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UNIVERSITY OF SAN DIEGO

San Diego

Distribution patterns of the invasive mussel *Arcuatula senhousia* in Mission Bay, San Diego, California: Effects of sediment grain size and byssus thread production on predation

by

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2022

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DEDICATION

To Aunt Julie who instilled in me forever an insatiable curiosity for the natural world.

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Table of Contents

List of Tables	viii
List of Figures.....	ix
Abstract	1
Chapter 1: Introduction	3
References	12
Chapter 2: Increased burrowing and byssus production in fine sediments may influence the distribution patterns of the invasive mussel <i>Arcuatula senhousia</i> in Mission Bay, San Diego, California.	18
Introduction	18
Methods	21
Results	30
Discussion	32
Tables and Figures	40
References	74
Chapter 3: Conclusion	84
Figures	88
References	90
Appendix.....	92

List of Tables

Table 2.1	Sediment grain size distribution of burned experimental sediment	39
Table 2.2	Summary of mortality experiment runs	41
Table 2.3	Summary of burrowing experiment runs	43
Table 2.4	% mortality two-way ANOVA	45
Table 2.5	% burial two-way ANOVA	47
Table 2.6	Mortality experiment byssus production three-way ANOVA	49
Table 2.7	Burrowing experiment byssus production Kruskal-Wallis test	51

LIST OF FIGURES

Figure 1.1 Mission Bay map with major creeks	8
Figure 2.1 Mission Bay map with sediment and <i>A. senhousia</i> distribution and sediment collection sites	53
Figure 2.2 Experimental beaker setup	55
Figure 2.3 Mortality experiment setup	57
Figure 2.4 Burrowing experiment setup	59
Figure 2.5 Relationship between sediment grain size and <i>A. senhousia</i> abundance	61
Figure 2.6 Sediment selection results	63
Figure 2.7 % mortality by run and treatment	65
Figure 2.8 % burial by run and treatment	67
Figure 2.9 Byssus production by run and treatment for the mortality experiment	69
Figure 2.10 Byssus production by run and treatment for the burrowing experiment	71
Figure 3.1 Conceptual diagram	87

ABSTRACT

The ability of bivalves to avoid predation by using defensive behaviors such as burrowing and byssus production may vary depending on the sediment characteristics of a given habitat. The varying sediment characteristics that change with water velocity within estuaries may influence the distribution of bivalves and limit them to areas that optimize their ability to defend against predators. We examined the distribution patterns of the invasive Asian date mussel *Arcuatula senhousia* relative to the sediment grain size distribution in Mission Bay, an urban estuary located in San Diego, California, USA. Mussels and sediment were collected using an Ekman grab at 76 stations sampled by University of San Diego students during October 2015, 2016, 2018, 2019, 2021, and March 2017. In 2020-2021, we also conducted a series of complementary laboratory experiments to evaluate the sediment preferences of *A. senhousia* and how *A. senhousia* mortality, burrowing behavior and byssal thread production was impacted by water temperature, sediment grain size, and predation by a native muricid snail (*Pteropurpura festiva*).

A. senhousia was associated with fine-grained sediment, in particular silts (<62.5 μm), that were most abundant in the back of the bay. Mussels also experienced lower mortality, burrowed deeper, and produced more byssus in fine-grained sediment, particularly in warmer water. These results likely indicate that sediment grain size in Mission Bay, in addition to the previously documented gradient in predator abundance, plays an important role in the distribution of mussels. Furthermore, given the strong effect of temperature on *A. senhousia*

mortality and byssus production that we observed, warming of Mission Bay related to climate change could enhance overall mortality for *A. senhousia*, irrespective of sediment type and byssal conditions, potentially shifting predator-prey dynamics.

CHAPTER 1: Introduction

Nonnative species are increasing in abundance throughout the world, and biological invasions now represent one of the most serious threats to the integrity of ecosystems (Vitousek et al. 1997). Exotic species can have a wide range of ecological interactions within invaded ecosystems, including competition with natives, alteration of the physical nature of habitats, or predation upon resident biota (Crooks and Khim 1999, Parker et al. 1999, Ruiz et al. 1999). Suspension-feeding bivalves are ubiquitous invaders of marine, estuarine, and freshwater ecosystems. Once established, introduced bivalves often achieve numerical dominance relative to natives (Grosholz 2005, Ruesink et al. 2005) and compete with them by altering the magnitude and seasonal dynamics of phytoplankton primary production (Alpine and Cloern 1992), or modifying the physical or biogeochemical conditions of the substrate and water column (Sousa et al. 2009).

In southern California estuaries, introduction of the Asian mussel, *Arcuatula* (formerly known as *Musculista*) *senhousia*, has been implicated in profound changes to native bivalve assemblages over the past 50 years (Crooks 1998, Dexter and Crooks 2000, Crooks 2001). *A. senhousia* is referred to as an “ecosystem engineer,” defined as the direct or indirect control of resource availability mediated by the organism's ability to cause physical changes in abiotic or biotic materials (*sensu* Jones et al. 1997). *A. senhousia* engineers ecosystems by creating a complex network of byssal threads, especially in mat-forming aggregations, that increase habitat complexity and sedimentation, and modify other physical characteristics of its surrounding environment including

oxygen and nitrogen content (Morton 1974, Creese et al. 1997, Reusch and Williams 1998, Crooks and Khim 1999, Takenaka et al. 2018). Such increased habitat complexity can result in increased biotic diversity/abundances, but is species- or functional group-specific (Crooks 2002a). For example, response to *A. senhousia*'s structurally complex byssal mats depends on size of associated biota: small invertebrates tend to live in higher abundances within the mat matrix while larger native suspension-feeding clams as well as eelgrass are inhibited by it (Crooks 2002a). Because mussels are so dense within the mats, there is little physical space for other species to inhabit and only smaller species or those which are able to readily move through the byssal threads (e.g., errant polychaetes) can live in the habitat created by *A. senhousia* (Creese et al. 1997).

A. senhousia is a short-lived mytilid mussel native to east Asia though it has successfully invaded New Zealand, Australia, the Mediterranean, and the Pacific coast of the United States. *A. senhousia* is a small mussel with a maximum length around 30mm but is most commonly 10-25mm in length and up to 12mm in width (GISD 2015). They have a smooth, thin shell and a well-developed byssus is used to construct a cocoon (also referred to as a “nest”) which may also contain sediment and protect the shell (GISD 2015). *A. senhousia* burrows into the sediment leaving only its posterior end protruding, allowing its siphons access to the water to enable suspension feeding (GISD 2015). *A. senhousia* eggs and larvae are planktonic and remain in the plankton for 45-55 days and can reach adult size within 9 months and growing up to 25mm within a year (GISD 2015). Life span is thought to be between 18 and 24 months (GISD 2015). *A. senhousia*

is an opportunistic species which can be found from intertidal to subtidal habitats (to a depth of 20m) and on soft or hard substrata (GISD 2015). *A. senhousia* possesses a suite of characteristics that allow it to thrive in fine-sediment habitats, including a style sac separate from the gut, which facilitates the processing of turbid water, and large labial palps and powerful rejectory currents, which aid in the removal of sediment (Morton 1974). However, it is also capable of fouling wharf pilings and other man-made structures (GISD 2015).

In Mission Bay, San Diego, California, *A. senhousia* attains a maximum length of about 32 mm in less than 2 years (Crooks 1996). Its thin shell aids the mussel in fast growth, and growth might vary seasonally in Mission Bay as a function of temperature or food availability (especially the latter in winter months) (Crooks 1996). Highly erratic distribution and abundance patterns of the mussel have been observed in San Diego Bay (Crooks 1992), Asia (Morton 1974, Mukai 1974) and New Zealand (Creese et al. 1997). Within its native range, densities of *A. senhousia* can exceed several thousand m⁻² (Kawaguchi and Shirai 1944, Morton 1974, Kulikova 1978, Sun and Tang 1989). Mussel densities can be up to 12,370m⁻² and 8,600m⁻² in San Diego Bay and Mission Bay, respectively, although densities lower than this are more common (Crooks 1992, Crooks 1996). *A. senhousia* is often patchily distributed but it remains unclear whether distributions result from preferential settlement with conspecifics, or from other factors such as the physical nature of the substrate, small-scale hydrodynamics, or the high predation risk of individuals that are not in clumps, which are all common factors affecting bivalve distributions (Woodin 1976, Eckman 1983,

Butman 1987). It has been suggested that a survivorship advantage may be afforded to those organisms living in aggregations (Bertness and Grosholz 1985, Lin 1991). The spawning and recruitment patterns of *A. senhousia* in both San Diego and its native Asia are inconsistent, with the magnitude of recruitment events varying substantially on relatively small temporal and spatial scales (Crooks 1996). Thus, *A. senhousia* is short-lived, suffers high mortality, can experience very high, but often variable population sizes, is small in body size, grows quickly, and has a long planktonic dispersal stage; all characteristics that are common to opportunistic species (Crooks 1996).

Exotic species can be eaten by native species, thus serving as a food resource for resident biota that can potentially limit the abundance of the invader (Crooks 2002b). This control of exotics by the feeding activities of native species represents a potentially important form of "ecological resistance" to invasions, whereby the extent and impact of invaders can be limited (Reusch 1998). In San Diego, native predators are responsible for a significant mortality in populations of the invasive bivalve *A. senhousia* (Reusch 1998). *A. senhousia* was not only consumed by native predators, but was preferred over at least one native bivalve species by the most conspicuous predator, a muricid gastropod, the festive murex *Pteropurpura festiva* (Reusch 1998). Several other predators native to southern California consume Asian mussels, including fishes such as yellowfin croaker (*Umbrina roncadore*), spotfin croaker (*Roncadore stearnsii*), and sargo (*Anisotrmmus davidsonii*) (Crooks 2002b), the California spiny lobster *Panulirus interruptus* (Reusch 1998, Cheng and Hovel 2010, Castorani and Hovel 2015), and wading

birds such as the willet (*Catoptrophorus semipalmatus*) and marbled godwit (*Limosa fedoa*) (Crooks 2002b). Asian mussels may experience extremely high mortality rates due to native predators in the subtidal and intertidal zone of Mission Bay however, over short time scales, proportional mortality appears to decrease with mussel density, and increasing eelgrass habitat structure seems to alter the behavioral response of native predators to Asian mussels (Kushner and Hovel 2006). Additionally, given that *A. senhousia* changed its feeding, burrowing, and aggregating behaviors in response to chemical cues from injured conspecifics and three prominent predators native to southern California (Castorani and Hovel 2016), introduced *A. senhousia* are not naïve to the threat of predation from native lobsters, drilling snails, or stingrays, which are among the most important agents of biotic resistance in San Diego estuaries (Reusch 1998, Crooks 2002b, Cheng and Hovel 2010).

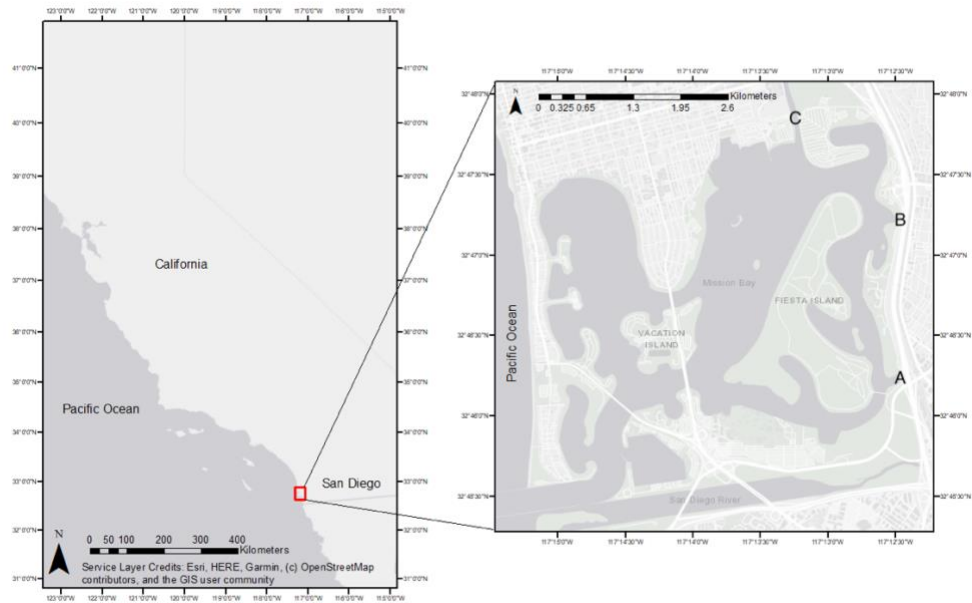


Fig. 1.1 Mission Bay study site (red box) in San Diego, California, USA with the locations of Tecolote Creek (A), Cudahy Creek (B), and Rose Creek (C) labeled.

Mission Bay is a highly modified urban estuary that was developed from a natural lagoon in the late nineteenth century through a sequence of engineering actions (Gabrielson 2002). The eastern portions of Mission Bay (“back-bay”) receive inflow from small creeks (Rose, Tecolote, Cudahy; Fig. 1) and tidal currents are weak (Largier et al. 2003, Kaufmann et al. 2004). The western portions of Mission Bay (“front-bay”) have limited natural freshwater inflow and are characterized by cooler ocean waters (Largier et al. 2003, Kaufmann et al. 2004). Storm-drains are located throughout Mission Bay and are diverted to the city’s wastewater facilities during dry weather; However, during rain, these diversions do not operate, and water flows directly into the Bay (Largier et al. 2003). This, combined with long residence times and often retentive dispersion of contaminants in the back-bay, make this area a water quality concern (Largier et al. 2003). Tidal currents are most important in the exchange of water in Mission Bay and the outer parts of Mission Bay are very well flushed and exhibit water properties very similar to those in the ocean off Mission Beach (Largier et al. 2003). With distance from the mouth of the bay, water residence times increase and waters may be retained in the region off Tecolote Creek for over a week with limited dilution, but with waters in the back-bay having been in Mission Bay for some time prior to being transported there the total time in the Bay may be closer to a month (Largier et al. 2003). Sediment characteristics in the Bay reflect this flow pattern as percentage of fine sediments increases with distance from the Bay mouth (Kaufmann et al. 2004). Finer sediments in Mission Bay also tend to be associated with higher water content, higher total organic carbon, and higher

metal concentrations (specifically Cu, Pb, Zn) (Kaufmann et al. 2004). The back-bay region is therefore categorized by fine, organic-rich sediments, and higher freshwater and nutrient/contaminant input (relative to the rest of the bay), all of which may affect which species can utilize back-bay habitats.

