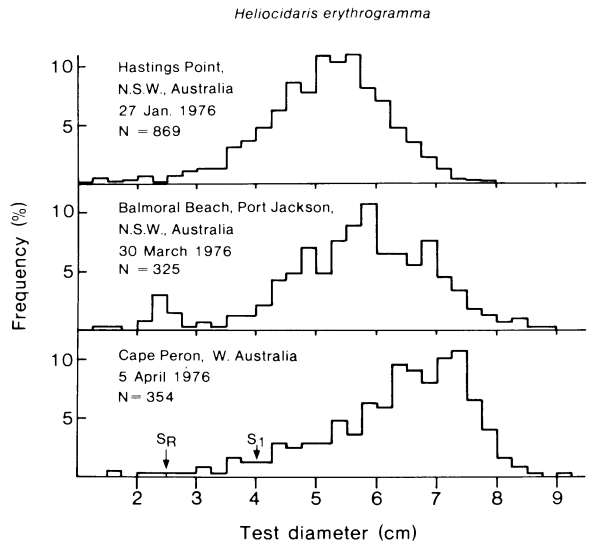Returns of tagged individuals were very poor; no animals were sent from Seychelles, no recaptures were

FIG. 13. Size structure of three populations of *Heliocidaris erythrogramma*. S_R is the mean of the first component of the size distribution as determined using the program of Macdonald and Pitcher (1979); S_1 is calculated size of a 1-yr-old urchin using the growth parameters estimated from Fig. 12. Exposure value is 5.0 for Hastings Point, 9.0 for Balmoral Beach, and 5.0 for Cape Peron.

obtained from Pupukea or Makua, just two tagged individuals were recovered from each site at Kapapa and Eilat, and only 19 from Ras Iwatine. The only small individuals were from Eilat; the two animals from Kapapa were both large, and all intermediate-sized urchins were from Kenya (Fig. 22). Furthermore, some of the animals from Ras Iwatine had additional fluorescing lines that made interpretation difficult or, in some cases, impossible. The origin of the confusing fluorescence patterns may be natural tetracycline in the environment (Bassett et al. 1980).

Because of the poor recovery of tagged individuals, I will not present an analysis of growth; the returns from Eilat were used to estimate the size of 1-yr-old urchins (S_1). Estimates of mortality will be based on Eq. 11 and an analysis of the size distributions (Figs. 23–25). Data and results are summarized in Table 12.

The first mode in the two distributions from Kapapa Island (Fig. 23) most certainly is age 0. This assertion is based on the rate at which the mode shifts from August to November, going from 4.4 to 5.6 cm in 3 mo, as well as the suggested rapid growth of *Tripneustes* sp. at Eilat. Figs. 22 and 24 show one individual growing from 1.5 to over 5.5 cm in 1 yr. Based on work done by McPherson (1965) and Lewis (1958), *Tripneustes ventricosus* (=*esculentus*) is able to attain a test diameter of 6–8 cm in 1 yr. Taken together, these arguments suggest that accepting the first mode as being equal to the young-of-the-year is quite reasonable. Applying Eq. 11 after separating the distribution into two components produced values of Z_π of 0.311 and 0.316/
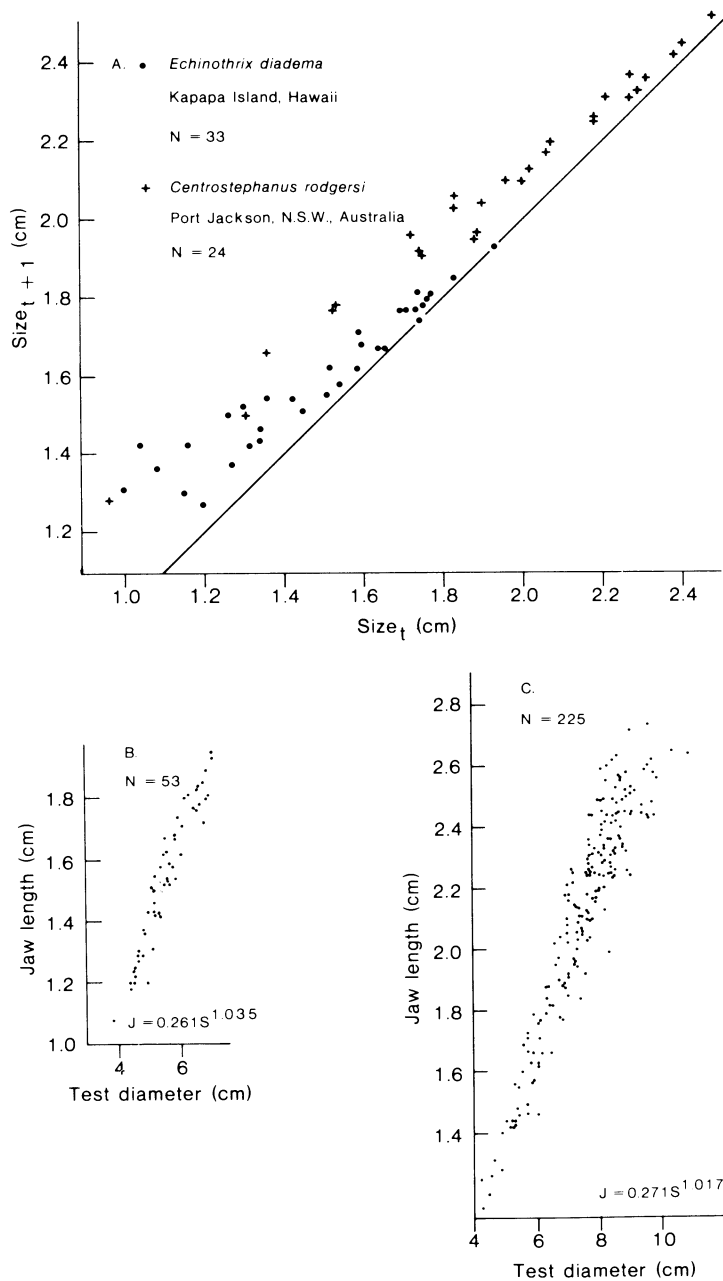
FIG. 14. (A) Growth of jaws for *Echinothrix diadema* and *Centrostephanus rodgersi*. Time interval is 1 yr. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$. (B) Jaw length vs. test diameter for *Echinothrix diadema*. (C) Jaw–test relationship for *Centrostephanus rodgersi*. Data summary is given in Table 10.

yr for August and November, respectively, with associated probabilities of annual survival of 0.73 for both distributions.

The distribution of *Tripneustes gratilla* from Ras Iwatine is more difficult to analyze. The position of the mode is at about the same location as the second modes of the Kapapa distributions, and furthermore there is a small shoulder on the left of the distribution which may represent age-0 urchins. If this is the cor-

rect interpretation, then the estimate of Z_π is 0.045 and $p = 0.96$ (Table 12). It is also possible, however, that the major mode is the age-0 class in which case p is close to 0, i.e., *Tripneustes* is an annual at Ras Iwatine. I have no good reason to accept one or the other of these interpretations, and so I choose to eliminate the *Tripneustes* population of Ras Iwatine from further analysis.

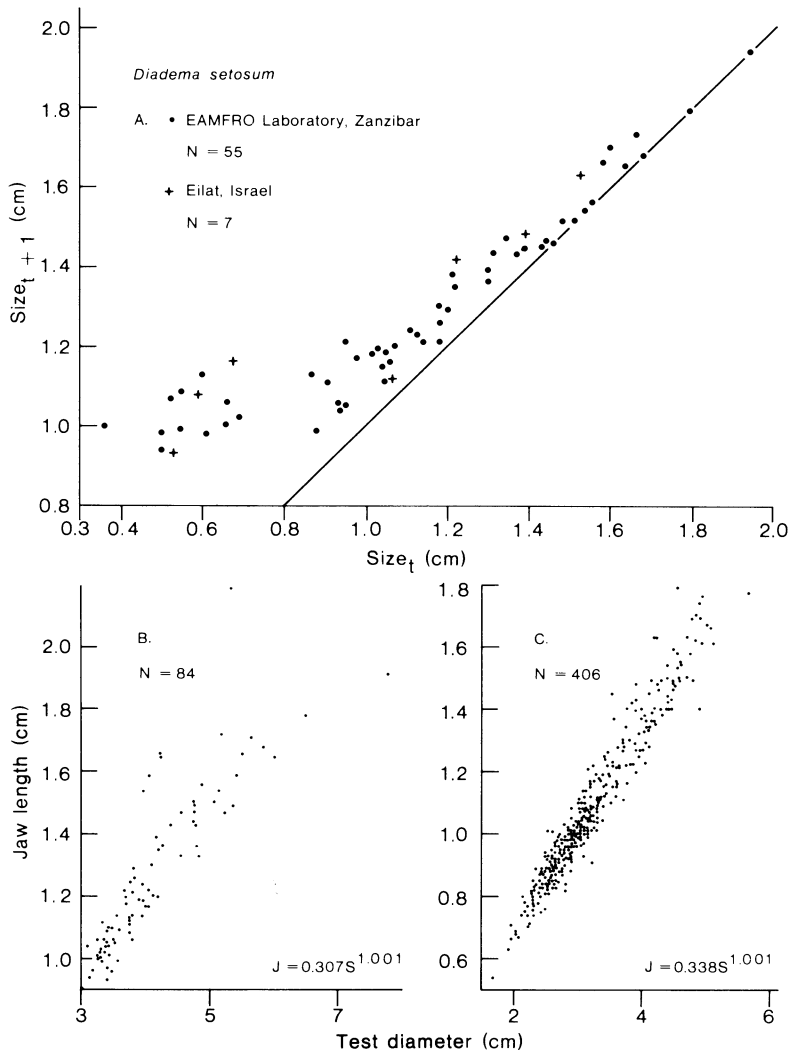The populations from Makua and Pupukea are either

