

The effect of water temperature on drilling and ingestion rates of the dogwhelk *Nucella lapillus* feeding on *Mytilus edulis* mussels in the laboratory

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Received: 7 December 2012 / Accepted: 13 February 2013 / Published online: 18 April 2013
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Abstract In highly seasonal intertidal habitats, changes in temperature through the year may drive substantial shifts in feeding and growth rates of organisms. For the dogwhelk *Nucella lapillus*, attacking and consuming *Mytilus edulis* mussels can take hours or days, depending on temperature. Handling time of dogwhelks feeding on mussels is therefore greatly affected by ocean temperature. I recorded attack time in the laboratory, partitioned into drilling and consumption time, for juvenile dogwhelks across a range of seawater temperatures representative of field seawater temperatures during the main growing seasons of summer and autumn. The combined length of a drilling attack and subsequent ingestion time tripled across the 10 °C decline in water temperatures from July through November, driven primarily by an increase in ingestion time. The observed reduction in handling time, coupled with projected sea surface warming in New England by the end of the twenty-first century, could extend the length of the growing season for *Nucella* and subsequently have cascading effects on the prey community.

Introduction

Foraging for food in the rocky intertidal zone brings a host of potential dangers. Leaving the relative safety of a crevice to forage for a meal can expose animals to predators as well as dangers from the environment, such as wave dislodgement or thermal stress (Denny et al. 2009). For predators feeding on well-defended prey, long handling times can exacerbate the risk posed by the environment and other predators (Pincebourde et al. 2008). Additionally, seasonal temperature changes may drastically impact the rates of physiological processes for ectothermic animals, which can affect both handling time and subsequent digestion rates (Sanford 2002a, b; Yee and Murray 2004). Future climate change, including warming sea surface temperatures, could alter the seasonality of feeding and growth, which will ultimately have cascading effects within the intertidal community (Sanford 2002a; Yamane and Gilman 2009; Gooding et al. 2009).

On the shores of the North Atlantic, the muricid dogwhelk *Nucella lapillus* feeds on mussels and barnacles (Connell 1961). To gain access to the tissue inside, *N. lapillus* must typically drill through the exterior shell of the prey before it can insert its proboscis and consume the animal (Rovero et al. 1999a). For dogwhelks feeding on the blue mussel *Mytilus edulis*, the process of drilling and consuming the mussel may take many hours or days. During this time, the dogwhelk must remain relatively stationary on the mussel to complete the attack, potentially leaving the dogwhelk exposed to threats to its own safety (Burrows and Hughes 1989).

The length of an attack by *N. lapillus* on *M. edulis* is determined by the initial amount of time necessary to gain entry into the mussel shell, plus the time required to consume the mussel tissue. Dogwhelks that are experienced

Communicated by M. G. Chapman.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-013-2202-z) contains supplementary material, which is available to authorized users.

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with feeding on mussels will often learn to quickly gain entry into the mussel shell by inserting the proboscis between the gape of the valves (Rovero et al. 1999a), while young and inexperienced dogwhelks must spend time rasping a hole in the shell with the radula, which takes much longer. The length of this drilling phase may be influenced by a number of factors, primarily where on the mussel shell the dogwhelk chooses to drill and the thickness of the mussel shell in that location. The amount of time needed to consume the mussel tissue after gaining entry can be affected by the relative sizes of predator and prey, the time since last feeding, and environmental influences such as temperature (Hughes and Drewett 1985).

Growth rates of *N. lapillus* during the cold winter and spring seasons are near zero (Largen 1967; Feare 1970). Juvenile *N. lapillus* emerge from egg capsules in the autumn and spend their first winter and spring seasons within the safety of crevices (Etter 1989). Warm temperatures in summer are associated with high growth rates in juveniles and rapid consumption rates in adults as well. Body mass of juvenile whelks can increase by 340 % and shell length can double during the summer and early autumn (Etter 1989; Palmer 1990). Feeding rates in adult whelks have been examined in more detail, with warmer temperatures leading to higher consumption rates and reduced digestion time between feeding bouts (Largen 1967; Bayne and Scullard 1978; Burrows and Hughes 1989). These same temperature effects likely exist for juvenile whelks, and the rates of feeding and growth may be particularly important at this life stage, when they determine the time needed to reach reproductive size and reach sizes large enough to be resistant to predation. Although there have been numerous recent studies on the feeding behavior of juvenile dogwhelks in response to predatory crab chemical cues, particularly during the summer growing season (Trussell et al. 2006a, b; Matassa and Trussell 2011), the effects of temperature on feeding rates of juvenile dogwhelks have received less attention. Climate models project future increases in sea surface temperature of several degrees through much of the year within the habitat range of *N. lapillus* (Meehl et al. 2007; IPCC 2007), which could extend the length of the growing season and have cascading effects on energy flow in the intertidal zone.

