Will the introduced mussel *Mytilus galloprovincialis* outcompete the native mussel *M. trossulus* in Puget Sound? A study of relative survival and growth rates among different habitats

Michelle Rensel, Joel Elliott, and Peter Wimberger
Department of Biology, University of Puget Sound

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Abstract
The Mediterranean mussel (*Mytilus galloprovincialis* = *Mg*) has become established throughout Puget Sound and the effects of this species introduction on the native mussel *M. trossulus* (*Mt*) are unknown. *Mg* and hybrids between *Mg* and *Mt* (*Mgt*) are abundant on floating docks and large *Mg* and *Mgt* mussels also occur at low frequencies in the intertidal zone and in areas of low salinity. A variety of factors (e.g., growth/survival rates, predation, larval recruitment) may be causing these observed distribution patterns. In this study we performed three field experiments to examine the relative survival and growth rates of *Mg* and *Mt*: 1) at different tide heights on pilings vs subtidal locations on docks, 2) when grown in single-species groups and mixed-species groups, and 3) at locations with different salinities. Individuals of *Mg* had higher survival and growth than *Mt* in all areas except the high intertidal. Each species had similar growth rates when grown in single and mixed-species groups. Mg had higher survival and growth rates than Mt under both high and low salinity. These results indicate that the introduced *Mg* has superior growth and survival to the native *Mt*, and *Mg* has the potential to outcompete *Mt* under certain environmental conditions.

Introduction
Introduced species are considered to be one of the greatest threats to biodiversity in marine ecosystems because they can displace and/or hybridize with native species and significantly alter food webs (Ruiz et al 2000). The Mediterranean mussel, *Mytilus galloprovincialis* (*Mg*) has been introduced into a wide variety of geographic locations (Wonham 2004). In South Africa *Mg* has become invasive and outcompetes a native mussel species, *Aulacomya ater* (Griffiths et al 1992; Hockey and Van Erkom Shurink 1992). In the Northeast Pacific, *Mg* has replaced the native mussel *M. trossulus* (*Mt*) in southern California (Geller 1999), and there is a stable hybrid zone between San Diego and Humboldt Bay. Relatively few mussels with *Mg* alleles have been found on the outer coast of Oregon and Washington, but *Mg* has been introduced into Puget Sound through ballast water and aquaculture where it has become widespread and is hybridizing with *Mt* (reviewed by Wonham 2004). The increasing frequency of *Mg* and hybrids in Puget Sound is of concern because *Mg* has a history of being a successful invader and it has the potential to compete with the native *Mt* and influence its genetic integrity. *Mt* is an integral member of the intertidal community in Puget Sound, and the disappearance or decline of this species could fundamentally change the ecology of intertidal habitats. Mussels beds provide shelter and protection for many other organisms (Seed and Suchanek 1992), and mussels are the major prey of a variety of marine predators. A decline in *Mt* could alter this important habitat and lead to a change in food sources for *Mt* predators. In addition, it may become more difficult for *Mt* predators to successfully handle prey since *Mg* shells are generally larger than those of *Mt* (Anderson et al 2002).

Previous studies of *Mg* and *Mt* in geographic locations other than Puget Sound have described *Mt* as a species that thrives in cooler waters with variable salinity, while *Mg* has a preference for warm, high salinity waters (Sarver and Foltz 1993; Hilbish 1994; Geller 1994; Hoffman and Somero 1996; Suchanek et al 1997). *Mg* may have a greater chance of thriving in Puget Sound than on the outer coast of Washington because of the relatively warmer temperatures in Puget Sound. They are common at a wide variety of locations (Wonham 2004), but they are relatively rare in areas of low or variable salinity (e.g., Elliott Bay, Commencement Bay). *Mg* and *Mt* have also been found to occur in different frequencies in intertidal and subtidal habitats. *Mg* and hybrids are commonly found in subtidal habitats on the sides and bottoms of floating docks, but *Mg* are relatively rare in intertidal habitats (Anderson et al 2002; Chambers 2003; Holmes 2003; Wonham 2004). In addition, Rensel (2005) found that *Mt* is most abundant near the surface on the sides of docks and *Mg* is most common lower down on the sides and bottoms of docks. The ecological factors causing these distribution and abundance patterns are only beginning to be studied. Matson et al (2003) found that larvae of *Mg* have lower growth rates than *Mt* at low salinities. Further experiments are needed to examine the survival and growth rates of these species under different environmental conditions and at different life history stages.

