Yearly shifts in shell quality for the hermit crab *Pagurus longicarpus* in coastal Massachusetts

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ABSTRACT: Global warming is expected to result in milder New England winters. In this study we monitored changes in hermit crab shell quality at Nahant, Massachusetts, USA, at intervals during 17 yr between 1997 and 2014 for a single species of hermit crab *Pagurus longicarpus* occupying the shells of the intertidal periwinkle *Littorina littorea*. The incidence of hermit crabs occupying damaged shells, shells housing the symbionts *Hydractinia*, *Crepidula plana*, and *C. convexa*, and showing poor shell fit varied significantly among years. Shell quality was especially bad in the summer of 2012, following one of the warmest winters on record: more than 60 % of the sampled hermit crabs were found living in damaged shells and more than 50 % of the shells bore symbionts. Moreover, an unusually low number (only 15 %) of the hermit crabs sampled that summer were found in shells that were undamaged, without symbionts, and of adequate size, compared with 50 to 55 % of hermit crabs being found in such 'perfect' shells in 1997 and 2013. We suggest that new, high-quality shells are added to hermit crab populations at our study site largely through the freeze-induced mortality of intertidal periwinkles, and that the poor shell quality documented in summer 2012 reflects reduced periwinkle mortality during the unusually warm preceding winter. If so, then *P. longicarpus* might serve as a coastal 'canary in the coal mine': documenting yearly shifts in the quality of shells used as shelters by coastal marine hermit crabs in New England may provide a convenient means of monitoring the impact of climate change on intertidal populations.

KEY WORDS: Hermit crabs · Climate change · Shell quality · *Littorina littorea* · *Pagurus longicarpus*

INTRODUCTION

'All hermit crabs are ultimately dependent upon gastropod mortality for new shells…. How these shells come to appear on the substrate is usually not known.' (Wilber & Herrnkind 1984 p. 149,145)

Marine hermit crabs seek empty gastropod shells for protection prior to metamorphosis (Reese 1962, Brodie 1999) and must then keep acquiring new shells as they grow (e.g. Vance 1972) and as the shells they occupy become damaged (e.g. Scully 1983, Mc-Clintock 1985, Tricarico & Gherardi 2007). Not all shells make equally suitable homes: shell quality affects susceptibility to predators (Buckley & Ebersole 1994, Angel 2000, Pechenik et al. 2001, Hazlett et al. 2005), reproductive output (Fotheringham 1976a,b, Wilber 1989, Turra 2003, Hazlett et al. 2005), growth rates (Markham 1968, Fotheringham 1976b,c, Bertness 1981, Angel 2000, Turra & Leite 2003), and vulnerability to eviction by other hermit crabs (Reese 1969) and to environmental stresses such as desiccation and fluctuating salinity (Shumway 1978, Taylor 1981, Pechenik et al. 2001). Not surprisingly, in laboratory studies marine hermit crabs carefully discrimi-

nate among empty shells for their homes, on the basis of size, weight, weight distribution, geometry, internal volume, and various types of damage (e.g. Reese 1962, Conover 1978, Bertness 1980, McClintock 1985, Hazlett 1987, 1989, Wilber 1990, Elwood 1995, Osorno et al. 1998, Turra & Leite 2002, Kaiser et al. 2005, Arce & Alcaraz 2012, reviewed by Hazlett 1981). Shells are also assessed with regard to the presence or absence of certain internal and external symbionts (Briffa & Elwood 2005; reviewed by Williams & McDermott 2004), such as hydrozoans (Buckley & Ebersole 1994) and the gastropods *Crepidula convexa* and *C. plana* (Conover 1976, Li & Pechenik 2004, Pechenik et al. 2015).

Hermit crabs can afford to be fussy in the field, too, as long as they have an abundance of shells of appropriate size and condition to choose from. This is not usually the case, however (e.g. Vance 1972, Hazlett 1981, Elwood & Neil 1992, Turra & Leite 2002), and hermit crabs must often battle each other to acquire shells of appropriate size and adequate quality (e.g. Vance 1972, Dowds & Elwood 1983, Briffa & Elwood 2000, 2002, Briffa & Dallaway 2007). What determines the degree to which hermit crabs in the field will need to compete with each other for shells of high quality? That will depend on the size of the hermit crab population, the rate at which high-quality shells of appropriate size enter the population, the rate at which occupied shells degrade, and how long empty shells of good quality remain accessible to the hermit crabs.

Hermit crabs have rarely been found to kill snails for their shells (Rutherford 1977, Laidre 2011). Instead, gastropods usually die of natural causes (e.g. freezing stress, high-temperature stress, salinity stress, dehydration, predation, and parasitic attack) (e.g. Orton 1933, Lewis 1954, Fraenkel 1960, Scully 1979, Murphy & Johnson 1980, Bertness & Cunningham 1981, Wilber & Herrnkind 1984, McKillup & McKillup 2000, Firth & Williams 2009, McGuire & Williams 2010) and the hermit crabs then evaluate the shells as they become available (Rittschof 1980, Hazlett 1997).

Empty, unoccupied shells are subject to burial (e.g. Conover 1975, Laidre 2011), erosion, transport away by currents, and damage by epibionts (reviewed by Wilber & Herrnkind 1984). Shells may also be damaged by animals mistakenly attacking empty shells or attempting to prey on hermit crabs occupying shells (Borjesson & Szelistowski 1990, Walker & Yamada 1993), or may be crushed by small stones during periods of intense water movement (Boulding & Van Alstyne 1993). Hermit crab populations thus require periodic input of high-quality shells of appro-

priate size, even in the absence of expanding populations. Gastropod mortality from parasitic infection (e.g. Lauckner 1987, Huxham et al. 1993) and from environmental factors such as salinity stress, high-temperature stress, and freezing stress (e.g. Kanwisher 1955, 1959, Murphy & Johnson 1980, Firth & Williams 2009) are likely to produce empty shells of especially high quality.

