Does Salinity Gradient Affect Distributions of Byssally-Attached Bivalves in Songkhla Lake, the Largest Estuary in Thailand?

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ABSTRACT

Bivalves are typically considered as ecosystem engineers, so knowledge of their distributions is important to understanding the structure of the benthic community in a lagoon system. This study aims to characterize the spatial distribution and examine mechanisms regulating the distribution of *Mytilopsis sallei, Mytella strigata* and *Perna viridis* in relation to salinity gradient, which is a key hydrographic feature, in Songkhla Lake, southern Thailand. Surveys showed that *M. sallei* was abundant in areas upstream with low salinity, while *My. strigata* were largely found in mid-range salinity. *P. viridis* was very rare and observed only at the mouth of the lagoon where it connects to the sea. Most *M. sallei* and *My. strigata* recruited at salinity conditions similar to where their adults were found. However, only a few recruits and adults of *P. viridis* was observed in the system, so their spatial relationship could not be evaluated. Results from an experiment testing the effect of different salinity levels on survival, growth, and condition of the bivalves showed that juveniles of *M. sallei* survived at all salinities (0, 20, 35 psu), while *My. strigata* and *P. viridis* survived only at 20 and 35 psu. Our study highlights the role of salinity as a key factor determining distribution of the byssally-attached bivalves in this estuarine system and demonstrates that the degree of influence recruitment and post-recruitment mechanisms have on distributions varies by species. The information obtained is crucial for understanding the dispersal mechanism of alien invasive species that is useful for species management.

Keywords: Bivalves, Distribution, Recruitment, Salinity, Songkhla Lagoon System

INTRODUCTION

Salinity is a key environmental factors in estuaries that determines the distribution and community structure of estuarine organisms (Udalov *et al*., 2005; Little *et al*., 2017). Freshwater and marine species decrease from the sea and river, respectively, toward the inner estuary. This area is dominated by a few true estuarine or brackish species that can survive in extremely dynamic environments (Remane, 1934; Telesh and Khlebovich, 2010). Additionally, species within the same functional or taxonomic groups may segregate spatially along a salinity gradient (Calliari *et al*., 2007; Dwyer *et al*., 2020), which consequently influences the community of associate organisms (Islam *et al*., 2006).

Byssally attached, filter-feeding bivalves are widely recognized as ecosystem engineers (Borthagaray and Carranza, 2007; Burlakova *et al*., 2012). Their filter-feeding activity can influence the structure of the pelagic zone by removing suspended particulate matter and plankton (MacIsaac, 1996; Dermott and Karec, 1997; Aldridge *et al*., 2008). Their three-dimensional biogenic structures can provide shelter and feeding grounds for other benthic species (Tsuchiya, 2002). It has been proposed that the spatial distribution of these bivalves is one of the key factors determining benthic

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community composition (Borthagaray and Carranza, 2007; Sousa *et al*., 2009; Hayeewachi *et al*., 2023). Therefore, understanding their distributions and the mechanisms that regulate them is important for elucidating the functioning of the aquatic systems.

The benthic community in the shallow waters of Songkhla Lake, a coastal lagoon located in the southern region of Thailand, and its tributaries has recently dominated by the Caribbean false mussel *Mytilopsis sallei* (Recluz, 1849) and the American brackish water mytilid *Mytella strigata* (Hanley, 1843) (Figure 1). Both species are recognized as alien invasive bivalves that have invaded the Indo-Pacific regions in recent years (Sanpanich and Wells, 2019; Yu *et al*., 2023). *M. sallei* was originally described from the Caribbean islands and the Bay of Mexico (Marelli and Gray, 1983), while *My. strigata* is native to both coasts of Central and South America (Lim *et al*., 2018). It has been suggested that the introduction of both species to the Indo-Pacific has occurred via hull fouling and transportation in ballast water (Lim *et al*., 2018; Tan and Tay, 2018).

A preliminary observation in 2022 found *M. sallei* in rivers or canals running into the lower part of the lagoon where salinity is relatively low. *My. strigata* was found in the southernmost part of the lagoon system where it opens to the sea at mid to high salinity levels. Differences in community composition of macroinvertebrates have been observed between those living in biogenic structures formed by *M. sallei* and in habitats not modified by the bivalves (Hayeewachi *et al*., 2023). Therefore, the distribution of these bivalves can impact the diversity and composition of other benthic faunas, consequently affecting the food webs in the system.

Another byssally-attached bivalve in the system is the green mussel Perna viridis (Linnaeus, 1758) (Figure 1), native to the Indo-Pacific region (Rajagopal *et al*., 2006). This bivalve is an economically important species that was abundant the lake system in the past but has been rarely observed in recent years (Angsupanich and Kuwabara, 1999; Mardnui and Plathong, 2009). The cause of its population decline has not yet been examined, but Wangkulangkul *et al*. (2022) suggested that space competition with the alien invasive bivalves might exclude *P. viridis* from the system.

While these bivalve species play an important role in structuring the aquatic community where they dominated (Wangkulangkul *et al*., 2022; Hayeewachi *et al*., 2023), knowledge of their distribution and the influence of salinity gradient, which is the key hydrographic feature in the lagoon system, on regulating their distributions is still limited. There are reports of the co-occurrence of *M. sallei* and *My. strigata* in the same estuaries (Lim *et al*., 2018; Sanpanich and Wells, 2019; Wangkulangkul *et al*., 2022), as well as reports demonstrating that *My. strigata* and *P. viridis* were found at the same sites (Spinuzzi *et al*., 2013; Sanpanich and Wells, 2019; Zuo *et al*., 2024). However, there is information suggesting that these species have different optimal salinity levels. Sa-nguansil and Wangkulangkul (2020) demonstrated that the survival of *M. sallei* larvae was highest at 12.5 and 16.25 psu, and the highest abundance was consistently found at mid-range salinity (approximately 15–20 psu). However, adults of *M. sallei* were found at a wide salinity range (0–35 psu) in natural habitats (Wangkulangkul, 2018). For *My. strigata*, experiments showed that adult mussels survived at 0–40 psu for long-term exposure.

