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Potential of Mussel Habitat Enhancement to Alleviate Eutrophication in Nutrient-Enriched Estuaries

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ABSTRACT

Through altered freshwater flow regimes and excessive anthropogenic nutrient input, many estuaries around the world are showing signs of eutrophication. As shellfish can alleviate some of these issues through their water filtration capacity, shellfish habitat restoration efforts have increased markedly in the past decade. This study quantifies, for the first time, the water filtration capacity of the Black Pygmy Mussel *Xenostrobus securis* and the potential for habitat enhancement to alleviate eutrophication issues in a hypereutrophic estuary in south Western Australia. Substrate, comprising coir matting, was deployed by community volunteers in four-panel arrangements in the rivers of the Swan-Canning Estuary onto which *X. securis* recruited naturally. In the Swan River, average mussel densities were 3377 individuals m^{-2}, based on 10% mat coverage. River water comprised relatively high particulate organic matter (POM) concentrations, particularly in spring (up to $9.2\,mg\,L^{-1}$). Standardised clearance rates (CR; g^{-1} mussel tissue) were typically greater ($>5.0\,L\,h^{-1}$) in summer when chlorophyll *a* concentrations, salinities and water temperature were elevated, whereas CR was often $<2.0\,L\,h^{-1}$ in early spring. In the Swan River, it was estimated that for every square metre of habitat enhanced, 9.2×10^5 L of water could be potentially cleared during spring and 1.7×10^6 L over summer, the latter incorporating 5.3 kg of organic matter into mussel biomass. On a larger scale, 1000 m^2 of deployed habitat over the course of summer has the potential to clear 24.5% of the volume of the tidal portion of the Swan River and 64.4% of the volume of the smaller Canning River. The results thus demonstrate the efficacy of using cost-effective soft substrates deployed by community volunteers to enhance habitat for mussels and its potential to assist in alleviating eutrophication issues.

1 | Introduction

Estuaries around the world have been subjected to the effects of rapidly expanding human populations (Jackson et al. 2001; Hallett et al. 2018). Consequently, many estuaries are now eutrophic due to excessive nutrient input from agricultural, industrial and urban developments in their catchments, and this is a particular problem for temperate estuaries (Jackson et al. 2001; Cottingham et al. 2014; Hallett et al. 2018). In addition, anthropogenic modifications, along with overharvesting, destructive fishing practices and disease, have led to the loss of important habitats, such as shellfish reefs, of which ~85% have been lost globally (Beck et al. 2011; Gillies et al. 2018; Cottingham, Bossie, Valesini, Maus, et al. 2023). As shellfish reefs provide a range of ecosystem services, including the improvement of water quality and clarity through water filtration, shellfish can help alleviate eutrophication problems (Cottingham, Bossie, Valesini, Tweedley, et al. 2023). Because of these services and the historic loss of these habitats, large-scale efforts to re-establish shellfish reefs have increased in recent decades (Carmichael

Summary

- Although small, the Black Pygmy Mussel is highly efficient at filtering water and can reach high densities.
- Large-scale mussel habitat enhancement has the potential to alleviate eutrophication issues in estuaries.
- Community volunteers can contribute substantially to shellfish restoration efforts on river banks.

et al. 2012; Fitzsimons et al. 2020; zu Ermgassen et al. 2020; Toone et al. 2021; McAfee et al. 2022).

While shellfish reef restoration projects, which have traditionally focused on oysters, have been largely confined to the United States, restoration projects in Australia have accelerated within the recent decade (McAfee et al. 2022). Shellfish reef restoration as a nature-based solution is particularly appropriate in Australia as > 80% of its population reside in estuary catchments, and the vast majority of shellfish reefs spread across > 7000 km of coastline have been lost since European settlement (Gillies et al. 2018; McAfee and Connell 2021). While the majority of the 46 shellfish reef projects initiated in Australia between 2015 and 2022 use oyster species, ~40% to some extent have also incorporated mytilid mussels (McAfee et al. 2022).

Larger-scale shellfish reef construction projects in Australia have typically involved the deployment of a reef base comprising boulders (usually limestone) that are then seeded with aquaculture-sourced mussels (*Mytilus galloprovincialis*) and/or oysters (*Ostrea angasi* and *Saccostrea glomerata*) (see McAfee et al. 2022). While such projects have been largely successful, there is growing interest among stakeholders to adopt approaches that can encourage environmental stewardship through community volunteer participation in on-ground activities and the development of citizen-science monitoring programmes (Weiner et al. 2022). Furthermore, shellfish construction projects have largely been constrained to coastal bays and lower reaches of estuaries, whereas eutrophication issues are typically more prominent upstream in the riverine reaches, which in temperate regions are often poorly flushed due to the low tidal water movement and highly seasonal freshwater discharge (Tweedley et al. 2016; Cottingham et al. 2018).

Eutrophication has been particularly evident in the upper region of the Swan-Canning Estuary, which flows through Perth (population ~ 2 million), the capital city of Western Australia (Cottingham et al. 2014). With ~60% of its main catchment (Swan-Avon) extensively modified (Brearley 2005), this estuary was among the most hypereutrophic of 131 coastal ecosystems examined globally by Cloern et al. (2014). Further exacerbating eutrophication issues, streamflow into the estuary declined by 89% between 1990 and 2015, leading to further reductions in flushing and the accumulation of allochthonous and autochthonous organic material (Cottingham et al. 2014, 2018). Given the cultural and societal importance of the Swan-Canning Estuary, its historic loss of extensive shellfish reefs and its eutrophication status, a large-scale multi-hectare *M. galloprovincialis* reef was constructed in the main estuary basin in 2022 (Cottingham, Bossie, Valesini, Maus, et al. 2023). During that construction phase, a small-scale pilot study was also initiated in the upper estuary region using, for the first time, the Black Pygmy Mussel *Xenostrobus securis* (Lamarck, 1819). This mytilid was selected as it is the only native reef-forming shellfish that prevails throughout the year in the upper estuary, where it is subjected to low salinities (5) and temperatures (15°C) during winter and high salinities (30) and temperatures (28°C) during summer (Cottingham, Bossie, Valesini, Maus, et al. 2023).

Xenostrobus securis is native to estuaries of southern Australia and New Zealand, where it can form extensive colonies on hard structures and occasionally on bare sediment (Wilson 1968; Zenetos et al. 2004; Iwasaki and Yamamoto 2014). This small mytilid (up to 30 mm) has a short life span (~2 years), attains maturity within its first year and has a protracted spawning season (Wilson 1968, 1969; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). While adults can survive in salinities between 2 and 58, early developmental stages are less tolerant, with spat settlement occurring in salinities between 17 and 33 (Wilson 1968, 1969; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). *Xenostrobus securis* was also once common throughout the Swan-Canning Estuary, but following marinisation of the estuary due to reduced streamflow, its population is now typically restricted to the upper estuary (Valesini et al. 2017; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). The limited tolerance range in salinities of the early developmental stages are also consistent with *X. securis* distribution throughout estuaries in Europe and Japan, where it has been introduced (Garci et al. 2007; Adarraga and Martinez 2012; Gestoso et al. 2012; Guerra et al. 2013).

Although there is limited information on the historical abundance of *X. securis* in the Swan-Canning Estuary, during the 1990s this species made a substantial contribution (~34%) to the diet of the sparid Black Bream *Acanthopagrus butcheri*, an important recreationally targeted fish species and one of its main predators (Sarre et al. 2000; Potter et al. 2022). However, by 2010 the contribution of *X. securis* to the diet of *A. butcheri* declined to < 5%, and low-calorie food, such as algae and detritus, increased (Potter et al. 2022). While a wide range of factors are likely attributing to these declines, Cottingham, Bossie, Valesini, Tweedley, et al. (2023) recently found *X. securis* larvae to be highly abundant in the upper estuary during its spawning season (October to April), as was demonstrated by substantial settlement (up to 15,000 ind. m^{-1} commercial spat rope) when appropriate habitat was provided.

