

Abstract.— Knowledge of population dynamics and production of dominant benthic organisms on the northwestern Atlantic continental shelf is important for developing or interpreting models addressing ecological or fishery management questions. This paper estimates the recruitment frequency and success, life span, growth rate, and production of a major component of the sand-bottom benthic community in this region: the common sand dollar *Echinarachnius parma* (Echinodermata: Echinoidea). These estimates are based on size-frequency data collected at least annually between 1977 and 1985 from three sites in the Middle Atlantic Bight and one site on Georges Bank. Larval recruitment of *E. parma* to the sites was mostly annual, but persistent cohorts were irregular. Average life span was about 8 years with some rare, larger, and presumably older animals present; the maximum size found was 54 mm. A time series of modal size progressions suggests mean growth in body width ranged from 3.5 to 6 mm/yr over a period of at least 5 years, with growth curves for cohorts appearing to be sigmoidal. Annual production: biomass ratios for definable cohorts varied with age, ranging from -0.04 for senescent older cohorts to 8.10 for juveniles.

Population Dynamics, Growth, and Production Estimates for the Sand Dollar *Echinarachnius parma*

Frank W. Steimle

Sandy Hook Laboratory, Northeast Fisheries Center
National Marine Fisheries Service, NOAA
Highlands, New Jersey 07732

Information on growth and production rates of major marine taxa can support the development of better ecological and fishery production theories or models (Winberg 1971, Greze 1978). Echinoderms are one of the major marine benthic taxa; however, information on their growth and production rates is scarce. For example, production estimates are currently available for little more than a dozen species worldwide (Richards and Riley 1967, Zaika 1972, Miller and Mann 1973, Buchanan and Warwick 1974, Greze 1978, Warwick et al. 1978, Warwick and George 1980).

On the Atlantic continental shelf north of Cape Hatteras, North Carolina, the sand dollar *Echinarachnius parma* is an abundant echinoderm of fine to medium-sand habitats (Coe 1972, Wigley and Theroux 1981). Because of its relatively large size (>50 mm) and population densities which can reach hundreds of adult individuals per m² (Caracciolo and Steimle 1983), it may be a "keystone" species as defined by Paine (1969), i.e., a major factor in structuring the benthic community by dominating habitat and detrital food use. Stanley and James (1971) conclude this species to be the second most important factor, after major storms, in reworking surface sediments. This sediment reworking can disturb smaller epifaunal benthic species and larval recruitment, which can include shellfish species of commercial interest. For example, Rich-

ardson et al. (1983) studied an *E. parma* community off Rhode Island, and studies of similar Pacific and Atlantic sand dollar species *Dendraster excentricus* and *Mellita quinquesperforata* by Smith (1981), Creed and Coull (1984), and J.A. Reidenauer (Dep. Oceanogr., Fla. State Univ., Tallahassee, FL 32306, pers. comm., July 1985) found that aggregations of sand dollars substantially alter benthic macrofauna community structure, especially for tube dwellers and meiofauna.

Besides its potential role in controlling benthic community structure, *E. parma* also occurs frequently in the diets of some commercially/recreationally valuable fish, including haddock *Melanogrammus aeglefinus*, summer flounder *Paralichthys dentatus*, American plaice *Hippoglossoides platessoides*, scup *Stenotomus chrysops*, tautog *Tautoga onitis*, and yellowtail flounder *Limanda ferruginea* (Bigelow and Schroeder 1953, Coe 1972, Maurer and Bowman 1975, Collie 1987). However, its food value (Kcal/g) is half that of other common benthic prey, e.g., polychaetes or crustaceans (Steimle and Terranova 1985). Despite wide use of *E. parma* as prey, extensive populations of this echinoderm, primarily of individuals too large to be eaten by most predators, may be an energy sink (Mercer 1982). For example, *E. parma* can comprise 40-50% of the total benthic macrofaunal biomass on Georges Bank (Steimle 1987).

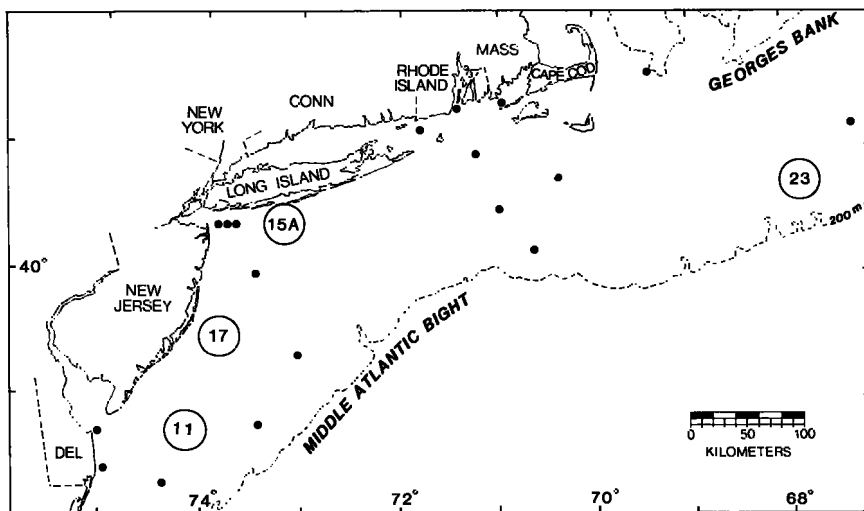


Figure 1

Station locations of the four study sites in the Middle Atlantic Bight-Georges Bank area. Other sites examined which did not produce reliable samples of *Echinarachnius parma* are also included (●).

