Disease outbreaks associated with recent hurricanes cause mass mortality of sea urchins in Nova Scotia

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ABSTRACT: Field observations and laboratory experiments support the hypothesis that disease-induced mass mortality of the sea urchin *Strongylocentrotus droebachiensis* can be associated with hurricane events that introduce a pathogenic amoeba *Paramoeba invadens* to coastal waters. The temporal pattern of morbidity and mortality of sea urchins observed in a large embayment on the Atlantic coast of Nova Scotia following Hurricane Juan in September 2003 and Hurricane Bill in August 2009, and in laboratory infection experiments during the 2009 event, closely conformed to that expected based on the known temperature-dependent dynamics of this amoebic disease.

KEY WORDS: Disease · Mass mortality · Sea urchin · Kelp beds · Temperature · Pathogen · Hurricane

INTRODUCTION

Outbreaks of disease can have catastrophic effects on marine populations that alter the structure and function of whole ecosystems (e.g. seagrass beds, Muelhstein 1989; coral reefs, Lessios 1988; kelp beds, Scheibling 1984). There is mounting evidence that the frequency and severity of disease outbreaks are increasing across a broad range of marine taxa (Harvell et al. 2002, Ward & Lafferty 2004). The increased prevalence of disease has been linked to anthropogenic stressors, including global climate change (Harvell et al. 1999, 2002, Lafferty et al. 2004, Mydlarz et al. 2006). Consequently, understanding the causes of disease and the spatial and temporal patterns of outbreaks in marine populations is becoming increasingly important to ecologists and resource managers.

Echinoderms are host to a variety of marine pathogens and parasites, and disease-mediated mass mortalities of sea stars and sea urchins provide striking examples of cascading trophic effects on community structure (reviewed by Tajima & Lawrence 2001, Uthicke et al. 2009). Along the Atlantic coast of Nova Scotia, an amoebic disease affecting the sea urchin *Strongylocentrotus droebachiensis* is the primary driver of transitions between alternative states of the rocky subtidal ecosystem (Scheibling 1984, Lauzon-Guay et al. 2009). Outbreaks of this disease are associated with warm sea temperatures in late summer and fall, and disease transmission and progression are strongly temperature dependent (Miller & Colodey 1983, Scheibling & Stephenson 1984, Miller 1985, Scheibling 1986, Scheibling & Hennigar 1997, Brady & Scheibling 2005). Scheibling & Hennigar (1997) reviewed evidence suggesting the pathogenic agent *Paramoeba invadens* (Jones 1985, Jones & Scheibling 1985) is a nonindigenous species, delivered episodically to this coast by warm water masses. They proposed 2 potential meteorologic/oceanographic mechanisms for advective transport of planktonic amoebae across the continental shelf: entrainment of water masses by Gulf Stream eddies and large-scale mixing by hurricanes. In support of the latter hypothesis, they found that an index of tropical storm or hurricane intensity in the northwest Atlantic Ocean south of Nova Scotia over a 20 yr period (1976 to 1995) was greatest in 5 out of 6 yr when disease outbreaks resulting in sea urchin mass mortality were documented.

Here we report on localized mass mortalities of sea urchins *Strongylocentrotus droebachiensis* in a large bay on the Atlantic coast of Nova Scotia after 2 hurricanes, Hurricane Juan and Hurricane Bill, which made landfall or passed close to the coast in 2003 and 2009, respectively.

MATERIALS AND METHODS

Field observations of sea urchin mortality. In summer and fall of 2003 and 2009, studies were underway to monitor grazing aggregations of sea urchins within kelp beds in St. Margarets Bay, Nova Scotia, when hurricanes struck: Hurricane Juan on 29 September 2003 and Hurricane Bill on 23 August 2009. These studies fortuitously provided prestorm measures of sea urchin abundance and enabled us to quantify rates of urchin morbidity and mortality following the passage of each storm. The study sites were located on the western shore near the mouth of the bay and within 1 km of each other: Birchy Head (44° 35′ N, 64° 03′ W) in 2003 and The Lodge (44° 33′ N, 64° 01′ W) in 2009 (Fig. 1). The rocky subtidal zone throughout much of St. Margarets Bay is composed of granitic boulders and cobbles that generally grade to fine sand at depths

between 8 and 20 m (below chart datum). This zone is covered by luxuriant algal beds (mainly kelps *Saccharina longicruris* and *Agarum clathrata*) during periods when sea urchins are in relatively low abundance (Mann 1972).

