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SPATIAL AND TEMPORAL VARIABILITY OF SPAWNING IN THE GREEN SEA URCHIN *STRONGYLOCENTROTUS DROEBACHIENSIS* ALONG THE COAST OF MAINE

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ABSTRACT The timing and spatial variation in spawning in the green sea urchin *Strongylocentrotus droebachiensis* (Müller) was investigated at three moderately protected sites in each of three geographic regions along the coast of Maine before the commencement of significant commercial harvesting. Urchins were sampled monthly (1987 to 1988) from subtidal hard bottoms, and test diameter (TD), height, total wet weight, and gonad wet weight were measured. To interpret reproductive and spawning patterns additional data were taken on habitat type, water temperature, salinity, urchin density, and diets. Over a range of TD (34.1–89.4 mm), 1,594 urchins were sampled. Gonad index (GI) increased as an allometric function of TD, and for urchins from the northeast and southwest regions, GI was independent of TD for animals ≥64 mm. In the central region, the size at independence was ≥55 mm. Analysis of variance with *a priori*, planned contrasts was used to quantify temporal changes in GI and spawning at two spatial scales (within and between regions). This information serves as a preharvest baseline for green urchin dynamics, analysis of reproductive cycles and spawning, and for current and future ocean changes. Gonad index and spawning varied seasonally, spatially and interannually. Gonad index increased during fall and early winter, and peaked in midwinter before a major spawning event in April at seven of nine sites. Gonad index ranged from 10% to 20% from December to April. Spawning [measured as a steep decline in GI (48%–78%) between successive sampling dates) occurred between early April and mid-May, except at one site in the central (Lamoine: March to April) and one in the northeast (Jonesport: May to June) regions. Gonad index patterns during spawning corresponded inversely to increasing seawater temperatures in the range of 2.5–5°C. Salinity, urchin density, and test size did not explain a significant proportion of the variability in mean GI through time. Diets consisted primarily of diatoms and microalgae on ledge, sediment, and coralline barrens and showed no regional trends. Sex ratio explained a significant portion of the variability in mean GI at only one site. Seawater temperature, however, explained 55%–77% of the variability in mean GI through time. Predicting when spawning occurs in natural populations is central to the sea urchin fishery by refining estimates of what are termed harvest windows (HW). The HW represents a segment of time during the general spawning season when GI are at, or above, a specified percent, for example, 10%. A review of the literature uncovered 19 different techniques to determine GI and assess spawning. Of 167 papers published between 1922 and 2013 in which methods of spawning in wild populations of sea urchins were described, 84 and 134 used histology and GI, respectively. This study contributes to the questions of dependence of GI on test size, first illuminated by Gonor (1972), and the general practice of interpreting minor declines in GI as fractional spawning events, rather than simply sampling noise. The use of statistical tests is encouraged to define aspects of the reproductive cycle in sea urchins.

KEY WORDS: green sea urchin, *Strongylocentrotus droebachiensis*, Maine, gonad index, spawning, spatial and temporal variability, gonad–test diameter relationship, fractional spawning, harvest window

INTRODUCTION

Variation is a fundamental tenant of life in all its forms and expressions. Recognizing variability in individuals, populations, and communities allows ecologists to test hypotheses about processes affecting distribution, growth, and abundance patterns (Underwood et al. 2000). Growth, behavior, reproduction, recruitment, and other life history traits of marine populations are commonly varied over several spatial and temporal scales (Underwood & Keough 2001, Navarette et al. 2005, Lester et al. 2007). In some corals, for example, fecundity varies spatially between reefs because of differences in depth, turbidity, and sedimentation rates (Kojis & Quinn 1984). Temporal variability in algal–herbivore interactions occurs with *Sargassum* on reef flats in Australia (Leferve & Bellwood 2011). Similarly, year-class phenomenon related to poor reproductive success can affect recruitment strength in rockfishes (*Sebastes* spp.) (MacFarlane & Norton 1999).

Also, variability may result from the interaction of genetic and environmental processes (Trussell & Etter 2001). For example, early embryos of sea urchins (*Centrostephanus rodgersii*) experimentally stressed at gastrulation showed heritable variation in thermal tolerance suggesting the potential to adapt to ocean warming and acidification (Foo et al. 2012). Additionally, intraspecific variation in developmental mode (poecilogony) may be an adaptive response to unpredictable environmental conditions (Krug 2009) and variation in predatory behavior, reproductive strategy, and rates of early development is phenotypically plastic and has a genetic underpinning (Sanford & Worth 2009, Jackson et al. 2012). For example, the dispersal strategy of an estuarine polychaete (via planktotrophy or lecithotrophy) maintained population growth rates in less predictable or fluctuating environments (Levin et al. 1987). Conversely, synchronizing processes that increase opportunities for spawning and recruitment may mask and/or decrease variability (Lessios 1991).

Understanding the dynamics of commercial marine fisheries relies on quantitative observations that include the variability in spatial and temporal life history patterns. Stocks of ovigerous

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lobsters (*Homarus americanus*) displayed consistent spatial variation in density over several years at seven sites along a 190-km region of the Nova Scotia coast (Miller 1997). The collapse of northern cod (*Gadus morhua*) stocks of Newfoundland and Labrador was associated with spatial and temporal changes in density and biomass as well as high fishing mortality with declining stock biomass (Hutchings 1996). Also, variation in sea urchin life history traits can occur over short geographic distances (Byrne 1990). In Maine, for example, variation in longevity and test growth occurs in sympatric populations of green sea urchins *Strongylocentrotus droebachiensis* (Vadas et al. 2002) and differential growth and survival occurs across tidal gradients in populations of softshell clams *Mya arenaria* (Beal et al. 2001).

Variation in reproduction and spawning patterns in commercially harvested, temperate–boreal sea urchins also occurs both spatially and temporally (Byrne 1990, Byrne et al. 1998, Meidel & Scheibling 1998). Most cold water urchins undergo an annual reproductive cycle, but different populations of the same species may spawn asynchronously (Fuji 1960a, Himmelman 1978). Similarly, some tropical, subtropical, and deep-sea urchins show temporal and spatial fluctuations in their reproductive cycles (e.g., Moore & Lopez 1972, Tyler & Gage 1984, Muthiga & Jaccarini 2005).

Numerous mechanisms have been proposed to trigger reproduction (i.e., gametogenesis) and spawning in field populations of boreal urchins. Various environmental cues, such as temperature (Lamare & Stewart 1998, Agatsuma 2001a, 2001b), photoperiod (Walker & Lesser 1998, Dumont et al. 2006), lunar conditions (Lamare 1998, Byrne et al. 1998), and salinity (Starr et al. 1993, Vaschenko et al. 2001) have been implicated in stimulating spawning. Endogenous cues such as the release of pheromones have also been shown to cause spawning in green urchins (Pennington 1985). Also, biotic factors may play a direct or indirect role in spawning. For example, trophic subsidies, in the form of drift kelp, influence gonadal development and spawning in intertidal urchins (*Tetrapygus niger*) along the central coast of Chile (Rodríguez 2003), and subtidal urchins of the coast of Nova Scotia (Kelly et al. 2012). Lang and Mann (1976) demonstrated a significant density-dependent effect on gonad size in *Strongylocentrotus droebachiensis* in kelp beds versus coralline barrens. Increasing intraspecific densities and aggregative behaviors may result in mass spawning responses (Lamare & Stewart 1998, Gaudette et al. 2006) and Starr et al. (1990, 1992) demonstrated that elevated concentrations of phytoplankton (chlorophyll *a*) induced spawning in green sea urchins in the laboratory.

This study was conducted over a 270-km stretch (66%) of the Maine coast at three subtidal locations within each of three coastal regions (southwest, central, and northeast) in Maine, United States, between September 1987 and September 1988, before the development of a commercial fishery in Maine (Vadas et al. 2000, Fig. 1; Chen et al. 2003, Berkes et al. 2006) and recent concerns about effects of ocean and coastal acidification on reproductive success in sea urchins (Stumpp et al. 2012, Kurihara et al. 2013). The green sea urchin occurs along the entire Maine coast which covers several degrees of latitude and longitude. It is likely that over this distance, gradients in biotic and abiotic properties could contribute to substantial variation in growth and reproduction (see Morgan et al. 2000, Blicher et al. 2007).

These data and analyses provide a baseline for resource managers to evaluate and predict differences in reproduction brought about by harvesting strategies and possibly climate change. Also, they contribute to quantitative evaluations of size, spawning, and gonad index (GI) in sea urchin populations (Cocanour & Allen 1967, Vadas & Beal 1999). Reproductive patterns are linked to diet, life history, and environmental factors, and the results are discussed with respect to sea urchin management in Maine. In addition, a review of how spawning has been assessed historically in *Strongylocentrotus droebachiensis* and other regular echinoids provides an in-depth evaluation of the relationship between GI and TD. In this process it was discovered that 19 different measures of GI have been used (1922–2013) to assess spawning.

Recently, there has been a renewed interest in what induces spawning and the means of assessing it (Ebert et al. 2011, Ouréns et al. 2012). Here, data are provided to assess spawning in *Strongylocentrotus droebachiensis*. Assumptions play a large part of deriving the formulae and logic in relying on the particular methodology used. This effort contributes to that dialog and to a new concept of "harvest windows" (HW).

STUDY SITES AND METHODS

General

In conjunction with the Maine Department of Marine Resources (DMR), nine sites were selected in a nonrandom fashion [i.e., based on ease of access for divers and from previous investigations (R. L. Vadas, unpublished data)] to reflect possible variation in reproduction and spawning in green sea urchins along the coast of Maine (Fig. 1, Table 1) (Vadas et al. 1997). Three general regions were specifically selected that ranged in linear distance from ~40 to 100 km, increasing in distance from the southwest to the central and northeast. Three moderately protected locations within each region were chosen based on urchin presence and diving accessibility from shore. Distance between research sites varied from a low of 7.7 km in the southwest to nearly 60 km in the northeast (Table 1). We consider these sites and regions as fixed factors in all statistical tests (see below). Urchins were sampled monthly from September 1987 to September 1988 by SCUBA from depths ranging from 2 to 8 m. To provide independence among urchins, 12–20 individuals [~40 mm (diameter) or larger] were sampled haphazardly each month along a belt transect. Animals were placed in coolers with seaweed and blue ice packs, returned to the laboratory, stored overnight at 4°C and dissected the following day. Sea urchin density and size were estimated at all locations, except Owl's Head, in May to June 1988 using 8–19 haphazardly placed quadrats (50 cm × 50 cm; Table 1). Temperature was measured monthly 15–30 cm beneath the surface using a calibrated stem thermometer. Salinity samples were taken at the same depth and analyzed using a hydrometer kit (G. M. Manufacturing Co.) and interpolated to the nearest part per thousand.

Site Descriptions and Habitat Quality

The three southwestern sites (Bailey Island, Five Islands, Boothbay Harbor) had similar, depauperate, floristic patterns. The understories contained relatively few macroalgae, were dominated by ledge with a high coverage of crustose coralline

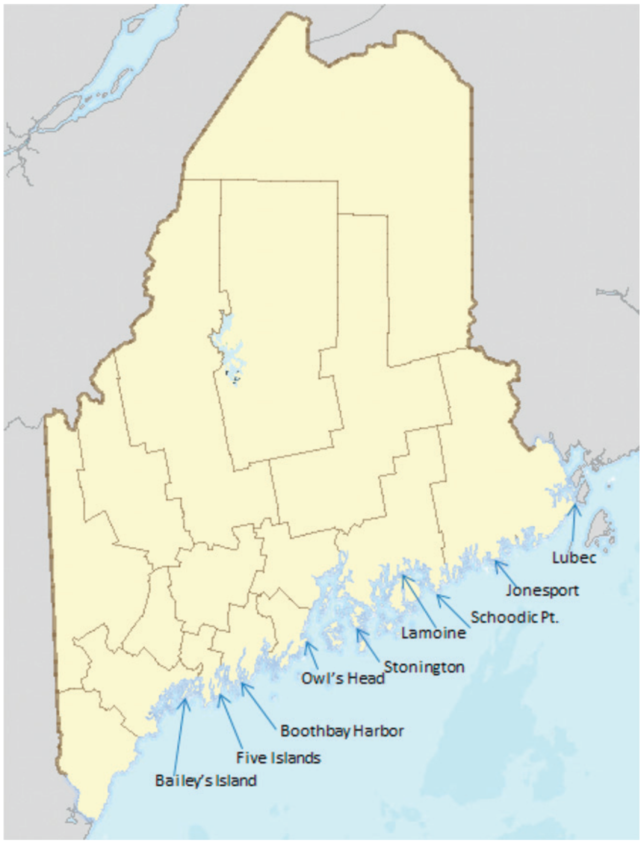

Figure 1. Nine study sites along the Maine coast where sea urchins were sampled approximately monthly from September 1987 to 1988.

algae and bare rock, and were considered "barren grounds" (sensu Lawrence 1975). At Bailey Island, however, a few small scattered kelp plants formed a patchy structure. Two of the central coastal sites (Stonington and Lamoine) were categorized as barren grounds. These two sites contained no edible fleshy algae. Nonedible *Desmarestia* sp. and *Agarum clathratum* were present at both sites. Our characterization of the benthos at Owl's Head (Table 1) is based on monthly observations by divers. Moderately high urchin densities and high littorinid densities (200–300 per m^2, Vadas 1992) contributed to the impoverished macroalgal flora at Lamoine. Northeastern sites contained higher abundances of macroalgae, including edible kelp. In particular, the shallow sublittoral fringe at Schoodic Point had the highest proportion of kelp of the nine sites and had a moderate canopy of *Saccharina latissima* (formerly known as *Laminaria saccharina*) and *Alaria esculenta*. The deeper depths, however, were typical of barren areas and contained *A. clathratum* and coralline algal crusts. The sites at Jonesport and Lubec had a moderate fleshy algal cover, and in the understory, contained exposed ledge and coralline crusts. Several sites contained sparse, patchy kelp in the deeper depths, but most of this was *A. clathratum*, a nonpreferred kelp which often persists in the presence of urchins (Vadas 1977, Himmelman et al. 1983). Herbivorous gastropods, mainly *Littorina littorea*, were present at most sites, but during late spring were concentrated in the low intertidal and sublittoral fringe. Green urchins were the major macrograzers at most sites.

Gonad Index and Sex Ratio

Quantitative GI values were determined monthly from each site. Test diameter (range = 34.1–89.4 mm) using Vernier calipers were measured to the nearest 0.1 mm. This size range was based on Gonor's (1972) recognition with *Strongylocentrotus purpuratus* that GI may not be independent of body size below a 40 mm TD. Wet test weight was recorded to the nearest 0.1 g. The peristomial membrane and body cavity were then pierced, the coelomic fluid was drained, and the animals were weighed a second time. Sex was determined by observing sperm or eggs (when present) or making smears on microscope slides. Gonads were placed on paper towels, allowed to dry for 1–2 min, and then weighed to the nearest 0.1 g. Gonad index is a ratio expressed as gonad weight (or volume) divided by live test weight (or volume) × 100. The validity of using gonad weight as an alternative to gonad volume (GV) was tested over all populations for the initial two (September and October 1987) sampling intervals. Gonad volume (read as displaced seawater in a graduated cylinder) served as the dependent variable and was regressed against gonad weight [$\mathrm{GV} = 0.127 + (0.9323) \times$ (gonad weight), $r^2 = 0.994$, $n = 353$]. In addition, analyses were conducted to test whether differences in the relationship between gonad weight and total (wet) weight occurred within and between regions.

