

Article

Quantifying the Potential Water Filtration Capacity of a Constructed Shellfish Reef in a Temperate Hypereutrophic Estuary

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Abstract: Shellfish reefs have been lost from bays and estuaries globally, including in the Swan-Canning Estuary in Western Australia. As part of a national program to restore the ecosystem services that such reefs once provided and return this habitat from near extinction, the mussel *Mytilus galloprovincialis* was selected for a large-scale shellfish reef construction project in this estuary. To assess the potential filtration capacity of the reef, estuary seston quality, mussel feeding behavior, and valve gape activity were quantified in the laboratory and field during winter and summer. In general, estuary water contained high total particulate concentrations (7.9–8.7 mg L^{−1}). Standard clearance rates were greater in winter (1.9 L h^{−1}; 17 °C) than in summer (1.3 L h^{−1}; 25 °C), the latter producing extremely low absorption efficiencies (37%). Mussel valves remained open ~97% and ~50% of the time in winter and summer, respectively. They often displayed erratic behavior in summer, possibly due to elevated temperatures and the toxic microalgae *Alexandrium* spp. Despite numerous stressors, the reef, at capacity, was estimated to filter 35% of the total volume of the estuary over winter, incorporating 42.7 t of organic matter into mussel tissue. The reefs would thus make a substantial contribution to improving estuary water quality.

Keywords: absorption efficiency; *Alexandrium* spp.; clearance rate; *Mytilus galloprovincialis*; restoration; seston quality; valvometers



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1. Introduction

Often referred to as ecosystem engineers, reef-forming shellfish, such as mussels and oysters, create habitats through the production of prominent reef or bed structures [1,2]. In such high abundance, shellfish provide a range of ecosystem services for coastal environments and communities, including the provision of habitat and prey communities for fish and crustaceans, the enhancement of biodiversity, and the improvement of water quality through filter feeding [3–6]. These habitats have historically suffered from anthropogenic impacts, such as over-harvesting, disease, and decreased water quality, which has led to the loss of ~85% of shellfish reefs worldwide, making them among the most threatened of all marine habitats [7,8]. The Swan-Canning Estuary supported vast shellfish reefs dominated by the native Flat Oyster *Ostrea angasi* in the middle Holocene, which later formed extensive shell deposits as the hydrology of the estuary changed with a drop in sea level and increasing siltation. These massive shell banks, which although non-living, provided vital habitat and shoreline buffering functions, were systematically destroyed through dredging for cement production in the first half of the twentieth century [9]. Over recent decades, increasing awareness of the ecosystem services provided by shellfish reefs and the scale of the loss of these habitats has led to large-scale efforts to restore them [8,10,11]. One such initiative is *Reef Builder*, Australia's largest marine restoration program. Led by The Nature Conservancy Australia (TNC), this program is currently working to restore shellfish reef

ecosystems at 13 sites nationally in a step towards a broader goal of restoring 30% of this lost habitat [12]. The Swan-Canning Estuary in Perth, Western Australia, is among those restoration sites.

Improving water filtration capacity would be particularly beneficial in temperate estuaries, which through excessive nutrient input are the most degraded of all marine ecosystems [13]. In South West Australia, eutrophication issues are further exacerbated by a highly seasonal climate and low tidal amplitude, resulting in long residence times of water and nutrients, particularly during the long, dry summers [14,15]. South West Australia has also experienced among the greatest declines in rainfall of any Australian region, substantially reducing streamflow into rivers and estuaries [16–18]. This has been particularly evident in the extensively modified Swan-Canning Estuary, in which annual streamflow has declined by ~90% over a recent 25-year period (1990–2015) [19]. This estuary was also among the most hypereutrophic of the 131 coastal ecosystems examined worldwide by Cloern et al. (2014) [20]. The environmental, cultural, and societal importance of the Swan-Canning Estuary, along with its historical loss of shellfish habitats and significant, increasing stressors through impacts such as harmful algal blooms, hypoxia, and contaminant loads [9,19], highlight this estuary as an excellent candidate for restoration using nature-based solutions (NbS), and specifically the reconstruction of shellfish reefs. While such habitat restoration is just one part of the broader management approach needed to sustain the health of complex waterways like the Swan-Canning Estuary, global evidence demonstrates the significant benefits restored shellfish reefs can bring to help recover ecosystem functioning, including improved water quality, greater fish productivity, and biodiversity gains [1]. This in turn supports benefits for local communities through enhanced recreational opportunities, support for local fishing and ecotourism industries, cultural reconnection and job opportunities.

While shellfish reef restoration efforts have typically focused on oysters, mussels have a similar water clearance capacity and can attain far greater densities [21,22]. This is of great importance when using mussels as NbS because the excess nutrients that lead to eutrophication may be removed more efficiently in the restored area. However, the rate and efficiency at which the nutrients can be removed vary according to environmental characteristics [23,24]. For example, at a certain threshold concentration of seston, mussels produce pseudofeces, i.e., seston retained in their gills but eliminated before ingestion [25,26]. Above that threshold, clearance rates may decrease, possibly due to sorting capacity reaching saturation [27]. The water clearance rate can be regulated by the opening and closing of the mussel's valves, which are held together by a ligament at the dorsal edge of the shell. Under optimal conditions, the adductor muscles are relaxed and the ligament holds the valves open to their maximum extent [28]. However, suboptimal environmental conditions can lead to modifications to valve behavior. For example, the Mediterranean mussel *Mytilus galloprovincialis* reduces valve gape in response to extremely low or high chlorophyll *a* concentration and increases the frequency of microclosures when exposed to toxic algae [29,30]. Long durations of valve closure have also been observed in *M. galloprovincialis* when exposed to elevated temperatures and in Blue Mussel *Mytilus edulis* when exposed to low dissolved oxygen concentrations [31].

