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The Relationship between Green Sea Urchin Spawning, Spring Phytoplankton Blooms, and the Winter-Spring Hydrography at Selected Sites in Maine

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THE RELATIONSHIP BETWEEN GREEN SEA URCHIN SPAWNING, SPRING PHYTOPLANKTON BLOOMS, AND THE WINTER-SPRING HYDROGRAPHY AT SELECTED SITES IN MAINE

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An Abstract of the Thesis Presented
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The relationship between green sea urchin spawning, spring phytoplankton blooms, and hydrography were examined at multiple spatial scales during the winter-spring of 2000 at selected sites along the coast of Maine. To determine factors contributing to the variation observed in the timing of green sea urchin spawning, sea urchins, phytoplankton, and oceanographic variables were sampled biweekly at four sites in central Maine and three sites in eastern Maine. Water column properties and phytoplankton was intensively examined at sites in central Maine, while sites in eastern Maine were less well characterized. Analysis of gonad indices showed that spawning was protracted in central Maine (occurring from late February to May and encompassing a period of 60 + days), while spawning was relatively discrete in eastern Maine (occurring from April to May and encompassing a period of 34 - 50 days). Despite significant variations in gonad indices between sites, changes in gonad indices were synchronous between males and females within each site. Female gonad indices were

significantly greater than males during the peak of the spawning period, although this difference diminished over time and varied between sites.

Spawning was significantly correlated with both the first, sustained increase in phytoplankton chlorophyll *a* and with increasing water temperatures at most sites. The strength of this relationship, however, varied between males and females and between sites. Further, sea urchin spawning times were similar between sites despite significant differences in temperature regimes (5-6° C in central Maine versus 4-5° C in eastern Maine) and water column properties. The coastal waters surrounding the sites in central Maine Islands during the winter-spring 2000 were characterized by high concentrations of inorganic nutrients ($SiO_4 > 8$ μM; $NO_3 + NO_2 > 5$ μM) and low phytoplankton standing biomass (chl *a* < 2 μg/L) and cell abundance ($< 5 \times 10^3$ cells L^{-1}) within a well-mixed water column. Phytoplankton abundance during 2000 exhibited trends inconsistent with a typical, pronounced spring phytoplankton bloom, which suggests that blooming phytoplankton may not be a reliable proximate spawning cue.

Despite the relatively consistent pattern, there is considerable variability in the timing, duration, and environmental correlates, especially water temperature and chlorophyll *a*, of spawning. The timing of spawning in the green sea urchin may influence the recruitment of this species, which furthermore may have important ecological and economic implications. Futhermore, micro- and meso-scale processes affect both phytoplankton bloom dynamics and sea urchin spawning, and the interaction between these factors may result in locally disparate or atypical patterns.

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PREFACE: GENERAL INTRODUCTION

A major goal of marine benthic ecologists is to understand the mechanisms controlling reproductive periodicity in free-spawning marine invertebrates. It is widely thought that a population can only maintain a synchronized seasonal rhythm through the transduction of an exogenous regulator or cue (Giese and Kananti 1987). Despite the extensive literature describing seasonal reproduction in marine invertebrates, the proximate factors (*sensu* Baker 1938) influencing seasonal reproduction within populations are unresolved in most taxa. There are numerous examples of annual breeding cycles in marine invertebrate taxa occurring in widely disparate regions, from temperate coastal waters to tropical and deep-sea areas, where the seasonality of environmental parameters varies significantly. Annual breeding cycles of marine invertebrates occurring in temperate or boreal regions that experience predictable, seasonality of environmental parameters may be correlated with numerous variables, such as temperature, photoperiod, or phytoplankton blooms (Pearse and Cameron 1991). In tropical and arctic climates or the deep-sea, where there is little or no seasonal variation in day length or temperature (but predictable annual periodicity in rainfall or phytoplankton), organisms with seasonal reproduction are also found (Orton 1920; Chao et al. 1995; Young and Tyler, 1999).

Synchronized breeding in seasonally reproducing populations of marine invertebrates is frequently associated with, but not limited to, external fertilization and pelagic development (Pearse 1990). Several non-exclusive hypotheses have been proposed to account for the observed seasonal, synchronized reproduction in marine invertebrates (Table P.1). These hypotheses make clear predictions that are testable and

Table P.1. Several hypotheses for synchronized seasonal reproduction in free-spawning marine invertebrates. (Modified from Olive 1992, 1995).

Hypotheses	Explanation
Orton's Rule (Orton 1920)	Seasonal reproduction is a result of a physiological relationship between gametogenic processes and temperature
Energy Limitation	Seasonal reproduction is restricted to times of energy surplus over that required to sustain metabolism
Genetic Legacy	Seasonal reproduction is a relict of previously strong selection
Larval Survival	Synchronous reproduction favors larval survival thus increasing fitness
1. Match - Mismatch	Synchronous reproduction occurs at times when conditions are optimal for larval development
2. Predator swamping	Synchronous reproduction results in large populations of larvae which swamps predators
Fertilization	Synchronous reproduction favors fertilization

much of the attention has focused on the "fertilization hypothesis" and "larval survival hypothesis" (Pearse and Cameron 1990; Yund 2000). Although not mutually exclusive, the factors influencing reproductive strategies must act to increase fitness and likely operate on both pre- and post-settlement processes. Based on empirical and theoretical work of *in situ* rates of fertilization, spawning synchrony may ensure successful fertilization (Pennington 1985; Yund 1990; Levitan et al. 1992; Yund 2000; Berndt et al. 2002), although fertilization does not seem to represent a major limiting step in population persistence or growth. Larval mortality, on the other hand, is frequently considered a bottleneck for both marine fishes and invertebrate populations with heteromorphic life cycles (Cushing 1975; Rumrill 1990). Not only must larvae successfully avoid predation, acquire nutrients, and cope with environmental stress, they must also locate suitable settlement habitat when physically competent to metamorphose into a juvenile (Young and Chia 1987; Morgan 1995; Lamare and Barker 1999). Rumrill (1990) showed larval survival for several species is generally on the order of only 10^{-4} to 10^{-7} which suggests that population growth and recruitment is likely limited by processes operating on pelagic larvae.

Beyond resulting in successful fertilization, synchronized seasonal gamete release in broadcast spawners has been viewed as a strategy to ensure that developing planktotrophic larvae will be coupled with favorable pelagic conditions, despite a lack of evidence supporting this contention. Favorable conditions for pelagic larvae include optimal environmental parameters for development (e.g., temperature, salinity), low predator abundance, and available food (Stephens 1972). The coupling of benthic processes to pelagic dynamics (especially phytoplankton-zooplankton blooms) has long

been recognized as an important factor influencing successful recruitment of marine fishes (e.g., Match-Mismatch Hypothesis: Hjort 1914; Cushing 1975), although this coupling remains surprisingly unexamined in marine invertebrate populations (Himmelman 1975). The coupling of benthic invertebrate spawning to phytoplankton blooms has been suggested for several taxa (Young 1945; Barnes 1959; Himmelman 1975; McEuen 1988; Chao et al. 1995), but experimental evidence supporting this relationship is equivocal (Starr et al. 1990). Unlike fish larvae, planktotrophic marine invertebrate larvae have little endogenous nutritional reserves and begin feeding on phytoplankton soon after fertilization. For example, sea urchin larvae begin feeding on nano- and ultraplankton one or two weeks after fertilization and may remain pelagic for more than 50 days before metamorphosing and settling to the benthos (Thorson 1946; Stephens 1972; Strathman 1978). Although it has been shown that there are significant larval losses in the plankton, there are few empirical studies documenting the relative importance of predation, starvation, or extreme environmental conditions resulting in these losses (Parsons et al. 1984).

This study was designed to (1) intensively examine the relationship between green sea urchin spawning and spring phytoplankton blooms in two hydrographically different regions of Maine and (2) develop predictive relationships for the induction of spawning in nature. Results of laboratory experiments predict that green sea urchins *(Strongylocentrotus droebachiensis)* should release gametes in response to the annual spring phytoplankton bloom in coastal waters (Starr et al. 1990). Based on the "match-mismatch hypothesis," the goal of this work was to relate spawning patterns to phytoplankton blooms and hydrographic conditions to make inferences regarding the

proximate cues for seasonal reproductive synchrony in the green sea urchin. As its tenet, this model of spawning links larval production to an optimal time for survival. Although it is frequently assumed that seasonal synchronous spawning is an adaptation to maximize fertilization success, there are few studies that have examined *in situ* rates of larval survival relative to spawning times. Phytoplankton blooms as a proximate cue for gamete release in the green sea urchin may be viewed as a strategy to couple pelagic larvae with abundant food, although it may also cause spawning in a way that maximizes fertilization success. Moreover, although basic information on annual spawning patterns in numerous marine invertebrate taxa exists, little is known about (1) the proximate cues for gamete release, (2) the degree of reproductive synchrony within populations, (3) or the hydrographic conditions at the time of spawning. This study addresses these issues by relating the hydrography and phytoplankton of selected sites in Maine to patterns of spawning in the green sea urchin at multiple temporal and spatial scales.

CHAPTER I

PATTERNS OF SPAWNING OF THE GREEN SEA URCHIN, *STRONGYLOCENTROTUS DROEBACHIENSIS* IN MAINE: A REGIONAL APPROACH

INTRODUCTION

Reproductive periodicity and synchrony in broadcast-spawning marine invertebrates has received a great deal of attention. The importance of synchronous reproduction at a time that is favorable for early developmental stages in organisms with external fertilization has been underscored in studies on marine algae (Serrao et al. 1996; Clifton 1997; Clifton and Clifton 1999) and marine invertebrates (Pennington 1985; Levitan 1990; Yund 1990; Pearse and Cameron 1991; Lamare 1998; Meidel and Yund 2000). However, the mechanisms entraining gametogenesis or stimulating spawning in organisms with annual reproductive cycles remain poorly understood (Pearse and Cameron 1991; Young 1999). The inability to determine cause based on observations of concurrence has resulted in much speculation on what factors control marine invertebrate reproductive cycles (Thorson 1946; Byrne 1990; Pearse and Cameron 1991). Despite the numerous papers correlating reproductive events with environmental parameters, the evidence for exogenous control of marine invertebrate reproduction remains equivocal (Bryne 1990; King et al. 1994; Pearse 2000). Several experimental studies have shown how single environmental factors cue spawning, however, intensive field studies examining exogenous control of reproductive events are lacking (Myazaki 1938; Smith and Stehlow 1983; Starr et al. 1990). Furthermore, the results of experimental studies

often cannot be extrapolated to nature and require further exploration (Starr et al. 1990, 1992).

Orton (1920) first reviewed the literature on environmental control of invertebrate reproduction and concluded that temperature was the proximate cause (*sensu* Baker 1938) coordinating the timing of reproductive events in organisms with annual reproductive cycles. He argued that "sea temperature must be the influence of paramount importance in controlling breeding in marine animals under normal biological conditions," and suggested that a critical temperature must be attained for breeding and that each species had a physiological constant. Orton's ideas became an important paradigm for environmental control of marine invertebrate reproductive cycles, and Thorson (1946), in his treatise on the reproductive cycles of numerous benthic invertebrate species in Danish waters, formalized Orton's ideas and suggested that species' distribution were determined by the temperature required for breeding. Now known as "Orton's Rule," the idea that temperature is consistently the proximate cue stimulating gamete release in marine animals has been challenged many times (Himmelman 1978; Starr et al. 1990; Pearse et al. 1991). However, there remains a lack of experimental evidence to support these claims that temperature indeed is not a proximate cue for spawning.

There is an extensive literature describing the annual reproductive cycles of echinoderms (Ernest and Blake 1981; Byrne 1990; Pearse and Cameron 1991; Meidel and Scheibling 1998; Brewin et al. 2000), but few studies have identified the proximate cues that synchronize reproductive events. Although endogenous regulation is possible, it is unlikely that an entire population can remain reproductively synchronous without an

exogenous entraining mechanism (Giese and Kananti 1987). Many environmental variables have been proposed to influence or control the timing of reproductive events in a number of temperate echinoderms. Examples of environmental variables that have been suggested or shown to regulate reproductive periodicity in echinoderms include: Photoperiod (Pearse 1981; Pearse et al. 1986; but see Cochran and Engelmann 1975), light intensity (McEuen 1988), lunar periodicity (Korringa 1946; Horii 1997), temperature (Byrne 1990; Sewell and Bergquist 1990; King et al. 1994), sex pheromones (McEuen 1988), and phytoplankton blooms (Himmelman 1975, 1978; McEuen 1988; Starr et al. 1990, 1993; Chao et al. 1995). Most of these studies have relied on correlation of reproductive events with environmental variables in the field, and the proposed spawning cues are unresolved. Despite the inability to determine the precise, proximate cues synchronizing the timing of reproductive events, the ability to predict either gametogenic or spawning events based on environmental correlates may be a useful construct for ecologists and an important tool for resource managers (Peters 1991).

The green sea urchin, *Strongylocentrotus droebachiensis*, is an ecologically (Paine and Vadas 1969; Breen et al. 1982; Scheibling 1986) and economically (NMFS 2000) important echinoderm with a circumpolar distribution. This species has an annual reproductive cycle and spawns during the early spring in northern temperate regions (Concanour and Allen 1967; Stephens 1972; Himmelman 1978; Falk-Petersen and Lønning 1983; Munk 1992; Meidel and Scheibling 1998). Photoperiod, or more specifically, short days, is a proximate cue synchronizing gametogenesis within *S. droebachiensis* populations (Walker and Lesser 1998). Seasonally variable environmental factors such as temperature, phytoplankton blooms, and water motion are

correlated with *S. droebachiensis* spawning, and have been suggested as proximate cues for gamete release (Himmelman 1975, 1978; Starr et al. 1990; Caron 1998). Starr et al. (1990) showed experimentally that phytoplankton cells, exudates from phytoplankton, and sperm from conspecifics stimulate spawning in *S. droebachiensis,* although multiple alternative hypotheses were not considered. Additionally, they show that exudates from the brown macroalga, *Fucus vesiculosus*, induce spawning in the green sea urchin (Starr et al. 1992). The wide range of stimuli inducing spawning in these, and other, studies suggest that the proximate factors stimulating gamete release in green sea urchins require further testing. Moreover, the incongruence between laboratory experiments and field observations necessitate rigorous laboratory studies and intensive field sampling at multiple temporal and spatial scales.

Here, I conducted extensive field sampling to evaluate patterns of natural spawning in the green sea urchin at selected sites along the coast of Maine. The general objectives of this work were to closely examine patterns of spawning of the green sea urchin to (1) determine the relationship between laboratory models of sea urchin spawning and spawning of natural populations, (2) determine the degree of reproductive synchrony between male and female sea urchins, (3) determine if environmental variables can be used to predict the time of spawning, and (4) assess the patterns of spawning at selected sites in hydrographically different regions of the Maine coast. Examining patterns of spawning at multiple spatial scales may provide insight on the factors influencing the timing of reproduction of wild green sea urchin populations and may be useful to resource managers entrusted by the public as stewards of the fishery.

MATERIALS AND METHODS

Site Description

Specimens of *Strongylocentrotus droebachiensis* and oceanographic variables were sampled at four subtidal sites in central Maine (Georges Islands Region) and three subtidal sites in eastern Maine (Jonesport Region), USA to determine spatial patterns of sea urchin spawning. The sites in central Maine are located near four coastal islands and include Allen Island (N 43°50'30'', W 69°18'45"), Benner Island (N 43°52'45'', W 69°19'45"), Davis Island (N 43°53'30'', W 69°18'15") and Hupper Island (N 43°54'45'', W 69°16'45"). The sites in northeastern Maine include Loon Point (N 44°32'30'', W 67°34'00'), Starboard Cove (N 44°36'15'', W 67°23'45"), and Black Duck Cove (N 44° 27'45", W 67° 35' 30") (Fig. 1.1). The Georges Island sites are characterized by having shallow depth (< 14 meters), rocky substrate, and moderate algal cover (including *Palmaria palmate, Alaria esculenta,* and *Laminaria* spp.), although Davis Island has substantially less algal cover than the other sites (T. Dowling, *personal communication).* The Jonesport Region sites are characterized by shallow depth (< 10 meters), mixed rock and sediment (i.e., sand) substrate, and abundant stands of *Laminaria* spp. and *Alaria esculenta.*

Sample Collection and Processing

Scuba divers haphazardly collected twenty sea urchins from each site biweekly from 30 January through 28 May 2000 in the Georges Islands region, and from 5 March

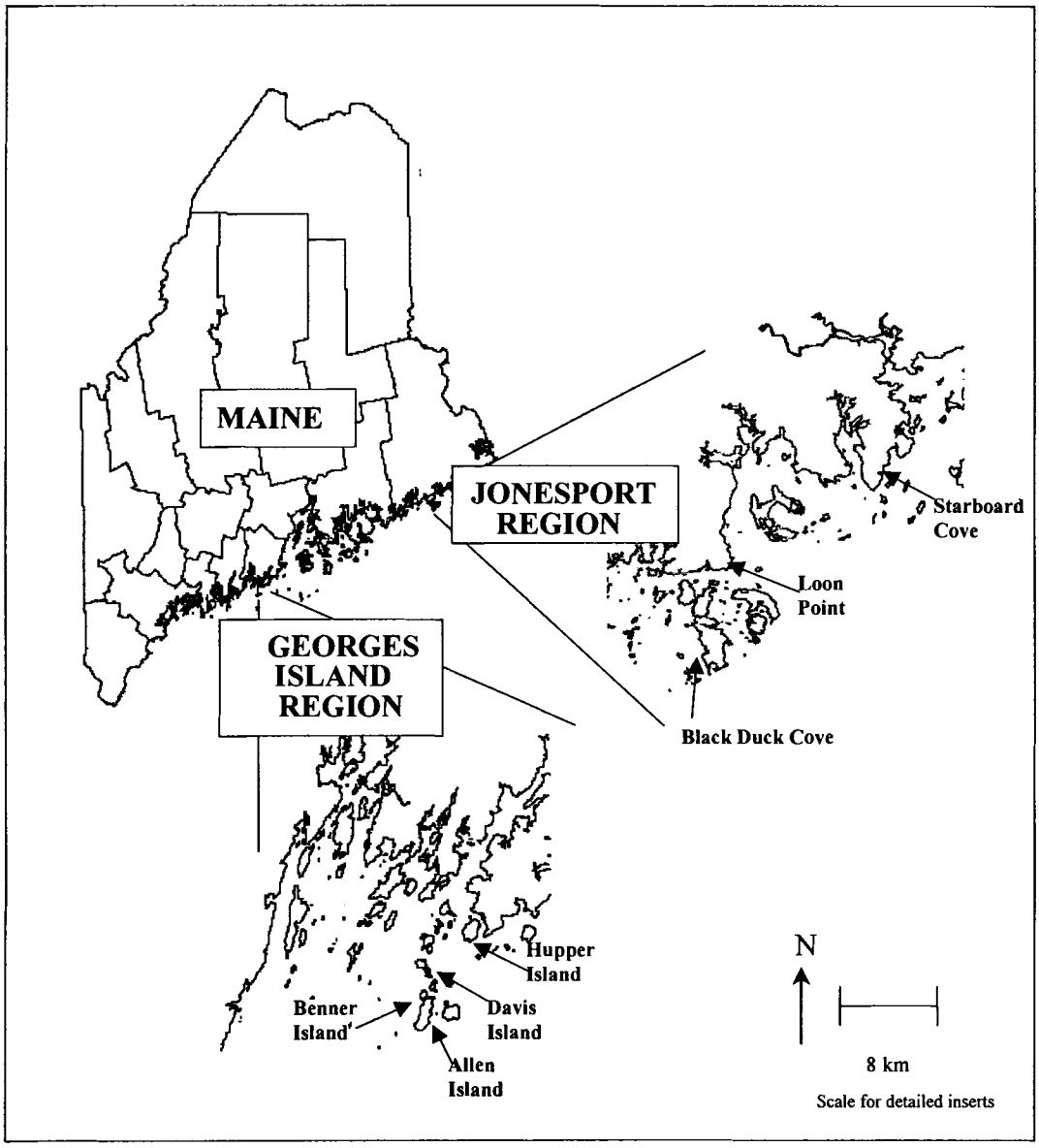

Figure 1.1. Location of sampling sites in the Georges Islands and the Jonesport Regions (scale applies only to detailed inserts).

through 30 May 2000 in the Jonesport Region. At one site in the Jonesport Region (Loon Point), sampling began on 20 February. Urchins from the two regions were sampled on alternating weeks. Test diameter (TD) of individuals was measured to the nearest 0.1 mm across the ambitus using vernier calipers. Total wet weight and total gonad weight (towel "blotted") were measured to the nearest 0.1 g with an electronic balance. Sex was determined by visually examining the gonads, or, when not obvious, with a slide smear under a compound light microscope. Several other variables (e.g., gonad color and texture, and gut fullness) were categorically determined for each individual, although they are not analyzed here.

Gonad index of males and females was used to determine spatial and temporal changes in sea urchin reproductive status. Only sea urchins greater than 45 mm TD were used to minimize variation in gonad index due to the size of the animal (Gonor 1972). The ratio of towel "blotted" gonad wet weight to total body wet weight was used to calculate the gonad index (GI), where GI = [Gonad wet weight / Total wet weight] x 100.

Phytoplankton

Phytoplankton biomass was quantified by measuring chlorophyll *a* concentrations using fluorometric methods (Parsons et al. 1984). Two water samples were collected at each site on each sampling date. One sample was collected 0.5 m below the surface and the other was collected 1 m above the bottom. One hundred millileters (ml) of water from each sample was filtered through a Gelman GFF (0.7 μm) filter. The filter was placed in a 20 ml glass scintillation vial and 10 ml of 90% acetone was added.

Chlorophyll *a* was extracted for 24 hours in vials stored on dry ice. Chlorophyll *a* and phaeophytin concentrations were determined using a Turner fluorometer.

Oceanographic Variables

Inorganic nutrient concentrations (i.e., phosphate, silicate, nitrate + nitrite, and ammonium) were determined using a Technicon AutoAnalyzer II by staff in D.W. Townsend's laboratory. Fifteen milliliters of both the surface and bottom water sample from each site on each sampling date were filtered separately using an inline syringe filter containing a 0.45 μm Millipore filter. Samples were kept dark and frozen on dry ice until analyzed.

Surface and bottom water temperature (°C) and salinity (practical salinity units) were determined using a calibrated thermometer and refractometer or salinometer. Extinction coefficient was determined by secchi disk measurements and calculated where extinction coefficient equals 1.7/depth (m) (Idso and Gilbert 1974). Secchi disk measurements were not made at the Jonesport Region sites.

Statistical Analysis

Analyses were performed using SAS Version 6.09 (SAS Institute, Inc. 1989) or SYSTAT Version 9 (SPSS Inc. 1998). Descriptive statistics were used to analyze changes in gonad index over time, between sites, and between regions. Comparisons of sex and date and their interactions on gonad index were done for each site separately using a two-factor Analysis of Variance (ANOVA), with sex and date as fixed factors. Gonad indices were arcsine-transformed to meet the assumption of normality (Zar 1998).

Differences in gonad indices between sites within each region on each date were analyzed with a single-factor ANOVA with an *aposteriori* Tukey's multiple comparison procedure with a Bonferroni corrected alpha to maintain a 5% risk of Type I error for each comparison (i.e., $\alpha = 0.05$/number of comparisons).

Variations in nutrient and phytoplankton pigment concentrations and environmental variables between surface and bottom water sample were analyzed using an Analysis of Covariance (ANCOVA) for each variable with date as a covariate (Appendix A). Because there were no significant differences between surface and bottom samples, data were pooled for further analyses. Phytoplankton chlorophyll *a* was log-transformed to meet the assumption of normality and homogeneity of variance (Zar 1998). The relationship between oceanographic variables at each site was examined using Pearson's product moment correlation analysis.

The relationship between temperature and chlorophyll *a* with gonad indices at each site was analyzed using linear regression analysis. Stepwise, multiple linear regression analysis was used to determine the dependence of arcsine-transformed gonad indices on oceanographic variables at each site separately and pooled sites within region. Variables considered in multiple regressions included salinity, temperature, extinction coefficient (Georges Island region only), chlorophyll *a*, phaeophytin, nitrate + nitrite, silicate, phosphate, and ammonium. Variables were forward selected into the overall model with an entry rule of $p = 0.15$. Despite high multicollinearity among oceanographic variables, predictive relationships may be developed using stepwise, multiple linear regression. However, direct associations between gonad indices and oceanographic variables are not demonstrable using stepwise, multiple linear regression

analyses (Zar 1998). Due to the high multicollinearity, significant predictor variables may be completely redundant with other variables, and thus, caution should be used interpreting the results of stepwise, multiple linear regression. Nonetheless, the predictive utility of stepwise, multiple linear regression analyses should not be overlooked. Again, due to the inter-correlation, especially between all other variables and temperature, stepwise, multiple linear regression analysis, was used to determine the dependence of arcsine-transformed gonad indices on oceanographic variables at each site separately and pooled sites within region, with temperature first forced into the model. Additionally, temperature was selected as a forced variable in the model because resource managers can readily measure temperature and this may be used as a predictive tool.

Because numerous oceanographic variables were inter-correlated, principal components analysis (PCA) was used for each region. The limited utility of linear and multiple regression analysis, especially with high multicollinearity among the variables, make PCA a valuable data reduction method (Ludwig and Reynolds 1988). PCA is a multivariate data reduction technique used to create a normalized, linear combination of variables, which account for the most variability in the data set (Handley 1998). Variables considered in the PCA were all of the multicolinearly related variables used in the multiple regression analyses (i.e., salinity, temperature, extinction coefficient (Georges Island region only), chlorophyll *a*, phaeophytin, nitrate + nitrite, silicate, phosphate, and ammonium). The resulting principal components can be considered an "oceanographic index," which is a linear combination of oceanographic variables that accounts for the high multicollinearity observed.

Principal components with an eigenvalue greater than 1.0 were used in the analyses of the relationship between oceanographic variables and gonad index. Each axis or principal component has an eigenvalue (also called latent root) associated with it, and they are ranked from the highest to the lowest (Dunteman 1989). Eigenvalues represent the amount of variation explained by the axis. Linear multiple regression analysis was used to determine the relationship between gonad index and the principal components (i.e., "the oceanographic index") for each site. This "oceanographic index" represents the dynamics and interrelationships between the oceanographic variables during the winter-spring period in the Gulf of Maine.

RESULTS

Central Maine: Georges Island Region

Mean biweekly gonad index values indicate disparate trends in spawning patterns among the four sites in 2000 (Fig. 1.2). Gonad indices of male and female *S. droebachiensis* changed significantly from January through late May at Allen, Benner, and Hupper Islands. However, gonad indices of females at Davis Island did not change significantly over the sampling period (ANOVA, $F_{8,74}$=1.526, p = 0.163). Pre-spawning gonad indices were high during late February and early March, and declined gradually until the end of the sampling period. Based on this gradual decline in gonad indices, spawning appears to have begun in late February at Allen and Hupper Islands and early March at Benner Island. It is unclear, however, when spawning occurred at Davis Island. Overall, there was significant variability in the precise changes of gonad index at each site. The difference between gonad indices of female urchins between sites was

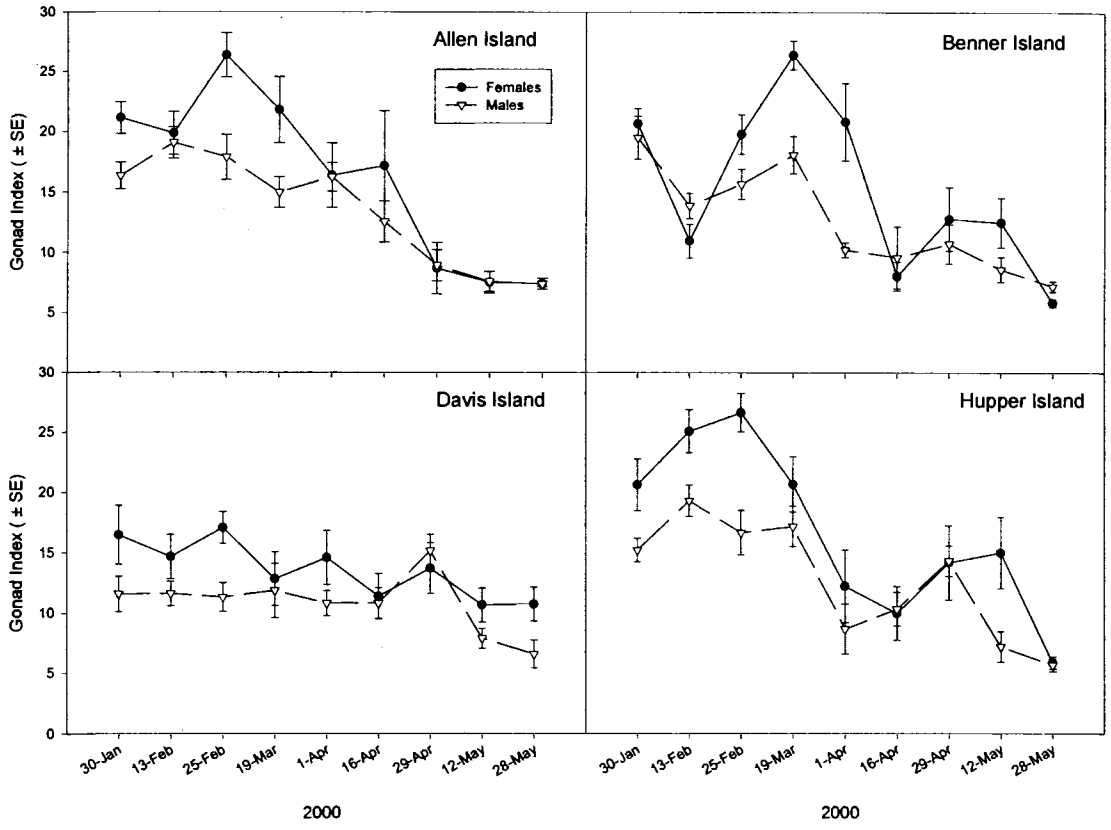

Figure 1.2. ***Georges Island Region.*** Changes in mean gonad index (± 1 SE) of female and male sea urchins at Allen, Benner, Davis and Hupper Islands (n=20).

significant on several dates, but not on others (Table 1.1a). Male gonad indices exhibited a similar pattern of variable differences, however, the dates on which they differed were not the same as the females (Table 1.1b).

Table 1.1. ***Georges Island Region.*** Mean gonad indices (± 95% CI) for (**A**) female and (**B**) male sea urchins on dates where gonad indices were significantly different. (Means with the same letter are not significantly different at $\alpha = 0.05$ using ANOVA and Tukey's *aposteriori* multiple comparison test with a Bonferroni adjusted alpha (0.05/9 = alpha / total # of comparisons).

A. ***Females***

Site	Mean ± 95% CI			
	13 Feb	25 Feb	19 Mar	28 May
Allen	19.87 ± 4.23 (AC)	26.40 ± 4.09 (A)	21.81 ± 6.06 (A)	7.41 ± 0.98 (A)
Benner	10.96 ± 3.18 (B)	19.79 ± 3.47 (B)	26.41 ± 2.74 (A)	5.84 ± 0.72 (A)
Davis	14.70 ± 5.08 (AB)	17.10 ± 3.08 (B)	12.86 ± 4.93 (B)	10.76 ± 3.08 (B)
Hupper	25.12 ± 3.96 (C)	26.68 ± 3.64 (A)	20.70 ± 5.32 (AB)	5.88 ± 1.17 (A)

B. ***Males***

Site	Mean ± 95% CI				
	30 Jan	13 Feb	25 Feb	1 Apr	29 Apr
Allen	16.37 ± 2.5 (AB)	19.09 ± 2.9 (A)	17.90 ± 4.4 (A)	16.25 ± 2.7 (A)	8.94 ± 2.8 (A)
Benner	19.50 ± 4.6 (B)	13.87 ● 2.4 (B)	15.66 ± 3.9 (AB)	10.21 ± 1.3 (B)	10.70 ± 3.8 (AB)
Davis	11.62 ± 3.2 (A)	11.65 ± 2.2 (B)	11.35 ± 2.6 (B)	10.85 ± 2.2 (B)	15.17 ± 3.1 (B)
Hupper	15.24 ± 2.1 (AB)	19.34 ± 3.0 (A)	16.69 ± 4.2 (AB)	8.70 ± 4.9 (B)	14.36 ± 2.8 (B)

The peak in mean gonad index of female urchins was consistent in magnitude between Allen, Benner and Hupper Islands, but not at Davis Island where gonad indices were significantly lower (ANOVA, $F_{3,\,36} = 7.271, p = 0.001$). Similarly, the peak in mean gonad index of male sea urchins was consistent in magnitude at Allen, Benner, and Hupper Islands, but Davis Island males had significantly lower gonad indices (ANOVA, $F_{3,\,30} = 4.819$, p = 0.007). The date on which the peak in female gonad indices occurred was 25 February at Allen, Benner, and Hupper Island, but on 19 March at Davis Island (Fig. 1.2). The time at which males had peak gonad indices was more variable than

females, with urchins at Allen and Hupper Island peaking on 13 February, and urchins at Benner and Davis reaching maximum gonad indices on 30 January and 29 April, respectively (Table 1.2).

Table 1.2. ***Georges Island Region.*** Peak gonad index (± 1 SE), date on which peak GI occurred, and Tukey's HSD grouping of female and male sea urchins. (Means with the same letter are not significantly different).

Site	Peak GI Females (date)	Peak GI Males (date)
Hupper Island	26.68 ± 1.61 (25 Feb) A	19.34 ± 1.29 (13 Feb) A
Benner Island	26.41 ± 1.21 (19 Mar) A	19.50 ± 1.79 (30 Jan) A
Allen Island	26.40 ± 1.86 (25 Feb) A	19.09 ± 1.31 (13 Feb) A
Davis Island	17.10 ± 1.30 (25 Feb) B	15.17 ± 1.34 (29 Apr) B

Sexual differences

Gonad indices of male and female *S. droebachiensis* at each site were significantly different on certain dates, but not on others (Fig. 1.2). There was a significant effect of date and sex, with females having greater or equal gonad indices than males during the period (Table 1.3). The interaction term was not significant at Allen, Davis and Hupper Islands, indicating that females consistently had higher or equal gonad indices than males throughout the sampling period, and that changes in gonad indices were synchronous between males and females. However, the interaction term was significant at Benner Island because males had significantly greater gonad indices than females on 28 May 2000 after spawning was completed. In general, male and female gonad indices varied similarly. Gonad indices of female urchins at Davis Island did not vary significantly during the study period, although a downward trend was observed from February through May (Fig. 1.2). At each site, females consistently had higher peak gonad index than males. Generally, peak gonad indices of females occurred on later dates than peak gonad indices of males (Table 1.2).