This study adopts a novel approach to shellfish bed restoration in which a habitat, comprising coir matting (erosion mesh nets made from coconut fibre), was deployed along the banks of Swan and Canning rivers onto which *X. securis* larvae would settle naturally. Guided by restoration practitioners, the project was largely community-based and provided the opportunity for community participation in planning, habitat installation and monitoring. One year after deployment, the potential for this habitat restoration approach to alleviating eutrophication issues was assessed by quantifying the water filtration capacity and organic matter removal rates of *X. securis*. The results of this study are of interest to environmental managers throughout the species' native range, and to restoration practitioners and citizen-scientists working in comparable environments.

2 | Material and Methods

2.1 | Study Location

The Swan-Canning Estuary, which covers an area of ~55 km^2, is a microtidal (0.6 m tidal amplitude) estuary on the temperate lower west coast of Australia (32·055° S; 115·735° E). The estuary comprises a narrow entrance channel permanently open to the Indian Ocean, a large central basin and the tidal portions of two rivers. Due to the Mediterranean climate, rainfall is highly seasonal with ~80% of rainfall (~600 mm) occurring between May and September and thus freshwater flow is largely restricted to the (austral) winter and early spring. While the focus of the current study was the saline reaches of the Swan River, which extends ~30 km upstream from its confluence with the basin and is ~4 m deep, less comprehensive data are also presented for the smaller Canning River, which is ~11 km and is typically < 2 m deep.

2.2 | Mussel Habitat Deployment and Monitoring

Coir matting, comprising 700 g m^{-2} coconut fibre mesh, was deployed by restoration practitioners and volunteers during the austral summer (December to February) of 2021 and 2022 at nine sites in the Swan River (S2–S10) and four sites in the Canning River (C2–C5; Figure 1). This material was chosen as it has been previously employed to enhance the settlement of other mytilids (van der Zee et al. 2015). At each site, 2 × 2 m coir matting panels were attached to the riverbank in the intertidal zone (−0.2 to 0.2 m depth) using wooden stakes, as either a single-layered panel, double-layered panel, or quadruple-layered panel, or as a 2 m long roll (noting that some sites had multiple pairs of panels whereas other sites could not accommodate all arrangements). These panel arrangements were used to explore which resulted in the highest density of mussels.

Each of the nine sites in the Swan River and four sites in the Canning River were linked to volunteers (individuals or groups) who monitored their restoration site using a 50 × 50 mm quadrat. Monitoring was undertaken during the day at low tide by randomly placing the quadrat on the surface of each layer of the mat at three different points, and the percentage coverage of *X. securis was* estimated to the nearest 10%. While the number of samples derived from a single-layered panel was three, that for the quadruple-layered panel was 12, that is three samples from each of the four layers. At sites with a roll, a total of nine samples

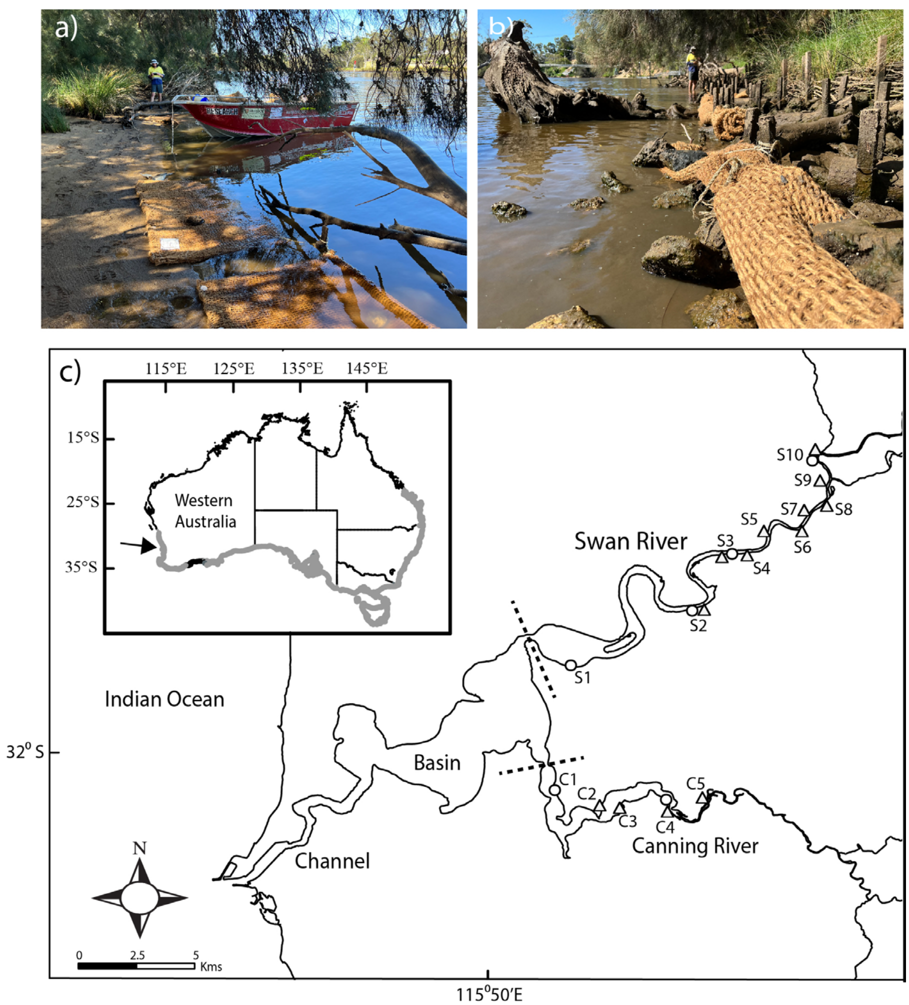

FIGURE 1 | Map of the Swan-Canning Estuary showing the locations of the restoration pilot sites in the Swan (S2–S10) and Canning rivers (C2–C5; triangles) and the six sites where water was collected for *Xenostrobus securis* feeding experiments (open circles). Dashed lines represent the downstream boundary of the riverine reaches. Distribution of *X. securis* in Australia is highlighted in grey in the insert.

were taken, that is three samples from each of three layers. At each site, data were also obtained from eight randomly placed quadrats on nearby unstructured habitat (control). No control samples contained *X. securis*.

While monitoring was undertaken every second month (from January 2022), *X. securis* did not become visible to the naked eye until late autumn (May 2022), and the panels were removed in September 2022. As such, the data collected by citizen scientists for percentage cover occurred from May to July 2022. As the resultant data did not conform to many of the assumptions of statistical tests, the data were only used to explore trends, in terms of percentiles of the data, among the two rivers and four panel arrangements.

2.3 | Mussel Densities and Mass-Length Relationship

During the removal of the coir matting in September, three 50 × 50 mm sections of coir matting, in which the density of *X. securis* appeared greatest, were removed from four sites (S3, S4, S5 and S8). In the laboratory, individual mussels were separated and counted, and their shell height was measured to 0.1 mm using vernier callipers. A total of 240 randomly selected individuals had their tissue removed from their shell, dried for > 24 h at 60°C and weighed. The mass-length relationship was then derived by fitting the equation $W = aL^b$ to the weights (W, g) and shell length (L, mm) of the 240 mussels.

