Filtration Efficiency in Bivalves: effects of species and size in oysters and mussels

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ABSTRACT

Filter-feeding bivalves possess the potential to naturally improve marine ecosystems suffering from an overabundance of particulate organic matter and anthropogenic pollution through their water filtration processes. However, differences in realized potentials related to species identity and size are poorly understood. This project strives to (1) analyze filtration rates as they correspond to species in *Pteria sterna, Pinctada mazatlanica,* and *Semimytilus algosus*, and (2) determine the independent influence of soft tissue volume on this phenomenon. I performed species-segregated filtration trials and analyzed the filtration efficiency per unit volume of soft tissue. *Pteria sterna* filters the fastest when considering species identity, but *Semimytilus algosus* filters most efficiently when considering water filtered per unit volume of soft tissue. Species and size are interconnected and codetermine filtration efficiency; size is the dominant factor regarding filtration, but species identity strongly predicts size. Microscope analysis of algae and bryozoans abundance before and after filtration trials implies that species differ in the organic matter they primarily consume. Furthermore, filtration rate does not increase linearly with larger group sizes, providing implications of social facilitation among bivalves.

RESUMEN

Los bivalvos que se alimentan por filtración tienen el potencial de mejorar naturalmente los ecosistemas marinos que sufren de una sobreabundancia de materia orgánica particulada y contaminación antropogénica a través de sus procesos de filtración de agua. Sin embargo, las diferencias en los potenciales realizados relacionados con la identidad y el tamaño de las especies son poco conocidas. Este proyecto se esfuerza por (1) analizar las tasas de filtración que correspondan a las especies en *Pteria sterna, Pinctada mazatlanica* y *Semimytilus algosus*, y (2) determinar la influencia independiente del volumen de tejidos blandos en este fenómeno. Realicé ensayos de filtración segregados por especies y analicé la eficiencia de filtrado por unidad de volumen de tejido blando. *Pteria sterna* filtra más rápido cuando se considera la identidad de una especie, pero *Semimytilus algosus* filtra más eficientemente cuando se considera agua filtrada por unidad de volumen de tejido blando. Las especies y el tamaño están interconectados y codifican la eficiencia de filtración; El tamaño es el factor dominante con respecto a la filtración, pero la identidad de la especie predice el tamaño. Además, el análisis microscópico de la abundancia de algas y briozoos antes y después de los ensayos de filtración implica que las especies difieren en la materia orgánica que consumen principalmente.

INTRODUCTION

Suspension feeder bivalves play an integral role in maintaining the health of marine ecosystems through water filtration and nutrient cycling (Buschmann et al. 2008, Newell 2004). Marine bivalves filter plankton, benthic algae, bryozoans, detritus, and other organic matter from the water column, simultaneously decreasing turbidity and maintaining ecosystem equilibrium (Gallardi 2014, Newell 2004). Decreasing turbidity is necessary to allow ample light to penetrate the water column, enabling organisms such as seagrasses and benthic microalgae to photosynthesize (Newell 2004). Furthermore, nitrogen and phosphorus are found in high densities in anthropogenically polluted water (Newell 2004). These mollusks sequester nitrogen, phosphorus, and carbon, utilizing a portion of it for tissue growth and depositing more into the sediment via their excrement (Gallardi 2014, Langdon et al. 1990, Newell 2004). Bivalves expel ammonia and undigested remains in the form of mucus-bound feces and pseudofeces that regenerate nitrogen and phytoplankton in moderation, stabilizing primary production and maintaining their own food source (Filgueira et al. 2015, Newell 2004). Additionally, their sequestration of carbon can aid in moderating the detrimental effects of global warming as carbon levels in the ocean are rising at an alarming rate (Hoegh-Guldberg et al. 2014). In these ways, bivalves exhibit both top-down grazer control as well as bottom-up production in marine ecosystems (Newell 2004).

Substantial data exists analyzing marine bivalve filtration processes in certain species, specifically interspecific differences in filtration rates and filtration-affiliated morphological characteristics (Ansell 1981, Kryger et al. 1988, Langdon et al. 1990). Langdon et al. found that the ribbed mussel *Geukensia demissa* sequesters more carbon and bacteria than the oyster *Crassostrea virginica* in a freshwater system (1990). Additionally, interspecific differences in filtration efficiency are affected by size, filtration rate, and gill particle retention ability (Riisgard 1988, Sylvester et al. 2005). However, these factors have largely been studied independently, resulting in a gap in our knowledge regarding whether species or size plays a more important role. Furthermore, the literature fails to emphasize the bivalve species most likely to thrive at aquaculture sites where such research holds the most relevant applications. A deeper understanding of bivalve filtration efficiency can minimize environmental impact and maximize sustainability.

Bivalve polycultures naturally recruit in the same coastal marine communities and aquaculture sites, resulting in ambiguity regarding individualistic filtration capacity. Since these organisms have been shown to greatly enhance the biotic conditions of their surrounding habitats, they demonstrate their potential to assist in the recovery of ecosystems suffering from anthropogenic pollution (Newell 2004, Strayer et al. 1999). Off-shore aquaculture systems serve as a prime example of anthropogenic establishments in need of ecological renovation in order to reach sustainability (Buschmann et al. 2008). The mariculture industry has alleviated substantial fishing pressure placed on the oceans in recent decades and is especially valuable for coastal communities that are economically reliant on their fishing industry (Buschmann et al. 2008). However, if not carefully executed, this system has potential to raise its own myriad of severe environmental consequences (Buschmann et al. 2008). Congregations of fish in high densities in mariculture modules produce a substantial amount of fish feces, detritus, bacteria, mercury, nitrogen, phosphorus, and other organic accumulations that flow into local reefs ecosystems, deeming them unsuitable for their inhabitants (Buschmann et al. 2008). This anthropogenic nutrient over-enrichment leads to detrimental shifts in primary production such as algal blooms, hypoxia, and red tides (Newell 2004).