Table 1.3. ***Georges Island Region.*** Two-way analysis of variance of the effects of date and sex and their interaction on gonad index (arcsine-transformed) at Allen, Benner, Davis and Hupper Islands, 2000.

Site	Source	SS	df	MS	F-ratio	P
Allen	Date	0.457	8	0.057	15.322	< 0.0001
	Sex	0.035	1	0.035	9.352	0.003*
	Date*Sex	0.045	8	0.006	1.515	0.156
	Error	0.585	157	0.004		
Benner	Date	0.381	8	0.048	18.082	< 0.0001
	Sex	0.030	1	0.030	11.237	0.001*
	Date*Sex	0.078	8	0.010	3.715	0.001
	Error	0.405	154	0.003		
Davis	Date	0.060	8	0.007	2.825	0.006
	Sex	0.029	1	0.029	11.078	0.001*
	Date*Sex	0.020	8	0.002	0.944	0.482
	Error	0.404	153	0.003		
Hupper	Date	0.482	8	0.060	14.872	< 0.0001
	Sex	0.068	1	0.068	16.831	< 0.0001*
	Date*Sex	0.051	8	0.006	1.571	0.138
	Error	0.620	153	0.004		

* Female gonad indices were significantly greater or equal to male gonad indices

Males at Davis Island had peak gonad indices on 29 April, which is inconsistent with the patterns observed at the other sites.

Oceanographic variables

Because there were no significant differences between oceanographic variables at the surface and bottom, data for each variable were pooled for subsequent analyses at each site (i.e., n = 2 for each variable at each site) (Appendix A). Sea temperature increased gradually and linearly throughout the study period. It was lowest on 13 February (1.5 °C) and highest on 28 May (10.5 °C). Chlorophyll *a* concentration was low throughout the late winter – early spring, but increased significantly on 12 May at all sites in central Maine to concentrations approaching 2 μg/L. The changes in inorganic nutrient concentrations were consistent between surface and bottom water samples and were consistent between sites (Appendix A). Silicate and nitrate + nitrite concentrations were high through the late winter at all sites, but decreased significantly as chlorophyll *a* concentrations increased (Fig 1.3). Nitrate + nitrite decreased in concentration gradually over the study period, while silicate concentration was high for most of the sampling period, and decreased rapidly from 12 May to 28 May at all sites. Mean (± 95% CI) ammonium concentration were high (2.63 ± 0.87 μM) on 30 January, low (0.219 ± 0.04 μM) throughout the sampling period, and increased to 1.00 ± 0.08 μM on 29 April. Phosphate concentrations were low throughout the sampling period and decreased at all sites in mid to late April. Extinction coefficient varied during the sampling period at and exhibited similar patterns at each site (Table 1.4). Generally, extinction coefficient was

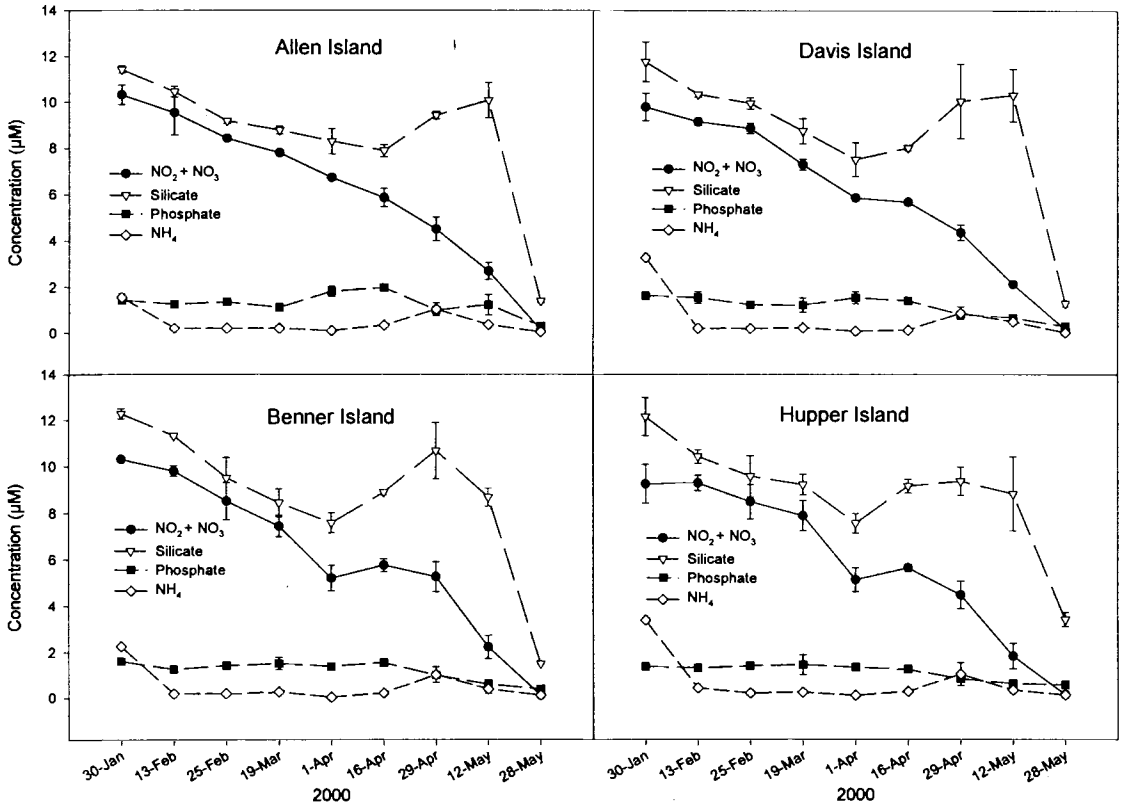

Figure 1.3. ***Georges Island Region.*** Mean concentrations (± 1 SE) of nitrate + nitrite, silicate, phosphate, and ammonium (µM) at Allen, Benner, Davis, and Hupper Islands, 2000 (n = 2 for each variable).

Table 1.4. ***Georges Island Region.*** Extinction coefficient (K,m^{-1}) (1.7/secchi depth (m)) from 30 January to 28 May 2000.

Date	Allen	Benner	Davis	Hupper
30 Jan	0.207	0.223	0.207	0.242
13-Feb	0.171	0.171	0.207	0.171
25-Feb	0.171	0.153	0.161	0.181
19-Mar	0.242	0.161	0.161	0.207
1-Apr	0.207	0.242	0.483	0.290
16-Apr	0.223	0.264	0.264	0.363
29-Apr	0.193	0.181	0.181	0.264
12-May	0.181	0.161	0.161	0.223
28-May	0.207	0.242	0.242	0.363

low from 30 January to mid-March, increased from mid to late April, declined in early May, and increased again in late May. Salinity changed significantly during the sampling period and changes were similar between the four sites (Fig. 1.4). Salinity varied between 32 and 33 psu from January to early April and was between 30 and 31.5 psu during late April and early May. At Davis Island, salinity increased to 33 psu on 28 May.

Pearson product moment correlation coefficients show a strong relationship between many oceanographic variables (Table 1.5). Correlation coefficients were calculated by site (Appendix B). Because the magnitude of and changes in oceanographic variables were consistent between sites, data from all sites were pooled to examine the overall relationship between the variables in the Georges Island region. Salinity, water temperature, chlorophyll *a*, phaeophytin, nitrate + nitrite, silicate, phosphate were significantly correlated. The strongest relationships were between temperature and nitrate + nitrite concentrations ($r = -0.975$, $p < 0.0001$), temperature and

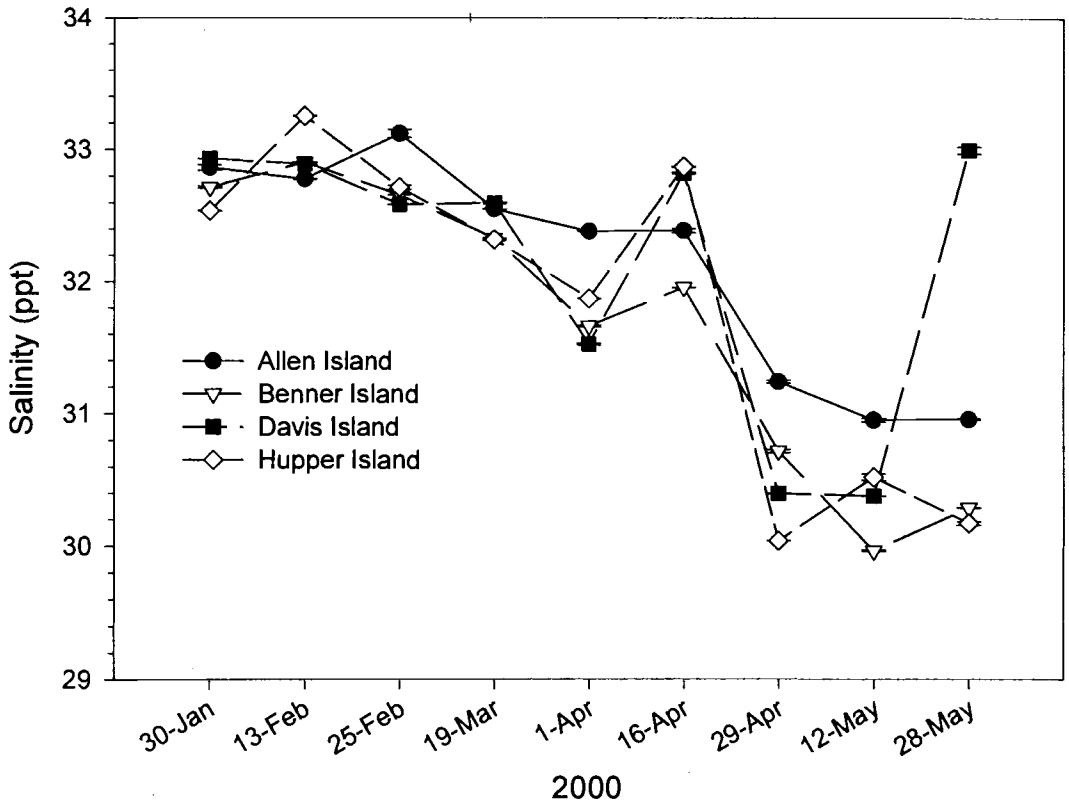

Figure 1.4. ***Georges Island Region.*** Mean (± 1 SE) bottom salinity (psu) at Allen, Benner, Davis, and Hupper Islands, 2000 (n = 3). Mean ± 1 SE determined by 3 replicate measurements for 1 water sample. These replicates were used to determine measurement errors, not to examine differences between water samples.

Table 1.5. ***Georges Island Region.*** Relationship between oceanographic variables, expressed as Pearson product correlation coefficients and Bonferroni adjusted probabilities at all sites, 2000.

Variable		Salinity	Ext. Coeff.	Temp	Chl a	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r*:	1.00								
	P:	0								
Ext. Coeff.	*r*:	-0.130	1.000							
	P:	1.000	0							
Temperature	*r*:	-0.730	0.295	1.000						
	P:	< 0.0001	0.432	0						
Chl a	*r*:	-0.649	0.201	0.912	1.000					
	P:	< 0.0001	1.000	< 0.0001	0					
Phaeophytin	*r*:	-0.615	0.047	0.757	0.773	1.000				
	P:	< 0.0001	1.000	< 0.0001	< 0.0001	0				
NO_3 +NO_2	*r*:	0.751	-0.245	-0.975	-0.916	-0.774	1.000			
	P:	< 0.0001	1.000	< 0.0001	< 0.0001	< 0.0001	0			
SiO_4	*r*:	0.303	-0.312	-0.730	-0.782	-0.561	0.743	1.000		
	P:	0.347	0.275	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0		
PO_4	*r*:	0.589	0.015	-0.674	-0.769	-0.689	0.736	0.572	1.000	
	P:	< 0.0001	1.000	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0	
NH_4	*r*:	0.101	-0.070	-0.362	-0.281	-0.108	0.365	0.492	0.198	1.000
	P:	1.000	1.000	0.063	0.611	1.000	0.057	< 0.0001	1.000	0

chlorophyll *a* ($r = 0.912$, $p < 0.0001$), and chlorophyll *a* and nitrate + nitrite ($r = -0.975$, $p < 0.0001$).

Relationships with gonad index

There is an inverse relationship between gonad index and temperature and chlorophyll *a* (Fig. 1.5). Linear regression analyses show a significant inverse relationship between gonad index and temperature and chlorophyll *a* (Appendix C). As a conservative estimate of the strength of the relationship between temperature and chlorophyll *a* and mean gonad index, coefficients of determination (r^2) were determined for pooled male and female sea urchins (Fig. 1.6 and 1.7). The strength of this relationship, however, varied between sites and between males and females. Coefficients of determination for the linear relationship between gonad indices and temperature ranged from 0.378 for females at Benner Island and 0.372 for males at Davis Island to 0.773 for females at Hupper Island and 0.817 for males at Allen Island. Similarly, coefficients of determination for the linear relationship between gonad indices and

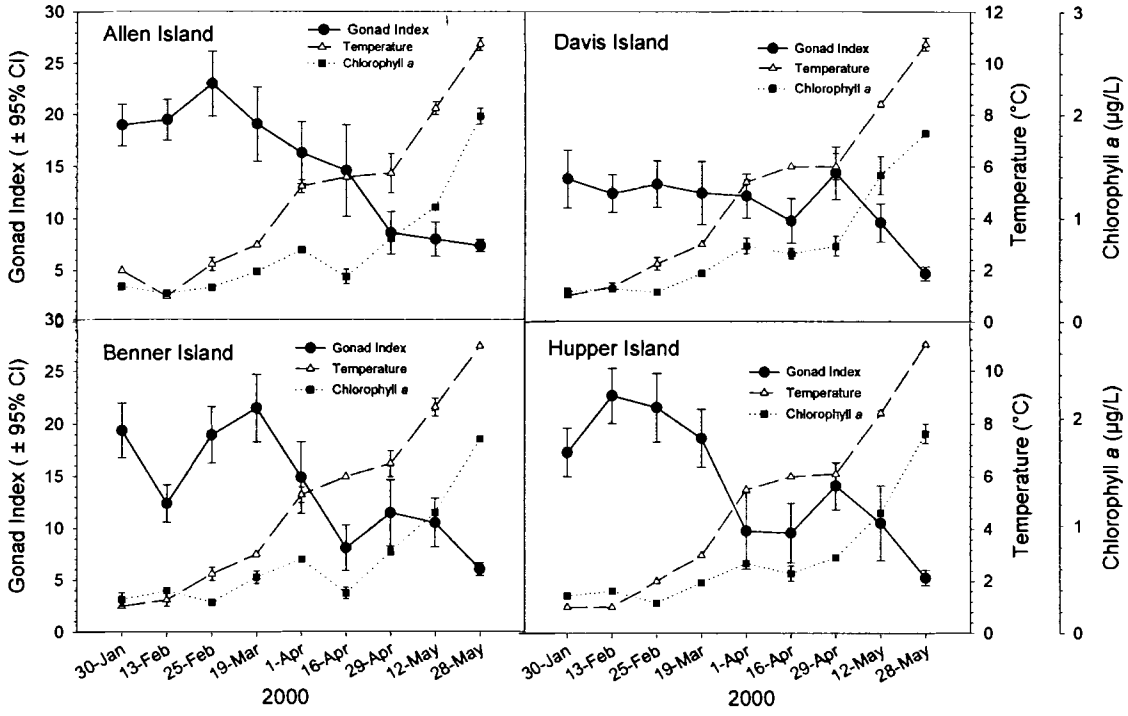

Figure 1.5. ***Georges Island Region.*** Variation in mean gonad index (± 95% CI) of male and female sea urchins (n=20), temperature (n=2), and chlorophyll *a* (n=2) concentration at Allen, Benner, Davis, and Hupper Islands from 30 January to 28 May 2000.

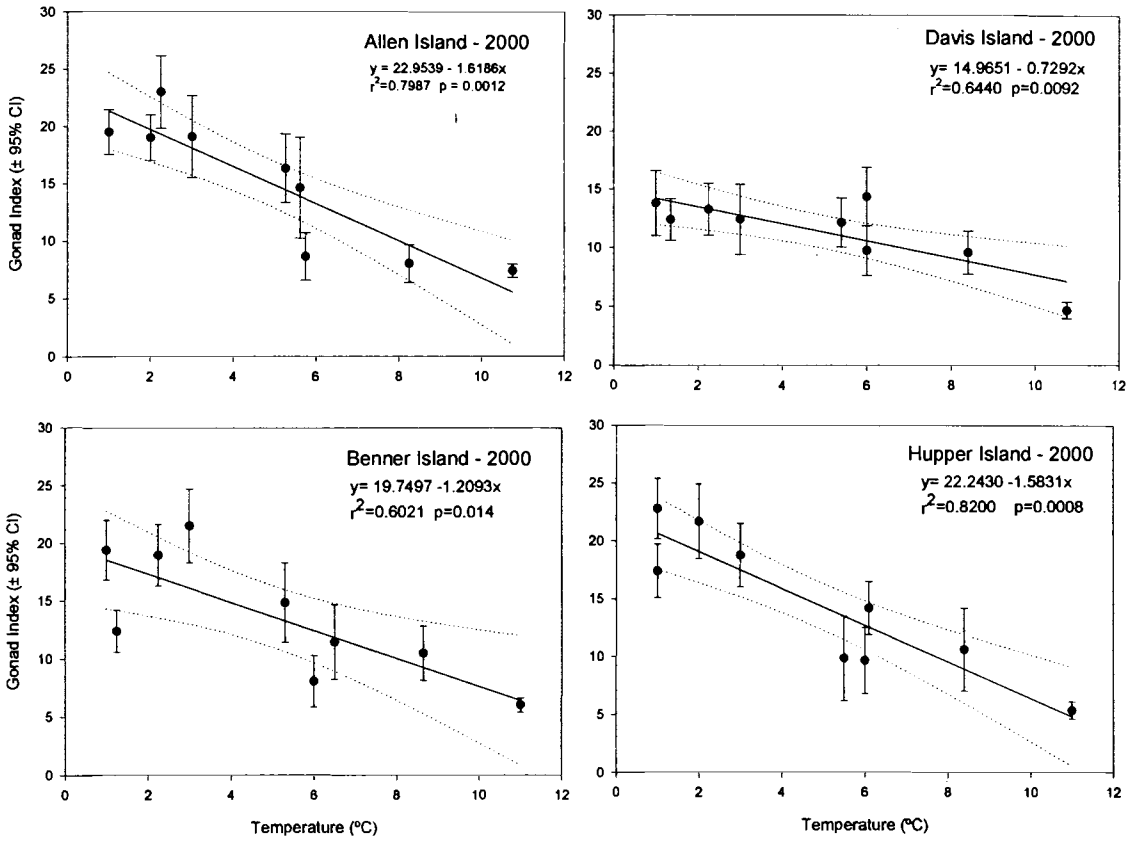

Figure 1.6. ***Georges Island Region.*** Linear regression analysis (± 95 % CI) of the relationship between mean gonad index of male and female sea urchins (n=20) at Allen, Benner, Davis, and Hupper Islands and mean temperature (n=2).

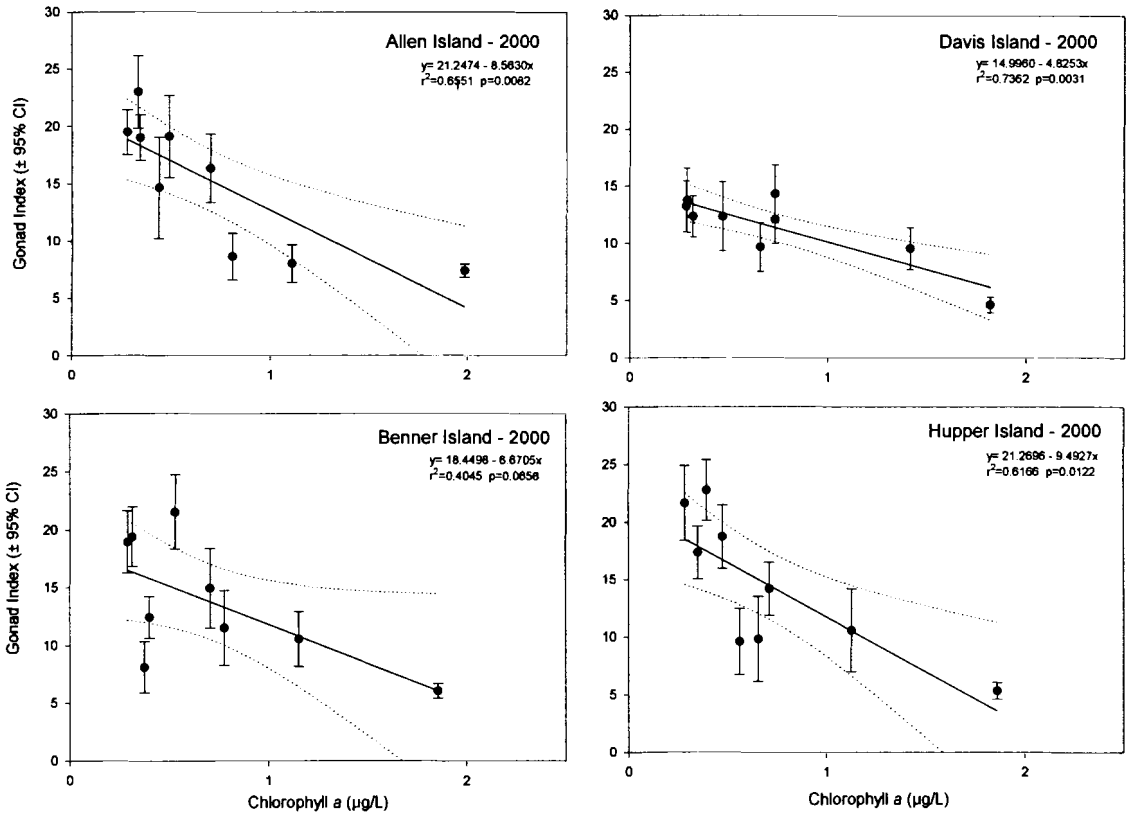

Figure 1.7. ***Georges Island Region.*** Linear regression analysis (± 95 % CI) of the relationship between mean gonad index of male and female sea urchins (n=20) at Allen, Benner, Davis, and Hupper Islands and mean chlorophyll *a* concentration (n=2).

chlorophyll *a* ranged from 0.266 for females at Benner Island and 0.488 for males at Davis Island to 0.640 for females at Hupper Island and 0.647 for males at Allen Island (Appendix C). Generally, the relationship between gonad index and temperature is stronger than the relationship between gonad index and chlorophyll *a*. Despite a significant relationship with relatively high coefficients of determination, linear regression analyses show, there is high variability in the relationship between gonad index and environmental variables.

Stepwise, multiple linear regression analyses show that the dependence of gonad indices on oceanographic variables varies between sites (Appendix D). However, as a conservative, predictive model for urchins in the Georges Islands Region, data were pooled from all sites. Most variables considered in the multiple regressions did not significantly contribute to the model (Appendix D). For pooled sites, nitrate + nitrite and silicate had significant effects on gonad indices ($R^2 = 0.626$) (Table 1.6). However, this coefficient of determination is much less than for each site individually. Changes in

Table 1.6. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=36) at Allen, Benner, Davis, and Hupper on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.626; SE of estimate = 0.032).

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	2	0.060	0.030	30.280	< 0.0001
Error	33	0.033	0.001		
Total	35				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.085	< 0.0001	0.018	
$NO_3 + NO_2$	0.016	< 0.0001	0.003	0.787
SiO_4	-0.005	0.114	0.003	-0.272

gonad indices at (1) Allen Island were significantly related to salinity and phosphate ($R^2 = 0.965$), (2) Benner Island were significantly related to temperature and nitrate + nitrite, ($R^2 = 0.747$), (3) Davis Island were significantly related to phaeophytin and salinity ($R^2 = 0.910$), and (4) Hupper Island were significantly related to chlorophyll *a*, salinity, and temperature ($R^2 = 0.982$) (Appendix D).

Stepwise, multiple linear regression analyses, with temperature forced first into the model, show that the dependence of gonad indices on oceanographic variables varies between sites. Again, as a conservative, predictive model for urchins in the Georges Island Region, data were pooled from all sites. Most variables used in the multiple regressions did not contribute significantly to the model (Appendix E). For pooled sites, temperature alone had significant effects on gonad indices ($R^2 = 0.624$) (Table 1.7).

Table 1.7. ***Georges Islands Region***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=18) at Allen, Benner, Davis, and Hupper Islands on oceanographic variables derived by stepwise, forward elimination procedure, with temperature forced first into the model (Adj. Model R^2 =0.624; SE of estimate = 0.032).

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	1	0.060	0.060	59.103	< 0.0001
Error	34	0.035	0.001		
Total	35				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.201	< 0.0001	0.010	
Temperature	-0.013	< 0.0001	0.002	-0.797

Coefficients of determination at each site were much greater than pooled sites and the variables that had a significant effect on gonad indices varied between sites. Changes in gonad indices at (1) Allen Island were significantly related to temperature and salinity

($R^2 = 0.950$), (2) Benner Island were significantly related to temperature and nitrate + nitrite ($R^2 = 0.747$), (3) Davis Island were significantly related to phaeophytin and salinity ($R^2 = 0.947$), and (4) Hupper Island were significantly related to chlorophyll *a*, salinity, and temperature ($R^2 = 0.916$) (Appendix E).

Principal components analysis of the oceanographic variables that may influence the time of urchin spawning showed that the first and second principal components accounted for 63.1% and 13.7 % of the variability in the data set, respectively. Nitrate + nitrite, silicate, phosphate, and salinity had a strong, positive influence on the first principal component (PC1), while temperature, chlorophyll *a*, and phaeophytin had a strong, negative influence on PC1. The component loadings for each variable indicate that ammonium and extinction coefficient were not important in the overall model, with low correlation coefficients (Table 1.8). All other variables showed a strong relationship with the first principal component. The first two principal components, or oceanographic indices, were then used in multiple regression analysis on gonad indices for each site.

Table 1.8. ***Georges Island Region.*** Component loadings for variables used in PCA. Component loadings are the linear relationships between the variable and each principal component (PC).

Variable	PC1	PC2
Ammonium (NH_4)	0.379	0.629
Extinction Coefficient	-0.244	-0.604
Silicate (SiO_4)	0.806	0.407
Salinity (ppt)	0.742	-0.340
Phaeophytin	-0.858	0.312
Phosphate (PO_4)	0.847	-0.287
Temperature	-0.967	-0.082
Chlorophyll *a*	-0.962	0.032
Nitrate + nitrite ($NO_3 + NO_2$)	0.980	0.000

Multiple regression analysis shows a significant relationship between arcsine-transformed gonad indices and the first two principal components (oceanographic index) (Table 1.9). Pooled gonad indices for female and male urchins at all sites were used as a

Table 1.9. ***Georges Island Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices from Allen, Benner, Davis, and Hupper Islands on principal components (Model R^2 =0.569).

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	3	0.056	0.028	24.095	< 0.0001
Error	33	0.039	0.001		
Total	36				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	-0.066	0.302	0.063
PC1	0.012	< 0.0001	0.002
PC2	-0.007	0.253	0.006

conservative estimate for the relationship between the oceanographic index and gonad indices. For all sites pooled in the Georges Islands region, the oceanographic index explained 57% of the variation in gonad indices. However, the strength of the relationship varied between sites. The oceanographic index explains 90%, 37%, 71%, and 67% of the variation in gonad index at Allen, Benner, Davis, and Hupper Islands, respectively (Appendix F). The overall regression model at Allen, Davis, and Hupper Islands was significant, although the model at Benner Island was not ($p = 0.104$).

Eastern Maine: Jonesport Region

Mean biweekly gonad index values indicate similar trends in spawning patterns among the three sites (Fig. 1.8). Gonad indices of male and female *S. droebachiensis* changed significantly from January through late May at all sites, although the precise changes in gonad indices varied between sites. Pre-spawning gonad indices were high during late February through mid- March, and declined in mid to late-April at all sites. Based on declining gonad indices, spawning appears to have begun in late April at Black Duck Cove, early April at Starboard Cove, and late March at Loon Point (Fig. 1.8). The peak in pooled gonad indices was consistent in magnitude between all three sites. Only on March 5 and 18 were pooled gonad indices significantly different between sites (ANOVA, $F_{2, 57} = 3.302, p = 0.044$; $F_{2,57} = 4.572, p = 0.014$), with Loon Point urchins having consistently higher gonad indices than Black Duck Cove (Tukey's HSD multiple comparison, $p = 0.056$ and $p = 0.01$ for March 5 and 18, respectively). Gonad indices of female urchins were not significantly different between sites on any date, while male urchins had significantly different gonad indices among sites on 18 March (Table 1.10).

Sexual differences

Gonad indices of male and female *S. droebachiensis* at each site changed synchronously over the study period (Fig. 1.8). Females generally had greater gonad indices than males, although the magnitude of difference varied between sites and over time. At Black Duck and Starboard Coves there was a significant effect of date and sex

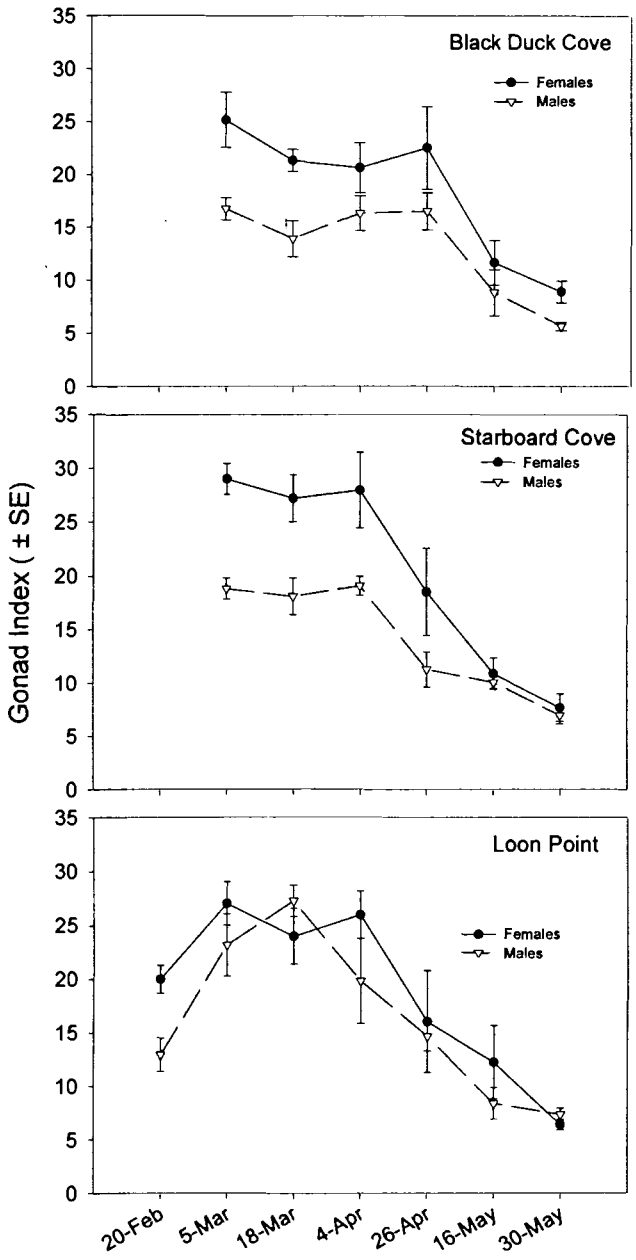

Figure 1.8. ***Jonesport Region***. Changes in mean gonad index (± 1 SE) of female and male sea urchins at Black Duck Cove, Starboard Cove, and Loon Point (n=20).

Table 1.10. ***Jonesport Region.*** Summary results of individual ANOVA on the effect of site on mean gonad index (arcsine-transformed) of female and male urchins at Black Duck Cove, Loon Point, and Starboard Cove at each sampling date.

