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journal homepage: www.elsevier.com/locate/jembeGrowth-mortality trade-offs along a depth gradient in *Cancer borealis*Cory J. Krediet^{a,c,*}, Megan J. Donahue^{b,c}^a Department of Biology, Drew University, 36 Madison Avenue, Madison, NJ 07940, United States^b Hawai'i Institute of Marine Biology, University of Hawai'i, PO Box 1346, Kāne'ohe, HI 96744, United States^c Shoals Marine Laboratory, Cornell University, G-14 Stimson Hall, Ithaca, NY 14853, United States

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ABSTRACT

Intertidal and shallow subtidal ecosystems experience steep environmental gradients over short distances. Individual foraging rate, predation risk, and physiologic stress vary along these gradients, resulting in growth-mortality trade-offs with depth. In the summer, *Cancer borealis* commonly forage in the shallow subtidal in the Gulf of Maine. *C. borealis* are the favored invertebrate prey of the Herring Gull and the Great Black-backed Gull, which consume 25%–50% of available *C. borealis* (those in <1 m water) during each daytime low tide. We investigated three possible explanations for the presence of *C. borealis* in the risky gull-predation zone. First, we tested whether predation risk in the gull-predation zone was matched at deeper depths by subtidal predators; we found predation risk decreases with depth. Second, we tested whether water temperatures were warmer in the gull-predation zone and whether these warmer temperatures resulted in increased growth rates. We found that, while waters were warmer in the gull-predation zone, crabs grew at similar rates above and below the thermocline when fed similar diets. Finally, we tested for differences in food availability with depth and whether these differences influenced *C. borealis* growth rates. Our results suggest a growth-mortality trade-off, where increased food availability provides sufficient growth benefit to outweigh the risk of foraging at shallower depths.

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1. Introduction

Trade-offs between growth and mortality arise when organisms balance foraging rate against predation risk and physiologic stressors (Mangel and Clark, 1986; Mangel and Stamps, 2001; McNamara and Houston, 1986; Werner, 1986; Werner and Anholt, 1993). Marine organisms exhibit a variety of adaptations to balance resource acquisition and predation risk: while organisms with limited mobility may respond to varying predator pressure and resource availability via phenotypic plasticity (Boeing et al., 2005; Lively et al., 2000; Miner et al., 2005; Molis et al., 2006; Trussell and Smith, 2000; Trussell and Nicklin, 2002), mobile organisms often move in response to changes in the growth-mortality landscape (Childress and Herrnkind, 1996; Farmer and Wiens, 1999; Jury et al., 1994; Richards, 1992; Taft and Haig, 2006).

Resource-rich habitats are often riskier (Werner et al., 1983) and classic foraging models predict a “minimize mortality to energy ratio” rule for landscapes with growth-mortality trade-offs (Gilliam, 1987). However, the correlation between risky and rich habitats can also result in a flat fitness distribution across the landscape (Mangel and Stamps, 2001). When this is the case, there may be a suite of equally optimal strategies, not all of which include the richest patches.

Intertidal and shallow subtidal ecosystems experience steep environmental gradients over short distances. Desiccation stress, thermal stress, wave exposure, food availability, and light penetration all change rapidly from the supralittoral to the shallow subtidal. Mobile animals can migrate vertically in response to tidal, seasonal, and ontogenetic changes to access food resources, avoid environmental stresses, and escape predators (e.g., Burrows and Gibson, 1995; Gibson, 2003; Hibino et al., 2006; Holsman et al., 2006; Takada, 1996). We expect that these migratory behaviors ultimately reflect the temporally varying fitness landscape.

The brachyuran crab, *Cancer borealis*, is widely distributed on the North American continental shelf and slope to 800 m from Newfoundland to the Bahamas (DFO, 2000; Haeffner, 1977; Stehlik et al., 1991; Wenner et al., 1992). Although most *C. borealis* live in deeper water, they are common in the shallow subtidal of the Gulf of Maine during the summer months (Jeffries, 1966; Krouse, 1980) where densities can reach 0.6 crab m⁻² (Witman, 1985). *C. borealis* move from the subtidal into the low intertidal (0 to –1 m MLLW) with the tide (Ellis et al., 2007), more than doubling in density between low tide (0.21 crabs m⁻²) and high tide (0.55 crabs m⁻²) and having dramatic top-down effects in the intertidal and shallow subtidal (Ellis et al., 2007). *C. borealis* are the favored prey of the Herring Gull (*Larus argentatus* Pontoppidan) and the Great Black-backed Gull (*Larus marinus* L.) (Ellis et al., 2005; Good, 1992), comprising 25%–60% of gull diet (Rome and Ellis, 2004). Predation pressure of gulls on accessible *C. borealis* is extreme, removing 30%–50% during each daytime low tide on shorelines throughout the Gulf of

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Table 1
Densities (\pm SE) of *C. borealis* in the intertidal and shallow subtidal of the Isles of Shoals.

