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Contribution to the Supplement: '*Lobsters in a Changing Climate*'

Original Article

American lobster nurseries of southern New England receding in the face of climate change

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Historically, southern New England has supported one of the most productive American lobster (*Homarus americanus*) fisheries of the northeast United States. Recently, the region has seen dramatic declines in lobster populations coincident with a trend of increasingly stressful summer warmth and shell disease. We report significant declines in the abundance, distribution, and size composition of juvenile lobsters that have accompanied the warming trend in Narragansett Bay, Rhode Island, since the first comprehensive survey of lobster nurseries conducted there in 1990. We used diver-based visual surveys and suction sampling in 1990, 2011, and 2012, supplemented by post-larval collectors in 2011 and 2012. In 1990, lobster nurseries extended from the outer coast into the mid-sections of the bay, but by 2011 and 2012 they were largely restricted to the outer coast and deeper water at the mouth of the bay. Among five new study sites selected by the lobster fishing industry for the 2011 and 2012 surveys, the deepest site on the outer coast (15–17 m depth) harboured some of the highest lobster densities in the survey. Separate fixed site hydrographic monitoring at 13 locations in the bay by the Rhode Island Division of Fish and Wildlife recorded an approximately 2.0°C increase in summer surface temperatures over the period, with 2012 being the warmest on record. Additional monitoring of bottom temperatures, dissolved oxygen and pH at our sampling sites in 2011 and 2012 indicated conditions falling below physiological optima for lobsters during summer. The invasion of the Asian shore crab, *Hemigrapsus sanguineus*, since the 1990s may also be contributing to declines of juvenile lobster shallow zones (<5 m) in this region. Because lobster populations appear increasingly restricted to deeper and outer coastal waters of southern New England, further monitoring of settlement and nursery habitat in deep water is warranted.

Keywords: American lobster, climate change, Narragansett Bay, nursery habitat, settlement.

Introduction

Climate change is having tangible impacts on commercially important fisheries of coastal and shelf waters worldwide (Harley *et al.*, 2006). This is especially true of the North Atlantic where ocean warming has outpaced that of other parts of the world, resulting in altered phenology and geographic range shifts for a host of marine fish and invertebrates with important implications for the future of the fisheries and their management (Nye *et al.*, 2009; Hare *et al.*, 2012; Mills *et al.*, 2013; Pinsky *et al.*, 2013). It is rare, however, to have the opportunity to evaluate the impact of climate change on the earliest life stages of marine species since most long-term datasets are derived from commercial catch or fishery-independent trawl surveys that selectively sample larger-bodied older juveniles and adults and do not target nursery habitat.

Southern New England has experienced dramatic changes in its population of American lobster, *Homarus americanus*, over the past two decades. These changes suggest that summer conditions in coastal areas are becoming inhospitable to this iconic, historically abundant and commercially important species. In the mid-1990s, lobster abundance and harvests were at historical highs in southern New England. Since then, the onset of shell disease and sharp declines in larval settlement to the region's coastal nurseries have preceded precipitous declines in adult abundance and landings that are now only a fraction of what they were two decades ago

(Wahle *et al.*, 2009a). Extreme summer temperatures, storm-induced mixing and rainfall during 1999–2000 triggered a massive die-off in Long Island Sound that resulted in a 75% drop in lobster landings and a local collapse of the commercial fishery (Pearse and Balcom, 2005). The Atlantic States Marine Fisheries Commission's (ASMFC) Lobster Technical Committee has deemed the southern New England lobster stock to be in a state of recruitment failure (ASMFC, 2009). In contrast, further north, where cooler temperatures prevail, abrupt warming events have caused shifts in phenology. Most recently, 2012 brought a record-breaking ocean heat wave that triggered an early molt and inshore migration in the Gulf of Maine, resulting in an over-supply of landed lobsters that overwhelmed processors and severely depressed the price (Mills *et al.*, 2013).

The American lobster is not the only species to have experienced dramatic changes associated with ocean warming in southern New England (Keller *et al.*, 1999; Nixon *et al.*, 2004, 2009). In the well-studied Narragansett Bay and nearby coastal waters, the winter–spring diatom bloom has all but disappeared (Keller *et al.*, 1999; Oviatt *et al.*, 2002; Nixon *et al.*, 2009), eelgrass has been on the decline (Bintz *et al.*, 2003), comb jellies have increased (Sullivan *et al.*, 2001), the composition of the groundfish assemblage has changed (Jeffries and Terceiro 1985; Jeffries, 2002), and the invasive green crab, *Carcinus maenas*, has been replaced by the equally invasive Asian shore crab, *Hemigrapsis sangineus* (Lohrer and Whitlatch, 2002).

Of particular relevance to lobster, summer water temperatures in southern New England have exceeded a long-recognized 20°C physiological threshold with historical frequency (McLeese and Wilder, 1958; Pearse and Balcom, 2005; Glenn and Pugh, 2006). The net result is the northward shift in the lobster's thermal niche, a scenario whereby coastal southern New England will no longer be a hospitable nursery to the American lobster in the coming decades (Frumhoff *et al.*, 2007). It is, therefore, valuable to compare current distributions with previous baselines.