FIG. 15. *Diadema setosum*. (A) Walford plot of jaw sizes separated by a time interval of 1 yr. S_t is original size, determined by tetracycline tagging, and S_{t+1} is size after 1 yr. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$. (B) Jaw length vs. test diameter for urchins from Zanzibar (Ebert 1980*a*). (C) Relationship of jaw vs. test size for urchins from Eilat. Data summary is given in Table 10.

stunted populations or annuals. If they were stunted, I would have expected to recover some tagged individuals, particularly from Pupukea, where 638 animals were tagged. I did not recover any tagged *Tripneustes* from Pupukea, and this reason, together with their small average size, suggests that p is zero or very close to zero. The even smaller average size for the Makua population indicates that they too are annuals.

The population of *Tripneustes* at Round Island, Seychelles, looks very much like the sample from Ras Iwatine or from Pupukea, except that the distribution is translated to an average size of over 10 cm. By far these are the largest *T. gratilla* I have seen. There were no small urchins in the area, based on the sample of 262 animals. It seems very unlikely that they are age 0, which then leads to the conclusion that $\pi_1 = 0$;

hence, by the analytical techniques that are being used, $Z_\pi = 0/\text{yr}$ and $p = 1.00/\text{yr}$.

The sample of *Tripneustes* from Eilat creates several problems in analysis. The first problem is associated with the small return of tagged urchins. With only two recaptures (Fig. 22), it is impossible to base further analysis on Eqs. 6 and 7. Furthermore, as shown in Fig. 24, the two individuals showed very different amounts of growth in 1 yr. If animal A is typical of the species, then analysis of the size distribution is difficult because there is no single mode that encompasses the correct sizes with appropriate gaps on either side. There should be a single mode in the interval up to ≈4 cm. Instead, there are about three modes. One solution is to assume that there were several episodes of recruitment and sum together the fractions for the
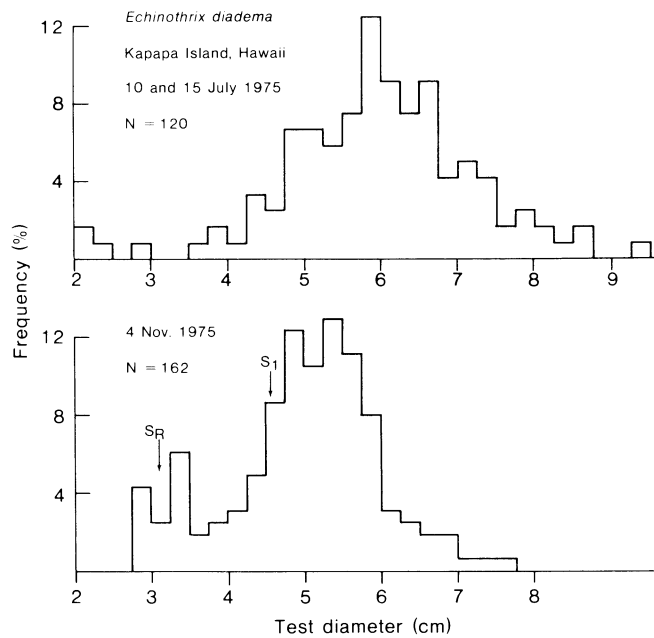
FIG. 16. Size-frequency distributions of *Echinothrix diadema* at Kapapa Island. S_R and S_1 are as in Fig. 13. Exposure value is 4.0.

first three modes, which gives $\pi_1 = 0.862$, and so $Z_\pi = 1.981$/yr. If urchin B is more typical of the species, then urchins up to ≈ 3 cm would be age 0, but still with more than one period of recruitment during the year. Under these circumstances, π_1 is 0.708 and Z_π would be 1.233/yr. The complicated size structure of the population also could be due to patchiness of growth and a combination of a number of subpopulations with different growth characteristics, but I do not believe that this is the case. *Diadema setosum* at Eilat also showed a complicated size structure (Fig. 19). Because microhabitat requirements are different for the two species and because the area appeared to be relatively homogeneous for each species, it seems best to conclude that the size distributions reflect multiple settlement episodes during a year rather than a combination of subpopulations with different growth characteristics.

The population of *Toxopneustes pileolus* at Round Island (Fig. 25) is negatively skewed with few individuals <7 cm. Based on the apparent growth of *Tripneustes gratilla*, it is highly unlikely that the large individuals with an average size of 9.87 cm and SD of 0.68 cm are age 0. The small tail on the left slope of the distribution may be age 0. A component with mean size of 7.06 cm can be separated from the distribution, comprising 2.6% of the total population. Using Eq. 11, Z_π is 0.022/yr and p is 0.97/yr (Table 12).

Salmacis belli

A single population of *Salmacis belli* was tagged in Moreton Bay, Queensland, Australia. Out of 251 animals shipped to me in 1977, 31 had tetracycline marks.

A total of 202 was tagged in 1976 (Table 12). The growth of tagged jaws is shown in Fig. 26, together with the scatter diagram of jaw length vs. test diameter. Size distributions for 1976 and 1977 are shown in Fig. 27 and were combined to estimate Z and p. The combined size distributions also were used to estimate π_1 and Z_π (Table 12). The shape of the distributions suggests either a low mortality rate or a declining population. The consistently low recruitment in both 1976 and 1977, together with the stable configuration of the size-frequency distributions (Fig. 27) suggests either that the population is stationary or that the decline has been going on for a long time and at a very low rate. In either event, the mortality rate would be low. The noncorrespondence of the estimate based on Eq. 11
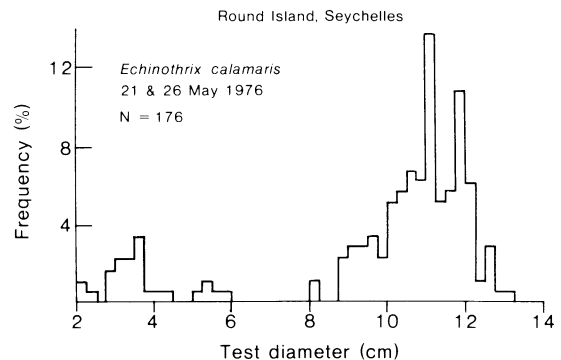

FIG. 17. Size structure of the *Echinothrix calamaris* population at Round Island. Exposure value is 11.0.

TABLE 10. Analysis of growth and survivorship of species of the Family Diadematidae: *Echinothrix diadema, E. calamaris, Centrostephanus rodgersi, Diadema setosum,* and *D. paucispinum.* Headings are as given in Tables 6 and 9; the common shape parameter for jaw growth (n_j) in *Diadema* is based on the sample from Zanzibar.

Species and location	$J = \alpha S^\beta$			Walford plot							Survivorship							
	N_1	α	β	N_2	N_3	n_j	K	J_∞	S_∞	n_t	S_R	S_1	Z	p	N_4	N_5	π_1	Z_π
Echinothrix diadema, Kapapa Island, Hawaii	53	.261	1.035 (0.041)	33	53	−0.180	0.050	2.185	7.781	−0.174	3.194 (0.109)	4.6	0.315	0.73	153	290	0.153 (0.036)	0.166
Echinothrix calamaris, Round Island, Seychelles											3.644 (0.198)				176		0.159 (0.026)	0.173
Kealakekua Bay, Hawaii											7.250 (2.919)				94		0.430 (0.178)	0.563
Centrostephanus rodgersi, Port Jackson, New South Wales	225	.271	1.017 (0.021)	24	229	−1.144	0.247	2.590	9.218	−1.132	1.561 (0.145)	1.7	0.064	0.94	220	220	0.023 (0.010)	0.023
Diadema setosum, Zanzibar	84	.307	1.001 (0.015)	55	86	−0.213	0.008	2.835	9.192	−0.213	1.803 (0.047)	3.0	0.288	0.75	153	200	0.451 (0.040)	0.600
Eilat, Israel	406	.338	1.001 (0.015)	7	406	−0.213	0.008	2.835	8.357	−0.213	1.862 (0.046)	3.0	0.654	0.52	985	963	0.543 (0.058)	0.783
Diadema paucispinum, Pupukea, Hawaii											3.851 (0.148)				17		1.00	
Kealakekua Bay, Hawaii											4.378 (0.082)				46		0.848 (0.053)	1.883

vs. the estimate based on Eqs. 6 and 7, $Z_\pi = 0.058$ vs. 0.203/yr, taken together with the stable configuration of the size distributions for the 2 yr suggests that the discrepancy may lie with the estimates of the growth parameters; animals may grow less rapidly than indicated in Fig. 26. The alternative explanation is that recruitment usually is much higher than shown in 1976–1977.