In habitats where both species survive and are at high population densities they have the potential to compete for limited space. In many intertidal habitats and on the sides of docks mussel beds can cover 100% of the substrate. Interspecific competition between *Mg* and *Mt* may play a role in determining their relative densities in these areas. However, there is no experimental evidence to suggest that these two species do compete in the Pacific Northwest. Wonham (2001) conducted competition experiments in the intertidal at Tatoosh Island on the exposed coast of Washington, but did not find any differences in the growth or survival of the two species when grown together vs alone. There have been no similar studies of these two mussel species in the more protected waters of central and south Puget Sound where *Mg* is reported to be more abundant (Anderson et al 2002; Wonham 2004). A variety of factors may influence the observed patterns of distribution, abundance, and size of these two species in Puget Sound (e.g., survival/growth rates under different salinities, predation, larval recruitment). Experiments are needed to determine the relative importance of these factors in causing the observed patterns.

In this study, we tested whether the different patterns of distribution, abundance, and size of *Mg* and *Mt* are the result of differential survival and growth rates of each species at different tidal heights and salinities. We also tested whether competition occurs between the two species by comparing the survival and growth rates of single-species and mixed-species groups of mussels. The experiments were conducted in South Puget Sound where pilings and docks are the major habitat of the two mussel species and there is little natural rocky intertidal habitat on which mussels can attach. To examine the effect of tidal height, we compared the survival and growth rates of both mussel species in the high and low intertidal zones of pilings and high and low subtidal zones of docks. We predicted that *Mt* would have higher survival and growth rates in the intertidal zone because *Mg* is relatively rare in this habitat, and *Mg* would have higher survival and growth rates in the lower subtidal zone on docks where it is most common. To examine the potential for competition between the two species, we compared the survival and growth rates of both mussel species when grown in single-species and mixed-species groups. In addition, we examined the effect of salinity on both species by comparing their survival and growth rates in the low subtidal zone at Fox Island (high salinity location) to Thea Foss Waterway, an area of relatively low and variable salinity. We predicted that *Mt* would have higher growth and survival in the low, variable salinity habitat, and *Mg* would have higher growth and survival in the high, constant salinity habitat.

Methods

Survival and growth experiments

Small *Mg* and *Mt* individuals (15-25 mm in length) were obtained from Taylor Seafood Farms in Shelton, Washington. The mussels were then kept in mesh socks and hung from a dock at Fox Island (47^{0} 15' 53''N, 122^{0} 38' 44" W) until used in experiments. To provide an enclosed space for mussels to grow in and to exclude predators, mesh cages were constructed using a design similar to Wonham (2001). A piece of plexiglass 15 x 15 cm^2 was roughened with an electric sander to provide a surface for mussel attachment. Plastic mesh with 1 cm^2 holes was used to create a cylindrical cage (10 cm diameter and 5 cm high) that was attached to the plexiglass plate using cable ties. The mesh cages prevented mussels from moving off of the plates and predators from gaining access to the mussels. Each plate was labeled with an electric etcher.

The length of each mussel was measured using digital calipers (to the nearest 0.1 mm), and groups of 40 individuals of the same species (size range 15-25 mm in length) were placed on individual caged plates. The mussels were allowed to attach in the cages with their byssal threads for approximately 3 days in the field before the cages were positioned in a particular tidal zone.