2.4 | Mussel Clearance Rates and Feeding Behaviour

Xenostrobus securis feeding experiments were undertaken in the laboratory at the beginning of the austral spring (September) of 2020 and the following summer (February 2021) using water collected at four sites in the Swan River (S1, S2, S3 and S10) and two sites in the Canning River (C1 and C4; Figure 1). On each occasion, ~600 L of estuary water was collected from 0.5 m below the surface into drums on the back of a utility vehicle using a submersible pump, and 30 *X. securis* individuals were collected from below the water level at the same location. The mussels and water were transferred to the laboratory where the feeding experiments were conducted.

The biodeposition apparatus was similar to that used by Cottingham, Bossie, Valesini, Maus, et al. (2023) to derive feeding physiological parameters for *M. galloprovincialis* in this estuary and broadly replicate that described by Galimany et al. (2011), Galimany, Rose et al. (2018, Figure 2). The design comprised 10 feeding chambers (175 (L) × 60 (W) × 60 (D) mm), each connected to a header tank (700 (L) × 300 (W) × 120 (D) mm) by a 13 mm diameter 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 (Galimany, Lunt, et al. 2018; Cottingham, Bossie, Valesini, Tweedley, et al. 2023).

To ensure a consistent flow to each feeding chamber, estuary water was continuously pumped from the sump tank to the header tank with an overflow return pipe to the sump to maintain the header tank's maximum capacity and thus also consistent flow rates (Figure 2). In each feeding chamber, permanent and removable baffles were used to force the water directly onto the mussels (Figure 2). A wave maker in the sump ensured the water was continuously mixed.

Each experiment was undertaken using a new group of 30 adult mussels (three mussels per feeding chamber, to account for their small size) with similar shell heights (14–17 mm). For each experiment, tissue from six mussels was removed, and their empty

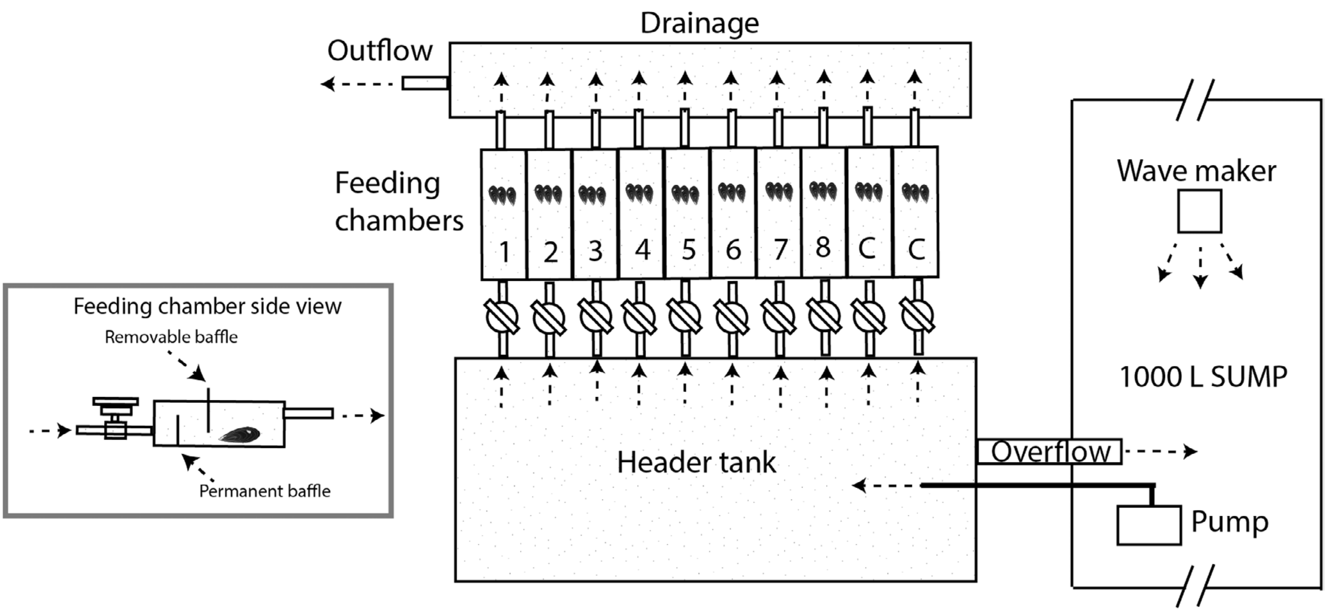

FIGURE 2 | Diagram of the experimental set-up used to measure the various feeding parameters of *Xenostrobus securis* using water collected from the Swan and Canning rivers. 1–8 are replicate samples of live mussels, and C is the control group of empty mussel shells. Arrows denote the direction of water flow. Insert shows a side view of a feeding chamber.

shells were used in the two control chambers (three shells in each chamber). On the day prior to each seasonal experiment, ten *X. securis* were collected 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 faeces, was recorded (Galimany et al. 2011).

Following the offset of the maximum GTT, each chamber was cleaned; that is faeces and pseudofaeces were removed. The experiments were then run over 2 h with the faeces and pseudofaeces collected when appearing and filtered onto pre-weighed 47 mm diameter Whatman GF/C glass fibre filters. The seston characteristics of the estuary water, that is the mass of total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM), were assessed at the outflow of each of the two control chambers at the beginning and end of the experiment by collecting and filtering 300 mL of water from each. The filters were then processed for TPM (dried at 60°C for 48 h) and PIM (burnt at 450°C for 4 h), with POM determined from the difference in mass between the two. The physiological components of the absorptive balance for *X. securis* for each site were derived in accordance with the biodeposition method in Iglesias et al. (1998) following the equations of Galimany et al. (2011; Table 1). Following analyses, where appropriate, the results were divided by three to account for three mussels in each chamber, and all feeding variables (Y_s) standardised to 1 g of dried tissue using the following equation:

$$Y_s = Y_e \cdot \left(\frac{1}{W_e}\right)^b \quad (1)$$

where Y_e is the experimentally determined physiological feeding rate, W_e is the dried mass of mussel tissue (g) and b is a predetermined constant (0.67) used in other studies for *Mytilus* spp. (Bayne et al. 1989; Galimany et al. 2011).

An additional 1 L of water was collected for chlorophyll *a* analyses at the beginning and end of each experiment from the control chambers. The water samples were then filtered separately and stored at −20°C and processed within 2 weeks. Chlorophyll *a* concentrations were determined by the spectrophotometric technique using the methods described by Baird (2017). Seston characteristics and feeding parameters were then compared among seasons and sites using ANOVA in SPSS (IBM Corp., New York, NY, USA, 2021, Version 28.0). Two-tailed *t*-tests were also employed to determine whether Pearson's correlation coefficients relating the water characteristics (TPM, POM, PIM and chlorophyll *a*) to feeding parameters (CR, FR, RP, OIR and AE, see Table 1) were statistically significant ($p < 0.05$).

TABLE 1 | Equations used to derive feeding behaviour parameters of *Xenostrobus securis* when subjected to water collected from the Swan and Canning rivers.

Parameter	Units	Calculation
Clearance rate (CR)	$L\,h^{-1}$	$(IM_F + IM_P) / \widehat{PIM}$
Filtration rate (FR)	$mg\,h^{-1}$	$CR \cdot \widehat{TPM}$
Rejection proportion (RP)	%	$100[IM_P + OM_P] / FR$
Organic ingestion rate (OIR)	$mg\,h^{-1}$	$[CR \cdot \widehat{POM}] - OM_P$
Absorption rate (AR)	$mg\,h^{-1}$	$OIR - OM_F$
Absorption efficiency (AE)	NA	AR / OIR

Note: IM and OM (inorganic and organic matter, respectively; $mg\,h^{-1}$) in F and P (faeces and pseudofaeces, respectively), PIM, POM and TPM (particulate inorganic, particulate organic and total particulate matter in estuary water, respectively, $mg\,L^{-1}$).

