

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

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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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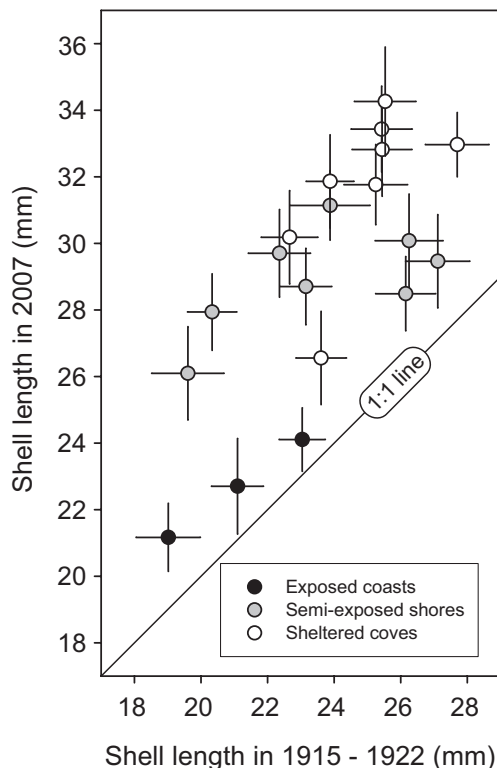


Fig. 1. Spatial and temporal variation in *N. lapillus* shell length. Average lengths (\pm 95% CIs) from 19 sites sampled from 1915–1922 (18, 19) were significantly shorter than those from the same sites resampled in 2007. The diagonal line indicates equal lengths; shading indicates relative wave exposure.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

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).

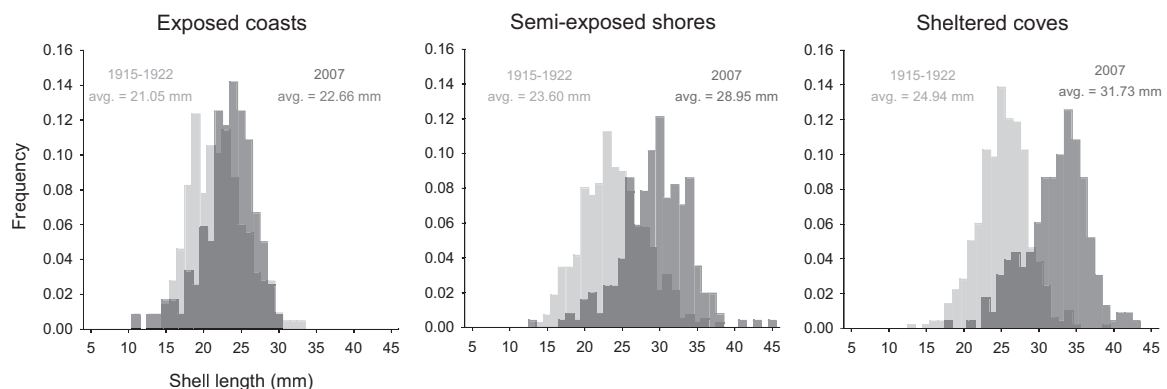


Fig. 2. Frequency distributions of *N. lapillus* shell lengths. Individuals are grouped by relative wave exposure, illustrating the 1915–1922 (light-gray bars) and 2007 periods (medium-gray bars). The dark-gray bars indicate size class overlap between periods. Average shell lengths are indicated on each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