At Birchy Head, sea urchins had formed a grazing aggregation (front) at 7 m depth along the lower margin of the algal bed when observations began at this site in spring 2003 (Lyons & Scheibling 2008). Sea urchin density was measured along a 60 m long section of the front on 16 June 2003, before Hurricane Juan, and on 18 October, after mass mortality of *Strongylocentrotus droebachiensis* had occurred (Lyons & Scheibling 2008).

At The Lodge, 14 000 sea urchins were transplanted to a dense kelp bed on 14 July 2009 as part of a large manipulative experiment we were conducting to test the effects of urchin density and disturbance (gaps in the kelp canopy) in triggering destructive grazing. The experimental urchins were collected at a site (Splitnose Point: 44° 29′ N, 63° 33′ W) 40 km ESE of The Lodge (Fig. 1) with the aid of urchin fishers, transported by boat in plastic fish crates and released in 5 m² circular plots, spaced at 7 m intervals (between plot centers) in a rectangular array (24 × 53 m) at 7 to 10 m (chart datum) depth. Sea urchin density treatments (0, 50, 100 and 200 urchins m^{-2}) were randomly assigned to 32 plots in a randomized block design. Density decreased sharply in the first 2 wk of the experiment, as urchins fell prey to lobsters and crabs and succumbed to injuries associated with collection and transplantation. Some urchins also may have dispersed into the kelp bed around the experimental plots, although urchins generally move little in dense kelp. Approximately 3500 urchins were distributed along the deep margin of the kelp bed at 18 m depth at the start of the experiment. To compensate for losses in the experimental array, an additional 10 % of the original number of urchins in each plot was added on 1 August from this pool of surplus urchins. Live urchins and their tests were counted in each plot at 1 wk intervals until 10 September in contiguous 0.25 m² quadrats along 4 radial transects (1.75 to 3.25 m long, transect length was progressively increased as urchins spread outwards to graze kelp) extending from the plot center in each cardinal direction (n = 13 to 25 quadrats per plot). On 17 September, once the
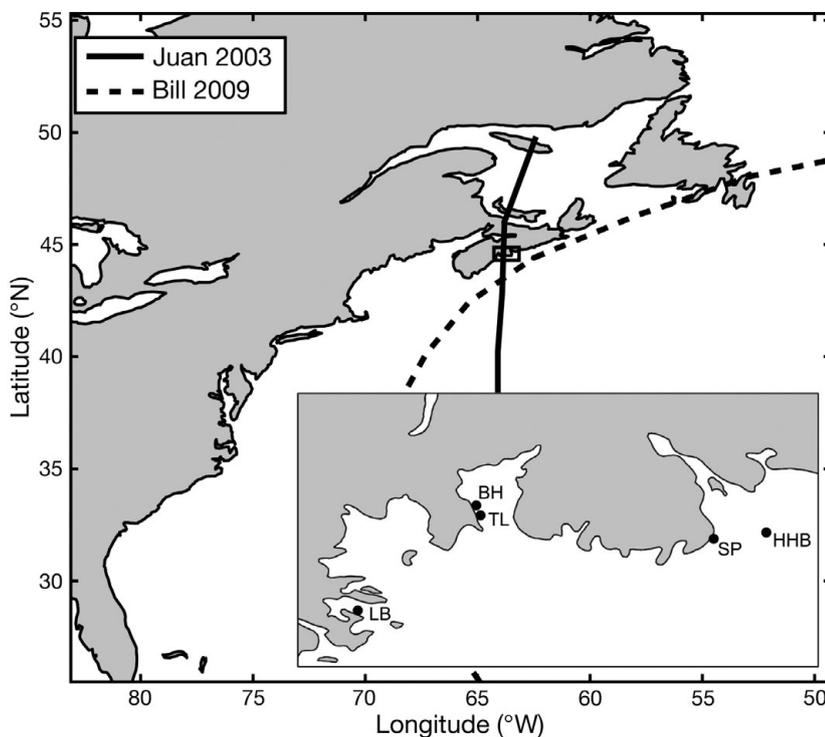