2.5 | Clearance Potential of Enhanced Habitat

Estimates of the potential water clearance capacity of the deployed substrate were based on average mussel densities (from four sites in the Swan River), percentage coverage (provided by citizen-scientists from 13 sites) and average individual clearance rates (derived from six sites). Individual clearance rates were derived from the mass (dried) of 240 mussels (Section 2.2) and rearranging Equation (1) to recalculate clearance rates of individuals based on their mass (rather than per gram), that is $Y_e = \frac{\hat{Y}_s}{W_e^{-b}}$, where $\hat{Y}_s$ is the average of the feeding variable (see Equation 1). To provide an estimation of potential to alleviate eutrophication, for each river (Swan and Canning) and season (spring and summer), the average individual clearance rate

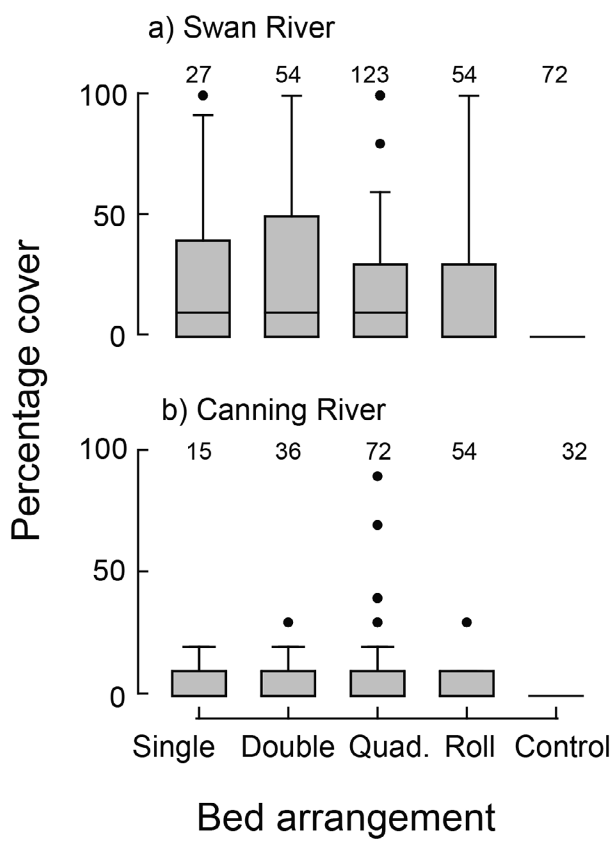

FIGURE 3 | Boxplots of percentage coverage of *Xenostrobus securis* on four different coir matting bed arrangements in (a) the Swan River (nine sites) and (b) the Canning River (four sites) in Western Australia. Boxplots show 10, 25, 50, 75 and 90th percentiles. Closed circles show outliers. The number of samples for each arrangement is shown above.

($\widehat{CR}$ h^{-1} ind.$^{-1}$) was then scaled up to account for the length of a season and the number of mussels on the substrate (density × percentage coverage × area).

3 | Results

3.1 | Mussel Percentage Coverage, Density, Size-Frequency and Mass-Length Relationship

Over the course of the project, 40 volunteers contributed a combined total of 118 h, which included participation in planning, habitat installation and monitoring. This provided percentage coverage data for 539 measurements across nine sites in the Swan River and four sites in the Canning River. These data demonstrated that the percentage coverage of *X. securis* on the deployed substrate varied among the two rivers and four-panel arrangements (Figure 3). Percentage coverage of *X. securis* on the deployed matting was typically greater in the Swan River than in the Canning River. In the Swan River, median percentage coverage (including all layers) was 10% for the single, double and quadruple bed arrangements and 0% for the roll, and the 75th percentile of the data was greatest for the double bed arrangement (50%) and least for the quadruple bed and the roll (30%). In the Canning River, median percentage coverages and the 75th percentile of those data were 0% and 10%, respectively, for all bed arrangements (Figure 3). While in the Swan River, 56% of all records contained 0% coverage; those for the Canning were 38%, with the single-layer bed arrangement producing the lowest percentage of 0% coverage (43%) and the double layer the greatest (56%).

Densities, based on samples collected by researchers at the four sites in the Swan (S3, S4, S5 and S8), ranged from an average (±1 SE) of 79 ± 2.5 individuals at Site S4 (31,600 ind. m^{-2}) to 118 ± 8.6 at Site S3 (47,200 ind. m^{-2}). Shell length of *X. securis* at those four sites ranged from 2.5 to 27.8 mm (Figure 4). Shell length distributions appeared to include multiple recruitment events, and thus the data in the length-frequency histograms were not distributed evenly around a single main peak. The overall modal length was greatest at site S8 (19 mm) and least at site S4 (6 mm; Figure 4).

The equation for the mass-length relationship provided a good fit to the mass (dry meat mass, g) and shell length (mm) data for *X. securis* as indicated by the coefficient of determination (R^2 = 0.90; Figure 5).

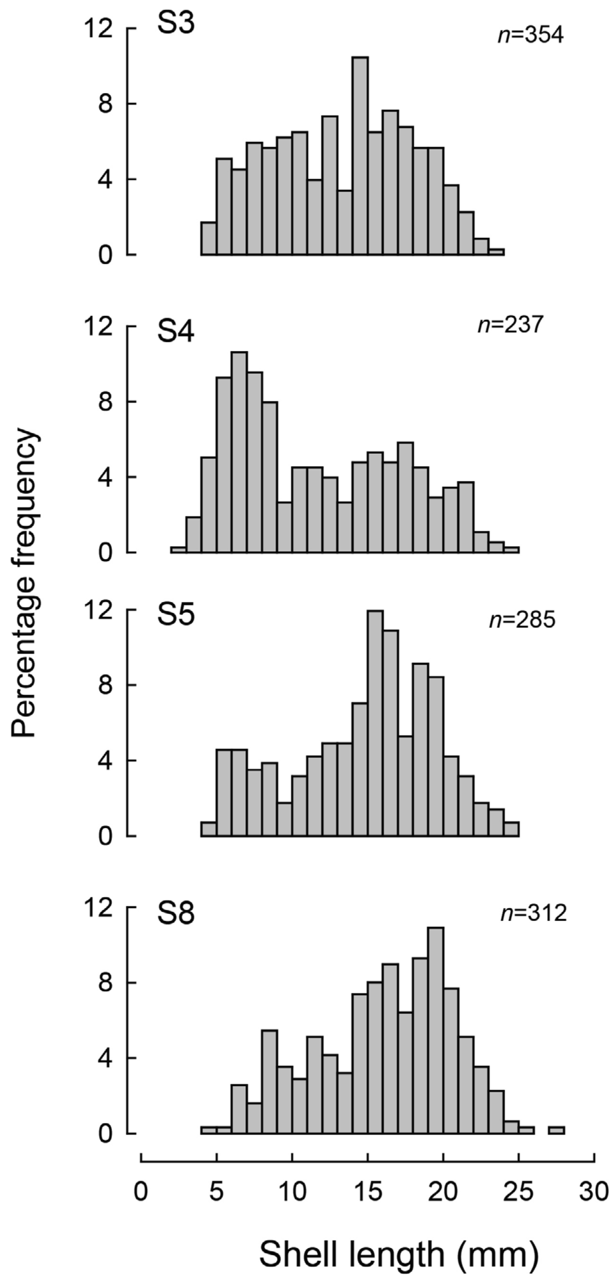

FIGURE 4 | Shell length-frequency distributions for *Xenostrobus securis* were collected from coir matting at four sites in the Swan River (S3, S4, S5 and S8) in spring 2022. Data for each site were derived from three 50 × 50 mm sections of matting from various panel arrangements.