In Mission Bay, *A. senhousia* tends to be more abundant in back-bay regions (Dexter 1983, Crooks 1996, Dexter and Crooks 2000, Cheng and Hovel 2010). Some possible explanations for this patchy distribution include preferential settlement with conspecifics, or results from factors such as the physical nature of the substrate, small-scale hydrodynamics, or the high predation risk of individuals that are not in clumps (Crooks 1996). One common explanation is that the distribution of *A. senhousia* in San Diego coastal embayments may be largely controlled by predation (Reusch 1998, Kushner and Hovel 2006, Cheng and Hovel 2010, Castorani and Hovel 2015). In Mission Bay, the pattern of biotic resistance along a steep environmental gradient was strongly aligned with high densities of native predators at front bay sites, though sediment instability may also play a role in limiting Asian mussels from this area (Cheng and Hovel 2010). Although hypoxia can also have strong effects on bivalve distribution and abundance (Mistri 2002, Altieri and Witman 2006), it is unlikely to explain the spatial mussel density gradient in Mission Bay because mussels were abundant in the back of the bay where hypoxia is most likely, and they were absent from the front bay where tidal forcing should keep water well oxygenated (Cheng and Hovel 2010). Though it is still unclear what restricts predators to front-bay sites, (Cheng and Hovel 2010) suggest these predators may be unable to tolerate

extreme environmental conditions in the back-bay relative to their invasive prey, as predicted by the consumer stress model (Menge and Sutherland 1987, Menge and Olson 1990). Biotic resistance may therefore be an important process that restricts invader distributions under conditions of low environmental stress, whereas invasive prey may obtain a refuge from predation in more stressful and perturbed habitats where their predators are unable to persist (Cheng and Hovel 2010). Given the gradient in abiotic conditions in Mission Bay, mussel distribution patterns may also reflect survival in varying environmental conditions. It remains unclear if sediment grain size impacts burrowing and anchoring ability of this thin-shelled bivalve, though a reduced ability of certain clams to burrow has been observed in sandy sediments (Alexander et al. 1993) and a reduced ability of *A. senhousia* to burrow in sandy sediments was observed in a preliminary study done by a marine ecology class taught by Nathalie Reyns at the University of San Diego. In addition, previous work (Dexter 1983, Crooks 1996, Reusch 1998, Dexter and Crooks 2000, Cheng and Hovel 2010, Castorani and Hovel 2015) did not address the role of byssal thread cocoons when evaluating predation risk. However, recent work (Zhao et al. 2020) suggests the importance of byssal threads in mitigating predation risk. Thus, this thesis seeks to better understand how the combination of sediment grain size and byssus production/condition may be affecting predation on *A. senhousia*.

REFERENCES

- Alexander, R. R., R. J. Stanton Jr, and J. R. Dodd. 1993. Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*:289-303.
- Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and oceanography* **37**:946-955.
- Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. *Ecology* **87**:717-730.
- Bertness, M. D., and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* **67**:192-204.
- Butman, C. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol* **25**:113-165.
- Castorani, M. C., and K. A. Hovel. 2015. Invasive prey indirectly increase predation on their native competitors. *Ecology* **96**:1911-1922.
- Castorani, M. C., and K. A. Hovel. 2016. Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. *Biological Invasions* **18**:169-181.
- Cheng, B. S., and K. A. Hovel. 2010. Biotic resistance to invasion along an estuarine gradient. *Oecologia* **164**:1049-1059.

- Creese, R., S. Hooker, S. De Luca, and Y. Wharton. 1997. Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **31**:225-236.
- Crooks, J. 1992. The ecology of the introduced bivalve, *Musculista senhousia*. Mission Bay, San Diego. MS Thesis, San Diego State University, San Diego, California.
- Crooks, J. A. 1996. The population ecology of an exotic mussel, *Musculista senhousia*, in a southern California bay. *Estuaries* **19**:42-50.
- Crooks, J. A. 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine ecology Progress series* **162**:137-152.
- Crooks, J. A. 2001. Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biological Invasions* **3**:23-36.
- Crooks, J. A. 2002a. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**:153-166.
- Crooks, J. A. 2002b. Predators of the invasive mussel *Musculista senhousia* (Mollusca: Mytilidae). *Pacific Science* **56**:49-56.
- Crooks, J. A., and H. S. Khim. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology* **240**:53-75.

- Dexter, D. 1983. Soft bottom infaunal communities in Mission Bay. California Fish and Game **69**:5-17.
- Dexter, D. M., and J. A. Crooks. 2000. Benthic communities and the invasion of an exotic mussel in Mission Bay, San Diego: a long-term history. Bulletin of the Southern California Academy of Sciences **99**:128-128.
- Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment 1. Limnology and Oceanography **28**:241-257.
- Gabrielson, E. 2002. Mission Bay Aquatic Park: the history of planning and land acquisitions. The Journal of San Diego History **48**:1-7.
- Global Invasive Species Database (GISD) 2015. Species profile *Musculista senhousia*. Available from:
<http://www.iucngisd.org/gisd/species.php?sc=1031> [Accessed 06 September 2017]
- Grosholz, E. D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proceedings of the National Academy of Sciences **102**:1088-1091.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Ecosystem engineering by organisms: why semantics matters. Trends in Ecology & Evolution **12**:275.
- Kaufmann, R., B. Stransky, J. Rudolph, D. Elliott, R. Griggs, J. Kittinger, B. Swope, J. Bolender, M. Boudrias, and H. Sarabia. 2004. Mission Bay Water and Sediment Testing Project, Final Report. City of San Diego.

- Kawaguchi, M., and K. Shirai. 1944. Studies on Bays of Setonakai, I. Benthic Community of Kasaoka Bay and a Quantitative Evaluation of *Brachidontes senhousia* as an Unutilized Natural Resource. *Contributions in Physiology and Ecology*, Kyoto Imperial University **8**:1-18.
- Kulikova, V. 1978. Morphology seasonal population dynamics and settlement of larvae of the bivalve mollusk *Musculista senhousia* in the Busse lagoon (South Sakhalin). *Biologiya Morya-Marine Biology*:61-66.
- Kushner, R. B., and K. A. Hovel. 2006. Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California. *Journal of Experimental Marine Biology and Ecology* **332**:166-177.
- Largier, J., M. Carter, M. Roughan, D. Sutton, J. Helly, B. Lesh, T. Kacena, P. Ajtai, L. Clarke, and D. Lucas. 2003. Mission Bay Contaminant Dispersion Study Final Report. City of San Diego, California.
- Lin, J. 1991. Predator-prey interactions between blue crabs and ribbed mussels living in clumps. *Estuarine, Coastal and Shelf Science* **32**:61-69.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology & Evolution* **5**:52-57.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**:730-757.

- Mistri, M. 2002. Ecological characteristics of the invasive Asian date mussel, *Musculista senhousia*, in the Sacca di Goro (Adriatic Sea, Italy). *Estuaries* **25**:431-440.
- Morton, B. 1974. Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhausia* Benson (Bivalvia, Mytilidae).
- Mukai, H. 1974. Ecological studies on distribution and production of some benthic animals in the coastal waters of central Inland Sea of Japan.
- Parker, I. M., D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, and J. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological invasions* **1**:3-19.
- Reusch, T. B. 1998. Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. *Marine Ecology Progress Series* **170**:159-168.
- Reusch, T. B., and S. L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. *Oecologia* **113**:428-441.
- Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual review of ecology, evolution, and systematics* **36**.

- Ruiz, G. M., P. Fofonoff, A. H. Hines, and E. D. Grosholz. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and oceanography* **44**:950-972.
- Sousa, R., J. L. Gutiérrez, and D. C. Aldridge. 2009. Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* **11**:2367-2385.
- Sun, D., and Z. Tang. 1989. Ecological characteristics of macrobenthos of the Huanghe river estuary and adjacent waters. *Studia Marina Sinica* **30**:260-274.
- Takenaka, R., T. Komorita, and H. Tsutsumi. 2018. Accumulation of organic matter within a muddy carpet created by the Asian date mussel, *Arcuatula senhousia*, on the Midori River tidal flats, Japan. *Plankton and Benthos Research* **13**:1-9.
- Vitousek, P. M., C. M. D'antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*:1-16.
- Woodin, S. A. 1976. Adult-Larval interactions in dense infaunal assemblages: Patterns of abundance.
- Zhao, L., J. Liang, J. Liang, B. Liu, Y. Deng, X. Sun, H. Li, Y. Lu, and F. Yang. 2020. Experimental study of transgenerational effects, pH and predation risk on byssus production in a swiftly spreading invasive fouling Asian mussel, *Musculista senhousia* (Benson). *Environmental Pollution* **260**:114111.

**CHAPTER 2: Increased burrowing and byssus production in fine sediments
may influence the distribution patterns of the invasive mussel *Arcuatula
senhousia* in Mission Bay, San Diego, California.**

2.1 Introduction

Biological invasions represent one of the most serious threats to the integrity of ecosystems with exotic species competing with native species, altering the physical nature of habitats, or preying upon resident biota (Vitousek et al. 1997, Crooks and Khim 1999, Parker et al. 1999, Ruiz et al. 1999). Additionally, suspension-feeding bivalves, which have become ubiquitous invaders of marine, estuarine, and freshwater ecosystems, often achieve numerical dominance relative to native species (Grosholz 2005, Ruesink et al. 2005) and compete by altering the magnitude and seasonal dynamics of phytoplankton primary production (Alpine and Cloern 1992), or modifying the physical or biogeochemical conditions of the substrate and water column (Sousa et al. 2009).

In southern California, USA, estuaries, introduction of the Asian mussel, *Arcuatula* (formally known as *Musculista*) *senhousia*, has been implicated in profound changes to native bivalve assemblages over the past 50 years (Crooks 1998, Dexter and Crooks 2000, Crooks 2001). *A. senhousia* acts as an “ecosystem engineer” by creating a complex network of byssal threads anchoring them to the sediment, resulting in mat-forming aggregations that increase habitat complexity and sedimentation, and modify other physical characteristics of the surrounding environment including oxygen and nitrogen content (Morton 1974, Creese et al. 1997, Reusch and Williams 1998, Crooks and Khim 1999, Takenaka et al. 2018).

A. senhousia grows as much as 25 mm in their first year, with such fast growth likely aided by their thin shell (Crooks 1996). In addition to rapid growth, within their native range, densities of *A. senhousia* can exceed several thousand m⁻² (Kawaguchi and Shirai 1944, Morton 1974, Kulikova 1978, Sun and Tang 1989). For example, densities in southern California have been observed of up to 12,370m⁻² in San Diego Bay and an extraordinary 170,000m⁻² in Mission Bay in the summer of 1995 following unusually heavy rainfall and strong red tides (Crooks 1992, Crooks 1996, Crooks and Soulé 1999). Highly erratic distribution and abundance patterns of the mussel have also been observed in Asia (Morton 1974, Mukai 1974) and New Zealand (Creese et al. 1997). Overall, *A. senhousia* is short-lived, suffers high mortality, can experience very large, but often variable population sizes, is small in body size, and grows quickly; all characteristics common to opportunistic species (Crooks 1996).

In Mission Bay, a highly modified urban estuary, *A. senhousia* tends to be more abundant in the eastern “back-bay” regions where tidal currents are weak (Dexter 1983, Crooks 1996, Dexter and Crooks 2000, Largier et al. 2003, Cheng and Hovel 2010). The western “front-bay” portions of Mission Bay are well flushed by tidal currents, have limited natural freshwater inflow, and are characterized by cooler ocean waters (Largier et al. 2003, Kaufmann et al. 2004). With distance from the mouth of the bay, tidal influence and flow decrease, and sediment characteristics in the bay reflect this flow pattern as percentage of fine sediments increases with distance from the bay mouth (Largier et al. 2003, Kaufmann et al. 2004). Finer sediments in Mission Bay also tend to be associated

with higher water content, higher total organic carbon, and higher metal (specifically Cu, Pb, Zn) concentrations (Kaufmann et al. 2004). The back-bay region is therefore categorized by fine, organic-rich sediments, has higher freshwater, and consequently, nutrient/contaminant input relative to the rest of the bay (Kaufmann et al. 2004), all of which may affect which species can utilize back-bay habitats. *A. senhousia* is often patchily distributed but it remains unclear whether distributions result from preferential settlement with conspecifics, or from other factors such as the physical nature of the substrate, small-scale hydrodynamics, or the high predation risk of individuals that are not in clumps, which are known to affect bivalve distributions (Woodin 1976, Eckman 1983, Butman 1987).

One explanation is that the distribution of *A. senhousia* may be largely controlled by predation (Reusch 1998, Kushner and Hovel 2006, Cheng and Hovel 2010, Castorani and Hovel 2015). *A. senhousia* is not only consumed by native predators including fishes (Crooks 2002), spiny lobster (Reusch 1998, Cheng and Hovel 2010, Castorani and Hovel 2015), and wading birds (Crooks 2002); but in one study, was preferred over at least one native bivalve species by the most conspicuous predator, a muricid gastropod, the festive murex *Pteropurpura festiva* (Reusch 1998). However, given that *A. senhousia* change their feeding, burrowing, and aggregating behaviors in response to chemical cues from conspecifics injured by native lobsters, drilling snails, and stingrays (Castorani and Hovel 2016), *A. senhousia* are not naïve to the threat of predation (Reusch 1998, Crooks 2002, Cheng and Hovel 2010). In Mission Bay, high

densities of native predators at front-bay sites results in greater potential for “biotic resistance”, whereby these predators control the invasion success of *A. senhousia* (Cheng and Hovel 2010). Furthermore, some predators may be unable to tolerate extreme environmental conditions in the back-bay relative to their invasive prey, as predicted by the consumer stress model (Menge and Sutherland 1987, Menge and Olson 1990). Biotic resistance may therefore be an important process that restricts invader distributions under conditions of low environmental stress, whereas invasive prey may obtain a refuge from predation in more stressful and perturbed habitats where their predators are unable to persist (Cheng and Hovel 2010).