When using shellfish as NbS for restoration purposes, native species should be chosen to mitigate negative ecosystem interactions [32]. Of the few reef-forming shellfish species that are native, relatively abundant, and suited to current environmental conditions in the Swan-Canning Estuary, *M. galloprovincialis* is considered the most appropriate for shellfish reef construction. This species has clearance rates greater than 4.5 L h^{-1} [26,33], is regularly found attached to jetty pylons and navigation markers in the estuary basin and channel, and is the main focus of the commercial shellfish aquaculture industry in the adjoining coastal embayment. While this species is euryhaline, tolerating salinities as low as 10 ppt and as high as 39 ppt, and thus suitable for the brackish waters of estuaries, its critical thermal maximum of ~26 °C is typically approached during summer in waters off Perth, which helps account for its absence in waters to the north [31,34–36].

Although the feeding and valve gaping behavior of *M. galloprovincialis* has been studied in European waters, the physico-chemical and seston quality of estuaries differ markedly over geographical scales. This is the first study to quantify the seasonal feeding behavior of *M. galloprovincialis* in an urbanized, temperate microtidal estuary, with the broader goal of applying those findings to estimate the filtration capacity of a fully-functioning constructed shellfish reef and promote the use of mussels as a NbS to restore water quality.

2. Materials and Methods

2.1. Feeding Experiments

The feeding experiments for *M. galloprovincialis* were undertaken during August 2020 (austral winter) and February 2021 (austral summer) in the laboratory using water collected from ~0.5 m above the substratum from three shallow (2–4 m) and three deep (5–8 m) sites in the main basin of the Swan-Canning Estuary (Sites 2, 4, 5; Figure 1). On each occasion, ~1000 L of estuary water was collected into surface drums using a submersible pump and transported to a 1000 L International Bulk Container (IBC) sump at the laboratory. Water temperature and salinity at the time of collection were 25 °C and 38 ppt in summer and 17 °C and 36 ppt in winter, and wind speed and streamflow leading up to and during water collection were low in both seasons.

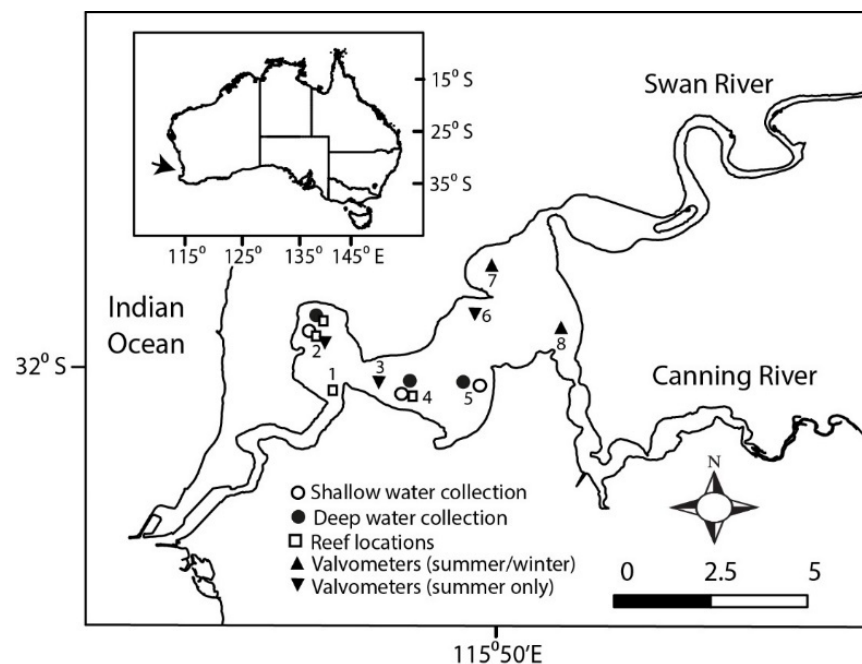


Figure 1. Map of the Swan-Canning Estuary showing the locations of the *Mytilus galloprovincialis* reefs, valve gaping monitoring sites, and collection sites for estuary water used in feeding experiments. Insert in the map shows the location of the estuary in Australia. Sites numbered 1 to 8.

The apparatus to measure feeding behavior, following the biodeposition method, was constructed to replicate that described by Galimany et al. (2011; Figure 2) [26]. The design comprised 20 feeding chambers, each connected to a header tank by a hose fitted with flow valves. The flow from each chamber was calibrated to 12 L h⁻¹ using a graduated cylinder over a 30 s interval [37].

On the day before the winter and summer experiments, 10 *M. galloprovincialis* were collected from subtidal jetty pylons in the estuary basin and used to derive estimates of gut transit times (GTTs). For this, the mussels were placed in individual beakers with 300 mL of seawater and 2 mL of *Tetraselmis* sp. monoculture, and the time taken for the algae to pass through the digestive tract, indicated through the production of bright green feces,

was recorded. It is important to calculate this time in biodeposition experiments because it accounts for the delay between water and mussel biodeposit collection. Each feeding experiment was then undertaken on successive days in each season using a new group of 20 mussels with similar shell heights (45–50 mm). The mussels were collected on the morning of each experiment from the same location and the shells cleared of epibionts. Tissue from four of the 20 mussels was removed and their shells were used in the control chambers [37].

Estuary water was pumped from the sump tank to the header tank (with an overflow to maintain constant water depth and thus consistent flow to each feeding chamber; Figure 2). In each feeding chamber, permanent and removable baffles were used to force the water directly onto the mussel at the bottom of each chamber (Figure 2). A wave maker in the sump ensured water was continuously mixed and prevented the settlement of particulate matter. Following the offset of the maximum GTT, each chamber was cleaned, i.e., feces and pseudofeces were removed. The experiment was then run over 2 h with the feces and pseudofeces removed when they appeared and separately filtered through washed, dried, and pre-weighed 47 mm diameter Whatman GF/C glass fiber filters. At the beginning, middle, and end of each experiment, 300 mL of water was collected from the header tank and each of the control chambers and filtered separately.

