Temporal and Spatial Variability in the Relationships Between Adult Size, Maturity and Fecundity in Green Sea Urchins: The Potential Use of a Roe-Yield Standard as a Conservation Tool

Report to the Maine Department of Marine Resources for the project entitled:

Research Necessary to Develop a Management Plan for the Green Sea Urchin, *Strongylocentrotus droebachiensis*, in the Territorial Waters of Maine

Robert L. Vadas
Department of Biological Sciences & School of Marine Sciences
University of Maine
Orono, Maine 04469
207-581-2974
vadas@maine.edu

Brian F. Beal
Division of Sciences
University of Maine at Machias
Machias, Maine 04654
207-255-3313
bbeal@acad.umm.maine.edu

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Summary

1) There is a predictable reproductive cycle and spawning period in green urchins in Maine. The timing varies by about 8 weeks along the coast, earlier in the southwest and later in the central and northeast regions. This supports the concept of zones.

2) There is a reasonably predictable spawning cycle in green urchins in central Maine. The timing or threshold for spawning correlates best with temperature and pigments. These results may be useful for regulating closure to preserve reproductive potential.

3) There are occasional minor spawning events in fall and early winter.

4) In the southwest, urchins from kelp had higher gonad indices than those in barrens.

5) Urchins from kelp habitats appear to spawn earlier than animals from barrens.

6) Roe color varies month to month throughout the reproductive cycle. The percent of grade A roe peaks just prior to spawning.

7) There is a trend of decreasing percent of grade A roe from west to east.

8) Roe texture shows no significant patterns regionally, monthly or by habitat.

9) Intensively (biweekly) sampled sites in central Maine show remarkably similar gonad index patterns and spawning periods (low within region variability). This supports the concept of having different zones.

10) The relationships between gonad index and both pigments (phytoplankton) and temperature provides the first step in developing predictive models for maximizing gonad yields and predicting spawning in Maine. These results may allow predicting when spawning begins in an area. Since the roe of urchins are "melting" in this phase, valid predictive models could provide the rationale for maintaining an area open or closing it.

11) Asymptotic gonad index (the size at which GI is independent of test diameter) for the 3 regions of Maine ranges from 42 mm - 54 mm (southwest - northeast). The pooled average is 45 mm or just below the legal size (50.8 mm). This provides only a slight margin of safety from harvesting urchins before they are capable of achieving their maximum gonadal index. Put another way, this confirms that the 2-inch size limit allows for some fully mature urchins to become part of the potential breeding stock, but there is not a large safety factor in this measure.

12) These data show that gonad index is a linear function of test size to approximately 2 inches (50.8 mm). Future decisions regarding minimum legal size limits must

consider the potential (detrimental) impact of harvesting urchins smaller than asymptotic size on future egg production.

13) We observed new lower limits on the size at which green sea urchins first release viable gametes, 11.5 mm for males and 16.2 for females. Release of gametes from both sexes shows a linear response with test diameter to 40 mm.

14) Based on the linear relationship between gonad index and test diameter, and the linear relationship of percent gamete release with size, the effective size for meaningful contribution to gamete production is between 30 and 40 mm.

15) Tagging urchins with oxytetracycline was successful and over 90% of the urchins examined could be correctly aged.

16) In region 1 urchins in kelp habitats grew faster than those in barrens. Data on growth for the urchins in kelp vs barren habitats were not significant in regions 2 and 3.

17) In the southwest urchins reach harvestable size sooner in kelp (5yr, range 3 - 8 yr) than in barrens (8yr, range 6 - 14yr). There was no difference in urchin growth rate between kelp and barrens in regions 2 and 3 suggesting that the habitats were not pure stands or that drift was available to urchins in the barrens thereby reducing differences. The age to attain commercial size ranged from 5 to 6.5 years in regions 2 and 3.

18) Multiple injections of a 2 M KCL solution were required to fully release gametes.

19) Some urchins are ready developmentally to release gametes (ready for spawning) as early as January, and possibly earlier. Nearly all large urchins from all regions released gametes in January and February, 2 to 3 months prior to spawning.

20) There is an allometric relationship between test diameter and eggs released. This results in small urchins (< 50 mm) contributing substantially fewer eggs to reproduction than urchins above legal harvestable size (50.8 mm). Large urchins (65 - 75 mm) contribute 1 to 2 orders of magnitude more eggs per individual than smaller urchins.

21) Urchins from the southwest showed differences in eggs released between kelp and barren habitat for January, but no other months. No significant differences in egg numbers occurred between habitats in regions 2 or 3 for any month. Some of the highest egg releases (8 to 10 million/ind) occurred in both February and March in the kelp bed in region 1. Urchins in kelp beds in region 2 also released high numbers of eggs (7 to 10 million/female) in March. In region 3 egg production (per ind) peaked in March in both habitats. A general trend in all data was that some animals in all size categories either could not be induced to release gametes, or, released very few. In some cases, these animals may have already spawned prior to sampling.

22) If induced egg release is a valid surrogate for *in situ* release, then urchins may be "hedging their bets" by being able to spawn over a 3 to 5 month period. However, as noted above, most of the spawning is synchronized in March, April or early May.

23) Our data suggests that egg number increases with increasing age (slope is positive), but the predictability is low. Generally, there was no significant relationship between these two variables for any habitat and month, except for urchins from region 1 for the kelp habitat in January).

24) The relationship between number of eggs released and sea urchin body weight generally follows an allometric relationship. This relationship shows that small urchins (< 70 g) contribute fewer eggs (50 - 80 % less) to the reproductive effort than larger urchins. The highest egg releases in all regions occurred in March and with the largest animals.

25) Stepwise multiple regression analysis with gonad index as the dependent variable was used to determine a roe standard for green urchins in Maine. Testing showed that five variables (test diameter, roe color, month of year, roe texture, and test weight) entered the model as significant and collectively explained 28.04 % of the variation. Of those entering the model, test diameter explained the greatest amount of variation, 18.1 %. It makes sense that test size, which controls the volume of an urchin, would correlate most strongly with gonad index.

26) These results show that sea urchins can be aged and that growth parameters can be extracted from the cumulative band widths. Growth curves developed by the aging and measuring techniques and the mixture model are sensitive to relatively subtle differences in growth rates.

27) These techniques allowed us to identify the presence and co-occurrence of two distinct growth (fast and slow) morphs at Allen Island. The two forms were not recognizable when viewing the animals in the field or laboratory.

28) The slower growing form does not live as long as the faster growing forms, and perhaps more importantly, the slow-growing form does not live long enough to attain legal size. Independent growth data from the three regions of Maine show a wide range of variation suggesting that the two morphs may be present elsewhere on the coast. These results may have important implications for sea urchin stocks and the industry.

I. Introduction

A) Objectives and Purposes of Research

The overall goal of this project was to better understand the reproductive ecology of green sea urchins, *Strongylocentrotus droebachiensis*, in Maine. The specific goals of this research are to provide both basic and applied information relevant to the management and sustained use of the sea urchin resource. Initially there were five major objectives outlined in our original proposal. A sixth objective was added in response to DMR's letter and questions regarding the proposed studies. A number of different approaches are utilized to address these objectives and the related questions. Our focus was directed toward providing answers to questions that will be of value to the Department of Marine Resources and the sea urchin industry. Hopefully these data will be useful to the industry and DMR in making decisions regarding the timing of harvesting and several variables including: the spawning cycle, which may influence the length of season; the relationships between size and age and maximum or optimum roe yield or gonad index, which may influence minimum and maximum legal sizes. Similarly, the relationships between size and age vs fecundity (# of eggs produced by different size or age animals) may influence decisions regarding size limits.

Our first main objective was to determine the patterns of reproduction and spawning at commercially harvested sites for four regions of the Maine coast and to correlate patterns of spawning in the field with environmental and oceanographic variables. This information is important for understanding reproductive cycles and some of the variables contributing to these cycles. We concentrated on gonad index, but also examined gonad color and gonad texture. We wanted to know if these variables were different at different times of the year and in the

different regions. We were also interested in how important such differences might be. We also wanted to know what environmental variables correlated with these patterns in the field. By understanding what processes are related to the spawning and reproductive patterns, we can (by monitoring these variables) better predict the spawning event in different waters in Maine. These studies also provide background information on some of the differences corresponding to the two zones established for harvesting. Such differences are likely to be of value if additional zones or subzones are considered for management options in the future.

Our second main objective was to determine the size and age of first reproduction and determine the specific relationship between size and age, and the asymptote for gonad index. This information is important for understanding reproductive maturity and at what time, and minimum size or age urchin roe can be harvested. These studies are also critical for understanding population growth and changes of this species. At what size do green urchins in Maine start spawning and contributing to future generations? How old are green sea urchins in Maine before they start spawning? This leads to two questions: how old are the urchins that the average harvester collects and how long does it take to replace a generation (population) in the field?

Our third main objective was to determine the effect of size and habitat on the percent of urchins producing gametes. This information is important for understanding what proportion various size classes of urchins within the population produce gametes. It provides an estimate of the potential contribution that various size classes make to the gene pool of the next generation. These studies are also important for understanding the effects that habitat (mainly kelp vs. barrens) have on this relationship. At what size do green urchins in Maine start spawning and

contributing to future generations?

Our fourth main objective was to determine the effect of urchin size and age, and habitat on fecundity or the number of eggs produced. This information is vital for understanding the maximum possible contribution of various size female sea urchins to the next generation. Information on egg production is necessary for any consideration of maximum or upper size limits on urchins. Like lobsters, if large females are producing a disproportionately high number of eggs, it may be wise to conserve them as broodstock. On the other hand, if these urchins consist primarily of old animals with little expectation of further life, then it might make more sense to harvest them. In addition, we wanted to know if these relationships differed for when urchins from kelp or barren habitats.

Our fifth main objective was to develop a roe-yield standard based on temporal and spatial patterns of growth (size or age) and gonad index. We constructed a simple regression model to help define the range of options available. This model provides an interim synthesis of the parameters contributing to the reproductive ecology of green sea urchins. The initial model is based on the various environmental data and meristic variables.

Our sixth main objective was to develop a technique and model for rapidly and inexpensively assessing the growth rates of various populations of green sea urchins. This information will be critical in providing a predictive model of long term population growth. This technique will allow decisions to be made about the intensity of harvest and the likely time frame for population regrowth. The technique allows for rapid field and laboratory assessment and could develop into an effective management tool.

B) Background

In a little more than the span of a decade sea urchins became a major fishery in Maine. This development occurred so rapidly that little could be done to establish comprehensive management policies. Also little time and few resources were made available initially for stock assessment. In addition, there was a paucity of biological and ecological data relevant to making management decisions. Despite these shortcomings, resource managers actively used available data and established a minimum size limit on harvestable urchins, a harvest season, and a two-zone system with staggered opening and closing dates. These regulations were enacted to prevent the resource from becoming overexploited and provided a starting point for managing this resource. Despite these efforts the fishery has continued to decline. Thus, the need for biological information on urchins in Maine is apparent, informed management decisions cannot be made without it.

The need for greater understanding of the biology of green sea urchins is related to the phenomenal growth of the fishery itself and the consequences to future urchins stocks. Relatively little biological information exists on green sea urchins in Maine. For example, they have an annual reproductive cycle and spawn in late winter and spring (Cocanour and Allen 1967; Larson et al. 1980; Vadas et al. 1989), but there are reports suggesting that some populations may spawn twice. Data taken in the 1980's at 10 sites along the coast indicate that late summer spawning may have occurred at one or two sites (Vadas et al. 1989). However, our recent studies in southwestern and northeastern Maine indicated that summer spawning is uncommon (Vadas, Beal and Dowling unpublished data). Our earlier data (Vadas et al. 1989) suggested that both temporal and spatial differences exist in the timing of spawning along the coast. Populations in the Casco Bay region spawned 4-6 weeks earlier (March-April) than those in eastern Maine. Whether this is a recurring, interannual pattern remains to be

tested. If it is, it provides the basis for maintaining or extending staggered harvest seasons along the coast.

Little is known about gamete production and gonad maturity. The minimum test diameter size at which green urchins first produce mature gametes varies from 18 - 40 mm (Paul and Paul 1984; Raymond and Scheibling 1987; Munk 1992). Whether eggs are viable from small (18 - 19 mm TD) and young urchins may be problematic. Gonad maturity appears to be less variable than first egg production and ranges from 40-50 mm test diameter (Gonor 1972; Vadas 1977; Larson et al. 1980; Munk 1992). Gonad indices are thought to reflect habitat or feeding conditions (Lang and Mann 1976) but also age (Thompson 1979; Munk 1992). An assumption made by most workers is that the gonad index follows a linear or sigmoidal relationship to ≈ 40 or 50 mm and thereafter is independent of size. Understanding size and gonad relationships are critical for determining minimal and maximal sizes of harvestable animals. Harvesting small or premature (below asymptotic levels) urchins with 10% roe content, for example, may not be conducive to a sustainable fishery. Similarly, it might be prudent to protect large animals, especially if they produce greater numbers of viable gametes than intermediate sized animals.

Several external factors potentially influence or control the temporal and spatial variability associated with maturation, fecundity and spawning. Food and urchin density may affect the amount of gonad produced (Larson et al. 1980), and may determine whether or not spawning will occur (Vadas and Grant 1973; Vadas et al. ms in prep.). Earlier studies on urchins suggested a strong relationship between spawning, and photoperiods and temperature (Giese 1959; Giese et al. 1991). More recently spawning in green urchins was thought to be related to phytoplankton blooms (Himmelman 1978; Starr et al. 1990). Attempts to correlate spawning with algal blooms

in Alaskan waters were inconclusive (Munk 1992). If spawning can be unambiguously related to phytoplankton abundance, then predictive relationships based on phytoplankton surveys can be developed and used to forecast spawning. A predictive relationship for timing of spawning would lead to better conservation of spawners and could translate into increased settlement and recruitment in future years. Thus, understanding temporal patterns and the mechanisms involved in the timing of release may be a valuable tool for managers. It has the potential to allow flexibility in closing particular areas or zones.

Little is known about the relationships between age, and maturity or fecundity. Estimates range from 2 - 4 years for some populations (Raymond and Scheibling 1987; Munk 1992; Mann 1973; Thompson 1979). The relationships between age and maturity may be confounded by spatial variability, including the diets available to urchins in the field (Vadas 1990). Urchins fed preferred seaweeds grew faster and produced more roe than those fed non-preferred algae or mussels (Vadas 1977, 1985; Larson et al. 1980; Briscoe and Sebens 1988). Sea urchins on barren grounds grow slower (Andrew and Choat 1985, Himmelman et al. 1983; Himmelman 1986; Kenner 1992) and contain significantly less roe (Vadas 1977; Lang and Mann 1976; Mann 1982; Keats et al. 1984).

Urchins exhibit considerable morphological plasticity (Ebert 1973; Russell 1987) and it is difficult to know if the smaller sizes reflect young age or the habitat. Urchins can be aged but there is considerable disagreement about the meaning of the bands on the calcareous plates (Jensen 1969; Ebert 1988; Pearse and Pearse 1975), but see Robinson and MacIntyre (1997); Meidel and Scheibling (1998). To understand differences in size frequency relationships, maturity and fecundity in different populations, it is necessary to accurately age animals. Aging also provides clues about

diet history and other life-history aspects that may be chronicled in the bands of an individual or a population: a large animal with few growth bands probably fed in kelp or algal beds whereas similar-sized animals, but with more bands, likely fed on coralline pavements where drift algae occur. The possibility exists that the urchins age and diet may affect the color of the roe as well.

C) Regional Approach

A regional approach was taken to provide answers to questions involving patterns along the coast of Maine. Temporal and spatial patterns can differ over relatively small scales and it is important to be able to document both similarities and differences in reproductive cycles and patterns over the coast. Sites were selected on the basis of depth (7 to 12 meters) and on the presence or absence of macroalgae and kelp. The sites were selected to provide broad coverage along the coast from Casco Bay to the Lubec-Jonesport area. Also, these sites will provide information on some of the differences corresponding to the two zones established for harvesting. Such differences are likely to be of value if additional zones or subzones are considered for management options in the future. Specific sites were selected on the basis of accessibility, active or potential for commercial harvest, and the relative amounts of kelp or barren ground present. These differences will provide information on the potential quality of the habitat to the reproductive biology of the urchins.

We have designated the regions 1 to 3 from southwestern to northeastern Maine. The southwest region (region 1) represents the Casco Bay area; the specific sites include Jewell Island and Green Island (Figure 1). The central region (region 2) represents the Rockland-Port Clyde areas; specific sites include Allen Island, Benner Island, Davis Island and Hupper Island (Figure 2). The northeast region (region 3) represents the area from Schoodic Point to the Lubec-Jonesport (Figure 3). Actually,

we had separated (and sampled) this area as two regions (Schoodic Region, consisting of Frazier Channel and Schoodic Peninsula, and Lubec-Jonesport Region, consisting of Sand Island and Ram Island). However inconsistent sampling due to storms and difficulties in obtaining regular boat use forced us to sample alternative sites or prevented us from sampling. As a result, we pooled the sites from these two areas.

III) Patterns of Reproduction and Spawning

Purpose: To determine if and how reproductive patterns and spawning vary at commercially harvested sites along the coast and to attempt to relate spawning patterns with environmental changes or cues. (Objective 1 from proposal)

Hypothesis: Based on our 1987 study and ongoing (Sea Grant) research, we proposed that gonad index and spawning along the coast of Maine would vary linearly from southwest to Northeast along the coast by 4 to 8 weeks with spawning occurring later in downeast waters. Our statistical nulls tested the model of no difference in gonad index, roe color, and texture between years, months within years, regions and habitats (kelp vs. barrens) and the interaction of these three main effects.

Methods: Systematic sampling for gonad cycle studies began in the spring of 1996 and ended in the spring of 1997 following spawning. All samples were collected by scuba diving. Generally, samples were taken monthly from November through June and bimonthly thereafter at two permanent sites (kelp vs barren) in each of the four (three) regions. In one region, two additional sub-sites (four total) were intensively sampled (biweekly) from January to June 1998 to determine if any one site within a region is representative of that region (a test of within-site variability, and to determine the relationship between gonad index and environmental conditions, see below). Sampling on a regular basis began earlier in regions 1 and 2 than in region 3 because of funding

delays and our inability to quickly locate suitable rental boats and appropriate dive/sampling sites. Twenty urchins approximately 50 mm or greater in test diameter were haphazardly collected by divers and immediately placed in ice chests. Specimens were kept in low temperature coolers (5° C) until dissected and measured, usually within 24 hours of collection. The following measurements or determinations were made on all urchins: test diameter, test weight, gonad weight, sex (when possible), roe color and texture, and gut fullness. Roe color and texture and gut fullness (an indication of recent feeding history) were estimated categorically by ranking. The gut contents of five urchins per collection per date were preserved in neutralized formalin for future diet analysis. Gonad index was calculated as [(gonad wt. ÷ test wt.) X 100]. Differences in gonad indices between sites, habitats (kelp vs barrens) and regions are presented graphically with mean and standard errors.

To determine possible relationships between spawning and environmental conditions, we employed an intensive (biweekly) sampling scheme during the winter and spring of 1998. Our other ongoing studies revealed that the regular "monthly" sampling program was not sensitive enough for clearly identifying patterns and developing predictive relationships between environmental variables and spawning. Sea urchins were sampled as above at Allen, Benner, Davis and Hupper Islands with gonad index being the response variable. The following environmental variables were determined biweekly: extinction coefficient (k', using a Secchi disk), water temperature (with calibrated thermometers), salinity (with a refractometer), nutrients (phosphate, nitrate, nitrite, NH_4, silicate; with an autoanalyzer), and chlorophyll *a* and phaeophytin (with a fluorometer) as a measure of phytoplankton abundance. The relationships between gonad index vs sampling date and environmental variables are presented graphically. Multiple stepwise regression analysis was used to define the statistically strongest (i.e., $P < 0.05$) relationships between these variables and gonad index for

each site.

Results and Discussion: Analysis of variance of mean gonad index for the monthly data collected in the three regions indicated three sources of variability that were significant ($P < 0.05$). None of the main effects (year, region, and habitat) could be assessed by themselves, except the nested main effect of month within year, because of significant interactions (Table 1). This analysis shows that when region and habitat are pooled, mean gonadal indices within year varies monthly ($P = 0.0046$). This indicates the presence of a clear reproductive cycle in Maine. This cycle, however, is influenced by region (Month x Region [Year]; $P = 0.0369$) indicating that the timing of reproduction varies regionally within a given year. Lastly, we detected differences in gonad index between habitats from region-to-region ($P = 0.0061$). Differences in gonad index between kelp and barren ground for 1996 and 1997 occurred only in region 1 (southwest coast) (Figure 4). The same trend for the first three sampling dates in 1997 is shown in Figure 5. At least two hypotheses may explain these data. First, the actual differences between barren and kelp habitats may not have been as dramatic in the central and eastern regions as it was in the southwest region. Second, there may have been more drift algae in the barren grounds in the central and eastern regions which might be expected with increased tidal currents in those vicinities.

Gonad indices for the three regions are shown in Figures 6a-c. There is a clear pattern to the reproductive cycles of urchins in the three regions. Variation within sites was low, which indicates that sample sizes were adequate and properly reflect the pattern at that site. Low variability also suggests there is a high degree of synchrony in gonad index among urchins at all sites. Gonad indices peak earliest in region 1 and latest in region 3. Peak values in region 1 occurred as early as December, but relatively high levels (in kelp areas) were present by September. Because Table 1

indicated that gonadal indices varied by month, region, and habitat, we describe the patterns for each region separately.

In the southwest (region 1; Figure 6a), spawning in 1996 occurred between March and April in the kelp habitat resulting in an 18% loss in gonad index (GI) (ca. 25% to 7%). In 1997, spawning occurred one month earlier in the kelp habitat (February to March) with a 10% reduction in GI (ca. 22% to 12%). There appeared to be a minor spawning event during the fall of 1996 in the kelp habitat only. In 1997, spawning in the barren area coincided with gamete release in the kelp habitat. However, maximum GI achieved in the barrens was only 14%. By March 1997, GI in the barren area was 7%. In general, GI in the kelp habitat was consistently higher than in the barren site in both years (Figure 4). This suggests that food limitation occurs in barren areas.

Spawning was slightly delayed in the midcoast (region 2; Figure 6b) in 1996 and 1997 compared to region 1. Gamete release in 1996 depended on habitat as barren ground urchins appeared to spawn later (March to July) than those in kelp (March to May). We detected a minor, early winter spawning in urchins from both habitats (December 1996 to January 1997). Maximum GI for barren ground urchins (ca. 21%) occurred in February 1997 whereas maximum GI for urchins from the kelp habitat was 22% and occurred two months later in April. Spawning in barren ground urchins occurred from February to April.

In the northeast (region 3; Figure 6c), urchins in kelp beds had spawned by May 1996 as GI was below 10%. Our data are inconclusive with respect to the exact timing of gamete release for urchins in barren habitats in 1996; however, it appears that spawning occurred after April as GI for urchins at that time was about 15%. We

detected a minor spawning event during late fall 1996 (November to December) in both habitats. Peak GI occurred in March for the barren population (ca. 17%) and in April for the kelp population (ca. 20%). In barren ground urchins, spawning had occurred by May 1997 whereas urchins in kelp habitats spawned between April and May 1997. The timing of gamete release is approximately eight weeks later in region 3 than in region 1. This is similar to the patterns observed along the coast for barren ground populations sampled in 1986-1987 (Vadas et al. 1997). At that time, urchins from Jonesport spawned from May to June while those from Owls Head and Boothbay Harbor spawned from April to May (see Appendix 1).

ANOVA was used to examine the mean of the ranked gonad color values. The index contained three classes (A, B, C), corresponding to the commercial grades used in Maine, The individual categories (ranks) for the three classes were as follows: Class A: 1 = yellow, 2 = yellow-orange, 3 = orange, Class B: 4 = light brown, 5 = orange brown, Class C: 6 = rust, 7 = dark brown. The ANOVA model was similar to that used to assess differences in mean gonad index (i.e., Table 1). The ANOVA revealed two significant sources of variability: Month nested within year ($P = 0.044$) and the year x region interaction ($P = 0.0142$; Table 2). The first significant source of variation indicates a difference in roe color from month-to-month within a given year. This means that roe color changes throughout the reproductive cycle. There was no region x month (year) interaction suggesting that the color changes observed between dates occurred along the entire coast. A year x region interaction indicates the relationship between region and roe color varied between years. Mean roe color index varied directly from region 1 to 3 in 1996 as urchin mean roe color became progressively darker from the southwest to the northeast. In 1997, however, urchins in regions 1 and 2 exhibited similar mean color index (3.44) which was lighter than the mean of urchins collected from northeast sites (4.42).

The seasonal pattern for color index for the three regions are presented, for kelp and barren habitats in Figures 7 a-c. The data are given as percent color grade in kelp and barren habitats for each sampling date. The two sources of variability identified in the ANOVA are supported by these figures. The variation in gonad color from month to month within a year are apparent. Further, it appears that percent of grade A color roe peaks in winter just prior to spawning. The percentage of grade A roe then declines in all regions where sampling dates are continuous. The second source of variation, year x region interaction, is less obvious. However, focusing on grade A roe shows a general trend of decreasing percentages of high quality roe in the northeast, but the pattern is not consistent between years. The presence of interactive terms and/or the absence of significant main effects suggests that color may not be related to habitat (diet) or that our qualitative ranking is not consistent between those scoring the index.

The means of the ranked texture data (index ranged from 1 = smooth to 5 = coarse) were evaluated with ANOVA. Again, the model was similar to that used in Table 1. The ANOVA (Table 3) revealed only one significant source of variation: the region x habitat interaction ($P = 0.016$). Urchins in regions 1 and 3 exhibited similar mean gonad textures between barren and kelp habitats. In region 2 urchins in kelp habitats appear to exhibit a smoother texture than conspecifics in barren areas. The seasonal pattern for mean texture ranking for the three regions are presented in Figures 8 a-c. Although there appears to be variation in gonad texture between sampling dates and habitats, these differences were not significant (Table 3). The lack of significance means that either texture is unrelated to diet and the reproductive cycle or that our qualitative ranking is not consistent between those scoring the index.

The patterns and degree of variability in gonad indices among the four intensively studied sites (two kelp and two barren habitats) within the central coast

(region 2) and the relationship between gonad index and various environmental factors during 1998 are given in Figures 9 a-c, 10 a-c, 11 a-c, 12 a-c. ANOVA was used to examine differences in mean GI based on habitat and sampling date. We found no habitat differences ($F = 1.18$, $P = 0.387$, $df = 1,9$) or habitat x date interaction ($F = 1.44$, $P = 0.239$, $df = 9,20$), but a significant sampling date effect ($F = 12.84$, $P < 0.0001$, $df = 9, 20$). This indicates a clear reproductive cycle in this region and low site-to-site and within-region variability. These intensively (biweekly) sampled sites show remarkably similar GI patterns and spawning periods. Although slight differences in GI patterns are evident from February to 1 April, they were not significant ($P < 0.05$).

The results from the multiple regression analysis on spawning show that at Allen and Hupper Island (kelp habitats) pigments (chlorophyll *a* and phaeophytin combined) explained 81% and 76%, respectively, of the variation in gonad index across all dates. At Benner and Davis (barren areas), temperature explained 77% and 46%, respectively, of variation in GI. For each site, we also fit the best 2- and 3-variable models to explain GI across all dates (Table 4). These results are suggestive but not conclusive as no combination of variables was the same across all sites. We also attempted to explain, using multiple regression analysis, variability in GI associated with the specific spawning period at each site (Table 5). At Allen Island, three variables (nitrogen, pigments, and the extinction coefficient) all explained greater than 90% of the variability in GI. At Benner Island, no variable explained 90% of the variability in GI, but nitrogen, the extinction coefficient and pigments explained between 61% - 81%. Both sampling date (Julian date) and seawater temperature explained between 91% and 99% of the variability in GI. Four variables (phosphate, pigments, the extinction coefficient and seawater temperature) explained more than 90% of the GI at Hupper Island.

In general, two variables, pigments and seawater temperature, had strong, predictive, relationships with spawning. Visual inspection of Figures 9b - 12b shows that the onset of spawning at all four sites occurred when chlorophyll *a* levels were rising and approached 1µg/L. Gonad indices declined precipitously as chlorophyll *a* levels rose dramatically (123% to 280%) over a two-week period. Seawater temperatures were also increasing during these spawning events and ranged from 5° - 6° C (Figures 9a - 12a). The relationships between gonad index and both pigments and temperature provides the first step in developing predictive models for maximizing gonad yields and predicting spawning events in Maine. These results are very encouraging and potentially useful to fisheries managers. They may provide a means of predicting when spawning begins in an area. Since the roe of urchins are at or near release or "melting" (as described by divers) in this phase, valid predictive models could provide the rationale for maintaining an area open or closing it. Closing an area to harvesting during spawning has the benefit of conserving the resource and aiding egg production and reproduction. Before implementing or applying these relationships, further testing is encouraged. These predictive relationships need to be verified intra-annually in region 2 and should be tested along other regions of the coast.

IV) Size and Age: First Reproduction, Asymptotic Size and Gonad Index, and Growth Rate to Commercial Size

Purpose: To determine the size and age of first reproduction and determine the specific relationship between size and age, and gonad maturity i.e., whether or not an asymptote for gonad index occurs. (Objective 2 from proposal)

Hypothesis: We recognize two states of gonadal maturation. The first is developmental. That is, the minimum size or age at which viable gametes are produced. Previous studies have shown this size to range from 18 - 40 mm. The

second maturation state is a morphological or volumetric ratio of gonad index to body weight. Earlier studies suggest that gonad index is directly proportional to urchin size in animals up to 40 - 50 mm test diameter (e.g., *S. purpuratus* [Gonor 1972] and *S. droebachiensis* [Vadas 1977; Larson et al. 1980]). Above that range of sizes, the assumption is that gonad index is independent of test diameter. That is, there is some asymptotic size above which gonad index levels off. Several alternative hypotheses regarding size and age were considered including: a linear, monotonic, relationship; a quadratic relationship peaking at an intermediate size or age, and a geometric or exponential relationship, similar to lobsters. No formal hypothesis was proposed for first reproduction, but it was assumed, based on literature, that no substantial roe production occurred in urchins below about 25 mm TD.

Methods: Sea urchins utilized in these analyses were taken from two types of collections, the ones sampled for reproductive cycle studies (see III above) and for gamete release studies (see V and VI, below). This was done to reduce logistics and the number of urchins sacrificed. A limited number urchins were provided by Steneck's group from three sites (these animals were aged but not included in these analyses). Individuals from the studies on reproductive cycles represent the larger size ranges (> 50 mm) at a site, whereas individuals from the gamete release studies contain all size ranges (10 to 100 mm TD). The latter size range enabled us to relate gamete release to size and sex of urchin, and, therefore, an estimate of age/size of first reproduction. Samples were collected from two or more sites in each of the three (four) regions. Determination of gonad indices were made just prior to and during spawning (January to April) to maximize gonad weights (and indices) and to minimize differences due to temporal, spatial or habitat variation (Vadas et al. 1989; 1997). Collections were made during both 1996 and 1997. Gonad indices were determined as described in objective 1 (III, above).

The ages of green sea urchins was determined by a modification of the technique originally employed by Jensen (1969) and Pearse and Pearse (1975). This is a relatively simple, non-toxic technique devised by colleagues at the Norwegian Institute for Nature Research (NINA). Samples of interambulacral plates or whole tests for small individuals, were taken from each animal and preserved in 50% ethyl alcohol. For processing, plates were lightly scrubbed with alcohol and a toothbrush. After scrubbing, plates were placed in an oven at 200° C for 1 hr or subsequently, placed in an oven at 60° C for 4 days. Upon cooling, individual plates were covered with vegetable oil, which enhanced the growth lines. The number and width of growth lines was determined under a dissecting microscope with a calibrated eyepiece. To verify that the growth lines were produced annually, approximately 750 urchins from a barrens at Lamoine were injected with a 1% solution of oxytetracycline (1mg per 10g of body weight) on August 6, 1997 (see also Robinson and MacIntyre 1997). The volume of fluid injected was adjusted according to test diameter (0.1 ml for each 10 mm in diameter).

Tagged animals were divided into three lots of 250 each. Each lot contained randomly selected individuals from a size range of 30 - 70 mm. One lot was placed in small mesh plastic lobster cages filled with brown macro algae that were contained in small mesh nylon bags. The cages were suspended from the pier in 3 meters of water (at low tide) at the Beals Island Shellfish Hatchery (BIRSH) near Jonesport, Maine. These animals were fed macroalgae intermittently in the fall and during the following spring and summer. Another 250 were transferred to a relatively isolated salt pond in Cobscook Bay. Lastly, 250 were returned to the Lamoine collection site. The latter two groups were released in highly localized areas (to facilitate recovery) but were allowed to roam free. The Lamoine site was a barren whereas the salt pond contained a dense cover of macroalgae and contained no resident sea urchins. Urchins were resampled

for tagged individuals at Lamoine and Cobscook Bay in August 1998. Tagged animals in cages at BIRSH were sampled in December of 1997 and August 1998. Plates were prepared as above, except for the heat treatment, which consisted of a short exposure at lower temperature. A subset of urchin plates from the cage experiments were examined for the incorporation of oxytetracycline (which fluoresces under ultraviolet light) and the development of growth ring(s) under an inverted fluorescent microscope with an ocular micrometer.

Regression analysis was used to determine the relationships between test diameter size and gonad index. Sequential regression analysis of gonad index on test diameter, from higher to lower test sizes, was used to determine asymptotic size. This was done by initially regressing all values greater than or equal to 55 mm test diameter and testing for significant fit to a linear model. A significant ($p = 0.05$) value for this relationship indicates a linear fit between GI and test diameter. If this test was not significant, the process was repeated with the addition of data from the next lowest 5 mm size class, and so on, until a significant linear relationship was found. Once the size class yielding a significant linear fit was found, we estimated the asymptotic size to the nearest millimeter by sequential regression within the 5 mm bracket. Regressions were performed for each region separately and as a pooled total.

Results and Discussion: The analyses and data are presented individually for the three regions and as a pooled value for the coast (Tables 6 and 7). Surprisingly, the asymptotic size (the point after which gonad index is independent of test diameter) for gonad index for the three regions is different, but the size for the pooled data, 45 mm (Table 7), was the same as that predicted in our original (proposal) hypothesis. The asymptotic test diameters for the southwest, central and northeast are 42 mm, 43 mm and 54 mm, respectively. This means that the 2-inch (50.8 mm) minimum legal size for

urchins is very close to the asymptotic size (45 mm) for urchins in Maine and provides only a slight margin of safety from harvesting urchins before they are capable of achieving their maximum gonadal index. Put another way, this confirms that the 2-inch size limit allows for some fully mature urchins to become part of the potential breeding stock, but there is not a large safety factor in this management scheme. If the value (54 mm) for the northeast region is essentially correct, then the margin of safety may be lower there than in the central and southwest regions.

The relationship between test diameter and gonad index for the three regions and all regions combined for the period between January and April 1996-1997 are shown as x - y plots in Figures 13a - 16a. As anticipated, and, despite limiting the analysis to four sampling periods in winter-early spring (prior to and during spawning), there was considerable variation in the data. A large percent of the variation was due to the presence of post-spawned animals on each sampling date. Our data on gamete release (below) indicates that some animals began releasing in January, and some began earlier than that. These animals would be spawned-out by February and March. Because this large variation in gonad index would tend to reduce our ability to estimate accurately whether or not an asymptotic size existed, we did not analyze the entire data set shown in Figures 13a - 16a. Instead, we analyzed data from each region based on maximum GI levels during the winter and early spring. For example, for the southwest region, we used gonad index data from the kelp habitat for four sampling dates: March 1996, and December 1996 through February 1997.

Animals equal to or greater than the asymptotic size and exhibiting gonad indices of 8% or less (during these times) were considered spawned-out (Figs 13b - 16b). Spawned-out individuals were plotted but excluded from the sequential regression analyses (Tables 6 and 7) . Despite the variation in these data, there are

clear linear relationships between gonad index and test diameter. These data show convincingly that gonad index is a function of test size to approximately 2 inches. Future decisions regarding minimum legal size limits must consider the potential impact of harvesting smaller urchins on future egg production. Conversely, raising the minimum size by 1/8- to 1/4-inch to about 55 - 58 mm would provide an added margin of safety.

Data presented in Figures 13a - 16a enable us to examine indirectly the question of size at first reproduction. Gonad index is one measure of reproductive potential in the population and, in Maine, a GI of 10% has generally been considered commercially acceptable. Using this criteria and a test diameter of 30 mm (approximate size of first reproduction), it can be seen that animals smaller than this rarely produce more than 10% GI and most produce less than 5% GI. It is apparent from examination of the smaller sized urchins that animals up to a test diameter of 15 - 16 mm, that there is no measurable gonad index. Hence, one would conclude that animals in this size range contribute little, if any, to the reproductive effort of the population.

A direct assessment of size at first reproductive is available from gamete release studies (see V and VI below, for details). Urchins were categorized by size and age, and, in the case of females, numbers of eggs counted (Tables 8 & 9). The smallest female induced to release gametes was 16.2 mm (region 1; Green Island, 4/24/1996) and produced 703 eggs. Female urchins released gametes in all 5 mm size categories from 20 mm to 40 mm (Table 8). Mean number of eggs released followed a power (allometric) function (r^2 = 0.93; Figure 17). Similarly, male urchins released gametes in all size categories (Table 9), with the smallest animal being 11.5 mm test diameter! Sperm counts were not made on male urchins; therefore, the relationship between

gamete number and test diameter was not examined.

Although urchins of both sexes released gametes in all size categories, only 6.3% of those less than 20 mm could be induced to spawn (Table 10). Percent gamete release followed a linear function with increasing size to 40 mm ($r^2 = 0.984$). It is clear that first reproduction begins at or near 15 mm, however, using data from Table 8 it would take 188 female urchins ≤ 20 mm to equal the gamete output of one 37.6 mm female urchin. This factor will be even larger when comparing small urchins to those in the legal or harvestable size categories.

The sea urchins from the cages incorporated the oxytetracycline and produced a narrow band of stained (fluorescent) plate material. All (28) of the urchins tested produced a single large white (under reflected light) band and portions of two colored bands (at the time of incorporation and nearest the suture). Twenty-five of the urchins examined could be clearly identified as producing one growth band or ring in the one year interval (Table 11). The bands on the plates on three of the urchins were not distinct and not scored. Two urchins appeared to be anomolous and warrant further investigation. These results indicate that about 90% of the urchins can be safely aged by counting bands on the plates of green urchins.