I tested the hypotheses that: (1) changes in ambient water temperature will affect drilling rates and the time required to successfully access mussel tissue, (2) ingestion time following a successful drilling attack will proceed faster at warmer water temperatures, and (3) total handling time from the start of an attack to the completion of ingestion will be shorter in warmer water. I used a hydrophone and time-lapse camera to measure the time course of drilling and consumption of *M. edulis* by juvenile

N. lapillus dogwhelks in mesocosms during the primary summer growing season and through the decreasing temperatures of autumn. In addition to the hypotheses above, these observations allowed me to assess the effect of the mussel shell thickness on drilling time, the effect of snail size on drilling and ingestion rate, and the effect of mussel size on ingestion rate. Using estimates of increasing sea surface temperatures in the future, I discuss the potential effects of rising temperatures and extended growing seasons for *N. lapillus*.

Materials and methods

Juvenile *N. lapillus* were collected from Pea Island, adjacent to the Marine Science Center at Nahant, MA (42.41554°N, 70.90925°W) during early June in the summers of 2010 and 2011. The dogwhelks were held in plastic containers in seawater tables at the Marine Science Center until they were used in the trials during the subsequent 6 months. Small *M. edulis* mussels, collected near Chamberlain, Maine (43.88554°N, 69.47387°W), were provided ad libitum as food. Prior to use in the experiment, each *N. lapillus* was starved for 5 days to standardize hunger levels and to clear the digestive tract so that previous meals would not influence ingestion. Experimental trials were carried out from July to November of 2010 and 2011 (Figure S1). Seawater temperatures in Nahant, MA typically peak at the end of July or during August, and decline through the autumn season. The dogwhelks ranged in size from 11.7 to 14.4 mm maximum shell length from spire to outer edge of aperture (mean length 13.2 mm), while mussels ranged from 10.3 to 16.8 mm in length (mean length 12.9 mm). These small *Mytilus edulis* were representative of the limited range of mussel sizes available on Pea Island where the *N. lapillus* were originally collected.

Using a piezo-electric hydrophone system similar to that described by Rovero et al. (1999b), I recorded the drilling noise of a dogwhelk attacking a mussel. The hydrophone housing was constructed of acrylic, with the piezo element epoxied directly to the inside of the acrylic housing. The audio cable was connected to a USB microphone pre-amplifier (Griffin iMic, Griffin Technology, Nashville TN, USA), hooked to a computer running a custom LabVIEW program (National Instruments Corporation, Austin, TX, USA) to record the audio stream continuously. For each trial, the right valve of a live *M. edulis* mussel was glued to the surface of the hydrophone with cyanoacrylate glue. This allowed the mussel to open and close its valves normally, and mussels were frequently observed to extend the foot to secrete byssal threads during the trial. The hydrophone was submerged in a 1.5-L tank hooked to a flow-through seawater system. A starved *N. lapillus* was placed

in the tank and allowed to attack and consume the mussel. Whelks appeared to crawl normally and explored the confines of the tank and the hydrophone surface when placed in the tank. The water level in the container was always kept full, so there was no tidal cycling in the experiment. Every trial was conducted outside under shade with natural day–night cycles. Water temperature was monitored continuously using a TMP-36 sensor (Analog Devices, Norwood, MA, USA).