Diet

To determine if GI was related to diet, quantitative estimates were made of prey items in the guts of urchins. The gut of five urchins (chosen randomly) was dissected and examined seasonally (late fall, late winter, spring, and summer = 34 sampling dates) from each site and placed in seawater with 10% buffered formalin to estimate temporal variation in diet. Two subsamples of fecal pellets were collected from each urchin and placed in separate beakers of seawater and stirred with a pipette to separate prey items. A 0.5-ml sample was pipetted onto a glass slide with cover slip. The area under each cover slip was examined and all algae and invertebrates were recorded and scored to obtain a relative estimate of frequency of occurrence. The relative importance of algal functional groups in the diet (Littler & Littler 1980, Steneck & Dethier 1994) was estimated from these counts. Data are expressed as relative abundance of each prey organism and as mean relative abundance of various algal functional groups (6 = abundant, 5 = common, 4 = present, 3 = infrequent, 2 = rare, 1 = absent). Thus, each site and date is represented by 10 counts from five urchins. Overall, a total of 180 urchins and 360 gut samples were examined.

Statistical Analyses

Comparison of GI, both temporally and spatially, assumes that GI is independent of urchin body size (diameter) (Gonor 1972, Ebert et al. 2011, Ouréns et al. 2012). Because it was unfeasible to sort underwater all urchins at or above 40 mm TD on each sampling date, this assumption was tested using regression analysis with GI (dependent variable) and TD (independent variable). Generally, internal volumes and heights increase linearly with body size (Gonor 1972); therefore, analysis was begun by examining a linear model between these two variables. A sequential lack-of-fit analysis (Steele & Torrie 1980) was performed beginning with animals >45 mm TD. The lack-of-fit

TABLE 1.

Description of nine study sites, covering a distance of 270 km, and mean density in 0.25 m^2 quadrats (mean number of individuals per 1 m^2 ± 95% CI in May to June 1988) of *Strongylocentrotus droebachiensis* in three coastal regions of Maine.

Region	Site*	Latitude	Longitude	Inhabits	Depth range (M)	N	Mean	95% CI
SW	BYI	43°43′06′′	70°00′16′′	BK†	2–3	12	68.8	42.9
	FVI	43°49′43′′	69°42′57′′	B‡	2–3	12	39.5	17.2
	BBH	43°48′91′′	69°35′72′′	B	2–3	12	43.8	23.7
CN	OWH	44°05′55′′	69°03′49′′	B	2–3	ND§	–	–
	STN	44°09′15′′	68°41′45′′	B	2–3	10	5.0	7.5
		–	–	–	4–7	10	5.0	7.5
	LMB	44°27′21′′	68°16′81′′	B	2–3	10	30.0	12.0
NE	SPT	44°20′27′′	68°02′72′′	BK¶	2–3	8	0.0	0.0
		–	–	–	4–5	8	28.0	8.0
		–	–	–	6–8	8	13.0	10.9
	JPT	44°32′36 ′′	67°33′69′′	BK¶	1–3	19	1.3	2.8
	LBC	44°48′45′′	66°58′62′′	BK¶	2–5	12	20.8	18.9

SW, southwest; CN, central; NE, northeast; BYI, Bailey Island; FVI, Five Islands; BBH, Boothbay Harbor; OWH, Owl's Head; STN, Stonington; LMB, Lamoine; SPT, Schoodic Point; JPT, Jonesport; LBC, Lubec.

* Sites ordered from southwest to northeast.

† Barrens with scattered, refugial kelp.

‡ Barrens.

§ No quantitative data; seasonally there was a bloom of green algae, but the yearly pattern was a barren.

¶ Kelp shallow; barrens deeper.

analysis used quadratic and cubic response variables. In addition, an allometric model was fit to the data.

To determine if GI varied temporally and spatially, a model I, two-factor analysis of variance (ANOVA) was performed using site and sampling date as fixed factors. The data were skewed and/or variances were heterogeneous before conducting an arcsine transformation (Sokal & Rohlf 1981). Because there was a highly significant interaction between site and date ($P < 0.0001$), using a model I, single-factor ANOVA, how GI varied temporally at each site was examined. The specific contrasts were based on observations before our study by Stephens (1972) who demonstrated that seawater temperatures near 4°C (both in the field and laboratory) were associated with green sea urchins from Maine and Massachusetts that were in a spawning condition. In addition, Stephens showed that the breeding season can be extended by 2 mo by holding ripe animals at 4°C. Also, field observations were made by Harvey (1956) and Cocanour & Allen (1967) who noted that temperatures above 4°C were associated with gamete release. For example, the first contrast ($\bar{x}_{\text{Jan.,Feb.,Mar.,Apr.}}$ versus $\bar{x}_{\text{May,Jun.,Jul.}}$) was based on seawater temperature values <4°C versus ≥4°C. The second contrast ($\bar{x}_{\text{Jan.,Feb.,Mar.}}$ versus $\bar{x}_{\text{Apr.}}$) examined if GI changed significantly during winter. The third contrast ($\bar{x}_{\text{May}}$ versus $\bar{x}_{\text{Jun.,Jul.}}$) tested whether changes in GI occurred when seawater temperatures were immediately >4°C. The fourth contrast ($\bar{x}_{\text{July}}$ versus $\bar{x}_{\text{Aug.,Sept.}}$) tested whether a late summer/early fall (fractional) spawning occurs as in Newfoundland (Keats et al. 1987) and Nova Scotia (Meidel & Scheibling 1998). A conservative decision rule was used for the four contrasts ($\alpha' = 1 - \alpha^{1/m}$; where $\alpha = 0.05$ and $m = 4$) based on Winer et al. 1991; therefore $\alpha' = 0.0127$. Unplanned comparisons of mean GI between sampling dates were carried out using the Bonferroni corrected *t*-tests using a decision rule of $\alpha = 0.05$, or the *a posteriori* Student–Neumann–Keuls (SNK) test. In addition, regional (fixed factor) and site-specific differences in mean maximum GI (reproductive potential sensu Lamare et al. 2002) were examined using a nested ANOVA followed by *a posteriori* SNK test.

Although the GI ratio was adjusted for differences in body size by attempting to sample urchins >40 mm TD, this may not have completely removed the effects of body size on this ratio (Packard & Boardman 1999, Harrington et al. 2007, Ebert et al. 2011). Therefore, the approach of Packard and Boardman (1999) and Ebert et al. (2011) was followed, and a more sensitive test [analysis of covariance (ANCOVA)] was conducted to determine the effect of date on reproductive cycle for each site. Least-squares regression lines were fitted to the data (gonad wet weight = dependent variable versus TD = independent variable). Slopes were compared using the least-square means for gonad wet weight to test for significant monthly variation in the dependent variable. In addition, *a priori* comparisons were used to test hypotheses concerning the least square means for pre- and postspawning events (as described above).

RESULTS

Sea Urchin Densities

Densities of sea urchins at the southwestern study sites were the highest of any region, but were highly variable, and ranged from 40 per m^2 to nearly 70 per m^2. Individuals were aggregated at one of the three sites [Bailey Island; Morisita's Index ($I_d = 1.57$, $P = 0.002$)]. Densities at central sites, Stonington and Lamoine, varied greatly (5 and 30 per m^2, respectively), and were aggregated at Lamoine ($I_d = 1.16$, $P = 0.012$). Among the northeastern sites, urchins at Schoodic Point were aggregated only at the deepest depth (6–8 m; $I_d = 1.48$, $P = 0.008$) and were rare in the shallowest depth (Table 1), where moderate wave exposure and surge were common. Urchin densities differed dramatically between the two other northeastern sites. Only a single urchin was sampled in the 19 quadrats taken at the Jonesport site ($\bar{x} =$

1.3 per m^2). The density estimate at this location may be biased low because of the shallow depth range of samples taken. Sea urchins were found mainly on boulders or ledge outcrops at Lubec where densities were moderately high (Table 1), and animals were not aggregated ($I_d = 1.87$, $P = 0.065$).

Sea Urchin Sizes

Urchins collected at all sites averaged >60 mm TD (Fig. 2) and >30 mm in height (data not shown), except Lamoine where animals consistently had the smallest test sizes [$\bar{x} \pm 95\%$ confidence interval (CI) = 49.7 ± 0.5 mm, $n = 173$]. Size–frequency distributions were not homogeneous among sites (G-test of independence, df = 24, $P < 0.0001$), and within each region ($P < 0.0001$). These data indicate that during the initial stages of intensive (4-fold increase) commercial harvesting, 1987 to 1988 (National Marine Fisheries Service 2014), the largest urchins occurred in the northeastern and southwestern regions of the state.

Validation of Gonad Index

Gonad index and urchin TD were related over the size range of animals sampled (Fig. 3). The allometric model ($y = ax^b$) produced the highest coefficient of determination for these data ($a = 0.004$, $b = 1.86$, $r^2 = 0.1437$, $n = 1594$, $P < 0.0001$; Table 2). The relatively low coefficient of determination may be a related to the fact that these data (Fig. 3) include information from all sites and all sampling dates. Subsequently, the same relationship on a subset of the data was examined (for sampling dates with peak GI values for each site—March or April 1987). The relationship was similar to the complete data set ($r^2 = 0.1393$, $n = 93$, $P = 0.0002$). Therefore, the site-specific body size–GI relationship for the larger data set was examined and found that the slopes of the regression lines were significantly different ($F = 9.43$, df = 8, 1576, $P < 0.0001$). For all data, a threshold TD was sought above which GI was independent of body size. Beginning at 40 mm, and testing in 5 mm increments, the four models presented in Table 2 were analyzed. At TD < 60 mm, each model yielded a statistically significant coefficient of determination. At TD ≥ 60 mm, the linear, quadratic, and allometric models yielded highly significant P values, although r^2 values were low. At TD ≥ 62.5 mm, only the quadratic model was statistically significant (Table 2). At TD ≥ 64 mm, however, each model demonstrated that GI was independent of urchin size. This relationship was similar between urchin populations in the northeast and southwest regions, but differed in the central region where GI was independent of TD for animals ≥55 mm.

Although GI depended on urchin size, and because our samples contained urchins as small as 34 mm TD, we decided to test if the pattern of GI varied differently through time for two size groups of urchins—all animals versus those ≥64 mm TD. We used a conservative approach and selected one site within each region [Five Islands (southwest), Stonington (central), Schoodic Point (northeast)] where there was a prevalence of smaller sized individuals (Fig. 2). Analysis of variance was used to compare mean GI for the two size groups separately for each site, and demonstrated no significant sampling date × urchin group interaction ($P > 0.55$) or significant group effect ($P > 0.15$; Fig. 4). Because of the similarity of GI patterns between the complete versus reduced data set (i.e., the ≥64 mm subset), we present mean GI data for the full range of urchin sizes from each site (Figs. 5–7).

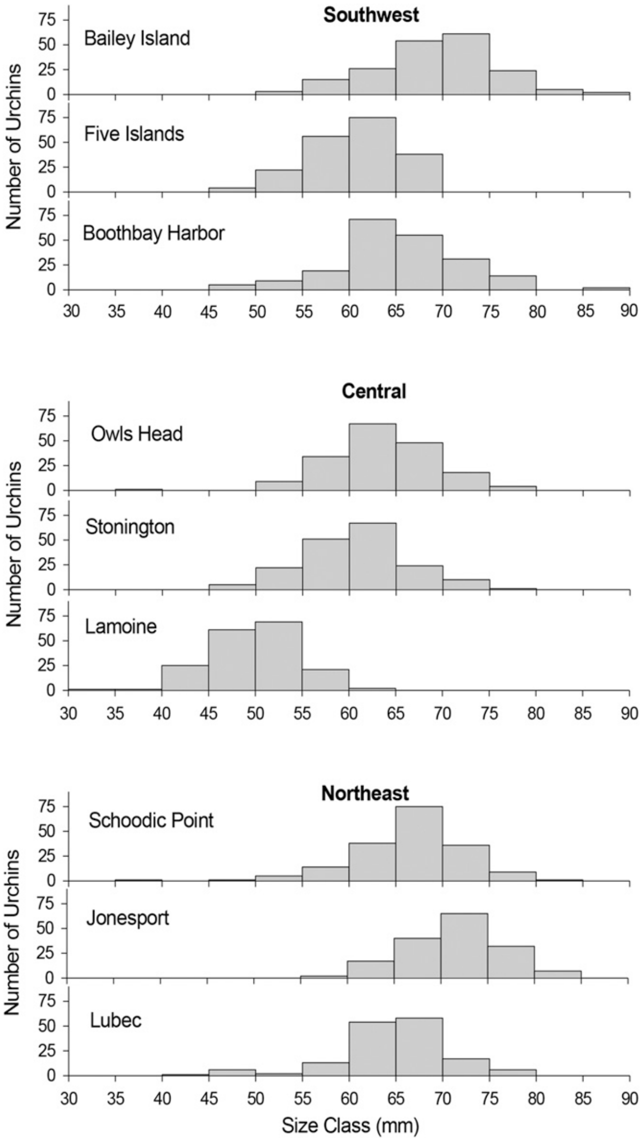

Figure 2. Sea urchin TD from nine sites representing three coastal regions of Maine. Divers were asked to collect urchins >50 mm diameter from each site; however, the average size of animals at Lamoine (barren grounds) was smaller than available elsewhere.

Hydrography

Temperature patterns were similar throughout the three regions and followed a typical profile for cold subarctic-boreal waters. Several features are worth noting from these data (Figs. 5–7). Most sites, except Five Islands and Lubec, had temperatures at or below zero for one or more months. Summer temperatures were 2–10°C cooler (maximum 10°C) at eastern sites, which likely resulted from greater tidal amplitudes in eastern Maine along with increased mixing with bottom and Bay of Fundy waters (Garside & Garside 2004). The greatest range of temperatures occurred in the central region. Overall, temperature ranges were more similar at central and western sites.

Three general patterns are evident from the salinity data (Figs. 5–7). First, all sites were influenced to some extent by snow melt and runoff during late winter and early spring. Second, salinities at Bailey Island, Boothbay Harbor, Five

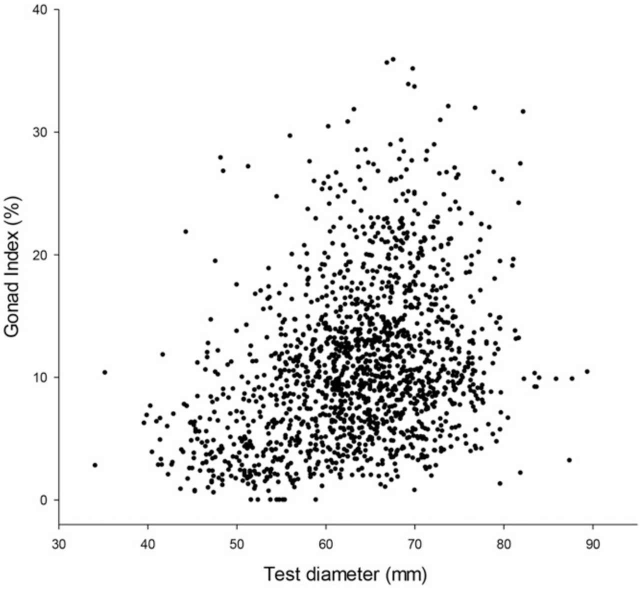

Figure 3. Relationship between GI and urchin TD for all sites and sampling dates (n = 1594). See Table 2 for lack-of fit-analyses and allometric model results for the relationship.

Islands, Owl's Head, and Jonesport generally were in the higher range of values for the nearshore Gulf of Maine (29–34 psu except during April). Third, Stonington, Lamoine, and Schoodic Point consistently had the lowest salinities with Lamoine ranging into the low 20s.

