HIGH PREDATION MAY HINDER NATIVE OYSTER

(*OSTREA LURIDA* CARPENTER, 1864) RESTORATION IN NORTH HUMBOLDT

BAY, CALIFORNIA

HUMBOLDT STATE UNIVERSITY

by

Julie A. Koeppel

A thesis

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We certify that we have read this study and that it conforms to acceptable standards of
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degree of Master of Science

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ABSTRACT

HIGH PREDATION MAY HINDER NATIVE OYSTER

(Ostrea lurida Carpenter, 1864) RESTORATION IN NORTH HUMBOLDT BAY, CALIFORNIA

By

Julie A. Koeppel

Oyster reefs serve an important role in estuarine ecosystems. Their shells create a complex habitat that serves as a home for future generations of oysters, other sessile invertebrates, and fishes. Native oysters, Ostrea lurida, are thought to have been historically abundant in Humboldt Bay. Populations of this species have failed to rebound from over harvesting and harvest practices that broke up existing reef structures. Early attempts to farm native oysters were unsuccessful, which lead to attempts to farm Crassostrea virginica in Humboldt Bay. Importing C. virginica is thought to have introduced the predatory Atlantic oyster drill, Urosalpinx cinerea.

In order to determine why populations of O. lurida have not rebounded, I examined predation as a potential limiting factor on native oysters in north Humboldt Bay, California. In 2008 and 2009, juvenile oysters were cultured at the Telonicher Marine Laboratory following spawning of adults from Mad River Slough, North Humboldt Bay, California. After rearing the oyster larvae released from these adults through settlement and metamorphosis to juvenile stage (approximately 8 weeks), plastic
tiles seeded with juvenile *O. lurida* were assigned to one of three treatments: (1) a treatment open to predation, (2) a caged treatment in which settlement panels were surrounded with stainless steel mesh to exclude predators, or (3) a fenced control, which allowed predators access while controlling for possible cage effects (with a strip of stainless steel mesh only along the top and two sides of the settlement panels which allowed predators access through a central opening). Results showed that mean survivorship of juvenile *O. lurida* in caged treatments was significantly greater than treatments open to predation (open and fenced “cage control”). The predominant predator at one site was *U. cinerea*, which was abundant at the site. In 2010, I repeated the study using one-year old oysters. As with juvenile oysters, survival was significantly greater in treatments protected from predation. This study suggests that mortality from predation is a significant factor which leads to high mortality of juvenile and one-year old oysters in Humboldt Bay. Predation pressure may therefore be a major hurdle to overcome before successful restoration efforts can be achieved in Humboldt Bay, California.
This project could not have happened without the support and funding of many people and organizations. First, I want to thank my major professor, Dr. Sean Craig and committee members, Dr. Tim Mulligan, Dr. Milt Boyd, and Dr. Frank Shaughnessy, for their contributions to my research. Special thanks to Dave Couch for his willingness to help with this project and share his knowledge of Ostrea lurida and Urosalpinx cinerea. Thank you to the City of Arcata Environmental Services Department for their support and for allowing me access to tidelands under their jurisdiction. Thank you to Karl Menard and the Bodega Marine Laboratory for sharing their research on culturing Ostrea lurida. Thank you to Marty Reed for converting my design for my three treatments from a drawing and description into a working model of plastic, metal and bolts. I want to thank Tom Moore of the California Department of Fish and Game for assistance with permits to transplant oysters to the field. Thank you to everyone in Dr. Craig’s Graduate Student Lab (Emily Wilson, Julie Kelly, Becca Langhans, Brendan Kelly and Robert Koeppel) and the summer REU students (Ariel Carter and Elsie Thomson) for early morning field work and help culturing microalgae and oysters at the marine lab. I want to thank Grant Eberle and Dave Hoskins, Humboldt State University Marine Laboratory for answering endless questions, providing equipment and for converting a “storage closet” into an “oyster culture” lab. I also want to thank Todd Van Herpe, Humboldt Bay Oyster Company, for supplying me with O. lurida brood stock, which settled on his floating docks in Mad River Slough.
A special thanks to my husband and research partner, Robert Koeppel, for getting up in the middle of the night to carry a heavy canoe and cement blocks to the launch site, helping me paddle a canoe through a narrow channel each low tide, culturing microalgae and oysters, tromping through mud, long days in the lab, and in general supporting and encouraging me throughout this project and my education.

