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Towards sustainable clam digging - estimating carrying capacity and assessing effects on clam populations and the macroinvertebrate community

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1. Introduction

Clam digging has a long history in Hong Kong. Traditionally, villagers collected clams from intertidal beaches during low tide using simple hand tools, primarily for household consumption or income generation. In recent decades, clam digging has become a popular recreational activity, particularly among families during holidays. However, increased participation on easily accessible beaches has resulted in intense harvesting pressure at some locations. Unregulated clam digging can deplete local clam populations and reduce biodiversity by disturbing benthic communities. Consequently, many countries have implemented sustainable management measures, including restrictions on the number and size of clams harvested, as well as the temporary closure of clamming grounds.

This study investigated the impacts of clam digging on clam populations and macrobenthic communities, and further assessed the genetic connectivity of individual clam species across different beaches on Lantau Island. Based on the findings, recommendations were developed to promote sustainable harvesting practices. The study comprised six parts. The first focused on comparing clam species diversity across six sites. Three sites—Shui Hau, Pui O and Tung Chung—were designated as treatment sites due to higher harvesting pressure, while the remaining three—Yi O, Tung Wan and Sha Lo Wan—served as control sites with minimal harvesting activity. In addition, stock assessments were conducted over two years to evaluate temporal variations in clam diversity.

The second part of the study evaluated visitor harvesting pressure through on-site surveys conducted at the same six beaches during both summer and winter. For each season, surveys were carried out on both weekdays and weekends to capture variability in visitor activity. During each survey, the number of clam diggers, the duration of harvesting activities, and the species and quantities of clams collected were recorded.

The third part of the study investigated the population dynamics of clam species targeted by harvesters at four sites over the course of one year, including two treatment sites (Shui Hau, Tung Chung) and two control sites (Yi O, Tung Wan). Key population parameters were examined, including recruitment period, size at maturity, number of cohorts, and the growth and mortality rates of individual cohorts. In addition, the theoretical life span of each species was estimated, and a length-converted catch curve analysis was performed.

The fourth part of the study consisted of a field manipulation experiment designed to determine the ecological impacts of clam digging on macrobenthic communities. The experiment was conducted at two treatment sites (Shui Hau and Tung Chung) and two control sites (Yi O and Tung Wan). Four experimental treatments were applied: Treatment A, an undisturbed control; Treatment B, in which sediment was dug but not removed from the experimental plot; Treatment C, in which sediment was dug and clams were removed while the sediment remained in place; and Treatment D, in which sediment was dug up, temporarily set aside, clams were removed, and the sediment was subsequently returned to the plot. Three replicates were established for each treatment.

The experiment lasted 12 weeks, during which simulated clam-digging activities were conducted weekly. Sediment and associated macrobenthic communities were sampled at

four-week intervals (Weeks 1, 5, 9, and 13). Multivariate analysis of species abundance were performed using non-metric multidimensional scaling (NMDS). Similarities in species composition among treatments, sites, and sampling periods were assessed, and changes in species richness and biodiversity indices were analyzed.

The fifth part of the study comprised a one-year caging experiment conducted at two treatment sites (Shui Hau and Tung Chung) and two control sites (Yi O and Tung Wan) to examine mortality and growth in shell length of clam species targeted by harvesters. Clams were maintained in cages, and mortality and shell-length growth were recorded at intervals of approximately one to one and a half months. During each sampling event, dead individuals were replaced with clams collected from the corresponding sites to maintain an approximately constant clam density within each cage. Three cages were used as replicates for each clam species at each site.

The sixth part of the study investigated the genetic connectivity of clam species on Lantau Island. Four high-quality chromosome-level genomes were generated for *Anomalocardia flexuosa* (= *Cryptonema producta*), *Meretrix petechialis*, *Meretrix meretrix*, and *Meretrix lamarckii*, and were published in two peer-reviewed journal papers (Law et al., 2025, 2026). Additionally, individuals of three *Meretrix* species (*M. petechialis*, *M. meretrix*, and *M. lamarckii*) were sampled from multiple locations across Lantau Island for population genetic analyses.