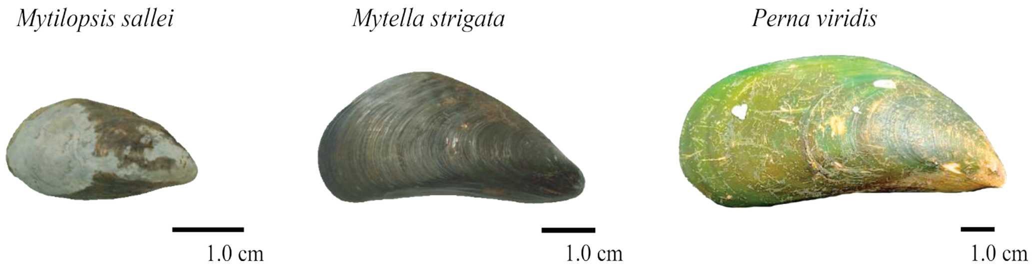

Figure 1. Three species of bivalves in this study: from left to right, *Mytilopsis sallei, Mytella strigata, Perna viridis.*

Huang *et al*. (2021) reported that *My. strigata* was abundant on the concrete embankments of estuaries in Taiwan at salinities between 15 and 42 psu, and the species was reported in Manila Bay, the Philippines, at salinities ranging from 21.8 to 31.4 psu (Vallejo *et al*., 2017). Compared to other species, the optimum salinity of *P. viridis* was relatively high at 35–37 psu (Yuan *et al*., 2016); however, it can tolerate a much wider salinity range of 0–64 psu (de Bravo *et al*., 1998). Information obtained from salinity tolerance experiments does not necessarily match the salinity range where bivalves were found in nature. Moreover, they do not demonstrate how species distribute across differing salinity regimes.

This study aims to quantify the spatial distribution in relation to salinity gradient of the three byssally attached, filter-feeding bivalves, *M. sallei, My. strigata* and *P. viridis* in Songkhla Lake and its tributaries. Furthermore, variations in recruitment of the bivalves were monitored along a salinity gradient to test if recruitment is the key process determining bivalves' distributions. Additionally, an experiment was conducted to examine whether bivalves' survival rates, growths and conditions in freshwater, mid-range and high salinity levels differ between species, to test if post-recruitment mortality when the bivalves are exposed to unfavorable salinity determine their distribution. The information obtained will shed light on the processes regulating populations of the byssally-attached filter-feeding bivalves that play important roles in estuarine systems.

MATERIALS AND METHODS

Study site

The Songkhla Lagoon System (7°08′N–7°48′N and 100°07′E–100°35′E, Figure 2a) is situated on the eastern side of Peninsular Thailand covering an area of 1,082 km^2. The system comprises four distinct lakes from north to south, with the lagoon connected to the sea: Thale Noi, Thale Luang, Thale Sap, and Thale Sap Songkhla (hereafter referred to as Songkhla Lake). The largest variations in salinity have been observed in Songkhla Lake and its tributaries (Pornpinatepong *et al*., 2010), whereas other lakes are almost freshwater throughout the year. *Mytilopsis sallei, Mytella strigata,* and *Perna viridis* were observed in the shallow waters of Songkhla Lake, as well as in rivers and canals that drain into the lake. Therefore, the study of bivalves' spatial distributions focuses on this section of the lagoon system. In Songkhla Lake, most of the bottom is muddy (Pornpinatepong *et al*., 2010), with an average depth of about 1 to 1.5 m (Lheknim and Yolanda, 2020). Several rivers and canals run into the lake, bringing freshwater and creating a salinity gradient from fresh to saline from the northern to the southern part of Songkhla Lake (Wangkulangkul and Lheknim, 2008).

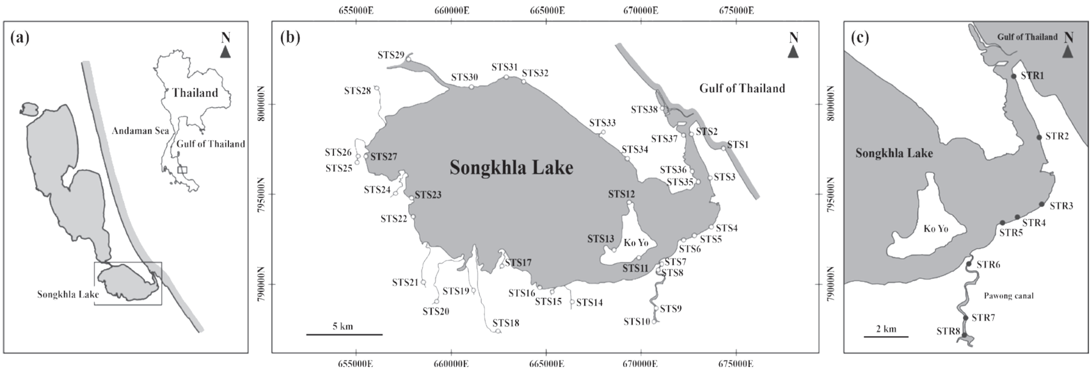

Figure 2. (a) Location of the Songkhla Lagoon System in Thailand, with Songkhla Lake indicated by a rectangle; (b) Locations of the sampling stations (STS1-STS38 = Station 1 to Station 38, labelled as open circle) on the banks of Songkhla Lake and its tributaries, as well as on the coast near the mouth of the lake; (c) Locations of sampling stations (STR1-STR8 = Station 1 to Station 8) labelled as black dots from the mouth of Songkhla Lake to Pawong canal. The grey areas represent water bodies.

Pawong canal (7°14′N, 100°34′E, Figure 2c) is one of the canals that drain into Songkhla Lake. Adults of *M. sallei* and *My. strigata* were observed in this canal (Wangkulangkul *et al*., 2022; Hayeewachi *et al*., 2023). Salinity generally decreases from the mouth of the canal toward the inner portion, ranging from 0 to 33 psu (Angsupanich and Kuwabara, 1999; Wangkulangkul, 2018). Since a salinity gradient was observed in this canal, the abundance of bivalves recruits was monitored from the mouth of the Lagoon System (or the mouth of Songkhla Lake) to the upstream section of the Pawong canal.

The climate of the eastern part of Peninsular Thailand is influenced by monsoons. Seasons can be classified as the northeast monsoon season (October–December); the dry season (February–April); and the southwest monsoon season (June–August). Generally, heavy rainfall is found during the northeast monsoon season, while there is lighter rain in the southwest monsoon season (Hayeewachi *et al*., 2023).

Surveys for the spatial distribution of the bivalves

Two surveys were conducted in 2022 to examine distribution of *M. sallei, My. strigata* and *P. viridis*. The first survey took place in late June, during the southwest monsoon, when the lake's salinity is relatively low due to rainfall. The second survey was conducted in early October, before the onset of the northeast monsoon, season, when salinity is relatively higher. These surveys covered 37 stations along the banks of Songkhla Lake, as well as canals, rivers and a coastal area near the lake's mouth (Figure 2b). Stations were not placed in areas with depth exceeding 1 meter, as most bivalves were found at shallow level.