This raises an important and intriguing question: how might future changes in environmental conditions alter the rate at which empty, good-quality shells of appropriate size enter the hermit crabs' habitat, and the timing of such entry?

Predation on gastropods makes shells potentially available to hermit crabs, but predators usually damage or completely destroy the shells in the act of killing the snails (e.g. Hamilton 1976, Bertness & Cunningham 1981, Walker & Yamada 1993, Turra et al. 2005; see Wilber & Herrnkind 1984, McGuire & Williams 2010 for 2 exceptions). Commercial trawling activities can also kill numerous gastropods, but the resulting shells are usually heavily damaged and avoided by potential hermit crab occupants (Kaiser et al. 2005). Hermit crabs of many species have been shown to avoid shells with apex and other forms of damage if intact shells of appropriate size are available (McClintock 1985, Wilber 1990, Pechenik & Lewis 2000, Pechenik et al. 2001, Kaiser et al. 2005).

In conducting a field survey of shell use by the hermit crab *Pagurus longicarpus* at Nahant, Massachusetts, USA, in the early summer of 2012, we encountered an unusually large percentage of individuals in shells of especially poor quality. This suggested that the unusually mild New England winter of 2011 to 2012 (indicated by data from the NOAA National Climatic Data Center) may have reduced the freeze-induced mortality of intertidal periwinkles, creating a very limited supply of high-quality shells to the hermit crab population in the following spring, and led us to consider how shell quality has varied at this site from year to year.

MATERIALS AND METHODS

Hermit crab and shell sampling

Field surveys of hermit crab *Pagurus longicarpus* shell quality were conducted at low tide near Castle Road in Nahant, Massachusetts, from late July to early October in 1997, 1998, 1999, 2000, 2002, 2003, 2006, and 2010 with undergraduate students as part of a class project. In August 2012, July and Septem-

ber 2013, and June 2014, we conducted additional, more detailed surveys at this same site. Nahant is a particularly convenient location for this study, since just one species of hermit crab is found there (*P. longicarpus*), and more than 94% of the hermit crabs at this site inhabit the shells of a single gastropod species, the common periwinkle *Littorina littorea* (Pechenik & Lewis 2000). Thus there are no complications in our study from differential preferences for shells of different gastropod species or from interspecific competition for shells. This seems to be an unusual situation (Vance 1972, Kellogg 1976, Spight 1977, Barnes & De Grave 2002, reviewed by Hazlett 1981), but one that greatly simplifies our survey design and data interpretation.

At least 115 hermit crabs were collected from the beach haphazardly by hand for each survey. For each individual collected each year, we recorded the shell condition ('intact' versus at least 2 categories of damage: 'drilled' by moonsnails, probably *Euspira heros*, and 'other damage', including apex, aperture, and/or lateral shell damage). We also assessed whether each hermit crab could withdraw completely into its shell—and not leave its chelipeds protruding—when prodded with a pencil, to estimate whether or not the hermit crab was in a shell appropriate for its size. In addition, for samples taken in 1997, 1998, 2002, 2012, 2013, and 2014, we recorded the presence of epibionts on or inside the shells: *Crepidula plana*, *C. convexa*, and *Hydractinia* spp.

In 1998 and 2014, we also collected 79 to 165 empty shells haphazardly by hand from the same location, to determine the incidence and size distribution of empty drilled shells, enabling comparison with data for hermit-crab-occupied shells.

Since most of our collections were made at slightly different times each year, we made collections twice in 2012 (2 wk apart) and twice in 2013 (2 mo apart) to determine if the frequencies of each variable tested changed over short periods of time. In 2012, none of the shell quality frequencies changed between sampling times (χ^2 = 0.02–2.39, df = 1, p = 0.13–0.97), so data from 2012 were pooled for analysis. In 2013, frequencies changed for the occurrence of *C. plana* (χ^2 = 16.04, df = 1, p < 0.0001) and *C. convexa* (χ^2 = 5.85, df = 1, p = 0.02), but did not change between sampling times for the other variables (other comparisons, χ^2 = 0.01–2.80, df = 1, p = 0.08–0.92); thus, data for all variables except incidence of *C. plana* and *C. convexa* were pooled for these samples for analysis. In 2012, 2013, and 2014 we also measured the aperture length of each crab-occupied shell to the nearest 0.1 mm with calipers.

In addition, for the 2012 and 2013 surveys, we brought hermit crabs in their periwinkle shells back to the laboratory for further study (n = 80 in 2012, n = 40 in 2013). Each hermit crab was brought to the laboratory in a separate container, so that there was no possibility of them exchanging shells during transport. After determining the aperture length of the shell inhabited by each hermit crab, we removed the crab from its shell by numbing it in warm seawater (34°C) for several minutes (Pechenik et al. 2015), blotted it quickly with a paper towel, and determined its wet weight. Individuals of *P. longicarpus* of a particular weight prefer shells of a particular size (Angel 2000), enabling us to assess more precisely the degree to which these hermit crabs were occupying shells appropriate to their size.

Analysis of historical winter air temperatures at Nahant, MA

In order to determine the lowest cold winter air temperatures that individuals of *L. littorea* experienced during low tides in the intertidal zone in different years, we found data for air temperatures at both extreme low tides on each day, from December 1996 to March 2014. Hourly winter temperature data were obtained from the NOAA buoy closest to Nahant, Buoy No. 44013 (42° 20′ 44″ N, 70° 39′ 4″ W). Because this buoy was missing air temperature data from January to March 2012, air temperature data from the nearby NOAA Buoy No. 8443970 (42° 21′ 18″ N, 71° 3′ 1″ W) were used instead for this time frame. The date and times of the 2 peak low tides each day from December 1996 to March 2014 were determined for Nahant using the following website: http://tbone.biol.sc.edu/tide/ (Pentcheff 2014).

