

An intertidal snail shows a dramatic size increase over the past century

Jonathan A. D. Fisher^{a,b,1}, Erika C. Rhile^{c,d}, Harrison Liu^d, and Peter S. Petraitis^d

^aDepartment of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada; ^bOcean Sciences Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, Canada; ^cCheverus High School, Portland, ME 04103; and ^dDepartment of Biology, University of Pennsylvania, Philadelphia, PA 19104

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Changes in the shell architecture of marine snails enhance defenses and greatly improve survival against predators. In the northwest Atlantic Ocean, shorter and thicker shells have been reported for several species following the introduction of predatory *Carcinus maenas* crabs early in the 20th century. But we report that the shell lengths of *Nucella lapillus* actually increased by an average of 22.6% over the past century, with no evidence of shell thickening after correcting for shell length. The increases in shell length were greatest on sheltered shores, highlighting the interaction between wave exposure and the sampling period. Comparisons were based on archived shells collected in 1915–1922 from sites that were resampled in 2007. *N. lapillus* is an important member of North Atlantic marine ecosystems, and our results suggest that the impacts of historical changes in species' key morphological traits on marine ecosystems remain underappreciated.

morphology | museum collections | natural history | rocky shores | trait variation

Because coastal marine ecosystems have been altered so radically in recent times, a complete understanding of contemporary observations and experiments requires analyzing historical data (1–6). Long-term shifts in ecological context occur on the scales of decades and centuries, underscoring the need for thorough natural history descriptions to guide the interpretation of experiments conducted even within apparently well-known systems (7, 8). Within the last century, coastal assemblages in the Gulf of Maine (northwest Atlantic Ocean) have experienced marked reductions in the size and abundance of exploited fish and invertebrates (1, 2, 9), temperature variability (10), and the introduction and spread of invasive species, including *Carcinus maenas* crabs (1, 11). Within this period, historical changes in shell shapes and thicknesses of *Nucella lapillus* (11) and other snails (12) within the Gulf of Maine have been interpreted solely as responses to the arrival of *C. maenas*. These patterns have since led to the development of experimental analyses of crab–snail interactions as a model system for the study of inducible and evolved morphological defenses (13–16). But although *N. lapillus* remains a common and extensively studied North Atlantic marine snail (17), no study has examined historical changes in its shell morphology on the scale of a century by exclusively resampling the same sites and evaluating site-specific wave exposures among sites, which alter shell size and shape (18–21). With the goal of exploring spatial and temporal variations in *N. lapillus* shell morphology and their implications across a century of dramatic ecological change, we resampled snails at locations originally described in museum collections.

Between 1915 and 1922, Harold Sellers Colton collected *N. lapillus* from >60 intertidal sites on and around Mount Desert Island (MDI), Maine, in an effort to correlate variations in shell color and shell size with local habitat conditions (18, 19). In addition to producing a remarkably complete depiction of the intertidal food web before the arrival of *C. maenas* (18, 22), Colton deposited his collections (many with >200 shells per lot)

at the Academy of Natural Sciences of Philadelphia (ANSP). We measured shell length, shell lip thickness, aperture length, and aperture width of *N. lapillus* shells from 19 ANSP lots, and then resampled the same 19 sites in 2007. We used the site description accompanying each lot [see supporting information (SI) Table S1] and maps of sampling locations (18, 19) and are confident that we were within 100–500 m of Colton's sampling sites. We also classified the relative wave exposure at each site as exposed coast, semiexposed shore, or sheltered cove. Our approach allowed us to test the influences of site, time period, and wave exposure on *N. lapillus* shell morphology.