Citation	This study	Donahue et al. (2009)	Perez et al. (2009)	Ellis et al. (2007)	Lozyniak (2003)	Ellis et al. (2005)	Novak (2004)	Witman (1985)
Year of study	2005	2006	2004	2002	2002	2000	1999	1982
Depth								
+0.5 m	–	–	0	–	–	–	–	–
0 m	0.06 (0.02)	0.25 (0.092)	0.2 (0.2)	0.28 (0.04)	–	0.18 (0.065)	–	–
–1 m	–	0.4 (0.13)	–	0.50 (0.05)	–	–	–	–
–2 m	0.16 (0.063)	0.6 (0.15)	0.8 (0.38)	–	0.56 (0.049)	–	0.075 (0.04)	–
–4 m	–	–	0.2 (0.2)	–	–	–	–	–
–6 m	–	–	–	–	0.25 (0.043)	–	0.06 (0.02)	–
–7–8 m	0.18 (0.056)	–	–	–	–	–	–	0.24 (0.023)
–10 m	–	–	–	–	0.23 (0.066)	–	0.17 (0.06)	–
Depth effect	No	Yes (+)	No	No	Yes (–)	–	Yes (+)	–

All studies estimated density by counts in quadrats or band transects; means and standard errors were scaled to density per m². In all studies, surveys between +0.5 m and –2.0 m MLLW were performed at high tide. Only surveys performed in summer daylight hours were included. Depth effect indicates whether the study reported a significant change in crab density with depth: + (–) indicates an increase (decrease) with increasing depth.

Maine (Ellis et al., 2005). However, gulls can forage to just 1 m of water depth (Good, 1998) and, therefore, crabs that remain below –1.5 m MLLW should be inaccessible to gull predation (minimum predicted tide in 2005 in the Isles of Shoals was –0.51 m). When gulls are experimentally excluded at low tide, *C. borealis* densities increased six-fold (to approx. 1.2 crabs m⁻²) in this “gull-predation zone” and were commonly found foraging above the waterline (Ellis et al., 2007). In this study, we investigated how growth–mortality trade-offs along a depth gradient may explain the movement of *C. borealis* into the shallow subtidal despite strong predation pressure from gulls.

We investigated three possible explanations for the frequent presence of *C. borealis* in the gull-predation zone. First, we tested whether predation risk in the gull-predation zone was matched at deeper depths by subtidal predators. Second, we tested whether water temperatures were warmer in the gull-predation zone and whether these warmer temperatures resulted in increased growth rates (as is typical in many invertebrates, especially decapods: (Cadman and Weinstein, 1988; Lellis and Russell, 1990; MacKenzie, 1988; Sanchez-Salazar et al., 1987). Finally, we tested for differences in food availability with depth and whether these differences influenced *C. borealis* growth rates.

2. Materials and methods

2.1. Site description

This study was conducted from 13 June 2005 to 12 August 2005 on the rocky, leeward shore of Appledore Island in the Gulf of Maine (42° 59' 21" N, 70° 37' 00" W). All experiments were conducted at depths of 0 m, –2 m, and –7 m mean lower low water (MLLW), chosen to capture the variation in temperature, food availability and predation risk with depth. The shallowest depth (0 m MLLW) is above the thermocline and is accessible to gull predation whenever the water level is <1 m MLLW during daylight hours (approximately 25% of the time). The middle depth (–2 m MLLW) is above the thermocline and should be just below the gull-predation zone: the maximum ebb tide in 2005 was –0.51 m MLLW (XTIDE 8.2, Flater 2008). The deepest depth (–7 m MLLW) is below the thermocline and below the gull-predation zone.

To characterize the temperature differences between 0 m, –2 m, and –7 m, temperature loggers (i-Button TMEX, model number: DS1921G) were sealed and secured to cages (see Growth experiment) at each depth, recording temperatures hourly. A single temperature logger was deployed at each depth on 30 June 2005; two additional loggers were installed at each depth on 20 July 2005; one logger was lost at –2 m.

2.2. Distribution of *C. borealis*

To measure the distribution of *C. borealis* across depth zones, we surveyed ten 15 m × 2 m transects at each depth (0 m, –2 m, –7 m MLLW). We tested for differences between depths using a one-way

ANOVA on log($x + 1$)-transformed data. We also reviewed the literature for density estimates of *C. borealis* in the Isles of Shoals.

