# Crab on a stick: assessing spatial variation in predator community and predation rate using tethered megalopae and underwater video

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## Abstract

Planktonic larval development, common in many benthic marine invertebrates, is associated with both costs and benefits relative to benthic larval development. Costs of being in the plankton include increased susceptibility to advection away from habitat and starvation. Potential benefits include reduction in predation for pelagic larvae. Few studies have measured predation rates on larvae in the field. Even fewer have directly observed larval predation events, documented the specific predator, mode of predation, and intervals between predator attacks. In this study we investigated benthic and pelagic differences in predator assemblage and predation interval on megalopae of the Dungeness crab, *Metacarcinus magister.* To observe the predation events, we combined methods of tethering larvae with automated motion analysis of underwater camera images from daytime deployments off the dock at Friday Harbor Laboratories, Friday Harbor, WA. We measured number of predation events, the interval in which those events happened, the species of predator, and of other non-predator species that comprised each visible community. Predation was higher on the benthos than the surface, with more total strikes and a shorter interval to predation. Only one predator species was seen during the trials, *Artedius harringtoni*. These results are consistent with previous studies, and support the novel combination of methods to better inform predation interactions of communities and their relative importance on each species.

## Introduction

Larval development in the plankton is common amongst benthic marine invertebrates (Marshall et al. 2012). Having a planktonic life stage incurs new risks compared to an entire life cycle in the benthos; these risks include advection away from habitat, starvation before metamorphosis, and predation on larvae as they transition to a pelagic habitat. Conversely, a planktonic stage can also provide additional benefits in the forms of escape from predation, additional food, and dispersal (Strathmann et al. 2002). Although a planktonic stage has been hypothesized to reduce predation on larvae, absolute mortality rates can still be substantial during the larval stage, which have major implications for the rates of juvenile recruitment back to the benthic environment (Strathmann 1985, Morgan 1995).

Reviews of both field and laboratory studies demonstrated predation on larvae to be a potentially significant source of mortality (Morgan, 1995; Allen and Vaughn, 2010). Estimates of larval mortality due to predation in the field have ranged from 0-100% (Rumrill, 1990; Johnson and Shanks, 2003; Allen and McAllister, 2007). Possible explanations include differences between species; differences in methods of measuring predation rates; and differences in geography, seasonality, and other spatiotemporal factors. Another possible explanation for large variance in predation rates could be that predation varies spatially over very short length scale, i.e/e.g. across water column depth and shallow subtidal environments. Predation can be substantially higher in near shore environments compared to offshore habitats (Morgan, 1990), and in another study, predation rates in tethered megalopae were shown to differ significantly between the benthos and the water column (Allen and McAllister 2007).

A lack of direct methods for observing larval predation has been an obstacle for previous studies. Methods, such as tracking a known amount of larvae, monitoring a volume of water over time (Johnson and Shanks, 2003), and quantifying the loss of tethered larval prey (Allen and McAllister, 2007; D'Alessandro and Sponaugle, 2011; Kerr et al. 2014) can provide invaluable estimates of predation rates. However, these studies do not establish exactly when a predation event occurs and therefore, are unable to resolve a precise attack interval on prey items. Indirect methods quantify predation loss after a set amount of time, overestimating the interval to a predation event, resulting in an underestimate of predation rate. If the attack interval is known, predation rates can be more accurate.

The other issue these methods have is discerning the predator assemblage for the study area. Predator assemblages can be inferred from environmental surveys (Kerr et al. 2014) or from attaching hooks to tethered larvae (Fernandez et al. 1993). But surveys might miss uncommon predators, and not all predators can be captured by hooks. Alternatively, stable isotope or gut analysis of potential predators could assess the predator assemblage, but attack interval cannot be found and choice of focal predators can bias the results.

In this study, we investigated spatial variation in the predator assemblages and the predation interval on megalopae of the Dungeness crab, *Metacarcinus magister* (Dana, 1852). To determine the species assemblage and predation interval at both the benthic and planktonic level, we used tethering methods in conjunction with a novel underwater camera housing that enabled direct observation of predation on the megalopae. Based on Allen and McAllister (2007), we predicted that attack interval would be quicker on the benthos compared to the plankton. We also predicted that the species assemblage would differ between the benthos and the plankton.

## Methods

To examine the predator community of *M. magister* megalopae, we tethered megalopae in close proximity to underwater camera housings and documented predation events over 2 hour intervals, during daylight from 30 July 2014 to 3 August 2014. We also recorded predator assemblage differences between the benthos and the surface.