Results and Discussion

Our most striking finding, which has not been reported previously in *N. lapillus*, is that shell length was increased at all 19 sites, by an average of 22.6%, between the 1915–1922 and 2007 sampling periods (Fig. 1). There is no evidence that the size increases were caused by Colton overlooking larger snails, because the frequency distributions were not truncated at large size classes (Fig. 2). Shell length also was significantly influenced by exposure, sites within exposure, and the interaction of time and exposure (Table S2). The increase in size was greatest at the wave-sheltered sites (27.2%), followed by semiexposed (22.7%) and fully wave-exposed locations (7.7%) (Fig. 2). This interaction of size increase and wave exposure is consistent with the increased risk of dislodgement of large *N. lapillus* at wave-exposed sites (18–21). This increase in shell length was unexpected, however, given the known influence of the recently introduced invasive *C. maenas* on *N. lapillus* shell morphology. When placed in the presence of continuous waterborne crab cues, *N. lapillus* shows a reduced growth rate, leading to consistently thicker but shorter shells (14, 15). The size increase in *N. lapillus*, which is not a commercially exploited species, also contrasts with decreased sizes of exploited fish and invertebrates in the coastal Gulf of Maine (1) and intertidal gastropods in California (4).

It is notable that the scarcity of large shells in the archived samples (Fig. 2) was apparently not exclusive to the 1915–1922 period or Colton's collection sites. Surveys of *N. lapillus* at ≥ 38 sites around MDI in the late 1920s and early 1930s led William Procter (23) to state that “one rarely finds a specimen over an inch and a half long [i.e., >38.1 mm], the majority being an inch and under [< 25.4 mm].” These qualitative descriptions are reflected in Colton's samples (Fig. 2), in which 0.1% of the shells were >38.1 mm long and 67% were <25.4 mm long. In our 2007 collections, the percentage of shells >38.1 mm long remained

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¹To whom correspondence should be addressed. E-mail: jonathan.fisher@queensu.ca.

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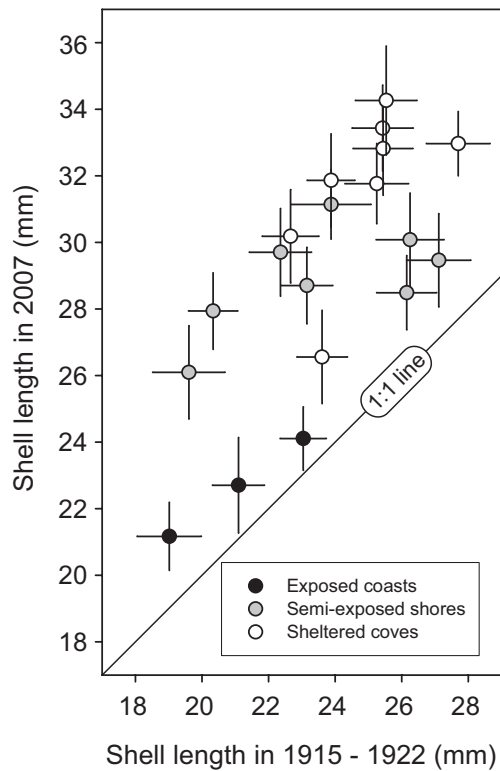


Fig. 1. Spatial and temporal variation in *N. lapillus* shell length. Average lengths (\pm 95% CIs) from 19 sites sampled from 1915–1922 (18, 19) were significantly shorter than those from the same sites resampled in 2007. The diagonal line indicates equal lengths; shading indicates relative wave exposure. The sites and sample sizes are described in Table S1.

low but still was increased 20-fold, to 2%, whereas the percentage of shells <25.4 mm long declined by >50%, to 26%. In another study, samples of mature snails collected in 1981 from 11 sites around MDI (21) revealed increased average length with decreased wave exposure (average length, 21.1 mm at 5 exposed sites, 29.8 mm at 2 semiexposed sites, and 29.9 mm at 4 sheltered sites), with lengths quite similar to our 2007 averages (Fig. 2). Together, these results demonstrate that Colton’s archived collections and our 2007 collections are representative of shell sizes within this region, and suggest that monitoring changes in shell morphology of *N. lapillus* and other marine snails should use paired designs to account for the influence of local conditions, such as wave exposure.