We assessed four different growth models (linear, allometric, von Bertalanffy, and Logistic) for size and age relationships for each region and habitat (Table 12). In each case, the unadjusted r^2 values are higher for the von Bertalanffy and Logistic models. Here, we present the von Bertalanffy equations and coefficients (Table 13) and show the data in Figures 18 a,b, 19 a,b and 20 a,b. Each figure shows a dotted line parallel to the x-axis at 50.8 mm which is the minimum harvestable size. In addition, age at minimum legal size (AMLS) is highlighted on the x-axis. Our data for

the southwest region support the patterns observed for differences in gonad indices between kelp and barren habitats (see III above). The slope (growth rates) of age-diameter curves from the two habitats appear vastly different, however, analysis of the log-transformed regression lines indicated that the slopes were equal (growth lines were parallel; $P = 0.07$). Analysis of covariance demonstrated that the intercepts were significantly different ($P = 0.005$) and that urchins in kelp habitats grow faster than those on barren grounds. Using mean age (5.98 ± 0.199 years) as a point of comparison, animals in kelp had a 49.1 mm test diameter versus 40.8 mm for animals in barren sites. Data from Figs 18 a,b show that on average, animals in the southwest reach harvestable size approximately in five years in the kelp habitat (Figure 18b) versus nearly eight years on barren grounds (Figure 18a). The actual range of age at commercial size in the kelp habitat is three to eight years. Although there was one individual from the kelp habitat that apparently attained legal size in two years, this may be an anomalous data point (Figure 18b). Fig 18a indicates that animals in barren habitats may take as little as six years (an individual was recorded as achieving legal size in three years, but this is probably anomalous) and as long as 14 years to reach commercial size. The marked distinction between growth rates in kelp vs. barren habitats observed in the southwest region was not detected elsewhere along the coast (Figures 19 a,b, 20 a,b). ANCOVA was unable to detect habitat differences in growth rate either for urchins from region 2 ($P = 0.302$) or region 1 ($P = 0.148$). This parallels patterns for gonad indices (see III above) seen in the central and northeast regions. The age to attain commercial size ranged from 5 to 6.5 years in these two regions. This lack of difference in urchin growth rate between kelp and barren grounds suggests that the habitats were not pure stands or that drift was available in the barren sites thereby ameliorating potential differences.

V) Effect of Size and Habitat on Percent Producing Gametes

Purpose: To determine the effect of size and habitat on the percent of sea urchins producing gametes. (Objective 3 from proposal)

Hypothesis: Our hypothesis predicts a sigmoidal relationship between urchin size and the percent of individuals producing gametes. We also proposed that spawning rate would be faster for individuals from kelp beds than from barren areas.

Methods: Sea urchins were collected from the two sites in each of the three (four) regions. Samples were stratified by habitat, kelp or macroalgae vs barren ground (coralline algae or other non-algal covered rock or cobble). A rigorous attempt was made to take animals from all size classes represented at a site. Gamete release studies were conducted during both 1996 and 1997. However studies in 1996 were not begun until late spring and were limited in scope. Approximately ten groups of 10 individuals each throughout the range of 10 to 100 mm test diameter were tested monthly from each of the four regions. Collections and runs required 2 consecutive days to complete. Specific runs for two sites in one of the four regions were conducted weekly, despite weather problems. To adjust for perceived spatial differences in the timing of spawning along the coast, sampling was initiated earlier in the southwest (during the earlier part of the month and sampling program) and later in the northeast (end of month). Experiments were run prior to spawning from January to March or April 1997, except for the northeast where releases were also done in May.

The percent of urchins in each size class producing gametes each month was determined as a dependent variable, and was assessed by natural and induced spawning. Urchins were stimulated to spawn by injecting animals with a 2 M KCL solution into the perivisceral cavity (Stephens, 1972). Initially a 0.5M KCl was tested but was marginally effective. Pilot studies indicated that relatively few animals

released large numbers of gametes at this initial concentration. Similarly, one injection was insufficient for full release. A 2M KCL solution was subsequently used and administered in multiple injections 45 to 60 min apart to release gametes. Animals were injected and placed, aboral side down, in a appropriate sized beaker filled with filtered ice-cold seawater. Animals were inspected every 15 min and scored for the presence of male or female gametes. A second and a third injection were given between 45 - 60 min and between 75 - 90 min after the initial injection, respectively. Ages and gonad indices were determined as described above.

Results and Discussion: Preliminary studies revealed that single injections of a 0.5 M solution of KCL failed to release all of the eggs from the gonads. Several pilot runs showed that three injections, approximately 1 hour apart, released over 99 % of the eggs. A representative set of data taken from animals collected from Lubec in May of 1996 shows the general pattern observed in all trials (Table 14; Figure 21). Most (80 - 98%) eggs were released after the first injection. Subsequent releases followed a negative exponential with repeated injections (Figure 21). The figure also shows that this pattern is independent of test size. The meristic data and specific patterns of release exhibited by these animals are given in Table 14. The table also shows the great variability associated with eggs released on any one date. Variation in egg numbers (Table 14) does not appear to be related to urchin size, but rather the late date (May) of the attempted release. Although this site is in the northeast, the date is nearing the end of the spawning period and many of the animals contained few or no eggs, e.g., numbers 7,11,12 and 14 (Table 14).

Data for percent of urchins releasing gametes within specific 5 cm class sizes (test diameter) are plotted by month for each region (Figures 22 a - c). These data generally show that urchins are developmentally capable of releasing gametes as early

as January, probably earlier. They also suggest that large urchins release proportionally earlier in the season, a pattern observed generally in our studies. In contrast a low percentage of the small (< 30 mm) urchins contribute to gamete production during the early part of the season. By the end of the season all size classes are contributing to gamete release. It is important to remember that despite small animals showing a high percentage of release during March-April, there are significantly fewer animals represented by the histograms (most are larger animals over 50 mm). As noted above (Figure 17, Table 10), relatively few (< 50 % of the small, ≤ 30 mm) urchins release gametes. Regions 1 and 3 (Figures 22 a,c) show similar seasonal trends, starting relatively high by January and being fully capable of spawning by March. By far, the most interesting aspect of these releases may be the fact that such a high percentage of the urchins are capable of spawning at least 2 months prior to the normal spawning period (Figures 6 a-c).

VI) Effect of Size, Age, and Habitat on Fecundity

Purpose: To determine the effect of urchin size and age, and habitat on fecundity or the number of eggs produced by female sea urchins. (Objective 4 from proposal)

Hypothesis: Our hypothesis predicts an allometric relationship between urchin size or age and the individual number of eggs produced (gametes). It predicts that larger individuals are proportionately contributing a greater number of eggs to future generations. However, several alternative hypotheses were possible including: a decreasing exponential relationship, a quadratic relationship, possibly indicating reproductive senility (*sensu* Peterson, 1986); and a linear, monotonic relationship. In addition, we suggest that urchins from kelp beds will be more fecund than from barren

areas (Lang and Mann, 1976; Vadas, 1977).

Methods: Determinations of egg numbers were made in 1996 & 1997, and on the same groups of animals utilized for IV and V (as above). Approximately ten groups of 10 individuals each throughout the range of 10 to 100 mm TD were collected from the two sites in each of the four regions. Samples were stratified by habitat type, kelp vs barren ground (coralline cover or other non algal covered rock or cobble). To adjust for the predicted spatial differences along the coast, sampling was staggered; earlier in the southwest, later in the northeast. Analyses were conducted monthly from January to March or April, prior to spawning as noted above. The percent of females producing eggs each month was determined and used as a dependent variable. Egg counts were assessed by inducing spawning with 2 M KCL (as above). Gonad tissue was also preserved for histological analysis (cf Andrew 1986), but there were insufficient funds to complete this component of our work. Urchins were stimulated to spawn (*sensu* Stephens, 1972) as described above (section V).

An estimate of egg numbers released from each female was made by taking three 1 ml samples from a beaker containing the injected urchin and then counting the eggs/sample using a Sedgwick Rafter Cell. Gonads from a subset of these animals were preserved in Bouin's fluid to be embedded in paraffin, and stained with haematoxylin and eosin stains for histological examination (Laegdsgaard et al., 1991). The number of eggs per female was utilized as a dependent variable for regression analysis against age and size. An analysis of covariance was used to determine relationships between size or age and, gonad index and fecundity. Region and habitat were used as co-variables.

Results and Discussion: The relationship between test diameter and egg numbers for

1996 for all regions are plotted in Figure 23. These data are pooled (March - May) and reflect only the latter part of the spawning effort during the first year of study. Several trends are evident in these data. Firstly, there is an apparent allometric relationship between test diameter and eggs released. This results in small urchins (< 50 mm) contributing substantially fewer eggs to the reproductive effort than urchins above legal harvestable size (50.8 mm). Secondly, large urchins (65 - 75 mm) contribute 1 to 2 orders of magnitude more per individual than smaller urchins.

The relationship between number of eggs released and test diameter (1997) generally appeared to follow an allometric relationship and there was a consistent pattern of greater egg release in larger urchins through time (Figures 24 - 26). Urchins from the southwest (region 1) showed differences in eggs released between kelp and barren habitat for January ($P = 0.005$; Figures. 24). No other significant differences in egg numbers occurred between habitats in February and March in region 1, or in any month for regions 2 and 3 ($P > 0.05$). Some of the highest egg releases (8 to 10 million per individual) occurred in both February and March in the kelp bed in region 1. Urchins in kelp beds in region 2 also released high numbers of eggs (7 to 10 million per female) in March (Figure 25). In region 3 (Figure 26), egg production per individual peaked in March in both habitats. A general trend observed for the data from Figures 24 - 26 was that some animals in all size categories either could not be induced to release gametes, or, released very few (i.e., < 10,000 per individual). In some cases, these animals may have already spawned prior to sampling.

Mean number of eggs released during the reproductive season (January to March) in kelp vs barren habitats for the three regions are shown in Figures 27 - 29. For the southwest, there are consistent patterns and differences between kelp vs barren habitats and between the three months shown (Figure 27). The data also show

consistent size-related patterns. Greatest mean number of eggs released came from urchins in kelp habitats and from the larger size classes of urchins. Also there is a trend for increased egg release from January to March as was seen in Figure 24. The fact that urchins in a population can release gametes over a 3- or 4-month period suggests that urchins are "hedging their bets" with regard to environmental cues for spawning. A similar, but delayed, pattern exists for the central region (Figure 28). Note the smaller mean numbers of eggs released in January and February from all size classes and the lack of a distinction between habitats in the numbers of eggs released (Figure 28). The pattern for the northeast shows that eggs are released over a 5-month period (Figure 29), but that peak egg release occurs in March and April (data not shown). Except for a few urchins in the 65 mm size category from the barren ground sites, the data from February and May are strikingly similar reflecting a pre- and post-spawning population. It is notable that in some regions of Maine, the spawning effort can apparently occur over a period of several months.

Our data enable us to examine the relationship between urchin age and numbers of eggs released per individual (Figure 30). We fit both an allometric (r^2 = 0.047, P = 0.075) and linear (r^2 = 0.131, P = 0.002) model to the 1996 data. Although the linear model is statistically significant and suggests that egg number increases with increasing age (slope is positive), its predictive ability is quite low. We also examined the relationship between age and number of eggs released in 1997 for each region and habitat (Figures 31 - 33). Generally, there was no significant relationship (P > 0.05 for both linear and allometric models) between these two variables for any habitat and month (except the kelp habitat in January). We also tested the relationship between gonad index and number of eggs released per female for the 1997 data for each region. We found no significant relationship (P > 0.05) for any region (months pooled) (region 1: n = 121, r^2 = 0.025, P = 0.0815; region 2: n = 84, r^2 = 0.000, P = 0.9683;

region 3: n = 155, r^2 = 0.002, P = 0.5649).

The relationship between sea urchin weight and egg numbers for 1996 for all regions are plotted in Figure 34. These data are pooled (March - May) and reflect only the latter part of the spawning effort during the first year of study. Several trends are evident in these data. Firstly, there is an apparent allometric relationship ($8.776X^{3.76}$, n = 125, r^2 = 0.125, p < 0.0001) between urchin weight and number of eggs released. Secondly, this relationship shows that small urchins (< 70 g) contribute fewer eggs (50 - 80 % less) to the reproductive effort than larger urchins.

The relationship between number of eggs released and sea urchin body weight for 1997 generally appeared to follow an allometric relationship. There was a consistent pattern of greater egg release in larger urchins through time in the three regions (Figures 35 - 37). There was no difference in the slopes (parallel) of the regressions and ANCOVA was used test for habitat differences. Sea urchins from the southwest (region 1) had higher numbers of eggs released from urchins collected from kelp beds than those taken from barren habitats for January (P = 0.0019; Figures. 35). No other significant differences in egg numbers occurred between habitats in February and March in region 1, or in any month for regions 2 and 3 (P > 0.05). Some of the highest egg releases (8 to 12 million per individual) occurred in March from the kelp beds in region 1. The low egg numbers associated with some of the larger urchins in region 3 probably reflect early spawners. Overall, highest egg releases in all regions occurred in March and with the largest animals.

VII) Roe-Yield Standard

Purpose: To develop a roe-yield standard based on temporal and spatial patterns of growth (size or age) and gonad index. (Objective 5 from proposal)

Hypothesis: Our hypothesis is that a global roe-yield standard for Maine is attainable. This is based on the fact that reproductive cycles of populations in different regions, although temporally variable, are similar enough on an annual basis to permit valid statistical comparisons within times, especially seasons. However, our alternative hypothesis is that seasonal and habitat factors are too variable to allow any roe standard to apply universally.

Methods: We are developing a multiple regression model that uses gonad index as the response variable with habitat, month, year, and site that will provide an interim synthesis of the parameters contributing to the reproductive ecology of green sea urchins.

Results and Discussion: As apparent from this report, numerous factors contribute to the production of gonad tissue and the determination of a gonad or roe index for sea urchins. In our studies some of the possible variables included: urchin size, age and weight, region along coast, habitat (kelp vs barren), month, and numbers of eggs released. Multiple regression requires that all variables entered in the model be available in each observation, which reduces the number of data points used from some categories. We conducted a stepwise multiple regression analysis with gonad index as the dependent variable to determine a roe standard for green urchins in Maine. Testing the above group of variables, except eggs, showed that five variables entered the model as significant ($p < 0.05$) and collectively explained 28.04 % of the variation (Table 15). These included test diameter, roe color, month of year, roe texture, and test weight. Of those entering the model and being potentially controlling (diameter, month, weight), test diameter explained the greatest amount of variation, 18.1 %. It makes sense that test size, which controls the volume of an urchin, would correlate most strongly with gonad index.

VIII) Model for Rapid Assessment of Growth Rates of Populations

Purpose: To develop a technique and model to rapidly and inexpensively assess the growth rates of various populations of green sea urchins. (Objective 6 outlined in letter dated 2/23/96 in response to DMR letter of 1/26/96)

Hypothesis: We have observed a relatively consistent pattern in the rings (age) structure of these urchins and propose that a predictable relationship may exist between the ring structure and the body size and age of animals. All of the populations examined critically for age structure show a consistent sequential narrowing between bands with increasing age, similar to the patterns described in classical growth curves, e.g., von Bertalanffy. Furthermore this relationship may be population-specific and provide insight on growth rates in different habitats and regions of Maine.

Methods: The first step consisted of preparing the sea urchins for aging and then determining the ages and the distances (using a micrometer on a dissecting microscope) between the various growth (age) rings or bands on the interambulacral plates. The second step was an attempt to correlate test diameter and distances between rings for different habitats and populations. In the third step, we assessed growth rates in different habitats from populations near Allen Island (region 2) and the Schoodic Peninsula (region 3). These relationships were investigated during 1997 (January, March) and 1998 (March, May).

Size, age and size distribution data were collected from samples from an area of approximately 225 m^2 using 0.25 m^2 quadrats placed at randomly pre-marked positions along fixed transect lines. Transect lines were placed approximately 5 m apart and aligned perpendicularly to the shore. Five quadrat samples were carefully taken along each of six (at Allen Island) or eight (at Schoodic peninsula) 10 m long transect lines in

both years. Firstly, larger sea urchins were gently removed from substrates. Secondly, quadrats were scanned for small (<10.0 mm) urchins. Thirdly, unconsolidated material was carefully removed and the area carefully searched for small urchins. Urchins were placed in 5 L mesh (1 mm) bags with string closures, and then placed in larger bags, returned to the surface, and placed in coolers.

In the laboratory, urchins were measured and prepared for aging as noted above (see section IV). A calibrated dissecting microscope with an ocular micrometer was used to count bands and measure linear distances between successive (growth) bands. For the growth analyses, we summed the interband distances. Here we use the term "Cumulative Interband Distance" (CID) to describe the cumulative growth in size of the inter-ambulacral rings. Our Initial analyses of size and age data from Allen Island revealed a wide range of variation that could not be described by a single trajectory of growth and growth variance. Subsequently, all data were subjected to a mixture model to partition the data into what visually appeared to be two separate growth morphs. A mixture model is a likelihood-based model used to statistically identify subsets of a distribution of values (e.g., sizes, ages) that can be characterized as more similar to each other than to values outside those subsets. The original growth model on which the mixture model is based was constructed by Smith and McFarlane (1990) to describe the size-at-age of lingcod. Their model assumed that size-at-age could be described by von Bertalanffy growth.

Results and Discussion: The mixture model estimated growth parameters for the two presumed growth forms based on the size (test diameter) -at-age for an urchin when it was collected (Vadas, Smith, Beal and Dowling ms in Prep.). More comprehensive estimates of growth parameters were obtained using the method of Smith et al. (1998)

and the growth increments in the CID measurements, since several growth increments from different years could be obtained from a single urchin. Model parameters for both the slow-growing and fast-growing urchins at Allen Island in 1997 and 1998, and the single growth form at Schoodic, yielded different estimates, based on their standard errors. Non-zero values of the parameter *b* for the fast-growing morph at Allen Island in 1997 and 1998 are responsible for the curvature in the growth increment plots (Figures 38a & 39a) and the slight inflection in the size-at-age plots (Figures 38d & 39c).

These figures show a number of interesting features about the populations at Allen Island and Schoodic Peninsula. First of all, there are different slopes to Figures a-c indicating that growth is faster in younger animals regardless of habitat. Secondly, Figures d-f show two striking features, higher growth rate in one of two populations at Allen Is. and at Schoodic. Thirdly, the co-occurrence of two growth forms in a population. Fourthly, that the slower growing form does not live as long as the faster growing forms, and perhaps more importantly, that the slow-growing form does not live long enough to attain legal size. This is clearly evident in the data from both years. Also, some of the growth data from the three regions (Figures 18-20) show a wide range of variation suggesting that the two morphs may be present elsewhere in Maine. Lastly, despite making the same sampling effort, there were fewer slow-growing forms in 1998. These results may have important implications for sea urchin stocks and the industry.

Expression of growth rates as a function of test diameter requires that the growth parameters be determined using the cumulative interband distance (CID) of the inter-ambulacral plates, and be converted to their test diameter equivalents. This requires

knowledge of the predictive relationship between band width and test diameter. Analysis of covariance was unable to reject the hypothesis of no difference in this relationship among sites and morphs ($p = 0.05$). Therefore, using data for both growth forms and both sites, a ln-linear relationship was determined with simple linear regression (Figure 40). The relationship is linear and clearly predictive. These data also show that the two forms are different as the forms sort out along different portions of the axis (relationship).

Using these techniques, we identified the presence of two distinct growth morphs at Allen Island. The two forms were not recognizable when viewing the animals in the field or laboratory. Visual scrutiny of the size-at-age data (Figure 41a) suggested the existence of at least two forms. The mixture model was used to search for two or more morphs, but only one fast- and one slow-growing form were statistically identified (Figure 41b). The model assigned each urchin to one of the two morphs. A likelihood ratio test judged that it was e^{53} times more likely that there were two, rather than just one, growth morphs at Allen Island in 1997. Similar results were obtained for Allen Island in 1998 (Figure 42). An attempt was also made to detect multiple morphs at Schoodic Peninsula, but the model confirmed the existence of only a single fast-growing morph there.

These results show that sea urchins can be aged and that growth parameters can be extracted from the cumulative band widths. Growth curves developed by the aging and measuring techniques are sensitive to relatively subtle (non-detectable at the whole organism level) differences in growth rates. This led to the identification of two growth morphs (fast-and slow-growing forms) on the coast of Maine. One of these, the slow-growing morph, does not appear to reach legal size. This raises some interesting and difficult questions for the industry. How important is this form in nature and what is its origin? Our growth data (Figures 18-20) suggest that it is present in

populations other than Allen Island. If it is confirmed to be present in reasonable numbers along the coast, it will be important to know if it has an environmental, genetic or some other basis. In particular, if it is genetic, it would mean that harvesting could be selecting against faster-growing forms, thereby leaving more of the slow-growing forms as breeding stock.

IX) Conclusions: Implications for Management

Our focus was directed toward providing answers to questions that were of direct and indirect value to the DMR and the sea urchin industry. The indirect information is part of the basic biology of a species that we need to understand before wise management decisions can be made. We think these data will be useful in making decisions regarding the timing of harvesting and several variables including: the spawning threshold, which may influence the length of season; the relationships between size and age and maximum or optimum roe yield or gonad index, which could influence minimum and maximum legal sizes. Similarly, the relationships between size and age vs fecundity (# of eggs produced by different size or age animals) could influence decisions regarding size limits. The presence of two types of urchins (fast- and slow-growing) on the Maine coast has some potentially serious implications for managers and the industry. If they are common and if the basis is genetic, continued harvesting could select for the slow-growing form because it does not appear to reach legal size. Our data on egg release and urchin size augers for a possible upper size limit on urchin in Maine. All of our egg release data showed the same response, substantially (order of magnitude) greater numbers of eggs released with increased body size (test diameter or weight).

The relationships between gonad index and both pigments and temperature provide the first step in developing predictive models for maximizing gonad yields and

predicting spawning events in Maine. Because the roe of urchins are at or near release or "melting" in this phase, valid predictive models could provide the rationale for maintaining an area open or closing it. Closing an area to harvesting during spawning has the benefit of conserving the resource and aiding egg production and reproduction. Before implementing or applying these relationships, further testing is encouraged. These predictive relationships need to be verified intra-annually in region 2 and should be tested along other regions of the coast.

Acknowledgments

We owe a large dept of gratitude to many individuals for helping us with many operations, logistics and tasks. First, we especially acknowledge Tim Dowling for coordinating all of the dive work, boat operations, and much of the lab studies. We also thank Corey Roberts and the "Island Institute" for providing a boat and assisting with urchin collections and intensive sampling in the Port Clyde region. We thank Torrey Sheafe and Lindsay Seward for coordinating the intensive sampling in region 2. We appreciate the assistance of the divers (Mark Grant, Torrey Sheafe, Mike Wall, Corey Roberts, Mary Robinson, and Joe Mariano) for their willingness to dive year-round. We also thank Steve Nickl, Jill Fegley, Jim Killarney, Mark Grant, Torrey Sheafe, Lindsay Seward, and Wes Wright for assistance with aging, injecting and dissecting urchins, counting eggs, entering data, and other laboratory studies. We also thank Mike Doan, Karen Mahar, Jeff Rodzen, and Sheri Emerson for assistance with pilot studies in 1996. We gratefully acknowledge Dave Townsend and Maura Thomas for analyzing the nutrient and chlorophyll samples. We thank Jill Fegley for running preliminary analyses and graphing. We owe special appreciation to Wes Wright and Lindsay Seward for round-the-clock preparation of final graphs and tables. We also owe special thanks to Barry Smith for conducting the mixture analyses and the

model work. We acknowledge funding support from the Maine Dept. of Marine Resources, The University of Maine Sea Grant program and the Maine Agricultural and Forestry Experiment Station.

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Table 1. Analysis of variance of mean gonad index as a function of month, year, habitat and region. Month is nested within year.

Source	df	SS	MS	F value	P
Year	1	5.90936	5.90936	1.20	0.2991
Month (Year)	12	342.04841	28.50403	5.79	0.0046
*Region	2	22.93517	11.46758	2.55	0.2816
Year x Region	2	8.98891	4.49446	0.91	0.4326
Month x Region (Year)	12	189.93092	15.82758	3.21	0.0369
*Habitat	1	29.98575	29.98575	7.85	0.2182
Year x Habitat	1	3.81846	3.81846	0.78	0.3993
Region x Habitat	2	87.28883	43.64442	8.86	0.0061
Month x Habitat (Year)	10	48.38108	4.83811	0.98	0.5112
Error	10	49.26940	4.92690		

*division using appropriate error term

see next page. M.H.

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Table 2. Analysis of variance of mean gonad color as a function of month, year, habitat and region. Month is nested within year.

Source	df	SS	MS	F value	P
Year	1	0.942755	0.942755	3.38	0.0958
Month (Year)	12	10.168253	0.847354	3.04	0.0439
*Region	2	3.2696469	1.634823	0.87	0.5335
Year x Region	2	3.739367	1.869683	6.70	0.0142
Month x Region (Year)	12	8.680631	0.723386	2.59	0.0704
*Habitat	1	0.0357344	0.035734	0.33	0.6690
Year x Habitat	1	0.109018	0.109018	0.39	0.5458
Region x Habitat	2	0.963851	0.481926	1.73	0.2267
Month x Habitat (Year)	10	1.118709	0.111871	0.40	0.9171
Error	10	2.788770	0.278877		

*division using appropriate error term

Table 3. Analysis of variance of mean gonad texture as a function of month, year, habitat and region. Month is nested within year.

Source	df	SS	MS	F value	P
Year	1	0.0078323	0.0078323	0.11	0.7489
Month (Year)	12	1.4037520	0.1169793	1.62	0.2272
*Region	2	0.2714002	0.1357001	1.44	0.4104
Year x Region	2	0.1888994	0.0944497	1.31	0.3135
Month x Region (Year)	12	0.7716576	0.0643048	0.89	0.5828
*Habitat	1	0.0013498	0.0013498	0.02	0.9163
Year x Habitat	1	0.0771207	0.0771207	1.07	0.3262
Region x Habitat	2	0.9298225	0.4649113	6.43	0.0160
Month x Habitat (Year)	10	1.1568037	0.115604	1.60	0.2356
Error	10	0.7234456	0.0723446		

*division using appropriate error term

Table 4. Regression analysis of best single, double, and triple-variable models for gonad indices by site (based on data for all dates).[1]

Site	Variable(s)	R^2
Model 1		
Allen Island	Pigments[2]	0.808
Benner Island	Temperature	0.769
Davis Island	Temperature	0.458
Hupper Island	Pigments	0.757
Model 2		
Allen Island	Pigments and Nitrogen[3]	0.853
Benner Island	Extinction coefficient and Temperature	0.845
Davis Island	Date[4] and Silica	0.721
Hupper Island	Date and Nitrogen	0.884
Model 3		
Allen Island	Salinity, Nitrogen and Phosphorous	0.879
Benner Island	Temperature, Nitrogen, and Phosphorous	0.889
Davis Island	Date, Silica, and Phosphorous	0.845
Hupper Island	Temperature, Nitrogen, and Phosphorous	0.923

[1]The following variables were available for entry into the model: Pigments, date, temperature, salinity, nitrogen, phosphorous, silica, and extinction coefficient.
[2]Chlorophyll *a* and phaeophytin
[3]Nitrate and nitrite
[4]Julian day

Table 5. Regression analysis for predicting spawning in *Strongylocentrotus droebachiensis* (based on three or four sampling dates, pre- and during spawning).

Site	Variable[1]	$R^{2\dagger}$
Allen Island[2]	Nitrogen[3]	0.998
	Pigments[4]	0.973
	Extinction coefficient	0.951
Benner Island[2, 5]	Nitrogen	0.812
	Extinction coefficient	0.720
	Pigments	0.612
Davis Island[6]	Date	0.997
	Temperature	0.912
Hupper Island[2]	Phosphorous	0.999
	Pigments	0.982
	Extinction coefficient	0.913
	Temperature	0.911

[1]The following variables were available for entry into the analysis: Pigments, date, temperature, salinity, nitrogen, phosphorous, silica, and extinction coefficient.
[2]Calculated using 3 sampling dates.
[3]Nitrate and nitrite
[4]Chlorophyll *a* and phaeophytin
[5]No R^2 values > 0.812
[6]Calculated using 4 sampling dates.
[†]Only R^2 values greater than 0.90 are shown, except for Benner Island

Table 6. Sequential regression analysis of gonad index on test diameter for three regions in Maine to determine asymptotic size and gonad maturity.

Southwest (Region 1)

Test Diameter (mm)	Number of Individuals	Probability	R^2
> 60	42	0.2183	0.0376
> 55	58	0.8274	0.0009
> 50	69	0.2315	0.0213
> 45	84	0.2608	0.0154
> 40	95	0.0126	0.0651

Asymptotic size = 42 mm

Central (Region 2)

Test Diameter (mm)	Number of Individuals	Probability	R^2
> 60	35	0.9175	0.0004
> 55	59	0.3992	0.0125
> 50	73	0.2575	0.0180
> 45	81	0.0814	0.0380
> 40	85	0.0115	0.0745

Asymptotic size = 43 mm

Northeast (Region 3)

Test Diameter (mm)	Number of Individuals	Probability	R^2
> 60	72	0.3992	0.0102
> 55	87	0.1935	0.0198
> 50	101	0.0128	0.0118

Asymptotic size = 54 mm

Table 7. Seqential regression analysis of gonad index on test diameter for three regions pooled in Maine to determine asymptotic size and gonad maturity.

Test Diameter	Number of Sea Urchins	Probability	R^2
> 60	149	0.9340	0.0001
> 55	204	0.8674	0.0001
> 50	244	0.2131	0.0064
> 45	279	0.0957	0.0010
> 40	297	0.0060	0.0253

Asymptotic size = 45 mm

Table 8. Reproductive statistics on female urchins (≤ 40 mm test diameter) from along the Maine coast (1996 - 1997).[1]

Size Class (mm)	n	Mean Age (yrs)	± 1 SE	n	Mean Number of Eggs	± 1 SE
≤ 20.0[2]	1	4.00	.	1	703	.
20.1 - 25.0	4	3.25	0.85	9	40,240	23,167
25.1 - 30.0	8	4.50	0.27	27	35,495	8,299
30.1 - 35.0	16	4.63	0.39	36	66,026	15,667
35.1 - 40.0	21	5.29	0.34	59	132,114	19,756

[1]Based on 2M KCl injections in the peristome.
[2]Smallest female urchin observed to spawn was 16.2 mm sampled from Green Island (region 1) on 24 April 1996 from a kelp habitat.

Table 9. Reproductive statistics on male urchins (≤ 40 mm test diameter) from along the Maine coast (1996 - 1997).[1]

Size Class[2] (mm)	n	Mean Age (yrs)	± 1 SE
≤ 20.0[3]	1	2.00	.
20.1 - 25.0	6	3.50	0.34
25.1 - 30.0	7	4.00	0.69
30.1 - 35.0	11	5.63	0.47
35.1 - 40.0	21	5.14	0.49

[1]Based on 2M KCl injections in the peristome.
[2]All males reported in this table released viable gametes.
[3]Smallest male urchin observed to spawn was 11.5 mm sampled from Allen Island(region 2) on 11 April 1997 from a kelp habitat.

Table 10. Percent gamete release by size class for urchins ≤ 40.0 mm along the Maine coast (1996-1997).

Size Class (mm)	Number Injected	Number of females releasing gametes	Number of males releasing gametes	Total percent releasing gametes
≤ 20	142	4	5	6.34
20.1 – 25.0	143	12	20	22.38
25.1 – 30.0	145	40	33	50.34
30.1 – 35.0	136	58	42	73.53
35.1 – 40.0	164	84	64	90.24

Table 11. Relationship between oxytetracycline marker and internal bands of *Strongylocentrotus droebachiensis*. (Samples injected with 1 mg/10g body weight on 8/06/97 and collected 8/11/98).

Urchin	Test Diameter (mm)	Mean distance between tetracycline marker and suture (± SE) (n=3)	Number of internal bands between tetracycline marker and suture[1]
1	33.4	0.31 (0.06)	1
2	35.8	0.48 (0.07)	1
3	37.2	0.65 (0.09)	1
4	37.4	0.25 (0.00)	*
5	37.8	0.31 (0.06)	**
6	38.5	0.66 (0.06)	1
7	44.1	0.63 (0.06)	1
8	44.1	0.53 (0.06)	1
9	46.7	0.84 (0.06)	1
10	48.7	0.33 (0.07)	1
11	48.7	0.19 (0.00)	1
12	50.2	0.56 (0.12)	1
13	50.4	0.38 (0.00)	1
14	50.8	0.29 (0.03)	1
15	51.5	0.19 (0.06)	1
16	51.6	0.66 (0.06)	1
17	51.7	0.33 (0.09)	*
18	51.7	0.33 (0.03)	1
19	52.0	0.47 (0.06)	*
20	52.5	0.56 (0.06)	1
21	53.9	0.51 (0.03)	1
22	54.4	0.39 (0.17)	**
23	56.7	0.24 (0.07)	1
24	57.0	0.26 (0.03)	1
25	57.1	0.35 (0.07)	1
26	57.6	0.66 (0.06)	1
27	59.5	0.22 (0.06)	1
28	65.3	0.27 (0.09)	1

[1]One "band" consists of a colored region and a white region.
*Internal bands not readable.
**Irregular band structure

Table 12. Coefficient of Determination for four models (linear, logarithmic, von Bertalanffy, and logistic) for the size-age relationship of *Strongylocentrotus droebachiensis* along the Maine coast.

Region	Habitat	N	r^2_{linear}	$r^2_{logarithmic}$	$r^2_{von\ Bertalanffy}$	$r^2_{logistic}$
Southwest	B	55	0.157	0.169	0.175	0.179
Southwest	K	154	0.349	0.360	0.365	0.363
Central	B	67	0.544	0.545	0.605	0.606
Central	K	76	0.493	0.587	0.613	0.611
Northeast	B	154	0.352	0.385	0.389	0.391
Northeast	K	188	0.477	0.478	0.506	0.503

Table 13. Von Bertalanffy growth coefficients for *Strongylocentrotus droebachiensis* in barren (B) and kelp (K) habitats along the Maine coast.

Region	Habitat	N	L_∞ (±SE)	K (±SE)	t_o (±SE)
Southwest	B	56	63.13 (15.25)	0.1404 (0.1698)	-3.438 (6.824)
Southwest	K	155	88.50 (19.84)	0.1263 (0.0686)	-1.643 (1.262)
Central	B	68	67.01 (5.613)	0.2315 (0.0820)	0.5412 (0.839)
Central	K	77	63.42 (4.091)	0.3268 (0.0809)	1.7200 (0.372)
Northeast	B	155	80.12 (7.937)	0.1776 (0.0705)	-0.4957 (1.321)
Northeast	K	189	95.19 (12.21)	0.1181 (0.0399)	-0.6638 (0.958)

ave = 76.23 .1868 -0.6632

Table 14. Eggs released from *Strongylocentrotus droebachiensis* after four injections with 2M KCl. Samples taken from Region 3, Lubec, Maine, on May 8, 1996.

Urchin	Age (yrs)	Diameter (mm)	Weight (g)	Gonad Weight (g)	Eggs Released per Injection					
					1		2		3	
					#	%	#	%	#	%
1	5	44.8	39.92	1.83	576990	97.07	9990	1.68	7440	1.25
2	4	51.6	68.65	3.85	26776	51.44	21653	41.60	3626	6.97
3	5	52.3	63.04	7.92	1242150	89.96	121840	8.82	16858	1.22
4	7	59.0	81.26	5.76	3332160	91.72	285665	7.86	14985	0.41
5	7	59.7	91.38	9.77	3169530	97.82	60188	1.86	10350	0.32
6	6	60.0	103.59	5.55	168480	99.30	1192	0.70	0	0
7	13	60.5	93.31	5.69	13440	98.42	1	0.01	215	1.57
8	8	60.7	105.57	4.19	31850	88.57	3960	11.01	152	0.42
9	.	62.1	85.98	5.23	13200	93.06	840	5.92	144	1.02
10	.	62.4	91.80	6.05	949960	93.67	57902	5.71	6347	0.63
11	.	62.5	101.59	.	20720	98.22	375	1.78	0	0
12	9	64.4	90.75	4.28	84630	99.62	327	0.38	0	0
13	6	64.4	108.55	16.62	2600260	92.26	165013	5.85	53190	1.89
14	11	65.0	112.34	6.45	12460	97.15	92	0.72	273	2.13
15	.	66.5	145.26	17.27	54600	92.62	4030	6.84	320	0.54
16	11	66.9	132.11	37.02	2809720	75.12	680350	18.19	250061	6.69
17	7	70.5	137.09	30.86	331320	92.54	23408	6.54	3313	0.93
18	9	71.3	141.73	24.12	1801140	94.89	78780	4.15	18275	0.96

* No eggs were released from the fourth injection

Table 15. Multiple regression analysis of gonad index as a dependent variable to determine a roe-yield standard[1].

Variable	Prob > F	Parameter Estimate	± SE	Partial R^2	Model R^2
Diameter	0.0001	0.3940	0.4864	0.1870	0.1870
Color	0.0001	-0.9011	0.1131	0.0542	0.2412
Month	0.0001	-0.7612	0.1384	0.0222	0.2634
Texture	0.0001	1.0302	0.2694	0.0100	0.2734
Weight	0.0037	-0.0401	0.0138	0.0070	0.2804

[1]Ranking based on R^2

Figure 1. Urchin sampling sites along the southwestern coast of Maine.