Several studies have examined aspects of *E. parma*'s life history (for review, see Caracciolo and Steimle 1983). Only two studies have examined its growth (Cocanour 1969, Graef 1977) and none its production. Since *E. parma* can be a major contributor to the overall benthic community biomass, estimates of its production could greatly support an estimate of total community production. Warwick (1980) has shown that a major proportion of total community production is often attributed to one or a few species.

The purpose of this study was to examine *E. parma* size frequencies from a series of at least annual collections to provide information on the species' population structure, dynamics, and growth, and to estimate its production at stations in the Middle Atlantic Bight and on Georges Bank. The term "production" is used in this paper to indicate the amount of biomass added to a unit of bottom area per year.

Material and methods

Echinarachnius parma were obtained from archived benthic collections made at three stations (11, 15A, 17) in the Middle Atlantic Bight and one station (23) on southwestern Georges Bank (Fig. 1). Water depths at these stations were 20 m (Stn. 17), 30 m (Stn. 15A), 50 m (Stn. 11), and 70 m (Stn. 23).

The archived collections consisted of 3-5 replicate 0.1-m² Smith-McIntyre grab collections at each station sampled on a quarterly to annual basis, 1978 to 1985, as part of the Northeast Monitoring Program (NEMP). Collection periods varied slightly between stations (see Figures 2-5 for specifics). Grabs were handled to minimize loss of sample by surficial material washout; grabs suspected of being excessively disturbed were

resampled. The samples were washed through 1.0-mm mesh sieves prior to 1980, and through 0.5-mm mesh sieves thereafter. While *E. parma* larvae are reported to undergo metamorphosis and settle to the seabed from the plankton at a width of about 0.4 mm (Cocanour 1969), the 1.0-mm sieve collected most postlarvae because few were collected on the 0.5-mm sieve when both sieve sizes were used together in 1980 and 1981. The sieved benthic samples were fixed in 10% buffered formalin, transferred to 70% ethanol within a few days, and later sorted.

Size-frequency distributions were based on measuring the diameter of each individual, parallel to the anal pore margin of the test, using either an ocular micrometer or vernier caliper. To estimate the ash-free dry weight (AFDW) of different cohort size classes, additional *E. parma* specimens were collected at the above sites and frozen, then sorted into 5-mm size groups covering the 5-50 mm size range, with each group containing 3-10 individuals, as available. Each size group was dried for 12 hours at 60°C and ashed for 4 hours at 500°C to produce a mean AFDW value per mean width (L in mm) and the regression; $AFDW = 0.02L^{2.55}$ ($r^2 = 0.991$). Overlapping cohorts were initially separated by probit graphical analysis (Cassie 1954), and these estimates were refined by the NORMSEP program (Tomlinson 1971) to separate overlapping distributions. Growth rates were estimated by modal progression analysis of the time series of size-frequency histograms (Figs. 2-5) for collections at each station. Production estimates are based on Crisp's (1971) growth-increment survivorship-curve method for populations with distinguishable recruitment and age classes (cohorts). Recruitment events in the Middle Atlantic Bight were assumed to be the result of fall-winter spawning, based on when recruits are first detected in

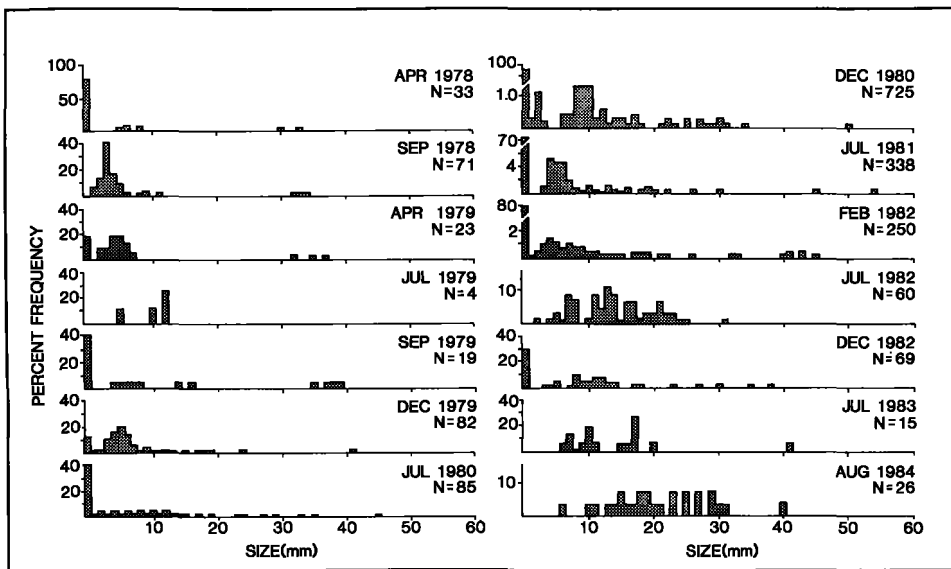


Figure 2
Echinarachnius parma size-frequency histograms per collection at station 11, Middle Atlantic Bight.