2.3. Predation experiment

To test whether predation rate on *C. borealis* varied with depth, we conducted a survivorship experiment from 20 July 2005 to 27 July 2005. Fifty-eight crabs (male, 63–104 mm CW) were attached to stainless steel wire tethers (50 cm long, 0.5 mm diameter) using epoxy (Z-spar Splashzone Compound A788). Crabs were randomly assigned to each depth (20 crabs each to 0 m and –2 m; 18 crabs to –7 m) and tethered to bricks (0 m) or a weighted trotline (–2 m and –7 m) at least 1 m apart. Crabs were tethered in areas with similar access to crevices across

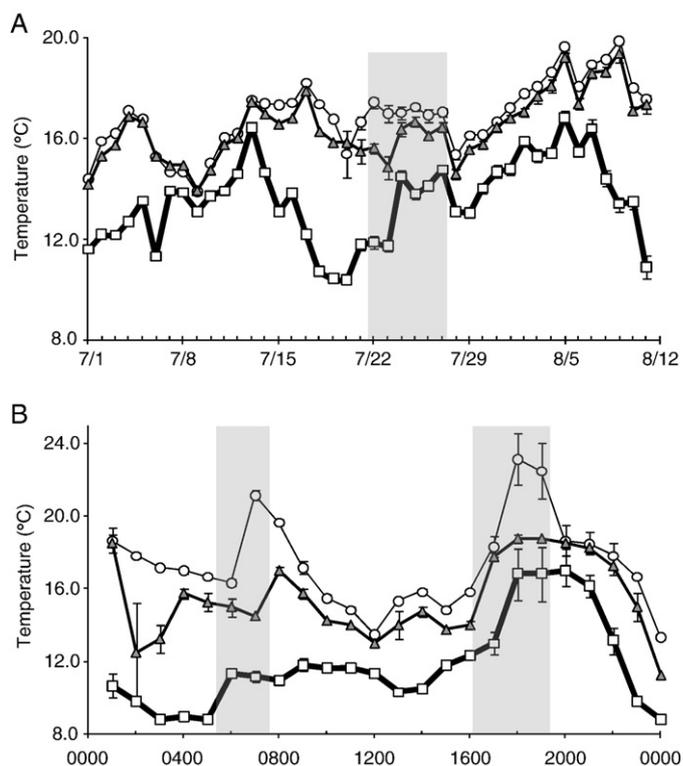


Fig. 1. (A) Daily mean temperature at 3 depths from 30 June to 11 August 2005: 0 m (open circles, solid line), –2 m (filled triangles, dashed line), and –7 m (open squares, dotted line). Shaded region indicates days with extreme daytime low tides: <0 m MLLW between 0530 and 1800. From 30 June to 21 July, there was a single logger at each depth; after 21 July, standard error is based on three loggers at 0 m and –7 m and two loggers at –2 m. (B) Mean hourly temperature on July 22, 2005 at 0 m (open circles, solid line), –2 m (filled triangles, dashed line), and –7 m (open squares, dotted line), illustrating the effect of a daytime low tide. Shaded regions indicate when the tide was below 0.5 m MLLW during daylight hours.

Table 2

Temperature (°C) statistics by depth based on hourly measurements over 35 days.

	0 m	-2 m	-7 m
Daily temperature ^a	16.9 (1.37)	16.4 (1.34)	13.5 (1.67)
Daily temperature range ^a	4.8 (3.4)	3.6 (1.9)	6.1 (2.2)
Maximum temperature	26	20.5	20

Maximum temperature is the maximum recorded temperature over the 35 day deployment.

^a Mean (standard error).

the three depths. Every day at dawn and dusk, we recorded the presence or absence of each crab using SCUBA or intertidal observations depending on the depth and tide. We used survival analysis to compare predation risk between depths. Survival analysis is the most appropriate and powerful tool to detect differences in survival when individual survival times are known; if some observations are censored (i.e., some crabs survived until the end of the experiment), survival times will not meet the assumptions of ANOVA. To test for the effect of depth on survivorship, we used a Cox proportional hazards survivorship model with planned contrasts between depths (Hosmer and Lemeshow, 1999).

Tethering artifacts can result in overestimates of mortality (e.g., tether failures are attributed to predation) or biased estimates of mortality (e.g., if tethering effectiveness differed between depths). For a control, five crabs were tethered in cages (one crab per cage) at each depth using 25 cm stainless steel tethers in 34 × 30 × 19 cm (*L* × *W* × *H*) coated-wire cages; crabs could reach the end of their tethers in the cages. In the control, tethers failed for one of the five crabs at each depth. Tether failure was independent of depth ($\chi^2 = 0$, *df* = 2, *p* = 1) and, in each case, the tether failed quickly (<24 h) and in the same way: the epoxy did not adhere to the carapace. During the experiment, we found two cases of this kind of tether failure, one at 0 m and one at -2 m. These cases were excluded from the survival analysis.