Gonad Indices

Typically maximum GI occurred in late winter or early spring at the nine sites (Figs. 5–7). Significant temporal variation in mean GI was observed at all sites ($P < 0.0001$). Although there was a highly significant interaction between site and sampling date in the two-way ANOVA, some consistent patterns are evident in the reproductive cycle and spawning in sea urchins in Maine. In general, gonads enlarge during fall and early winter and urchins spawn in early spring. Gonad indices typically were lowest immediately after spawning and throughout summer. Indices began increasing during early fall. Mean GI for the nine sites ranged from a low of 2.4% (Lamoine, October 1987) to a high of 22.9% (Lubec, March 1988) (Figs. 5–7). Prespawning indices generally ranged from 14% to 19%, whereas postspawning indices ranged from 5% to 11% at all sites, except Lamoine and Stonington, which were lower. Gonad indices remained relatively low ($\bar{x}$ ± 95% CI = 8.3 ± 0.34, n = 600) from May through early fall during the recovery phase (sensu Fuji 1960b, Byrne 1990, Meidel & Scheibling 1998, Walker & Lesser 1998, Harrington et al. 2007). Generally, GI increased by 80% between November 1987 and February 1988, except at Lamoine where the increase was insignificant (ca. 2%).

We examined mean maximum GI loss between successive sampling dates, which we assume represents the major (i.e., annual) spawning period, for each site (Table 3). This loss in mean GI ranged from 48% to 78%, and generally occurred between April and May (Figs. 5–7). We analyzed these data by preplanned, orthogonal contrasts (Table 4; contrast 1), which demonstrated a significant decline (major spawning pulse) in mean GI between the January–April and May to July sampling dates at seven sites. This pattern did not occur at two sites [Lamoine, where spawning occurred between March and April (Fig. 6); Jonesport, where spawning occurred between May and June (Fig. 7)]. During the prespawning period (January to April) mean GI increased significantly at only three of the sites (Five Islands, Boothbay Harbor, Stonington) (Table 4; contrast 2). For example, the mean detectable increase in mean GI during this period was 7.4% whereas the mean increase at the other sites was <1%. The same contrast for urchins at Lamoine was significant, but for a different reason. Mean GI increased from January 13 to March 16, 1988, but declined rapidly after this date (Fig. 6). No differences in mean GI occurred in larger urchins (≥64 mm) between January and April at any site (Table 4). Immediate (statistically significant) recovery of mean GI after spawning was detected at only two sites (Owl's Head, ca. 50%, Fig. 6; and Jonesport, ca. 60%, Fig. 7). No differences in mean GI were detected at any site from July to September 1988 for either the full data set or for the >64 mm set (Table 4; contrast 4); however, these tests may have been too conservative because August and September sampling dates were pooled, and Figure 5 suggests a fall spawning event at all sites in the southwestern region at the end of summer 1988, immediately after seawater temperatures had reached their annual maxima. The loss in mean GI also was associated with a 45.5%–76.7%

TABLE 2.

Lack-of-fit analysis and allometric model results for the relationship between urchin TD and GI.

	Lack-of-fit analysis							
	Linear		Quadratic		Cubic		Allometric	
	P	r^2	*P*	r^2	*P*	r^2	*P*	r^2
All data (n = 1,594)	**<0.0001**	0.1030	**<0.0001**	0.1138	**0.0009**	0.1200	**<0.0001**	0.1437
≥45 mm (n = 1,553)	**<0.0001**	0.0923	**<0.0001**	0.1090	0.1251	0.1103	**<0.0001**	0.1308
≥50 mm (n = 1,480)	**<0.0001**	0.0661	**<0.0001**	0.0867	0.9621	0.0868	**<0.0001**	0.0863
≥55 mm (n = 1,348)	**<0.0001**	0.0255	**0.0002**	0.0354	0.8848	0.0354	**<0.0001**	0.0268
≥60 mm (n = 1,139)	**0.0029**	0.0078	**0.0201**	0.0125	0.7899	0.0125	**0.0056**	0.0067
≥62.5 mm (n = 943)	0.0851	0.0031	**0.0359**	0.0078	0.7283	0.0079	0.0749	0.0034
≥64 mm (n = 834)	0.2978	0.0013	0.0714	0.0052	0.6533	0.0055	0.2691	0.0015

Overall TD for complete data set ranged from 34.1 to 89.4 mm. Significant *P* values are shown in boldface.

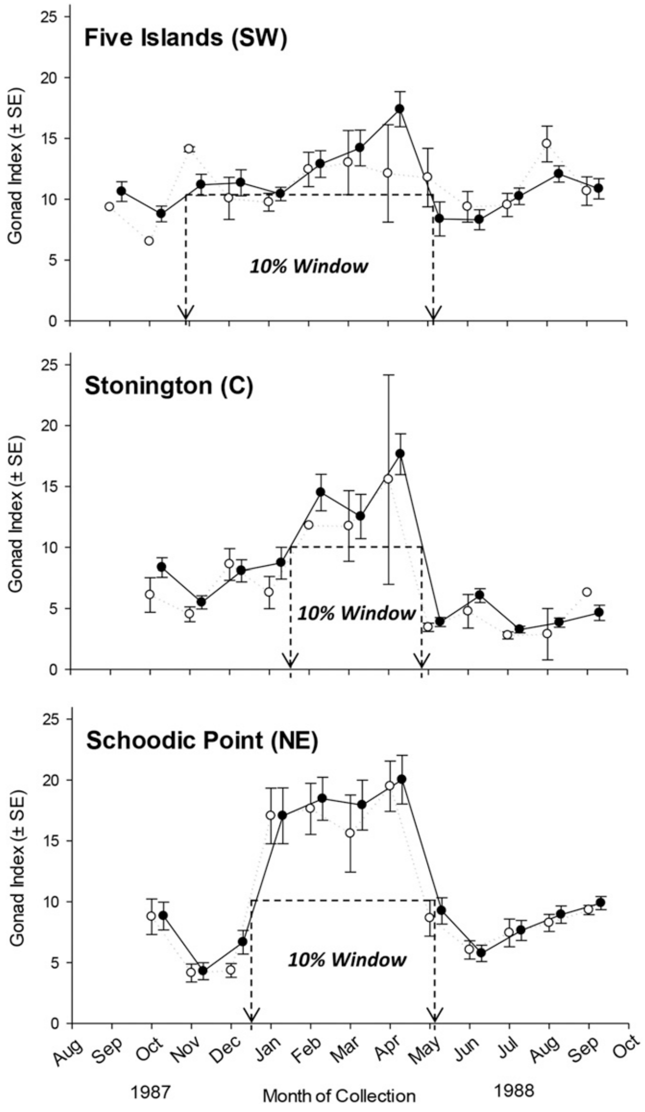

Figure 4. Mean GI (%) patterns for a selected site within each coastal region (see Table 1). Solid circles represent all data from each sampling date (complete data); open circles represent data only for urchin TD ≥ 64 mm (reduced data set). SW, southwest; C, central; NE, northeast.

loss in mean gonad wet weight over all sites ($\bar{x} \pm 95\%$ CI $= 61.1 \pm 7.45\%$, $n = 9$).

Analysis of least-square regression lines (gonad wet weight versus TD) demonstrated homogeneous slopes for all months and sites ($P > 0.15$). For each site, analysis of adjusted gonad weights (least-square means) confirmed results (both overall *F*-test and preplanned contrasts) from the single-factor ANOVA on mean GI (Table 4). Mean GI, unadjusted, and adjusted mean gonad weight varied similarly through time at all sites, and an example from each region is presented (Fig. 8). These analyses indicate that the GI measurements (Figs. 5–7) are reasonable estimates of site-specific reproductive cycles (sensu Harrington et al. 2007), and highlight the utility (sensitivity) of this technique to discern patterns of reproduction (Packard & Boardman 1999, Ebert et al. 2011).

Further examination of mean GI versus mean temperature in the three regions (Fig. 9) indicates that GI decreases linearly with sea surface temperature for central and northeast urchin populations. The southwestern populations, however, appeared to respond differently as the addition of a quadratic term to the linear model was significant ($P = 0.004$), suggesting that mean GI increases with temperatures above 12°C. Seawater temperature explained 55%–77% of the variability in mean GI through time across the three regions (Fig. 9). A reanalysis of the August (mean GI $= 12.2 \pm 0.5\%$, $n = 39$) and September 1988 ($10.1 \pm 0.5\%$, $n = 39$) GI data for the southwestern populations (Fig. 5) was carried out to determine whether the apparent decrease [noise or possible fall (fractional spawning)] in mean GI (–17.2%) was statistically different from zero. We used the *post hoc* Tukey [honestly significant difference HSD)] procedure (Winer et al. 1991) which demonstrated that the two means were not equal ($P < 0.01$). A similar test for the central ($n = 83$) and northeastern ($n = 84$) populations for the same two sampling dates in 1988 showed that the mean difference in GI (+9.5%) was not significantly different from zero ($P = 0.26$). In addition, a fall spawning event may have occurred in 1987 at Schoodic Point (northeast; Fig. 7). One could ask whether the change in the transformed mean GI during the period between October and December could have occurred by random chance alone ($F = 6.3$; df = 2, 42; $P = 0.0041$). A Bonferonni test indicated that the 51% decrease from October to November was statistically significant ($P = 0.05$). A similar analysis for Five Islands (southwest; Fig. 5; $F = 2.68$; df = 2, 42; $P = 0.081$) indicated no significant change in mean GI.

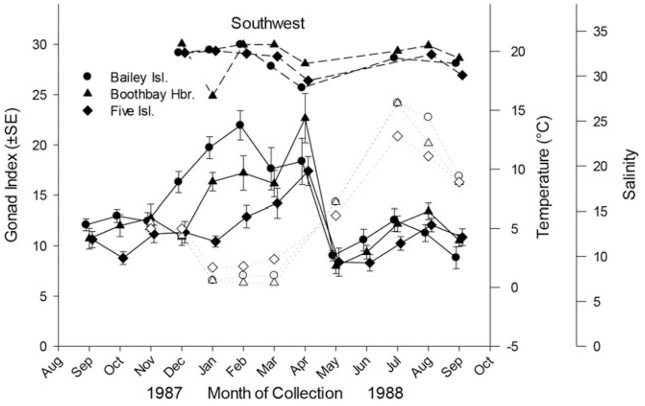

Figure 5. Seawater temperature (open symbols with dotted lines), salinity (solid symbols and dashed lines), and mean GI (%) patterns (solid symbols and lines) for three sites comprising the southwest coast of Maine. Gonad index data include full range of test sizes.

Mean maximum gonad index (max GI) varied between regions (Table 5). The Student–Neumann–Keuls test revealed that mean max GI did not differ significantly between the southwest and northeast regions ($20.2 \pm 1.5\%$, $n = 79$), and was ~52% higher than the mean maximum from the central region ($13.3 \pm 2.2\%$, $n = 43$). Only the central region showed significant site-to-site variability in mean max GI (Table 5). The Student–Neumann–Keuls test demonstrated that urchins from Owl's Head and Stonington had significantly higher max GI values ($15.5 \pm 2.3\%$, $n = 28$) than urchins from Lamoine ($9.1 \pm 4.1\%$, $n = 15$).

Inter- and Intraregional Differences in Gonad Weight versus Total Weight

The relationship between gonad weight and total weight of all urchins measured was weakly linear ($r^2 = 0.442$, $P < 0.0001$,

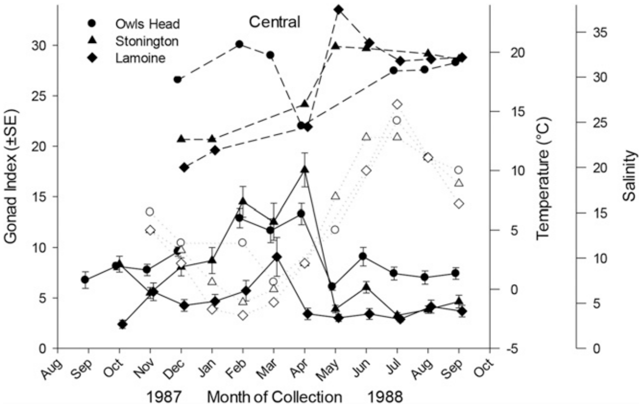

Figure 6. Seawater temperature (open symbols with dotted lines), salinity (solid symbols and dashed lines), and mean GI (%) patterns (solid symbols and lines) for three sites comprising the central coast of Maine. Gonad index data include full range of test sizes.

$n = 1586$), but an allometric model gave a significantly better fit ($a = 0.00347$, $b = 1.721$, $r^2 = 0.564$, $P < 0.0001$). For the southwest and northeast regions, the log-transformed lines were not parallel ($P = 0.011$ and $P < 0.001$, respectively). The lines for each of the three sites within the central region were parallel ($P = 0.1140$), and an ANCOVA indicated that there was a significant difference between sites ($P < 0.0001$). Analysis of the adjusted means (sensu Packard & Boardman 1999) demonstrated that each site was significantly different from one another ($P < 0.0001$). Mean adjusted gonad weight (i.e., least-square means) for a given total weight for urchins at Owl's Head was 33.2% greater than urchins at Stonington, which was 94.7% greater than urchins at Lamoine.

Sex Ratio

Sex was determined in 977 (61.3%) of 1,594 individuals examined. The remainder (617 or 38.7%) could not be accurately sexed. Most of the ambiguity in gender occurred during the recovery phase (postspawning) between May and September 1988. Of the animals sexed successfully, the ratio was not significantly different from 1:1 (female = 505; male = 472; G = 1.115, df = 1, $P = 0.2910$). This ratio did not vary across regions (G = 5.128, df = 2, $P = 0.0770$), but differed significantly over sampling dates (G = 89.733, df = 13, $P < 0.0001$). For example, from June through September, the sex of 81 urchins (pooled over all sites) was determined and 69 (85%) were male ($P < 0.025$). In October, November, and February, females ($n = 206$) occurred in a higher proportion (62.8%) than males ($n = 122$; $P < 0.05$). In addition, sex ratio depended on sampling date at three of the nine sites [Boothbay Harbor: $P = 0.0172$, no bias (nb) =9, female bias (fb) = 3; Five Islands: $P = 0.0313$, nb = 6, fb = 2, male bias (mb) = 4; Schoodic Point: $P = 0.0005$, nb = 6, fb = 4, mb = 2].

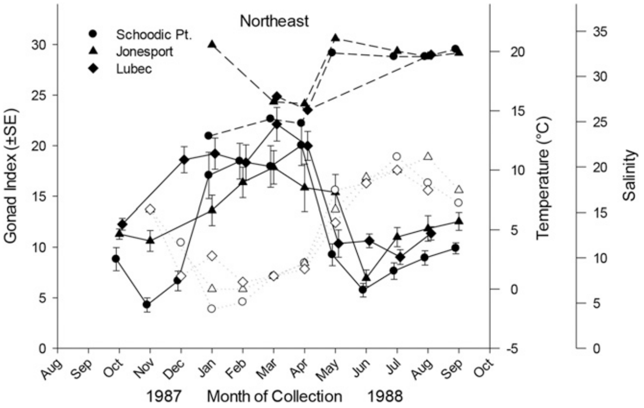

Figure 7. Seawater temperature (open symbols with dotted lines), salinity (solid symbols and dashed lines), and mean GI (%) patterns (solid symbols and lines) for three sites comprising the northeast coast of Maine. Gonad index data include full range of test sizes.