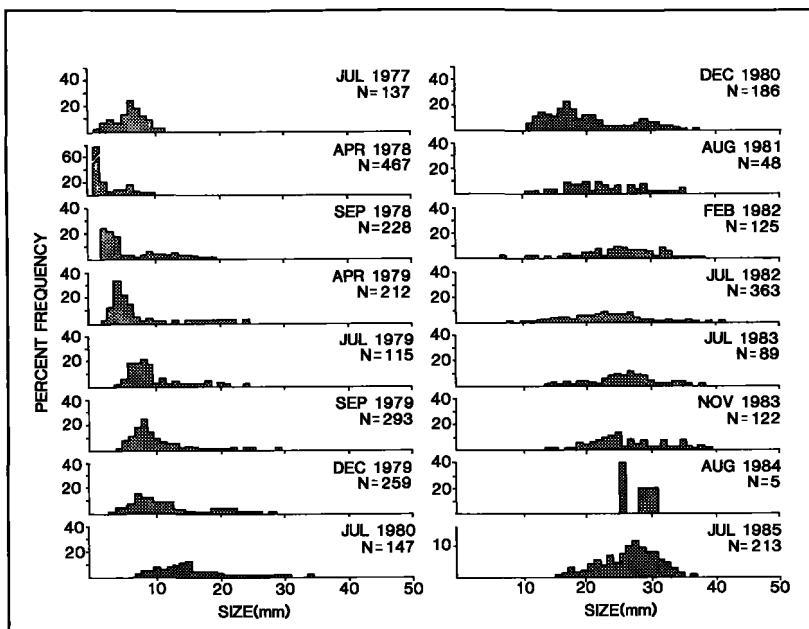


Figure 3
Echinarachnius parma size-frequency histograms per collection at station 17, Middle Atlantic Bight.

the samples (winter-spring) and thus identified by the pair of years covering the probable peak spawning period. The recruitment season was estimated, in some cases, from back-calculations based on growth curves. Ages assigned to each cohort are based on inspecting the length-frequency histograms and noting when recruitment, i.e., >2 mm size mode, was apparent. These can be considered relative ages, although it is highly probable they represent absolute age (± 3 months) if it is assumed that a delayed metamorphosis of the larvae is not normally a major problem; there is no evidence to suggest otherwise.

The reliance on size-frequency analysis for growth and production estimates assumes (1) frequency modes represent cohorts, a reasonable assumption when recruitment period can be determined and modal shifts can be traced over a period of time, and (2) that the size distribution within each cohort was normal or representative of the true population and unbiased. A departure from normality may not be critical to the accuracy of mean size estimates (McNew and Summerfelt 1978). The sample sizes were often below the minimum (400) suggested by Cohen (1966) to separate accurately two cohorts in a single size-frequency analysis, with a larger sample needed for separating more than two

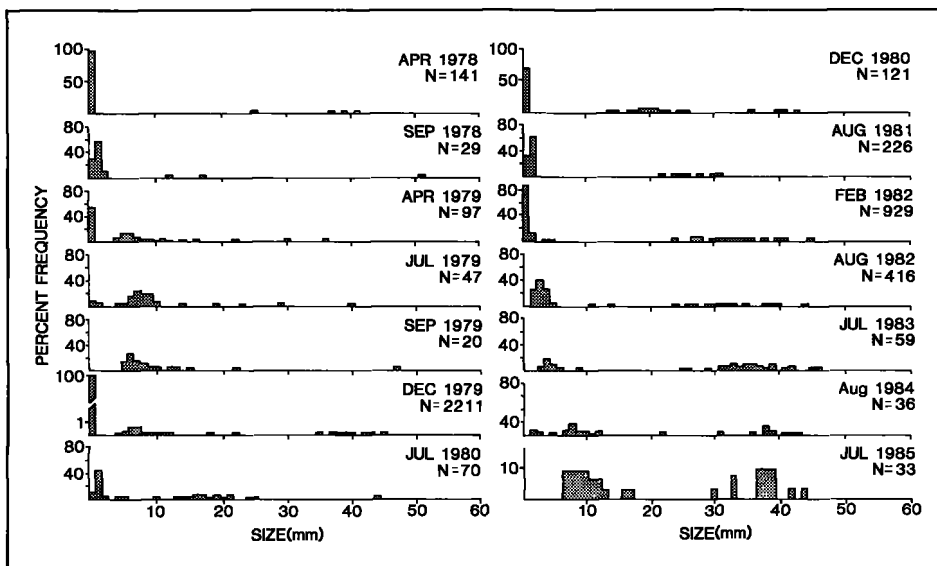


Figure 4
Echinarachnius parma size-frequency histograms per collection at station 15A, Middle Atlantic Bight.

groups. The time series of population size-frequencies available in this study could estimate poorly defined cohorts and modal peaks by visual examination of the overall modal patterns in the time series.