Prionocidaris baculosa

No growth information exists for *Prionocidaris baculosa,* and few comparative data exist for other members of the family Cidaridae. Results presented by McPherson (1968) suggest that *Eucidaris tribuloides* may grow to a test diameter of 2 cm in 1 yr and have a maximum size of ≈4.5 cm. *Prionocidaris baculosa* has a larger maximum size (Fig. 28) than *E. tribuloides,* and so quite possibly achieves a larger size during its 1st yr after settlement. It is very unlikely, however, that individuals in Fig. 28, which have an average test diameter of over 5 cm, are age-0 animals. It is more reasonable to say that $\pi_1 = 0$, and hence p would be estimated as 1.00 for this population.

General comments on growth, survivorship, and size

Three major points must be made concerning growth, survivorship, and size before survivorship is related to relative body wall size in the next section. First, the general shape of the Walford plot for all urchin species with good recapture data (e.g., *Echinometra mathaei* at Rottnest Island [Fig. 7], *Diadema setosum*

at Zanzibar [Fig. 15], or *Stomopneustes variolaris* from Negombo [Fig. 20]) all show a scatter of points in the graphs that do not follow a straight line. Small urchins grow very rapidly, and large urchins grow slowly for many years. The very rapid initial growth and prolonged slow growth is shown in the negative fractional values of the shape parameter n in the Richards function in all cases except *Heliocidaris erythrogramma* at Port Jackson (Table 9), for which a positive shape parameter was estimated. However, as noted in the section on *Heliocidaris,* there is reason to question this estimate. Rapid initial growth and prolonged slow growth appears to be the pattern shown by urchins.

Yamaguchi (1975) has suggested that early growth of echinoderms is exponential. It seems reasonable that newly settled animals would not have the maximum growth rate possible and that some time would be required after metamorphosis and settlement to attain the maximum growth rate. With the possible exception of *Heliocidaris erythrogramma,* none of the sets of urchin data suggests that an exponential phase, if it exists under field conditions, extends to the smallest sizes that were tagged. If early exponential growth was present, then it would be evident in the Walford plots. A short segment of the curve for the smallest sizes would have an average slope >1.0. If an exponential phase was a significant feature of growth, then the shape parameters of the Richards function would be positive (e.g., $n = +1.0$ for the logistic).

It must be made clear that contrary to the implications of Yamaguchi's work, a time interval of 1 yr does not interfere with detecting early exponential growth.
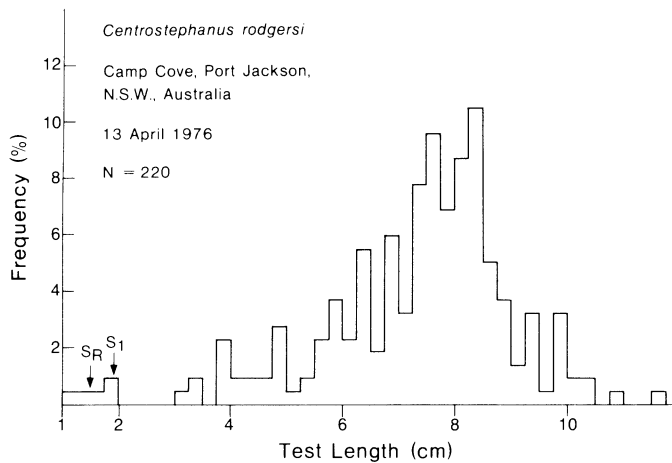
FIG. 18. Distribution of test diameter measurements of *Centrostephanus rodgersi* at Camp Cove, Port Jackson. S_R and S_1 are as in Fig. 13. Exposure value is 8.0.

Time interval was a problem in his work (Yamaguchi 1975), but only because of the manner he chose to analyze growth, namely examining the consequences of approximating instantaneous growth rate, ds/dt by $(S_2 - S_1)/(t_2 - t)$. I conclude that, for the sizes that were tagged, an exponential phase is not an important part of the growth curve.

Rapid growth in urchins appears to take place for just the 1st yr, and the change to slower growth may be associated with the onset of sexual maturity. For example, Dix (1977) shows the relationship between gonad mass and test diameter for *Heliocidaris erythrogramma*. As shown in his figures, sexual maturity begins at a test diameter of ≈4 cm, which is the size at 1 yr that was estimated for this species at Cape Peron (Table 9).

A second general point concerns the estimates of mortality rates. The estimates based on growth and size, Eqs. 6 and 7, and Ebert (1981), frequently were not the same estimates as those obtained from using the fraction of the population in the first mode (Eq. 11). A variety of errors are certainly involved; however, the major violation of assumptions is probably with respect to the presence of a stable age or size distribution with stationary structure. Although I have no direct evidence, it is most likely that annual variation in growth is less important than variation in recruitment and survival. The resolution of this difficulty is not possible with the data on hand. Two possible ways of resolving the problems of variation are through long-term observations of urchin populations or direct observation of age structure and density over a period of several years. Natural growth lines are evident in some species; *Echinometra mathaei*, *Colobocentrotus atratus* and *Echinostrephus aciculatus* have particularly clear pigmented lines in the jaws. The results from tetracycline tagging in *E. mathaei* suggest that the natural lines in jaws are annual. More subtle growth

lines may be present in other species and may now be interpretable in light of the results from tetracycline, as has been suggested by Pearse and Pearse (1975). Ion ratios that change in response to seasonal changes
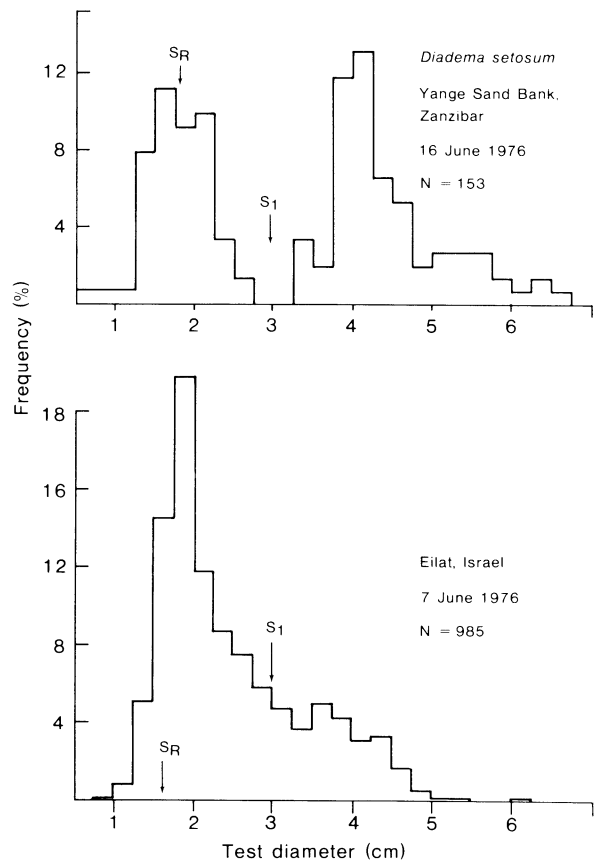

FIG. 19. Size-frequency distributions of *Diadema setosum* at Yange Sand Bank, Zanzibar (Ebert 1981), and Eilat, Israel. Exposure value is 6.0 for both Zanzibar and Eilat.
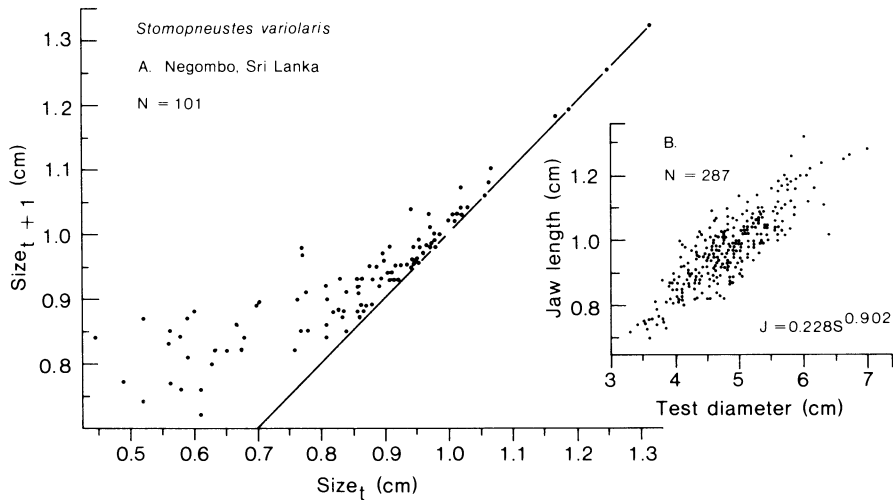
FIG. 20.   Growth of *Stomopneustes variolaris* jaws (A) and relationship between jaw length and test diameter (B). Summary of data is given in Table 11. The 45° diagonal in (A) is the line of zero growth where $S_{t+1} = S_t$.

in temperature might be used, as has been done by Fowler (1972), or X-ray analysis might be used to reveal density differences (Pearse and Pearse 1975).