Each extreme low tide was paired with an air temperature from the same hour and date using the NOAA buoy data, and the single lowest air temperature occurring during low tide for each winter was determined. Assuming that individuals of *L. littorea* may be more likely to die during repeated exposures to extreme low air temperatures, monthly 'cold stretches' were also determined. Here, a sliding window of 6 consecutive peak low tides (i.e. low tides occurring over all 3-d intervals) was used to find the lowest mean air temperature during 6 consecutive extreme low tides for each month. All calculations and data pairing were completed using R version 3.0.2 (R Core Team 2013) and the R package Zoo version 1.7-11 (Zeileis & Grothendieck 2005).

Data analysis

All data were analyzed using GraphPad Prism version 4.3 (http://www.graphpad.com). To determine whether the condition of hermit-crab-occupied shells changed over our 17 yr sampling period, we first isolated each shell parameter as a nominal variable, and then used a chi-squared test for heterogeneity of frequencies in each category over time. For shell condition, we tested the frequency of drilled shells, the frequency of shells with 'other' damage (any shell damage other than a drill hole), and the frequency of intact shells over time. For epibiont load, we tested the frequency of shells associated with the hydroid *Hydractinia* spp., the gastropod *C. plana*, and the gastropod *C. convexa* over time. For shell fit, we tested the frequency of shells containing hermit crabs whose major cheliped remained protruding when the crabs were prodded, crabs whose major cheliped was flush with the shell aperture, and crabs that were able to withdraw well into the shell when prodded (Pechenik & Lewis 2000). Finally, we tested the frequency of hermit crabs found in 'perfect' shells — those of adequate size and exhibiting no damage and no epibionts. We know that hermit crabs of this species dislike being in shells that they cannot withdraw into (Angel 2000); however, we do not know whether they distinguish between shells into which they can completely withdraw and those in which, when fully withdrawn, they can only be flush with the aperture. In this study, we refer to such hermit crabs as 'protruding', 'hidden', or 'flush', respectively. Analyses for 'perfect' shells were therefore run 3 different times: once assuming that the criterion for being in a 'perfect' shell was to be flush with the aperture when fully withdrawn, once assuming that the criterion was to be hidden within the shell when fully withdrawn, and once assuming that the criterion included all crabs that were either hidden or flush with the aperture when withdrawn.

For data collected in 2012 and 2013, we determined the degree of shell size adequacy (or inadequacy) by comparing our data to the shell-fit index determined for these species (the hermit crab *P. longicarpus* and shells of the gastropod *L. littorea*) by Angel (2000). The wet weights of the hermit crabs and the aperture lengths of the shells that they were found to be occupying were log transformed before linear regression. We then compared the resulting regression slope with the slope from the equation found in Angel (2000, m = 0.2623) using an *F*-test. We generated size-frequency distributions for the shells of hermit crabs collected in 2012, 2013, and 2014, and subsequently compared those distributions using the Komolgorov-Smirnov test.

RESULTS

Hermit crab shell quality

In Nahant, Massachusetts, at least 98% of hermit crabs collected during the 17 yr study period were found occupying shells made by *Littorina littorea*, but those shells varied considerably from year to year in condition, epibiont load, and fit for the hermit crabs within them. The frequency of hermit crabs found in shells that were intact, drilled, or that exhibited other forms of damage differed significantly among the years in which we sampled (Fig. 1; intact: χ^2 = 247.8, df = 10, p < 0.0001; drilled: χ^2 = 93.04, df = 10, p < 0.0001; other damage: χ^2 = 220.1, df = 10, p < 0.0001). Among those 3 categories, the frequency of hermit crabs found in drilled shells varied the least over time, never comprising more than 13% of hermit-crab-occupied shells and usually 5% or less (Fig. 1). When empty *L. littorea* shells were surveyed in 1998 and 2014, drilled shells comprised between 44 and 57% of the population sampled (Table 1); in previous
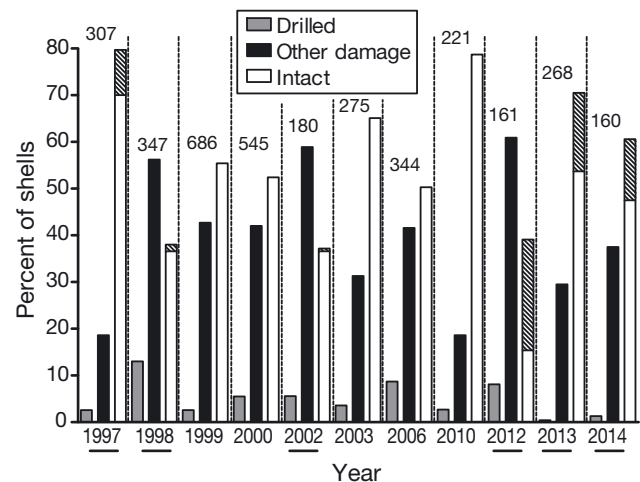

Fig. 1. Extent to which shells occupied by the hermit crab *Pagurus longicarpus* at Nahant, Massachusetts, were found to be damaged over a 17 yr period. At this site, >98% of the shells occupied by hermit crabs were made by the gastropod *Littorina littorea*. The number of crabs collected each year is indicated above each set of bars. Shells that were 'drilled' (gray bars) contained a single hole made by a predatory moonsnail; shells that had 'other damage' (black bars) had some combination of a broken apex, broken aperture, or broken lateral area; and shells that were 'intact' (white bars) showed no damage. In the underlined years, we also recorded presence of the symbionts *Hydractinia* spp. and *Crepidula convexa* on the outside of the shells, and *C. plana* on the inside; presence of symbionts in or on intact shells is shown by shading at the top of the white ('intact') bars. In 1997, 2012, 2013, and 2014, the percentage of damaged shells bearing symbionts was 53, 56, 43 and 31.5%, respectively (data not shown)

Table 1. Characteristics of drilled *Littorina littorea* shells collected at Nahant, Massachusetts. Shells were collected in the years indicated to determine the incidence of those that were empty or occupied by hermit crabs, and the size characteristics of the shells in those 2 categories. Statistics refer to comparisons of mean shell aperture length. n = total number of shells examined in each category