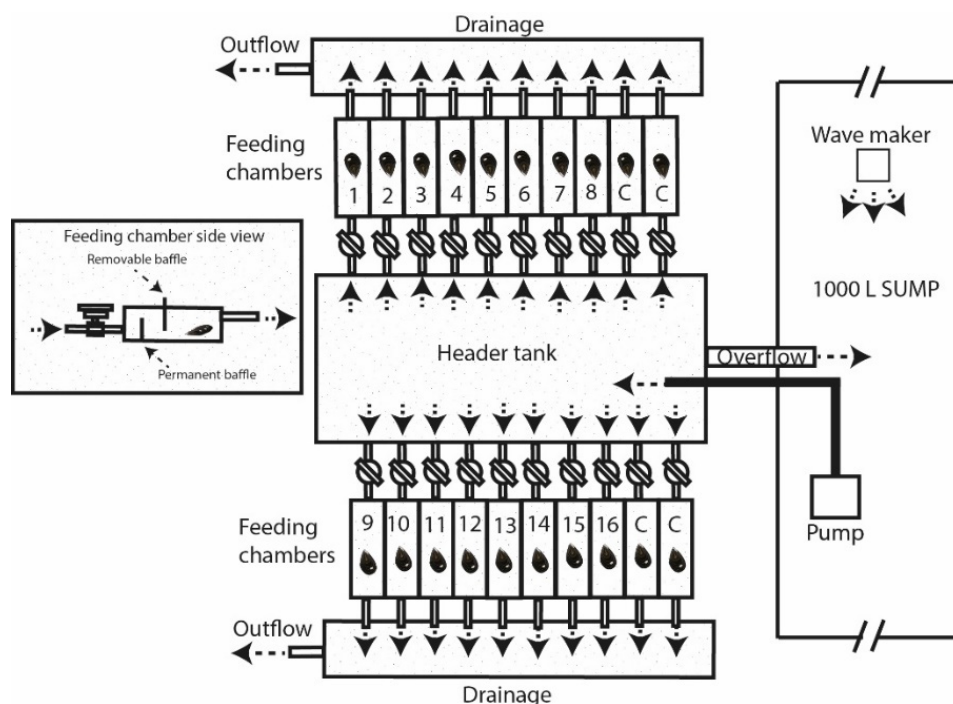


Figure 2. Diagram of the apparatus used to measure the filter-feeding behavior of *Mytilus galloprovincialis* using water collected from the Swan-Canning Estuary. ‘C’ denotes control mussels (empty shells). Arrows denote the direction of water flow.

The samples thus comprised 16 filters containing feces, 16 containing pseudofeces, 12 containing seston from the control chambers, and three filters containing seston from the header tank. The filters were then processed for particulate organic matter (POM, mg L⁻¹; dried at 60 °C for 48 h) and particulate inorganic matter (PIM mg L⁻¹; burnt at 450 °C for 4 h), with TPM equal to the sum of POM and PIM. Seston quality (*f*) was estimated by dividing POM by TPM. The feeding behavior parameters for *M. galloprovincialis* for each site were then derived in accordance with the equations of Galimany et al. (2011) [26] (Table 1). All the feeding variables were standardized (*Y_s*) to 1 g of dried bivalve flesh using the following equation:

$$Y_s = Y_e \times (1/W_e)^b$$

where Y_e is the experimentally determined physiological feeding rate, and W_e is the dry body mass measured for the bivalves. The constant b value used for each predetermined feeding rate was 0.67, as used in other studies for *Mytilus* spp., including *M. galloprovincialis* [25,26]. Data from the few mussels that closed their valves for extended periods during the experiments were excluded from the analyses.

Table 1. Equations used to derive feeding behavior parameters of *Mytilus galloprovincialis* when subjected to water collected from the Swan-Canning Estuary. IM and OM (inorganic and organic matter, respectively; mg h^{-1}) in F and P (feces and pseudofeces), PIM, POM, and TPM (particulate inorganic, particulate organic, and total particulate matter in estuary water, mg L^{-1}).

Parameter	Units	Calculation
Clearance Rate (CR)	L h^{-1}	$[\text{IM}_F + \text{IM}_P] / \text{P}\hat{\text{M}}$
Filtration Rate (FR)	mg h^{-1}	$\text{CR} \cdot \text{T}\hat{\text{P}}\text{M}$
Rejection Proportion (RP)	%	$100 \cdot (\text{IM}_P + \text{OM}_P) / \text{FR}$
Organic Ingestion Rate (OIR)	mg h^{-1}	$(\text{CR} \cdot \text{P}\hat{\text{O}}\text{M}) - \text{OM}_P$
Absorption Rate (AR)	mg h^{-1}	$\text{OIR} - \text{OM}_F$
Absorption Efficiency (AE)	na	AR / OIR

Additional 1 L samples of water were collected for chlorophyll *a* analyses at the beginning, middle, and end of each experiment from the header tank, sump, two control chambers, and six experiment chambers. The water samples were then filtered separately and stored at -20°C for <2 weeks before being processed using the spectrophotometric technique described by Baird (2017) [38]. Seston characteristics and feeding behavior parameters were then compared among seasons, depths, and sites using ANOVA in SPSS (IBM Corp. New York, NY, USA, 2021, Version 28.0). Two-tailed *t*-tests were then employed to determine whether Pearson's correlation coefficient. Relating the water characteristics (TPM, POM, and PIM) to feeding parameters (CR, FR, RP, OIR, and AE, see Table 1) was statistically significant ($p < 0.05$); such relationships have been observed in previous studies [25–27]. Prior to the ANOVA analyses, the water parameters were tested for collinearity. POM and *f* were found to be highly correlated ($r > 0.9$), thus *f* was not subjected to analysis.

2.2. Valve Gape Recordings

Valve gape recorders (valvometers) were used to monitor shell gaping activity for six mussels at five different sites in the basin region of the Swan-Canning Estuary (Figure 1). The valvometers were deployed in December 2019 and August 2020, encompassing the austral summer and winter, respectively. While reliable data was produced for all five sites in summer when the study commenced, comparable data was only produced for two sites in winter (Sites 7, 8; Figure 1) due to leaking seals on the valvometer housing. Note also that the summer deployment of the valvometers was ~one year before the feeding experiments were conducted.