It remains unclear if sediment grain size impacts burrowing and anchoring ability of this thin-shelled bivalve, as burrowing success for other bivalve species can be determined by sediment characteristics (Alexander et al. 1993, De la Huz et al. 2002). In addition, previous work (Dexter 1983, Crooks 1996, Reusch 1998, Dexter and Crooks 2000, Cheng and Hovel 2010, Castorani and Hovel 2015) did not address the role of byssal threads when evaluating predation risk. However, a more recent study (Zhao et al. 2020) suggests the importance of byssal threads in reducing predation risk. Thus, the objective of this study was to determine whether *A. senhousia* mortality, burrowing behavior, and byssus production varied with predation risk and sediment grain size.

2.2 Methods

2.2.1 Field Study of Arcuatula senhousia and Sediment Grain Size Distribution

To document the spatial distribution of *A. senhousia* and sediment grain size in Mission Bay, we used samples collected October 2015, 2016, 2018, 2019, 2021 and March 2017 by University of San Diego students taking EOSC 301: Research Applications course. A Wildco standard (15.24 x 15.24 x 15.24 cm) Ekman grab was used to collect two replicate benthic samples at 76 different stations throughout Mission Bay with a minimum of 12 and a maximum of 48 of those stations sampled each semester (Fig. 2.1). To collect *A. senhousia*, the grab sample was rinsed through a 1mm box sieve, and the remaining macrofauna was placed into a reusable plastic bag for transport to the lab in a cooler on ice. Two replicate macrofauna samples were collected at each station, and samples were frozen (~ 2 weeks) until *A. senhousia* were identified and counted. *A. senhousia* counts were standardized to abundance ($\#/m^2$), and values from the two replicates were averaged by station.

To collect sediments at each station, approximately 50g of sediment from each replicate grab (n=2) was placed into a quart-sized reusable plastic bag and transported to the lab. Sediment was dried and analyzed for mean particle size and composition (% clay, silt, and sand) using a CILAS 1190 Particle Size Analyzer laser particle sorter (LPS). Mean sediment grain diameter (in microns) was averaged by station from the two replicates.

To compare mussel and sediment grain size distributions, mean *A. senhousia* abundance and sediment grain size were mapped using ArcGIS ([GIS software]. Version 10.0. Redlands, CA: Environmental Systems Research Institute, Inc., 2010.) An inverse distance weighted (IDW) interpolation in the

Spatial Analyst geoprocessing tool pack was used to visualize the spatial gradient in sediment grain size. Additionally, the Wentworth scale was used to categorize sediment as silt ($\leq 62.5\mu\text{m}$), very fine sand ($62.5\text{--}125\mu\text{m}$), fine sand ($125\text{--}250\mu\text{m}$), medium sand ($250\text{--}500\mu\text{m}$) and coarse sand ($500\text{--}1000\mu\text{m}$), and *A. senhousia* abundance and mean sediment grain sizes were averaged within each sediment category. *A. senhousia* abundance was log-transformed to meet ANOVA assumptions (Shapiro-Wilks test: $p=0.97$, Levene's test: $p=0.38$). A one-way ANOVA and Tukey's HSD Test for multiple comparisons were used to determine if there were significant differences in *A. senhousia* abundance by sediment category. All statistical analyses were performed using SPSS (IBM Corp. Released 2021. IBM SPSS Statistics for Windows, Version 28.0. Armonk, NY: IBM Corp) or R studio (v4.0.3; R Core Team 2020).

Laboratory Experiments

2.2.2 Sediment and Mussel Collections

Coarse-grained sediment was collected from the western, front-bay portion of Mission Bay near the mouth of the estuary (where mussels were least prevalent during the field study) and fine sediment was collected from the north-western portion of Mission Bay (where mussels were prevalent, see Fig. 2.1). To remove organic matter, all sediment was burned prior to experimentation in a muffle furnace at 550°C for four hours. To verify that the sediment grain size

distribution was preserved throughout experimentation, the LPS was used to calculate the % clay, silt and sand used during each experimental run (Table 1).

Mussels were collected from the subtidal sediments of Mission Bay using the same Ekman grab employed during the field study described above. Contents of the grab were placed in a 1mm mesh box sieve, and gently rinsed with seawater. An effort was made to collect individual mussels as well as mussel aggregations formed by a larger collective byssal network. Once isolated, the mussels were stored in a cooler filled with seawater and transported to the lab. Based on the experiment (see below), mussels were separated into three byssus classifications: “naked” mussels (either collected without byssus, or with byssal threads carefully removed with scissors), “cocoon” mussels with intact and distinct byssal cocoons (individuals surrounded by byssus), and “mat” mussels whose byssal threads were left intact and interconnected to some degree to other mussels.

All experiments were conducted in a temperature-controlled room at the University of San Diego, where environmental conditions were set to reflect the ambient water temperature recorded on the day of mussel collection

2.2.3 Sediment Selection Experiment

To assess whether mussels prefer coarse or fine-grained sediment, a sediment selection experiment was conducted. The experiment was run twice at 20°C. For each experimental run, five 1000mL beakers were divided in half using a rectangular piece of plastic secured to the bottom of the beaker with tape, and each side filled with 150mL of coarse or fine-grained sediment (Fig. 2.2). The

beakers were carefully filled to the 1000mL line with seawater, to prevent mixing of the sediments. An air stone was suspended in the water above the sediment surface. Ten mussels were placed in each beaker, with five evenly distributed on each sediment type (Fig. 2.2). Every 24h for 6d, the number of mussels found atop or within each sediment type was recorded, as well as the number of mussels found along the beaker walls or on the air stone above each sediment type.

The proportion of mussels on and above each sediment type was used to examine mussel sediment selection. Proportions were arcsine, square root-transformed to reduce the heterogeneity in variances (Levene's test: $p=0.33$), and distributions were normal (Shapiro-Wilks test: $p=0.88$). A paired t-test was used to compare the proportion of mussels associated with each sediment type.

2.2.4 Mortality Experiment

Experiments were conducted to quantify mussel mortality with respect to byssus classification (naked, cocoon, mat), sediment grain size (coarse, fine, and a “no sediment” control group), and presence/absence of a predator. We ran four mortality experiments: 2 during the winter and 2 during the summer (Table 2.2). Each experiment consisted of fifty-four (three replicates for each mussel classification; but see Table 2.2 for details when not all planned replicates were completed), 1000mL beakers that contained 300mL of sediment and seawater of ambient Mission Bay salinity (~34) filled to the 1000mL mark for sediment treatments, and with only 1000mL of seawater for no sediment controls (Fig. 2.3). Each beaker received an individual air stone to maintain oxygen content. Water

temperature and salinity were checked and maintained daily using a Milwaukee MA887 digital refractometer.

Five mussels were randomly scattered atop the sediment in each beaker, equivalent to 633 mussels m⁻², which is within the range of mussel densities commonly found in Mission Bay (Crooks 1996; Fig. 2.3). The drilling gastropod, *P. festiva*, one of the dominant native predators of *A. senhousia* in Mission Bay (Reusch 1998, Cheng and Hovel 2010, Castorani and Hovel 2015), was used in the predator treatments. *P. festiva* were collected along the rock jetty near Ventura Point in Mission Bay (32.770894, -117.243479) and held in a holding tank with the same temperature and salinity as the experimental beakers. Snails were fed mussels *ad lib.* prior to experimentation until 48 hours prior to the start of each experiment when they underwent a short period of starvation based on another *A. senhousia* study using predatory crabs (Zhao et al. 2020).

For each experimental run, date/temperature was applied as a blocking variable, and treatments (byssus classification, sediment grain size, predator presence/absence were assigned to beakers (experimental unit), and randomly placed on a shelf in the temperature-controlled room). After three days, mussel mortality (number of dead mussels/beaker) was quantified. Mussels were considered dead if the shell was open and deaths were attributed to the snail if there was also a drill hole present in the shell. Mussel mortality was low (total mortality = 0.69%) in the no-predator control treatments, and thus these data were excluded from the analysis to avoid a bimodal distribution. Mussels classified as cocoon and nest treatments were combined and re-classified as ‘nest’ since

cocooned mussels almost always joined together partially or completely by the end of the three-day experiment. Despite numerous transformations, the mortality data did not meet the assumptions of a randomized block three-way ANOVA to simultaneously test the effects of temperature, sediment type, and byssal classification. Thus, a non-parametric Kruskal-Wallis test was used to determine if % mussel mortality varied by treatment. Given a significant temperature effect on mussel mortality (Kruskal-Wallis: $H_{(1)} = 15.45$, $p < 0.001$), runs were combined by temperature and analyzed separately. As such, it was possible to run a two-way ANOVA for the cold runs, with sediment and byssus classification as factors after applying an arcsine, square-root-transformation to % mortality to meet ANOVA assumptions (Shapiro-Wilks: $p = 0.88$; Levene's test: $p = 0.14$). Warm runs did not meet ANOVA assumptions, so a Kruskal-Wallis test was used to analyze sediment and byssus classification treatments separately.

Byssal thread production of naked mussels was also measured at the end of the mortality experiment to determine if production varied by temperature, sediment type and predator exposure. Byssal threads were carefully removed from all naked mussels in each beaker and left to dry (byssal threads grouped by beaker). Total organic content of the byssal threads was measured using a loss on ignition (LOI) technique, in which the dried threads were weighed using a Sartorius BP221S analytical balance with 0.001g precision, burned in a muffle furnace at 550°C for 2 hours, then re-weighed to calculate the loss of organic carbon from byssal threads (%LOI). Since mussel sizes varied slightly in each experimental run and treatment (Tables 2.2, 2.3), %LOI for each beaker was

standardized by mussel size. Estimated dry mass of each mussel was calculated using the equation derived by Reusch and Williams (1998), where:

$$\text{mussel dry mass (in grams)} = 0.0763 \times 10^{-3} \times \text{mussel length(mm)}^{2.67}.$$

Then, %LOI per beaker was divided by the total estimated mussel mass per beaker and used as a proxy for byssus thread production (%LOI g⁻¹). The response variable (%LOI g⁻¹) was log-transformed to meet the homogeneity of variances assumption (Levene's test, $p = 0.94$) and a three-way ANOVA was used with temperature (warm vs. cold), sediment (coarse, fine, no sediment), and predator (presence vs. absence) as factors. A Tukey HSD post-hoc test was used to determine where differences existed between levels of significant factors.

2.2.5 *Burrowing Experiment*

To determine if mussel burrowing behavior was influenced by sediment grain size and predator presence, experiments were conducted to quantify the degree of burrowing. Three runs of the burrowing experiment took place: 1 each during the winter, spring, and summer (Table 2.3). The experimental coarse and fine-grained sediment treatments were set-up in beakers as described above for the mortality experiments. However, while constant temperatures were maintained during the first and third burrowing experiment runs, a shut-down of the temperature-controlled room led to a mixed temperature Run 2 with water reaching 22°C for approximately 24h before returning to 13.5°C.

All mussels used in the burrowing experiment were naked, having their byssal threads carefully removed. Mussels were exposed to a combination of one of three predator treatments (direct, indirect, none), and one of two sediment

treatments (coarse, fine). Since previous work found that chemical cues from *P. festiva* had weak influences on burrowing (Castorani and Hovel 2016), we included two predator treatments: snails were either placed directly (direct treatment) into the beaker with the mussels so mussels could burrow in response to physical cues, or suspended within the beaker inside a mesh bag (indirect treatment) to allow chemical cues in the water while preventing mussel death from affecting burrowing (as dead mussels cannot bury). Each beaker received a mesh bag whether it contained a snail or not, to eliminate any potential variation caused by the presence of the mesh bag. Within each experimental run, each treatment was tested in triplicate (total of eighteen beakers: Fig. 2.4). After three days, degree of burrowing (length of shell that protruded above the sediment surface measured at the highest part of the shell in mm, and mussel orientation), and byssal thread production (%LOI g⁻¹ as described above in the mortality experiment) were measured.

The response variable, % burial, was calculated using the length (if vertically orientated) or width (if horizontally orientated) of the shell that protruded above the sediment surface. Since only mussel length was recorded, mussel width was estimated after generating a standard curve such that:

$$\text{mussel width} = 0.4509x + 1.1374$$

where x = mussel length; created by fitting a regression line to the length and width measures of 160 mussels ($R^2 = 0.97$, $p < 0.001$; Appendix A).

Dead mussels were excluded from the analysis (only one death occurred outside direct predator treatments when a mussel climbed up the side of the

beaker and was eaten by a snail in a mesh bag). As temperature differed between the three experimental runs, each run was analyzed separately. After ensuring assumptions were met for run 1 (Levene's Test: $p = 0.35$), run 2 (Levene's Test: $p = 0.12$), and run 3 (Levene's Test: $p = 0.23$), a two-way ANOVA was used to determine if % burial varied with sediment and predator treatments for each run separately.

To analyze byssal thread production during the burrowing experiment, various transformations failed to improve the homogeneity of the variances, so non-parametric Kruskal-Wallis tests were used to examine temperature, sediment, and predator treatment effects separately.