At each station, the percentage cover of bivalves was visually estimated within a 2×2 m area and categorized as absent (0%), rare (<10%), common (10–80%), and abundant (>80–100%). Additionally, salinity was measured using a hand-held refractometer. It was impractical to access the actual percentage cover of bivalves in plots or quadrats due to the high heterogeneity of the substrates to which the bivalves attach. Observations revealed that some bivalve individuals attached to hard submerged substrates such as mangrove roots, wooden poles, or concrete structures, while others formed dense patches covering the water bodies' bottoms.

Samplings of bivalves' recruitment

To quantify the recruitment of bivalves along a salinity gradient, samplings were carried out at 8 stations from the mouth of Songkhla Lake to the inner part of Pawong canal (Figure 2c), which ranged from high to low salinity. Although the reproductive season was known for *M. sallei* (Wangkulangkul, 2009), knowledge of *My. strigata* and *P. viridis*'s reproduction is lacking. Therefore, sampling for the recruitment of all three species was conducted monthly throughout the year from December 2021 to December 2022. In this study, plastic scouring pads (14×16×0.5 cm) were used as artificial filamentous substrates to facilitate the settlement of the bivalves. At each station, 5 scouring pads were randomly tied to the polyester rope and attached to concrete poles. The pads were suspended below the water surface at a depth of 0.5 m. Scouring pads were collected and replaced at monthly intervals. During sampling, salinity was measured at each station using a multiparameter digital water quality meter (YSI ProQuatro). In the laboratory, scouring pads from each station were kept separately in a glass aquarium (22×45×28 cm), filled with artificial seawater. The salinity of the water in each aquarium matched the salinity of the natural habitat where the pads were collected. The artificial seawater was changed every 2 days for all aquariums. The pads with recruits were kept for 14 days to allow the recruits to grow until they are identifiable. Bivalves were fed daily with *Nannochloropsis* sp. The concentrated algal solution was poured into the aquarium to meet a concentration of 4×10^4 cells·mL^{-1} (Wang *et al*., 2011). Afterwards, the total number of bivalve individuals on each pad was identified to the species, counted, and recorded as the density of the recruits.

Salinity tolerance of the juvenile bivalves

The effects of salinity on growth, condition, and survival of bivalves were tested for individuals at juvenile stage as they are more susceptible to environmental condition than adults (Jermacz *et al.*, 2021). *M. sallei* matures at 8 mm, *My. strigata* at 12.5 mm, and *P. viridis* at 15–30 mm shell length (Siddall, 1980; Morton, 1989; Stenyakina *et al.*, 2010). Therefore, a salinity tolerance experiment was performed on juveniles with shell lengths of 5.0–8.0 mm for *M. sallei*, 9.0–12.5 mm for *My. strigata*, and 12.0–15.0 mm for *P. viridis*. It was unlikely to retrieve needed specimens from the same location at the same time. Juveniles of *M. sallei* were collected from Songkhla Lake (salinity = 0 psu). *My. strigata* specimens were retrieved from Pak Panang estuary, located approximately 70 km north of the northern part of the Songkhla Lagoon System (salinity = 8 psu). Meanwhile, *P. viridis* were collected at Kao Seng beach and Sakom beach, located on the coast of the gulf of Thailand, 6 and 20 km south of the mouth of Songkhla Lake (salinity = 32 psu). All specimens were collected in March 2022. After collection, specimens of each species were acclimated separately for 24 h at a salinity similar to their natural habitat. Each bivalve was labelled by an individual number, its wet weight was measured, and then it was randomly assigned to treatments. Twelve bivalve individuals of each species were placed in a 900 mL plastic container and exposed to 500 mL of continuously aerated test solution at different salinities. Specimens of each bivalve species were exposed to three treatments: salinity 0, 20 and 35 psu. The salinity levels used were determined from the fact that salinity in the Songkhla Lake system is highly variable. Therefore, small scale change in salinity presumably might not affect the bivalves. These salinity levels (0, 20 and 35 psu) represent freshwater, mid-range, and marine condition, respectively. Each treatment consisted of three replicated containers. The positions of all containers were randomized. The solution was changed every 2 days. Bivalves were fed daily with *Nannochloropsis* sp. The concentrated algal solution was poured into each container to meet the concentration of 4×10^{4} cells·mL^{-1} (Wang *et al.*, 2011). All treatments were exposed to the same light conditions and temperature. After 5 weeks, survivors were counted, growth rate and condition index (CI) of each individual were measured and analyzed. The survival rate of bivalves in each container was calculated as [Survival rate = (number of survivors×100)/12], and the growth rate of each individual was calculated as [Growth rate = (wet weight of survivors at the end of the experiment (g) - wet weight of the bivalves before the experiment (g))×1,000/35]. Additionally, the survival of bivalves was examined daily, and dead bivalves were removed from the treatment. To analyze the condition index (CI), the shells and tissue samples were oven-dried at 60 °C for 48 h, and then the dry mass (g) was measured to the nearest 0.0001 g using a digital weighing scale. The CI was calculated as [CI = (tissue dry mass (g)×100)/dry shell weight (g)] (Davenport and Chen, 1987).

Data analysis

To examine spatial and temporal variation in bivalves' recruitment, two-way permutational multivariate analysis of variance (PERMANOVA) with pairwise comparisons was performed to test the effects of stations (fixed factor, 8 levels) and months (fixed factor, 13 levels) on density of *M. sallei* and *My. strigata*. Additionally, to specifically analyze the effect of locations along a salinity gradient on recruit density, a one-way PERMANOVA with pairwise comparison was performed to test the differences in abundance of *M. sallei* and *My. strigata* recruits between stations (fixed factor, 8 levels). In this analysis, the data of recruit density were pooled across months. Since *P. viridis* recruits were only found at one station in one month, these analyses were not performed for this species.

To examine variations in salinity between recruitment sampling stations, a Kruskal-Wallis test was performed, treating data from sampling months as replicated. Pairwise comparisons were conducted using the Mann–Whitney U test. Moreover, a Kruskal-Wallis test was used to compare salinity levels between species in locations where adults were found and where most recruits were observed. Separate tests were also conducted to examine the differences in salinity levels between where adults were observed and where most recruits were found for each species individually. In these latter two analyses, data of salinity where selected from stations that contributed the top 80% of overall recruit numbers for each species.

For instance, if recruits were found at stations 5, 6, 7, and 8 (ranked by total numbers of recruits found at each station), and 80% of the overall recruits were from station 5 and 6, then the salinity values used were those measured at station 5 and 6 during the months when recruitment was observed. This approach was adopted due to the significant variation in recruit density, particularly notable for *M. sallei*, where on some occasions, a thousand recruits were found on a pad, whereas only a few individuals were observed in others. Consequently, data from stations and months with very low recruit density were excluded from the analysis.

