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Authors

Sorte, Cascade JB
Davidson, Victoria E
Franklin, Marcus C
et al.

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Long-term declines in an intertidal foundation species parallel shifts in community composition

CASCADE J. B. SORTE[1], VICTORIA E. DAVIDSON[2], MARCUS C. FRANKLIN[3], KYLLA M. BENES[1], MEREDITH M. DOELLMAN[4], RON J. ETTER[5], ROBYN E. HANNIGAN[6], JANE LUBCHENCO[7] and BRUCE A. MENGE[7]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA,* [2]*Whitman College, Walla Walla, WA 99362, USA,* [3]*Cornell Institute for Public Affairs, Cornell University, Ithaca, NY 14853, USA,* [4]*Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA,* [5]*Department of Biology, University of Massachusetts, Boston, MA 02125, USA,* [6]*School for the Environment, University of Massachusetts, Boston, MA 02125, USA,* [7]*Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA*

Abstract

The earth is in the midst of a biodiversity crisis, and projections indicate continuing and accelerating rates of global changes. Future alterations in communities and ecosystems may be precipitated by changes in the abundance of strongly interacting species, whose disappearance can lead to profound changes in abundance of other species, including an increase in extinction rate for some. Nearshore coastal communities are often dependent on the habitat and food resources provided by foundational plant (e.g., kelp) and animal (e.g., shellfish) species. We quantified changes in the abundance of the blue mussel (*Mytilus edulis*), a foundation species known to influence diversity and productivity of intertidal habitats, over the past 40 years in the Gulf of Maine, USA, one of the fastest warming regions in the global ocean. Using consistent survey methods, we compared contemporary population sizes to historical data from sites spanning >400 km. The results of these comparisons showed that blue mussels have declined in the Gulf of Maine by >60% (range: 29–100%) at the site level since the earliest benchmarks in the 1970s. At the same time as mussels declined, community composition shifted: at the four sites with historical community data, the sessile community became increasingly algal dominated. Contemporary (2013–2014) surveys across 20 sites showed that sessile species richness was positively correlated to mussel abundance in mid to high intertidal zones. These results suggest that declines in a critical foundation species may have already impacted the intertidal community. To inform future conservation efforts, we provide a database of historical and contemporary baselines of mussel population abundance and dynamics in the Gulf of Maine. Our results underscore the importance of anticipating not only changes in diversity but also changes in the abundance and identity of component species, as strong interactors like foundation species have the potential to drive cascading community shifts.

Keywords: Atlantic, benchmarks, biodiversity, community ecology, foundation species, global change, historical ecology, mussel, *Mytilus edulis*, population biology

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Introduction

Direct and indirect effects of human-induced global changes have caused rapid and extreme shifts in community composition across ecosystems worldwide (Sala *et al*., 2000; Lotze *et al*., 2006). Environmental conditions can influence species directly (Levin *et al*., 2001), and many studies reporting ‘fingerprints’ of global change have focused on these direct effects on responding species (e.g., Parmesan & Yohe, 2003; Root *et al*., 2003). However, indirect effects are pervasive in communities (Menge, 1995), so climate change-driven declines in individual, strongly interacting species may lead to chain reactions causing shifts in overall community composition (Jackson *et al*., 2001; Ellison *et al*., 2005; Bracken *et al*., 2007). Cascading extinctions (Borrvall *et al*., 2000) can occur from the top-down (e.g., due to the loss of keystone predators; Paine, 1966; Estes *et al*., 1989) or from the bottom-up (e.g., in the absence of a basal food source or foundation [habitat-providing] species; Pandolfi *et al*., 2003). Here, we use comparisons over a 40-year time period and 450-km spatial extent to investigate declines in an important coastal foundation species and to evaluate the potential implications for overall community structure.

The blue mussel, *Mytilus edulis*, is a critical foundation and prey species in coastal systems (Seed, 1969; Menge,

Correspondence: C. J. B. Sorte, tel. +949 824 6971, fax +949 824 2181, e-mail: csorte@uci.edu

1976) and appears to be facing an increasing risk of extinction in locations along the USA east coast. Historically (before 1960), blue mussels occurred widely across the northern Atlantic from the Arctic Sea to North Carolina and from Svalbard, Norway to the French/Spanish border (reviewed by Jones *et al.*, 2009). Over the past 50 years, the southern range limit of established blue mussel populations in the USA has shifted by 350 km to the north, from Cape Hatteras, NC (35.2°N), to the current limit at Lewes, DE (38.8°N; Jones *et al.*, 2010). This range contraction in the southeastern USA raises the question of whether blue mussels are also declining in the Gulf of Maine, between Cape Cod, Massachusetts, and southern Canada (Fig. 1).

Declines of blue mussel populations may have severe ecological and economic impacts. As filter feeders, mussels form a link between marine and terrestrial productivity by consuming particulate materials in the nearshore ocean and biofiltration in general (e.g., Widdows *et al.*, 1979; Altieri & Witman, 2006; Bracken *et al.*, 2012). Mussels exist within relatively well-characterized interaction webs in intertidal habitats, often excluding competitors such as barnacles and seaweeds unless kept in check by the top carnivores such as whelks and sea stars (Paine, 1966; Menge, 1976). Mussels not only 'feed' intertidal food webs, they create beds with a three-dimensional matrix that provides essential habitat for a diverse assemblage of associated invertebrates (Suchanek, 1987; Smith *et al.*, 2006). Blue mussels are also harvested as food by humans. In 2014, almost 4 million pounds of blue mussels – amounting to over \$10 million – were harvested in the USA, and approx. 85% of USA mussel landings are from the Gulf of Maine (NOAA National Marine Fisheries Service, 2016). The majority of these mussel landings are from wild beds, and cultured mussels, which account for <20% of Maine landings, are initially seeded from wild sources (Maine Department of Marine Resources, 2016). Therefore, the persistence of mussels within the Gulf of Maine is critical for sustaining both ecological and economic systems, as loss of mussels could precipitate changes in the abundance of interacting species, overall community structure, and ecosystem functioning.