This work was funded through several grants and scholarships: Humboldt State University Department of Biological Sciences Masters Student Grant, the American Association of University Women (AAUW) Scholarship, Malcom Oliphant Marine Science Scholarship, Gary J Brusca Award, The Nature Conservancy (TNC) and National Oceanic and Atmospheric Administration (NOAA) community-based grant and the National Science Foundation. Thank you all for the generous support of my project.
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INTRODUCTION

Oyster reefs serve an important role in estuarine ecosystems. As oysters grow their shells rise vertically from the substrate, creating a hard three-dimensional structure that serves as substratum for future generations of oysters, other sessile invertebrates, and seaweeds. The complex habitat that these oysters create allows for increased abundance and diversity in the entire ecosystem (Grabowski et al. 2005; Rodney and Paynter 2006; Kimbro and Grosholz 2006). Juvenile fish and invertebrates are able to find refuge from predation among living oysters and the interstices of empty shells (Rodney and Paynter 2006). Additionally, oysters and other filter-feeding species improve water quality by decreasing turbidity and recycling nutrients (Haven and Morales-Alamo 1966; Coen et al. 2007). During filter-feeding, organic and inorganic matter is caught in gill lamellae of oysters; the inorganic particles are packaged as pseudo-feces and voided from the oyster, sinking to the estuary floor. Restoration of *Ostrea lurida* (Carpenter 1864) reefs may therefore improve water quality by decreasing suspended particulate matter through packaging of pseudo-feces as well as through suspension feeding, thereby increasing water clarity. Additionally, abundant populations of *O. lurida* may increase overall species diversity and abundance because they create habitat with refuges from predation for many different invertebrates and juvenile fish.

The taxonomy of the Olympia oyster has been in question since 1985. Genetic evidence suggests oysters ranging from Sitka, Alaska to Baja California, Mexico are a separate species from the more southern *O. conchaphila* (Polson et al. 2009). Throughout
this paper *Ostrea lurida* is used to refer to the native oyster in Humboldt Bay, California. *Ostrea lurida* is considered a native oyster thought to have been historically abundant in Humboldt Bay. Their shells are prevalent in Native American kitchen middens in the Humboldt Bay area (Couch and Hassler 1989). Populations were depleted in Humboldt Bay and throughout much of *O. lurida*’s range beginning in the mid-1800s due to over-harvest and harvest practices that broke up reef structures. (Barrett 1963). There were attempts to farm *O. lurida* after natural populations were depleted. In 1929, diked beds were constructed on the mud flats to keep water over the oysters during low tide. Farming relied on natural recruitment on to wooden slates (Bonnet 1937). During that same time period there were attempts to farm the eastern oyster *Crassostrea virginica* (Gmelin 1781) within bays along the Pacific Coast (Barrett 1963). Importing *C. virginica* is thought to have introduced the predatory Atlantic oyster drill, (*Urosalpinx cinerea* Say 1822) to Humboldt Bay, California (Boyd et al. 2002). *C. virginica* juveniles are extremely vulnerable to predation by *U. cinerea* (Manzi 1970, Newell et al. 2000), and predation on juveniles may be a key reason that *O. lurida* populations have not rebounded.

Some known predators of *O. lurida* are red rock crabs (*Cancer productus* Randall 1839), Dungeness crabs (*C. magister* Dana, 1852), graceful crabs (*C. gracilis* Dana 1852), Pacific oyster drills (*Ceratostoma inornatum* Carlton 1979), Atlantic oyster drills (*U. cinerea*) and bat rays (*Myliobatis californica* Gill 1865) (Barrett 1963). Previous studies indicate that predator species vary among sites due to variation in temperature or
salinity (Kimbro et al. 2009, Buhle and Ruesink 2009) and differences in substrate type and vegetation (Micheli and Peterson 1999). Studies conducted in Tomales Bay, California suggest that mortality of *O. lurida* caused by drill predation is reduced through a trophic cascade, in which rock crabs (*C. antennarius* Stimpson 1856 and *C. productus*) consume both native and invasive predatory drills (Kimbro et al. 2009). Rock crabs reduce predation indirectly because their presence decreases native drill foraging time (Kimbro et al. 2009). Studies in Willapa Bay, Washington indicated a trophic cascade similar to that found in Tomales Bay. In that system, there are two invasive drills (*C. inornatum* and *U. cinerea*). Crabs (*Cancer* spp.) consumed invasive drills, and may limit their local distribution and abundance (Buhle and Ruesink 2009). However, when drills are present in both of these West coast ecosystems, oyster mortality due to predation is high.