Experiment #1: One cage with *Mt* and one with *Mg* were attached at the high (3 m above MLLW) and low (1 m above MLLW) intertidal zones on the northeast sides of five pilings at Fox Island (Fig. 1). Plates with each species were also placed near the surface of the water (high dock) and 45 cm below the surface (low dock) at five locations along the side of the dock at Fox Island.

Experiment #2: To determine whether the mussel species influence the survival or growth of each other, 20 *Mt* and 20 *Mg* individuals were put together (40 individuals total) in five separate cages placed in the low subtidal on the same dock as for the single-species cages (Fig. 1). To identify individuals of the different species, a small section on the shell of each mussel was sanded and painted with a red dot (*Mg)* or a yellow dot (*Mt)* with enamel paint.

Experiment #3: To assess the effects of low and variable salinity on *Mg* and *Mt* survival and growth, five cages with 40 *Mg* and five more with 40 *Mt* were attached to the side of a dock in Thea Foss Waterway (47^{0} 15'27''N, 122^{0} 26'08"W) in the low subtidal (Fig. 1). This location experiences low and variable salinity because of the influences of the Puyallup river and storm water runoff into the waterway. The survival and growth of the mussels in Thea Foss Waterway were compared to those from the low subtidal on the dock at Fox Island (high constant salinity).

The mussels were left in the cages at Fox Island and Thea Foss Waterway for approximately one month (33 and 28 days respectively) in July and August of 2004. The cages were monitored every few days for survival and the subtidal cages were periodically scrubbed to clear away algae. At the end of the experiment all of the mussel cages were collected from the field and brought back to the lab. The percent survival and average growth of the mussels in each cage were determined. Average growth rate was calculated as the difference in mean length of the mussels in each cage between the start and end of the experiment standardized by the number of growing days.