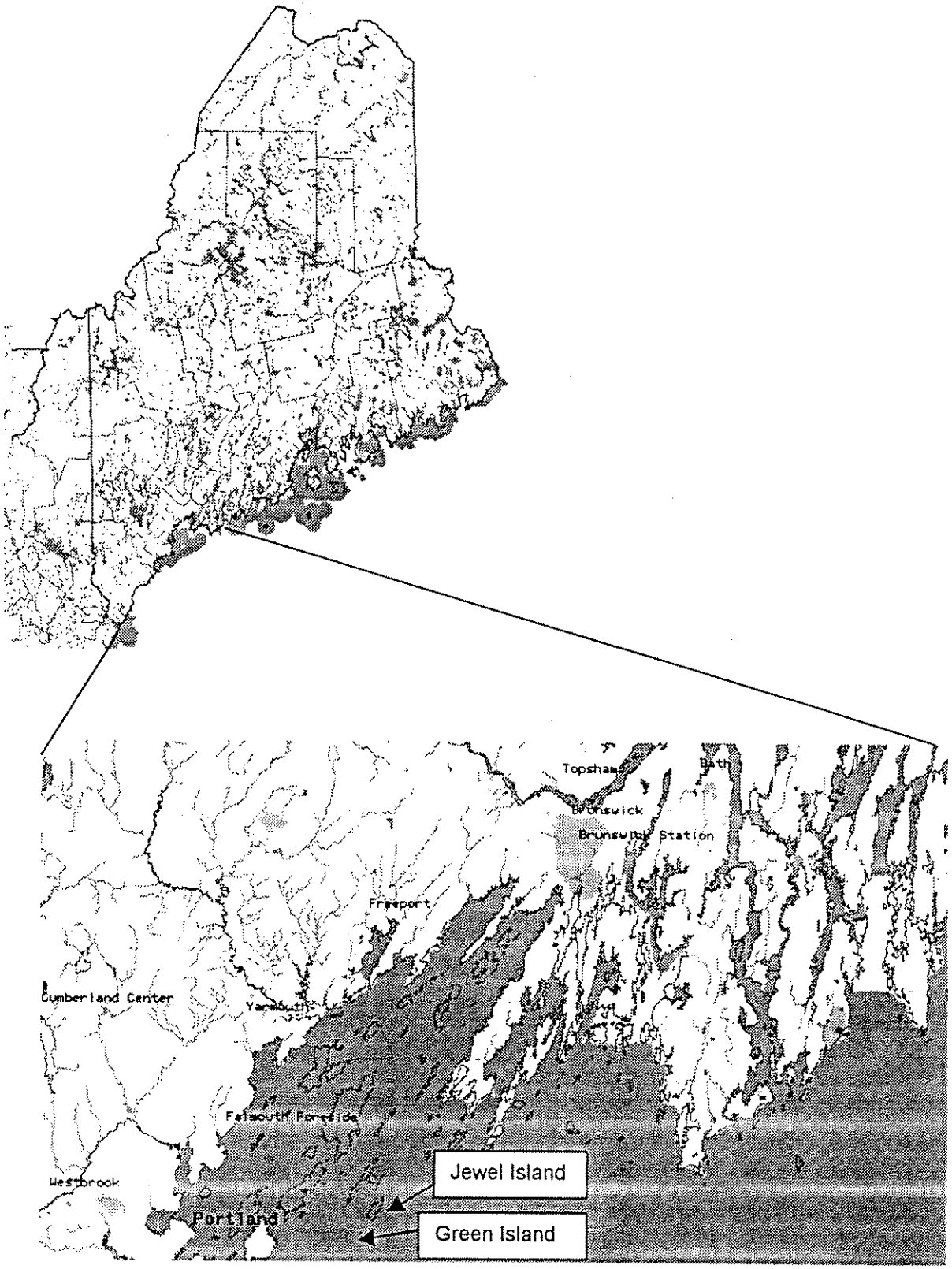


Figure 2. Urchin sampling sites along the central coast of Maine.

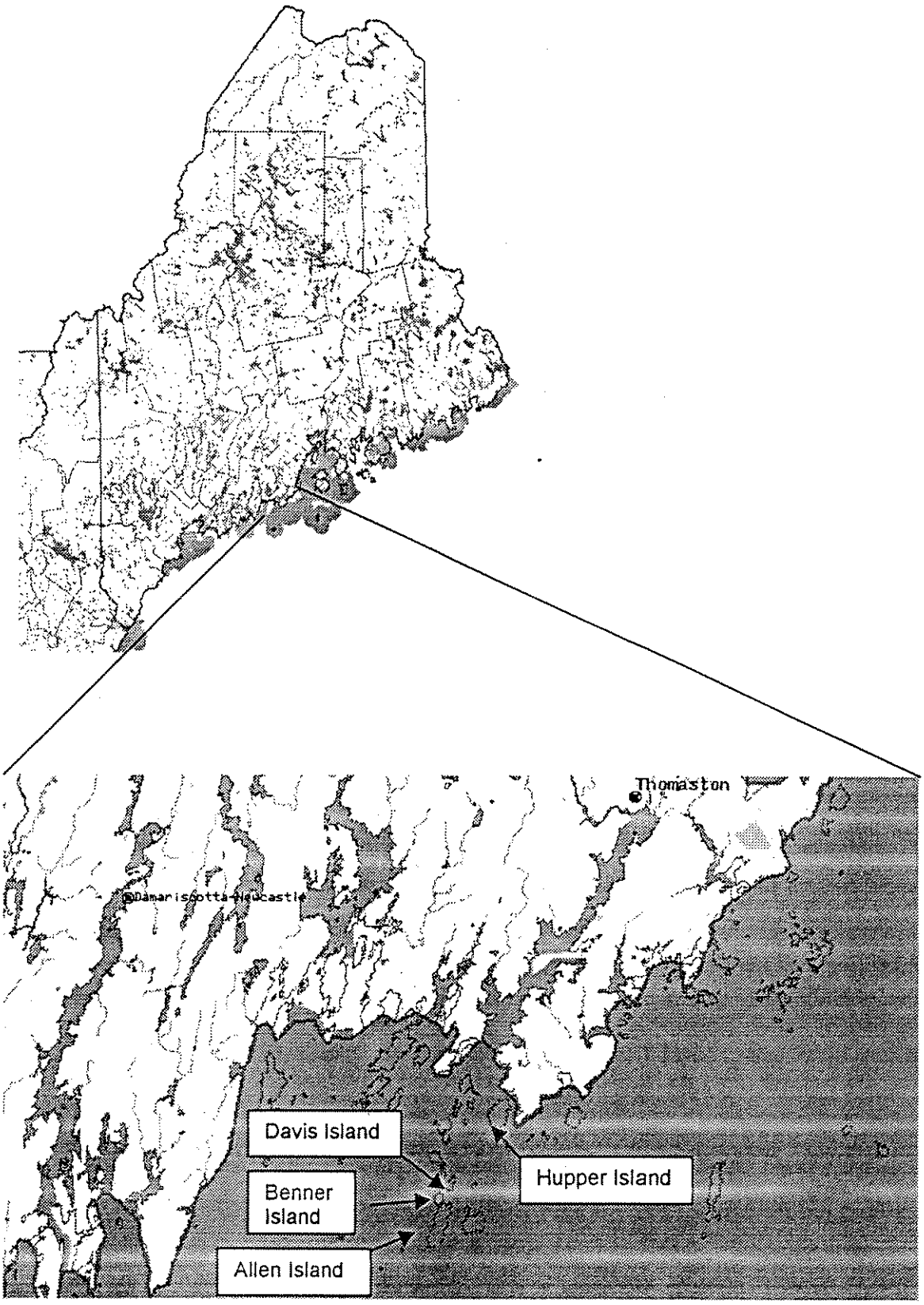


Figure 3. Urchin sampling sites along the northeastern coast of Maine.

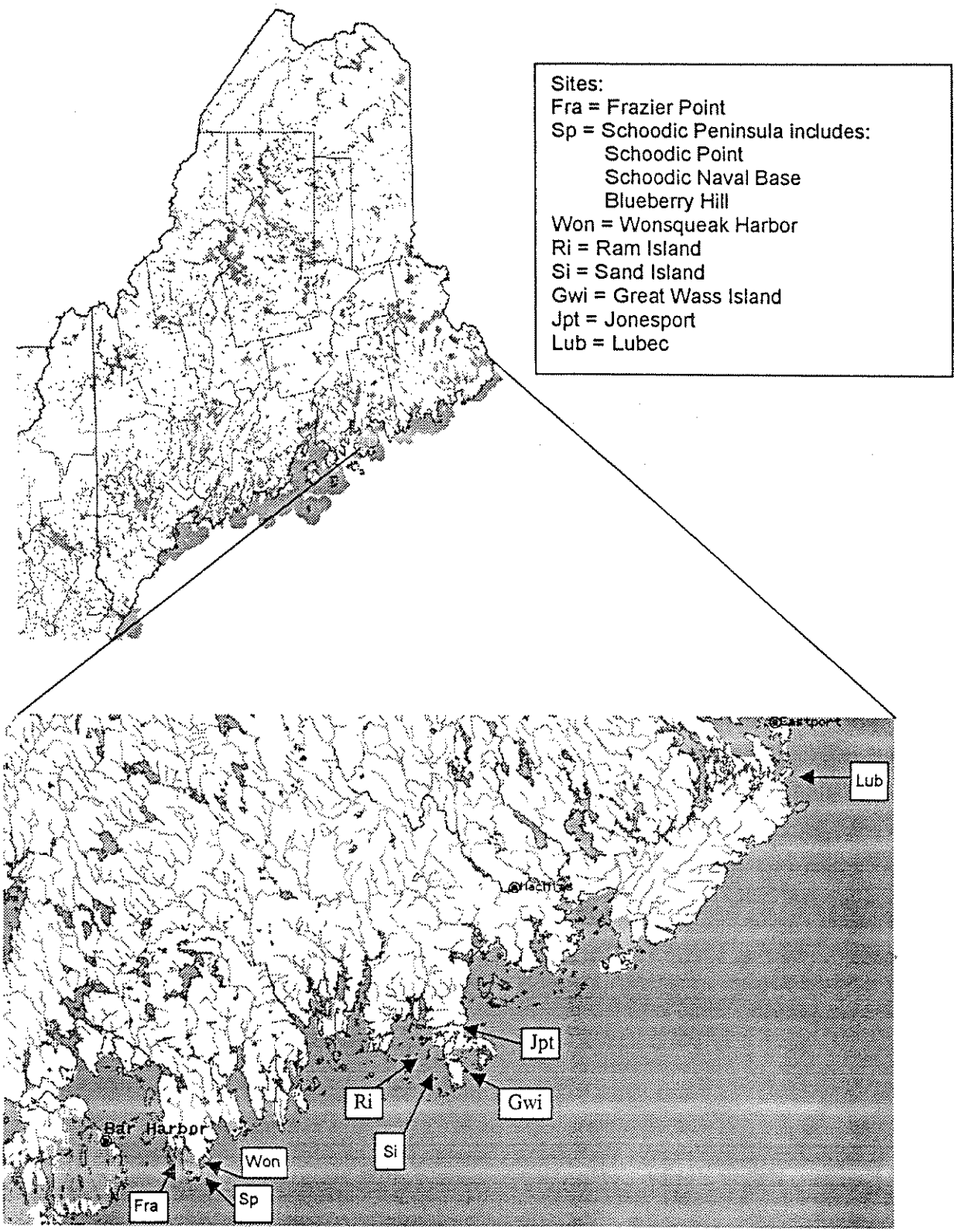


Figure 4. Mean gonad index (+SE) of *Strongylocentrotus droebachiensis* occurring in three regions of Maine and in barren and kelp habitats for 1996 and 1997. (Sample sizes are indicated within bars. See region x habitat source of variation in Table 1.)

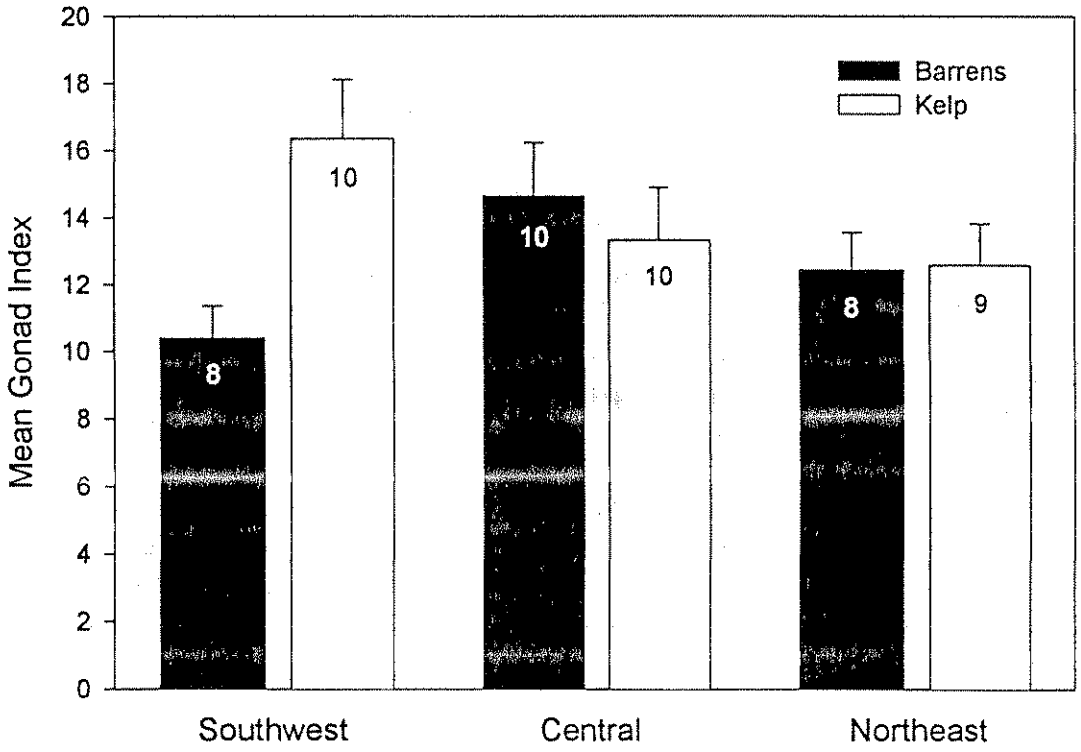


Figure 5. Mean gonad index (+ SE) of *Strongylocentrotus drobachiensis* occuring in three regions of Maine and in barren and kelp habitats, January through March. (Sample sizes are indicated within bars.)

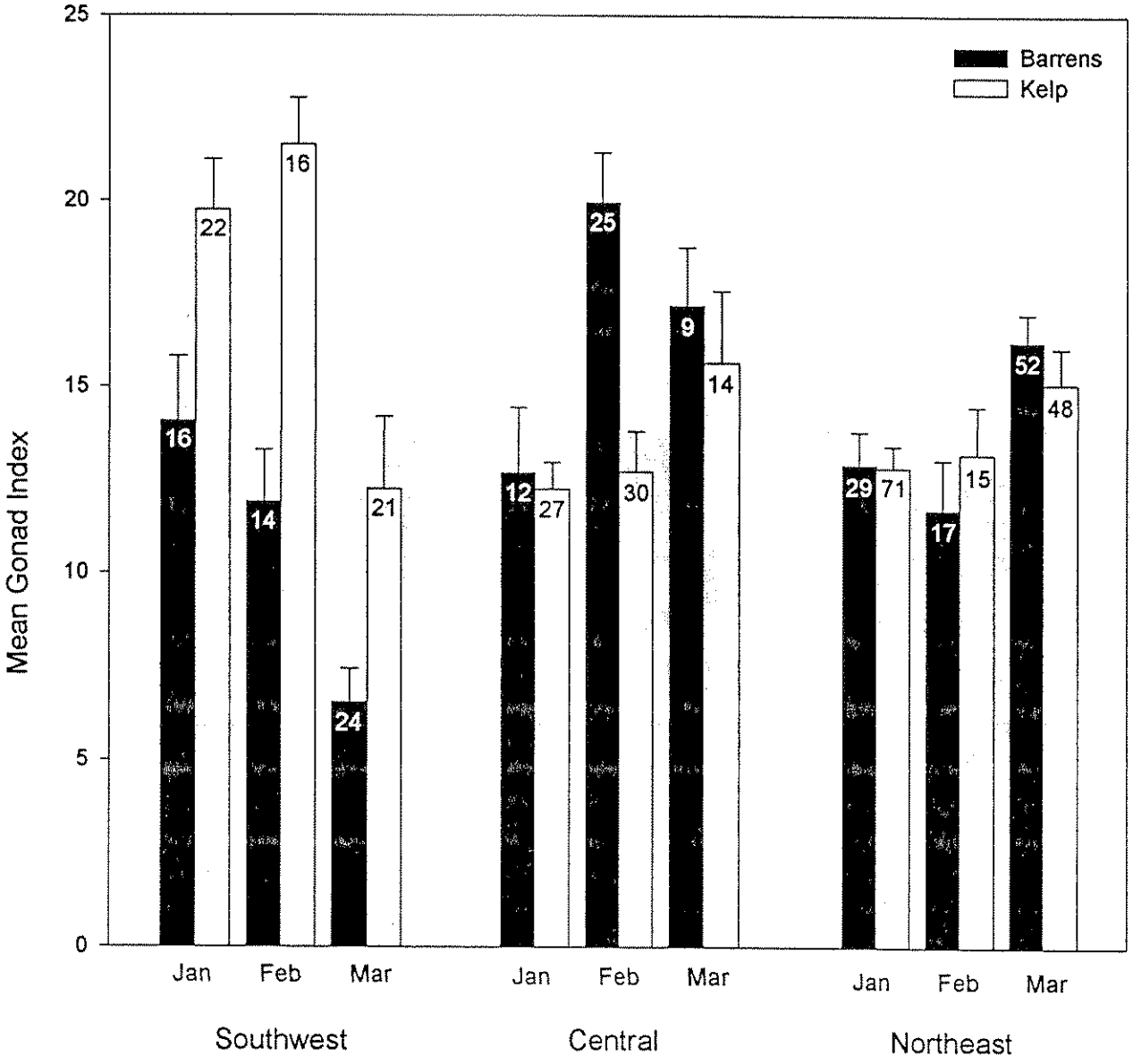


Figure 6a. Mean gonad indices (± SE) of *Strongylocentrotus droebachiensis* for the southwestern coast of Maine, 1996-1997.

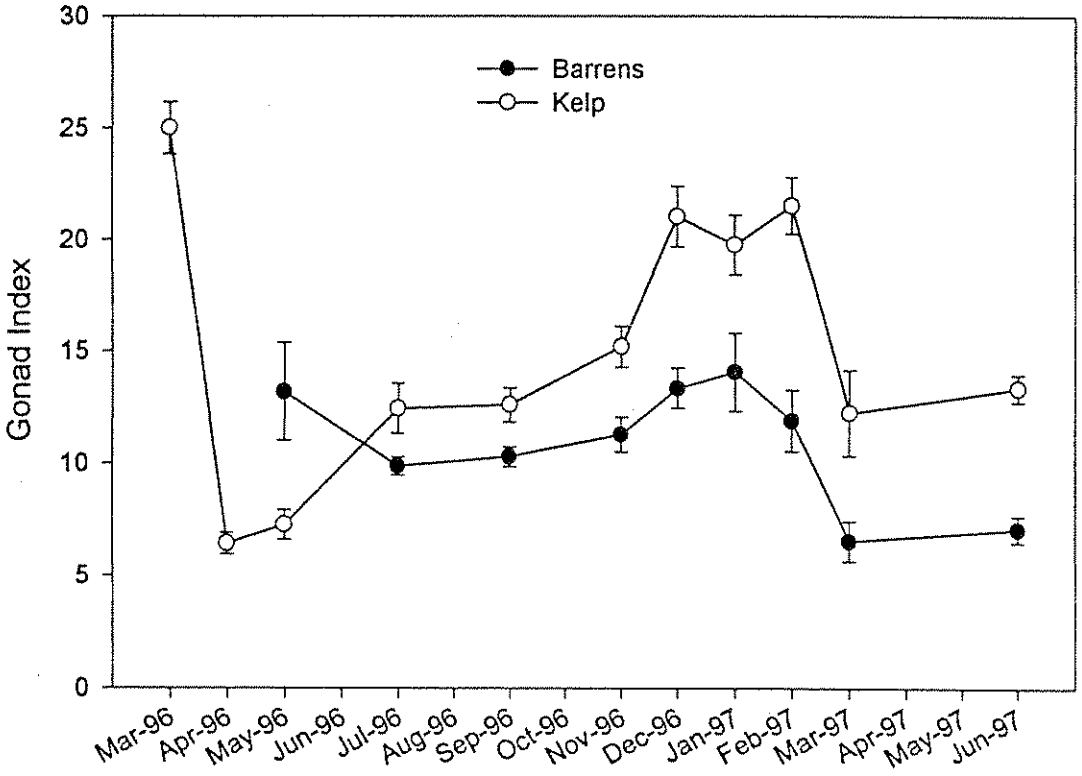


Figure 6b. Mean gonad Indices (± SE) of *Strongylocentrotus droebachiensis* for the central coast of Maine, 1996-1997.

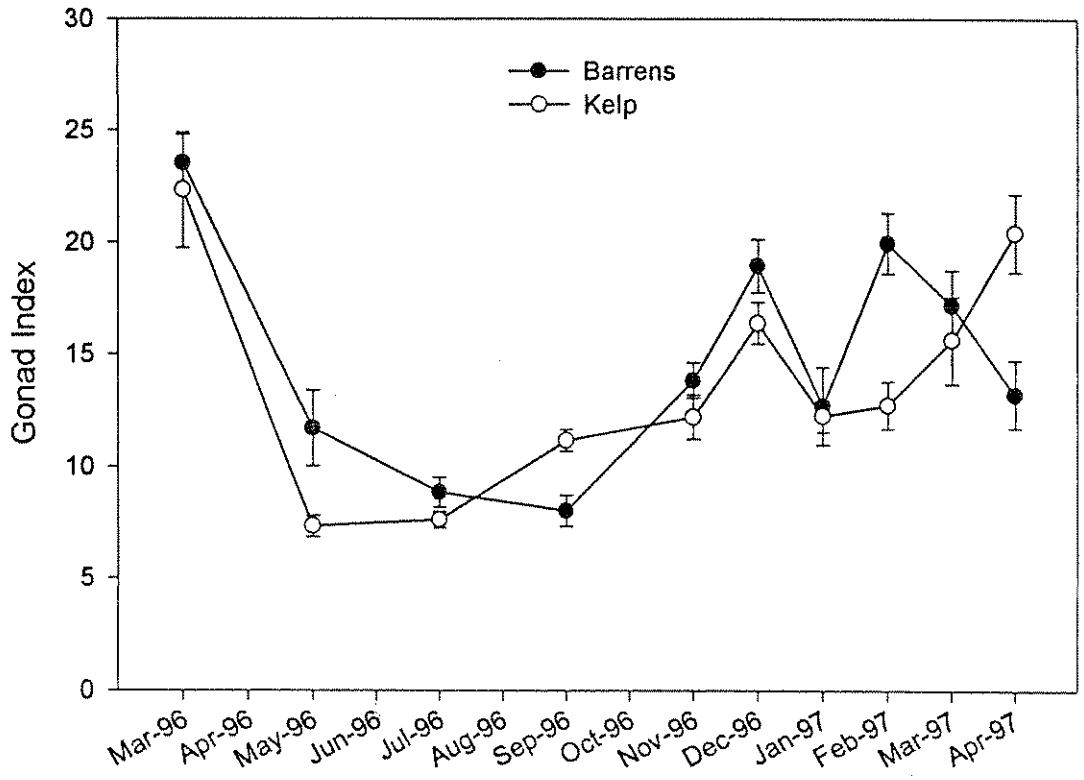


Figure 6c. Mean gonad indices (± SE) of *Strongylocentrotus droebachiensis* for the northeastern coast of Maine, 1996-1997.

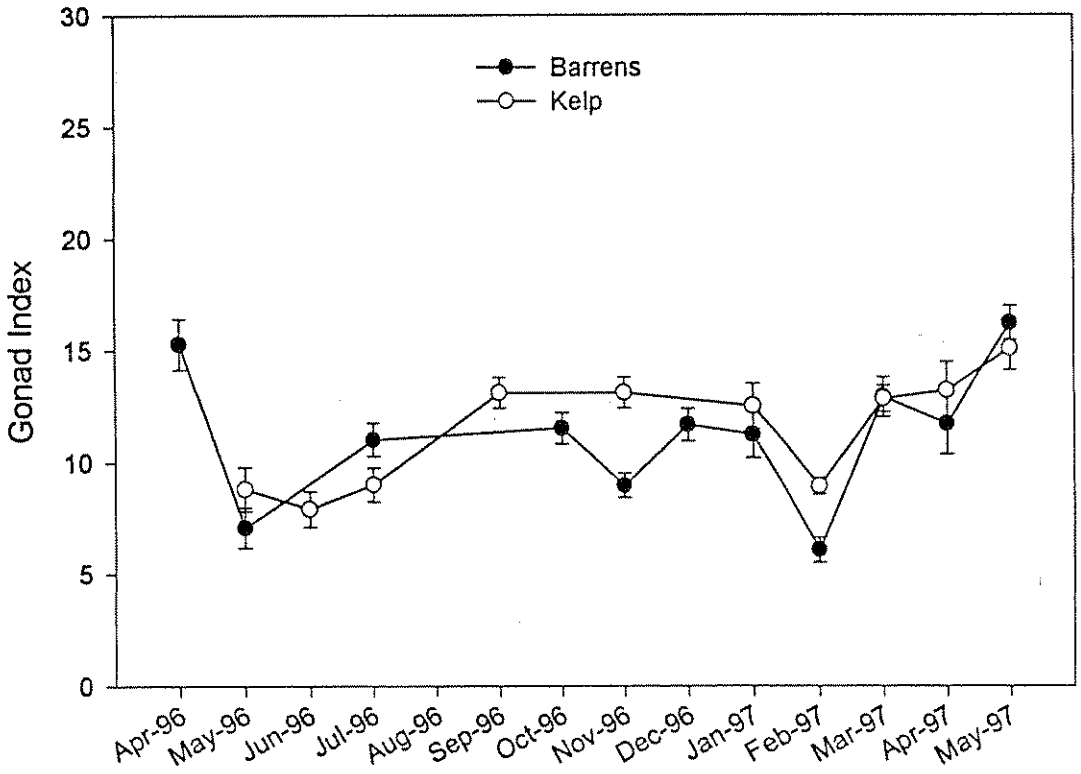


Figure 7a. Market grade roe (based on color) of *Strongylocentrotus droebachiensis* gonads sampled from the southwest coast of Maine during 1996 and 1997 from barren and kelp habitats.

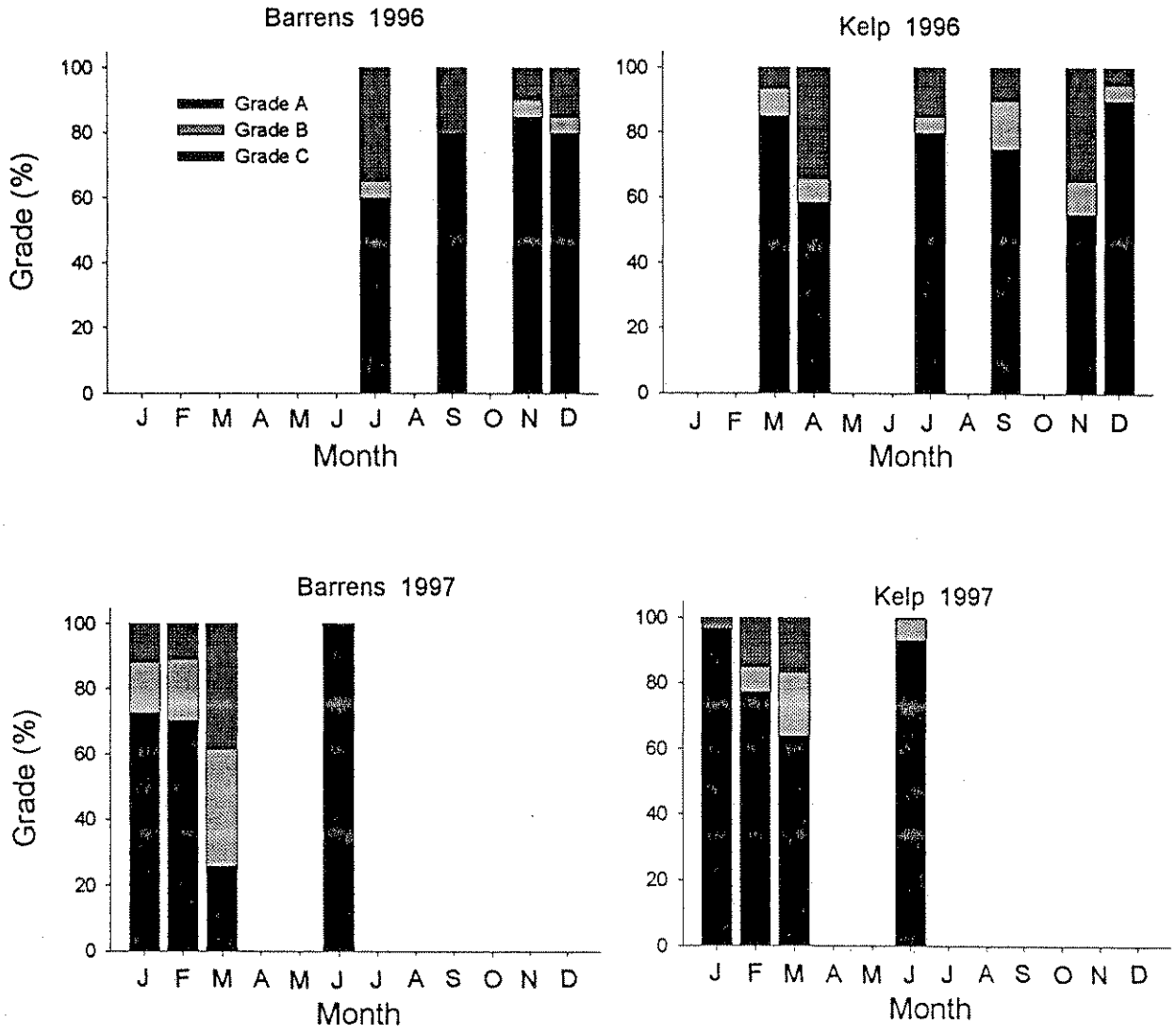


Figure 7b. Market grade roe (based on color) of *Strongylocentrotus droebachiensis* gonads sampled from the central coast of Maine during 1996 and 1997 from barren and kelp habitats.

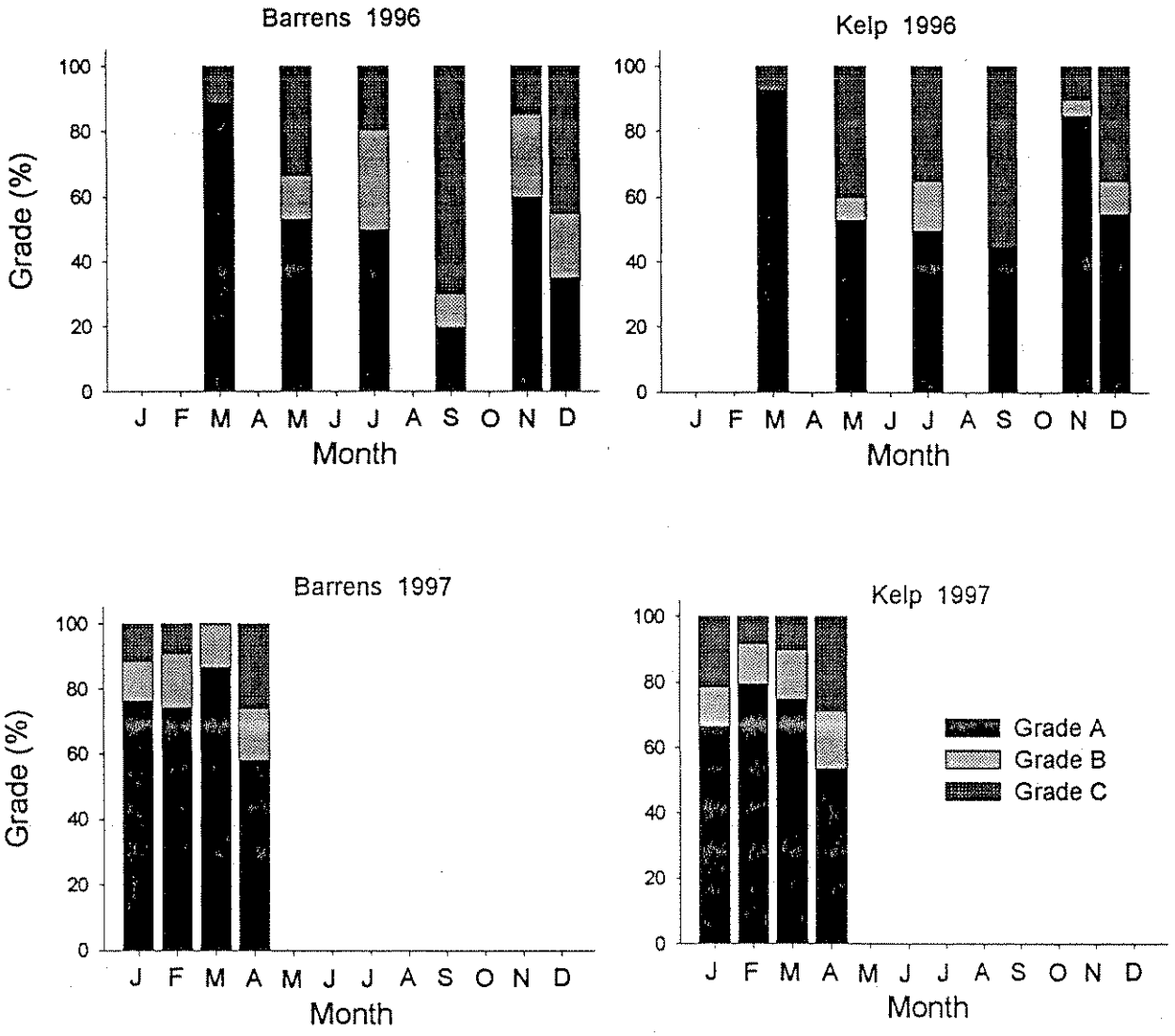


Figure 7c. Market grade roe (based on color) of *Strongylocentrotus droebachiensis* gonads sampled from the northeast coast of Maine during 1996 and 1997 from barren and kelp habitats.

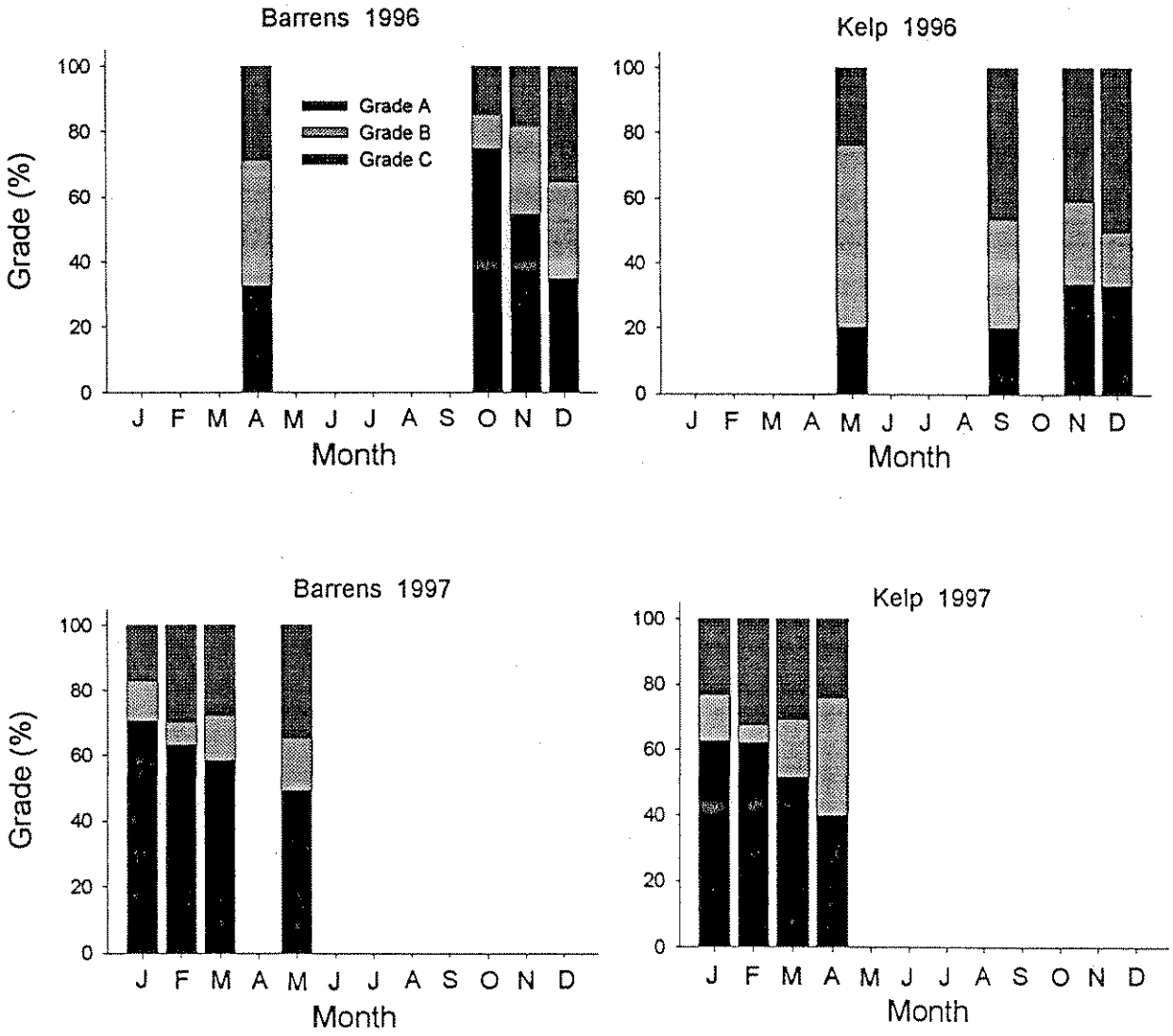


Figure 8a. Mean texture + SD of roe (1 = smooth to 5 = coarse) of *Strongylocentrotus droebachiensis* gonads sampled from the southwest coast of Maine during 1996 and 1997 from barren and kelp habitats.

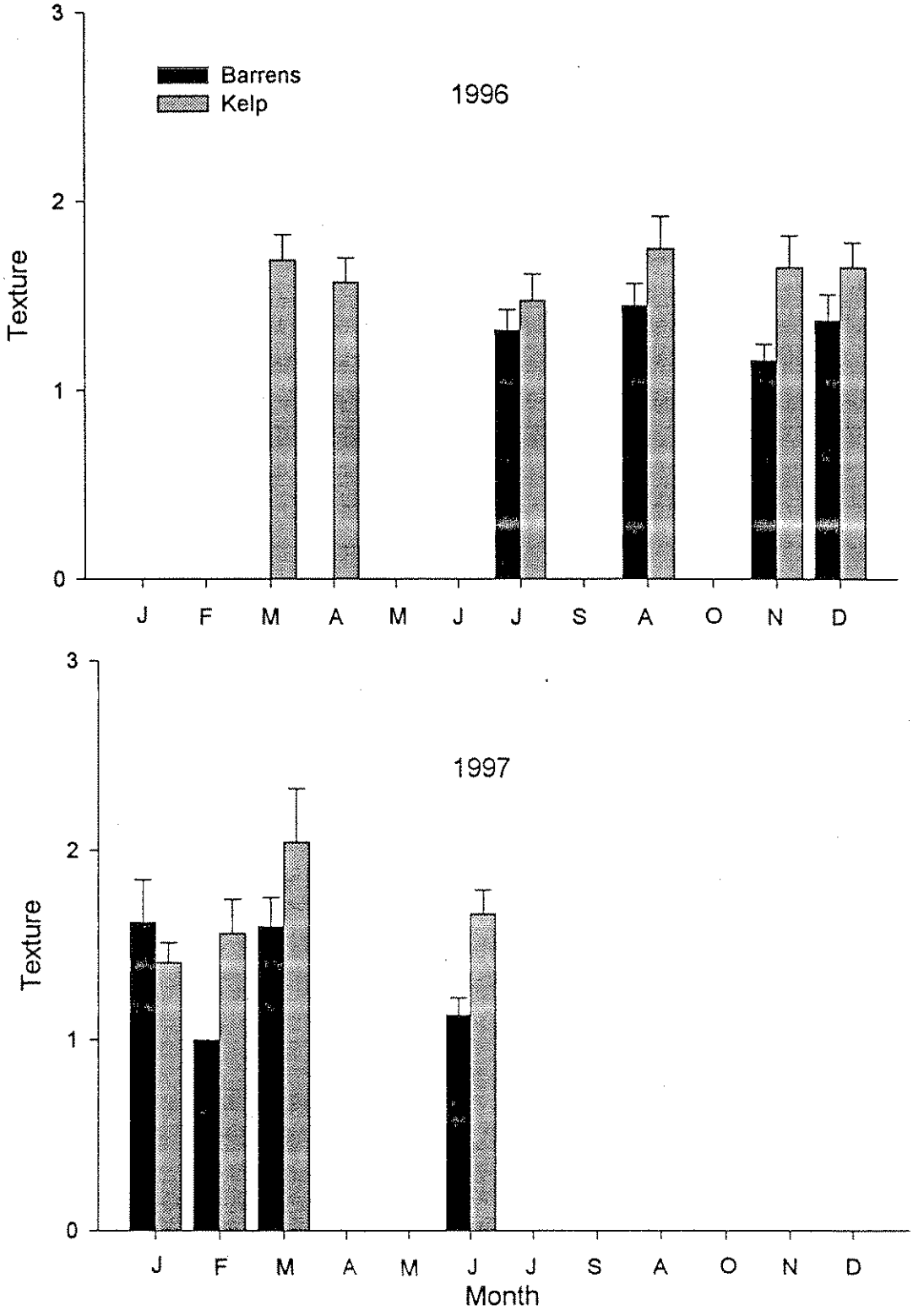


Figure 8b. Mean texture + SD of roe (1 = smooth to 5 = coarse) of *Strongylocentrotus droebachiensis* gonads sampled from the central coast of Maine during 1996 and 1997 from barren and kelp habitats.