Sex	Date	df (source, error)*	F-ratio	Probability
Male	5 March	2, 27	3.223	0.056
Female	5 March	2, 26	0.900	0.419
Male	18 March	2, 23	13.128	<0.0001
Female	18 March	2, 30	1.855	0.174
Male	4 April	2, 27	0.809	0.456
Female	4 April	2, 27	1.965	0.160
Male	26 April	2, 33	2.825	0.074
Female	26 April	2, 20	0.607	0.555
Male	16 May	2, 18	0.289	0.752
Female	16 May	2, 34	0.095	0.909
Male	30 May	2, 20	1.893	0.177
Female	30 May	2, 31	1.070	0.355

*Variable sample sizes due to the inability to determine the sex of a small number of individuals at each date.

on gonad indices, with females having either equal or greater gonad indices than males during the pre-spawning period (Table 1.11). The interaction between sex and date was significant at Starboard Cove, and is attributable to female urchins having significantly greater gonad indices than males from 5 March through 26 April and equal gonad indices following spawning. Female urchins at Black Duck Cove had significantly greater gonad indices than males on 5 March, 18 March, and 30 May. At Loon Point, there was a significant effect of date, but not sex, on gonad indices. Females at Loon Point did have significantly greater gonad indices than males on 20 February (ANOVA, $F_{1, 18} = 10.805$, $p = 0.004$), but this difference was not detected for the rest of the sampling period. Overall, females had peak gonad indices at the same (Black Duck Cove) or earlier dates than male urchins (Table 1.12). In addition, female sea urchins had significantly greater

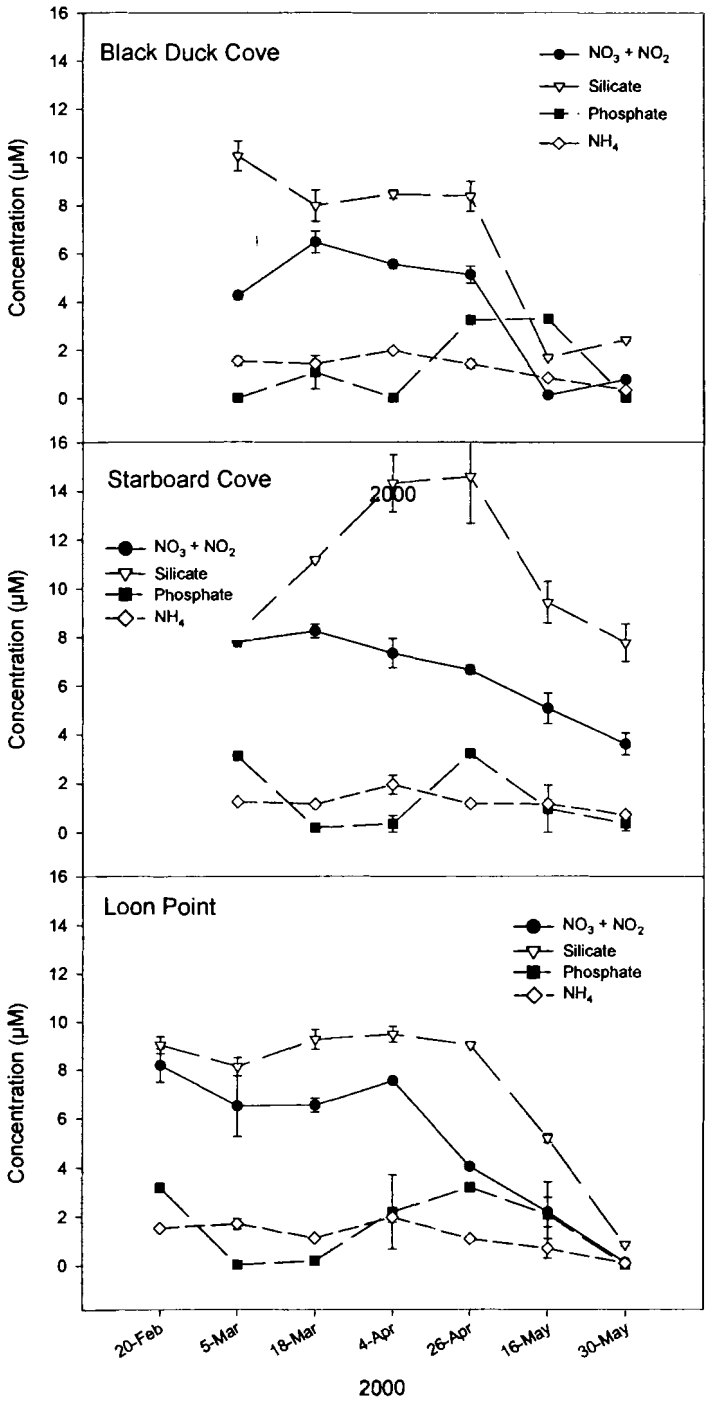

Figure 1.9. ***Jonesport Region.*** Mean concentrations (± 1 SE) of nitrate + nitrite, silicate, phosphate, and ammonium (µM) at Black Duck Cove, Starboard Cove, and Loon Point, 2000 (n=2 for each variable).

to < 3 μM. At Starboard Cove, silicate concentrations were significantly higher than at the other sites (> 12 μM) during April, and only decreased moderately to about 8 μM by 30 May. Nitrate-nitrite concentration decreased gradually over the study period at all sites although the concentrations varied between sites. Phosphate and ammonium concentrations were low throughout the sampling period, and no distinct trend was detected (Fig. 1.9).

Pearson product moment correlation coefficients indicated a strong relationship between many oceanographic variables (Table 1.13). Correlation coefficients were computed by site, although the pooled coefficients are presented here (Appendix B). Because the magnitude of and changes in oceanographic variables were consistent between sites, data from all sites were pooled to examine the overall relationship between the variables in the Jonesport region. Water temperature, chlorophyll *a*, phaeophytin, nitrate + nitrite, silicate, phosphate were significantly correlated. The strongest relationships were between chlorophyll *a* and nitrate + nitrite ($r = -0.809$, $p < 0.0001$), chlorophyll *a* and silicate ($r = -0.761$, $p < 0.0001$), and nitrate + nitrite and silicate ($r = -0.761$, $p < 0.0001$). Temperature was significantly correlated with chlorophyll *a*, phaeophytin, and nitrate + nitrite (Table 1.13). Inorganic nutrient concentrations were inversely correlated with temperature and chlorophyll *a*.

Relationships with gonad index

There is a significant inverse relationship between gonad index and temperature and chlorophyll *a*, although the strength of this relationship varied between sites (Fig 1.10). Coefficients of determination (r^2) for the relationship between gonad

Table 1.13. ***Jonesport Region.*** Relationship between oceanographic variables, expressed as Pearson correlation coefficients and Bonferroni probabilities at all Downeast sites.

Variable		Salinity	Temp	Chl a	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r:*	1.00							
	P:	0							
Temperature	*r:*	0.477	1.000						
	P:	0.070	0						
Chl a	*r:*	0.185	0.665	1.000					
	P:	1.000	< 0.0001	0					
Phaeophytin	*r:*	0.324	0.669	0.670	1.000				
	P:	1.000	< 0.0001	< 0.0001	0				
NO_3 +NO_2	*r:*	0.022	-0.675	-0.809	-0.688	1.000			
	P:	1.000	< 0.0001	< 0.0001	< 0.0001	0			
SiO_4	*r:*	-0.052	-0.457	-0.761	-0.619	0.782	1.000		
	P:	1.000	0.110	< 0.0001	0.001	< 0.0001	0		
PO_4	*r:*	0.021	0.046	0.041	-0.158	0.111	0.074	1.000	
	P:	1.000	1.000	1.000	1.000	1.000	1.000	0	
NH_4	*r:*	0.068	-0.565	-0.585	-0.515	0.721	0.632	0.107	1.000
	P:	1.000	0.006	0.003	0.026	< 0.0001	0.001	1.000	0

index and temperature and chlorophyll *a* were determined for both male and female sea urchins (Fig 1.11 and 1.12). The strength of this relationship varied between sites and between males and females. Coefficients of determination for the linear relationship between gonad indices and temperature ranged from 0.696 for females at Loon Point and 0.4133 for males at Loon Point to 0.932 for females at Starboard Cove and 0.911 for males at Starboard Cove (Fig 1.11). Similarly, coefficients of determination for the linear relationship between gonad indices and chlorophyll *a* ranged from 0.673 for females at Starboard Cove and 0.521 for males at Loon Point to 0.871 for females at Black Duck Cove and 0.806 for males at Black Duck Cove (Fig 1.11). In addition, linear regression analyses show that despite a significant relationship with relatively high coefficients of determination, there is high variability in the relationship between gonad index and environmental variables.

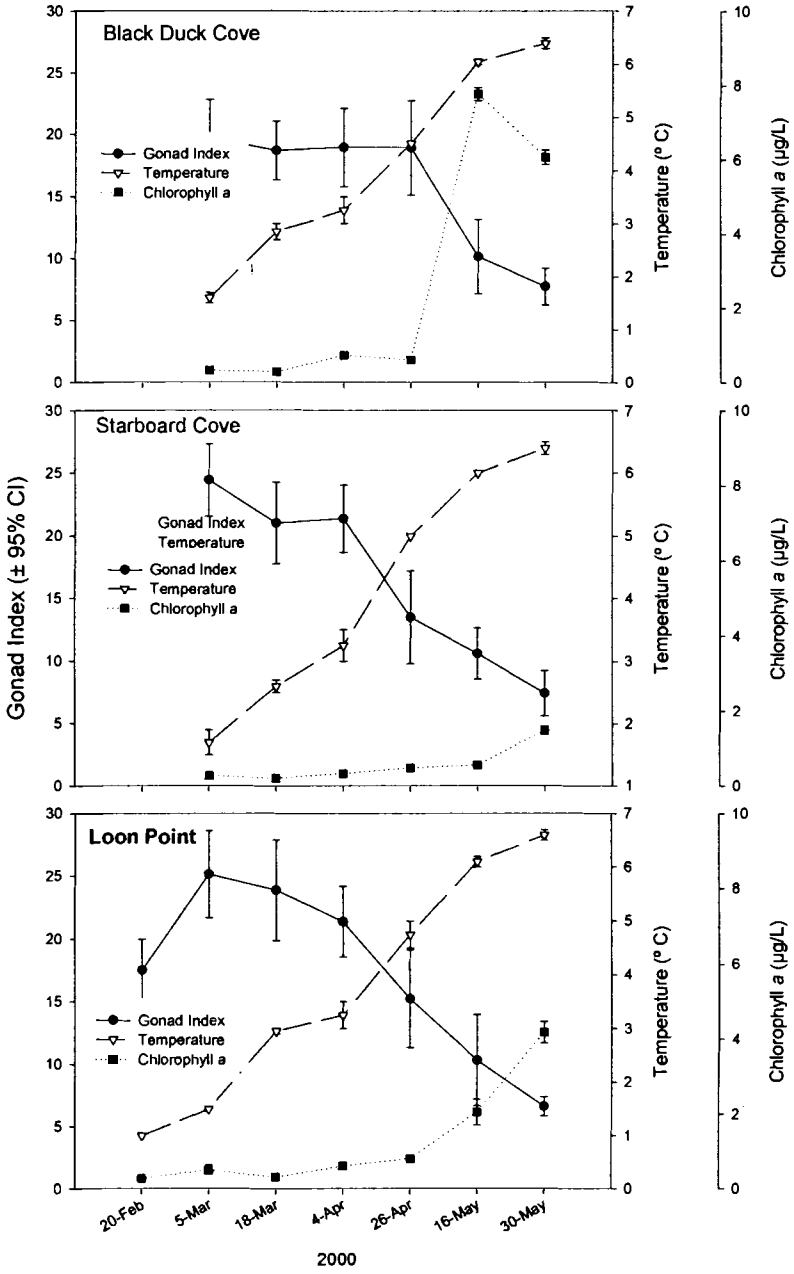

Figure 1.10. ***Jonesport Region***. Variations in mean gonad index (± 95% CI) of male and female sea urchins (n=20), temperature (n=2), and chlorophyll *a* (n=2) concentration at Black Duck Cove, Starboard Cove, and Loon Point from 20 February to 30 May 2000.

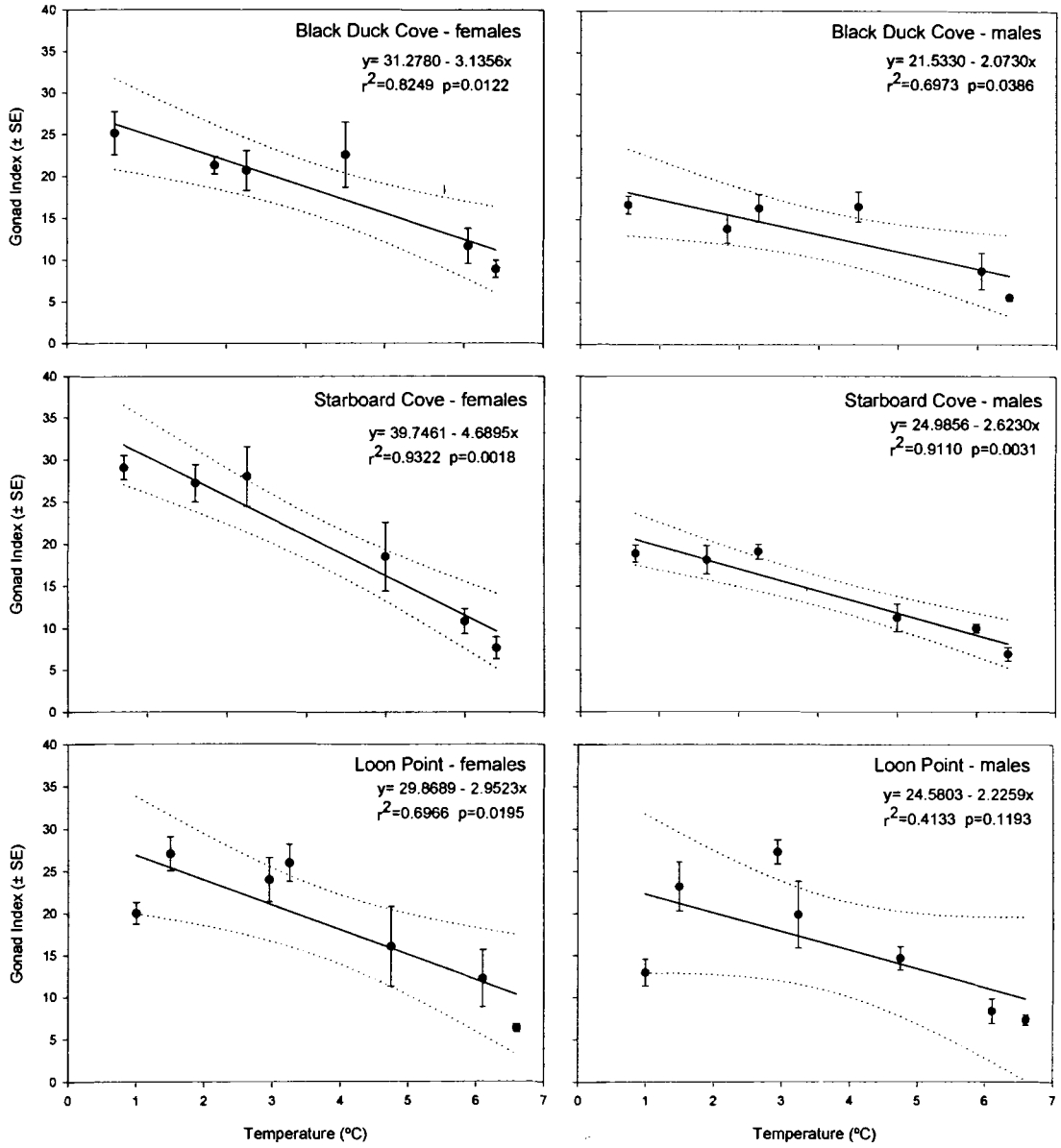

Figure 1.11. ***Jonesport Region.*** Linear regression analysis (± 95 % CI) of the relationship between mean gonad index of male and female sea urchins (n=20) at Black Duck Cove, Starboard Cove, and Loon Point and mean temperature (n=2).

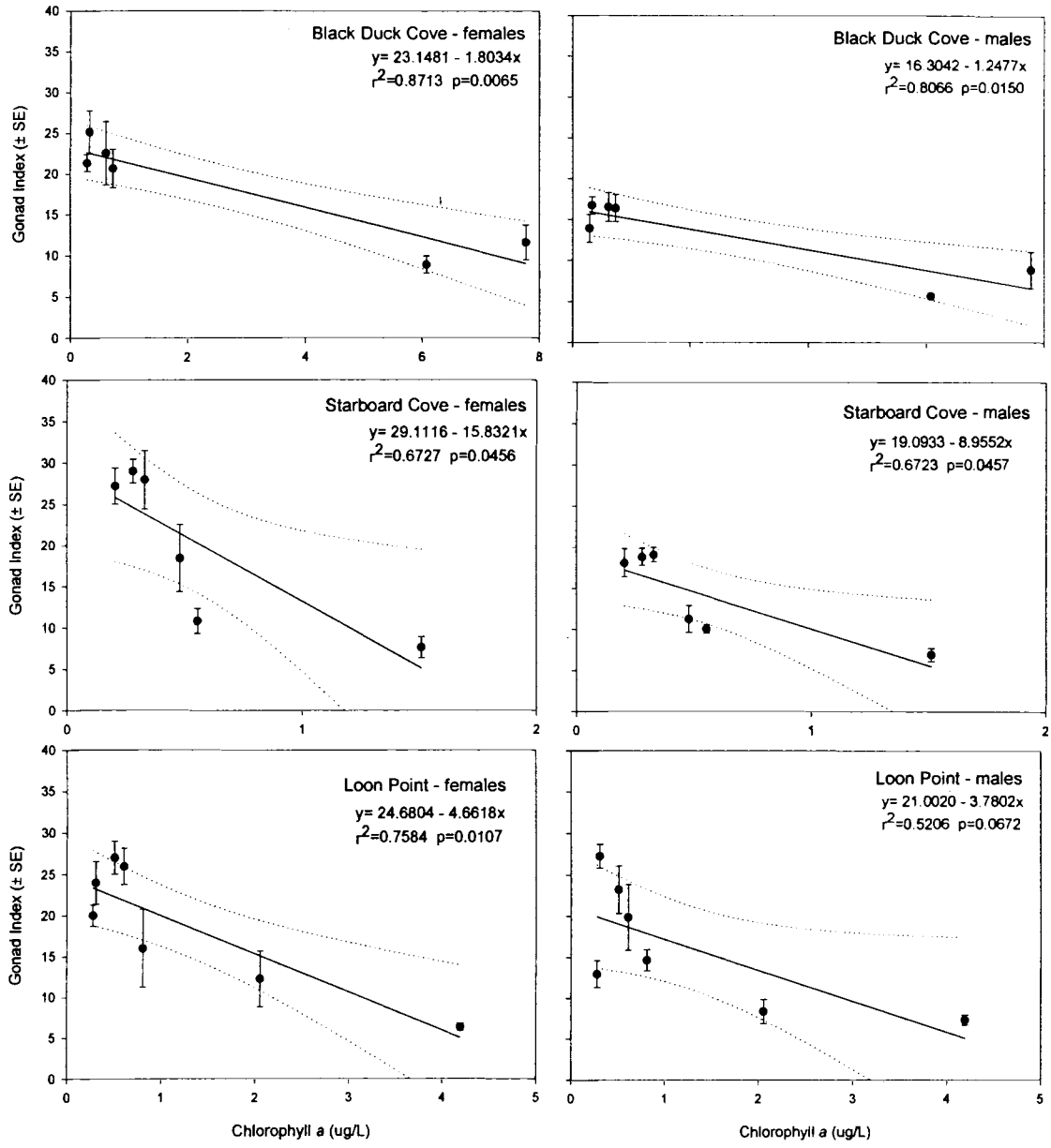

Figure 1.12. ***Jonesport Region***. Linear regression analysis (± 95 % CI) of the relationship between mean gonad index of male and female sea urchins (n=20) at Black Duck Cove, Starboard Cove, and Loon Point and mean chlorophyll *a* (n=2) concentration.

Stepwise, multiple linear regression analyses show that the dependence of gonad indices on oceanographic variables varies between sites. However, as a conservative, predictive model for the Jonesport Region, data were pooled from all sites. Most variables used in the multiple regressions did not contribute significantly to the model (Appendix D). For pooled sites, temperature and ammonium had significant effects on gonad indices ($R^2 = 0.802$) (Table 1.14). Coefficients of determination at each site were much greater than pooled sites and the variables that had a significant effect on gonad indices varied between sites. Changes in gonad indices at (1) Black Duck Cove were significantly related to silicate, phaeophytin, and ammonium ($R^2 = 0.992$), (2) Loon Point were significantly related to nitrate + nitrite, phosphate, salinity, and temperature ($R^2 = 1.00$), (3) Starboard were significantly related to temperature and phaeophytin ($R^2 = 0.997$) (Appendix D).

Table 1.14. ***Jonesport Region***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=18) at Black Duck Cove, Loon Point, and Starboard Cove on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.802; SE of estimate = 0.027).

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	2	0.056	0.028	37.499	< 0.0001
Error	16	0.012	0.001		
Total	18				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.215	< 0.0001	0.040	
Temperature	-0.022	< 0.0001	0.005	-0.889
NH_4	0.032	0.095	0.018	0.406

Stepwise, multiple linear regression analyses with temperature forced first into the model show that the dependence of gonad indices on oceanographic variables varies

between sites. Again, as a conservative, predictive model for the Jonesport Region, data were pooled from all sites. Most variables used in the multiple regressions did not contribute significantly to the model (Appendix E). For pooled sites, temperature, salinity, and nitrate + nitrite had significant effects on gonad indices ($R^2 = 0.849$) (Table 1.15). Coefficients of determination at each site were much greater than pooled sites and the variables that had a significant effect on gonad indices varied between sites. Changes in gonad indices at (1) Black Duck Cove were significantly related to temperature, salinity and silicate ($R^2 = 0.965$), (2) Loon Point were significantly related to temperature, salinity, phaeophytin, phosphate ($R^2 = 1.00$), (3) Starboard were significantly related to temperature and phaeophytin ($R^2 = 0.997$) (Appendix E).

Table 1.15. ***Jonesport Region***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=18) at Black Duck Cove, Loon Point, and Starboard Cove on oceanographic variables derived by stepwise, forward elimination procedure, with temperature forced first into the model (Adj. Model R^2 =0.849; SE of estimate = 0.024).

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	2	0.060	0.020	34.829	< 0.0001
Error	16	0.009	0.001		
Total	18				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	1.268	0.006	0.398	
Temperature	-0.014	0.023	0.006	-0.889
Salinity	-0.033	0.019	0.012	-0.484
$NO_3 + NO_2$	-0.007	0.057	0.003	0.470

Principal components analysis of the oceanographic variables that may influence the time of urchin spawning showed that the first and second principal components accounted for 58.2% and 16.6 % of the variability in the data set, respectively. Silicate,

ammonium, and nitrate + nitrite had a strong, negative influence on the first principal component, while temperature, chlorophyll *a,* and phaeophytin had a strong positive influence on PC1. The component loadings for each variable indicate that salinity and phosphate were not important in the overall model, with low correlation coefficients (Table 1.16). However, salinity had a strong influence on PC2 (r = 0.838).

Table 1.16. ***Jonesport Region.*** Component loadings for variables used in PCA for Black Duck Cove, Loon Point, and Starboard Cove. Component loadings are the linear relationships between the variable and each principal component.

Variable	PC1	PC2
Ammonium (NH_4)	-0.839	0.061
Silicate (SiO_4)	-0.832	0.382
Salinity (ppt)	0.381	0.838
Phaeophytin	0.832	-0.208
Phosphate (PO_4)	-0.070	0.552
Temperature	0.845	0.361
Chlorophyll *a*	0.887	-0.038
Nitrate + nitrite ($NO_3 + NO_2$)	-0.959	0.010

The first two principal components, or oceanographic index, were used as independent variables in multiple regression analyses on gonad indices for each site. Multiple regression analyses show a significant relationship between arcsine-transformed gonad indices and the first two principal components (oceanographic index) (Table 1.17). Pooled gonad indices for female and male urchins at all sites were used as a conservative estimate for the relationship between the oceanographic index and gonad indices. For all sites pooled in the Jonesport region, the oceanographic index explained 80% of the variation in gonad indices. However, the strength of the relationship varied between sites. The oceanographic index explains 94%, 85%, and 72% of the variation in gonad index at Black Duck Cove, Loon Point, and Starboard Cove, respectively (Appendix F).

The overall regression model at Black Duck Cove and Loon Point was significant, although the model at Starboard Cove was not ($p = 0.068$).

Table 1.17. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices from Black Duck Cove, Starboard Cove, and Loon Point on principal components (Model $R^2 = 0.797$)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.056	0.028	36.384	< 0.0001
Error	16	0.012	0.001		
Total	18				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	1.801	< 0.0001	0.404
PC1	-0.563	0.001	0.138
PC2	0.277	0.001	0.070

Large-scale Spatial Patterns - Between Regions

Variations in gonad indices of sea urchins at sites within the Jonesport Region were more similar to each other than variations in gonad indices of sea urchins at sites within the Georges Islands Region. Male and female urchins were generally more synchronous at the Jonesport region than the Georges Islands, with gonad indices closely mirroring each other. The changes in gonad indices of urchins in the Jonesport region followed the typical trajectory of temperate sea urchins, while urchins in the Georges Island region had a less defined (i.e, protracted) spawning season. The spawning period of urchins between the two regions was generally similar, despite the differences in environmental variables.

Peak arcsine-transformed gonad indices of male and female sea urchins at all sites were typically similar, although peak gonad index of female urchins at Davis Island were

significantly smaller than female gonad indices at all other sites (ANOVA, $F_{6, 62} = 4.128$, $p = 0.002$) and peak gonad index of males at Loon Point were significantly greater than male gonad indices at all other sites (ANOVA, $F_{6, 59} = 7.740$, $p < 0.0001$) (Table 1.18). Peak gonad indices of female sea urchins within each region occurred at similar times, while peak gonad indices of male sea urchins within each region occurred at different times (Table 1.18). Variations in gonad indices of males and females between sites within the Georges Islands region was greater than between sites within the Jonesport region (see Tables 1.1 and 1.10).

Table 1.18. Peak mean (± 1 SE) gonad index (n=20), date on which peak GI occurred, and Tukey's HSD grouping of arcsine-transformed female and male gonad indices in the Georges Islands and Jonesport Regions. (Means with the same letter are not significantly different).

Site	Peak GI Females (date)	Peak GI Males (date)
Georges Islands Region		
Hupper Island	26.68 ± 1.61 (25 Feb) A	19.34 ± 1.29 (13 Feb) A
Benner Island	26.41 ± 1.21 (19 Mar) A	19.50 ± 1.79 (30 Jan) A
Allen Island	26.40 ± 1.86 (25 Feb) A	19.09 ± 1.31 (13 Feb) A
Davis Island	17.10 ± 1.30 (25 Feb) B	15.17 ± 1.34 (29 Apr) A
Jonesport Region		
Starboard Cove	29.06 ± 1.43 (5 Mar) A	19.13 ± 0.87 (4 Apr) A
Loon Point	27.08 ± 1.98 (5 Mar) A	27.30 ± 1.45 (18 Mar) B
Black Duck Cove	25.17 ± 2.59 (5 Mar) A	16.74 ± 1.06 (5 Mar) A

Mean test diameter of sea urchins in the Georges Islands region and the Jonesport region were significantly different, with urchins in the Georges Island region being smaller than urchins in the Jonesport region. Urchins collected in the Jonesport region had mean (± SE) test diameters ranging from 67.3 ± 0.61 to 69.2 ± 0.66 mm (range 50.1 mm to 92.9 mm), while mean (± SE) test diameter of urchins in the Georges Island region ranged from 60.8 ± 0.25 to 64.8 ± 0.37 mm (range 37.5 to 75.4 mm) (Table 1.19). The

size range of animals in both regions was minimized to avoid the effect of size on gonad index (Gonor 1972), and reflects the upper size range of the animals available at each site.

Table 1.19. Summary statistics for test diameter (TD) and peak gonad index in males and females at all sites (mean ± SE (date)).

Site	Mean (± SE) TD	Min TD	Max TD	Peak GI Females (date)	Peak GI Males (date)
GEORGES ISLANDS					
Allen	61.4 ± 0.38	37.5	75.3	26.40 ± 1.86 (25 Feb)	19.09 ± 1.31 (13 Feb)
Benner	61.6 ± 0.42	47.5	75.3	26.41 ± 1.21 (19 Mar)	19.50 ± 1.79 (30 Jan)
Davis	60.8 ± 0.25	52.6	70.7	17.10 ± 1.30 (25 Feb)	11.89 ± 2.24 (19 Mar)
Hupper	64.8 ± 0.37	53.3	75.4	26.68 ± 1.61 (25 Feb)	19.34 ± 1.29 (13 Feb)
DOWNEAST					
Black Duck Cove	69.2 ± 0.66	50.1	86.3	25.17 ± 2.59 (5 Mar)	16.74 ± 1.06 (5 Mar)
Loon Point	67.3 ± 0.61	50.1	83.3	27.08 ± 1.99 (5 Mar)	27.30 ± 1.46 (18 Mar)
Starboard Cove	67.5 ± 0.70	50.1	92.9	29.06 ± 1.43 (5 Mar)	19.13 ± 0.87 (4 Apr)

DISCUSSION

Spawning and Gonad Indices

Spawning in sea urchins with annual reproductive cycles results in an observable decline in gonad indices (Giese and Pearse 1974; Giese and Kanatani 1987), but few authors have provided a quantitative definition of spawning (i.e., based on changes in gonad index). Vadas and Beal (1989) define spawning in the green sea urchin as "the greatest significant decline in gonad index between two consecutive months," although they did not corroborate this definition with histological analyses. Studies that have coupled histological analyses with changes in gonad index show that a sharp decline in gonad index is generally indicative of spawning in some species (e.g., *S. droebachiensis:* Meidel and Scheibling 1998), but not in all species (e.g., *Centrostephanus rodgersii*: King et al. 1994). It has been suggested that decreases in gonad index may be due to utilization of nutrient resources stored in the gonad in addition to spawning (Byrne 1990). During the spawning period, there is high variability in the reproductive stage of sea urchins (Byrne 1990; King et al. 1994; Meidel and Scheibling 1998), which indicates reproductive asynchrony among individuals in a population. Moreover, although a sharp decline in gonad index may generally indicate spawning, there are intrinsic problems with defining spawning quantitatively based on changes in gonad index.

There are two fundamental challenges to defining spawning using changes in gonad index. The first difficulty is due to a lack of information about an individual sea urchin's spawning behavior. For most species, it is not known if an individual releases all of its gametes in a single spawning event or if it releases a fraction of its gametes several times during the spawning period. Also, the degree of reproductive synchrony in sea

urchin populations is poorly understood, although it is probable that some individuals in a population spawn at different times, while others spawn at the same time. Individual spawning behavior and population-level spawning patterns interact and may result in several types of spawning. In populations where individuals release all of their gametes during one spawning event and all members of a population spawn synchronously, a quantitative definition of spawning based on declining gonad indices is possible and meaningful (Fig. 1.13a). However, in populations where individuals are reproductively asynchronous or where individuals release a portion of their gametes during multiple spawning events, a quantitative definition of spawning becomes more difficult (Fig. 1.13b). Exact spawning behavior is generally unknown and is difficult to determine because spawning is rarely observed in nature (Pearse and Cameron 1991). Further, destructive sampling is required to determine the reproductive condition of an animal, therefore making determinations of specific spawning behavior impossible. Despite this, there is some evidence to suggest that some urchin species have the capacity to release a portion of its gametes several times. For example, in *S. droebachiensis*, multiple injections of KCl are necessary to stimulate the release of all of an individual's gametes (Vadas et al. *unpublished data).* Additionally, in time-integrated fertilization assays using *S. droebachiensis*, Wahle and Gilbert (2002) observed near continuous male spawning during the spawning season, although this was likely due to different individuals spawning at different times rather than a single individual spawning continuously. Moreover, precise spawning behaviors in nature are virtually unknown and complicates the development of quantitative definition of spawning.

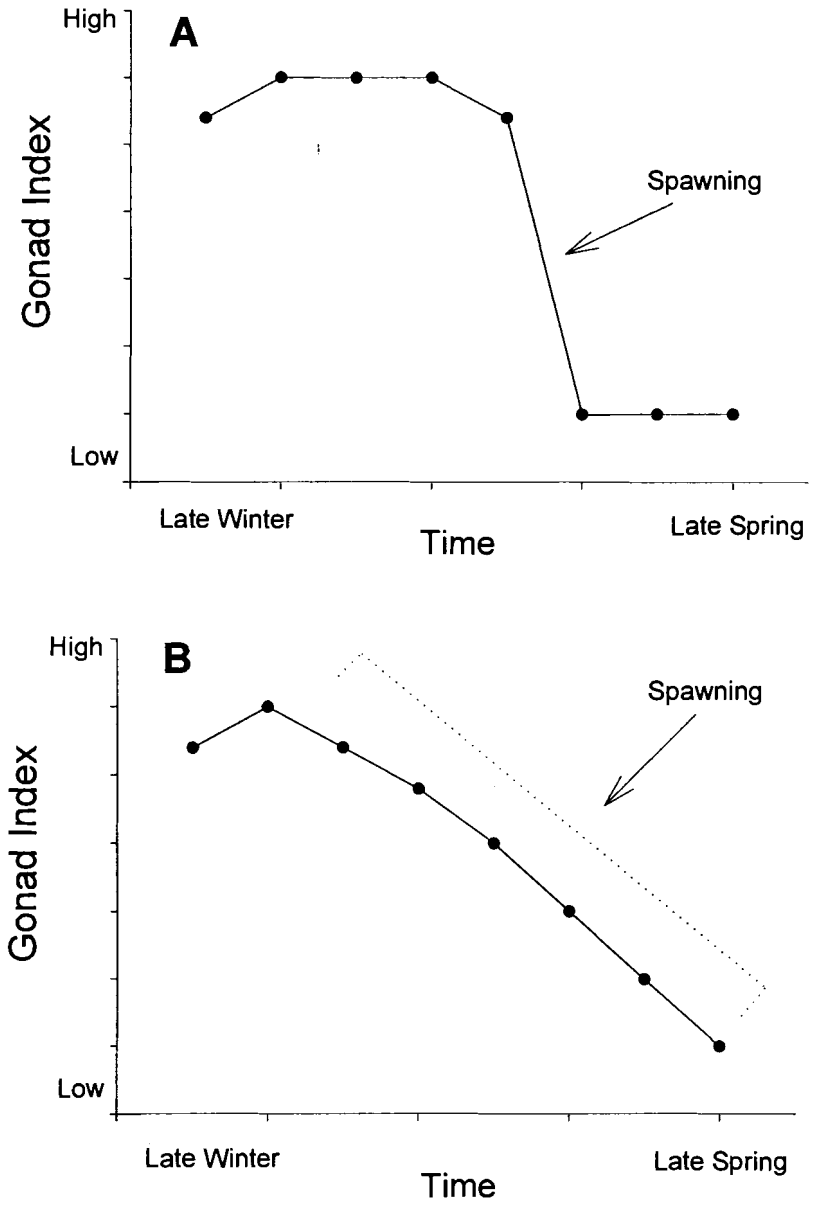

Figure 1.13. Diagrammatic illustration of two types of spawning that might occur in temperate sea urchins: (A) Discrete or synchronous spawning and (B) Protracted ("dribble") spawning.

Without knowledge of an individual's spawning behavior, inferences about population-level spawning based on changes in gonad index may be weak. The few documented observations of natural spawning indicate that sea urchins spawn both in aggregations and as scattered individuals (Pennington 1985), males spawn first, and once spawning is initiated, conspecifics are stimulated to spawn (Gieses and Pearse 1974), and spawning is highly temporally and spatially variable (Pennington 1985; Levitan 2002). For example, in natural spawning of *S. franciscanus*, Levitan (2002) observed (1) less than 50% of sea urchins in a 5 x 5 m^2 area were spawning, (2) a higher percentage of males were spawning, and (3) that spawning occurred in highly local aggregations. In this study, sea urchins were sampled irrespective of their spatial distribution and therefore, it is possible that the high variability in changes in gonad indices was due to very local effects; that is, urchins spatially proximate may have been spawning synchronously, while non-adjacent individuals may not have been spawning. The lack of information about the spatial distribution of animals coupled with temporal variability of natural spawning further complicates a definition of spawning based only on variations in gonad index.