Naming issue of Anomalocardia flexuosa

In the present study of clam species in Shui Hau, *Anomalocardia flexuosa* was identified as the most dominant species, consistent with previous studies. The species name has been used consistently since at least the 1980s and is recorded in two authoritative references: The Seashore Ecology of Hong Kong by Prof. Brian Morton (Hong Kong University Press, 1983) and Coloured Illustrations of Aquatic Molluscs in China, edited by Wang RC (Zhejiang Publishing House of Science and Technology 1988). In recent years, the name *A. flexuosa* has also been adopted in peer-reviewed journal publications, including So et al. (2021) and Lam et al. (2023). Consistent with this usage, the genomic resource generated from the present study was published under the name *A. flexuosa* (Law et al., 2025).

Recently, questions have been raised within local communities regarding the taxonomic identity of *A. flexuosa*, particularly whether it should instead be referred to as *Cryptonema producta*. This query arises from information in the World Register of Marine Species (WoRMS), where both *A. flexuosa* and *C. producta* are currently regarded as valid species. Based on diagnostic photographs available on the WoRMS website and Chinese molluscan references (Qi, 2004; Zhang, 2008; Xu and Zhang, 2008), the specimens we collected appear to be more closely aligned morphologically with *C. producta*.

Nevertheless, preliminary analyses using molecular markers generated from our specimens, together with comparisons against sequences available in public databases, suggest that *A. flexuosa* and *C. producta* likely represent the same species and are distinct

from other *Anomalocardia* species. Further systematic investigations combining molecular and morphological data, and incorporating samples from multiple geographic locations, will be necessary to clarify the current taxonomic status of these taxa.

2. Study 1: Stock assessment for clams on Lantau Island

2.1 Methodology

The stock assessment was conducted at six beaches. Three of these—Pui O, Shui Hau, and Tung Chung—were designated as clam-digging sites due to their popularity among visitors for recreational activities, including clam collection. The remaining three sites—Tung Wan, Yi O, and Sha Lo Wan—are relatively remote, receive very few visitors, and therefore served as control sites.

At each beach, three or four transect lines were established from the backshore to the waterfront, with the number determined by beach size. Four transects were set at Shui Hau and Pui O, whereas three transects were used at the other sites. Along each transect, quadrats measuring 0.5 m × 0.5 m were placed adjacent to the transect line at elevations of 0.5, 0.7, 0.9, 1.1, and 1.3 m above Chart Datum (CD). This resulted in 12 quadrat samples per tidal height at sites with four transects and nine samples per tidal height at sites with three transects.

Within each quadrat, the top 15 cm of sand was excavated and sieved through a 2-mm mesh. All clams were collected, identified, and measured for shell length. A sediment sample was also taken from each quadrat using a corer (5-cm diameter, 15-cm length). The three samples from each tidal elevation along a transect were combined to form a composite sample. Sediment analyses included determination of median particle size, organic content, and calcium carbonate content.

Stock assessments were conducted in 2022 and 2024 to evaluate temporal variation. At Tung Chung, the sampling locations differed between the two years. The 2022 site represented a typical sandy beach in the area; however, subsequent observations revealed that clam-digging activity was concentrated at a site characterized by a mixture of sand, oysters, and pebbles. As a result, the sampling site was relocated in 2024. Consequently, data from Tung Chung in 2022 and 2024 are not directly comparable.

2.2 Results and Discussion

2.2.1 *Characteristics of the site and sediment characteristics*

The mean calcium carbonate content and total organic content differed significantly among sites in both surveys (Table 1). Shui Hau consistently recorded the highest calcium carbonate content, whereas Sha Lo Wan showed the lowest in both years. In contrast, no consistent inter-site pattern was observed for total organic content.

The median particle diameter (expressed in phi units) (Fig. 1) differed significantly among sites in both surveys, and all sites were statistically distinct from one another (2022: $F = 244.7$, $df = 5, 24$, $p < 0.001$; 2024: $F = 623.8$, $df = 5, 23$, $p < 0.001$). Sha Lo Wan had the largest median particle diameter, whereas Yi O had the smallest.

Table 1. Mean calcium carbonate content (%) and total organic content (%) ($\pm$ SD) at each site in both surveys. Sites sharing the same superscript letter are statistically indistinguishable.

