Disease as a control of sea urchin populations in Nova Scotian kelp beds

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ABSTRACT: In Nova Scotia, Canada, periodic outbreaks of amoebic disease (paramoebiasis) cause mass mortality of sea urchins *Strongylocentrotus droebachiensis* in subtidal barrens. However, in kelp beds, where sea urchins are cryptic and generally less dense than in barrens, disease outbreaks are not readily observed and the importance of disease in regulating these populations is unknown. To determine whether sea urchin populations in kelp beds are controlled by disease, we analyzed population data from kelp beds at a single location (St. Margarets Bay) across a span of 44 yr (1968 to 2012) to compare changes in size structure and density in relation to the timing of disease outbreaks in adjacent sea urchin aggregations and barrens. We found that sea urchin density, maximum test diameter and percentage of adults decreased following disease outbreaks and increased during intervening periods without disease, indicating that disease regulates the population in kelp beds by limiting survival to adulthood. Our results suggest that disease has replaced predation as a major agent controlling sea urchin populations in Nova Scotian kelp beds.

KEY WORDS: *Strongylocentrotus droebachiensis* · Disease · Phase shift · Predation · Kelp beds

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INTRODUCTION

Sea urchins are dominant grazers in kelp forests worldwide and can destructively graze kelps to the extent of causing a phase shift to barrens — which is generally considered an alternative state of a collapsed kelp ecosystem (Filbee-Dexter & Scheibling 2014). Shifts to barrens are associated with a marked loss of species diversity, habitat complexity, and community productivity (Mann 1982). Therefore, understanding factors that control sea urchin populations and maintain resilience of the kelp state is of urgent concern for conservation and management of these valued ecosystems. Historically, predation is thought to have been the major controlling agent of sea urchin abundance in kelp-dominated ecosystems (reviewed by Estes & Duggins 1995, Scheibling 1996, Sala et al. 1998). Overfishing or overhunting of urchin predators, such as sea otters, demersal fish or large crustaceans, has had cascading trophic-level

effects leading to the formation of urchin barrens in cold temperate regions throughout the world (reviewed by Tegner & Dayton 2000, Jackson et al. 2001, Steneck et al. 2002). Disease also can play an important role in controlling sea urchins, and accounts for the boom-bust population dynamics (Uthicke et al. 2009) observed in some kelp systems (Scheibling 1984a, Lafferty 2004). Overfishing of predators can have indirect negative effects on sea urchins if the incidence of disease increases with the density of the host population (Tegner & Dayton 2000, Behrens & Lafferty 2004, Lafferty 2004). However, the extent to which disease can replace the functional role of predation as the major agent of population control of sea urchins in kelp ecosystems remains equivocal (Lafferty 2004).

Along the Atlantic coast of Nova Scotia, population outbreaks of green sea urchins *Strongylocentrotus droebachiensis* drive phase shifts from kelp beds to barrens (Johnson & Mann 1988, Scheibling et al.

1999, Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007), whereas outbreaks of amoebic disease (paramoebiasis) cause mass mortality of sea urchins in barrens and aid the reverse shift back to kelp beds (Miller 1985, Scheibling 1986). Population outbreaks of *S. droebachiensis* were first documented in Nova Scotia in the late 1960s and early 1970s in St. Margarets Bay, a large semi-protected embayment near Halifax, and were attributed to a release from predation as a result of overfishing of sea urchin predators such as finfish (reviewed by Scheibling 1996). During the 1970s, kelp beds in St. Margarets Bay transitioned to barrens due to destructive grazing by dense aggregations of adult sea urchins within and along the margins of the beds (Breen & Mann 1976). Prior to these sea urchin outbreaks, kelp beds in the bay were thought to represent a stable ecosystem (Mann 1972a,b). Barrens persisted as the dominant state of the rocky subtidal ecosystem until the early 1980s, when outbreaks of paramoebiasis decimated sea urchins in barrens within the bay and along the entire Atlantic coast of Nova Scotia (Scheibling 1984a). Outbreaks of paramoebiasis have since increased in frequency along this coast in association with severe storm events and warming temperatures, which may play a role in the introduction and spread of the pathogenic agent (Scheibling & Lauzon-Guay 2010, Scheibling et al. 2013). Since the early 1980s, kelp beds have persisted in St. Margarets Bay, and barrens have not been observed (except on 2 occasions). In the summer/fall of 1992 and 2003, aggregations of sea urchins migrating from offshore sand bottoms, where temperatures are below a threshold for disease (~10°C, Brady & Scheibling 2005), began destructively grazing kelps along the western shore of the bay (Scheibling et al. 1999, Lyons & Scheibling 2008). However, these advancing grazing fronts were eliminated by outbreaks of paramoebiasis (in the fall of 1995 and 2003) before the transition to barrens was complete.

