

Testing rates of planktonic versus benthic predation in the field

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Predation is a major source of mortality for the eggs, embryos, and larvae of marine invertebrates. Many studies have measured rates of predation on the developmental stages of marine invertebrates in the lab, but few studies have estimated predation rates in the field. Field studies of predation on developmental stages have generally been limited to organisms in a single environment, with few comparisons of equivalent prey items between habitats. These limitations have prevented comparisons of the relative risks of development in planktonic and benthic habitats. To determine the relative risks of predation for free-living eggs, embryos, and larvae, we measured loss rates for agarose baits flavored with the eggs of two species of marine invertebrates on separate coasts of the United States. First, we deployed agarose baits flavored with eggs of the sand dollar, *Echinocardium* (Eschscholtz), in planktonic and benthic habitats in Parks Bay, Shaw Island, Washington. We subsequently deployed agarose baits flavored with eggs of the sipunculan *Parapionosoma* (Fisher), in planktonic and benthic habitats in Ewin Narrows, Harpswell, Maine. In addition, we measured loss rates of live, tethered megalopae of the Dungeness crab, *Cancer magister* (Dana) in Washington. For both agarose baits and tethered megalopae, loss rates were highest in benthic habitats. Loss rates of agarose baits flavored with sand

different habitats are correlated with changes in developmental trajectories. For example, [Werner \(1988\)](#) argued that the size at which organisms should switch habitats could be predicted from the ratio of growth rates to mortality rates in the potential habitats. Many models of marine invertebrate life-history evolution make use of estimates of planktonic mortality rates as important parameters (e.g. [Vance, 1973](#); [Christiansen and Fenchel, 1979](#); [McEdward, 1997](#); [Levitan, 2000](#)). However, they often neglect to discuss the possible implications of high benthic mortality rates for larvae, settling juveniles, or recent metamorphs (but see [Pechenik, 1979](#) and [Havenhand, 1993](#)). As a result, these models do not consider the potential costs or benefits of unencapsulated benthic development as an alternative to planktonic larval development. Without accurate estimates of relative mortality rates for offspring developing in benthic versus planktonic habitats, it is difficult to predict the life-history strategies that will be evolutionarily favorable.

To our knowledge, no field data currently exist com-

Ewin Narrows and occur at densities of $37.6 \pm 9.5 \text{ m}^{-2}$
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direct contact with the benthos but were occasionally disturbed by strong currents in which case they were lifted off of the benthos for brief periods. Baits deployed in the plankton were attached to the weight/float assembly in a similar manner, with the fishing swivel affixed ~3 m above the concrete weight. During the summer of 2002, a single bait was attached to each