Large-scale mariculture establishments have attempted to dilute such pollution with submarine blowers, siphon waste with remote-operated vehicles, or collect it via accessories attached to the bottom of modules (Buschmann et al. 2008). However, these remedies are not within the realm of accessibility for small mariculture sites with limited resources. Therefore, more accessible organic environmental control is the key to waste management for such establishments. Some small-scale aquaculture sites actively recruit filter-feeding seaweed and young bivalves as biocontrol, but not all have taken this kind of initiative (Buschmann et al. 2008, Soto et al. 1999).The INMAR mariculture site off the coast of Cuajiniquil is an example of an establishment that has only minimally evaluated the present marine species and possibilities to increase sustainability. Just as terrestrial farms utilize animals as biocontrol of pests, mariculture benefits from the presence of filter-feeders as natural waste management (Cardinale et al. 2003, Soto et al. 1999).

Oyster species *Pteria sterna* and *Pinctada mazatlanica* as well as mussel *Semimytilus algosus* can colonize together in large magnitudes at mariculture sites, resulting in polycultures with unknown segregations of filtering efficiencies. The objectives of this project include (1) analyzing how filtration rates differ between *Pinctada mazatlanica, Pteria sterna,* and *Semimytilus algosus*, and (2) determining the influence of individual soft tissue volume on the filtration rate. Analyzing these factors will allow me to determine whether species or size is more influential regarding filtration. I predicted that *Pinctada mazatlanica* filters the fastest and possesses the highest filtration rate per unit volume of soft tissue since it is the largest in size.

MATERIALS AND METHODS

My data was collected and analyzed at the INMAR mariculture site in Bahia Thomas off the coast of Cuajiniquil, Costa Rica from 16 November – 24 November, 2018. I completed ten trails with three species: *Pteria sterna*, *Pinctada mazatlanica*, and *Semimytilus algosus*. Species were identified using a bivalve seashell guidebook (Coan et al. 2012).

Turbidity Trials

I recorded filtration rates by measuring the decrease in turbidity over time as each species independently filtered water. With the assistance of the mariculture staff, I free dove at the mariculture site to collect bivalves of each species, algae, and bryozoans from the modules. Species were separated into respective white buckets with two conspecific individuals per bucket (35 cm height, 30 cm diameter, 88 cm circumference) and compared to a control bucket with no bivalves. I added 18 liters of water and approximately 0.8 liters of algae to each bucket to increase the water turbidity. This water quantity was determined by the quantity and depth required to effectively measure the turbidity as a gradient. I used two individuals per bucket to filter the water efficiently enough to complete ten trials of the experiment.

To measure the turbidity of the water, I held a 15-centimeter ruler parallel to the bucket bottom paired with an attached perpendicular measuring tape that ran parallel to the bucket wall. This device served as a small-scale, precise Secchi Disk. I lowered it into the water and recorded the deepest vertical centimeter depth at which I could distinguish the horizontal millimeter lines. I shaded the buckets to minimize water warming due to sunlight exposure and consistently recorded turbidity measurements from the same angle to avoid unequal light exposure from shadows of the bucket walls. I measured turbidity at the start of the experiment to ensure that each bucket had the same turbidity. If necessary, I added small quantities of algae to less-turbid buckets to match the most turbid bucket. Additionally, I photographed the buckets at the start and finish of each experiment.

Every 20 minutes, I measured the turbidity in each bucket. I concluded the trial when all three bivalve buckets reached maximum clarity, meaning I could differentiate the millimeter lines when the ruler rested at the bottom of the bucket, or when two hours and 20 minutes passed.

<u>*Individual Dimensions and Volume*</u>

I took size measurements of each individual with measuring tape and water displacement. I recorded vertical and horizontal circumferences, total volume (shell with soft tissue), and soft tissue volume. I measured the volume of only the soft tissue as a parameter because that is the anatomical part of the bivalve that filters. I dissected and measured the soft tissue volume for six individuals of each species and created species-specific ratios between soft tissue volume, the circumferences, and total volume. Then I extrapolated the soft tissue volume of every other conspecific.

<u>*Intraspecific Filtration Comparison*</u>

For two of the ten trails, I also observed filtration in two extra buckets with four and six individuals, respectively, of *Pinctada mazatlanica*. This allowed me to compare how a larger group size affects filtration rate, specifically whether the rate increases linearly, logistically, exponentially, or otherwise.

<u>*Microscope Analysis*</u>

For four of the ten trails, I took samples of water from each bucket before and after the trial for microscope analysis. I briefly stirred the water in the bucket to create a homogenous mixture and filtered 0.5 gallons through a plankton net (13 cm diameter, 38 cm length, 50 mL flask) to concentrate the algae, plankton, and other contents. Using a compound microscope, I conducted qualitative observations and quantitative analysis viewing 25 drops per sample on a 400 square spot slide. I compared the percent coverage of algae and bryozoans from samples before filtration to their respective samples after filtration.

RESULTS

Pteria sterna filters faster than the other two species, and filters significantly faster than *Semimytilus algosus* (Figure 1, ANOVA, F=4.20, p = 0.026, Tukey-Kramer, see Appendix 1). *Pinctada mazatlanica* filters at an intermediate rate, and *Semimytilus algosus* filters the slowest (Figure 1).