In kelp beds, where sea urchins are cryptic and generally less dense than in grazing fronts or barrens (Meidel & Scheibling 1998), disease outbreaks are not readily observed and the importance of disease in regulating urchin populations is unknown. To determine whether the populations within kelp beds have been controlled by outbreaks of disease, we analyzed sea urchin population data collected over 44 yr (1968 to 2012) from kelp beds in St. Margarets Bay. We compared changes in population size structure and density in relation to the timing of outbreaks of paramoebiasis in adjacent sea urchin aggregations

and barrens, and our results suggest that disease has replaced predation as a major agent controlling sea urchin populations in Nova Scotian kelp beds.

MATERIALS AND METHODS

To characterize sea urchin populations in kelp beds in St. Margarets Bay, we compiled records of sea urchin population size structure and density in kelp beds at Mill Cove (44° 36' N; 64° 04' W) or adjacent sites (within a 10 km radius) within the bay, from 17 yr of published and unpublished data collected over a span of 44 yr between 1968 and 2012 (Table 1). Sampling protocols varied slightly among studies. In surveys conducted in 1968, 1973, and 1977, 1992 to 1995, and 2009 to 2012, divers destructively sampled 0.25, 0.5 or 1.0 m^2 quadrats placed randomly along transect lines or haphazardly on the seafloor within the kelp bed, and counted and measured (test diameter, mm) all sea urchins within each quadrat. In surveys from 1982 to 1990 divers haphazardly sampled the kelp bed by overturning boulders over an area of ~1000 m^2 and counted and measured (test diameter, mm) all sea urchins encountered in 2 to 5 person-hours of searching. Sampling from 1982 onwards was conducted in kelp beds that were re-established following mass mortality of sea urchins in former sea urchin barrens in 1980 and 1981 (Miller 1985). In all studies, divers searched for small and cryptic sea urchins under boulders and cobbles, in crevices and amongst turf algae. Kelp biomass varied from 1.1 to 5.2 kg m^{-2} (Table 1) with two exceptions: in 1968 when biomass was unusually high (20.1 kg m^{-2}; Breen & Mann 1976) and in 2012 when it was unusually low (~0.1 kg m^{-2}; J. O'Brien & R. E. Scheibling unpubl. data).

To examine whether disease regulates population size structure of sea urchins within kelp beds, we examined 14 yr of available data (between 1982 and 2012) for changes in (1) the mean test diameter of the largest 5% of the population and (2) the percentage of the population composed of adults (>20 mm test diameter, Meidel & Scheibling 2001) in relation to the timing of outbreaks of paramoebiasis recorded in adjacent barrens or among experimentally transplanted sea urchins in kelp beds in St. Margarets Bay. These metrics of population size structure indicate whether recruits are surviving to adulthood and adults are increasing in size (age). Since only size-frequency distributions (rather than individual urchin test diameters) are available for some years, the mean test diameter of the largest 5% of the pop-

Table 1. *Strongylocentrotus droebachiensis.* Sampling protocols of studies used to construct a time series (1968 to 2012) of sea urchin population data in kelp beds in St. Margarets Bay (SMB). 'Data' is the type of data available from each study: population density (D) and/or size frequency (S). TD = sea urchin test diameter. ND = no data. A single 0.5 m^2 quadrat was also sampled within a barren patch in the kelp bed in 1973