Fig. 1. Eastern seaboard of the USA and Atlantic Canada showing storm tracks of Hurricanes Juan and Bill in the Northwest Atlantic Ocean. Inset: Atlantic coast of Nova Scotia showing the location of study sites in St. Margarets Bay (Birchy Head [BH] and The Lodge [TL]), Splitnose Point (SP), and the meteorological buoy off Halifax Harbour (HHB) and thermograph in Lunenburg Bay (LB)

urchins had begun exhibiting symptoms of infection by the amoeboid pathogen *Paramoeba invadens* (loss of attachment, gaping peristome and jaws, drooping and disheveled spines; Jones & Scheibling 1985) after the passage of Hurricane Bill, a graduated 4.5 m line was rotated through 360° around the plot center and apparently healthy or moribund urchins were counted separately in a series of concentric belts (0.5 m wide). This procedure was repeated on 22 October, after the mass mortality of sea urchins. For all sampling dates, the bottom was carefully searched for experimental individuals (>30 mm test diameter), without overturning boulders and cobbles. Small urchins (usually <10 mm) belonging to the natural population at this site occasionally were observed, but not counted in these samples.

Significant wave height (average height of the highest one-third of waves in a wave field) was recorded at a meteorological buoy (www.meds-sdmm.dfo-mpo.gc.ca) located at the mouth of Halifax Harbour (buoy identification no. C44258; 44° 30′ N, 63° 24′ W) and 45 km east of Birchy Head (Fig. 1). Water temperature was recorded at 10 min intervals using a temperature logger (StowAway TidbiT Temp Logger, Onset Computer) at 8 m depth at The Lodge from 15 August to 21 October 2009. We obtained measures from Coastal Time Series database (www.mar.dfo-mpo.gc.ca/science/ocean/database/Doc2003/cts2003app.html) for 8 m depth from a thermograph in Lunenburg Bay (32 km SW of Birchy Head, Fig. 1) from 1 July to 31 October 2003.

Laboratory infection experiments. To determine whether the rates of morbidity and mortality of *Strongylocentrotus droebachiensis* that we observed at The Lodge conformed to the temperature-mediated dynamics of paramoebiasis, we conducted 2 waterborne disease transmission experiments using the same methods and experimental system as Scheibling & Stephenson (1984). For Expt 1, healthy sea urchins (30 to 70 mm test diameter) were collected at 8 m depth by divers from a grazing front at Splitnose Point on 21 September 2009. Groups of 20 urchins were placed in 47 l glass aquaria supplied with oxygenated flowing seawater at controlled temperature and illuminated on a 12 h light:12 h dark cycle. All individuals were carefully inspected to exclude any with external lesions or abnormalities. Haphazard samples of urchins from the same stock were inverted to ensure that they could right themselves within <3 min, an indication of normal healthy condition (Scheibling & Stephenson 1984). Moribund urchins were collected from the experimental area at The Lodge on 20 September and placed in groups of 4 to 10 in similar aquaria in a separate quarantine laboratory. These urchins were supplied with oxygenated seawater (changed on a daily basis) and maintained in a flowing ambient seawater bath at