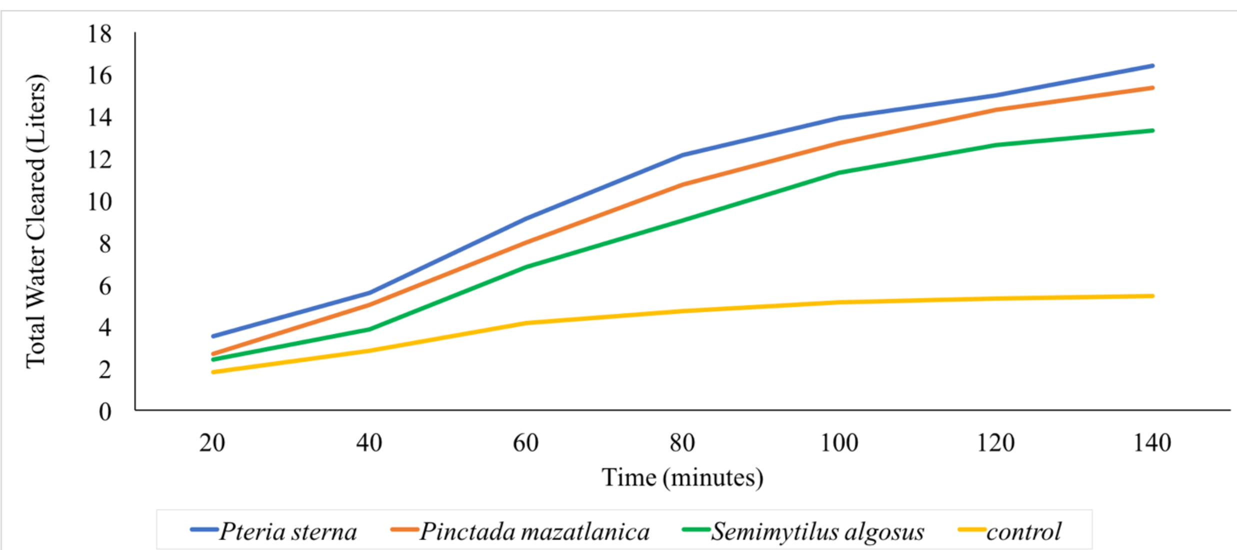

Figure 1: Average filtration rate of each species and the control at 20 minute intervals through 10 trials.

Pteria sterna and *Pinctada mazatlanica* individuals have similar volumes, and both tended to be larger than *Semimytilus algosus* (Figure 2). *Pteria sterna* and *Pinctada mazatlanica* were distinctly on the higher end of the spectrum (volume > 20 mL), while *Semimytilus algosus* individuals congregated on the lower end of the spectrum (volume < 20 mL) (Figure 2). Despite this size difference, all three species have similar average filtration rates. The filtration rate is the volume of fluid that flows per unit time, representing the volumetric flow rate. The respective averages for *Pteria sterna*, *Pinctada mazatlanica*, and *Semimytilus algosus* are 6.3 L/hr, 5.8 L/hr, and 4.8 L/hr (Figure 2).

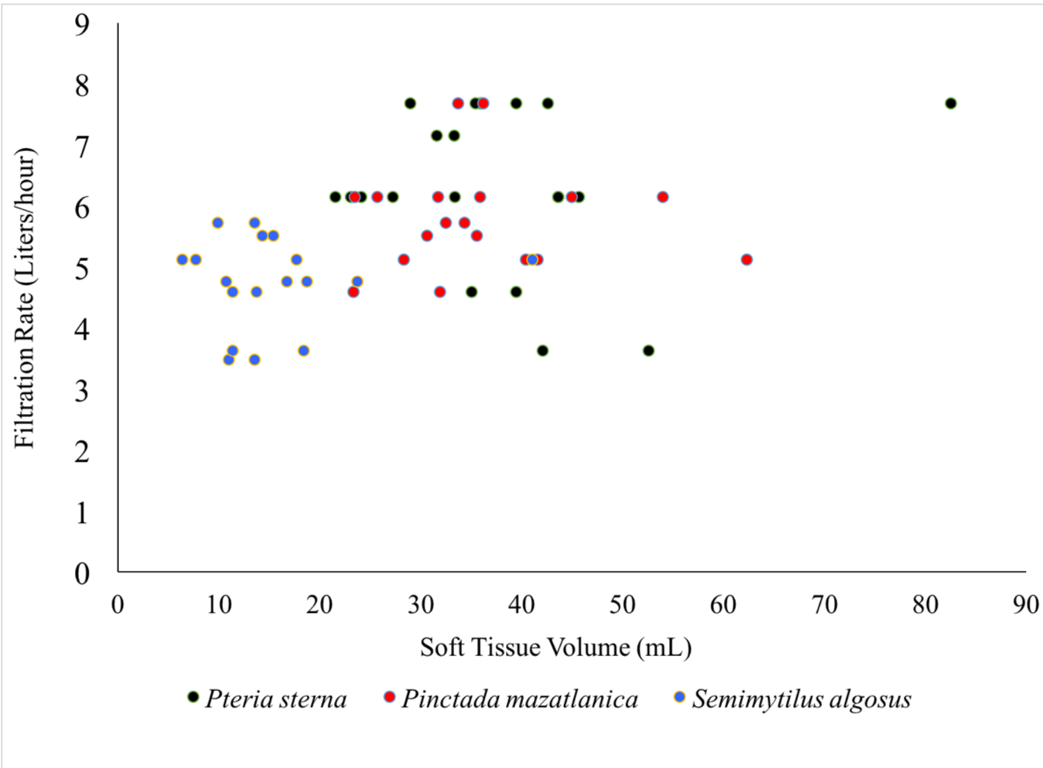

Figure 2: Filtration rate and volume of soft tissue for each individual.