Date	Location	Depth (m)	Sampling method	Urchin size sampled (TD, mm)	Data	Source
1968	Within SMB	0–20	0.25 m^2 quadrats (n = 165)	>9	D	Miller & Mann (1973)
1973	Western shore SMB	4–12	0.5 m^2 quadrats (n = 6)	>5	D,S	Breen & Mann (1976)
1977	Boutilier Point, SMB	0–10	0.25 m^2 quadrats (n = 10)	ND	D	Chapman (1981)
Dec 1982, Jun, Sep 1983, Jun, Jul, Sep 1984, Jul 1985, May 1986	Mill Cove, SMB	8–10	Haphazard search (2–4 person-hours)	>1–2	S	Raymond & Scheibling (1987)
Jul 1989 Jun 1990	Mill Cove, SMB	5–6 5–9	Haphazard search (4–5 person-hours)	>1–2	S	R. E. Scheibling (unpubl. data)
Jun 1992, Oct 1993, Aug 1994, Aug 1995	Mill Cove, SMB	6–10	1 m^2 quadrats (n = 4–10)	>2	D, S	Scheibling et al. (1999)
Jun 2009 Jun 2010 Jun 2012	Birchy Head, SMB Birchy Head & Mill Cove, SMB Mill Cove, SMB	8–10	1 m^2 quadrats (n = 8–15)	>2	D, S	This study

ulation was calculated as a weighted mean of the median test diameters of the sea urchin size classes containing the largest 5 % of the population ($\bar{x}_w$):

$$\bar{x}_w = \frac{\sum_{i=1}^{N} (w_i x_i)}{\sum_{i=1}^{N} w_i}$$

where x_i is the median test diameter of size class i, w_i is the proportion of sea urchins within that size class, and N is the total number of sea urchin size classes. For each weighted mean, we calculated a weighted standard deviation (sd_w):

$$sd_w = \sqrt{\frac{\sum_{i=1}^{N} w_i (x_i - \bar{x}_w)^2}{\frac{(N-1)\sum_{i=1}^{N} w_i}{N}}}$$

The package 'SDMTools' for R (Institute for Statistics and Mathematics of the Wirtschaftsuniversität (WU) Wien) was used for both calculations.

To determine whether disease regulates sea urchin abundance within kelp beds, we also examined changes in sea urchin density within the kelp bed in relation to the timing of disease outbreaks for 7 yr of available data between 1992 and 2012.