A few populations of *Ostrea lurida* within Coos Bay, Oregon have increased in spatial distribution and overall abundance (Groth and Rumrill 2009). However restoration of *O. lurida* throughout much of its range is limited by lack of hard substratum, poor juvenile survival, competition, and predation (Brumbaugh and Coen 2009, Groth and Rumrill 2009, Trimble et al. 2009). I compared survivorship of oysters both exposed and protected from predators at a site with and a site without *U. cinerea* to determine whether predation by Atlantic oyster drills, *U. cinerea* would be a limiting factor in restoration of native oysters, *O. lurida* in North Humboldt Bay, California.
METHODS

Study Sites

The study sites are located in the tidal mudflats of north Humboldt Bay, Humboldt County, California (Fig. 1). The “Railroad Levee” site is located east of the City of Arcata’s wastewater treatment oxidation ponds at a breech in the railroad dike reinforced with quarry rock (N 40°50.972’, W 124°5.108’). Predatory Atlantic oyster drills, *Urosalpinx cinerea*, are present at this site. The Railroad Levee site is surrounded by exposed unvegetated mud flats during low tides (Fig. 2). The second site used in this study (in 2009 and 2010) is located within the Arcata channel near the State Native Oyster Preserve (N 40°50.721’, W 124°06.388’). There is hard substrate at this site from ballast rock that was unloaded from ships sometime between the mid 1800s to early 1900s (Fig. 3). During low tide this “Arcata Channel” site remains surrounded by water within the channel. Both sites contain a sparse population of adult *O. lurida* (mean oysters/m² and SD, 4.9 ±3.3). These sites are accessible only during tides equal or lower than 0.0’ MLLW.

Oyster Culture

As part of the City of Arcata native oyster restoration project, hard substrate consisting of rock, concrete pieces and mesh bags filled with *C. gigas* shells were placed at four sites within North Humboldt Bay. I helped monitor the sites for evidence of natural recruitment from July through September during 2007 and 2008. We did not find
any evidence of natural recruitment during that time. Because native oyster populations are sparse in North Humboldt Bay, and no natural recruitment was observed, I cultured *O. lurida* for use in field predation experiments. Juvenile oysters were cultured at the Humboldt State Marine Laboratory, following a protocol developed at the Bodega Marine Laboratory by Karl Menard, which was modified to adjust for differences in laboratory equipment. Oysters for brood stock were collected from the Mad River Slough, Humboldt Bay, California and transported in mesh bags to the marine laboratory. Prior to being placed in culture tanks, these adult oysters were soaked in fresh water for ten minutes to reduce epifaunal organisms on their surfaces, which could otherwise contaminate lab culture tanks; *O. lurida* can tolerate short exposures to fresh water. Twenty adult *O. lurida* (50-80 mm) were conditioned for spawning in each of two 18” x 3’ conical bottom cylindrical tanks (Solar Components Corporation). Seawater in the tanks remained at an average temperature of 24.7°C (ambient air temperature in the culture room ranged from 22-26.5°C). Airflow for each tank was supplied via three glass tubes, each connected to a portable Tetra® Whisper air pump to keep microalgae and larvae suspended in the water column. I cultured the haptophyte *Isochrysis galbana* Parke (University of Texas Number LB 2307) for feeding larvae, juvenile and adult stages. *Isochrysis* (T-ISO) is a small, unicellular (4-8 µm cell length) golden-brown flagellated alga commonly used in aquaculture. For daily feeding, 16 liters of seawater was removed from each tank and replaced with 16 liters of densely cultured T-ISO (1.5 x 10⁶ to 2.0 x 10⁶ cells/ml). Microalgal cell density was estimated using a secchi density measuring
stick and conversion table. The seawater in the tanks was completely exchanged every three days. Filtered UV sterilized seawater was drawn the preceding day and allowed to warm to room temperature prior to this exchange. The outflow was sieved through a 73-micron screen to retain larvae while emptying the culture tank. Larvae were kept in a glass container and returned to the culture tank once refilled.