Semimytilus algosus is significantly smaller in volume than both *Pteria sterna* and *Pinctada mazatlanica* (Figure 3, ANOVA, $F = 13.1$, $p < 0.0001$, Tukey-Kramer, see Appendix 2).

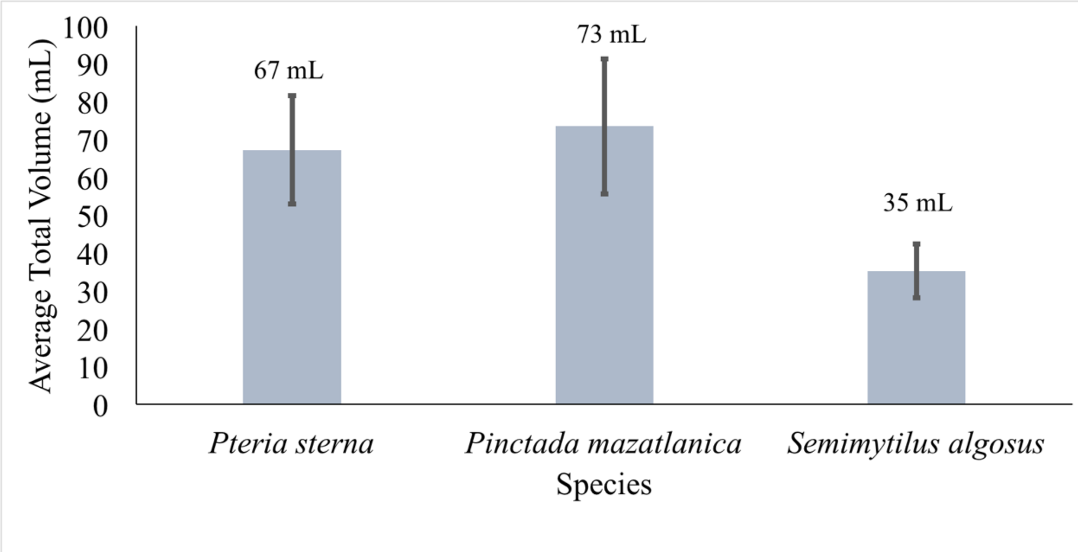

Figure 3: Average total volume of individuals by species. Total volume directly correlates with soft tissue volume.

The volumetric flow rate of each individual is standardized per unit volume of soft tissue, revealing that *Semimytilus algosus* is significantly more efficient at filtration than both oyster species (Figure 4, ANOVA, $F = 19.6$, $p < 0.0001$, Tukey-Kramer, see Appendix 3). The average volumetric flow rate per milliliter soft tissue for *Pteria sterna*, *Pinctada mazatlanica*, and *Semimytilus algosus* are 182 (mL/hr), 172 (mL/hr), and 371 (mL/hr), respectively. The respective standard deviations are 65 (mL/hr), 47 (mL/hr), and 172 (mL/hr) (Figure 4).

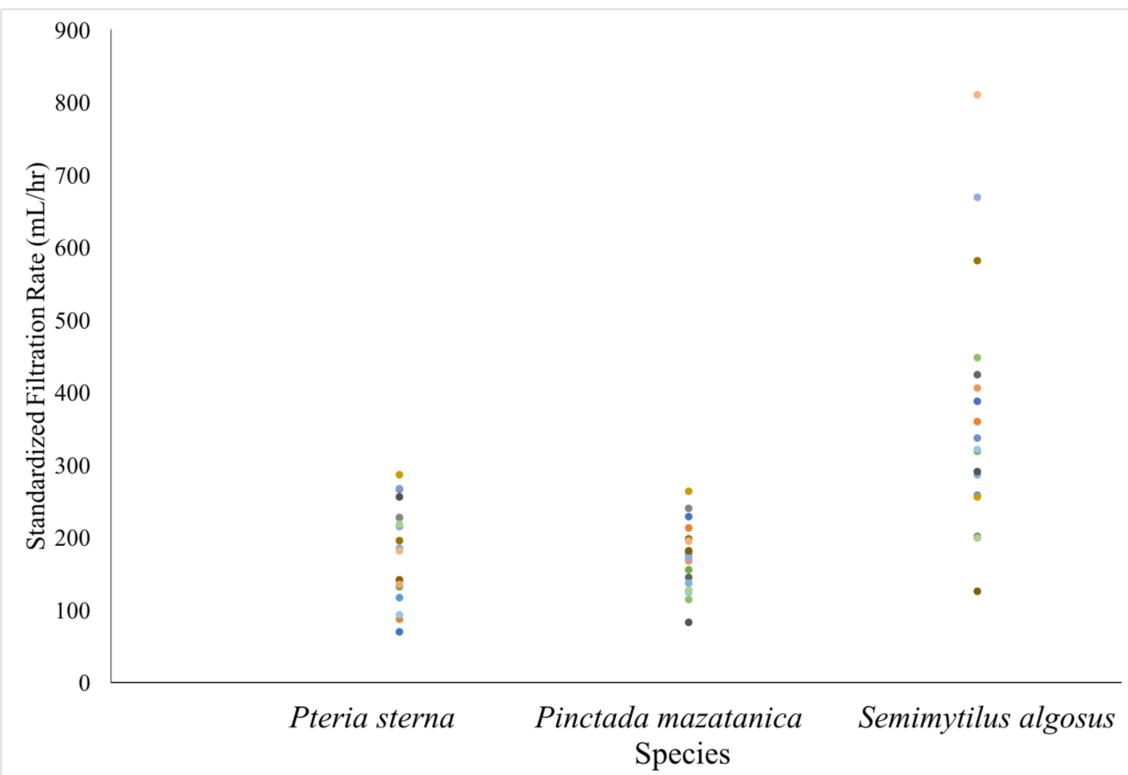

Figure 4: Standardized values for filtration rate per unit volume of soft tissue. This represents the milliliters of water filtered per hour per milliliter of soft tissue. Each data point represents one individual.