On the day before valvometer deployment, mussel clumps were collected from jetty pylons in the estuary and carefully separated in the laboratory. On each mussel, a sensor mounting bracket (to attach a Hall effects sensor) and a small disk magnet (6×4 mm, diameter \times depth) were attached to opposing posterior valve margins. Hall effects sensors have been employed to monitor bivalve gaping activity in several previous studies [39–42].

Each valvometer unit comprised eight Hall effects sensors and a digital thermometer (DS18B20, Maxim Integrated, San Jose, CA, USA) connected to a small microcontroller (Nano ATmega328, Arduino, New York, NY, USA). Data were transferred to a micro SD card (Class 10, Industrial Delkin Devices, San Diego, CA, USA) via a micro SD card breakout board (Adafruit Industries). As Hall effects sensors output signals are a function of magnetic field density, the resultant data (mV) thus reflects the distance between the magnet and sensor, with the readings ranging from ~500 mV when valves are fully open,

to ± 50 mV when closed (depending on magnetic polarity). To improve efficiency, 300 (mV) was subtracted from each reading to enable data storage as bytes, i.e., values between 0 and 255.

The electronics and battery packs were housed in a PVC pipe and deployed inside a 15 L commercial oyster basket at each of the five sites, allowing sufficient distance between mussels to avoid magnetic interference. The baskets were suspended 0.5 m above the estuary bottom in waters 4–8 m deep using a combination of anchors and floats, and retrieved ~one month after deployment.

The data recorded for each mussel was transformed using the following logistic equation:

$$P_j = \frac{100}{1 + e^{-[v_j - (v_{closed} + \frac{v_{open} - v_{closed}}{2})]}}$$

where P_j is the percentage of maximum gape of the j th reading, v_j is j th value (mV) recorded by the valvometer, v_{closed} and v_{open} are the minimum and maximum values of v_j . The percentage of time a mussel's valves were open was then calculated as the number of times the resultant value was $>20\%$ divided by the number of recordings. A value of 20% was also used to derive the number of valve closures, which were compared statistically between summer and winter using a two-tailed t -test in SPSS.

2.3. Filtration Capacity of a Shellfish Reef

The shellfish reef constructed in the Swan-Canning Estuary in late 2022 comprises ~1.2-hectares of limestone rubble reef spread over an 8-hectare area across four sites in the estuary basin. The reefs were initially seeded with *M. galloprovincialis* (shell heights ~45–50 mm) grown on a local aquaculture lease. Once the reefs become self-sustaining and have fully matured (~5–7 years), it is expected they will contain adult mussel densities of 1000 ind·m⁻². The mussel filtration capacity of the reef was estimated using the total number of adult mussels multiplied by the average clearance rate of individual mussels and the average proportion of time the mussel valves were open and thus clearing water. The potential organic matter removal (OMR) rate (kg of organic matter removed from the water and incorporated as mussel tissue h⁻¹) was then calculated separately for summer and winter as:

$$\text{OMR} = \text{OIR} \times \text{mass of full reef} \times (\text{AE}/100)$$

where OIR is the organic ingestion rate (mg h⁻¹ g⁻¹ of mussel), the mass of full reef (t) is derived from the anticipated density of adult mussels (assuming that adult mussels are about 45–50 mm in length and have an average dried mussel meat mass of 0.366 g per individual) and AE is absorption efficiency (as a proportion). The total organic matter removal of the reef was then calculated for summer and winter using those values and the average percentage of time the mussel valves were open and thus feeding.

3. Results

3.1. Characteristics of the Estuary Water

Estuary water contained greater total particulate matter (TPM) concentrations in winter than summer (8.7 vs. 7.9 mg L⁻¹; $p < 0.001$) and a greater proportion of particulate organic matter (POM) resulting in higher values of seston quality (f) (55 vs. 35%; $p < 0.001$; Figure 3). Shallow waters contained greater amounts of POM than deep waters (4.1 vs. 3.4 mg L⁻¹; $p < 0.001$), whereas the reverse applied to particulate inorganic matter (PIM = 4.3 vs. 4.7 mg L⁻¹; $p = 0.011$), and thus f was greater in shallow (49%) than deep waters (42%; $p < 0.001$). TPM ranged from 7.7 mg L⁻¹ at site 2 to 8.5 mg L⁻¹ at site 5 ($p = 0.002$) and POM followed a similar trend (3.4–4.3 mg L⁻¹; $p < 0.001$). Seston quality ranged from 40 to 50% ($p < 0.001$) and was greatest at site 5. Overall, chlorophyll a was greater during summer (3.0 µg L⁻¹), at shallow sites (3.9 µg L⁻¹), and greatest at site 5 (3.6 µg L⁻¹; all $p < 0.001$; Figure 3).