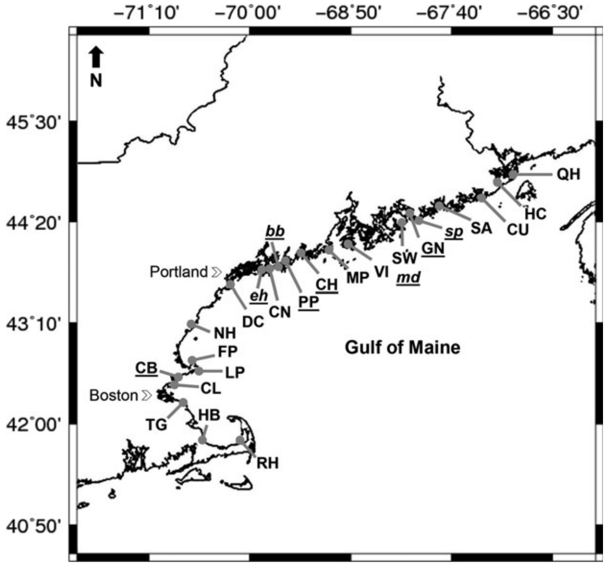

Fig. 1 Field sites in the Gulf of Maine. Sites were surveyed for the historical comparisons (underlined), contemporary community analyses (capitals), or both. Site names are as follows: Quoddy Head (QH), Hamilton Cove (HC), Cutler (CU), South Addison (SA), Schoodic Point (sp), Grindstone Neck (GN), Seawall, Mount Desert Island (SW), Somes Sound, Mount Desert Island (md), Vinalhaven Island (VI), Marshall Point (MP), Chamberlain (CH), Pemaquid Point (PP), Cape Newagen (CN), Boothbay (bb), East Harpswell (eh), Dyer Cove (DC), Rye Beach, NH (NH), Folly's Point (FP), Loblolly Point (LP), Canoe Beach (CB), Cunner Ledge (CL), The Glades (TG), Horizon Beach (HB), and Rock Harbor (RH). Geographic coordinates are available in Data set S1.

In this study, we used historical and contemporary survey data to evaluate changes in blue mussel abundance and community composition. Our objective was to answer the following specific questions: (1) Have mussels declined in abundance in the Gulf of Maine over the past 40 years? (2) Has community composition changed over this same time period, particularly the contribution of mussels to compositional patterns? (3) Is intertidal species diversity related to mussel abundance? (4) Which locations are most susceptible to future population declines, as indicated by the lowest population sizes, proportion of juveniles, and reproductive potential?

Materials and methods

Approach

We quantified changes in mussel abundances and community composition by compiling historical records and conducting site resurveys. To establish current baselines, we extended our contemporary surveys to 20 sites across the Gulf of Maine. We investigated the links between mussels and two interacting species (the predatory whelk *Nucella lapillus* and another space competitor, the barnacle *Semibalanus balanoides*) as well as overall community diversity and composition using comparisons across time (historical vs. contemporary survey data) and space (sites). Finally, to evaluate future mussel population growth trajectories, we quantified mussel fecundity and size structure within these 20 contemporary populations.

Historical data compilation

Historical blue mussel abundance data from the Gulf of Maine were gathered using a three-step process, including: (1)

database searches, (2) literature reviews, and (3) data extraction. We used species- and location-specific keywords to search online databases [ISI Web of Knowledge (1800–2013), BioOne, Google Scholar, Sea Grant Publication Index, Biodiversity Heritage Library, EBSCOhost Wildlife & Ecology Studies Worldwide, and University of Maine Dissertation Index]. We also reviewed cited references and included papers from our own reference files. Our main criterion for inclusion was the reporting of site-specific, quantitative mussel abundance data. In total, we reviewed over 8100 titles, 500 abstracts, and 180 papers, eventually including data from 36 published sources representing a total of over 500 abundance estimates [by year × site × location (e.g., tide height)]. Although we focused our field study on hard-bottom, intertidal sites, the database also includes some data from soft-bottom and subtidal sites. Abundance values were extracted from text, tables, or figures [using ImageJ (Rasband, 2009) or WebPlotDigitizer (Rohatgi, 2015)] or were provided by the authors as raw data. Our most extensive historical dataset, published by Menge (1976) and Lubchenco & Menge (1978), was transcribed from original data notebooks. The full database of historical mussel abundances is provided in Data set S1.

Historical resurveys

We identified five historical studies, reporting mussel abundances quantified between 1972 and 2007, which provided adequate methodological information that allowed us to resurvey each study location (e.g., site and tide height; Fig. 1) using the same survey methods, as described below. All historical and contemporary abundance data were from quadrat counts conducted along horizontal transects or intertidal zones. Where specified, locations of random quadrats were determined using a random numbers table, and point-count abundance estimates relied on plexiglass quadrats containing 100 points randomly located in x, y space.

Menge (1976) and Lubchenco & Menge (1978) surveyed Grindstone Neck (GN), Chamberlain (CH), Pemaquid Point (PP), and Canoe Beach (CB) between 1972 and 1976. We transcribed abundance estimates for all species from all surveys (Data set S2). Historical data from summer months (May through August) were used for analyses (but differed by year; thus, month was not included in our statistical analyses). We resurveyed these sites in May and July of 2013 and 2014. For the resurveys, three 30-m horizontal transects were laid at low (0 m), mid (1 m), and high (2 m) tide heights at each site. Ten 0.25-m^2 quadrats were randomly placed along each transect, and mussel abundances were determined using both visual percent cover estimates and point-count estimates (both methods were used at different times by Lubchenco & Menge, 1978). For subsequent analyses, we used the contemporary visual percent cover estimates, which were slightly (0.85 ± 0.22%) higher than point-count estimates and, thus, more conservative in identifying declines (also see Dethier *et al.*, 1993).

Larsen (2012) counted mussels at three rocky intertidal sites in July 1975: Somes Sound on Mount Desert Island (MD), McKown Point in Boothbay Harbor (BB), and Pinkham Point at East Harpswell (EH). All organisms were scraped from two haphazard 0.25-m^2 quadrats at each of three tide heights (low, mid, and high) and were sorted and counted in the laboratory. We resurveyed these sites in July 2014 with the one methodological difference that we counted the few mussels present *in situ*.