Snail movement during the same trial was recorded using time-lapse images taken with a USB web camera positioned above the tank. A set of red LEDs provided minimal illumination at night. Images were captured every 3 minutes by the LabVIEW program. The time-lapse images were used to mark the time when a dogwhelk first contacted the mussel, and when the dogwhelk finally departed from the consumed mussel. The time course of the drilling phase was analyzed using Audacity software (version 1.3beta 2010) to visualize each audio recording as a spectrogram where the noise from the discrete rasps of the drilling attack could be seen. The start and end time of each rasping bout, comprised of many discrete rasping noises occurring about two seconds apart, was recorded to the nearest second. Pauses in drilling lasting more than ten seconds marked the end of a rasping bout. The period between individual rasp strokes was sampled at the start, middle, and end of the drilling phase of the attack for each snail. The end of the drilling phase and beginning of the ingestion phase were taken as the point where rasping noise permanently ceased. This transition was accompanied by the snail beginning to shift its shell repeatedly, presumably to allow the proboscis to reach all interior portions of the mussel shell through the drill hole. The end of the ingestion phase was marked as the time when the snail crawled away from the mussel. After the snail departed the mussel, I measured the exterior dimensions of the mussel to the nearest 0.01 mm using digital calipers, and measured the thickness of the shell immediately surrounding the drill hole to the nearest 0.001 mm using a digital micrometer. In order to account for the possible influence of the smaller amount of shell material removed when a dogwhelk drilled on the lip of a mussel valve compared to drilling wholly on the valve, I estimated the volume of shell material that made up the drill hole. I measured the area of the drill hole (to the nearest 0.01 mm²) using ImageJ software (Rasband 2013), and multiplied that area by the average thickness around the drill hole to estimate the volume of shell material removed. The maximum shell length of the dogwhelk, from the tip of the spire to the end of the siphonal canal, was measured with calipers to the nearest 0.01 mm. I measured dogwhelk weight by poking the snail to encourage it to retract fully into the shell, wiping away any excess water with a paper towel, and weighing on a balance

to the nearest 0.1 mg. In every trial, the dogwhelk consumed all of the tissue in the mussel shells, except for occasional remnants of the adductor muscles and small sections of the mantle edge. Each dogwhelk was only used once during these trials.

Prior to carrying out multiple regression analyses, I assessed potential collinearity of predictor variables using scatterplots and by calculating variance inflation factors for the available predictors (Fox and Weisberg 2011). Of the available predictors, I removed mussel shell width and height, along with snail mass, due to high collinearity with other predictors. The remaining variables—water temperature, mussel shell length, the volume of shell material removed from the drill hole, and dogwhelk shell length—were used as predictors in the multiple regression models. The response variables in these analyses were drilling time, rasping rate, ingestion time, and total attack length. All analyses were carried out in R 2.14.1 (R Development Core Team 2012). I fit a series of preliminary models including all interactions among the predictor variables, and used likelihood ratio tests to examine the potential for interactions. None of the interaction terms were significant, but the small sample size ($n = 18$ snails) limits the ability to elucidate interactions. Due to the small sample size, I subsequently restricted the set of linear models reported here to additive models without interaction terms to avoid overfitting. For the multiple regression of drilling time, I used water temperature, snail length, and the volume of shell material removed from the drill hole as predictor variables. Mussel length was not included in this model, as it was assumed drill hole size would have a more direct relationship to drilling time. For the analyses of ingestion time and total attack length, mussel shell length was substituted for drill hole volume as a predictor variable, as the time taken to ingest the mussel was likely driven by the amount of tissue available (a function of shell size) rather than the shell thickness that had already been penetrated. In general, it is likely that pairing larger snails with smaller mussels, or vice versa, would result in significant interactions affecting the duration of the different phases of attack discussed here (Hughes and Dunkin 1984). The narrow range of snail and mussel sizes used here should help mitigate the potential influence of these interactions within the sample, but extrapolating results to other size classes or temperature ranges should be cautioned against. The distributions of model residuals and quantile–quantile plots were inspected to ensure that the assumption of homogeneity of variances was met. There were no obvious patterns in the residuals, and all analyses were carried out with untransformed variables.

I derived estimates of historical and future whelk feeding rates from a combination of the total attack length regression model (converted to a feeding rate, mussels per

day) and climate model projections of sea surface temperature. I extracted sea surface temperature projections for grid cells adjacent to the study site from a set of eight atmospheric-ocean global circulation models obtained from the World Climate Research Program's Coupled Model Intercomparison project (Meehl et al. 2007, Table S1). Modeled monthly average sea surface temperatures were sampled for the last two decades of the twentieth century and twenty-first century, using the SRES A1B emissions scenario results for the twenty-first century models (IPCC Working Group III 2000). The projected sea surface temperatures were bootstrap resampled to produce a feeding rate estimate for each month separately by first resampling the set of pooled temperatures from the 20 years of estimates of a given month from the eight models. The bootstrapped mean temperature value for each of the 10,000 iterations was used to predict the mean feeding rate and standard deviation from the multiple regression model for that temperature, using the average size of mussels and whelks in the experiment. A final feeding rate for the temperature was then sampled from a random normal distribution around that mean using the associated standard deviation. The 10,000 estimates of feeding rate for a month were then used to calculate a mean feeding rate and confidence intervals. The bootstrap estimation was carried out separately for each month when historical ocean temperatures in the models were within the bounds of the experimental trial temperatures (May to December).