### Study site

We conducted our study off the docks at Friday Harbor Laboratories, Friday Harbor, WA (N 48° 32' 46" N, W 123° 0' 46"). This dock is protected by a floating breakwater, but boat traffic causes wakes to the floating dock. Pier pilings are spaced on either side roughly 3.3m apart from shore to sea and roughly 5m apart perpendicular to shore. The benthic deployment site is a soft sediment bottom with patchy kelp as well as debris algae and eelgrass transported by tidal exchanges. The depth to the benthos is 2.13m when tide is at 0m MLLW.

### Camera housing

We used a 4.50m x 5.08cm and a 1.80m x 5.08cm PVC tube for the benthic and surface camera housings respectively. With PVC cement and silicone sealant, we glued one end of each PVC tube to half of a coupler and an L-shaped elbow to the other half of the coupler and screwed the couplers together to create a watertight seal. 78.0mm x 80.0mm x 5.0mm pieces of acrylic plastic were glued to the open ends of the L-shaped elbows using epoxy. A 5.83kg weight was tied to the 4.5m housing, and an 8.5kg weight was used for the 1.8m housing, to provide negative buoyancy and stabilization of the camera and the prey.

### Camera

We used modified web cameras (Logitech QuickCam Pro 9000) for the experiment, which slid into the PVC housing until they reached the elbow, facing out of the acrylic window. The camera was modified by altering the focal distance to be approximately 5cm. The cameras were powered by a laptop connected with USB extension cables to reach out of the PVC tubes. iSentry and iCamSource, the applications we used, were designed to capture pictures from the external webcams when motion was detected in the field of view. Both applications were set to the highest sensitivity setting and recorded images at 5 frames per second (fps) when triggered. The pictures from each deployment were then assembled into a movie using Time Lapse Assembler. We used the movies to note when the first predation events occurred and identified all the animals that approached the megalopae. For the purposes of this study, we defined a predation event is as an attempt by a predator to consume the megalopa, whether or not the attack was successful.

In order to steady the cameras within the housings, we attached them to separate 2x4 blocks of wood using U-Bolts. The 2x4x12 wood block for the benthic camera housing was nailed to pilings that were attached to the substrate, while the 2x4x6 wood block for the surface camera housing was nailed to the floating dock. This allowed the benthic camera to remain near the bottom and the surface camera to always be 1.05m below the water line even as the tides fluctuated.

**Tethering megalopae**

Megalopae were collected off the Friday Harbor Laboratories docks at night using a nightlight and glass jars. The tethers consisted of a 4cm length of 0.85mm diameter fishing line with a 1cm Nitex thread superglued, to it, adjusted to place the megalopa within the focal plane and the field of view. The fishing line provided rigidity to the tether, allowing the megalopae to stay within the field of view of the cameras, while the Nitex thread was flexible enough to allow the megalopae some movement. Before tethering, we measured the carapace length of the megalopae here defined as from the eye to the start of the abdomen to the nearest 0.5mm. We superglued the megalopae onto the Nitex thread and attached the tether to the acrylic using binder clips.

### Capturing footage

Housings with tethered megalopae were placed into the water for 2 hours, consistent with the sampling intervals of Allen & McAllister (2007). Megalopae were replaced, even if not consumed before the beginning of the next trial. Trials started at approximately 8am and ended at approximately 9pm each day, when light levels became too low for photography.

### Control

As a positive control, we crushed 17 recently molted *M. magister* juveniles, released them under the docks, and tracked their trajectories until they were either advected out of view or consumed by a predator. If predation by surface predators is typically high, but these predators were deterred by the presence of the camera housings, freely floating crushed *M. magister* should still be consumed. All of the *M. magister* sank out of sight without any predation event by potential predators.

## Results

Out of the 19 trials on the benthos, 8 predation events occurred all with *Artedius harringtoni* as the predator. In contrast, none of the tethered megalopae were attacked near the surface (Figure 1). Using a binomial logistic regression, there is a significant difference between the proportion of predation events between surface and benthos ($X^2 = 12.781$, $p = 0.0003$).

Because we did not observe predation events on the surface, we are unable to compare the predation intervals, defined here as the time from the introduction of the megalopa until it was attacked, across treatment levels. However, we calculated upper and lower bounds for attack rates in both the benthic and surface treatments (Table 1) If a megalopa was attacked on the benthos, the predation interval averaged 50.11 minutes +/- 21.79 minutes (Table 1).