In *O. lurida*, eggs are fertilized and brooded inside the anterior branchial chamber to the veliger stage (Couch and Hassler 1989). Mature veliger larvae (185-187 μm) are released after approximately 10 days of development within the branchial chamber. Nine days after release, some of the veliger larvae in my culture tanks developed eyespots and were competent to settle. During the first spawning event, most of the larvae settled on the shells of the brood stock. Thereafter, I removed the brood stock from the tank when larvae became competent to settle. For larval settlement, the inner perimeter of each tank was lined with 10x10 cm plastic tiles attached to a Vexar plastic mesh screen. Juvenile oysters were grown out for approximately one month in these culture tanks prior to use in predation studies. All tiles were groomed so there was approximately 1 cm free space surrounding each oyster to minimize the potential for mortality due to overcrowding. Each tile was photographed prior to use in predation studies in the field.

**Predation Studies**

**Juvenile Oyster Predation Study Trials**

The first juvenile oyster trial was conducted in 2008 to investigate whether predation by oyster drills, *U. cinerea* is a key factor in oyster mortality. The Railroad
Levee site was selected because it contained a population of *U. cinerea* and therefore proved to be a good place to test the design of exclusion cages. I used a randomized block design with three treatments to examine predation on juvenile *O. lurida*: (1) open (open to predators), (2) caged (predator exclusion) and (3) fenced control, which allowed predators access but controlled for possible cage effects. Three 10 x 10 cm plastic tiles containing attached juvenile oysters were bolted to each side of a crossbar attached to a 3.8 x 20 x 40 cm concrete garden stone (Fig. 4). These tiles were positioned vertically with the bottom of the tile touching the garden stone. Two tiles per stone were haphazardly assigned to each of the three treatments. For the predator exclusion treatment, 14 x16 cm rectangles of stainless steel mesh with 0.64 cm openings were molded to wrap around and fully enclose the plastic tiles. The fenced treatment was identical to the predator exclusion treatment, with the exception of a 6 x 8 cm central opening that allowed either swimming or crawling predators access to the juvenile oysters on the panel inside. Six concrete garden stones (12 replicates of each treatment) were deployed at the Railroad Levee site on September 13, 2008 and July 8, 2009 and at the Arcata Channel site on July 10, 2009. I cleared drift plant material and debris from the mesh screen on these treatments every two-weeks (the next low tide cycle) in order to assure continuous water flow to the oysters. In 2008, the study was ended after two months in the field after many of the oysters had been consumed. While cleaning the mesh at that time, it was noted that there were many juvenile oysters with drill holes on the open treatments. The second juvenile oyster predation trial (2009) was ended after
approximately two months as well, when some of the stainless steel screws holding the mesh in place on exclosure and fenced control treatments began to fail.

All tiles were transported on their garden stones to the HSU marine laboratory after exposure to predators in the field. Live juvenile oysters were counted using a dissecting microscope; the number of surviving oysters was compared with their initial abundance. I digitally photographed each tile at the end of the study. Oyster lengths (hinge to shell margin) were measured using National Institutes of Health Image J software and compared to measurements from initial photographs to estimate growth.

One-Year Old Oyster Predation Trial (2010)

Settlement of *O. lurida* onto tiles in the laboratory was not as successful in 2010 as in previous years. Larvae settled heavily only on a small number of tiles (n= 15). Attempts to transplant juvenile oysters to tiles were unsuccessful, however, because their bottom valves were tightly secured to the rough surface of these tiles. Their bottom valves were extremely thin and fragile; the valves became damaged when I attempted to remove the juvenile oysters for transplantation. Alternatively I used *O. lurida* cultured in 2009 that had settled on the Vexar plastic mesh which held the tiles inside the perimeter of the culture tanks, because these oysters were easily removed. These one-year old oysters ranged in length (measuring from umbo to outer shell edge) from 1.7 cm to 5.4 cm, with an average length of 3.58 cm. Four one-year old oysters were attached to each 10 x 10 cm plastic tile using Z-spar splash zone epoxy (Gregalis et al. 2008). The block
design was identical to the earlier study in 2009. Five cement blocks (10 replicates of each treatment) were deployed at the Arcata Channel site on July 14, 2010 and the Railroad Levee site on July 15, 2010. The study at the Arcata Channel site was ended on August 11, 2010 because the mesh cages had somehow been removed from two of the predator exclusion treatments and one mesh fence had been pried away from a fenced control treatment. Each tile was then photographed and live oysters were counted. A census of live oysters was taken at the Railroad Levee site on August 12, 2010. However, these treatments were left in place to observe further drill predation and were not retrieved until September 9, 2010.