Year	Occupied shells			Empty shells			t	df	p
	n	Drilled (%)	Mean shell aperture (mm) ± SE	n	Drilled (%)	Mean shell aperture (mm) ± SE			
1998	307	10.1	15.3 ± 0.33	79	57.0	14.2 ± 0.28	2.57	75	0.012
2014	366	8.0	13.3 ± 0.385	189	44.3	13.4 ± 0.183	0.29	162	0.77

surveys made at this study site, drilled shells comprised about one-third of the population of empty shells (Pechenik & Lewis 2000). In both years, the proportion of occupied shells that were drilled was significantly lower than the proportion of empty shells that were drilled (1998: χ^2 = 87.21, df = 1, p < 0.0001; 2014: χ^2 = 102.50, df = 1, p < 0.0001). There was little or no difference in the mean aperture size of empty and occupied drilled shells in the sampled years (Table 1).

In 1998, 2002, and 2012, fewer than 40% of hermit crabs occupied intact shells. Hermit crabs were found living in damaged shells most frequently in 2012 (69% of the population sampled): 8.1% of the occupied shells had been drilled, and 60.9% exhibited other forms of shell damage (Fig. 1). Moreover, a remarkable proportion (16.1%) of the 161 hermit crabs sampled in 2012 were found living in shells

that were damaged extensively (i.e. with at least ~25% of the shell missing; Fig. 2), to an extent not seen in any previous or subsequent year; in 2013 only 3 such shells were encountered out of 268 hermit-crab-occupied shells examined, and in 2014 only 1 out of 160 hermit-crab-occupied shells was so badly damaged.

The frequency of hermit crabs found in shells bearing the epibionts *Crepidula plana* and *C. convexa* also varied significantly over the sampling period (Figs. 1 & 3; *C. plana*: χ^2 = 179.7, df = 5, p < 0.0001; *C. convexa*: χ^2 = 106.4, df = 3, p < 0.0001), while the frequency of hermit-crab-occupied shells bearing *Hydractinia* spp. changed only slightly (Fig. 3; χ^2 = 6.82, df = 3, p = 0.07). More than 50% of the sampled intact shells bore symbionts in 2012; thus of the 161

Fig. 2. Hermit crab *Pagurus longicarpus* in an extensively damaged shell, from a sample taken at Nahant, Massachusetts, in summer 2012. An unusually high proportion of hermit crabs (about 16% of the 161 individuals sampled) were found occupying such shells that summer
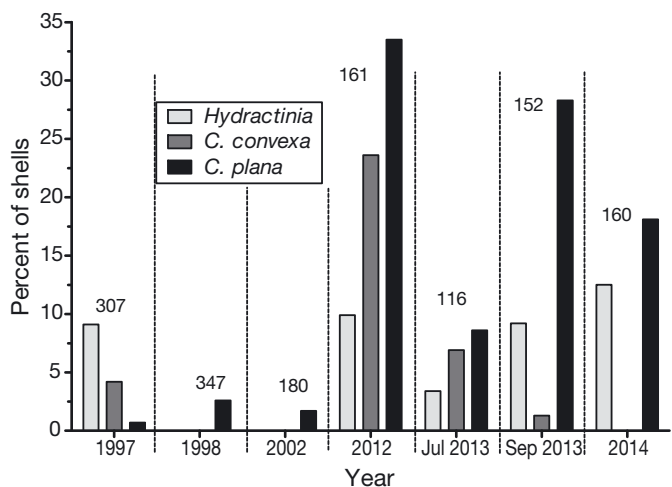

Fig. 3. Extent to which shells occupied by *Pagurus longicarpus* from Nahant, Massachusetts, bore epibionts over a 17 yr period. At this site, >98% of the shells occupied by hermit crabs were made by the gastropod *Littorina littorea*. The number of crabs collected each year is indicated above each set of bars. The hydroid *Hydractinia* spp. (light gray bars) and the gastropod *Crepidula convexa* (dark gray bars) are found on the outside of *L. littorea* shells, while the gastropod *C. plana* (black bars) lives on the inside of *L. littorea* shells
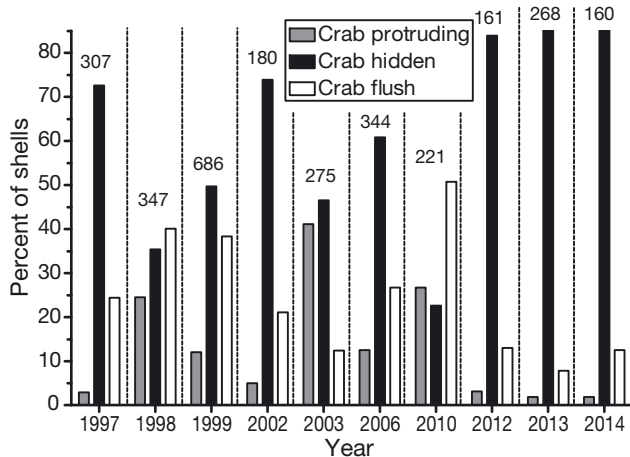
Fig. 4. Adequacy of shell fit by *Pagurus longicarpus* hermit crabs from Nahant, Massachusetts, over a 17 yr period. At this site, >98% of the shells occupied by hermit crabs were made by the intertidal gastropod *Littorina littorea*. The number of crabs collected each year is indicated above each set of bars. Hermit crabs were observed either to fit into their shells with their major cheliped protruding (gray bars, protruding), to withdraw deep into their shells (black bars, hidden), or to fit into shells with their cheliped lying flush with the aperture (white bars, flush)

hermit-crab-occupied shells sampled in that year, more than 90% were either damaged or bearing symbionts (Fig. 1). Among the years sampled, 2012 showed the highest frequencies of shells (both damaged and intact) bearing the epibionts *C. plana* (33.5% of shells sampled) and *C. convexa* (23.6% of shells sampled), while *Hydractinia* spp. was most frequent in 2014 (12.5% of shells sampled) (Fig. 3).