2.3 Results

*2.3.1 Sediment grain size and *Arcuatula senhousia* distribution and abundance*

On average, sediment grain size increased towards the mouth of Mission Bay with the largest mean grain size ($506.1\mu\text{m}$) collected nearest to the bay mouth and Pacific Ocean. The smallest mean grain size ($21.5\mu\text{m}$) was collected in the northeastern portion of the bay (Fig. 2.1). The highest mean *A. senhousia* abundance (5678 mussels m^{-2}) across years was along the eastern portion of Mission Bay. No mussels were found at 11 stations across all years sampled, most being in the middle to western regions of the bay. The mean grain size at stations where mussels were not collected ranged from $27.97\mu\text{m}$ to $304.32\mu\text{m}$.

A one-way ANOVA revealed that *A. senhousia* abundance was significantly different across sediment grain size categories ($F_{(4, 177)} = 7.47$, $p < 0.001$). Tukey's HSD Test for multiple comparisons found that the mean *A.*

senhousia abundance in silt was significantly greater than mussel abundances in all other sediment categories ($p < 0.001$, 95% C.I. = 0.2822, 1.5359; Fig. 2.5)

2.3.2 Sediment association

A greater proportion of mussels was associated with the fine-grained sediment rather than the coarse-grained sediment side of the beakers; this difference was marginally insignificant (paired t-test: $t_{(9)} = -1.6$, $p = 0.07$; Fig. 2.6). Additionally, a greater proportion of mussels resided above (climbed the side of the beaker) the coarse sediment side of the beakers than the fine sediment side, though the difference was insignificant (paired t-test: $t_{(9)} = 1.10$, $p = 0.15$; Fig. 2.6).

2.3.3 Mortality

Overall, mussels experienced significantly lower snail mortality in cold water than warm water (Kruskal-Wallis: $H_{(1)} = 15.45$, $p < 0.001$; Fig. 2.7a). Furthermore, in cold water, mussel mortality differed significantly in sediment and byssal condition treatments, and there was no significant sediment x byssal condition interaction (Table 2.4). These mussels experienced the lowest mortality when they were in sediment rather than the no-sediment controls (Fig. 2.7b), and when they were within byssal thread nests rather than without byssal threads (Fig. 2.7c). In contrast, in warm water, mussel mortality was not significantly different between sediment (although there was slightly lower mortality in fine-grained sediment; Kruskal-Wallis: $H_{(2)} = 0.84$, $p < 0.66$) or byssal condition treatments (Kruskal-Wallis: $H_{(1)} = 0.001$, $p < 0.98$; Fig. 2.7c).

2.3.4 Burrowing

In general, mussel burrowing did not vary in response to direct or indirect predator cues, and there were no significant predator x sediment interactions (Table 2.5). Mussels did not alter their % burial in coarse and fine-grained sediments in the cold and variable temperature runs but were burrowed significantly deeper in fine rather than coarse-grained sediment in the third (warm) run of the burrowing experiment (Table 2.5; Fig. 2.8).

2.3.5 Byssus Production

Byssus production increased significantly with temperature in the mortality (Table 2.6; Fig. 2.9) and burrowing experiments (Table 2.7; Fig. 2.10) and interactions were not significant in the mortality experiment (Table 2.6). Byssus production was also significantly different between sediment treatments, with highest production in the no-sediment treatment in the mortality experiment (Table 2.6; Fig. 2.9) and fine sediment in the burrowing experiment (Table 2.7; Fig. 2.10). Predator treatment did not have a statistically significant effect on byssus production in the mortality (Table 2.6) or burrowing experiments (Table 2.7).

2.4 Discussion

In Mission Bay, the distribution of *A. senhousia* corresponded to the sediment grain size gradient, whereby more mussels were found in siltier sediments in the back bay (Dexter 1983, Dexter and Crooks 2000, Cheng and Hovel 2010). Many factors are likely involved in shaping these patterns, but these field distributions can be explained, in part, by our laboratory experiments that indicated that *A. senhousia* are more associated with finer-grained sediment than coarser-grained

sediment. Furthermore, mussels in fine-grained sediment experienced lower mortality than when they were outside of sediment, but mortality patterns with respect to sediment grain size and byssus conditions was temperature dependent.

In warm water, mussel mortality and byssus production were both higher than in cold water. The significant difference in mortality between warm and cold water experiments were likely related to increased predation by the snail *P.*

festiva, as temperature increases rates of metabolism (Hochachka and Somero 2002, Yee and Murray 2004) and food consumption (Edwards and Huebner 1977, Bayne and Scullard 1978, Stickle et al. 1985, Sanford 2002) in ectothermic snails. Only 8 total non-snail deaths occurred (3 in no predator treatments, 5 in predator treatments) across all runs of the mortality experiment so mortality can be almost entirely attributed to snail feeding. Increased metabolism and activity of *P. festiva* would have potentially increased speed and capacity for feeding, and therefore predation on mussels. While mussels were slightly bigger on average in the warm experimental runs (two mortality runs and one burrowing run), given that shell length and strength are correlated in other mussel species (Penney et al. 2007), and that handling and processing time might be increased with larger prey (Elner and Hughes 1978, Peharda and Morton 2006), the presence of bigger mussels may have reduced mortality rather than increased it. This suggests that mussel size should not be the cause of the greater observed mortality in the warm runs.

Previous work suggests that Asian mussels may experience extremely high mortality rates due to native predators in the subtidal and intertidal zones of Mission Bay; however, over short time scales, proportional mortality appears to

decrease with mussel density as such densities can over saturate potential predators (Kushner and Hovel 2006). While mussel densities within beakers did reflect moderate field densities (633 mussels m^{-2}), densities of *A. senhousia* have been observed of up to 8,600 m^{-2} (and 170,000 m^{-2} in one extreme case) in Mission Bay (Crooks 1992, Crooks 1996, Crooks and Soulé 1999). Thus, the density of mussels in our experimental beakers may have been low enough for more active snails in warm temperatures to consume rapidly.

One approach that mussels may adopt to decrease predation risk when water temperatures are warm, and snails are more active is to burrow deeper and produce more byssus in fine sediment. We observed significantly greater burial in fine sediment in the warm runs of the burrowing experiment. Byssus production also increased with temperature in all experiments and was greater in fine sediment. Increased byssus production in warmer temperatures has been observed in other studies (Young 1985, Rajagopal et al. 1996) and is likely related to increased metabolism of the molluscs, or in response to increased predatory activity of snails as *A. senhousia* increased byssus production when exposed to chemical cues from predators and injured conspecifics (Castorani and Hovel 2016, Zhao et al. 2020). Along with increased burial and byssus production in fine sediment and warm water temperature, mortality was slightly lower in fine sediment and warm water, indicating there may be some survival advantage afforded to mussels in fine sediment that burrow deeper and produce more byssus.

Based on our field study and laboratory experiment, mussels were preferentially associated with fine sediments. Higher abundances in fine-grained

sediment likely result from the adaptations that allow *A. senhousia* to do well in soft sediment (Morton 1974). Over small spatial scales (likely on the order of centimeters to meters), adult *A. senhousia* can travel across the sediment surface and up hard structures using their muscular foot and byssal threads (Morton 1974). Presumably this allows *A. senhousia* to select post-settlement/recruitment substrates in which they reside, although such movements are unlikely to alter to their broad distribution patterns. While hydrodynamic conditions are more likely to redistribute mussels over larger estuary-scales as has been observed for other bivalve species undergoing secondary dispersal via bedload transport (Hunt 2004, Hunt et al. 2007), areas with fine-grained sediment in Mission Bay also have the weakest tidal currents (Largier et al. 2003). Fine sediment seems to promote byssus production which may help stabilize and accumulate sediment and anchor mussels (Morton 1974, Tsutsumi et al. 2013, Takenaka et al. 2018), limiting redistribution and providing the thin shelled mussel with protection from predation. Given that *A. senhousia* readily accumulates fine sediments in their byssal networks (Tsutsumi et al. 2013, Takenaka et al. 2018), it is possible that these mussels reach high enough abundance in the back-bay that they are changing slightly the sediment distribution in Mission Bay. Future work should look at sediment cores in Mission Bay to see if sediment characteristics have changed since the introduction of *A. senhousia*.

In contrast, mussels in coarse-grained sediment moved around more, burrowed less, and produced less byssus, following previously observed trends in other bivalves (Alexander et al. 1993, De la Huz et al. 2002). Mussels climbing

above the coarse-grained sediment may indicate a prevalence for redistribution if they initially settle in sand, especially since sandier sediment deposits are indicative of more energetic environments (Hjulstrom 1939, Meade 1972, Traykovski et al. 2004) which might not be preferable for this species. Additionally, mussels that move around more, burrow less, and produce less byssus in coarse-grained sediment are more vulnerable to predation. At front-bay sites in Mission Bay where benthic predators are most abundant (Cheng and Hovel 2010) and sediment is the coarsest, the increased vulnerability to predation of mussels and potential for redistribution of mussels in the coarse sediment may act synergistically to restrict them from this area.

While sediment characteristics certainly play a role in the distribution patterns of the benthic subtidal *A. senhousia*, several other physical factors like water and overall environmental quality may also play a role in mussel distribution. Given the contaminated freshwater input (Schiff and Kinney 2001, Kaufmann et al. 2004), high water residence times (Largier et al. 2003), and fine sediments (which are usually associated with less oxygen, more organic content) in the back-bay, refuge may be afforded to the r-selected, “weedy” and invasive *A. senhousia* in these regions of degraded environmental quality where natives are less successful. This pattern would correspond well with the Pearson-Rosenberg Model (Pearson 1977, Pearson and Rosenberg 1978) in which a “peak of opportunists” near organic outputs create an area of high abundance and low diversity, making it an ideal place for fast growing, opportunistic invaders like *A. senhousia*. Although hypoxia can also have strong effects on bivalve distribution

and abundance (Mistri 2002, Altieri and Witman 2006), it is unlikely to explain the spatial mussel density gradient in Mission Bay because mussels were abundant in the back of the bay where hypoxia is most likely, and they were absent from the front bay where tidal forcing should keep water well-oxygenated (Cheng and Hovel 2010). While *A. senhousia* tends to be tolerant of degraded conditions, organic pollution has resulted in population declines in Tomioka Bay, Japan (Tsutsumi et al. 1991).

It is also worth noting that our experiments dealt only with adult mussels in completely still water; given *A. senhousia*'s long planktonic dispersal stage (Crooks, 1996) it is possible that the hydrodynamic properties of the bay play a more important role in the earlier planktonic life stages of these mussels. In one bivalve study, correlations between the hydrodynamic factors and the observed larval abundances were only significant for early recruits and became insignificant within 2 weeks (Armonies and Hellwig-Armonies 1992). Additionally, we did not look at the impact of seagrass on the distribution of *A. senhousia* though physical structure and reduction of water velocity provided by seagrass (Fonseca et al. 1982) may assist larval bivalves in settling and recruiting (Bologna and Heck 2000). This does not appear to be the case for *A. senhousia* in Mission Bay as recruitment of mussels or adult distributions were not enhanced in seagrass beds (Williams et al. 2005), and in some cases eelgrass inhibited *A. senhousia* recruitment (Reusch and Williams 1999). Increasing eelgrass habitat structure also seemed to alter the aggregative behavioral response of native predators to Asian mussels in a previous study (Kushner and Hovel 2006), thus

the abundance of adult *A. senhousia* is likely negatively related to eelgrass abundance.

2.4.1 Conclusions

Past studies of *A. senhousia* distributions in Mission Bay have placed greater focus on predator effects rather than sediment effects; given that sediment characteristics often play an important role in the distribution and abundance of intertidal and subtidal bivalves (Alexander et al. 1993, Nel et al. 1999), the influence of sediment characteristics on the distribution of the invasive *A. senhousia* provide important insight. The results of our study suggest that in Mission Bay, and at moderate mussel densities: (1) warmer temperatures increase both mortality by a conspicuous predator (*P. festiva*), and byssus production of *A. senhousia*; and in particular, (2) fine-grained sediment increases byssus production and burrowing; while (3) in cold temperatures, increased byssus coverage reduces mussel mortality. Collectively, these results imply that a survivorship advantage may be afforded to mussels that settle in or choose fine sediment regions of Mission Bay where they might increase burial, byssus coverage, and sediment accumulation (and therefore protection). The structure of a community is controlled by a complex combination of processes, and our study provides new insight that helps further our understanding of the biotic and abiotic factors that influence *A. senhousia* distributions in Mission Bay; byssus production, burrowing, and predation play important roles across a sediment gradient, but temperature modifies the relative importance of these factors. Furthermore, given the strong effect of temperature on *A. senhousia* mortality and

byssus production that we observed, these results may have implications for climate change in the future. Warming of Mission Bay could enhance overall mortality for *A. senhousia*, irrespective of sediment type and byssal conditions, potentially shifting predator-prey dynamics and impacting the distribution of *A. senhousia* among other potential ecological consequences.

2.5 Tables and Figures

Table 2.1 Sediment grain size distribution used in experiments. Grain size distribution of unburned (original) sediment collected from Mission Bay and compared after burning for 4 hours at 550°C to remove organic matter. For runs, “M” indicates use in a mortality experiment, while “B” indicates use in a burrowing experiment; numbers refer to replicate runs as described in Tables 2 and 3).

Run	Coarse			Fine		
	%clay	%silt	%sand	%clay	%silt	%sand
Unburned	0.50	6.75	92.75	2.52	87.10	10.38
M1	0.44	5.24	94.32	2.09	57.64	40.27
M2/M3	0.30	2.14	97.56	2.98	75.64	21.38
M4	0.40	3.36	96.24	2.78	74.34	22.88
B1/B2	0.30	2.48	97.22	3.31	77.64	19.05
B3	0.39	3.47	96.14	3.10	74.52	22.38

Table 2.2 Summary of mortality experimental runs, including dates, environmental conditions, and sample sizes.

	Cold		Warm	
	M1	M2	M3	M4
Date of mussel collection	12/08/20	01/28/21	07/09/21	08/03/21
Temperature	13.5°C	13.5°C	20°C	20°C
# Beakers	47	36	54	54
Mean \pm SE mussel length	14.8 \pm 0.3	14.1 \pm 0.3	15.3 \pm 0.2	16.7 \pm 0.2
	3x all naked			
	3x all nest			
Completed replicates	2x all cocoon – 1 beaker	2x all	3x all	3x all

Table 2.3 Summary of burrowing experimental runs.