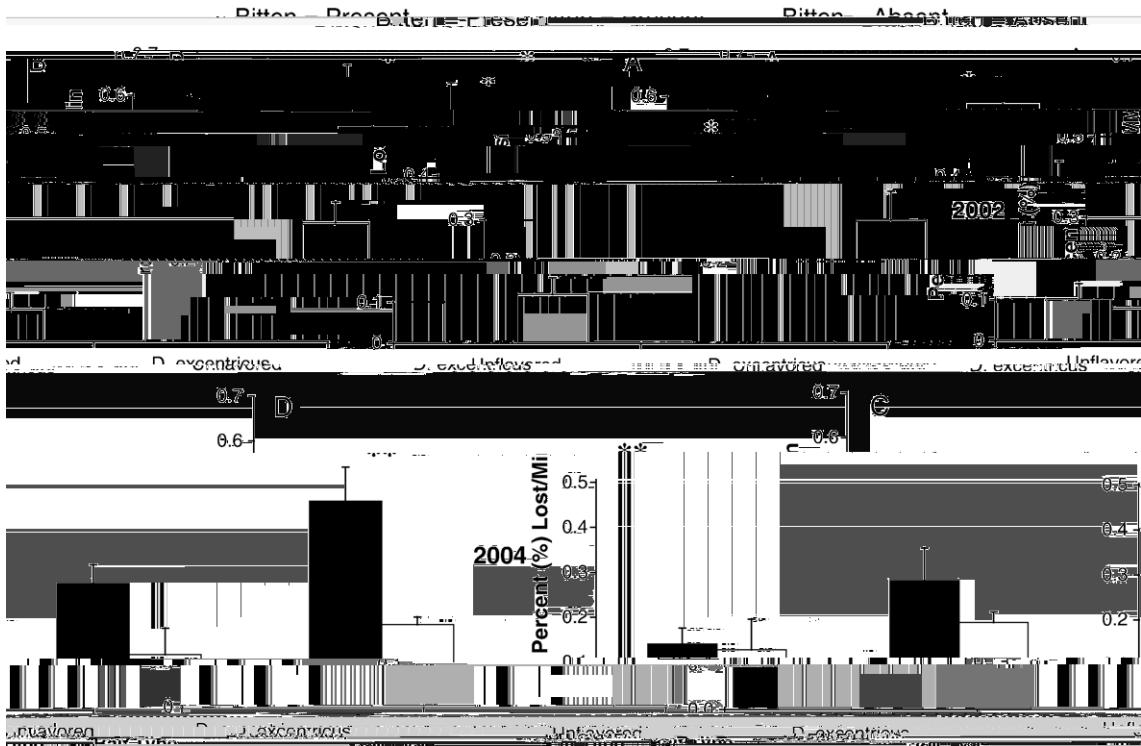


Fig. 2. Percent loss per minute (mean ± SE) of unflavored and flavored agarose baits. Black bars represent benthic baits and white bars represent planktonic baits. Data in (A) and (B) are from 2002. Data in (C) and (D) are from 2004. Bitten baits are scored as present in (A) and (C). Bitten baits scored as absent in (B) and (D). Indicates $p < 0.05$; indicates $p < 0.001$ for contrast tests on the effect of habitat.

data collected in 2002, when bitten baits were scored as present, the logistic regression indicated that there was a significant effect of bait type but not of date, habitat, or the interaction between bait and habitat on loss rates (Table 1A). The bait by habitat contrasts conducted as part of the logistic regression analysis indicate that there was a significantly greater loss of *P. ginsengensis*-flavored baits in benthic habitats than planktonic habitats (Wald Chi-Square=7.039; $p = 0.008$). However, there was no significant difference in loss rates of unflavored baits between the plankton and the benthos (Wald Chi-Square=0.984; $p = 0.321$). In addition, *P. ginsengensis*-flavored baits were more likely to be consumed than unflavored baits in both benthic (Wald Chi-Square=12.211; $p < 0.001$) and planktonic (Wald Chi-Square=5.177; $p = 0.023$) habitats. When the data from 2002 were analyzed with bitten baits scored as absent, the logistic regression indicated that there was a significant effect of date, bait type, and habitat but no significant bait by habitat interaction (Table 1B). The bait by habitat contrast tests showed that *P. ginsengensis*-flavored baits were consumed at significantly higher rates on the benthos than in the plankton (Wald Chi-Square=9.699; $p = 0.002$). Unflavored baits also were consumed at significantly higher

rates on the benthos than in the plankton (Wald Chi-Square=6.609; $p = 0.010$). *P. ginsengensis*-flavored baits were no more likely to be consumed than unflavored

Table 1
Results of logistic regression for loss rates of unflavored and *P. ginsengensis*-flavored agarose baits deployed in 2002 and 2004

Year	Effect	DF	Wald Chi-Square	p
A) 2002	Date	3	7.426	0.059
	Bait	1	14.686	<0.001
	Habitat	1	3.728	0.053
	Bait habitat	1	0.009	0.921
B) 2002	Date	3	7.942	0.047
	Bait	1	7.987	0.00
	Habitat	1	14.235	<0.001
	Bait habitat	1	0.425	0.515
C) 2004	Date	8	7.617	0.472
	Bait	1	7.594	0.00
	Habitat	1	0.055	0.815
	Bait habitat	1	5.150	0.023
D) 2004	Date	8	9.892	0.273
	Bait	1	6.153	0.013
	Habitat	1	19.329	<0.001
	Bait habitat	1	3.998	0.04

In separate analyses bitten baits were scored as present (A, C) or bitten baits were scored as absent (B, D). Significant effects ($p < 0.05$) are in bold.

baits in benthic habitats (Wald Chi-Square=3.297; $p=0.069$) but were more likely to be consumed in planktonic habitats (Wald Chi-Square=4.765; $p=0.029$).