The frequency of hermit crabs found in shells in which they were protruding, hidden, or flush with the aperture when prodded also differed significantly among years (Fig. 4; protruding: $\chi^2 = 343.4$, df = 9, p < 0.0001; hidden: $\chi^2 = 476.9$, df = 9, p < 0.0001; flush: $\chi^2 = 250.4$, df = 9, p < 0.0001). Except for the years 1998 and 2010, most hermit crabs occupied shells into which they could fully withdraw when prodded ('hidden'; Fig. 4), and only in 2010 were more than 50% of the sampled hermit crabs flush with the shell opening when prodded (Fig. 4). Substantial numbers of hermit crabs (more than 25% of the sampled populations) were found in shells that were much too small for them (i.e. the animals protruded from the their shells when prodded) only in 1998, 2003, and 2010. In 2012, 2013, and 2014, more than 80% of the sampled hermit crabs were found living in relatively large shells, into which they could fully withdraw, and about 95% of the hermit crabs could either withdraw fully into their shells or were flush with the aperture when prodded (Fig. 4); in the 2012 samples, most of those shells were otherwise in poor condition, as noted earlier.

In both 2012 and 2013 (these measurements were not made in 2014), the relationship between the hermit crabs' wet weight and the aperture size of the shells they occupied was significantly different (p < 0.0005) from the same relationship obtained from hermit crabs of this species that had been allowed to choose from an abundance of shells in the laboratory (Angel 2000) (Fig. 5). In both of those sampled years, the smaller hermit crabs tended to be in shells that were too large for them, while the largest hermit crabs were usually found in shells of the preferred size (Fig. 5). Although the range of shell sizes was similar in all 3 yr (2012 to 2014), small hermit-crab-occupied shells were significantly rarer in 2012 and
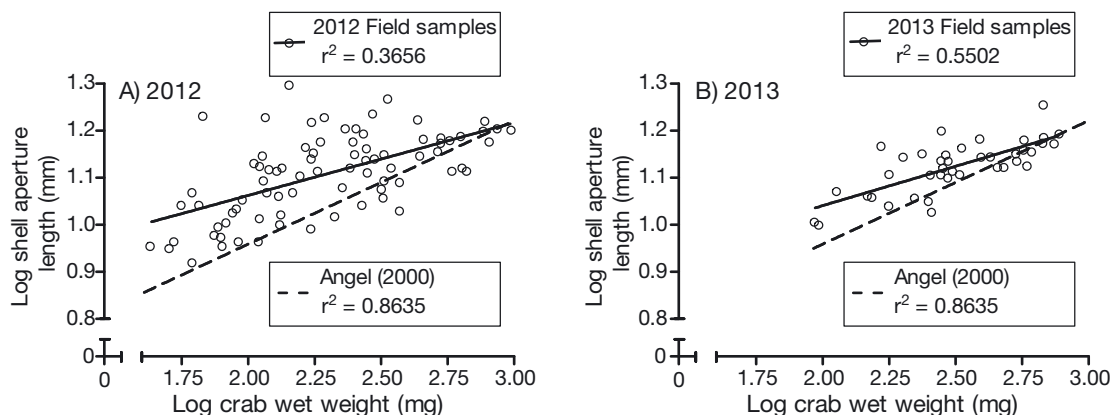

Fig. 5. Extent of shell-size inadequacy for hermit crabs collected at Nahant, Massachusetts, in (A) 2012 (n = 80) and (B) 2013 (n = 40). The linear regression slopes from the 2012 and 2013 sampling periods (solid lines) were significantly different from the slope of the regression found for hermit crabs occupying shells of a preferred size (dashed line, adapted from Angel 2000) (2012: $F_{1,78} = 21.81$, p < 0.0001; 2013: $F_{1,38} = 14.96$, p = 0.0004)

2013, and less rare in 2014 (Fig. 6) (Kolmogorov-Smirnov tests: 2012 vs. 2013: D = 0.139, p = 0.136; 2012 vs. 2014: D = 0.216, p = 0.001; 2013 vs. 2014: D = 0.310, p < 0.001).

The frequency with which hermit crabs were found in 'perfect' shells (i.e. shells that were intact and without symbionts, and into which the hermit crabs could withdraw at least far enough for their chelipeds to be flush with the aperture when prodded) varied over the sampling period, regardless of the shell-fit criteria used to determine 'perfect' shells (Fig. 7; hidden only: χ^2 = 176.5, df = 5, p < 0.0001; flush only: χ^2 = 40.93, df = 5, p < 0.0001; hidden or flush: χ^2 = 185.3, df = 5, p < 0.0001). Regardless of how 'adequate' shell fit was assessed (Fig. 7), hermit crabs occupying 'perfect' shells showed the poorest shell fits in 2012. Moreover, in that summer only about 15% of the hermit crabs were found to be living in shells that showed no damage and no symbionts, and into which they could at least withdraw reasonably well (Fig. 7C).

