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

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8

9 **Abstract**

10 In highly seasonal intertidal habitats, changes in temperature through the year may drive substantial shifts  
11 in feeding and growth rates of organisms. For the dogwhelk *Nucella lapillus*, attacking and consuming *Mytilus*  
12 *edulis* mussels can take hours or days, depending on temperature. Handling time of dogwhelks feeding on mussels is  
13 therefore greatly affected by ocean temperature. I recorded attack time in the laboratory, partitioned into drilling and  
14 consumption time, for juvenile dogwhelks across a range of seawater temperatures representative of field seawater  
15 temperatures during the main growing seasons of summer and autumn. The combined length of a drilling attack and  
16 subsequent ingestion time tripled across the 10°C decline in water temperatures from July through November,  
17 driven primarily by an increase in ingestion time. The observed reduction in handling time, coupled with projected  
18 sea surface warming in New England by the end of the 21<sup>st</sup> century, could extend the length of the growing season  
19 for *Nucella* and subsequently have cascading effects on the prey community.

20 **Keywords**

21 Feeding rate; handling time; climate change; sea surface temperature; seasonality; rocky intertidal zone

## 22 **Introduction**

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

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

38 The length of an attack by *N. lapillus* on *M. edulis* is determined by the initial amount of time necessary to gain  
39 entry into the mussel shell, plus the time required to consume the mussel tissue. Dogwhelks that are experienced  
40 with feeding on mussels will often learn to quickly gain entry into the mussel shell by inserting the proboscis  
41 between the gape of the valves (Rovero et al. 1999a), while young and inexperienced dogwhelks must spend time  
42 rasping a hole in the shell with the radula, which takes much longer. The length of this drilling phase may be  
43 influenced by a number of factors, primarily where on the mussel shell the dogwhelk chooses to drill and the  
44 thickness of the mussel shell in that location. The amount of time needed to consume the mussel tissue after gaining  
45 entry can be affected by the relative sizes of predator and prey, the time since last feeding, and environmental  
46 influences such as temperature (Hughes and Drewett 1985).

47 Growth rates of *N. lapillus* during the cold winter and spring seasons are near zero (Largen 1967; Feare 1970).  
48 Juvenile *N. lapillus* emerge from egg capsules in the autumn and spend their first winter and spring seasons within

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

63 I tested the hypotheses that 1) changes in ambient water temperature will affect drilling rates and the time  
64 required to successfully access mussel tissue, 2) ingestion time following a successful drilling attack will proceed  
65 faster at warmer water temperatures, and 3) total handling time from the start of an attack to the completion of  
66 ingestion will be shorter in warmer water. I used a hydrophone and time lapse camera to measure the time course of  
67 drilling and consumption of *M. edulis* by juvenile *N. lapillus* dogwhelks in mesocosms during the primary summer  
68 growing season and through the decreasing temperatures of autumn. In addition to the hypotheses above, these  
69 observations allowed me to assess the effect of the mussel shell thickness on drilling time, the effect of snail size on  
70 drilling and ingestion rate, and the effect of mussel size on ingestion rate. Using estimates of increasing sea surface  
71 temperatures in the future, I discuss the potential effects of rising temperatures and extended growing seasons for *N.*  
72 *lapillus*.

### 73 **Materials and methods**

74 Juvenile *N. lapillus* were collected from Pea Island, adjacent to the Marine Science Center at Nahant, MA  
75 (42.41554° N, 70.90925° W) during early June in the summers of 2010 and 2011. The dogwhelks were held in

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

86         Using a piezo-electric hydrophone system similar to that described by Rovero et al. (1999b), I recorded the  
87 drilling noise of a dogwhelk attacking a mussel. The hydrophone housing was constructed of acrylic, with the piezo  
88 element epoxied directly to the inside of the acrylic housing. The audio cable was connected to a USB microphone  
89 pre-amplifier (Griffin iMic, Griffin Technology, Nashville TN, USA), hooked to a computer running a custom  
90 LabVIEW program (National Instruments Corporation, Austin, TX, USA) to record the audio stream continuously.  
91 For each trial, the right valve of a live *M. edulis* mussel was glued to the surface of the hydrophone with  
92 cyanoacrylate glue. This allowed the mussel to open and close its valves normally, and mussels were frequently  
93 observed to extend the foot to secrete byssal threads during the trial. The hydrophone was submerged in a 1.5 L tank  
94 hooked to a flow-through seawater system. A starved *N. lapillus* was placed in the tank and allowed to attack and  
95 consume the mussel. Whelks appeared to crawl normally and explored the confines of the tank and the hydrophone  
96 surface when placed in the tank. The water level in the container was always kept full, so there was no tidal cycling  
97 in the experiment. Every trial was conducted outside under shade with natural day-night cycles. Water temperature  
98 was monitored continuously using a TMP-36 sensor (Analog Devices, Norwood, MA, USA).