A second difficulty in defining spawning quantitatively is the temporal resolution used to examine changes in gonad index of a population. Most studies examining sea urchin reproductive cycles have sampled urchin populations at monthly, or less frequent, intervals, which may have masked the potentially high variability in the changes in gonad indices during the spawning period. In this study, changes in gonad indices of sea urchins in central Maine were highly variable and consistent with a protracted type of spawning (see Fig. 1.13b). Defining spawning based on declining gonad indices is

especially difficult in this scenario as it is unclear when (specifically) spawning occurred. Without histological analyses, it would not be prudent to quantitatively define spawning, as there are numerous "peaks" and "valleys" in gonad indices, which may or may not be indicative of spawning.

These limitations notwithstanding, the spawning season in the Georges Island region occurred between March and May and encompassed a period of 30 to 60 days. Similarly, the spawning season in the Jonesport region, which occurred between April and May, encompassed a period of 34 to 56 days. The temporal changes in gonad indices during the spawning period of green sea urchins from different sites along the coast of Maine, however, exhibited disparate trends. Sea urchins from the Jonesport sites and females at Allen Island followed the typical trajectory for spawning in the green sea urchin in Maine, with maximum gonad indices reached in late February followed by a linear decline in gonad indices to < 10% in late May (Vadas et al. 1989). In contrast, the spawning patterns observed at the other Georges Islands sites were not typical of the green sea urchin and appears to be protracted compared to other studies (Himmelman 1978; Meidel and Scheibling 1998; Vadas et al. 1989; *unpublished data*). Wahle and Gilbert (2002) observed a similar protracted spawning period of urchins sampled in West Boothbay Harbor, Maine in 2000, which indicates that the spawning patterns in the Georges Islands Region were not unusual relative to other sites in Maine in 2000. Although gonad indices at Benner, Davis and Hupper Islands exhibited a downward trend over the sampling period, the precise changes in gonad index were highly variable and the exact spawning time was difficult to determine. Further, female sea urchin gonad indices at Davis Island did not change significantly over the study period, which indicates

that a sharp decline in gonad indices does not necessarily occur during the spawning period.

Others have shown a distinct spawning period in temperate sea urchins, based on a significant decrease in gonad indices (Himmelman 1978; Starr et al. 1993; Meidel and Scheibling 1998), although infrequent sampling may have masked the high variability of changes in gonad index. Few have sampled urchin populations at biweekly intervals, and this sampling resolution may provide insights into the reproductive variability at the population level. The high inter-site variability coupled with the high variability in gonad indices at each sampling date suggests that green sea urchins have a prolonged spawning period lasting several months. Although the majority of the population likely releases its gametes synchronously, many individuals may spawn at different times. That is, the duration of the spawning period does not imply that the populations spawned continuously, but rather that portions of the population spawn at different times.

The high variability in gonad indices at each date during the pre-spawning period may reflect individual differences in nutrient acquisition, energy allocation, and patterns of gonad development. Meidel and Scheibling (1998) determined histologically that the greatest variability in reproductive stage in the green sea urchin occurred during the spawning period. This high variability in gonad condition during the mature phase has been reported for numerous temperate echinoids, and thus, results in a prolonged spawning period relative to tropical and deep-sea echinoids (Thorson 1948; Young et al. 1992; Byrne 1990; Young 1999).

These data also contribute to our understanding of temporal variation of spawning of green sea urchins. Two previous years of data from biweekly sampling at the Georges

Islands sites revealed sharper declines and more recognizable spawning period (Vadas et al. *unpublished*). Changes in gonad indices of green sea urchins in the Georges Island region in 2000 contrast with changes in both 1998 and 1999 (Appendix G). Despite high variability in gonad indices from January to mid-April, gonad indices declined significantly and sharply at most sites in 1998 and 1999. Gonad indices of urchins at Davis Island are an exception, where patterns in 1998 most closely resemble those seen in 2000. Additionally, the precise changes in gonad indices at each site varied between years. This inter-annual variation in the changes in and magnitude of gonad indices coupled with the high variation between sites highlights the importance of intensive field sampling at multiple temporal and spatial scales. Moreover, this temporal and spatial variability in green sea urchin spawning raises questions about the effects of this variation on recruitment, and consequently, the dynamics of sea urchin populations.

Spatial variation in Gonad Indices

The spawning season in the Georges Island region occurred between March and May, while the spawning season in the Jonesport region occurred between April and May. Although it appears that spawning began slightly later in the Jonesport region, there is some overlap in the spawning season. Without histological analyses of gonads, it is difficult to determine the precise time of spawning and inter-site and inter-region comparisons of spawning times are speculative except where gonad indices show a steep decline. Intra-population variability in the development of nutritive, nongametogenic tissue versus gametes *per se* have been shown for other urchins and underscore the

importance of histological analyses (Fuji 1960; Giese and Pearse 1974; Byrne 1990; Meidel and Scheibling 1998).

Changes in gonad indices were highly variable over distances of < 10 km in the Georges Island region, but were relatively synchronous between males and female sea urchins at all sites. Conversely, changes in and magnitude of gonad indices of urchins in the Jonesport region were relatively consistent between sites. It appears, however, that spawning began about two weeks later at Black Duck Cove than at Starboard Cove or Loon Point. The variability of changes in and magnitude of gonad indices between sites within each region suggest differences in food quality and quantity and availability (Vadas 1977). For example, Davis Island is characterized by low algal biomass relative to the other Georges Island sites (T. Dowling *personal communication)*, and this difference is reflected in the lower urchin gonad indices at this site. Additionally, Black Duck Cove is characterized by dense stands of kelp beds (*Alaria esculenta* and *Laminaria* spp.), while Starboard Cove and Loon Point have relatively less kelp (T. Scheafe *personal communication*). These differences in habitat characteristics may influence the reproductive stage of urchins inhabiting each site. Small-scale spatial variability in gonad indices has been reported for other echinoids, including the green sea urchin, and has been attributed to differences in food or habitat characteristics (Fuji 1960; Ebert 1968; Vadas 1977; Keats et al. 1984; Meidel & Scheibling 1998; Brevin et al. 2000).

Sexual Differences in Gonad Indices

At the peak of the reproductive cycle, female sea urchins had higher gonad indices than males at all sites. The changes in gonad indices of male and female urchins

within a site, however, were relatively synchronous. Differences between male and female gonad indices have been observed in *S. droebachiensis* in several studies, although the magnitude and direction of the difference is variable (Munk 1992; Meidel and Scheibling 1998; Oganesyan 1998). Meidel and Scheibling (1998), sampling green sea urchins on the east coast of Nova Scotia, Canada showed that female urchins had consistently higher gonad indices than males until the animals are "spent," at which time there was no significant difference. On the other hand, Oganesyan (1998), sampling green sea urchins in a fjord in the Barents Sea, showed that male sea urchins had significantly higher gonad indices than females. This contradictory data suggests that green sea urchin populations occurring in different geographical regions have different patterns of gonad development.

Despite the high inter-site variability, male and female sea urchins spawned synchronously within a site. In free spawning marine invertebrates with planktotrophic larvae, some degree of reproductive synchrony within populations of dioecious species is necessary for successful fertilization (Thorson 1946; Pennington 1985). When spawned, approximately 80% of eggs are fertilized either on the aboral surface of female sea urchins or relatively close to the female (Meidel and Yund 2001), while sperm is rapidly diluted in the water column and is viable for less than 20 minutes (Pennington 1985). These characteristics of gametes once spawned indicate that sexual synchrony at small spatial-scales may be more important for successful fertilization, and thus individual fitness, than inter-population reproductive synchrony at large spatial-scales.

Environmental Control of Sea Urchin Spawning

The observed sexual synchrony in spawning times at each site indicates that spawning is exogenously controlled. Exogenous control of green sea urchin reproductive cycles has long been recognized, although the proximate factors affecting gametogenesis or stimulating spawning remain poorly understood (Himmelman 1978; Starr et al. 1990; Pearse and Cameron 1991). The similar spawning times between urchins from the Georges Island and Jonesport regions, despite hydrographic differences, suggest that site-specific factors influence gamete release by green sea urchins. The relationship between spawning time and environmental parameters across the green sea urchin's geographic range is highly variable, which is consistent with the hypothesis that very local hydrographic conditions influence sea urchin reproduction (Table 1.20).

Phytoplankton

There was a significant relationship between phytoplankton chlorophyll *a* and sea urchin spawning at sites in both regions. However, the strength of this relationship varied between sexes, between sites, and between regions. Sea urchin spawning occurred between March and May at all sites and coincided with increasing chlorophyll *a* concentrations. The coincidence of green sea urchin spawning and phytoplankton blooms in nature has been shown for urchin populations in the northeast Pacific (Himmelman 1978), the northwest Atlantic (Himmelman 1978), and the St. Lawrence Estuary (Starr et al. 1993). In this study, sea urchins spawned when phytoplankton chlorophyll *a* concentrations were low (~2 μg/L), although this concentration is well below typical concentrations for a pronounced winter-spring phytoplankton bloom (see

Table 1.20. Relationship between spawning time of *Strongylocentrotus droebachiensis* and (1) the temperature range during spawning and (2) the timing of the spring phytoplankton bloom in different geographical regions (modified from Starr et al. 1993)

Locality	Spawning time	Temperature	Spring Phytoplankton Bloom
Northeast United States			
Cape Cod, MA	Late April (Stephens 1972)		Begins late March through late April (Bigelow et al. 1940)
Woods Hole, MA	March (Boolootian 1966)	1-2°C (Taylor et al. 1957)	Mid-winter (Fish 1925)
Boothbay Harbor, ME	Early April (Stephens 1972)	8°C (Taylor et al. 1957)	Begins mid- to late March (Bigelow et al. 1940)
Salisbury Cove, ME	April to mid-May (Harvey 1956)		Starts in April or May (Bigelow et al. 1940)
Lamoine, ME	April (Cocanour & Allen 1967)		Starts in April or May (Bigelow et al. 1940)
Georges Islands, ME	Mid-late April (present study)	4-8°C (present study)	Starts mid-April or May (present study)
Jonesport, ME	Mid-late April (present study)	4-6°C (present study)	Starts late April or May (present study)
Northeast Canada			
St. Margaret's Bay, Nova Scotia	March – April (Miller & Mann 1973; (Meidel & Scheibling 1998)	2-4°C (Miller & Mann 1973)	April (Platt & Irwin 1970)
Mahone Bay, Nova Scotia	March – April (Meidel & Scheibling 1998)		
Portugal Cove, Newfoundland	March – April (Himmelman 1978)	< 3°C (Himmelman 1969)	April (Himmelman 1978)
Pointe-au-Pere, Quebec	June (Starr et al. 1993)	4-10°C (Starr et al. 1993)	Begins in June, maximum in July (Starr et al. 1993)
Norway			
Bergen	Late March (Runnstom 1927a, 1927b)	4-5°C (Brown 1984)	Begins mid-March, maximum March-April (Gran 1928)
Trömso	February to March (Vasseur 1952)	2°C (Brown 1984)	Begins mid-March, maximum March-April (Gran 1928)
Tromsösundet	March (Falk-Petersen & Lonning 1983)		Begins mid-March, maximum March-April (Gran 1928)
British Columbia			
First Narrows	April (Himmelman 1976)	6-8°C (Himmelman 1976)	April (Himmelman 1976)
Botanical Beach	April (Himmelman 1976)	8-9°C (Himmelman 1976)	Mid-April (Himmelman 1976)
White Sea	Mid-June to mid-july (Kaufmann 1974)	3-5°C (Kaufmann 1974)	
Barents Sea	February to April (Oganesyan 1998)	0-2°C (Oganesyan 1998)	Begins March, Maximum in April (Propp 1971; Kuznetsov 1991)

Chapter 2), except at Starboard and Black Duck Coves. Sea urchins at Black Duck Cove spawned when chlorophyll *a* concentrations rapidly increased to about 8 μg/L, which supports the hypothesis that phytoplankton stimulates gamete release in this species. There was no significant change, however, in phytoplankton abundance at Starboard Cove and the maximum chlorophyll *a* concentration attained was approximately 1.5 μg/L. Starr et al. (1990) showed experimentally that sea urchins could be induced to spawn by exposure to phytoplankton and phytoplankton filtrates. They also showed that the spawning response of field-collected sea urchins (collected in January) was dependent on the concentration of chlorophyll *a*. A maximum spawning response (~50%) was achieved at very high phytoplankton abundance (i.e., 24 μg/L), while at low phytoplankton abundance (i.e, 2 μg/L for >3 days), a 20% spawning response occurred. The incongruence between laboratory experiments and field studies cast doubt on the role of phytoplankton as the sole proximate cue for spawning and necessitate further exploration. Moreover, although the idea that sea urchins spawn to couple their larvae with their food is theoretically attractive, the field evidence supporting this hypothesis is inconclusive.

Sea urchin larvae begin feeding on nano- and ultraplankton one or two weeks after fertilization and may remain pelagic for more than 50 days before metamorphosing and settling to the benthos (Thorson 1946; Stephens 1972; Strathman 1978). Spawning at the onset of the spring phytoplankton bloom may permit sea urchin larvae to experience peak phytoplankton biomass when they begin feeding. However, the magnitude and duration of the spring phytoplankton bloom in the Gulf of Maine is highly variable and may not be at peak biomass when urchins reach the planktotrophic stage (Townsend and

Spinrad 1986). Despite the significant relationship between chlorophyll *a* and sea urchin spawning, there does not appear to be a critical or threshold concentration of chlorphyll *a* that induces spawning. A confounding factor to the idea that phytoplankton or extracts from phytoplankton stimulate spawning is that sea urchins feed on benthic diatoms, which are common during the spring in Maine (Vadas *personal communication*). Furthermore, extracts from *Fucus vesiculosus,* have been shown to stimulate green sea urchin spawning (Starr et al. 1992). The influence of algal compounds on spawning raises questions about the value of phytoplankton as a spawning stimulus under natural conditions. Moreover, the sensitivity of individuals to low concentrations of this proposed stimuli remain unknown.

The lack of a pronounced or distinct spawning period or winter-spring phytoplankton bloom in 2000 may be attributed to interannual differences in the hydrography of the coastal waters surrounding the Georges Islands and Jonesport regions. It is well known that the duration of the spring phytoplankton bloom in the Gulf of Maine may be limited to 2 weeks (Townsend and Spinrad 1986), and biweekly sampling may not have detected the bloom *per se*. However, with gradually declining concentrations of nitrate + nitrite, and silicate during the sampling period, it is possible that a winter-spring phytoplankton production bloom occurred without a corresponding increase in phytoplankton biomass. Keller et al. (2000) report the absence of a spring phytoplankton bloom in Massachusetts Bay in 1998, and attribute this to higher than average sea temperatures, which was optimal for zooplankton grazing to minimize phytoplankton growth. Additionally, in other shallow water bodies, grazing by benthic filter feeders has been shown to be a significant source of phytoplankton losses (Cloern 1982). Although

zooplankton or benthic grazer abundance was not determined here, it is possible that low concentrations of chlorophyll *a* are attributable to grazing pressure, which inhibited the development of a pronounced winter-spring phytoplankton bloom (see Chapter 2).

Temperature

There is a significant relationship between temperature and sea urchin spawning at sites in both regions. As with phytoplankton chlorophyll *a*, the strength of the relationship between temperature and gonad indices varied between sexes, between sites, and between regions. Sea urchins spawned when temperature increased from 3 to 6 °C in both the Georges Islands and Jonesport Region. Spawning times in other populations of green sea urchins occur within this temperature range (Cocanour and Allen 1967; Stephens 1972; Miller and Mann 1973; Kaufmann 1974; see Table 1.20), although in other regions, this relationship varies (Taylor et al. 1957; Himmelman 1976; Oganesyan 1998). A corollary to the hypothesis that temperature is a proximate spawning cue is that spawning will commence earlier in central Maine than eastern Maine, which was not observed in 2000. However, the temperature range between the two regions was similar during the spawning period, despite higher maximum temperatures in the Georges Islands region. The possibility that temperature is the proximate cue for spawning in green sea urchins has been challenged (Himmelman 1978; Starr et al. 1990, 1993), although the evidence supporting this claim is equivocal.

It is unclear whether green sea urchins spawn in response to a critical temperature, although it is possible that high temperatures, which are lethal to developing larvae, inhibit spawning (Pearse 1980). Stephens (1972) showed in laboratory experiments that

S. droebachiensis larvae develop synchronously and normally at 0 – 4 °C and asynchronously and abnormally at 10 °C, while at 12 °C, cell division is arrested and larvae mortality occurs. This inhibitory effect of high temperatures on larval development raises the possibility that spawning occurs at temperatures that minimize larval development times, while maximizing larval survival. Green sea urchin larval periods range from 4 to 21 weeks, depending on temperature (Strathmann 1978), and it is thought that mortality during this period for echinoid larvae is high (Afatsuma 2001*a*). Similarly, predatory zooplankton abundance is typically low at cold temperatures (0 – 4 °C), and increase at warmer temperatures (> 5 °C) (Thorson 1948). Thus, it is possible that populations of *S. droebachiensis* spawn semi-continuously from late-January to mid-May, during a period when temperature regimes act to minimize grazing pressure, while minimizing larval development times (which alone may reduce the probability of predation).

Despite the inability to determine causation based on observations of concurrence, temperature can be used to predict the spawning period of the green sea urchin (*sensu* Peters 1991). Further, the influence of changing photoperiod on spawning (via its effect on vernal warming) may be considered the underlying cause of the relationship between temperature and spawning. Linear regression models provide a predictable coupling between spawning times and increases in temperature. In addition, when temperature is first forced into the stepwise, multiple regression model, variation in gonad indices are significantly related to temperature at all sites. The significant relationship between temperature and males and female gonad indices, and combined gonad indices, may allow for site-specific spawning models to be developed. Additionally, although the

timing of spawning is difficult to determine for several sites (e.g., Davis Island), the relationship between temperature and changing gonad indices can be determined and used in general predictive models. Resource managers may therefore monitor temperature to determine the spawning times of field populations of green sea urchins.

Other variables

The relationship between gonad indices and other variables showed disparate patterns between sites and regions. Stepwise, multiple regression analyses show gonad indices of animals inhabiting different sites are predicted by different variables (Appendix D). These dissimilar patterns suggest that site-specific hydrographic or other factors influence the spawning period for the green sea urchin, which has been suggested for other temperate sea urchins (*Paracentrotus lividus*: Byrne 1990; *Psammechinus miliaris*: Kelly and Cook 2001; *Evechinus chloroticus*: Barker 2001; *Strongylocentrotus purpuratus*: Tegner 2001). Furthermore, general predictive models of sea urchin spawning are be difficult to develop, as different variables are significant predictors at each site. Temperature, which is correlated with several other variables, including chlorophyll *a*, silicate, and nitrate + nitrite, may be more useful in developing general predictive models. These general models may be more applicable to populations of green sea urchins along the coast of Maine, rather than for other regions and areas.

The results of principal components analysis show a significant relationship between the principal components and gonad indices at all sites. These principal components, or "oceanographic index," are significantly related to gonad indices, although the predictive utility of these principal components may be limited. Because the

oceanographic index is a linear combination of oceanographic variables, it would be necessary to measure all the variables to predict changes in gonad indices. This would be of little use to resource managers, although it may provide insights into the dynamic hydrographic conditions during the spawning period of the green sea urchin.

Ultimate factors

It is well recognized that the timing and duration of the spawning season in strongylocentrotid sea urchins is highly variable among locations and between years (Giese and Pearse 1974; Young 1999; Agatsuma 2001*a*, 2001*b*; Tegner 2001). This spatial and temporal variability in spawning may be attributable to differences in habitat characteristics, population dynamics, and/or hydrographic factors, which may also vary in space and time. The long spawning season (~ 3-4 months) documented for *S. droebachiensis* may be influenced by several of these factors, or possibly a combination of them. Young (1999) discussed the length of marine invertebrate breeding seasons over a latitudinal gradient and suggested that populations in highly seasonal, yet variable environments, such as temperate-boreal regions, have prolonged reproductive seasons relative to populations occurring in more stable, less seasonal areas, such as tropical region or deep sea environments. This widespread phenomenon of increasing spawning duration with latitude and lack of discrete spawning events raises questions about (1) whether population-level reproductive synchrony exists in temperate sea urchin populations, (2) whether spawning is indeed exogenously controlled, and (3) how individual reproductive success is influenced by spawning time.

Long spawning seasons may also be influenced by differences in spawning times between old and young individuals in a population. Vadas et al. (2002) showed at Allen Island that individuals of the same size were of different ages. This introduces the possibility, that, although urchins in this study were of a limited size range, they may have differed in age. This age difference may influence the length of the spawning season, with urchins in different age classes spawning at different times. Thus, segments of sea urchin populations may be synchronized, although overall, the individuals may spawn at different times.

Given the high variability in the gonad indices on any date, due to asynchronous gametogenesis at the individual level, it seems reasonable to assert that portions of the population may spawn synchronously at different times. That is, asynchronous gametogenesis at the individual level may result in semi-continuous or prolonged spawning at the population level (Young 1999). In environments that are seasonal, yet variable, such as the northwest Atlantic, it is adaptive for a species to time it's reproduction at times when (1) other members of the population spawn, (2) conditions are favorable for fertilization, and (3) conditions are favorable for early-developmental stages. To have different portions of a population release gametes throughout a period that is unpredictable can be viewed as a "bet-hedging" strategy (*sensu* Stearns 1976), and may confer advantages to those individuals who wager correctly.

CHAPTER II

THE WINTER-SPRING HYDROGRAPHY AND PHYTOPLANKTON OF SELECTED SITES IN THE GEORGES ISLANDS REGION, MAINE, USA

INTRODUCTION

The onset of the winter-spring phytoplankton bloom in both coastal and oceanic waters involves a complex interaction between several physical and biological factors and is temporally and spatially variable. Water column stability, temperature, and nutrient and light availability have been shown to influence bloom initiation (Riley 1942; Sverdrup 1953; Townsend and Spinard 1986; Townsend et al. 1994), while phytoplankton losses due to grazing (Martin 1970; Cloern 1982), self-shading (Agustí et al. 1987; Timm et al. 1990), and nutrient exhaustion (Sieraki et al. 1993; Townsend and Thomas 2001) may result in the curtailment of the bloom. Temporal and spatial variability in the onset, magnitude, and duration of the spring bloom has been observed in numerous coastal and oceanic systems and is due primarily to variations in light availability, vertical mixing, and grazing intensity (Bigelow 1940; Pennock and Sharp 1986; Cloern 1991; Townsend et al. 1994; Kelly and Doering 1997). Patterns of bloom development are also related to sea temperature, which not only directly influence phytoplankton growth rates (Eppley 1972; Smayda 1973) but indirectly affect zooplankton abundance and grazing rates (Deason 1980; Keller et al. 1999; Keller et al. 2000). Further, the negative effects of benthic grazing on phytoplankton standing biomass have been observed in nature (Cloern 1982; Carlson et al. 1984) and have been

demonstrated in mesocosm experiments (Prins et al. 1995; Keller et al. 1999) and model simulations (Officer et al. 1982).

In the presence of an adequate nutrient supply, phytoplankton blooms occur when total, vertically integrated production exceeds cumulative phytoplankton losses and this occurs above the depth at which total production exactly equals losses (i.e., the critical depth). Sverdrup (1953) formalized this mechanism for bloom initiation and showed empirically that the shoaling of the upper mixed layer (above the critical depth) releases phytoplankton populations from light limitation and phytoplankton respond with increasing growth rates (Sverdrup's Critical Depth Model). This model has been independently corroborated in both coastal (e.g., Narragansett Bay: Hitchcock and Smayda 1977) and oceanic waters (e.g., Sargasso Sea: Riley 1953), although it does not accurately predict bloom inception in some shallow estuaries (e.g., San Francisco Bay: Lucas et al. 1998).

Empirical and theoretical models of phytoplankton bloom dynamics in shallow (<50 m), coastal waters show that these systems function differently than deeper, oceanic systems (Riley 1957; Hitchcock and Smayda 1977; Townsend and Spinrad 1986; Townsend et al. 1994; Lucas et al. 1998). Seasonal development of phytoplankton biomass in response to vertical stratification due to vernal warming (Sverdrup 1953; Riley 1957) or the absence of vertical mixing (Townsend et al. 1992) characterizes open ocean systems. However, in regions influenced by freshwater, salinity and thermal stratification may be counteracted by strong turbulent mixing by tidal currents, wind stress, and the interactive effects of bottom roughness (Officer 1976). In addition, the depth of the upper mixed layer often extends to the bottom in shallow waters, making

vertical stratification an unnecessary prerequisite for the initiation of the winter-spring phytoplankton bloom since phytoplankton are unlikely to be light limited (Hitchcock and Smayda 1977; Koseff et al. 1993; Keller et al. 2001). Consequently, stratification and bloom dynamics in shallow coastal systems are more variable than in open ocean systems due to stochastic (e.g., storms) and regular (e.g., tidal stirring) mixing events coupled with the temporal and spatial variability of seasonal freshwater input (Simpson et al. 1990).

During the winter-spring period in shallow, coastal waters of the Gulf of Maine, inorganic nutrient concentrations are high and sufficient to fuel phytoplankton production (Eppley et al. 1969; Townsend et al. 1994). Light availability primarily limits primary production during this high-nutrient period and the spring phytoplankton bloom is triggered when the depth-averaged, vertically-integrated irradiance within the upper mixed layer reaches approximately 40 langleys (Ly) day^{-1} (Hitchcock and Smayda 1977; Townsend and Spinrad 1986). However, when the upper mixed layer extends to the bottom (i.e., above the critical depth), light available to phytoplankton is a function of weather and water column clarity. Cloud-cover primarily influences interannual variability in the inception of the winter-spring bloom by determining the amount of solar radiation reaching the sea, and thus the critical depth (Sverdrup 1953; Townsend et al. 1994). Similarly, the spatial and temporal patterns of blooming phytoplankton throughout the Gulf of Maine is partially a function of variation in incident solar radiation reaching the sea surface. The variability in the magnitude and duration of the spring bloom coastal waters may be influenced by the interaction between temperature and both pelagic and benthic grazers, which can deplete the water column of both primary and

secondary producers (Martin 1970; Deason 1980; Cloern 1982; Carlson et al. 1984; Keller et al. 1999). Sverdrup's critical depth model, although shown to predict the onset of the spring phytoplankton bloom in other shallow water systems, may not consistently predict shallow water blooms because it fails to incorporate small-scale tidal effects and the dynamics of phytoplankton biomass losses (e.g., due to rapid consumption by benthic grazers or by horizontal advection) (Lucas et al. 1998; Keller et al. 2001).

Phytoplankton species composition and abundance have been described and quantified for shallow coastal sites (Pratt 1959; Petrie 1975; Karentz and Smayda 1984; Wong and Townsend 1999) and deeper oceanic sites in the western North Atlantic (Bigelow 1926; Sieracki et al. 1993; Townsend and Thomas 2001). The winter-spring phytoplankton bloom in the western North Atlantic consists primarily of diatoms (Bigelow et al. 1926; Pratt 1965; Smayda 1965), which rapidly deplete the water column of dissolved silicate and inorganic nitrogen (Sieracki et al. 1993; Townsend and Thomas 2001). Moreover, diatom production at oceanic sites is first limited by silicate depletion, then by nitrogen limitation (Sieracki et al. 1993; Townsend and Thomas 2001; Townsend and Thomas 2002). Following this nutrient depletion, there is a shift in phytoplankton communities from diatoms to small flagellates. Common spring phytoplankton species in coastal waters of Maine include the neritic diatoms, *Chaetoceros* sp., *Thalassiosira nordenskioldi, Skeletonema costatum, Nitszchia* sp. and the prymnesiophyte, *Phaeocystis* sp. (Petrie 1975; Wong and Townsend 1999).

The general objective of this work was to characterize the phytoplankton and hydrography of the Georges Islands region by intensively sampling four coastal stations biweekly from January through May 2000. My specific objectives were (1) to determine

the relationship between light, nutrients, temperature, and phytoplankton community species composition in the waters surrounding the Georges Islands; (2) to relate species succession to water properties; and (3) to examine the small-scale (< 10 km) variability of water properties and phytoplankton species composition and abundance.

MATERIALS AND METHODS

Site Description

Water samples were collected biweekly at 4 stations in central Maine near Allen Island (N 43°50'30'', W 69°18'45"), Benner Island (N 43°52'45'', W 69°19'45"), Davis Island (N 43°53'30'', W 69°18'15") and Hupper Island (N 43°54'45'', W 69°16'45") from 30 January to 28 May 2000 (Fig. 2.1). Two 1000 ml water samples were collected at each site on each sampling date. One sample was collected 0.5 m below the surface and the other was collected 1 m above the bottom. These stations are within 10 kilometers of each other and are located within 500 m of each island. Sites varied in depth and depth at each station varied with tides (Table 2.1).

Table 2.1. Mean depth (± 1 SE) (m), range, and coefficient of variation (CV) for stations sampled biweekly from 30 January to 28 May 2000 (n=8).

Station	Mean depth (± 1 SE)	Mimimum	Maximum	CV
Allen Island	12.037 (0.46)	10.2	14.4	0.11
Benner Island	8.0625 (0.53)	5.7	10.2	0.19
Davis Island	8.0625 (0.41)	6.6	9.6	0.14
Hupper Island	9.0375 (0.43)	7.5	10.5	0.13

Oceanographic Variables

Samples for dissolved inorganic nutrients (i.e., phosphate, silicate, nitrate + nitrite, and ammonium) were filtered using an inline syringe filter containing a 0.45 μm

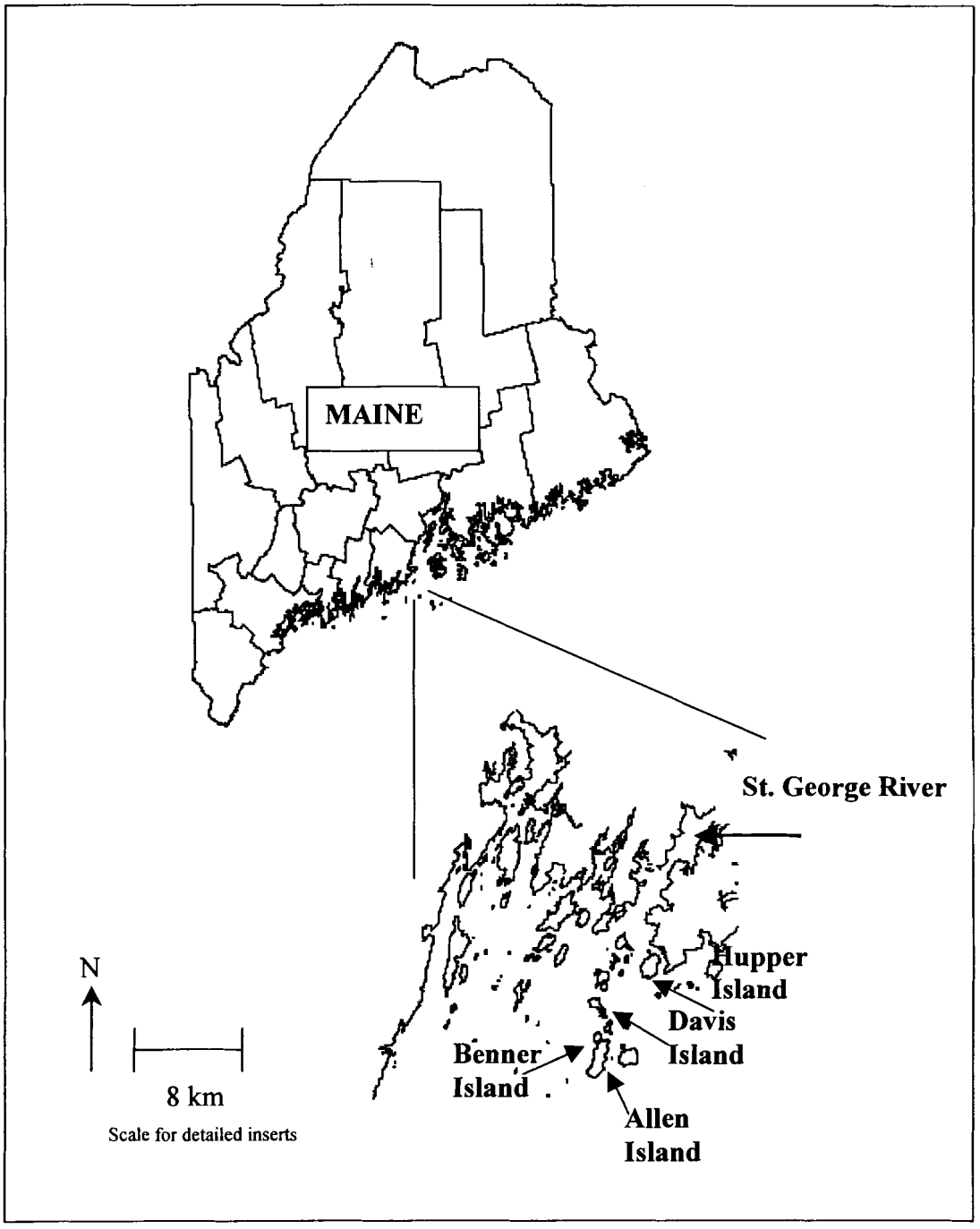

Figure 2.1. Location of stations near Allen, Benner, Davis, and Hupper Islands in the Georges Islands region.

Millipore acetate membrane filter, after first flushing the filters with sample water. Samples were kept dark and frozen on dry ice until analyzed with a Technicon AutoAnalyzer® II using standard techniques by staff in D.W. Townsend's laboratory. Fifteen milliliters of both the surface and bottom water sample from each site on each sampling date were filtered separately. Surface and bottom water temperature were determined using a calibrated thermometer. Salinity samples were collected at about 0.5 m above the bottom in 300 ml Boston Round, flint glass bottles with screw caps equipped with Poly-Seal cones to prevent leakage and evaporation. Water samples collected in this way can be stored for six months with a salinity change of less than 0.001 practical salinity units (psu) (Stalcup 1991). Salinity was measured in the laboratory using Guildline Portasal® Portable Salinometer (8410A) which has an accuracy of ± 0.003 on the psu scale. Light extinction coefficients (K, m^{-1}) were determined by secchi disk measurements and calculated where extinction coefficient equals 1.7/depth (m) (Idso and Gilbert 1974).