The estimates of Z and p obtained by using growth parameters and size structure are potentially better than estimates based on just the fraction of the size distribution in the first mode because more information is used; hence, the estimate of Z is consistent not only with a feature of the size distribution, but also with features of individual growth. Because more information is used in Eqs. 6 and 7, I will accept such estimates of Z and p as the best estimates for a particular population and use the estimates based on Eq. 11 to indicate whether the assumption of a stable age distribution is consistent with the results. Results from Eq. 11 are used when no growth parameters are known or where it is reasonable to suspect that there is substantial error in the estimates of the growth constants.

Relationship between α and survival probability

The stated goal of this paper was to examine the relationship between relative body wall size, which is a measure of allocation to maintenance, and survivorship, adjusting comparisons for differences in surf conditions. Tables 13 and 14 present the analysis for 17 species of sea urchins with a total of 38 populations. The analysis is based on results presented in Tables 6 through 12. Table 13 presents the regression analysis using the BIOMED program for stepwise multiple regressions BMDP2R (Dixon and Brown 1979). What is clear is that both relative size of the body wall and exposure provide reductions in the residual sums of squares with a highly significant F ratio.

The first variable to enter the multiple regression was α because the correlation between p and α is .316 vs. .273 for p and exposure. In step 2 of the multiple

regression the partial coefficients are .528 and .507 for α and exposure, respectively; each is explaining about the same amount of variation in p. The correlation between α and exposure is $-.476$, and the multiple correlation coefficient R is .576. About one-third of the variation in p is explained by α and exposure (E). The detailed presentation of variables, predicted val-
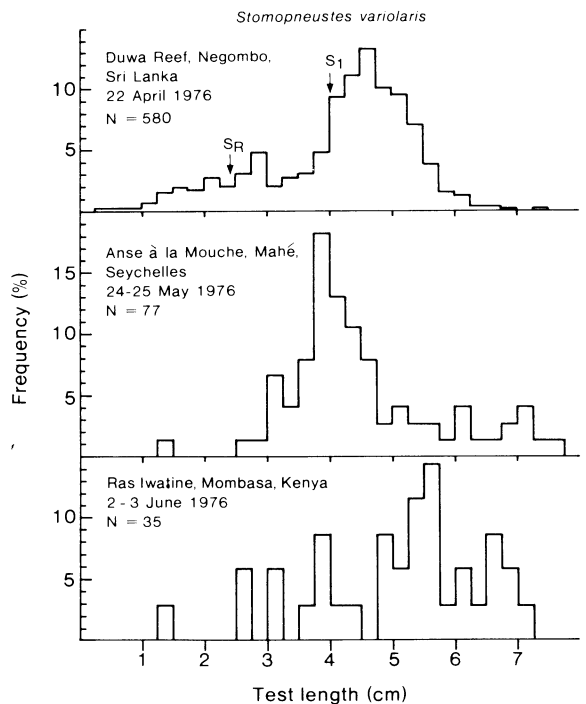

FIG. 21.   Size structure of three populations of *Stomopneustes variolaris*. Exposure values are 6.0 for Duwa Reef and 5.0 for both Anse à la Mouche and Ras Iwatine.
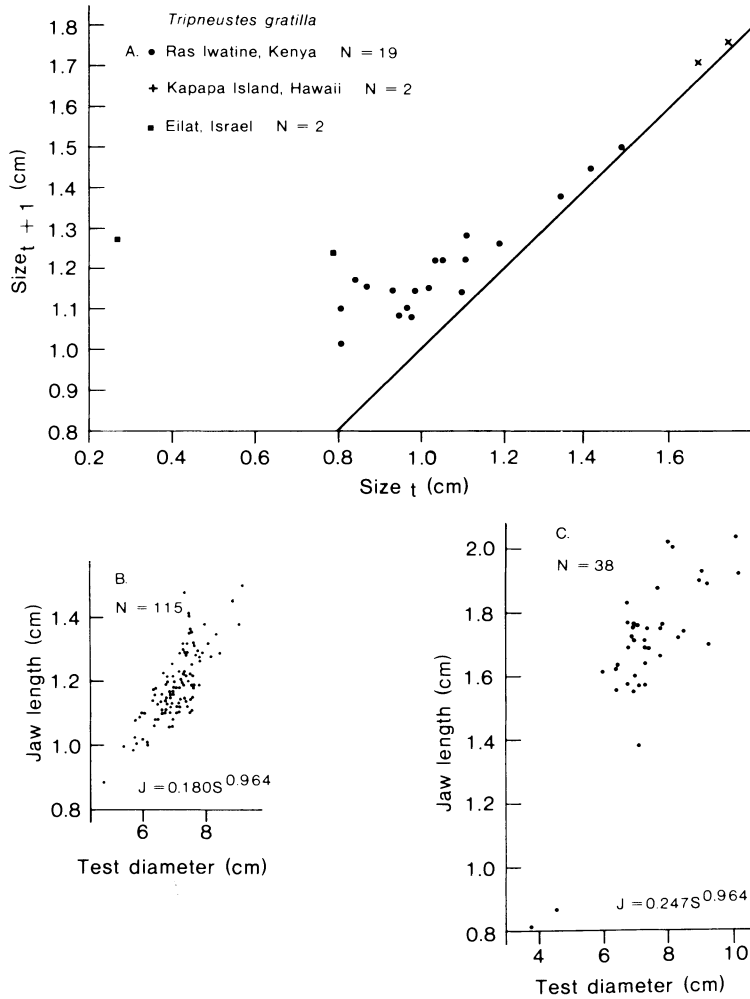
FIG. 22. Growth of jaws of *Tripneustes gratilla* from Kenya and Hawaii and for *Tripneustes* sp. at Eilat, Israel (A), jaw length vs. test diameter for the Ras Iwatine population (B), and the population from Kapapa Island (C). Data are summarized in Table 12.

ues of p, and residuals is given in Table 14. The regression equation is:

$$p = 1.20\alpha + 0.06E - 0.350. \qquad (13)$$

The first conclusion is that survival is related to relative body size; the larger the value of α the higher the value of p, given a constant exposure. Within a restricted area (e.g., the reef edge of a bay or a large pool), urchins with massive body walls will live longer on the average than urchins with thin body walls.

The second conclusion is that survival also is related to exposure. Given the same relative body wall size (α), the greater the degree of exposure to surf, the lower the survival probability; the same species of sea

TABLE 11. Analysis of growth and survivorship of *Stomopneustes variolaris*. Headings are as given in Tables 6 and 9.

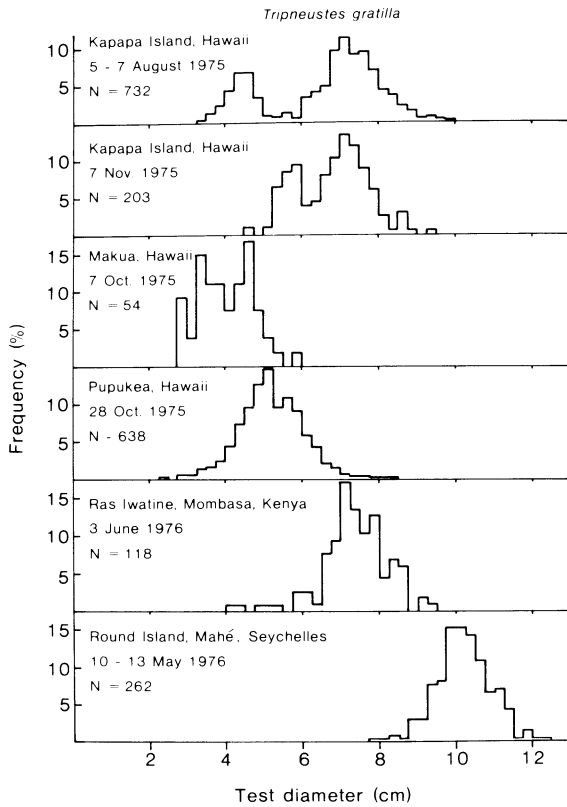| Study area	$J = \alpha S^\beta$			Walford plot							Survivorship								
	N_1	α	β	N_2	N_3	n_j	K	J_x	S_x	n_t	S_R	S_1	Z	p	N_4	N_5	π_1	Z_π	p
Negombo, Sri Lanka	287	.248	0.871 (0.026)	101	359	−0.120	0.013	1.368	7.109	−0.138	2.456 (0.143)	3.9	0.187	0.83	580	647	0.233 (0.030)	0.265	
Anse à la Mouche, Seychelles											3.983 (0.179)				77	77	0.790 (0.122)	1.561	0.210
Ras Iwatine, Kenya											3.193 (0.886)				35	35	0.263 (0.192)	0.305	0.737

FIG. 23. Size structure of six populations of *Tripneustes gratilla*. Exposure value is 4.0 for Kapapa, 2.0 for Makua, 4.0 for Pupukea, 5.0 for Ras Iwatine, and 11.0 for Round Island.

urchin that can survive over a wide range of surf conditions will tend to have the longest lifespan in the calmest water.