The respective filtration rate trends of two, four, and six *Pinctada mazatlanica* individuals appear to increase non-linearly; there is a substantial increase from two to four individuals and relatively small increase from four to six individuals (Figure 5, Table 1).

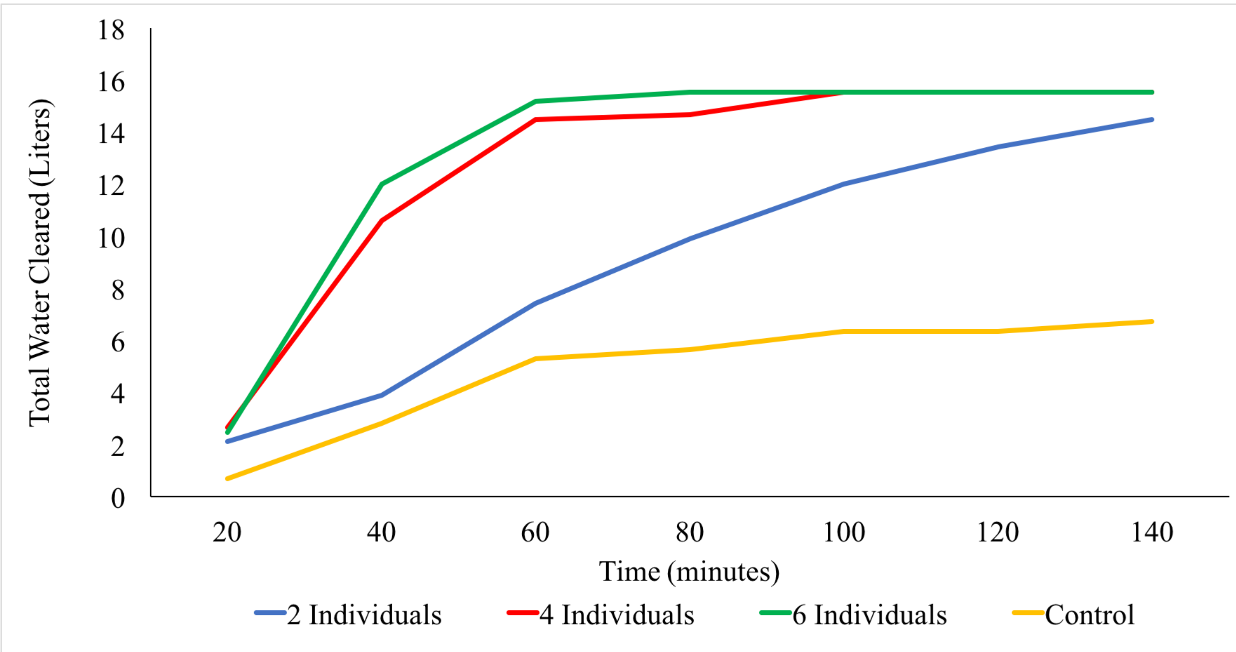

Figure 5: *Pinctada mazatlanica* filtration rates with two, four, and six individuals showing the median values from two trials.

Table 1: Temporal filtration data for comparison between two, four, and six individuals of *Pinctada mazatlanica.*

Trial	Number of Individuals	Completely cleared water within 140 minutes?	Minutes needed to completely clear water
A	2	No	N/A
B	2	Yes	120
A	4	Yes	100
B	4	Yes	80
A	6	Yes	80
B	6	Yes	60
A	0 (control)	No	N/A

B	0 (control)	No	N/A

Qualitatively, I took note that the before-filtration samples were much denser with algae, bryozoans, and plankton while the after-filtration samples contained much less, with most of the minimal contents being brown bivalve excrement.

For quantitative analysis, the average percent cover of algae and bryozoans on spot sides shows decreases in abundance in the post-filtration samples (Table 2).

Table 2: Decrease in average percent coverage of algae and bryozoans after 4 filtration trials.

Species	Average decrease after filtration
Pteria sterna	53%
Pinctada mazatlanica	35%
Semimytilus algosus	42%
Control	+2%

DISCUSSION

Filtration trials show that *Pteria sterna* filtered the fastest and filtered significantly faster than *Semimytilus algosus*, which was the slowest (Figure 1). This does not agree with my prediction that *Pinctada mazatlanica* would filter the fastest. Species identity certainly contributes to filtration rate. The slight decrease in turbidity in the control bucket was due to sediment settling.

Considering filtration rate and total soft tissue volume, *Semimytilus algosus* filtered at a similar rate as both the oyster species, despite being smaller (Figure 2). *Semimytilus algosus* almost completely dominates the small end of the soft tissue volume spectrum, but the averages of all three species are similar as they are within 1.5 L/hr of each other. This implies that *Semimytilus algosus* is most efficient and does not agree with my prediction that *Pinctada mazatlanica* would be most efficient. This further implies that species identity contributes to filtration rate because if only size determined filtration rate, *Semimytilus algosus* would filter many fewer liters per hour due to its smaller size. The standardized filtration rates per unit soft tissue volume further elucidates this trend (Figure 4). *Semimytilus algosus* filters most efficiently than the other two species by a significant margin (Appendix 3). *Pteria sterna* is less efficient, and *Pinctada mazatlanica* filters the least efficiently by a relatively small margin. Although *Semimytilus algosus* filtered the slowest in the filtration trials and has the smallest average volume, it filtered more efficiently than individuals of *Pteria sterna* and *Pinctada mazatlanica* per unit soft tissue volume (Figures 1, 3 and 4). This data implies that if timed filtration trials were held between equally-sized individuals of *Pteria sterna* and *Semimytilus algosus, Semimytilus algosus* would filter faster. Species identity is undoubtedly a factor for determining filtration efficiency.