Overall mean TD varied significantly as a function of urchin gender ($P = 0.0006$). Females were, on average, 1.7 mm larger than males ($\bar{x}_{\text{female}} \pm 95\%\ \text{CI} = 64.6 \pm 0.72$ mm, $n = 505$; $\bar{x}_{\text{male}} = 62.9 \pm 0.70$ mm, $n = 472$). In addition, mean GI pooled across all sites and sampling dates varied by sex ($P = 0.0002$). Females had a higher mean GI (13.2 ± 0.65%) than males (11.7 ± 0.47%). Overall mean GI of urchins that could not be accurately sexed (mostly during the post spawning period) was ~30% lower than the average of those urchins whose sex was not ambiguous (8.5 ± 0.41%, $n = 617$).

Sea Urchin Diets

Twenty-eight taxa of algae were identified in the gut of green sea urchins from the nine sites and were categorized as five functional groups (Table 6). Gut analyses revealed that diatoms and microalgae were consistently the dominant prey items at our sites, accounting for nearly 80% of the algal items ingested. Diatoms were the dominant algal form in 19 of the 36 sample dates (based on site and season). The diet of urchins in the central and western region was dominated by diatoms. Microalgae (which included cyanobacteria, coccoid green algae, chrysophytes, individual cells and fragments, and relatively unbranched filaments of red, brown, and green algae) dominated 10 sample dates. Filamentous algae were the only other algal group of some importance in the guts of these urchins. Foliose forms and large macrophytes were unimportant components in the diet, and usually were rated as patchy and rare (2) or absent (1) (Table 6). In addition, six groups (mainly orders) of invertebrates were identified from gut analyses, but were rare or infrequent. These included amphipods, bivalves, cladocerans, isopods, nematodes, and ostracods. Although rare, these invertebrates occurred more often, in descending order, from Five Islands, Bailey Island, Owl's Head, Stonington, and Schoodic Point. Surprisingly, none were observed in individuals from samples taken at Lamoine, Jonesport, and Lubec.

DISCUSSION

Study Sites and Reproductive Patterns

In Maine, *Strongylocentrotus droebachiensis* has an annual reproductive cycle (Cocanour & Allen 1967, Vadas & Grant 1973, Vadas et al. 2000, Seward 2002, Gaudette et al. 2006, Harrington et al. 2007, this study). Urchins at the nine sites spawned between March and May. Similar annual cycles in wild populations of green sea urchins have been observed elsewhere in the northwest Atlantic Ocean (e.g., Himmelman 1978, Keats et al. 1984a, Meidel & Scheibling 1998). Relatively few studies on regular sea urchins have investigated reproductive cycles over the broad geographic scale encompassed by the three regions

TABLE 3.

Mean GI (±95% CI) and mean percent loss of GI for each region and site for the month before and after spawning.

Region	Site	*n*	Prespawn	*n*	Postspawn	Percent loss
SW	BYI	12	18.4 (10.1%)	12	9.0 (2.3%)	51.1
	FVI	15	17.4 (6.2%)	15	8.3 (3.5%)	52.3
	BBH	12	22.7 (10.8%)	12	7.9 (3.3%)	64.8
						$\bar{x} = 55.8$
CN	OWH	13	13.1 (4.8%)	13	5.9 (1.3%)	54.9
	STN	15	17.6 (7.2%)	15	3.9 (1.6%)	77.8
	LMB	15	9.1 (8.2%)	15	3.4 (2.4%)	62.6
						$\bar{x} = 65.6$
NE	SPT	15	20.0 (8.6%)	15	9.2 (4.7%)	54.0
	JPT	13	15.4 (7.7%)	13	6.9 (3.6%)	55.2
	LBC	12	19.9 (6.6%)	12	10.4 (5.9%)	47.7
						$\bar{x} = 52.5$
						Overall $\bar{x}$ = **58.2**

SW, southwest; CN, central; NE, northeast; BYI, Bailey Island; FVI, Five Islands; BBH, Boothbay Harbor; OWH, Owl's Head; STN, Stonington; LMB, Lamoine; SPT, Schoodic Point; JPT, Jonesport; LBC, Lubec.
n = number of urchins sampled on each date—see Figs. 5–7.

examined here (but see McPherson 1968, 1969, Pearse 1968, 1970, Byrne et al. 1998, Viktorovskaya & Matveev 2000, Kino & Agatsuma 2007, Lester et al. 2007). See also Ouréns et al. 2011 for a geographic evaluation of reproduction in *Paracentrotus lividus*. In addition, Sivertsen and Hopkins (1995) found considerable variation in gonad growth and maturation of *S. droebachiensis* over a wide geographic scale along the Norwegian West Coast. A number of investigators have studied annual changes in gonadal weights or indices at single or multiple locations in close proximity (Bennett & Giese 1955, Lewis 1958, Himmelman 1978, Falk-Peterson & Lönning 1983, Munk 1992, Meidel & Scheibling 1998, Brady & Scheibling 2006).

Here, statistically significant changes in monthly GI were used to evaluate objectively when urchins spawned (Meidel & Scheibling 1998, Lamare et al. 2002), with the assumption that the maximum mean difference in GI between two successive monthly collections (range = 48%–78%; Table 3) represented the interval over which spawning occurred. Similar assumptions were made by Himmelman (1975) for *Strongylocentrotus droebachiensis*, and by Spirlet et al. (1998), Guettaf et al. (2000), and Leoni et al. (2003) for other urchin species. The analyses (Table 4) indicated a single, major spawning in late winter/early spring 1987 (Figs. 5–8). For example, spawning occurred between the April 6–16 and May 10–18 collections at seven of the nine sites. This was followed by a recovery period (summer) and a growth phase when gonad mass increased by nearly 80% (fall/early winter). This temporal pattern, however, varied within and between regions (Figs. 5–7). After November 1987 GI varied widely at the three southwestern sites, whereas spawning and recovery phases (April to September 1988) were relatively synchronous (Fig. 5).

Variation in reproductive patterns can occur over long (years) temporal scales at the same site. For example, in 2002, Gaudette et al. (2006) collected urchins near one of our southwestern sites near West Boothbay Harbor, ME, and showed that mean GI between March and May was greater (ca. GI 25%) than that was observed over a similar sampling date15 y earlier (ca. GI 15%). This difference could be explained by the return of kelp (Steneck et al. 2002) (mainly *Saccharina* sp.) due to the reduced density of grazing sea urchins caused by commercial harvesting. Also, Gaudette et al. (2006) found that urchins spawned about 2–3 wk later than they did in 1987 (based on a biweekly mean that was 3.7 SD lower than the mean

TABLE 4.

Summary of single-factor ANOVA results.

		Complete data			>64 mm		
		Contrasts*			Contrasts†		
Site	df	1	2	3	1	2	3
BYI	12	**<0.0001**	0.2549	0.0645	**<0.0001**	0.2687	0.0470
FVI	12	**<0.0001**	**0.0002**	0.2467	0.2387	0.9122	0.3253
BBH	12	**<0.0001**	**0.0006**	0.0239	**<0.0001**	0.0220	0.0465
OWH	11	**<0.0001**	0.4069	**0.0082**	**<0.0001**	0.0992	0.3607
STN	11	**<0.0001**	**<0.0001**	0.4652	**0.0002**	0.1919	0.9360
LMB	11	**0.0003**	**0.0046**	0.9946	–‡	–	–
SPT	11	**<0.0001**	0.1983	0.0723	**<0.0001**	0.1578	0.2927
JPT	10	**<0.0001**	0.3481	**0.0001**§	**0.0002**	0.3583	**0.0003**§
LBC	10	**<0.0001**	0.9108	0.8748	**<0.0001**	0.8230	0.2526

BYI, Bailey Island; FVI, Five Islands; BBH, Boothbay Harbor; OWH, Owl's Head; STN, Stonington; LMB, Lamoine; SPT, Schoodic Point; JPT, Jonesport; LBC, Lubec.
Dependent variable: arcsine-transformed monthly GI data for green sea urchins at each of nine sites along the Maine coast from September 1987 to 1988. Independent variable: month (10–14 dates per site). Four single degree-of-freedom, *a priori* contrasts were conducted for each ANOVA. To control for excessive type I error, a decision rule of $\alpha' = 0.0127$ was used (Winer et al. 1991). Boldface *P* values are statistically significant. $6 \le n \le 15$.
* Contrast 1: January, February, March, April versus May, June, July; contrast 2: January, February, March versus April; contrast 3: May versus June, July; contrast 4 (not shown): July versus August, September (no contrast was significant, $P > 0.0127$). Analyses were performed using complete size range of urchins (34.1–89.4 mm).
† Analyses performed on urchins with TD ≥ 64 mm.
‡ All urchins had TD < 64 mm at Lamoine.
§ Postspawning recovery contrast = June versus July, August, September (see Figure 7).

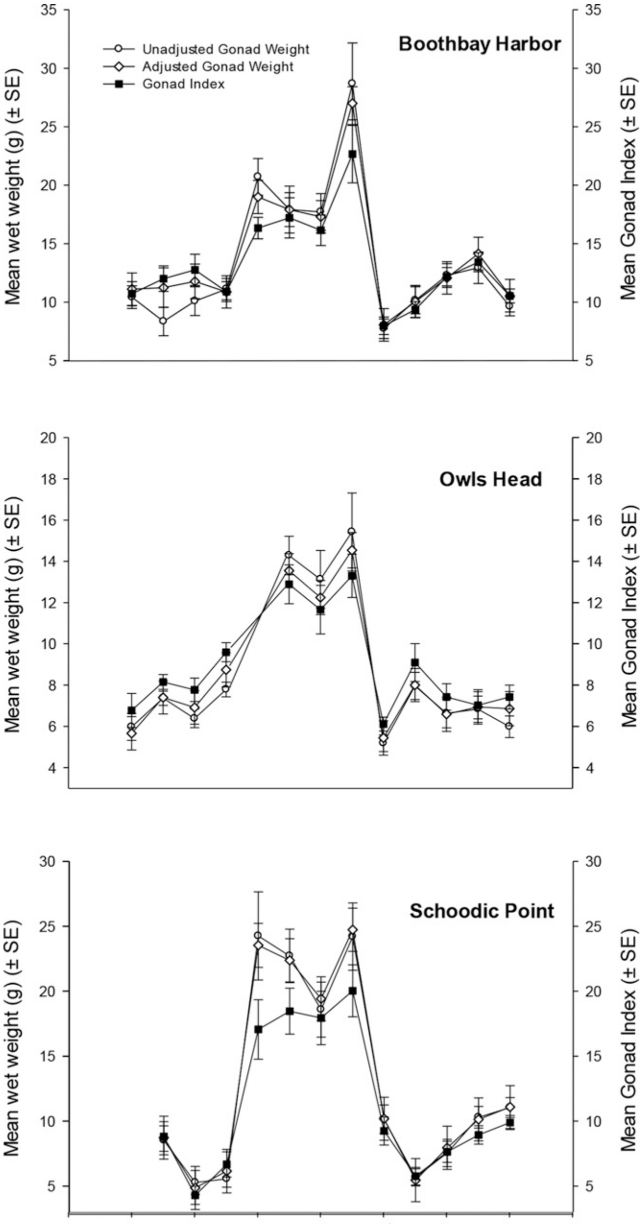

Figure 8. Mean GI (%) patterns (black squares) for a randomly selected site within each coastal region (see Table 1). Least square, adjusted means (open diamonds) and unadjusted means (open circles) for gonad wet weight. Adjusted means based on an overall mean urchin TD for Boothbay Harbor (65.5 mm), Owl's Head (63.6 mm), and Schoodic Point (66.5 mm).

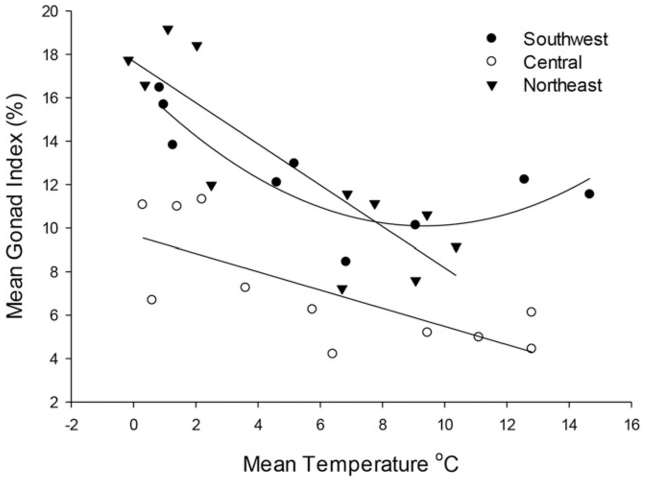

Figure 9. Relationship between mean GI and mean ambient seawater temperature for each of the three regions: southwest: $Y = 16.8 - 1.43x + 0.077x^2$, $r^2 = 0.771$, $n = 9$, $P = 0.012$; central: $Y = 9.7 - 0.42x$, $r^2 = 0.553$, $n = 11$, $P = 0.009$; northeast: $Y = 17.7 - 0.95x$, $r^2 = 0.739$, $n = 11$, $P = 0.0007$. (Values for the central coast do not include information from Lamoine because animals there were smaller and GI were lower than elsewhere—see Results.)

of their previous 10 sampling dates (Fig. 3 in Gaudette et al. 2006). In the central region, variation in the timing of spawning occurred between sites as urchins at Lamoine Beach spawned 1 mo earlier (March to April) than urchins at the other sites. In addition, mean GI at Lamoine was significantly lower (GI rarely exceeded 5%) than those at other central region sites in and on most sampling dates (Fig. 6). This is in contrast to what Cocanour and Allen (1967) found at the same site during 1965 to 1966, as mean GI was ≥8% in 8 of 13 monthly samples. In the northeast region, gonad development in the fall/early winter of 1987 was more variable than the other two regions (Fig. 7). In addition, spawning in the northeast region was asynchronous as urchins at Jonesport spawned approximately 1 mo later (May to June) than those at the other two sites. Seward (2002) found that spawning in 2000 at the same Jonesport site (Table 1) occurred between early March and late May 2000. Taken together, these data indicate that spawning varies spatially and temporally along the Maine coast.

Assumptions about GI

Because GI is a relative measure of reproductive effort, it is not clear whether changes in this variable represent a real change in gonad mass or in one or more of the other variables. For example, in this study mean GI values on the sampling date before spawning (usually the peak value, Figs. 5–7) varied across the three regions from 12.9% to 19.5% and then declined to a mean ranging from 4.2% to 8.5% a month later (ca. 55%–65% decrease in 1 mo). It is important to note that the apparent loss of gonadal tissue may have occurred as a result of changes in spatial and temporal dynamics of coelomic fluid, food intake, and defecation, as implied by Fuji (1967). That is, gonad weight could remain constant through time, yet GI show peaks and troughs due to changes in gut fullness, fluid content, and/or diet, and this could affect the gonadal/somatic ratio (Leoni et al. 2003). Several studies have shown a strong, positive correlation between GI and availability of food (Fuji 1960a, Ebert 1968, Gonor 1973a, Spirlet et al. 1998) or food quality (Keats et al. 1983). Specifically, if diet and gut fullness were responsible for the observed changes in GI between pre- and postspawning dates (Figs. 5–7), then there should be no relationship between GI and gonad mass. Conversely, if a relationship exists between these two variables, the highest values of GI should be associated with the highest values of gonad weight before spawning. Concomitantly, the lowest GI values should be associated with the lowest values of gonad weight after spawning. Therefore, a positive relationship should exist between GI and gonad weight over these two sampling dates. Figure 10 shows a positive relationship between these two

TABLE 5.

Analysis of variance on the arcsine-transformed mean maximum GI for nine sites and three regions of the Maine coast.