To assess differences in survival rate, growth rate, and condition index of juvenile bivalves exposed to different salinities (fixed factor, 3 levels), a one-way PERMANOVA with pairwise comparisons was performed. Data of growth rate and condition index of *My. strigata* and *P. viridis* were not obtained at 0 psu as all specimens died, therefore, the effect of salinity was tested only between salinities of 20 and 35 psu.

For univariate PERMANOVA, Euclidean distance resemblance matrices (with a dummy variable added) were constructed from untransformed data. PERMANOVAs analyses were conducted in PRIMER v7 add-on package PERMANOVA+ (Anderson *et al*., 2008) and Kruskal-Wallis tests and Mann–Whitney U tests were performed using PAST (Paleontological Statistics) 4.06 (Hammer *et al*., 2001).

RESULTS

Surveys for the distribution of the bivalves

The first survey of bivalve distribution in June 2022 (Figure 3a), conducted when the salinity in Songkhla Lake was relatively low, revealed that *Mytilopsis sallei* were observed in the rivers and canals draining into the lake, with some also observed in the shallow areas of the lake, spanning a range of salinities from 0 to 7 psu. *Mytella strigata* were observed from the southernmost part to the mouth of the lake, with salinity ranging from 6 to 27 psu. *Perna viridis*, on the other hand, was found along the coast around the mouth of the lake, thriving in marine conditions at a salinity of 32 psu. There was only one location where both *M. sallei* and *My. strigata* co-occurred (STS6).

The second survey in October 2022 (Figure 3b), conducted when salinity was relatively higher, showed *M. sallei* maintaining its presence in the same locations but expanding towards the mouth of the lake (STS5-4). It was found across a wide range of salinities, from 0 to 32 psu, with higher abundance noted in areas with low salinity, particularly in rivers or canals. *My. strigata*, meanwhile, were primarily observed near the mouth of the lake at salinities ranging from 15 to 32 psu. There were 7 locations where both *M. sallei* and *My. strigata* coexisted. Additionally, a few individuals of *P. viridis* were found at the mouth of Songkhla Lake at 32 psu, a location where they had not been previously observed (STS2).

The Kruskal-Wallis test revealed that salinity measured at stations where adults of *M. sallei* were present was lower than those of *My. strigata* (Figure 6b, $p<0.05$). These analysis pooled data across all sampling occasions.

Spatial and temporal variation in recruitment of the bivalves

During the study period, the maximum density of *M. sallei* recruits was 9,743.60 individuals per pad at station 7 (STR7). There were 2 peaks of *M. sallei* recruitment at stations 7 and 8 (STR8), occurring in February and August 2022. At station 7, the number of recruits was approximately four times higher in August than in February 2022 (Figure 4b, Table 1, pairwise comparison, $p<0.05$). Recruitments at other stations were rare. The maximum density of *My. strigata* recruits was 2,017 individuals per pad at station 3 (STR3). Recruitment of *My. strigata* peaked at station 3 and station 4 (STR4) in February

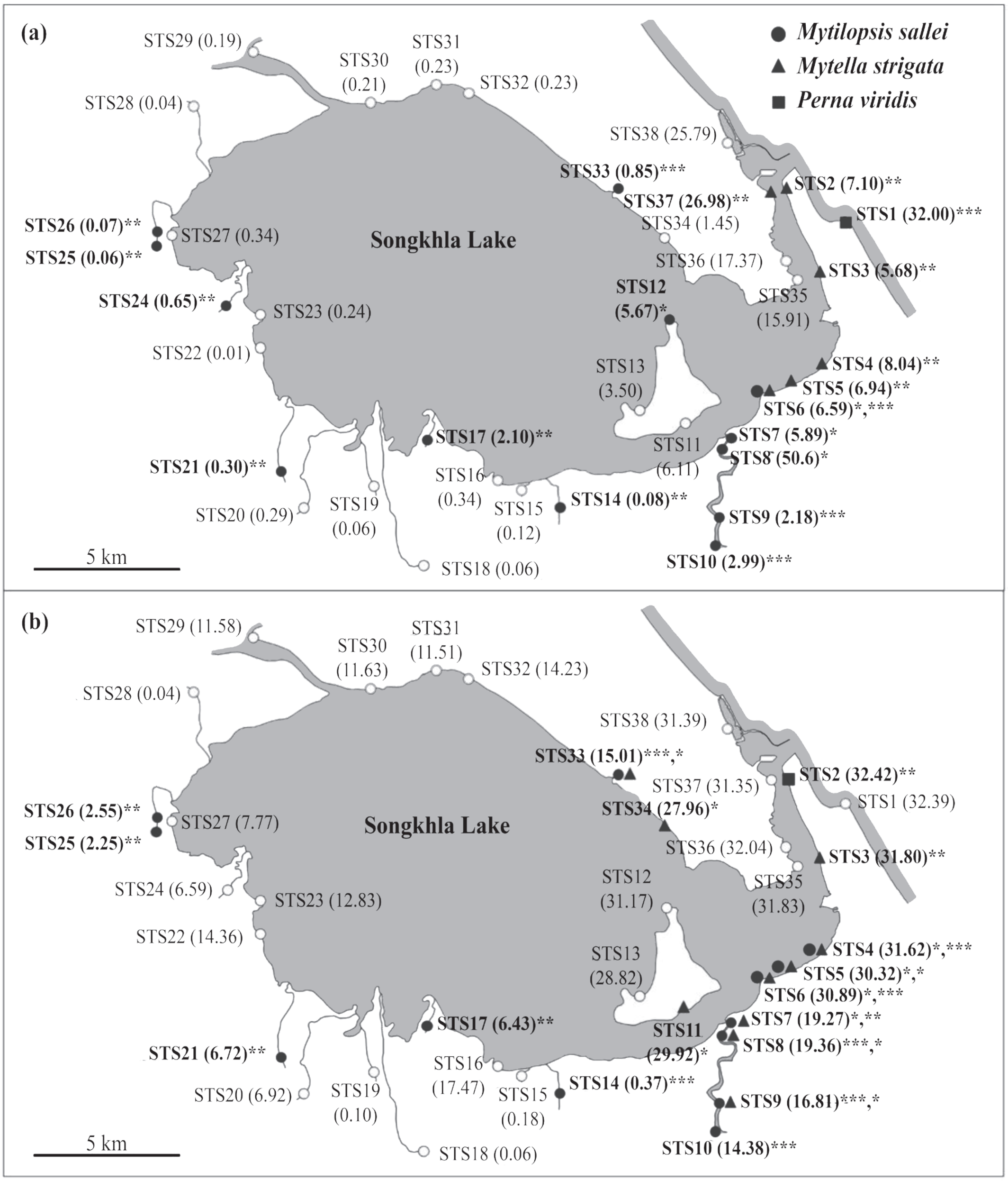

Figure 3. Maps show distribution of *Mytilopsis sallei, Mytella strigata* and *Perna viridis* in Songkhla Lake and its tributaries: (a) in June 2022; (b) in October 2022.
STS1-STS38 denote sampling station 1–38; Stations are labelled as open circles except for stations where bivalves were observed, which are marked by icons indicating each species (See the figure legend); Numbers in brackets represent salinity; Asterisks denote the relative abundance of species marked by the icons (single asterisk = rare, double asterisks = common, triple asterisks = abundant).