3.2 | Characteristics of the Estuary Water

Water temperatures at the time of the feeding experiments in spring and summer were ~18°C and 26°C, respectively. Salinities in the Swan River increased with distance downstream and ranged from 2 to 8 during spring and 14 to 30 during summer. Salinities in the Canning River similarly increased with distance downstream and ranged from 14 to 24 in spring and 30 to 34 in summer.

The seston characteristics of the water collected at each site typically differed in concentrations of total particulate matter (TPM), particulate organic matter (POM), particulate inorganic matter (PIM), seston quality (*f*; POM / TPM × 100) and chlorophyll *a* (Figure 6). In the Swan River, average ± SE TPM ranged from 7.7 ± 0.6 to 16.8 ± 0.8 mg L^{-1} during spring and 7.1 ± 0.5 to 17.6 ± 0.5 mg L^{-1} during summer, typically increasing with distance upstream. However, in the Canning River, TPM values varied greatly in spring and ranged from 6.5 ± 0.5 to 314 ± 1.9 mg L^{-1} but were less variable in summer, 8.9 ± 0.4 to 13 ± 0.8 mg L^{-1}. POM was greater during spring than summer and ranged from 2.7 ± 0.2 to 6.4 ± 0.2 mg L^{-1} in the Swan and 4.0 ± 0.3 to 9.2 ± 0.6 mg L^{-1} in the Canning. Thus, PIM was greater in summer than in spring and typically declined with distance upstream. In the Swan, PIM ranged from 2.7 ± 0.5 to 10.4 ± 0.8 mg L^{-1} during spring and from 4.3 ± 0.4

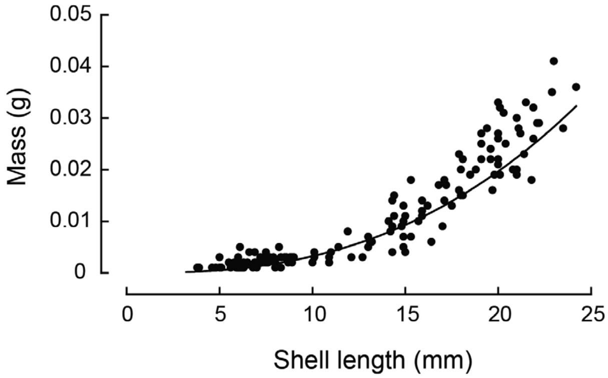

FIGURE 5 | Mass-length relationship (dry weight- shell length) derived for *Xenostrobus securis* collected during spring 2022 from deployed mussel habitat in the Swan River (M = 1.8×10^{-6} $L^{3.15}$; $R^2 = 0.90$).

to 12.2 ± 0.4 mg L^{-1} during summer, and in the Canning from 1.6 ± 0.3 to 305 ± 1.6 mg L^{-1} during spring and 4.3 ± 0.3 to 9.0 ± 0.8 mg L^{-1} during summer. With the exception of C1, *f* was greater during spring. Despite the higher concentrations of POM during spring, chlorophyll *a* concentrations were typically greater during summer (Figure 6).

3.3 | Clearance Rates and Feeding Behaviour of *Xenostrobus Securis*

Clearance rate (CR) of *X. securis* differed significantly with the season ($p = 0.02$), site ($p < 0.001$) and the interaction season × site ($p < 0.001$). Standardised CR (g^{-1} dry tissue) was typically greater in summer when values ranged from 5.0 ± 0.5 to 6.1 ± 0.6 L h^{-1} in the Swan and 3.0 ± 0.2 to 6.6 ± 1.3 L h^{-1} in the Canning (Figure 7). During spring, CR was greatest at the two most downstream sites in the Swan River (3.5–6.6 L h^{-1}) and <2 L h^{-1} at the upper two sites in the Swan and at both sites in the Canning (Figure 7).

Filtration rate (FR) differed significantly with site and season × site (both $p < 0.001$), but not season ($p = 0.07$). Average FR was lower at sites further upstream and was typically greater in summer, ranging from 43.3 ± 4.1 to 105.8 ± 22.1 mg h^{-1} in the Swan and 38.5 ± 2.6 to 58.8 ± 11.3 mg h^{-1} in the Canning (Figure 7). During spring, FR in the Swan ranged from 7.8 ± 0.7 to 55.8 ± 8.5 mg h^{-1} and reached 361.3 ± 9.3 mg h^{-1} in the Canning (Figure 7).

Rejection proportion (RP) differed significantly with site ($p = 0.009$) and season ($p < 0.001$) and season × site ($p < 0.001$). RP was typically greater during spring, ranging from 44% to 84% in the Swan, and was as high as 100% at the lower site in the Canning, meaning that in some cases, every particle cleared was rejected (Figure 7). During summer, RP ranged from 45% to 67% in the Swan and 42% to 63% in the Canning (Figure 7).

Organic ingestion rate (OIR) differed significantly with the site ($p < 0.001$) and the season × site interaction ($p = 0.017$) but not season ($p = 0.199$), noting that, due to small values for FR, OIR could not be confidently estimated during spring in the Canning and the two upstream sites in the Swan. Average OIR at the two sites during spring in the Swan ranged from 9.8 to 26.1 mg h^{-1}

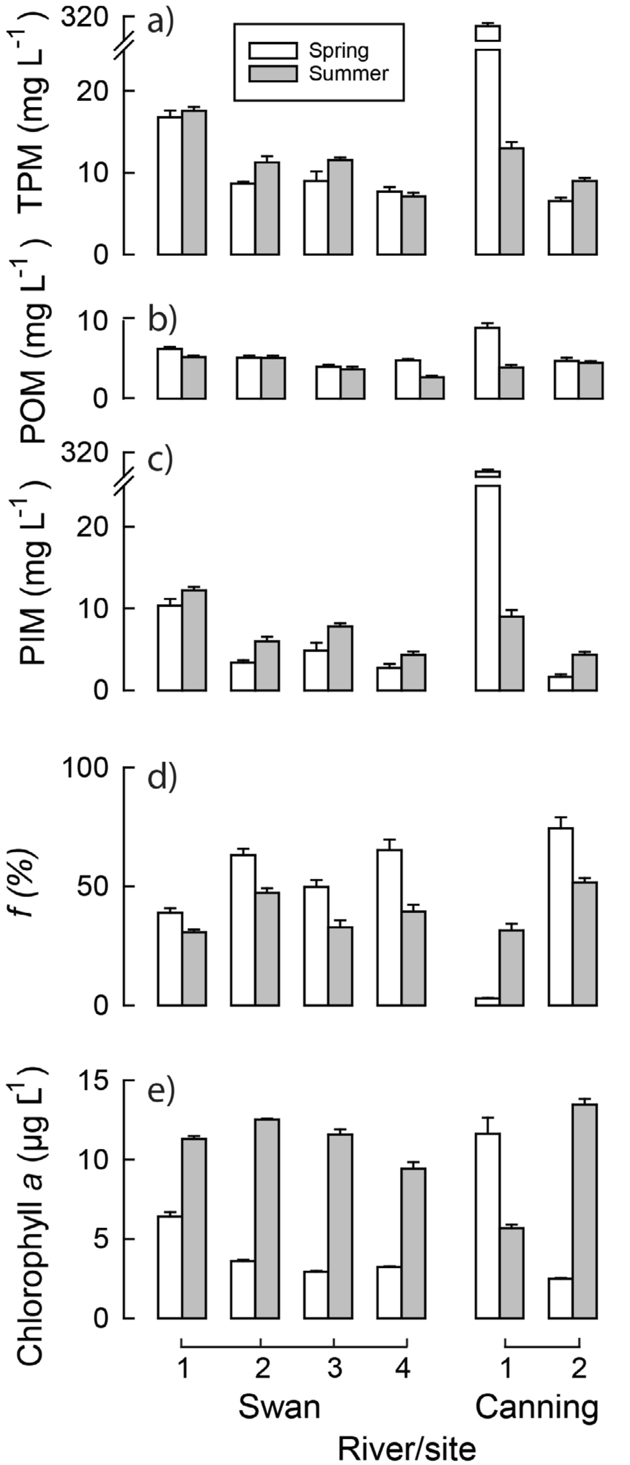

FIGURE 6 | Mean + SE of (a) total particulate matter (TMP), (b) particulate organic matter (POM), (c) particulate inorganic matter (PIM), (d) seston quality (*f*) and (e) chlorophyll *a* concentration of the water in austral spring of 2020 and summer of 2020/21 at each site in the Swan and Canning rivers.