RESULTS AND DISCUSSION

The population size structure of *Strongylocentrotus droebachiensis* in kelp beds in St. Margarets Bay varied in relation to outbreaks of paramoebiasis between 1980 and 2012. Outbreaks of disease were observed in sea urchin aggregations or barrens in the bay in fall 1980 and 1981 (Miller 1985), 1995 (Scheibling & Hennigar 1997) and 2003 (Lyons & Scheibling 2008), and at the site of sea urchin transplantation experiments (that measured spatial patterns of disease) in fall 2009 (Scheibling et al. 2010), 2010 (Feehan et al. 2012), 2011 (Feehan et al. 2013) and 2012 (Scheibling et al. 2013) (Fig. 1). The mean test diameter of the largest 5 % of the sea urchin population in the re-established kelp bed at Mill Cove increased significantly from December 1982 to August 1995, when there was no sign of disease in St. Margarets Bay (Figs. 1A & 2). This is consistent with a significant increase in the percentage of adults in the population, from 0 to ~30 %, over the same period (Figs. 1B & 2). The mean test diameter of the largest 5 % of the population in 1984 (20 mm) approximates the size at maturity of *S. droebachiensis*, indicating that the population was composed almost exclusively of juveniles at this time. Growth experiments by Raymond & Scheibling (1987) indicate that *S. droebachiensis* takes ~2.5 yr to reach maturity. The sea
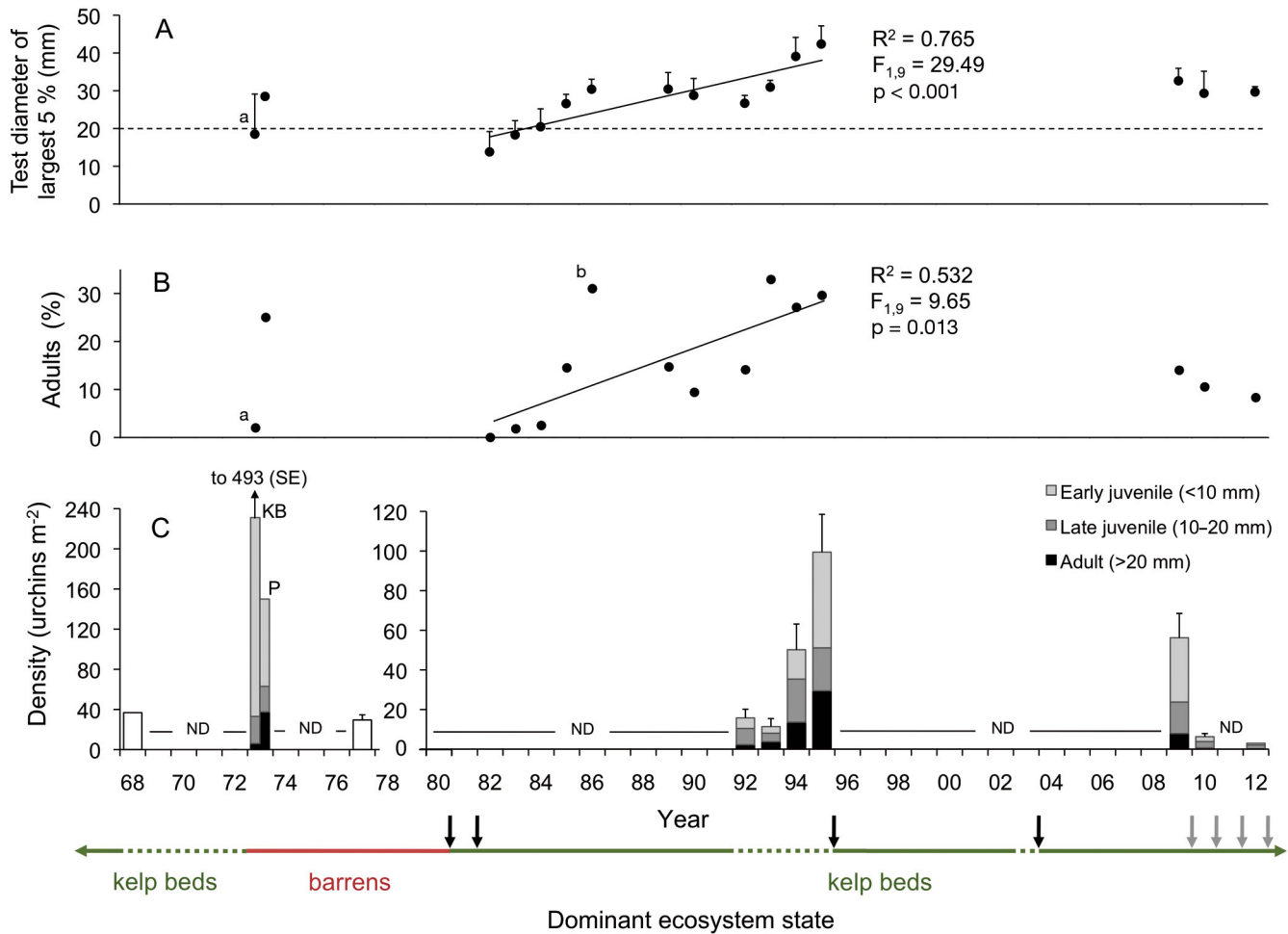
Fig. 1. *Strongylocentrotus droebachiensis.* (A) Mean test diameter (mm) of the largest 5% of the sea urchin population in kelp beds in St. Margarets Bay (SMB). The horizontal dashed line indicates average size at maturity (20 mm). Error bars are standard deviation of mean test diameter of the largest 5% of the population. (B) Percent of the population composed of adults (>20 mm test diameter) in 15 years for which data were available between 1973 and 2012. For the years 1982 to 1995 (n = 11 for each regression), linear regression shows a significant positive relationship between mean test diameter of the largest 5% of the population and year (A), and percent of the population composed of adults and year (B). (C) Mean sea urchin density in kelp beds in SMB (urchins m^{-2}, total bar) divided into 3 size groups of sea urchins (early juvenile, <10 mm; late juvenile, 10–20 mm; adult, >20 mm) in 10 yr for which data were available (1968–2012). Bars with no shading are total density when size-class data were not available. Error bars are standard error (SE) of mean total population density. Data in 1973 are for sea urchins in grazed patches within the kelp bed (P) and in the surrounding kelp bed (KB). The dominant ecosystem state in SMB is shown for the timeframe of the study: dashed sections indicate the initiation of urchin barrens due to destructive grazing by sea urchins. Black arrows (1980–2003) indicate outbreaks of paramoebiasis in barrens in SMB. Grey arrows (2009–2012) indicate outbreaks of paramoebiasis in experimentally transplanted sea urchins in the kelp bed. ND = No data. Data sources and sampling protocols are given in Table 1. [a]Data in 1973 were strongly influenced by a heavy sea urchin recruitment event within the kelp bed (Meidel & Scheibling 2001). [b]The outlier is based on a sample collected in May 1986, prior to the annual peak in settlement of *S. droebachiensis* in Nova Scotia (June/July; Balch & Scheibling 2000). Because sampling was conducted prior to a peak in settlement, early juveniles were rare in the kelp bed and the percent of the population composed of adults was consequently high (see also Fig. 2)