Results

Out of 44 experimental trials with feeding snails, 18 trials yielded usable data for this study. Data from the other trials had to be excluded for a variety of reasons, typically due to poor sound quality from the hydrophone when dogwhelks drilled the valve of the mussel that was not directly glued to the hydrophone. Of the 18 dogwhelks retained in the data set, 8 drilled on the lip of the mussel valve, leaving a semi-circular hole, while the remaining dogwhelks drilled entirely on the valve, leaving a circular hole.

When drilling, dogwhelks made a rasping stroke every 1.9 s (± 0.56 s, 1 SD) on average. The rasp stroke period was significantly influenced by water temperature (Fig. 1), which ranged from 9.1 to 19.6 °C during the summer and autumn seasons. Dividing the total length of all rasping bouts by the rasping stroke period for each snail's drilling phase, it took between 568 and 4060 rasps, with an average of 2,072 rasps ($\pm 1,036$, 1 SD), to penetrate a mussel shell. The shell thickness around each drill hole ranged from 0.097 to 0.276 mm (mean thickness, 0.183 mm), and the volume of shell material removed from drill holes ranged

from 0.005 to 0.076 mm³ (mean 0.044 \pm 0.021 mm³, 1 SD).

The drilling phase of the attack lasted 6.4 h on average (± 3.9 h, 1 SD), and ranged from 0.9 to 14.2 h. During the drilling phase, active rasping bouts lasted an average of 4.1 min (± 2.0 min, 1 SD). Between active rasping bouts, when the hydrophone did not detect any noise, it is assumed that the snail was dissolving the organic matrix of the mussel shell inside the drill hole using secretions from the accessory boring organ (Rovero et al. 1999b). These quiet periods lasted 17.1 min (± 7.9 min, 1 SD) on average.

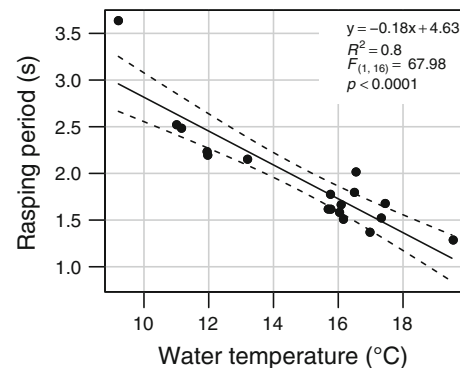


Fig. 1 Rasping stroke period (seconds per stroke) versus water temperature. Dashed lines represent 95 % confidence intervals

Table 1 Coefficient estimates for multiple regression models of (A) drilling time, (B) ingestion time, and (C) total attack time (drilling and ingestion time combined). Bold values represent significant partial regression slopes. Shell lengths were measured in millimeter

Coefficients	Estimate	SE	<i>p</i>
(A) Drilling time (h)			
Intercept	-13.90	23.01	0.555
Water temperature	-0.094	0.389	0.813
Drill hole volume (mm ³)	91.35	59.40	0.146
Snail length	1.373	1.386	0.339
$F_{(3,14)} = 1.33$, $p = 0.305$, adjusted $R^2 = 0.05$			
(B) Ingestion time (h)			
Intercept	119.04	38.91	0.0085
Water temperature	-3.648	0.782	0.0003
Mussel length	6.045	1.328	0.0005
Snail length	-8.791	3.125	0.0138
$F_{(3,14)} = 16.73$, $p = <0.0001$, adjusted $R^2 = 0.74$			
(C) Total attack time (h)			
Intercept	132.5	43.33	0.0085
Water temperature	-4.083	0.895	0.0004
Mussel length	7.312	1.460	0.0002
Snail length	-10.05	3.438	0.0111
$F_{(3,14)} = 17.78$, $p = <0.0001$, adjusted $R^2 = 0.75$			

Bold values represent significant partial regression slopes. Shell lengths were measured in millimeter