99         Snail movement during the same trial was recorded using time-lapse images taken with a USB web camera  
100 positioned above the tank. A set of red LEDs provided minimal illumination at night. Images were captured every  
101 three minutes by the LabVIEW program. The time lapse images were used to mark the time when a dogwhelk first  
102 contacted the mussel, and when the dogwhelk finally departed from the consumed mussel. The time course of the

103 drilling phase was analyzed using Audacity software (version 1.3beta2010) to visualize each audio recording as a  
104 spectrogram where the noise from the discrete rasps of the drilling attack could be seen. The start and end times of  
105 each rasping bout, comprised of many discrete rasping noises occurring about two seconds apart, was recorded to  
106 the nearest second. Pauses in drilling lasting more than ten seconds marked the end of a rasping bout. The period  
107 between individual rasp strokes was sampled at the start, middle, and end of the drilling phase of the attack for each  
108 snail. The end of the drilling phase and beginning of the ingestion phase was taken as the point where rasping noise  
109 permanently ceased. This transition was accompanied by the snail beginning to shift its shell repeatedly, presumably  
110 to allow the proboscis to reach all interior portions of the mussel shell through the drill hole. The end of the  
111 ingestion phase was marked as the time when the snail crawled away from the mussel. After the snail departed the  
112 mussel, I measured the exterior dimensions of the mussel to the nearest 0.01 mm using digital calipers, and  
113 measured the thickness of the shell immediately surrounding the drill hole to the nearest 0.001 mm using a digital  
114 micrometer. In order to account for the possible influence of the smaller amount of shell material removed when a  
115 dogwhelk drilled on the lip of a mussel valve compared to drilling wholly on the valve, I estimated the volume of  
116 shell material that made up the drill hole. I measured the area of the drill hole (to the nearest 0.01 mm<sup>2</sup>) using  
117 ImageJ software (Rasband, 2013), and multiplied that area by the average thickness around the drill hole to estimate  
118 the volume of shell material removed. The maximum shell length of the dogwhelk, from the tip of the spire to the  
119 end of the siphonal canal, was measured with calipers to the nearest 0.01 mm. I measured dogwhelk weight by  
120 poking the snail to encourage it to retract fully into the shell, wiping away any excess water with a paper towel, and  
121 weighing on a balance to the nearest 0.1 mg. In every trial, the dogwhelk consumed all of the tissue in the mussel  
122 shells, except for occasional remnants of the adductor muscles and small sections of the mantle edge. Each  
123 dogwhelk was only used once during these trials.

124           Prior to carrying out multiple regression analyses, I assessed potential collinearity of predictor variables  
125 using scatterplots and by calculating variance inflation factors for the available predictors (Fox and Weisberg 2011).  
126 Of the available predictors, I removed mussel shell width and height, along with snail mass, due to high collinearity  
127 with other predictors. The remaining variables - water temperature, mussel shell length, the volume of shell material  
128 removed from the drill hole, and dogwhelk shell length - were used as predictors in the multiple regression models.  
129 The response variables in these analyses were drilling time, rasping rate, ingestion time, and total attack length. All  
130 analyses were out in R 2.14.1 (R Development Core Team 2012). I fit a series of preliminary models including all

131 interactions among the predictor variables, and used likelihood ratio tests to examine the potential for interactions.  
132 None of the interaction terms were significant, but the small sample size ( $n = 18$  snails) limits the ability to elucidate  
133 interactions. Due to the small sample size, I subsequently restricted the set of linear models reported here to additive  
134 models without interaction terms to avoid overfitting. For the multiple regression of drilling time, I used water  
135 temperature, snail length, and the volume of shell material removed from the drill hole as predictor variables.  
136 Mussel length was not included in this model, as it was assumed drill hole size would have a more direct  
137 relationship to drilling time. For the analyses of ingestion time and total attack length, mussel shell length was  
138 substituted for drill hole volume as a predictor variable, as the time taken to ingest the mussel was likely driven by  
139 the amount of tissue available (a function of shell size) rather than the shell thickness that had already been  
140 penetrated. In general, it is likely that pairing larger snails with smaller mussels, or vice versa, would result in  
141 significant interactions affecting the duration of the different phases of attack discussed here (Hughes and Dunkin  
142 1984). The narrow range of snail and mussel sizes used here should help mitigate the potential influence of these  
143 interactions within the sample, but extrapolating results to other size classes or temperature ranges should be  
144 cautioned against. The distributions of model residuals and quantile-quantile plots were inspected to ensure that the  
145 assumption of homogeneity of variances was met. There were no obvious patterns in the residuals, and all analyses  
146 were carried out with untransformed variables.