Low-temperature stress experienced in the field

There was considerable variability in the level of single-episode low-temperature stress exhibited during low tides in the winters of different years, from about −8.5°C in 2002 to about −15°C in 2003 (Fig. 8, solid dots). The patterns of low-temperature stress over periods of 6 consecutive tidal cycles were even more variable among years. For example, in the winter of 2002, intertidal *L. littorea* would not have experienced average low temperatures colder than −2°C over any 6 consecutive tidal cycles (Fig. 8A, ver-

tical bars), while periwinkles in winter 2003 would have experienced repeated exposures to temperatures averaging about −10°C in both January and February. In the winter of 2012, the worst continuous run of low temperatures was seen in January, and was only about −5.5°C (Fig. 8A). The patterns of repeated low-temperature stress appear to have been less stressful in winters preceding those sum-
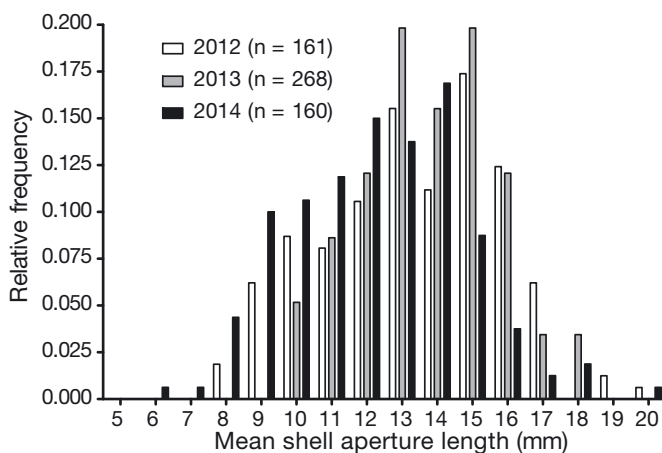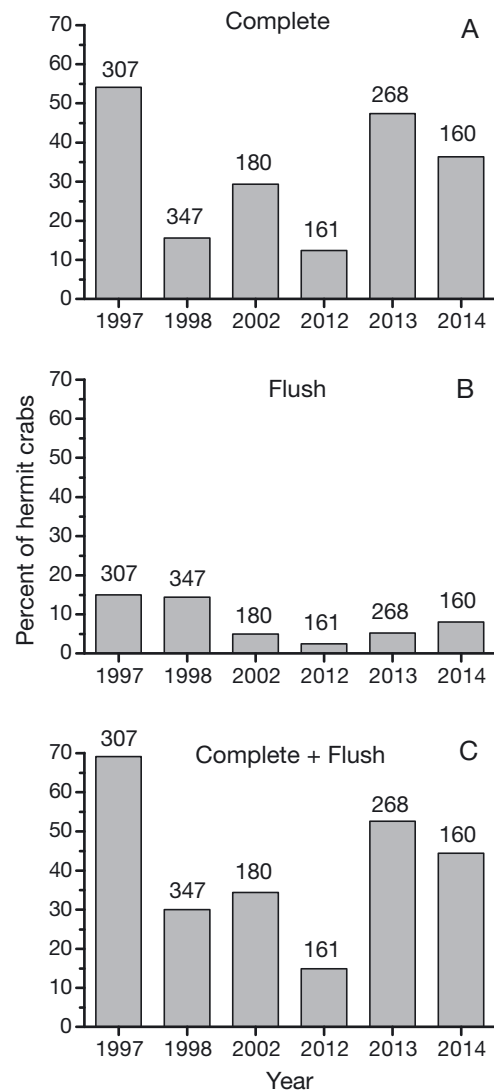

Fig. 7. Percentage of *Pagurus longicarpus* hermit crabs from Nahant, Massachusetts, that were found occupying 'perfect' shells over a 17 yr period. At this site, >98% of the shells occupied by the hermit crabs were made by the gastropod *Littorina littorea*. 'Perfect' shells were those that had no damage, bore no epibionts, and were of a size that (A) allowed a hermit crab to withdraw completely inside the shell when prodded, (B) allowed a hermit crab to withdraw enough so that its cheliped was flush with the aperture, or (C) allowed a hermit crab to either withdraw fully or remain flush with the aperture. The number of hermit crabs collected each year is indicated above each set of bars

Fig. 6. Size distributions of *Pagurus longicarpus* hermit-crab-occupied *Littorina littorea* shells in summers 2012 to 2014
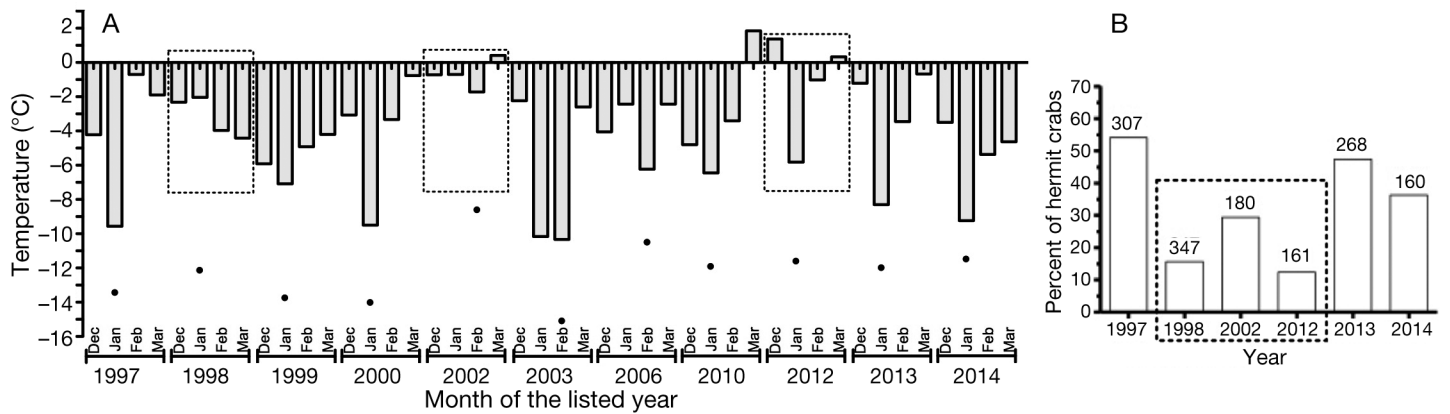
Fig. 8. (A) Extreme low winter air temperatures during hermit crab *Pagurus longicarpus* collection years at Nahant, Massachusetts. A sliding window of 6 consecutive extreme low tides (i.e. low tides occurring in sequence over 3 d) was used to find the lowest mean air temperature stretch for each month (gray bars). (●) Single coldest air temperature recorded during low tide in each winter. The 3 dotted rectangles correspond to data enclosed within the dotted rectangle in B. (B) Percentage of hermit crabs that were found living in 'perfect' shells (shells with no damage and no symbionts, and into which they could fully withdraw their chelipeds). The number of hermit-crab-occupied shells sampled is indicated above the bars

mers in which the hermit crabs were found in shells of unusually poor quality, and more stressful in winters preceding those summers in which the hermit crabs were found occupying shells of unusually high quality (Fig. 8B and dotted rectangles).