2.4. Food availability

To test for differences in food availability with depth, we collected all mobile invertebrates and scraped all sessile invertebrates and macroalgae in fifteen 20 × 20 cm quadrats on rocky substrate at each depth stratum (0 m, -2 m, and -7 m). Samples were preserved in 95% ethanol and sorted within one week of collection. Invertebrates

were dried to constant weight and grouped into the following taxa for analysis: mussels (primarily *Mytilus edulis*), snails (primarily *Littorina littorea*), sea urchins (*Strongylocentrotus droebachiensis*), polychaetes, crabs, other arthropods (primarily amphipods and isopods), and seastars (*Asterias* spp.). Algae were sorted, measured by wet weight, and grouped into the following taxa for analysis: *Chondrus crispus*, *Corallina*, *Polysiphonia*, *Alaria esculenta*, *Urospora penicilliformis*, *Polyides rotundus*, and other green algae (including *Codium* and *Ulva*). We used discriminant analysis to assess differences in invertebrate assemblages and algal assemblages across depths. Invertebrate dry weights and algal wet weights were $\log(x + 1)$ transformed to meet the assumptions of multivariate analysis.

2.5. Growth experiment

We expected that the primary factors influencing *C. borealis* growth rate across depth would be temperature and food availability. To distinguish the effects of these two factors, we conducted an *in situ* growth experiment by caging *C. borealis* at 0 m, -2 m, and -7 m from 7 July 2005 and 11 August 2005. Twenty coated-wire enclosures (34 × 30 × 19 cm *L* × *W* × *H*; 1.27 cm mesh size) were bolted to cleared, rocky substrate at each depth at least 3 m apart; ten cages at each depth were randomly assigned to each food treatment (ambient or standardized). The ambient food treatment consisted of all invertebrates and algae scraped from a 20 × 20 cm area of substrate surrounding the cages to simulate the diet of crabs foraging at that depth. The standardized food treatment included 50 g of *Scomberomorus maculatus* (mackerel) and five crushed *L. littorea*; this ensured that food availability was similar across depths and reduced food limitation as a potential limit of growth. For both treatments, food was added to the enclosures every 2–3 days for the 35 days of the growth experiment. Comparing growth rates by depth under ambient and standardized food treatments allowed us to distinguish whether growth at each depth was limited by food and/or by temperature (or another non-food factor varying with depth).

To control for variability in growth rate and differences in growth-mortality trade-offs with reproductive stage (Hartnoll, 2006; Perry and Pianka, 1997), all *C. borealis* used in the growth experiment were 60–80 mm carapace width (CW) males. At this size, male *C. borealis* are undergoing gonadal maturation; they attain morphometric and functional maturity at 120–135 mm CW (Moriyasu et al., 2002). We tracked

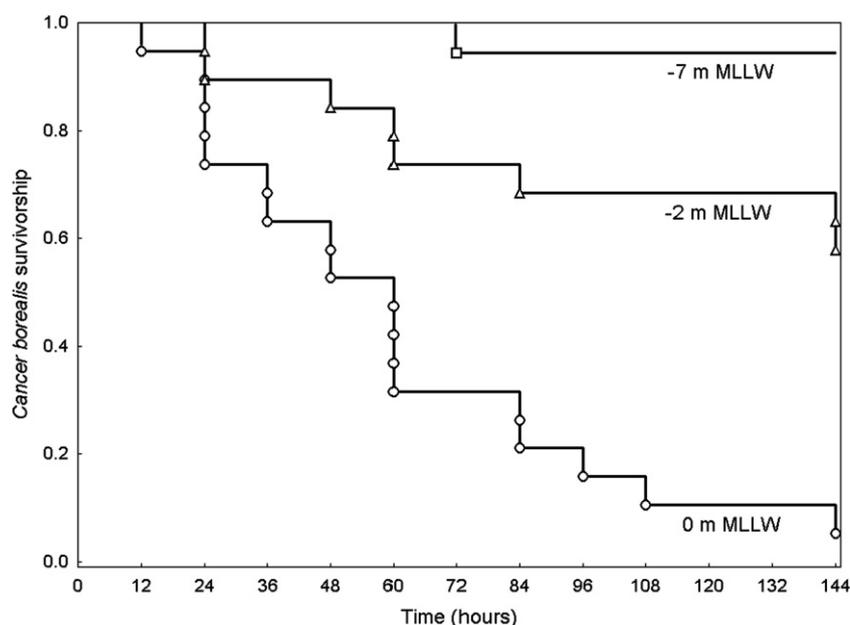


Fig. 2. Survivorship of *C. borealis* at 0 m, -2 m, and -7 m over the six day tethering experiment. Each line represents the proportion of crabs surviving at each depth; each symbol indicates the loss of one crab.