Fig. 2. *Strongylocentrotus droebachiensis.* Size-frequency distribution of sea urchin test diameters (mm) in kelp beds in St. Margarets Bay (SMB), Nova Scotia for 14 yr for which data were available between 1982 and 2012, and in barren patches grazed by sea urchins within the kelp bed in 1973. Red arrows indicate a disease outbreak in adjacent sea urchin aggregations and barrens. Vertical lines indicate size-groups of sea urchins (early juvenile, <10 mm; late juvenile, 10–20 mm; adult, >20 mm). The percent of the population composed of adults is shown for each year. Horizontal dashed lines indicate breaks in the data record. n = number of individuals sampled. Data sources and sampling protocols are given in Table 1
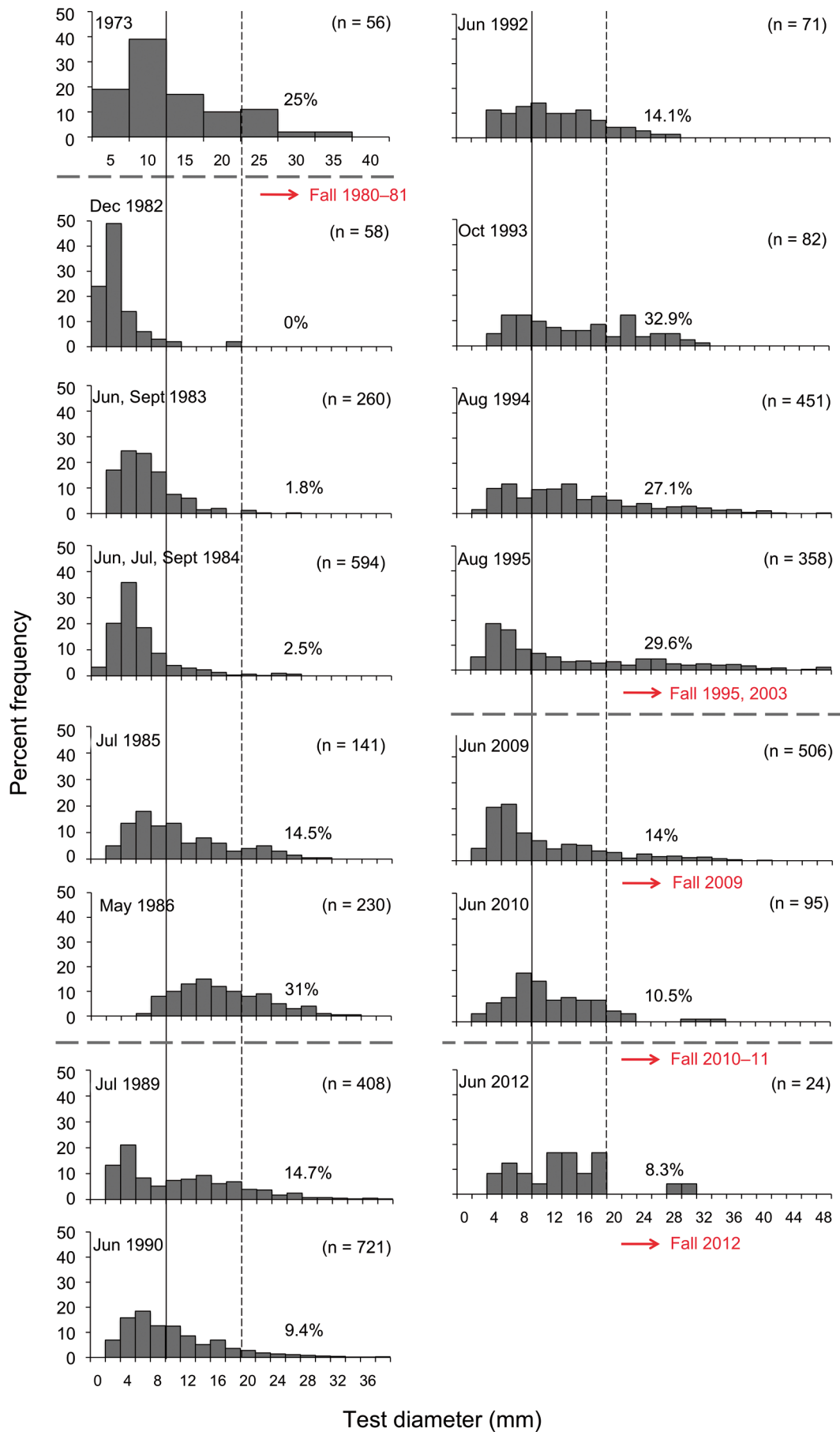
Test diameter (mm)