Source of variation	df	SS	MS	*F*	Pr > *F*
Region	2	919.66	459.83	18.01	**<0.0001**
Site (Region)	6	665.44	110.91	4.34	**0.0006**
SW region	2	111.00	55.50	2.17	0.1189
CN region	2	492.36	246.18	9.64	**0.0001**
NE region	2	62.08	31.04	1.22	0.2991
Error	113	2885.39	25.53		
Total	121	4470.50			

SW, southwest; CN, central; NE, northeast.
Maximum values for GI occurred between February and April 1988. To control for excessive type I error, a decision rule of $\alpha' = 0.0170$ was used (Winer et al. 1991). Boldface *P* values are statistically significant. $12 \leq n \leq 15$.

variables for each of the three regions, suggesting that the changes in GI that were attributed to a spawning event reflects a loss of gonadal tissue rather than an increase in gut fullness or fluid content. Without assessing this relationship, the use of GI to estimate the timing of spawning events in urchin populations may lead to erroneous inferences (Spirlet et al. 1998). In addition, changes in gonad weight also are a reflection of changes in the composition of gonadal tissue (i.e., nutritive phagocytes or gametes—see Harrington et al. 2007) that could be observed via histology. Another way to assess spawning is to examine the relative difference in mean gonad wet weight over the two successive sampling dates, immediately before and after spawning. The data for all sites combined revealed a drop in mean gonad weight of 61.1% over that period (range = 45.1%–76.7%). Similar observations were noted in other studies with *Strongylocentrotus droebachiensis* (Harrington et al. 2007) and with other sea urchin species (Drummond 1995).

Relationship between TD and GI

The relationship between TD and GI can influence estimates of reproductive condition. A number of biologists recognized earlier that a relationship existed between these variables (Fuji 1967, Pearse 1970). Fuji (1960b) and Moore (1963 a, 1963b) were among the earliest investigators to demonstrate a positive relationship between urchin size and GV or mass. Gonor (1972) critically analyzed the GI-TD relationship in *Strongylocentrotus purpuratus* and showed that for small urchins (<40 mm) GI varied directly with TD. This relationship is important because including animals below a species-specific minimum threshold size could bias estimates of GI and inferences about spawning. Before 2000, 45 of 105 studies (42.8%; Table 7) recognized the relationship between GI and TD, whereas since 2000, 77.4% of studies (48 of 62) used animals above a threshold minimum to assess spawning. Here, it was determined that an overall (nine sites) threshold size of 64 mm, above which, GI and TD were independent.

Two approaches have emerged to assess spatial or temporal changes in reproductive output. Both recognize an allometric relationship between TD (body size) and total weight, gonad weight, mass or GI that is a general phenomenon in marine invertebrates (McKinney et al. 2004, Hemachandra & Thippeswamy 2008) and sea urchins in particular (Gonor 1972, Lozano et al. 1995, Russell 1998, Muthiga 2005). The first involves a size-independent estimate of GI that uses information from the larger (mature) individuals in a population (Gonor 1972, Falk-Peterson & Lönning 1983, Brewin et al. 2000, Lamare et al. 2002) that may be site-specific (Sánchez-España et al. 2004). Below a certain threshold TD, GI increases directly with body size (Fig. 3, Ebert et al. 2011). In Newfoundland, Keats et al. (1984a) saw no relationship between TD and GI for *Strongylocentrotus droebachiensis* between 20 and 50 mm. Comparisons of mean GI between sample dates and/or sites using ANOVA or other statistical tests assume that the gonad-to-body size ratio is consistent throughout the population (e.g., Himmelman 1978, Brady & Scheibling 2006). Use of urchins below the threshold size would bias estimates toward lower GI values. Three sites chosen deliberately to reflect smaller individuals (Fig. 4) showed no significant difference in mean GI through time for data using a restricted (i.e., ≥64 mm TD) versus a complete size range (34.1–89.4 mm). It is likely that this lack of a significant difference

TABLE 6.

Relative seasonal abundance of five algal functional groups in the gut of green sea urchins within three regions of the coast of Maine.

	Functional algal	Region		
Season	Groups	Southwestern	Central	Northeastern
Late fall	Diatoms	X	XXXX	XXX
	Microalgae	XXX	XXXX	XX
	Filamentous	XX	XXXXX	X
	Foliose	X	XX	XX
	Macrophytes	X	XX	XX
	Relative abundance	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Late winter	Diatoms	XX	XXXX	XXX
	Microalgae	XXXX	XX	XXXXX
	Filamentous	X	XXX	X
	Foliose	XX	XX	XX
	Macrophytes	XX	X	XX
	Relative abundance	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Spring	Diatoms	XX	XXX	XXXXX
	Microalgae	XX	XXXX	XX
	Filamentous	XX	XXXX	XXXX
	Foliose	XX	XX	XX
	Macrophytes	XX	XX	XX
	Relative abundance	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Summer	Diatoms	XXX	XXXX	XX
	Microalgae	XX	XXX	X
	Filamentous	XX	XXXX	XX
	Foliose	XX	XX	X
	Macrophytes	X	X	X
	Relative abundance	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6

Summary data are presented from three sites within each coastal region (see Table 1). The gut of five randomly chosen urchins was dissected seasonally from each site. 1 = absent, 2 = rare, 3 = infrequent, 4 = present, 5 = common, 6 = abundant (e.g., relative abundance of diatoms in the central region during the late fall ranged from rare to common; macrophytes in the northeastern region during summer were absent).

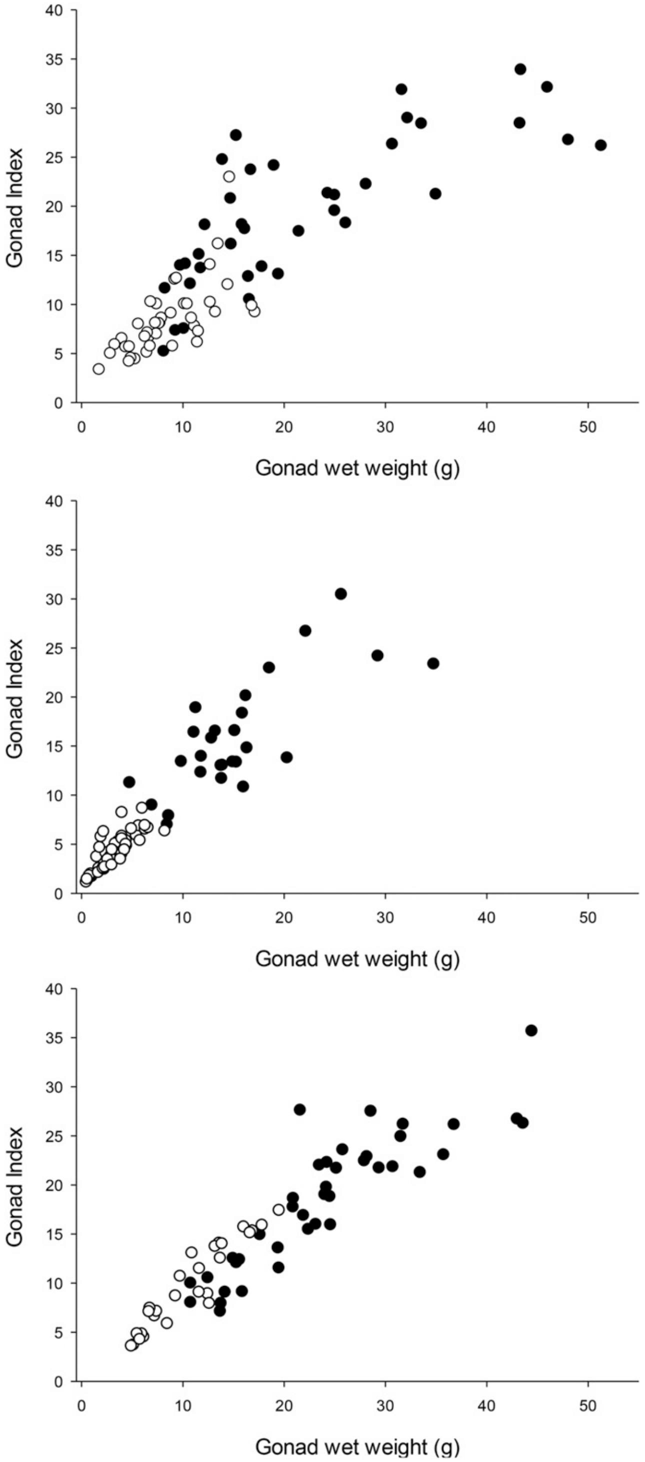

Figure 10. Relationship between GI and gonad wet weight for individual green sea urchins in each region. Closed circles (n = 39, 28, and 40 for southwest, central, and northeast, respectively) represent the immediate prespawning date (see Figs. 5–7). Open circles (n = 39, 43, 27 for southwest, central, and northeast, respectively) represent the immediate postspawning date.

reflects the large variability in the GI versus TD relationship for the >1,500 urchins sampled (Fig. 3).

The second approach (Grant & Tyler 1983, Packard & Boardman 1999) does not use size-specific indices such as GI, but relies on measuring a physiological variable, such as gonad weight, over the entire range of sizes of individuals in the population. Regression analysis followed by ANCOVA was used to remove the effects of body size allowing spatial and/or temporal comparisons of adjusted means (Ebert et al. 2011). If slopes of lines relating the physiological variable such as gonad weight are homogenous then ANCOVA can be used to compare adjusted means between monthly samples (Harrington et al. 2007) or between locations. This approach was used here to compare adjusted mean gonad weights, which supported earlier interpretations regarding site- and region-specific reproductive cycles made on unadjusted mean GI data (Fig. 8).

Causes of Variability

The geographic spread and diversity of bottom habitats of study sites (Table 1) allows for speculation on the possible causes of the observed variability in reproductive cycles. Mechanisms that trigger spawning are not well understood (Lamare & Stewart 1998, Oganesyan 1998). Both correlative and experimental approaches have been used to investigate spawning triggers in echinoids (Himmelman 1975, 1978, Levitan 1988a, Starr et al. 1990, Wahle & Peckham 1999, Gaudette et al. 2006). Several biotic and abiotic factors have been associated with spawning, including feeding/diets, habitat, water motion, intraspecific density, temperature, salinity, lunar phase, termination of the polar night, water depth, phytoplankton abundance, presence of gametes or pheromones, and temperature-dependent embryogenesis (Fujisawa 1989, Starr et al. 1993, Lamare & Stewart 1998, Oganesyan 1998, Himmelman 1999). Here, changes in GI were correlated with several of these factors.

Seawater temperature has long been cited to explain seasonal reproductive patterns in temperate urchins (Elmhirst 1923, Stott 1931, Bennett & Giese 1955, Fuji 1960b, Stephens 1972, Byrne 1990, Oyarzún et al. 1999, Brady & Scheibling 2006, but see Gonor 1973a, Himmelman 1978). Spawning in some tropical and subtropical urchins has been shown to vary with seawater temperature as well. Muthiga and Jaccarini (2005) showed that mean monthly GI in *Echinometra mathaei* in three Kenyan reef lagoons was positively correlated with mean monthly seawater temperatures ($r^2 = 0.75$). Similarly, Vaïtilingon et al. (2005) showed GI was negatively correlated with seawater temperature ($r^2 = 0.20$) for *Tripneustes gratilla* in the southern Indian Ocean. Seawater temperature explained 56% of the variation in GI over 12 mo for *Lytechinus variegatus* at one of four sampling stations near Miami, FL (Ernest & Blake 1981). Hernández et al. (2006) and Tuason and Gomez (1979) reported the existence of a clear seasonality in the GI of *Diadema antillarum* (Canary Islands), and *T. gratilla* (near Mindoro Island, Philippines). The data presented here for *Strongylocentrotus droebachiensis* showed that mean seawater temperature explained between 55% and 77% of the variation in mean GI (Fig. 9). This does not imply that seawater temperature is a spawning trigger because the photoperiod cue and the temperature cue (decrease) occur simultaneously. Rather, the relatively high coefficient of determination can be used as a predictive tool (sensu Low-Décarie et al. 2014) to assess the timing of spawning in green urchins. Several authors have downplayed the role of temperature as a spawning cue (Himmelman 1978, Bayed et al. 2005, Scheibling & Hatcher

TABLE 7.

Methods of assessing spawning in wild populations of regular sea urchins. (Taxonomy after World Register of Marine Species. www.marinespecies.org).

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
Direct observation	nd	x	*Diadema setosum*	Suez, Egypt	Fox 1922
Extrusion of ripe ova; appearance of larvae and early juveniles	nd	x	*Psammechinus miliaris* *Echinus esculentus*	Keppel, Millport, Scotland, Clyde Sea	Elmhirst 1923
Fertilization trials	nd	x	*E. esculentus*	Plymouth, United Kingdom	Orton 1929
Observation of spent individuals†; microscopy	nd	x	*E. esculentus*	Port Erin, Isle of Man, Irish Sea	Stott 1931
GI‡; microscopy	nd	No relationship between TD and gonad size	*E. esculentus*	Port Erin, Isle of Man, Irish Sea	Moore 1934
Direct observation of gonad releasing gametes; microscopy; histology	12.5–57.5	Gonad volume linear *f*(*x*) of test volume	*Echinocardium cordatum*	Port Erin, Isle of Man, Irish Sea	Moore 1936
Sperm agglutination tests both species	nd nd	x x	*Strongylocentrotus droebachiensis* *Strongylocentrotus pallidus*	Dröback, Trondheim, Tromsö, Norway	Vasseur 1952
GI§	nd	x	*Strongylocentrotus purpuratus*	Pescadero Point, CA Yankee Point, CA	Lasker and Giese 1954
GI ± 95% CI§	nd	x	*Mesocentrotus franciscanus*	Pescadero Point, CA	Bennett and Giese 1955
GI ± 95% CI§	nd	x	*S. purpuratus*	Hopkins Marine Station	
Visual assessment of gonad ripeness	nd	x	*S. droebachiensis*	Salisbury Cove, ME	Harvey 1956
GI distribution plots§	nd	x	*S. purpuratus*	Yankee Point, CA Moss Beach, CA	Giese et al. 1958
GI¶; plankton tows for larvae	nd	x	*Tripneustes ventricosus*	Barbados, West Indies	Lewis 1958
GI§	nd	x	*S. purpuratus*	Baja California Coos Head, OR	Boolootian and Giese 1959
GI§; fertilization studies	55–96	xo	*Strongylocentrltus fragilis*	Monterey Bay, CA	Boolootian et al. 1959
GI ± 95% CI§	nd	x	*S. purpuratus*	Yankee Point, CA Pescadero Point, CA	Giese 1959
GI ± SE‖; histology for both species	>40 for both species	xo xo	*Mesocentrotus nudus* *Strongylocentrotus intermedius*	Muroran, Ishiya, and Shinori southern Hokkaido, Japan	Fuji 1960a
GI‡	>40	Gonad volume is an allometric function of TD	*Lytechinus variegatus*	Virginia Key, Miami, FL Richardson's Cove Bermuda	Moore et al. 1963a
GI‡	>50	Gonad volume is an allometric function of TD	*T. ventricosus*	Virginia Key, Miami, FL	Moore et al. 1963b
GI ± SD§	146–715 g	x	*Stomopneustes variolaris*	Madras Harbor, India	Giese et al. 1964
Direct observation	32–67	x	*Diadema antillarum*	St. John, U.S. Virgin Islands	Randall et al. 1964

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TABLE 7.