changes in total dry weight and hepatopancreas dry weight for each individual. The hepatopancreas is a storage organ (Fox, 2001) and can be sensitive to changes in condition (J.J. Stachowicz, *personal communication*). Each of 80 crabs was marked with a small tag, measured for initial carapace width, and weighed. To decrease variation in wet weight, water was drained from each crab's gill chambers for 45 min by balancing each crab over a glass on the anterior edge of its carapace (A.R. & R.F. Uglow, *personal communication*). Sixty crabs were randomly selected and assigned to the growth experiment in the field enclosures. The remaining 20 crabs were a random sub-sample of the initial population, which we used to predict initial values of total dry weight and hepatopancreas dry weight for the experimental population using linear regression. The hepatopancreas was dissected out of each crab and dried at 60 °C to constant weight. Total dry weight (TDW) was well-predicted from wet weight (WW) by the regression equation $TDW = 0.3704 WW - 0.6092$ ($R^2 = 0.97$, $p < 0.001$). The relationship between hepatopancreas dry weight (HDW) and carapace width (CW) was described by the regression equation $HDW = 0.0694 CW - 2.6844$ ($R^2 = 0.40$, $p = 0.003$).

Nine crabs were lost during the experiment: one crab escaped at -7 m, three crabs were lost to gull predation at 0 m, and five crabs were lost to apparent thermal stress at 0 m. For the remaining 51 crabs, individual growth rates (IGR) based on total dry weight and on hepatopancreas dry weight were calculated as $IGR = \ln(\text{Final Weight} /$

predicted Initial Weight) and analyzed in separate two-factor (depth, diet), fixed-effect ANOVAs (JMP Statistical Software Version 5.1). For total dry weight only, we excluded the two crabs that molted during the experimental period. To meet the assumptions of homoscedasticity, hepatopancreas growth rate was transformed as $y = \ln(1 - IGR)$; however, the data are plotted as IGR for interpretability. We used Tukey's Honest Significant Difference test for post-hoc comparison of means.

3. Results

3.1. Crab distribution

This and other studies in the Isles of Shoals demonstrate a persistent presence of *C. borealis* in intertidal depths of 0 to -1 m MLLW (Table 1). We found no significant difference in mean *C. borealis* density between depths ($F_{2,27} = 1.66$, $p = 0.2$) with an observed power of 0.32. Previous studies have found increases (3/6), decreases (1/6), and no effect (2/6) of depth on crab density (Table 1).

3.2. Temperature

Daily average temperatures at 0 m and -2 m were similar and approximately 3 °C higher than daily average temperatures at -7 m