Irradiance reaching the sea surface (I_o) was measured with a Li-Cor® 200SA pyranometer mounted on an unobstructed dock on Allen Island. Surface irradiance was recorded every 15 minutes with a Campbell 10x datalogger from 19 March to 14 May 2000 (corresponding to Julian Days 79 – 133) and was used to examine variation in total surface irradiance (both direct and sky-reflected light) during part of the study period. The depth of the euphotic zone (I_z) was calculated according to Beer's Law, $I_z = I_o * e^{-k*z}$, using average values of I_o on overcast (500 W m^{-2}) and sunny (900 W m^{-2}) days from 19 March to 14 May and the mode, minimum, and maximum values of K (0.207, 0.161 and 0.463 m^{-1}, respectively) with depths (z) ranging from 1 – 35 m. These

values of K were chosen to reflect the range in water column transparency at all sites during the study period to conservatively estimate the depth of the euphotic zone. Assuming 1.0% surface irradiance for the compensation light intensity, I_z was determined by comparing calculated values to 1% surface irradiance, equal to 5 and 9 W m^{-2} when surface irradiance is equal to 500 and 900 W m^{-2}, respectively. These calculations were used to roughly estimate if light was limiting to phytoplankton growth during the sampling period. However, this coarse measure of light as limiting fails to incorporate mixing of phytoplankton to depths deeper than the critical depth beyond the sampling stations. This limitation notwithstanding, it appears that the water column at each sampling station was well illuminated during the sampling period. Descriptive statistics were used to examine changes in oceanographic variables between sites and over the sampling period.

Phytoplankton

Phytoplankton biomass was quantified by measuring chlorophyll *a* concentrations using fluorometric methods (Parsons et al. 1984). One hundred ml of water from each sample was filtered through a Gelman GFF (0.7 μm) filter. The filter was placed in a 20 ml glass scintillation vial and 10 ml of 90% acetone was added. Vials were stored on dry ice for 24 hours for extraction. Chlorophyll *a* and phaeophytin concentrations were determined in the laboratory using a Turner B fluorometer. Descriptive statistics were used to examine temporal changes in chlorophyll *a* and phaoephytin concentrations.

Water samples of 300 mls were collected at each site at 1 m below the surface for phytoplankton identification and enumeration. Phytoplankton cell densities were determined by settling a 50 ml sub-sample of seawater preserved in acidified Lugol's

iodine solution in a 50 ml graduated cylinder for 48 hours. The top 40 ml of the water sample was extracted using a pipette attached to a vacuum pump leaving a 5 times concentrated sample. The remaining 10 ml of sample was placed into a scintillation vial for analysis. A 1.3 ml sub-sample was placed into a counting chamber and allowed to settle before cells were identified and enumerated at 100-400x magnification using a Nikon TMS inverted microscope. The cells were identified as diatoms, dinoflagellates, or other flagellates. Cells were identified to genera to note dominant taxa, although analyses were not done for this taxonomic level.

RESULTS

Oceanographic Variables

Pearson product moment correlation coefficients show a strong relationship between many oceanographic variables (Appendix C). There was no significant difference of oceanographic variables or phytoplankton chlorophyll *a* between surface and bottom water samples and data for each variable were pooled for subsequent analyses at each site (i.e., n = 2 for each variable at each site) (Appendix A). Additionally, bottom water salinity indicates that freshwater runoff had a significant effect throughout the water column (see below). This uniform distribution of water properties coupled with bottom salinity provides evidence that the water column at each of these sites was vertically well-mixed. Therefore, data for surface and bottom waters within station were subsequently pooled for further analysis.

Sea temperature increased gradually and linearly throughout the study period. It was coldest on 13 February (1.5 °C) and warmest on 28 May (10.5 °C) at all sites (Fig. 2.2). The rate of springtime warming was low from 30 January to 19 March (≈ 1 °C per 2 week interval) and accelerated from 19 March to 1 April, when temperatures increased about 2.5 °C from 3 to 5.5 °C. Temperature increased at this rate after 29 April, when maximum temperature approached ≈ 11 °C on 28 May at all sites. Mean (± 95% C.L.) salinity decreased from 32.553 ± 0.175 psu during the period from 30 January to 16 April to 30.723 ± 0.461 psu in late April and early May (Fig. 2.3). Decreases in salinity coincide with above-average streamflow (110 % of normal) of the St. George River in March and April 2000 and was also likely influenced by the input of spring melt-water from terrestrial runoff (USGS 2002, http://waterdata.usgs.gov/).

Chlorophyll *a* and phaeophytin concentration increased gradually during the sampling period and was significantly and positively correlated with temperature ($r = 0.912$, $p < 0.0001$ and $r = 0.757$, $p < 0.0001$, respectively) (Fig. 2.2). Mean (± 95% C.L.) chlorophyll *a* concentration was 0.366 ± 0.04 µg/L from 30 January to 19 March, increased to 0.791 ± 0.135 µg/L from 1 April to 12 May and increased significantly to 1.88 ± .07µg/L on 28 May 2000 at all sites. Mean (± 95% C.L.) phaeophytin concentrations were low from 30 January to 16 April (0.269 ± 0.022) but increased significantly in late April through late May to 0.615 ± 0.081 µg/L at all sites. Chl *a*: phaeophytin ratios were always >1, but increased to > 2 –3 in May indicating that live, actively growing cells were present in the plankton community throughout the sampling period, and prevalent in the plankton during May.

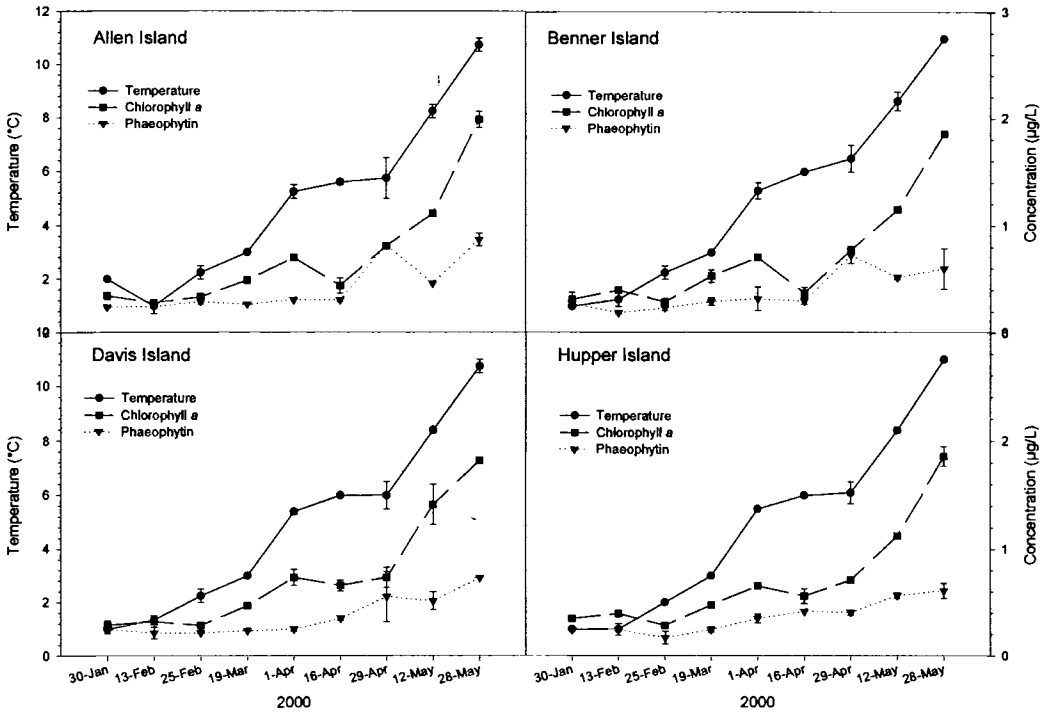

Figure 2.2. Mean temperature and concentrations (± 1 SE) of chorophyll *a* and phaeophytin at Allen, Benner, Davis, and Hupper Islands, 2000 (n=2 for each variable).

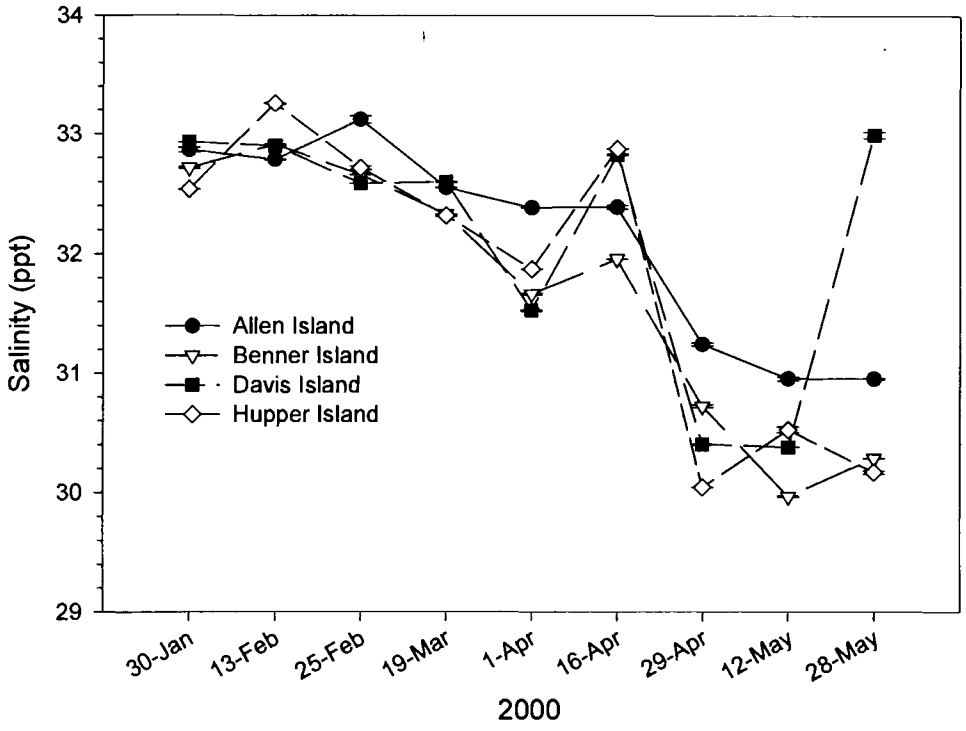

Figure 2.3. Mean (± 1 SE) bottom salinity (practical salinity units) at Allen, Benner, Davis, and Hupper Islands, 2000. Mean ± 1 SE determined by 3 replicate measurements for 1 water sample. These replicates were used to determine measurement errors, not to examine differences between water samples.

Changes in inorganic nutrient concentrations were similar between stations (Fig 2.4). Nitrate + nitrite concentrations were gradually depleted through the sampling period. Concentrations of nitrate + nitrite were highest on 30 January, ($\approx$ 10 μM) and declined linearly through 28 May to < 1 μM at all sites. On April 16, there was a slight increase in nitrate + nitrite concentrations and was likely related to spring runoff. Nitrogen was depleted well before silicate at each of the four stations. Mean (± 95% CI) silicate concentration gradually and linearly declined from 11.92 ± 0.38 μM on 30 January to 7.75 ± 0.37 μM on 1 April at all sites. Between 1 April and 12 May, silicate concentration increased linearly to 9.9 ± 0.61 μM followed by a rapid depletion of silicate to 1.90 ± 0.99 μM on 28 May. Mean (± 95% CI) ammonium concentration were relatively high (2.63 ± 0.87 μM) on 30 January, low (0.219 ± 0.04 μM) through the sampling period, and increased to 1.00 ± 0.08 μM on 29 April, coinciding with spring runoff and a storm event (NASA 2002). After 29 April, mean ammonium concentrations were depleted to 0.25 ± 0.12 μM. Mean (± 95% CI) phosphate concentrations were low (1.39 ± 0.07 μM) from 30 January to 19 March, increased slightly, but not significantly to 1.54 ± 0.17 μM between 1 April to 16 April, then decreased at all sites to 0.705 ± 0.16 μM by 28 May.

Light extinction coefficients (K) were variable over time and between sites and ranged from 0.161 to 0.483 m^{-1} during the study period (Table 2.2). Mean (± 95% CI) K at all sites from 30 January to 28 May was 0.22 ± 0.02 m^{-1} with a mode was 0.207 m^{-1}. On 1 April at Davis station, K reached 0.483 m^{-1} and represents high turbidity throughout

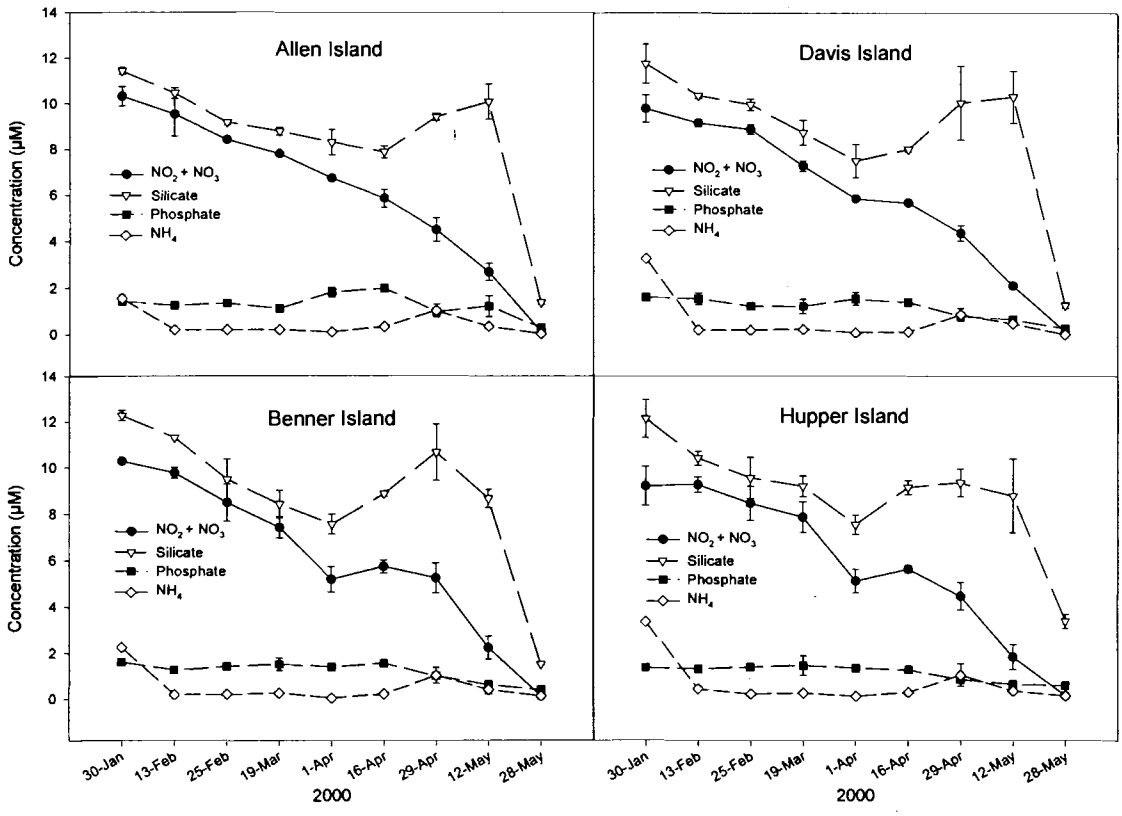

Figure 2.4. Mean concentrations (± 1 SE) of nitrate + nitrite, silicate, phosphate, and ammonium (µM) at Allen, Benner, Davis, and Hupper Islands, 2000 (n=2 for each variable).

Table 2.2. Extinction coefficient (K, m^{-1}) from 30 Jan to 28 May 2000. at each station.

Date	Allen	Benner	Davis	Hupper
30 Jan	0.207	0.223	0.207	0.242
13-Feb	0.171	0.171	0.207	0.171
25-Feb	0.171	0.153	0.161	0.181
19-Mar	0.242	0.161	0.161	0.207
1-Apr	0.207	0.242	0.483	0.290
16-Apr	0.223	0.264	0.264	0.363
29-Apr	0.193	0.181	0.181	0.264
12-May	0.181	0.161	0.161	0.223
28-May	0.207	0.242	0.242	0.363

the water column. On average, extinction coefficient increased on 1 April and remained high for several weeks and coincided with a storm event as well as the spring runoff period.

Solar irradiance reaching the sea surface was highly variable and this was likely due to variations in cloud cover. Data collected from 19 March to 14 May 2000 show peak-light intensity reached about 1000 W m^{-2} and daily variation in the amount of light reaching the sea surface was high (Fig. 2.5). Surface irradiance was relatively low on days 88, 94 –95, 113-119, and 129- 131 and corresponded to overcast days and stormy conditions (NOAA 2000). Although surface irradiance was typically high, there was high variation within and between days.

The results show that the euphotic zone (I_z) was generally deeper than the bottom during the study period (Table 2.3). Three models of possible light limiting conditions were developed based on the observed mode and minimum and maximum values of extinction coefficients (K) and mean incident solar irradiance (I_o) on overcast (500 W m^{-2}) and sunny (900 W m^{-2}) days. In scenario 1 ($k=0.161\ m^{-1}$), depth of the euphotic

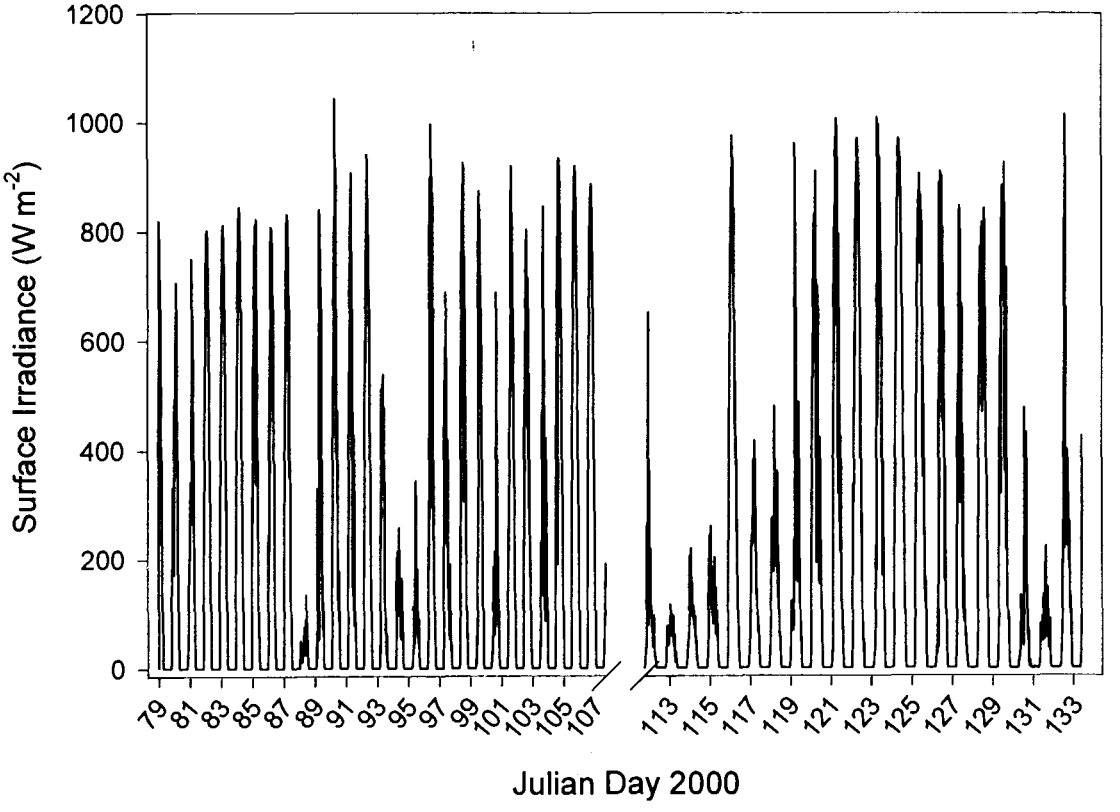

Figure 2.5. Surface irradiance (Watts (W) m^{-2}) at Allen Island from 19 March to 14 May 2000.

zone ($0.01 * I_o = 5$ and 9 W m^{-2}) is between 25 and 30 meters. In scenario 2, ($k = 0.207$ m^{-1}), depth of the euphotic zone ($0.01 * I_o = 5$ and 9 W m^{-2}) is between 20 and 25 meters. In scenario 3 ($k = 0.483$ m^{-1}), depth of the euphotic zone ($0.01 * I_o = 5$ and 9 W m^{-2}) is close to 10 m. The value of *K* in scenario 2 represents typical conditions in the Georges Islands region during the winter-spring period and provides a conservative estimate of water transparency throughout the sampling period. The value of *K* in scenario 3 represents atypical conditions in this region during the sampling period, and therefore, is considered an extreme estimate of the depth of the euphotic zone. In scenarios 1 and 2, the depth of the euphotic zone is much deeper than the depths of Allen, Benner, Davis, and Hupper stations (Table 2.1).

Table 2.3. Calculated light intensity (I_z) at different depths in the water column based on 3 different light extinction coefficients (*K*) according to Beers Law ($I_z = I_o * e^{-k*z}$). *K* represent minimum, maximum, and mode values from all sites. Surface irradiance represents average on overcast (500 W m^{-2}) and sunny (900 W m^{-2}) days. Bolded values represent depths where $I_z = 0.01 * I_o$.

Depth (z) (m)	**Scenario 1** $K = 0.161$ m^{-1} (mimimum)		**Scenario 2** $K = 0.207$ m^{-1} (mode)		**Scenario 3** $K = 0.483$ m^{-1} (maximum)	
	$I_o = 500$	*$I_o = 900$*	*$I_o = 500$*	*$I_o = 900$*	*$I_o = 500$*	*$I_o = 900$*
1	425.65	766.16	406.51	731.72	308.46	555.24
5	223.54	402.38	177.61	319.70	**44.68**	**80.43**
10	99.94	179.90	63.09	113.57	**3.99**	**7.19**
15	44.68	80.43	22.41	40.34	0.36	0.64
20	19.98	35.96	**7.96**	**14.33**	0.03	0.06
25	**8.93**	**16.08**	**2.83**	**5.09**	0.00	0.01
30	**3.99**	**7.19**	1.00	1.81	0.00	0.00
35	1.79	3.21	0.36	0.64	0.00	0.00

Phytoplankton

Densities of diatoms, dinoflagellates, and other phytoplankton groups (primarily flagellates between 5 – 10 μm in diameter) were relatively low throughout the sampling period at all sites (Fig. 2.6). On average, cell densities at the Hupper Island station were greater than at the other 3 stations. Total phytoplankton densities remained well below 10×10^3 cells L^{-1} from 30 January to mid-March, at which time, diatom densities increased to about 5×10^3 cells L^{-1} at Benner, Davis, and Hupper Islands. The dominant taxa during this time were *Thalassiosira* spp. and *Navicula* spp. and other benthic diatoms (e.g., *Biddulphia* spp., *Licmophora* spp., *Gyrosigma* spp.) were present in most samples (Appendix H). Dinoflagellate densities were very low ($< 10 \times 10^2$ cells L^{-1})throughout the sampling period at all stations, but increased slightly in late May. In addition to relatively high densities of diatoms, water samples collected on 28 May consisted of a mixed dinoflagellate species assemblage and included low numbers of *Amphididium* spp., *Peridinium* spp., *Heterocapsa* spp. and *Ceratium* spp. In late April and early May, large numbers ($> 14 \times 10^3$ cells L^{-1}) of solitary cells and colonies of the prymnesiophyte, *Phaeocystis* spp. were abundant at Allen and Benner stations but were less numerous at Hupper and Davis stations. Diatom densities increased again by 28 May at Benner, Davis, and Hupper stations and dominant taxa included *Thalassiosira* spp., *Chaetoceros* spp., and *Skeletonema costatum.* Small flagellates (< 10 μm) were present in low numbers throughout the sampling period, although Lugol's preservation makes identification as autotrophic difficult. Further, identification of calcareous phytoplankton, such as coccolithophorids (Haptophyta), was not possible due to degradation by Lugol's solution.

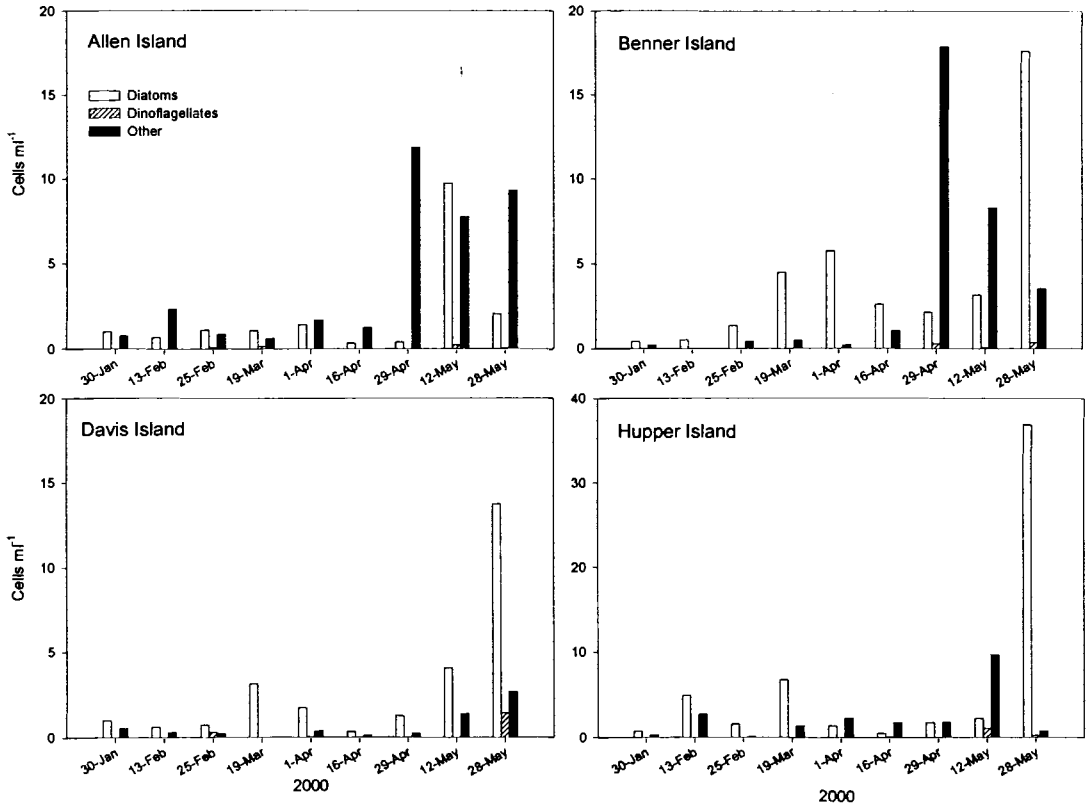

Figure 2.6. Cell densities (number of cells per ml) of diatoms, dinoflagellates, and other flagellates at Allen, Benner, Davis, and Hupper Islands from 30 January to 28 May 2000 (Note change of scale at Hupper Island).

DISCUSSION

The coastal waters surrounding the Georges Islands during the winter-spring 2000 were characterized by high concentrations of inorganic nutrients ($SiO_4 > 8$ μM; $NO_3 + NO_2 > 5$ μM) and low phytoplankton standing biomass (chl *a* < 2 μg/L) within a well-mixed water column. Phytoplankton abundance and chlorophyll *a* concentrations were well below values typically attained during winter-spring blooms in the western North Atlantic (Smayda 1957; Townsend and Thomas 2002) despite favorable conditions for bloom inception (Hitchcock and Smayda 1977; Keller et al. 2001). Water transparency was variable, but was generally high throughout most of the sampling period and the depth of the euphotic zone typically extended to the bottom (i.e., less than the critical depth, although the critical depth was not determined empirically). Increased turbidity and silicate concentrations in early April was due to a storm event, which resulted in the re-suspension of particulate matter from the bottom. The water column remained well-mixed throughout the sampling period regardless of being influenced by freshwater inputs during March and April. The effects of tidal stirring, storms, and high winds may counteract development of vertical stratification (due to freshwater input and/or surface warming) and this has been observed in other shallow water systems (Cloern 1991; Keller et al. 2001). However, vertical stratification is not a necessary prerequisite for bloom development (Townsend et al. 1992; Keller et al. 2001) and a spring bloom was expected during the sampling period. The phytoplankton in the Georges Island region during the winter-spring 2000 exhibited trends inconsistent with a typical, pronounced spring phytoplankton bloom. Futhermore, meso-scale phytoplankton bloom dynamics in shallow, tidal waters involves the complex interaction between numerous physical (e.,g.,

nutrient and light availability, water column stability, and lateral advection) and biological factors (e.g., grazing and phytoplankton self-shading) and these interactions may result in locally disparate or atypical patterns.

Phytoplankton densities and chlorophyll *a* were low until 28 May 2000, when there was an increase in both chlorophyll *a* and diatom densities coinciding with the rapid depletion of silicate (from ≈ 9 μM to 1 μM over 2 weeks). These patterns indicate the onset of a diatom bloom in late May. However, empirical and conceptual models of phytoplankton bloom dynamics predict the inception of a winter-spring phytoplankton bloom in these waters as early as December or January, given the observed nutrient and light regimes (Sverdrup 1953; Smayda and Hitchcock 1977; Boyton et al. 1982; Townsend and Spinrad 1986). The gradual decline of inorganic nutrient concentrations from January to May suggests that phytoplankton were actively growing throughout the water column. Based on measured surface irradiance and light extinction coefficients, light was unlikely limiting growth of phytoplankton populations, as the euphotic zone extended to the bottom during most of the study period (i.e., above the critical depth). Additionally, hydrographic conditions (e.g., light, high inorganic nutrient concentrations) were favorable for a phytoplankton bloom well prior to May. It is possible, therefore, that a phytoplankton production bloom commenced in late January without a corresponding increase in phytoplankton biomass. If the bloom did not commence until late May, how were the nutrients depleted? And if a bloom did begin in January, what processes resulted in phytoplankton losses?

Several separate, but not mutually exclusive, scenarios may explain the lack of a pronounced spring phytoplankton bloom during the winter-spring period in the Georges

Islands region. To account for the undetected phytoplankton bloom (i.e., in terms of phytoplankton chlorophyll *a* and cell densities), I propose four hypotheses to explain the observed patterns. First, interannual differences in the hydrography of the coastal waters surrounding the Georges Islands may have resulted in a phytoplankton bloom with a relatively limited duration, magnitude, and extent. The duration of the spring phytoplankton blooms may be limited to 2 weeks or less in coastal waters (Cloern 1991; Li and Smayda 2001) and biweekly sampling may not have detected the bloom *per se*. Also, it is well known that phytoplankton populations are patchily distributed and exhibits variability at fine spatial (meters to 100s meters) (MacAlice 1970; Pastuszak et al. 1982; Kelly and Doering 1997; Smayda 1998) and temporal (intratidal to days) scales (Cloern et al. 1989; Li and Smayda 2001). Because water samples were collected without regard to tidal phase, intratidal variability in chlorophyll *a* concentrations and phytoplankton abundance may have been greater than bi-weekly variability, thus resulting in poor estimates of phytoplankton biomass (Sinclair 1978; Li and Smayda 2001). Higher biomass occurs during ebbing tides than flooding tides and this tidally induced diurnal variability of phytoplankton biomass may have been an important variable in this study (Cloern et al. 1989). However, the gradual decline of nitrate + nitrite and silicate concentrations and Chl *a*: phaeophytin ratios > 1 during the sampling period provides evidence that actively growing phytoplankton cells were depleting the water column of nutrients throughout the late winter and early spring. This "undetected bloom hypothesis" seems unlikely given the observed gradual decline of nitrate + nitrite and silicate concentrations which supports the idea that production was occurring *in situ*.

A second hypothesis accounting for the depletion of inorganic nutrients, despite low chlorophyll *a* and phytoplankton densities, is that a winter-spring phytoplankton bloom was absent and depletion of inorganic nitrogen was due to uptake by benthic macro- and micro-algae. It seems unlikely that the observed decline in nitrate + nitrite starting in January is due to benthic macroalgae utilization because the benthos at these stations is dominated by perennial species (i.e., with low rates of N-uptake) (Pedersen and Borun 1997). In addition, rapid growth of ephemeral species (i.e., with high rates of N-uptake) would not be expected until late spring (Chapman and Craige 1977; Pedersen and Borum 1996, 1997). Benthic diatoms (e.g., *Navicula* spp., *Biddulphia* spp., *Licmophora* spp.), however, were frequently found in water samples throughout the study period introducing the possibility that attached benthic phytoplankton might have depleted the water column of inorganic nutrients. Furthermore, the decline in silicate concentration during the late winter (30 January to 1 April) may possibly be attributed to the growth of benthic diatoms. This "benthic diatom hypothesis" can be rejected, however, because it is unlikely that a population of benthic diatoms can deplete an entire water column of silicate (S. B. Brawley *personal communication).*

A third hypothesis explaining the observed decline in inorganic nutrients coupled with low chlorophyll *a* and phytoplankton densities is that phytoplankton cells were lost due to vertical or horizontal transport via sedimentation or lateral advection, respectively. Numerous islands and highly variable bathymetry (due to the presence of shoals) characterize the Georges Islands region. It is dissected by the St. George River and is situated west of Penobscot Bay and downstream of the eastern Maine coastal current (Brooks and Townsend 1989). This region is influenced both by adjacent offshore waters

of the Gulf of Maine and terrestrial runoff, that likely interact to create high spatial and temporal variability in the dynamics of phytoplankton populations. Circulation patterns in other near-shore bays along the Maine coast (e.g., Penobscot Bay) are complex and are influenced by freshwater inputs, coastal currents, bathymetry, juxtaposition of islands, and wind forcing (Pettigrew 1998). It is possible that the circulation patterns of the Georges Islands region coupled with tidal effects resulted in the lateral advection of phytoplankton populations away from the sampling stations. Sedimentation of phytoplankton is unlikely since the water column was vertically well-mixed throughout the sampling period and because of the presence of benthic grazers (see below). The lateral advection scenario, although possible, seems unlikely given the dynamics of nitrate + nitrite and silicate at each site, which suggests that production was occurring *in situ*. Nitrate + nitrite declined linearly and gradually over the sampling period, which indicates uptake by algae. Silicate declined from 30 January to 1 April, then increased, coinciding with a decrease in salinity. This decrease in silicate was likely due to diatom production, while the increase after 1 April was likely due to both terrestrial runoff and a storm event, which re-suspended silicate from the bottom. Changes in nutrient concentrations suggest that the sampled water masses were not being laterally advected from the study area.