147 I derived estimates of historical and future whelk feeding rates from a combination of the total attack length  
148 regression model (converted to a feeding rate, mussels  $\text{day}^{-1}$ ) and climate model projections of sea surface  
149 temperature. I extracted sea surface temperature projections for grid cells adjacent to the study site from a set of  
150 eight atmospheric-ocean global circulation models obtained from the World Climate Research Programme's  
151 Coupled Model Intercomparison project (Meehl et al. 2007, Table S1). Modeled monthly average sea surface  
152 temperatures were sampled for the last two decades of the 20<sup>th</sup> century and 21<sup>st</sup> century, using the SRES A1B  
153 emissions scenario results for the 21<sup>st</sup> century models (IPCC Working Group III 2000). The projected sea surface  
154 temperatures were bootstrap resampled to produce a feeding rate estimate for each month separately by first  
155 resampling the set of pooled temperatures from the 20 years of estimates of a given month from the eight models.  
156 The bootstrapped mean temperature value for each of the 10,000 iterations was used to predict the mean feeding rate  
157 and standard deviation from the multiple regression model for that temperature, using the average size of mussels  
158 and whelks in the experiment. A final feeding rate for the temperature was then sampled from a random normal

159 distribution around that mean using the associated standard deviation. The 10,000 estimates of feeding rate for a  
160 month were then used to calculate a mean feeding rate and confidence intervals. The bootstrap estimation was  
161 carried out separately for each month when historical ocean temperatures in the models were within the bounds of  
162 the experimental trial temperatures (May to December).

## 163 **Results**

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

169 When drilling, dogwhelks made a rasping stroke every 1.9 s ( $\pm 0.56$  s, 1SD) on average. The rasp stroke  
170 period was significantly influenced by water temperature (Figure 1), which ranged from 9.1 to 19.6°C during the  
171 summer and autumn seasons. Dividing the total length of all rasping bouts by the rasping stroke period for each  
172 snail's drilling phase, it took between 568 and 4060 rasps, with an average of 2072 rasps ( $\pm 1036$ , 1 SD), to  
173 penetrate a mussel shell. The shell thickness around each drill hole ranged from 0.097 to 0.276 mm (mean thickness,  
174 0.183 mm), and the volume of shell material removed from drill holes ranged from 0.005 to 0.076 mm<sup>3</sup> (mean 0.044  
175  $\pm 0.021$  mm<sup>3</sup>, 1 SD).

176 The drilling phase of the attack lasted 6.4 hr on average ( $\pm 3.9$  hr, 1SD), and ranged from 0.9 to 14.2 hr.  
177 During the drilling phase, active rasping bouts lasted an average of 4.1 min ( $\pm 2.0$  min, 1 SD). Between active  
178 rasping bouts, when the hydrophone did not detect any noise, it is assumed that the snail was dissolving the organic  
179 matrix of the mussel shell inside the drill hole using secretions from the accessory boring organ (Rovero et al.  
180 1999b). These quiet periods lasted 17.1 min ( $\pm 7.9$  min, 1 SD) on average. The length of the drilling phase was not  
181 well predicted by the linear model (Table 1A, Figure 2A). Drilling through a greater volume of shell material tended  
182 to increase the length of the drilling phase, though not significantly.

183 The length of the ingestion phase, after the completion of drilling, was significantly affected by water  
184 temperature, the size of the mussel, and the size of the snail (Table 1B, Figure 2B). Warming water temperatures by



185 1°C reduced the average length of the ingestion phase by 3.6 hr ( $\pm$  1.7 hr, 95% CI) in the regression model.  
186 Increasing mussel length by 1 mm, which should increase the mass of tissue available to feed on, increased ingestion  
187 time by 6.0 hr ( $\pm$  2.8 hr, 95% CI). Larger snails ingested their prey faster, leading to a reduction of ingestion time by  
188 8.8 hr ( $\pm$  6.7 hr, 95% CI) for each 1mm increase in snail length.