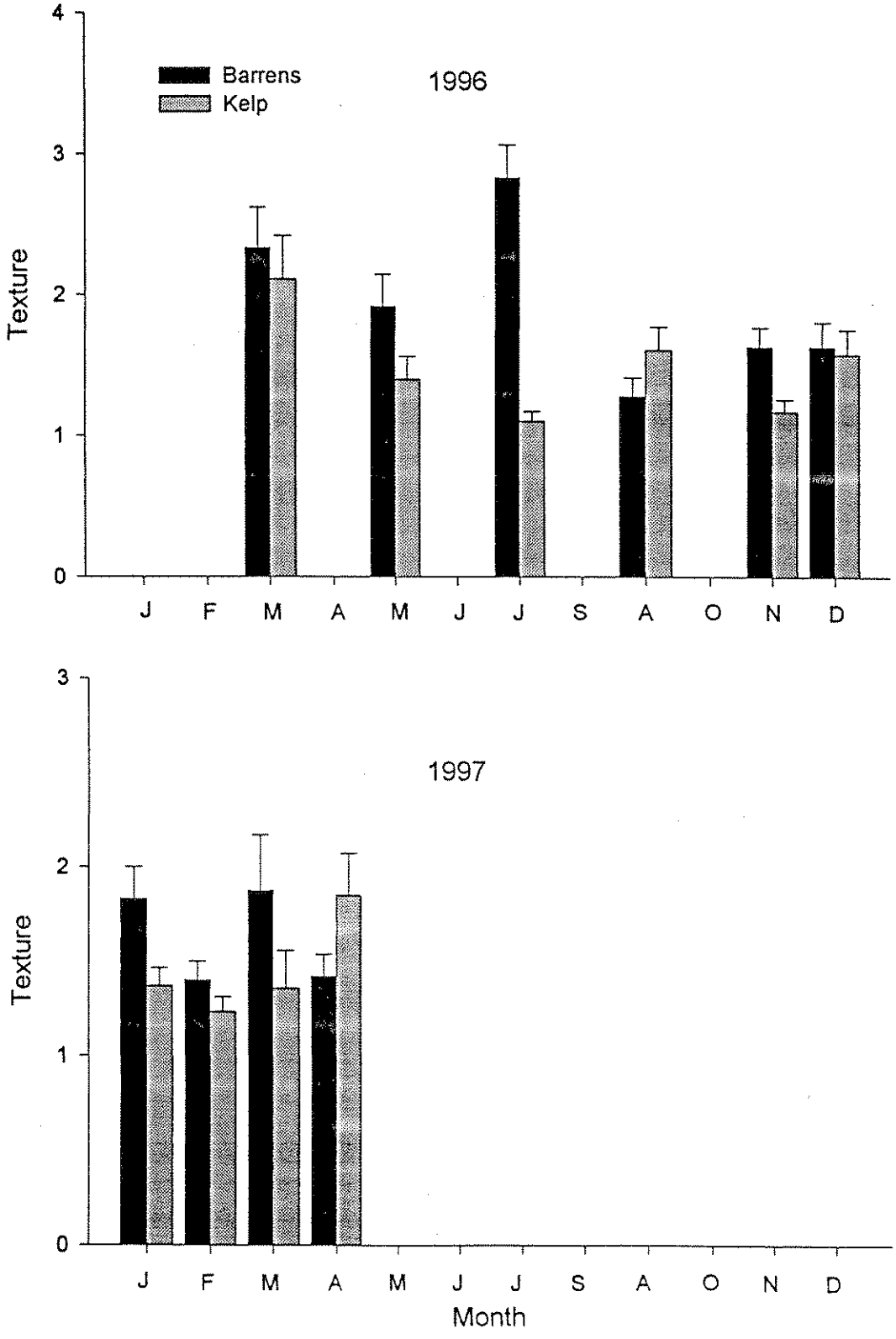


Figure 8c. Mean texture + SD of roe (1 = smooth to 5 = coarse) of *Strongylocentrotus droebachiensis* gonads sampled from the northeast coast of Maine during 1996 and 1997 from barren and kelp habitats.

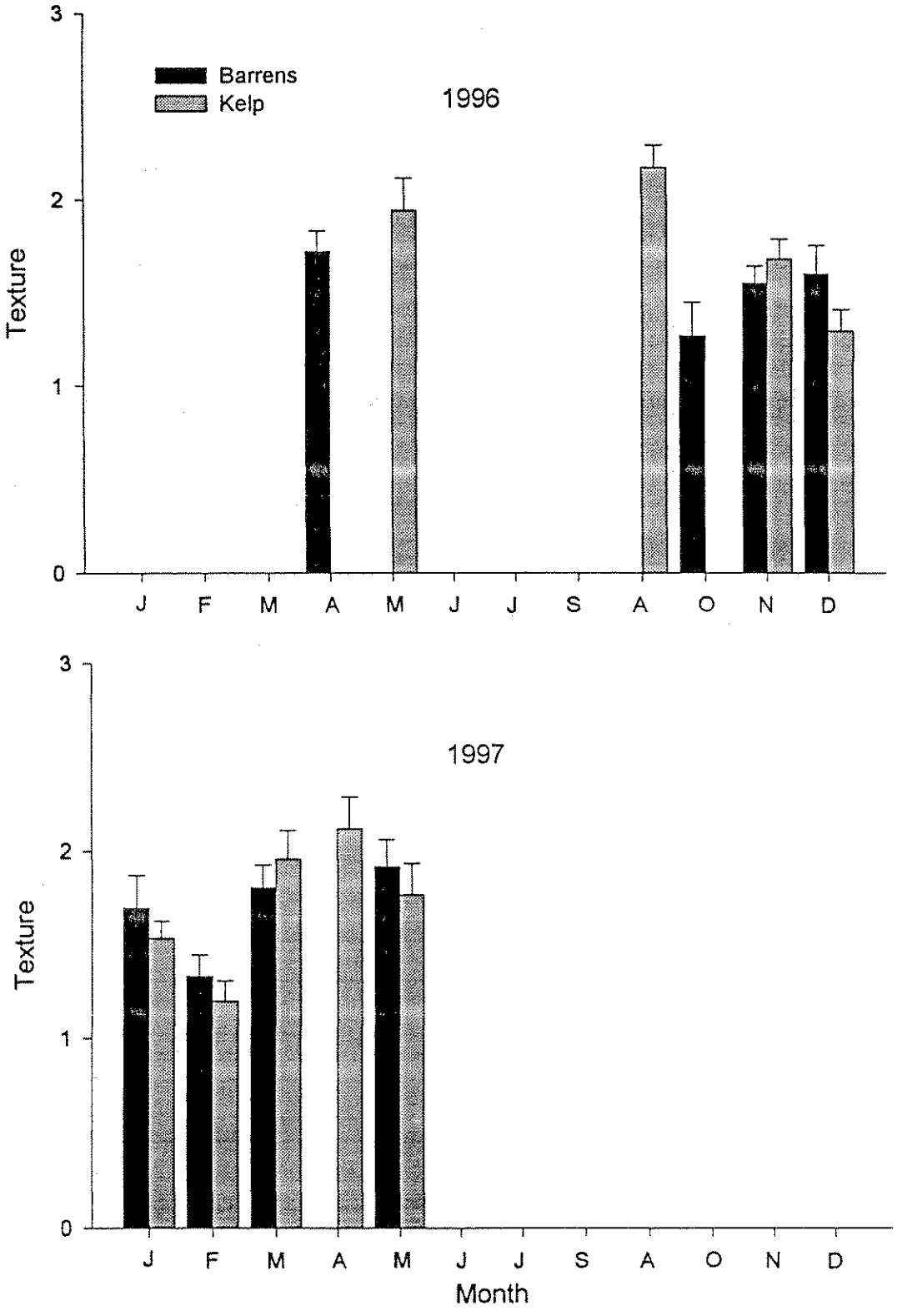


Figure 9a. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and temperature and salinity at Allen Island, Maine.

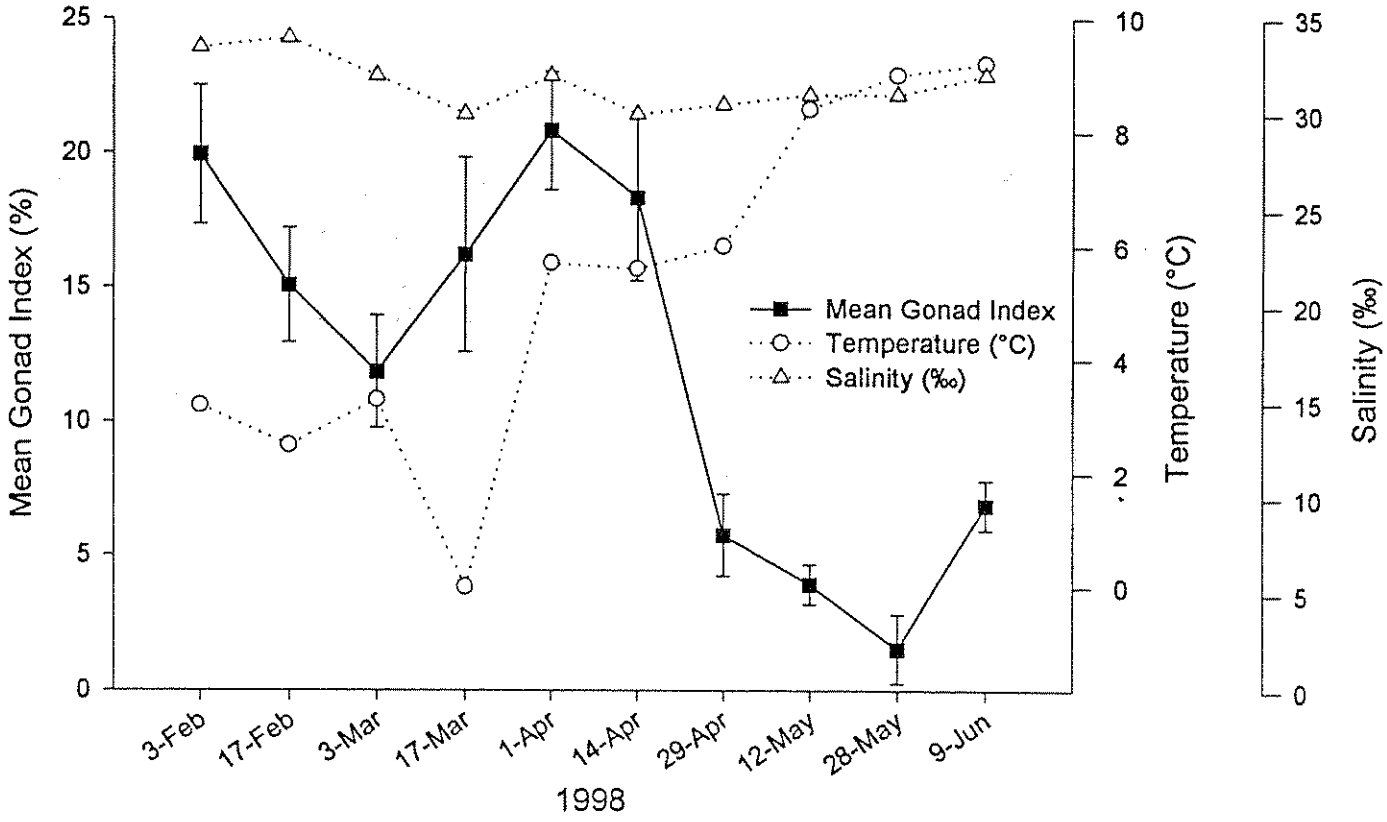


Figure 9b. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and pigment concentrations (µg/L) at Allen Island, Maine.

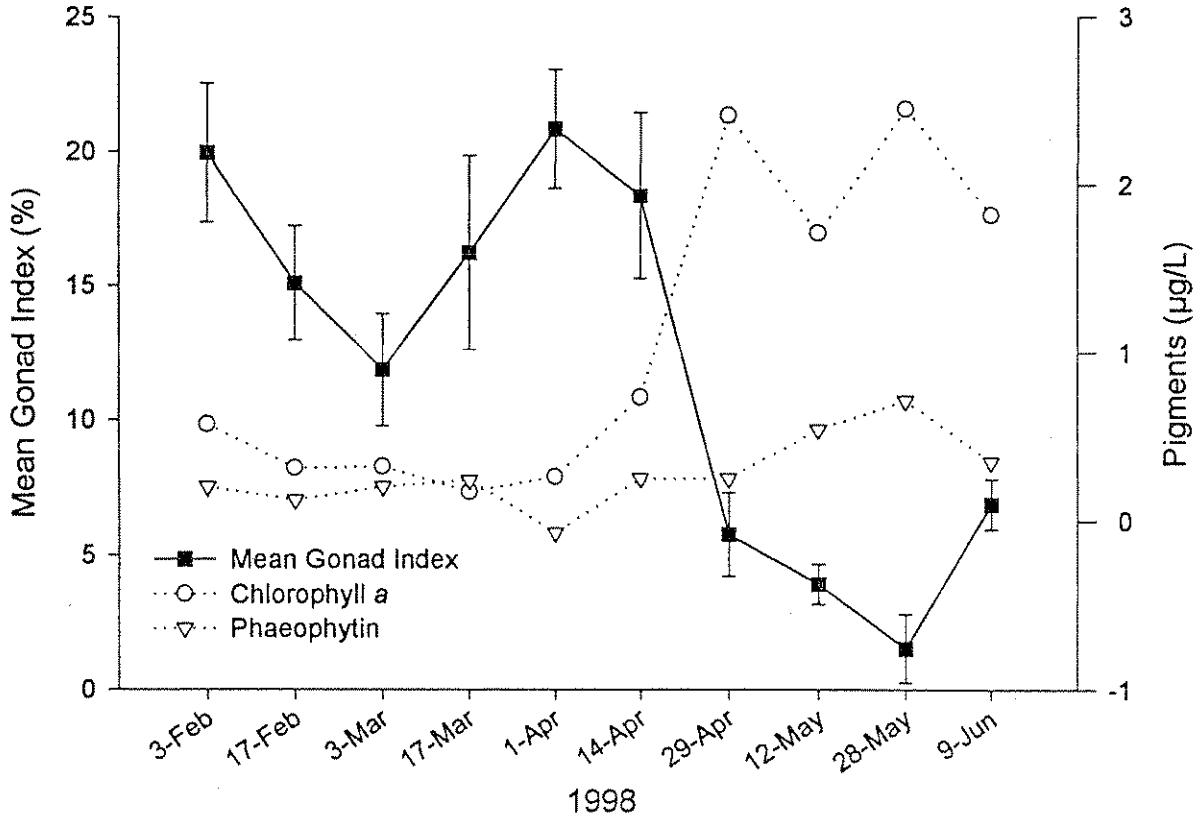


Figure 9c. Relationship between mean gonad index (± 95% confidence intervals) and inorganic nutrient concentrations (µM) at Allen Island, Maine.

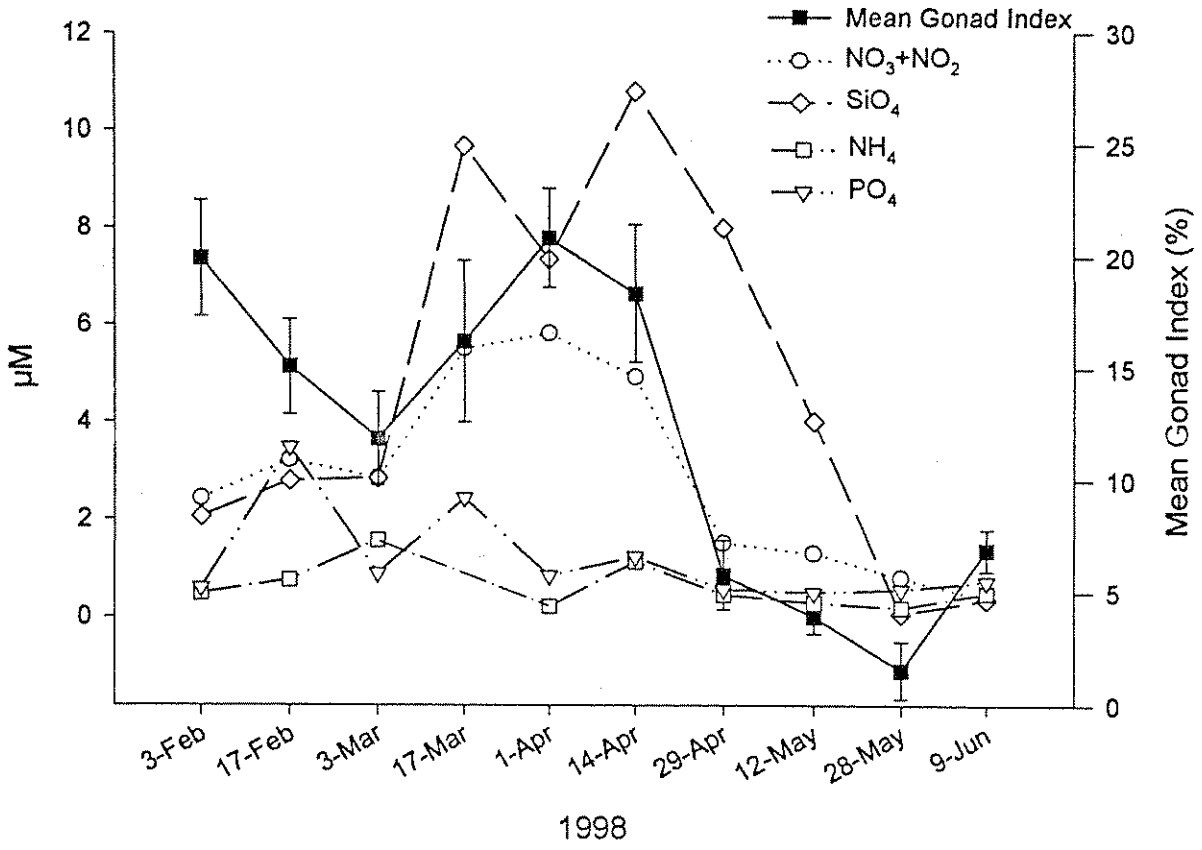


Figure 10a. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and temperature and salinity at Benner Island, Maine.

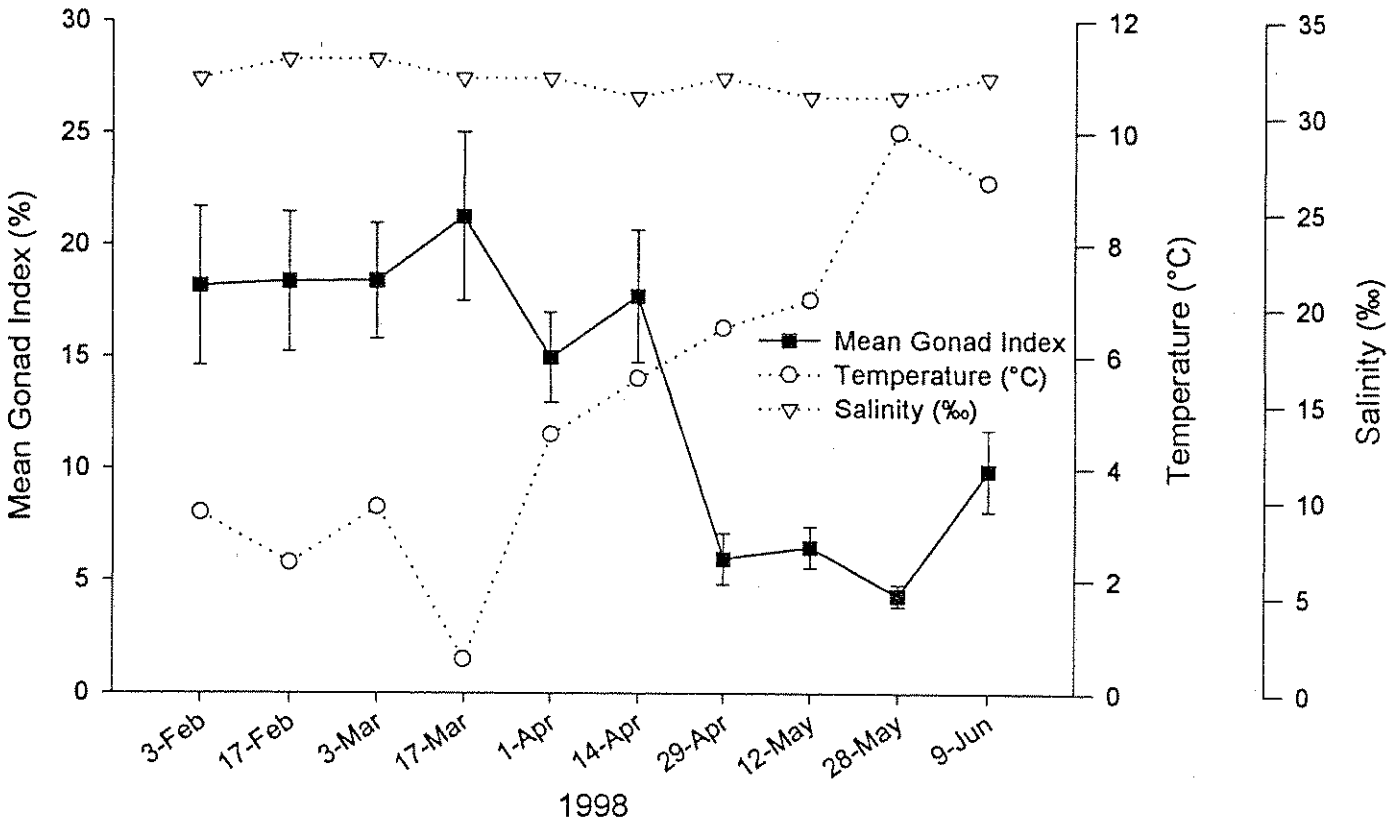


Figure 10b. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and pigment concentrations (µg/L) at Benner Island, Maine.

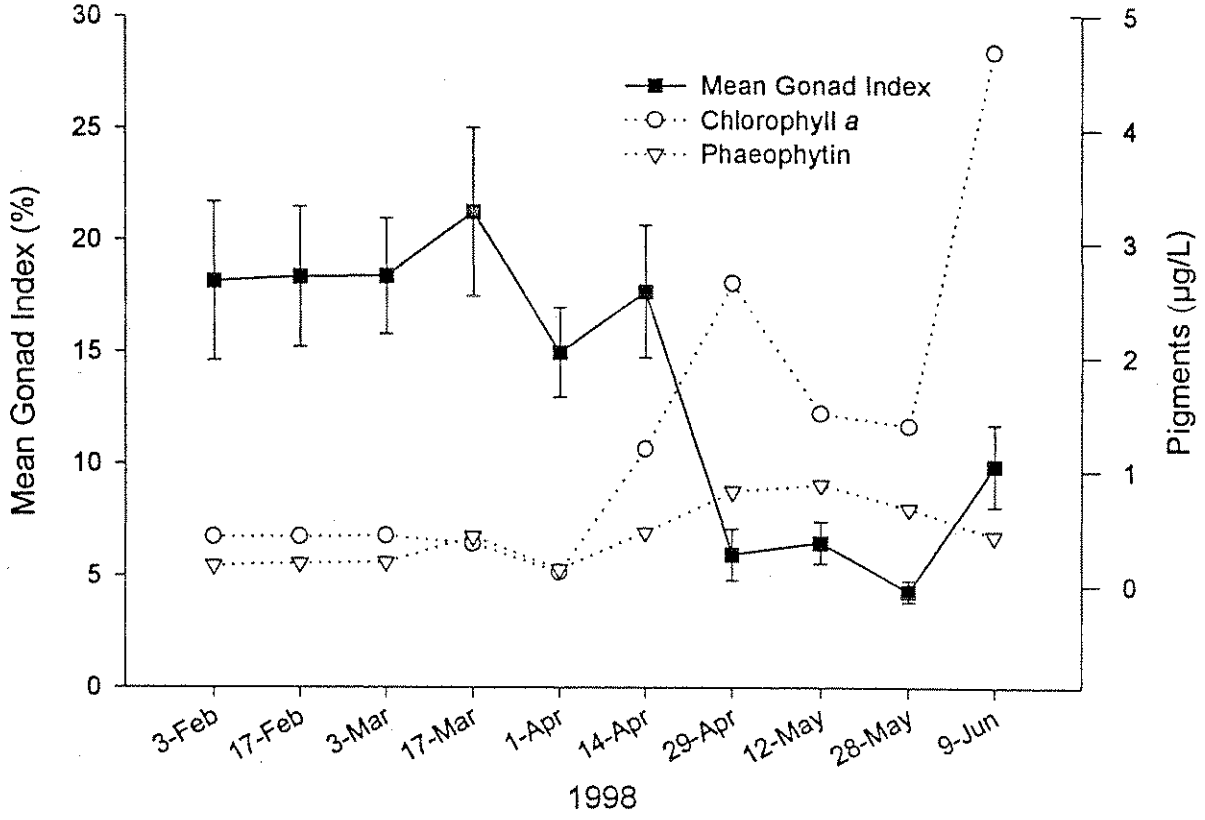


Figure 10c. Relationship between mean gonad index (± 95% confidence intervals) and inorganic nutrient concentrations (µM) at Benner Island, Maine.

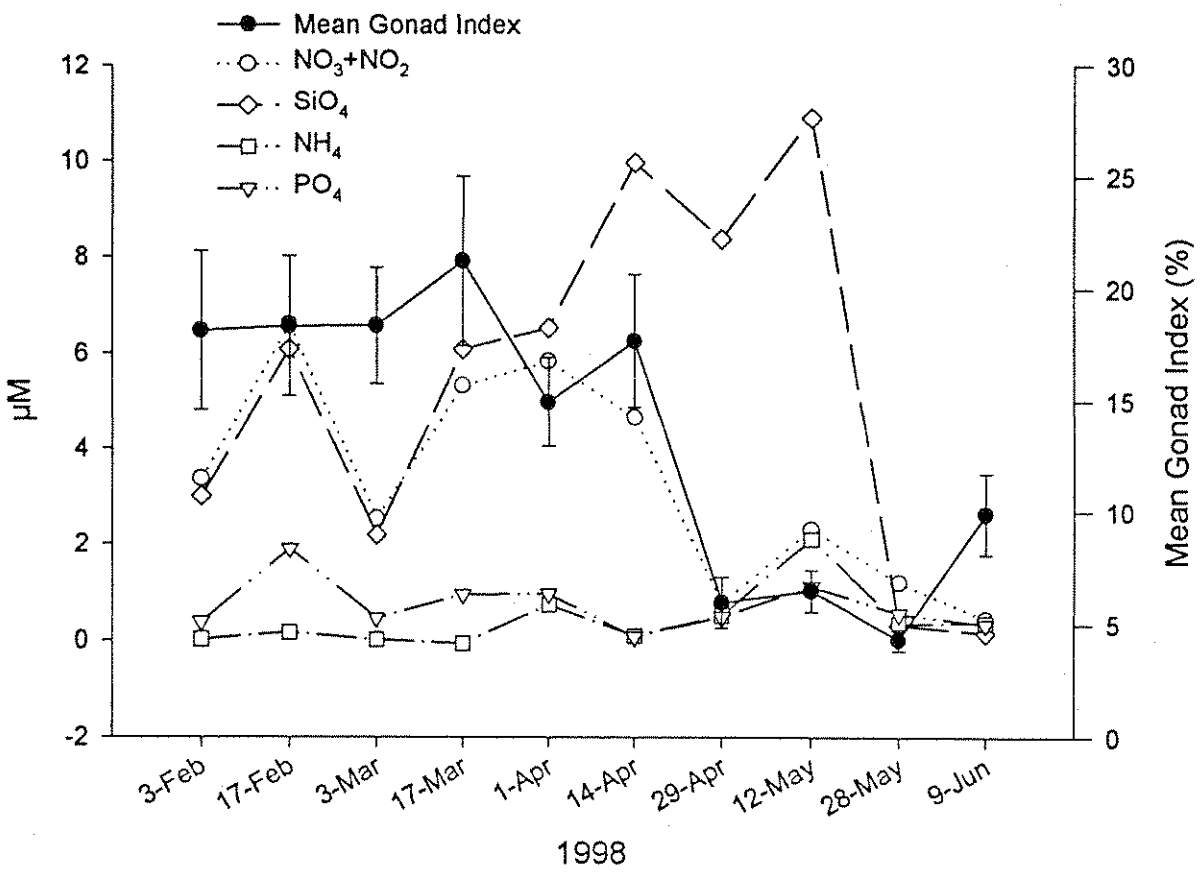


Figure 11a. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and temperature and salinity at Hupper Island, Maine.

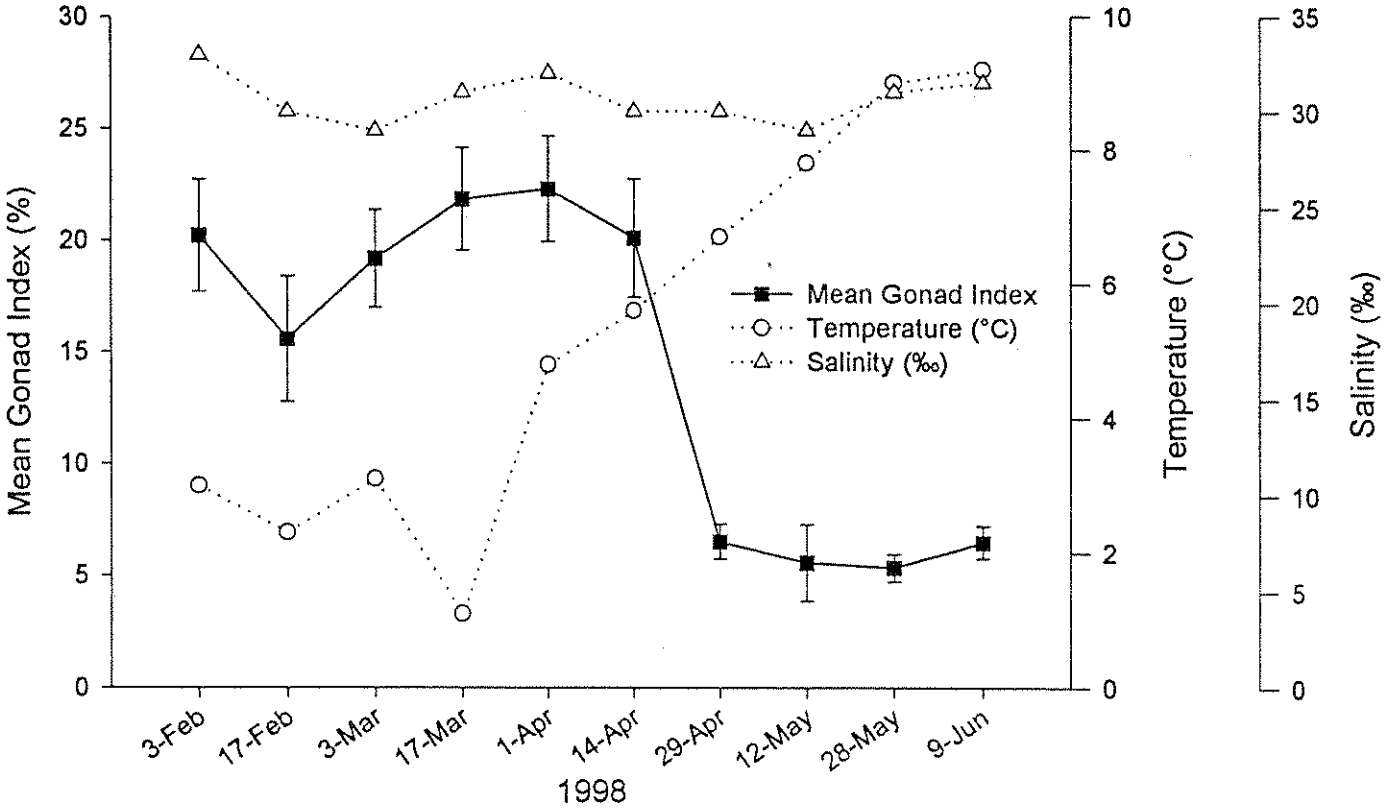


Figure 11b. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and pigment concentrations (µg/L) at Hupper Island, Maine.

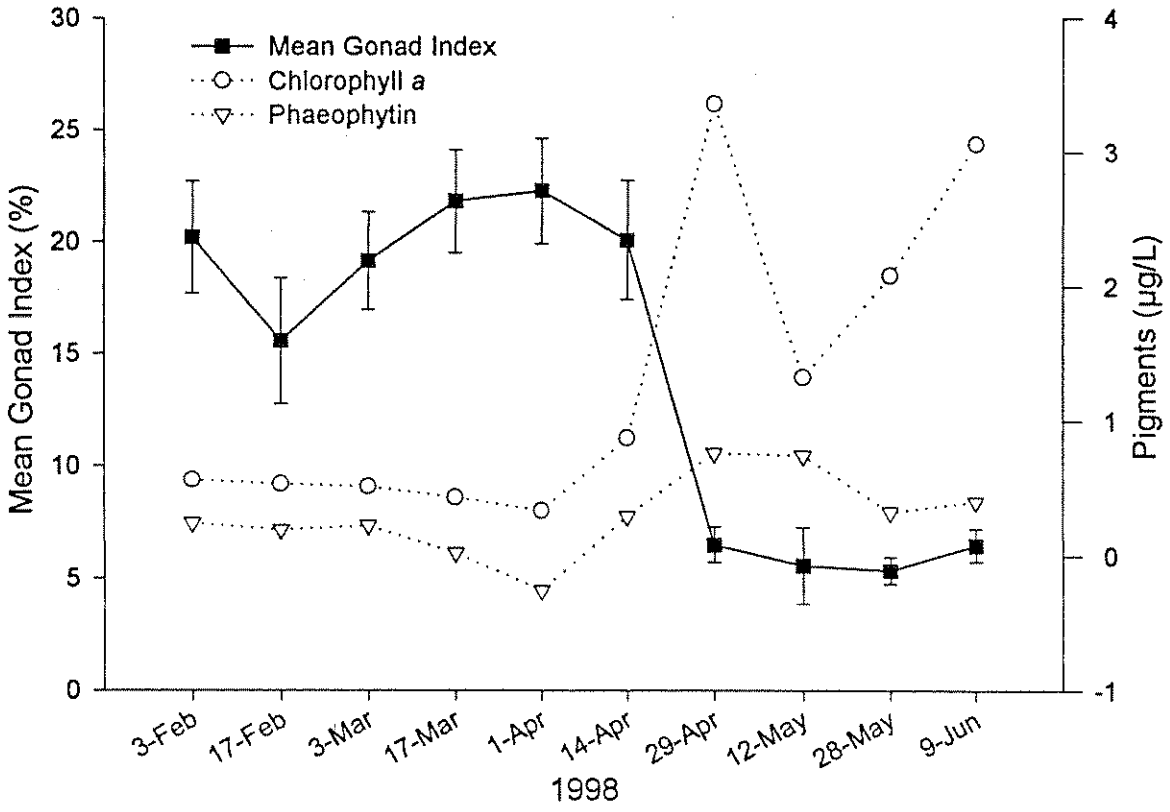


Figure 11c. Relationship between mean gonad index (± 95% confidence intervals) and inorganic nutrient concentrations (µM) at Hupper Island, Maine.

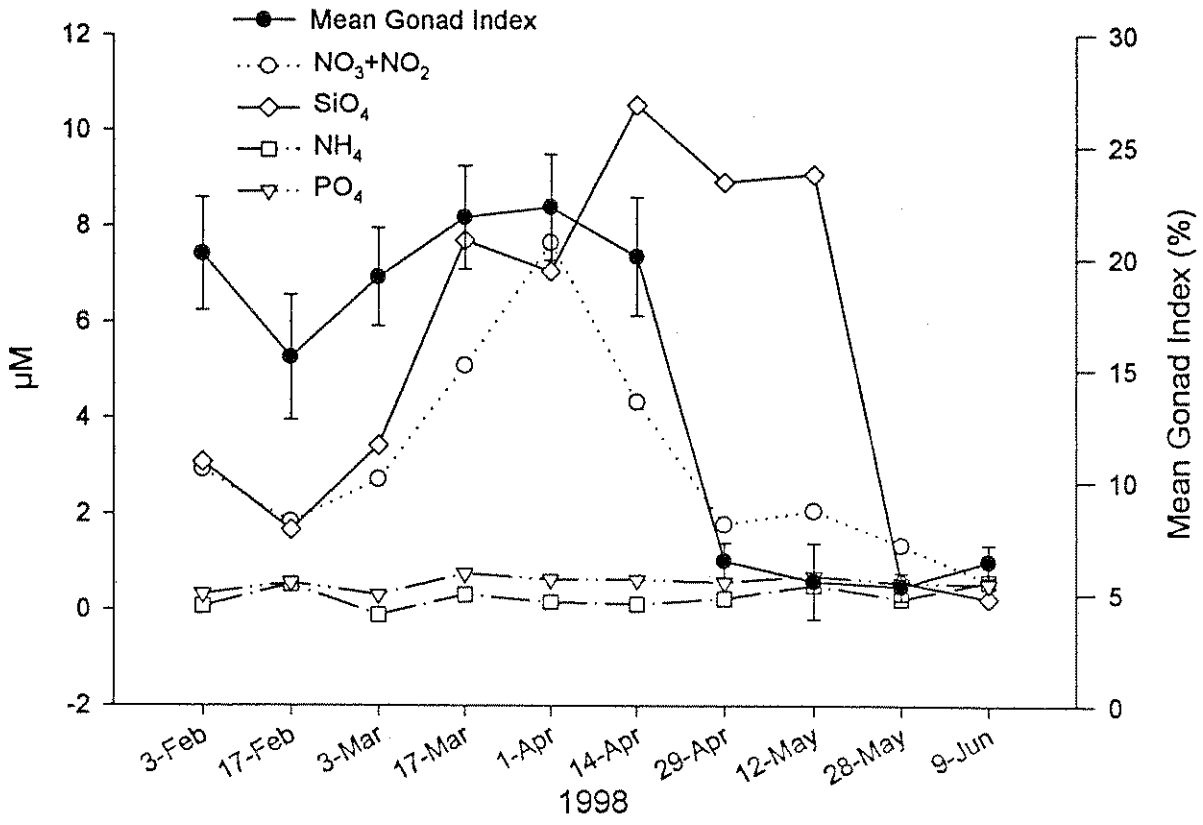


Figure 12a. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and temperature and salinity at Davis Island, Maine.