continued

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SD	nd	x	*S. purpuratus*	Yankee Point, CA	Lawrence et al. 1965
GI‡; microscopy	>50	xo	*T. ventricosus*	Virginia Key, FL	McPherson 1965
GI§	nd	x	*S. purpuratus*	Pacific Grove, CA	Boolootian 1966
GI ± 95% CI§	nd	x	*Arbacia punctulata*	Woods Hole, MA	
GI¶; microscopy	nd	x	*D. antillarum*	St. James, Barbados, West Indies	Lewis 1966
GI ± SE§	50–70	xo	*S. droebachiensis*	Lamoine, ME	Cocanour and Allen 1967
GI ± SE‖; microscopy	>40	Gonad volume is an allometric function of TD	*S. intermedius*	Volcano Bay, Tugaru Straits, and Japan Sea, southern Hokkaido, Japan	Fuji 1967
Histology	10–40 g	x	*Stylocidaris affinis*	Between Isle of Capri and Bocca Piccola, Italy	Holland 1967
GI‡; microscopy; KCl injection	(18–110 ml)	xo	*D. setosum*	Seto (Aichi Prefecture), Japan	Kobayashi and Nakamura 1967
GI ± 95% CI§; histology ; % mature	nd	x	*Arbacia lixula*	Villenfranche, France	Fenaux 1968
	nd	x	*Paracentrotus lividus*		
	nd	x	*Psammechinus microtuberculatus*		
GI ± 95% CI‡; microscopy; histology	8–39	xx**	*Eucidaris tribuloides*	Margot Fish Shoal, Virginia Key, Long Reef, South Florida, FL	McPherson 1968
Direct observation; histology	31–98	xo	*D. setosum*	Indo-Pacific region	Pearse 1968
	32–81		*Echinometra mathaei*		
Histology	40–67	xo	*E. mathaei*	Rottnest Island, Western Australia	Pearse and Phillips 1968
Histology	6–10 g	x	*P. microtuberculatus*	Gulf of Naples, Italy	Holland and Holland 1969
GI ± error bars‡; microscopy	nd	x	*Tripneustes gratilla*	Seto (Aichi Prefecture), Shirahama (Wakayama Prefecture), Japan	Kobayashi 1969
	nd	x	*E. mathaei*		
	nd	x	*Heliocidaris crassispina*		
	nd	x	*Echinostrephus aciculatus*		
GI‡; microscopy; histology	25–65	xo	*Echinometra lucunter*	Virginia Key to Pigeon Key, South Florida, FL	McPherson 1969
	25–65	xo	*Echinometra viridis*		
GI ± SD; ANOVA; direct observation; histology	33–69	xo	*Prionocidaris baculosa*	Wadi el Dome, northwestern Gulf of Suez	Pearse 1969a
	40–76	xo	*Lovenia elongata*		
GI ± SD; direct observation; histology	40–69	xo	*E. mathaei*	Gulf of Suez, northwestern Red Sea, Egypt	Pearse 1969b
GI‡; microscopy	45–81	Decrease in GI with increasing TD	*Evechinus chloroticus*	Kaiteriteri, South Island	Dix 1970
	95–150			Kaikoura, South Island New Zealand	

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TABLE 7.

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How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SD; histology	36–95	xx	*D. setosum*	Gulf of Suez and northern Red Sea	Pearse 1970
GI‡	nd	x	*L. variegatus*	Bear Cut Flats and Sewage Beach, Miami, FL	Moore and Lopez 1972
Microscopy; histology††	nd	x	*Centrostephanus coronatus*	Santa Catalina Island, CA	Pearse 1972
GI; microscopy (proportion of ripe eggs from the population)	51–102	x	*S. droebachiensis*	Cape Cod Bay, MA	Stephens 1972
	nd	x	*S. droebachiensis*	Boothbay Harbor, ME	
Histology	>45	xx	*S. purpuratus*	Central Oregon	Gonor 1973a
GI ± 95% CI‡‡; histology	>45	xx	*S. purpuratus*	Central Oregon	Gonor 1973b
Direct observation	0.9–47.3 g	x	*S. droebachiensis*	St. Margaret's Bay, Nova Scotia	Miller and Mann 1973
Percent of urchins oozing gametes	nd	x	*S. purpuratus*	Palos Verdes, CA	Cochran and Engelmann 1975
GI ± 95% CI§§	45–70	xx	*P. lividus*	Bantry Bay, Ireland	Crapp and Willis 1975
Direct observation; GI ± 95% CI	nd	x	*S. droebachiensis*	Burrard Inlet, Vancouver, British Columbia	Himmelman 1975
Percent of urchins oozing gametes; oocyte size–frequency distribution; histology	nd	x	*C. coronatus*	Santa Catalina Island, CA	Kennedy and Pearse 1975
GI‡; histology	nd	x	*D. antillarum*	Indian Key and Key West, FL	Bauer 1976
GI ± error bars (undefined)¶¶; histology	>100 mm	Linear relationship to 95	*M. franciscanus*	Amphitrite Point, Vancouver Island, British Columbia	Bernard 1977
GI ± SE; microscopy; histology	>60	xx	*Heliocidaris erythrogramma*	Derwent Estuary, Blubber Heads, southeastern Tasmania	Dix 1977
GI ± error bars (undefined); microscopy; histology	nd	x	*H. crassispina* *Hemicentrotus pulcherrimus*	Mouth of Tokyo Bay, Japan	Masuda and Dan 1977
GI¶¶	>40	xx	*S. droebachiensis*	San Juan Islands, WA	Vadas 1977
GI‖‖; histology	$\bar{x}$= 70.7 (SD ± 1.59)	x	*Loxechinus albus*	Valparaiso, Chile	Bückle et al. 1978
GI ± 95% CI; ANOVA (undefined *a posteriori* test)	>30 g for each species	xx	*S. droebachiensis*	Portugal Cove, Newfoundland	Himmelman 1978
		xx	*S. droebachiensis*	First Narrows & Botanical Beach, Vancouver Island, British Columbia	
		xx	*S. purpuratus*		
GI ±2 SE‡; histology (for each species)	nd	X	*Centrostephanus rodgersii*	Solitary Islands, New South Wales, Australia	O'Connor et al. 1978
	nd	x	*Phyllacanthus parvispinus*		
	nd	x	*Heliocidaris tuberculata*		
	Nd	x	*T. gratilla*		

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TABLE 7.

continued

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI for both species; histology for *T. gratilla*	nd	x	*T. gratilla*	Puerto Galera, Mindoro Island, Philippines	Tuason and Gomez 1979
	nd	x	*D. setosum*		
GI	>30	x	*Parechinus angulosus*	Robben Island; Oatland Point. near Capetown, South Africa	Greenwood 1980
Histology for each species	nd	x	*Asthenosoma ijimai*	Kanagawa, Japan	Mori et al. 1980
	nd	x	*Araeosoma owstoni*		
	nd	x	*H. pulcherrimus*		
	nd	x	*H. crassispina*		
	nd	x	*Pseudocentrotus depressus*		
GI ± SE; histology	30–110	x	*T. gratilla*	Kuei-hou and Yeh-liu, northern Taiwan	Chang-Po and Kun-Hsiung 1981
GI ± SD‡‡; histology	55–65	xx	*L. variegatus*	Anclote Estuary, FL	Ernest and Blake 1981
Adjusted mean GI ± 95% CI***; microscopy for all species	nd	Allometric between GI and body weight for each species	*Diadema mexicanum*	Island of Urabá, Panama	Lessios 1981
	nd		*Echinometra vanbrunti*	Culebra Island, Panama	
	nd		*D. antillarum*	Maria Chiquta, Panama	
	nd		*E. viridis*	Fort Randolph, Panama	
	nd		*E. lucunter*		
GI ± SD‡; histology; oocyte size–frequency distribution	nd	x	*D. antillarum*	Castle Harbour, Bermuda	Iliffe and Pearse 1982
Changes in adjusted GV through time; histology	>40	xx	*E. chloroticus*	Hauraki Gulf, New Zealand	Walker 1982
GI ± SD; seawater-induced gamete release; histology for both species	ca. 60	xx	*S. droebachiensis*	Tromsøysundet, Norway	Falk-Petersen and Lönning 1983
		xx	*S. pallidus*		
GI ± SE	20–50	No significant relationship	*S. droebachiensis*	Conception Bay, Newfoundland	Keats et al. 1984b
GI‡; microscopy	8–70	x	*E. lucunter*	Little Bay, Graves End, Barbados	Lewis and Storey 1984
Oocyte size–frequency distribution; histology	nd	xx	*Gracilechinus affinis*	Rockall Trough, northeast Atlantic Ocean	Tyler and Gage 1984
KCl injection	nd	x	*T. ventricosus*	San Blas Islands, Panama	Lessios 1985
	nd	x	*L. variegatus*		
	nd	x	*E. viridis*		
	nd	x	*Lytechinus williamsi*		
	nd	x	*E. lucunter*		
GI ± 95% CI†††; oocyte size–frequency distribution; histology	nd	xx	*E. esculentus*	Plymouth and Cornwall, England	Nichols et al. 1985

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TABLE 7.
continued

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
Proportion of population observed to be spawning	nd	x	*S. droebachiensis*	Eastern Newfoundland (4 sites)	Keats et al. 1987
Direct observation; KCl injection; $\bar{x}$ percent spawning ± SD	20–85	xx‡‡‡	*D. antillarum*	Lameshur Bay, St. John U.S. Virgin Islands	Levitan 1988b
$\bar{x}$ ± 95% CI gonad dry weight through time; % mature gonads; microscopy	nd	xx	*E. esculentus*	Duart and Cuan, Scottish West Coast	Comely and Ansell 1989
GI ± SD‡‡; histology	30–65	xx	*P. lividus*	Ballynahown and Glinsk, western coast of Ireland	Byrne 1990
GI ± SD; histology; KCl injection; microscopy	>40	xx	*Heterocentrotus mamillatus*	Gulf of Aqaba, Red Sea	Dotan 1990
GI ± SE; histology	nd	x	*S. variolaris*	Oslo Beach, South Africa	Drummond 1991
GI ± SE‡‡; ANOVA, SNK; histology	55–80 55–95	xx xx	*H. erythrogramma* *H. tuberculata*	Botany Bay, New South Wales, Australia	Laegdsgaard et al. 1991
GI ± SE	60–80	No relationship after TD > 50	*S. droebachiensis*	Womens Bay, Kodiak, AK	Munk 1992
Microscopy; histology	nd	x	*Stylocidaris lineata*	Northern Bahamas (deep water)	Young et al. 1992
GI ± SD; histology	55–76	xx	*L. albus*	Punta Lagunillas, Chile	Zamora and Stotz 1992
GI ± SD§§§	80–90	xx	*Sphaerechinus granularis*	Glenan Archipelago, Western Brittany, France	Guillou and Michel 1993
GI ± 95% CI; ANOVA, Scheffé's test; direct observation; microscopy	40–60	xx	*S. droebachiensis*	St. Lawrence Estuary, Quebec, Canada	Starr et al. 1993
GI ± SD; histology	55–76	xx	*Tetrapygus niger*	Punat Lagunillas, Bhaía La Herradura de Guayacán, Chile	Zamora and Stotz 1993
GI ± 95% CI; histology	nd nd	x	*S. droebachensis* *Strongylocentrotus polyacanthus*	Avachinskaya Inlet, Kamchatka, Russia	Arkhipova and Yakovlev 1994
GI ± SD	80–90	xx	*S. granularis*	Glenan Archipelago, Western Brittany, France	Guillou and Michel 1994
GI ± SE‡‡; ANOVA, SNK test; KCl injection; histology	70–100	xx	*C. rodgersii*	Sydney, New South Wales, Australia	King et al. 1994
GI	45–95	xx	*P. lividus*	Galicia, Spain	Catoira 1995
GI ± SE; *t*-test; histology for both species	nd nd	x x	*Diadema savignyi* *E. mathaei*	Ispingo Beach, Ramsgate, Natal Province, South Africa	Drummond 1995

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TABLE 7.

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How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SE¶¶¶; ANOVA, Tukey's test; histology	>30	xx	*P. lividus*	Tossa de Mar, Cubelles, northeast coast of Spain	Lozano et al. 1995
GI ± SE§; ANOVA, SNK test	50–130+	No relationship at northern sites; quadratic relationship found at southern site	*E. chloroticus*	North and southwest coast South Island, New Zealand	McShane et al. 1996
GI ± 95% CI‖‖‖; ANOVA, Tukey's HSD test	31–50	xx	*P. lividus*	Urbinu lagoon; East coast of Corsica, France	Fernandez and Boudouresque 1997
GI ± 95% CI; histology	>40	xx	*H. crassispina*	Mera Bay, within Suruga Bay, Shizuoka Prefecture, Japan	Horii 1997
GI ± SE; histology	66–120	No relationship from 66 to 119****	*C. rodgersii*	New South Wales, Australia (4 locations)	Byrne et al. 1998
Seasonal changes in mean gonad dry weight	>70	x	*E. esculentus*	Isle of Cumbrae, Clyde Estuary, Scotland	Emson and Moore 1998
GI ± 95% CI‖‖‖	41–50	xx	*P. lividus*	Urbinu lagoon; East coast of Corsica, France	Fernandez 1998
GI ± SD§§§; histology	80–90	xx	*S. granularis*	Bay of Brest, West Brittany, France	Guillou and Lumingas 1998
GI ± SE¶¶; direct observations	nd	x	*E. chloroticus*	Doubtful Sound, South Island, New Zealand	Lamare 1998
GI ± SE¶¶; direct observations	nd	x	*E. chloroticus*	Doubtful Sound-Thompson Sound, South Island, New Zealand	Lamare and Stewart 1998
GI ± SD; ANOVA; histology	35–50	No relationship between 35 and 50	*S. droebachiensis*	Mahone Bay and St. Margaret's Bay, Nova Scotia	Meidel and Scheibling 1998
GI ± 95% CI, histology	60–70	xx	*S. droebachiensis*	Motovsky Bay, Barents Sea, Russia	Oganesyan 1998
GI ± SD; histology	35–50	xx	*P. lividus*	Morgat, southern Brittany, France	Spirlet et al. 1998
KCl injection; field observations of larvae	nd	x	*Sterechinus neumayeri*	Borge Bay, Signy Island, Antarctica	Stanwell-Smith and Peck 1998
GI ± SD§§§; Wilcoxon–Mann–Whitney test	80–115	xx	*S. granularis*	Bay of Brest, Britanny, France	Guillou and Lumingas 1999
GI ± error bars (not defined); histology	≥70	x	*L. albus*	Cockburn Channel; Dawson Isl. Magallanes, Chile	Oyarzún et al. 1999
GI ± SE¶¶; ANOVA, SNK test; histology	27.9–105.1 g 23.6–66.3 g	xx	*D. setosum* *E. mathaei*	Kubbar Island reef, Kuwait	Alsaffar and Lone 2000
GI††††; microscopy; KCl injection	35–45	xx	*L. variegatus*	St. Joseph Bay, FL	Beddingfield and McClintock 2000

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TABLE 7.