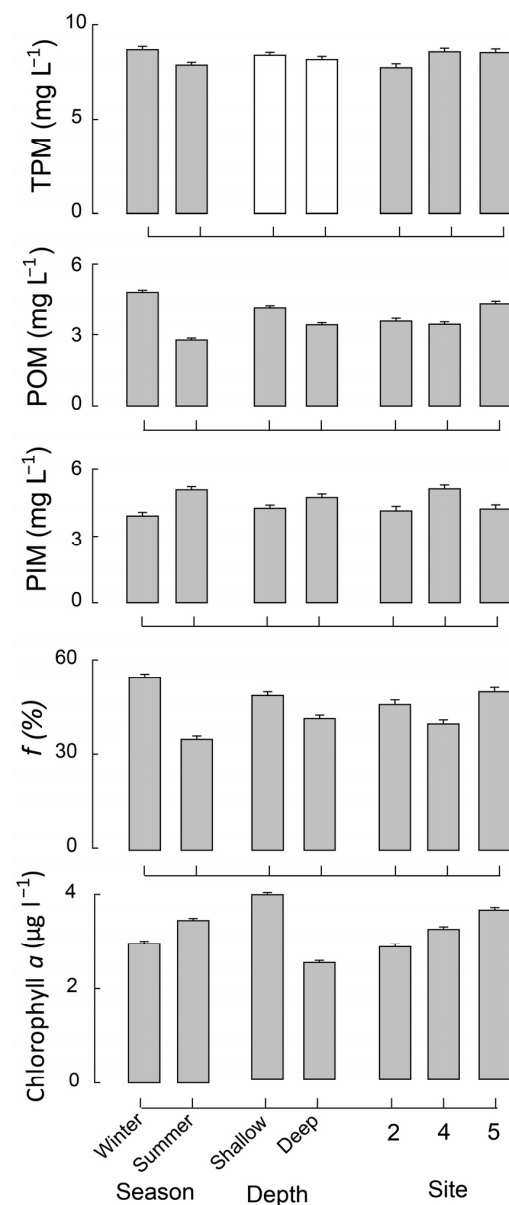


Figure 3. Mean (+SE) of total particulate matter (TPM), particulate organic matter (POM), particulate inorganic matter (PIM), quality of seston (f), and chlorophyll a of the water sampled in the different seasons, depths, and sites in the basin of the Swan-Canning Estuary. Bars were shaded grey when the levels within a factor were statistically significant from each other.

3.2. Mussel Feeding Parameters

Average clearance rates (CR) and filtration rates (FR) per gram dry weight of *M. galloprovincialis* during winter were 1.9 L h⁻¹ and 16.3 mg L⁻¹, respectively, which were significantly greater than those recorded in summer, i.e., 1.3 L h⁻¹ and 10.1 mg L⁻¹ (both $p < 0.001$; Figure 4). CR and FR did not differ significantly with depth or site. Rejection proportion (RP) was greater in summer (40%) than in winter (30%; $p = 0.005$), and in deeper (38%) than shallow water (30%; $p > 0.001$), and did not vary among sites. Organic ingestion rate (OIR) of 7.1 mg h⁻¹ per gram of mussel dry weight was greater in winter than summer (2.5 mg h⁻¹; $p < 0.001$) and in shallow than deeper water (5.8 vs. 4.5 mg h⁻¹; $p = 0.026$) but did not vary among sites ($p = 0.47$). Absorption efficiency (AE) was greater in winter (63%) than in summer (37%; $p < 0.001$) but did not vary with depth or site.

There was a significant positive relationship between FR of *M. galloprovincialis* and POM of estuary water ($\text{FR} = 2.52 \text{ POM} + 3.75$; $p = 0.026$, $r = 0.64$, Figure 5; Table 2). Rejection

proportion was negatively related to POM ($RP = -5.16 \text{ POM} + 54.04$, $p < 0.001$, $r = -0.86$) and positively related to PIM ($RP = 5.45 \text{ PIM} + 10.01$, $p = 0.013$, $r = 0.69$). Organic ingestion rate was positively related to POM ($OIR = 2.13 \text{ POM} - 3.02$, $p < 0.001$, $r = 0.89$) and negatively related to PIM ($OIR = -2.36 \text{ PIM} + 15.66$, $p = 0.005$, $r = -0.75$). Absorption efficiency was positively related to TPM ($AE = -10.49 \text{ TPM} + 98.16$, $p = 0.011$, $r = 0.70$) and POM ($AE = 12.89 \text{ POM} + 2.58$, $p < 0.001$, $r = 0.84$, Table 1, Figure 5).

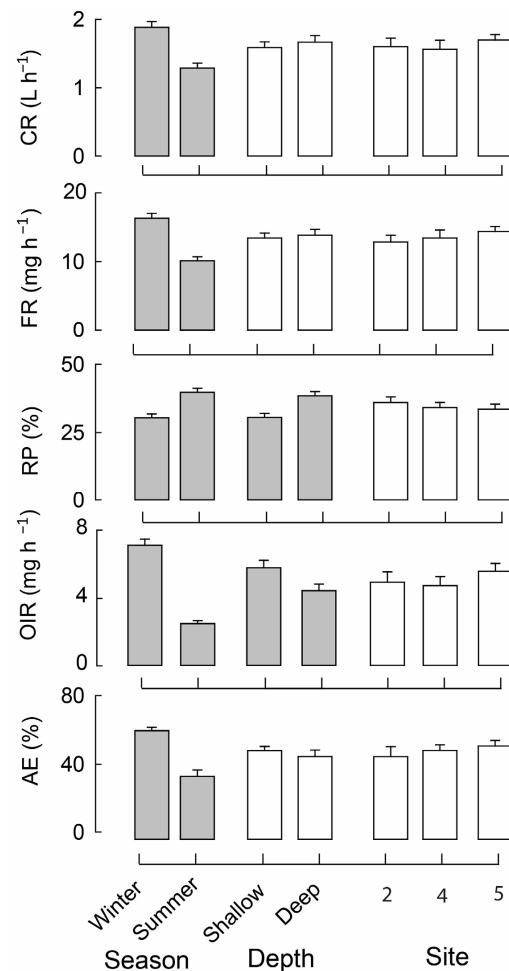


Figure 4. Mean (+SE) feeding parameters of *Mytilus galloprovincialis* during winter and summer and in shallow and deep waters at three sites of the Swan-Canning Estuary. CR is clearance rate, FR filtration rate, RP rejection proportion, OIR organic ingestion rate, and AE absorption efficiency. Bars were shaded grey when levels within each factor were statistically significant from each other.

Table 2. p -values (two-tailed) for relationships between Swan-Canning Estuary water parameters and *Mytilus galloprovincialis* feeding parameters. Pearson's r values are reported for $p < 0.05$. TPM (total particulate matter, mg L^{-1}); POM (particulate organic matter, mg L^{-1}); PIM (particulate inorganic matter, mg L^{-1}); CR (clearance rate L h^{-1}); FR (filtration rate mg h^{-1}); RP (rejection proportion, %); OIR (organic ingestion rate mg h^{-1}); AE (absorption efficiency, %).