The third general conclusion is that urchins appear to conform to the predictions of the Gadgil-Bossert model that relate allocation to life history features (Gadgil and Bossert 1970), in that an increase in apparent allocation to a structure associated with maintenance leads to an increase in survival. Sea urchins fulfill one of the requirements for dealing with the allocation model in terms of investigating life history evolution. It would now be reasonable to analyze allocation in greater detail because the foundation to believe that allocation is related to survival has been provided.

The analysis in Table 14 ignores qualitative differences in the structure of the body wall such as sharp spines vs. blunt spines or the relative proportions of spines vs. test plates. Qualitative differences may be very important in determining how well α predicts survival rate p. Furthermore, qualitative differences may reflect sources of mortality other than surf conditions, such as the actions of predators or competitors.

Data on species from three families listed in Table 14 were subjected to an analysis of covariance (BMDP2V, Dixon and Brown 1979). Grouping was done by family (Table 15). Species in the Echinometridae have the most massive body walls ($\bar{\alpha} = 0.717$) and tend to live in high-energy environments ($\bar{E} = 3.2$). Species in the Toxopneustidae have much less massive bodies ($\bar{\alpha} = 0.399$) and tend to live in more protected habitats ($\bar{E} = 6.1$). Species in the family Diadematidae have intermediate body wall size ($\bar{\alpha} = 0.483$) and live in habitats that are similar in surf conditions ($\bar{E} = 6.4$) to those inhabitated by species in the Toxopneustidae.

When survival values are adjusted for the two covariates α and E, the three families are not significantly different ($F = 0.22$, tail probability $= .80$). There do not seem to be strong qualitative differences among sea urchins of the three families; the sharp, thin

TABLE 12. Analysis of growth and survivorship of species in the Family Toxopneustidae and *Salmacis belli* (Family Temnopleuridae). Headings are as given in Tables 6 and 9.

| Species and location	$J = \alpha S^\beta$			Walford plot							Survivorship								
	N_1	α	β	N_2	N_3	n_j	K	J_x	S_x	n_j	S_R	S_1	Z	p	N_4	N_5	π_1	Z_π	P
Tripneustes gratilla, Ras Iwatine, Kenya	115	.180	0.964 (0.046)								4.826 (0.619)				118		0.044 (0.030)	0.045	0.96
Kapapa Island, Hawaii	38	.247	0.964 (0.046)																
August 1975											4.405 (0.030)				732		0.267 (0.017)	0.311	0.73
November 1975											5.649 (0.082)				203		0.271 (0.055)	0.316	0.73
Tripneustes sp., Eilat, Israel	271	.201	1.074 (0.030)								4.2				858		0.862	1.981	0.14
Toxopneustes pileolus											7.063 (0.256)				459		0.026 (0.008)	0.022	0.97
Salmacis belli	246	.197	0.941 (0.036)	31	251	−0.163	0.077	1.801	10.478	−0.174	4.931 (0.243)	6.7	0.203	0.82	453	202	0.056 (0.011)	0.058	
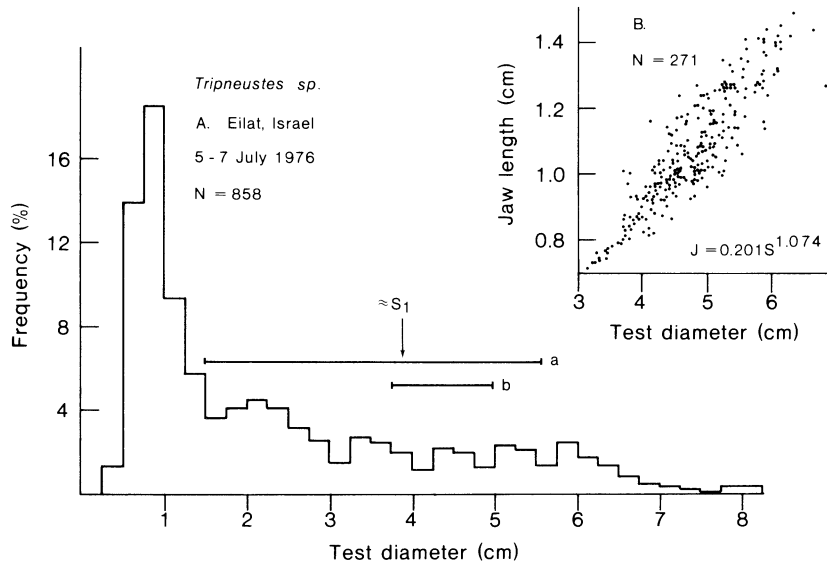
FIG. 24. (A) Size structure of the *Tripneustes* sp. at Eilat (exposure value 6.0); lines a and b show growth estimates for the two tagged individuals shown in Fig. 22, and S_1 is an approximation based on the growth of individual a. (B) Relationship between jaw length and test diameter.

spines of the Diadematidae are no more or less effective for their mass than the more massive spines of the Echinometridae or very small spines of the Toxopneustidae. I conclude that qualitative differences are not important in modifying survival rates.

DISCUSSION

An important question for urchins specifically and all organisms generally is: what is the significance of longevity? There are at least five views. The first view is that longevity is significant because it is a positive benefit to an organism in its own right: it is good for an organism to live a long time, and so selection favors long life (Sacher 1978).

In many papers there are elements of the idea that living a long time, in itself, is good, and this suggestion sometimes is lurking even in papers written by authors who argue against such a line of reasoning. For example, in their discussion of the evolution of longevity, Kirkwood and Holliday (1979) suggest that if a species gains an adaptation that enables it to colonize a more secure niche, then there will be selection against aging factors so the organism can realize full benefit of the adaptation. Gaining full benefit in such a case seems to mean living a long time. My impression is that such suggestions are rooted in anthropocentrism: I like the idea of living a long time and am very sure that living a long time would be good for me. Everyone I have discussed this with also would like to live a long time and believes that it would be beneficial; however, just because I want to live a long time is no reason to believe that my pet hamster would have greater fitness if it too lived a long time. Cole's (1954)

analysis of the benefits of long life vs. short, all other things being equal, still makes good sense and contradicts the view that long life of itself should be selected for.

A second view of longevity is that is has no significance but is merely a result of success in suppressing the expression of deleterious genes and the time of onset of senescence (Medawar 1957, Williams 1957). Deep down inside, this view seems to be much the same as the first: longevity is good all by itself and were it not for the decrease in the force of selection with increasing age, creatures would live much longer than they do. This second view has been attacked on logical grounds by Kirkwood (1977).
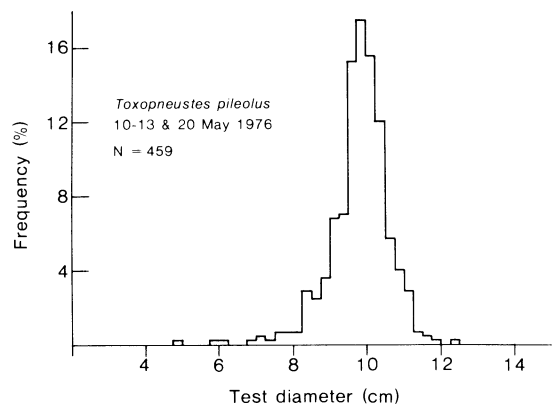

FIG. 25. Distribution of diameter measurements of *Toxopneustes pileolus* at Round Island, Seychelles. Exposure value is 11.0.
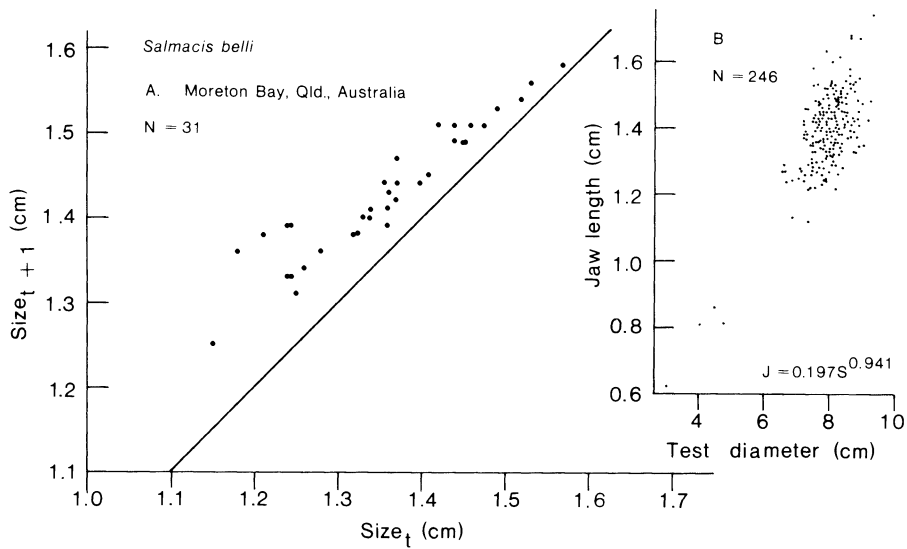
FIG. 26. (A) Walford plot of jaw growth for *Salmacis belli*. The 45° diagonal is the line of zero growth where $S_{t+1} = S_t$. (B) Scatter diagram of jaw length vs. test diameter, which is used to convert growth parameters of the jaws into the appropriate parameters for test growth. Data are summarized in Table 12.