Dudgeon *et al.* (1999) conducted surveys at CH and PP in May of 1989 and Schoodic Point (SP) in September of 1990. At each site, mussel abundance was measured in 6–14 quadrats (0.04 m^2) randomly placed along 20-m horizontal transects at each of three tide heights: low (0 m), mid-low (0.5 m), and mid-high (1.0 m). Whereas photographic abundance estimates were presented in Dudgeon *et al.* (1999), our analyses (Table 1) are based on raw point-count data provided by the authors. We resurveyed in July 2013 and May 2014, also quantifying abundance via N = 12–26 point-count estimates across the two sampling dates.

Bertness *et al.* (2004) compared mussel abundance between habitats dominated by mussels or the alga *Ascophyllum nodosum* across two sites (CH and PP) in July 2001. Eight to 10 0.25-m^2 quadrats were haphazardly counted approx. 2 m apart at two different tide heights: low (0 m to lower limit of *Ascophyllum* canopy) and high (upper limit of *Ascophyllum* canopy to bare rock). Mussel abundance was estimated as visual percent cover. We resurveyed these sites (10 quadrats per habitat × tide height × site) in July of 2013 and 2014.

Tam & Scrosati (2014) surveyed mussels in May to July 2007 at 'exposed' and 'very exposed' sites, which included CH and PP. Raw data were provided by the authors, and resurveys were conducted at CH and PP in May 2014 and July of 2013 and 2014. At each site, a 10-m horizontal transect was laid at 1 m tide height, and mussel abundance [visual percent cover (values used in analyses) and total individuals] was quantified in 15 randomly placed, 0.25-m^2 quadrats. Because the identities of all field sites surveyed by Tam & Scrosati (2014) were not available, CH and PP values were compared to the average values for exposed and very exposed sites, respectively.

Contemporary latitudinal surveys

We conducted community surveys at 20 rocky intertidal sites across the Gulf of Maine in both May and July of 2013 and 2014 (Fig. 1). At each site, we laid a 50-m horizontal transect parallel to the waterline and then N = 5 vertical transects perpendicular to the waterline at randomly determined locations. The horizontal transect was laid in the same general vicinity during each site visit, but vertical transect locations differed by sampling date (i.e., these were not 'permanent' transects or quadrats). Along each vertical transect, we surveyed all species in 0.0625-m^2 quadrats from 0 m mean lower low water to the upper edge of the intertidal zone (i.e., end of the barnacle zone/bare rock) at 0.5-m elevation intervals. In each quadrat, we determined percent cover of sessile species and bare space (using visual estimates; values could be >100% due to canopy layering) and individual counts for mobile species. Given variation in tidal amplitude between sites (2–6 m), each transect included between 5 and 13 quadrats. To assess population growth dynamics (e.g., Westerbom *et al.*, 2002), we also

Table 1 Mussel abundance from historical and contemporary surveys (2013–2014). Historical data are from 1972–1976 (Menge, 1976; Lubchenco & Menge, 1978), 1975–1976 (Larsen, 2012), 1989–1990 (Dudgeon *et al.*, 1999), 2001 (Bertness *et al.*, 2004), and 2007 (Tam & Scrosati, 2014). Abundance values are percent cover except for those from 1975–1976 (Larsen, 2012) which are individual counts. Detailed survey methodologies are provided in the text. P values are from nonparametric Mann–Whitney U-tests (1972–1976 and 2007 comparisons) or t-tests when analyses were based on summary data (1975–1976, 1989–1990, and 2001 comparisons) (nd = no data). Arrows indicate direction of significant changes between historical and contemporary surveys based on a Bonferroni-corrected P value of 0.00179

			Historical abundance			Contemporary abundance				
Year	Site	Location	Mean	SE	*N*	Mean	SE	*N*	*P*	Change
1972–1976	Grindstone Neck	High	4	1	63	5	2	40	0.29	
1972–1976	Grindstone Neck	Mid	17	2	96	10	3	40	<0.001	↓
1972–1976	Grindstone Neck	Low	32	4	78	12	3	40	<0.0001	↓
1972–1976	Chamberlain	High	5	1	28	9	1	40	0.03	
1972–1976	Chamberlain	Mid	62	5	40	15	4	40	<0.0001	↓
1972–1976	Chamberlain	Low	69	5	40	0	0	40	<0.0001	↓
1972–1976	Pemaquid Point	High	19	2	89	4	1	40	<0.0001	↓
1972–1976	Pemaquid Point	Mid	57	4	75	2	0	40	<0.0001	↓
1972–1976	Pemaquid Point	Low	70	4	50	4	1	40	<0.0001	↓
1972–1976	Canoe Beach	High	12	2	39	8	2	40	0.01	
1972–1976	Canoe Beach	Mid	15	3	45	2	1	40	<0.001	↓
1972–1976	Canoe Beach	Low	1	0	24	0	0	40	<0.01	↓
1975–1976	Mount Desert Island	Low to High	1184	nd	6	3	1	6	<0.0001	↓
1975–1976	Boothbay	Low to High	861	nd	6	1	1	6	<0.0001	↓
1975–1976	East Harpswell	Low to High	133	nd	6	2	1	6	<0.0001	↓
1989–1990	Chamberlain	Low	1	1	13	0	0	26	0.14	
1989–1990	Chamberlain	Mid–Low	2	1	12	14	6	24	0.16	
1989–1990	Chamberlain	Mid–High	9	5	9	15	6	26	0.55	
1989–1990	Pemaquid Point	Low	2	1	11	0	0	26	0.01	
1989–1990	Pemaquid Point	Mid–Low	0	0	14	1	0	26	0.30	
1989–1990	Pemaquid Point	Mid–High	0	0	6	2	0	26	0.01	
1989–1990	Schoodic Point	Low	14	4	8	3	2	12	0.02	
1989–1990	Schoodic Point	Mid–Low	1	1	8	7	3	26	0.22	
1989–1990	Schoodic Point	Mid–High	12	5	8	5	2	26	0.15	
2001	Chamberlain & Pemaquid Point	*Ascophyllum*	5	3	10	3	1	80	0.52	
2001	Chamberlain & Pemaquid Point	Mussel Bed	74	4	8	16	2	80	<0.0001	↓
2007	Chamberlain	Mid	22	2	150	16	3	45	<0.0001	↓
2007	Pemaquid Point	Mid	1	0	150	6	1	45	<0.0001	↑

determined mussel size structure during each site survey by removing all mussels from $N = 5$ random quadrats ($0.0625\ \mathrm{m}^2$) and transporting them to the laboratory on ice, where they were sorted into 5-mm-size bins. We also measured gonadosomatic index (GSI), an index of reproductive potential, of $N = 40$ mussels sampled haphazardly from the size structure quadrats. Each mussel used for GSI analysis was measured with calipers and dissected to determine shell dimensions and tissue wet weights, respectively. GSI was calculated as gonad weight ÷ total soft tissue mass.