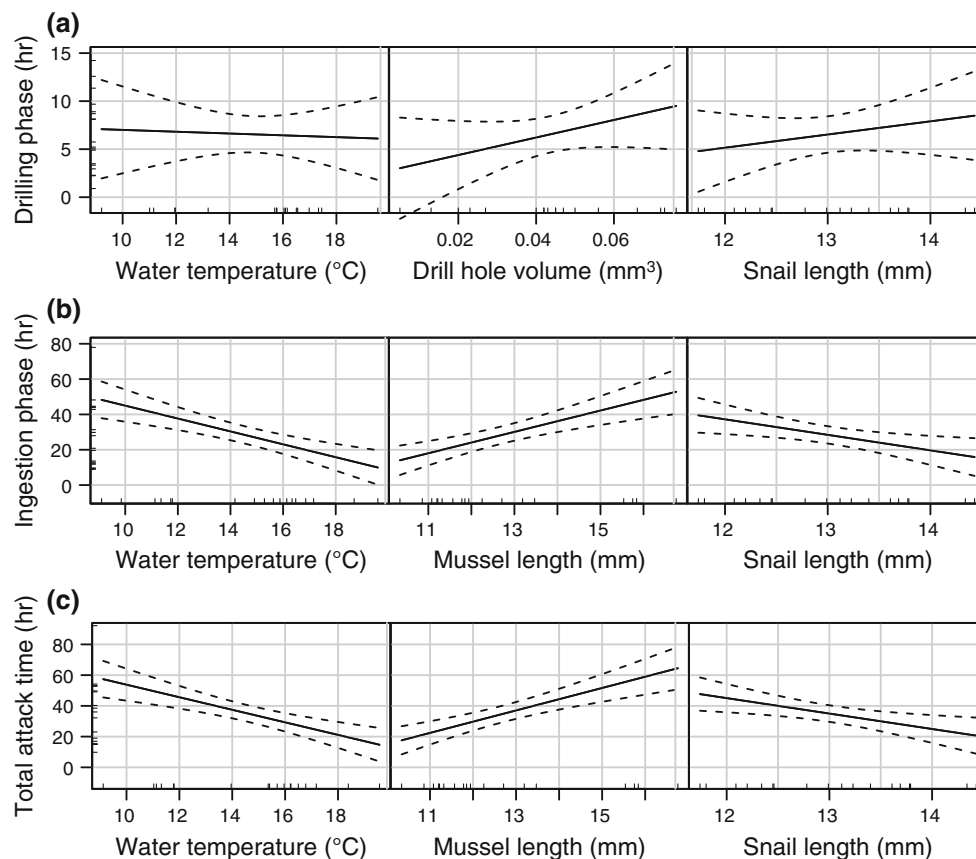


Fig. 2 Marginal effects plots showing fitted partial regressions for **a** drilling time, **b** ingestion time, and **c** total attack time (drilling and ingestion combined) against each predictor variable, when each of the other predictors was held at its mean value. The rug of points along

the borders represents the distribution of the original data points used to fit the linear models. Dashed lines represent 95 % confidence limits. Coefficient estimates are given in Table 1

The length of the drilling phase was not well predicted by the linear model (Table 1A; Fig. 2a). Drilling through a greater volume of shell material tended to increase the length of the drilling phase, though not significantly.

The length of the ingestion phase, after the completion of drilling, was significantly affected by water temperature, the size of the mussel, and the size of the snail (Table 1B; Fig. 2b). Warming water temperatures by 1 °C reduced the average length of the ingestion phase by 3.6 h (± 1.7 h, 95 % CI) in the regression model. Increasing mussel length by 1 mm, which should increase the mass of tissue available to feed on, increased ingestion time by 6.0 h (± 2.8 h, 95 % CI). Larger snails ingested their prey faster, leading to a reduction in ingestion time by 8.8 h (± 6.7 h, 95 % CI) for each 1 mm increase in snail length.

When the drilling phase and ingestion phase lengths were combined to estimate total attack time, water temperature, mussel length, and snail length each remained significant predictors (Table 1C; Fig. 2c). Increasing water temperature by 1 °C reduced the overall length of the attack by 4.1 h (± 1.9 h, 95 % CI), while increasing mussel length by 1 mm increased the length of the attack by 7.3 h

(± 3.1 h, 95 % CI), and increasing snail length by 1 mm reduced the total attack time by 10.1 h (± 7.4 h, 95 % CI).

Sea surface temperatures during May through December near the study site are projected to rise 2.8 °C by the end of the twenty-first century under the A1B emissions scenario. Rising sea surface temperatures could increase the feeding rates of dogwhelks by 25 % on average, though there is substantial overlap in the historical and future estimates of average monthly feeding rate (Fig. 3).