2022 (Figure 4c, Table 1, PERMANOVA pairwise comparison, $p<0.05$). A few recruits occurred at other stations in February, July, and September 2022. The recruitment rate of *P. viridis* was very low (maximum of 4 individuals per pad), with recruits observed only at station 3 in February 2022 (Figure 4d).

When considering the recruitment of bivalves along a salinity gradient (Figure 5), recruits of *M. sallei* were found at all stations except station 2 (STR2). PERMANOVA on the effect of stations showed that the highest density was found at station 7 (STR7) (Figure 5, Table 1, PERMANOVA pairwise comparison, $p<0.05$). Throughout the year, it was only at locations with relatively low salinities (STR7-8) that the density of *M. sallei* recruitment exceeded 900 individuals per pad. Recruits of *My. strigata* were found at all stations; however, the mean density was higher than 100 individuals per pad only at stations 3 and 4 (Figure 5, Table 1, PERMANOVA pairwise comparison, $p<0.05$) with mid to high-range salinity. Across all months, only a few individuals of *P. viridis* recruits were found at station 3.

From recruitment sampling stations 1 to 8, median salinity decreased from approximately 15 psu to less than 5 psu (Figure 6). The Kruskal-Wallis test demonstrated that salinity differed between recruitment sampling stations ($p<0.05$). However, variation within stations was very high, and only the differences between station 1 and stations 6–8 were significant (Figure 6a, Mann–Whitney U tests,

Table 1. PERMANOVA testing the effects of 1) months and stations; and 2) stations on density of bivalves' recruits.

Source of Variation	df	MS	Pseudo-F	p (perm.)
Two-way PERMANOVA				
Mytilopsis sallei				
Month (Mo)	12	1.13×107	92.534	**<0.05**
Station (St)	7	2.10×107	172.81	**<0.05**
Mo×St	83	5.72×106	47.01	**<0.05**
Residual	406	1.22×105		
Total	508			
Mytella strigata				
Month (Mo)	12	7.78×105	295.76	**<0.05**
Station (St)	7	2.32×105	88.293	**<0.05**
Mo×St	83	2.44×105	92.619	**<0.05**
Residual	406	2631.2		
Total	508			
One-way PERMANOVA				
Mytilopsis sallei				
Station	7	2.14×107	16.227	**<0.05**
Residual	501	1.32×106		
Total	508			
Mytella strigata				
Station	7	2.34×105	3.8196	**<0.05**
Residual	501	61201		
Total	508			

p<0.05). Although the salinity measured at stations where adults of *M. sallei* were present was lower than those of *My. strigata* (Figure 6b, Kruskal-Wallis test, p<0.05), this pattern was not statistically significant for recruitment, even though the mean salinity at stations where most *M. sallei* recruited seemed lower than that of *My. strigata*. Additionally, the salinities measured where adults were distributed and where most bivalves recruited were not different for both *M. sallei* and *My. strigata* (Figure 6b, Kruskal-Wallis test, p>0.05).

Salinity tolerance of the juvenile bivalves

For *M. sallei*, there were no differences in percent survival rates between treatments (PERMANOVA, pairwise comparison), and the species had more than 80% survival rates across all treatments (Figure 7). All *M. sallei* specimens survived at a salinity 0 psu but all *My. strigata* and *P. viridis* specimens died at this salinity (Figure 7). The number of surviving *My. strigata* began to decrease on the 5th day, with 100% mortality by the 11th day from the onset of the experiment. The number of surviving *P. viridis* specimens decreased rapidly, with all individuals dying by the 6th day. Survival of *My. strigata* did not differ between 20 and 35 psu (Figure 7), while more *P. viridis* individuals survived at 20 psu than at 30 psu (Figure 7). The growth rate of *M. sallei*, *My. strigata* and *P. viridis* did not differ between treatments (Figure 7, PERMANOVA pairwise comparison). The condition index of *M. sallei* increased as salinity increased, whereas the condition of *My. strigata* and *P. viridis* did not vary between salinity levels (Figure 7, PERMANOVA pairwise comparison).

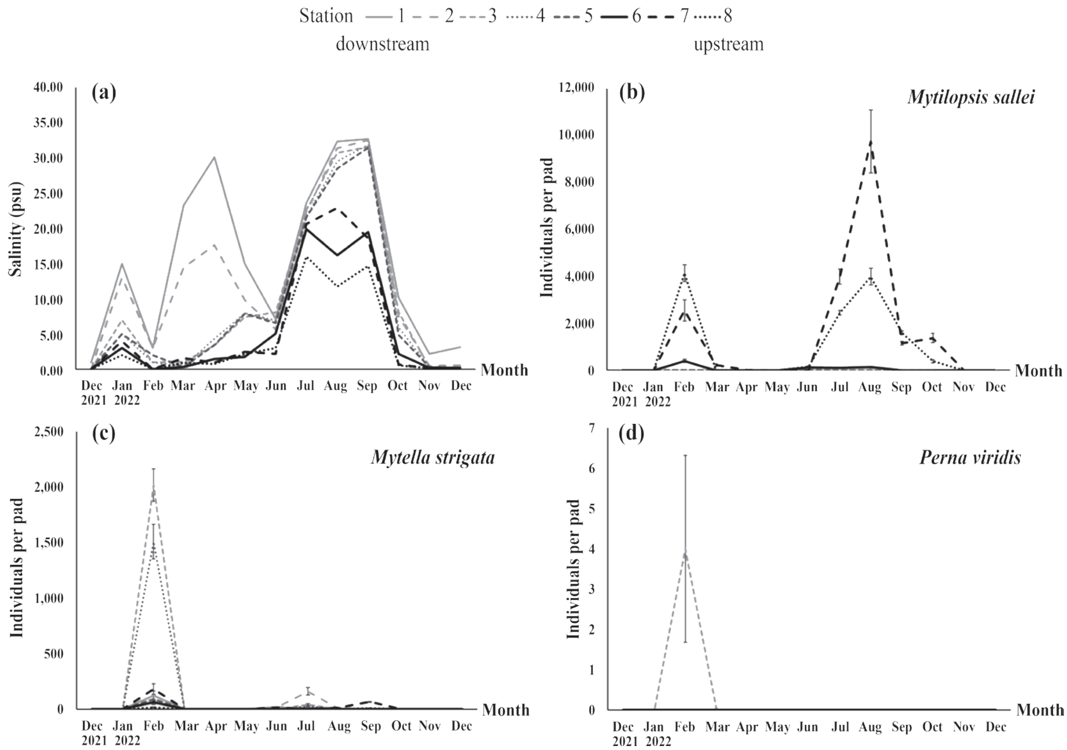

Figure 4. Salinity and density of bivalve recruits (Mean±SD) from December 2021 to December 2022 at stations 1 to 8 (STR 1–8): (a) Salinity; (b) *Mytilopsis sallei* recruits; (c) *Mytella strigata* recruits; (d) *Perna viridis* recruits.