Our cameras also allowed us to identify other in the field. With the exception of one ctenophore (*Pleurobrachia* sp.) found on the surface, all of the other potential predators were observed near the benthos (Table 2). *A. harringtoni* and *Hexagrammos* spp. were the most common fish recorded, but several crustaceans, such as cancrid crabs and *Pugettia* sp., were also observed. Since we observed multiple individuals of the same species in one trial, it is possible that the animals we documented were not independent of each other. The lack of independence would violate statistical assumptions needed to determine if certain organisms were more common than others.

## Discussion

Our results support the findings of Allen and McAllister (2007) that predation of *M. magister* megalopae is significantly higher in the benthos compared to the surface. Our estimate of the percent of megalopae lost per minute, 0.35%, at the benthos was consistent with the findings of Allen and McAllister (2007), 0.29%. Both study suggest that, for megalopae and possible other similarly large and well-protected larvae, benthic predation in multiple sites is significantly higher than at the surface. The absence of predation at the surface also corresponds to the low predation in the plankton observed by Johnson and Shanks (2003). A limitation of our method came from the surface camera being fixed onto a floating dock allowing for disturbances from people being on the dock to potentially scare predators away. The results of our positive control hint that predation is still low on the surface even without a camera housing. Tethering megalopae may lead to an overestimate of predation rates because it precludes effective responses from predators. Similarly, a tethered megalopa could have a lower encounter rate with predators since it has relatively low motion with respect to the water and benthos compared to its normal swimming speed of 4.2cm/s (Jacoby 1982). Since 100% of the predation events involved *Artedius harringtoni* (Table 1), we concluded that it is the primary predator of megalopae at this site during the day.

**Potential predator assemblage**

In addition to identifying the predator species on the megalopae, the camera allowed us to observe other organisms in the different habitats. Data from the surface camera showed that potential predators were not abundant near the top of the water column. This supports our control where crushed *M. magister* deployed near the surface did not elicit any predation events despite the absence of a camera housing.

The benthic camera, however, recorded several other species of fish and crustaceans that could have been potential predators of megalopae. Various species of crabs and fish came into close contact with the megalopae, perhaps attracted by the L-shaped elbow which resembled a potential shelter, but made no attempts to consume the megalopae. While it would be unreasonable to conclude that these species do not consume megalopae, their relatively frequent occurrence on the benthos and the fact that only *Artedius harringtoni* preyed on megalopae imply that these other species might not be major predators of megalopae. Our observation contrasts with other studies, in which cannibalism from juvenile crabs was a significant source of mortality (Fernandez et al. 1993; Moksnes et al. 1997). Interestingly, Fernandez et al. (1993) also found that another species of sculpin, *Leptocottus armatus*, was the only predator in their tethering experiments using *M. magister* megalopae at Gray Harbor estuary near the southern Washington coast. This suggests that this group of fishes is an important, perhaps the most important, factor determining the relative cost of the benthic environment as habitat for larval development. In sites that lack sculpins a follow up study is needed to investigate whether other types of predators assume the role of larval predators or whether those habitats are favorable for larval development.

The conventional explanation for vertical migration rests upon the supposition that predation risk for zooplankton is highest during the day (Lampert 1989). While we do not have data on predation rates and intervals for night, we are still able to conclude that, under the limitations of our experimental approach, the benthos appears to be more dangerous for megalopae during the day than the surface. It is possible that other explanations for vertical migration, such as aversion to UV light and reducing metabolism during the day, are driving the movement of zooplankton.

Kerr et al. (2014) proposed another explanation for their observed lack of reduction in predation between day and night. Although large zooplankton may face substantial predation risk in the water column during the day, predation risk could actually increase at night since nocturnal planktivorous fish target larger prey items (Holzman and Genin 2003). Kerr et al. (2014) noticed a shift in predation risk when *Artemia franciscana* grew into adults of 3.7mm in length. The megalopae we used had carapace width between 4 and 5 mm, so it is plausible that they face similar predation risks as adult *A. franciscana*. This explanation of similar nighttime predation to daytime predation for large zooplankton does not explain the lack of predation events near the surface for our megalopae.

The results from this study support the idea proposed by Strathmann et al. (2002) that the planktonic stage is an adaptation for larvae to escape predation from the benthos since we observed a significant reduction in predation in the water column. Identifying the components of mortality and how they change spatially can be important for this commercially valuable species.

Further observations of predation on megalopae at night, with infrared lighting, are needed to fully understand how predation rates differ between surface and the benthos. Additional studies at sites outside of the Friday Harbor Lab dock would aid in expanding the scope of the study and better the understanding of surface predation rates.