189 When the drilling phase and ingestion phase lengths were combined to estimate total attack time, water  
190 temperature, mussel length, and snail length each remained significant predictors (Table 1C, Figure 2C). Increasing  
191 water temperature by 1°C reduced the overall length of the attack by 4.1 hr ( $\pm$  1.9 hr, 95% CI), while increasing  
192 mussel length by 1mm increased the length of the attack by 7.3 hr ( $\pm$  3.1 hr, 95% CI), and increasing snail length by  
193 1mm reduced the total attack time by 10.1 hr ( $\pm$  7.4 hr, 95% CI).

194 Sea surface temperatures during May through December near the study site are projected to rise 2.8 °C by  
195 the end of the 21<sup>st</sup> century under the A1B emissions scenario. Rising sea surface temperatures could increase the  
196 feeding rates of dogwhelks by 25% on average, though there is substantial overlap in the historical and future  
197 estimates of average monthly feeding rate (Figure 3).

## 198 **Discussion**

199 Several factors influence the behavior, feeding rate, and growth rate of *N. lapillus* foraging on rocky shores,  
200 which in turn affect their impact on prey species and ultimately, the community composition as a whole. Predatory  
201 crabs, wave exposure, desiccation, and heat stress influence when and where *N. lapillus* elects to forage for food  
202 (Burrows and Hughes 1989; Vadas et al. 1994; Matassa and Trussell 2011). These limitations on the foraging rates  
203 of dogwhelks may be partially offset by the accumulation of experience preying on mussels (Rovero et al. 1999a) or  
204 by inherently higher foraging rates of dogwhelks from wave-exposed sites (Menge 1978; Burrows and Hughes  
205 1990). The current study highlights the role that seasonal temperature shifts can play in determining dogwhelk  
206 feeding rates. Feeding rates peak during the warmest summer temperatures to support the fastest growth, as shown  
207 here and in earlier studies (Largen 1967; Bayne and Scullard 1978; Etter 1989; Palmer 1990). As the ocean cools  
208 through the autumn, the time needed for ingestion lengthens, more than tripling the total handling time in the span of  
209 the 10°C seawater temperature decline encompassed in this study ( $Q_{10} = 3.7$  for feeding rate, mussels day<sup>-1</sup>).

210 Over the narrow range of mussel shell thicknesses measured in this study (0.098 to 0.276 mm), shell  
211 thickness had only a small effect on drilling time. The average drilling rate measured here,  $1.03 \pm 0.78$  mm day<sup>-1</sup> (1  
212 SD), was faster than previous estimates for *N. lapillus* feeding on larger *M. edulis* (Hughes and Dunkin 1984;  
213 Rovero et al. 1999a, 0.36 and 0.29 mm day<sup>-1</sup>, respectively). The rasp stroke period (seconds between the start of two  
214 rasp strokes) observed here is similar to the value (1.5 s) measured by Rovero et al. (1999b) for rapidly drilling adult  
215 whelks (35 mm shell length) at 17°C, although adult whelks were also often observed to have longer periods of 5 –  
216 10 s between individual rasp strokes. Due to the large variation in drilling phase length in this study, there is little  
217 evidence that drilling through *Mytilus* shell is affected by water temperature, even though the time between rasp  
218 strokes increased significantly at colder water temperatures. A similar change in rasping rate with temperature has  
219 been observed in grazing herbivorous gastropods in the field (Petraitis 1992). Drilling through a *M. edulis* shell  
220 involves alternating phases of active rasping and phases of dissolution of the shell by the accessory boring organ  
221 secretions (Chétail and Fournié 1969; Carriker 1981). Colder temperatures should slow the rates of chemical  
222 reactions causing shell dissolution, although the solubility of CaCO<sub>3</sub> structures rises in cold waters (Fabry et al.  
223 2008), which could make the drilling process easier. However, the lack of evidence for an increase in drilling phase  
224 length with decreasing temperature in these trials may simply be due to behavioral variation in drilling effort  
225 between snails masking any temperature effect.