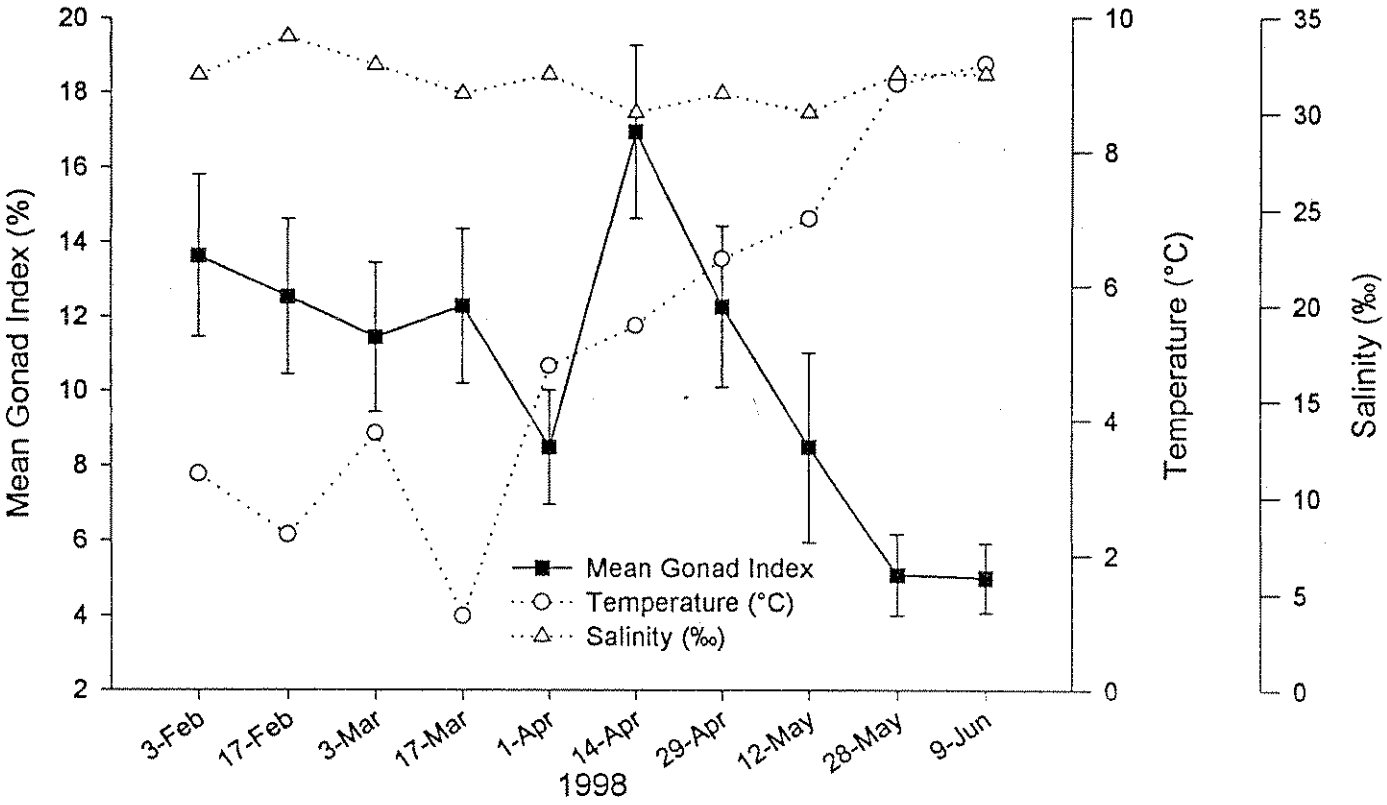


Figure 12b. Relationship between mean gonad index (± 95% confidence intervals) of *Strongylocentrotus droebachiensis* and pigment concentrations (µg/L) at Davis Island, Maine.

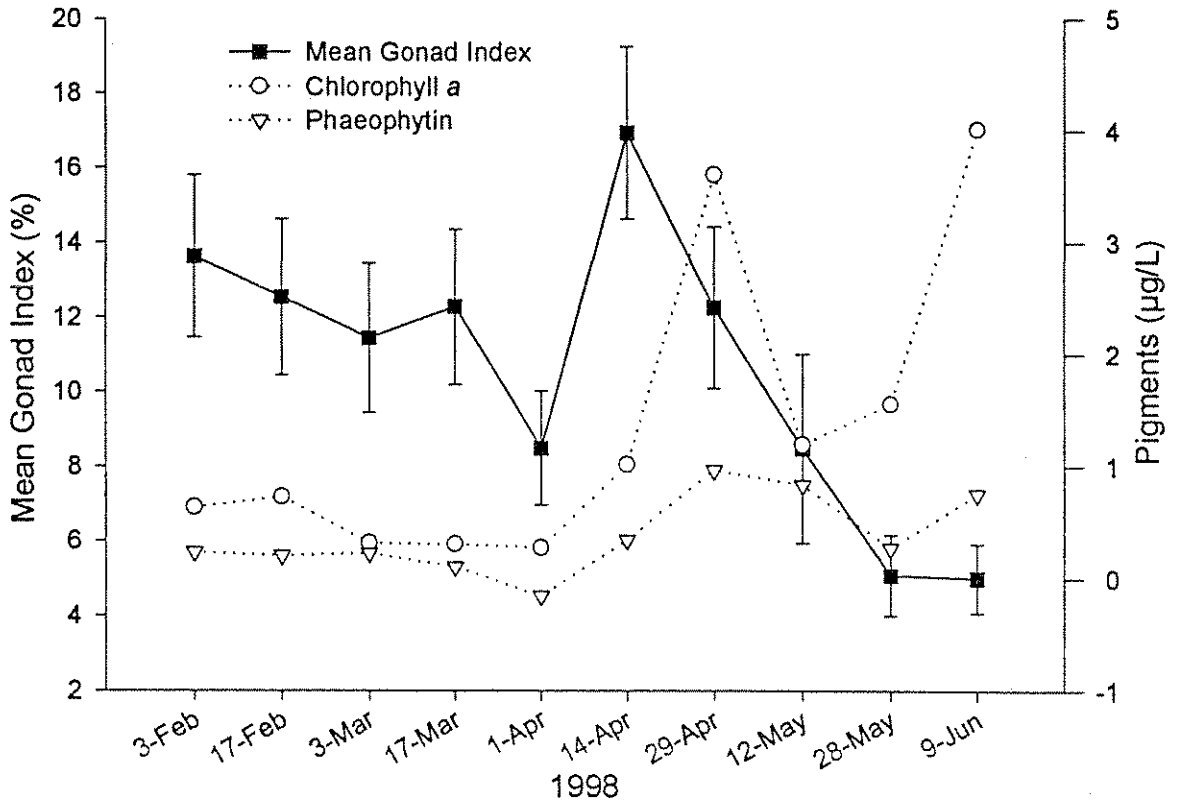


Figure 12c. Relationship between mean gonad index (± 95% confidence intervals) and inorganic nutrient concentrations (µM) at Davis Island, Maine.

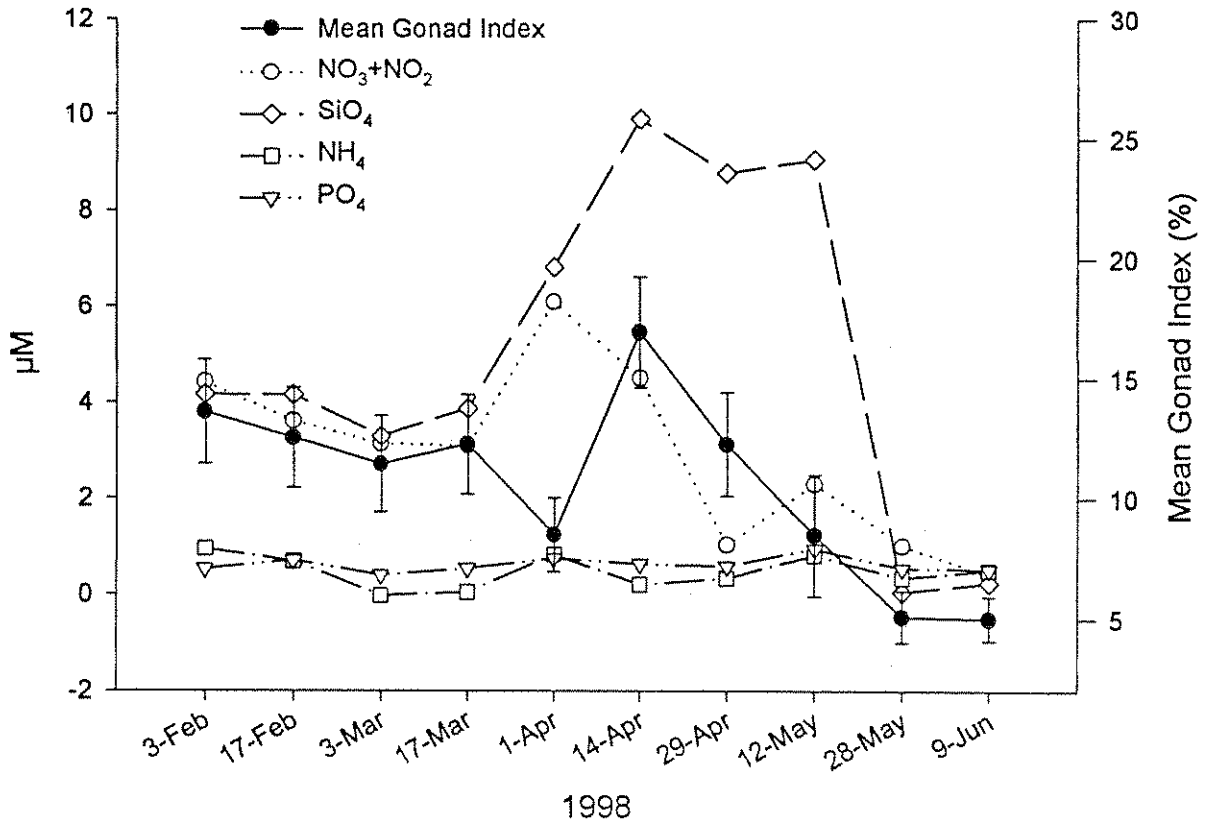


Figure 13a. Relationship between gonad index and test diameter for urchins sampled during January through April from the southwest coast of Maine (N = 269).

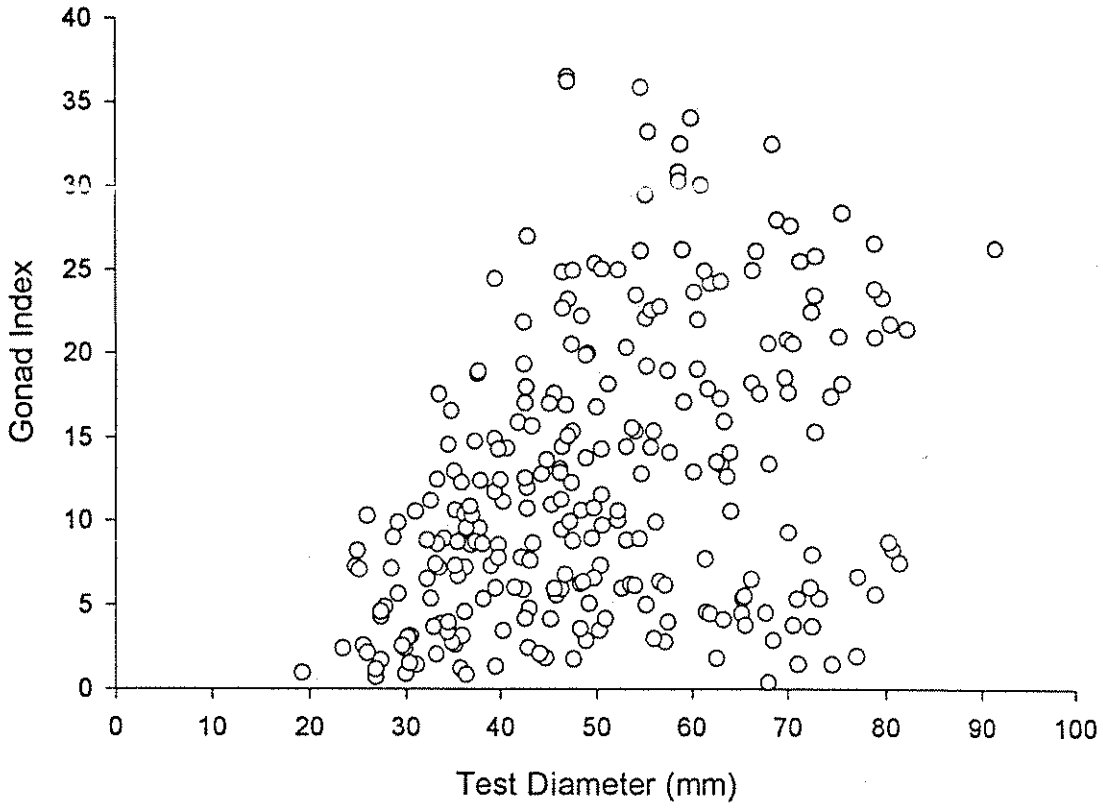


Figure 13b. Asymptotic test diameter showing gonad index is independent of size above 42 mm for urchins sampled from the southwest coast of Maine, N = 138.

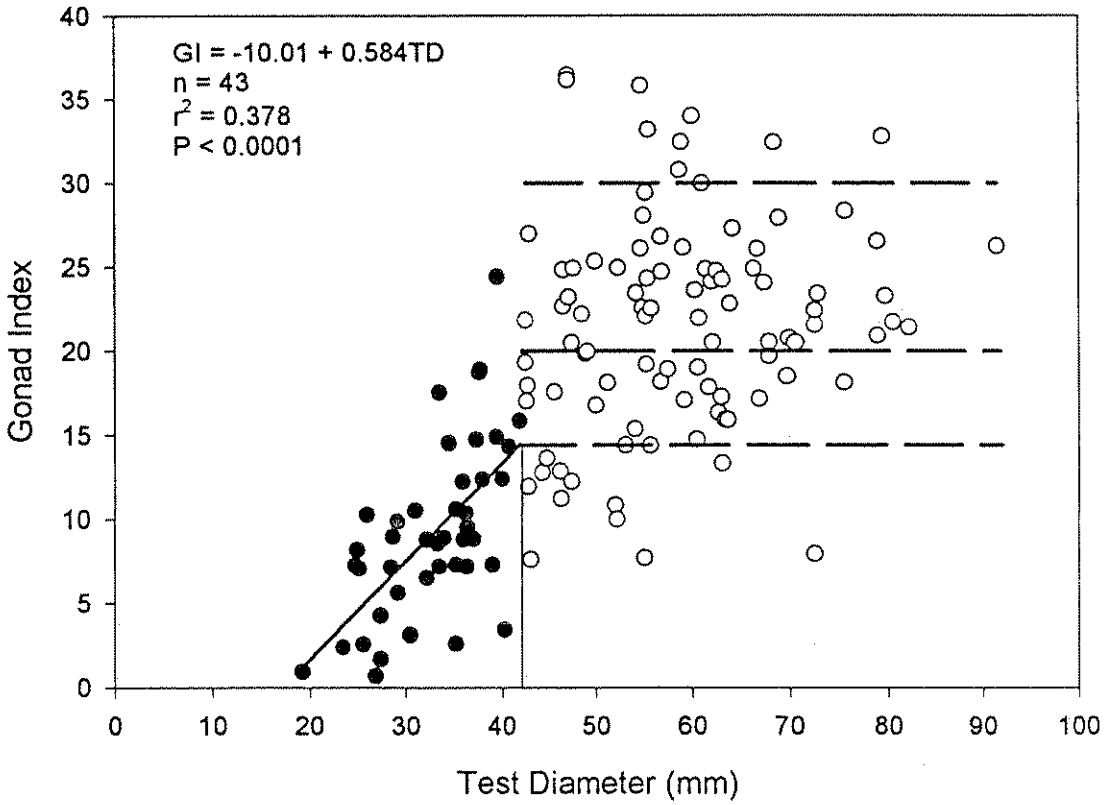


Figure 14a. Relationship between gonad index and test diameter for urchins sampled during January through April from the central coast of Maine (N = 255).

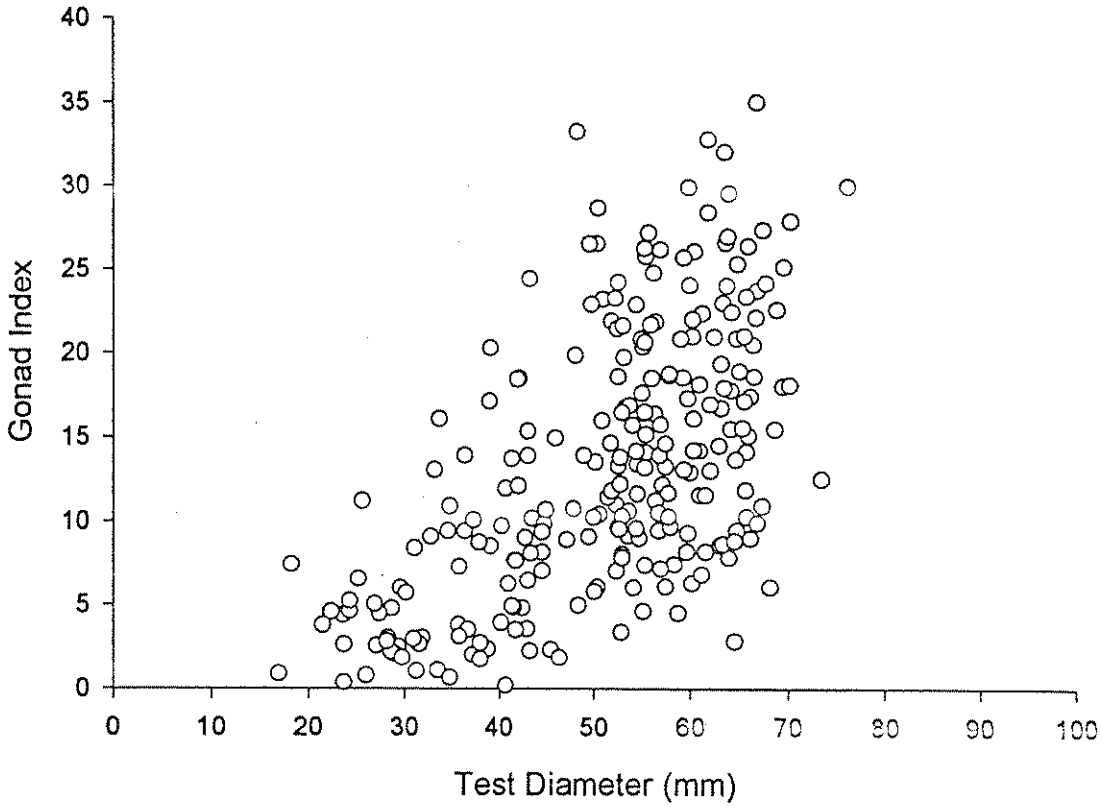


Figure 14b. Asymptotic test diameter showing gonad index is independent of size above 43 mm for urchins sampled from the central coast of Maine, N = 112.

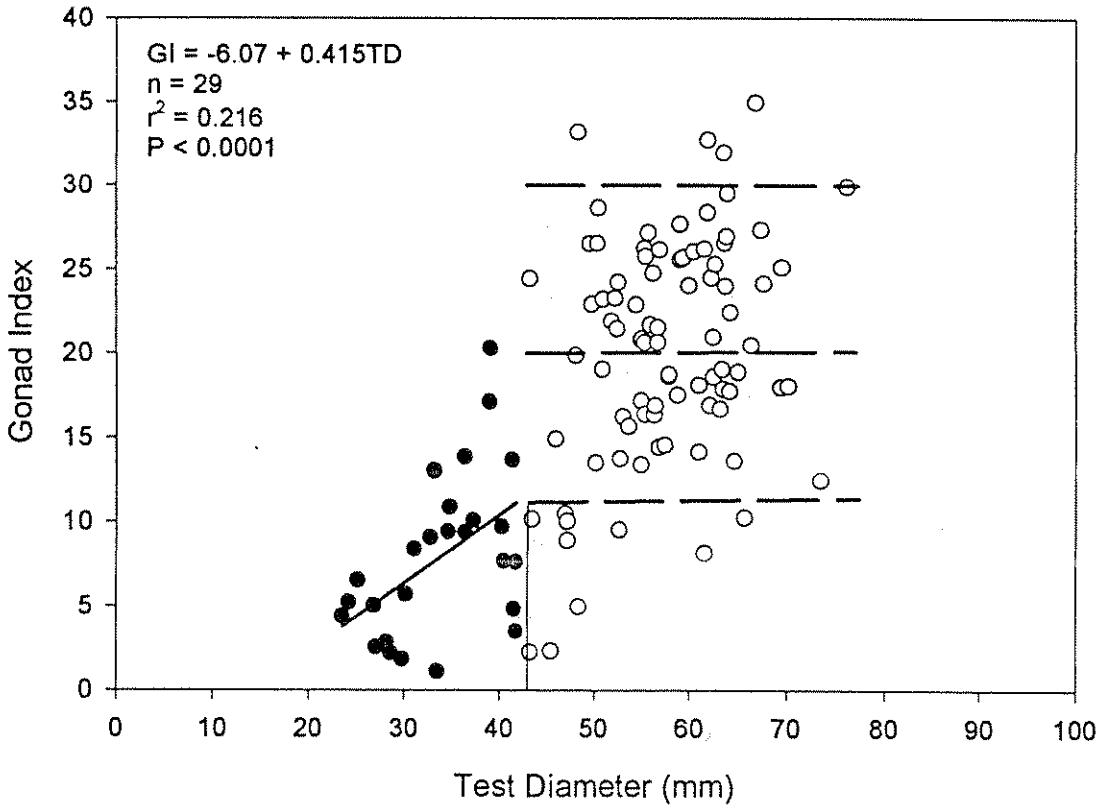


Figure 15a. Relationship between gonad index and test diameter for urchins sampled during January through April from the northeast coast of Maine (N = 391).

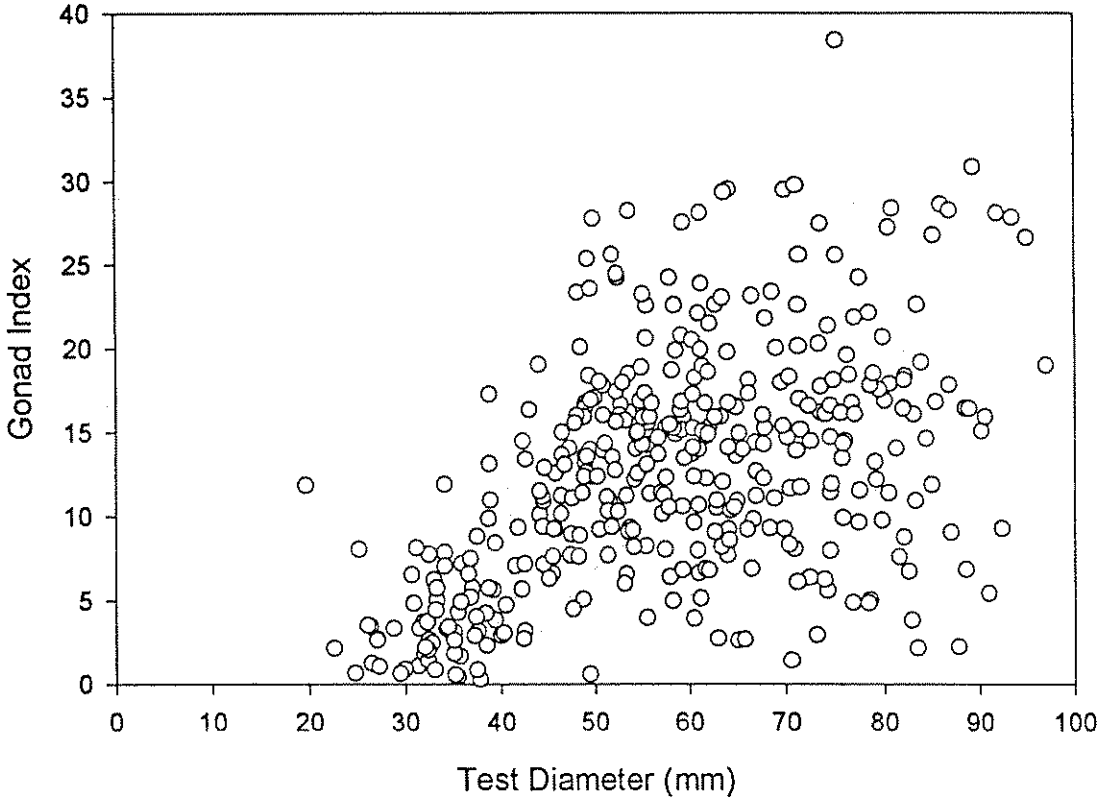


Figure 15b. Asymptotic test diameter showing gonad index is independent of size above 55 mm for urchins sampled from the northeast coast of Maine, N = 151.

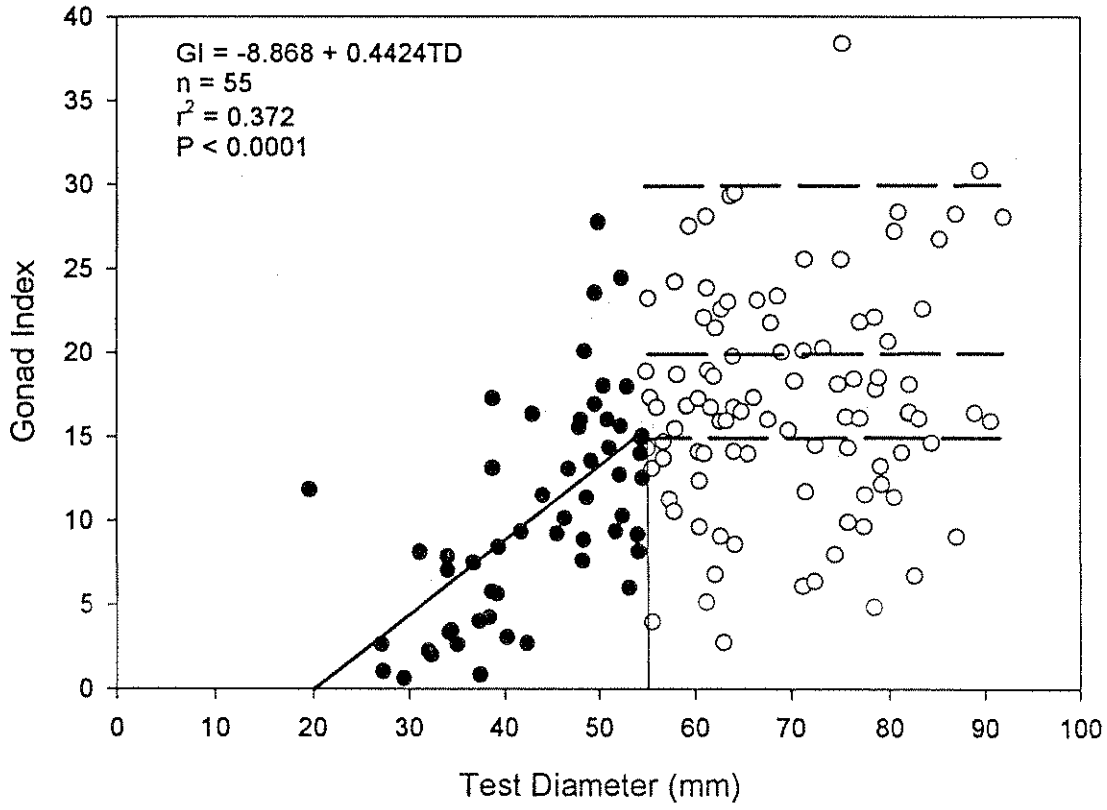


Figure 16a. Relationship between gonad index and test diameter for urchins sampled during January through April pooled from all regions along the coast of Maine (N = 915).

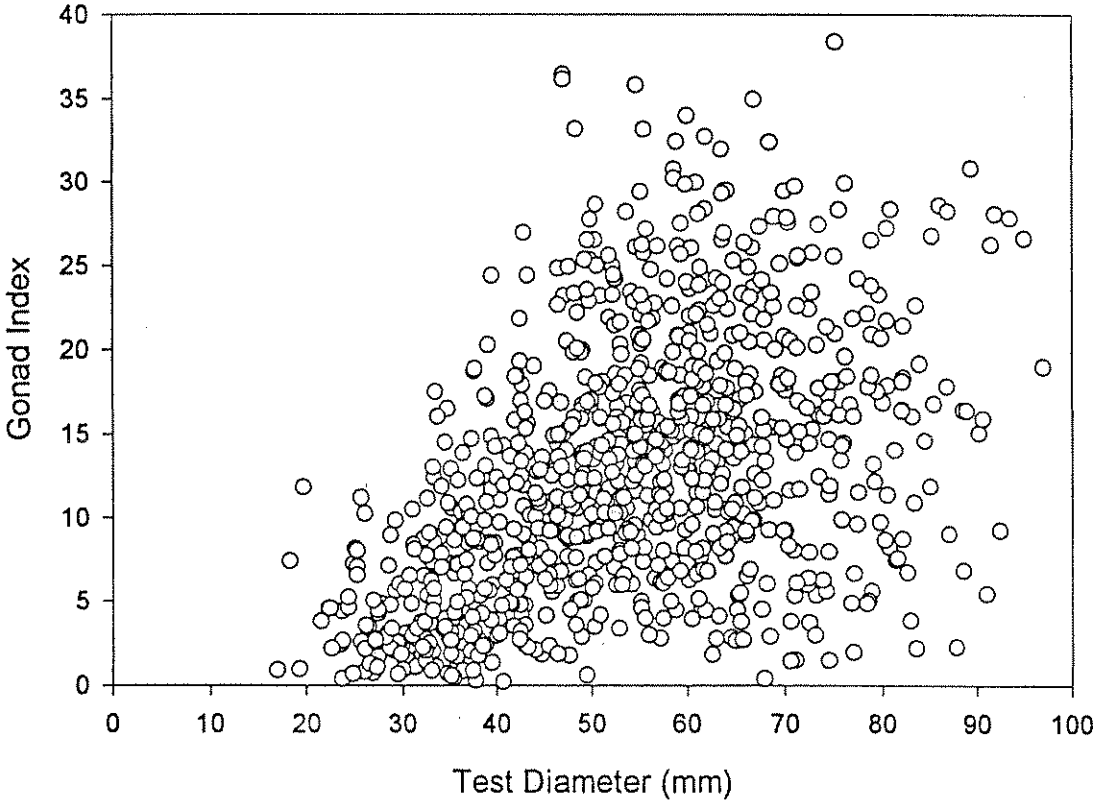


Figure 16b. Asymptotic test diameter showing gonad index is independent of size above 45 mm for urchins pooled from all regions along the coast of Maine, N = 401.

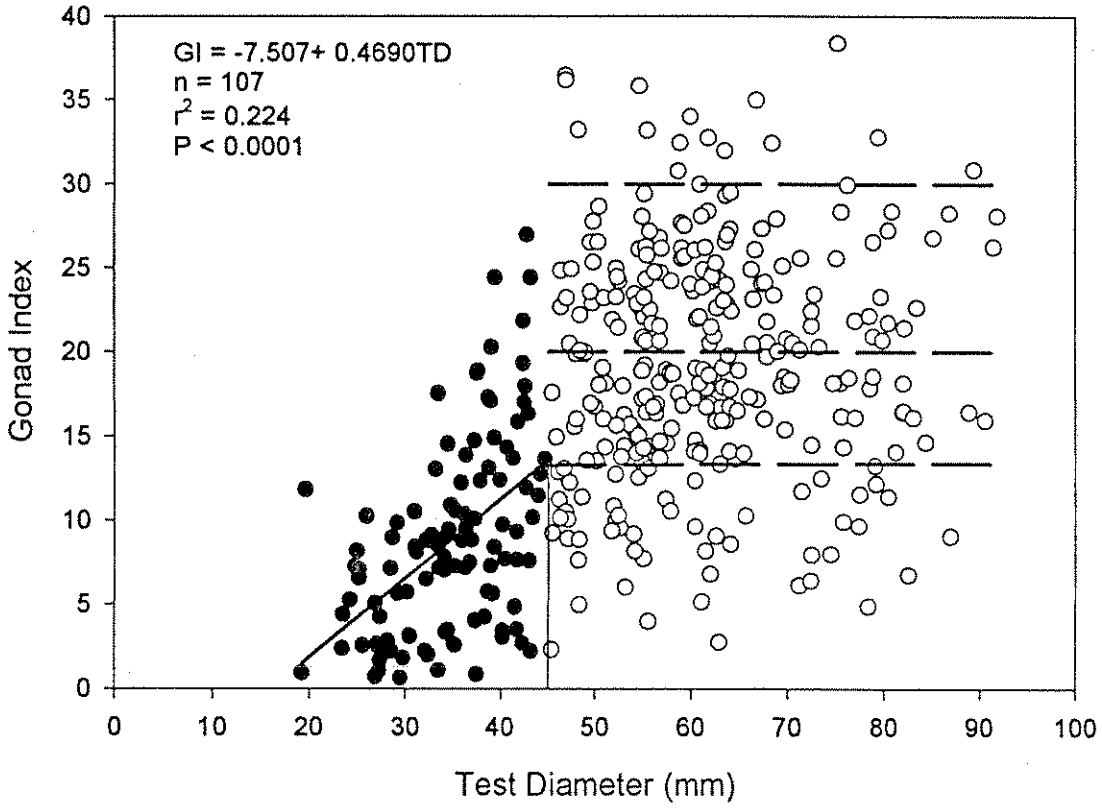


Figure 17. Size at first reproduction expressed as mean number of eggs released from female urchins (< 40 mm test diameter) along the Maine coast (1996 - 1997).