	Cold	Mixed	Warm
	B1	B2	B3
Date of mussel collection	02/25/21	05/25/21	08/25/21
Cold room temp	13.5°C	13.5°C - 22°C	20°C
# Beakers	18	18	18
Mean \pm SE mussel length	16.2 \pm 0.4	15.7 \pm 0.2	18.2 \pm 0.2
Completed replicates	3x all	3x all	3x all

Table 2.4 Two-way ANOVA results of effects of sediment treatment and byssus classification on the % mortality of *A. senhousia* in cold treatments. Bold values indicate significant p-values < 0.05.

Cold				
	<i>df</i>	MS	<i>F</i>	<i>p</i>
Sediment	2	0.27	3.7	0.034
Byssus	1	0.66	9.07	0.005
Sediment x byssus	2	0.17	2.3	0.11
Error	36	0.073		

Table 2.5 Two-way ANOVA results of effects of sediment treatment and predator treatment on the % burial of *A. senhousia*.

	Cold				Mixed				Warm			
	df	MS	F	p	df	MS	F	p	df	MS	F	p
Sediment	1	214.26	0.20	0.66	1	1164.46	1.40	0.24	1	7728.03	6.53	0.012
Predator	2	64.72	0.061	0.94	2	17.72	0.021	0.98	2	2420.23	2.05	0.14
Sediment x predator	2	1183.98	1.11	0.33	2	47.78	0.057	0.94	2	33.86	0.029	0.97
Error	84	1062.99			84	834.62			84	1181.75		

Table 2.6 Three-way ANOVA results of effects of temperature, sediment treatment, and predator treatment on byssus production (%LOI g⁻¹) of *A. senhousia* in the mortality experiment.

	<i>df</i>	MS	<i>F</i>	<i>p</i>
Temperature	1	0.16	4.75	0.033
Sediment	2	6.80	207.84	<0.001
Predator	1	0.0020	0.073	0.79
Temperature x sediment	2	0.042	1.25	0.29
Temperature x predator	1	0.0020	0.058	0.81
Sediment x predator	2	0.018	0.53	0.59
Temperature x sediment x predator	2	0.028	0.83	0.44
Error	60	0.033		

Table 2.7 Kruskal-Wallis results of effect of temperature, sediment treatment, and predator treatment on byssus production (%LOI g⁻¹) of *A. senhousia* in the burrowing experiment.

	Kruskal-Wallis H	<i>df</i>	<i>p</i>
Temperature	14.89	2	<0.001
Sediment	15.90	1	<0.001
Predator	4.48	2	0.10

Fig. 2.1 Map of Mission Bay, San Diego, California with the background gradient representing the mean sediment grain diameter (microns) and black dots representing mean *A. senhousia* abundance, with dots increasing in size proportionally to mussel abundance. Green symbols represent experimental coarse (triangle) and fine (square) sediment collection sites used in the laboratory experiments.

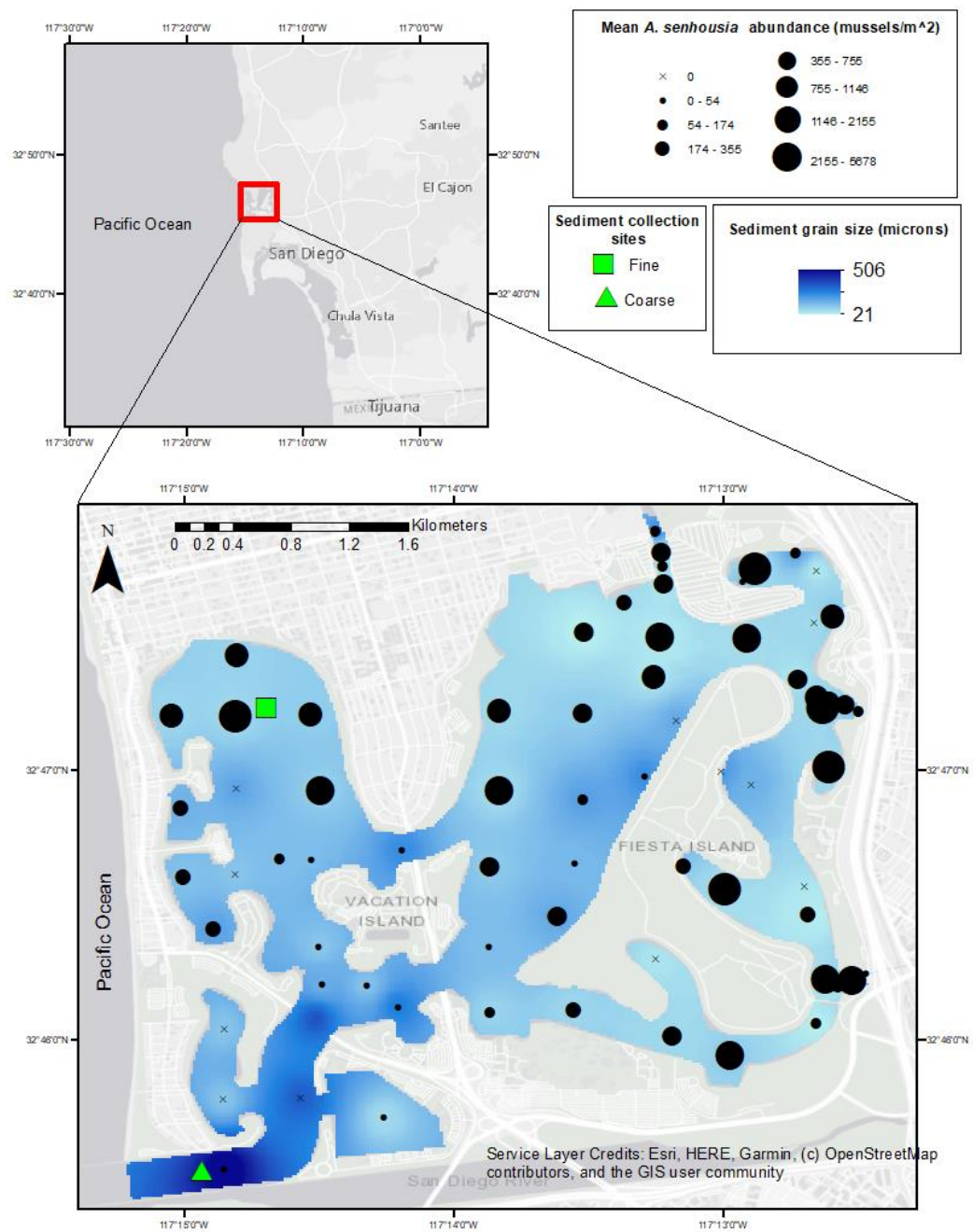


Fig. 2.2 Beaker setup for sediment selection experiment with side view (left panel) and top view showing mussel placement (right panel).

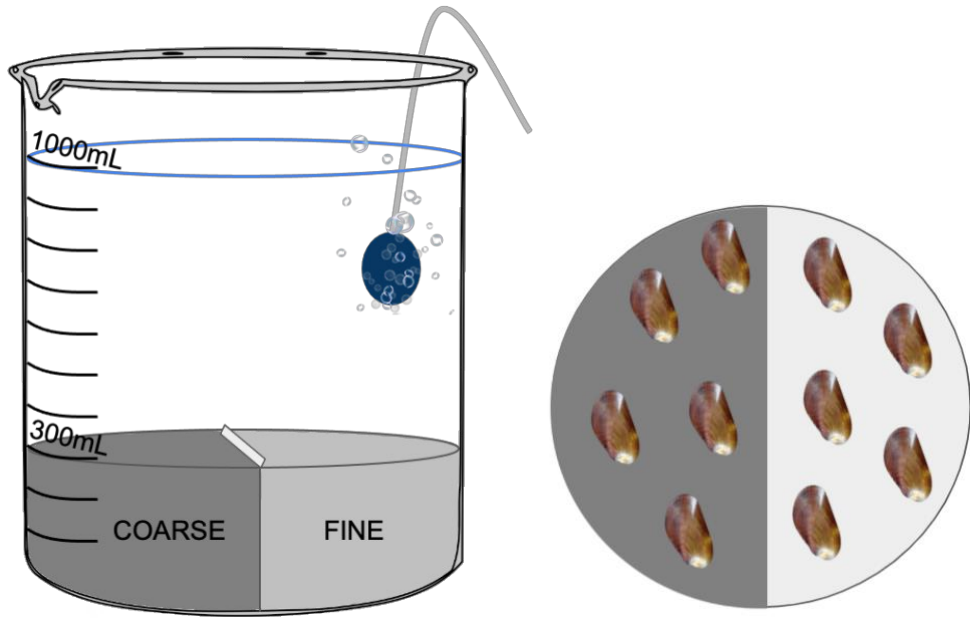


Fig. 2.3 Setup showing the sediment (no-sediment control, fine-grained, and coarse-grained) and predator (with and without) treatments in the mortality experiments. Controls are circled in red. The dark black outer box indicates one round of experiments for each mussel type (naked, cocoon, or mat), with three replicates (blue circles representing each beaker) of each treatment. Each beaker housed five mussels, and the response variables measured included: mortality and byssal thread production. Although not depicted here, treatments (beaker placement) were randomized.

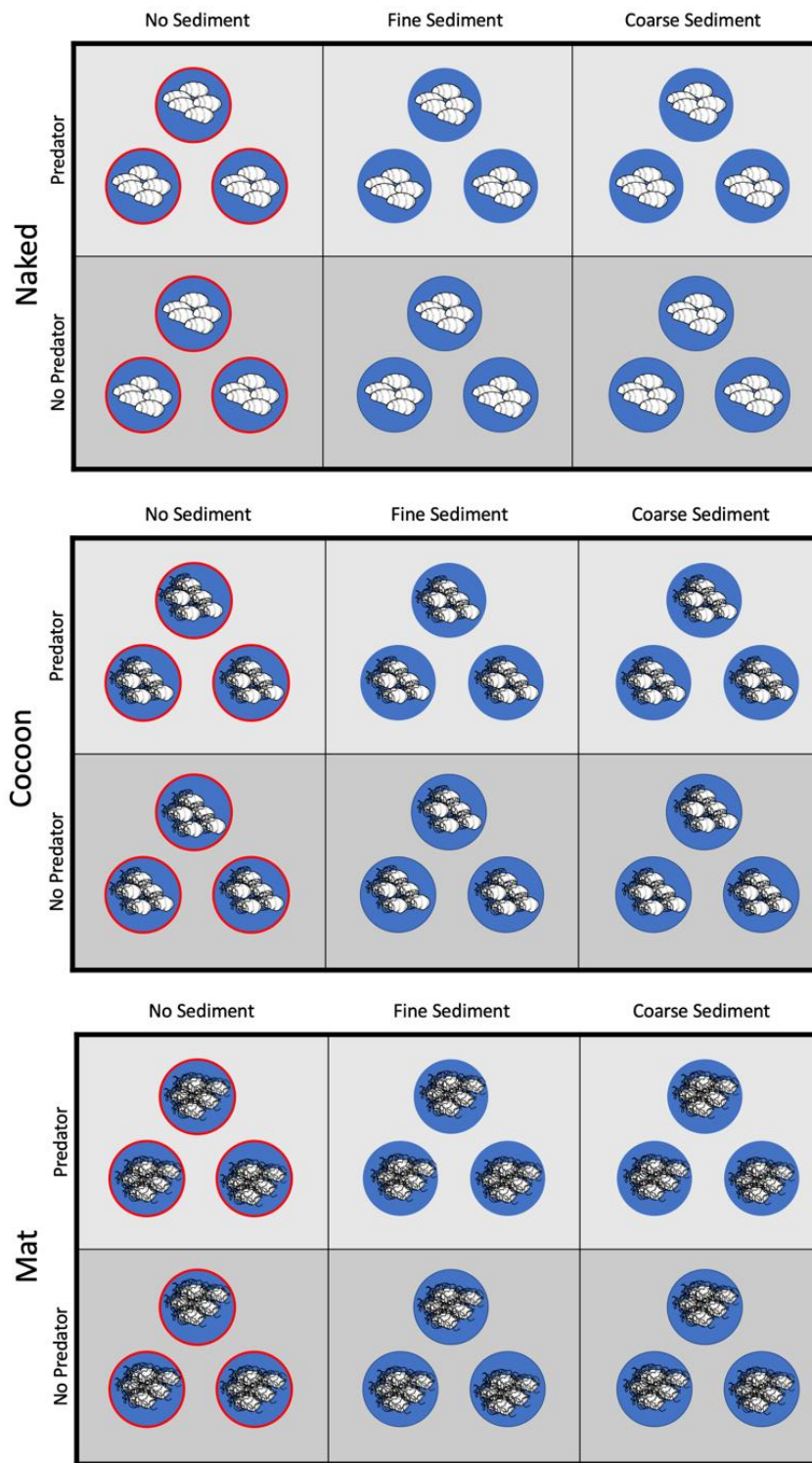


Fig. 2.4 Setup showing the sediment (fine-grained, and coarse-grained sediment) and predator (no predator, direct contact with predator, indirect contact with predator) treatments in the burrowing experiments. Controls are circled in red. The dark black outer box indicates one round of experiments with three replicates (blue circles representing each beaker) of each treatment. Each beaker housed five naked mussels, and the response variables measured included: shell length above the sediment surface and byssal thread production. Although not depicted in this schematic, the treatments (beaker placement) were randomized.