Furthermore, considering Figures 1, 3 and 4 together demonstrates that size is also an important factor. *Pteria sterna* filters fastest because individuals of that species tend to be larger, not because that species is more efficient, because *Semimytilus algosus* is more efficient (Figure 4). This data implies that size is more influential than species, since the larger species filtered faster than the more efficient species. Future research is necessary in order to pinpoint the precise tipping point of these factors, meaning at what volume the efficiency is more influenced by species identity.

The observed correlation between large size and low filtration efficiency is realistic when considering organism energy investment. Considering the average total volume of each species, *Semimytilus algosus* has significantly the smallest volume, implying this species invests relatively less energy in a large shell and more into its soft tissue processes (Figure 3). Similar flexible energy allocation in order to enhance fitness is observed in zebra mussels (Stoeckmann et al. 2001). Therefore, its soft tissue can be more efficient in filter feeding. *Pinctada mazatlanica* has the largest shell and lowest filtration efficiency of all three species, corresponding with the opposite trend of energy investment; more towards size and mechanical protection than filtration processes (Figures 3 and 4). Similar reasoning explains why *Semimytilus algosus* has the highest standard deviation in filtration efficiency per soft tissue volume; even a tiny difference in soft tissue volume will more drastically alter the filtration efficiency since each unit of soft tissue has a relatively higher filtration capacity (Figure 4).

The filtration rate trends of two, four, and six *Pinctada mazatlanica* individuals show a substantial increase from two to four individuals but a relatively small increase from four to six individuals (Figure 5, Table 1). I chose to use *Pinctada mazatlanica* for this intraspecific analysis based on the data from the turbidity trials; this species proved to have the intermediate filtration rate so I strived to determine the number of individuals of *Pinctada mazatlanica* that rivals or surpasses the filtration rate of the faster *Pteria sterna*. As only two trials were conducted, no statistics can be applied. However, this data serves as interesting preliminary observations for future research regarding filtration rate trend as population size increases. A non-linear increase in filtration rate could have implications for social facilitation among bivalves, as is observed in other marine invertebrates such as red sea urchins (Breen et al. 1985).

Quantitative microscope analysis shows trends in algae and bryozoan reduction post-filtration. This analysis estimates the quantity of algae and bryozoans consumed by each species to complement the filtration speeds gathered from the time trials (Table 2, Figure 1). The filtration trials observed water clearance rate, therefore observing the reduction in all water contents over time, but the microscope analysis specifically focuses on algae and bryozoans. *Pteria sterna* filtered the most algae, followed by *Semimytilus algosus,* and *Pinctada mazatlanica* consumed the least amount of algae. This data gives important insight regarding the specific water contents that each species consumes. The fact that *Pinctada mazatlanica* filtered faster than *Semimytilus algosus* in the time trials but *Semimytilus algosus* consumed more algae can be explained by two possible phenomenons. One explanation is that *Pinctada mazatlanica* selectively feeds on other biotic material in the water, such as zooplankton. Newell found support for a similar pattern in oysters and mussels in freshwater systems, as they filtered algal material from the water first, then filtered detrital material and bacteria only when there was low abundance of algae (1990). These mollusks might show food preference comparable to that of animals in higher trophic levels. An alternate explanation is that the gills of *Pinctada mazatlanica* do not retain phytoplankton particles as well as those of *Semimytilus algosus,* but instead more efficiently retain particles of a different range. *Semimytilus algosus* might possess larger latero-frontal cirri on their gills that enhance retention of phytoplankton particles. This more effective gill morphology is found in the clam species *Mercenaria mercenaria*, allowing it to achieve a greater retention rate of particles larger than four μm compared to the oyster *Crassostrea virginica* (Riisgard 1988). This is an area for future research.

Understanding interspecific rates of filtration while simultaneously considering the impact of individual size could potentially revolutionize the composition of suspension feeders that conservationists deliberately recruit to polluted marine regions.