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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1. Steneck RS, Carlton JT (2001) in *Marine Community Ecology*, eds Bertness MD, Gaines SD, Hay ME (Sinauer, Sunderland, MA), pp 445–468.
2. Jackson JBC (2001) What was natural in the coastal oceans? *Proc Natl Acad Sci USA* 98:5411–5418.
3. Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267:672–675.
4. Roy K, Collins AG, Becker BJ, Begovic E, Engle JM (2003) Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecol Lett* 6:205–211.
5. Lotze HK, Milewski I (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecol Apps* 14:1428–1447.
6. Lotze HK, et al. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.
7. Polis GA, et al. (1998) in *Experimental Ecology: Issues and Perspectives*, eds Reseratis WJ, Jr, Bernardo J (Oxford, New York), pp 254–280.
8. Underwood AJ, Chapman MG, Connell SD (2000) Observations in ecology: You can't make progress on processes without understanding the patterns. *J Exp Mar Biol Ecol* 250:97–115.
9. Witman JD, Sebens KP (1992) Regional variation in fish predation intensity: A historical perspective in the Gulf of Maine. *Oecologia* 90:305–315.
10. Lazzari M (2001) *Monthly and Annual Means of Sea Surface Temperature: Boothbay Harbor, Maine 1905 Through 2001* (Maine Dept. of Marine Resources, Augusta, ME), Research Reference Document 02/1.
11. Vermeij GJ (1982) Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature* 299:349–350.
12. Seeley RH (1986) Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc Natl Acad Sci USA* 83:6897–6901.
13. Appleton RD, Palmer AR (1988) Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proc Natl Acad Sci USA* 85:4387–4391.
14. Palmer AR (1990) Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). *Hydrobiologia* 193:155–182.
15. Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology* 84:629–640.
16. Edgell TC, Neufeld CJ (2008) Experimental evidence for latent developmental plasticity: Intertidal whelks respond to a native but not an introduced predator. *Biol Lett* 4:385–387.
17. Crothers JH (1985) Dog-whelks: An introduction to the biology of *Nucella lapillus* (L.). *Field Studies* 16:291–360.
18. Colton HS (1916) On some varieties of *Thais lapillus* in the Mount Desert region: A study of individual ecology. *Proc Acad Nat Sci Phila* 68:440–458.
19. Colton HS (1922) Variation in the dog whelk, *Thais* (*Purpura* auct.) *lapillus*. *Ecology* 3:146–157.
20. Kitching JA, Muntz L, Ebling FJ (1966) The ecology of Lough Ine XV: The ecological significance of shell and body forms in *Nucella*. *J Anim Ecol* 35:113–126.
21. Crothers JH (1983) Some observations on shell-shape variation in North American populations of *Nucella lapillus* (L.). *Biol J Linn Soc* 19:237–274.
22. Fisher JAD (2005) Exploring ecology's attic: Overlooked ideas on intertidal food webs. *Bull Ecol Soc Am* 86:145–151.
23. Procter W (1933) *Biological Survey of the Mount Desert Region, Part 5: Marine Fauna* (Wistar Institute of Anatomy and Biology, Philadelphia).
24. Woodward G, et al. (2005) Body size in ecological networks. *Trends Ecol Evol* 20:402–409.
25. Bayne BL, Scullard C (1978) Rates of feeding by *Thais* (*Nucella*) *lapillus* (L.). *J Exp Mar Biol Ecol* 32:113–129.
26. Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecol Monogr* 65:21–74.
27. Hughes RN, Elner RW (1979) Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. *J Anim Ecol* 48:65–78.
28. Bigelow HB, Welsh WW (1925) *Fishes of the Gulf of Maine* (Department of Commerce, Washington, DC), U.S. Bureau of Fisheries Bulletin 40.

Supporting Information

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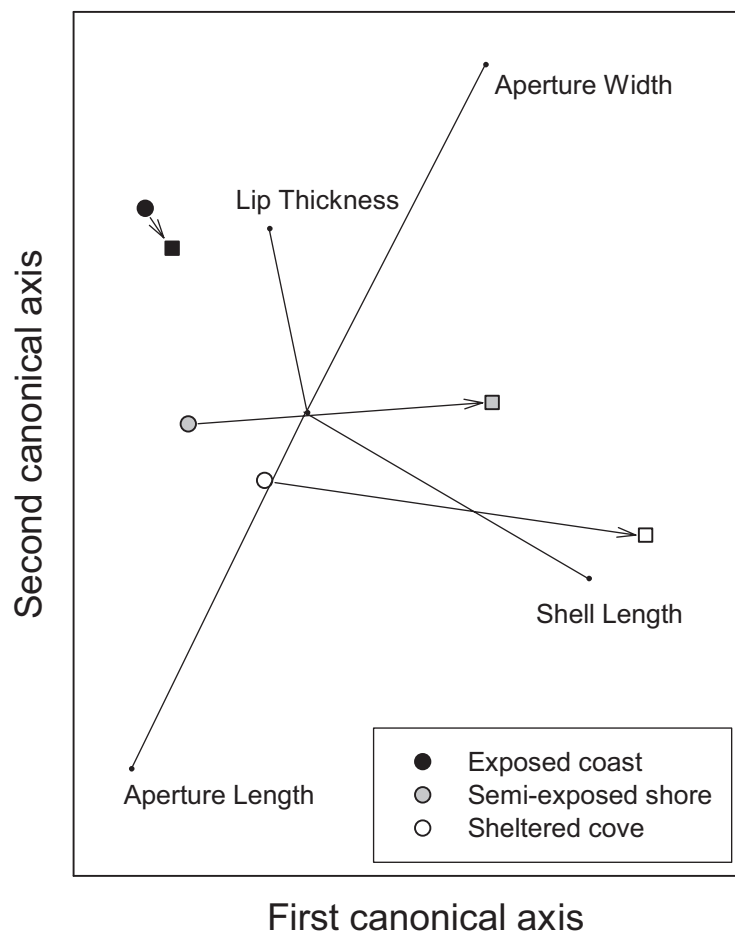