In 1990, Wahle (1993) undertook the first comprehensive survey of Rhode Island lobster nurseries in Narragansett Bay, including 17 sites surveyed visually by divers, 6 of which were also suction-sampled (Figure 1; Supplementary Table S1). In retrospect, it is apparent that these surveys were done at a time when the lobster fishery and larval settlement were at historical highs. After the 1990 survey, a subset of the lower bay sites plus additional outer coastal sites continued to be monitored by suction sampling under what would become the American Lobster Settlement Index (ALSI), a collaborative monitoring programme of lobster nurseries throughout New England and Atlantic Canada. Larval settlement in Rhode Island has fallen to historical lows in recent years (Wahle *et al.* 2009a, 2012; Supplementary Figure S1). Concurrently, since 1990, summer surface temperatures in the bay have risen at an average rate of 0.09°C per year (Olszewski, 2013; Supplementary Figure S2). However, the original Narragansett Bay sites have not been re-surveyed since 1990, despite the dramatic changes reported over the intervening years. In this study, we repeated and augmented the Narragansett Bay lobster nursery survey in a collaborative project among the University of Maine, the Rhode Island lobster fishing industry, and Rhode Island Division of Fish and Wildlife (RI DFW) to evaluate how lobster nurseries within the bay had changed over the two decades since the first survey.

Methods

This study repeated the diver-based visual and suction sampling surveys at the same sites visited in 1990 and augmented them at several locations using passive post-larval collectors to provide an independent comparison to the diver-based methods. We also sampled five additional study sites selected by participating lobster fishers to address industry concerns that previous sampling was insufficient to characterize current juvenile lobster distributions. Visual surveys and suction sampling were completed and passive collectors were deployed at these new sites. In addition to the methodology outlined below, further details for visual and suction sampling appear in Wahle (1993), and for the use of passive collectors, Wahle *et al.* (2009b).

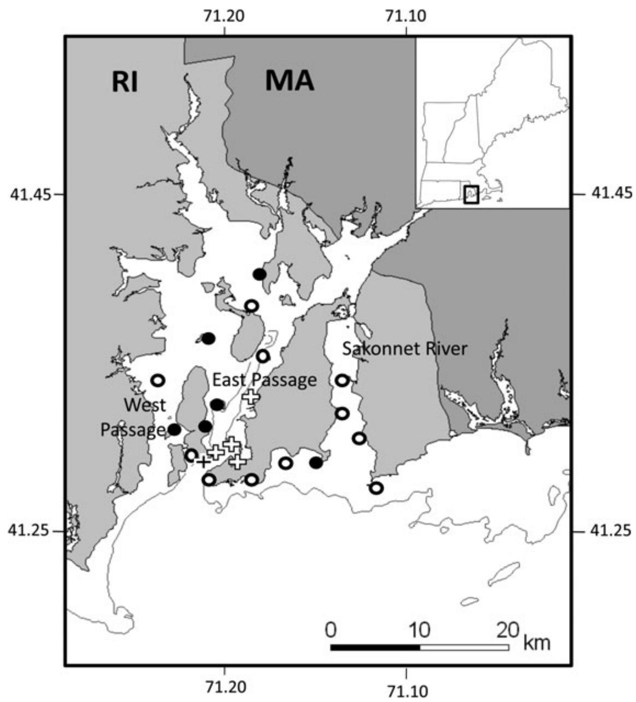

Figure 1. Narragansett Bay and Rhode Island's outer coast showing the 17 sites surveyed in 1990 and resurveyed in 2011 and 2012 (circles). Black circles denote sites subject to both visual surveys and suction sampling by divers; white circles are sites where only visual surveys were conducted. Crosses indicate industry-selected sites for the 2011–2012 survey; white crosses denote the site where collectors and visual and suction samples were done; black cross denotes the sole industry-selected site where collectors were not deployed. RI, Rhode Island, MA, Massachusetts. Map includes 20 m isobath. Inset shows Narragansett Bay on a map of New England, USA.

Visual surveys

We conducted visual surveys in July and early August to provide a rapid assessment of general bay-wide patterns in the benthic lobster population. Divers haphazardly placed 1-m^2 quadrats on cobble–boulder habitat at each site. Four divers surveyed in all 20 quadrats in ~30 min. Divers carefully overturned rocks and searched crevices, working slowly so as to avoid suspending sediment that hampers visibility. Data recorded for each quadrat included cobble and algae coverage and counts of lobster, crab, and other larger fauna. We also measured lobster carapace length and crab carapace width to the nearest millimetre.

We conducted visual surveys in 2011 and 2012 at all 17 sites surveyed in 1990 (listed in Supplementary Table S1). Each year, we included two additional industry-selected sites which were only sampled for 1 year. These sites ranged in depth from 3 to 5 m below mean low water. In 2012, we added one additional "deep" site, Fort Wetherill, at 17 m below MLW.

Suction sampling surveys

Suction sampling was necessary because visual methods are less effective for recently settled young-of-year (YoY) and 1-year-old lobsters. However, all sizes of lobster were sampled in the process. We conducted suction sampling from late August to the first week of September to coincide with RI DFW long-term monitoring of stations on Rhode Island's outer coast at the end of the settlement season. Diver pairs worked together to vacuum the contents of 0.5 m^2 quadrats placed in cobble–boulder habitat. Rocks were removed during the process to expose hidden infauna. Samples were retained in a mesh bag secured to the top of the sampler; bags were changed between quadrats. We sampled 20 quadrats per site. Two diver pairs completed this task in <1 h, making it feasible to have completed 3–4 sites in a day. Sample bags were returned to the laboratory where they were sorted fresh or were frozen to be sorted later. Lobsters were measured, sex was determined, and claws counted. Associated fauna of interest included several species of native and introduced crabs (*C. maenas*, *Dyspanopeus sayi*, *Cancer borealis*, and *Hemigrapsus sanguineus*) and benthic fish which were also identified to species, counted, and measured (see Supplementary Tables S2 and S3 for a full list of crabs, lobsters, and fish collected by suction sampling).