~11°C. To propagate the disease, healthy urchins from Splitnose Point were added to these aquaria, and those with advanced symptoms (discoloration, lesions, extensive spine loss) were removed. On 23 September, healthy urchins in experimental aquaria were continuously exposed to water flowing (~3 l min⁻¹) over 5 moribund urchins or 5 healthy ones (a procedural control) in 0.7 l cylindrical glass tubes (4.5 cm diameter) spliced into the incurrent seawater line. Moribund urchins in tubes were replaced regularly; only individuals 30 to 70 mm in diameter with early symptoms of paramoebiasis were used. Aquaria were supplied with ambient seawater that was heated to 16 ± 0.3°C (mean ± SD) or chilled to 6 ± 1.0°C within the Aquatron facility of Dalhousie University. There were 2 replicate aquaria (with 20 urchins each) for each combination of disease exposure and temperature. Temperature levels were selected to reflect a warm temperature that results in the onset of morbidity in sea urchins infected by *Paramoeba invadens* within ~1 wk, and a cooler temperature at which overt symptoms of this disease do not occur, based on previous studies (Scheibling & Stephenson 1984).

For Expt 2, apparently healthy sea urchins were collected at 18 m depth along the deep margin of the kelp bed at The Lodge on 24 September and transported directly to flowing aquaria in the same array as in Expt 1. To determine whether these urchins had been infected with *Paramoeba invadens* but were asymptomatic because of the lower temperatures they experienced at greater depth, they were exposed to water flowing over healthy conspecifics from Splitnose Point at 16 or 6°C. There were 2 replicate aquaria (with 20 urchins each) for each temperature level.

The experiments were monitored at daily intervals. Individuals were considered moribund when they displayed symptoms of paramoebiasis and could no longer attach to aquarium surfaces or right themselves within 20 min of being inverted (Scheibling & Stephenson 1984). Moribund sea urchins were removed from aquaria after 12 h if they had not righted and placed in separate quarantine aquaria for observation until death. Experiments were terminated after 3 wk, after all individuals in disease exposure treatments had died. Urchins were not fed during the experiments (but can survive for months without food) and fecal material and debris were regularly removed.

RESULTS

Urchin mass mortality following recent hurricanes

At Birchy Head, the mean density of *Strongylocentrotus droebachiensis* in a grazing front along the deep

margin of the algal bed was 28 urchins m^{-2} in mid-June 2003 (Lyons & Scheibling 2008). Hurricane Juan made landfall at Halifax on 29 September (Fig. 1) as a strong Category 1 or weak Category 2 storm with maximum sustained winds of 160 km h^{-1} and maximum significant wave heights up to 8.5 m (at the Halifax Harbour buoy, Fig. 2). By 16 October, there were numerous tests of dead sea urchins in the barrens and along the edge of the algal bed, and the few live urchins remaining displayed symptoms of paramoebiasis (Fig. 2). Clusters of small and apparently healthy urchins were observed on detached drift algae on the sand bottom at depths down to ~22 m during a diving survey at this time. No surviving sea urchins were found along the deep margin of the algal bed or adjacent barrens in subsequent dives at this site in 2003. The mass mortality in St. Margarets Bay appeared to be localized. Sea urchin fishers observed no unusual mortality along the headland between the bay and Halifax Harbour in fall 2003 (D. Gray pers. comm.).