Laboratory Feeding Trials

The Arcata Channel site did not show any signs of mortality due to drill predation. However, there was mortality due to a predator which was capable of chipping away and/or crushing the oyster shells. As a follow-up to the predation field studies, I therefore conducted feeding trials in the laboratory to ascertain whether crabs, which were common at the Arcata Channel site, could have caused this sort of shell damage. *Cancer productus* and *C. antennarius* Stimpson (1856) were collected at the Arcata Channel site. One crab and one tile containing four one year old *O. lurida* individuals were placed in each of eight 10-gallon aquaria to observe predation in the lab. These aquaria were placed within a sea table supplied with continuous seawater flow. A sheet of plywood was placed over these aquaria to maintain darkness at all times because *C. productus* and *C. antennarius* are primarily nocturnal foragers (Robles et al. 1989).
observed the results of these lab experiments on crabs and oysters for nine days to determine if predation by crabs could account for the observed damage to oysters observed in the field.

Statistical Analysis

Data were analyzed using R version 2.7.2. Survivorship and growth of juvenile oysters among treatments and between sites were analyzed using ANOVA when the assumptions of parametric tests could be met. There were varying numbers of juvenile *O. lurida* on the tiles at the beginning of the study. I used logistic regression to tease out whether the number of oysters on experimental tiles at the start of the experiment was an important predictor of the number of surviving oysters at the end of the study. Data from the juvenile oysters (second trial) at the Railroad Level site did not meet the assumptions of normality; therefore they were analyzed using a non-parametric Kruskal-Wallis rank sum test. Analysis of juvenile oyster survival for the second trial at the Arcata Channel site was completed using a one-way ANOVA (comparing across treatments only). Survival data from the one-year old oyster trial did not meet the assumptions of normality and the survival variable was ordinal (0 to 4 oysters) due to the small number of oysters glued onto each panel at the start. Therefore, these data were analyzed using a Kruskal-Wallis rank sum test.
Figure 1: Map of field study sites in North Humboldt Bay, California. 1) Railroad Levee Site, 2) Arcata Channel Site
Figure 2: A breech in the Railroad Levee reinforced with quarry rock (Railroad Levee site) North Humboldt Bay, California
Figure 3: Rocky mound in the Arcata channel (Arcata Channel Site), North Humboldt Bay, California
Figure 4: Example of experimental design with three treatments (1) open to predation, (2) caged with stainless steel mesh to exclude predators and (3) fenced control, which allowed predator access while controlling for possible cage effects.
RESULTS

Juvenile Oyster Predation Trial 1 (2008)

The percent growth of oysters was estimated using the change in length from umbo to shell margin during the approximately two month growth period in the field at the Railroad Levee site. Growth was slightly higher for the open treatment, but did not differ significantly among treatments \( (F=1.145, \text{df} 2,12, p =0.35) \) (Fig. 5). Therefore, filter-feeding did not seem to be significantly affected by the mesh fence or enclosure treatments.

The mean survivorship of juvenile *O. lurida* in caged treatments was 47 percent, which was significantly greater \( (F=8.041, \text{df} 2, p=0.0016) \) compared to treatments that were open to predation (17.6 percent) or fenced to allow predator access but control for cage effects (14.7 percent). The open and fenced treatments were not significantly different from one another (post hoc Tukey multiple comparison of means, adjusted p-value 0.94) (Fig. 6). The number of oysters at the start was not a significant predictor of the number of oysters alive at the end of the study (p-value=0.8), however, treatment was a significant predictor of the number of live *O. lurida* at the end of the experiment (p-value=0.012).
Juvenile Oyster Predation Trial 2 (2009)

**Railroad Levee Site**

In the field study conducted in 2009, growth was similar among treatments and between sites (two-way ANOVA with site and treatment as factors, F: 0.435 df 3, 51, p-value 0.73) (Fig. 7). Oysters within all treatments at the Railroad Levee site had low initial survivorship, possibly due to environmental factors. Survivorship did not differ significantly among treatments at the Railroad Levee site (Kruskal-Wallis chi-squared =0.0424, df 2, p-value = 0.979). Predation by drills accounted for 4.6 percent of total mortality over the two month study.