Collector surveys

Passive post-larval collectors were also deployed to provide a measure of settlement independent of the diver-based method. Previous studies have documented the comparability of the collector- and suction sampling-based methods (Wahle *et al.*, 2009b, 2012). Passive collectors were made of 10-gauge vinyl-coated wire with a 3.7-cm (1.5 inch) mesh. They measured 61.0 × 91.5 × 15.0 cm deep, providing 0.55 m^2 in the floor area. A cover made of the same wire mesh served to retain the rocks and allow the free passage of post-larval lobsters. The floor and walls were lined inside with 2-mm plastic mesh (Petmesh™) to retain newly settled lobsters, crabs, and other organisms during retrieval. Collectors were filled with clean, rounded cobbles ranging in diameter from 10 to 15 cm. Collectors filled with rocks weighed ~80 kg. Each collector was fitted with a bridle to enable lifting in a horizontal position, which is important to retaining collections during retrieval. An earlier pilot study demonstrated that losses of organisms were negligible when retrieved in this manner (Wahle *et al.*, 2009b).

Collectors were deployed in late May/early June each year. Twenty collectors were deployed at each of the six original and two industry-selected sites, comprising in all 160 collectors per year. We retrieved collectors at the end of the settlement season at the same time suction sampling was conducted (late August–early September). Once on deck, lids were removed, rocks rinsed with a hose to remove sediment, and then carefully removed to inspect for lobsters and other organisms. All lobsters, crabs, and fish were measured. Lobsters were further inspected to determine sex and the number of claws, noted for evidence of shell disease, and then released.

Water quality

RI DFW provided surface and bottom temperatures from 1990 to 2013 for 13 fixed locations throughout the bay sampled during its monthly bottom trawl survey (Supplementary Figure S2; Olszewski, 2013). In addition, we collected water quality data specific to our benthic sampling sites in 2011 and 2012, although no hydrographic data were collected in 1990. At the subset of six original sites and two industry-selected sites subject to the more intensive sampling, we deployed continuously recording Tid-Bit™ temperature loggers set to record temperature hourly. Temperature loggers were fastened to post-larval collectors and deployed at 5–7 m depth. Furthermore, we conducted SeaBird CTD casts in July and August to assess thermal profiles at selected deeper mid-channel locations next to sampling sites. We conducted hydrographic surveys of our benthic sampling sites during 22–24 August 2012, by measuring surface and bottom temperature, salinity, dissolved oxygen (DO), and pH at using a YSI 556 Multiparameter System.

Statistical analysis

We evaluated the statistical significance of lobster demographic changes between 1990, 2011, and 2012 using the visual survey dataset encompassing the 17 sites originally visited in 1990. Although visual surveys may undersample the smallest size classes of lobster, this dataset comprised the largest number of lobsters and the greatest spatial coverage compared with the suction sampling and collector-based methods. To evaluate changes in lobster population density, we used a Wilcoxon signed-ranks test to assess the three possible between-year comparisons of site means. Differences in mean carapace length among years were tested using a single-factor ANOVA, with each year treated as a separate level (numbers of lobsters for each year denoted in Figure 2b). Similarly, we used a single-factor ANOVA to assess spatial shifts in occupied lobster nurseries from 1990 to 2011 and 2012, by evaluating differences in the latitude for sites where lobsters were present (not weighted by density) in each year's survey. Latitude runs perpendicular to the roughly N–S axis of the bay's basin, and therefore served as the most useful dimension with which to assess spatial shifts; the northern and southern most sites of the 17 are separated by 0.227° of latitude or 25.2 km (0.227° × 111 km $degree^{-1}$ latitude). Finally, to evaluate the link between hypoxia and acidification at our sampling sites, we used a least-squares linear regression to test the statistical relationship between dissolved oxygen concentration and pH measured at the surface and bottom during our hydrographic survey.

Results

Visual surveys

Diver visual surveys of Narragansett Bay lobster nurseries conducted in 2011 and 2012 revealed a dramatic reduction in lobster density, distribution, and size composition compared with 1990 levels (Figure 2). In 1990, lobster densities among the 17 sites averaged 0.51 lobsters per m^2 (±0.14 SE). By 2011 and 2012, densities had fallen to 0.13 (±0.05 SE) and 0.06 (±0.02 SE) individuals per m^2, respectively, representing a statistically significant nearly 10-fold overall decline from 1990 to 2012 (Wilcoxon signed-ranks test: 1990 vs. 2011, $Z = -2.86$, $P = 0.002$; 1990 vs. 2012, $Z = -3.17$, $P = 0.004$; 2011 vs. 2012, $Z = -2.03$, $P = 0.04$). Notably, most of the lobsters counted in the 2012 visual survey were from the single deep site, Fort Wetherill, selected by the fishing industry, that was not part of the 1990 survey.

The spatial distribution of lobster nurseries also receded south towards the outer coast from 1990 to 2011 and 2012 (Figure 2a). Whereas juvenile lobsters in 1990 extended well into the mid-section of the bay, they were largely restricted to the lower bay and outer coastal locations in the recent surveys. In the context of the

Figure 2. Visual surveys of *H. americanus* nurseries in Narragansett Bay, 1990, 2011, and 2012. (a) Lobster density (n $m^{-2} + 1$ SE) listed by the site north-to-south ($n = 20$ 1-m^2 quadrats sampled per site), and (b) lobster size composition. Industry selected denoted with asterisks.

sampling domain of 17 visual sampling sites, spanning 0.227° of latitude (25.2 km), this represents a statistically significant southward shift of 0.038° (4.2 km) in the centre of the nursery population from 41.506°N (±0.014° SE) in 1990 to 41.468°N (±0.006° SE) in both 2011 and 2012 (one-way ANOVA, $F = 3.94$, d.f. $= 2$, $P = 0.03$).