Results

The size-frequency distributions, grouped into 2-mm size classes for all collections at each station, show a high degree of variability in population structure (Figs. 2–5). The distributions for Station 11, off Delaware Bay (Fig. 2), show a population with a variety of size classes evident in all collections; cohort definition is often weak, largely because of small sample sizes for most collections. Size-frequency distributions at Station 17, off Central New Jersey (Fig. 3), in contrast to Station 11, show a very limited population, restricted entirely to two annual recruitments in 1976 and 1978. Both of the two cohorts at Station 17 appear to persist until at least 1985 (the last collection of the study), although they were inseparable after 1981. There is no evidence of any additional recruits, even though the population reached a size, >27 mm, when spawning should occur (Ruddell 1977). The situation at Station 15A, off Fire Island, is similar to that of Station 11, with several sizes present in the population subsequent to initial collections (Fig. 4). There appear to be two recent strong cohorts, that of 1978 and 1982. Some non-persistent recruitment was evident in other years, however. The *E. parma* population structure at station 23, on northeast Georges Bank, was similar to that of Station 17, with no evidence of a population prior to 1978 and with the 1978 and 1979 cohorts the strongest, although non-persistent recruitment was noted for other years sampled.

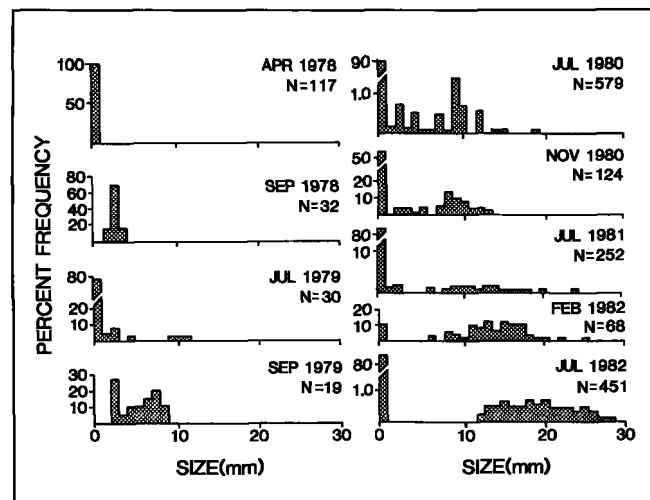
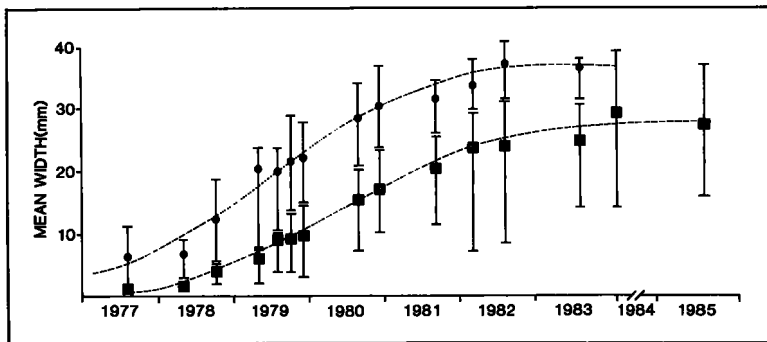


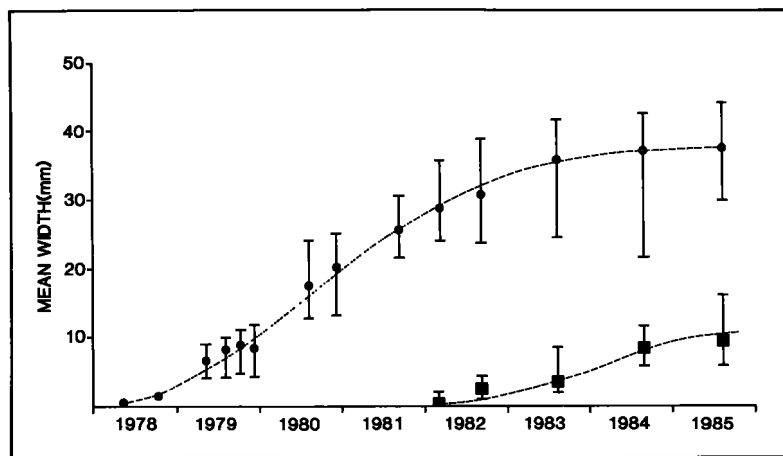
Figure 5
Echinarachnius parma size-frequency histograms per collection at station 23, southwestern Georges Bank.

The estimated growth curves (based on change in cohort's modal size progressions over time) of persistent and prominent cohorts at Stations 15A, 17 and 23, were sigmoidal (Figs. 6–8). The highly variable size-frequency distributions at Station 11 (Fig. 2) did not produce reliable modal trends to use for growth estimates. The mean cohort growth rates, approximated from modal progression analysis for definable cohorts ranged from 4.0 to 6.5 mm per year (Table 1).