urchin population recovered from the 1981 disease outbreak after ~4 yr, as indicated by the test diameter of the largest 5% of the population and percentage of adults from 1985 to 1995 (31.9 ± 2.0 mm and 21.7 ± 3.3%, mean ± SE), which are comparable to baseline data from 1973 (28.5 mm and 25%, in a grazed patch within the kelp bed) before paramoebiasis was recorded in Nova Scotia (Fig. 1A,B). Recurrent disease outbreaks from 2009 to 2012 were followed by a decrease in both the mean test diameter of the largest 5% of the population and the percentage of adult sea urchins (Fig. 1A,B). Collectively, these temporal patterns in the size structure of the population suggest that disease has been limiting the survival of sea urchins to adulthood in kelp beds in St. Margarets Bay.

Changes in sea urchin density within kelp beds in relation to the timing of outbreaks of paramoebiasis provides a second line of evidence that disease is controlling sea urchin populations in St. Margarets Bay. Annual records of sea urchin density in kelp beds in the bay are available from 1992 to 1995 and 2009 to 2012 (excluding 2011). In the absence of disease outbreaks between June 1992 and August 1995, sea urchin population density increased significantly within the kelp bed (ANOVA, $F_{3,23} = 9.05$, p < 0.001), from ~16 to 100 urchins m^{-2}, with adult density increasing 15-fold (Fig. 1C). Sea urchin density decreased significantly ($F_{2,29} = 21.49$, p < 0.001), from ~60 to 3 urchins m^{-2}, following recurrent outbreaks of paramoebiasis from 2009 to 2011. By June 2012, adult sea urchins were rare within the kelp bed (0.25 urchins m^{-2}). The density of adult sea urchins observed in the kelp bed in 1995 (~29 urchins m^{-2}) is below that observed in the early 1970s, during a sea urchin population outbreak that led to destructive grazing of the kelp bed (38 urchins m^{-2} in 1973). These results, combined with the observed mass mortality events in 1995 and 2003, which arrested destructive grazing by an advancing sea urchin front at the deep margin of the kelp bed (Scheibling et al. 1999, Lyons & Scheibling 2008), suggest that disease exerts an important control on sea urchin populations within kelp beds in St. Margarets Bay. In consequence, there is a reduced potential for a phase shift from kelp forest to barrens.

Although this study covers a large temporal scale, it is limited spatially to a single site. To investigate potential variability in sea urchin density on the scale of kilometres, we sampled 10 sites throughout St. Margarets Bay in June 2010 (including Mill Cove), separated by 1.5 to 12.5 km (linear distance). These results indicate that mean sea urchin density (sam-pled in 1 m^2 quadrats, n = 8 per site) ranged from 1.1 to 11.2 urchins m^{-2}, with a grand mean (± SD) of 5.0 ± 3.3 urchins m^{-2} for the 10 sites (C. J. Feehan unpubl. data). Mean densities in June 2010 at Mill Cove (6.9 ± 7.7 urchins m^{-2}) and Birchy Head (5.0 ± 1.4 urchins m^{-2}), the sites used in our analysis (Table 1), approximate the grand mean for all 10 sites.