Site	CaCO ₃ Content (%)				Total Organic Content (%)			
	2022		2024		2022		2024	
Pui O	13.57	(1.34)	14.05	(2.15)	2.21	(0.23)	1.97	(0.30)
Sha Lo Wan	1.96	(1.84)	2.42	(0.89)	1.36	(0.73)	1.02	(0.57)
Shui Hau	16.62	(3.24)	19.81	(2.11)	2.20	(0.33)	2.27	(0.56)
Tung Chung	2.81	(1.03)	20.07	(8.08)	1.35	(0.25)	3.08	(0.72)
Tung Wan	7.90	(1.57)	8.33	(1.09)	1.15	(0.15)	0.89	(0.24)
Yi O	6.65	(0.47)	5.67	(0.53)	1.85	(0.18)	0.71	(0.10)
CaCO ₃ Content (%)	SH ^a , PO ^a , TW ^{a,b} , YO ^{a,b} , TC ^b , SLW ^b (2022) SH ^a , TC ^a , PO ^{a,b} , TW ^{a,b} , YO ^b , SLW ^b (2024)							
Total Organic Content (%)	PO ^a , SH ^a , YO ^{a,b} , TC ^{a,b} , SLW ^{a,b} , TW ^b (2022) TC ^a , SH ^b , PO ^b , SLW ^c , TW ^{c,d} , YO ^d (2024)							

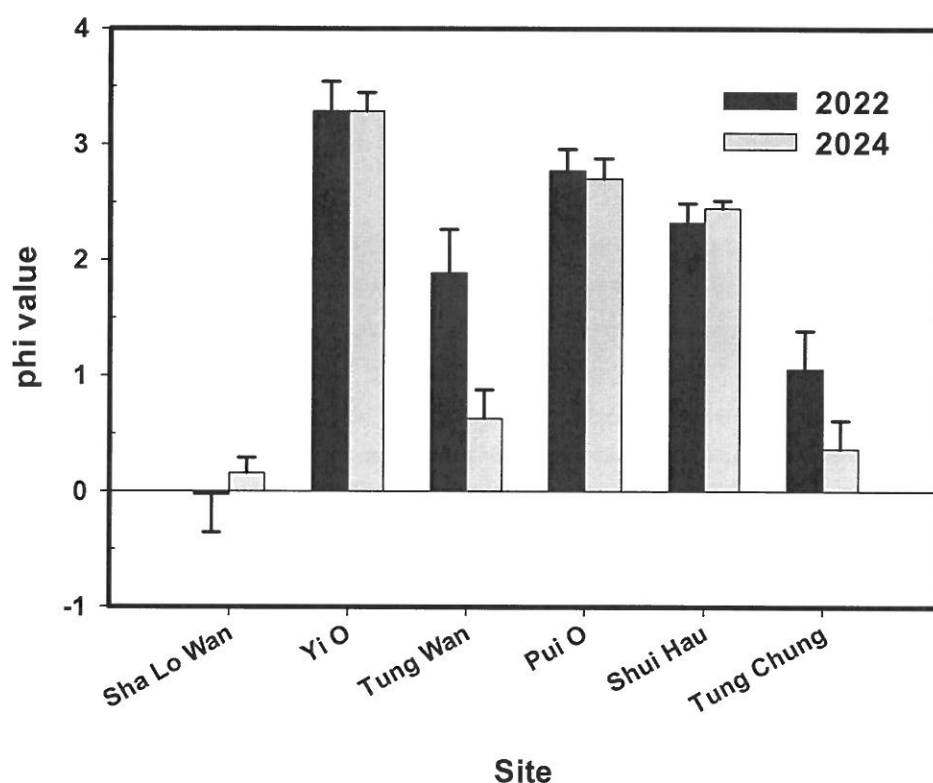


Fig. 1. Comparison of median particle diameter (phi units) among the six sampling sites in 2022 and 2024.

2.2.2 Clam species diversity

A total of 41 clam species were recorded across the two summer surveys. In 2022, 38 species were collected, whereas 25 species were recorded in 2024 (Table 2). The total number of individuals collected was 1153 in 2022 and 1412 in 2024.

Table 2: Total number of species recorded at the six sampling sites (Pui O, Sha Lo Wan, Shui Hau, Tung Chung, Tung Wan, Yi O) in 2022 and 2024. Filled cells indicate that the species was not recorded in that survey.