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How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SE¶¶; ANOVA; histology	≥70	No relationship after TD > 70	*E. chloroticus*	Tory Channel, Marlbrorough Sounds, New Zealand	Brewin et al. 2000
GI ± SD‡,***	>30	xx	*D. antillarum*	Gran Canaria, Canary Islands	Garrido et al. 2000
GI ± 95% CI‖‖‖; Kruskal–Wallis, SNK tests	45–58	xx	*P. lividus*	Bay of Algiers; Bou Ismail, Algeria	Guettaf et al. 2000
GI ± 95% CI‡‡‡‡; histology	20–30	xx	*P. miliaris*	Loch Creran, West Scotland	Kelly 2000
GI‖; histology	nd	x	*S. intermedius*	Cape Zolotoi Cape Povorotnyi, Primor'e Far Eastern Russia	Viktorovskaya and Matveev 2000
GI ± SE‡‡	>40	xx	*S. polyacanthus*	Shemya Island, AK	Konar 2001
GI ± SE¶¶; ANOVA; histology	70–140	xx	*E. chloroticus*	Doubtful Sound, New Zealand	Lamare et al. 2002
GI ± SD; histology	nd	x	*L. variegatus*	Biscayne Bay, FL	McCarthy and Young 2002
GI ± SE§§§§; ANOVA, Tukey's test; KCl injection; histology	30–60	xx	*Holopneustes purpurascens*	Bare Island, Botany Bay, Australia	Williamson and Steinberg 2002
GI ± 95% CI	>12	x	*P. lividus*	Cabo Raso, Portugal	Gago et al. 2003
GI ± SD	21.7–50.8 44–80.8¶¶¶¶	x x	*A. punctulata* *L. variegatus*	Tampa, FL, nearshore and offshore	Hill and Lawrence 2003
GI****; Kruskal–Wallis; histology	40–60	xx	*P. lividus*	Corsica, France	Leoni et al. 2003
GI ± SD; ANOVA, Tukey's test; histology	>20	xx	*P. lividus*	Strait of Gibraltar, Spain	Martínez et al. 2003
GI ± SD; ANOVA, Tukey's B test	54.5–60.3 (without spines)	xx	*P. lividus*	Lorbé, Galicia, Northwestern Spain	Montero-Torreiro and Garcia-Martinez 2003
GI ± SE; KCl injection; histology	61.2 ± 0.4 68.3 ± 0.4‖‖‖‖	xx	*D. savignyi* *D. setosum*	Kanamai lagoon, Kenya	Muthiga 2003
GI ± SE¶¶,*****; histology	40–84	xx	*E. lucunter*	Arraial do Cabo. Abrolhos Archipelago, Brazil	Ventura et al. 2003
GI ± SD	>30	xx	*H. pulcherrimus*	Oshoro Bay, Hokkaido, Japan	Agatsuma and Nakata 2004
GI ± SD; histology	>12	x	*Pseudechinus magellanicus*	Puerto Madryn, Argentina	Bigatti et al. 2004
GI ± SE; ANOVA, Tukey's test; histology	>20	xx	*P. lividus*	Near Strait of Gibraltar (4 sites); Western Mediterranean (2 sites)	Sánchez-España et al. 2004
GI ± SD*****; histology	>40	xx	*H. crassispina*	Kodomari, Wakasa Bay, Central Japan Sea	Yatsuya and Nakahara 2004
GI ± SE‖‖‖; ANOVA, Tukey's HSD test	30–35	xx	*P. lividus*	Atlantic coast of Casablanca, Morocco	Bayed et al. 2005
GI ± SD§§§§; microscopy (for each species)	nd	x	*D. savignyi* *D. setosum* *Echinothrix calamaris* *Echinothrix diadema*	Viti Levu, Fiji	Coppard and Campbell 2005

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TABLE 7.

continued

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SE; KCl injections; histology	45–80	No significant relationship between 45 and 80	*T. gratilla*	Kanamai lagoon, Kenya	Muthiga 2005
GI ± SE; ANOVA; KCl injections; histology	25–60	x	*E. mathaei*	Vipingo, Kanamai, Diani lagoons, Kenya	Muthiga and Jaccarini 2005
GI	≥22	xx	*L. variegatus*	Margarita Island, Venezuela	Quijano and Gaspar 2005
GI ± SD; ANOVA; histology	70–90	xx	*T. gratilla*	Beloza fringing reef lagoon, southwestern coast of Madagascar	Vaïtilingon et al. 2005
GI ± SD; ANOVA; Scheffé test; histology	>30	xx	*H. pulcherrimus*	Onagawa Bay, Miyagi Prefecture, Japan	Agatsuma et al. 2006
GI ± SD; ANOVA*****	35–69	No significant relationship over size range	*S. droebachiensis*	Chedabucto Head, Halifax Harbor, Nova Scotia	Brady and Scheibling 2006
GI ± SE; ANOVA, Fisher's LSD, Mann–Whitney tests	nd	x	*S. droebachiensis*	Pemaquid Point and West Boothbay Harbor, ME	Gaudette et al. 2006
GI ± SE***; ANOVA(ns)	nd	x	*D. antillarum*	Abades and Boca Cangrejo, Canary Islands	Hernández et al. 2006
GI ± SD§§§; ANOVA, LSD	32–36 22–25	xx	*P. lividus* *P. miliaris*	Bay of Brest	Jacquin et al. 2006
GI ± SE; histology; ANOVA on mean oocyte diameter, Tukey's test	9.3–24.1	xx	*P. magellanicus*	Golfo Nuevo, Patagonia Argentina	Marzinelli et al. 2006
GI ± SE; ANOVA(ns); histology	nd	x	*P. lividus*	Ligurian coast of Italy (Bergeggi, SV)	Barbaglio et al. 2007
Dry gonad mass ± SE; KCl injection; histology	28–33	xx	*S. neumayeri*	Rothera Point, Adelaide Island, Antarctica	Brockington et al. 2007
GI ± SD; Kruskal–Wallis, Tukey's tests; macroscopic observation of gonads	>45 >26	xx	*M. nudus* *H. pulcherrimus*	Coast of Tsubaki, Oga Peninsula, Honshu Prefecture, Japan	Endo et al. 2007
GI ± SD; ANOVA, SNK test; histology	>30	xx	*S. droebachiensis*	Isles of Shoals, NH	Harrington et al. 2007
GI ± SD†††††, megascopic observation of oozing gonads	≥60	xx	*L. albus*	Chiloé Island, Chile	Kino and Agatsuma 2007
GI ± SD§§§,*****; Histology	35–70	Increasing GI with increasing TD at two locations	*P. lividus*	Bay of Tunis, Tunisia	Sellem and Guillou 2007
GI ± SE; macroscopic smears	35–70	xx	*S. droebachiensis*	Bodø, Norway	Hagen et al. 2008
GI ± SE; KCl injection	80–110	xx	*C. rodgersii*	Eastern Tasmania	Ling et al. 2008
GI ± SD; ANOVA, Tukey's test; histology	41–100	xx	*S. granularis*	Southeast coast of Spain	Martínez-Pita et al. 2008

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TABLE 7.

continued

How spawning was assessed	Urchin size (mm or g)	Relationship between GI* and TD* (mm)	Species	Location	Reference
GI ± SD; histology	Mean sizes ranged from 46–59	xx	*S. intermedius*	Hirota Bay, Iwate Prefecture, Japan	Matsui et al. 2008
GI (as boxplot); Kruskal–Wallis, Dunn's tests	65–85	xx	*L. albus*	Bridges Island, Beagle Channel, Argentina	Pérez et al. 2008
GI ± SE§§§§; ANOVA, Tukey's test, histology	30–60	xx	*E. mathaei*	Bostaneh, Persian Gulf, Iran	Shahri et al. 2008
GI ± SD‡‡‡‡‡; Kruskal–Wallis test; histology	>33	xx	*E. lucunter*	Southern coast of Pernambuco, Brazil	Lima et al. 2009
GI ± SE; Kruskal–Wallis, Tukey's tests	>23	xx	*E. lucunter*	Praia da Casta, Vila Velha, Espirito Santo, Brazil	Mariante et al. 2009
GI ± SD‖‖‖	45–55	xx	*P. lividus*	Algers Bay and Bay of Boou-Ismail, Algeria	Soualili and Guillou 2009
GI ± SE; Kruskal–Wallis, Dunn's tests; histology	>16	xx	*Arbacia dufresnii*	Golfo Nuevo, Patagonia, Argentina	Brogger et al. 2010
GI ± SD§§§§§; paired sample tests; KCl injection	>40	xx	*P. lividus*	Southeastern Bay of Biscay	Garmendia et al. 2010
GI ± 95% CI; histology	30–43¶¶¶¶¶ 55–70‖‖‖‖‖	xx	*P. lividus*	Cantabrian Sea, Bay of Biscay, France	González-Irusta et al. 2010
GI (Q_2 with 5th and 95th) percentiles; Kruskal–Wallis, Dunn's tests; histology	65–85	xx	*L. albus*	Bridges Island, Beagle Channel, Argentina	Pérez et al. 2010
GI ± 95% CI; Kruskal–Wallis, Dunn's tests; histology	60–102	xx	*L. albus*	Port William and Berkeley Sound, Falkland Islands	Schuhbauer et al. 2010
GI******	<10–65††††††	x	*P. lividus*	Bistrina Bay, Adriatic Sea, Croatia	Tomšić et al. 2010
GI ± SE***; ANOVA; KCl injection; histology	>21	x	*D. antillarum*	Tenerife Island, Canary Islands	Hernández et al. 2011
GI ± SE; Kruskal–Wallis, Steel–Dwass tests; histology	28.1–44.9	xx	*H. pulcherrimus*	Matsushima Bay, Miyagi Prefecture, Japan	Ogasawara et al. 2011
GI ± SD; ANOVA, Tukey's multiple comparisons	nd	xx	*P. lividus*	Gulf of Tunis, Tunisia	Arafa et al. 2012
Mean gonadal weight ± 95% CI	25–130 g (median wet weight)	x	*S. purpuratus*	Seppings Island, British Columbia to Punta Baja, Baja California	Ebert et al. 2012
SGI‡‡‡‡‡‡‡; nonlinear mixed regression model	>40.5	xx	*P. lividus*	Galacia coast (NW Spain)	Ouréns et al. 2013
GI ± SE¶¶; ANOVA, Tukey's HSD test; histology; oocyte size–frequency distribution	62.9–121.0	xx	*C. rodgersii*	Mokohinau Islands, Northeast New Zealand	Pecorino et al. 2013
GI ± SE; Kruskal–Wallis, Dunn's tests; histology	35.0–58.6	x	*A. lixula*	Tossa de Mar, NE Spain	Wangensteen et al. 2013

LSD, least significant difference; nd, no data given; x, no analyses performed; xx, indicated knowledge about size/gonad relationship (sensu Fuji 1960b; Moore et al. 1963a; Pearse 1970; Gonor 1972); xo, size of the urchins was restricted to a specific range, but no indication of a size/gonadal relationship was given.

Direct observation refers to visual examination of the gonads either in the field and/or the laboratory.

ANOVA indicates an overall (global) significant ($P \leq 0.05$) *F*-test for temporal variability without an *a posteriori* test; ANOVA(ns) indicates an overall (global) nonsignificant ($P > 0.05$) *F*-test for temporal variability.

ANOVA, SNK, or some other *a posteriori* or *a priori* test indicates an overall *F*-test for temporal variability and a subsequent comparison of means to pinpoint when spawning occurred.

In some cases, higher stats may have been used, but not as a test to determine when spawning occurred.

* GI = wet weight of gonad divided by total wet weight of animal × 100 (unless otherwise noted). TD = Test diameter.

† Chemical and graphical determinations on gonad-specific gravity, dry weights, and glycogen levels.

‡ GI = (10 × GV) divided by test volume. GV = gonad volume.

§ GI = GV divided by total wet weight of urchin.

¶ GI = GV divided by TD (for Lewis 1966, GI = GV divided by TD cubed)

|| GI = gonad wet weight divided by total volume of urchin.

** Showed a positive relationship between GV and TD between 20 and 30 mm; no trend after 30 mm TD.

† † Spawning assessed using gross observations (size of gonads), change in thickness of spermatocytes, spermatozoa, oocyte diameter, and nutritive phagocytes.

‡‡ GI = gonad dry weight divided by total dry weight.

§§ GI = gonad wet weight divided by total wet weight minus the gonad wet weight.

¶¶ GI = gonad wet weight divided by drained test weight.

|||| GI = gonad wet weight divided by TD cubed (i.e., TD^3).

*** GI = GV divided by dry body weight

† † † GI = eviscerated dry weight (g) divided by total body volume (ml).

‡‡‡ Gamete volume increased allometrically with TD.

§§§ GI = gonad dry weight divided by eviscerated test dry weight.

¶¶¶ GI = gonad dry weight (of four lobes) divided by dry body weight (we assume "body weight" and total weight are the same).

|||||| GI = gonad dry weight divided by TD cubed (expressed either in cm^3 or mm^3).

**** "Gonad retrieval rate, GRR" = slope of a regression of gonad weight against total weight; GRR used instead of GI; ANOVA used to determine location and habitat effects on GRR, but not used to determine when spawning occurred.

† † † † Data were purportedly analyzed statistically, but no *P* values, error bars, etc. are provided.

‡‡‡‡ GI = gonad wet weight divided by the wet weight of the eviscerated test expressed as a percentage.

§§§§ GI = gonad dry weight (of four lobes, corrected to five lobes) divided by total dry weight.

¶¶¶¶ Ranges were estimated from Table 3 in Hill and Lawrence (2003).

|||||||| Standard error (Table 1 in Muthiga 2003)

***** ANOVA or Mann–Whitney *U*-test was used to determine difference in mean GI between sites, years, or depths, but not used to assess spawning

† † † † † Error bars given, and it is assumed that they represent 1 SD (Table 1 in Kino & Agatsuma 2007)

‡‡‡‡‡ GI = [dry weight of 4 gonads/dry weight of dissected test – (gonads + gut contents)] × 100.

§§§§§ GI was calculated using four methods (three are listed here as footnotes *, ‡‡, ||||||), and dry gonad weight divided by whole animal wet weight.

¶¶¶¶¶ Intertidal collection.

|||||||||| Subtidal collection.

****** GI given with some estimate of error that was undefined.

† † † † † † Ranges were estimated from Figures 2 and 3 in Tomšić et al. (2010).

‡‡‡‡‡‡ Standardized GI defined in Ouréns et al. 2012.

TABLE 8.

Comparison of various formulas used to calculate GI in sea urchins.

		Gonad indices of *Strongylocentrotus droebachiensis* calculated using formulae from:						
Site	**n**	**GI***	**Moore et al. 1963**	**Lasker and Giese 1954**	**Lewis 1958**	**Fuji 1960a**	**Crapp and Willis 1975**	**Bückle et al. 1978**
BBH	11	17.4 (4.1)	0.63 (0.16)	17.2 (4.2)	0.27 (0.07)	6.4 (1.6)	21.7 (6.3)	0.06 (0.02)
OWH	14	12.9 (2.1)	0.47 (0.08)	12.7 (2.0)	0.21 (0.03)	4.7 (0.7)	14.9 (2.7)	0.05 (0.01)
SPT	15	18.5 (3.8)	0.67 (0.14)	16.9 (3.4)	0.31 (0.06)	7.3 (1.5)	23.5 (6.2)	0.07 (0.01)

BBH, Boothbay Harbor; OWH, Owl's Head; SPT, Schoodic Point.

Values are means ± 95% CI from a site selected from each region in this study from February 1988. (See Table 7 footnotes for GI formulas associated with each reference.).

* (Total wet weight of gonad/total body weight) × 100; this study.

2001). Himmelman (1999) indicated that support for a "temperature hypothesis" is weak because few studies have examined alternative environmental factors.

Variation in diet has been associated with concomitant responses in GI in both the laboratory and field (Larson et al. 1980, Keats et al. 1983, Minor & Scheibling 1997, Meidel & Scheibling 1998, Vadas et al. 2000, James et al. 2007). Shallow-water habitats at most sites were dominated by crustose coralline barrens and filamentous algae. Patches of opportunistic macroalgae and refugial kelp reflect high, preharvest urchin densities (Table 1). Diets of urchins mirrored barren-dominated habitats where benthic diatoms and filamentous microalgae were the abundant prey items at all sites for each season (Table 6). Others working in similar habitats have indicated the presence of diatoms in sea urchin diets (Vadas & Grant 1973, Chapman 1981, Duggins 1981). Generally kelps, which are among the more preferred prey in the diets of green urchins (Larson et al. 1980, Keats et al. 1984b, Lemire & Himmelman 1996), were absent or rare at most of our sites. The relatively minor differences in diet within and between regions through time (Table 6) cannot explain the significant spatial and temporal variation in GI.