Data analysis

Historical and contemporary mussel abundance data were averaged across replicate quadrats and sampling dates, and Table 1 shows parallel comparisons between time periods based on results of nonparametric Mann–Whitney U-tests or t-tests when analyses were based on summary data. We assessed significance at $P < 0.00179$ using a Bonferroni correction for multiple comparisons. We addressed differences between contemporary data and the Menge (1976) and Lubchenco & Menge (1978) studies using a generalized linear model (Proc GENMOD, using a gamma distribution with a log link function) in SAS Statistical Software (Cary, NC, USA). Specifically, we evaluated mussel abundance as a function of time period (1972–1976 vs. 2013–2014), tide height (low, mid, high), and site (GN, CH, PP, CB).

To assess changes in interacting species (barnacles and whelks) and community composition, we compared the transcribed community data from Menge (1976) and Lubchenco &

Menge (1978) to those from our 2013–2014 community survey at the same tide heights (0, 1, and 2 m). We investigated the effect of differences in quadrat size between these two community survey data sets (0.25 m^2 vs. 0.0625 m^2) by comparing contemporary mussel cover estimates using both quadrat sizes (from surveys across four sites and tide heights) and found an average difference of $3.75 \pm 1.14\%$ cover. We evaluated changes in barnacle and whelk abundance with a generalized linear model as for the mussel comparisons, described above, except using a Poisson distribution for analyses of whelk count data. We identified the percentage contribution of each sessile species to the similarity and dissimilarity of community composition between time periods (1972–1976 vs. 2013–2014) using a SIMPER analysis, and we used PERMANOVA, run in PRIMER v. 6 (Clarke & Gorley, 2006), to compare the sessile community composition between time periods.

To evaluate contemporary patterns of mussel abundance, GSI, and size structure, as well as species richness, we used generalized linear models, as described above. Mussel abundance (averaged across $N = 1–5$ transects depending on site and tide height) was modeled as a function of month and year of survey, site, emersion time, site × month, and site × emersion time. Emersion time for each 0.5-m interval was calculated as the proportion of time each tide height was above the projected tide level (i.e., emersed), based on tide height data for the 1 year period of 01 July 2013 to 01 July 2014 (tbone tides; http://tbone.biol.sc.edu/tide/). This allowed us to correct for variation in tidal amplitude across sites. We addressed the role of mussels in driving local diversity (at the quadrat level) by modeling sessile species richness and mobile species Fisher's alpha (Hammer *et al.*, 2001) as a function of year, month, site, emersion time, mussel cover, and mussel cover × emersion time. We also evaluated factors driving GSI (including year, month, site, month × site, and mussel length) and proportional abundance of the smallest mussel size class (0–4.9 mm; including year, month, and site). All values are reported as means ± SE unless specified otherwise.

Results

Blue mussels declined over the past 40 years at seven sites spanning 450 km of the Gulf of Maine coast (Table 1). Declines detected by our resurveys of the Menge (1976) and Lubchenco & Menge (1978) studies (time period $\chi^2 = 393.78$, df = 1, $P < 0.0001$) were particularly evident at locations where mussels were historically present in high abundance. Across four sites (GN, CH, PP, and CB), mussel cover declined by an average of 84%, 74%, and 6% at low, mid, and high tide heights, respectively (tide height × time period $\chi^2 = 128.57$, df = 2, $P < 0.0001$; Table 1). Mid-zone mussel cover at these sites has declined from a range of 15–62% in the 1970s to the current range of 2–15% cover. Mussel abundance also declined by 99% across the three sites originally surveyed by Larsen (2012) in 1975–1976. Comparisons to more recent baselines indicated a decreasing trend but fewer differences (Table 1).

Community composition changed between 1972–1976 and 2013–2014, the same interval during which blue mussels declined (PERMANOVA pseudo-$F = 53.67$, $P = 0.001$; Fig. 2; Data sets S2 and S3). In 1972–1976, the dominant space holders were the barnacle *S. balanoides* and mussels, respectively contributing 38.8% and 34.1% to similarity within sites and surveys; three algal species (*Chondrus crispus*, *A. nodosum*, and *Fucus* spp.) contributed a total of 19.6%. However, in 2013–2014, mussels were not among the species that accounted for >90% of similarity within the sessile community. Instead, the main contributors to similarity between sites and surveys were *S. balanoides* (48.3%) and five algal species (*Ralfsia verrucosa*, *Hildenbrandia* sp., *Mastocarpus stellatus*, *A. nodosum*, and *Fucus* spp.), which contributed a total of 41.8% (4.7–13.2% each). Mussels were the second most important contributor to differences in community composition between historical and contemporary time periods, with a contribution of 11.7%, after 19.2% by the abundant species *S. balanoides* (Table S1). Single-species comparisons showed that *S. balanoides* increased (time period $\chi^2 = 18.71$, df = 1, $P < 0.0001$) and the predatory whelk *N. lapillus* decreased (time period $\chi^2 = 1793.19$, df = 1, $P < 0.0001$) between 1972–1976 and 2013–2014 (Fig. 3).

Across the Gulf of Maine, within-site analyses indicated that mussels characterized the sessile community (based on species accounting for >90% of similarity) at only two of 20 sites in 2013–2014 – Cunner Ledge (CL) and Grindstone Neck (GN) – contributing ≤6% to month and year comparisons. Mussel abundance did not vary between years during our contemporary surveys ($\chi^2 = 0.27$, $P = 0.6052$) but did vary seasonally and within and among sites ($n = 595$; Fig. 4). Mussels were more abundant in May than July ($\chi^2 = 19.49$, $P < 0.0001$) and at lower tide heights (emersion time $\chi^2 = 22.17$, $P < 0.0001$). There was a great amount of variability across sites ($\chi^2 = 326.89$, $P < 0.0001$) as well as interactive effects of site × month ($\chi^2 = 119.80$, $P < 0.0001$) and site × emersion time ($\chi^2 = 153.45$, $P < 0.0001$) on mussel abundance.