At The Lodge, sea urchin density within the experimental area (calculated by averaging counts in the 24 experimental plots that received urchins) had stabilized at ~4 urchins m^{-2} in August (Fig 2). Hurricane Bill passed along the Atlantic coast of Nova Scotia as a Category 1 storm on 23 August 2009 (Fig. 1), with maximum sustained winds of 130 km h^{-1}, and maximum significant wave heights exceeding 6 m (Fig. 2). Sea urchins exhibiting symptoms of paramoebiasis were first observed on 10 September, particularly in shallower parts of the experimental grid. The number of moribund sea urchins increased within the next week, and by 17 September, 35% of all live urchins sampled in experimental plots (n = 2440) exhibited symptoms of disease, and recently dead urchins, intact tests and test fragments were abundant on the seabed. By 22 October, only 9 live sea urchins were observed in all plots combined, indicating near complete mortality (>99%) over the last sampling interval (Fig. 2). Along the deep margin of the kelp bed at 18 m depth, only 1 out of
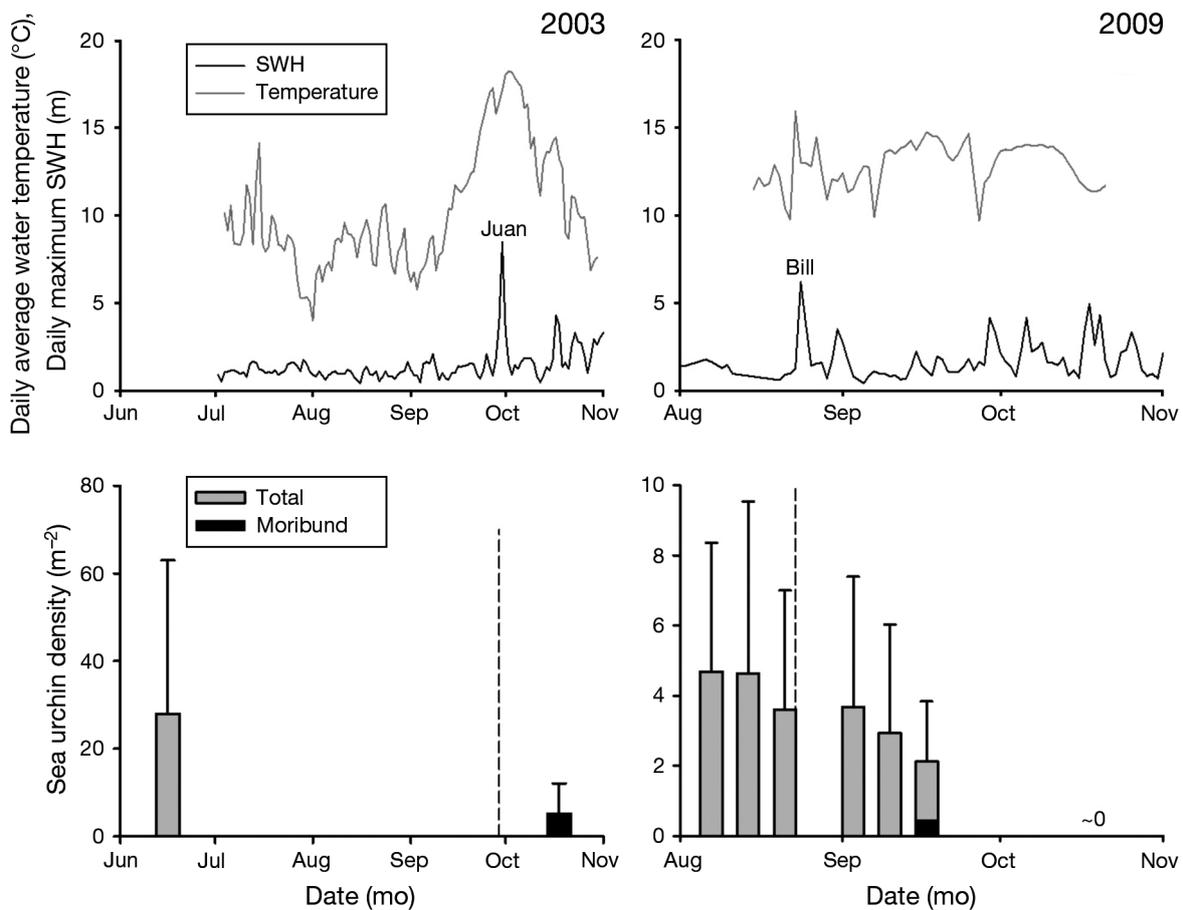

Fig. 2. *Strongylocentrotus droebachiensis*. Top row: Significant wave height (SWH) and temperature at 8 m depth in the summer/fall, showing spikes in SWH and changes in temperature associated with the passage of Hurricane Juan at Birchy Head in 2003 and Hurricane Bill at The Lodge in 2009. Bottom row: Change in density of sea urchins showing decrease in density and proportion of moribund urchins after the passage of each hurricane. Dashed vertical lines indicate the dates the hurricanes struck or passed by the coast

92 urchins collected on 24 September exhibited weak attachment and gaping jaws. (These were the surplus urchins released in this area when the experiment was set up.) We observed no morbidity or unusual mortality of sea urchins at Splitnose Point or Chebucto Head (the western headland of Halifax Harbour) during 2 to 3 dives at each location in September/October, nor did sea urchin fishers working in this area report any mortality (D. Gray pers. comm.).