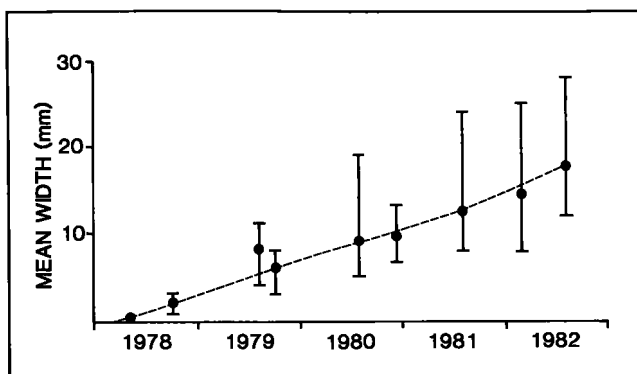
Table 2 summarizes the estimated annual production (P), mean biomass (B), and P:B ratio for each cohort, and the total annual population production and P:B ratio for each station, showing much variability. A comparison of individual-cohort annual P:B ratios with

**Figure 6**

Growth curves from the shift of the mean widths of prominent *Echinarachnius parma* cohorts, over time, at station 17, Middle Atlantic Bight.

**Figure 7**

Growth curves from the shift of the mean widths and ash-free dry-weight values of the prominent 1977-78 *Echinarachnius parma* cohort, over time, at station 15A, Middle Atlantic Bight.

**Figure 8**

Growth curves from the shift of the mean widths of the prominent 1978 *Echinarachnius parma* cohort, over time, at station 23, southwestern Georges Bank.

Table 1

Mean estimates of *Echinarachnius parma* growth rate, based on cohort-size modal shifts at three stations in the Middle Atlantic Bight and southwestern Georges Bank.

Station	Cohort	Approx. mean growth rate (mm/yr)
17	1976-77	6.0
	1977-78	4.5
15A	1977-78	5.5
23	1978	4.0

estimated cohort age (Fig. 9), based on the modal progression analysis or estimated growth rates, for all stations combined produced a skewed normal curve.

Discussion

The population dynamics of *E. parma*, with variable annual recruitment and cohort survival patterns (Figs. 2-5), are in general agreement with population dynamics reported for other echinoderms (Ebert and Dexter 1975, Lane and Lawrence 1980, Ebert 1983, Beukema 1985). Recruitment is evident as peaks in the 0-2 mm size-frequency columns of Figures 2-5. Station 17 (Fig. 3) was the exception, however, to the almost annual or frequent recruitment pattern; detectable recruitment was evident there in only 2 years. This recruitment pattern may be associated with anoxic conditions that defaunated this area during the summer of 1976 (Steimle and Radosh 1979). The definition of the first definable cohort at this station in July 1977 included some animals larger (to 12 mm) than the 6-mm estimated maximum annual growth rate, although the size-frequency mode was about 6 mm for the initial July 1977 collection (Fig. 3). It must be assumed any preanoxia recruitment in 1976 did not survive the event, as few living *E. parma* were found in the area

Table 2

Estimates of annual cohort production and P:B ratios for *Echinarachnius parma* and total annual population production and P:B at all stations in the Middle Atlantic Bight and southwestern Georges Bank. Production (P) values are mg ash-free dry weight (AFDW)/m⁻²·year, and biomass (B) values are mg AFDW. Conversions to energy equivalents are based on a mean conversion of 24 KJ/g AFDW (5.74 Kcal/g AFDW) (from Steimle and Terranova 1985).

Station/ annual period	Cohort 1972-73?			Cohort 1976-77			Cohort 1978-79			Cohort 1979-80			Cohort 1981-82			Total P/m ²			
	P	B	P:B	P	B	P:B	P	B	P:B	P	B	P:B	P	B	P:B	mg AFDW	Kcal	P:B	
Station 11																			
Nov-Oct																			
1977-78	184	1217	0.15	21	71	0.30										205	1.18	0.16	
1978-79	599	2843	0.21	270	208	1.30	180	94	1.91							1049	6.02	0.31	
1979-80	781	717	1.09	1004	810	1.24	952	541	1.75	30	10	3.00				2767	15.88	1.34	
1980-81	211	2288	0.09	102	429	0.24	611	848	0.72	170	185	0.92	9	345	0.03	1103	6.33	0.27	
1981-82				369	697	0.53	974	722	1.35	371	344	1.08	14	9	1.56	1728	9.92	0.98	
1982-83				179	518	0.35							2	1	2.00	181	1.04	0.35	
																\bar{X} = 1172	6.72	0.57	
				Cohort 1976-77			Cohort 1977-78												
Station 17																			
1976-77	802	667	1.19													802	4.60	1.19	
1977-78	1556	1092	1.42	310	101	3.07										1866	10.71	1.56	
1978-79	2967	1420	2.09	1479	1523	0.97										4446	25.52	1.51	
1979-80	3405	4707	0.72	4675	3564	1.31										8080	46.38	0.98	
1980-81	1632	6072	0.27	5305	5534	0.96										6937	39.82	0.60	
1981-82	2801	7054	0.40	2796	27870	0.10										5597	32.13	0.16	
																\bar{X} = 5068	29.09	0.94	
				Cohort 1972-74?			Cohort 1977-78			Cohort 1978-79?			Cohort 1979-80?			Cohort 1980-81			
Station 15A																			
1977-78	-13	1584	-0.01	49	13	3.77										36	0.21	0.02	
1978-79	-65	1936	-0.03	550	556	0.99										485	2.78	0.19	
1979-80	-58	4554	-0.01	2369	965	2.45	86	44	1.95							2397	13.76	0.43	
1980-81				1887	2404	0.78										1887	10.83	0.78	
1981-82	-65	2403	-0.03	1927	5092	0.38				218	27	8.10	239	101	2.37	2319	13.31	0.30	
1982-83	53	1362	0.04	371	14960	0.02							202	25	8.10	626	3.59	0.04	
																\bar{X} = 1292	7.41	0.29	
				Cohort 1976-77			Cohort 1977-78			Cohort 1978-79			Cohort 1979-80			Cohort 1980-81			
Station 23																			
May-April																			
1978-79				27	8	3.39										27	0.15	3.39	
1979-80	70	107	0.65	83	84	0.99										153	0.88	0.80	
1980-81	246	353	0.70	310	377	0.82	30	9	3.33	7	06	1.17				593	3.40	0.80	
1981-82	466	579	0.80	1019	1327	0.77	40	41	0.98	23	3	7.67	2	2	1.00	1550	8.90	0.79	
1982-83	236	1838	0.13	1178	3131	0.38										1414	8.12	0.28	
																\bar{X} = 747	4.29	1.21	