**Arcata Channel Site**

Oysters protected from predation (caged treatment) showed a 59.3 percent survivorship, which was significantly greater when compared with oysters exposed to predation (fenced and open treatments) which had a 25 and 17 percent survivorship, respectively (F= 26.16, df 2,33 p < 0.0001). Post hoc analysis using Tukey HSD showed that there was no statistical difference between the fenced and open treatments (adjusted p-value 0.39: see Fig. 8).

One-Year Old Oysters Predation Trial 1 (2010)

**Railroad Levee Site**

After one-month in the field, there was no significant difference in survivorship among treatments at the Railroad Levee site (Kruskal-Wallis chi-squared=4.87, df=2, p-value = 0.0875, see Fig. 9). However, after two months in the field, oysters protected
from predation had 100 percent survivorship (four out of four oysters survived on each tile), which was significantly greater than oysters exposed to predation (fenced treatments had on average 3.4 oysters surviving, while open treatments had an average of 2.4 oysters per tile surviving) (Kruskal-Wallis chi-squared = 12.9627, df = 2, p-value = 0.0015, see Fig. 10). After 2 months, oyster drill predation accounted for 21 percent of the overall mortality at the Railroad Levee site during this trial. Mortality at the Railroad Levee site was due to a combination of predation by drills and crabs or other predators capable of chipping/crushing their shells. Potential crab predation accounted for 73 percent of mortality. Only one oyster shell was found intact and gaping: mortality was not likely to have been due to predation for this individual (Fig. 11).

**Arcata Channel Site**

At the Arcata Channel site, oysters protected from predation (caged treatments) had an average survivorship of 93.75 percent (average of 3.75 out of 4 oysters survived per tile), which was significantly greater than oysters exposed to predation (fenced treatments averaged a survival of 25 percent (average of 1 out of 4 oysters surviving per tile), whereas open treatments had 37.5 percent survival (1.5 oysters out of 4 on average surviving per tile) (Kruskal-Wallis chi-squared = 8.8912, df = 2, p-value = 0.01173) (Fig. 9). Data from two of the caged treatments from the Arcata Channel site were dropped from the analysis because their mesh cages had been removed somehow during the period of study. At the Arcata Channel site, all mortality was due to crabs or possibly other predators capable of chipping/crushing their shells (Fig. 11).
Crab Impact - Laboratory Feeding Study

Three of the four red rock crabs (*C. productus*) used in lab studies consumed an average of 96 percent of the oysters placed in their tanks, while the fourth *C. productus* specimen died on the second day in the lab. Bottom valve fragments that remained attached to the tiles were very similar to fragments observed on settlement panels deployed in field studies at both sites. *C. antennarius* did not consume oysters in the lab over the nine day period.
Figure 5: Average percent growth of the native oyster, *Ostrea lurida*, among caged, fenced and open treatments at the Railroad Levee site in 2008. Mean ± SE
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Figure 9: Average number of surviving one year old oysters, out of four total, on each of 10 replicate panels deployed to the Railroad Levee and Arcata Channel sites, North Humboldt Bay, California.
**Figure 10:** Mean ± SE number of surviving one year old oysters per tile after two months at the Railroad Levee Site, North Humboldt Bay in 2010.
Figure 11: Comparison of causes of mortality between sites. Drilled=mortality due to predation by the oyster drill, *U. cinerea*. Chipped=mortality most likely due to predation by crabs (see section “crab impact” in results), Gaper=mortality not due to predation, or at least without evidence of predation.
DISCUSSION

This three-year study indicates that predation is likely to play a strong role in limiting native oyster survivorship in North Humboldt Bay, particularly among juvenile and one-year old oyster recruits. I found evidence of predation by *U. cinerea* in all three years at the Railroad Levee site. Predation by drills accounted for an average of 12.9 percent of juvenile oyster mortality at the Railroad Levee site. The average survivorship of juvenile oysters exposed to predation was only 16.2 percent over the two-month study in 2008. There was a high rate of juvenile oyster mortality thought to be unrelated to predation at both sites during 2008 and 2009. However, unlike oyster drills that leave a distinct rasped hole, other predation may be less easily documented.