Discussion

Several factors influence the behavior, feeding rate, and growth rate of *N. lapillus* foraging on rocky shores, which in turn affect their impact on prey species and ultimately, the community composition as a whole. Predatory crabs, wave exposure, desiccation, and heat stress influence when and where *N. lapillus* elects to forage for food (Burrows and Hughes 1989; Vadas et al. 1994; Matassa and Trussell 2011). These limitations on the foraging rates of dogwhelks may be partially offset by the accumulation of experience

preying on mussels (Rovero et al. 1999a) or by inherently higher foraging rates of dogwhelks from wave-exposed sites (Menge 1978; Burrows and Hughes 1990). The current study highlights the role that seasonal temperature shifts can play in determining dogwhelk feeding rates. Feeding rates peak during the warmest summer temperatures to support the fastest growth, as shown here and in earlier studies (Largen 1967; Bayne and Scullard 1978; Etter 1989; Palmer 1990). As the ocean cools through the autumn, the time needed for ingestion lengthens, more than tripling the total handling time in the span of the 10 °C seawater temperature decline encompassed in this study ($Q_{10} = 3.7$ for feeding rate, mussels per day).

Over the narrow range of mussel shell thicknesses measured in this study (0.098–0.276 mm), shell thickness had only a small effect on drilling time. The average drilling rate measured here, 1.03 ± 0.78 mm per day (1 SD), was faster than previous estimates for *N. lapillus* feeding on larger *M. edulis* (Hughes and Dunkin 1984; Rovero et al. 1999a, 0.36 and 0.29 mm per day, respectively). The rasp stroke period (seconds between the start of two rasp strokes) observed here is similar to the value (1.5 s) measured by Rovero et al. (1999b) for rapidly drilling adult whelks (35 mm shell length) at 17 °C, although adult whelks were also often observed to have longer periods of 5–10 s between individual rasp strokes. Due to the large variation in drilling phase length in this study, there is little evidence that drilling through *Mytilus* shell is affected by water temperature, even though the time between rasp strokes increased significantly at colder water temperatures. A similar change in rasping rate with temperature has been observed in grazing herbivorous gastropods in the field (Petraitis 1992). Drilling through a *M. edulis* shell involves alternating phases of active rasping and phases of dissolution of the shell by the accessory boring organ secretions (Chétail and Fournié 1969; Carrier 1981). Colder temperatures should slow the rates of chemical reactions causing shell dissolution, although the solubility of CaCO_3 structures rises in cold waters (Fabry et al. 2008), which could make the drilling process easier. However, the lack of evidence for an increase in drilling phase length with decreasing temperature in these trials may simply be due to behavioral variation in drilling effort between snails masking any temperature effect.

The conditions in these experimental trials represent a low-stress scenario for dogwhelks feeding on mussels. In the field, prey handling times in the range observed here would encompass multiple low tides and potentially expose the dogwhelk to predators, to wave disturbance at high tide, or to desiccation stress at low tide (Hughes and Drewett 1985; Burrows and Hughes 1989; Vadas et al. 1994). Aerial exposure at moderate temperatures may increase respiration rates (Sandison 1967), which comes with an

energetic cost. Feeding rates may also increase with moderate aerial exposure (Stickle et al. 1985), though stressful high temperatures tend to depress feeding rates in intertidal gastropods (Brown and Stickle 2002; Yamane and Gilman 2009). *N. lapillus* foraging rates decrease during extreme high temperatures at low tide and when water temperatures approach 25 °C (Largen 1967; Menge 1978). The peak in the future estimated feeding rates shown in Fig. 3 in July, August, and September is an extrapolation beyond the temperature range of the feeding experiment, and feeding rates during those months may not increase as much as is shown, due to curtailed feeding rates at peak summer temperatures. However, there may be unexplored physiological capacity for acclimation and effective feeding at seawater temperatures near 25 °C. While increasing peak summer temperatures may negatively impact foraging by increasing the threat of thermal stress, warming seawater temperatures in the spring, early summer, and fall may prolong the season of high feeding and growth rates (Stickle et al. 1985; Stickle and Bayne 1987), possibly offsetting the effects of reduced feeding during peak summer temperatures. Excluding July, August and September, the increase in the future projected feeding rates for May to December shown in Fig. 3 ranges from 21 to 42 % on average, although the 95 % confidence intervals overlap with the historical estimates.