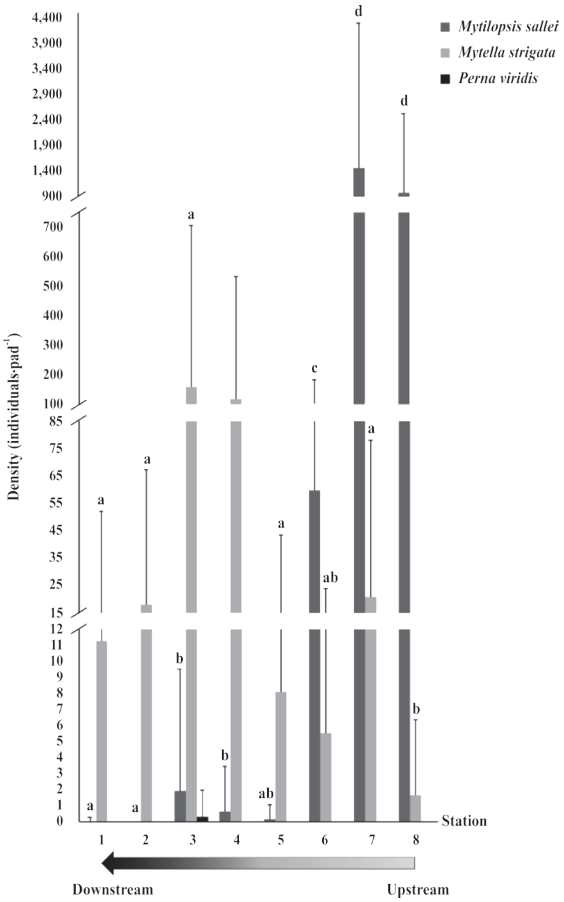

Figure 5. Density of recruits (Mean±SD) at stations 1 to 8. Data were pooled across months. Different letters above bars indicate significant difference between stations (Pairwise comparison, p<0.05).

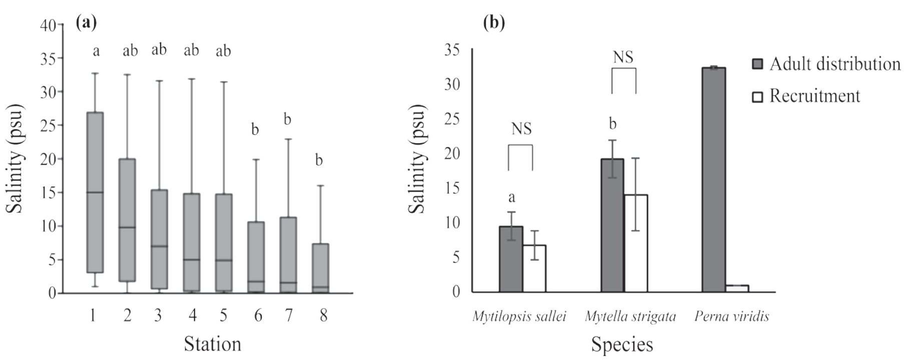

Figure 6. (a) Boxplot of salinity measured at stations where recruitment was monitored. Data for each station were collected across all months. Different letters above bars indicate significant difference between stations (Mann–Whitney U test; p<0.05); (b) Salinity (Mean±SD) measured at sampling stations where adult bivalves were found (dark grey bars) and salinity measured at stations where most bivalve recruits were observed (light grey bars). Different letters above bars indicate significant difference between species (Kruskal-Wallis test; p<0.05; data of *P. viridis* were omitted). NS = no significant difference in salinity between where adults were observed and where recruits were found (Kruskal-Wallis test; p>0.05; the test was not performed for *P. viridis*).

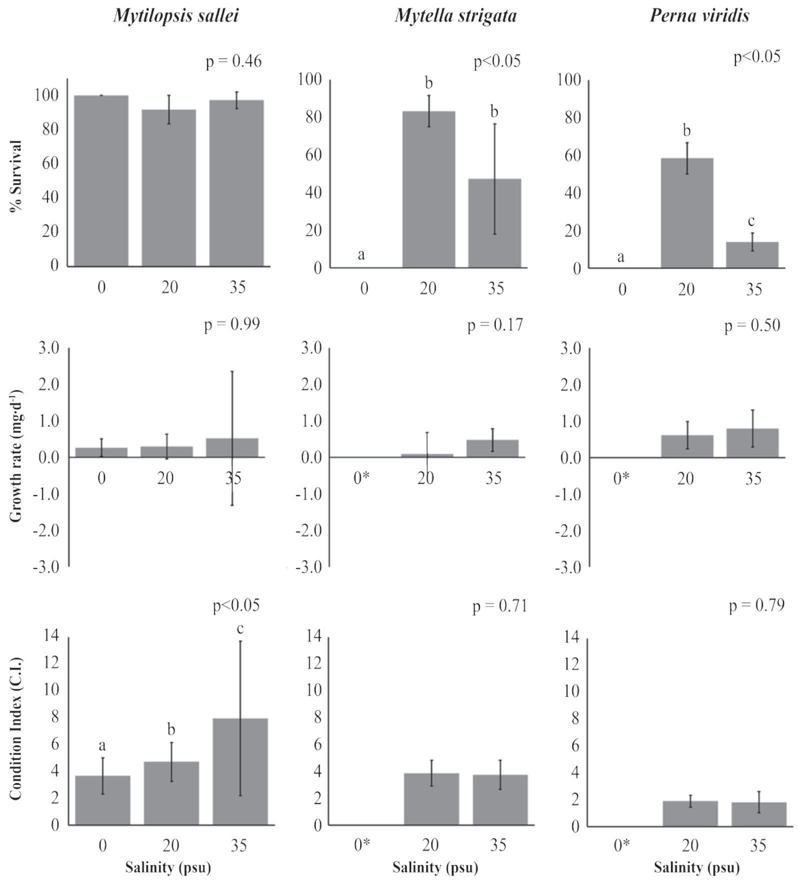

Figure 7. Percentage of survival, growth rate and condition index of *Mytilopsis sallei*, *Mytella strigata*, and *Perna viridis* at different salinities. The p-values were obtained from PERMANOVA testing the effect of salinity on survival rate, growth rate, and condition index of bivalves. Different letters above the bars indicate differences between treatments (pairwise comparisons, $p<0.05$); 0* = data were unavailable.