We also recorded a significant upwards shift in the size composition of the nursery population in the recent surveys, reflecting the absence of the smaller juveniles that were prevalent two decades earlier (Figure 2b). Mean carapace length significantly increased from 31.5 mm ($\pm$1.2 mm SE) in 1990 to 36.7 ($\pm$1.9 SE) and 41.0 ($\pm$2.2 SE) in 2011 and 2012, respectively (one-way ANOVA, $F = 6.74$, d.f. $= 2$, $P = 0.001$).

Suction sampling surveys

Suction sampling reinforced evidence of diminishing lobster recruitment of YoY lobsters (Figure 3). In the 1990 survey, YoY lobsters extended from the outer coast to mid-bay locations (Figure 3a). In 1990, YoY lobsters also represented the dominant mode in the size distribution, but in 2011 they were absent from the suction samples, and in 2012 only one was found (Figure 3b). In 2012, all the lobsters collected by suction sampling came from Fort Wetherill, the single deep site, and the only site, historical or industry-selected, where lobsters of any size were collected by this method.

Passive collectors

All collectors were retrieved, except for 15 lost at Southwest Point and 5 lost at Sachuest Point, as a result of Hurricane Irene in 2011. All lobsters found in collectors in 2011 came from the lower bay

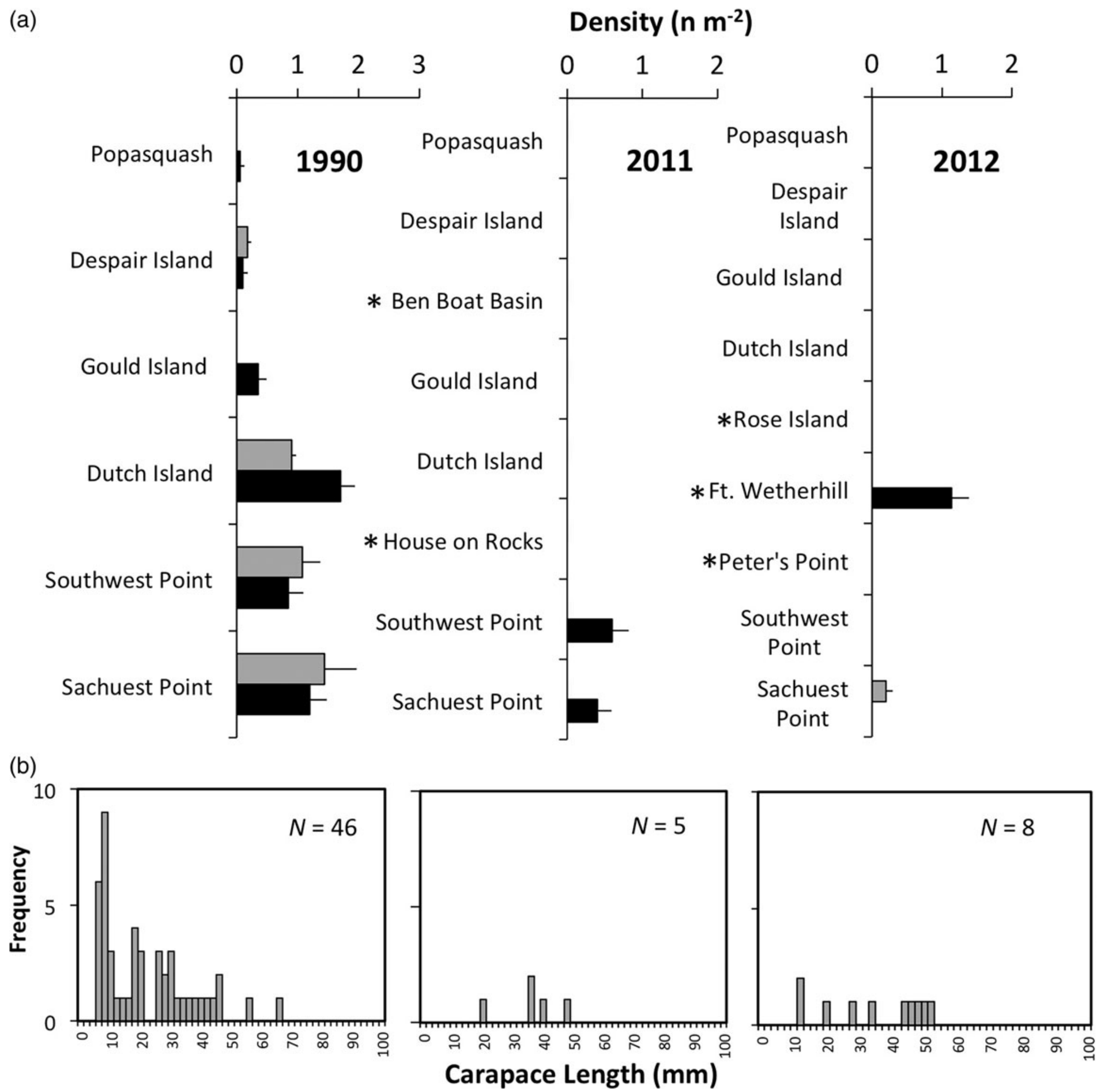

Figure 3. Suction sampling of *H. americanus* nurseries in Narragansett Bay 1990, 2011, and 2012. (a) Lobster density (n m^{-2} +1 SE) listed by the site north-to-south, ($n = 200.5$-m^2 quadrats sampled per site), and (b) lobster size composition. Industry selected denoted with asterisks.

and outer coast, whereas lobsters from 2012 collectors were exclusively from the outer coast. We recorded only one YoY in 2011, and five in 2012, all at the two outermost coastal sites (Figure 4a). No YoY lobsters were found in collectors deployed at the industry-selected sites. Overall, the size composition of lobsters in collectors was similar to that of suction samples (Figure 4b).