This study demonstrates a strong relationship between prey handling time and seawater temperature for juvenile dogwhelks, but predicting the eventual community-level responses to decreasing handling time and increased feeding rates of dogwhelks will require further information. The feeding rates derived here do not include subsequent digestion time that may be required before snails can begin foraging for their next meal (Burrows and Hughes 1991; Stickle et al. 1985), though the time required for digestion has also been shown to decrease in adult dogwhelks at higher temperatures (Bayne and Scullard 1978). Incorporating an estimate of the digestion time between meals would lower the absolute value of the estimated feeding rates shown here, but could enhance the relative increase in feeding rates projected under warming sea surface temperature conditions if snails in warmer waters finish digesting their meals faster than those in cooler waters. This comparison also assumes that search time and encounter rates do not change appreciably in the future climates, but these factors might change significantly as the community responds to climate change. Estimating the transfer of energy from lower to higher trophic levels will also require estimates of metabolism and the growth efficiency of dogwhelks across a range of temperatures. Past work with eastern Atlantic adult *N. lapillus* populations showed highest growth efficiencies at moderate temperatures (10–15 °C), with negative growth efficiencies at low

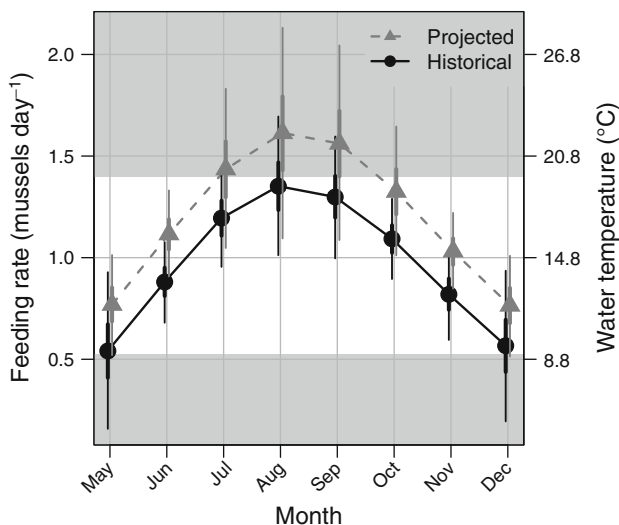


Fig. 3 Bootstrapped estimates of *N. lapillus* feeding rates (mussels per day) under historical and future projected sea surface temperatures. The secondary ordinate axis shows corresponding sea surface temperature estimates from the model ensemble for the ocean grid cell closest to Nahant, Massachusetts. The *thick* and *thin* error bars represent 50 and 95 % confidence intervals, respectively. The *gray background* regions represent temperature conditions outside of the range of observed temperatures on which the feeding rate regression model was based

(5 °C) and high (20 °C) temperatures (Stickle and Bayne 1987). Projected warming trends around Nahant, MA could keep winter sea surface temperatures above 5 °C, allowing dogwhelks to forego winter torpor, continue feeding, and grow more than recent historical winter temperatures allowed. But for these same dogwhelks operating in a warming environment in summer, the rate of increase in metabolic costs may outstrip increased feeding rates, as demonstrated in other systems (Rall et al. 2010; Lemoine and Burkepille 2012). Thus, at peak temperatures in summer, the ingestion efficiency (ingestion rate divided by metabolic rate) may decrease until a dogwhelk is burning more calories through metabolic maintenance pathways than it can effectively consume, leading to negative growth rates. Higher feeding rates could increase the *per capita* effect of *N. lapillus* on prey populations of *M. edulis*, and could negatively affect mussel populations where dogwhelks occur in high densities.

Rising temperatures will not impact dogwhelks in isolation, so the parallel effects of warmer seawater temperatures on predatory crabs, *M. edulis*, and other predators and prey resources in the system will shape the community response. Fisher et al. (2009) found evidence for increasing *N. lapillus* body sizes relative to early twentieth century samples, and they present several hypotheses for the increase, including faster growth in warmer waters, increased coastal productivity driving increases in prey abundance and value, and the loss of non-crab predators of

dogwhelks. Predatory crab distributions have been shifting in concert with warming trends in the Gulf of Maine, and with the introduction of new species through human activities (Welch 1968; Freeman and Byers 2006). The mussel *M. edulis* can also thicken its shell in response to predator cues (Freeman and Byers 2006), and warmer climate conditions can decrease *M. edulis* growth efficiency and bring it closer to its thermal tolerance limits (Widdows and Bayne 1971; Jones et al. 2009). So while the present study provides insight into how changing seawater temperature might affect dogwhelk feeding rates, this represents only one piece of a much larger puzzle composed of the numerous species-specific physiological responses to climate warming and the emergent patterns resulting from the interactions between these species.