Increases in intraspecific density of tropical and temperate sea urchins can result in reduced fecundity (Levitan 1989, Guillou & Lumingas 1998, Muthiga & Jaccarini 2005). Sea urchin densities at most of our study sites were relatively high (Table 1) and compare favorably with barren ground density estimates for this species in other northwestern Atlantic locations (Breen & Mann 1976, Scheibling & Hennigar 1997). For example, at shallow sites in the Gulf of Maine, Wahle and Peckham (1999) found a 50% decline in urchin (*Strongylocentrotus droebachiensis*) GI over a range of population densities from 0.1 to 250 ind./m^2. To determine whether a relationship existed between the density of green urchins at the study sites (May to June 1988, Table 1) and maximum GI (typically March to May 1988, see Figs. 5–7), these two variables were regressed for all sites except Owl's Head, where no density measurements were taken and found no relationship ($F = 0.56$, df = 1, 6, $P = 0.48$). Thus, over the range observed in this study, density did not show an expected inverse relationship with GI (sensu Levitan 1988b, Worthington & Blount 2003 as cited in Hill et al. 2003). Perhaps the lack of a significant relationship is the result of extensive barren habitats at our sites. Spawning in some sea urchins (e.g., *Strongylocentrotus* spp.) has been shown to correlate indirectly with seasonal increases in salinity (Starr et al. 1993, Vaschenko et al. 2001). We also examined the relationship between mean GI and salinity for all sites and sampling dates, and found no significant correlation between these variables ($F = 0.75$, df = 1, 57, $P = 0.389$, $r^2 = 0.013$; see Figs. 5–7).

In recent decades, seasonal phytoplankton blooms, along with their metabolites, have been considered as spawning cues in green and pale sea urchins (Himmelman 1978, Starr et al. 1990, 1992, Viktorovskaya & Zuenko 2005, Gaudette et al. 2006). This implies that larvae and phytoplankton abundance are closely synchronized (Thorson 1950), and that having urchin larvae in the water column concomitant with high concentrations of microalgae represents an evolutionary strategy (Himmelman 1999, Scheibling & Hatcher 2001). Others have reported similar findings with other urchin species. For example, López et al. (1998) and González-Irusta et al. (2010) showed that variations in larval abundance of *Paracentrotus lividus* from the northeast coast of Spain correlated closely with chlorophyll *a* concentrations. Muthiga and Jaccarini (2005) demonstrated that peak spawning activity in *Echinometra mathaei* coincided with a peak in phytoplankton abundance. Spawning in other echinoderms (e.g., *Cucumaria frondosa*, *Ophionotus victoriae*) has been correlated with increasing concentrations of chlorophyll *a* (Hamel & Mercier 1995, Grange et al. 2004).

The perception that a particular variable induces spawning is not straightforward. Often, two or more variables appear to be correlated. For example, the distinction between temperature and chlorophyll *a* acting as an inducer for spawning is ambiguous because several field studies in arctic, temperate, and tropical waters have shown that the two variables are autocorrelated (Platt et al. 1970, Bisagni et al. 1996, Stanwell-Smith & Peck 1998, McGillicuddy et al. 2001, Grange et al. 2004). Seward (2002) found that phytoplankton blooms in eastern Maine were correlated with many oceanographic variables including seawater temperatures, chlorophyll *a*, pheophytin, nitrate + nitrite, silicate, and phosphate. This suggests that a suite of variables may be responsible in the field for stimulating spawning in green sea urchins.

Also, spawning in sea urchins could be related more to thermal dependence of embryogenesis than other variables. Three species of cold- to warm-temperate urchins coexist on the Pacific coast of Japan near Kanagawa Prefecture (Fujisawa 1989), yet each species spawns during a different season. Although different species of phytoplankton may induce spawning during these seasons, an alternative hypothesis is that seawater temperature and/or photoperiod (sensu Kelly 2000) induces gametogenesis. Walker and Lesser (1998) showed that ovaries of animals exposed to a photoperiod advanced by 4 mo were significantly larger by as much as 175% than control (field) animals mostly due to accelerated development of nutritive phagocytes. New, vitellogenic primary oocytes occupied <1% of the volume fraction of the gonads compared with nutritive phagocytes (ca. 90%). Fujisawa and Shigei (1990) demonstrated that optimum temperature range for development in eight species of temperate and tropical sea urchins was closely related to seawater temperatures during the spawning season. The results suggest that gametes are shed during times when seawater temperature is increasing from ca. 1–7°C (Figs. 5–7), which corresponds to optimum embryo and larval development in *Strongylocentrotus droebachiensis* (Stephens 1972).

Assessment of Spawning

Early attempts to assess spawning (e.g., Fox 1922, Elmhirst 1923) were qualitative, usually graphical presentations. A progression of techniques has followed including direct observations in the field, gonadal smears, changes in GI, gonadal weight, or volume through time, microscopy, and histology (Fuji 1967, Pearse 1968, Keats et al. 1987, Young et al. 1992, King et al. 1994, Viktorovskaya & Matveev 2000, Brady & Scheibling 2006, Sellem & Guillou 2007, Pecorino et al. 2013, Wangensteen et al. 2013, see Table 7). Moore (1934) was the first to use GI to assess spawning in urchins. Of 167 papers published between 1922 and 2013 in which methods of spawning in wild populations of regular sea urchins (species number = 54) were described (Table 7), 84 (50.2%) and 134 (80.2%) used histology and GI, respectively.

Here, spawning was assessed by analyzing changes in GI through time rather than examining gonads histologically. The use of both histology and GI to assess spawning has increased in recent years. Histology can demonstrate whether ovaries contain large percentages of nutritive phagocytes (prespawning), mature ooyctes (spawning is imminent), and relict oocytes (partly spawned to spent). Interestingly, there may be considerable variation in spawning associated with the number of mature oocytes. For example, King et al. (1994), indicated that mature oocytes are not necessarily released at initial maturity but can be held within the test indefinitely. Also, ''the temporal pattern in the gametogenic index of females was similar across depth strata and concordant with the pattern in gonad index'' (Brady & Scheibling 2006). In a few species, however, only weak correlations existed between GI and histological condition of the gonad, [e.g., *Centrostephanous rodgersii* (King et al. 1994) and *Heliocidaris* species (Laegdsgaard et al. 1991)].

Generally, there is good concordance between GI and histology. Harrington et al. (2007) examined stereologically nutritive phagocytes and gametogenic cells during the annual reproductive cycle of *Strongylocentrotus droebachiensis*, and stated that GI serves as a good assessment of the seasonal reproduction cycle. The histology of the gonads of two tropical species (*Diadema setosum* and *Echinometra mathaei*) was correlated with GI and was similar to that of other urchins (Alsaffar & Lone 2000). Bigatti et al. (2004) indicated that GI in *Pseudechinus magellanicus* appeared to be a good indicator of the reproductive cycle, corroborated by gonad histology. Byrne (1990) and King et al. (1994) also verified spawning times by the histological condition of the gonads. Ouréns et al. 2011, concluded that histology was the most reliable tool for determining the reproductive cycle of *Paracentrotus lividus*.

Mature gametes, however, are not necessarily an indication of spawning (Mahdavi Shahri et al. 2008). The presence of ripe gonads with mature gametes only indicates a readiness to spawn given the right cue. Spawning may not occur until the animal experiences certain cues or stimuli (Byrne 1990, Starr et al. 1990, Byrne et al. 1998). Where both GI and histological data have been reported, maximum gonad size usually corresponds to periods when highest percentages of ripe individuals occur in collections (e.g., McPherson 1965—*Tripneustes ventricosus*; Dix 1970—*Evechinus chloroticus*; Gonor 1973a—*Strongylocentrotus* purpuratus), (see Ernest & Blake 1981). Furthermore, for *Centrostephanus rodgersii* near the Solitary Islands, New South Wales, Australia, histological examination confirmed that maximum spawning activity was in August (winter) (O'Connor et al. 1978) and the GI figure (Fig. 1, p. 2) shows a major decline in GI between the July and August (1973–1974) sampling dates.

Gonad Index: Assumptions, Calculations, and Statistics

Surprisingly, 19 different techniques and/or formulae have been used for calculating GI in echinoids (Table 7; see Table 8 for a subset of comparisons of these formulas applied to data from sites selected from each region in this study). Also, Ebert et al. (2011) described multiple ways GI was calculated for echinoids and other echinoderms. Earlier, Spirlet et al. 1998 argued for the inclusion of both the GI and maturity index (histological data on the change from nutritive cell to gametogenic cells). Historically, GI measures have changed from volumetric to mass based. Before 1970, 21 of 25 papers used volumetric measures to calculate GI. Kelly (2000) refined techniques for estimating GI by eviscerating the test and removing food items, sediments, etc. from the test before weighing and calculating the index. Previous indices may have been too conservative because of the presence of these items in the test before weighing the roe. Since 1989, the trend has been to use a GI similar to the one used in this study (57.6%, or 49 of 85 papers). Overall, the use of GI to assess spawning has increased over time (G-statistic = 23.82, df = 4; $P < 0.0001$). Before 1970, 48% of papers used this metric, however, since 2000 GI has been used nearly 95% (59 of 62) of the time. Before 2000, 37 of 105 papers (ca. 35%) used both GI and histology, whereas after 2000, the rate was 33 of 61 papers (54%) (Table 7). Recently there has been an emphasis on the need to standardize the methodology for calculating GI (Ebert et al. 2011, Ouréns et al. 2012, 2013).

Many of the qualitative estimates used to assess spawning that are described in Table 7 included means ± a measure of error (e.g., SE, SD, 95% CI), but no statistical analyses (i.e., hypothesis tests) were conducted. On the other hand, quantitative assessment of reproductive cycles has become more common in recent decades. To the best of our knowledge, the first attempt to quantify statistically the timing of spawning in sea urchins was by Pearse (1969a) who used ANOVA to detect differences in mean GI in *Prionocidaris baculosa* from the Gulf of Suez. It is not clear, however, how results from the ANOVA were interpreted. That is, whether an overall F-statistic and its P value were used to assess variability over an annual cycle or, if a series of F-statistics were used to compare discrete periods (usually monthly) of time within the annual cycle (e.g., March versus April or May and June versus July). For example, a significant *F*-value for a set of monthly GI means (temporal variability) does not give precise information about when spawning occurred. Instead, *a posteriori* tests (e.g., SNK, Tukey, Scheffé) or a series of *a priori* contrasts should be used to further draw out the information about specific temporal patterns. Here, ANOVA was used to determine spatial and temporal variation in mean GI and preplanned orthogonal contrasts to delineate spawning within the annual cycle. In addition, there has been a trend to use statistical methods to assess spawning over time (Table 7). Before 2000, 11 of 105 papers (ca. 10%) used a statistical test to determine when spawning occurred. Since then, 34 of 62 papers (ca. 55%) have used these techniques.

Maine Management Plan

Green sea urchins have been harvested commercially in Maine, United States, because landings have been recorded (1964, 55 mt) (DMR 2014). A large-scale fishery developed subsequent to the sampling conducted in 1987. Peak landings occurred in 1993 (18,800 mt, worth $26.8 million); however, by 1997, landings fell below 10,000 mt, and, by 2012, had declined to precommercial levels at 863 mt (DMR 2014). Currently, the DMR management plan focuses on four major harvesting constraints. The first is based on perceived regional differences in the timing of reproduction that is denoted by a line near mid-coast that divides the state into two management zones. ‘‘Zone 1’’ extends from the Maine/New Hampshire boarder to the mouth of the Penobscot River. ‘‘Zone 2’’ continues from the off-shore islands in Penobscot Bay to the Canadian border (see Fig. 2 in Chen & Hunter 2003). A person may hold a license from only one zone. The second constraint relates to urchin reproductive cycles within each zone that sets the harvest seasons. The third and fourth address limited entry and minimum and maximum size limits, respectively. The zones reflect inherent differences in seawater temperatures and nutrients between the two regions (Townsend et al. 2010), and because this study found that between 55% and 77% of the variation in mean GI can be explained by seawater temperature, it would appear that continued use of these zones is justified. Four of the nine sites in this study are in Zone 1, with spawning at each occurring between April and May (Figs. 5–6). Spawning at the remaining five sites was more variable temporally (Figs. 6–7). Also, the interannual variability shown by a comparison with earlier and later urchin studies in Maine (Cocanour & Allen 1967—Lamoine, Gaudette et al. 2006—Boothbay Harbor) attests to the extreme variability in spawning along the coast of Maine. Because of the large variability observed in GI both within and between sampling sites, and interannually within a subset of the sampling sites through time (Cocanour & Allen 1967, Seward 2002, Gaudette et al. 2006), potential differences in reproduction and spawning (even if not so subtle) were unable to be discerned, and limits the refinement of current management practices in Maine.

Gonad Index and a HW

Because GI is a relative measure of reproduction (timing and effort), it is readily subject to differing views and interpretations (Ebert et al. 2011, Ouréns et al. 2012). It would be desirable to standardize the measure of GI so that researchers, resource managers, and commercial enterprises have a common reference and understanding of what the results mean. To this end, Ebert et al. (2011) (using gonad wet weight) and Ouréns et al. (2012) (using gonad dry weight) both developed allometric models to calculate GI. A detailed understanding of spawning cycles, especially possible triggers (Kirchhoff et al. 2010) and duration (Byrne et al. 1998), would provide the basis for developing specific models for identification of what is termed here as ‘‘harvest windows’’. These windows (based on location-specific GI, e.g., estuaries, bays, inlets, lagoons, and islands) represent segments of time (days, weeks, months, etc.) during the general spawning season when GI are at or above 10% (e.g., see Fig. 4, Schoodic Point) (10% represents the minimal commercial standard in Maine (Vadas et al. 2000). By focusing on initiation of harvesting at 10% and termination at the first signs of ‘‘melt’’ (wide-spread) release of gametes from goniducts on the aboral surface), the windows would retain (conserve) a residual population of small urchins for further growth and large urchins for breeding stock. These windows could be adjusted by increasing or decreasing GI values to enhance sustainability and conservation efforts. Ouréns et al. (2011) concluded that understanding the reproductive cycle would provide a tool (guide) for management, allowing sea urchins to spawn several times during their life span before being harvested. The concept of HW would be a refinement of this management tool.

A typical cycle for *Strongylocentrotus droebachiensis* in Maine would include ‘‘prematuration’’ (fall development of roe contents and gonad growth), ‘‘maturation’’ (winter), ‘‘spawning and melt’’ (spring) and ‘‘recovery’’ (summer) (see also Byrne 1990, Harrington et al. 2007). Unless tested statistically, the small peaks and downturns in GI (fractional spawning) should be considered as sampling noise. A statistical approach for identifying and analyzing these events may permit the development of predictive relationships at local scales. Such predictors may enhance the analysis of multiple factors (different salinities, foods, temperatures, etc.) and therefore provide greater insight for determining when to set the initiation and termination points of HW. Detecting the termination phase (as soon as melting is recognized at the site) will be difficult because of the wide variability in spawning (as shown here). Such information will permit the integration of predictions into management strategies to provide better estimates of marketing and conservation of immature urchins with little roe and legal sized urchins with melted roe, respectively. The search for appropriate HW may provide another tool for harvesting and sustaining urchin populations with quality roe.

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