Data from experiments in 2004 yielded qualitatively similar results to those collected in 2002 (Fig. 2C–D). When bitten baits were scored as present, there were significant effects of bait type and bait by habitat interaction, but not of date or habitat on loss rates (Table 1C). Contrast analysis of the bait by habitat interaction indicated that while flavored baits were consumed at a higher rate on the benthos than in the plankton, this difference was only marginally significant (Wald Chi-Square=3.669; $p=0.056$). Unflavored baits showed no significant difference in loss rate in benthic versus planktonic habitats (Wald Chi-Square=1.809; $p=0.179$). Flavored baits were consumed at significantly higher rates than unflavored baits on the benthos (Wald Chi-Square=12.190; $p<0.001$) but there was no differ-

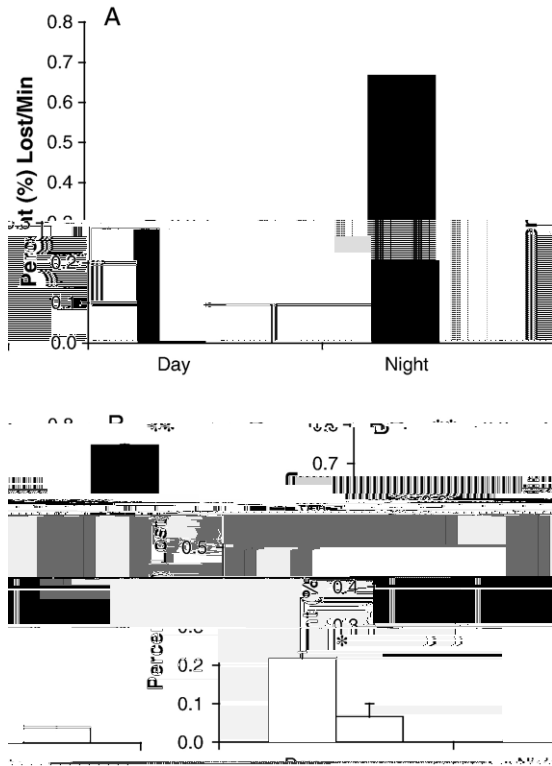


Fig. 4. Percent loss per minute (mean±SE) of tethered C megalopae. Black bars represent benthic baits and white bars represent planktonic baits. Data in (A) are from 2002 and data in (B) are from 2004. *Indicates $p < 0.05$; ** $p < 0.001$ for contrast tests on the effect of habitat.

plankton (Fig. 4). For a single day–night comparison in 2002, megalopae tethered on the benthos suffered loss rates of 0.29%/min during the day and 0.67%/min at night. In contrast, megalopae tethered in the plankton suffered lower rates of predation both during the day (0.10%/min) and at night (0%/min; Fig. 4A). There were, however, no significant effects of time, habitat or time by habitat interaction on loss rates (Table 3A). Contrast test results for habitat yielded no significant differences between benthic and planktonic loss rates either during the day (Wald Chi-Square=1.148; $p = 0.284$) or at night (Wald Chi-Square=0.001; $p = 0.971$). Contrast tests for time showed no significant difference between planktonic loss rates during the day and at night (Wald Chi-Square<0.001; $p = 0.977$), but there were significantly higher loss rates on the benthos at night than during the day (Wald Chi-Square=4.531; $p = 0.033$).