during the fall of 1976. These few were found at sites, nearby, that were on the tops of sand ridges near or in the thermocline, offering less anoxia-stressed conditions (Steimle and Radosh 1979). This suggests there may have been accelerated growth of some recruits

spawned in nearby areas unaffected by anoxia, possibly a response to a rich detrital food supply remaining from the related phytoplankton bloom (Mahoney and Steimle 1979) and an absence of competitors or predators.

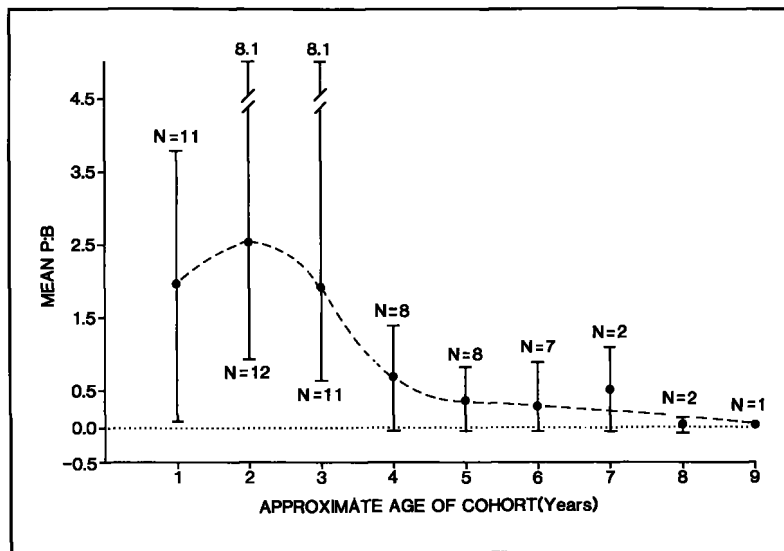


Figure 9

Relationship between production (P) to biomass (B) ratios (mean and ranges) and estimated age for all definable *Echinarachnius parma* cohorts from all stations, Middle Atlantic Bight and Georges Bank.

The period of peak recruitment varied slightly between the Middle Atlantic Bight stations and that of Georges Bank. Recruitment was heaviest or most consistent in the winter to early spring (December–April) at Stations 11 and 15A (Figs. 2, 4) which is consistent with most reports of fall *E. parma* spawning (Fewkes 1886, Cocanour and Allen 1967, Ruddell 1977). Recruitment of the two cohorts found at Station 17 (Fig. 3) occurred prior to when sampling began, but the 1978 cohort was probably recruited in the winter of 1977–78. On Georges Bank (Fig. 5), however, recruitment appeared in all collections except those of September, and most did not persist. Collie's (1987) observation of yellowtail flounder selectively feeding on <12 mm size *E. parma* on Georges Bank is relevant to the poor survival of most new cohorts there.

The life span for persistent cohorts in the Middle Atlantic Bight, estimated from recruitment in 1976 to the end of the study, was at least 7–8 years, e.g., see Figure 3. The presence of a few larger individuals, to 54 mm, suggests a maximum life span of perhaps 15+ years, given the probable very slow growth rates of the larger/older segment of the population. However, maximum widths were generally below 40 mm which suggests that most of the population did not live much more than 8 years. At the Georges Bank station, recruitment prior to the 1978 cohort was not evident, thus reasonable estimates of maximum size, life span, or other population variables were not possible because collections there covered less than 5 years.