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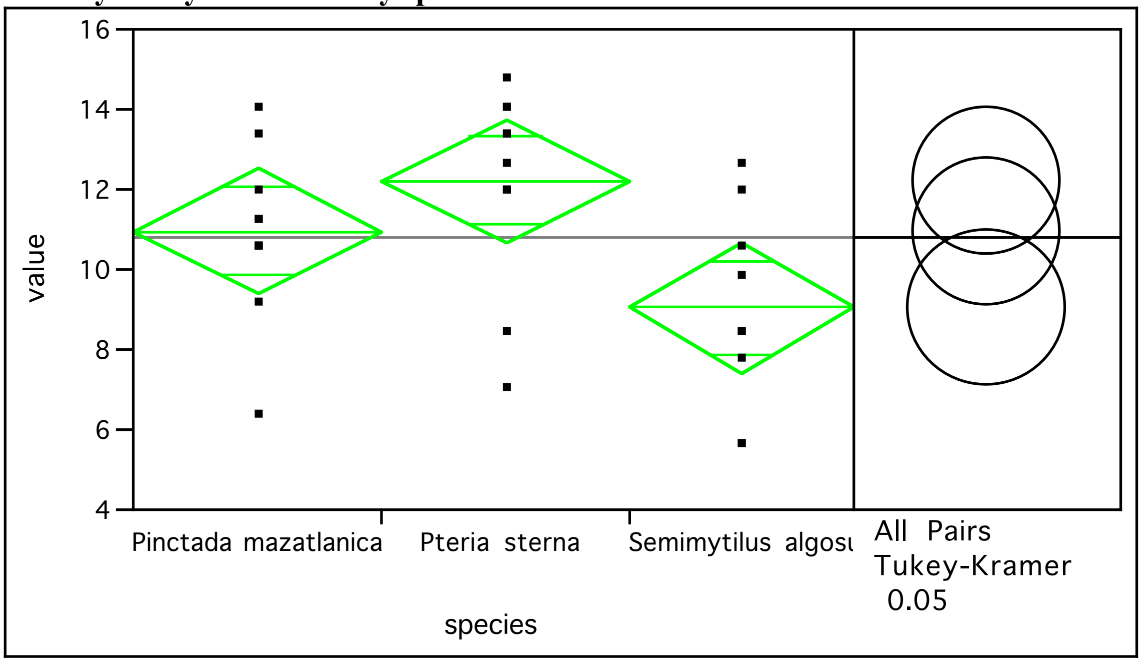
APPENDICES

Appendix 1
Oneway Analysis of value By species



Oneway Anova
Summary of Fit

Rsquare	0.24422
Adj Rsquare	0.186083
Root Mean Square Error	2.386309
Mean of Response	10.7931
Observations (or Sum Wgts)	29

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
species	2	47.84240	23.9212	4.2008	0.0263
Error	26	148.05622	5.6945		
C. Total	28	195.89862			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
Pinctada mazatlanica	10	10.9500	0.75462	9.399	12.501
Pteria sterna	10	12.2100	0.75462	10.659	13.761
Semimytilus algosus	9	9.0444	0.79544	7.409	10.679

Std Error uses a pooled estimate of error variance

Means Comparisons

Dif=Mean[i]-Mean[j]	Pteria sterna	Pinctada mazatlanica	Semimytilus algosus
Pteria sterna	0.0000	1.2600	3.1656
Pinctada mazatlanica	-1.2600	0.0000	1.9056
Semimytilus algosus	-3.1656	-1.9056	0.0000

Alpha=

0.05
Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2.48489	0.05

Abs(Dif)-LSD	Pteria sterna	Pinctada mazatlanica	Semimytilus algosus
Pteria sterna	-2.6519	-1.3919	0.4410
Pinctada mazatlanica	-1.3919	-2.6519	-0.8190
Semimytilus algosus	0.4410	-0.8190	-2.7953

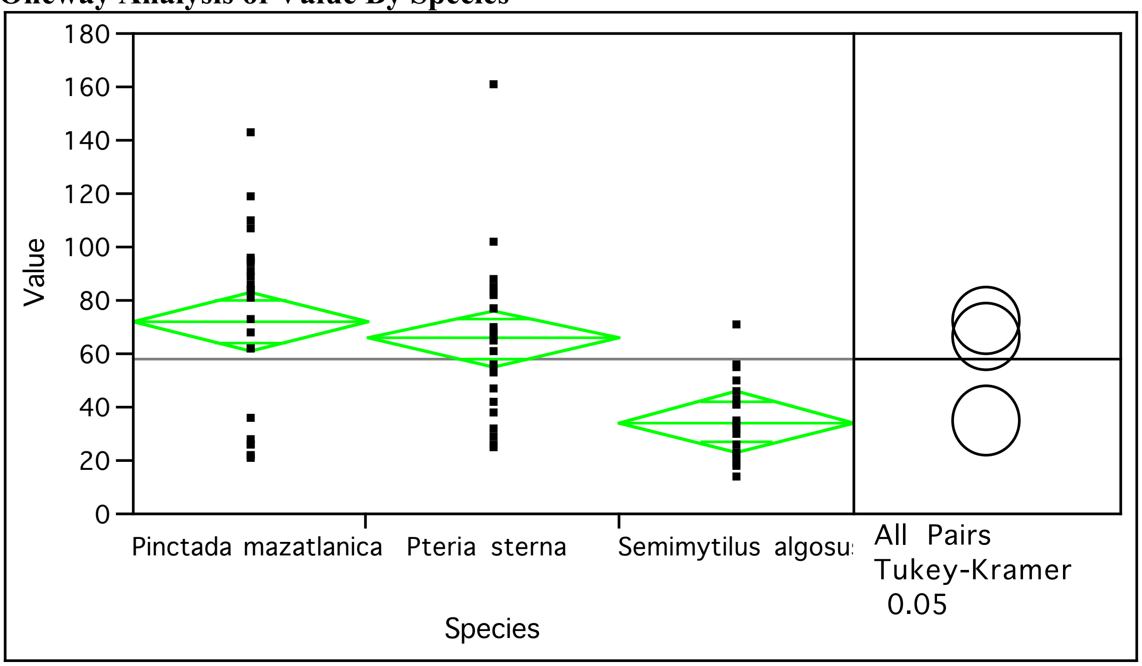
Positive values show pairs of means that are significantly different.