Our contemporary surveys indicated that the diversity of sessile species varied with mussel abundance and tide height in the Gulf of Maine (Table S2). Sessile species richness differed with mussel cover × emersion time ($P = 0.01$) as well as the main effects of emersion time ($P < 0.0001$), site ($P < 0.0001$), and year ($P = 0.03$). *Post hoc* analysis showed that sessile species richness increased with increasing mussel abundance in the upper intertidal (emersion time > 50%) ($\chi^2 = 9.78$, $P = 0.0018$), but was not related to mussel abundance in the lower intertidal ($P > 0.38$ for all groups).

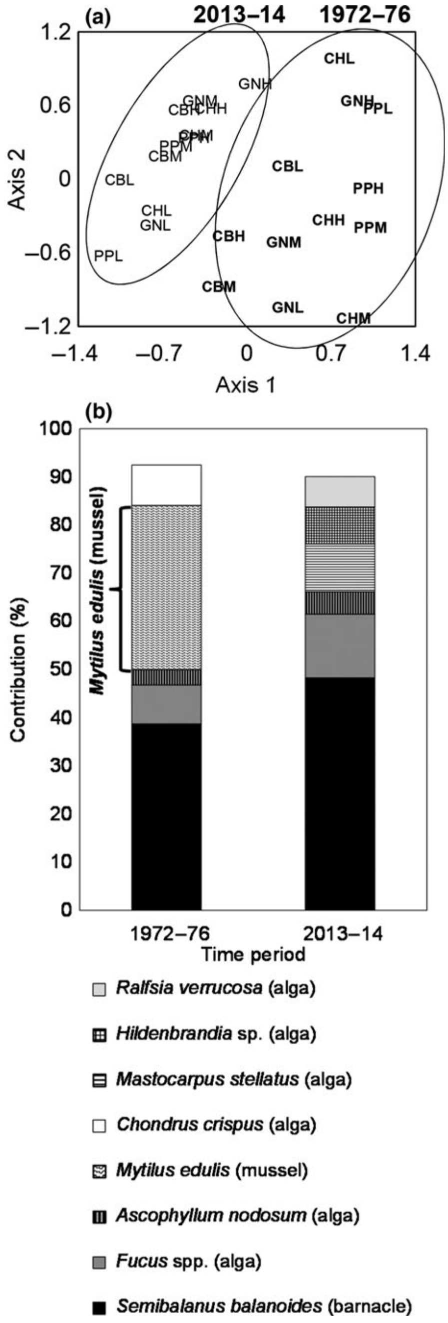

Fig. 2 Changes in community composition between 1972–1976 and 2013–2014 at four sites across the Gulf of Maine. (a) Non-metric multidimensional scaling plot of differences by site (GN, CH, PP, and CB) × tide height (L = low, M = mid, H = high) between 1972–1976 (bold text) and 2013–2014. Values are from a Bray–Curtis resemblance matrix after square-root transformation (3-D stress = 0.07). (b) Contributions to community composition of sessile species collectively comprising >90% of the similarity within time periods. Values are based on percent cover estimates from $N = 820$ and 228 quadrats surveyed in 1972–1976 and 2013–2014, respectively, across four sites (GN, CH, PP, and CB) and during the summer months (May to August).

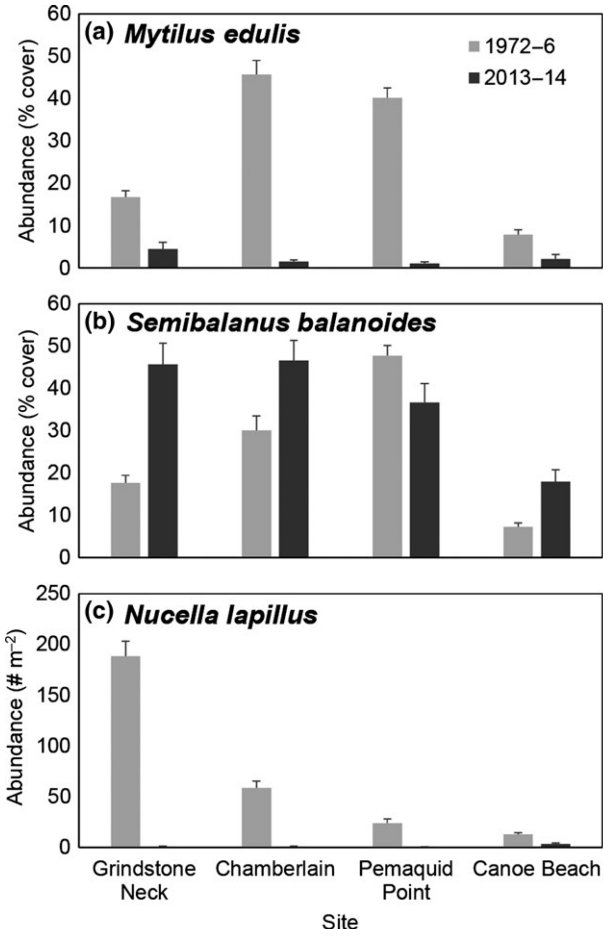

Fig. 3 Abundance of (a) mussels *Mytilus edulis*, (b) barnacles *Semibalanus balanoides*, and (c) whelks *Nucella lapillus* from two time periods spanning 40 years. Abundance is based on estimates of visual percent cover (mussels and barnacles) or counts (whelks) in quadrats surveyed between May and August during 1972–1976 ($N = 140–270$) and 2013–2014 ($N = 56–58$). Values are site means + SE across quadrats at three tide heights (0, 1, 2 m). Details are given in 'Materials and methods' and Data set S1.

Diversity (Fisher's alpha) of mobile species differed by emersion time ($P < 0.0001$) and site ($P < 0.0001$) but was not related to the main or interactive effect of mussel cover ($P = 0.80$).