(Figure 7). During summer, OIR ranged from 13.4 ± 1.8 to 22.8 ± 5.6 mg h^{-1} in the Swan and 5.9 ± 0.6 to 21.3 ± 2.3 mg h^{-1} in the Canning (Figure 7).

Absorption efficiency (AE) did not vary with any factor or interaction ($p > 0.05$ in all cases), noting that AE could only

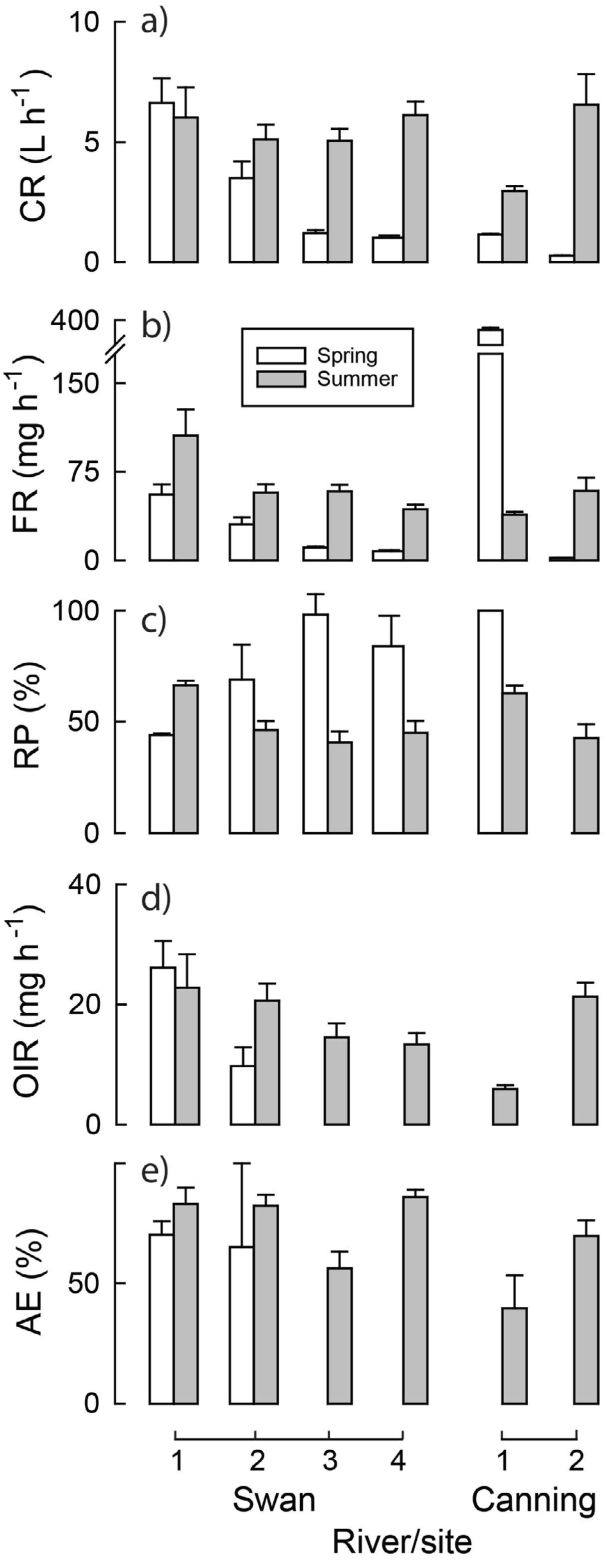

FIGURE 7 | Mean (+1 SE) feeding parameters of *Xenostrobus securis* during the austral spring 2020 and summer 2020/21 in the Swan and Canning rivers. (a) clearance rate (CR), (b) filtration rate (FR), (c) rejection proportion (RP), (d) organic ingestion rate (OIR) and (e) absorption efficiency (AE). Note, in the cases where CR was low, RP, OIR and AE could not be confidently quantified.

be calculated in the cases where values of OIR were derived. During summer, average AE ranged from 56.3% to 85.8% in the Swan and from 40.0% to 70.0% in the Canning. During spring, AE was 65.0% and 70.2% at those two lower Swan River sites (Figure 7).

No relationships were evident between TPM, POM and PIM and any of the feeding parameters (CR, FR, RP, OIR and AE). However, significant relationships did exist between f and CR ($p=0.03$, $r=-0.66$), FR ($p=0.04$, $r=-0.625$) and RP ($p=0.04$, $r=0.62$), and between chlorophyll a and CR ($p=0.002$, $r=0.82$), FR ($p=0.002$, $r=0.81$) and RP ($p=0.003$, $r=-0.80$; Figure 8). Note that in some case collinearity existed between the water quality variables.

3.4 | Potential Filtration Capacity of Deployed Habitat

While the average individual clearance rates in the Swan River in spring (0.13 $\mathrm{L\,h^{-1}}$ ind.) and summer (0.23 $\mathrm{L\,h^{-1}}$ ind.) were relatively low at the individual mussel level, these values still correspond to 3.0 and 4.5 L per mussel per day, respectively, and thus 272 and 490 L over the ~90 days in each season. As average densities per square metre of deployed habitat were 3377 ± 787 individuals (accounting for 10% coverage), one square metre of the substrate could thus facilitate the clearance of $9.2 \pm 2.1 \times 10^5\ \mathrm{L\,m^{-2}}$ over the course of spring and $1.7 \pm 0.4 \times 10^6\ \mathrm{L\,m^{-2}}$ over the course of summer, the latter incorporating 5.3 ± 1.2 kg of organic material (dry mass) into mussel tissue.

When assessing the different bed arrangements in the Swan River and employing the 75th percentiles, the double bed matting arrangement (50% coverage) could potentially clear five times the amount of water as the values provided above ($4.6 \pm 1.1 \times 10^6$ and $8.2 \pm 1.9 \times 10^6\ \mathrm{L\,m^{-2}}$ in those respective seasons) and remove 26.5 ± 6.2 kg of organic matter during summer. The corresponding values for the single bed (40% coverage) and the quadruple bed and roll arrangements (30% coverage) were thus four and three times those above values.

In the Canning River, based on the 75th percentiles and thus 10% coverage, one square metre of substrate could thus facilitate, on average, the clearance of $2.1 \pm 0.5 \times 10^5\ \mathrm{L\,m^{-2}}$ over the course of spring and $1.4 \pm 0.3 \times 10^6\ \mathrm{L\,m^{-2}}$ over the course of summer, the latter incorporating 4.1 ± 0.9 kg of organic material (dry mass) into mussel tissue.