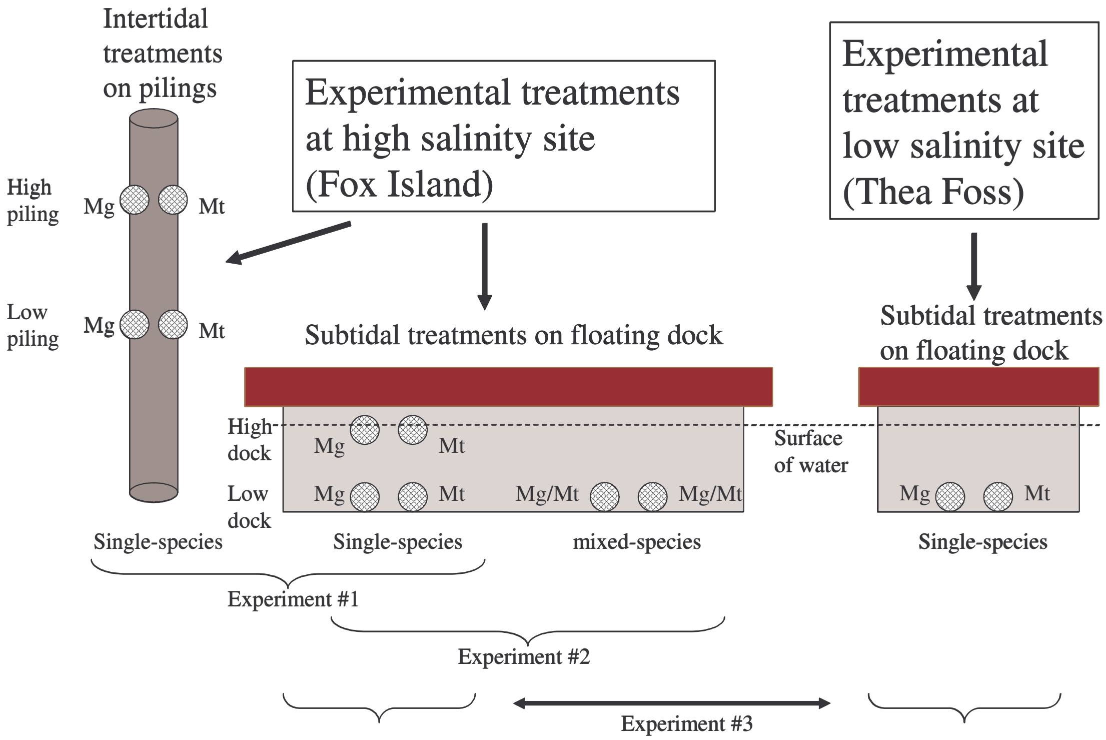

Figure 1. Diagram of experimental treatments in which 40 mussels were put in mesh cages and then allowed to grow under different conditions. Experiment #1: At the high salinity site (Fox Island) cages were attached at two different tidal heights on pilings (High piling = 3 m above MLLW; Low piling =1 m above MLLW) and at different depths on docks (High dock = water surface; Low dock = 45 cm below the surface). Experiment #2: Mussels were grown in mixed-species groups (20 *Mg* and 20 *Mt*) and in single-species cages at the low dock position of the high salinity location (Fox Island). Experiment #3: At the low salinity site (Thea Foss Waterway) mussels were grown in single-species cages at the low dock position. There were five replicates of each treatment.

Statistical Analyses

All statistical analyses were performed using the statistical software SPSS. The data from each experiment were analyzed using a Two-way ANOVA. Any data that did not meet the assumptions of normality and homogeneity of variance were transformed prior to statistical analysis. Post-hoc comparisons were conducted using the Least Significant Difference test.

Temperature Analyses

In order to determine the relative temperatures that mussels were exposed to in the high and low intertidal and high and low subtidal zones of docks during the summer, small temperature loggers (Smartbutton brand) were wrapped in plastic wrap and then encased in silicone within small mussel shells, a procedure similar to that used by Helmuth

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and Hofmann (2001). The temperature loggers provided measurements of the internal temperatures that a mussel would experience during a low tide series in the summer when there were maximum temperature extremes. The loggers were attached to the same areas as the experimental plates at Fox Island: high and low intertidal zones on the north sides of a piling and in the high subtidal and low subtidal zones on the side of the dock. We also put temperature loggers on the south side of pilings at the high and low intertidal regions where mussels are not typically found as a comparison with the north side where mussels are found in abundance.

Results

Experiment #1: Overall, mussel survival was significantly lower in the intertidal zone on pilings than in the subtidal zone on the sides of docks (*P*=0.002; Fig. 2). Post-hoc analyses revealed significant differences in survival between all zones except for comparisons between high and low piling and high and low dock zones (*P*=0.517 and *P*=0.592, respectively). The survival of *Mg* was consistently higher than *Mt* but this difference was not statistically significant (*P*=0.083). There was no significant interaction between treatment and species (*P*=0.927). Growth rates were significantly higher in the low tide zone of pilings and on the sides of docks than at the high tide on pilings (*P*<0.0001; Fig.2). Post-hoc analyses revealed a significant difference in average growth between all zones (*P*<0.05 for all combinations). Across all zones, *Mg* individuals had a significantly higher growth rate of 0.23 mm ± 0.11 SD per day while *Mt* individuals had a growth rate of 0.17 mm ± 0.07 SD per day (*P*=0.001). Average growth values were greater for *Mg* than for *Mt* in the subtidal zones, but similar between the two species in the intertidal zones. This pattern is reflected in a significant interaction between treatment and species (*P*=0.013).