226 The conditions in these experimental trials represent a low-stress scenario for dogwhelks feeding on  
227 mussels. In the field, prey handling times in the range observed here would encompass multiple low tides and  
228 potentially expose the dogwhelk to predators, to wave disturbance at high tide, or to desiccation stress at low tide  
229 (Hughes and Drewett 1985; Burrows and Hughes 1989; Vadas et al. 1994). Aerial exposure at moderate  
230 temperatures may increase respiration rates (Sandison 1967), which comes with an energetic cost. Feeding rates may  
231 also increase with moderate aerial exposure (Stickle et al. 1985), though stressful high temperatures tend to depress  
232 feeding rates in intertidal gastropods (Brown and Stickle 2002; Yamane and Gilman 2009). *N. lapillus* foraging  
233 rates decrease during extreme high temperatures at low tide and when water temperatures approach 25°C (Largen  
234 1967; Menge 1978). The peak in future estimated feeding rates shown in Figure 3 in July, August, and September is  
235 an extrapolation beyond the temperature range of the feeding experiment, and feeding rates during those months  
236 may not increase as much as is shown, due to curtailed feeding rates at peak summer temperatures. However, there  
237 may be unexplored physiological capacity for acclimation and effective feeding at seawater temperatures near 25°C.

238 While increasing peak summer temperatures may negatively impact foraging by increasing the threat of thermal  
239 stress, warming seawater temperatures in the spring, early summer, and fall may prolong the season of high feeding  
240 and growth rates (Stickle et al. 1985; Stickle and Bayne 1987), possibly offsetting the effects of reduced feeding  
241 during peak summer temperatures. Excluding July, August and September, the increase in future projected feeding  
242 rates for May to December shown in Figure 3 ranges from 21% to 42% on average, although the 95% confidence  
243 intervals overlap with the historical estimates.

244 This study demonstrates a strong relationship between prey handling time and seawater temperature for  
245 juvenile dogwhelks, but predicting the eventual community-level responses to decreasing handling time and  
246 increased feeding rates of dogwhelks will require further information. The feeding rates derived here do not include  
247 subsequent digestion time that may be required before snails can begin foraging for their next meal (Burrows and  
248 Hughes 1991; Stickle et al. 1985), though the time required for digestion has also been shown to decrease in adult  
249 dogwhelks at higher temperatures (Bayne and Scullard 1978). Incorporating an estimate of the digestion time  
250 between meals would lower the absolute value of the estimated feeding rates shown here, but could enhance the  
251 relative increase in feeding rates projected under warming sea surface temperature conditions if snails in warmer  
252 waters finish digesting their meals faster than those in cooler waters. This comparison also assumes that search time  
253 and encounter rates do not change appreciably in future climates, but these factors might change significantly as the  
254 community responds to climate change. Estimating the transfer of energy from lower to higher trophic levels will  
255 also require estimates of metabolism and the growth efficiency of dogwhelks across a range of temperatures. Past  
256 work with eastern Atlantic adult *N. lapillus* populations showed highest growth efficiencies at moderate  
257 temperatures (10 -15 °C), with negative growth efficiencies at low (5°C) and high (20°C) temperatures (Stickle and  
258 Bayne 1987). Projected warming trends around Nahant, MA could keep winter sea surface temperatures above 5°C,  
259 allowing dogwhelks to forego winter torpor, continue feeding, and grow more than recent historical winter  
260 temperatures allowed. But for these same dogwhelks operating in a warming environment in summer, the rate of  
261 increase in metabolic costs may outstrip increased feeding rates, as demonstrated in other systems (Rall et al. 2010;  
262 Lemoine and Burkepile 2012). Thus, at peak temperatures in summer, the ingestion efficiency (ingestion rate  
263 divided by metabolic rate) may decrease until a dogwhelk is burning more calories through metabolic maintenance  
264 pathways than it can effectively consume, leading to negative growth rates. Higher feeding rates could increase the

265 *per capita* effect of *N. lapillus* on prey populations of *M. edulis*, and could negatively affect mussel populations  
266 where dogwhelks occur in high densities.

267 Rising temperatures will not impact dogwhelks in isolation, so the parallel effects of warmer seawater  
268 temperatures on predatory crabs, *M. edulis*, and other predators and prey resources in the system will shape the  
269 community response. Fisher et al. (2009) found evidence for increasing *N. lapillus* body sizes relative to early 20<sup>th</sup>  
270 century samples, and they present several hypotheses for the increase, including faster growth in warmer waters,  
271 increased coastal productivity driving increases in prey abundance and value, and the loss of non-crab predators of  
272 dogwhelks. Predatory crab distributions have been shifting in concert with warming trends in the Gulf of Maine, and  
273 with the introduction of new species through human activities (Welch 1968; Freeman and Byers 2006). The mussel  
274 *M. edulis* can also thicken its shell in response to predator cues (Freeman and Byers 2006), and warmer climate  
275 conditions can decrease *M. edulis* growth efficiency and bring it closer to its thermal tolerance limits (Widdows and  
276 Bayne 1971; Jones et al. 2009). So while the present study provides insight into how changing seawater temperature  
277 might affect dogwhelk feeding rates, this represents only one piece of a much larger puzzle composed of the  
278 numerous species-specific physiological responses to climate warming and the emergent patterns resulting from the  
279 interactions between these species.