One-year old *O. lurida* had low mortality due to reasons unrelated to predation. There was one dead oyster that did not show signs of predation (chipping or drill hole). Mean survivorship of one-year old oysters at the Railroad Levee site that were exposed to predation (fenced and open treatments) was 88.8 percent after one month and 73.8 percent after two months. *Urosalpinx cinerea* has a long prey handling time of approximately 10 days for *O. lurida* (Hanks 1957, Buhle and Ruesink 2009). Evidence from outplanting of *O. lurida* in Willapa Bay, Washington suggests that the predation impacts of drills on *O. lurida* over short-term studies translate into large impacts over longer periods (Buhle and Ruesink 2009). The mortality from drill predation documented during my two month field trials would likely amount to substantial mortality over several years.
*Urosalpinx cinerea* bores a hole through its prey’s shell by alternating the apposition of the accessory boring gland and the radula. The accessory boring gland secretes chemicals that weaken the prey’s shell prior to rasping by the radula (Person et al. 1967). The accessory boring gland does not function under anaerobic conditions and drills may then detach from their prey (Person et al. 1967). Drills may become detached from the oyster, during low tide, prior to completely boring through the oyster’s valve. *Ostrea lurida* higher in the intertidal zone may thus experience less predation by drills which are dislodged during low tides. This study was conducted at 0.0 MLLW, so the results may be indicative of the lower ranges of drill predation only.

Survivorship of juvenile oysters that were exposed to predators was only 21 percent at the Arcata Channel site. The survivorship of one-year old oysters exposed to predation was 31.3 percent, which is low compared with the Railroad Levee site. Because the Arcata Channel site did not have any invasive Atlantic oyster drills, I expected better oyster survival. There was high mortality of juvenile and one year old oysters in treatments open to predators at the Arcata Channel site even though there was no evidence of predation by drills.

Oyster mortality due to a predator capable of crushing the oyster’s shell and prying up mesh cages was evident at both field sites. Mortality from crabs or other predators accounted for 60 percent of the mortality at the Railroad Levee site and 100 percent of the mortality observed at the Arcata Channel site over a one month period.
during 2010. Fragments of the bottom valves of oysters on settlement panels used in this study were left imbedded in the Z-spar used to attach them to the experimental tiles. Results from laboratory studies suggested that red rock crabs, *C. productus*, are likely predators of native oysters in Humboldt Bay.

My results differ from studies elsewhere along the Pacific Coast which found native crabs reduced invasive drill predation on *O. lurida*. In Willapa Bay, Washington native crabs (*Cancer* spp.) had a positive indirect affect on oysters by consuming drills in that system (Buhle and Ruesink 2009). Studies in Tomales Bay, California indicated that *C. antennarius* has a positive indirect affect on *O. lurida* by consuming *U. cinerea* as well as native oyster drill species (Kimbro et al. 2009). Further investigation is needed to examine whether trophic cascades impacting native oysters exist within Humboldt Bay. In contrast to results from my study, predation on adult *O. lurida* by *Cancer* spp. was not indicated in Willapa Bay and Tomales Bay.

Results from this study are similar to a five-week study in Willapa Bay, Washington that found mortality caused by invasive drills (*U. cinerea* and *Ceratostoma inornatum*) was highly variable among their field sites. Predation by drills was found at only 7 out of 28 total sites (Buhle and Ruesink 2009). The life history of *U. cinerea* is likely to foster isolated populations, because this species has direct development with no pelagic larval stage which might disperse the offspring. *Urosalpinx cinerea* attaches its egg cases to firm substrates. Juvenile drills emerge from the egg cases; they then locate their prey by chemical attraction (Ritchoff et al. 1983). Localized drill populations may
make it possible to find a restoration site free from predation by drills within Humboldt Bay.

There was high juvenile *O. lurida* mortality among all treatments at both field sites during the two trials. Mortality of juvenile oysters protected from predators ranged from 41 to 81 percent. High mortality unrelated to predation in juvenile oysters is consistent with other studies of *O. lurida* as well as *Crassostrea* spp. (Newell et al. 2000, Brumbaugh and Coen 2009, Buhle and Ruesink 2009, Trimble et al. 2009). Mesh “grow-out” bags may increase survivorship of juvenile oysters. Juvenile oysters, settled on empty shell, are placed in mesh bags that are then suspended in the water column. The oysters are “grown-out” through juvenile size prior to transplant to the restoration site. The mesh bags protect the oysters from predators. In addition, positioning in the water column allows for increased water flow around the oysters, providing greater feeding opportunity and decreasing siltation that may smother juvenile oysters. Mesh grow-out bags are often used as part of *C. virginica* restoration projects in recruitment limited systems (Brumbaugh and Coen 2009).