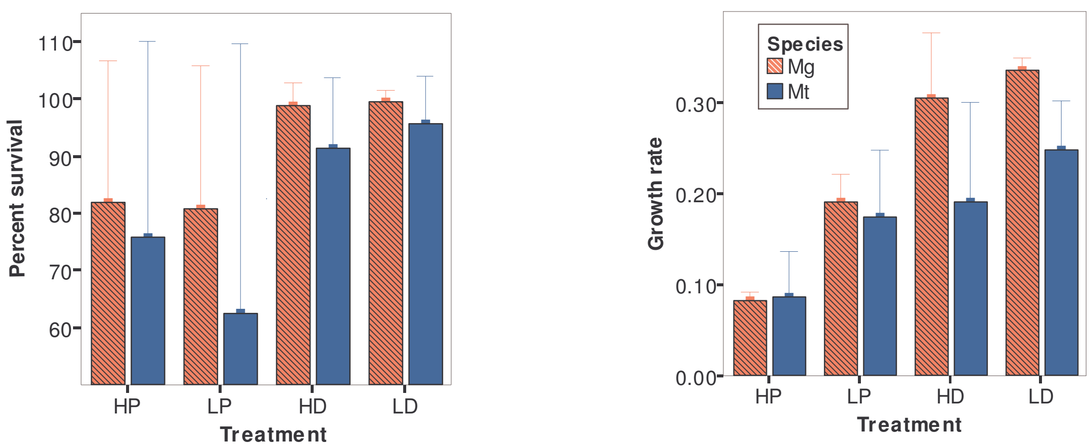

Figure 2. Average (±95% confidence limits) percent survival and growth rates (mm d^{-1}) of *Mg* and *Mt* at high piling (HP) and low piling (LP) and high dock (HD) and low dock (LD) locations at Fox Island.

Experiment #2: There were no significant differences in the percent survival of mussels in mixed-species cages versus single-species cages (*P*=0.112) or between species (*P*=0.185; Fig. 3). However, the average percent survival in the mixed-species cages was slightly lower (94.0% ± 4.59 SD) than in the single-species cages (97.5% ± 4.01 SD). Also, *Mg* had a slightly higher percent survival (96.9% ± 3.49 SD) than *Mt* (94.2% ± 5.30 SD). There was also no significant difference in the average growth rates of each species in single-species vs mixed-species cages (*P*=0.929; Fig. 3). However, *Mg* individuals across both treatments grew significantly faster (0.32 mm ± 0.03 SD per day) than *Mt* (0.27 mm ± 0.03 SD per day; *P*=0.026). There was no interaction between treatment and species (*P*=0.136).

Experiment #3: Mussel survival was significantly higher in low subtidal cages at the high salinity location (Fox Island) than at the low salinity location (Thea Foss Waterway) (*P*=0.006; Fig. 4). Across both locations, average survival was significantly greater for *Mg* (97.2% ± 4.32 SD) than for *Mt* (91.3% ± 5.98 SD; *P*=0.011). There was no significant interaction between species and treatment (*P*=0.292). Growth rates were also significantly higher at Fox Island than at Thea Foss Waterway (*P*<0.0001; Fig. 4). When the values were pooled from both locations, *Mg* individuals had significantly greater growth (0.27 mm ± 0.07 SD per day) than *Mt* (0.18 mm ± 0.07 SD per day;

P<0.0001). There was no significant interaction between treatment (Fox Island or Thea Foss) and species (*P*=0.635).