Species No.	Species List	2022 Survey	2024 Survey
1	<i>Anomalocardia flexuosa</i>		
2	<i>Anomalodiscus squamosus</i>		
3	<i>Arcuatula senhousia</i>		
4	<i>Atactodea striata</i>		
5	<i>Borniopsis sagamiensis</i>		
6	<i>Cyclina sinensis</i>		
7	<i>Dosinia japonica</i>		
8	<i>Exolaternula spengleri</i>		
9	<i>Gafrarium tumidum</i>		
10	<i>Geloina expansa</i>		
11	<i>Gonimyrtea sp.</i>		
12	<i>Hiatula acuta</i>		
13	<i>Hiatula diphos</i>		
14	<i>Hiatula sp.</i>		
15	<i>Jactellina clathrata</i>		
16	<i>Jitlada culter</i>		
17	<i>Jitlada philippinarum</i>		
18	<i>Joannisiella cumingii</i>		
19	<i>Kellia porculus</i>		
20	<i>Latona cuneata</i>		
21	<i>Latona faba</i>		
22	<i>Latona semisulcata semigranosa</i>		
23	<i>Macridiscus aequilatera</i>		
24	<i>Mactra dissimilis</i>		
25	<i>Marcia hiantina</i>		
26	<i>Meretrix lamarckii</i>		
27	<i>Meretrix lyrata</i>		
28	<i>Meretrix meretrix</i>		
29	<i>Meretrix petechialis</i>		
30	<i>Nitidotellina soyoae</i>		
31	<i>Ruditapes philippinarum</i>		
32	<i>Rugalucina vietnamica</i>		
33	<i>Solen grandis</i>		

34	<i>Solen strictus</i>		
35	<i>Strigilla tomlini</i>		
36	<i>Tapes conspersus</i>		
37	<i>Tapes literatus</i>		
38	<i>Tapes sp.</i>		
39	<i>Tellinella cruciata</i>		
40	<i>Tellinides timorensis</i>		
41	<i>Unknown 1</i>		
Total Number of Species		38	25

The number of clam species collected at each site is shown in Table 3. For most sites, similar numbers of species were collected in the two surveys. However, notable declines were observed at two locations: species richness at Shui Hau decreased by more than half (from 23 species in 2022 to 10 in 2024), and at Yi O, it decreased by 25% (from 12 to 9 species).

In 2022, the number of species was positively correlated with site area, whereas no such relationship was observed in 2024 (Fig. 2). With the exception of Shui Hau in 2022, clam digging sites tended to have lower species richness than expected based on the species-area relationship, as they fell below the regression line. In contrast, all control sites fell above the line, indicating relatively higher species richness.

The numbers of individuals, densities and average sizes of each clam species collected in 2022 and 2024 are shown in Appendices 1-2.

Table 3. Number of clam species recorded at each site in both surveys.

Site	2022 Survey	2024 Survey
	No. of species	No. of species
Shui Hau	23	10
Sha Lo Wan	12	13
Yi O	12	9
Pui O	7	7
Tung Wan	6	7
Tung Chung	4	4

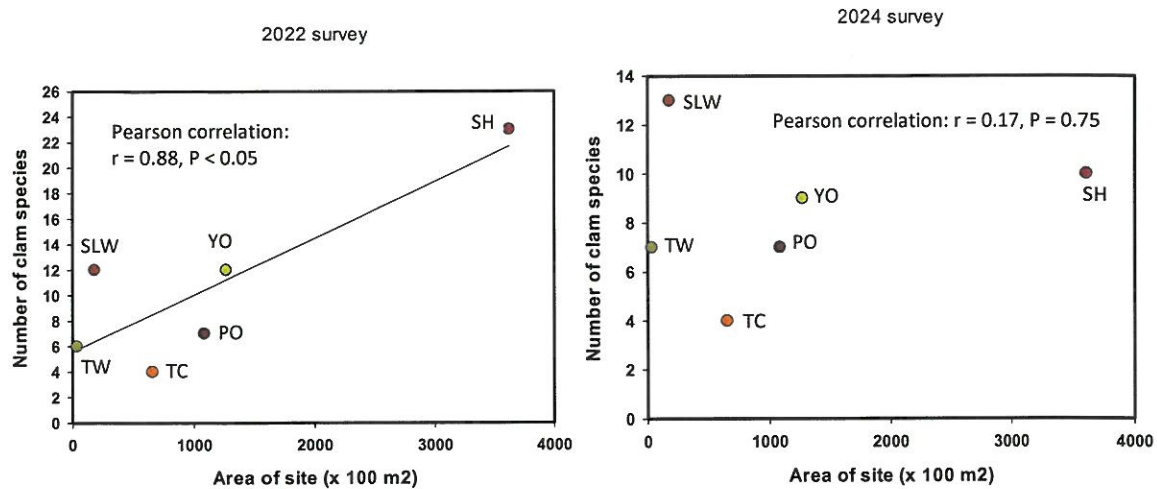


Fig. 2. Regression relationship between the number of clam species and site area in 2022 and 2024. (PO: Pui O, SH: Shui Hau, SLW: Sha Lo Wan, TC: Tung Chung, TW: Tung Wan, YO: Yi O)