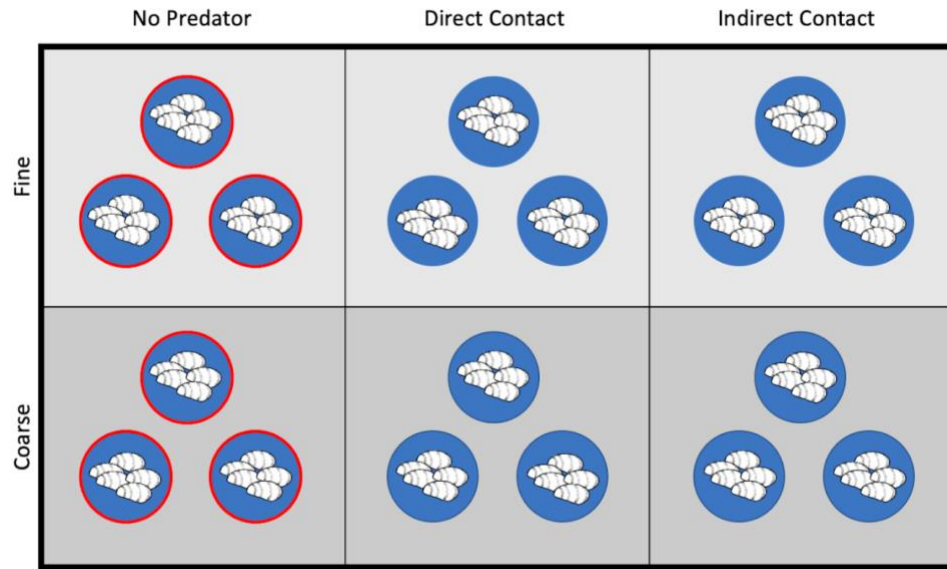


Fig. 2.5 Relationship between mean *A. senhousia* abundance and mean sediment grain size diameter from samples collected throughout Mission Bay (stations in Fig. 2.1) during October 2015, 2016, 2018, 2019, and 2021 and March 2017. Letters denote the significant differences in *A. senhousia* abundance between sediment categories detected by Tukey's HSD post-hoc test for multiple comparisons.

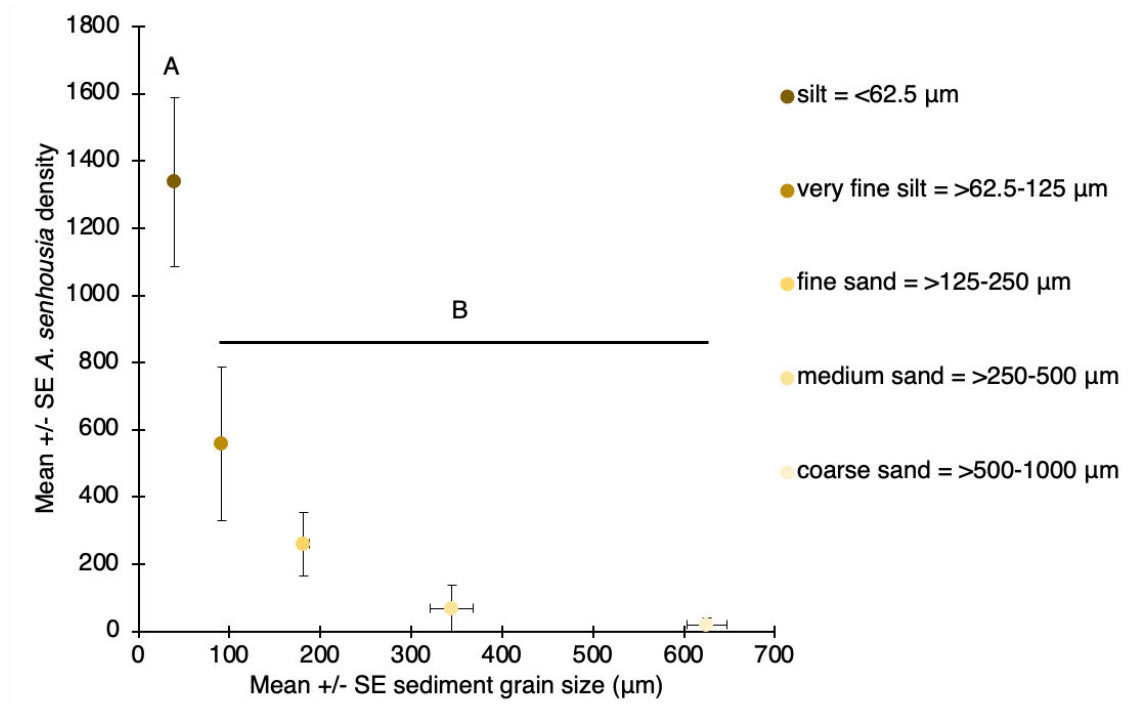


Fig. 2.6 Mean proportion of mussels associated with each sediment type during the 6 days of observation. The grey portion of each column represents the mean proportion of mussels that were atop or within the sediment (“on”). The white portion of each column represents the mean proportion of mussels that climbed along the beaker sides or air stone above each sediment (“off”) type.

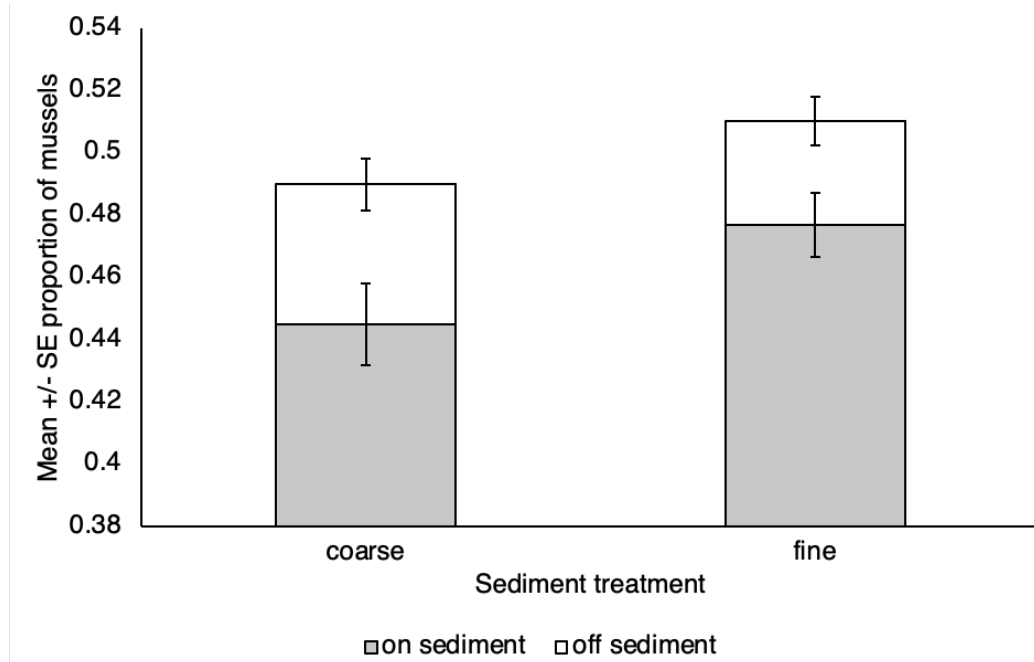


Fig. 2.7 Mean % mussel mortality grouped by (a) temperature runs, (b) sediment treatments, and (c) byssus classification (c) and separated by cold and warm runs.

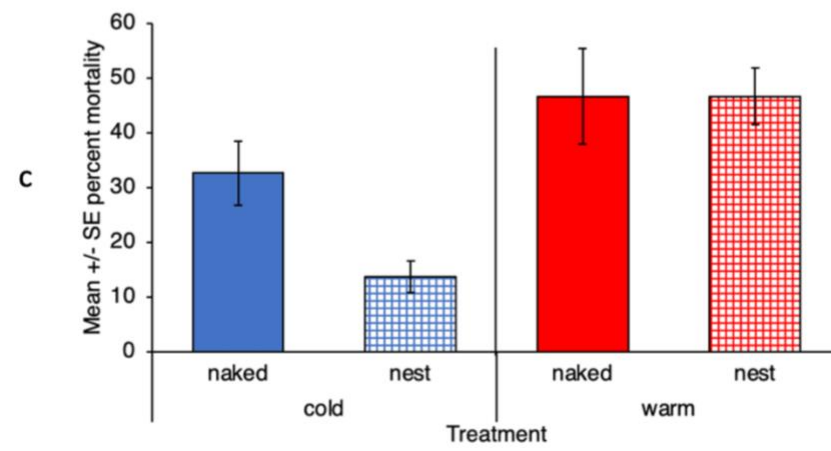
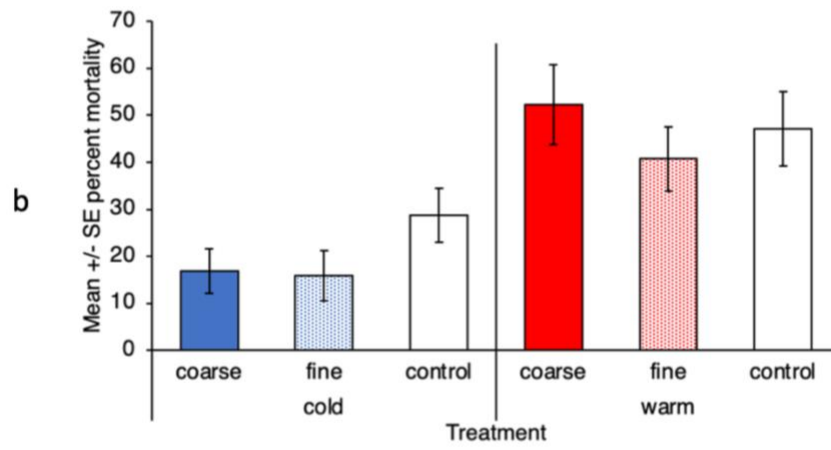
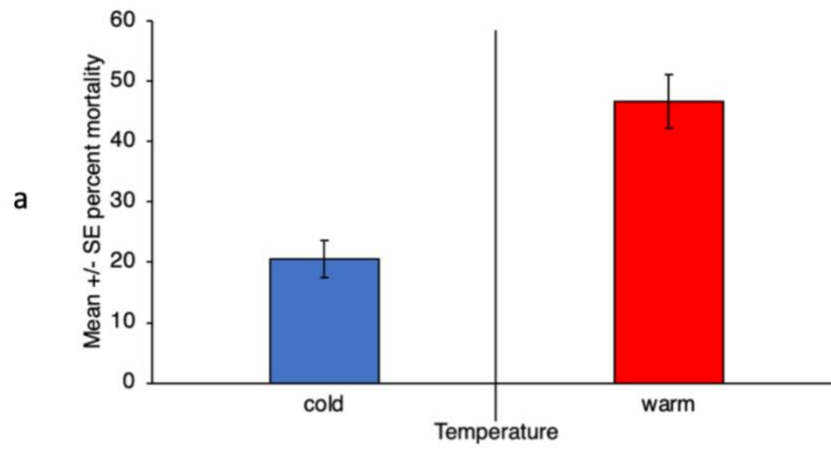


Fig. 2.8 (a) Mean % burial of mussels in the cold run (1), mixed temperature run (2), and warm run (3) during the burrowing experiment.

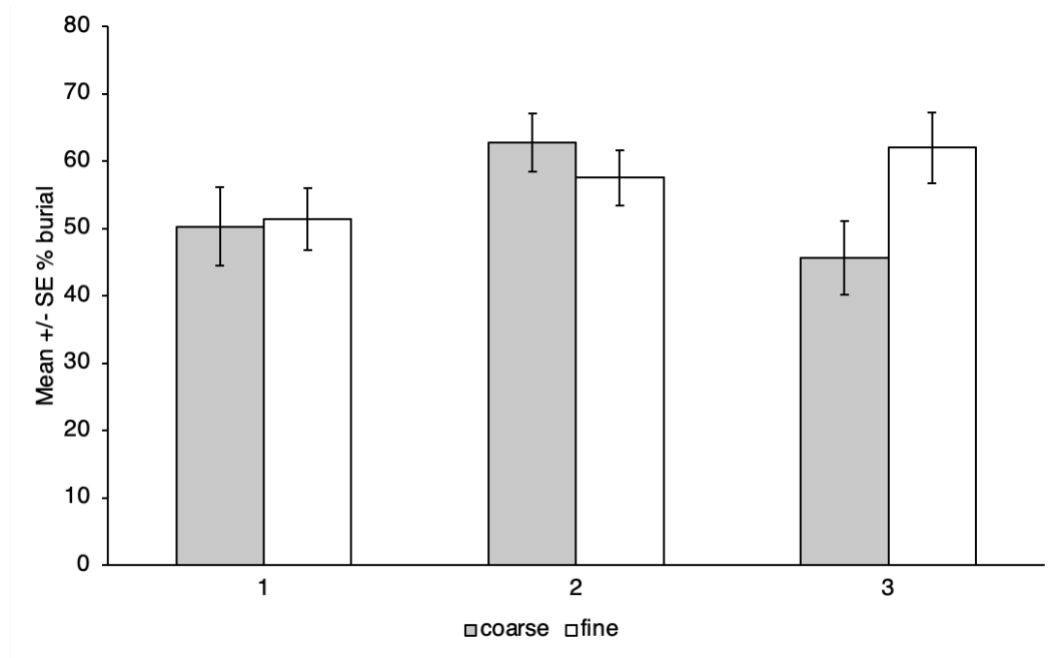


Fig. 2.9 Mean byssus production (%LOI g⁻¹ of mussels in each beaker) for all four runs of the mortality experiment. Two runs took place in the warmer summer/early fall and two took place in the colder late fall/winter. Letters denote the significant differences in byssus production between sediment categories detected by Tukey's HSD post-hoc test for multiple comparisons.