The estimated life span of *E. parma* in the study area is most likely less than the estimated 21 years reported by Brykov (1975) for a Pacific population of this disjunctly trans-subboreal species, based on assumed annual growth-ring counts to estimate age. However,

individuals of *E. parma* have been measured that generally exceed 80 mm (maximum reported is 92 mm) in the northern Gulf of Maine (Lohavanijaya 1964, Cocanour 1969), and if one uses a mean growth rate of about 3 mm per year (range 1.5–4 mm/year) as determined from tagged, middle-sized (33–55 mm) individuals measured after 2 years in the Gulf of Maine (Cocanour 1969), then 20+ year life spans could occur in boreal waters. If annual ring counts to size estimates of Cocanour (1969) alone were used, it appears a lesser age would be reasonable because 60–70 mm animals had only 6–7 growth rings. The reduced growth rates of a cohort as it reaches senescence may not produce distinguishable growth rings and juvenile rings may also be weak or obscure, so ring counts could underestimate age. Also, Cocanour (1969) has suggested that mature *E. parma* may alternate years of growth and gametogenesis, at least in the Gulf of Maine; there is no evidence of this alternate-year growth pattern in the growth curves (Figs. 6–8). The maximum width measured in the Middle Atlantic Bight was 54 mm. This apparent difference in maximum size, and possibly life spans, between populations in the temperate Middle Atlantic Bight and the boreal Gulf of Maine suggests a latitude or temperature-related size cline for this species, as predicted for echinoids in general by Ebert (1975). Other factors, e.g., food supply, genetic variability, differences in methodologies, or habitat or predation pressure, could also be involved.

Although the collection periods caused some problems in accurately defining the specific time of peak recruitment, the quarterly-to-semiannual sampling over at least the initial 5-year period of the study was probably sufficient to estimate growth and production. Parsons et al. (1977), for example, suggest the

sampling period for growth and production estimates should be no greater than 10% of the generation time (from egg to sexual maturity) of a species. Ruddell (1977) reports *E. parma* reaches sexual maturity at a width of about 27 mm in the Middle Atlantic Bight. This width suggests an age of approximately 5 years from the growth curve at Stations 17 and 15A (Figs. 7 and 8); thus, semiannual sampling appears to meet this suggested minimum.

The slightly sigmoidal growth curves, for most prominent cohorts (Figs. 6–8), differ from the more parabolic growth curves reported for other sand dollar species (Ebert and Dexter 1975, Lane and Lawrence 1980) and sea urchins (Ebert 1982). However, Sime and Cranmer (1985) and Nichols et al. (1985) report sigmoidal growth curves in North Sea echinoid species. Some of the irregularities in growth curves in the present study may be due to a sigmoidal, intra-annual, seasonal growth cycle that would have highest rates in the early summer and lowest in the early winter (Cocanour 1969). These curves, based on defined cohort means, may be somewhat imprecise because of the small sample sizes; however, the modes are basically congruent with the means and support the general shapes of the curves. The apparent growth curves for Stations 17 (1976/77 cohort, Fig. 6) and 15A (1977/78 cohort, Fig. 7) are almost congruent although the Station 17 (1977/78) cohort has a lower slope, similar to that of the Station 15A (1981/82) cohort or that of the Station 23 (1977/78) cohort curve. The cause of difference in these two sets of slopes is unknown, at present.

The mean annual growth rates (Table 1), estimated by modal progression analysis, ranged from 4.0 to 6.5 mm per year and were greater than the average 1.5–4.0 mm per year rates reported by Cocanour (1969), based on tagged individuals, for an intertidal population along the northern Maine coast. However, the ratios of number of apparent growth rings to diameter were generally higher, ranging from about 7.5 to 15 mm per ring. The rates estimated in the present study are less, however, than the approximate 7 mm per year from Woods Hole, Massachusetts (Durham 1955) or the 7.5 mm per year off northern New Jersey (Graef 1977), both determined by growth ring counts for 45–48 mm specimens. The diameter-to-ring ratio ranged from 4.3 to 11.3 mm per ring for eight smaller specimens in Graef's study and appeared to peak at about 34 mm with three rings evident. The size range examined by these two studies is near the predicted size asymptote, and senescence may be involved with zero or negative growth which would underestimate the age and overestimate overall growth rates. Negative growth (shrinkage), evident as slope declines on the right side of curves found for some older cohorts, agrees with similar findings by Cocanour (1969) for this species and

for other sand dollars (Lane and Lawrence 1980). Senescence is thought by these authors to be the cause of this negative growth in older populations, although Gordon (1929) and Cocanour (1969) report some shrinkage in all age classes during winter months. There is better agreement between the growth-ring count estimates and the size-frequency estimates of growth rate if it can be assumed that the relatively slow juvenile growth, suggested by the sigmoid growth curves and reported by Gordon (1929) and Highsmith and Emler (1986) for a Pacific population, may leave an obscure ring for the first or perhaps even second year of survival, thus lowering the size-age estimates based on ring counts. On Georges Bank, the most persistent or dominant cohort was the 1978 recruitment. The growth patterns (Fig. 8) suggest a mean growth rate of about 4 mm per year for the first 4 years of this cohort, although there was some irregularity in July 1979. This rate is slightly lower than most rates for similar cohorts at other stations.