The three most dominant species at each site are listed in Table 4. The proportion of the most dominant species ranged from 28.9% to 86.7%. The same dominant species occurred in both years at Sha Lo Wan, Shui Hau and Yi O. Species highlighted in yellow represent the target clam species at each site. At the clam digging sites, the target clam species was the most abundant species at Pui O in 2022 and at Tung Chung in 2024. However, at Pui O, its relative abundance declined markedly from 55% in 2022 to 26% in 2024. At Shui Hau, the target clam species consistently comprised approximately 80% of the total clam population.

Among the control sites, the target clam species was the most abundant only at Tung Wan, not at Yi O or Sha Lo Wan. These patterns indicate that clam digging does not necessarily reduce target species densities to the point where they become minor components of the assemblage, as seen at Pui O and Tung Chung. Similarly, the target species are not always dominant at sites without digging pressure. This suggests that, beyond harvesting impacts, intrinsic site characteristics also play a major role in shaping species composition. Nonetheless, the substantial reduction of the target species at Pui O in 2024 warrants attention.

Table 4. The three most dominant species and their percentage abundances at each site. *Note: The survey sites in Tung Chung in 2022 and 2024 differed. Species highlighted in yellow are species targeted by clam diggers.*

Site	2022		2024	
	Species	%	Species	%
Pui O	<i>Meretrix lamarckii</i>	35.6	<i>Solen strictus</i>	57.6
	<i>Latona semisulcata semigranosa</i>	25.3	<i>Meretrix lamarckii</i>	15.0
	<i>Meretrix petechialis</i>	19.9	<i>Meretrix meretrix</i>	11.0
Sha Lo Wan	<i>Joannisiella cumingii</i>	28.9	<i>Joannisiella cumingii</i>	35.4
	<i>Tapes sp.</i>	16.7	<i>Anomalodiscus squamosus</i>	13.8
	<i>Ruditapes philippinarum</i>	11.1	<i>Geloina expansa</i>	12.3

Shui Hau	<i>Anomalocardia flexuosa</i>	78.5	<i>Anomalocardia flexuosa</i>	81.9
	<i>Jitlada philippinarum</i>	4.2	<i>Anomalodiscus squamosus</i>	6.1
	<i>Anomalodiscus squamosus</i>	3.1	<i>Meretrix petechialis</i>	4.6
Tung Chung	<i>Joannisiella cumingii</i>	42.9	<i>Ruditapes philippinarum</i>	86.7
	<i>Cyclina sinensis</i>	28.6	<i>Tapes literatus</i>	8.0
	<i>Meretrix meretrix</i>	28.6	<i>Anomalodiscus squamosus</i>	2.7
			<i>Joannisiella cumingii</i>	2.7
Tung Wan	<i>Macridiscus aequilatera</i>	72.2	<i>Ruditapes philippinarum</i>	46.2
	<i>Meretrix lamarckii</i>	8.3	<i>Arcuatula senhousia</i>	19.2
	<i>Meretrix meretrix</i>	8.3	<i>Nitidotellina soyoae</i>	15.4
	<i>Meretrix petechialis</i>	5.6		
Yi O	<i>Jitlada philippinarum</i>	60.5	<i>Jitlada philippinarum</i>	83.6
	<i>Gonimyrtea sp.</i>	19.6	<i>Gonimyrtea sp.</i>	8.0
	<i>Jitlada culter</i>	9.7	<i>Meretrix petechialis</i>	3.7