A third view is that individual longevity is associated with maintaining stable population sizes near the carrying capacity of the environment (Southwood et al. 1974), though of itself longevity apparently is of no significance. Long life in K-selected forms is the result of an increase in individual size caused by interspecific competition, and large size requires long generation times. Rapid return to population equilibrium following disturbance can be attained with varying clutch or litter size in a density-dependent manner. This is the r- and K-selection paradigm.

A fourth view is that longevity is a response to variation in juvenile survival (Murphy 1968, Schaffer 1974). If prereproductive survival is constant, then maximum fitness can be attained with massive investment in reproduction with minimum investment in mechanisms that prolong life. This is the bet-hedging point of view (Stearns 1976, 1977).
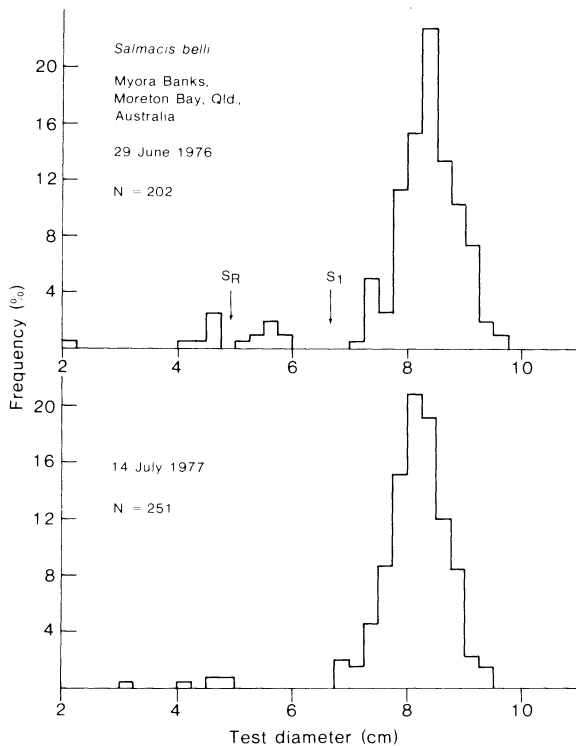

FIG. 27. Size structure of the *Salmacis belli* population in Moreton Bay, Queensland. Exposure value is 10.0.
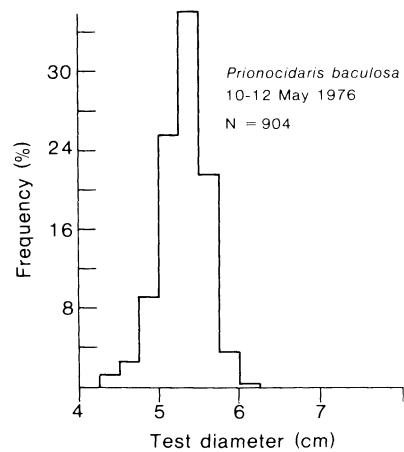

FIG. 28. Size-frequency distribution of diameter measurements for *Prionocidaris baculosa* at Round Island. Exposure value is 11.0.

TABLE 13. Regression analysis of relationship of α and exposure E in determining probability of annual survivorship p. Variables, predicted values for p, and residuals are presented in Table 14. Analysis is for both independent variables entering the multiple regression using the BIOMED program BMDP2R (Dixon and Brown 1979).

Analysis of variance	Sums of squares	df	Mean square	F ratio	
Regression	1.2234	2	0.6117	8.70	$.0005 < P < .001$
Residual	2.4622	35	0.0703		

Variables in regression equation with dependent variable p the probability of annual survival:

Variable	Coefficient	SE of coefficient	F to remove
Y-intercept	−0.350		
α	1.206	0.328	13.50
Exposure	0.061	0.017	12.13

Partial correlations with P:

Step	α	Exposure
0	.3161	0.2725
1	.3169	0.5073
2	.5276	0.5073

Summary table:

Step	Variable entered	Multiple R	R^2	Increase in R^2
1	α	0.3169	0.1004	0.1004
2	Exposure	0.5761	0.3319	0.2315

Finally, a fifth view is derived from the simple deterministic model of Schaffer (1974), together with Stearns' (1977) arguments concerning design constraints. Very high but constant juvenile mortality could act as a constraint barrier on how short life could be, and longevity in different species could reflect the presence of the barrier at different positions in the species' adaptive space.

The annual growth rate λ of a population, as presented by Schaffer (1974) or Schaffer and Gadgil (1975) is:

$$\lambda = cB + p, \qquad (14)$$

where B is the total number of newborn individuals, c is the juvenile survival rate to the age of first reproduction, and p is the adult survival rate. Changes in c, B, or p can influence λ. If c is very small, then one way of having $\lambda \geq 1$ is for p to be large; large p means long life. In terms of resource allocation, an increase in p may be at the expense of B (total births) or size of individual offspring, which may, though by no means' certainly, result in even poorer juvenile survival.

It seems that for long life to persist in this deterministic scheme, very small c and very large B must be given as constraints. That is, c is very small because of the basic design of the organism, and B is limited by the total amount of resource that can be devoted to reproduction without a substantial evolutionary design breakthrough.

In both views four and five, a balance exists between allocation of resources to reproduction and to maintenance. Sufficient resources are allocated to maintenance to make it likely that an individual will replace itself. This is Kirkwood and Holliday's (1979) "disposable soma" theory and is a reasonable game strategy in the sense used by Slobodkin and Rapaport (1974).

Within the context of these five views on the significance of longevity, two questions can be posed for the urchins in this study: (1) what selective pressures are most likely responsible for the resulting longevities, and (2) how can one tell whether any particular population that is selected for study is a suitable subject for evolutionary questions, i.e., how does one know that a population is in the mainstream of evolution?

Concerning the first question, it is necessary to return to the ideas of r- and K-selection, bet hedging, and design constraints, views three through five on the significance of longevity. I wish to argue that basic aspects of r- and K-selection are untestable because of, in part, the requirement that density-dependent components of birth and death be recognizable from density-independent components. The theory would predict that short-lived urchins such as *Diadema setosum* or *D. paucispinum* would suffer more deaths due to density-independent factors compared with such long-lived urchins as *Heterocentrotus trigonarius*. Hickman (1979) has suggested that the distinction between density-independent and density-dependent mortality may be "inoperational" in nature, and if this assertion is generally true, then the r- and K-selection paradigm is useless.

When food is scarce, gonad development in urchins is poor (Ebert 1968), but there is no indication that low urchin densities result in increased recruitment or that

TABLE 14. Observed and predicted values of p, the probability of annual survival using α, the coefficient of relative body size, and E, a subjective ranking of severity of surf conditions as independent variables. An $E = 1$ is most severe surf. Predicted values are based on the analysis of the regression shown in Table 13; regression equation is $p = 1.206\alpha + 0.061E - 0.350$; each * is equal to one standard deviation; (π) shows survival probabilities estimated using Eq. 11; other observed probabilities were determined from Eq. 7.