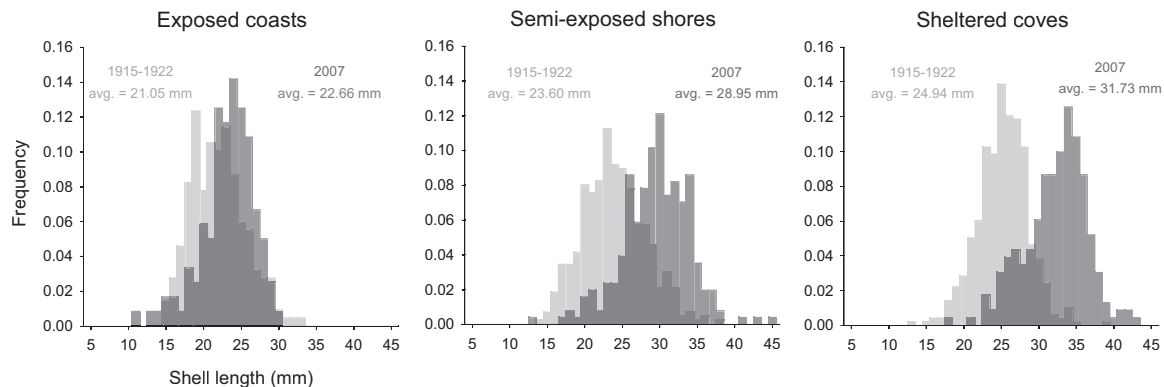


Fig. 2. Frequency distributions of *N. lapillus* shell lengths. Individuals are grouped by relative wave exposure, illustrating the 1915–1922 (light-gray bars) and 2007 periods (medium-gray bars). The dark-gray bars indicate size class overlap between periods. Average shell lengths are indicated on each plot.

Aperture width, aperture length, and lip thickness also demonstrated significant increases over the last century, indicating that shells were larger overall and not simply elongated (Table S2). Multivariate ANOVA (MANOVA) of all 4 shell measures illustrates the combined influence of exposure and time on shell morphology, with a tendency for exposed shore snails to have shorter shells with wider apertures compared with snails from semiexposed and wave-sheltered coves and a tendency for the change in overall size to be the least dramatic on exposed shores (Fig. S1). If changes in shell length are not taken into account, then it appears that the shells had thinner lips (1.32 ± 0.06 mm vs. 1.82 ± 0.09 mm) and shorter spires in 1915–1922 than in 2007 (shell length/aperture length: 1.374 ± 0.006 vs. 1.426 ± 0.008 ; see Table S2). These results are nearly identical to earlier reports of changes in shell characteristics of *N. lapillus* before and after the arrival of *C. maenas* (11); however, we found that these increases in lip thickness and changes in shell shape over the last century were driven largely by increases in shell length (Table S2) and are allometric. Most measures demonstrate no significant differences between sampling dates or among wave exposures when corrected for shell length (Tables S2 and S3). The only exception is aperture width, which showed a 3.4% decline from 1915–1922 to 2007 at exposed sites (Table S3).

A previous study of *N. lapillus* from northern Wales, UK examined allometric relationships of aperture length, aperture width, and lip thickness against shell length using log-log regressions (14), and we found similar relationships in our study. All 3 shell metrics demonstrated significant allometric scaling relationships against shell length within all exposures and time periods (Table S4). Contemporary relationships tended to have shallower slopes compared with the 1915–1922 data, but not in every comparison (Table S4). The significant differences in shell lip thickness are remarkable in that contemporary snails actually increased lip thickness more slowly with increasing size compared with snails from 1915–1922. Slopes from previous regressions (14) are similar to ours for sheltered sites (slope averages \pm 2 SE overlap in all cases) but differ from ours for exposed sites (slope averages \pm 2 SE do not overlap).

The effects of temporal changes in body size remains an important open question for food webs (24), and the observed size increases that we report here have implications for *N. lapillus* as both predator and prey. Larger-than-average *N. lapillus* tend to prey on larger mussels (*Mytilus edulis*) and spend less time between foraging bouts compared with smaller snails (25). *N. lapillus* also preys on barnacles (*Semibalanus balanoides*), and thus size-specific predation also may affect the size structure of barnacles. Size-specific predation by *N. lapillus* also may influence mussels and barnacles indirectly, because these species compete for limited attachment space in the intertidal zone (26).