Indicators of future population growth trajectories differed between sites (Figs S1 and S2). In particular, the proportional abundance of the youngest individuals (within the smallest size class of 0–4.9 mm) – an index of recruitment – differed between populations and over time ($n = 380$; Fig. 5). Size distribution varied by site ($\chi^2 = 136.37$, $P < 0.0001$) and month × site ($\chi^2 = 95.14$, $P < 0.0001$). Across sites, the youngest size class represented an average of 22.53 ± 3.33% of mussels, with a range of 0% (at South Addison in northern Maine) to 65% (in New Hampshire). There were also more

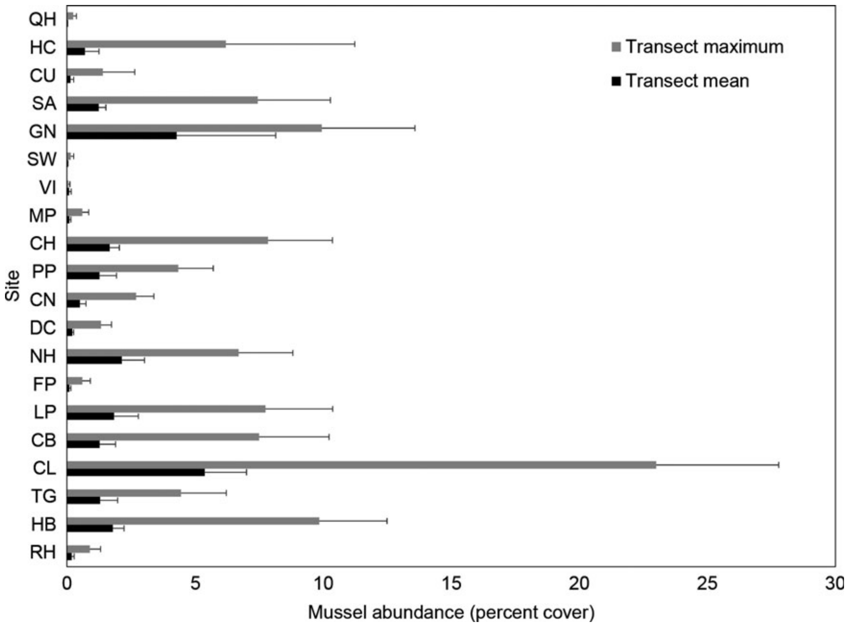

Fig. 4 Contemporary (2013–2014) mussel abundance at 20 sites in the Gulf of Maine (organized from north to south; see Fig. 1). Maximum values are from the quadrat (i.e., tide height) of maximum abundance on each transect, averaged across five transects from four survey dates ($N = 20$ total). Mean values represent an estimate of abundance across the entire intertidal zone from $N = 4$ surveys, after first averaging abundance by tide height across transects and then across all tide heights to get the mean for each survey. Error bars are 1 SE.

individuals 0–4.9 mm found in May than in July ($\chi^2 = 12.99$, $P = 0.0003$) and in 2014 than in 2013 ($\chi^2 = 25.66$, $P < 0.0001$). GSI, an index of reproductive potential, varied by month ($\chi^2 = 114.89$, $P < 0.0001$) and site ($\chi^2 = 109.57$, $P < 0.0001$) and increased with mussel length ($\chi^2 = 133.68$, $P < 0.0001$).

Discussion

Using consistent methodology across time, our results show that blue mussels have declined in the Gulf of Maine over the past 40 years. These declines occurred across all seven sites surveyed in the 1970s, which span >400 km of coastline. Our comparisons across time and space showed that changes in mussel abundance were associated with major shifts in community structure. Over 40 years, mussels have gone from being a defining species of intertidal habitats in the Gulf of Maine to being a minor contributor to compositional patterns and a spatial subdominant. In addition, an increase in competitors (the barnacle *S. balanoides*) and decrease in the predatory whelk *N. lapillus* support the prediction that mussel declines influence the community via changing species interactions. The sharp decline in whelk abundance indicates a strong bottom-up effect, with declines in mussel prey having a major impact on the trophic structure of this system. Furthermore, our contemporary surveys showed that mussel abundance was positively related to species richness – suggesting a positive effect of habitat provisioning – in the relatively stressful upper intertidal across 20 sites. These findings of our contemporary surveys across sites mirrored those of the historical comparisons, reinforcing the importance of this foundation species to the broader intertidal community, even as captured in visual surveys (i.e., without destructively sampling to assess all species that live in the mussel bed matrices; Suchanek, 1987; Smith *et al*., 2006).

Comparisons to historical surveys conducted between 1972 and 2001 suggest that mussel declines have been consistent over time, with increasing differences from baseline data collected further back in time. Although few data are available prior to the 1970s (Data set S1), some of the observed declines likely started before the 1970s. For example, at Canoe Beach (CB), albeit a site with relatively high human traffic (C. Sorte, personal observations), Pearse (1913) observed that in June 1912 '*[Semi]balanus*. . .is everywhere. *Mytilus* and *Littorina* are almost as ubiquitous'. However, by 1972–1976, average cover for mussels was approximately 6% (Data set S2). Repeating the surveys across months and years within each time period allowed us to compare seasonal and annual variability to differences between time periods as well as to minimize