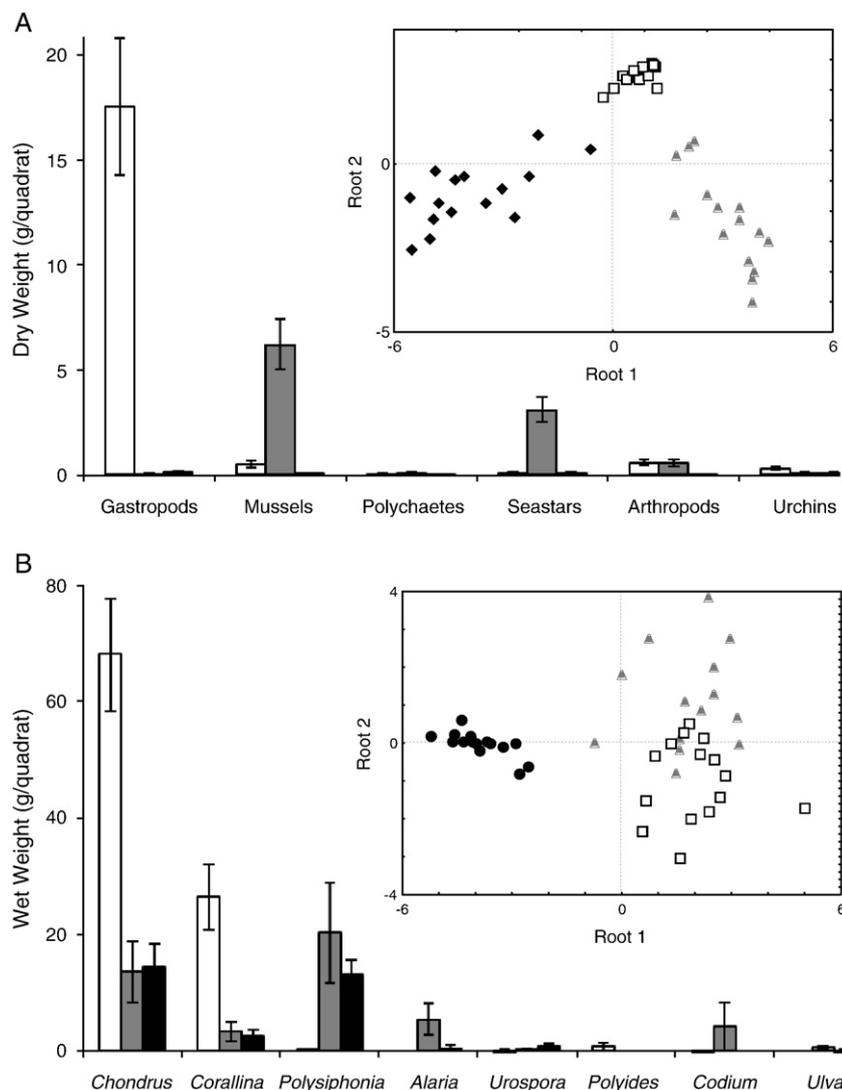


Fig. 3. (A) Dry weight of invertebrates and (B) wet weight of algae in fifteen 20 × 20 cm quadrats at 0 m (open), -2 m (gray), and -7 m (black) MLLW, mean ± standard error. Inset graphs plot the discriminant roots of each quadrat for the (A) invertebrate and (B) algal assemblages. See Table 3 for the eigenvectors that comprise the canonical roots.

Table 3
Standardized discriminant function coefficients for assemblages across depths (Fig. 3A,B).

	Discriminant root 1	Discriminant root 2
(A)		
Eigenvalue	8.932	3.821
Mussels	0.317	-0.619
Seastars	0.396	-0.604
Snails	-0.946	-0.456
Crabs	0.119	-0.706
Urchins	-0.543	-0.22
(B)		
Eigenvalue	7.982	0.756
Chondrus	-0.645	-0.14
Corallina	-1.019	0.15
Polysiphonia	0.976	-0.07
Alaria	0.178	0.75
Urospora	0.493	0.643
Green algae	0.103	0.615

Both roots of the discriminant function contribute to classification. (A) Invertebrate assemblages (root 2 only: $R^2 = 0.79$, $\chi^2_{df=4} = 62.4$, $p < 0.0001$; roots 1 and 2: $R^2 = 0.90$, $\chi^2_{df=10} = 154.8$, $p < 0.0001$). (B) Algal assemblages (root 2 only: $R^2 = 0.43$, $\chi^2_{df=5} = 22.2$, $p = 0.0005$; roots 1 and 2: $R^2 = 0.89$, $\chi^2_{df=12} = 109.0$, $p < 0.0001$).

(Fig. 1A, Table 2). This pattern is consistent throughout the daily tidal cycle, although temperatures rise rapidly at 0 m when aerial exposure occurs during daylight hours (Fig. 1B). The daily temperature fluctuation was largest at -7 m (Table 2). Crabs experienced maximum temperatures at 0 m during aerial exposure (Fig. 1A, Table 2), especially during a week of daytime low tides where daily maximum temperatures at 0 m exceeded 21.5 °C.

3.3. Predation experiment

C. borealis survivorship increased with depth (Fig. 2): at the end of the experiment, 5% of crabs remained at 0 m, 58% of crabs remained at -2 m, and 94% of crabs remained at -7 m. Survivorship was 3.5× higher at -2 m depth than 0 m (Hazard Ratio = 0.29, Wald $\chi^2 = 9.30$, $p = 0.002$) and 10× higher at -7 m than -2 m (Hazard Ratio = 0.10, Wald $\chi^2 = 4.82$, $p = 0.03$). While the -2 m treatment was intended to be below the gull-predation zone, this experiment coincided with a week of extreme daytime low tides (maximum ebb was -0.41 m MLLW) and crabs at -2 m experienced moderate gull predation.

3.4. Food availability

Invertebrate assemblages differed across depth (MANOVA, approx $F_{14,72} = 31.4$, $p < 0.0001$, Fig. 3A). Differences across depth in the biomass of mussels ($F_{2,36} = 5.91$, $p = 0.006$), snails ($F_{2,36} = 80.5$, $p < 0.0001$), seastars ($F_{2,36} = 11.14$, $p = 0.0002$), crabs ($F_{2,36} = 9.09$, $p = 0.0006$), and urchins ($F_{2,36} = 4.4$, $p = 0.019$) contributed to the change in invertebrate assemblage with depth. Using these five taxa in the discriminant function (Table 3A), 43/45 quadrats were correctly classified by depth (Fig. 3A inset). Gastropods were abundant at 0 m, mussels were abundant at -2 m, and there was low invertebrate abundance at -7 m (Fig. 3A, Table 3A).