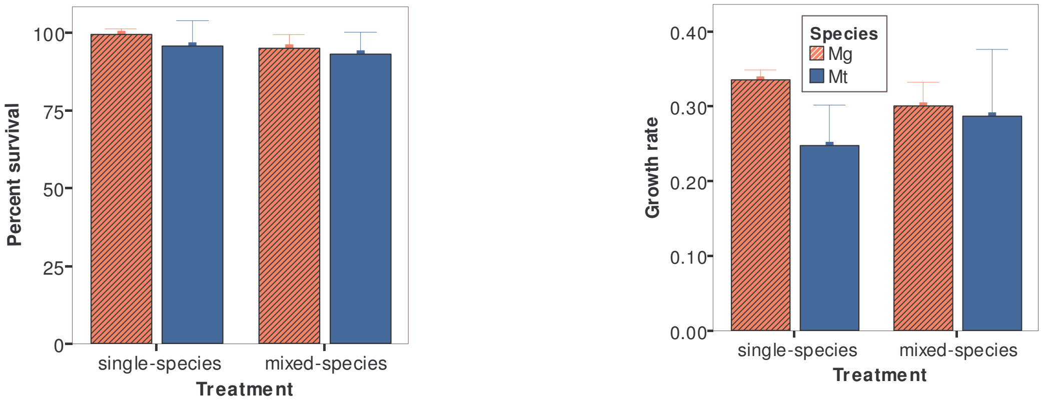

Figure 3. Average (±95% confidence limits) percent survival and growth rates (mm d^{-1}) of *Mg* and *Mt* on single-species and mixed-species plates at low dock (LD) locations at Fox Island.

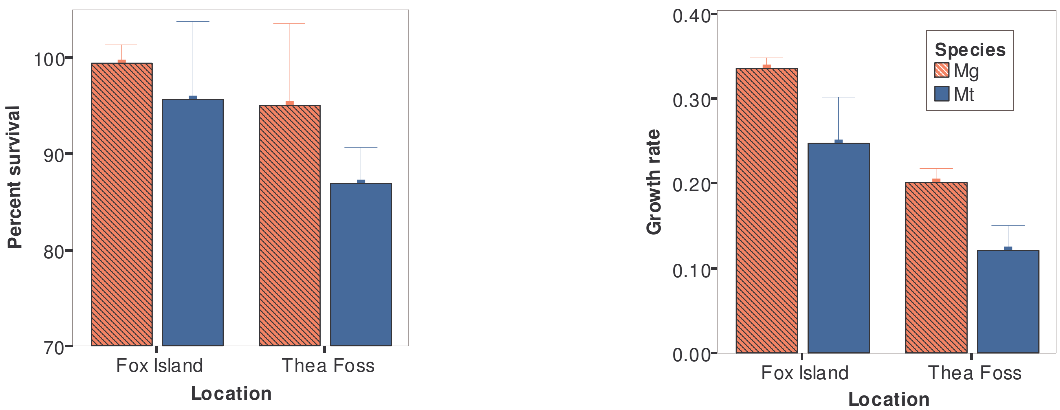

Figure 4. Average (±95% confidence limits) percent survival and growth rates (mm d^{-1}) of *Mg* and *Mt* at Fox Island (high, constant salinity) and Thea Foss Waterway (low, variable salinity).

Temperature Logger Data

The high and low subtidal temperature loggers that were continuously submerged showed relatively constant baseline temperatures (±2^{0}C) over the tidal cycle (Fig. 5). However, the intertidal loggers recorded large changes in temperature over the tidal cycle, especially on the south side of pilings where mussels do not typically occur in nature. For example, temperatures from 21 July, 2004 at the high intertidal level reached 32°C on the south side of the piling within minutes of being exposed to the air, whereas on the north side of the pilings at the high tide level the temperatures rose slowly over the tidal cycle to a maximum of 25°C. The low intertidal temperatures were approximately 3^{0}C cooler during the low tide series than the high intertidal logger when exposed to the air. Also, the low tide mussels were only exposed to air for approximately half of the time in comparison to the high tide mussels.

Discussion

Ecological studies have suggested that individuals of *Mg* are most common in the subtidal zone on the sides and bottoms of docks and they are relatively rare on pilings, especially in the high intertidal zone (Wonham 2004; Chambers 2003; Holmes 2003). Thus, we predicted that *Mg* would exhibit higher growth and survival than *Mt* in the low subtidal zone since this is where *Mg* is most abundant in nature. Our results indicate that growth for both species was greatest in the low subtidal zone, and that *Mg* displayed greater growth than *Mt*. Survival was also