Laboratory infection experiments

In Expt 1, sea urchins in the disease-exposed treatment at 16°C displayed symptoms of disease within 5 to 7 d (Fig. 3). The incidence of morbidity was ≥50% by 10 to 12 d, and all urchins were dead within 17 d. There was no morbidity or mortality in the disease-exposed treatment or control at 6°C after 21 d, when the experiment was terminated. There was 10 to 20% morbidity in the controls at 16°C after 10 to 13 d, although 1 urchin in each replicate aquarium was cannibalized at 10 and 15 d, respectively, before it could be definitively classified as moribund. We continued to observe some morbidity and mortality in control sea urchins for another 10 d after the end of the experiment, before all were euthanized. We attribute this to the presence of background levels of the pathogen in the ambient water from the Northwest Arm of Halifax Harbour at this time (see also Miller & Colodey 1983).
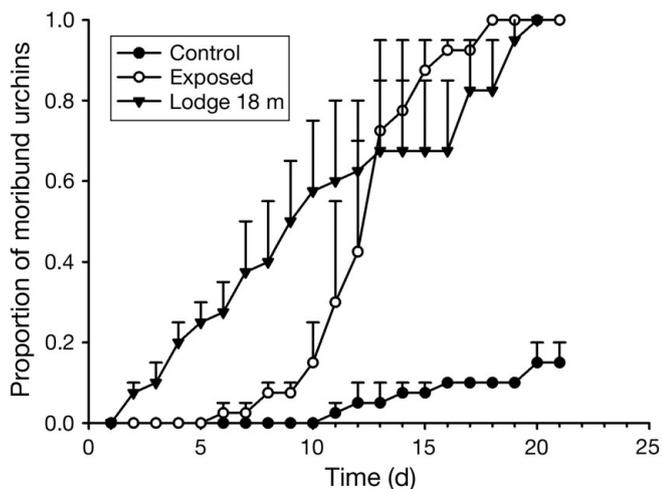

Fig. 3. *Strongylocentrotus droebachiensis*. Cumulative morbidity of sea urchins over a 21 d period in 3 treatments at 16°C in waterborne infection experiments: disease-exposed healthy urchins from Splitnose Point and controls (Expt 1), urchins from 18 m depth at The Lodge (Expt 2). Data are mean + SE for 2 replicate aquaria. There was no morbidity in treatments at 6°C in either experiment (disease-exposed healthy urchins and controls, Expt 1; urchins from 18 m, Expt 2)

The proportion of moribund urchins at 16°C was significantly greater (*t*-test adjusted for heterogeneous variance) in disease-exposed aquaria than in control tanks at Day 15 ($t_1 = -10.12$, p = 0.031) and Day 21 ($t_1 = -17.00$, p = 0.019) of the experiment.

In Expt 2, sea urchins collected from 18 m depth at The Lodge began showing symptoms of disease after 1 d at 16°C and ≥50% were moribund within 6 to 12 d; all urchins were dead within 19 d (Fig. 3). No morbidity or mortality was observed in these urchins at 6°C. Sea urchins in Expt 2 showed a progressive increase in the incidence of morbidity throughout the experiment, in contrast to those in Expt 1, which showed a lag of ~1 wk before the incidence of morbidity increased rapidly from 5 to 95% within 5 to 7 d.