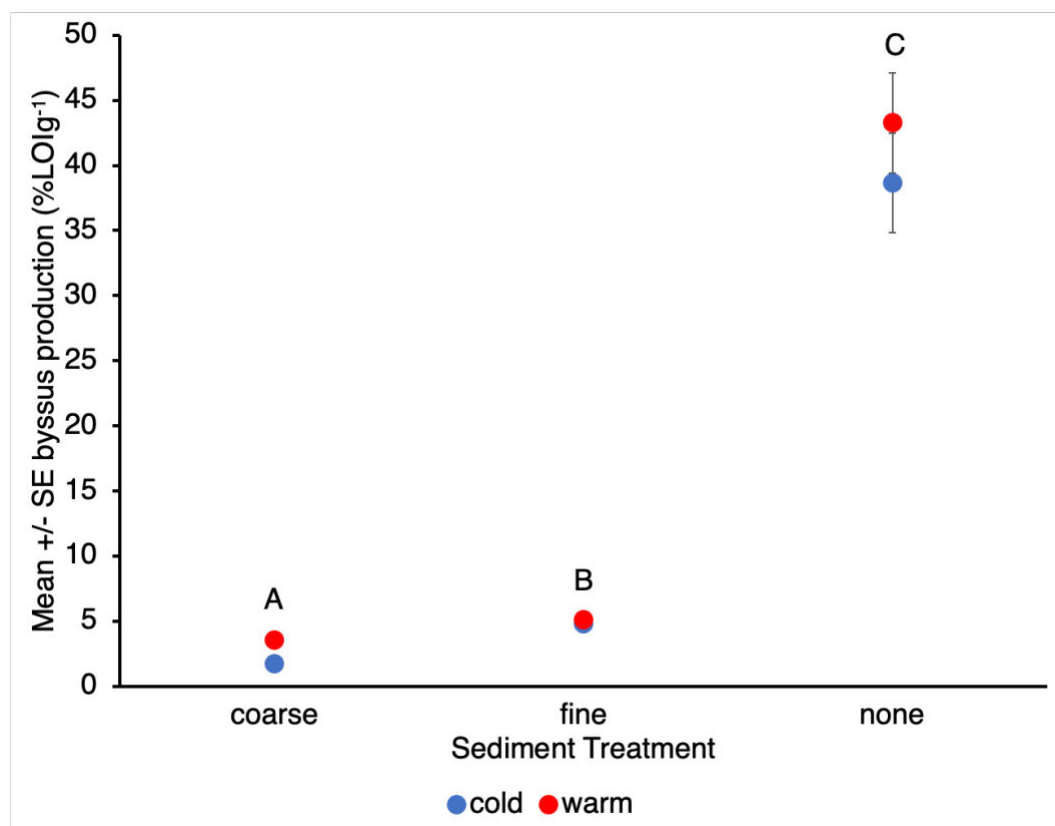
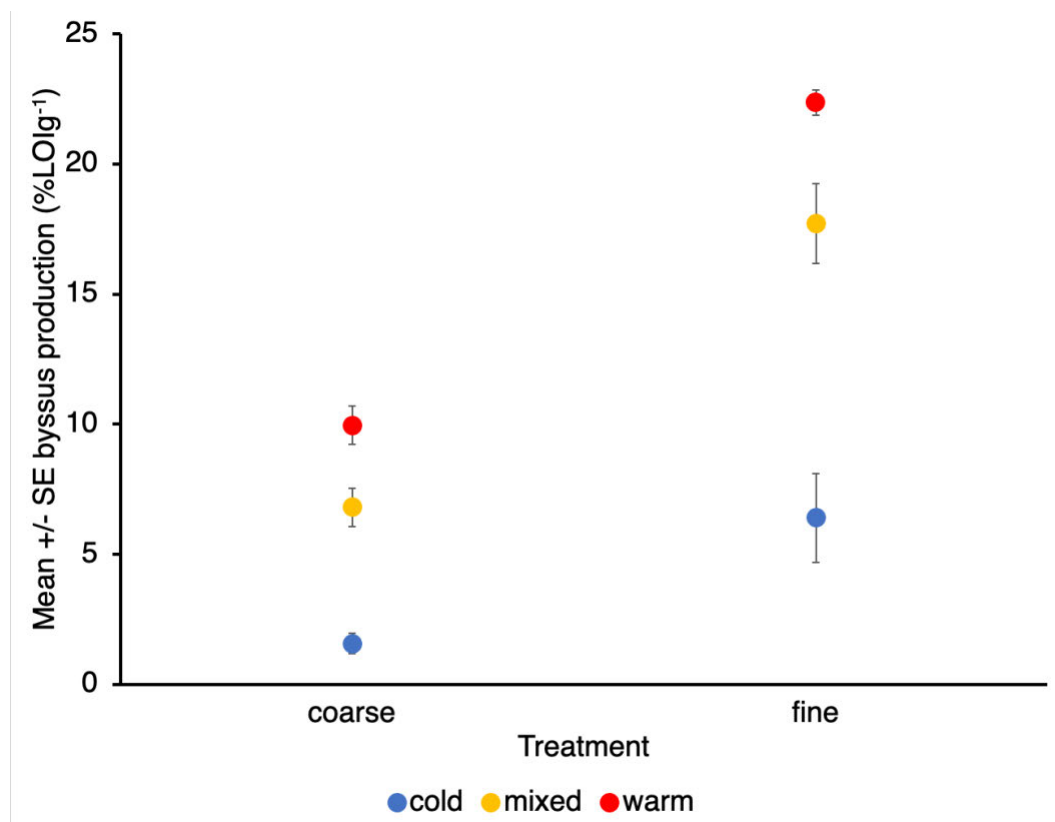


Fig. 2.10 Mean byssus production (%LOI g⁻¹ of mussels in each beaker) for all four runs of the burrowing experiment. One run took place in the winter, one in spring, and one in summer. The temperature-controlled room shut down in the middle of the second run of the experiment resulting in a mixed temperature treatment.



REFERENCES

- Alexander, R. R., R. J. Stanton Jr, and J. R. Dodd. 1993. Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*:289-303.
- Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and oceanography* **37**:946-955.
- Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. *Ecology* **87**:717-730.
- Armonies, W., and M. Hellwig-Armonies. 1992. Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. *Netherlands Journal of Sea Research* **29**:371-378.
- Bayne, B., and C. Scullard. 1978. Rates of feeding by *Thais* (*Nucella*) *lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **32**:113-129.
- Bologna, P. A., and K. L. Heck. 2000. Impacts of seagrass habitat architecture on bivalve settlement. *Estuaries* **23**:449-457.
- Butman, C. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol* **25**:113-165.
- Castorani, M. C., and K. A. Hovel. 2015. Invasive prey indirectly increase predation on their native competitors. *Ecology* **96**:1911-1922.

- Castorani, M. C., and K. A. Hovel. 2016. Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. *Biological Invasions* **18**:169-181.
- Cheng, B. S., and K. A. Hovel. 2010. Biotic resistance to invasion along an estuarine gradient. *Oecologia* **164**:1049-1059.
- Creese, R., S. Hooker, S. De Luca, and Y. Wharton. 1997. Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **31**:225-236.
- Crooks, J. 1992. The ecology of the introduced bivalve, *Musculista senhousia*. Mission Bay, San Diego. MS Thesis, San Diego State University, San Diego, California.
- Crooks, J., and M. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. Sandlund OT, Schei PJ, Viken A editors. *Invasive species and biodiversity management*. Kluwer: Dordrecht.
- Crooks, J. A. 1996. The population ecology of an exotic mussel, *Musculista senhousia*, in a southern California bay. *Estuaries* **19**:42-50.
- Crooks, J. A. 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine ecology Progress series* **162**:137-152.
- Crooks, J. A. 2001. Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biological Invasions* **3**:23-36.

- Crooks, J. A. 2002. Predators of the invasive mussel *Musculista senhousia* (Mollusca: Mytilidae). *Pacific Science* **56**:49-56.
- Crooks, J. A., and H. S. Khim. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology* **240**:53-75.
- De la Huz, R., M. Lastra, and J. López. 2002. The influence of sediment grain size on burrowing, growth and metabolism of *Donax trunculus* L.(Bivalvia: Donacidae). *Journal of Sea Research* **47**:85-95.
- Dexter, D. 1983. Soft bottom infaunal communities in Mission Bay. California *Fish and Game* **69**:5-17.
- Dexter, D. M., and J. A. Crooks. 2000. Benthic communities and the invasion of an exotic mussel in Mission Bay, San Diego: a long-term history. *Bulletin of the Southern California Academy of Sciences* **99**:128-128.
- Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment 1. *Limnology and Oceanography* **28**:241-257.
- Edwards, D. C., and J. D. Huebner. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* **58**:1218-1236.
- Elner, R. W., and R. N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *The Journal of Animal Ecology*:103-116.
- Fonseca, M., J. Fisher, J. Zieman, and G. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine, Coastal and Shelf Science* **15**:351-364.

- Grosholz, E. D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences* **102**:1088-1091.
- Hjulstrom, F. 1939. Transportation of detritus by moving water: Part 1. Transportation.
- Hochachka, P. W., and G. N. Somero. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford university press.
- Hunt, H. L. 2004. Transport of juvenile clams: effects of species and sediment grain size. *Journal of Experimental Marine Biology and Ecology* **312**:271-284.
- Hunt, H. L., M.-J. Maltais, D. C. Fugate, and R. J. Chant. 2007. Spatial and temporal variability in juvenile bivalve dispersal: effects of sediment transport and flow regime. *Marine Ecology Progress Series* **352**:145-159.
- Kaufmann, R., B. Stransky, J. Rudolph, D. Elliott, R. Griggs, J. Kittinger, B. Swope, J. Bolender, M. Boudrias, and H. Sarabia. 2004. Mission Bay Water and Sediment Testing Project, Final Report. City of San Diego.
- Kawaguchi, M., and K. Shirai. 1944. Studies on Bays of Setonakai, I. Benthic Community of Kasaoka Bay and a Quantitative Evaluation of *Brachidontes senhousia* as an Unutilized Natural Resource. *Contributions in Physiology and Ecology, Kyoto Imperial University* **8**:1-18.
- Kulikova, V. 1978. Morphology seasonal population dynamics and settlement of larvae of the bivalve mollusk *Musculista senhousia* in the Busse lagoon (South Sakhalin). *Biologiya Morya-Marine Biology*:61-66.

- Kushner, R. B., and K. A. Hovel. 2006. Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California. *Journal of Experimental Marine Biology and Ecology* **332**:166-177.
- Largier, J., M. Carter, M. Roughan, D. Sutton, J. Helly, B. Lesh, T. Kacena, P. Ajtai, L. Clarke, and D. Lucas. 2003. Mission Bay Contaminant Dispersion Study Final Report. City of San Diego, California.
- Meade, R. H. 1972. Transport and deposition of sediments in estuaries. *Geological Society of America* **133**:91-120.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology & Evolution* **5**:52-57.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**:730-757.
- Mistri, M. 2002. Ecological characteristics of the invasive Asian date mussel, *Musculista senhousia*, in the Sacca di Goro (Adriatic Sea, Italy). *Estuaries* **25**:431-440.
- Morton, B. 1974. Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhausia* Benson (Bivalvia, Mytilidae).
- Mukai, H. 1974. Ecological studies on distribution and production of some benthic animals in the coastal waters of central Inland Sea of Japan.

- Nel, R., A. McLachlan, and D. Winter. 1999. The effect of sand particle size on the burrowing ability of the beach mysid *Gastrosaccus psammodytes* Tattersall. *Estuarine, Coastal and Shelf Science* **48**:599-604.
- Parker, I. M., D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, and J. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological invasions* **1**:3-19.
- Pearson, T. a. R. R. 1977. Pearson TH, Rosenberg R.. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Ann Rev* **16**: 229-311. *Oceanography and Marine Biology* **16**.
- Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment.
- Peharda, M., and B. Morton. 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator–prey interactions with the Black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). *Marine Biology* **148**:1011-1019.
- Penney, R. W., M. J. Hart, and N. D. Templeman. 2007. Shell strength and appearance in cultured blue mussels *Mytilus edulis*, *M. trossulus*, and *M. edulis* × *M. trossulus* hybrids. *North American Journal of Aquaculture* **69**:281-295.
- Rajagopal, S., G. Van der Velde, H. Jenner, M. Van der Gaag, and A. Kempers. 1996. Effects of temperature, salinity and agitation on byssus thread

- formation of zebra mussel *Dreissena polymorpha*. *Netherlands Journal of Aquatic Ecology* **30**:187-195.
- Reusch, T. B. 1998. Native predators contribute to invasion resistance to the non-indigenous bivalve *Mytilus senhousia* in southern California, USA. *Marine Ecology Progress Series* **170**:159-168.
- Reusch, T. B., and S. L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Mytilus senhousia*. *Oecologia* **113**:428-441.
- Reusch, T. B., and S. L. Williams. 1999. Macrophyte canopy structure and the success of an invasive marine bivalve. *Oikos*:398-416.
- Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual review of ecology, evolution, and systematics* **36**.
- Ruiz, G. M., P. Fofonoff, A. H. Hines, and E. D. Grosholz. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and oceanography* **44**:950-972.
- Sanford, E. 2002. The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *Journal of Experimental Marine Biology and Ecology* **273**:199-218.

- Schiff, K., and P. Kinney. 2001. Tracking sources of bacterial contamination in stormwater discharges to Mission Bay, California. *Water Environment Research* **73**:534-542.
- Sousa, R., J. L. Gutiérrez, and D. C. Aldridge. 2009. Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* **11**:2367-2385.
- Stickle, W., M. Moore, and B. Bayne. 1985. Effects of temperature, salinity and aerial exposure on predation and lysosomal stability of the dogwhelk *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **93**:235-258.
- Sun, D., and Z. Tang. 1989. Ecological characteristics of macrobenthos of the Huanghe river estuary and adjacent waters. *Studia Marina Sinica* **30**:260-274.
- Takenaka, R., T. Komorita, and H. Tsutsumi. 2018. Accumulation of organic matter within a muddy carpet created by the Asian date mussel, *Arcuatula senhousia*, on the Midori River tidal flats, Japan. *Plankton and Benthos Research* **13**:1-9.
- Traykovski, P., R. Geyer, and C. Sommerfield. 2004. Rapid sediment deposition and fine-scale strata formation in the Hudson estuary. *Journal of Geophysical Research: Earth Surface* **109**.
- Tsutsumi, H., T. Kikuchi, M. Tanaka, T. Higashi, K. Imasaka, and M. Miyazaki. 1991. Benthic faunal succession in a cove organically polluted by fish farming. *Marine Pollution Bulletin* **23**:233-238.