Species	Location	α	Exposure	$P_{observed}$	$P_{calculated}$	Residual
Heterocentrotus trigonarius	Ananij Reef, Enewetak Atoll	.966	1.5	0.971	0.906	0.065
Heterocentrotus mammillatus	Honaunau Bay, Hawaii	.919	4.0	0.895	1.000	−0.105
Colobocentrotus atratus	Ulupau reef bench, Hawaii	.788	1.0	0.672	0.661	0.010
Prionocidaris baculosa	Round Island, Victoria Harbor, Seychelles	.727	11.0	1.000 (π)	1.192	−0.192
Echinometra oblonga	Reef bench at Kapapa Island, Hawaii	.687	3.0	0.868	0.660	0.208
	Lani Overlook, Hawaii	.687	1.5	0.686	0.569	0.117
	Ulupau reef bench, Hawaii	.687	1.0	0.649 (π)	0.539	0.110
Echinometra mathaei	Reef bench at Kapapa Island, Hawaii	.672	3.0	0.831	0.642	0.189
	Lani Overlook, Hawaii	.672	1.5	0.604	0.551	0.053
	Pools at Makua, Hawaii	.672	2.0	0.650 (π)	0.582	0.069
	Pool at Pupukea, Hawaii	.672	4.0	0.881 (π)	0.702	0.178
	Rottnest Island, Western Australia	.672	4.0	0.865	0.702	0.163
	Ras Iwatine, Kenya	.672	5.0	0.855	0.763	0.092
	Anse à la Mouche, Mahé, Seychelles	.672	5.0	0.967 (π)	0.763	0.204
	Sand Island Channel, Enewetak Atoll	.672	5.0	0.420 (π)	0.763	−0.343*
	Eilat, Israel	.604	6.0	0.084	0.741	−0.658**
Stomopneustes variolaris	Duwa Reef, Negombo, Sri Lanka	.647	6.0	0.829	0.793	0.036
	Anse à la Mouche, Mahé Seychelles	.647	5.0	0.210 (π)	0.733	−0.523*
	Ras Iwatine, Kenya	.647	5.0	0.737	0.733	0.004
Echinothrix diadema	Lee of Kapapa Island, Hawaii	.570	4.0	0.730	0.580	0.151
Centrostephanus rodgersi	Camp Cove, Port Jackson, New South Wales	.560	8.0	0.938	0.809	0.129
Heliocidaris erythrogramma	Cape Peron, Western Australia	.537	5.0	0.907	0.600	0.307*
	Hastings Point, New South Wales	.537	5.0	0.964 (π)	0.600	0.364*
	Balmoral Beach, Port Jackson, New SouthWales	.537	9.0	0.930	0.842	0.088
Diadema paucispinum	Cook Monument, Kealakekua Bay, Hawaii	.532	6.0	0.152 (π)	0.644	−0.492*
	Pool at Pupukea, Hawaii	.532	4.0	0.000 (π)	0.523	−0.523*
Toxopneustes pileolus	Round Island, Victoria Harbor, Seychelles	.439	11.0	0.974 (π)	0.845	0.130
Diadema setosum	Yange Sand Bank, Zanzibar	.422	6.0	0.750	0.522	0.228
	Eilat, Israel	.422	6.0	0.520	0.522	−0.002
Echinothrix calamaris	Round Island, Victoria Harbor, Seychelles	.411	11.0	0.841 (π)	0.811	0.030
	Cook Monument, Kealakekua Bay, Hawaii	.411	6.0	0.411 (π)	0.509	0.061
Tripneustes gratilla	Lee of Kapapa Island, Hawaii	.398	4.0	0.731 (π)	0.372	0.359*
	Pools at Makua, Hawaii	.398	2.0	0.000 (π)	0.251	−0.251
	Pool at Pupukea, Hawaii	.398	4.0	0.000 (π)	0.372	−0.372*
	Palemano Point, Kealakekua Bay, Hawaii	.398	5.0	0.508 (π)	0.433	0.076
	Round Island, Victoria Harbor, Seychelles	.398	11.0	1.000 (π)	0.796	0.205
Tripneustes sp.	Eilat, Israel	.367	6.0	0.138 (π)	0.456	−0.318*
Salmacis belli	Moreton Bay, Queensland	.360	10.0	0.841	0.689	0.152

high adult densities lead to low recruitment. In fact, the evidence indicates the opposite (Moore et al. 1963, Ebert 1968, Tegner and Dayton 1977): recruitment is positively related to adult density.

The significance of exposure in the multiple regression (Eq. 13) and the lack of qualitative differences among families (Table 15) both suggest a significant role of the physical environment in shaping lifespan. Massive body walls of *Heterocentrotus* sp. or *Colobocentrotus atratus* appear to be more a response to the physical environment than to interspecific competitive abilities. Both *Heterocentrotus trigonarius* and *C. atratus* live in very restricted environments with

no other urchin species. If competition is so important, where are their competitors? The obvious response is to point out that because there are no other urchins living in the high-energy environments occupied by *H. trigonarius* or *C. atratus,* we have strong evidence showing that they are capable of keeping all other urchins out of the surf zone. However, this is the untestable elephant-bane hypothesis: "I'm ringing this bell to keep elephants away." "I don't see any elephants." "Successful, isn't it?"

Knowledge of the intensity of intraspecific competition is equally elusive. Are populations of long-lived species existing near the upper limit of available re-

TABLE 15. Analysis of annual survival rates of species in three sea urchin families. Data are a subset of Table 14. The families are Echinometridae (*Heterocentrotus trigonarius, H. mammillatus, Colobocentrotus atratus, Echinometra mathei,* and *E. oblonga*), N = 15 families; Diadematidae (*Echinothrix diadema, E. calamaris, Centrostephanus rodgersi, Diadema paucispinum,* and *D. setosum*), N = 8; and Toxopneustidae (*Toxopneustes pileolus, Tripneustes gratilla,* and *T.* sp. from Eilat), N = 7. Grouping was done by family; survival rate is the dependent variable. α, the coefficient of relative body size and E, the ranking of surf condition, are covariates. Analysis was done using BMDP2V analysis of covariance (Dixon and Brown 1979).

Source	Sum of squares	df	Mean square	F value	Tail probability	Slope (β)
Mean	0.1148	1	0.1148	1.56	.22	
Families	0.0323	2	0.0161	0.22	.80	
α	0.2980	1	0.2980	4.04	.055	1.326
E	0.7299	1	0.7299	9.89	.004	0.071
Both α and E	0.8733	2	0.4366	5.91	.008	
Error	1.8458	25	0.0738			

Mean survival values *p* after adjusting for α and E are not significantly different for the three families of sea urchins (F = 0.22, tail probability = .80).

Variable	Echinometridae	Diadematidae	Toxopneustidae
N	15	8	7
p	0.658	0.552	0.614
Mean α $\pm$ SE	0.7174 $\pm$ 0.0258	0.4825 $\pm$ 0.0254	0.3994 $\pm$ 0.0079
Mean E $\pm$ SE	3.1667 $\pm$ 0.4328	6.3750 $\pm$ 0.8004	6.1429 $\pm$ 1.3350

sources of food or space and short-lived species generally well below environmental carrying capacity? Density-dependent mortality could be explored either by long-term monitoring of density and survival rates or by the manipulation of densities; to date, however, no convincing studies exist for urchins. Some data suggest that food availability may modify individual size but not survival (Ebert 1968, 1977).

Subjectively, there does not appear to be any relationship between lifespan and filling available space. *Diadema setosum* at Yange Sand Bank (*p* = 0.75) appeared to saturate the environment to a greater degree than did *Heterocentrotus trigonarius* at Enewetak Atoll (*p* = 0.97).

Finally, it is clear that both relatively short-lived species (*Diadema setosum*) and relatively long-lived species (*Strongylocentrotus purpuratus*) both possess adaptive machinery for dealing with food shortage. When food is in short supply these two species develop relatively larger jaws compared with development under conditions of greater food availability (Ebert 1980*b*). Overall, the theory of r- and K-selection seems either to be untestable, or urchins appear not to conform to its predictions.

Bet-hedging theory is more attractive than r- and K-selection theory if for no other reason than basic assumptions can be tested. The keystone of bet-hedging theory is that lifespan reflects variability in prereproductive survival. This central point is testable as shown by Murphy (1968) for clupeids and, in principle, is testable for urchins, although for very long-lived species the length of time between successful recruitment episodes may exceed both the patience and good will of most funding agencies, and possibly the lifespan of the investigator. Buchanan (1967) presents recruitment data

for two heart urchins which show, for *Echinocardium cordatum,* a long-lived species, just two successful recruitment periods in 15 yr.

Strongylocentrotus purpuratus in Sunset Bay, Oregon, had a major recruitment in 1963 (Ebert 1968). I have returned to Sunset Bay every year or two since 1969 and have not seen major recruitment since the 1963 year-class. During a 15-yr period, *Strongylocentrotus purpuratus* had only one major recruitment (Ebert 1982), and observation of the shift of the 1963 year-class in size distributions indicates that major recruitment had not occurred in 1962, 1961, 1960, or 1959. It is difficult to project backward to pre-1959 size distributions; however, it is reasonable to state that there was only one good year for recruitment during a period of 20 yr. If the urchins of Sunset Bay are typical of long-lived urchins, then it might be necessary to examine urchins for at least 20 yr in order to document recruitment variability. They are long lived and, following the massive recruitment in 1963, continue to readjust very slowly, contrary to the expectations of r- and K-selection theory.

Low recruitment is not at all the same as variable recruitment, and the evolutionary consequences of the two should be different, even though low and variable recruitment frequently are lumped together (e.g., Lynch 1980). Average low recruitment may set a lower limit for longevity as suggested by the model of Charnov and Schaffer (1973). Under conditions of low but predictable recruitment, those individuals that produce more offspring should have a greater chance of contributing to the next generation than would those individuals that allocate fewer resources to reproduction and more to maintenance. The long-term result of predictable recruitment would be selection for ever

greater allocation to reproduction. Because this would require a shift of resources away from maintenance, there would be an associated increase in mortality rate until the lifespan was so short that any further shortening would decrease the chances that an individual would contribute to the next generation.