A fourth hypothesis is that a grazing (by zooplankton and/or benthic invertebrates) cropped phytoplankton standing biomass so that chlorophyll *a* and phytoplankton densities were below levels indicative of a bloom. It is widely accepted that zooplankton (Pratt 1965; Martin 1970; Deason 1980; Keller 1999) and benthic grazers (Cloern et al. 1982; Officer et al. 1982; Carlson et al. 1984) strongly influence the

development, duration, and curtailment of phytoplankton blooms. Before the significant role of light in bloom inception was elucidated, early work in coastal waters suggested that the onset of the winter-spring phytoplankton bloom was caused by release from zooplankton grazing pressure due to low winter sea temperatures (Pratt 1965; Martin 1970; Hitchock and Smayda 1977). Once initiated, the extent that zooplankton grazing affects phytoplankton biomass is dependent on temperature (Deason 1980; Keller et al. 1999). During the winter-spring period in coastal Maine, there is a high abundance of pelagic grazers, including planktotrophic larvae such as barnacle nauplii (Martin 1990). It is possible that these grazers significantly reduced phytoplankton standing biomass during the winter-spring period in the Georges Island region. Keller et al. (2000) report the absence of a spring phytoplankton bloom in Massachusetts Bay in 1998 due to higher than average sea temperature, which was optimal for zooplankton grazing, thus curtailing phytoplankton bloom development. Although sea temperature in the Georges Islands region in 2000 did not deviate from long-term averages (NDBC 2002), the role of zooplankton should not be overlooked as a possibly important mechanism resulting in phytoplankton biomass losses.

In shallow coastal waters, high abundance of benthic bivalve filter feeders have also been shown to remove significant fractions of phytoplankton biomass, especially relative to sites without benthic filter-feeders (Cloern 1982). In this study, grazing by benthic filter feeders, especially *Mytilus edulis*, may have depleted the water column of phytoplankton, thus explaining the trends in nutrient concentration, low phytoplankton standing biomass, and low concentrations of chlorophyll *a*. Benthic communities in these shallow coastal stations in the Georges Island region are characterized by moderately

high algal biomass and abundant blue-mussels (T. Dowling, *personal communication*) making this hypothesis viable. Keller et al. (1999) showed in mesocosm experiments that *Mytilus edulis* are capable of removing significant fractions of the phytoplankton standing biomass and that this response was positively related to temperature. Dense populations of *Mytilus edulis* and infaunal bivalves on intertidal mud flats also significantly reduced the standing crop of both phytoplankton and zooplankton in a northern, temperate estuary (Carlson et al. 1984). It seems plausible that benthic grazing removed significant fractions of phytoplankton biomass during the study period, although there is no empirical evidence to support this hypothesis.

Temporal and spatial variability in the timing, magnitude, and duration of the winter-spring phytoplankton blooms in oceanic and coastal waters has long been recognized. The importance of macro-, meso-, and micro- scale processes when considering the factors involved in bloom inception, development, and curtailment has been underscored in numerous studies, but fully predictive models are still lacking. However, based on historical recurrence of winter-spring phytoplankton blooms in coastal waters of the Northwest Atlantic, it seems probable that a typical, pelagic bloom did in fact occur (Bigelow et al. 1940; Smayda 1958; Li and Smayda 2001; but see Keller et al. 2001), but went undetected due to phytoplankton losses.

The uncoupling of phytoplankton production and removal processes, which facilitates bloom inception, involves complex interactions between physical and biological processes at multiple temporal and spatial scales. Developing a complete understanding of phytoplankton bloom dynamics requires the incorporation of meso- and micro- scale processes in addition to less predictable events (e.g., storms, rainfall) into

dynamic models. Further, sampling programs that examine patterns at macro- scales may fail to detect phenomena occurring at finer resolutions.

SYNTHESIS

This study examined the relationships between hydrographic variables, phytoplankton, and patterns of green sea urchin spawning (1) to make inferences about the proximate causes of reproductive synchrony within and between populations inhabiting different sites and (2) to develop predictive models of spawning in nature. Spatial and temporal variability in spawning times of green sea urchins (Vadas et al. 1989) and the timing, magnitude, and duration of winter-spring phytoplankton blooms has long been recognized (Townsend and Cammen 1988), although the relationship between the two has not been intensively examined until now. During the 2000 winter-spring period, there were disparate patterns of green sea urchin spawning between sites within the Georges Islands region, although there were consistent trends between males and females at each site. In the Jonesport Region, there was a high degree of reproductive synchrony both between sites and between male and female urchins at each site. Based on declining gonad indices, spawning appears to have occurred at similar times between the two regions, even though the precise changes in gonad indices were highly variable. Generally, sea urchins inhabiting sites in the Georges Islands Region appeared to have a protracted spawning period while urchins spawning in the Jonesport region were temporally more discrete.

Results of laboratory experiments suggest that the timing of gamete release in the green sea urchin should be coupled with the winter-spring phytoplankton bloom (Starr et al. 1990), although the current study does not entirely support this hypothesis. The phytoplankton in the Georges Island region during the winter-spring 2000 exhibited

trends inconsistent with a typical, pronounced spring phytoplankton bloom. Relatively low chlorophyll *a* concentrations (< 2 μg/L) and phytoplankton abundance (< 10 x 10^3 cells L^{-1}) characterized the coastal waters of the Georges Island region, which suggests that blooming phytoplankton may not be a reliable proximate spawning cue. It appears that phytoplankton loss processes were equal to or greater than production during the 2000 winter-spring period in the Georges Islands region. Consequently, sea urchins were not exposed to the high concentrations of chlorophyll *a* shown to induce spawning (i.e., >24 μg/L for 50% of individual urchins to spawn). This incongruence between laboratory experiments and field observations suggests that the models of spawning in the green sea urchin are more complicated than previously thought. Furthermore, if phytoplankton losses were due to grazing (by either zooplankton or benthic filter-feeders), the observed variability in urchin spawning times may be due to complex multi-species interactions occurring at fine temporal and spatial scales.

To date, there is an extensive literature speculating on proximate factors synchronizing seasonal reproduction in free-spawning marine invertebrates, but there remains a lack of empirical studies examining these factors. To fully understand patterns of recruitment and population dynamics, we need more detailed information on, the degree of temporal and spatial reproductive synchrony within populations, individual spawning dynamics, the portion of gametes released by individuals during each spawn, natural rates of fertilization, and the hydrographic conditions at the time of spawning. It is nonetheless possible to accurately predict spawning events in nature even without this detailed information on reproduction, which may provide both a useful construct for ecologists and a powerful tool for resource managers.

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Appendix A

Analysis of covariance on the effect of location (surface vs bottom) with date as a covariate on oceanographic variables in the Georges Island and Jonesport Regions

Table A1. ANCOVA on the effect of location (surface versus bottom) on salinity in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.0000	1	0.0000	0.0000	1.0000
Date	45.1710	1	45.1710	97.7430	0.0000
Error	31.8880	69	0.4620		

Table A2. ANCOVA on the effect of location (surface versus bottom) on temperature in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.4510	1	0.4510	0.6670	0.4170
Date	672.6070	1	672.6070	993.4640	0.0000
Error	46.7150	69	0.6770		

Table A3. ANCOVA on the effect of location (surface versus bottom) on log transformed chlorophyll *a* in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.0020	1	0.0020	0.0280	0.8670
Date	21.3530	1	21.3530	304.2610	0.0000
Error	4.8420	69	0.0700		

Table A4. ANCOVA on the effect of location (surface versus bottom) on phaeophytin in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.0380	1	0.0380	2.4410	0.1230
Date	1.6840	1	1.6840	107.4030	0.0000
Error	1.0820	69	0.0160		

Table A5. ANCOVA on the effect of location (surface versus bottom) on nitrate + nitrite in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.2950	1	0.2950	0.3700	0.5450
Date	663.9460	1	663.9460	832.6340	0.0000
Error	55.0210	69	0.7970		

Table A6. ANCOVA on the effect of location (surface versus bottom) on silicate in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	1.3530	1	1.3530	0.3000	0.5860
Date	249.0480	1	249.0480	55.1300	0.0000
Error	311.7070	69	4.5170		

Table A7. ANCOVA on the effect of location (surface versus bottom) on phosphate in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.0560	1	0.0560	0.4810	0.4900
Date	6.2290	1	6.2290	53.9100	0.0000
Error	7.9720	69	0.1160		

Table A8. ANCOVA on the effect of location (surface versus bottom) on ammonium in the Georges Islands region.

Source	SS	df	MS	F-ratio	P
Location	0.0260	1	0.0260	0.0450	0.8330
Date	8.8750	1	8.8750	15.4620	0.0000
Error	39.6070	69	0.5740		

Table A9. ANCOVA on the effect of location (surface versus bottom) on temperature in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.3600	1	0.3600	3.6700	0.0640
Date	127.1080	1	127.1080	1294.9360	0.0000
Error	3.4360	35	0.0980		

Table A10. ANCOVA on the effect of location (surface versus bottom) on salinity in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.0070	1	0.0070	0.0260	0.8720
Date	4.1640	1	4.1640	16.6420	0.0000
Error	8.7570	35	0.2500		

Table A11. ANCOVA on the effect of location (surface versus bottom) on log transformed chlorophyll *a* salinity in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.0320	1	0.0320	0.0710	0.7910
Date	27.5500	1	27.5500	60.6460	0.0000
Error	15.8990	35	0.4540		

Table A12. ANCOVA on the effect of location (surface versus bottom) on phaeophytin in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.0020	1	0.0020	0.0180	0.8950
Date	2.3010	1	2.3010	18.4780	0.0000
Error	4.3580	35	0.1250		

Table A13. ANCOVA on the effect of location (surface versus bottom) on nitrate + nitrite in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.1640	1	0.1640	0.0510	0.8220
Date	150.1020	1	150.1020	46.6570	0.0000
Error	112.6010	35	3.2170		

Table A14. ANCOVA on the effect of location (surface versus bottom) on silicate in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	5.8030	1	5.8030	0.5050	0.4820
Date	110.5280	1	110.5280	9.6120	0.0040
Error	402.4710	35	11.4990		

Table A15. ANCOVA on the effect of location (surface versus bottom) on phosphate in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.7280	1	0.7280	0.3120	0.5800
Date	0.1380	1	0.1380	0.0590	0.8090
Error	81.6440	35	2.3330		

Table A16. ANCOVA on the effect of location (surface versus bottom) on ammonium in the Jonesport region.

Source	SS	df	MS	F-ratio	P
Location	0.0000	1	0.0000	0.0020	0.9640
Date	4.4870	1	4.4870	24.2980	0.0000
Error	6.4640	35	0.1850		

Appendix B

Relationship between oceanographic variables expressed as Pearson product correlation coefficients and Bonferroni adjusted probabilities at all sites

Table B1. Relationship between oceanographic variables, expressed as Pearson product ment correlation coefficients and Bonferroni probabilities at Allen Island, 2000.

Variable		Salinity	Ext. Coeff.	Temperature	Chl a	Phaeophytin	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r*:	1.000								
	P:	0								
Ext. Coeff.	*r*:	0.012	1.000							
	P:	1.000	0							
Temperature	*r*:	-0.889	0.139	1.000						
	P:	< 0.0001	1.000	0						
Chl a	*r*:	-0.844	0.063	0.919	1.000					
	P:	< 0.0001	1.000	< 0.0001	0					
Phaeophytin	*r*:	-0.836	-0.051	0.754	0.815	1.000				
	P:	0.001	1.000	0.011	0.001	0				
NO_3 +NO_2	*r*:	0.915	-0.059	-0.970	-0.914	-0.820	1.000			
	P:	< 0.0001	1.000	< 0.0001	< 0.0001	0.001	0			
SiO_4	*r*:	0.484	-0.264	-0.724	-0.811	-0.626	0.723	1.000		
	P:	1.000	1.000	0.024	0.002	0.195	0.025	0		
PO_4	*r*:	0.533	0.085	-0.425	-0.679	-0.686	0.516	0.574	1.000	
	P:	0.817	1.000	1.000	0.070	0.060	1.000	0.456	0	
NH_4	*r*:	0.073	0.016	-0.247	-0.272	0.011	0.305	0.490	0.087	1.000
	P:	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0

Table B2. Relationship between oceanographic variables, expressed as Pearson product moment correlation coefficients and Bonferroni probabilities at Benner Island, 2000.

Variable		Salinity	Ext. Coeff.	Temp	Chl a	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r*:	1.000								
	P:	0								
Ext. Coeff.	*r*:	-0.107	1.000							
	P:	1.000	0							
Temperature	*r*:	-0.934	0.325	1.000						
	P:	< 0.0001	1.000	0						
Chl a	*r*:	-0.842	0.199	0.885	1.000					
	P:	< 0.0001	1.000	< 0.0001	0					
Phaeophytin	*r*:	-0.797	0.044	0.693	0.656	1.000				
	P:	0.003	1.000	0.051	0.113	0				
NO_3 +NO_2	*r*:	0.919	-0.276	-0.982	-0.897	-0.641	1.000			
	P:	< 0.0001	1.000	< 0.0001	< 0.0001	0.150	0			
SiO_4	*r*:	0.561	-0.364	-0.750	-0.828	-0.378	0.796	1.000		
	P:	0.556	1.000	0.012	0.001	1.000	0.003	0		
PO_4	*r*:	0.822	0.053	-0.799	-0.884	-0.614	0.822	0.612	1.000	
	P:	0.001	1.000	0.002	< 0.0001	0.243	0.001	0.252	0	
NH_4	*r*:	0.174	0.061	-0.353	-0.262	0.092	0.417	0.500	0.282	1.000
	P:	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0

Table B3. Relationship between oceanographic variables, expressed as Pearson product moment correlation coefficients and Bonferroni probabilities at Davis Island, 2000.

Variable		Salinity	Ext. Coeff.	Temp	Chl a	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r:*	1.000								
	P:	0								
Ext. Coeff.	*r:*	-0.017	1.000							
	P:	1.000	0							
Temperature	*r:*	-0.365	0.156	1.000						
	P:	1.000	1.000	0						
Chl a	*r:*	-0.280	0.073	0.942	1.000					
	P:	1.000	1.000	< 0.0001	0					
Phaeophytin	*r:*	-0.307	-0.115	0.774	0.804	1.000				
	P:	1.000	1.000	0.006	0.002	0				
NO_3 +NO_2	*r:*	0.416	-0.079	-0.982	-0.954	-0.839	1.000			
	P:	1.000	1.000	< 0.0001	< 0.0001	< 0.0001	0			
SiO_4	*r:*	-0.257	-0.303	-0.687	-0.687	-0.633	0.683	1.000		
	P:	1.000	1.000	0.059	0.059	0.173	0.065	0		
PO_4	*r:*	0.327	0.290	-0.776	-0.799	-0.827	0.821	0.561	1.000	
	P:	1.000	1.000	0.005	0.002	0.001	0.001	0.559	0	
NH_4	*r:*	0.078	-0.188	-0.415	-0.321	-0.186	0.404	0.494	0.303	1.000
	P:	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0

Table B4. Relationship between oceanographic variables, expressed as Pearson product moment correlation coefficients and Bonferroni probabilities at Hupper Island, 2000.

Variable		Salinity	Ext. Coeff.	Temp	Chl a	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r:*	1.000								
	P:	0								
Ext. Coeff.	*r:*	-0.364	1.000							
	P:	1.000	0							
Temperature	*r:*	-0.804	0.703	1.000						
	P:	0.002	0.040	0						
Chl a	*r:*	-0.766	0.584	0.911	1.000					
	P:	0.007	0.391	< 0.0001	0					
Phaeophytin	*r:*	-0.748	0.633	0.917	0.884	1.000				
	P:	0.013	0.173	< 0.0001	< 0.0001	0				
NO_3 +NO_2	*r:*	0.836	-0.620	-0.972	-0.909	-0.906	1.000			
	P:	0.001	0.219	< 0.0001	< 0.0001	< 0.0001	0			
SiO_4	*r:*	0.553	-0.587	-0.786	-0.831	-0.648	0.803	1.000		
	P:	0.619	0.378	0.004	0.001	0.130	0.002	0		
PO_4	*r:*	0.777	-0.348	-0.753	-0.755	-0.754	0.837	0.587	1.000	
	P:	0.005	1.000	0.011	0.010	0.011	0.001	0.373	0	
NH_4	*r:*	0.116	-0.112	-0.413	-0.301	-0.264	0.393	0.569	0.176	1.000
	P:	1.000	1.000	1.000	1.000	1.000	1.000	0.494	1.000	0

Table B5. Relationship between oceanographic variables, expressed as Pearson product moment correlation coefficients and Bonferroni probabilities at Black Duck Cove, 2000.

Variable		Salinity	Temp	Chl a	Phaeo	$NO_3 + NO_2$	SiO_4	PO_4	NH_4
Salinity	*r*:	1.00							
	P:	0							
Temperature	*r*:	0.639	1.000						
	P:	0.709	0						
Chl a	*r*:	0.392	0.861	1.000					
	P:	1.000	0.009	0					
Phaeophytin	*r*:	0.459	0.735	0.716	1.000				
	P:	1.000	0.182	0.246	0				
$NO_3 + NO_2$	*r*:	-0.442	-0.778	-0.953	-0.737	1.000			
	P:	1.000	0.081	< 0.0001	0.175	0			
SiO_4	*r*:	-0.511	-0.795	-0.866	-0.682	0.810	1.000		
	P:	1.000	0.056	0.008	0.408	0.039	0		
PO_4	*r*:	0.137	0.416	0.286	-0.184	-0.186	-0.238	1.000	
	P:	1.000	1.000	1.000	1.000	1.000	1.000	0	
NH_4	*r*:	-0.677	-0.777	-0.808	-0.657	0.816	0.806	-0.114	1.000
	P:	0.437	0.083	0.041	0.568	0.033	0.043	1.000	0

Table B6. Relationship between oceanographic variables, expressed as Pearson productoment correlation coefficients and Bonferroni probabilities at Loon Point, 2000.

Variable		Salinity	Temp	Chl *a*	Phaeo	$NO_3 + NO_2$	SiO_4	PO_4	NH_4
Salinity	*r*:	1.000							
	P:	0							
Temperature	*r*:	0.540	1.000						
	P:	1.000	0						
Chl *a*	*r*:	0.639	0.807	1.000					
	P:	0.387	0.014	0					
Phaeophytin	*r*:	0.369	0.665	0.769	1.000				
	P:	1.000	0.263	0.036	0				
$NO_3 + NO_2$	*r*:	-0.602	-0.905	-0.883	-0.746	1.000			
	P:	0.638	< 0.0001	0.001	0.062	0			
SiO_4	*r*:	-0.692	-0.736	-0.970	-0.734	0.881	1.000		
	P:	0.171	0.075	< 0.0001	0.079	0.001	0		
PO_4	*r*:	0.134	-0.068	-0.272	-0.208	0.255	0.393	1.000	
	P:	1.000	1.000	1.000	1.000	1.000	1.000	0	
NH_4	*r*:	-0.644	-0.775	-0.796	-0.671	0.901	0.835	0.363	1.000
	P:	0.365	0.032	0.19	0.239	< 0.0001	0.006	1.000	0

Table B7. Relationship between oceanographic variables, expressed as Pearson product moment correlation coefficients and Bonferroni probabilities at Starboard Cove, 2000.

Variable		Salinity	Temp	Chl *a*	Phaeo	NO_3 +NO_2	SiO_4	PO_4	NH_4
Salinity	*r*:	1.000							
	P:	0							
Temperature	*r*:	0.706	1.000						
	P:	0.290	0						
Chl *a*	*r*:	0.454	0.778	1.000					
	P:	1.000	0.080	0					
Phaeophytin	*r*:	0.822	0.908	0.560	1.000				
	P:	0.029	0.001	1.000	0				
NO_3 +NO_2	*r*:	0.516	-0.128	-0.326	0.152	1.000			
	P:	1.000	1.000	1.000	1.000	0			
SiO_4	*r*:	0.343	0.318	-0.052	0.524	0.431	1.000		
	P:	1.000	1.000	1.000	1.000	1.000	0		
PO_4	*r*:	0.021	-0.136	-0.189	-0.172	0.274	0.128	1.000	
	P:	1.000	1.000	1.000	1.000	1.000	1.000	0	
NH_4	*r*:	0.270	-0.059	-0.215	0.243	0.477	0.472	-0.057	1.000
	P:	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0

Appendix C

Linear regression analysis of the relationship between selected oceanographic variables and female and male gonad indices at all sites

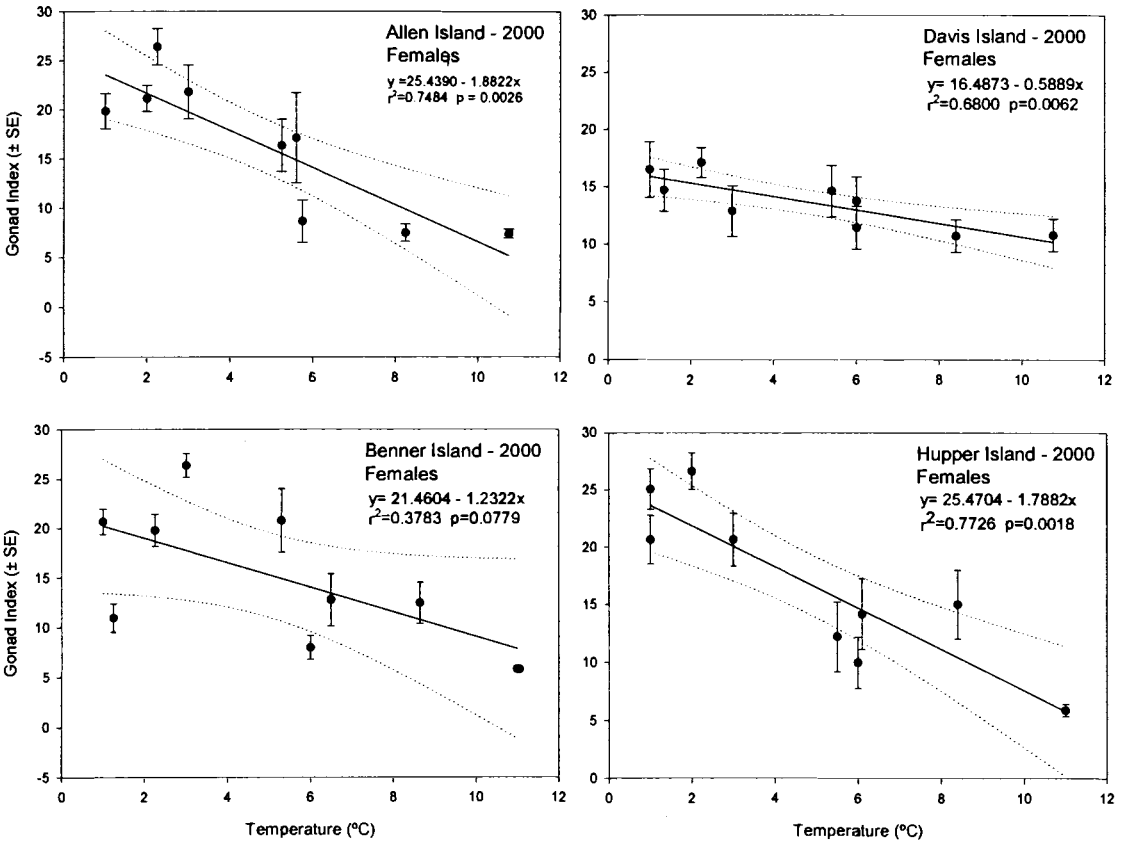

Figure C1. Linear regression analysis of the relationship between mean gonad index of female sea urchins at Allen, Benner, Davis, and Hupper Islands and mean temperature (n=2).

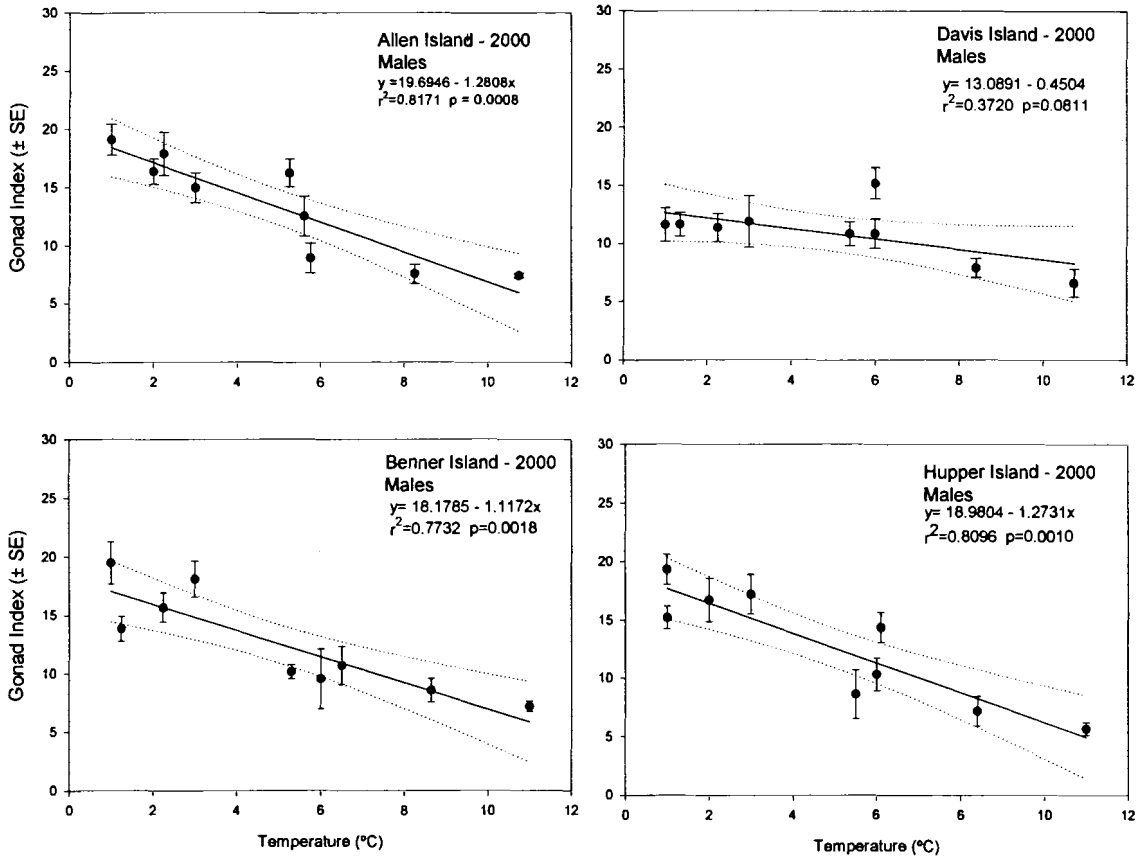

Figure C2. Linear regression analysis of the relationship between mean gonad index of male sea urchins at Allen, Benner, Davis, and Hupper Islands and mean temperature (n=2).

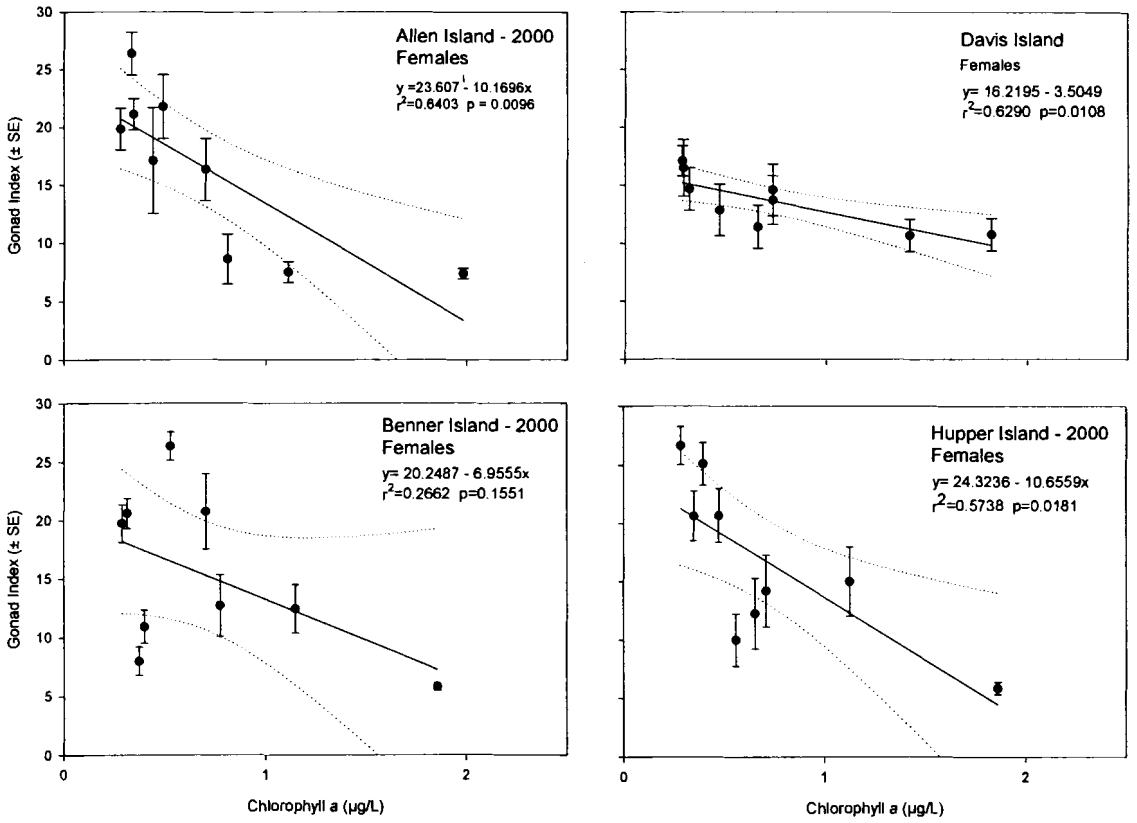

Figure C3. Linear regression analysis of the relationship between mean gonad index of female sea urchins at Allen, Benner, Davis, and Hupper Islands and mean chlorophyll *a* concentrations (n=2).

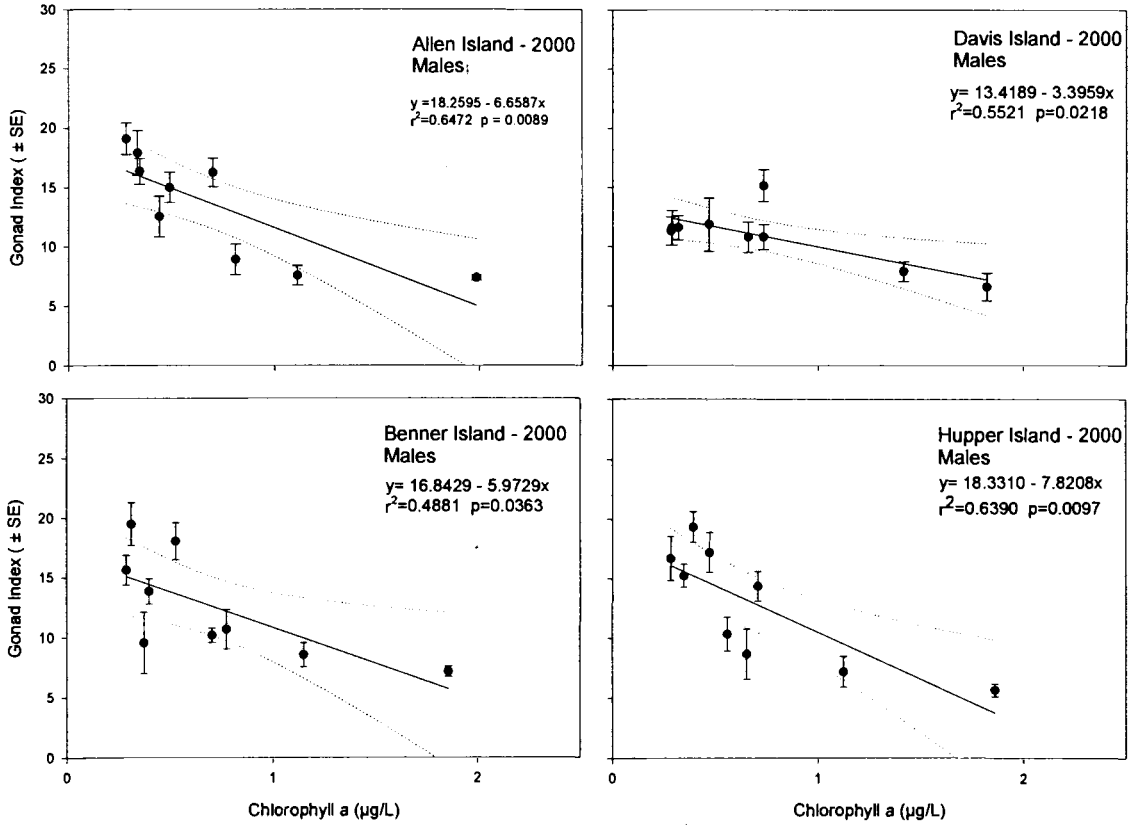

Figure C4. Linear regression analysis of the relationship between mean gonad index of male sea urchins at Allen, Benner, Davis, and Hupper Islands and mean chlorophyll *a* concentrations (n=2).

Appendix D

Stepwise, multiple linear regression for the dependence of arcsine-transformed gonad indices at the Georges Islands and Jonesport sites on oceanographic variables

Table D1. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Allen Island on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.965; SE of estimate = 0.011).