DISCUSSION

Urchin mass mortality following hurricanes

The mass mortality of *Strongylocentrotus droebachiensis* that we observed in 2003 and 2009 in St. Margarets Bay occurred within 2 to 3 wk of the passage of Hurricane Juan and Hurricane Bill, respectively. At these times, moribund sea urchins all exhibited the characteristic external symptoms of paramoebiasis, and there were numerous tests of dead urchins on the seabed. These observations are consistent with the hypothesis that hurricane-induced mixing can deliver a nonresident pathogenic agent to the Atlantic coast of Nova Scotia. Another possibility is that local or regional populations of *Paramoeba invadens*, resistant to low temperature (perhaps in a cyst form), are mixed into the water column with the passing of major storms. *Paramoeba* are found in marine sediments, although a cyst form has not been observed (Jellett & Scheibling 1988, Jellett et al. 1989).

Given the strong temperature dependence of the progression of paramoebiasis in *Strongylocentrotus droebachiensis* (Scheibling & Stephenson 1984), the timing of the onset of morbidity and mortality after Hurricanes Juan or Bill is in accordance with that expected based on sea temperature during the post-storm period, assuming the pathogen was introduced and infected sea urchins when the storm struck. We estimated the expected time to 50% morbidity of sea urchins (t_{50}, d) for a given seawater temperature (*T*, °C) from results of multiple waterborne infection experiments at 12, 16 and 20°C (Table 2 in Scheibling & Stephenson 1984): $t_{50} = 23492T^{-2.7476}$ ($r^2 = 0.939$). At Birchy Head, the expected t_{50}, based on an average temperature of 14.9°C at 8 m depth over the 17 d period between the arrival of Hurricane Juan and the first record of mass mortality at Birchy Head (16 Octo-

ber 2003), was 13.6 d, which is consistent with our observation of extensive morbidity and mortality at this time. Similarly, the expected t_{50} based on an average temperature of 12.7°C at 8 m depth over the 24 d period between the passage of Hurricane Bill and our first record of extensive morbidity (35% of the remaining population) and mortality at The Lodge (17 September 2009) was 22.9 d.

Sea urchins at 18 m depth, along the deep margin of the kelp bed at The Lodge, showed little or no sign of morbidity or unusual mortality on 24 September, 1 mo after the passage of Hurricane Bill. Temperature at 18 m at this time was 12°C, compared with 16°C in the experimental area at 8 to 10 m depth. At 12°C, the time to 50% morbidity in experimental sea urchins continually exposed to *Paramoeba invadens* is ~1 mo (Scheibling & Stephenson 1984). Consistently cooler temperatures at 18 m probably slowed the progression of disease in the deeper population at The Lodge. Large numbers of asymptomatic urchins also were observed in deeper cooler waters after the mass mortality at Birchy Head in October 2003 after Hurricane Juan.

Laboratory infection experiments

The average time to morbidity of healthy *Strongylocentrotus droebachiensis* in our waterborne infection experiments at 16°C is comparable with that measured in similar experiments (10 d) after outbreaks of disease in the early 1980s (Scheibling 1984, Scheibling & Stephenson 1984). *Paramoeba invadens* (Jones 1985) was identified as the pathogenic agent in the previous studies (Jones & Scheibling 1985). The high degree of concordance between these 2 sets of infection experiments, as well as the consistent symptomatology, supports the conclusion that paramoebiasis was also the cause of morbidity and death in our study. Furthermore, we did not observe any morbidity in sea urchins exposed to morbid conspecifics at 6°C, which is below the thermal threshold (~10°C) for transmission and progression of this disease (Scheibling & Stephenson 1984, Jellett & Scheibling 1988). Scheibling & Stephenson (1984) found that urchins infected by morbid conspecifics at 16°C recovered when transferred to aquaria at 5 to 8°C.

Sea urchins from 18 m depth at The Lodge, which were asymptomatic when collected 1 mo after Hurricane Bill (24 September) and transferred to aquaria at 16°C, all developed signs of paramoebiasis within 1 to 19 d and died. The cumulative morbidity curve for these urchins was approximately linear and without a lag phase (unlike that for healthy urchins exposed to morbid conspecifics), suggesting these deep-living urchins were infected during the hurricane event but remained asymptomatic at the low temperatures they experienced *in situ*. Interestingly, of 6 live urchins collected from the experimental area at The Lodge on 22 October and transferred to an aquarium at 16°C, one survived for 25 d before being sacrificed. Dissection revealed no internal or external signs of morbidity, indicating that this individual was resistant to disease. A few survivors also were observed after previous urchin die-offs (Scheibling & Hennigar 1997).