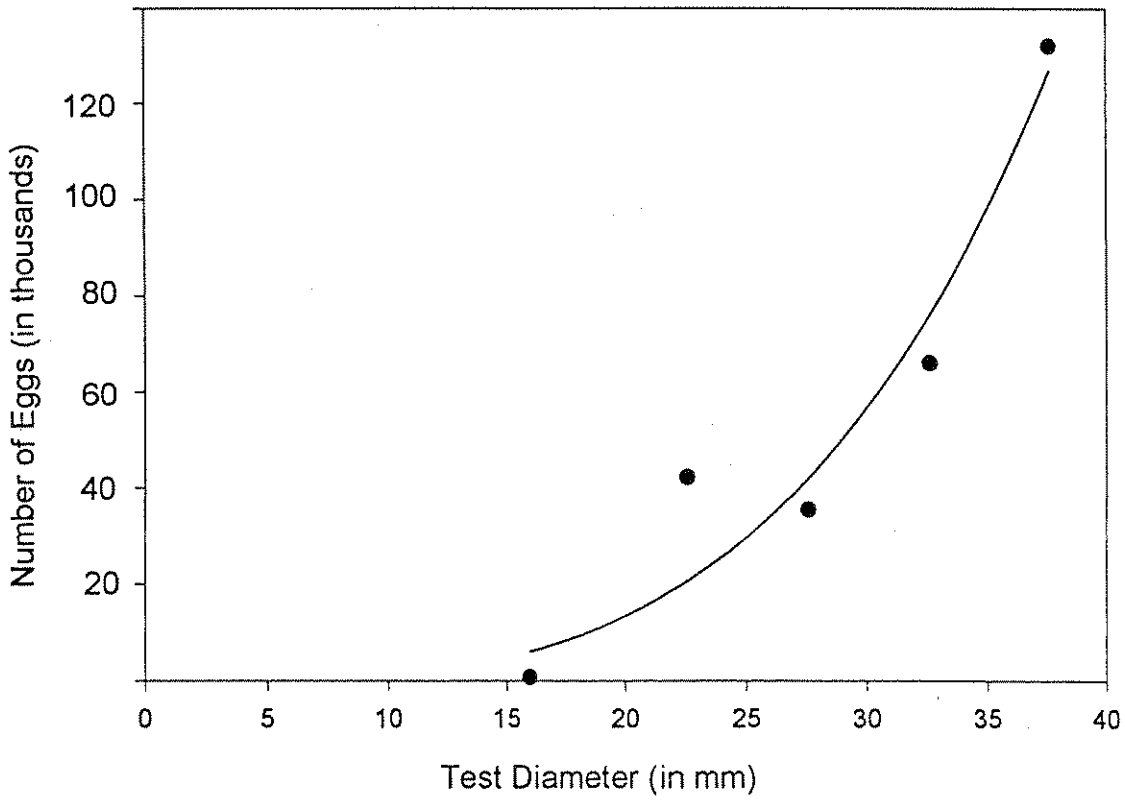


Figure 18a. Relationship between age and test diameter for urchins from the southwest coast of Maine (1996 - 1997) sampled from barren habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

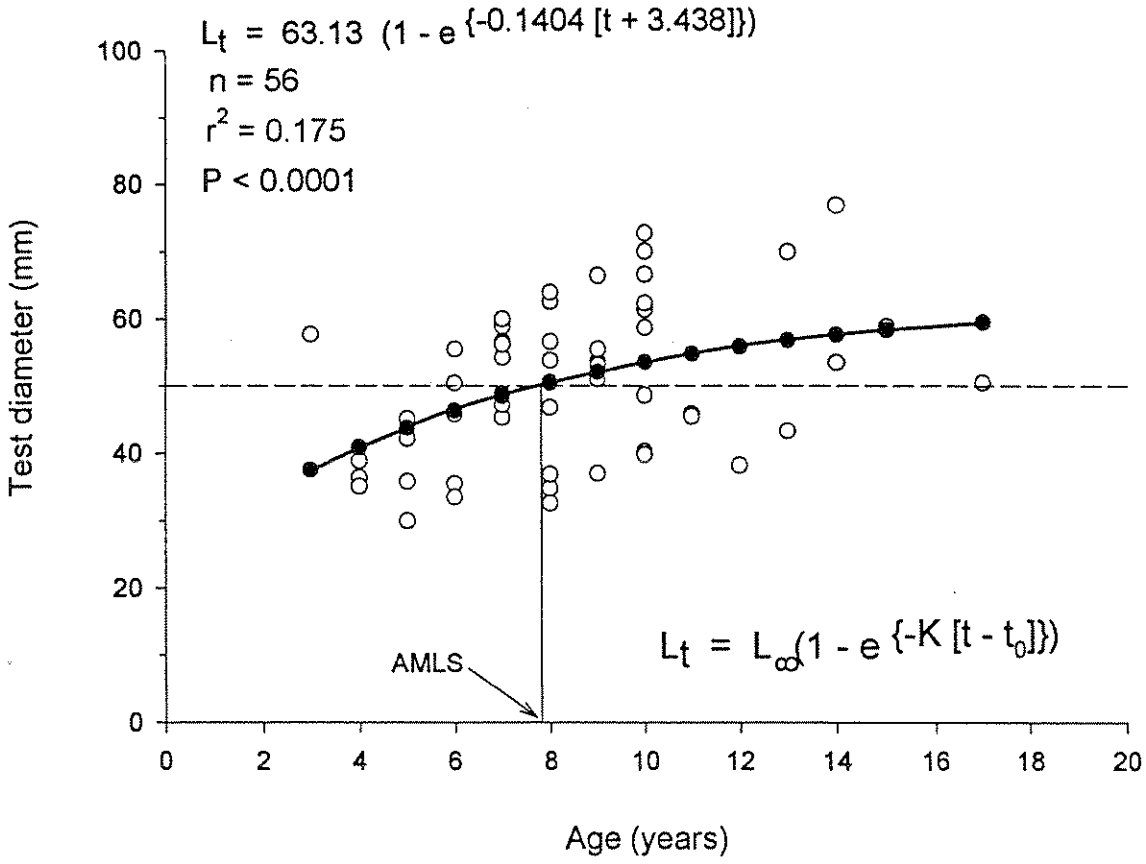


Figure 18b. Relationship between age and test diameter for urchins from the southwest coast of Maine (1996 - 1997) sampled from kelp habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

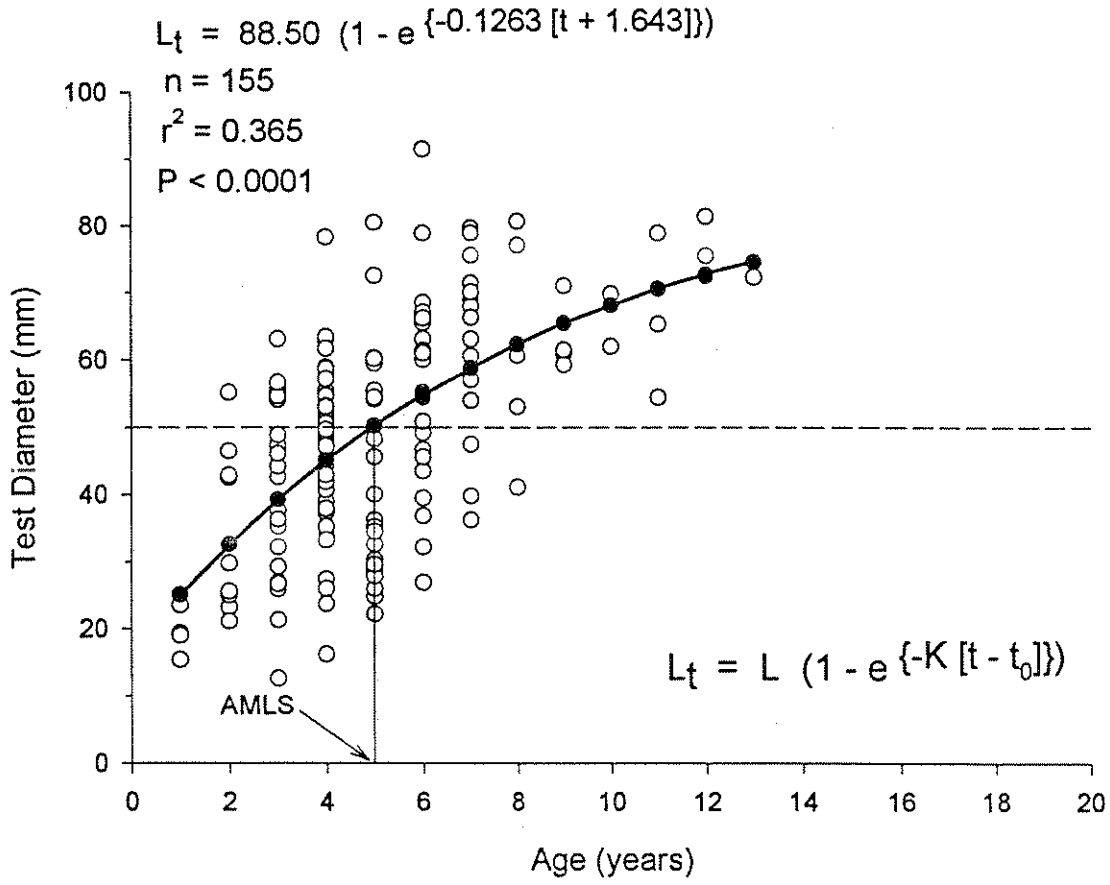


Figure 19a. Relationship between age and test diameter for urchins from the central coast of Maine (1996 - 1997) sampled from barren habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

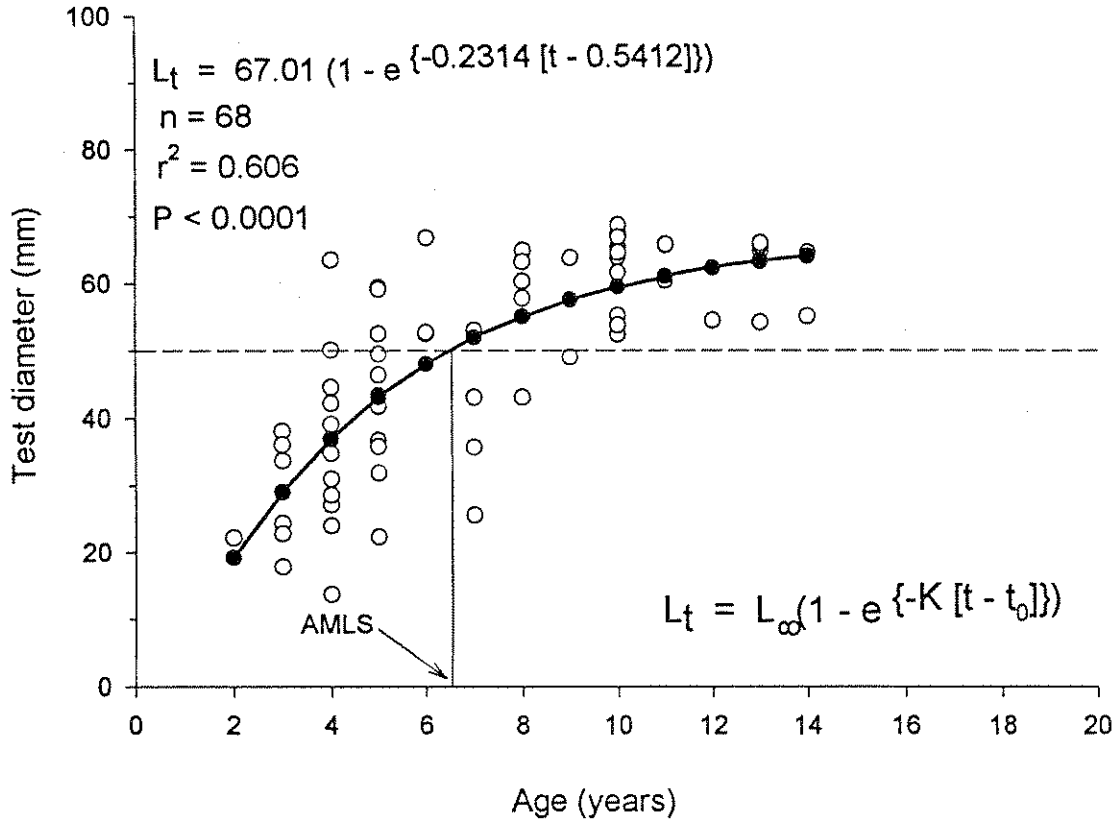


Figure 19b. Relationship between age and test diameter for urchins from the central coast of Maine (1996 - 1997) sampled from kelp habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

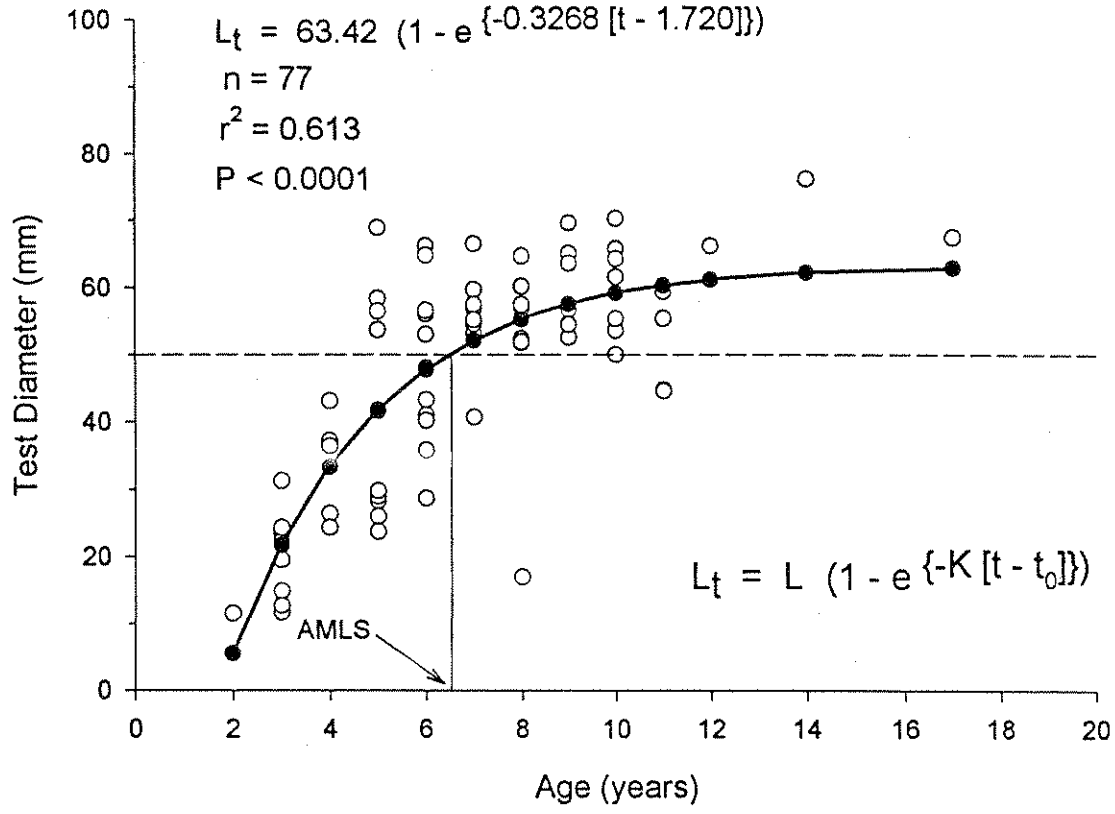


Figure 20a . Relationship between age and test diameter for urchins from the northeast coast of Maine (1996 - 1997) sampled from barren habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

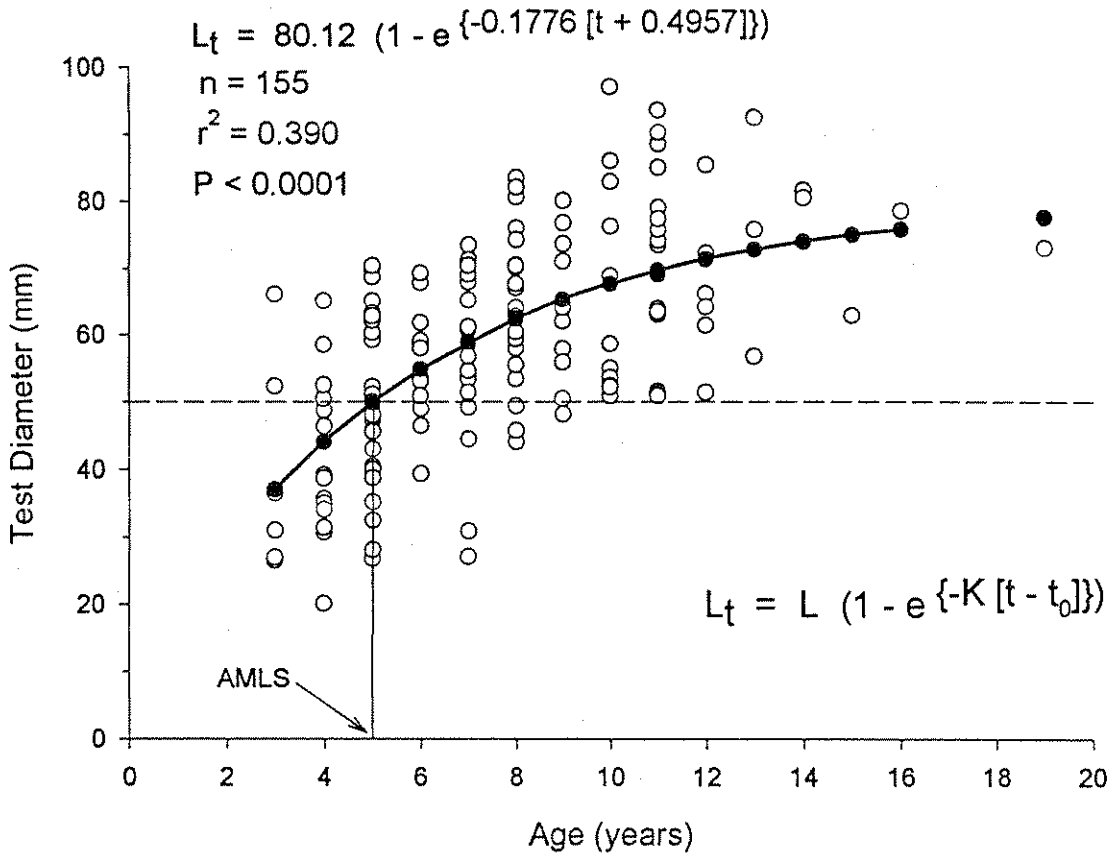


Figure 20b. Relationship between age and test diameter for urchins from the northeast coast of Maine (1996 - 1997) sampled from kelp habitat. (AMLS = age at minimum legal size as defined by the von Bertalanffy growth function.)

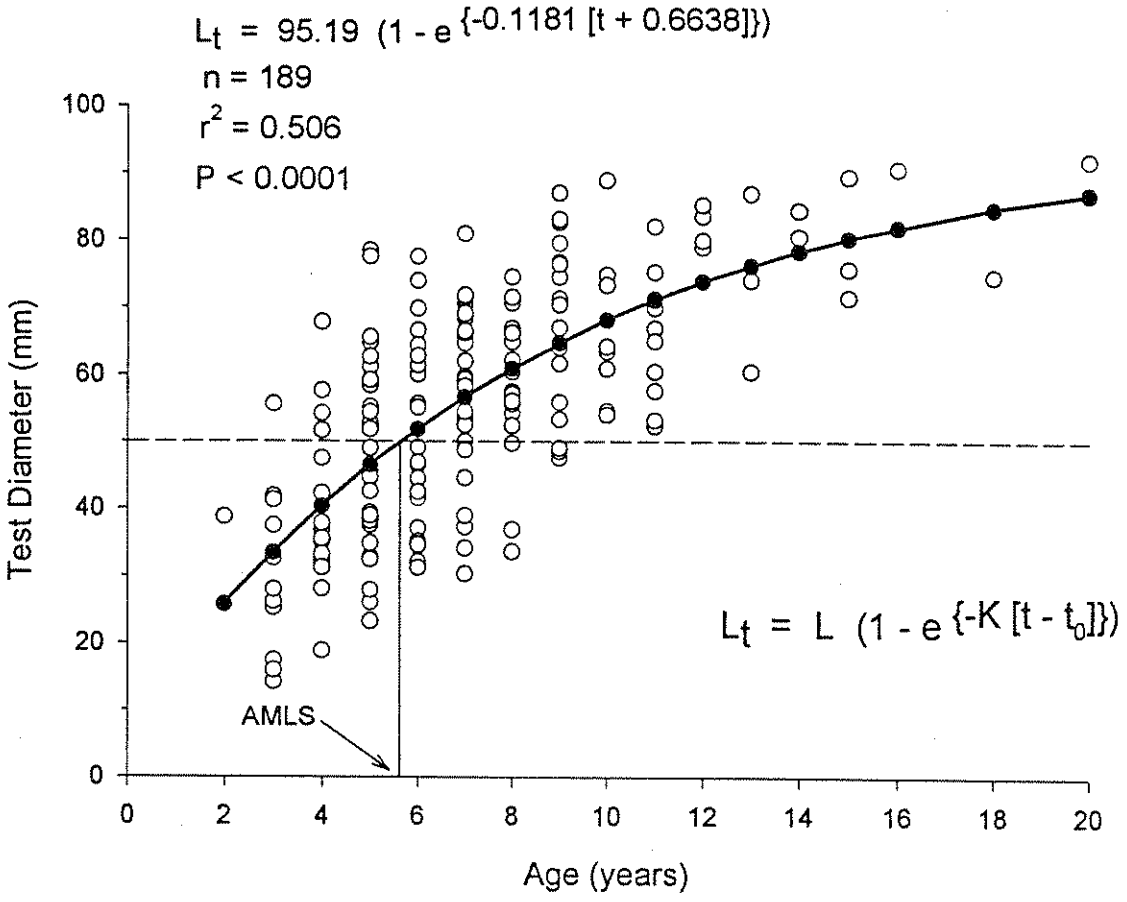
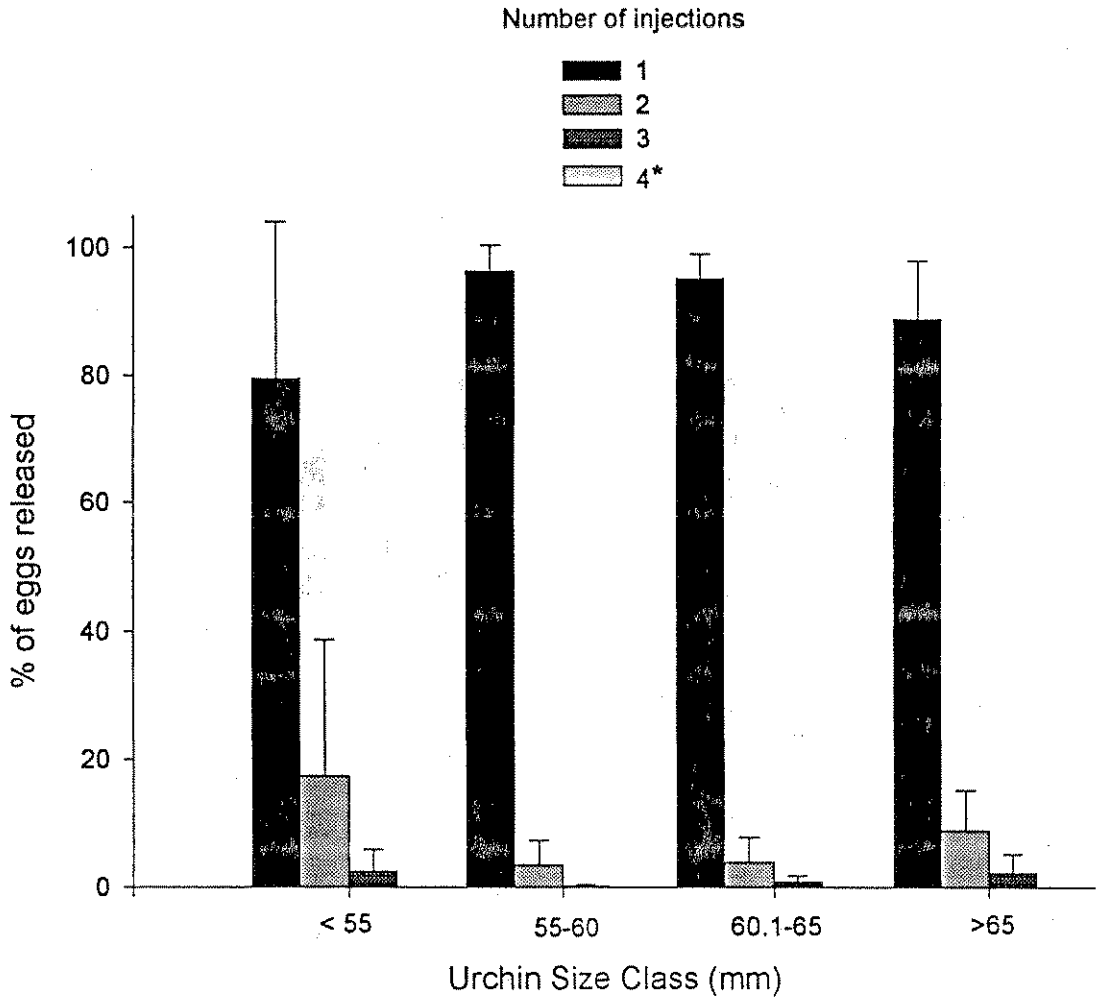


Figure 21. Percent of eggs released by *Strongylocentrotus droebachiensis* in four size classes (test diameter range of 44.8 - 71.3 mm) after multiple injections with 2M KCl. (Samples from Lubec)



*No release with fourth injection.

Figure 22a. Percent spawned in each of 14 size classes for urchin from the southwest coast of Maine.

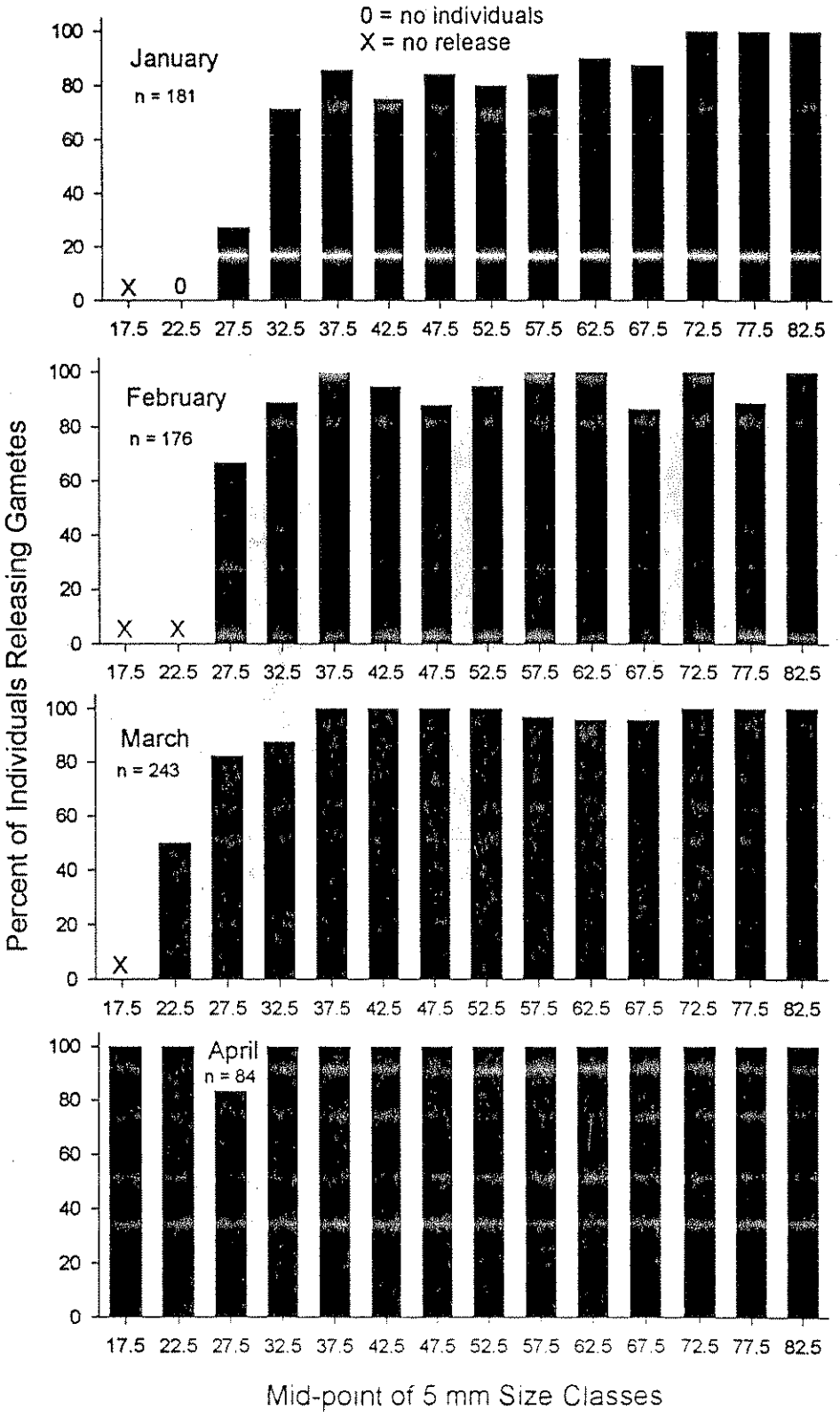


Figure 22b. Percent spawned in each of 14 size classes for urchin from the central coast of Maine.

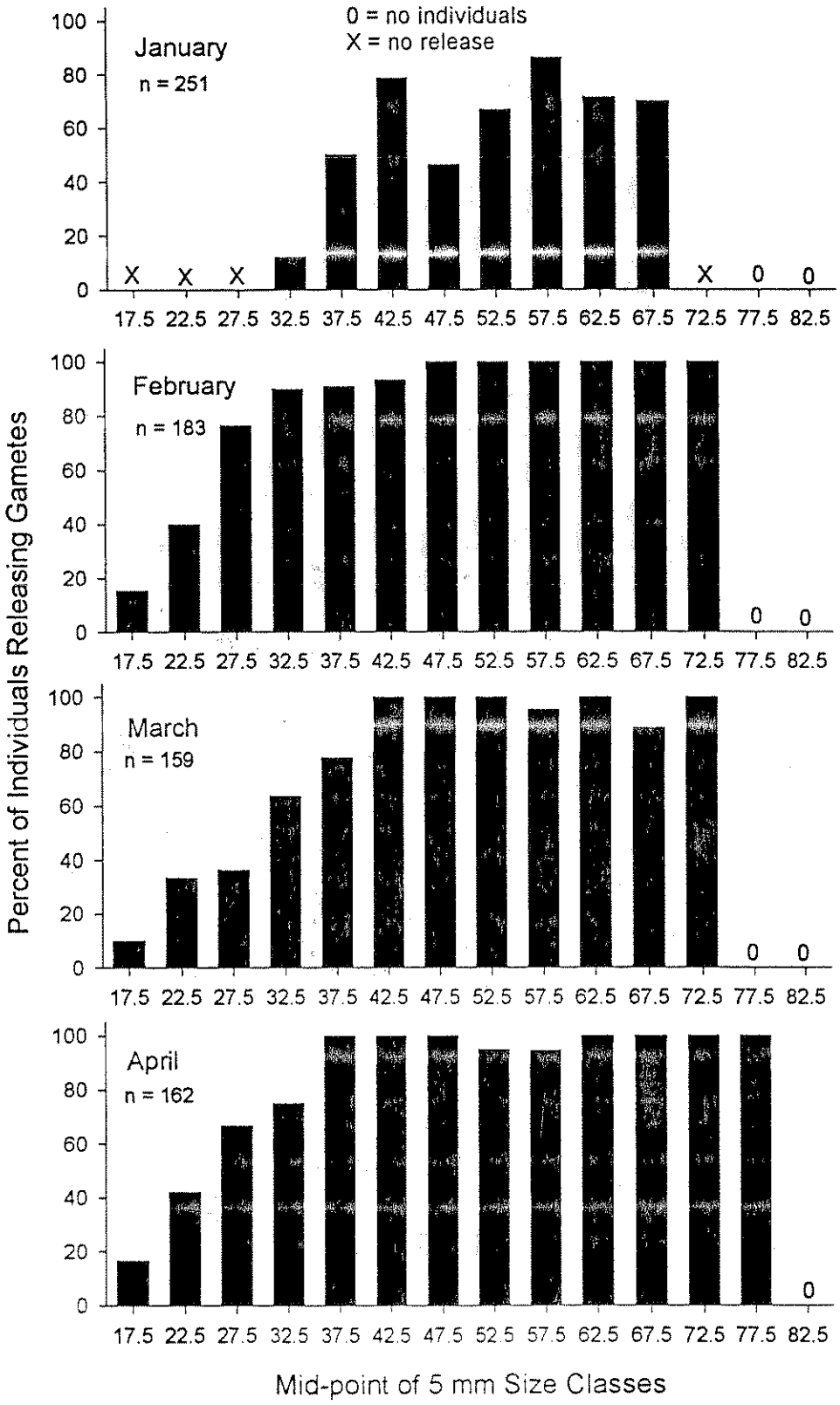


Figure 22c. Percent spawned in each of 14 size classes for urchin from the northeast coast of Maine.

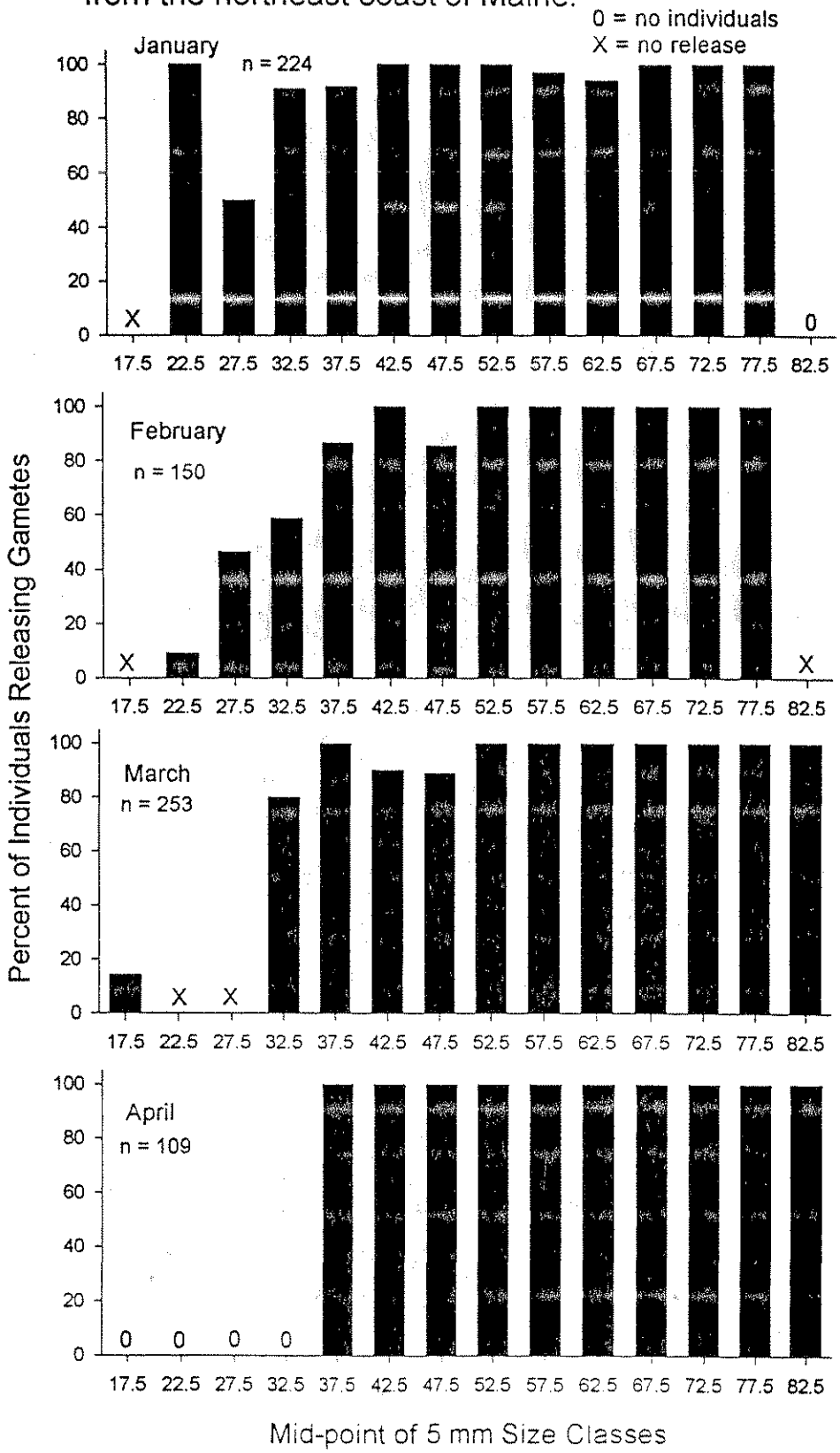


Figure 23. Relationship between urchin test diameter and number of eggs for urchins along the Maine coast during 1996 (March - May).

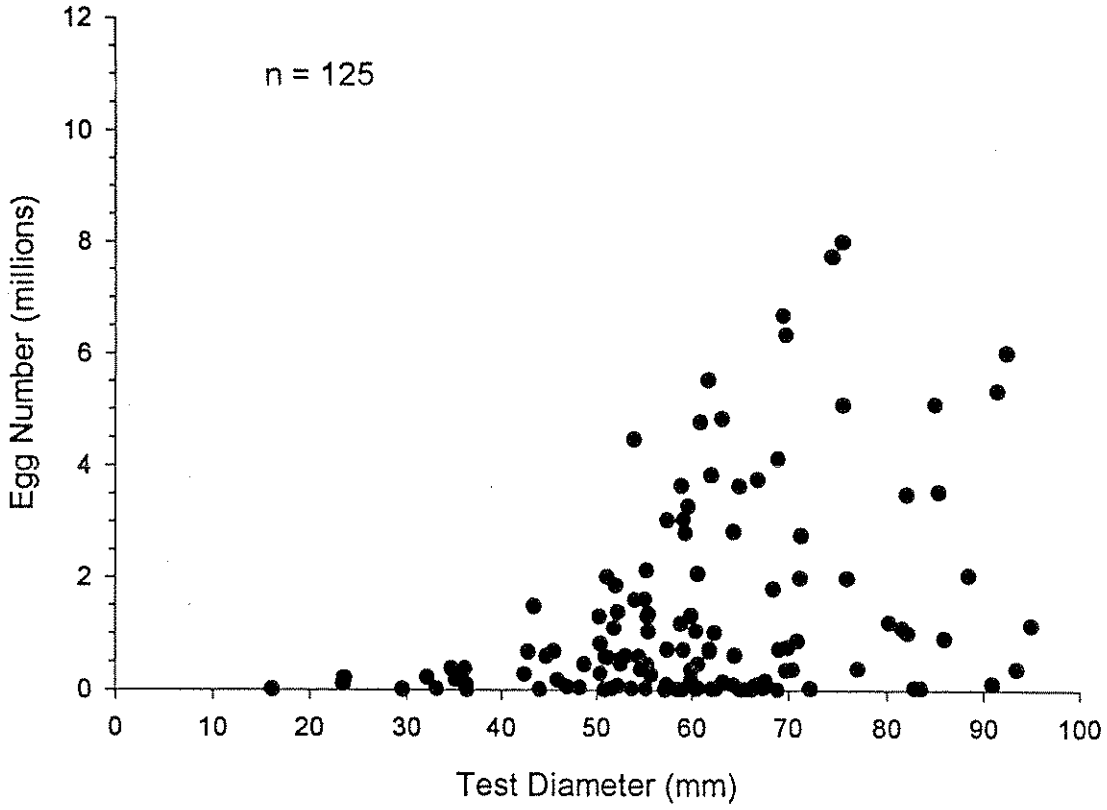


Figure 24. Relationship between urchin test diameter and number of eggs from two habitats along the southwest coast of Maine for January - March, 1997.

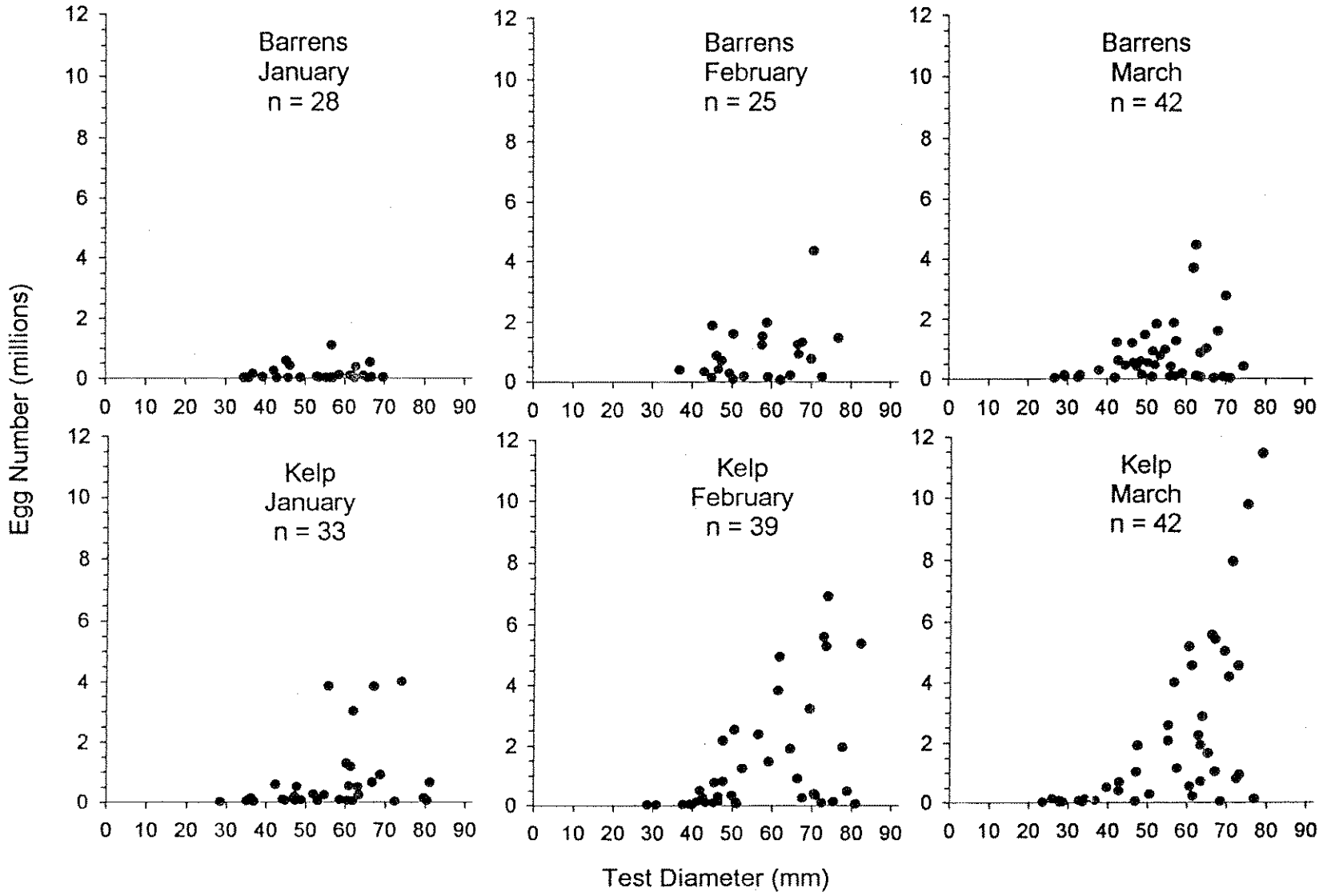


Figure 25. Relationship between urchin test diameter and number of eggs from two habitats along the central coast of Maine for January - April, 1997.