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.026	0.013	112.761	< 0.0001
Error	6	0.001	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	-2.154	< 0.0001	0.170	
Salinity	0.072	< 0.0001	0.005	0.981
PO_4	-0.016	0.148	0.010	-0.561

Table D2. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Benner Island on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.747; SE of estimate = 0.027)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.019	0.009	12.838	0.007
Error	6	0.004	0.001		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.728	0.014	0.213	
Temperature	-0.061	0.021	0.020	-0.785
$NO_3 + NO_2$	-0.048	0.048	0.019	-0.711

Table D3. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Davis Island on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.910; SE of estimate = 0.017)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.025	0.013	41.652	< 0.0001
Error	6	0.002	< 0.0001		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	-0.226	0.304		
Phaeophytin	-0.261	< 0.0001	0.035	-0.931
Salinity	0.015	0.052	0.006	0.702

Table D4. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Hupper Island on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.982; SE of estimate = 0.004)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	3	0.007	0.002	142.533	< 0.0001
Error	5	0.000	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.774	< 0.0001	0.064	
Chl *a*	-0.065	<0.0001	0.008	-0.878
Salinity	-0.019	< 0.0001	0.002	-0.915
Temperature	-0.004	0.021	0.001	-0.830

Table D5. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=6) at Black Duck Cove on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.992; SE of estimate = 0.005)

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	3	0.014	0.005	210.886	0.005
Error	2	0.000	0.000		
Total	5				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.094	0.015	0.012	
SiO_4	0.008	0.029	0.001	0.970
Phaeophytin	-0.031	0.057	0.008	-0.745
NH_4	0.028	0.061	0.007	0.939

Table D6. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=7) at Loon Point on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =1.00; SE of estimate = 0.001)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	4	0.030	0.007	8508.355	< 0.0001
Error	2	0.000	0.000		
Total	6				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	-3.150	< 0.0001	0.051	
$NO_3 + NO_2$	0.038	< 0.0001	0.000	0.855
PO_4	-0.045	< 0.0001	0.000	-0.745
Salinity	0.099	< 0.0001	0.002	0.996
Temperature	-0.003	0.031	0.001	-0.969

Table D7. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=6) at Starboard Cove on oceanographic variables derived by stepwise, forward elimination procedure (Adj. Model R^2 =0.997; SE of estimate = 0.004)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.024	0.012	942.067	< 0.0001
Error	3	0.000	0.000		
Total	5				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.285	< 0.0001	0.006	
Temperature	-0.045	< 0.0001	0.002	-0.986
Phaeophytin	0.178	0.006	0.025	0.971

Appendix E

Stepwise, multiple linear regression for the dependence of arcsine-transformed gonad indices at the Georges Islands and Jonesport sites on oceanographic variables (with temperature forced first into the model)

Table E1. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Allen Island on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model R^2 =0.950; SE of estimate = 0.013).

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.026	0.013	77.588	< 0.0001
Error	6	0.001	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	-1.913	0.002	0.359	
Temperature	-0.001	0.003	0.774	-0.862
Salinity	0.064	0.011	0.001	0.925

Table E2. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Benner Island on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model R^2 =0.747; SE of estimate = 0.027)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.019	0.009	12.838	0.007
Error	6	0.004	0.001		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.728	0.014	0.213	
Temperature	-0.061	0.021	0.020	-0.785
$NO_3 + NO_2$	-0.048	0.048	0.019	-0.711

Table E3. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Davis Island on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model R^2 =0.947; SE of estimate = 0.007)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	3	0.007	0.002	48.421	< 0.0001
Error	5	< 0.0001	< 0.0001		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.616	0.001	0.079	
Temperature	-0.004	0.255	0.003	-0.831
Salinity	-0.014	0.002	0.002	-0.893
Chlorophyll *a*	-0.035	0.091	0.017	-0.683

Table E4. ***Georges Islands.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=9) at Hupper Island on oceanographic variables derived by stepwise, forward elimination procedure with temperature first forced into the model (Adj. Model R^2 =0.916; SE of estimate = 0.018)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.028	0.014	44.734	< 0.0001
Error	6	0.002	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.299	< 0.0001	0.025	
Temperature	-0.010	0.007	0.003	-0.909
Extinction coefficient	-0.344	0.018	0.106	-0.798

Table E5. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=6) at Black Duck Cove on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model R^2 =0.965; SE of estimate = 0.010)

A. *Analysis of variance*

Source	df	SS	MS	F-ratio	P
Model	3	0.014	0.005	47.343	0.021
Error	2	0.000	0.000		
Total	5				

B. *Regression parameter estimates*

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	1.663	0.117	0.625	
Temperature	0.021	0.017	0.006	-0.891
Silicate	0.022	0.072	0.005	0.844
Salinity	-0.052	0.124	0.020	-0.876

Table E6. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=7) at Loon Point on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model R^2 =1.00; SE of estimate = 0.001).

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	4	0.030	0.007	3613.682	< 0.0001
Error	2	0.000	0.000		
Total	6				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	2.169	< 0.0001	0.035	
Temperature	-0.009	0.002	0.000	-0.827
Salinity	-0.059	< 0.0001	0.001	-0.870
Phaeophytin	-0.051	0.001	0.002	-0.797
PO_4	-0.009	0.002	0.000	-0.998

Table E7. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices (n=6) at Starboard Cove on oceanographic variables derived by stepwise, forward elimination procedure, with temperature first forced into the model (Adj. Model $R^2 = 0.997$; SE of estimate = 0.004).

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.024	0.012	942.067	< 0.0001
Error	3	0.000	0.000		
Total	5				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE	Partial correlation
Intercept	0.285	< 0.0001	0.006	
Temperature	-0.045	< 0.0001	0.002	-0.986
Phaeophytin	0.178	0.006	0.025	0.971

Appendix F

Multiple regression for the dependence of arcsine-transformed gonad indices at the Georges Islands and Jonesport sites on principal components

Table F1. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices at Allen Island on principal components (Model R^2 =0.909)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.025	0.013	41.142	<0.0001
Error	6	0.002	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	-0.354	0.004	0.078
PC1	0.019	<0.0001	0.002
PC2	-0.034	0.004	0.007

Table F2. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices at Benner Island on principal components (Model R^2 =0.373)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.012	0.006	3.375	0.104
Error	6	0.011	0.002		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	-0.059	0.739	0.168
PC1	0.011	0.080	0.005
PC2	-0.008	0.648	0.016

Table F3. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices at Davis Island on principal components (Model R^2 =0.715)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.006	0.003	11.057	0.010
Error	6	0.002	0.000		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	0.117	0.077	0.055
PC1	0.004	0.095	0.002
PC2	0.008	0.147	0.005

Table F4. ***Georges Islands***. Multiple regression for the dependence of arcsine-transformed gonad indices at Hupper Island on principal components (Model R^2 =0.672)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.022	0.011	9.204	0.015
Error	6	0.007	0.001		
Total	8				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	-0.070	0.603	0.128
PC1	0.014	0.014	0.004
PC2	-0.005	0.713	0.013

Table F5. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices from Black Duck Cove on principal components (Model R^2 =0.938)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.014	0.007	39.066	0.007
Error	3	0.001	0.000		
Total	5				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	0.481	0.438	0.539
PC1	-0.106	0.606	0.184
PC2	0.048	0.641	0.093

Table F6. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices from Loon Point on principal components (Model R^2 =0.854)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.027	0.013	18.574	0.009
Error	4	0.003	0.001		
Total	6				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	1.889	0.062	0.734
PC1	-0.597	0.079	0.254
PC2	0.294	0.084	0.128

Table F7. ***Jonesport Region.*** Multiple regression for the dependence of arcsine-transformed gonad indices from Starboard Cove on principal components (Model R^2 =0.721)

A. Analysis of variance

Source	df	SS	MS	F-ratio	P
Model	2	0.020	0.010	7.469	0.068
Error	3	0.004	0.001		
Total	5				

B. Regression parameter estimates

Variable	Parameter Estimate	*P*	± SE
Intercept	2.768	0.186	1.619
PC1	-0.895	0.198	0.544
PC2	0.442	0.207	0.276

Appendix G

Patterns of spawning in the green sea urchin at Allen, Benner, Davis, and Hupper Islands in 1998 and 1999

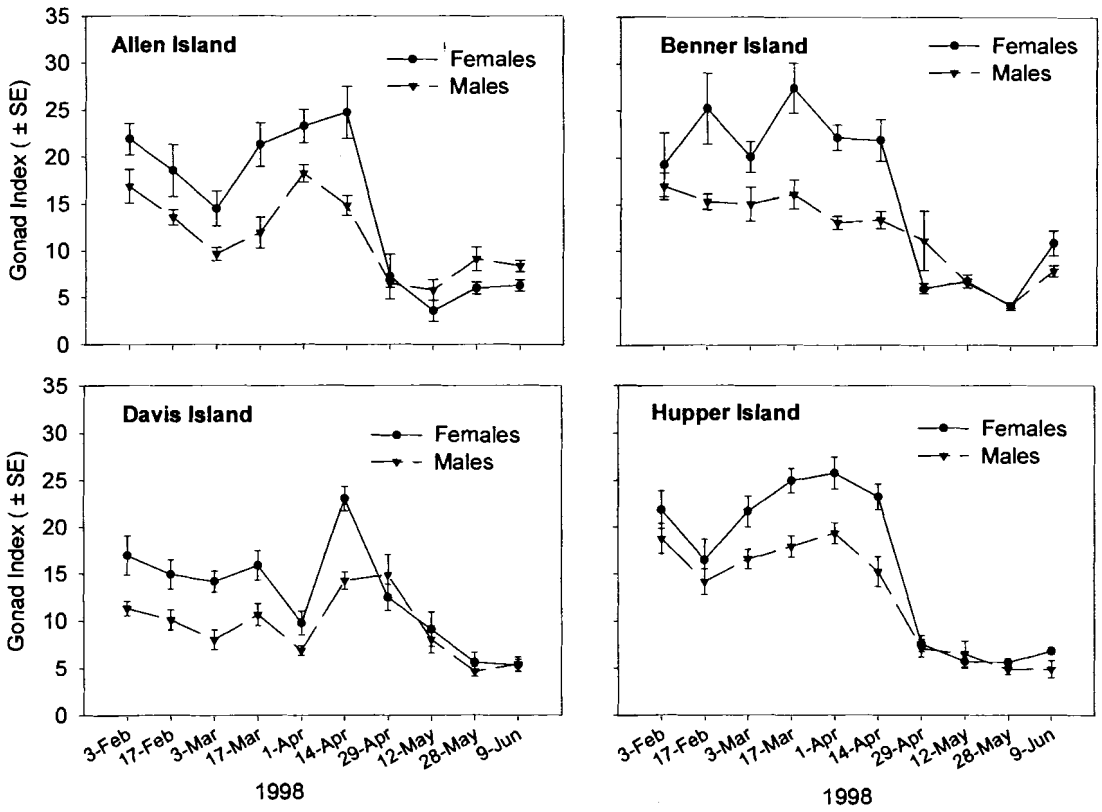

Figure G1. ***Georges Islands Region***. 1998. Changes in mean gonad index (± 1SE) of female and male sea urchins at Allen, Benner, Davis, and Hupper Islands (n=20).

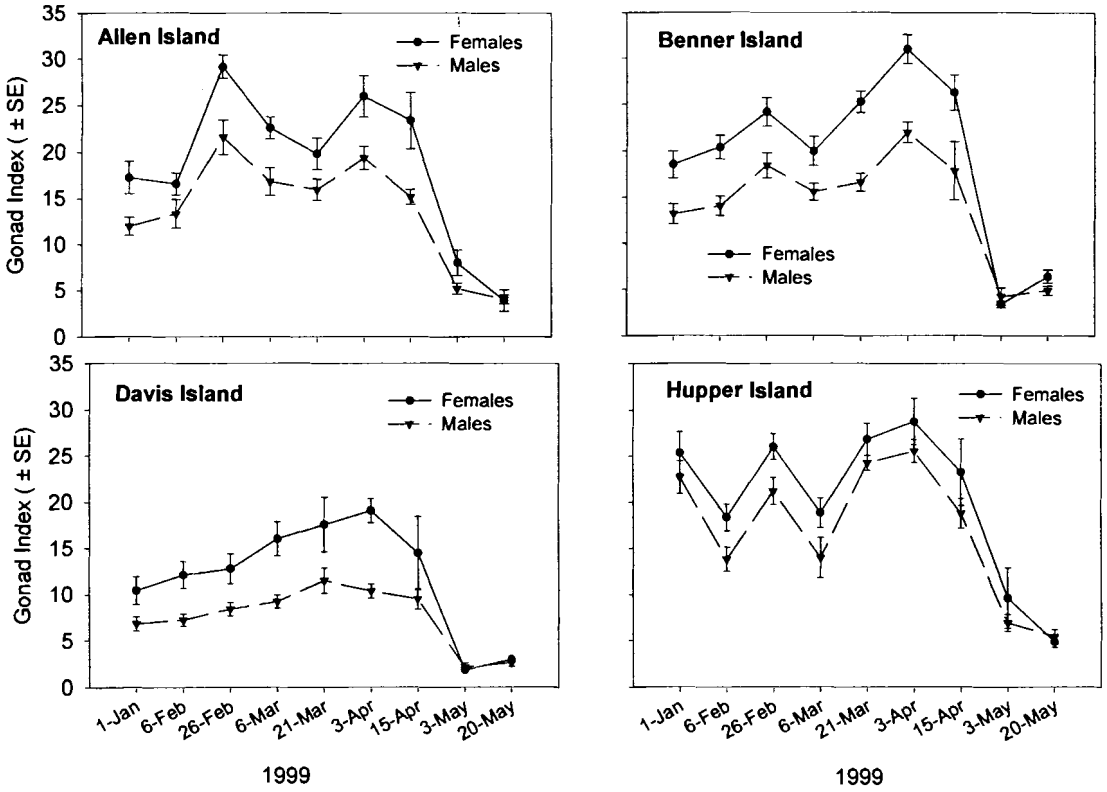

Figure G2. ***Georges Islands Region***. 1999. Changes in mean gonad index (± 1SE) of female and male sea urchins at Allen, Benner, Davis, and Hupper Islands (n=20).

Appendix H

Phytoplankton cell counts (raw data, cells ml^{-1}, and cells L^{-1}) at Allen, Benner, Davis, and Hupper Islands from 30 January to 28 May 2000

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Allen	1/30/2000	*Cocinodiscus*	1	0.03	30.76923
Allen	1/30/2000	*Thalassiosira*	3	0.09	92.30769
Allen	1/30/2000	*Fragilaria*	6	0.18	184.6154
Allen	1/30/2000	*Skeletonema*	10	0.31	307.6923
Allen	1/30/2000	*Navicula*	12	0.37	369.2308
Allen	1/30/2000	miscellaneous flagellates	12	0.37	369.2308
Allen	1/30/2000	other	13	0.40	400
Allen	2/13/2000	*Cocconeis*	1	0.03	30.76923
Allen	2/13/2000	*Rhizoselenia*	1	0.03	30.76923
Allen	2/13/2000	*Ditylum*	1	0.03	30.76923
Allen	2/13/2000	*Chaetocerros*	5	0.15	153.8462
Allen	2/13/2000	*Thalassiosira*	14	0.43	430.7692
Allen	2/13/2000	miscellaneous flagellates	18	0.55	553.8462
Allen	2/13/2000	Tear-drop flagellates > 10 um	22	0.68	676.9231
Allen	2/13/2000	Tear-drop flagellates < 10 um	36	1.11	1107.692
Allen	2/25/2000	*Coscinodiscus*	1	0.03	30.76923
Allen	2/25/2000	*Licmophora*	1	0.03	30.76923
Allen	2/25/2000	*Rhizoselenia*	2	0.06	61.53846
Allen	2/25/2000	*Pleurosigma*	3	0.09	92.30769
Allen	2/25/2000	*Nitschia*	3	0.09	92.30769
Allen	2/25/2000	miscellaneous dinos.	3	0.09	92.30769
Allen	2/25/2000	larvae	3	0.09	92.30769
Allen	2/25/2000	*Navicula*	4	0.12	123.0769
Allen	2/25/2000	*Guinardia*	4	0.12	123.0769
Allen	2/25/2000	*Thalassionema*	5	0.15	153.8462
Allen	2/25/2000	*Thalassiosira*	13	0.40	400
Allen	2/25/2000	other	28	0.86	861.5385
Allen	3/19/2000	*Cocconeis*	2	0.06	61.53846
Allen	3/19/2000	*Rhizoselia*	3	0.09	92.30769
Allen	3/19/2000	*Nitschia*	3	0.09	92.30769
Allen	3/19/2000	miscellaneous dinos.	3	0.09	92.30769
Allen	3/19/2000	*Coscinodiscus*	5	0.15	153.8462
Allen	3/19/2000	larvae	5	0.15	153.8462
Allen	3/19/2000	miscellaneous flagellates	5	0.15	153.8462
Allen	3/19/2000	*Navicula*	10	0.31	307.6923
Allen	3/19/2000	other	10	0.31	307.6923
Allen	3/19/2000	*Chaetocerus*	12	0.37	369.2308
Allen	4/1/2000	*Rhizoselenia*	1	0.03	30.76923
Allen	4/1/2000	*Ceramium*	1	0.03	30.76923
Allen	4/1/2000	*Coscinodiscus*	1	0.03	30.76923
Allen	4/1/2000	*Grammatophora*	2	0.06	61.53846
Allen	4/1/2000	*Fragilaria*	2	0.06	61.53846
Allen	4/1/2000	*Licmophora*	3	0.09	92.30769
Allen	4/1/2000	*Nitschia*	4	0.12	123.0769
Allen	4/1/2000	*Skeletonema*	4	0.12	123.0769
Allen	4/1/2000	*cocconeis*	9	0.28	276.9231
Allen	4/1/2000	miscellaneous flagellates	9	0.28	276.9231
Allen	4/1/2000	Other	15	0.46	461.5385
Allen	4/1/2000	*Navicula*	20	0.62	615.3846
Allen	4/1/2000	*Phaeocystis*	31	0.95	953.8462

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Allen	4/16/2000	*Grammatophora*	1	0.03	30.76923
Allen	4/16/2000	*Navicula*	10	0.31	307.6923
Allen	4/16/2000	miscellaneous flagellates	12	0.37	369.2308
Allen	4/16/2000	*Phaeocystis*	28	0.86	861.5385
Allen	4/29/2000	*Nitschia*	1	0.03	30.76923
Allen	4/29/2000	*Cocconeis*	1	0.03	30.76923
Allen	4/29/2000	*Grammatophora*	1	0.03	30.76923
Allen	4/29/2000	*Thalassiosira*	1	0.03	30.76923
Allen	4/29/2000	*Licmophora*	1	0.03	30.76923
Allen	4/29/2000	Foraminifera	1	0.03	30.76923
Allen	4/29/2000	*Navicula*	4	0.12	123.0769
Allen	4/29/2000	*Skeletonema*	4	0.12	123.0769
Allen	4/29/2000	miscellaneous flag.	5	0.15	153.8462
Allen	4/29/2000	*Phaeocystis*	382	11.75	11753.85
Allen	5/12/2000	*Gramminophora*	1	0.03	30.76923
Allen	5/12/2000	*Cocconeis*	1	0.03	30.76923
Allen	5/12/2000	*Pleurosigma*	1	0.03	30.76923
Allen	5/12/2000	*Fragilaria*	3	0.09	92.30769
Allen	5/12/2000	*Nitschia*	6	0.18	184.6154
Allen	5/12/2000	*Eucampia*	6	0.18	184.6154
Allen	5/12/2000	*Prorocentrum*	7	0.22	215.3846
Allen	5/12/2000	*Rhizoselenia*	8	0.25	246.1538
Allen	5/12/2000	*Navicula*	13	0.40	400
Allen	5/12/2000	*Licmorpha*	21	0.65	646.1538
Allen	5/12/2000	*Thalassiosira*	33	1.02	1015.385
Allen	5/12/2000	*Chaetocerus*	36	1.11	1107.692
Allen	5/12/2000	miscellaneous flagellates	50	1.54	1538.462
Allen	5/12/2000	*Skeletonema*	188	5.78	5784.615
Allen	5/12/2000	*Phaeocystis*	203	6.25	6246.154
Allen	5/28/2000	*Cocconeis*	2	0.06	61.53846
Allen	5/28/2000	*Ditylum*	2	0.06	61.53846
Allen	5/28/2000	*Peridinium*	2	0.06	61.53846
Allen	5/28/2000	*Grammatophora*	3	0.09	92.30769
Allen	5/28/2000	*Pleurosigma*	4	0.12	123.0769
Allen	5/28/2000	*Nitschia*	7	0.22	215.3846
Allen	5/28/2000	*Eucampia*	13	0.40	400
Allen	5/28/2000	*Fragilaria*	16	0.49	492.3077
Allen	5/28/2000	*Navicula*	20	0.62	615.3846
Allen	5/28/2000	Tear-drop flagellates < 10 um	117	3.60	3600
Allen	5/28/2000	*Phaeocystis*	186	5.72	5723.077

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Benner	1/30/2000	*Pleurosigma*	1	0.03	30.76923
Benner	1/30/2000	*Licmophora*	3	0.09	92.30769
Benner	1/30/2000	*Cocconeis*	1	0.03	30.76923
Benner	1/30/2000	*Thalassiosira*	4	0.12	123.0769
Benner	1/30/2000	*Navicula*	5	0.15	153.8462
Benner	1/30/2000	miscellaneous flagellates	5	0.15	153.8462
Benner	1/30/2000	other	2	0.06	61.53846
Benner	2/13/2000	*Thalassiosira*	9	0.28	276.9231
Benner	2/13/2000	*Navicula*	4	0.12	123.0769
Benner	2/13/2000	*Cocconeis*	1	0.03	30.76923
Benner	2/13/2000	*Grammatophora*	1	0.03	30.76923
Benner	2/13/2000	*Nitschia*	2	0.06	61.53846
Benner	2/25/2000	*Pleurosigma*	1	0.03	30.76923
Benner	2/25/2000	*Nitschia*	1	0.03	30.76923
Benner	2/25/2000	*Grammatophora*	1	0.03	30.76923
Benner	2/25/2000	*Coscinodiscus*	1	0.03	30.76923
Benner	2/25/2000	*Leptocylindrus*	1	0.03	30.76923
Benner	2/25/2000	oak pollen	1	0.03	30.76923
Benner	2/25/2000	*Eucampia*	2	0.06	61.53846
Benner	2/25/2000	*Licmophora*	3	0.09	92.30769
Benner	2/25/2000	Tear-drop flagellates > 10 um	6	0.18	184.6154
Benner	2/25/2000	Tear-drop flagellates < 10 um	8	0.25	246.1538
Benner	2/25/2000	*Navicula*	10	0.31	307.6923
Benner	2/25/2000	*Thalassiosira*	24	0.74	738.4615
Benner	3/19/2000	*Coscinodiscus*	1	0.03	30.76923
Benner	3/19/2000	*Nitschia*	1	0.03	30.76923
Benner	3/19/2000	*Rhizoselenia*	1	0.03	30.76923
Benner	3/19/2000	*Biddulphia*	3	0.09	92.30769
Benner	3/19/2000	*Grammatophora*	3	0.09	92.30769
Benner	3/19/2000	*Thalassiosira*	5	0.15	153.8462
Benner	3/19/2000	*Pleurosigma*	8	0.25	246.1538
Benner	3/19/2000	*Cocconeis*	15	0.46	461.5385
Benner	3/19/2000	miscellaneous flagellates	16	0.49	492.3077
Benner	3/19/2000	*Navicula*	109	3.35	3353.846
Benner	4/1/2000	*Pleurosigma*	1	0.03	30.76923
Benner	4/1/2000	*Ceramium*	1	0.03	30.76923
Benner	4/1/2000	*Nitschia*	2	0.06	61.53846
Benner	4/1/2000	*Coscinodiscus*	2	0.06	61.53846
Benner	4/1/2000	*Thalassionema*	4	0.12	123.0769
Benner	4/1/2000	*Fragilaria*	5	0.15	153.8462
Benner	4/1/2000	*Chaetocerros*	5	0.15	153.8462
Benner	4/1/2000	*cocconeis*	7	0.22	215.3846
Benner	4/1/2000	*Skeletonema*	7	0.22	215.3846
Benner	4/1/2000	miscellaneous flagellates	7	0.22	215.3846
Benner	4/1/2000	*Thalassiosira*	38	1.17	1169.231
Benner	4/1/2000	*Navicula*	55	1.69	1692.308
Benner	4/1/2000	*Licmophora*	62	1.91	1907.692

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Benner	4/16/2000	*Biddulphia*	1	0.03	30.76923
Benner	4/16/2000	*Thalassionema*	1	0.03	30.76923
Benner	4/16/2000	*Cocconeis*	1	0.03	30.76923
Benner	4/16/2000	oak pollen	1	0.03	30.76923
Benner	4/16/2000	*Guinardia*	2	0.06	61.53846
Benner	4/16/2000	*Thalassiosira*	2	0.06	61.53846
Benner	4/16/2000	*Paralia*	6	0.18	184.6154
Benner	4/16/2000	*Licmophora*	8	0.25	246.1538
Benner	4/16/2000	*Pleurosigma*	9	0.28	276.9231
Benner	4/16/2000	large tear shaper flagellates	15	0.46	461.5385
Benner	4/16/2000	miscellaneous flagellates	21	0.65	646.1538
Benner	4/16/2000	*Navicula*	56	1.72	1723.077
Benner	4/29/2000	*Coscinodiscus*	1	0.03	30.76923
Benner	4/29/2000	*Thalassionema*	1	0.03	30.76923
Benner	4/29/2000	*Grammatophora*	1	0.03	30.76923
Benner	4/29/2000	*Nitschia*	2	0.06	61.53846
Benner	4/29/2000	*Eucampia*	2	0.06	61.53846
Benner	4/29/2000	*Peridinium*	2	0.06	61.53846
Benner	4/29/2000	*Biddulphia*	3	0.09	92.30769
Benner	4/29/2000	*Skeletonema*	4	0.12	123.0769
Benner	4/29/2000	*Licmophora*	8	0.25	246.1538
Benner	4/29/2000	miscellaneous dinos	8	0.25	246.1538
Benner	4/29/2000	*Thalassiosira*	13	0.40	400
Benner	4/29/2000	*Navicula*	15	0.46	461.5385
Benner	4/29/2000	*Cocconeis*	20	0.62	615.3846
Benner	4/29/2000	Tear-drop flagellates > 10 um	29	0.89	892.3077
Benner	4/29/2000	Tear-drop flagellates < 10 um	78	2.40	2400
Benner	4/29/2000	*Phaeocystis*	474	14.58	14584.62
Benner	5/12/2000	*Licmorpha*	1	0.03	30.76923
Benner	5/12/2000	*Nitschia*	1	0.03	30.76923
Benner	5/12/2000	*Thalassionema*	1	0.03	30.76923
Benner	5/12/2000	*Navicula*	2	0.06	61.53846
Benner	5/12/2000	*Guinardia*	3	0.09	92.30769
Benner	5/12/2000	*Alexandrium*	3	0.09	92.30769
Benner	5/12/2000	*Cocconeis*	5	0.15	153.8462
Benner	5/12/2000	*Paralia*	7	0.22	215.3846
Benner	5/12/2000	*Chaetoceros*	10	0.31	307.6923
Benner	5/12/2000	large heterokonts > 10 um	12	0.37	369.2308
Benner	5/12/2000	*Thalassiosira*	17	0.52	523.0769
Benner	5/12/2000	Tear-drop flagellates < 10 um	29	0.89	892.3077
Benner	5/12/2000	*Skeletonema*	56	1.72	1723.077
Benner	5/12/2000	miscellaneous flagellates	93	2.86	2861.538
Benner	5/12/2000	*Phaeocystis*	136	4.18	4184.615

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Benner	5/28/2000	*Chaetoceros*	368	11.32	11323.08
Benner	5/28/2000	*Coscinodiscus*	1	0.03	30.76923
Benner	5/28/2000	*Navicula*	6	0.18	184.6154
Benner	5/28/2000	*Eucampia*	12	0.37	369.2308
Benner	5/28/2000	*Amphidinium*	2	0.06	61.53846
Benner	5/28/2000	*Peridinium*	4	0.12	123.0769
Benner	5/28/2000	*Dinophysis*	1	0.03	30.76923
Benner	5/28/2000	Tear-drop flagellates < 10 um	26	0.80	800
Benner	5/28/2000	*Skeletonema*	94	2.89	2892.308
Benner	5/28/2000	*Licmorpha*	2	0.06	61.53846
Benner	5/28/2000	*Thalassiosira*	71	2.18	2184.615
Benner	5/28/2000	*Thalassionema*	19	0.58	584.6154
Benner	5/28/2000	*Phaeocystis*	58	1.78	1784.615
Benner	5/28/2000	*Bacteriastrum*	2	0.06	61.53846
Benner	5/28/2000	*Alexandrium*	5	0.15	153.8462
Benner	5/28/2000	miscellaneous flagellates	19	0.58	584.6154
Benner	5/28/2000	large flagellates > 10 um	11	0.34	338.4615

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Davis	1/30/2000	*Cocconeis*	2	0.06	61.53846
Davis	1/30/2000	*Thalassiosira*	4	0.12	123.0769
Davis	1/30/2000	*Fragilaria*	9	0.28	276.9231
Davis	1/30/2000	*Skeletonema*	10	0.31	307.6923
Davis	1/30/2000	*Navicula*	8	0.25	246.1538
Davis	1/30/2000	miscellaneous flagellates	10	0.31	307.6923
Davis	1/30/2000	other	8	0.25	246.1538
Davis	2/13/2000	*Thalassiosira*	9.00	0.28	276.9231
Davis	2/13/2000	*Navicula*	4.00	0.12	123.0769
Davis	2/13/2000	*Cocconeis*	1.00	0.03	30.76923
Davis	2/13/2000	*Grammatophora*	1.00	0.03	30.76923
Davis	2/13/2000	*Nitschia*	2.00	0.06	61.53846
Davis	2/13/2000	*Rhizoselenia*	2.00	0.06	61.53846
Davis	2/13/2000	*Ditylum*	1.00	0.03	30.76923
Davis	2/13/2000	miscellaneous flagellates	10.00	0.31	307.6923
Davis	2/25/2000	*Navicula*	4	0.12	123.0769
Davis	2/25/2000	*Pleurosigma*	2	0.06	61.53846
Davis	2/25/2000	*Nitschia*	1	0.03	30.76923
Davis	2/25/2000	*Rhizoselenia*	1	0.03	30.76923
Davis	2/25/2000	*Coscinodiscus*	1	0.03	30.76923
Davis	2/25/2000	*Guinardia*	1	0.03	30.76923
Davis	2/25/2000	*Thalassiosira*	5	0.15	153.8462
Davis	2/25/2000	*Thallasionema*	3	0.09	92.30769
Davis	2/25/2000	*Licmophora*	6	0.18	184.6154
Davis	2/25/2000	other	8	0.25	246.1538
Davis	2/25/2000	miscellaneous dinoflagellates	10	0.31	307.6923
Davis	3/19/2000	*Biddulphia*	18.00	0.55	553.8462
Davis	3/19/2000	*Gramatophora*	6.00	0.18	184.6154
Davis	3/19/2000	*Fragillaria*	25.00	0.77	769.2308
Davis	3/19/2000	*Cocconeis*	1.00	0.03	30.76923
Davis	3/19/2000	*Navicula*	37.00	1.14	1138.462
Davis	3/19/2000	*Gyro/pleurosigma*	11.00	0.34	338.4615
Davis	3/19/2000	*Licmophora*	4.00	0.12	123.0769
Davis	4/1/2000	*Navicula*	22.00	3.38	3384.615
Davis	4/1/2000	*cocconeis*	4.00	0.62	615.3846
Davis	4/1/2000	*Rhizoselenia*	1.00	0.15	153.8462
Davis	4/1/2000	*Nitschia*	9.00	1.38	1384.615
Davis	4/1/2000	*Grammatophora*	2.00	0.31	307.6923
Davis	4/1/2000	*Corethron*	2.00	0.31	307.6923
Davis	4/1/2000	*Gyro/pleurosigma*	13	2.00	2000
Davis	4/1/2000	*Coscinodiscus*	1.00	0.15	153.8462
Davis	4/1/2000	*Licmophora*	2	0.31	307.6923
Davis	4/1/2000	*Paralia*	1	0.15	153.8462
Davis	4/1/2000	*Alexandrium*	2	0.31	307.6923
Davis	4/1/2000	miscellaneous flagellates	13	2.00	2000

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Davis	4/16/2000	*Navicula*	11.00	0.34	338.4615
Davis	4/16/2000	miscellaneous flagellates	1.00	0.03	30.76923
Davis	4/29/2000	*Navicula*	18.00	0.55	553.8462
Davis	4/29/2000	*Nitschia*	1.00	0.03	30.76923
Davis	4/29/2000	*Cocconeis*	2.00	0.06	61.53846
Davis	4/29/2000	*Rhizoselenia*	1.00	0.03	30.76923
Davis	4/29/2000	*Biddulphia*	3.00	0.09	92.30769
Davis	4/29/2000	*Thalassiosira*	16.00	0.49	492.3077
Davis	4/29/2000	*Pleurosigma*	1.00	0.03	30.76923
Davis	4/29/2000	miscellaneous flagellates	9.00	0.28	276.9231
Davis	5/12/2000	*Guinardia*	1	0.03	30.76923
Davis	5/12/2000	*Distephanus*	1	0.03	30.76923
Davis	5/12/2000	*Cocconeis*	1	0.03	30.76923
Davis	5/12/2000	*Pleurosigma*	1	0.03	30.76923
Davis	5/12/2000	*Nitschia*	1	0.03	30.76923
Davis	5/12/2000	*Rhizoselenia*	2	0.06	61.53846
Davis	5/12/2000	Tear-drop flagellates > 10 um	2	0.06	61.53846
Davis	5/12/2000	*Navicula*	3	0.09	92.30769
Davis	5/12/2000	*Licmorpha*	4	0.12	123.0769
Davis	5/12/2000	miscellaneous flagellates	16	0.49	492.3077
Davis	5/12/2000	*Thalassiosira*	25	0.77	769.2308
Davis	5/12/2000	Tear-drop flagellates < 10 um	28	0.86	861.5385
Davis	5/12/2000	*Chaetocerus*	44	1.35	1353.846
Davis	5/12/2000	*Skeletonema*	50	1.54	1538.462
Davis	5/12/2000	*Phaeocystis*	517	15.91	15907.69
Davis	5/28/2000	*Guinardia*	1	0.03	30.76923
Davis	5/28/2000	*Rhizoselenia*	1	0.03	30.76923
Davis	5/28/2000	*Gyrodidium*	1	0.03	30.76923
Davis	5/28/2000	*Navicula*	2	0.06	61.53846
Davis	5/28/2000	*Amphididium*	2	0.06	61.53846
Davis	5/28/2000	*Alexandrium*	2	0.06	61.53846
Davis	5/28/2000	*Nitschia*	4	0.12	123.0769
Davis	5/28/2000	*Peridinium*	7	0.22	215.3846
Davis	5/28/2000	*Eucampia*	19	0.58	584.6154
Davis	5/28/2000	*Thalassionema*	22	0.68	676.9231
Davis	5/28/2000	miscellaneous flagellates	29	0.89	892.3077
Davis	5/28/2000	Tear-drop flagellates < 10 um	29	0.89	892.3077
Davis	5/28/2000	Tear-drop flagellates > 10 um	30	0.92	923.0769
Davis	5/28/2000	*Heterocapsa*	35	1.08	1076.923
Davis	5/28/2000	*Thalassiosira*	57	1.75	1753.846
Davis	5/28/2000	*Skeletonema*	153	4.71	4707.692
Davis	5/28/2000	*Chaetocerus*	188	5.78	5784.615