N. lapillus is also prey, and the majority of snails at semiexposed sites and in sheltered coves in the 2007 samples are large enough so as to possibly escape shell-crushing predation by *C. maenas* with carapace widths <6–7.5 cm (20, 27). Together, the direct and indirect effects of size increases within all sites may have altered the structure and dynamics of intertidal assemblages in the Gulf of Maine, regardless of which factors contributed to the size increases.

Although the size increase from 1915–1922 to 2007 is clear, our results appear to be at odds with some aspects of previous comparative (11) and experimental results (14, 15). Vermeij (11) found changes in shell spire height and lip thickness before and after the introduction of *C. maenas*; our results were nearly identical. We suspect that Vermeij (11) did not find changes in shell length because his choice of sites confounded the effects of *C. maenas* invasion with the effects of wave exposure. Previous experimental studies (14, 15) demonstrated that the presence of waterborne cues from crabs induced thickening of shell lips and slower growth rates; but although we found an increase in lip thickness between 1915–1922 and 2007, this increase was due to an overall increase in size, not to a change in shape [see the analysis of covariance (ANCOVA) results in Tables S2 and S3]. Studies of induced responses used much smaller snails [average length, 14.7–21.6 mm (14); average length, \approx 6.5 mm (15)] than were found in either the 1915–1922 samples (23.6 mm) or the 2007 samples (28.9 mm). We hypothesize that when exposed to crab cues, snails first experience shell thickening, and then, once better defended against shell-crushing predators, grow in length to a size at which crabs cannot successfully attack them. This scenario would explain the findings of both the induction experiments (14, 15) and our study.

Other possible factors exist, and distinguishing among multiple potential factors that may have caused an increase in size between 1915–1922 and 2007 and the variation in the increase among sites is difficult. Directional selection by *C. maenas* may have contributed to this pattern; the greatest increases in *N. lapillus* size occurred in sheltered areas, which are most suitable for crabs (20, 27). But our results cannot provide unequivocal support for this hypothesis, because other concomitant changes have occurred within this ecosystem as well. Contemporary *N. lapillus* could be larger because they grow faster, perhaps due to water temperature differences between periods; annual average sea surface temperatures at a coastal long-term monitoring site \approx 120 km southwest of MDI were 1.9 °C higher during 1994–2001 than during 1915–1922 (10). In addition, nutrient enrichment in the region has increased over the past century, and contemporary eutrophied rocky shores exhibit increased cover of mussels and barnacles relative to noneutrophied sites (5); thus, a long-term increase in coastal productivity could have increased snail growth rates by increasing the availability of prey. Finally, although *C. maenas* is currently considered an important predator (11, 15), *N. lapillus* may now actually experience a lower rate of predation or higher rate of growth than in 1915–1922 due to a loss of other predators. Colton did not report crabs as a source of mortality for *N. lapillus*, but did identify fish and gulls as predators (18, 19). Whereas those early inferences about fish predation were based on indirect evidence (22), the large, abundant predatory fish that formerly existed close to shore (28) are now conspicuously absent, making it extremely difficult to compare contemporary rates of predation by invasive species with those generated by previously abundant native predators within this region (1, 2, 9).

Our results demonstrate that within a species known for extensive morphological variation among sites on both sides of the North Atlantic (17), a directional change in shell length occurred within sites during the past century, associated with apparent increases in correlated shell measures (Table S3). Our results are striking given that *N. lapillus* is an intensively studied

organism (17) within an intensively studied region (11, 18, 19, 21, 22, 23, 26), and they demonstrate the importance of archived data to both reveal temporal variation and provide a natural history context in which to evaluate experimental results (7, 8). Although perhaps more prevalent in marine assemblages subjected to direct fisheries exploitation (1, 2, 5, 6), we show that shifting baselines occur in unexploited species within model ecosystems. Thus, variations in key traits of marine species on similar time scales might be more prevalent than currently documented.