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387 **Tables**

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

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

391

392 **Figure legends**

393 **Fig. 1** Rasping stroke period (seconds per stroke) vs. water temperature. Dashed lines represent 95% confidence  
394 intervals.

395 **Fig. 2** Marginal effects plots showing fitted partial regressions for A) drilling time, B) ingestion time, and C) total  
396 attack time (drilling and ingestion combined) against each predictor variable, when each of the other predictors was  
397 held at its mean value. The rug of points along the borders represents the distribution of the original data points used  
398 to fit the linear models. Dashed lines represent 95% confidence limits. Coefficient estimates are given in Table 2.

399 **Fig. 3** Bootstrapped estimates of *N. lapillus* feeding rates (mussels day<sup>-1</sup>) under current and future projected sea  
400 surface temperatures. The secondary ordinate axis shows corresponding sea surface temperature estimates from the  
401 model ensemble for the ocean grid cell closest to Nahant, Massachusetts. The thick and thin error bars represent  
402 50% and 95% confidence intervals, respectively. The gray background regions represent temperature conditions  
403 outside of the range of observed temperatures on which the feeding rate regression model was based.

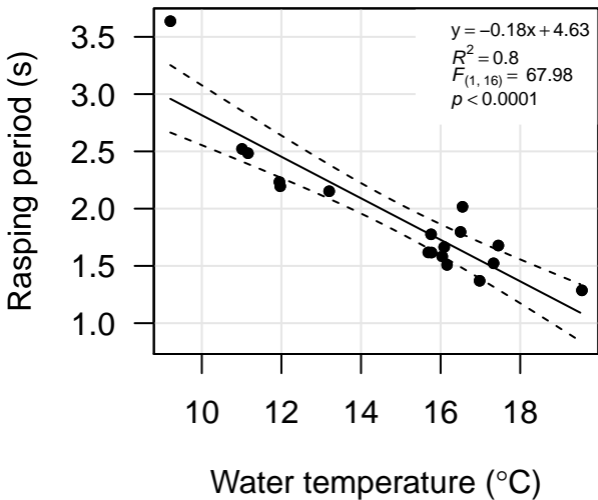
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405 **Supplemental figure legend**

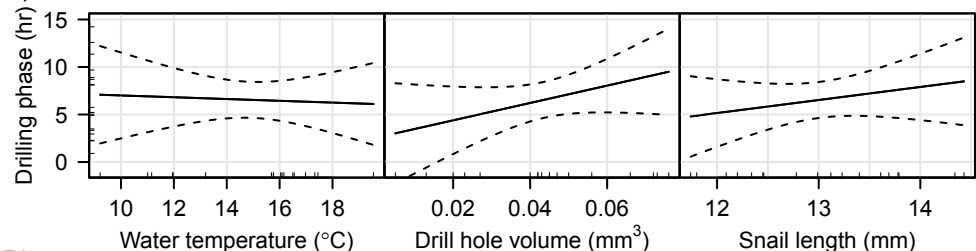
406 Fig S1. Seawater temperatures at the Marine Science Center, Nahant, MA, USA during 2010 and 2011 (upper and  
407 lower panels, respectively). Gray bars represent the timing of the feeding trials included in this data set.

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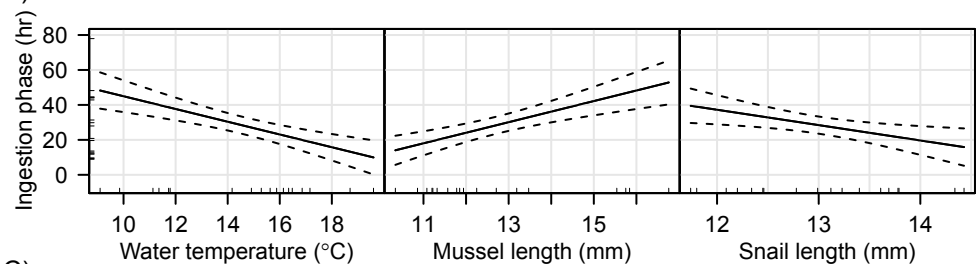




A)



B)



C)