Although a quantitative assessment of associated fauna is not included in this report, several points are worth highlighting on the decapod crustacean and fish assemblages (Supplementary Table S2). The Asian shore crab (*H. sanguineus*) is a notable recent introduction, not reported in the 1990 survey, but counted at all sites except the deep one (Fort Wetherill) in the recent survey. At least 16 species of fish were identified and counted in collectors deployed during this study (Supplementary Table S3). Several species of fish, such as cunner, black sea bass, toad fish, and eels, were reported at remarkable densities of tens per collector. Several of these species are known to be predators of juvenile lobster (Wahle *et al.*, 2013). Despite the high predator diversity and abundance in collectors, it is noteworthy that YoY and juvenile lobster densities were still found at comparable or even larger numbers than those in suction samples of the natural nursery habitat at the same location, which has been the case in previous studies (Wahle *et al.*, 2009b, 2012).

Water quality

Temperatures at all sites rose well above the thermal threshold of 20°C for lobsters during the 2-year study (Figure 5). Coincidentally, summer of 2012 proved to be the warmest on record since the initiation in 1990 of RI DFW fixed site temperature monitoring at 13 sites in the bay (Supplementary Figure S2; Olszewski, 2013). Loggers were lost from our outer coastal stations at Sachuest Point and Southwest Point during the hurricane in 2011, so we used data from a more protected site nearby, House-on-Rocks. Temperatures at upper bay sites exceeded 20°C ~2 weeks ahead of the lower bay sites, and reached maximum temperatures of ~25°C (Figure 5).

Representative upper and lower bay profiles for 2011 and 2012 revealed considerable thermal stratification (Figure 6). The entire water column exceeded 20°C down to a depth of 10 m in the upper bay. At the mouth of the bay, only the first few meters of depth were >20°C, with temperatures at 15–20 m ranging from 17 to 18°C, which approximates the thermal optimum for lobsters.

The hydrographic survey also revealed considerable differences between surface and bottom conditions and bay-wide gradients in water quality (Supplementary Figure S3). Salinity ranged from 29 to 31 psu in a down-bay direction, and was slightly higher near bottom than at the surface, as is typical in estuaries. Temperature ranged from a high of 25°C in the upper bay to a low of 19°C on the outer coast, and was consistently a degree or two warmer at the surface than at the bottom. Dissolved oxygen levels were generally higher at the surface than at the bottom, ranging from about 6.8 to 8.1 mg l^{-1}. There were two sites with exceptionally low DO concentrations: Fogland and Easton Point, both in the Sakonnet River, with bottom readings below 6 mg l^{-1}. Levels of pH varied from typical ocean levels of ~8.1 to <7.0, and were also generally lower near the seabed than at the surface. Levels of pH also correlated significantly with DO concentrations, especially near the seabed (surface: $r^2 = 0.39$, $P = 0.004$; bottom: $r^2 = 0.83$, $P < 0.001$), which would be consistent with near-bottom O_2 depletion and CO_2 generation and acidification resulting from benthic respiration (Supplementary Figure S4).

Discussion

These results indicate significant declines in abundance and a receding distribution of juvenile lobsters in Narragansett Bay since the early 1990s. The three independent and parallel sampling protocols revealed consistent patterns of declining lobster numbers in shallow nurseries. The change in lobster abundance we detected within Narragansett Bay is also consistent with trends observed in juvenile populations at sites monitored continuously by suction sampling from 1990 to the present along the Rhode Island's outer coast (Wahle *et al.*, 2009a; Pershing *et al.*, 2012; Supplementary Figure S1). Supplemental sampling of additional industry-selected sites, with one important exception, agreed with observations at the original sites. Densities of juvenile lobster were as low at these sites as they were at nearby locations in the bay. The exception was the deep site (15–17 m) at Fort Wetherill where relatively high densities of juvenile lobsters were found. Taken together, the three sampling methods, the added sampling locations, and long-term monitoring outside the bay, strongly indicate a decline and receding distribution of juvenile lobster from shallow nurseries. In short, the relative rarity of YoY lobsters represents a demographic hole in the nursery population, which now comprises only a few remaining juveniles most likely from previous years of settlement.

Water quality indicators suggest that midsummer conditions have become increasingly stressful for lobster in the upper and mid-bay sections of Narragansett Bay. The American lobster begins to experience physiological stress at temperatures above 20°C (McLeese and Wilder 1958; Pearse and Balcom 2005). Lobsters were absent in the upper bay where water temperatures ranged above 25°C for extended periods during summer and where salinity was reduced. Independent RI DFW hydrographic surveys indicate that mean summer surface temperatures in these same areas of the bay were 2–3°C warmer in 2011 and 2012 than they were in 1990 (Supplementary Figure S2). Coincidently, summer temperatures in 2012 happened to be the warmest on record, not only in Narragansett Bay (Olszewski, 2013; Supplementary Figure S2), but over a large portion of the Northwest Atlantic (Mills *et al.*, 2013). Despite this warming trend, much of the bay and outer coast thermal stratification during summer can create a thermal refuge for lobsters in deeper water that may be within reach of settling post-larvae or larger juvenile and adult lobsters. These changes in the distribution of lobster nurseries suggest that favourable conditions have shifted considerably southward towards the mouth of the bay. Furthermore, Glenn *et al.* (2011) recently observed that with increasingly warm summer temperatures in nearshore shallows, egg bearing lobsters were being caught at greater depths, and therefore greater distances, from shore. This suggests that larvae are hatching further from shore and are more likely to be exported from coastal nurseries, further exacerbating the effects of a declining broodstock in nearshore waters.