Materials and Methods

Sampling. All samples were collected from the shores of MDI or nearby islands. Colton's (18, 19) collections housed at ANSP are searchable by lot number online at <http://clade.ansp.org/malacology> (Table S1). We resampled Colton's sites in July–August 2007. The choice of sites to resample was based on our ability to relocate and access the sites; many are on private islands or land to which we could not gain access. Colton (18, 19) also collected *N. lapillus* in summer, and because many of his samples include hundreds of shells, the samples likely are representative of the size range of snails present in 1915–1922 (although we cannot be sure that he collected snails from the smallest of size classes). Small *N. lapillus* snails (less than \approx 15 mm) seek refuge in rock crevices (18, 19); Colton may have overlooked these snails. Collectors often tend to collect larger snails (4, 21); thus, if there is a bias in Colton's collecting, it is most likely in the direction of larger animals. During the resampling, 1–3 people slowly walked on separate lines parallel to the shore in the mid-intertidal zone. Every *N. lapillus* encountered was taken, whether on or under rocks or in crevices, until 25–50 snails were collected. At 1 site (ANSP lot 142360), only 19 snails were found.

Shell Measurements. Each shell's length, shell lip thickness, aperture length, and aperture width (14) were measured using electronic calipers (Fowler Ultra-Cal EDP 13522) with a resolution of 0.01 mm. Lip thickness and aperture width were measured slightly differently from the techniques used in previous studies (14). Lip thickness was measured near the suture of the body whorl, and aperture width was measured from the columella to the inside edge of the outer lip. Shell weights were not compared, because many archived samples contained dried tissues within the shells and could not be measured nondestructively. Shells from Colton's collections were subsampled in lots with >100 shells. The total number was estimated, and then shells were picked up one at a time; depending on the number estimated, every second, third, fourth, or fifth shell was measured to subsample \approx 50 shells. All shells in the 2007 samples were measured.

Analyses. Data were analyzed using a paired design of time (i.e., 1915–1922 vs. 2007) by the 19 sites; the sites were further partitioned into 3 exposure classes (exposed coast, semiexposed shore, and sheltered cove). The complete design contained effects of time, exposure, time \times exposure interaction, sites nested within exposure, and time \times sites nested with exposure. Sites nested within exposure and time \times sites nested within exposure were treated as random effects, and the remaining sources were treated as fixed effects. MANOVA, ANOVA, and ANCOVA were used to analyze the data. Post hoc tests were done using Tukey's honestly significant differences tests. All 4 measures were used in MANOVA, and each measure was analyzed with ANOVA. Shell spire height (shell length/aperture length) also was analyzed, because this measure was used by Vermeij (11). Although ratios tend to not be normally distributed, quantile plot of residuals to the fitted model show near-normality, with a slight skewness to the right and slight leptokurtosis. The shells in the 2007 samples were clearly larger; thus, shell lip thickness, aperture length, aperture width, and spire height also were analyzed by ANCOVA, with shell length as the covariate. The reported analyses used untransformed data, because residuals showed no signs of curvilinearity and because previous studies used untransformed data in similar analyses (11, 14, 15). Tests for parallel slopes, done by adding an interaction term for shell length \times time \times sites nested within exposure, were significant for lip thickness, aperture height, and spire height, but not for aperture width. But these tests were significant because of the high degrees of freedom (16 and 1,705), and the variance component for the interactions ranged from 0.04% to 0.5%. Given that such a small amount of the variation was explained by the interaction, we assumed the slopes to be homogeneous. Analyses of residuals were consistent with this assumption. ANCOVA and tests of parallel slopes using log-transformed data gave the same results. Palmer (14) analyzed allometry using regressions based on log-transformed data; thus, we performed the same regressions of lip thickness, aperture length, and aperture width on shell length to allow a compar-

ison of results. Allometry was tested using *t*-tests with the null hypothesis of a slope = 1, and differences in allometry between the 1915–1922 and 2007 samples were tested using *F*-tests for differences in slopes.

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