DISCUSSION

In the Songkhla Lake system, although there were sites where species co-occurred, *Mytilopsis sallei, Mytella strigata* and *Perna viridis* showed spatial segregation along a salinity gradient. *M. sallei* preferred areas with lower salinity compared to *My. Strigata* and was occasionally found in freshwater environments where the other species were absent. In contrast, *P. viridis* was predominantly abundant in fully marine conditions outside the lake. Previous observations in the Songkhla Lake system revealed that *M. sallei* was present across a wide salinity range (0–35 psu) but thrived in sites with relatively low salinity (Wangkulangkul, 2018). *My. strigata*, as reported by Huang *et al.* (2021), thrived in salinities between 15 and 42 psu, with records in Manila Bay, the Philippines, showing occurrences in salinities ranging from 21.8 to 31.4 psu (Vallejo *et al*., 2017). While *P. viridis* could be found in salinities ranging from 2 to 38 psu (Spinuzzi *et al*., 2013), Yuan *et al*. (2016) found that its optimum salinity range was relatively high (35–37 psu). The differences in physiological adaptations of these bivalves to salinity likely drive this habitat partitioning. However, a comparative analysis of how these bivalves respond physiologically to salinity has not been conducted.

Changes in the distribution of these bivalves were observed between two surveys. When salinity levels were higher, *M. sallei* expanded their range into areas with generally higher salinity, whereas *My. strigata* and *P. viridis* were found in more upstream areas. A high number of *M. sallei* recruits found in August 2022 at stations upstream suggested a massive spawning event had occurred previously. Thus, it is possible that some larvae were transported to downstream areas, where they settled and recruited. For *My. strigata* and *P. viridis*, the increase in salinity might have allowed them to settle in more upstream areas as salinity conditions became more favorable.

The recruitment of the bivalves exhibited strong temporal variation throughout the year. *M. sallei* had a major peak in August, with a smaller one in February. Wangkulangkul (2009) observed two peaks of *M. sallei* recruitment in a small lagoon connected to the mouth of Songkhla Lake: a major peak in January and a small one in July. Thus, her work and the present study support the notion that the *M. sallei* population in this estuarine system reproduces twice per year. In Brazil, ripe gonads and recruitment of *M. sallei* could be observed throughout the year, with the highest recruitment occurring when salinity was low (Queiroz *et al*., 2022).

In the present study, the major peak of *My. strigata* was in February, with a few recruits found in July and September. On the coast of the upper Gulf of Thailand, Wells *et al*. (2024) suggested that *My. strigata* spawned once per year. Similarly, populations of *My. strigata* on the south American coasts exhibited one reproductive season (Cárdenas and Aranda, 2000; Monteles *et al*., 2023).

In February, only a few recruits of *P. viridis* were found on settlement pads. On the coast of Southeast India and Bangladesh, *P. viridis* reproduces twice per year (Rajagopal *et al*., 1998; Khan *et al*., 2010). Conversely, in the Malacca Strait, a population of *P. viridis* showed a peak of recruitment in July and August (Al-Barwani *et al*., 2007). Low salinity can induce spawning in bivalves (Morton, 1989). Given the observed decrease in salinity in Songkhla Lake at the end of the year (Phasook and Sojisuporn, 2005; Bunsom and Prathep, 2012), a spawning event might have been induced when salinity dropped at the end of 2021, resulting in the peak of recruitments of *M. sallei* and *My. strigata* in February 2022.

The spatial pattern of recruitment along a salinity gradient was less conspicuous. *M. sallei* settled at all stations except those near the mouth of the lake (STR1–2). However, a greater density of *M. sallei* recruits (mean density >900 individuals per pad) was found in the upstream areas with a relatively low salinity. Sa-nguansil and Wangkulangkul (2020) showed that most larvae of *M. sallei* died when salinity exceeded 25 psu. Consequently, it is possible that the majority of *M. sallei* larvae died before settlement at stations downstream stations. *My. strigata* recruits were found across a wider range than *M. sallei*, i.e., they were present at all stations; however, the highest recruitment rate was observed in areas with mid-range salinity (STR3–4). Although there is no report on the salinity tolerance of *My. strigata* larvae, it is likely that its optimum salinity might be higher than that of *M. sallei*'s. Knöbel *et al*. (2021) compared the growth, mortality, and settlement success between larvae of two *Mytilus* species living at high and low salinity conditions. They discovered that the larvae performed better when reared at their respective native salinities. For *P. viridis*, a few recruits were found at stations near the mouth of the lake. However, the number of recruits was very low, making the interpretation of the data difficult. The low recruitment might result from the absence of adults in the lake system, and larvae produced by the population on the open coast might not disperse in sufficient numbers into the lake. Additionally, the percentage of *P. viridis* eggs that developed into normal D-veligers and the survival rate of larvae decreased as salinity decreased (Tan, 1996). This could explain why recruits of *P. viridis* were found only at the mouth of the lake, where salinity was high.

When bivalves face unfavorable external environments, such as non-optimal salinities, they typically close their valves to isolate and defend themselves (McFarland *et al*., 2013). This closure halts activities like respiration, feeding, and filtration, leading to potential challenges in gas exchange and food uptake, resulting in anoxic respiration and reduced energy input (Picoy-Gonzales and Laureta, 2022). These factors can significantly impact the survival, growth, and condition of the bivalves. There was a difference in survivorship patterns between juveniles of *M. sallei* and the other two species. *M. sallei* survived across all salinities, whereas all *My. strigata* and *P. viridis* specimens died at 0 psu. This aligns with previous studies showing that juveniles of all three bivalve species can survive in a wide range of salinities, but only *M. sallei* that can endure salinities as low as 0 psu (McFarland *et al*., 2015; Rice *et al*., 2016; Sa-nguansil and Wangkulangkul, 2020). The salinity tolerance pattern of *My. strigata* and *P. viridis* in our study corresponds to findings by Yuan *et al*. (2010) and Yuan *et al*. (2016), respectively. In Yuan *et al*. (2010), the survival rate of *My. strigata* juveniles was higher at a mid-range (14, 23 psu) and high salinities (40 psu) than low salinity (5 psu). Similarly, in Yuan *et al*. (2016), more *P. viridis* juveniles died at low salinity of 5 psu compared to 20 and 30 psu across all temperature levels. At 31°C, more *P. viridis* individuals survived at 20 psu than at 36 psu, which is similar to the result of the present study (20 *vs* 35 psu).