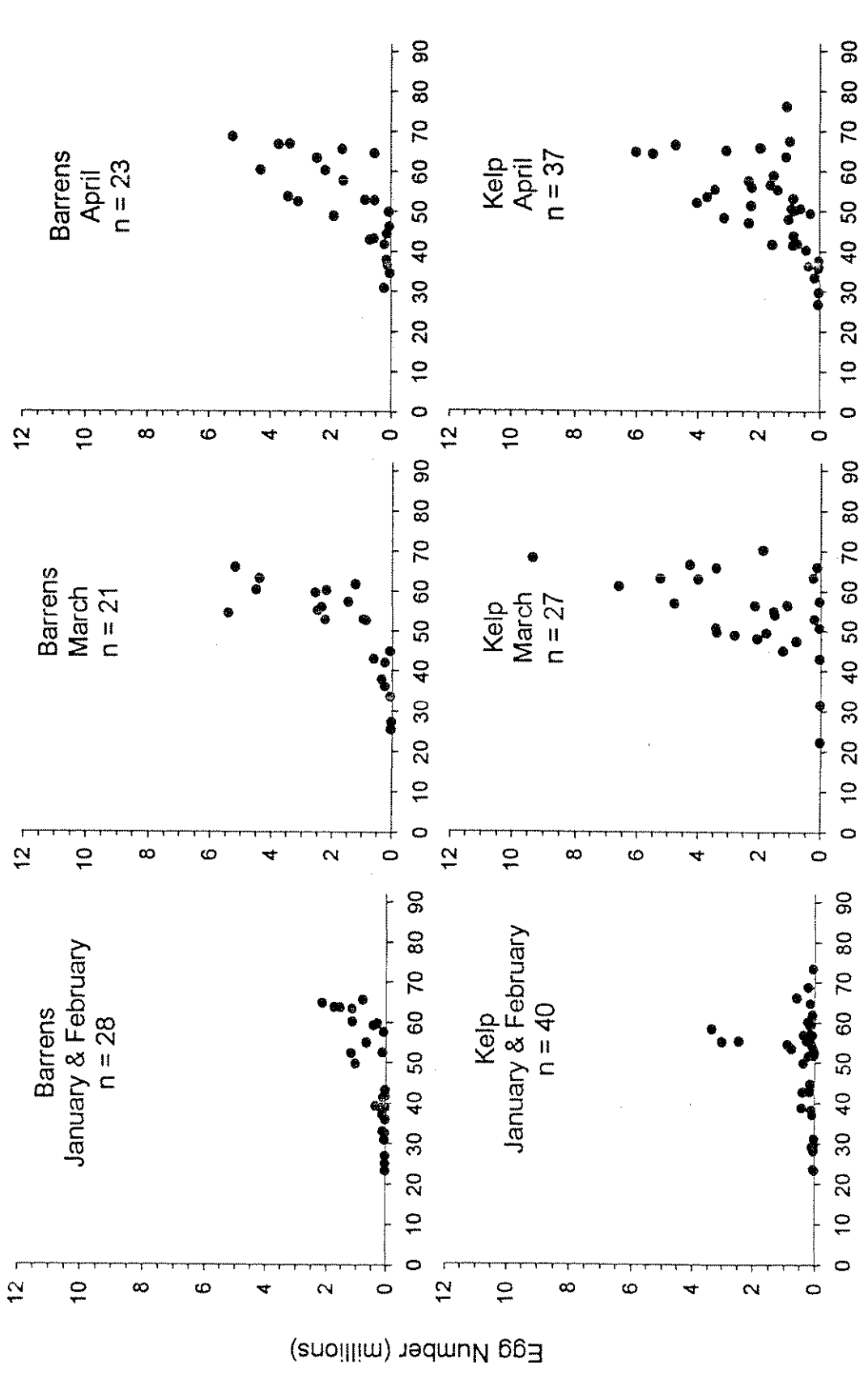


Figure 26. Relationship between urchin test diameter and number of eggs from two habitats along the northeast coast of Maine for January - March, May, 1997.

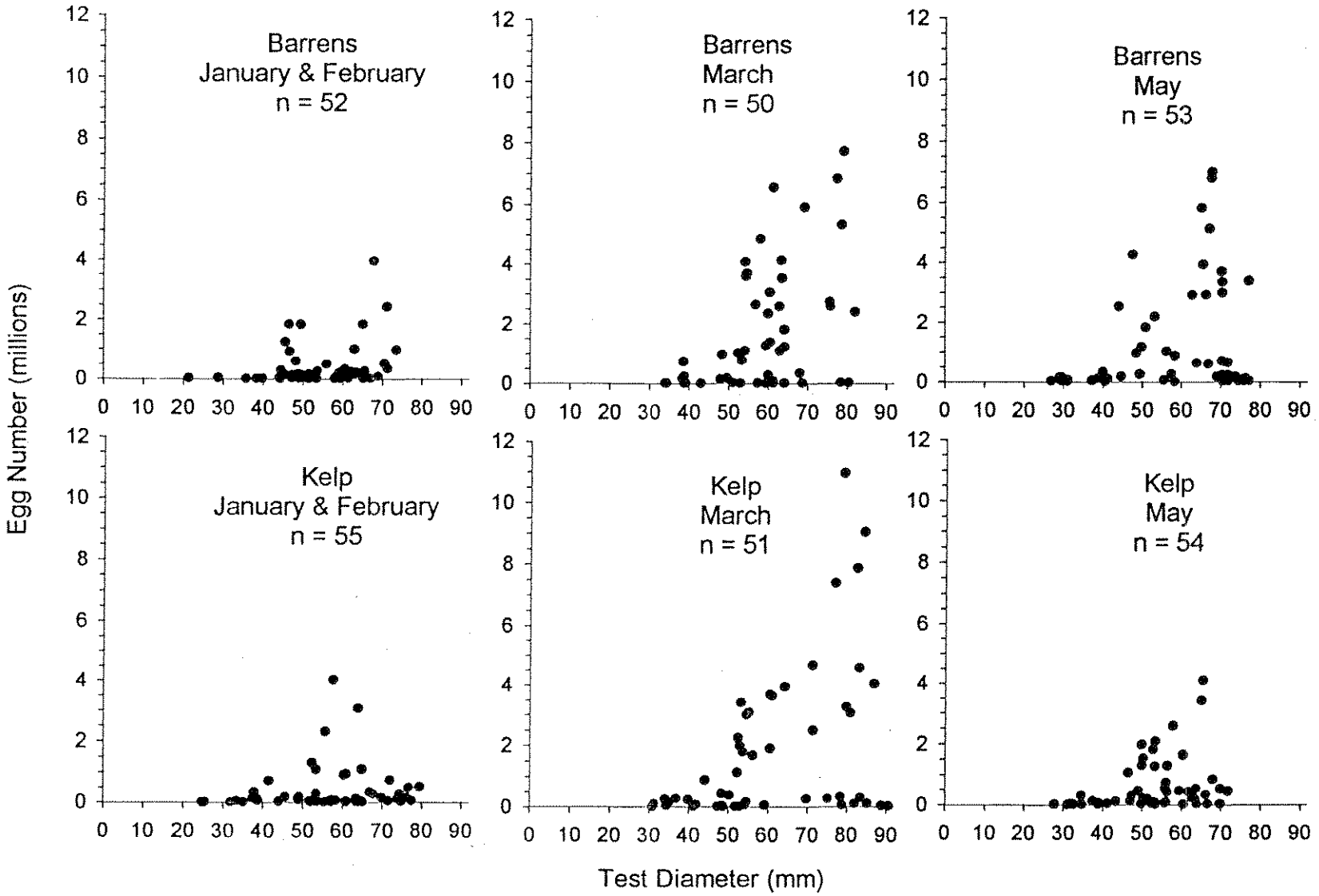


Figure 27. Mean number of eggs (-1 SE) in eight size classes of *Strongylocentrotus droebachiensis* samples from the southwest coast for January - March, 1997.

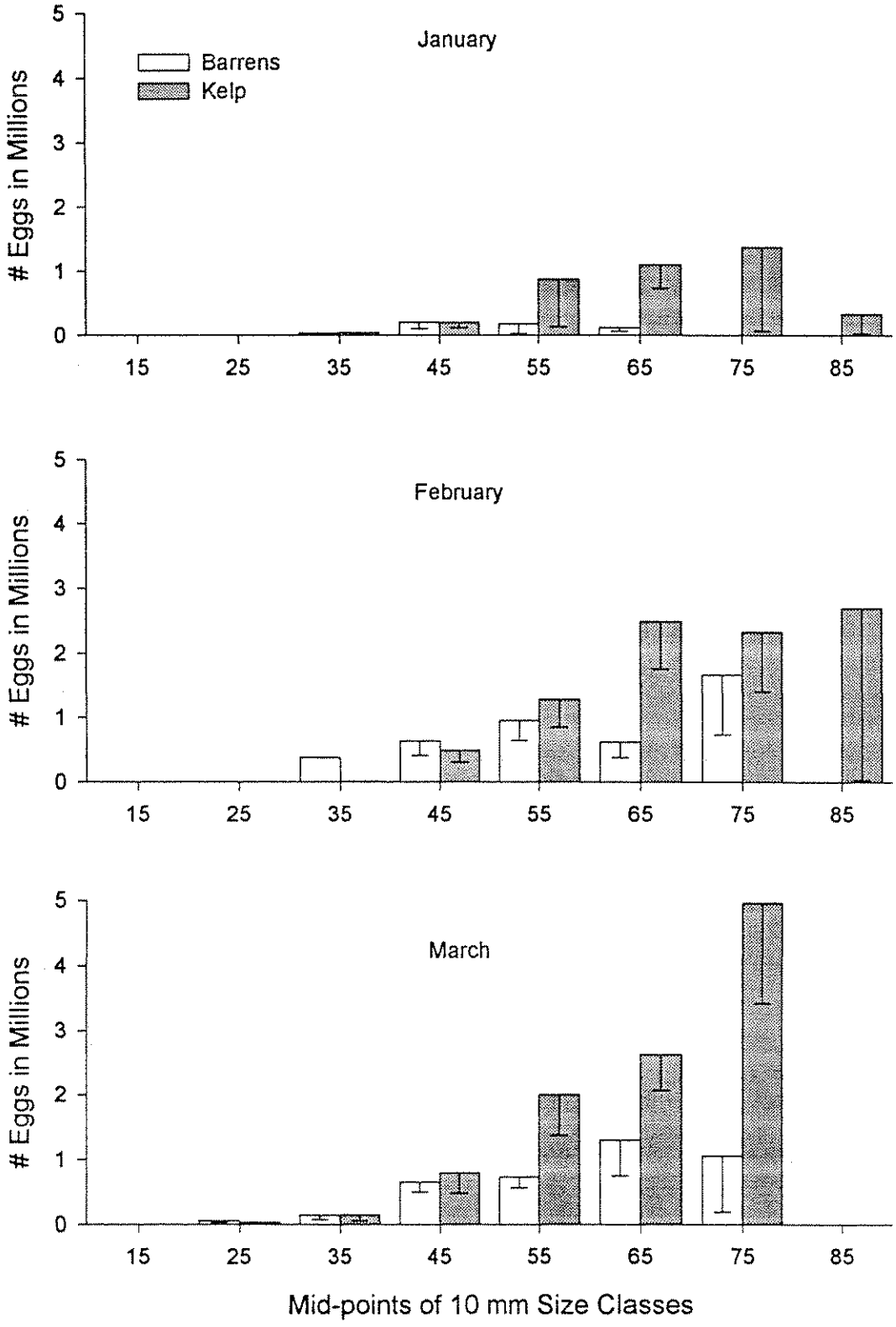


Figure 28. Mean number of eggs (-1 SE) in eight size classes of *Strongylocentrotus droebachiensis* samples from the central coast for January - April, 1997.

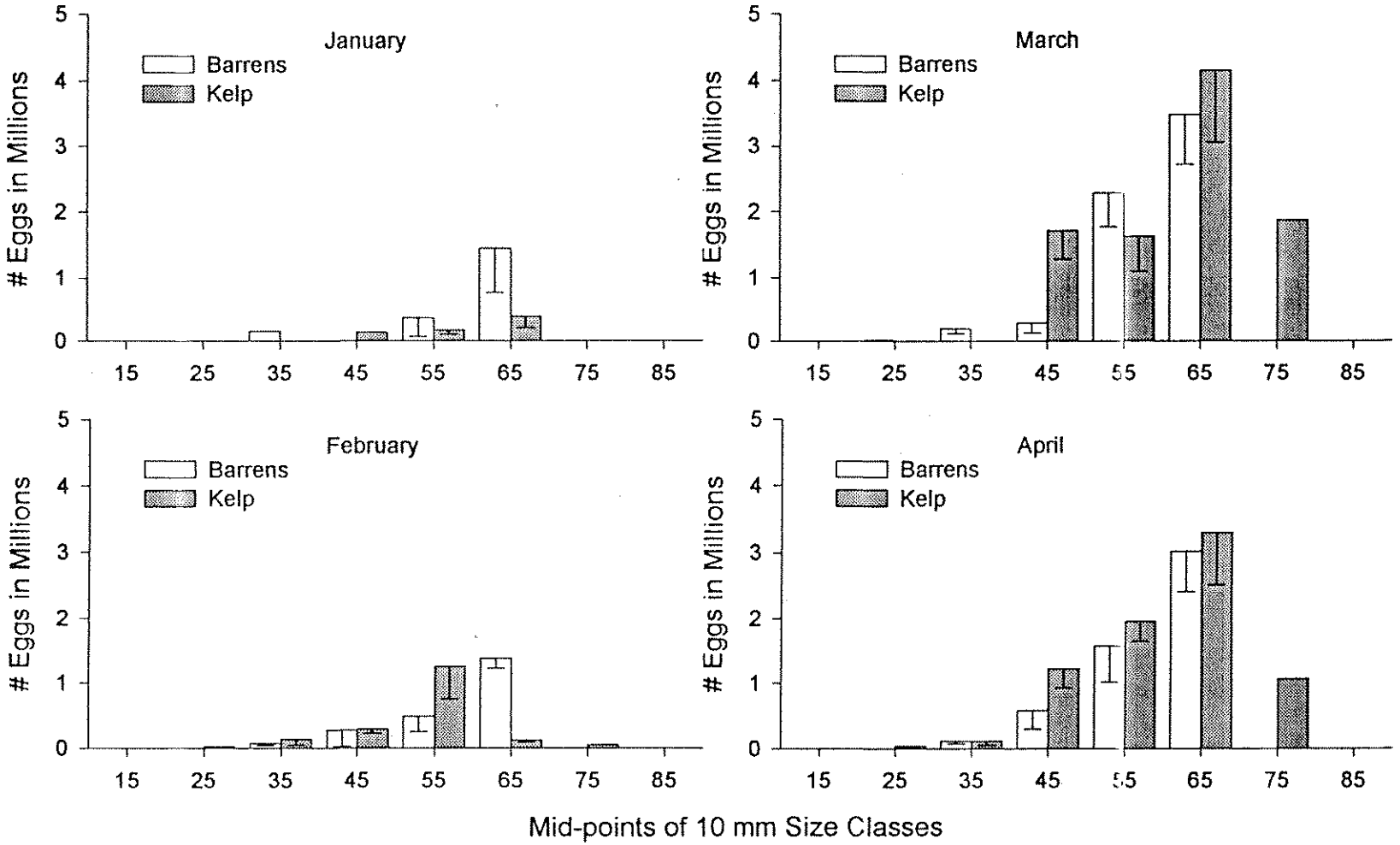


Figure 29. Mean number of eggs (-1 SE) in eight size classes of *Strongylocentrotus droebachiensis* samples from the northeast coast for January - March, May, 1997.

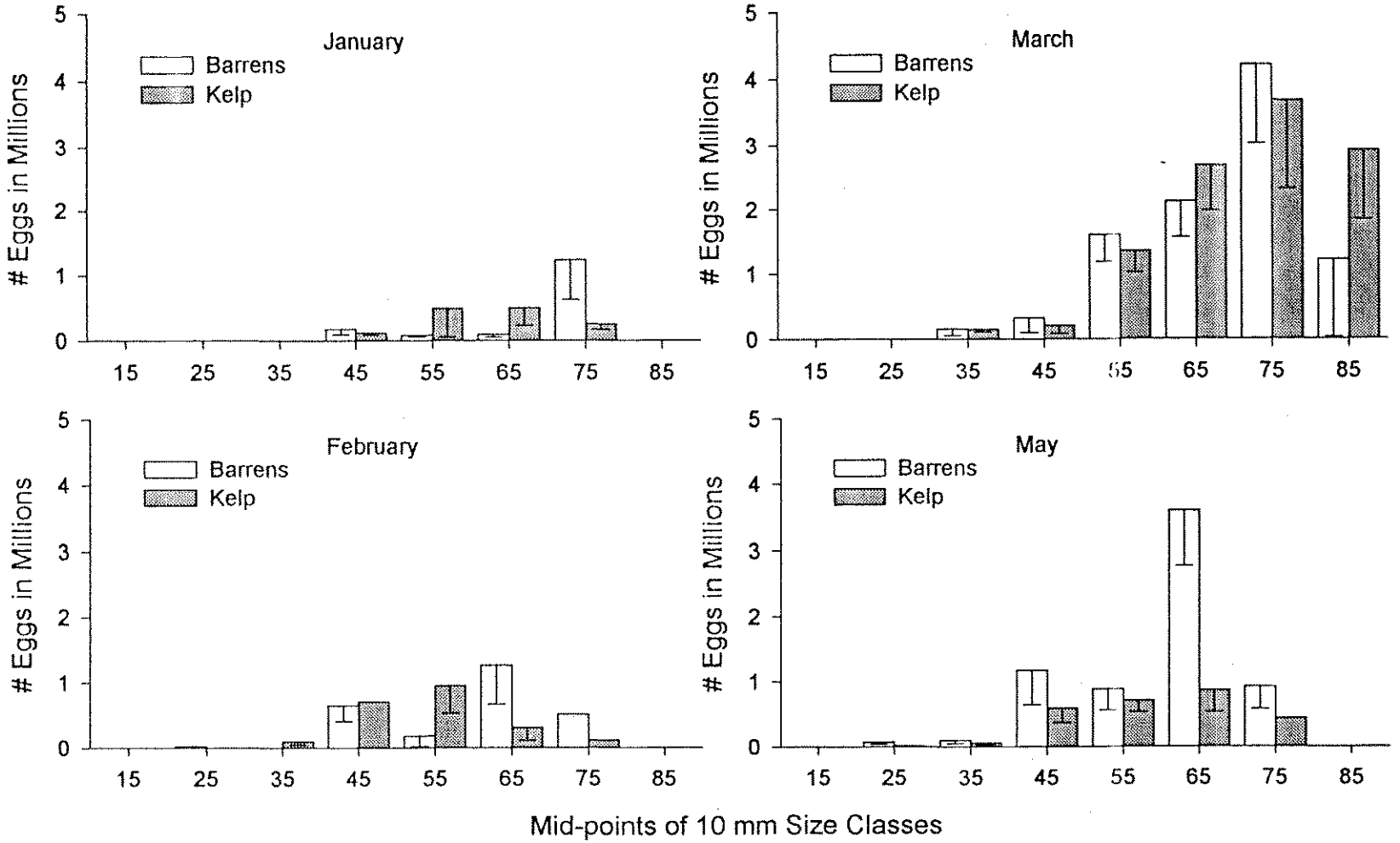


Figure 30. Relationship between urchin age and number of eggs for urchins along the Maine coast during 1996 (March - May).

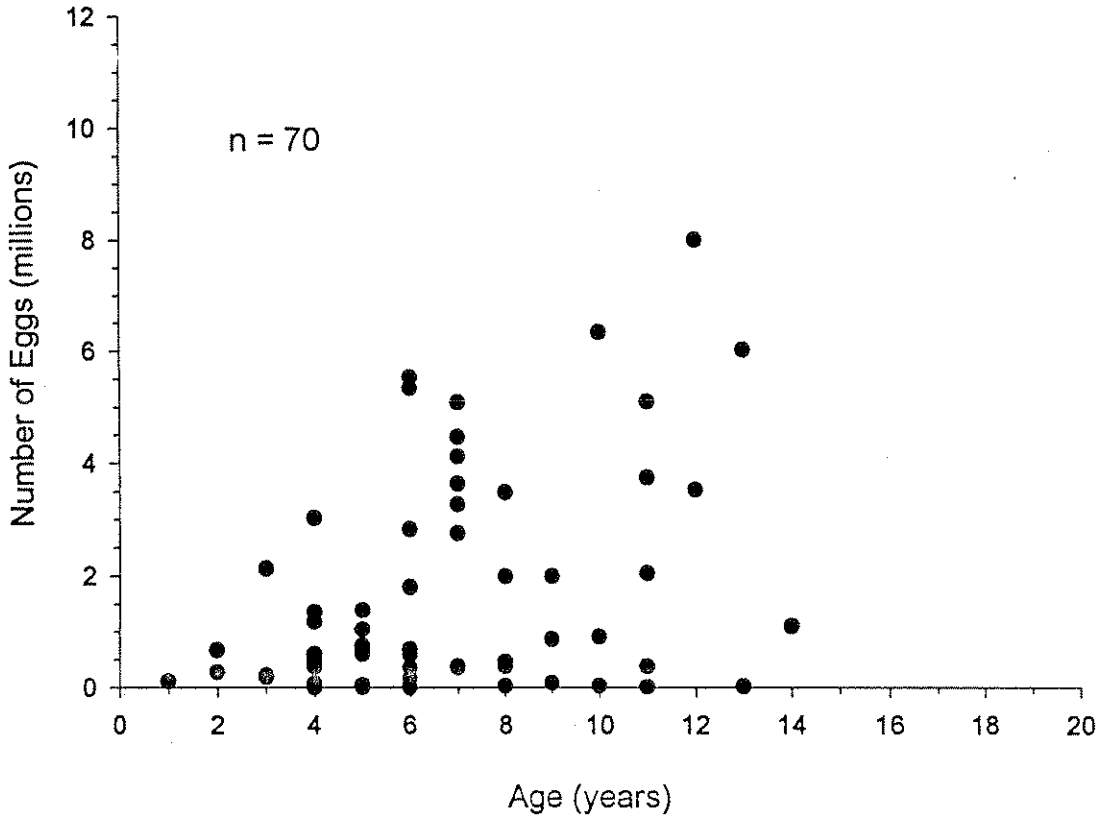


Figure 31. Relationship between urchin age and number of eggs from two habitats along the southwest coast of Maine for January - March, 1997.

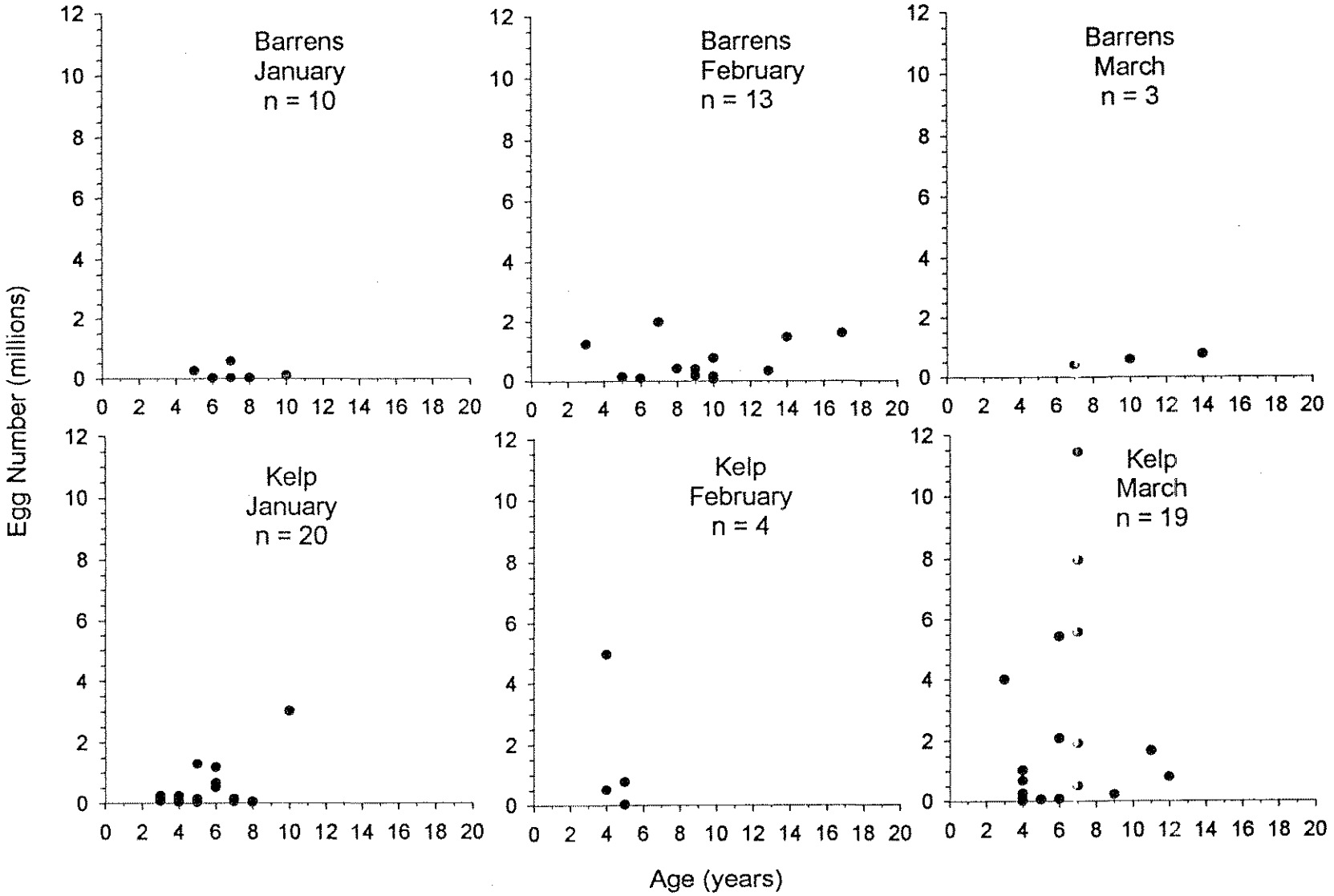


Figure 32. Relationship between urchin age and number of eggs from two habitats along the central coast of Maine for January - April, 1997.

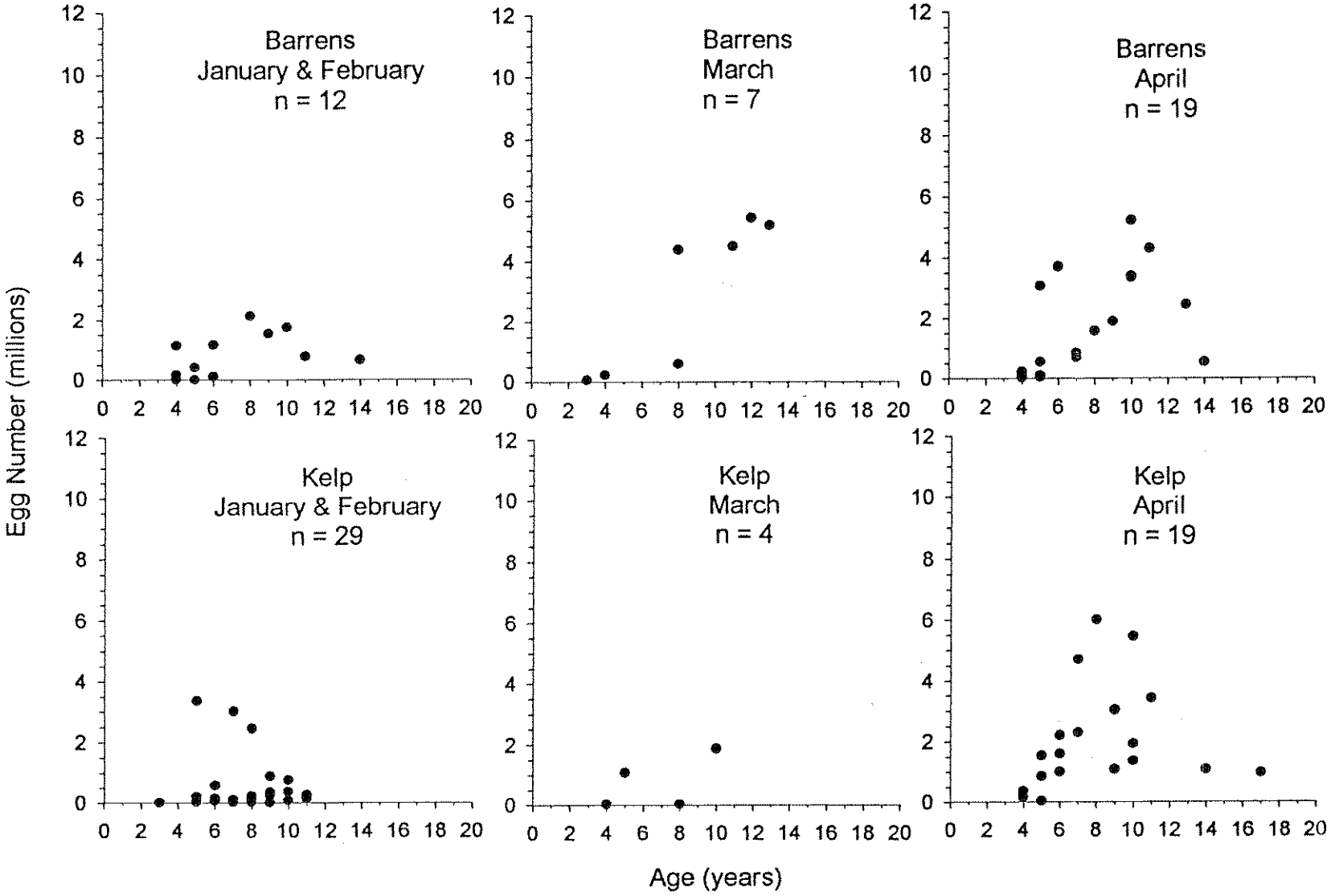


Figure 33. Relationship between urchin age and number of eggs from two habitats along the northeast coast of Maine for January - March, May, 1997.

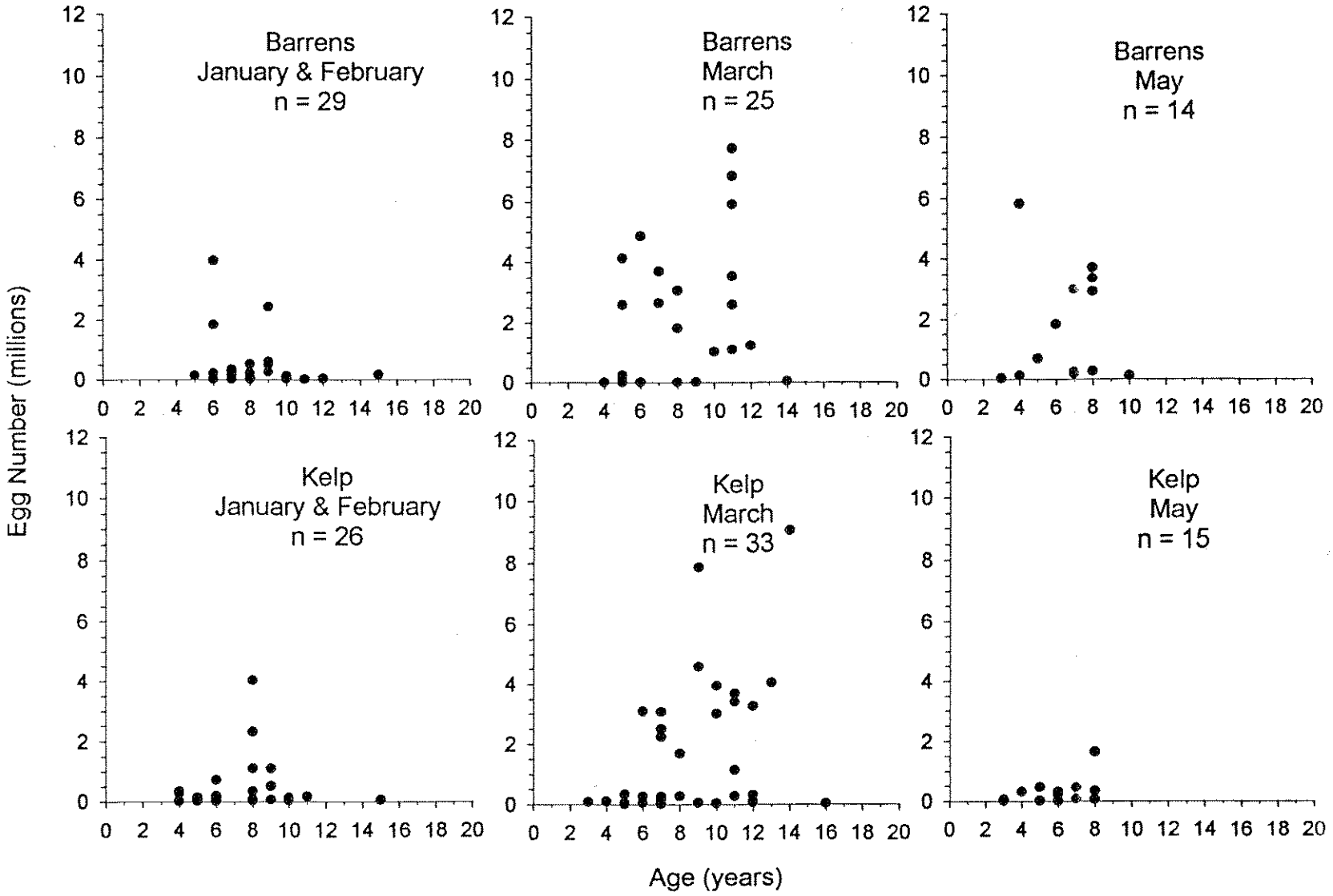


Figure 34. Relationship between urchin weight and number of eggs for urchins along the Maine coast during 1996 (March - May).

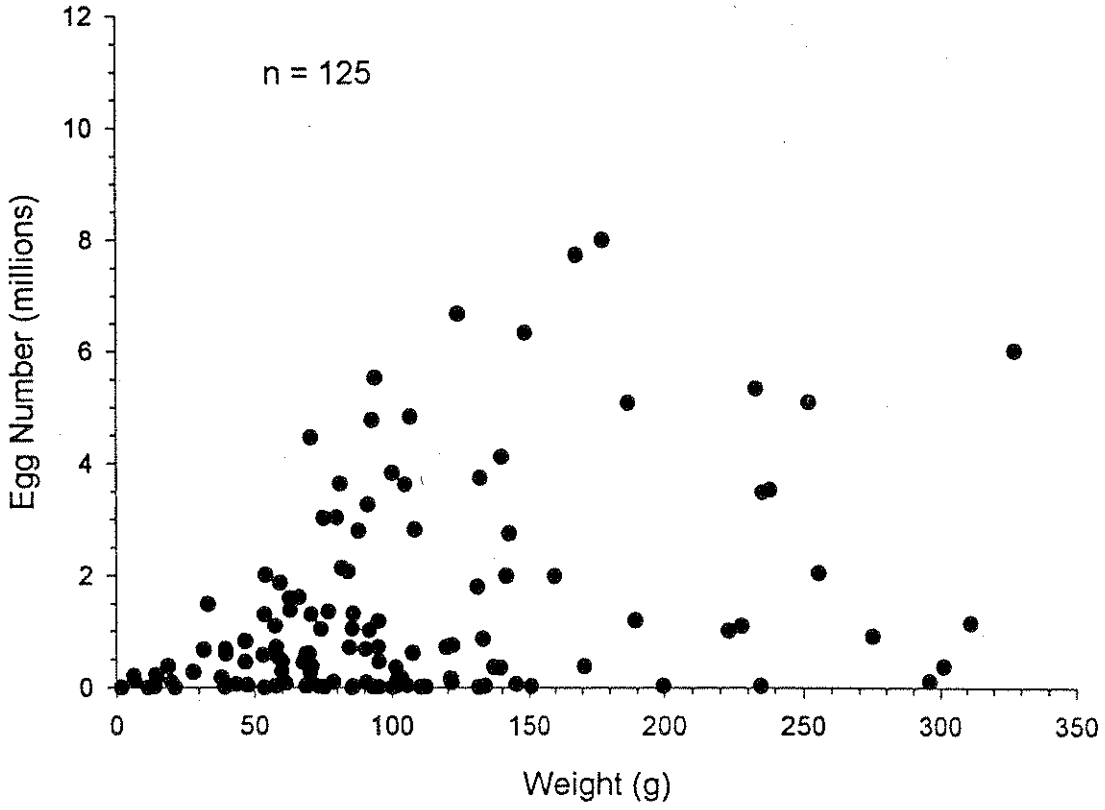


Figure 35. Relationship between urchin weight and number of eggs from two habitats along the southwest coast of Maine for January - March, 1997.