With the use of this novel combination of methods, we were able to support previous findings who found low predation rates on the surface (Johnson and Shanks, 2003) and increased predation rates on the benthos (Allen and McAllister 2007), determine predator assemblage, as well as attain more precise estimates of predation intervals on megalopae. By directly observing predation events with underwater camera housings, we were able to obtain accurate estimates of predation intervals and document a predator assemblage. Better estimates of predation intervals allowed us to calculate improved predation rates, which have implications for population dynamics. Recognizing the major predators on larvae refines our understanding of larval food web ecology.

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Table 1. Table presenting the number of predation events, the predator species for each event, the predation interval, the % loss per minute for the two different depths, and the 95% confidence interval for attack rate.

| Depth | Number of predation events | Predator species | Predation Interval (minutes) | % Loss per Minute | 95% Confidence Interval for Attack Rate (# of attacks per second) |
|---|---|---|---|---|---|
| Surface | 0 | N/A | N/A | 0 | 0 to 1.7e-5 |
| Predation | 8 | *Artedius harringtoni* | 50.11 +/- 21.79 | 0.034231921 | 3.3e-5 to 1.4e-4 |

Table 2. A list of organisms found within the field of view of the camera during a trial that did not consume a megalopa. An observation is defined when an organisms enters the field of view until it leaves.

| Species observed near the benthos | Number of observations |
|---|---|
| *Hexagrammos stelleri* | 4 |
| *Hexagrammos* sp. | 6 |
| *Artedius harringtoni* | 11 |
| *Chirolophis* sp. | 4 |
| *Pholis laeta* | 4 |
| *Embiotoca lateralis* | 3 |
| *Pugettia* sp. | 1 |
| Embiotocidae | 4 |
| Cancridae | 4 |
| Shrimp | 4 |
| *Pleurobrachia* sp. (surface) | 1 |

Figure 1. The proportion of predation events between megalopae tethered to the benthos and those tethered near the surface ($X^2$ = 12.781, p = 0.0003523)

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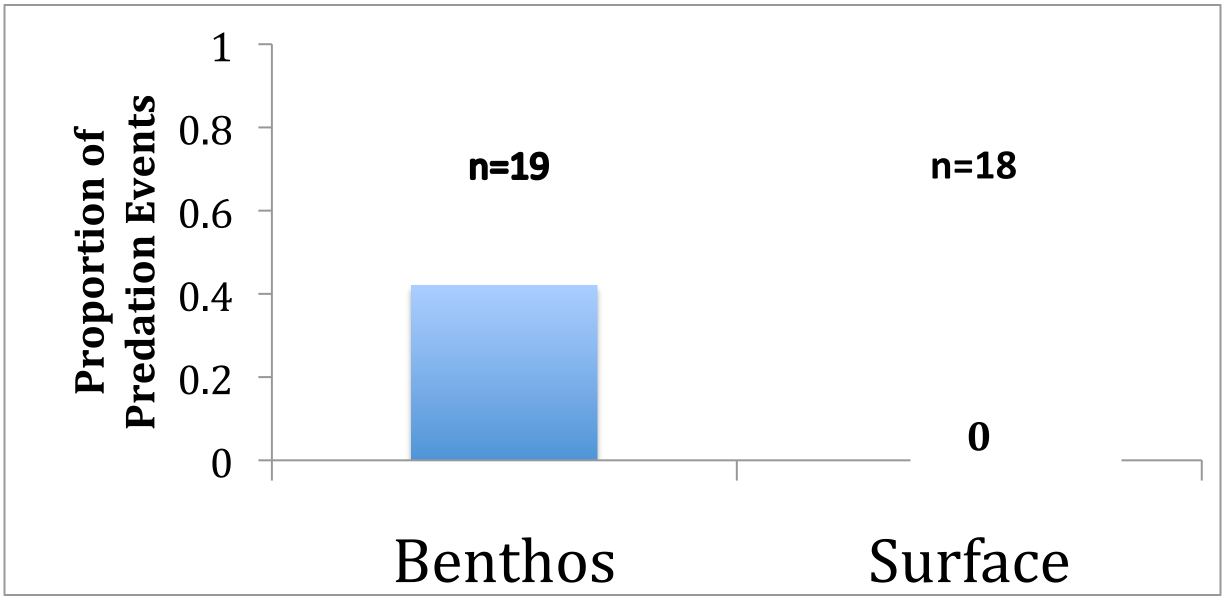
Proportion of Predation Events
1
0.8
0.6
0.4
0.2
0
n=19
n=18
0
Benthos
Surface