Previous studies of trophic cascades in other systems have identified predators that reduce crab predation on oysters. Mortality of juvenile oysters (*C. virginica*) from predation by the mud crab (*Panopeus herbstii*), is reduced by the presence of oyster toadfish (*Opsanus tau*), through consumption of mud crabs and reduction of their foraging by this fish. Even when oyster toadfish were absent, habitat complexity reduced oyster mortality from predation because crab foraging was less efficient (Grabowski
A complex habitat may therefore increase survivorship of oysters by decreasing the predator’s ability to locate and consume its prey (Lenihan 1999, Grabowski 2004).

Although predation would have also occurred within historic *O. lurida* reefs, the impact on the population may have been less than documented in this study because of the existence of a complex reef structure. Complex structure provides habitat for greater diversity and abundance of mobile and sessile invertebrates (Kimbro and Grosholz 2006). The greater diversity may have included more desirable prey items for *Cancer* spp. which feed on a wide range of invertebrates. Native oysters may have had greater refuge from predation in a more complex reef. A complex habitat reduces predator foraging efficiency resulting in decreased mortality from predation (Grabowski 2004). Additionally, the historic population would have had a greater number of sexually mature adult oysters spawning each season. Recruitment in to the population may have offset loss to predation.

Heavy predation by both *U. cinerea* and *C. productus* may hinder restoration of *O. lurida* at sites within North Humboldt Bay where these predators are present. The Arcata Channel site is surrounded by vegetated substrate and remains surrounded by water during low tide, which may have contributed to the abundance of red rock crabs at this site. Vegetated mudflats provide habitat for predators and increase predator movement to the prey area (Micheli and Peterson1999).

There are clearly challenges to overcome if native oyster restoration is to be successful in North Humboldt Bay. To decrease predation, a location should be selected
where oyster drills are not established. Oyster drill populations are isolated, but once drills are established at a site they are difficult to eradicate. Programs to remove adult drills and egg cases are expensive and serve to limit, but not eradicate drill populations (Buhle et al. 2005). It may be more cost effective to find a location free of *U. cinerea* within Humboldt Bay and work to avoid accidental introduction.

The location for restoration work within Humboldt Bay should also have good water flow and fresh water input. Areas with higher water flow rates may increase oyster survival by both increasing food delivery and decreasing detection by predators. Increased food delivery could mean faster growth and therefore less time at a more vulnerable, smaller size. Oyster drills preferentially consumed smaller oysters when offered a range of sizes in field studies (Buhle and Ruesink 2009). Both predators identified in this study follow chemical clues to locate prey, so faster water flow should decrease the predator’s detection of *O. lurida*. Faster water flow increases the dissipation of bivalve scent plumes, decreasing the ability of predators to locate their prey (Grabowski et al. 2005). Reduced salinity from fresh water input will limit predators of *O. lurida* in Humboldt Bay. Salinity influences *U. cinerea* feeding rate and reproduction. Feeding of this Atlantic oyster drill stops at salinities of 12.5 ppt. and reproduction stops at salinities at or below salinities of 15 ppt. (Manzi 1970). *Urosalpinx cinerea* is absent from areas with river input in Willapa Bay, Washington (Buhle and Ruesink 2009). Additionally, *C. productus* distribution and abundance within Coos Bay was correlated to salinity. In laboratory studies salinity of 13.1 ppt. is the lethal limit for *C. productus*
(Carroll and Winn 1989). Although *O. lurida* survives best at salinities of 25 ppt. and above, it can tolerate periods of lower salinity, which may serve to decrease its predator abundance.

Restoration may be possible if a location can be found that has high water flow, freshwater input, an unvegetated mudflat border, and has not been invaded by predatory oyster drills. Along with the selection of a proper location for restoration within Humboldt Bay, another important consideration is the addition of complex substrate and stock enhancement. Restoration will require the addition of hard substratum (natural rock, artificial reef structure or oyster shell). Stock enhancement can be done with either juvenile or adult oysters. However, stock enhancement using *O. lurida* that have been grown to sexual maturity in suspended mesh bags may increase stock survival and subsequent recruitment success. Dense populations of *O. lurida* have an increased change of fertilization success due to the proximity of other sexually mature adults. The goal of restoration is to form reefs which naturally “self-seed” and persist through time, despite losses due to predation.
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