Since the 1970s, temperatures in Narragansett Bay have been rising at a rate of ~0.3°C per decade (Nixon *et al.*, 2004). This is consistent with the long-term trend reported by Mills *et al.* (2013) for the Gulf of Maine, although their more recent study also suggests that the pace of warming has accelerated over the past decade. Even at the more conservative rate, future warming projected by the International Panel on Climate Change models is likely to make southern New England shallow coastal areas increasingly inhospitable to lobsters in the coming decades (Frumhoff *et al.*, 2007).

Abrupt warming events can play an especially important role in altering species distribution and abundance. The lobster die-off of

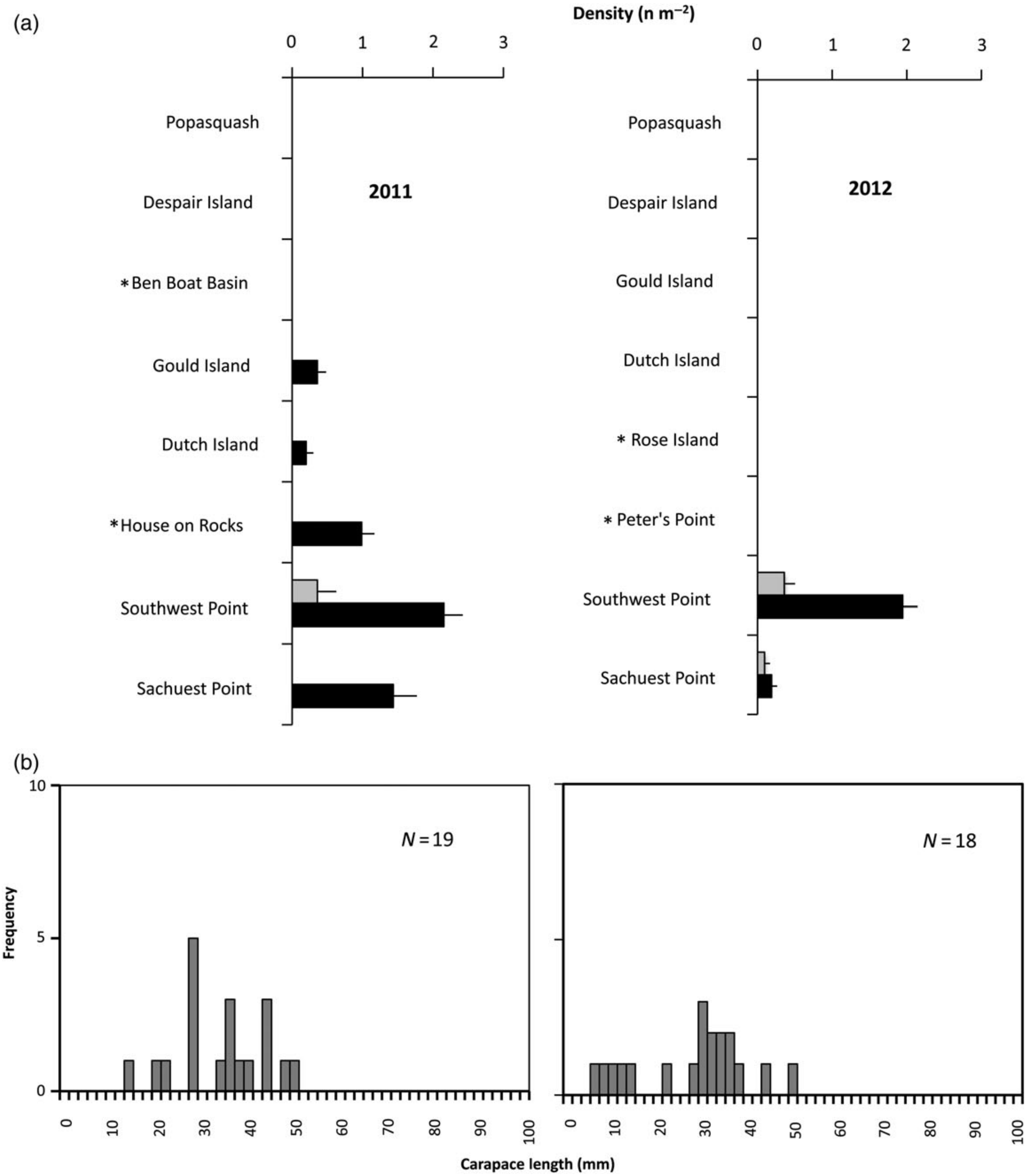

Figure 4. Passive collectors deployed in *H. americanus* nurseries of Narragansett Bay, 2011, and 2012. (a) Lobster density (n m^{-2} + 1 SE) listed by the site north-to-south ($n = 20$ collectors sampled per site), and (b) lobster size composition. Collectors were not used in 1990. Industry selected denoted with asterisks.

1999 in Long Island Sound, next to Rhode Island waters, may be a prime example (Pearse and Balcom, 2005). Mass mortality of lobster and associated fauna in the Sound resulted from a combination of warmer than average temperatures and wind-induced turnover of the water column that mixed warm, oxygen-poor water down to deeper channels that are normally a cool refuge from the midsummer heat in the shallows. Although the 2012 ocean heat wave was a record-breaker, it was not accompanied by mass mortality event in southern New England, even though it dramatically impacted lobster molting phenology further north (Mills *et al.*, 2013). We speculate that the absence of a late summer storm-related mixing event, such as occurred in 1999, may have allowed the southern New England to avert another catastrophic die-off.