DISCUSSION

'Low temperature is frequently the chief environmental stress which eliminates a species in a given location.' (Kanwisher 1955, p. 56)

Although periwinkle *Littorina littorea* shell quality and shell fit varied considerably among samples taken in different years for hermit crabs *Pagurus longicarpus* collected over the 17 yr sampling period at our study site in Nahant, Masachusetts, the quality of occupied shells sampled in 2012 stands out as being particularly poor: fewer than 40% of the occupied shells were intact, and more than half of those intact shells bore symbionts that are actively avoided by *P. longicarpus*, when given other choices in the laboratory (Buckley & Ebersole 1994, Li & Pechenik 2004, Pechenik et al. 2015) (Fig. 1). Moreover, the integrity of the damaged shells was unusually poor that year (Fig. 2); indeed, only about 15% of the 161 hermit crabs sampled in 2012 were found to be living in shells with no damage and no epibionts, and that were large enough to allow substantial withdrawal into the shell when the crab was prodded (Fig. 7C). *P. longicarpus*, like other hermit crabs, avoids damaged shells when given the option (McClintock 1985, Wilber 1990, Pechenik & Lewis 2000). Considering the gen-

erally poor quality of the occupied shells in 2012, it seems intriguing that occupancy of drilled shells did not increase that year despite the abundance of appropriately sized drilled shells at the study site, whereas that of *Crepidula plana*-occupied shells did. Previous work (Pechenik et al. 2015) found that when presented in the laboratory with shells of similar and appropriate size, *P. longicarpus* were equally reluctant to occupy drilled shells and those containing large individuals of *C. plana*. It may be that many of the *C. plana* and *C. convexa* symbionts recorded in our surveys were not yet of sufficient size to have been noticed by the hermit crabs (Li & Pechenik 2004, Pechenik et al. 2015). With continued growth over time, though, those symbionts would make the shells less and less desirable (Li & Pechenik 2004, Pechenik et al. 2015). Our results imply, then, that competition for high-quality shells was especially severe for this hermit crab population in summer 2012. We suggest that this was caused by the unusually warm winter that year (December 2011 to March 2012), the second warmest New England winter on record since 1898 (www.ncdc.noaa.gov, www.capitalclimate.blogspot.com).

Competition for high-quality shells might have been unusually great in summer 2012 because hermit crab survival was unusually high in the previous winter. However, *P. longicarpus* migrates into deeper water (at least 5 m deep) in the late autumn when temperatures fall below ~10°C and does not reappear in the intertidal zone until spring (Rebach 1974). *Clibanarius vitattus* behaves similarly (Fotheringham 1975). Thus, unlike periwinkles, which remain inter-

tidal throughout the year (Murphy & Johnson 1980), the hermit crabs are not exposed to intertidal air temperatures during winter. The poor quality of the shells occupied by hermit crabs in the summer of 2012 is more likely due to a poor supply of new, high-quality shells than to increased hermit crab population size, but more studies are needed to resolve this issue.

This brings us back to 3 compelling issues that were mentioned earlier: What controls the supply of new empty shells to the hermit crab population? What determines how long those shells remain of high quality and available to hermit crabs? And how might warmer winters affect the availability of high-quality shells in the future?

Surprisingly few studies have focused on how new shells enter hermit crab populations (McGuire & Williams 2010). The green crab *Carcinus maenas* has been reported to be one of the major predators of *L. littorea* in some areas (Rangeley & Thomas 1987). However, at our Nahant study site this species has been almost completely replaced for at least the past 10 yr by the invasive Asian shore crab *Hemigrapsus sanguineus* (J. Pechenik pers. obs.), which tends to feed primarily on macroalgae and bivalves (Tyrell & Harris 1999, Brousseau et al. 2000, Bourdeau & O'Connor 2003); it also consumes juvenile periwinkles, but does so by cracking the shell or breaking the shell aperture (Gerard et al. 1999, Bourdeau & O'Connor 2003). Moreover, *C. maenas* feeds by crushing, chipping, and cracking the shells of its prey (Hadlock 1980), so that good-quality shells would not be made available to hermit crabs by their feeding activities. Naticid gastropods are also major predators of *L. littorea* at our study site (Pechenik & Lewis 2000), but they also obtain their prey by damaging (through drilling) the shell (Pechenik & Lewis 2000, Pechenik et al. 2001). Spider crabs *Libinia emarginata* will also prey on live periwinkles (McGuire & Williams 2010), although we have never seen these crabs at our study site.

Freezing stress is another potentially major source of gastropod mortality, and one that will always leave the shells intact. Periwinkle tissues may freeze twice each day in winter as the animals are exposed to air during low tides for hours at a time; as noted earlier, these snails remain intertidal throughout the year (Murphy & Johnson 1980). The tissues will also thaw twice daily when the water levels again rise and cover the animals; at −10°C, 60 to 80% of the water in the tissues of this species is frozen (Kanwisher 1955, 1959). Although *L. littorea* has a high tolerance to freezing at temperatures as low as −10°C (Kanwisher

1959, Murphy & Johnson 1980, Churchill & Storey 1996), individuals collected in the winter died within 6 h following a single exposure to temperatures of −11 and −13°C (Murphy & Johnson 1980). In their natural environments in New England, these snails may be subjected to temperatures of −20°C or lower (Kanwisher 1959), so freezing stress may indeed be a major source of gastropod mortality for *L. littorea* at Nahant. If so, warmer winters would be expected to reduce the supply of new empty shells to the hermit crab population. Murphy & Johnson (1980) showed that smaller periwinkles were more susceptible to freezing stress than larger periwinkles, which may help to explain the relative rarity of small hermit-crab-occupied shells at our study site — hermit crabs tended to be found in shells that were substantially larger than the preferred size (Fig. 5) following the relatively warm winter of 2012. On the other hand, many hermit crabs were also in larger shells than expected in the 2 subsequent seasons, following more normal, cold winters. Smaller empty shells may simply be more likely to be buried or swept into deeper waters than larger shells.