	TPM		POM		PIM	
	p -values	r values	p -values	r values	p -values	r values
CR	0.488	-	0.090	-	0.112	
FR	0.166	-	0.026	0.64	0.113	
RP	0.073	-	<0.001	-0.86	0.013	0.69
OIR	0.089	-	<0.001	0.89	0.005	-0.75
AE	0.011	0.70	<0.001	0.84	0.085	

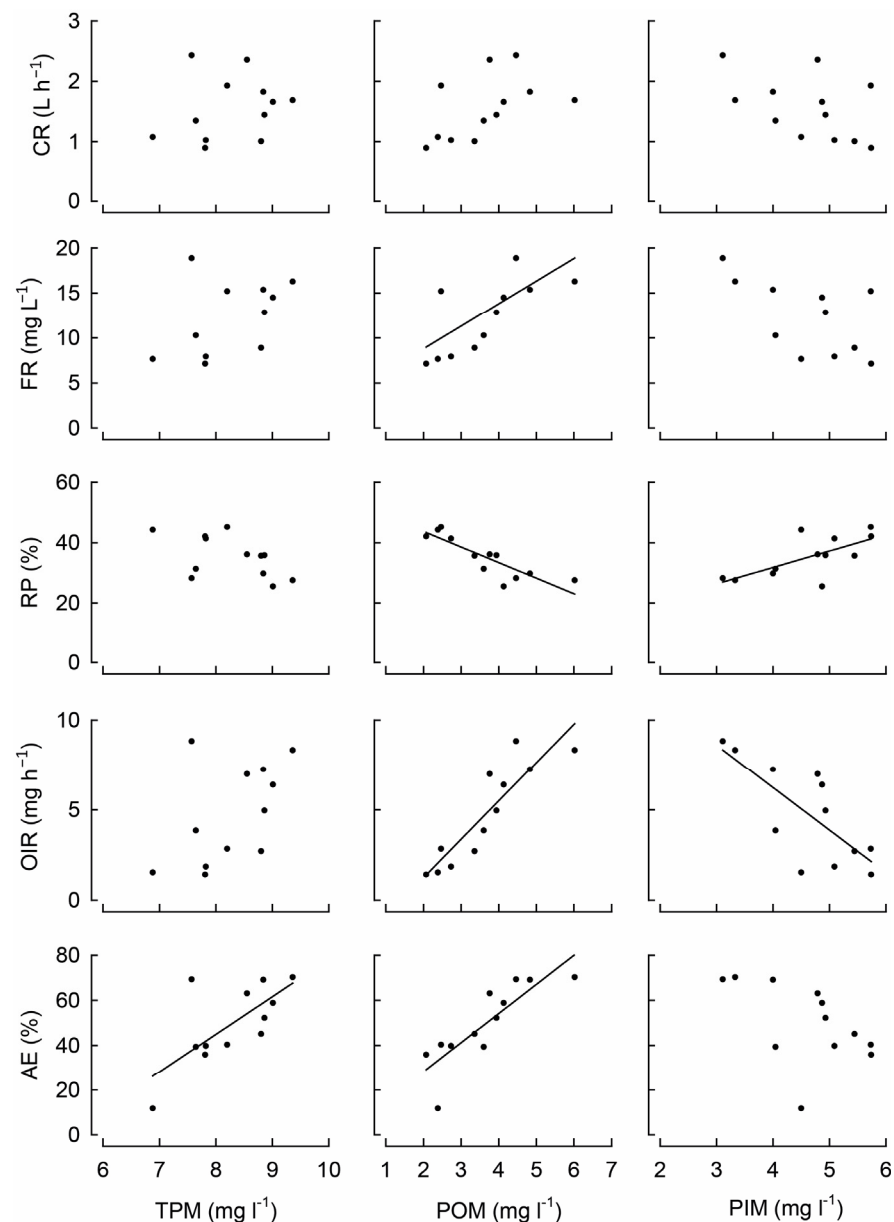


Figure 5. Relationships between Swan-Canning Estuary water parameters and *Mytilus galloprovincialis* feeding parameters; TPM (total particulate matter), POM (particulate organic matter), PIM (particulate inorganic matter), *f* (seston quality), and CR (clearance rate), FR (filtration rate), RP (rejection proportion), AE (absorption efficiency), OIR (organic ingestion rate). Lines represent significant relationships.

3.3. Water Temperature and Valve Gape Activity

The water temperature during the valvometer field trials ranged from 14.8 to 16.9 °C in winter and 24.1 to 26.6 °C in summer (Figure 6). Valve closures were more frequent at the beginning of the trial in winter (Figure 6), probably related to a cold front producing wind gusts >100 km h⁻¹ off the coast (Australian Bureau of Meteorology, 2020), which would be sufficient to re-suspend sediment loads [43]. Irrespective, valves of *M. galloprovincialis* were open 95–97% of the time in winter compared with an average of 53% (45–81%) in summer. The maximum duration valves remained closed (based on data obtained at one-minute intervals) was 148 min in winter and 973 min in summer, and the average number of closures per day during winter was significantly lower than in summer (9.2 vs. 26.6 closures day⁻¹; *p* = 0.047). During summer, the greater number of closures reflected

the erratic behavior of the mussels, which was followed by mortality, illustrated by the valves being open at their fullest extent with no further movement (Figure 6).