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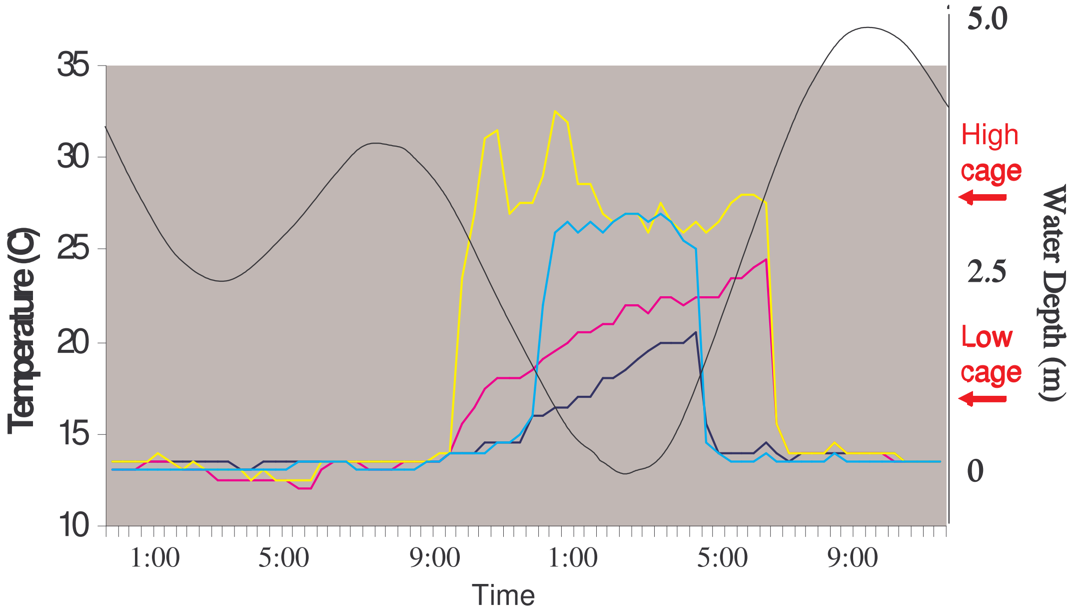

Figure 5. Temperature logger data (left axis) from the high (3 m above MLLW) and low (1 m above MLLW) intertidal zones on the north and south sides of a piling at Fox Island from July 21, 2004. Tide height (right axis) with tide levels over the 24 hour period.

highest for both species in the subtidal, and *Mg* had higher survival than *Mt,* but this difference was not statistically significant. These results suggest that *Mg* has the potential to outcompete *Mt* in the subtidal zone by taking over space more quickly through its higher survival and growth rates. The percent cover of mussels and other invertebrates reaches 100% on the sides of some docks and pilings, and the survival and growth rates of mussels may strongly influence their ability to compete for space. Longer term studies over many years are needed to determine whether *Mg* can outcompete *Mt* in the subtidal zone on docks where both species can be abundant.

Within the subtidal zone on docks, *Mt* is mostly present near the surface, or swash zone (Rensel 2005). We predicted that *Mt* would exhibit higher survival and growth in this zone than *Mg*. However, we found that *Mg* had higher survival than *Mt*, although this was not statistically significant. In addition, the growth of *Mg* was significantly higher than *Mt*. These results indicate that while *Mg* has the capability to survive and successfully grow in the swash zone, it does not do so. This could be because it prefers to settle lower in the subtidal zone where there is greater access to food and the environmental conditions (i.e., salinity and temperature) are more constant. Also, the high densities of *Mt* near the surface may prevent the settlement of *Mg* in this area.

Mg are relatively rare in the high intertidal zone on pilings, and we predicted that it would have lower survival and growth in this zone than the native mussel, *Mt.* However, *Mg* grew and survived equally well with *Mt* in the high intertidal zone on pilings. Growth of both species was lowest in the high intertidal, which was expected because of the shorter submersion time for feeding and harsh environmental conditions (high temperatures and desiccation stress). The high intertidal may be a potential refuge for *Mt* where it will not experience competition from *Mg*.