The overall, estimated annual cohort and population production varied from station-to-station and from year-to-year (Table 2), reflecting the variable dynamics of recruitment, growth, and mortality of each population. It is interesting to note that population production peaked in the November 1979–October 1980 production year at all three Middle Atlantic Bight stations and later, during the May 1981–April 1982 production year for Georges Bank. The *E. parma* population at Station 17 was the most productive for the period examined, and its total production peaked in 1979–80 at 8080 mg AFDW/m² per year. This production level (46 Kcal/m² per year), when converted to energy equivalence (24 KJ or 5.7 Kcal/g AFDW; Steimle and Teranova 1985), is greater than the total benthic community production reported in many North Atlantic continental shelf areas (table 5, Steimle 1985); even the mean value for this station, 29 Kcal/m² per year is comparable to some total community values. The high production at Station 17 is probably related to the 1976 anoxia episode, mentioned previously.

The P:B ratios (Table 2) varied from negative values for older cohorts to a maximum of about 8.1 for some juvenile cohorts at Station 15A. A comparison of mean cohort P:B ratios against approximate cohort age (Fig. 9) for all stations combined shows a skewed normal curve, with mean ratios per age group ranging from a maximum of about 2.4 for 1–2 year-old cohorts to less than 0.5 for cohorts older than 5 years. The declining part of this curve appears to be common in other marine organisms, e.g., Warwick (1980). The low P:B ratios for 0–1 year-old cohorts could suggest a relatively slow growth of young-of-the-year juveniles (Figs. 6–8). The apparently low initial ratios could also be influenced by accurately establishing time of recruitment.

Table 3
Summary of production (P) to biomass (B) ratios for some echinoderms.

Class Species	P:B (range)	Reference
Holothuroidea		
<i>Cucumaria elongata</i>	0.26	Zaika (1972)*
Echinoidea		
<i>Strongylocentrotus droebachiensis</i>	0.80	Miller and Mann (1973)
<i>Echinocardium cordatum</i>	(-0.002-3.7)	Warwick et al. (1978)
<i>Brissopsis lyrifera</i>	0.30	Buchanan and Warwick (1974)
<i>Moira atrops</i>	0.82-1.0	Moore and Lopez (1966)
<i>Echinarachnius parma</i>	(0.02-3.39)	Present study
Stelleroidea		
<i>Astropecten irregularis</i>	0.005	Warwick et al. (1978)
<i>Asterias forbesi</i>	2.64	Richards and Riley (1967)
<i>Asterias rubens</i>	(3.6-7.3)	Zaika (1972)*
<i>Ophiura albida</i>	0.84	Arntz (1971)
<i>Ophiura texturata</i>	0.68	Warwick et al. (1978)
	0.48	Warwick and George (1980)
<i>Amphiura filiformis</i>	1.97	O'Connor et al. (1986)
<i>Amphioplus conioartode</i>	2.26	Moore (1972)
<i>Amphipholus squamata</i>	1.8	George and Warwick (1985)
<i>Ophiothrix fragilis</i>	1.8	George and Warwick (1985)
<i>Ophionephthys limicola</i>	2.33	Moore (1972)
<i>Amphoidia arctica</i>	(0.6-0.8)	Zaika (1972)*

*Ratios calculated from published data.

Mean P:B ratios for *E. parma*, although generally declining with the age of the cohort (Fig. 9), are comparable to the range of P:B ratios determined for other echinoderms (Table 3). Because of the variable relationship of P:B ratios to the (1) specific population age structure (Fig. 9), (2) segment of the life span, or (3) other factors, the significance of this comparison is uncertain. This problem has attracted the attention of other authors who have attempted to improve the utility of interspecific comparisons of P:B ratios by scaling them to either temperature (Parsons et al. 1977), body mass at maturity (Banse and Mosher 1980), or life span (Winberg 1971, Zaika 1972).

The results could be affected by a number of sources of error or variability that commonly affect similar studies and are usually difficult to assess, e.g., sampling error. We did not have samples near the end of the presumed winter-spring peak of larval settlement to obtain accurate estimates of the time and density of larval recruitment. This could affect the growth curves or production estimates. The production of any missed recruits during the few weeks or months before they were sampled would probably be minor because of their small size and high mortality rate. It could influence the cohort P:B-to-age curve (Fig. 9) and partially explain the initial low ratio and rise. Later, semi-annual sampling also made it difficult to determine if

E. parma spawns more than once per year. There are suggestions of substantial recruitment outside of the approximate peak periods (or delayed recruitment) in some of the histograms, especially for the Georges Bank station (Fig. 5).

Another source of error may be systematic, e.g., annual mean production or P:B values do not adequately consider a cyclic annual growth and production patterns. These appear to have maximum values in the warmer months, based on the study of Cocanour (1969), when specific rates would be much higher than the mean annual values.

The final source of error is statistical, especially considering the small sampling sizes available to estimate many of the variables, e.g., the size mode of each cohort. The relatively long time series of data examined, however, allowed a better definition of cohort size modes and growth than is normally possible by attempts to interpret a limited number of collections over a short time and reduced the necessity for alternate aging estimates.

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