Along the coasts of Norway and Maine (USA) the major factors thought to control populations of *Strongylocentrotus droebachiensis* are settlement failure due to temperature-related mortality of sea urchin larvae (Fagerli et al. 2013) and predation by large decapods (Steneck et al. 2013), respectively. Peak settlement of sea urchins on artificial (plastic turf) collectors at Mill Cove in 2010 (mean ± SD, n = 4 collectors: 100 ± 68 settlers m^2; C. J. Feehan unpubl. data) was similar to that recorded on similar collectors from 1992 to 1994 (mean ± SD, n = 4 yr: 110 ± 143 settlers m^{-2}; Balch & Scheibling 2000), indicating little change in peak settlement over ~2 decades. Despite mass mortalities of shallow populations of sea urchins in St. Margarets Bay, reproductive populations in deeper waters (where sea urchins have a thermal refuge from disease) may provide a relatively constant source of larvae (Filbee-Dexter & Scheibling 2012 and unpubl. data). The only predator abundance data available for St. Margarets Bay over the period of our study is catch per unit effort (CPUE) for lobster *Homarus americanus* (Lobster Fishing Area 33 East, Department of Fisheries and Oceans Canada [DFO] 2011). Although CPUE increased from 1990 (~0.15 kg trap^{-1}) to 2010 (~0.35 kg trap^{-1}), there was no change in CPUE between 1992 and 1995 (~0.15 kg trap^{-1}) when sea urchin density increased significantly in St. Margarets Bay (Fig. 1C). These data provide no evidence for a link between lobster abundance and sea urchin density in St. Margarets Bay, which is consistent with results of an earlier study (Scheibling 1984b).

Outbreaks of paramoebiasis are increasing in frequency along the coast of Nova Scotia due to changing oceanographic conditions associated with a changing ocean climate (Scheibling & Lauzon-Guay 2010, Scheibling et al. 2013). Large embayments such as St. Margarets Bay may be hotspots for paramoebiasis due to warmer peak temperatures and longer residence times of seawater, relative to the exposed coast (Feehan et al. 2012). Recurrent disease outbreaks between 2009 and 2012 have nearly eliminated sea urchins in St. Margarets Bay. Based on the observed trend in disease outbreaks, we predict that populations of *Strongylocentrotus droebachiensis* will likely not recover in the shallow

subtidal zone of the bay. In the absence of destructive grazing aggregations of sea urchins, kelp beds along the coast of Nova Scotia should persist for the foreseeable future. However, these kelp beds may be undergoing a new phase shift to turf algae dominance (e.g. filamentous red algae *Polysiphonia lanosa* and *Bonnemaisonia hamifera*), as evidenced by unusually low kelp density in St. Margarets Bay in 2012 (J. O'Brien & R. E. Scheibling unpubl. data). In recent years, large-scale shifts of perennial macrophytes to ephemeral filamentous algae have occurred in temperate regions throughout the world, in association with eutrophication, climate change, and changes in grazing pressure, epibionts and sedimentation (Eriksson et al. 2002, Connell et al. 2008, Anderson et al. 2011, Moy & Christie 2012, Wernberg et al. 2013). It remains to be seen whether large-scale shifts to turf algae also are occurring along the coast of Nova Scotia, and how this may alter the dynamics of kelp beds, sea urchins and disease.

Transmission of paramoebiasis is dosage dependent (Scheibling & Stephenson 1984); therefore, the extent and severity of a disease outbreak in barrens will likely influence the rate of mortality of sea urchins in adjacent kelp beds. In 1980 and 1981, widespread disease outbreaks caused near complete mortality of sea urchins in shallow barrens (<25 m depth) across 100s of kilometres (linear distance) of Nova Scotian coastline (Scheibling 1986). The broad spatial extent of the host population in barrens at this time likely facilitated the propagation of the amoebic pathogen, accounting for the absence of adult sea urchins within the kelp bed in St. Margarets Bay in December 1982 (Figs. 1A,B & 2). In contrast, there were some surviving adult sea urchins in the kelp bed following disease outbreaks in 2009 to 2011 (Figs. 1A,B & 2). In recent years sea urchin barrens have been discontinuous along the coast, and absent within St. Margarets Bay. This lower density of the host sea urchin population may account for the survival of some sea urchins following recent disease outbreaks.