Algal assemblages also differed across depth (MANOVA, approx $F_{12,74} = 18.3$, $p < 0.0001$, Fig. 3B). Differences across depth in the abundance of *Chondrus* ($F_{2,37} = 6.5$, $p = 0.003$), *Corallina* ($F_{2,37} = 22.0$, $p < 0.0001$), *Polysiphonia* ($F_{2,37} = 19.1$, $p < 0.0001$), *Alaria* ($F_{2,37} = 5.67$, $p = 0.007$), *Urospora* ($F_{2,37} = 7.3$, $p = 0.002$) and green algae ($F_{2,37} = 3.46$, $p = 0.04$) contributed to the changes in algal community with depth. Using these six taxa in the discriminant function (Table 3B), 38/45 quadrats were correctly classified by depth (Fig. 3B inset). *Chondrus* and *Corallina* were most abundant at 0 m, *Polysiphonia* was most abundant at -2 m, and overall algal abundance was lower at -7 m (Fig. 3B, Table 3B).

3.5. Growth experiment

Overall, crabs at -2 m gained weight under both food treatments, but crabs at -7 m crabs gained weight under the standardized diet and lost weight under the ambient diet (Fig. 4A,B). At 0 m, crabs lost weight or did not grow under both food treatments; this is likely due to thermal stress during a week of daytime low tides when air temperatures reached 26 °C, resulting in the deaths of five crabs caged at 0 m.

3.5.1. Hepatopancreas-based growth rates (HGR)

HGR was higher in the standardized diet (diet: $F_{1,45} = 34.5$; $p < 0.0001$) and varied with depth (depth: $F_{2,45} = 9.83$; $p = 0.0005$), and there was an interaction between diet and depth (diet × depth: $F_{2,45} = 9.33$; $p = 0.0004$; Fig. 4A). Under the standardized diet, crabs grew similarly at -2 m (60%) and -7 m (67%) over the 35 day experiment, but there was no growth at 0 m (Fig. 4A). Under the ambient diet, hepatopancreas weights increased at -2 m (27%), decreased at -7 m (47%), and remained the same at 0 m (Fig. 4A).

3.5.2. Total dry weight-based growth rates (WGR)

WGR was marginally higher under the standardized diet (diet: $F_{1,43} = 3.93$, $p = 0.054$) and varied with depth (depth: $F_{2,43} = 8.77$; $p = 0.0006$). There was a marginally significant interaction between depth and diet (diet × depth: $F_{2,43} = 2.81$; $p = 0.071$): growth rate at -7 m strongly depended on food treatment (Fig. 4B). Under the standardized diet, total dry weight decreased at 0 m (-6%) but increased at -2 m (10%) and -7 m (12%) (Fig. 4B). Under the ambient diet, total dry weight increased at -2 m (10%) and decreased at -7 m (-5%) and 0 m (-10%).

4. Discussion

Predation risk decreased from the intertidal into the subtidal (Fig. 2), consistent with observations of high gull predation in shallow

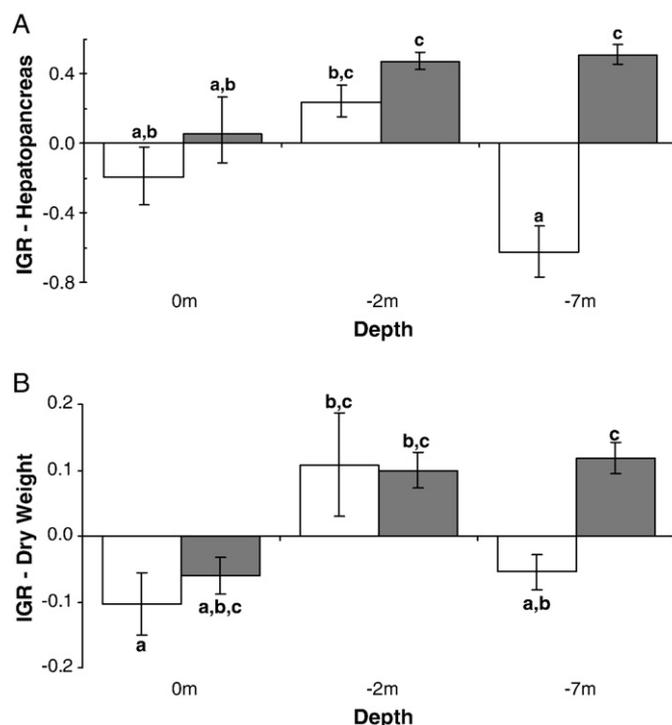


Fig. 4. Individual growth rate based on (A) hepatopancreas dry weight and (B) total dry weight in response to ambient food treatment (white bars) or standardized food treatment (grey bars) at 0 m, -2 m, and -7 m MLLW. Error bars are ± 1 standard error and letters indicate homogeneous groups based on post-hoc Tukey's HSD tests.

water (Ellis et al., 2005; Ellis et al., 2007; Good, 1992). Contrary to expectation, -2 m was not an absolute refuge from gull predation, although crabs at -2 m had $3.5\times$ higher survivorship than crabs at 0 m. The unusual diurnal foraging habits of *C. borealis* (Novak, 2004) may make this species more vulnerable to predation by gulls.