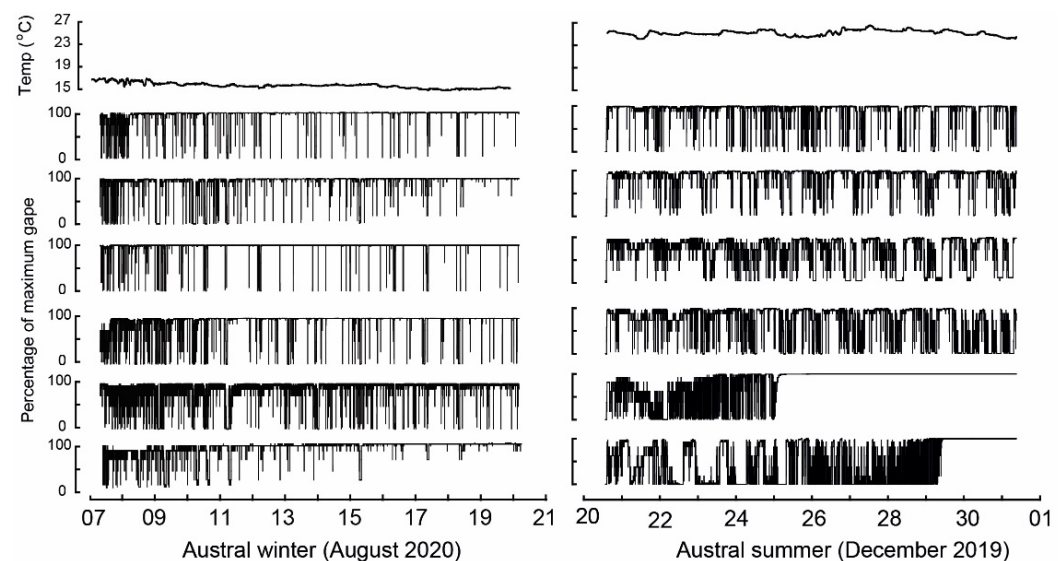


Figure 6. Temperature (top graphs) and valve gape activity of six *Mytilus galloprovincialis* in the Swan-Canning Estuary in South West Australia over ~two weeks where 0% was full closure and 100% open to their maximum extent. All data were derived from Site 7. **Left;** austral winter. **Right;** austral summer.

3.4. Potential Filtration

Based on the average clearance rate and valve open duration, once fully functioning, the *M. galloprovincialis* reef (~1.2 ha with 1000 ind·m⁻²) would filter between 7.2×10^7 L day⁻¹ in summer and 1.9×10^8 L day⁻¹ in winter. As the basin of the Swan-Canning Estuary holds $\sim 5 \times 10^{10}$ L, 35% of the entire volume of the estuary basin could potentially be filtered throughout winter (June–August) and 13% throughout summer (December to February). Based on the organic matter removal rate, the potential total organic matter removed and incorporated as mussel tissues would be 42.7 t over winter and 4.7 t over summer.

4. Discussion

The global loss of shellfish reefs has resulted in the loss of ecosystem services, with water filtration being among the most important in temperate microtidal estuaries that are prone to eutrophication. The extensively modified Swan-Canning Estuary, which has been recognized globally for its hypereutrophication, and within which a shellfish reef construction project has recently been completed, provided an excellent model to predict the potential capacity of those shellfish reefs to help restore estuarine water quality. The fully constructed and mature mussel reef (~1.2 ha with 1000 ind·m⁻²) has the potential to clear 35% of the entire volume of the estuary ($\sim 5 \times 10^{10}$ L) throughout winter (three months), removing 42.7 t of organic matter. This demonstrates the efficiency of NbS in helping remediate eutrophic environments, as has been exemplified by studies on natural and farmed populations of *M. edulis* elsewhere. For example, despite high nutrient loads in the Oosterschelde Estuary in the Netherlands, extensive *M. edulis* beds cleared the total volume of the estuary (2.7×10^{12} L) in four to five days [44,45]. In the Bay of Königshafen (Germany) extensive intertidal *M. edulis* beds cleared its volume in ~2 days, in the Western Wadden Sea, ~20 days, and, under intensive raft culture, the entire volume of the relatively large Ría de Arosa (228 km²) in ~12 days [44]. The differences between the predicted clearance potential of the man-made *M. galloprovincialis* reef in the Swan-Canning Estuary and those in other locations worldwide where extensive beds or rafts of *M. edulis* occur, may

not only be related to the mussels-to-water volume ratio but also to the reduced capacity of mussels to clear water under suboptimal conditions.

The values for TPM ($7.9\text{--}8.7\text{ mg L}^{-1}$) in the Swan-Canning Estuary were among the highest recorded compared to other locations in *M. galloprovincialis* feeding behavior studies (Table A1). However, many of those studies were undertaken in coastal waters where lower concentrations of TPM would be expected compared to a relatively shallow estuarine environment with substantial terrigenous sediment [26,46]. Thus, as was consistent with previous studies [45,46], elevated concentrations of suspended particles, in particular particulate inorganic matter, affected feeding behavior and increased pseudofeces production. The first feeding physiological response to seston changes tends to be clearance rate, which adapts to the amount and quality of food [47]. However, in the Swan-Canning Estuary, filtration was the first response to food changes. Filtration rate, i.e., the amount of seston removed from the water column trapped on the bivalves' gills, was greater for the Swan-Canning Estuary than in the other reported studies (Table A1). This may have been an adaptation to the high seston quantity and quality, allowing the mussels to filter high amounts of organic particles, which resulted in greater amounts of material being ingested and thus making the feeding process efficient in winter.

Another relevant environmental characteristic that modulates mussel feeding behavior is water temperature, which is the most likely reason for the reduced feeding ability in summer. The effect of high temperatures on clearance rates of mytilids has been previously studied in the laboratory, with clearance rates of *Mytilus californianus* declining at $26\text{ }^{\circ}\text{C}$ and for *M. galloprovincialis* and *M. edulis* at $25\text{ }^{\circ}\text{C}$ [31,48,49]. Thus, water temperatures during the summer feeding trials of $25\text{ }^{\circ}\text{C}$ were close to the critical thermal maxima at which clearance rates would be expected to decline. It is hypothesized that this resulted in lower clearance and filtration rates and, in combination with reduced seston quality (f) led to very low absorption efficiencies, which also occurred in this species in a Mediterranean embayment during summer [26]. As low absorption efficiencies are likely to equate to a net energy loss, this would imply mussels are using, or are close to using, energy reserves that are unsustainable over long durations [50,51].