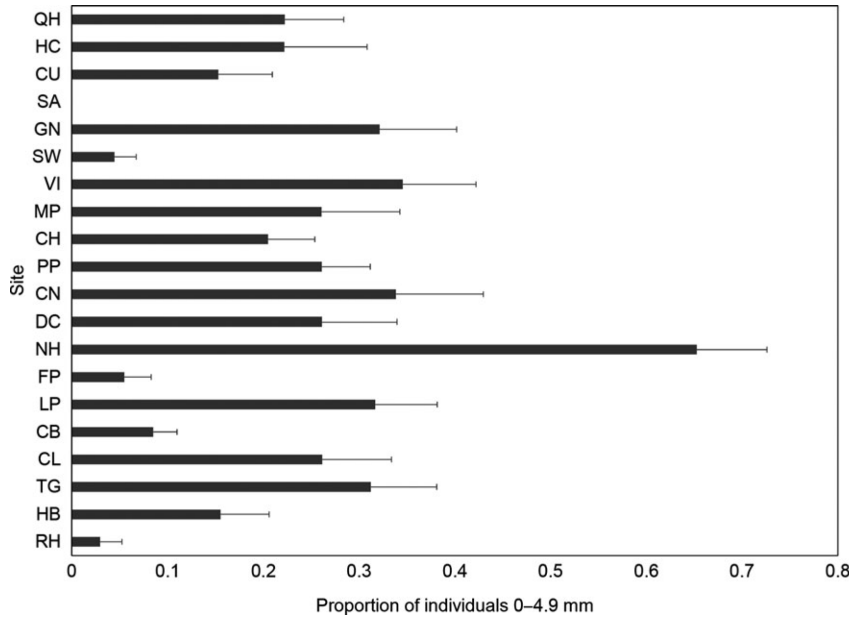

Fig. 5 Proportion of individual mussels in the smallest size class (0–4.9 mm) at 20 sites in the Gulf of Maine (organized from north to south; see Fig. 1). Values are mean (+1 SE) proportional abundance in $N = 20$ quadrats across four survey dates (May and July of 2013 and 2014), except at QH, HC, CU, and RH where $N = 16$, 15, 11, and 18, respectively.

potential effects of between-period climatic differences (e.g., Denny & Paine, 1998).

Declines in Gulf of Maine mussel populations are analogous to the trajectories of populations between Delaware and North Carolina where blue mussels are now rare and/or locally extinct (Jones *et al.*, 2010). Thus, in the northwestern Atlantic, blue mussels have experienced both a contraction of their southern range edge (Jones *et al.*, 2010) and significant decreases in their region of historically maximum abundance (Tam & Scrosati, 2011; Petraitis & Dudgeon, 2015). At the same time, there is evidence that blue mussels have extended their northern range edge into the Arctic by recolonizing an area of historical extirpation at Svalbard (Berge *et al.*, 2005). Future work could utilize recently reported quantitative benchmarks to broaden the spatial extent of these comparisons, including to the coast of eastern Canada (Tam & Scrosati, 2011), Greenland (Blicher *et al.*, 2013), and the North Sea (Folmer *et al.*, 2014).

It is important to note that both our study and other studies that have not included a genetic component likely overestimate *M. edulis* populations, as the visually indistinguishable congener *Mytilus trossulus* becomes increasingly common at more northern sites. Genetic analyses have shown that *M. trossulus* coexists with *M. edulis* at low frequency (<10%) in southern to mid-coast Maine (i.e., the northernmost sites included in our historical comparisons) but up to 50% frequency in northern Maine (SA, CU, HC, and QH; Hayhurst & Rawson, 2009) and north of our study region (Tam & Scrosati, 2011). Such cases of morphological crypsis can obscure attempts to track population shifts (Geller, 1999).

The causes of these changes in mussel abundance and distribution patterns are likely multifold, including direct and indirect effects of human activities and global change. A significant factor in the decline of blue mussels in the Gulf of Maine has been the increase in their harvesting over the past 40 years. Commercial harvest (in units of mussel biomass taken annually) has increased approx. 10-fold over this time period (NOAA National Marine Fisheries Service, 2016), and the development of mussel aquaculture has also increased harvesting due to its reliance on wild spat (Maine Department of Marine Resources, 2016). Future work would ideally improve tracking of harvesting activities across the Gulf of Maine, as recreational regulations allow collection of two bushels (approx. 50 kg) per day (Webber & Maine Department of Resources, 2013), removal that is unmonitored. Particularly impactful would be the harvesting of likely mussel source populations in the northern Gulf of Maine (e.g., Sorte *et al.*, 2013), as further evidenced by concurrent declines in mussel recruitment rates (Petraitis & Dudgeon, 2015).

Declines due to direct removal by humans are likely exacerbated via indirect effects of human activities including climate change and species invasions, with feedbacks involving alterations in productivity, food availability, large-scale storm disturbances, and, ultimately, recruitment. Jones *et al.* (2009, 2010) used a combination of laboratory tolerance experiments and hindcasting with climate models to show that the blue mussel's southern range contraction appears to be a consequence of ocean warming. Episodic warming periods occurred in the Gulf of Maine between the 1930s and 1980s, including in the late 1960s (Drinkwater, 1996), whereas sea surface temperature seems to have continually increased from the 1980s to the present (Pershing *et al.*, 2015). Multiple exposures to temperatures of >32 °C – a low tide temperature that is not uncommon during summer months – caused 50% mortality in experiments with mussels from Nahant, MA (Sorte *et al.*, 2011). Even more moderate temperature exposures can elicit mussels' stress responses and hinder normal functions of growth and reproduction (Hofmann & Somero, 1995; Halpin *et al.*, 2002). Declines in mussel populations would also be consistent with increases in hurricane activity (i.e., storm frequency) in the North Atlantic (Carrington, 2002), as field mortality rates of mussels in Rhode Island were accurately predicted by models of wave intensity combined with observed temperature extremes (Carrington *et al.*, 2009). In addition, there is evidence of changing productivity in the region (Greene & Pershing, 2007; Balch *et al.*, 2012), and predation intensity has changed due to the introduction of nonnative species (e.g., green crabs can be important predators in wave-protected habitats; Leonard *et al.*, 1999) and to alterations in trophic structure resulting from overfishing (Harris & Tyrrell, 2001).

Patterns of disturbance and recruitment are known to play a key role in mussel population dynamics (Dayton, 1971), particularly in highly seasonal systems like the north Atlantic (e.g., Menge, 1976; Dudgeon & Petraitis, 2001; Witman *et al.*, 2003). Indeed, our size frequency data (Fig. S1) indicate that recruitment does occur but that postsettlement mortality is high, preventing new recruits from surviving to enter the larger size classes. Thus, as human activities directly and indirectly increase disturbance, declining source populations and subsequent recruitment are expected to impede future population replenishment, and this feedback loop seems to already be underway (e.g., Petraitis & Dudgeon, 2015).