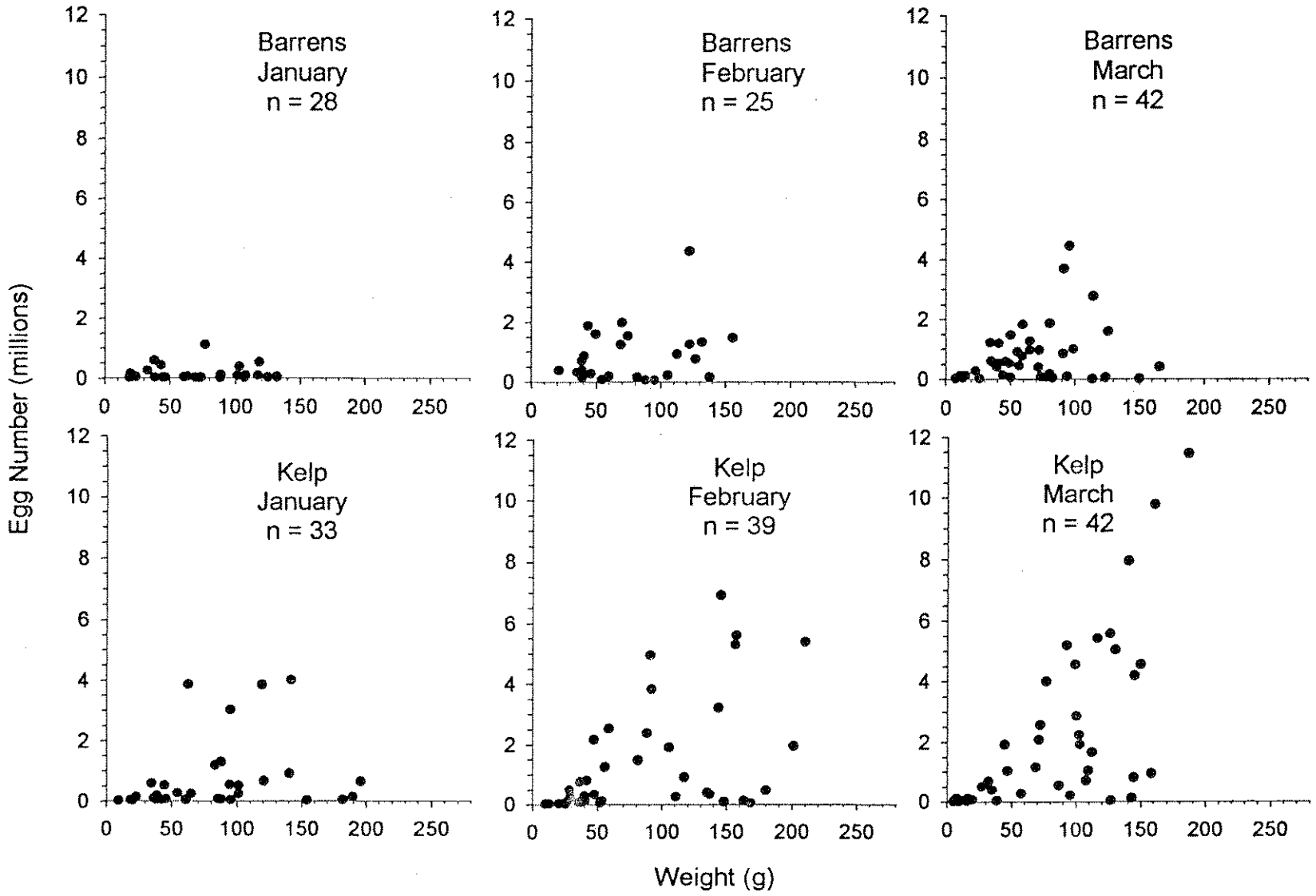


Figure 36. Relationship between urchin weight and number of eggs from two habitats along the central coast of Maine for January - April, 1997.

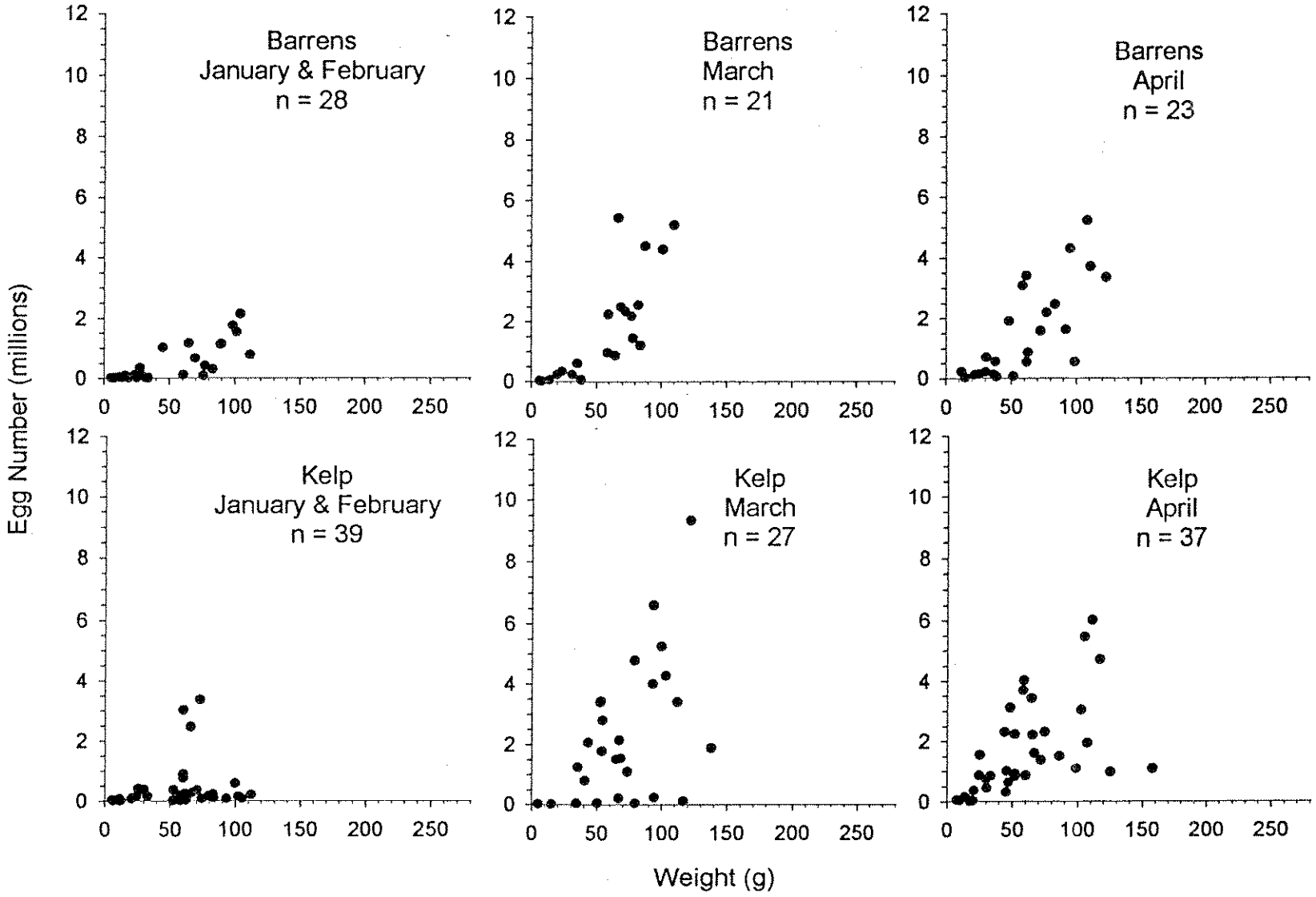


Figure 37. Relationship between urchin weight and number of eggs from two habitats along the northeast coast of Maine for January - March, May, 1997.

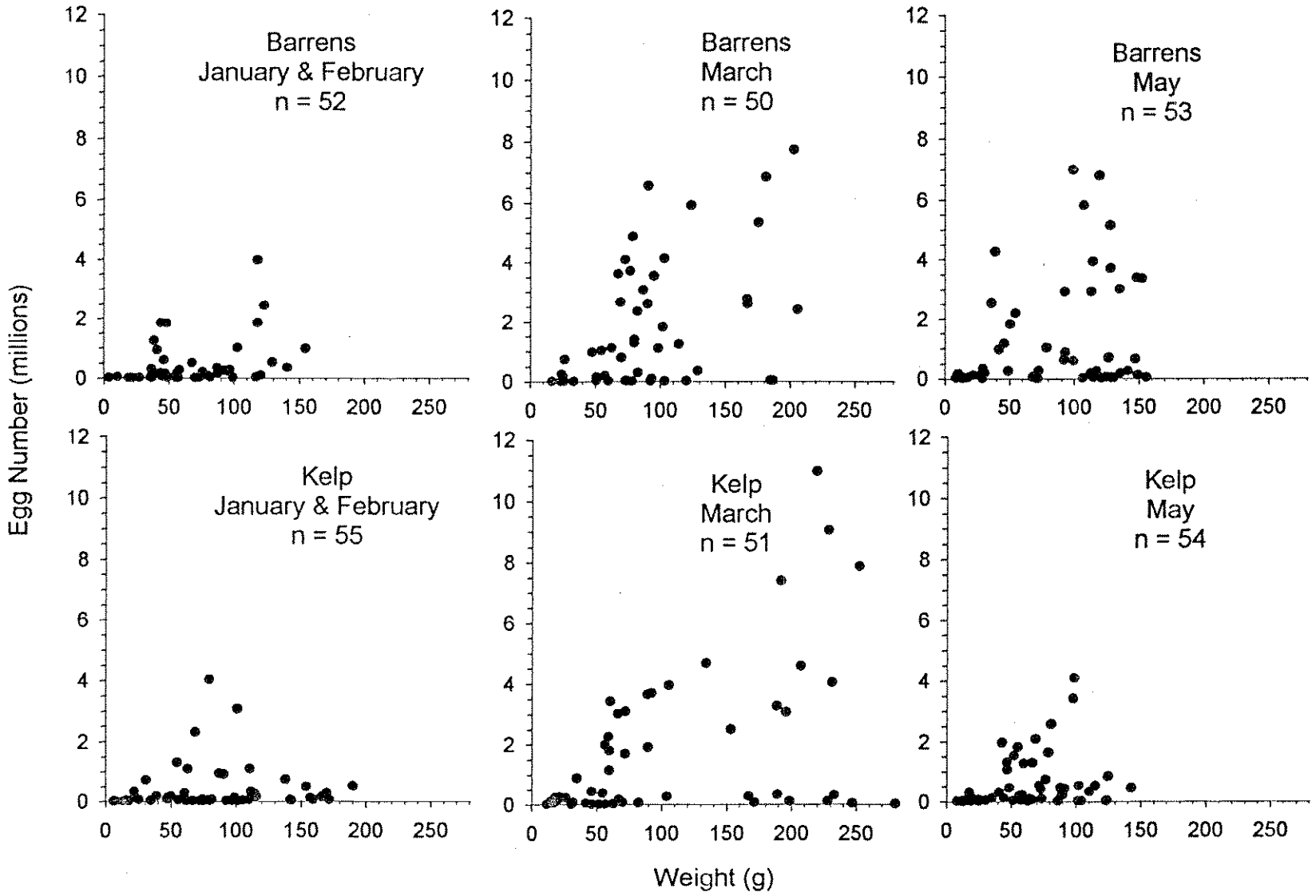


Fig. 38. (a-c): Observed (+) and predicted (solid circles) annual growth increments in interambulacral plate size for the fast-growing and slow-growing morphs at Allen Island in 1997, and the single morph at Schoodic in 1997. Year-effects are evident in plots a-c as parallel strings of growth increment predictions, each string portraying the growth function for one year. The data in plots a-c are expressed as size (cumulative interband distance, CID) -at-age plots in plots d-f. In this portrayal only the mean predicted size-at-age is indicated (i.e., year-effects are not separated as in plots a-c).

Figure 38

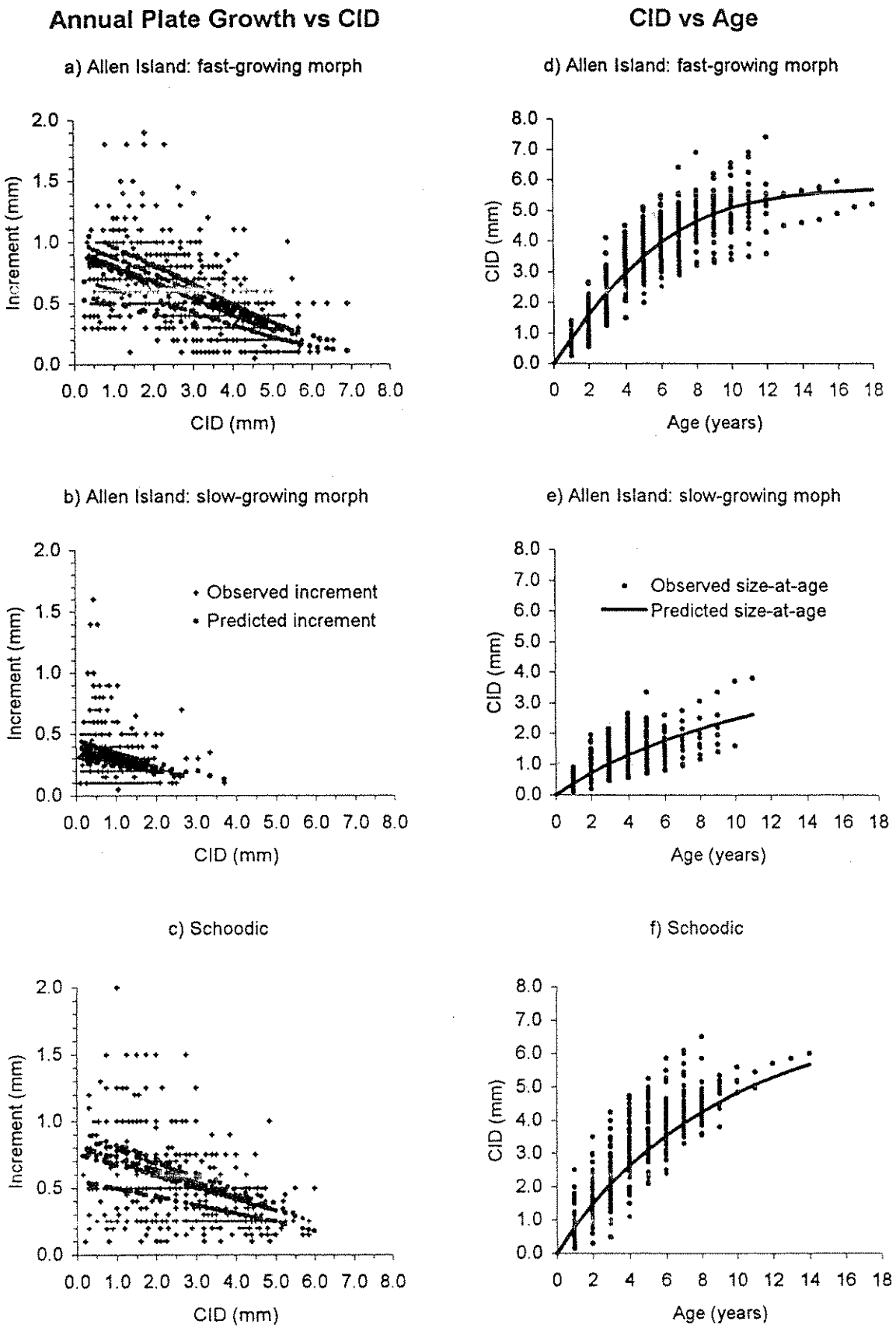

Annual Plate Growth vs CID
CID vs Age
a) Allen Island: fast-growing morph
d) Allen Island: fast-growing morph
Increment (mm)
CID (mm)
Age (years)
b) Allen Island: slow-growing morph
e) Allen Island: slow-growing moph
Observed increment
Predicted increment
Observed size-at-age
Predicted size-at-age
c) Schoodic
f) Schoodic

Fig. 39. (a and b): Observed (+) and predicted (solid circles) annual growth increments in interambulacral plate size for the fast-growing and slow-growing morphs at Allen Island in 1998. Year-effects are evident in plots a-c as parallel strings of growth increment predictions, each string portraying the growth function for one year. The data in plots a and b are expressed as size (cumulative interband distance, CID) -at-age plots in plots c and d. In this portrayal only the mean predicted size-at-age is indicated (i.e., year-effects are not separated as in plots a and b).

Figure 39

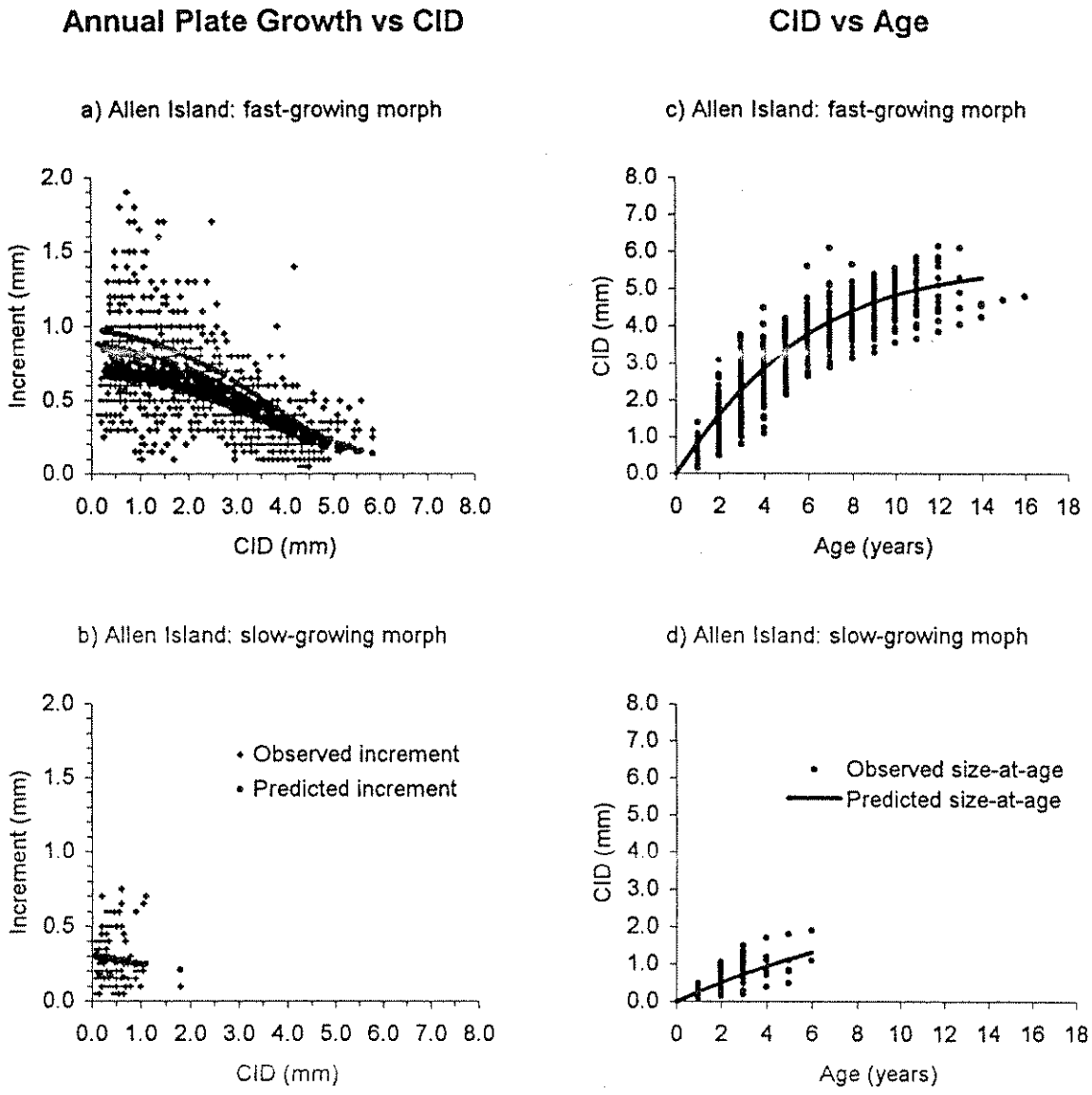

Annual Plate Growth vs CID
CID vs Age
a) Allen Island: fast-growing morph
c) Allen Island: fast-growing morph
Increment (mm)
CID (mm)
Age (years)
b) Allen Island: slow-growing morph
d) Allen Island: slow-growing moph
Observed increment
Predicted increment
Observed size-at-age
Predicted size-at-age

Fig. 40. Ln-linear relationship between test diameter (TD, mm) and cumulative interband distance (CID, mm) for the fast-growing and slow-growing morphs at Allen Island in 1997 and 1998, and at the Schoodic site in 1997.

Figure 40

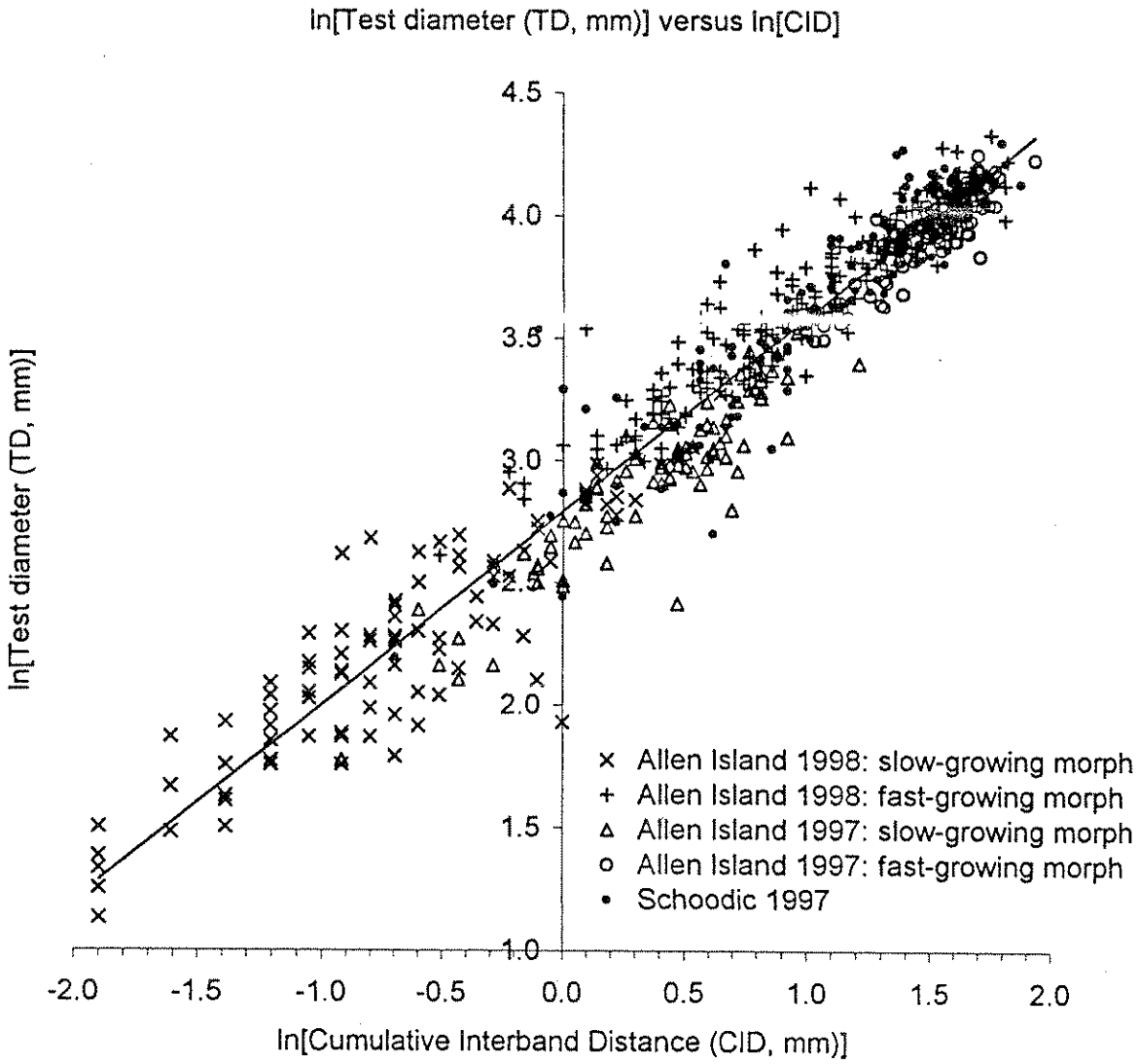
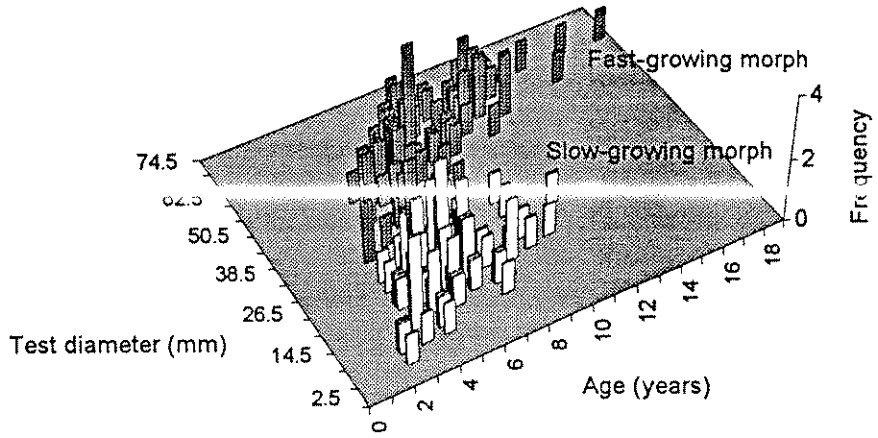

ln[Test diameter (TD, mm)] versus ln[CID]
ln[Test diameter (TD, mm)]
ln[Cumulative Interband Distance (CID, mm)]
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Allen Island 1998: slow-growing morph
Allen Island 1998: fast-growing morph
Allen Island 1997: slow-growing morph
Allen Island 1997: fast-growing morph
Schoodic 1997

Fig 41. (a) Observed frequencies and (b) predicted density distributions of the slow-growing (n=92) and fast-growing (n=98) morphs at Allen Island in 1997, as determined by a mixture analysis of ages and test diameters. (c) The sampled (histogram) and estimated (lines) mixture of the slow-growing and fast-growing morphs at Allen Island in 1997.

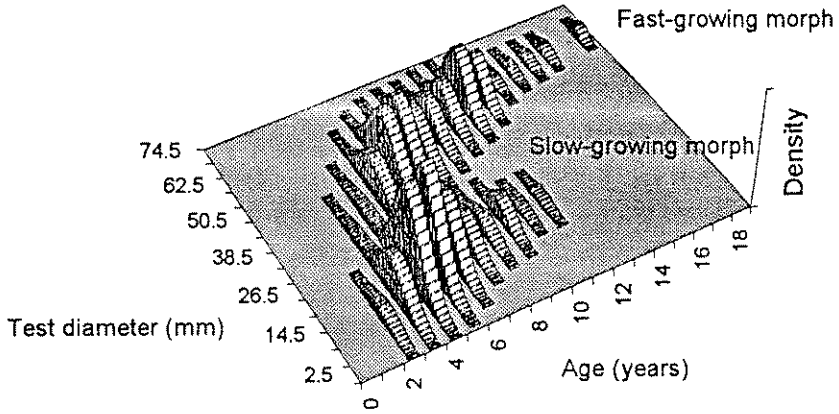
Figure 41

Identification of growth morphs at Allen Island 1997

a) Observed size-at-age by growth morph



b) Predicted growth morph densities



c) Distribution of growth morphs

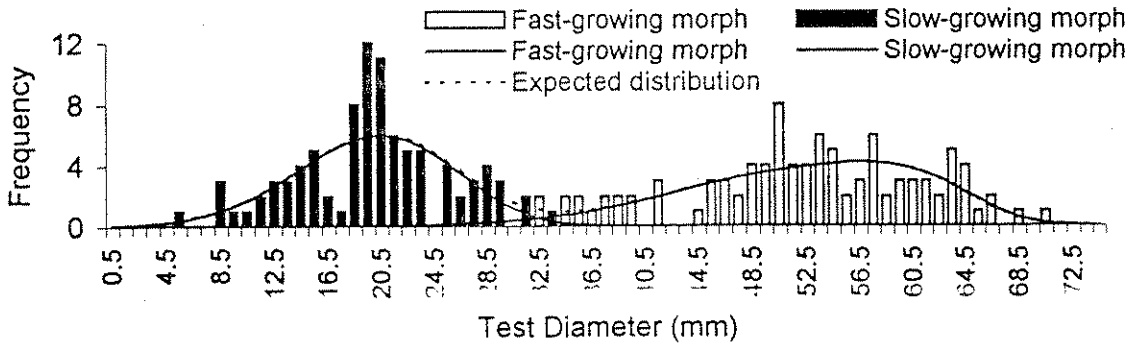
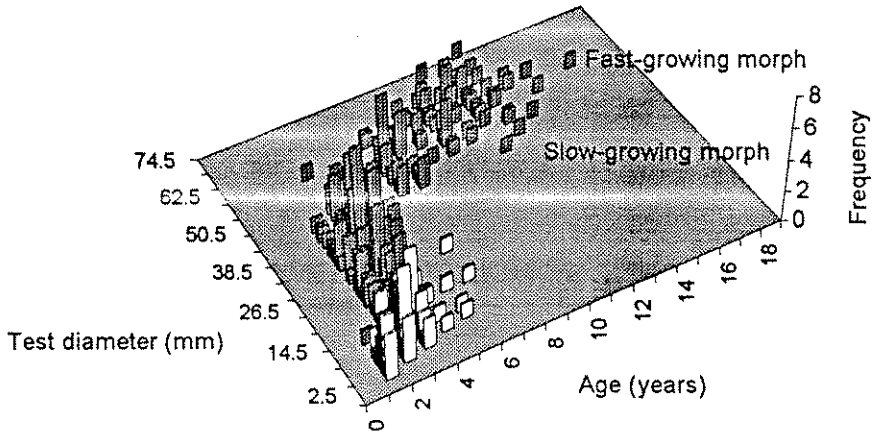


Fig. 42. (a) Observed frequencies and (b) predicted density distributions of the slow-growing (n=96) and fast-growing (n=226) morphs at Allen Island in 1998, as determined by a mixture analysis of ages and test diameters. (c) The sampled (histogram) and estimated (lines) mixture of the slow-growing and fast-growing morphs at Allen Island in 1998.

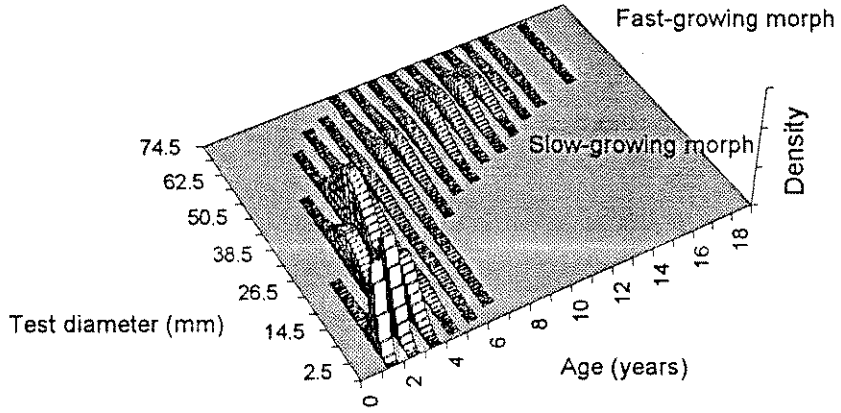
Figure 42

Identification of growth morphs at Allen Island 1998

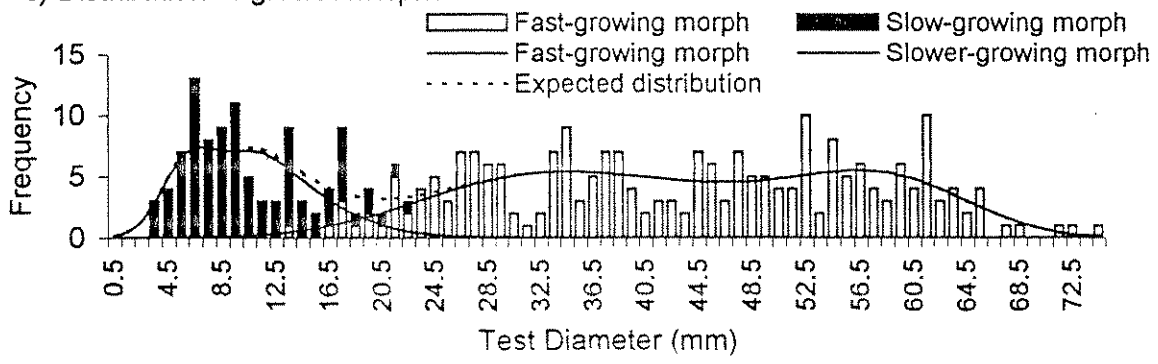
a) Observed size-at-age by growth morph



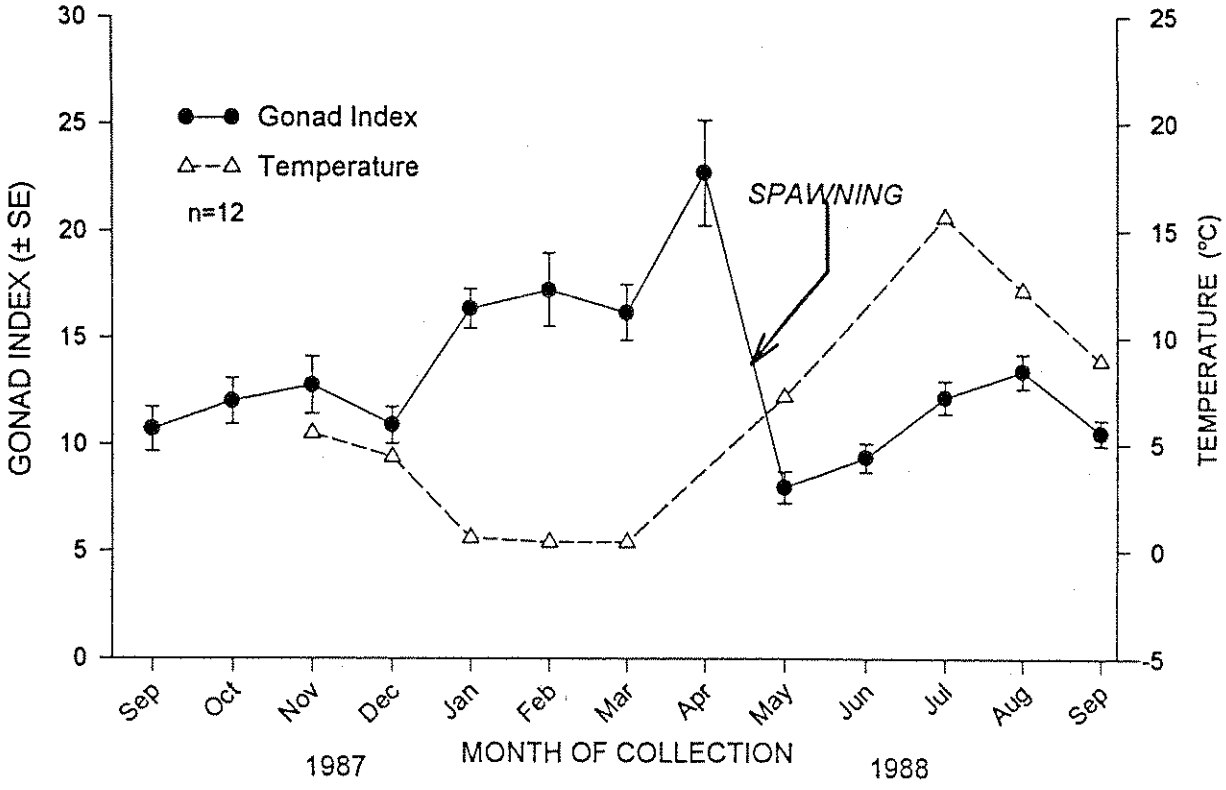
b) Predicted growth morph densities



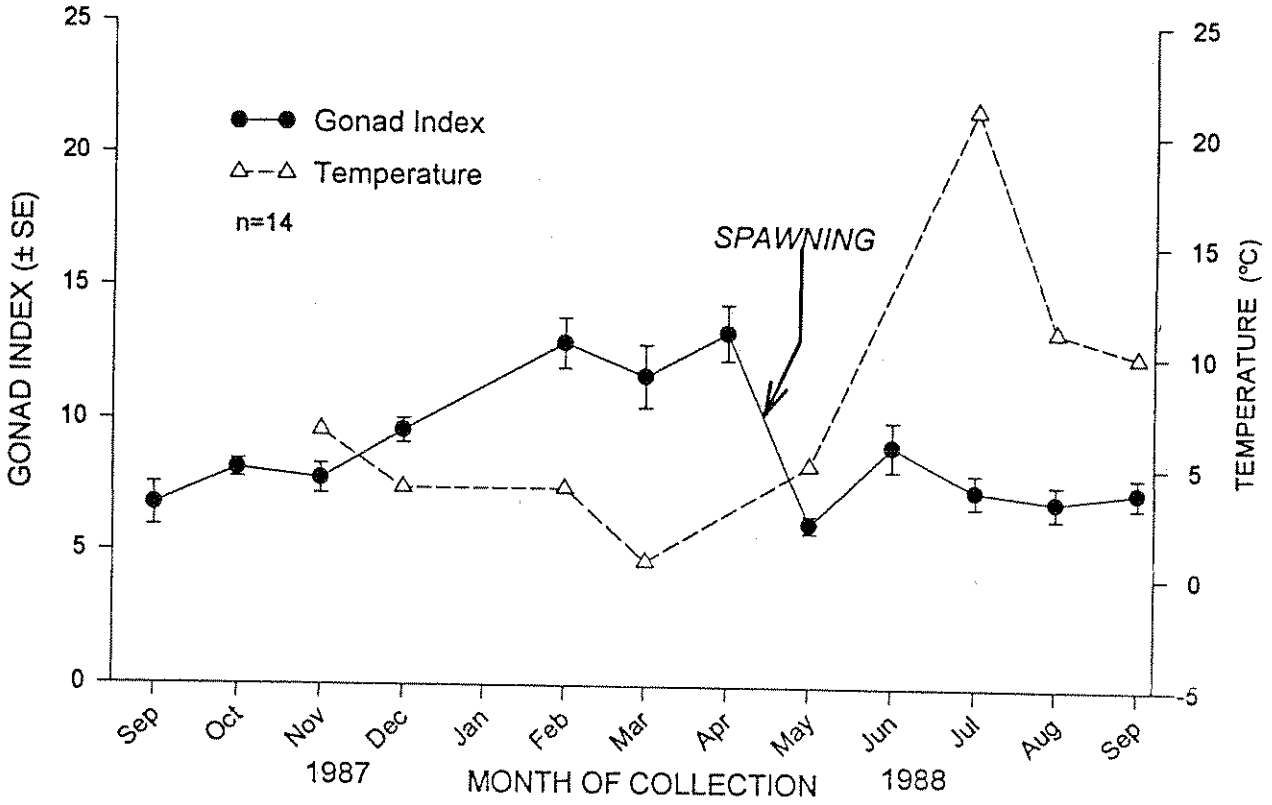
c) Distribution of growth morphs



Appendix (Figure 1). Mean gonad indices (± SE) of *Strongylocentrotus droebachiensis* for Boothbay Harbor, Maine (southwest region), 1987 -1988.



Appendix (Figure 2). Mean gonad indices (± SE) of *Strongylocentrotus droebachiensis* for Owl's Head, Maine (central region), 1987 -1988.



Appendix (Figure 3). Mean gonad indices (± SE) of *Strongylocentrotus droebachiensis* for Jonesport, Maine (northeast region), 1987 -1988.