Predation has long been considered the major controlling agent of sea urchin abundance in kelp beds (Scheibling 1996). Although the settlement rate of *Strongylocentrotus droebachiensis* is similar in kelp beds and barrens in Nova Scotia, populations are generally less dense in kelp beds (Balch & Scheibling 2000). This pattern has been attributed to higher post-settlement mortality of sea urchins in kelp beds due to a higher abundance of predators. Sea urchin population outbreaks in St. Margarets Bay in the late 1960s and early 1970s were associated with a long-

term reduction in predation pressure due to overfishing (reviewed by Scheibling 1996), and this may have contributed to major recruitment pulses during this period (Hart & Scheibling 1988, Meidel & Scheibling 2001). Despite the impact of historical overfishing, predation likely remains an important source of sea urchin post-settlement mortality in Nova Scotian kelp beds.

Strongylocentrotus droebachiensis is most susceptible to predation during the late juvenile to early adult life stage, since small juveniles can effectively utilize spatial refuges from predators (e.g. small-mouthed fish, decapod crustaceans, sea stars) and larger adults have a size refuge from most predators (Scheibling & Hamm 1991). This can create a bottleneck in the development of an adult population that results in a bimodal size frequency distribution (Scheibling 1996). Therefore, in a situation where predation is the primary control of population growth, we expect that the size of the largest adults in a developing population would progressively increase as some individuals escape predation, but there would be a lag in the increase in the proportion of adults due to the bottleneck. We did not observe a bimodal size distribution (Fig. 2), providing evidence that predation is not the major control of sea urchin populations in kelp beds in St. Margarets Bay. There does appear to be a slight lag in the increase in the percentage of adults from 1982 to 1984, which may indicate that predation was impeding the initial establishment of the sea urchin population. However, recruitment in the early 1990s resulted in an exponential increase in the adult density (Fig. 1C), suggesting that predation alone cannot prevent the establishment of sea urchin populations within these kelp beds. In contrast, sea urchins were decimated by recurrent disease outbreaks in 2009 to 2011 (Fig. 1C). The non-occurrence of sea urchin population outbreaks and the attendant formation of barrens in St. Margarets Bay in recent decades (since disease was first recorded in 1980) suggests that disease has replaced predation as the major agent controlling sea urchin populations.

Lafferty (2004) investigated the effects of fishing for sea urchin predators on sea urchin density and incidence of disease. Using a 20 yr dataset of kelp forest communities at Channel Islands National Park, California, he found that outbreaks of bacterial disease in sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus* and *Lytechinus anameus*) were more frequent outside of a marine reserve than inside the reserve (where protected populations of spiny lobster

Panulirus interrutus limited the population abundance of sea urchins). In Nova Scotia, the first documented outbreaks of paramoebiasis also were associated with high sea urchin densities in barrens. However, in contrast to the situation in Nova Scotia, bacterial disease in California did not fully replace predation in controlling sea urchin populations, as evidenced by sustained high densities of urchins and overgrazing of algae outside of the reserve.

Herbivorous sea urchins have been impacted by disease in other coastal ecosystems worldwide. However, apart from Nova Scotia, the only documented case of widespread (100s of km) mass mortality was an outbreak of an unidentified pathogen that decimated *Diadema antillarum* on coral reefs throughout its geographic range in the Caribbean in 1983 (Lessios 1988). In Norway, *Strongylocentrotus droebachiensis* is infected by an endoparasitic nematode, *Echinomermella matsi,* which decreases reproductive output and survival of adult sea urchins (Hagen 1992, Stien et al. 1998, Stien 1999) but does not cause mass mortality or phase shifts from barrens to kelp beds (Stien et al. 1995, reviewed by Norderhaug & Christie 2009). Bald sea urchin disease, a bacterial infection of sea urchins, has caused localized mass mortalities of sea urchins *Diadema* aff. *antillarum* in the Canary Islands, Spain (Dyková et al. 2011), *Paracentrotus lividus* in the Canary Islands and northwest Mediterranean (Boudouresque & Verlaque 2007, Girard et al. 2012), and *Strongylocentrotrus franciscanus* and *S. purpuratus* in the North Pacific (Rogers-Bennett 2007). While these systems are characterized by localized transitions from sea urchin barrens to macroalgal beds, the role of bacterial or macroparasitic disease in mediating these phase shifts is yet to be determined. This may be due in part to the interplay of multiple factors affecting sea urchin populations, such as recruitment variability and harvesting (Sala et al. 1998, Boudouresque & Verlaque 2007). Longitudinal studies, as we have shown here, can be particularly useful in elucidating the role of disease in controlling sea urchin populations in complex and dynamic marine ecosystems.

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