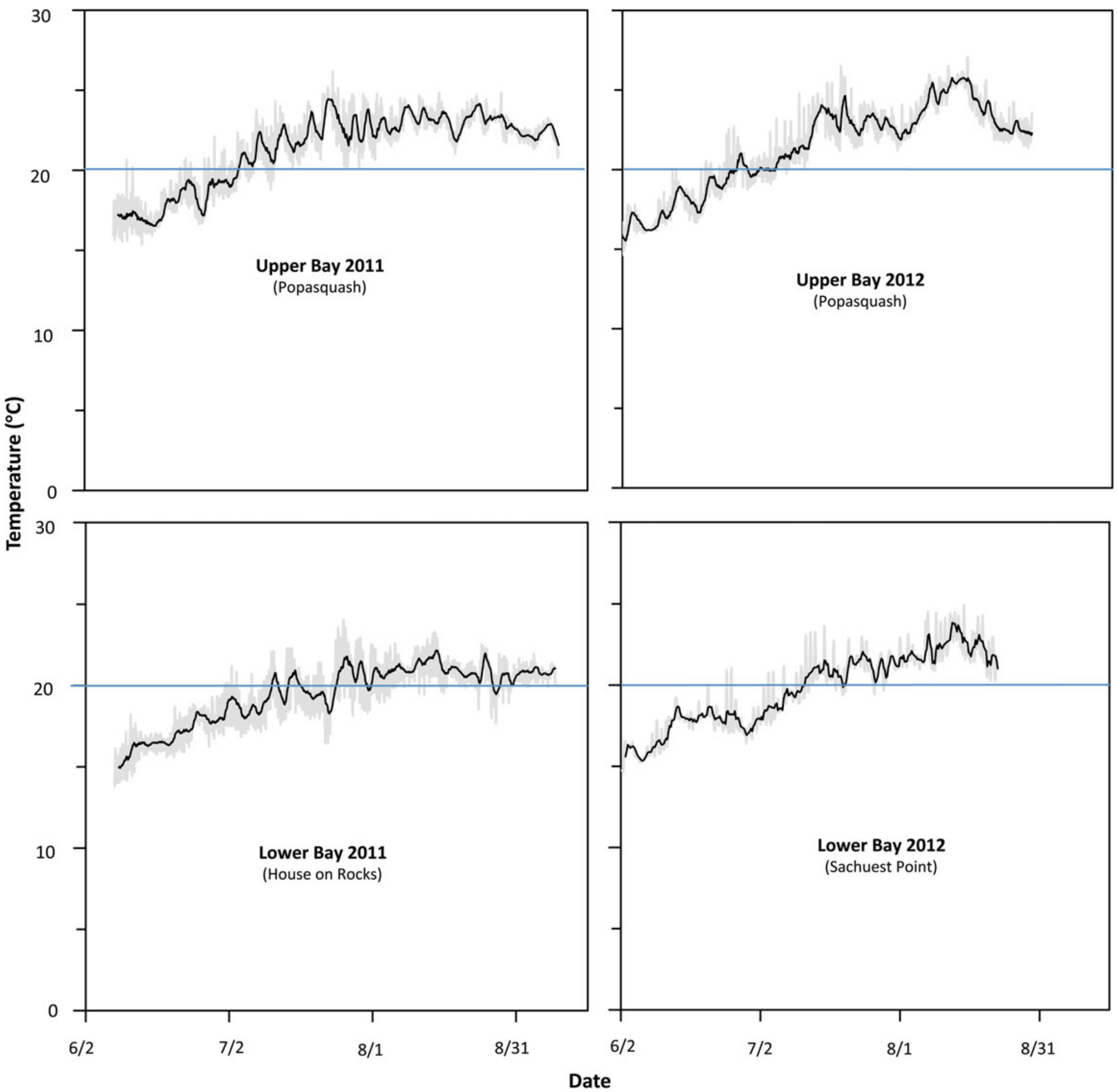

Figure 5. Temperature logger data at upper (Popasquash 41.6743°N, −71.3083°W) and lower (House on Rocks 41.4815°N, −71.3561°W and Sachuest Point 41.4733°N, −71.2483°W) Narragansett Bay locations during collector deployments in 2011 and 2012. Grey, hourly record; black, 24-h running mean.

Adverse secondary effects of warming, such as hypoxia and possibly shell disease, may only exacerbate conditions for lobster, and may also contribute to the receding distribution of lobster nurseries in Narragansett Bay. The onset of the shell disease epizootic in southern New England, for example, followed almost a decade of above normal summer temperatures (Glenn and Pugh, 2006), although the role of toxic pollutants in the epizootic remains in question (Laufer *et al.*, 2013). At some of our study sites, high temperatures were accompanied by hypoxic and acidified conditions. The extent to which these conditions also contributed to the absence of lobsters is unclear. Narragansett Bay is a particularly urbanized estuary prone to summer hypoxia events related to local anthropogenic eutrophication (Altieri and Witman, 2006; Nixon *et al.*, 2009). Reducing nutrient supplies into the bay, therefore, could mitigate adverse effects of hypoxia and low pH.

We also cannot rule out the possibility that the invasion of the Asian shore crab, *H. sanguineus*, may have contributed to declining numbers of juvenile lobsters in Rhode Island's shallow lobster nurseries. Asian shore crabs were not present in our 1990 survey, but were abundant in the recent sampling at all sites except the deepest one at Fort Wetherill in Narragansett Bay. This introduced species is an aggressive predator, and has excluded or limited distributions of the green crab, *C. maenas*, from some shores in southern New England (Lohrer and Whitlatch, 2002). It is not unreasonable to suspect this crab could have a similar impact on juvenile lobsters to the extent the two species overlap. On the other hand, the depth