Comparisons of growth and survival of *Mg* and *Mt* under different salinity levels indicated that survival and growth were lower in the less-saline location at Thea Foss Waterway. This result is consistent with those of previous studies in which *Mg* is described as being intolerant of low salinities (Sarver and Foltz 1993; Hilbish 1994; Geller 1994; Hoffman and Somero 1996). The average growth rate of *Mt* at Fox Island (0.22 mm d^{-1}) in the low subtidal was similar to the maximum growth rate of *Mt* on aquaculture farms at Penn Cove, WA (0.204 mm d^{-1}) (Mueller 1996). However, the growth rate of *Mt* at Thea Foss Waterway (0.12 mm d^{-1}) was lower than the minimum growth rates reported for Penn Cove, WA (0.162 mm d^{-1}). This indicates that Fox Island was an optimal location for mussel growth but Thea Foss was a poor location. It is important to note, however, that factors other than salinity such as nutrient levels and pollution likely vary between Thea Foss and Fox Island and could influence the growth and survival of these mussel species. Further research is needed to determine the influence of salinity on *Mg* and *Mt* in the field without the effects of confounding factors such as water temperature and pollution levels.

If individuals of *Mg* were better competitors that *Mt* in the subtidal zone on docks where their distributions overlap, we expected that the survival and growth of *Mt* would be reduced in the mixed species cages in relation to the single-species cages (interspecific competition > intraspecific competition). However, the results of our experiments show that *Mg* had greater growth than *Mt* in the mixed-species cages, but growth of both species was not significantly different between the single-species and mixed-species cages. This result indicates that neither species was having a strong competitive effect on the survival or growth of the other species.

If *Mg* is not limiting the survival or growth of *Mt* in the low subtidal zone on docks, a variety of other factors may limit the frequencies of *Mt* in this zone. The distribution patterns of *Mg* and *Mt* may be due to larval settlement behavior and viability as well as post-settlement movement. In a study of larval settlement of *Mg* and *M. edulis,* Gilg and Hilbish (2000) found that mussel larvae of both species did not settle out of the plankton in particular zones. Instead, their results suggest that mussel species distribution patterns were caused by differential selection on the two species in the different tidal zones. It is possible, however, that *Mg* and *Mt* in Puget Sound preferentially settle out of the plankton in certain tidal zones. Freeman et al. (2002) found that the largest percentage of *Mt* larvae settled at the surface, which is consistent with the distribution pattern of this species near the surface on docks and in the intertidal zone. Caceres-Martinez and Figueras (1998) reported that *Mg* recruit at slightly higher densities at 5-10 m than at 1 m depths, which is consistent with the deeper distribution pattern of *Mg* than *Mt* on docks. However, it is also possible that both species settle in all zones but that the early post-settlement larvae experience differential survival or movement that leads to the observed distributions. The settlement patterns of *Mg* and *Mt* in the field should be studied to determine their importance in determining adult distribution patterns.

Rensel (2005) observed that *Mt* individuals are highly mobile post-settlement and exhibit upward movement when provided with a vertical surface, whereas *Mg* remain relatively stationary. Hunt and Scheibling (2002) found that small *Mt* and *M. edulis* individuals displayed post-settlement movement. *Mt* individuals that settle in the low subtidal zone may move up into the swash zone for several reasons. *Mg* may monopolize available space in the low subtidal, making it beneficial for *Mt* to move out of the area. In addition, *Mt* may seek a refuge from common sea star predators such as *Pisaster ochraceus* and *Evasterius troschelii* by moving to the swash zone where it could be more difficult for sea stars to feed. The fast growth rates and large size of *Mg* and hybrids (Anderson et al 2002) may make them less susceptible to predators and alter predator-prey relationships in the intertidal and subtidal zones.

The results of this experimental study showed that *Mg* had higher survival and growth than *Mt* in all habitats except the high intertidal, suggesting that *Mg* has the potential to outcompete *Mt* in the low intertidal and low subtidal zones in areas of high salinity. Further research is required to determine whether *Mg* or hybrids between *Mg* and *Mt* will have a significant influence on populations of the native mussel *Mt* in Puget Sound.

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