- Tsutsumi, H., R. Nomura, T. Tanoue, T. Komorita, T. Iwasaki, and T. Fujimori.
2013. Influence of the Development and Destruction of Muddy Byssal Mats Made by a Mytilid Mussel, *Musculista senhousia* , on Seasonal Fluctuations of the Macrobenthic Community on Sandy Tidal Flats. Japanese journal of benthology **67**:47-55.
- Vitousek, P. M., C. M. D'antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks.
1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology:1-16.
- Williams, S., T. Ebert, and B. Allen. 2005. Does the recruitment of a non-native mussel in native eelgrass habitat explain their disjunct adult distributions? Diversity and distributions **11**:409-416.
- Woodin, S. A. 1976. Adult-Larval interactions in dense infaunal assemblages: Patterns of abundance.
- Yee, E., and S. Murray. 2004. Effects of temperature on activity, food consumption rates, and gut passage times of seaweed-eating Tegula species (Trochidae) from California. Marine Biology **145**:895-903.
- Young, G. 1985. Byssus-thread formation by the mussel *Mytilus edulis*: effects of environmental factors. Marine ecology progress series. Oldendorf **24**:261-271.
- Zhao, L., J. Liang, J. Liang, B. Liu, Y. Deng, X. Sun, H. Li, Y. Lu, and F. Yang.
2020. Experimental study of transgenerational effects, pH and predation risk on byssus production in a swiftly spreading invasive fouling Asian

mussel, *Musculista senhousia* (Benson). *Environmental Pollution*
260:114111.

CHAPTER 3: Conclusion

Understanding the combination of processes that influence the distribution of invasive, ecosystem engineering bivalves like *Arcuatula senhousia* is crucial for monitoring and management. Before this study, the influence of sediment characteristics on the soft sediment-dwelling mussel's burrowing behavior and byssus production (important survival adaptations for this thin shelled bivalve) had not been closely examined, with previous studies focusing more on the role of native predators in mussel distribution (Crooks 2002, Cheng and Hovel 2010, Castorani and Hovel 2015, 2016).

In Chapter 2, the associated distribution of *A. senhousia* with fine sediments as well as differences in mussel mortality, burrowing, and byssus production in different temperatures and sediment grain sizes were discussed, with temperature having the greatest affect. This is consistent with other studies of predation and temperature of ectothermic invertebrates; feeding behavior (Edwards and Huebner 1977, Bayne and Scullard 1978, Stickle et al. 1985, Sanford 2002) and metabolism (Hochachka and Somero 2002, Yee and Murray 2004) generally increasing with water temperature. The increase in byssus production with temperature is consistent with previous work as well (Young 1985, Rajagopal et al. 1996) and the lower mortality we observed in mussels with greater byssus coverage suggests the importance of byssus in mussel mortality. While we observed significantly deeper mussel burial in the warm run, a consistent temperature effect was not seen in our burrowing experiments though previous work has found a strong relationship between burrowing behavior and

temperature (Block et al. 2013). Given the equipment issues we experienced, temperature is likely still an important factor in *A. senhousia* burrowing behavior that requires further investigation. Strong responses in mortality and byssus production to temperature may have climate change implications in the future. Though we saw increased byssus production and snail mortality with increasing temperature, experimental temperatures were likely within the species' thermal niche and thermal stress beyond the temperatures we tested could have varying effects. Further investigation of *A. senhousia* response to temperature and thermal stress as warming continues will become more relevant and important.

Sediment also played a role in *A. senhousia* mortality and behavior with presence of sediment having significant effects on mortality and byssus production, the increase in both likely relating to limited options for avoiding predation outside of sediment. Burrowing behavior was significantly affected by sediment grain size in one experimental run with mussels burrowing deeper in fine sediment which is consistent with previous work (Alexander et al. 1993, De la Huz et al. 2002). Fine sediment seemed to promote byssus production which may help stabilize and accumulate sediment and anchor mussels (Morton 1974, Tsutsumi et al. 2013, Takenaka et al. 2018), limiting redistribution and providing the thin shelled mussel with protection from predation. Additionally, given that a higher proportion of mussels were associated with fine sediment in our sediment selection experiment, fine sediment may be preferred by *A. senhousia*, and upon settling in fine sediment mussels may spend more time and energy burrowing and producing byssus and less time and energy relocating.

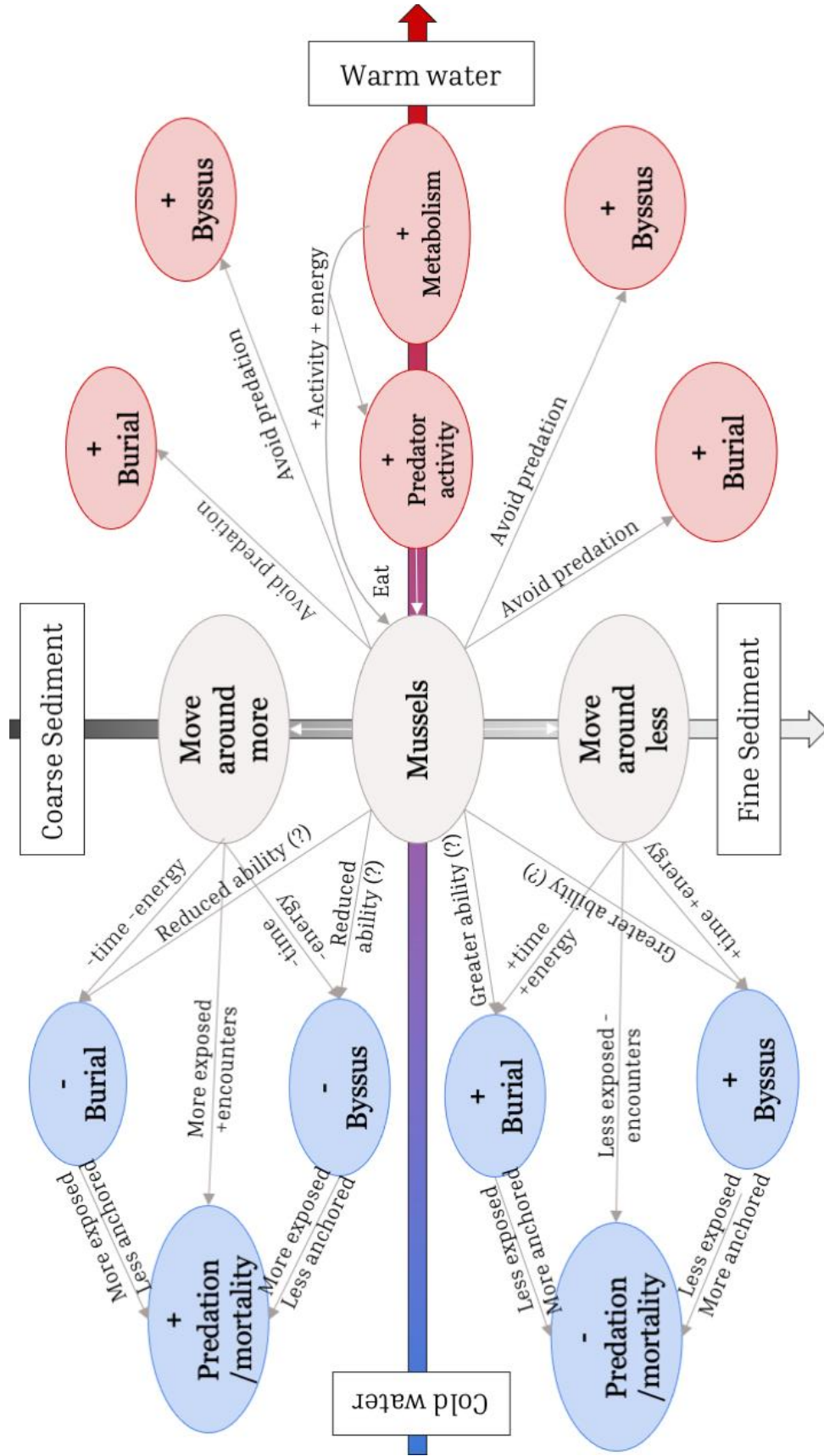
Based on the results of this study and previous findings, we propose the following conceptual model for the effect of sediment grain size on *A. senhousia* survival and distribution in Mission Bay (Fig. 3.1). In warm water we saw higher mortality, byssus production and burial which could be related to increased metabolism of mussels that are ectothermic (their activity being highly dependent on the temperature of surroundings). The experimental snail *P. festiva* are also ectothermic so trends may be more related to increased snail metabolism and activity. One approach mussels may take to reduce predation risk might be to burrow deeper and produce more byssus when it is warm and snails are more active (especially in fine-grained sediment). In warm water, the lack of significant differences between treatments may be because the increased snail activity swamped any trends we might've seen given the moderate mussel density in our experimental beakers. From the sediment choice experiments we know that mussels are preferentially associated with fine-grained sediment, moving around less when initially placed on fine sediment. They seem to spend more time redistributing in coarse-grained sediment which may leave them more exposed and increase the rate at which they encounter predators, ultimately increasing mortality in coarse sediments. Additionally, energy spent moving around is not energy spent burrowing or producing byssus, so in coarse sediment mussels may spend less time and energy doing these things, again making them more vulnerable to predation. In contrast, when mussels move around less on fine sediment, they are less exposed and may experience fewer encounters with predators and are able to spend more time and energy burrowing and producing

byssus, making them less vulnerable to predation. Finally, mussels may simply be able to burrow and produce byssus better or more easily in fine sediment. Some bivalves are more generalists when it comes to burrowing ability in different sediment grain sizes, but previous work has not addressed specifically how sediment grain size affects *A. senhousia*'s physical ability to burrow.

Invasive species, especially ecosystem engineers like *A. senhousia*, interact with their invaded ecosystems in many ways and have the capacity to create major changes to ecosystems. Invasive bivalves can become widespread, often achieving numerical dominance relative to natives, which can have implications for primary production and food availability within invaded ecosystems. It is for this reason that the distribution of invasive bivalves is important to understand and track. For soft sediment dwelling bivalves like *A. senhousia*, sediment characteristics certainly play a large role in where they can exist and where they distribute, as suggested by this study. This study sheds light on how sediment characteristics across an environmental gradient may affect the distribution of a potentially harmful invasive bivalve.

3.1 Figures

Figure 3.1 Conceptual diagram illustrating some of the trends and relationships discussed in this study with the x-axis representing temperature treatments (cold on the left and warm on the right) and the y-axis representing sediment treatments (coarse on the top and fine on the bottom).



REFERENCES

- Alexander, R. R., R. J. Stanton Jr, and J. R. Dodd. 1993. Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*:289-303.
- Bayne, B., and C. Scullard. 1978. Rates of feeding by *Thais* (*Nucella*) *lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **32**:113-129.
- Block, J. E., G. W. Gerald, and T. D. Levine. 2013. Temperature effects on burrowing behaviors and performance in a freshwater mussel. *Journal of Freshwater Ecology* **28**:375-384.
- Castorani, M. C., and K. A. Hovel. 2015. Invasive prey indirectly increase predation on their native competitors. *Ecology* **96**:1911-1922.
- Castorani, M. C., and K. A. Hovel. 2016. Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. *Biological Invasions* **18**:169-181.
- Cheng, B. S., and K. A. Hovel. 2010. Biotic resistance to invasion along an estuarine gradient. *Oecologia* **164**:1049-1059.
- Crooks, J. A. 2002. Predators of the invasive mussel *Musculista senhousia* (Mollusca: Mytilidae). *Pacific Science* **56**:49-56.
- De la Huz, R., M. Lastra, and J. López. 2002. The influence of sediment grain size on burrowing, growth and metabolism of *Donax trunculus* L.(Bivalvia: Donacidae). *Journal of Sea Research* **47**:85-95.

- Edwards, D. C., and J. D. Huebner. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* **58**:1218-1236.
- Hochachka, P. W., and G. N. Somero. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford university press.
- Morton, B. 1974. Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae).
- Rajagopal, S., G. Van der Velde, H. Jenner, M. Van der Gaag, and A. Kempers. 1996. Effects of temperature, salinity and agitation on byssus thread formation of zebra mussel *Dreissena polymorpha*. *Netherland Journal of Aquatic Ecology* **30**:187-195.
- Sanford, E. 2002. The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *Journal of Experimental Marine Biology and Ecology* **273**:199-218.
- Stickle, W., M. Moore, and B. Bayne. 1985. Effects of temperature, salinity and aerial exposure on predation and lysosomal stability of the dogwhelk *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **93**:235-258.
- Takenaka, R., T. Komorita, and H. Tsutsumi. 2018. Accumulation of organic matter within a muddy carpet created by the Asian date mussel, *Arcuatula*

senhousia, on the Midori River tidal flats, Japan. Plankton and Benthos Research **13**:1-9.

Tsutsumi, H., R. Nomura, T. Tanoue, T. Komorita, T. Iwasaki, and T. Fujimori.

2013. Influence of the Development and Destruction of Muddy Byssal Mats Made by a Mytilid Mussel, *Musculista senhousia* , on Seasonal Fluctuations of the Macrobenthic Community on Sandy Tidal Flats. Japanese journal of benthology **67**:47-55.

Yee, E., and S. Murray. 2004. Effects of temperature on activity, food consumption rates, and gut passage times of seaweed-eating Tegula species (Trochidae) from California. Marine Biology **145**:895-903.

Young, G. 1985. Byssus-thread formation by the mussel *Mytilus edulis*: effects of environmental factors. Marine ecology progress series. Oldendorf **24**:261-271.

APPENDIX A