Fig. S1. Canonical correlation plot of the significant ($P < .0001$) exposure \times time interaction from MANOVA analysis of *N. lapillus* shell characteristics. Four measured shell characteristics are represented as biplot rays, with the length and direction of each vector defined by its relative correlations with the first 2 axes. Circles represent centroids from the 1915–1922 collections; squares represent centroids from the 2007 collections. Sites were pooled by relative wave exposures (shaded points). Shells from exposed sites underwent little temporal changes in morphology, whereas shells from semiexposed and sheltered sites underwent morphological changes caused primarily by significant increases in shell length. The first axis explains 80.7% of the total variation, and the second axis explains the remaining 19.3%.

Table S1. Details of the 19 sites sampled by H. S. Colton in 1915–1922 and resampled by us in 2007

Lot	Year	Site description	Exposure	N _C	N _F	Latitude	Longitude	Other ANSP lots
142335	1915	Goose March Cove, east shore near pond, Blue Hill Bay, Maine	Sheltered cove	57	25	44.2552051	−68.4037318	142370
142342	1915	Latty's Cove, Blue Hill Bay, Maine	Sheltered cove	88	25	44.2542943	−68.4183517	
142343	1915	Buckel Island, west side <i>Fucus</i> zone, Blue Hill Bay, Maine	Semiexposed shore	57	38	44.1802699	−68.4768424	
142344	1915	East side Buckel Island, Blue Hill Bay, Maine	Sheltered cove	51	33	44.1790321	−68.4740261	
142360	1915	Southwest Harbor, Stanley House Point, Mt. Desert Island, Maine	Sheltered cove	54	19	44.2668000	−68.2991000	142361, 142362, 142368
142363	1915	Gilpatricks Cove, West Point, Mt. Desert, Maine	Sheltered cove	55	29	44.2868287	−68.2909639	
142364	1915	Placentia Island, south end, Red Rocks, Maine	Semiexposed shore	53	28	44.2004144	−68.3328989	142386
142371	1915	Black Island, south end, west side of point, Blue Hill Bay, Maine	Semiexposed shore	50	25	44.1750000	−68.3539000	
142373	1915	Seal Harbor Cliffs halfway to Hunters Beach, Mount Desert, Maine	Exposed coast	50	45	44.2942172	−68.2301185	142372
142374	1915	Seal Harbor, Steamboat Wharf, Blue Hill Bay, Maine	Semiexposed shore	33	43	44.2826351	−68.4018562	
142376	1915	Salisbury Cove, south point, Frenchman's Bay, Maine	Sheltered cove	79	25	44.4320422	−68.2859914	
142385	?	Seal Cove, south side, Blue Hill Bay, Maine	Sheltered cove	51	50	44.2857372	−68.3976791	142379, 142387
142398	1922	Sea Wall, Mt Desert, Maine	Exposed coast	75	24	44.2469159	−68.3098012	
142404	1922	Great Gott Island, Head south side, Mt. Desert, Maine	Semiexposed shore	83	36	44.2004144	−68.3328989	
142405	1922	Great Gott Island, Head north side, Mt. Desert, Maine	Semiexposed shore	75	36	44.1627958	−68.4410794	14206
142407	1922	Black Island, east side, Mt. Desert, Maine	Semiexposed shore	40	25	44.1705000	−68.3413000	
142408	1922	Black Island, east side, wharf, Mt. Desert, Maine	Semiexposed shore	45	25	44.1707000	−68.3400000	
142411	1922	Thomas Bay, south shore, Frenchmans Bay, Maine	Sheltered cove	63	25	44.4342403	−68.3338685	142412
142417	1922	Blue Hill Falls, Mt. Desert, Maine	Exposed coast	94	51	44.3739000	−68.5581000	

Colton's lots were deposited at the ANSP. ANSP lot number, year collected by Colton, and site description are provided for each collection together with the relative wave exposure and geographic coordinates of the paired location sampled in 2007. N_C represents the number of shells subsampled and measured from ANSP lots, and N_F represents the number of shells collected and measured in 2007. "Other ANSP lots" refers to lots collected at locations close the lot used; these lots were initially used as replicates nested within sites in analyses, although their inclusion did not affect the analyses, and thus they were not included.