Although the cited studies demonstrate that single exposures to extremely low air temperatures can indeed kill periwinkles, no studies to our knowledge have explored how repeated exposures to somewhat milder freezing air temperatures affect periwinkle survival. The winters of 2012 and 2013 had very similar single lowest extreme air temperatures at low tide, −11.6 and −12.0°C, respectively, so it is unlikely that these single acute exposures to low temperature resulted in the recorded differences in the quality of available shells (Fig. 8). However, the lowest mean temperatures experienced during a series of 6 low tides (a 'cold stretch') were quite different for those 2 winters: an average of −5.8°C in 2012 and −8.3°C in 2013. This difference in prolonged exposure to mild freezing temperatures could be responsible for differential periwinkle survival in these 2 yr. Similarly, whereas the winters of 1997 and 1998 had relatively close single minimum temperatures at extreme low tides, −13.4 and −12.1°C, respectively (Fig. 8), the same winters had very different minimum mean 'cold stretches' at low tides, averaging −9.6 and −4.0°C, respectively. We suggest that future studies examine how repeated exposures to freezing air temperatures and repeated freeze–thaw cycles brought upon snails by the tidal cycle affect periwinkle survival.

Parasites may also play a role in affecting the susceptibility of *L. littorea* to freezing. *L. littorea* serves as an intermediate host in the life cycles of 5

trematode species, particularly *Cryptocotyle lingua* (Blakeslee & Byers 2008, Lambert et al. 2012, Pechenik et al. 2012). Infection rates exceeding 30% have been commonly reported from some natural populations (Lauckner 1987, Huxham et al. 1993, Byers et al. 2008, Lambert et al. 2012). However, although trematode infection is known to decrease the tolerance of *L. littorea* to high temperatures (discussed below), we are not aware of any studies that have examined how infection affects its freeze tolerance. This is again something that could be looked at in future studies: if parasitic infection weakens the snails and decreases their tolerance to freezing temperatures, then warmer winter air temperatures may reduce gastropod mortality in proportion to the incidence of parasitism.

Climate change, bringing increased air and water temperatures, is predicted to continue far into the future (e.g. Helmuth et al. 2006), with routinely milder winters as a predicted consequence in New England. As far as we are aware, no previous studies have considered the potential impact of milder winters on the availability of good-quality shells to hermit crabs. However, our study suggests that such impact might be expected. Indeed, Beukema & Dekker (2014) found an interesting correlation between the intensity of winters and the extent of recruitment to bivalve populations in the Wadden Sea, a relationship that may be controlled by the effect of winter severity on the population size of the crustaceans that prey on bivalve recruits. The authors suggest that severe winters reduce the crustacean populations without interfering with bivalve reproduction, so that post-recruitment bivalve survival is correspondingly high following severe winters. Milder winters, in contrast, correlate with larger crustacean populations, and thus higher levels of predation on young bivalves. The severity of winters may have a similar impact on *P. longicarpus* in New England, by altering the availability of high-quality shells through changes in the extent of intertidal gastropod mortality. Milder winters might also increase hermit crab survival and thus the subsequent competition for good-quality shells, although, as mentioned earlier, this seems less likely as hermit crabs migrate into deep water in the late autumn and remain dormant there until spring (Rebach 1974), and thus are not subject to the extreme low temperatures faced by intertidal animals. To the extent that increasing ocean temperatures and acidification accelerate the weakening of empty gastropod shells (Nienhuis et al. 2010), competition for high-quality shells should increase, and the rate at which new empty shells enter the population will increase in importance correspondingly.

On the other hand, substantially warmer summers at Nahant may eventually increase shell availability to hermit crabs in this population through heat-stress-induced periwinkle mortality, as mentioned earlier; such mortality would probably be proportional to the degree to which the periwinkles are infected by trematode parasites, as infected periwinkles are more readily killed by exposure to high temperatures (McDaniel 1969, Newell et al. 1971, Lauckner, 1987, Huxham et al. 1993, reviewed by Sousa & Gleason 1989). Parasitic infection also lowers the resistance of at least some gastropods to desiccation and osmotic stress (Berger & Kondratenkov 1974, as cited in Lauckner 1987), although this does not seem to have been investigated yet for *L. littorea*.

One additional, but potentially fascinating, complication is the possibility that an acidifying ocean might increase host parasite loads or parasite pathogenicity, if the parasites are less affected by declining pH than their hosts (MacLeod & Poulin 2012). On the other hand, Lefcort et al. (2002) found that some trematode parasites were more sensitive to heavy metal pollution than were their gastropod hosts, so that parasite loads decreased in polluted environments. How changing climate conditions and ocean chemistry will alter the extent of trematode-inspired mortality of periwinkles exposed to thermal extremes remains to be examined, and should be explored (see MacLeod & Poulin 2012).

P. longicarpus might serve as a coastal 'canary in the coal mine': if the relative rarity of high-quality shells in summer 2012 in our study did indeed reflect reduced periwinkle mortality caused by the unusually warm winter that year, then monitoring changes in the quality of shells occupied by hermit crabs could be a useful way to monitor and document the integrated impact of global climate change on intertidal ecology. *P. longicarpus* ranges from New England (e.g. Buckley & Ebersole 1994) to Florida (e.g. Conover 1978, Wilber 1989). In New England, such monitoring of shell quality should be done twice each year: once in the early spring, to take into account the mortality of periwinkles caused by freezing, and again towards the end of the summer, to take into account the potential mortality of periwinkles caused by high-temperature stress.

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