Acknowledgments The author was supported by a National Science Foundation grant OCE-0727628 to G. C. Trussell. C. M. Matassa collected the whelks and mussels, M. E. Bracken provided space for the monitoring equipment. C. A. Blanchette provided the original motivation for the project, and M. Jelenic provided thoughtful discussion on monitoring feeding behavior.

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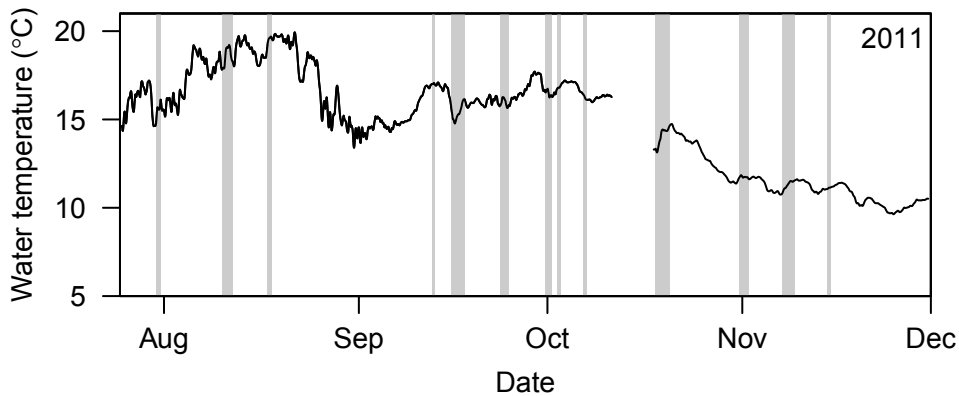
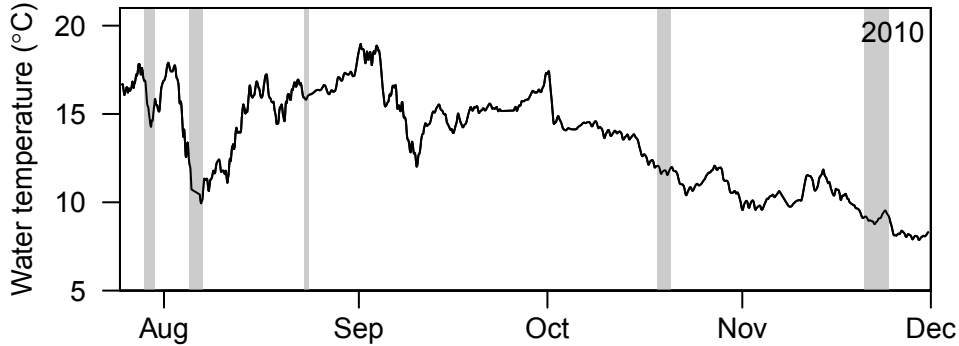


Table S1. Climate models used to estimate water temperatures near Nahant, Massachusetts at the end of the 20th and 21st centuries. Data from the 20th century were taken from the 20C3M run for each model, and data for the 21st century were taken from the SRES A1B emissions scenario run. Model results were downloaded from the World Climate Research Programme's Coupled Model Intercomparison Project 3 multi-model archive at http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php

CMIP3 Model ID	Originating Group	Citation
BCCR-BCM2.0	Bjerknes Centre for Climate Research	(Furevik et al. 2003)
CSIRO-Mk3.0	CSIRO Atmospheric Research	(Gordon et al. 2002)
GFDL-CM2.0	US Dept. of Commerce / NOAA / Geophysical Fluid Dynamics Laboratory	(Delworth et al. 2006)
GFDL-CM2.1	US Dept. of Commerce / NOAA / Geophysical Fluid Dynamics Laboratory	(Delworth et al. 2006)
MIROC3.2 (medres)	Center for Climate System Research (The University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC)	(K-1 Model Developers 2004)
ECHAM5/MPI-OM	Max Planck Institute for Meteorology	(Jungclaus et al. 2006)
MRI-CGCM2.3.2	Meteorological Research Institute	(Yukimoto et al. 2001)
UKMO-HadCM3	Hadley Centre for Climate Prediction and Research / Met Office	(Gordon et al. 2000)

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