4 | Discussion

This is the first study to derive estimates of the potential filtration capacity of enhanced mussel (*X. securis*) habitat employing a relatively inexpensive substrate and deployment method. Shellfish restoration programmes are key to understanding the potential of bivalves to help remediate eutrophication, among restoring other ecosystem services. But these programmes are usually labour demanding and time intense, thus collaboration between scientists, restoration practitioners, estuarine managers and community volunteers can be key in achieving restoration, environmental and scientific goals. The current study exemplifies a highly successful collaboration for such purposes, which involved university researchers, natural resource managers (Perth NRM), government (Department of Biodiversity,

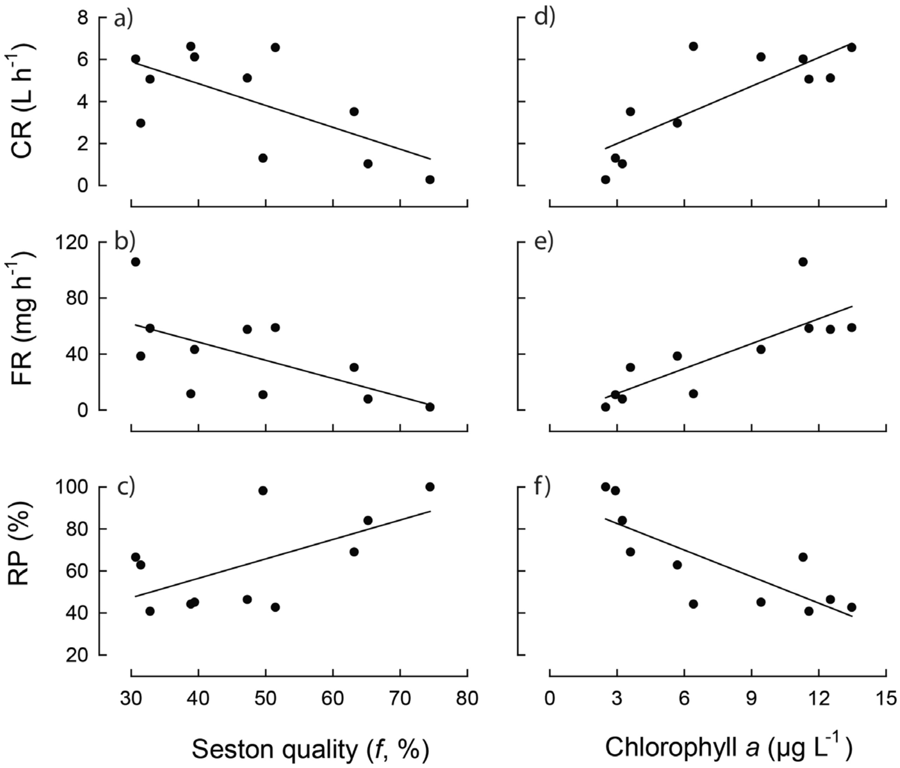

FIGURE 8 | Relationship between (a–c) seston quality (*f*) and (d–f) chlorophyll *a*, and *Xenostrobus securis* clearance rate (CR), filtration rate (FR) and rejection proportion (RP) derived from six sites in the Swan and Canning rivers during the austral spring 2020 and summer 2020/21. Note, the lower site in Canning River in spring was not included in analyses.

Conservation and Attractions) and 40 volunteers who participated in the planning, habitat installation and monitoring programme, and provided over 500 records of mussel percentage coverage estimates.

4.1 | Factors Influencing Mussel Abundance

Median values for each bed arrangement in each river were relatively consistent given the number of volunteers. The double-layer matting arrangement contained the greatest coverage in the Swan River when employing the 75th percentiles of those data. This may be due to mussels having a preference towards the outer layer of the matting, but with the added benefits of maintaining moisture and shading during periods of aerial exposure. This would be particularly crucial at low tide during the day in summer, when air temperatures can exceed 40°C and for which exposure can be prolonged due to the diurnal tidal cycle.

While predation has been an important consideration for many other mussel restoration projects throughout the world, and particularly that from crabs (Moody et al. 2020), predation was not likely to be a major factor in the current study as few aquatic predators are found in the rivers over winter and early spring when the experiments were undertaken. For example, *A. butcheri* has a tendency to overwinter in the lower region of the estuary (basin) and move upstream to spawn during late spring (Cottingham et al. 2014). On the land, the resident water rat Rakali *Hydromys chrysogaster* has a preference for large mature mussels, that is those that are approaching their second year of life, as indicated by middens present on river banks (Anonymized, pers. obs.).

Average densities of *X. securis* on the enhanced habitat of 3377 ind. m^{-2}, when accounting for percentage coverage, were lower than densities recorded in other studies. For example, Garci et al. (2007) recorded *X. securis* densities of 67,000 ind. m^{-2} in Ria of Vigo, Spain, and Iwasaki and Yamamoto (2014) encountered average densities of 19,600 ind. m^{-2} in Japan. The maximum densities of *X. securis* on the coir matting in this study were, however, far greater than the mean density of the much larger Ribbed Mussel *Geukensia demissa* on coir logs in Florida of 30 ind. m^{-2} (Moody et al. 2020). There also appeared to be several settlement events of *X. securis* onto the coir matting in the current study, as indicated by the length-frequency histograms, which would be consistent with this species having a protracted spawning period (Wilson 1969; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). Multiple recruitment events within the same spawning season were also consistent with previous studies in the Swan River (Wilson 1969) and in Japan (Iwasaki and Yamamoto 2014).

4.2 | Swan and Canning Rivers Seston Characteristics

The seston characteristics of the waters from the Swan and Canning rivers, which constitute the upper, saline region of the Swan-Canning Estuary, were generally slightly greater than temperate estuaries elsewhere. For example, the range of TPM values in the Swan Rivers of 7.1–17.6 mg L^{-1} was greater than that of two estuaries in New South Wales, Australia (3.5–12.3 mg L^{-1}), but was within the range of those recorded in Gwangyang Bay, Korea (2.0–18.5 mg L^{-1}; Table 2) and likewise declined with distance upstream (Paterson et al. 2003; Bibi et al. 2020). Although TPM concentrations in the current study were typically less than those of macrotidal estuaries, such as those in Marennes-Oléron Bay, France, which ranged from 100 to 721 mg L^{-1} (Mallet et al. 1990) (Table 2), they were typically greater than those used in mussel feeding experiments (Cottingham, Bossie, Valesini, Tweedley, et al. 2023). This includes that of a recent study on *M. galloprovincialis* in the main basin of the Swan-Canning Estuary, where TPM concentrations were 7.9–8.7 mg L^{-1} (Cottingham, Bossie, Valesini, Maus, et al. 2023).

Particulate organic matter concentrations recorded in the Swan and Canning rivers of 2.7–9.2 mg L^{-1} were likewise greater than eleven of the twelve studies on mussel feeding experiments collated by Cottingham, Bossie, Valesini, Maus, et al. (2023), which ranged from 0.2 to 10.6 mg L^{-1} and included a study undertaken in the lower region of the Swan-Canning Estuary where eutrophication issues are less pronounced. The average seston quality in the Swan and Canning rivers of 31%–74% (excluding CR1 in spring) was also typically greater than those recorded in other estuaries (see Table 2), but more similar to that of 48%–73% in the Mediterranean Sea (Galimany et al. 2011). However, despite the high organic matter content of the seston in the Swan and Canning rivers, no relationship between POM and any mussel-feeding parameters was significant, despite the relatively large range in the data. This may indicate that the organic material was not suitable mussel food, and mussels are more likely to select phytoplankton, which would be consistent with the relationships between feeding parameters and chlorophyll *a* concentrations and also the lack of a relationship between POM and chlorophyll *a*.

The greater values for TPM and PIM during summer were likely related to sediment resuspension due to wind mixing, with strong and persistent southerlies that generally occur across the region during summer (Pattiaratchi and Woo 2009). Resuspension of sediments by wind-generated waves would be particularly dominant in shallow estuaries such as the Swan-Canning Estuary, which has a large width-to-depth ratio. This conclusion is also consistent with TPM and PIM being greatest at the most downstream sites, which have limited wind protection, and least at the upper most sites, where the rivers become narrow and the riverbanks provide a buffer from the wind. This relationship was similar to the findings by Galimany, Lunt, et al. (2018) in Florida, with the highest TPM values recorded closest to the ocean.