Elevated temperatures can also have serious detrimental effects on other physiological processes, such as valve gaping. During winter, when temperatures were $<17\text{ }^{\circ}\text{C}$, valves were open for 97% of the time, which was almost identical to that recorded for this species in the Ría de Arousa (Spain) [40]. In contrast, in the Swan-Canning Estuary in summer, when temperatures were $>24\text{ }^{\circ}\text{C}$, valve opening duration was 53%. Such a phenomenon has been observed in previous studies [31] and the detrimental effects of elevated temperature in summer have also been related to mussel mortality events elsewhere in the world [52–54]. For example, high mortality of *M. galloprovincialis* in the Aegean Sea occurs when temperatures are greater than $26\text{ }^{\circ}\text{C}$ for extended periods [31], and to some degree, this was consistent with greater summer mortality that was evident in the valvometer field trials in the current study.

Experimental studies also provide evidence that valve activity can become modified when exposed to toxic microalgae. It is thus relevant that, in December 2019, blooms of the saxitoxin-producing dinoflagellates *Alexandrium* spp. (*A. minutum* and *A. pacificum*) occurred throughout the estuary, with concentrations reaching cell densities of $>15,000\text{ cells mL}^{-1}$ [55]. Although the response to such high concentrations of toxic microalgae has not been explored, Comeau et al. (2019) found the number of microclosures by *M. galloprovincialis* increased when exposed to low concentrations of *A. minutum* ($1\text{--}5\text{ cell mL}^{-1}$) [29]. This behavior was also evident in Akoya Pearl Oysters (*Pinctada fucata*) when exposed to the toxic dinoflagellate *Heterocapsa circularisquama* [42].

Based on the findings of this study, it would appear that while *M. galloprovincialis* is living close to its thermal maximum during summer in the Swan-Canning Estuary, along with other stressors common in urbanized waterways, a fully functioning reef has the potential to remove substantial amounts of organic matter from the environment. Reef-forming bivalves have been successfully used as NbS to improve water quality around

the globe, especially in eutrophic environments [56,57]. Despite restoration efforts traditionally focusing on oysters, bivalves, in general, have constraints on their distribution and abundance. Thus, the use of local bivalves with high rates of filter-feeding should be encouraged, such as those in mussel restoration [58,59]. The results of this research align with the UN decade of restoration [60] and demonstrate the potential of mussels to be used as NbS in addition to other management strategies, such as nutrient reduction, to have healthy and fully functioning estuarine ecosystems.

5. Conclusions

This study derived estimates of the feeding behavior and valve gape activity of *M. galloprovincialis* in a hypereutrophic temperate estuary in which a shellfish reef construction project has recently been completed. Although at an individual level, mussel clearance rates in the Swan-Canning Estuary were lower than those recorded for this species at other locations, the fully functioning and mature mussel reef has the potential to clear between 13 and 35% of the total volume of the estuary and remove between 4.7 and 42.7 of organic matter throughout summer and winter, respectively. The differences in the efficiency of individual mussels to clear water were clearly influenced by the characteristics of the water [26,47,61,62]. For example, excess inorganic matter triggers pseudofeces production but, at the same time, it prevents mussels from ingesting higher loads of organic matter, thus decreasing the removal of organic matter from the water column. This physiological response, along with a suppression of feeding in high water temperatures or the presence of toxic phytoplankton, suppresses feeding, and the mussels' efficiency to remove organic matter gets compromised. However, these suboptimal conditions were less of a concern in winter. The use of mussels for NbS in estuaries should thus be encouraged to recover, not only water quality but also other ecosystem services that bivalves provide, such as habitat provision and biodiversity enhancement [1,2,57].

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Appendix A

Table A1. Water seston and feeding parameters of *Mytilus galloprovincialis* in this and various previous studies; total particulate matter (TPM, mg L⁻¹), particulate organic matter (POM, mg L⁻¹), particulate inorganic matter (PIM, mg L⁻¹), seston quality (*f*, %), chlorophyll *a* (Chl *a*, µg L⁻¹, clearance rate (CR, L h⁻¹), filtration rate (FR, mg h⁻¹), rejection proportion (RP, %), absorption efficiency (AE, %). Range in values presented for the current study represents means of values derived in summer and in winter.

Region	TPM	POM	PIM	<i>f</i>	Chl <i>a</i>	CR	FR	RP	AE	Temp (°C)	Reference
Swan-Canning	7.9–8.7	2.8–4.8	3.9–5.1	35–55	1.0–5.3	0.6–0.9	4.5–8.1	33–40	16–63	17–25	Current study
Alfacs Bay (Med.)	1.0–2.3	0.7–1.4	0.5–1.2	48–73		0.9–4.8	1.5–7.2	0.2–16	22–88	10–26	[26]
Milford * (Atlantic)	3.4–9.6	1.6–4.1	1.3–5.5	37–63		1.0–3.1	9.0–17.5	25–45		18–25	[62]
Hunts * (Atlantic)	4.1–12.7	1.1–2.3	2.9–10.5	18–27		0.8–2.3	7.8–22.4	36–73		17–24	[62]
Wellington (Pacific)	9.2–14.0	2.4–7.0		21–60		2.8–5.0			0–80	10–16	[63]
Galicia (Atlantic)	0.4–2.4	1.7–2.0	0.02–1.9	21–97					35–98		[51]
Bay of Fundy (Atlantic)	1.7–2.0	0.5–0.7	0.9–1.5	27–45					55–69		[51]
Gulf of Gaeta (Tyrr.)	4.3	0.2	4.1	5.5	0.5–2.1	2.2				17	[64]
Gulf of Castellammare (Tyrr.)	4.4	0.3	4.1	7	0.02–0.06	3.2				16	[64]
Ria de Arousa (Atlantic)	0.9–2.7	0.3–1.1		35–55		1.3–3.2					[65]
Little Swanport (Tas.)	4.5–22.0	1.9–6.0	2.5–14.0	25–48	0.1–6.0						[46]
Pipeclay Lagoon (Tas.)	6.0–42.5	2.0–10.6	3.8–33.5	18–49	0.2–8.0						[46]

* study conducted on the Ribbed Mussel *Geukensia demissa*, Med. = Mediterranean, Tyrr. = Tyrrhenian Sea, Tas. = Tasmania.

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