Severity of hurricane-mediated disease outbreaks

The localized disease outbreaks that we observed in 2003 and 2009, unlike the widespread mass mortality observed in the 1980s and 1990s (Miller 1985, Scheibling 1986, Scheibling & Hennigar 1997, Miller & Nolan 2008), suggests that *Paramoeba invadens* may be patchily distributed in water masses. The difference in the extent of urchin die-off between the recent posthurricane disease outbreaks and earlier ones along this coast is probably due at least in part to differences in the distribution and abundance of shallow water (<25 m depth) urchin populations. In the early 1980s and throughout the 1990s, sea urchins occurred in high densities in extensive barrens along the Atlantic coast of Nova Scotia. Following the last major die-off in 1999, sea urchins have been slow to repopulate the shallows except in localized areas near Halifax (Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007). We predict that a storm event that delivers *Paramoeba invadens* to the Nova Scotia coast at a time when sea urchins are highly abundant is more likely to trigger an epizootic. Local hydrodynamics also may play an important role in dispersing the pathogen once it begins to infect urchins at the point of introduction. The long residence time of water in large embayments such as St. Margarets Bay (10 to 30 d; Heath 1973) may retain introduced amoebae, and limit the spread of the disease to outside areas.

Another key factor determining the extent and severity of an outbreak of paramoebiasis is variation in sea temperature at the time of pathogen introduction and during the period of disease propagation that follows. Previous studies (Scheibling & Stephenson 1984, Miller 1985, Scheibling 1986, Scheibling & Hennigar 1997, Brady & Scheibling 2005) have shown that widespread and near complete mortality of sea urchins occurred in years (1981, 1983, 1995, 1999) when disease outbreaks occurred during an extended period of relatively high peak temperatures. In contrast, more localized and partial mortality was observed during years when peak temperatures were

lower or of shorter duration (1980, 1993) or when outbreaks began later in the year (1982). Therefore, the effect on sea urchin populations of major storms that potentially introduce the pathogen will be determined by the timing of these events in relation to the annual temperature cycle. Storms occurring late in the hurricane season (October/November) when temperatures are below 12°C are likely to have no effect, as the disease is not propagated under these conditions. For example, Hurricane Noel made landfall as an extratropical storm along the southwestern coast of Nova Scotia on 3 to 4 November 2007, causing major spikes in both wave action and sea surface temperature (maximum wave height: 9 m, maximum sea surface temperature: 16°C; measured at the Halifax Harbour buoy). However, sea temperature immediately dropped to 8°C after the storm and continued to decline towards winter. Therefore, even if *Paramoeba invadens* was introduced during this event, temperatures were too low for an outbreak of disease to occur. Indeed, there was no evidence of morbidity in a dense population of *Strongylocentrotus droebachiensis* at Splitnose Point sampled in November and December 2007 (J. S. Lauzon-Guay & R. E. Scheibling unpubl. data).

If hurricane events in the North Atlantic Ocean increase in frequency and intensity with global warming, as some models predict (Emanuel 2005, Elsner et al. 2008), we are likely to see more frequent introductions of *Paramoeba invadens* to the coastal waters of Atlantic Canada and the northeastern USA. If this is the case, we predict that more frequent and perhaps more localized outbreaks of disease will occur along the coast of Nova Scotia. This could result in the persistence of algal assemblages such as kelp beds and seriously disrupt or destroy the sea urchin fishery. However, nothing is known about the source populations of *P. invadens* or how these amoebae are dispersed by large-scale advective processes, such as hurricanes. Future studies that address these knowledge gaps are crucial to understanding the dynamics of these disease outbreaks and their ecological and economical consequences.

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