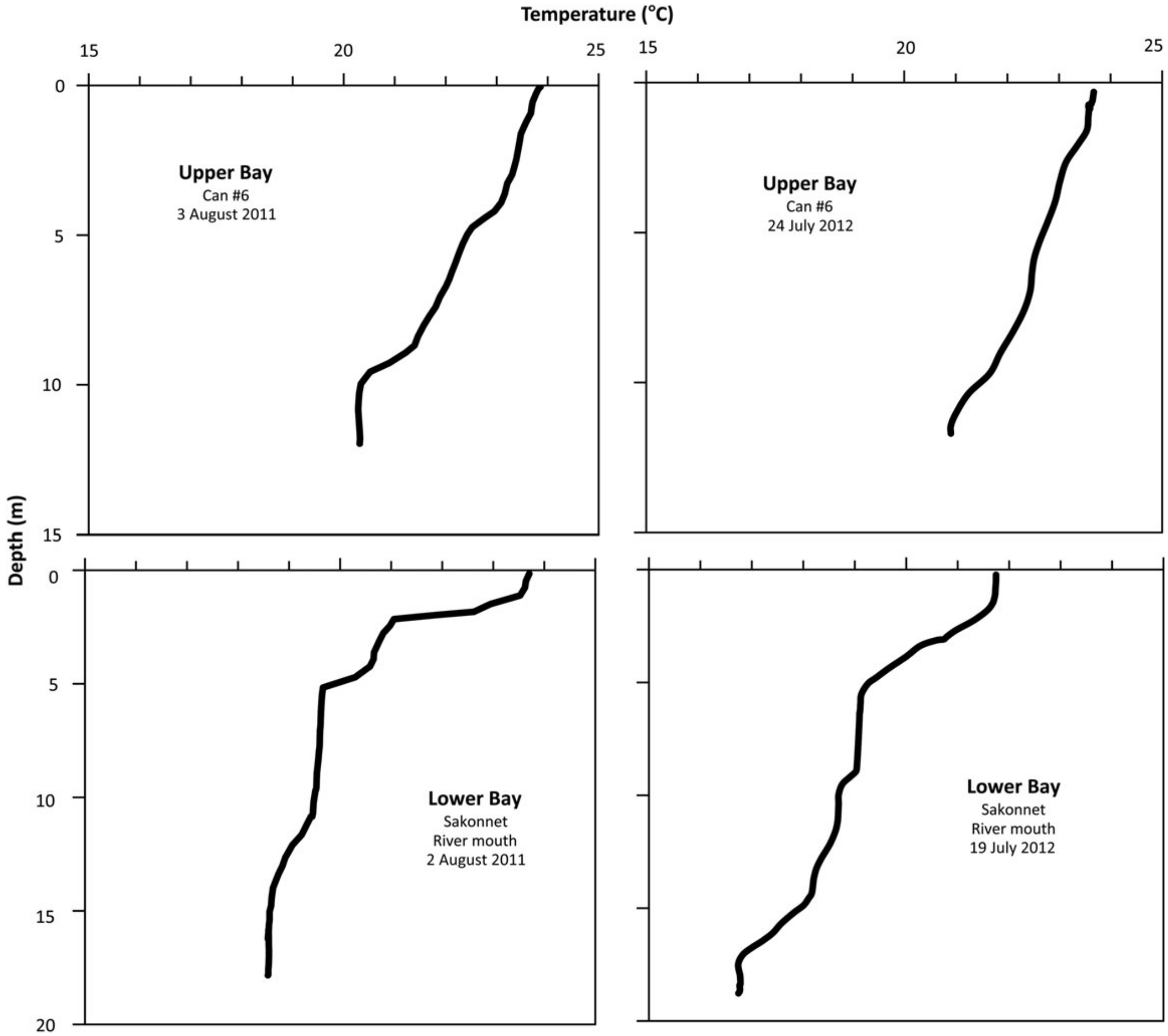

Figure 6. Midsummer temperature profiles at upper (41.6647°N, −71.3904°W) and lower (41.4624°N, −71.2168°W) Narragansett Bay locations taken in 2011 and 2012.

range of the Asian shore crab does not extend greatly into the lobster habitat, so its impact, if any, would be restricted to the shallowest subtidal locations. Therefore, further monitoring of lobster settlement and nursery habitat in deep water is warranted.

It is likely that with increasingly inhospitable summer temperatures in shallow coastal areas, lobster settlement in southern New England will be further restricted to deeper zones, provided suitable shelter-providing habitat is available. To date, there has been only limited sampling, mostly by passive collectors, to evaluate lobster settlement in >10 m of water (Glenn *et al.*, 2011; Wahle *et al.*, 2012). These studies were done during the recent dearth of larval settlement in southern New England, and not surprisingly have produced only a few records of YoY lobsters. Collector deployments in other parts of New England and Atlantic Canada, where settlement has remained strong, have reported settlement at depths as great as ∼80 m. Collectors have not been deployed to greater depths to date. This raises the possibility that settlement may be occurring at depths greater than previously thought, and that there is a need for further deep water monitoring. To monitor lobster settlement in deeper water will likely require the expanded use of passive collectors. Furthermore, high-resolution mapping of available nursery habitat will enable extrapolation of estimated settlement densities to the area of suitable habitat.

In conclusion, this study reports the receding distribution of American lobster early benthic life stages in previously well-populated nurseries of Narragansett Bay. Since 1990, when the first survey was conducted, lobsters have suffered mass mortalities, shell disease, and diminishing fishery recruitment on a larger scale in southern New England. Climate warming has been implicated in these events. But, coastal ocean warming is not the only stressor associated with climate change. It will be important to gain a greater understanding of how hypoxia, ocean acidification, and the shifting ranges of predators and competitors impact the changing geography of lobster distributions. Monitoring the most vulnerable life stages of commercially important species and their environment can provide the early warning that coastal and fishery managers need to anticipate and adapt to the impacts of a warming climate.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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