This argument seems reasonable regardless of whether there is significant competition between or predation on adults or prereproductives, or whether the major sources of mortality are due to physical conditions. Whether mortality is density dependent or independent is irrelevant. The only significant force directing evolution of long life is variability of prereproductive survival. Thus, the prediction for urchins or any other species would be that over evolutionary time long life has been a response to variable survival of individuals up to the age of first reproduction.

If low and constant recruitment can be a constraint on how short life can be, then, in principle, it is possible to explain the variation in life spans of the urchins I have studied as being due to different degrees of mismatching of juvenile survival and total births. That is, if total number of births exactly equals the reciprocal of juvenile survival, then λ can equal 1.0 when adult survival p is zero. As total number of births B becomes ever smaller relative to the juvenile survival rate, p must become larger. If c is outside the adaptive abilities of the species, then c forms a constraint on p, and decreasing c "ups the ante" for allocation to maintenance mechanisms that increase p. This is not really "bet hedging" but rather "forced ante." For the urchins in this study it may be that the ante is different for different species and is highest for such species as *Heterocentrotus trigonarius* and lowest for such species as *Tripneustes* sp. at Eilat, Israel.

With the data I have, I cannot distinguish between "bet hedging" and "forced ante." Population trends for species evolving under these two different sets of rules would be different, and it should be possible to gather data that would aid in distinguishing between the two views. For a long-lived species operating under the rules of bet hedging, populations would usually be declining (births < deaths), but there would be occasional recruitment episodes that increase the population substantially. Under the rules of "forced ante" the usual conditions would be for populations to remain at the same density (births = deaths).

It should be obvious that it is possible to combine "bet hedging" and "forced ante." When juvenile mortality is constant, life will become shorter and shorter, up to the constraint barrier. If juvenile mortality is variable, then life will be longer, and the more variable prereproduction mortality is, the greater will be the difference between the potential survival at the barrier and the actual survival.

The problem of deciding whether any particular population is in the mainstream of evolution is extremely difficult to deal with and, I would argue, is a perennial bugbear in all studies of field populations that use evolutionary arguments to interpret data. The difficulty is well illustrated in the summary of data in Table 14, which shows such species as *Echinometra mathaei* with estimates of p ranging from 0.084 to 0.967 or *Tripneustes gratilla* with estimates ranging from 0.000 to 1.000. All areas can be considered as being "marginal," "typical," or "superior." Typical habitats would be those that have the individuals of a species that contribute most genetic information to future generations and so show the clear relationship between maintenance and p. Many habitats, for various reasons, are marginal for survival of urchins after settlement, and the probability of annual survival approaches zero, regardless of investment in maintenance. Finally, there are few highly favorable sites in which species with very thin body walls can survive, as well as species with heavy body walls.

The marginal natures of Pupukea and Makua are further indicated by the fact that other species found in the pools all were represented by only small individuals that probably were <1 yr old. Six *Echinothrix diadema* were collected at Makua with a size range from 2.01 to 3.96 cm; 27 *Eucidaris metularia* collected at Makua had a size range of 0.44–1.64 cm; 2 *Pseudoboletia indiana* collected at Pupukea were 4.18 and 4.31 cm, and 2 collected at Makua were not measured, but were <2 cm diameter.

Victoria Harbor, Seychelles, seems to be an example of a superior habitat. All species were represented by large individuals, and if the size distributions of *Tripneustes gratilla*, *Toxopneustes pileolus*, *Echinothrix calamaris*, and *Prionocidaris baculosa* can be accepted as stationary, then all species are very long lived in the region near Round Island.

The criteria for designating a habitat "marginal," "typical," or "superior" have been based on adult survival. A second way of classifying habitats would be in terms of recruitment. It now seems reasonable to conclude from the data in Table 14 and the presentation of species occurrences in the section on areas and organisms that recruitment may be best for most species under conditions of high water movement. The marginal habitats for adult survival have many species, but the large number of species are represented by young animals only. The pool at Pupukea, given an exposure ranking of 4.0, contains 10 of the 12 shallow-water regular echinoids (subclass Regularia) of Hawaii; I have not seen *Colobocentrotus* or *Heterocentrotus* in the pool. Other than *Echinometra* sp., urchins are represented solely by young-of-the-year. The reef bench at Ulupau, the most exposed site where urchins were tagged, had a few small individuals of *Tripneustes*, *Heterocentrotus*, *Pseudoboletia*, and *Echinometra mathaei*. In contrast, more-protected sites did not have conspicuous numbers of small animals. Small urchins were conspicuously absent in the calm

waters of Round Island, Seychelles ($E = 11.0$), but small *Tripneustes* and *Toxopneustes* as well as a small *Prionocidaris baculosa* (2.82 cm) were observed at Anse à la Mouche ($E = 5.0$).

A further complicating feature with the idea of marginal, typical, and superior habitats comes from the multiple regression analysis. As executed, the analysis assumes a linear relationship between p and exposure. This assumption is quite likely incorrect, or at least incorrect for some species, but I do not believe that the data in Table 14 are sufficient to justify making the model more complicated at this time. The relationship between survival rate (p) and exposure would be better described with a second-order equation. The argument for this is based on the distribution of such species as *Heterocentrotus trigonarius* and *Colobocentrotus atratus* and their response to being held in aquaria. Both of these urchin species are very narrowly confined to high-energy environments; they do not occur in calmer water. What I think this suggests is that the urchins may have lower limits as well as upper limits for tolerance of water movement. Because of poor performance in aquaria, the lower limits for *Heterocentrotus* and *Colobocentrotus* seem to be due to physiological stress (respiratory?), whereas the upper limits probably are set by the strength of the test and spines in resisting a pounding surf. The gradients would be surf action with associated physical stress and the opposing gradient, physiological (respiratory?) stress, associated with decreasing water motion. If this analysis is correct, it would suggest the reason for only thin-wall species in bays and harbors, with the notable exception of species in the Family Cidaridae. *Prionocidaris baculosa* was common near Round Island in Seychelles and its α value is .727. Cidarids frequently are sold in aquarium shops, indicating excellent tolerance to low water movement, and, finally, they are the only heavy-bodied group of echinoids that is present in the deep sea. They are capable of living in areas with high water motion (*Eucidaris* at Makua), as well as in protected areas. They obviously possess the machinery for dealing with low water movement while maintaining a massive body wall, whereas members in the Family Echinometridae (*Heterocentrotus* and *Colobocentrotus* in particular) lack such machinery. This argument suggests that there are qualitative differences among the urchins, and I am quite willing to entertain the argument that the results in Table 15 may change when additional data are added.

The evolution of life history characteristics of shallow-water urchins can, I believe, be placed within a reasonable set of constraints, some of which can be deduced from the data in this paper. The first constraint appears to be the settlement requirements of the larvae: they seem to settle best in areas of high water motion. I suggest that this is a constraint; otherwise I would expect to see good recruitment of thin-bodied urchins in protected bays and little or no recruitment of these species in areas of high surf. (*Tripneustes gratilla* should not be settling at Ulupau if settlement were related to the expectation of long life of adults.)

Larvae appear to be very conservative parts of the life cycle, and the only deviation from the norm in the group I studied was *Heliocidaris erythrogramma*, with its highly modified development and exceptionally short planktonic period of only 5 d (Williams and Anderson 1975), in contrast with more typical urchins such as *Lytechinus anamesus* (=*pictus*), which require 3 wk (Hinegardner 1975). With such a development in larval biology, I predicted that the recruitment rate should have been high and with low variability, and hence *H. erythrogramma* should be very short lived. *H. erythrogramma* is a species that broke through some of the constraints on larval development and ended up with what seems to be an inferior mechanism for making recruitment more predictable. The solution to the apparent problem may be provided by Jackson and Strathmann (1981). The short period of development of *H. erythrogramma* may mean that it also has a very short period of time in which it is capable of settling. Species with long development times probably have potentially longer times in the plankton during which they can settle, if a suitable substrate is encountered. Consequently short development time does not necessarily promote more certain settlement and would do so only if coupled with a long period during which settling could take place. The "competent" period for *H. erythrogramma* is unknown. The overall survival of larvae may form a constraint on how short adult life can be, that is, the shortest life possible when prereproductive survival is constant.

A second constraint appears to be the basic design of regular echinoids. I would suggest that the requirement of exchanging gases across the body wall through tube feet (Farmanfarmaian 1959, 1966, Fenner 1973, Smith 1980) places a constraint on the test thickness that can function under different degrees of surf action. The best design for gas exchange probably is a thin test, but it is an inferior design for withstanding the surf.

Within these constraints, I believe that it is reasonable to ask whether there are patterns of resource allocation that result in differences in expenditures on growth, reproduction, and maintenance that are consistent with the theoretical considerations of allocation and life history (Gadgil and Bossert 1970). The particular goals for future inquiry into urchin biology, or that of other species, must center on both a clearer analysis of the constraints (Stearns 1977, Gould and Lewontin 1979), an increased understanding of the variation of age-specific survivorship in populations that contribute to future generations, and the development of energy budgets with sufficient detail to permit allocation comparisons.

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