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Hupper	1/30/2000	*Cocinodiscus*	1	0.03	30.76923
Hupper	1/30/2000	*Pleurosigma*	2	0.06	61.53846
Hupper	1/30/2000	*Skeletonema*	8	0.25	246.1538
Hupper	1/30/2000	*Thalassiosira*	4	0.12	123.0769
Hupper	1/30/2000	*Navicula*	10	0.31	307.6923
Hupper	1/30/2000	miscellaneous flagellates	7	0.22	215.3846
Hupper	1/30/2000	other	4	0.12	123.0769
Hupper	2/13/2000	*Distephanus*	1	0.03	30.76923
Hupper	2/13/2000	*Biddulphia*	1	0.03	30.76923
Hupper	2/13/2000	*Corethron*	1	0.03	30.76923
Hupper	2/13/2000	*Nitschia*	3	0.09	92.30769
Hupper	2/13/2000	*Cocconeis*	4	0.12	123.0769
Hupper	2/13/2000	*Coscindiscus*	4	0.12	123.0769
Hupper	2/13/2000	*Grammatophora*	6	0.18	184.6154
Hupper	2/13/2000	*Licmophora*	8	0.25	246.1538
Hupper	2/13/2000	*Thallasionema*	11	0.34	338.4615
Hupper	2/13/2000	*Pleurosigma*	13	0.40	400
Hupper	2/13/2000	*Paraphilia*	17	0.52	523.0769
Hupper	2/13/2000	*Thalassiosira*	23	0.71	707.6923
Hupper	2/13/2000	Tear-drop flagellates < 10 um	40	1.23	1230.769
Hupper	2/13/2000	Tear-drop flagellates > 10 um	49	1.51	1507.692
Hupper	2/13/2000	*Navicula*	69	2.12	2123.077
Hupper	2/25/2000	*Pleurosigma*	1	0.03	30.76923
Hupper	2/25/2000	*Cocconeis*	1	0.03	30.76923
Hupper	2/25/2000	*Rhizoselinia*	1	0.03	30.76923
Hupper	2/25/2000	*Corethron*	2	0.06	61.53846
Hupper	2/25/2000	Tear-drop flagellates > 10 um	4	0.12	123.0769
Hupper	2/25/2000	*Thallasionema*	6	0.18	184.6154
Hupper	2/25/2000	*Thalassiosira*	18	0.55	553.8462
Hupper	2/25/2000	*Navicula*	22	0.68	676.9231
Hupper	3/19/2000	*Cocconeis*	1	0.03	30.76923
Hupper	3/19/2000	*Coscinodiscus*	1	0.03	30.76923
Hupper	3/19/2000	*Nitschia*	1	0.03	30.76923
Hupper	3/19/2000	*Pleurosigma*	3	0.09	92.30769
Hupper	3/19/2000	*Thallasionema*	3	0.09	92.30769
Hupper	3/19/2000	*Grammatophora*	3	0.09	92.30769
Hupper	3/19/2000	*Corethron*	5	0.15	153.8462
Hupper	3/19/2000	miscellaneous flagellates	6	0.18	184.6154
Hupper	3/19/2000	*Thalassiosira*	7	0.22	215.3846
Hupper	3/19/2000	Tear-drop flagellates > 10 um	8	0.25	246.1538
Hupper	3/19/2000	*Paralia*	9	0.28	276.9231
Hupper	3/19/2000	*Chaetocerous*	10	0.31	307.6923
Hupper	3/19/2000	*Skeletonema*	14	0.43	430.7692
Hupper	3/19/2000	*Navicula*	28	0.86	861.5385
Hupper	3/19/2000	Tear-drop flagellates < 10 um	32	0.98	984.6154
Hupper	3/19/2000	*Biddulphia*	54	1.66	1661.538
Hupper	3/19/2000	*Bacillaria*	82	2.52	2523.077

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Hupper	4/1/2000	*Pleurosigma*	1	0.03	30.76923
Hupper	4/1/2000	*Nitschia*	2	0.06	61.53846
Hupper	4/1/2000	*Biddulphia*	3	0.09	92.30769
Hupper	4/1/2000	large flagellates	7	0.22	215.3846
Hupper	4/1/2000	Tear-drop flagellates > 10 um	10	0.31	307.6923
Hupper	4/1/2000	*Thalassiosira*	16	0.49	492.3077
Hupper	4/1/2000	*Navicula*	23	0.71	707.6923
Hupper	4/1/2000	miscellaneous flagellates	26	0.80	800
Hupper	4/1/2000	Tear-drop flagellates < 10 um	31	0.95	953.8462
Hupper	4/16/2000	*Gyrosigma*	1	0.03	30.76923
Hupper	4/16/2000	*Ceramium fuscum*	1	0.03	30.76923
Hupper	4/16/2000	*Guinardia*	1	0.03	30.76923
Hupper	4/16/2000	*Cocconeis*	2	0.06	61.53846
Hupper	4/16/2000	*Navicula*	2	0.06	61.53846
Hupper	4/16/2000	*Peridinium*	2	0.06	61.53846
Hupper	4/16/2000	*Thalassiosira*	3	0.09	92.30769
Hupper	4/16/2000	miscellaneous flagellates	5	0.15	153.8462
Hupper	4/16/2000	Tear-drop flagellates > 10 um	5	0.15	153.8462
Hupper	4/16/2000	*Leptocylindrus*	7	0.22	215.3846
Hupper	4/16/2000	Other	21	0.65	646.1538
Hupper	4/16/2000	Tear-drop flagellates < 10 um	26	0.80	800
Hupper	4/29/2000	*Thalassionema*	2	0.06	61.53846
Hupper	4/29/2000	Tear-drop flagellates > 10 um	4	0.12	123.0769
Hupper	4/29/2000	*Nitschia*	4	0.12	123.0769
Hupper	4/29/2000	*Thalassiosira*	5	0.15	153.8462
Hupper	4/29/2000	*Biddulphia*	6	0.18	184.6154
Hupper	4/29/2000	*Navicula*	20	0.62	615.3846
Hupper	4/29/2000	Fragilaria	20	0.62	615.3846
Hupper	4/29/2000	miscellaneous flagellates	21	0.65	646.1538
Hupper	4/29/2000	Tear-drop flagellates < 10 um	33		
Hupper	5/12/2000	*Scrippsiella*	1	0.03	30.76923
Hupper	5/12/2000	*Pleurosigma*	1	0.03	30.76923
Hupper	5/12/2000	*Gymnodinium*	2	0.06	61.53846
Hupper	5/12/2000	*Ceratium*	2	0.06	61.53846
Hupper	5/12/2000	*Amphidinium*	2	0.06	61.53846
Hupper	5/12/2000	*Thalassionema*	3	0.09	92.30769
Hupper	5/12/2000	*Peridinium*	3	0.09	92.30769
Hupper	5/12/2000	*Nitschia*	4	0.12	123.0769
Hupper	5/12/2000	*Gyrodinium*	6	0.18	184.6154
Hupper	5/12/2000	*Chaetoceros*	15	0.46	461.5385
Hupper	5/12/2000	*Thalassiosira*	20	0.62	615.3846
Hupper	5/12/2000	miscellaneous dinoflagellates	20	0.62	615.3846
Hupper	5/12/2000	*Skeletonema*	27	0.83	830.7692
Hupper	5/12/2000	miscellaneous flagellates	39	1.20	1200
Hupper	5/12/2000	Tear-drop flagellates < 10 um	67	2.06	2061.538
Hupper	5/12/2000	*Phaeocystis*	209	6.43	6430.769

Site	Date	Genus or group	Count	Cells/mL	Cells/L
Hupper	5/28/2000	*Peridinium*	1	0.03	30.76923
Hupper	5/28/2000	*Guinardia*	1	0.03	30.76923
Hupper	5/28/2000	*Distephanus*	1	0.03	30.76923
Hupper	5/28/2000	*Gyrosigma*	2	0.06	61.53846
Hupper	5/28/2000	*Rhizoselenia*	3	0.09	92.30769
Hupper	5/28/2000	*Grammatophora*	4	0.12	123.0769
Hupper	5/28/2000	*Cocconeis*	4	0.12	123.0769
Hupper	5/28/2000	miscellaneous dinoflagellates	8	0.25	246.1538
Hupper	5/28/2000	*Licmorhora*	9	0.28	276.9231
Hupper	5/28/2000	*Nitschia*	11	0.34	338.4615
Hupper	5/28/2000	Tear-drop flagellates < 10 um	26	0.80	800
Hupper	5/28/2000	*Thalassionema*	33	1.02	1015.385
Hupper	5/28/2000	*Navicula*	34	1.05	1046.154
Hupper	5/28/2000	*Thalassiosira*	189	5.82	5815.385
Hupper	5/28/2000	*Chaetoceros*	294	9.05	9046.154
Hupper	5/28/2000	*Skeletonema*	617	18.98	18984.62

Appendix I

Literature Review

Reproductive Synchrony

A diverse array of reproductive modes is evident in the natural world, although the mechanisms underlying these strategies are poorly understood. These strategies can be viewed as a suite of physiological adaptations aimed at minimizing offspring mortality or maximizing reproductive output (Stearns 1976). Despite the extensive literature describing these reproductive modes, the proximate factors influencing reproductive synchrony within populations remain unresolved in numerous taxa. Although endogenous regulation is possible, it is unlikely that an entire population can remain reproductively synchronous without an exogenous entraining mechanism (Giese and Kananti 1987). Empirical studies and theoretical models show that reproductive synchrony within a population is imperative for successful reproduction (Pennington 1985; Yund 1990; Levitan et al. 1992; Serrão et al. 1996; Clifton 1997; McCurdy et al. 2000; Berndt et al. 2001). Furthermore, exogenous entraining mechanisms ensure that some degree of temporal and spatial reproductive synchrony exists within populations (Sweeney and Vannote 1982; Pearse and Cameron 1991; Bacon and Vadas 1991).

Reproductive synchrony is broadly defined as a population of organisms in the same locale reproducing at the same time. This definition includes both the spawning of populations of different species, as in temperate echinoderms or coral reef organisms (Babcock et al. 1986, 1994; Pearse et al. 1988; McEuen 1988; Clifton 1997), or populations of the same species (Korringa 1947; Sweeney and Vannote 1982; Zeeck et al. 1988; Clifton and Clifton 1999). Single species ("epidemic") and multispecific ("mass") spawning at a given locale have both generated much research on the factors controlling or influencing reproductive synchrony (Babcock et al. 1986; Starr et al. 1990; Serrão et

al. 1996; Young 1999). In organisms with external fertilization, which includes many marine invertebrates and algae, the importance of reproductive synchrony for successful fertilization has been underscored in a variety of taxa (Pennington 1985; Levitan 1990; Yund 1991; Serrão et al. 1996; Berndt et al. 2001). For free spawning marine invertebrates and algae, high fertilization rates and maximal larval survival occur if gametes are released simultaneously when conditions are favorable for early developmental stages (Pearse and Cameron 1991).

The timing of gamete release in free spawning marine invertebrates with planktotrophic larvae is a result of past selective pressures that may have operated on several life-history stages. Although not mutually exclusive, these ultimate factors have selected for reproductive strategies that enhance the success of the species and operate on both pre- and post-settlement processes. First, the timing of gamete release must be synchronized between individual's who are spatially proximate so that successful fertilization may occur (Pennington 1985; Levitan 1990; Serrão et al. 1996). Without mechanisms to ensure successful fertilization, selective pressures at later developmental stages are irrelevant. The next critical life-history stage at which selection is strong is the larval stage. As larvae, there are several separate, yet related, factors that exert strong selective pressures. Larval survival to settlement is considered a bottleneck for marine invertebrate populations with heteromorphic life cycles. Not only must larvae successfully avoid predation, acquire nutrients, and cope with environmental stress, but they must also locate suitable habitat to settle to when physically competent to metamorphose into a juvenile (Young and Chia 1987; Morgan 1995; Lamare and Barker

1999). These ultimate factors have likely operated at many temporal and spatial scales and have undoubtedly influenced the types of reproductive strategies we now observe.

Reproductive periodicity in marine invertebrates

Reproductive periodicity and synchrony in marine invertebrates has received a great deal of attention. In temperate regions, which experience predictable, yet variable, seasonality of environmental parameters, many marine invertebrate taxa have an annual breeding cycle with synchronous spawning (Pearse and Cameron 1991). In tropical and arctic climates or the deep-sea, where there is less variation in environmental parameters, annual breeding cycles are also found (Orton 1920; Thorson 1946; Chao et al. 1995; Young and Tyler, 1999; Van Dover 1999). Many have suggested that a number of environmental variables may influence or control reproductive periodicity, although endogenous regulation is possible. However, Giese and Pearse (1974) underscore that "it is unlikely that any population of individuals can maintain a synchronized seasonal rhythm completely independent of an exogenous regulator or cue". Nonetheless, some degree of reproductive synchrony, within a population and/or species with external fertilization, is necessary if gametes are to be successfully fertilized.

The factors influencing the timing of reproduction in marine invertebrates has received a great deal of attention. There is considerable interest and controversy over what induces spawning in several marine invertebrate taxa, although, the evidence supporting any one spawning stimuli is equivocal. Although the ultimate or selective factors controlling gamete or larvae release are often considered, only the proximate factors controlling reproduction have been examined experimentally.

Proximate Factors

When analyzing the factors influencing reproductive periodicity, it is first necessary to define the reproductive stages. Olive (1995) suggested the following general sequence for invertebrates: (i) Prepubescent development; (ii) Gonad activation and/or gametocyte proliferation; (iii) Gametocyte development; (iv) Period of readiness to spawn; (v) Spawning period; and (vi) Gonad resting period/period of energy accumulation. Byrne (1990) and King et al. (1994) delimit six maturity stages for sea urchins, including: (I) recovering; (II) growing; (III) premature; (IV) mature; (V) partly spawned; and (VI) spent. This classification scheme is identical to Olive (1995) and is based on changes in the relative abundance of different cell types present in gonads during the maturation process. Yakolev (1993) divides the reproductive cycle in sea urchins into two categories, gametogenic and agametogenic, to emphasize that a portion of the "reproductive cycle" does not involve the proliferation of gametes *per se*, but rather a period of nutritional gain. Walker and Lesser (1998) employ the approach of Fuji (1960a, b), who describes five stages for gametogenesis based on histological studies. For the purposes of examining factors regulating reproductive periodicity, Olive's (1995) scheme seems more appropriate. Olive separates the period just prior to spawning (stage iv) and spawning (stage v), which is conceptually meaningful when examining factors stimulating synchronous spawning. Fuji, however, does not distinguish between the period of readiness to spawn and spawning; he delimits only a "mature stage" followed by the "spent stage".

Research on environmental control of the timing of reproduction has focused on gametogenesis and spawning, although most attention has been devoted to gametogenesis

(Pearse and Cameron 1991). Proximate cues (mechanisms) regulating the period of gametocyte development have been intensively examined in a variety of taxa. Photoperiod and temperature usually have been cited as important environmental parameters (Pearse et al. 1986; McClintock and Watts 1990; Byrne 1990; Sewell and Bergquist 1990; Olive 1995; Walker and Lesser 1998). Stimuli for spawning have received relatively less attention, and most evidence for different spawning cues is correlative rather than experimental (McEuen 1988; Sewell and Bergquist 1990; Byrne 1990; Babcock et al. 1994; Chao et al. 1995).

Many environmental variables have been suggested as cues to spawning in marine invertebrates: Photoperiod (Pearse 1981; Pearse et al. 1986; but see Cochran and Engelmann 1975), light intensity (McEuen 1988), lunar periodicity (Korringa 1946; Babcock et al. 1994; Kenyon 1995; Horii 1997), temperature (Byrne 1990; Sewell and Bergquist 1990; King et al. 1994), water motion (Caron et al. 1999), air pressure (Watson et al. 2000), sex pheromones (McEuen 1988; Zeeck et al. 1996; Hardege et al. 1998), and phytoplankton blooms (Young 1945; Barnes 1959; Jordan 1972; Himmelman 1975, 1978; Smith and Strehlow 1983; McEuen 1988; Starr et al. 1990, 1991, 1993, 1994; Chao et al. 1995; Stanwell-Smith and Clarke 1998). Although most of these studies have relied on environmental correlates to identify spawning cue(s), several have used an experimental approach. Sex pheromones as a spawning cue in several marine polychaetes have been rigorously tested in both the field in laboratory, and the mechanisms by which these cues induce spawning have been well described (Hardege et al. 1998; Zeek et al. 1996, 1998). Phytoplankton abundance as a spawning cue in several species of mollusks and echinoderms (e.g., *Ciona intestialis, Mytilus edulis M.*

californianus, Ostrea gigas, Strongylocentrotus droebachiensis), have also been rigorously tested (Myazaki 1938; Smith and Strehlow 1983; Starr et al. 1990).

Biology and Ecology of *Strongylocentrotus droebachiensis*

The green sea urchin, *Strongylocentrotus droebachiensis* O. F. Müller, is an echinoderm (Echinodermata: Echinoidea) with a circumpolar distribution (Stephens 1972). It is the dominant shallow-subtidal grazer on rocky shores (see Elner and Vadas 1990 for critique of studies in the northwest Atlantic). *S. droebachiensis* is a generalist; it is primarily an herbivore, consuming mainly macroalgae (Vadas 1977; Larson et al. 1980; Briscoe and Sebens 1988). Field studies in the northwest Atlantic and northeast Pacific have shown that *S. droebachiensis* grazing has a significant effect on benthic algal-community structure (Paine & Vadas 1969; Breen and Mann 1976; Miller 1985; Scheibling 1986). Both experimental removals of *S. droebachiensis* (Vadas 1968; Paine and Vadas 1969; Breen and Mann 1976) and natural reductions in sea urchin numbers (Breen et al. 1982; Scheibling 1986) result in the colonization of macroalgae in formerly algae-depauperate areas. Similarly, shifts from kelp-dominated communities to those dominated by crustose, coralline algae ("barrens") due to green sea urchin grazing has been well documented (Breen and Mann 1976; Miller 1985; Scheibling 1986).

Reproductive cycle

Green sea urchins have an annual reproductive cycle and spawn during the early spring in northern temperate regions (Cocanour and Allen 1967; Stephens 1972; Himmelman 1978; Falk-Petersen and Lønning 1983; Munk 1992; Meidel and Scheibling 1998). A number of researchers have also detected late summer-early autumn spawning

in the northwest Atlantic (Keats et al. 1984a; Meidel and Scheibling 1998; Vadas *pers. comm).* However, it is generally thought that there is little recruitment from autumn spawning (Meidel and Scheibling 1998). As broadcast spawners, *S. droebachiensis* release their gametes into the water column, where fertilization and embryonic development occur. Pennington (1985) showed that sea urchin sperm is viable for less than 20 minutes and that successful fertilization requires high sperm densities ($> 10^6$ sperm l^{-1}). Reproductive synchrony and high population densities in shallow water marine invertebrates may mitigate the difficulties of external fertilization. Sea urchin larvae begin feeding one or two weeks after fertilization and may remain pelagic for more than 50 days before metamorphosing and settling to the benthos (Thorson 1946; Stephens 1972; Strathman 1978).

Most determinations of seasonal reproductive cycles of urchins have employed gonad indices to assess relative gonad mass throughout the year. Gonad index is the ratio of gonad weight to total body weight and is widely used to describe sea urchin reproductive cycles. The use of gonad indices acts to minimize variation of gonad weight due to the size of the animal (Gonor 1972). In *S. droebachiensis*, gonad indices are lowest in the summer (<10%), increase during the autumn and early winter, and are at a maximum immediately prior to spawning, attaining values up to 37% (Scheibling and Meidel 1998; Vadas *et al.* 1989). Although gonad indices alone may not provide precise information regarding reproductive chronology, several recent studies have coupled gonad indices with histological analysis (Meidel and Scheibling 1998; Walker and Lesser 1998). These histological studies have shown that changes in the relative abundance of gametes and other cell types are generally concordant with changes in gonad indices.

The green sea urchin exhibits distinct temporal patterns in the relative abundance of gametes and nutritive phagocytes in the gonads (Walker and Lesser 1998; Meidel and Scheibling 1998). Meidel and Scheibling (1998) showed that after spawning in spring, female urchins in Nova Scotia remain in the recovering stage (stage i) for 2-4 months before beginning the growing stage (stage ii) during the summer. By late summer and early fall, females enter the premature stage (stage iii) where they remain until late winter or early spring. Female gonads then become mature (stage iv), and proceed rapidly through the partly spawning (stage v) and spent stages (stage vi). A new gametogenic cycle commences several weeks after spawning is complete. Male sea urchins show a similar pattern of maturation, although the periodicity is less distinct than females. Several weeks after spawning is completed, males enter the recovering (stage i) and growing stages (stage ii). Unlike female urchins, however, 30% of the males remained in the spent stage (stage vi) through the late summer. During the fall, most males enter the premature stage (stage iii) where they remain until late winter or early spring, although 25% of the males at one study site were still in the growing stage (stage ii) in February. In the late winter and early spring, most male gonads become mature (stage iv), and proceed rapidly through the partly spawning (stage v) and spent stages (stage vi). A new gametogenic cycle commences several weeks after spawning. Despite the sexual differences in gonad condition over the annual cycle, both male and female sea urchins exhibited the greatest variation in reproductive stage during the spawning period (Meidel and Scheibling 1998).

The periodicity of gametogenesis and spawning may be governed by exogenous cues, but the exact proximate cues influencing both gametogenesis and spawning in *S.*

droebachiensis have been only partially elucidated (Himmelman 1975; Starr *et al.* 1990, 1991, 1993, 1994; Walker and Lesser 1998). Although much is known about gonad indices and the reproductive cycle of *S. droebachiensis,* there is a paucity of experimental evidence on the factors influencing and/or controlling gametogenesis and spawning (Himmelmann 1975; Scheibling and Meidel 1998; Walker and Lesser 1998). Due to the economic importance of the roe or gonads in *S. droebachiensis* and the implications for aquaculture, several studies have investigated the physiological and environmental variables influencing gametogenesis (Thompson 1983; Minor and Scheibling 1997; Walker and Lesser 1998; Garrido and Barber 1998). Studies examining proximate factors influencing spawning have been limited to a few investigators (Himmelman 1975; Starr et al. 1990, 1992; 1993), whose focus has been exclusively phytoplankton blooming as the spawning cue. These studies have coupled experimental laboratory studies with correlative field studies to determine if phytoplankton can induce spawning.

Spawning

Several studies in northern latitudes have shown that that there is a good correlation of sea urchin spawning with the spring phytoplankton bloom (Himmelman 1975, 1978; Starr et al. 1990, 1992). The strategy to spawn coincident with the phytoplankton bloom is advantageous in that planktotrophic sea urchin larvae will be in the water column when their primary food is present (Strathman 1978; Starr et al. 1990). Thorson (1946) showed that several species of larval echinoderms feed on nano- and ultraplankton, including species of *Thalassiothirix*, *Nitzschia, Chaetoceras,* and small flagellates (range diameter 5 - 25 μm). This concept of benthic-pelagic coupling has been an important idea in fishery science, where the timing of the spring bloom may lead

to interannual variability in the recruitment of fish (the "match-mismatch theory") (Townsend and Cammen 1988; Sinclair 1988). Most studies on the coupling of the spring bloom and sea urchin spawning, however, have provided only correlative data. These studies have shown that *S. droebachiensis* from different geographical and hydrographic regions spawn over a range of water temperatures and phytoplankton bloom periods (Table H1). With the exception of Starr et al. 1990, there is little or no experimental data.

The evidence is ambiguous that phytoplankton can be a proximate cue for spawning in *S. droebachiensis*,. First, the authors (i.e., Starr et al. 1990) demonstrate that when exposed to four species of cultured phytoplankton (at two concentrations) or culture filtrates, only 31.3% - 52.5% of the individuals spawn. The spawning response of field-collected sea urchins (collected in January) was dependent on the concentration of chlorophyll *a*, where the maximum response was achieved at very high (i.e., 24 μg/L) phytoplankton abundance. The phytoplankton concentrations that Starr et al. (1990) used, however, are not usually attained during the sea urchin spawning period in Maine (Vadas et al. *unpublished*). Vadas et al. (*unpublished*) show that sea urchins in central Maine spawn when phytoplankton concentrations approach about 1 – 2 μg/L. Furthermore, Starr et al. (1990) show that sperm from conspecifics (suspended in seawater) stimulated spawning in 39.2% of the individuals tested. Generally, Starr et al. (1990) suggest that phytoplankton stimulates the most receptive males to release gametes, and that sperm acts synergistically with phytoplankton to elicit a spawning response from other sea urchins. The authors do not, however, speculate on what the spawning cue may be for the other 47.5% - 68.7 that did not spawn. It is possible that the urchins that did

Table H1. Relationship between spawning time of *Strongylocentrotus droebachiensis* and (1) the temperature range during spawning and (2) the timing of the spring phytoplankton bloom in different geographical regions (modified from Starr et al. 1993)

Locality	Spawning time	Temperature	Spring Phytoplankton Bloom
Northeast United States			
Cape Cod, MA	Late April (Stephens 1972)		Begins late March through late April (Bigelow et al. 1940)
Woods Hole, MA	March (Boolootian 1966)	1-2°C (Taylor et al. 1957)	Mid-winter (Fish 1925)
Boothbay Harbor, ME	Early April (Stephens 1972)	8°C (Taylor et al. 1957)	Begins mid- to late March (Bigelow et al. 1940)
Salisbury Cove, ME	April to mid-May (Harvey 1956)		Starts in April or May (Bigelow et al. 1940)
Lamoine, ME	April (Cocanour & Allen 1967)		Starts in April or May (Bigelow et al. 1940)
Georges Islands, ME	Mid-late April (present study)	4-8°C (present study)	Starts mid-April or May (present study)
Jonesport, ME	Mid-late April (present study)	4-6°C (present study)	Starts late April or May (present study)
Northeast Canada			
St. Margaret's Bay, Nova Scotia	March – April (Miller & Mann 1973; (Meidel & Scheibling 1998)	2-4°C (Miller & Mann 1973)	April (Platt & Irwin 1970)
Mahone Bay, Nova Scotia	March – April (Meidel & Scheibling 1998)		
Portugal Cove, Newfoundland	March – April (Himmelman 1978)	< 3°C (Himmelman 1969)	April (Himmelman 1978)
Pointe-au-Pere, Quebec	June (Starr et al. 1993)	4-10°C (Starr et al. 1993)	Begins in June, maximum in July (Starr et al. 1993)
Norway			
Bergen	Late March (Runnstom 1927a, 1927b)	4-5°C (Brown 1984)	Begins mid-March, maximum March-April (Gran 1928)
Trömso	February to March (Vasseur 1952)	2°C (Brown 1984)	Begins mid-March, maximum March-April (Gran 1928)
Tromsösundet	March (Falk-Petersen & Lonning 1983)		Begins mid-March, maximum March-April (Gran 1928)
British Columbia			
First Narrows	April (Himmelman 1976)	6-8°C (Himmelman 1976)	April (Himmelman 1976)
Botanical Beach	April (Himmelman 1976)	8-9°C (Himmelman 1976)	Mid-April (Himmelman 1976)
White Sea	Mid-June to mid-july (Kaufmann 1974)	3-5°C (Kaufmann 1974)	
Barents Sea	February to April (Oganesyan 1998)	0-2°C (Oganesyan 1998)	Begins March, Maximum in April (Propp 1971; Kuznetsov 1991)

not spawn had already spawned prior to collection. Additionally, Starr et al. (1990) did not consider alternative hypotheses, such as photoperiod, water temperature, pH, or a combination of environmental variables. Other evidence that casts doubt on the possibility that phytoplankton or phytoplankton extracts stimulate spawning in the green sea urchin comes from Starr et al. (1993). The author's showed how compounds found within the brown macroalga, *Fucus vesiculosus,* stimulated spawning in laboratory studies, which suggest that phyco-compounds in general may act synergistically to stimulate gamete release. The value of phytoplankton as a spawning stimulus under natural conditions and the sensitivity of individuals to low concentrations of the proposed stimuli remains unknown. One possible alternative hypothesis, that spring photoperiod can induce spawning, seems unlikely given the interannual and spatial variability of the timing of spawning along the coast of Maine. Water temperature, however, may be one viable alternative hypothesis (Vadas et al. *unpublished).*

Several studies have shown that there is a positive relationship between the quantity and quality of available food and growth and reproduction (Vadas 1977; Larson et al. 1980; Thompson 1982; Keats et al. 1984b; Meidel and Scheibling 1998). Differences in food availability may affect gametogenesis, and consequently be responsible for the observed interannual and spatial variability in the timing of spawning (Himmelman 1978; Falk–Peterson and Lönning 1983; Minor and Scheibling 1997). Differences in gametogenic phase (see Walker and Lesser 1998) may influence spawning time, which suggests that there may be several spawning stimuli, or alternatively, that those animals not "ready to spawn" when the spring bloom commences do not contribute to that years synchronous gamete pool. An experimental analysis of environmental

control of spawning in *S. droebachiensis* considering multiple factors is necessary to determine precisely the proximate spawning cue.

Spring Phytoplankton Blooms in the Gulf of Maine

The onset of the spring phytoplankton bloom in both coastal and oceanic waters of the Gulf of Maine involves the interaction of several physical and biological factors and may vary between years. Water column stability and nutrient and light availability have been shown to influence the timing of the onset of the bloom (Riley 1957; Hitchcock and Smayda 1977; Boynton et al. 1982; Townsend et al. 1994), while phytoplankton losses due to grazing, self-shading, and nutrient exhaustion may result in the curtailment of the bloom (Martin 1970; Deason 1980; Sieracki et al. 1993; Kelley et al. 2000; Townsend and Thomas 2001). Temporal and spatial variability in the timing of the spring phytoplankton bloom in the Gulf of Maine has long been recognized, with the bloom beginning earlier in the southern part of the Gulf and progressing northward (Bigelow et al. 1940). Additionally, it is possible that the spring phytoplankton bloom may not occur, and is directly related to grazer abundance and indirectly related to water temperature during the vernal period (Keller et al. 2000).

In shallow, near-shore waters in the Gulf of Maine, where the critical depth extends to the bottom, the spring phytoplankton bloom is triggered when the depth-averaged, vertically-integrated irradiance within the upper mixed layer reaches approximately 40 Ly day^{-1} (Riley 1957; Hitchcock and Smayda 1977; Townsend and Spinrad 1986). Inter-annual variability in the timing of the bloom is primarily influenced by cloud-cover, which determines the amount of solar radiation reaching the sea, and thus

the critical depth. Similarly, the spatial and temporal pattern of phytoplankton blooms in the Gulf of Maine is partly a function of this inter-annual variation in incident solar radiation reaching the ocean surface. An important aspect of the temporal variability in the timing of spring phytoplankton blooms in temperate oceans is that it is possible that a bloom does not always occur (Keller et al. 2000). Keller et al. (2000) reported the absence of the spring phytoplankton bloom in Massachusetts Bay and attributed this to warmer than average sea temperatures that resulted in abundant zooplankton populations that actively grazed, and thus, thwarted the development of a high phytoplankton standing crop.

Phytoplankton species composition and abundance have been described and quantified for a number of coastal sites in Maine (Bigelow 1926; Petrie 1975; Wong and Townsend 1999). The spring phytoplankton bloom in the North Atlantic consists primarily of diatoms, which rapidly deplete silicate and nitrogen (Sieracki et al. 1993). Following this depletion, there is a shift in phytoplankton communities from diatoms to small flagellates. Common spring phytoplankters in coastal Maine include the neritic diatoms, *Chaetoceros* sp., *Thalassiosira nordenskioldii,* and the chrysophyte, *Phaeocystis* sp. (Petrie 1975).

The small-scale spatial distribution of phytoplankton has received little attention, although it has long been recognized that phytoplankton tend to be over-dispersed (MacAlice 1979; Parson and Takahashi 1984). This nonrandom distribution may limit the utility of a single water sample in oceanographic studies. That is, the characterization of a single station based on single sample may not provide an accurate description of the composition or abundance of phytoplankton.

BIOGRAPHY OF THE AUTHOR

Lindsay Seward was born in beautiful New Haven, Connecticut on the 29th day of April in 1976. Fortunately, she was moved away from the Nutmeg State and settled down in another New England town, Hopkinton, Massachusetts, now known for its rapid rate of suburban development. Lindsay graduated from Hopkinton High School, right on time, in 1994. Lindsay went on to attend the University of Rhode Island and graduated *summa cum laude* with a Bachelor's of Science degree in Wildlife Biology, right on time in 1998. While attending the University of Rhode Island, Lindsay went on a year-long sabbatical and attended the University of Maine, where she discovered her strange fondness for algae. Upon graduating from URI, Lindsay explored her interests in forested wetlands and songbirds while living in a bungalow by the sea. In keeping with her tradition of attending public schools, Lindsay enrolled at the University of Maine to pursue a Master's degree in Zoology (although really, it's more like marine biology). While at the University of Maine, Lindsay was a research and teaching assistant (*Field Natural History of Maine, Vascular Plant Taxonomy, and Field Marine Ecology)*, co-authored a paper on endangered species published in Ecological Applications and gave several presentations at professional meetings. When a special friend pointed out that she could not "make a career out of TAing," Lindsay wrapped-up her degree toot sweet and acquired an Instructor position in the Department of Wildlife Ecology at the University of Maine. Despite not finishing "on time", Lindsay had splentabulous experiences during her graduate student days. In her spare time, she enjoys puzzles, lying about on the floor, and cataloguing her collection of Ziggy comics. Lindsay is a candidate for the Master of Science degree in Zoology from The University of Maine in May, 2002.