The average chlorophyll *a* concentration recorded in the Swan and Canning rivers in the current study (2.5–13.5 μg L^{-1}) was broadly consistent with the annual averages recorded by Thompson (2001) in this estuary in the 1990s, which ranged from 6.3 to 14 μg L^{-1}. The maximum concentrations in the current study of 13.5 μg L^{-1}, recorded during summer in the Canning River, were, however, substantially less than the maximums recorded by Thompson (2001), which during phytoplankton blooms regularly exceeded 100 μg L^{-1} and reached ~1000 μg L^{-1}, measures which awarded this estuary its status as the second most eutrophic system of the 131 waterways analysed by Cloern et al. (2014).

4.3 | Clearance Rates and Feeding Behaviour

Clearance rates of *X. securis* in the Swan and Canning rivers were highly variable, as low as 0.3 in spring and as high as 6.6 L h^{-1} in summer. Although there are no comparable data for this species,

TABLE 2 | Water seston characteristics of temperate estuaries, TPM (total particulate matter, mg L^{-1}), PIM (particulate inorganic matter, mg L^{-1}), POM (particulate organic matter, mg L^{-1}), *f* (organic content, %) and chlorophyll *a* (Chl. *a*, μg L^{-1}).

Estuary	Region	TPM	PIM	POM	*f*	Chl. *a*	References
Swan River	SWA	7.1–17.6	2.7–10.4	2.7–6.4	32–65	2.9–12.5	This study
Canning River	SWA	6.5–314	1.6–305	4.8–9.1	3–74	2.5–11.6	This study
Swan-Canning Estuary	SWA	7.9–8.7	3.9–5.1	2.8–4.8	35–55	1.0–5.3	Cottingham, Bossie, Valesini, Tweedley, et al. (2023)
Brisbane Water	NSW	3.5–7.0	2.6–5.1	1.0–1.9	27–28[a]	1.8–4.0	Paterson et al. (2003)
Lake Macquarie	NSW	5.8–12.3	3.8–8.7	1.6–3.5	21–34[a]	2.7–9.4	Paterson et al. (2003)
Gwangyang Bay	Korea	2.0–29.1	0.9–20.6[a]	1.1–8.5	29–55[a]	0.2–7.2	Bibi et al. (2020)
Port Stephens Estuary	NSW	2.9–7.5	2.3–6.5[a]	0.6–1.0	14–21		Bayne (2009)
Great Sound	USA	37.1–78.1	28–75[a]	2–14[a]	6–22[a]	2–6.8[a]	Fegley et al. (1992)
Choptank River	USA	4.0–30	2.5–22[a]	1.5–8[a]	20–40[a]	1–16.5[a]	Berg and Newell (1986)
Marennes-Oléron Bay[b]	France	100–721	90–700[a]		16	5–15	Mallet et al. (1990)

Note: Regions: SWA (south-western Australia), NSW (New South Wales, Australia).
[a]Estimates based on figures within publication.
[b]Macrotidal estuary for comparison.

the clearance rates of *X. securis* in the Swan and Canning rivers were typically greater than those recorded for *M. galloprovincialis* in the Swan-Canning Estuary basin (1.2–1.9 $L h^{-1}$) (Cottingham, Bossie, Valesini, Tweedley, et al. 2023), but were more within the range of those recorded for that species in Alfacs Bay (Mediterranean Sea; 0.9–4.8 $L h^{-1}$), Wellington (New Zealand; 2.8–5.0 $L h^{-1}$), Ria de Arousa (Spain; 1.3–3.2 $L h^{-1}$) and two locations in the Tyrrhenian Sea (2.2–3.2 $L h^{-1}$) (Navarro et al. 1991; Gardner 2002; Sarà and Mazzola 2004; Galimany et al. 2011). They were likewise typically in the range of those derived for *G. demissa* at two locations in Long Island Sound (USA) (0.8–3.1 $L h^{-1}$) (Galimany et al. 2013).

The often slightly greater CR of *X. securis* is consistent with previous studies that have demonstrated that filtering rates as a function of mass decline with increasing size and this is consistent among numerous bivalve families, including mytilids and unionids (Wagner 1976). It is also consistent with the empirically derived equation used to standardise mussel feeding parameters to grams per mussel tissue (Bayne et al. 1989; Moody and Kreeger 2020; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). Clearance rate also appeared to be impacted by salinity, with values being greater in downstream sites where salinity was greater, and this was particularly evident in spring when salinities ranged from 2 to 8. Positive relationships between salinity and CR have previously been found in other estuarine mytilids in Florida, such as the Green Mussel *Perna viridis* (McFarland et al. 2013), but were negatively correlated in the case of the Hooked Mussel *Ischadium recurvum* (Galimany, Lunt, et al. 2018).

Despite the poorer seston quality in summer, the filtration and clearance rates of *X. securis* were greater, indicating that the seston characteristics were well within the range that this species can feed on. The average rejection proportion of 43%–67% in summer and 44%–100% in spring in this study, however, was typically greater than that recorded for other mytilids. For example, the rejection proportion of *M. galloprovincialis* ranged from 0.2%–16% in the Mediterranean Sea to 42%–47% in the lower reaches of the Swan-Canning Estuary (Galimany et al. 2011; Cottingham, Bossie, Valesini, Tweedley, et al. 2023). They were also typically greater than that recorded for *G. demissa*, which ranged from 25% to 73% (Galimany et al. 2013).

As small mytilids have the ability to clear greater amounts of water per gram of mussel tissue, the small maximum size of *X. securis* in combination with its formations of high densities makes *X. securis* more efficient compared to other mytilids, which grow to a larger size and aggregations are lower in density. These values for *X. securis* derived in this study were thus greater than those estimated for the *M. galloprovincialis* reef constructed further downstream in the estuary, where the same size area (1000 m^2) at the desired adult mussel density of 1000 ind. m^{-2} would clear up to 1.4×10^9 L over a three-month period incorporating 3.6 t of organic material into mussel biomass (Cottingham, Bossie, Valesini, Tweedley, et al. 2023).

Based on the approximate average length, width and depth of the Swan River (45 km × 50 m × 3 m) and thus a volume of 6.7×10^9 L, 1000 m^2 of enhanced *X. securis* habitat (at 10% coverage) could filter 13.6% of its volume in spring and 24.5% in summer. In the smaller Canning River (11 km × 200 m × 1 m = 2.2×10^9 L), 1000 m^2 of enhanced mussel habitat could filter 9.6% of the river's volume over the course of spring and 64.4% over summer. These values were, however, far less than those recorded for mussel beds elsewhere. For example, in the Oosterschelde Estuary (The Netherlands), beds of *Mytilus edulis* potentially clear the estuary (2.7×10^{12} L) in four or five days (Smaal et al. 1986; Dame and Prins 1998). Similarly, in the Bay of Königshafen (Germany), beds of *M. edulis* cleared its volume in ~2 days (Dame and Prins 1998).

The results of this study have thus demonstrated the efficacy of using soft substrates deployed by community volunteers to enhance habitat for mussels and their potential to assist in alleviating eutrophic issues. It also represents a cost-efficient approach that takes advantage of natural recruitment rather than seeding from aquaculture or a shellfish hatchery, which can incur substantial costs. Through further exploration, advances could be made on trialling different bed formations and also the timing of deployment that will likely increase *X. securis* settlement and resulting percentage coverage.

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Conflicts of Interest

The authors declare no conflicts of interest.

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