A combination of anthropogenic and other global change drivers has been invoked to explain community shifts in adjacent subtidal communities within the Gulf of Maine. In the 1970s, shallow subtidal communities in New Hampshire and southern Maine were dominated by kelps and red algae in natural benthic habitats (Harris & Tyrrell, 2001) and invertebrates (mussels and barnacles) on experimental settlement plates (Dijkstra & Harris, 2009; Dijkstra *et al.*, 2011). However, over an approx. 25-year period (by the late 1990s), both communities had shifted to dominance by non-native species, primarily invasive algae on the natural substrata (Harris & Tyrrell, 2001) and invasive sea squirts on the experimental plates (Dijkstra & Harris, 2009; Dijkstra *et al.*, 2011). Harris & Tyrrell (2001) attributed the shift on subtidal rocky reefs to indirect effects of global change – population explosion and herbivory by the urchin *Strongylocentrotus droebachiensis* – while Dijkstra *et al.* (2011) correlated shifts in experimental outcomes to a suite of direct environmental changes, particularly temperature and nutrient availability. Further offshore, Lucey & Nye (2010) found that the pelagic fish assemblage in this region shifted over the past 45 years, becoming more similar to southern assemblages. Emerging evidence for accelerating climate change (Pershing *et al.*, 2015) and profound community shifts across the Gulf of Maine identifies the region as a 'hot spot' and a 'test bed' of global change impacts (also see Hobday & Pecl, 2014), similar to marine ecosystems in Northern Europe (Southward *et al.*, 1995; Hawkins *et al.*, 2003, 2009) and Australia (Wernberg *et al.*, 2011).

Clearly, the shifts that we observed in the intertidal community are part of a larger phenomenon of global and regional changes. However, attributing the causes of these changes is problematic given the number of concurrent and interacting drivers, such as the anthropogenic threats described above, as well as the many potential indirect pathways through which impacts may be manifested. Previous studies documenting the importance of mussels in intertidal interaction webs and to intertidal diversity (e.g., Paine, 1966; Seed, 1969; Menge, 1976; Suchanek, 1987; Smith *et al.*, 2006) – and our own comparisons across space and time presented here – suggest that the loss of mussels has precipitated a number of the observed changes in strongly interacting species and overall community composition. However, it is also likely that some portion of these community-level changes are caused by alternate drivers and/or are themselves the drivers of changes in the mussel populations. The ability to ascribe causality in longitudinal datasets is improved with increased frequency of sampling (see Mieszkowska *et al.*, 2014). For example, sampling that encompasses periods of warming and cooling has allowed researchers to link climate to population dynamics across a wide range of species, including marine foundation species (Southward & Crisp, 1956; Southward *et al.*, 1995; Stenseth *et al.*, 2002; Hawkins *et al.*, 2003; Wethey & Woodin, 2008; Genner *et al.*, 2009). Observations have been paired with modeling (see Helmuth *et al.*, 2006; Poloczanska *et al.*, 2008) or, rarely, experiments (reviewed in Wernberg *et al.*,

2012) to disentangle the direct effects of changing environmental context from the indirect effects of species interactions. These studies point to the importance of following the population trajectories of foundation species as potential harbingers of community-level changes (Hawkins *et al*., 2009).

Global change is not only continuing but in many cases accelerating, particularly within the Gulf of Maine: sea surface temperature increased at a rate of 0.03 °C yr^{-1} during 1982–2004 but 0.23 °C yr^{-1} during 2004–2015 (Pershing *et al*., 2015). It is, therefore, concerning that we have already documented significant shifts in intertidal mussel populations and the potential for such shifts to successively impact diversity and community composition. This raises the question of how populations will continue to change in the future. Mussel population dynamics varied between sites, and we might anticipate the most severe population declines at locations with currently lower population sizes, lower abundance of juveniles (i.e., less successful recruitment), or lower abundance of medium size classes (i.e., lower establishment and higher postsettlement mortality). Locations of possible concern include South Addison, Maine (where no mussels <5 mm were found), and Seawall, Maine (the site with the lowest mean abundance and few mussels < 5 mm). On the other hand, several sites had higher than average proportion of mussel recruits, and relatively high current population sizes, including Grindstone Neck (Maine), Rye (New Hampshire), and Loblolly Point, Cunner Ledge, and The Glades in Massachusetts. The most vulnerable populations may increasingly depend on replenishment via colonization by new recruits from the broader metapopulation (i.e., less vulnerable source sites). This dependence calls for a better understanding of larval connectivity in the Gulf of Maine, as climate-induced shifts in physical transport processes have the potential to either promote or impede dispersal to declining populations (Byers & Pringle, 2006; Sorte, 2013; Sorte *et al*., 2013). It is encouraging to find evidence for reproductive viability – that is, seasonal changes in GSI indicative of spawning – in all of the populations we sampled. Where natural processes of population replenishment are insufficient to counteract population declines, conservation and management can play important roles in protecting particular populations, especially if such populations are critical for seeding multiple habitats linked by larval dispersal (Carson *et al*., 2011).

In conclusion, we have uncovered declines in an important coastal foundation species and changes in community structure that were consistent across a broad region and across a 40-year time period. Future predictions and the mobilization of conservation efforts depend on broadscale and long-term survey and monitoring efforts that provide quantitative baselines of population sizes, and we aim for the database published here (Data sets S1–S3) to serve this purpose. To the extent that global change processes have driven past declines of blue mussel populations, future increases in temperatures, storm intensity, invasions, harvesting, and impacts to marine food webs present further threats to the currently dwindling populations. Our results provide a scientific basis for future decision-making aimed at preventing continued declines of foundation species whose persistence fosters diversity and whose disappearance could drive an escalation in community-level extinctions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Sessile species contributing to community dissimilarity between time periods.
Table S2. Results of a generalized linear model evaluating the relationship between contemporary mussel abundance and species diversity.
Figure S1. Mussel population size structure across four surveys and 20 sites in the Gulf of Maine.
Figure S2. Mussel gonadosomatic index across 20 sites in the Gulf of Maine.
Data set S1. Historical and contemporary baselines of mussel abundance in the Gulf of Maine.
Data set S2. Historical (1972–1976) community data from four sites in the Gulf of Maine.
Data set S3. Contemporary (2013–2014) community data from 20 sites in the Gulf of Maine.