Level			Mean
Pteria sterna	A		12.210000
Pinctada mazatlanica	A	B	10.950000
Semimytilus algosus		B	9.044444

Levels not connected by same letter are significantly different

Appendix 2

Oneway Analysis of Value By Species



Oneway Anova
Summary of Fit

Rsquare	0.268969
Adj Rsquare	0.248377
Root Mean Square Error	27.31609
Mean of Response	57.55405
Observations (or Sum Wgts)	74

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Species	2	19492.287	9746.14	13.0616	<.0001
Error	71	52977.997	746.17		
C. Total	73	72470.284			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
Pinctada mazatlanica	24	71.8750	5.5759	60.757	82.993
Pteria sterna	26	65.6923	5.3571	55.011	76.374
Semimytilus algosus	24	34.4167	5.5759	23.299	45.535

Std Error uses a pooled estimate of error variance

Means Comparisons

Dif=Mean[i]-Mean[j]	Pinctada mazatlanica	Pteria sterna	Semimytilus algosus
Pinctada mazatlanica	0.000	6.183	37.458
Pteria sterna	-6.183	0.000	31.276
Semimytilus algosus	-37.458	-31.276	0.000

Alpha=
0.05

Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2.39384	0.05

Abs(Dif)-LSD	Pinctada mazatlanica	Pteria sterna	Semimytilus algosus
Pinctada mazatlanica	-18.877	-12.327	18.582
Pteria sterna	-12.327	-18.136	12.766
Semimytilus algosus	18.582	12.766	-18.877

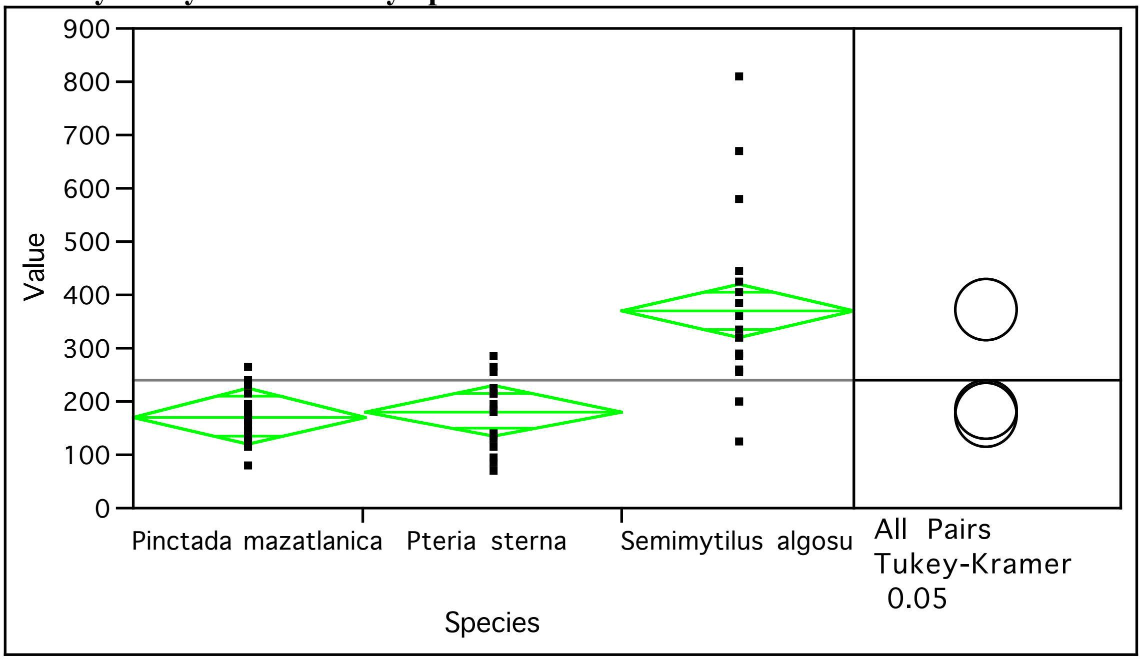
Positive values show pairs of means that are significantly different.

Level			Mean
Pinctada mazatlanica	A		71.875000
Pteria sterna	A		65.692308
Semimytilus algosus		B	34.416667

Levels not connected by same letter are significantly different

Appendix 3

Oneway Analysis of Value By Species



Oneway Anova
Summary of Fit

Rsquare	0.425485
Adj Rsquare	0.403805
Root Mean Square Error	107.9557
Mean of Response	239.6125
Observations (or Sum Wgts)	56

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Species	2	457455.8	228728	19.6258	<.0001
Error	53	617685.2	11654		
C. Total	55	1075141.0			

Means for Oneway Anova

Level	Number	Mean	Std Error	Lower 95%	Upper 95%
Pinctada mazatlanica	18	171.939	25.445	120.90	222.98
Pteria sterna	20	182.465	24.140	134.05	230.88
Semimytilus algosus	18	370.783	25.445	319.75	421.82

Std Error uses a pooled estimate of error variance

Means Comparisons

Dif=Mean[i]-Mean[j]	**Semimytilus algosus**	**Pteria sterna**	**Pinctada mazatlanica**
Semimytilus algosus	0.00	188.32	198.84
Pteria sterna	-188.32	0.00	10.53
Pinctada mazatlanica	-198.84	-10.53	0.00

Alpha=
0.05

Comparisons for all pairs using Tukey-Kramer HSD

q*	Alpha
2.41127	0.05

Abs(Dif)-LSD	Semimytilus algosus	Pteria sterna	Pinctada mazatlanica
Semimytilus algosus	-86.77	103.75	112.07
Pteria sterna	103.75	-82.32	-74.05
Pinctada mazatlanica	112.07	-74.05	-86.77

Positive values show pairs of means that are significantly different.

Level			Mean
Semimytilus algosus	A		370.78333
Pteria sterna		B	182.46500
Pinctada mazatlanica		B	171.93889

Levels not connected by same letter are significantly different