Table S3. Averages and SEs (in mm; except for spire height ratios) based on ANOVA and ANCOVA reported in Table S2

Exposure	Time	Length	Aperture length	Aperture width	Lip	Spire height
ANOVA						
Exposed	Colton	21.05 ± 0.61 ^d	15.49 ± 0.38 ^d	6.76 ± 0.16 ^b	1.28 ± 0.13 ^b	1.36 ± 0.01 ^b
Exposed	Present	22.66 ± 0.84 ^{c,d}	16.34 ± 0.53 ^{c,d}	6.89 ± 0.22 ^b	1.50 ± 0.18 ^{a,b}	1.39 ± 0.02 ^{a,b}
Semiexposed	Colton	23.60 ± 0.43 ^c	17.09 ± 0.27 ^c	6.94 ± 0.11 ^b	1.35 ± 0.10 ^b	1.38 ± 0.01 ^b
Semiexposed	Present	28.95 ± 0.55 ^b	20.03 ± 0.35 ^b	8.21 ± 0.14 ^a	2.01 ± 0.12 ^a	1.44 ± 0.01 ^a
Sheltered	Colton	24.94 ± 0.40 ^c	17.99 ± 0.25 ^c	7.29 ± 0.10 ^b	1.34 ± 0.09 ^b	1.39 ± 0.01 ^b
Sheltered	Present	31.73 ± 0.59 ^a	21.86 ± 0.37 ^a	8.84 ± 0.15 ^a	1.95 ± 0.13 ^a	1.45 ± 0.01 ^a
ANCOVA						
Exposed	Colton		18.14 ± 0.18	7.86 ± 0.10 ^a	1.68 ± 0.13	1.39 ± 0.01
Exposed	Present		18.02 ± 0.23	7.59 ± 0.13 ^{a,b}	1.76 ± 0.17	1.41 ± 0.02
Semiexposed	Colton		18.19 ± 0.12	7.40 ± 0.07 ^b	1.52 ± 0.09	1.39 ± 0.01
Semiexposed	Present		17.89 ± 0.16	7.32 ± 0.09 ^b	1.68 ± 0.12	1.41 ± 0.01
Sheltered	Colton		18.29 ± 0.11	7.41 ± 0.06 ^b	1.38 ± 0.08	1.39 ± 0.01
Sheltered	Present		18.04 ± 0.19	7.25 ± 0.11 ^b	1.37 ± 0.14	1.40 ± 0.01

Superscripts refer to significantly different groupings ($P \leq .05$) based on Tukey's honestly significant differences post hoc tests.

Table S4. Results from regressions of log-transformed shell metrics "Variable" against log-transformed *N. lapillus* shell lengths from different exposure levels (see Fig. 1) and different time periods

Exposure	Time	Variable	N	Intercept	SE	Slope	SE	R ²	T	F	P
Exposed	Colton	A-length	219	0.150	0.033	0.784	0.025	0.816	8.57	0.12	NS
Exposed	Present	A-length	120	0.159	0.045	0.775	0.033	0.824	6.82		
Exposed	Colton	A-width	219	−0.256	0.037	0.819	0.028	0.797	6.46	0.34	NS
Exposed	Present	A-width	120	−0.253	0.043	0.803	0.032	0.841	6.14		
Exposed	Colton	Lip	219	−2.321	0.155	1.817	0.117	0.528	7.01	9.58	.0021
Exposed	Present	Lip	120	−1.801	0.197	1.459	0.146	0.459	3.15		
Semiexposed	Colton	A-length	436	0.027	0.013	0.879	0.010	0.949	12.42	76.21	<.0001
Semiexposed	Present	A-length	256	0.172	0.024	0.773	0.016	0.900	13.99		
Semiexposed	Colton	A-width	436	−0.241	0.024	0.789	0.018	0.821	11.98	1.91	NS
Semiexposed	Present	A-width	256	−0.198	0.036	0.760	0.025	0.788	9.69		
Semiexposed	Colton	Lip	436	−2.319	0.111	1.763	0.082	0.518	9.34	13.51	.0003
Semiexposed	Present	Lip	256	−1.808	0.142	1.433	0.098	0.459	4.44		
Sheltered	Colton	A-length	498	−0.033	0.019	0.922	0.014	0.901	5.72	26.15	<.0001
Sheltered	Present	A-length	231	0.091	0.035	0.831	0.023	0.847	7.26		
Sheltered	Colton	A-width	498	−0.476	0.029	0.958	0.021	0.810	2.03	7.07	.0080
Sheltered	Present	A-width	231	−0.392	0.044	0.890	0.029	0.799	3.74		
Sheltered	Colton	Lip	498	−2.445	0.152	1.822	0.109	0.360	7.53	0.28	NS
Sheltered	Present	Lip	231	−2.353	0.216	1.753	0.144	0.393	5.23		

Variables: A-length, aperture length; A-width, aperture width; Lip, shell lip thickness; T, t-test for slope = 1. All have highly significant *P* values. *F*, *F*-ratio from the test of a time period effect. *P*, *P* values for tests of a time period effect. NS, not significant.