We found no evidence that *C. borealis* forages in shallow water to take advantage of increased temperatures and, thereby, increased growth rates. Despite consistently 3 °C warmer temperatures at -2 m than at -7 m (Fig. 1, Table 2), crabs fed the same diet at -2 m and -7 m grew similarly (Fig. 4). Despite similar mean temperatures at 0 m and -2 m (Fig. 1, Table 2), crabs fed the same diet at 0 m grew more slowly than those at -2 m (Fig. 4). This difference in growth is likely due to thermal stress during a week of daytime low tides (shaded region of Fig. 1A,B). Five caged crabs died at 0 m from apparent thermal stress during this period, despite shading the cages with *Ascophyllum nodosum* (which reduce mortality for caged *C. borealis* in Menge, 1983). Growth rates at 0 m were similarly depressed in both food treatments, indicating that thermal stress, rather than food availability, suppressed growth. Although thermal stress could be disregarded as a cage effect, Ellis et al. (2007) also found evidence of thermal stress in unmanipulated *C. borealis* foraging in their gull exclusion treatment: 5% of *C. borealis* foraging above the water line died during a period of daytime low tides. Taken together, these results indicate that 0 m has higher mortality risk than -2 m due to both higher predation and higher thermal stress. Overall, our study does not indicate an advantage of increased temperature on crab growth; rather, it indicates a risk of thermal stress from aerial exposure during daytime low tides.

C. borealis may forage in the gull-predation zone in order to exploit the greater food resources at 0 m and -2 m despite higher predation risk, i.e., a growth-mortality trade-off. There are clear changes in prey availability with depth (Fig. 3A,B). At 0 m, *L. littorea* is the primary food source for *C. borealis* (Fig. 3A). *L. littorea* was preferred (over *L. obtusata*, *M. edulis*, amphipods, and isopods) by *C. borealis* in a lab choice experiment (Donahue et al., 2009) and *C. borealis* has been noted as an important predator of *L. littorea* in previous studies (Menge, 1983; Perez et al., 2009). At -2 m, *M. edulis* is the primary prey available to *C. borealis* (Fig. 3A). Mussels are an important component of *C. borealis* gut contents ($>60\%$, Donahue et al., 2009, 35%, Ojeda and Dearborn, 1991), but mussel availability can be highly episodic (Witman et al., 2003). In summer 2005, newly recruited mussels were abundant at -2 m in mid-June but had declined noticeably by August (personal observation). At -7 m, none of the prey commonly found in *C. borealis* gut contents (gastropods, bivalves, and polychaetes: Ojeda and Dearborn, 1991; Steneck et al., 2004) were abundant (Fig. 3A,B). The growth experiment indicates that crabs at -7 m are food limited (Fig. 4): crabs at -7 m lost weight on the ambient diet but gained weight on the standardized diet, while crabs at 0 m and -2 m grew similarly on both diets. Although growth rates of caged crabs at 0 m were lower than -2 m, uncaged crabs that successfully retreat with the ebbing tide would likely benefit from the abundant prey at 0 m without suffering growth impairment due to thermal stress.

Optimal foraging theory suggests a “minimize mortality to energy ratio” rule for growth-mortality trade-offs (e.g., Gilliam, 1987). There are clear trade-offs in this landscape: -7 m is a classic refuge with low predation risk but low resource availability, while -2 m and 0 m are rich but increasingly risky habitats. Based on our estimates of mortality rate (Fig. 2) and assuming the “minimize mortality:energy” rule, the energy payoff must be $11\times$ greater at -2 m compared to -7 m to move out of the -7 m refuge. While this study does not provide direct comparisons of the energy payoffs of foraging at each depth, the ambient-diet growth rates and prey densities at -7 m were so low compared to -2 m that this is a viable explanation for movement into shallower waters. More interestingly, the energy payoff must be just $1.6\times$ higher at 0 m than at -2 m to justify the risk

of foraging in the gull-predation zone ($1.7\times$ higher if we include an additional 5% mortality from thermal stress at 0 m, Ellis et al., 2007). While an energetic analysis of available prey and handling times at 0 m and -2 m would be necessary to test this hypothesis, it is likely that patches of high snail abundance at 0 m exist where this threshold is exceeded.

Despite low resource availability at -7 m, densities of *C. borealis* are often similar to shallower depths (Table 1). This is not surprising. Growth-mortality trade-offs often result in a flat fitness surface (Mangel and Stamps, 2001) where a range of habitat choices are equivalent; i.e., the net fitness effects of foraging at -7 m (low predation risk and low resource abundance) and shallower depths (high predation risk and high resource abundance) are similar. The presence of not only abundant but also preferred prey of *C. borealis* at 0 m and -2 m supports a growth-mortality trade-off model: enhanced prey availability allows for increased growth rates, which compensate for the increased mortality risks.

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