Despite being abundant in areas with low salinity in its natural habitat, *M. sallei* exhibited the highest condition index in marine condition (35 psu). Sa-nguansil and Wangkulangkul (2020) found that the condition index of adult *M. sallei* surviving at 40 psu did not differ from those reared at 0–25 psu. These findings highlight the resilience of *M. sallei* when exposed to unfavorable environments. The growth rate and condition indices of *My. strigata* and *P. viridis* did not differ between 20 and 35 psu. All specimens died at 0 psu, so data were not obtained for both species. Galimany *et al*. (2018) observed that higher salinity enhanced feeding in *My. Strigata*, whereas for *P. viridis* feeding decreased at salinities that were too low or too high. Additionally, Tan (1996) found that the growth of *P. viridis* larvae was greatest at 24 ppt. The results suggest that salinities of 20 and 35 psu did not affect the growth and condition of both mussel species and might still fall within their optimal range.

To understand whether the adult distribution of bivalves along a salinity gradient is determined by recruitment, density of recruits was monitored along such a gradient. Larvae of *M. sallei* and *My. strigata* recruited in the same salinity regimes where the adults live. In the life cycles of these bivalves, once gametes fertilize, an embryo develops and metamorphoses into a pediveliger before settling (Gosling, 2015). The larvae must survive before settling, and it is likely that salinity conditions optimal for both species are similar to where adults are found. According to the recruitment limitation hypothesis, the size of an adult population can largely be determined by the input of new individuals (Doherty and Fowler, 1994; Armsworth, 2002; Jenkins *et al*., 2009). Successful establishment of adults where salinity conditions are favorable for larvae to recruit is, therefore, possible.

For *M. sallei*, the optimal salinity for larvae was around 5–20 psu (Sa-nguansil and Wangkulangkul, 2020) which is similar to the salinity range of adults' habitat. Results from a salinity tolerance experiment revealed that juveniles of *M. sallei* can survive in a wide salinity range from 0 to 35 psu. Moreover, their nutritional states, suggested from the condition index, did not decline when exposed to marine conditions. Therefore, we suggest that the distribution of *M. sallei* along a salinity gradient in Songkhla Lake is determined by recruitment, and the impact of post-recruitment mortality due to unfavorable salinity conditions is trivial in regulating adults' distribution.

For *My. strigata*, although mean salinity where recruits were observed was in the mid-range, similar to where adults live, recruitment monitoring showed that recruits were found at all stations from upstream to downstream. Yuan *et al*. (2010) found that juvenile *My. strigata* (shell length <19 mm.) can tolerate salinities as high as 40 ppt, while adults survived best at lower maximum salinity levels (23 ppt) than juveniles. This suggests that *My. strigata* might be able to settle and recruit in a wide range of salinities but died at a later stage. Therefore, for *My. strigata*, distribution is not strongly limited by recruitment, but potentially determined by post-recruitment mortality due to unfavorable salinity.

For *P. viridis*, it is difficult to demonstrate the relationship between recruitment and adults because the recruitment rate was negligible. However, the low rate of recruitment helps explain why the number of *P. viridis* has become considerably lower in the lake system.

Both negative and neutral interactions between the bivalve species were reported. After *M. sallei* invasion in the Songkhla Lake system, farming of the green mussel *P. viridis* has completely collapsed, and one of the main possible causes was being outcompeted by *M. sallei* (Wangkulangkul *et al*., 2022). Sanpanich and Wells (2019) demonstrated that both *M. sallei* and *P. viridis* competed with *My. Strigata*, which was likely to be a superior competitor in the inner Gulf of Thailand. In Singapore, observations on suspended netting in fish farms revealed that the abundance of *P. viridis* decreased when the number of *My. strigata* increased (Lim *et al*., 2018). In contrast, Galimany *et al*. (2018) suggested that there was no competition between *My. strigata* and *P. viridis* because their optimal water characteristics differed. In the present study, although there were locations where *M. sallei* and *My. strigata* occurred together, there was no evidence of direct competition (one being smothered by the other). Moreover, locations where *M. sallei* and *My. strigata* (both recruits and adults) were most abundant were not in the same area. Therefore, whether they are in competition with each other remains unclear. For *P. viridis*, the number of the specimens was too low and there were no other bivalves observed in the same vicinity.

To properly manage the impact of invasive species, understanding what factors control their spread and establishment in an area is crucial (Sakai *et al*., 2001). *M. sallei* was recognized as a brackish species (Tan and Tay, 2018). Its distribution in Thailand was restricted to brackish water bodies (Klangnurak *et al*., 2022), and survival of larvae in saline and freshwater was low (Sa-nguansil and Wangkulangkul, 2020). The high recruitment and adult abundance in upstream areas of the Songkhla Lake system support the hypothesis in Klangnurak *et al*. (2022) that the occurrence of *M. sallei* in several locations along Thailand's coasts is a result of multiple introductions from outside sources, and connectivity between populations through planktonic larval dispersal is poor. If larvae of *M. sallei* were transported seawards, recruitment would increase in the same direction. For. *My. strigata*, high rate of recruitment was found in areas near the mouth of the lake where salinity was relatively higher. Therefore, *My. strigata* has a higher potential to migrate to other brackish waters via larval dispersal compared to *M. sallei*. However, the survival of its larvae in salinity levels of fully marine conditions needs to be tested.

CONCLUSIONS

The difference in optimum salinity for survival and reproduction of each species could lead to habitat partitioning between species along a salinity gradient. In our study, *Mytilopsis sallei* primarily occupied areas upstream with low salinity, *Mytella strigata* were in areas with mid-range salinity, while *Perna viridis* were abundant in fully marine conditions. Recruitment played an important role in determining *M. sallei* distribution but might have influenced the distribution of *My. strigata* to a lesser degree. All three species in this study are byssally-attached filter-feeding bivalves considered ecosystem engineers, which can impact benthic and pelagic community compositions and food web structures. The information gained from this study will serve as a baseline for further research to understand the functioning of the lake ecosystem. Information on the reproduction of alien invasive bivalves also shed some light on the mechanisms of their dispersal, which is useful for species management.

Future research should consider populations in other estuaries. Experiments on the salinity tolerance of *My. strigata* and *P. viridis* at different life-history stages will provide further understanding of how salinity influences the distribution of these species.

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