Experiments using tethered megalopae over three days and two nights in 2004 also resulted in higher loss rates in benthic habitats (Fig. 3B). Megalopae tethered on the benthos suffered loss rates during the day of

0.22%/min and 0.75%/min at night. In contrast, megalopae tethered in the plankton suffered loss rates of 0.07%/min during the day and 0.04%/min at night. There were significant effects of time, habitat, and the time by habitat interaction but not of date on the rates of loss for tethered megalopae (Table 3B). Megalopae tethered on the benthos had significantly higher loss rates than those tethered in the plankton both during the day (Wald Chi-Square=9.370; $p = 0.002$) and at night (Wald Chi-Square=51.103; $p < 0.001$). Benthic megalopae also suffered significantly greater loss rates at night than during the day (Wald Chi-Square=35.772; $p < 0.001$), however there was no significant difference between day and night loss rates for planktonic megalopae (Wald Chi-Square=0.016; $p = 0.899$).

3.3.

Estimates of survival (S) were calculated and used to produce rates of mortality ($-\ln(S)/t$) per day for all of the baits used in this study (Table 4). Baits that were present or had suffered partial predation were scored as “surviving” baits, whereas baits that were lost completely were counted as “dead”. A review by Rumrill (1990) gives S values for planktonic freely developing larvae and benthic protected larvae, which we averaged within each developmental mode to produce values of 0.247 and 0.027, respectively. The present study contributes values to two developmental categories, planktonic freely developing and benthic freely developing. Two additional studies of predation on larvae in the field provide measures of extreme mortality rates (both high and low), which we include for comparison. First, a study by Olson and McPherson (1987) provides an estimate of an extremely high mortality rate due to fish predation for ascidian larval tadpoles of *Ascidia* (Gottschaldt) that were followed in the field. Their value of 0.407 s^{-1} , was converted to a per diem value and is included in Table 4.

Table 3 Results of logistic regression for day–night deployments of tethered megalopae in 2002 (A) and in 2004 (B)

Effect	DF	Wald Chi-Square	
(A) Time	1	<0.001	0.982
Habitat	1	0.002	0.968
Time habitat	1	0.001	0.973
(B) Date	2	2.7797	0.249
Time	1	13.272	<0.001
Habitat	1	57.333	<0.001
Time habitat	1	16.138	<0.001

Significant effects ($p < 0.05$) are in bold.

measuring predation on adult brine shrimp on coral reefs also found that predation was relatively much higher on the benthos compared to habitats 1.5 to 6.0 m above the seafloor (Motro et al., 2005). While none of these studies (nor the current study), provide measures of absolute rates of predation, all of them suggest that predation rates on small zooplankton (whether larval or adult stages) are relatively much higher on the benthos.

In the current study, by analyzing bitten baits in two different ways (as either present or absent), we were able to show that the high rates of loss on the benthos were due to actual predation events and were not an artifact related to tethering on a complex substrate (the seafloor). For example, baits were not simply being dislodged by eel grass or kelp blades upon retrieval from the benthos. For data collected in Parks Bay, when unflavored baits, which were intended as controls, were analyzed with bitten baits scored as being present, there was no significant effect of habitat on loss rates. In contrast, when this same data set was analyzed with bitten baits scored as being absent, loss rates on the benthos increased and there was a significant effect of habitat (Table 1). Because bitten baits showed direct evidence of predation events (i.e. clear bite marks present on the remaining bait), we attribute the high levels of loss on the benthos directly to predation events and not

megalopal stage of this species makes consistent migrations up into surface waters at night (Shanks, 1986; Hobbs and Botsford, 1992) as well as in the early morning (Park and Shirley, 2005). For megalopae that are not tethered to the benthos, such a behavioral change may reduce the susceptibility of megalopae to benthic predators during the night as has been shown for the larvae of spiny lobsters (Acosta and Butler, 1999).

4.3. *Implications for larval mortality*

With few exceptions, previous studies of larval mortality have compared predation rates on free-swimming planktonic larvae with rates of loss for brooded or encapsulated embryos developing on the benthos (Rumrill, 1990; Morgan, 1995). Loss rates for benthic developing embryos may be greatly reduced by the addition of protective structures, placement in sheltered sites, or other