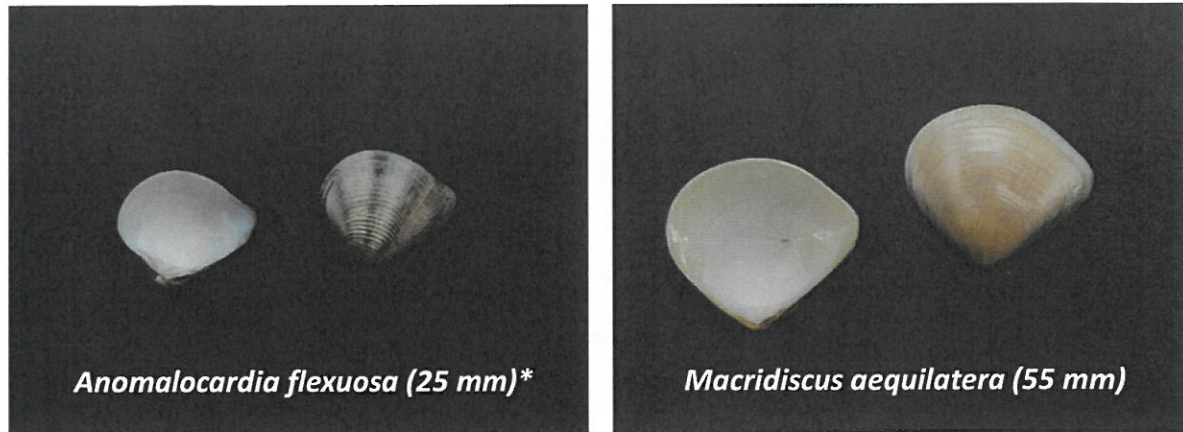


Fig. 3. The photos above show the clam species targeted by clam diggers.

The six sites were grouped into clam digging and control categories. Neither the Shannon-Weiner diversity index (H') nor Pielou's evenness index (J) differed significantly between the two site types in either survey year (H' : 2022: $t = -0.907$, $df = 3,3$, $p = 0.416$; 2024: $t = -0.77$, $df = 3,3$, $p = 0.483$) (J : 2022: $t = -1.241$, $df = 3,3$, $p = 0.283$; 2024: $t = -0.783$, $df = 3,3$, $p = 0.478$). Nonetheless, both H' and J were consistently higher at the control sites in both years (Fig. 4).

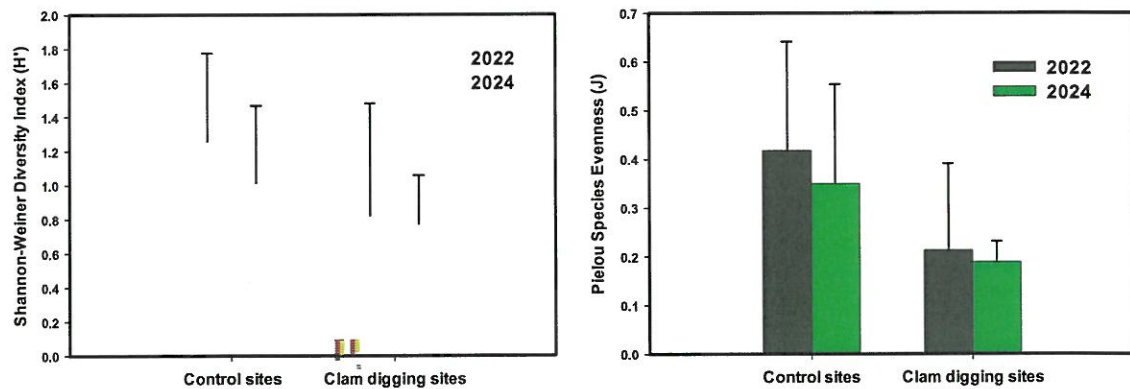


Fig. 4. (a) Shannon-Weiner diversity index and (b) Pielou's species evenness for control sites and clam digging sites in 2022 and 2024.

Shannon-Weiner diversity (H') and Pielou's evenness (J) values for each site are presented in Table 5. In 2022, Sha Lo Wan had the highest species diversity, which was significantly greater than that of all other sites except Pui O ($F = 19.49$, $df = 5,14$, $p < 0.001$) (Fig. 5a). Tung Chung exhibited significantly lower species diversity than all remaining sites. In 2024, species diversity did not differ significantly among sites ($F = 2.51$, $df = 5,14$, $p = 0.08$) (Fig. 5a), although Sha Lo Wan still recorded the highest species diversity and Tung Chung the lowest.

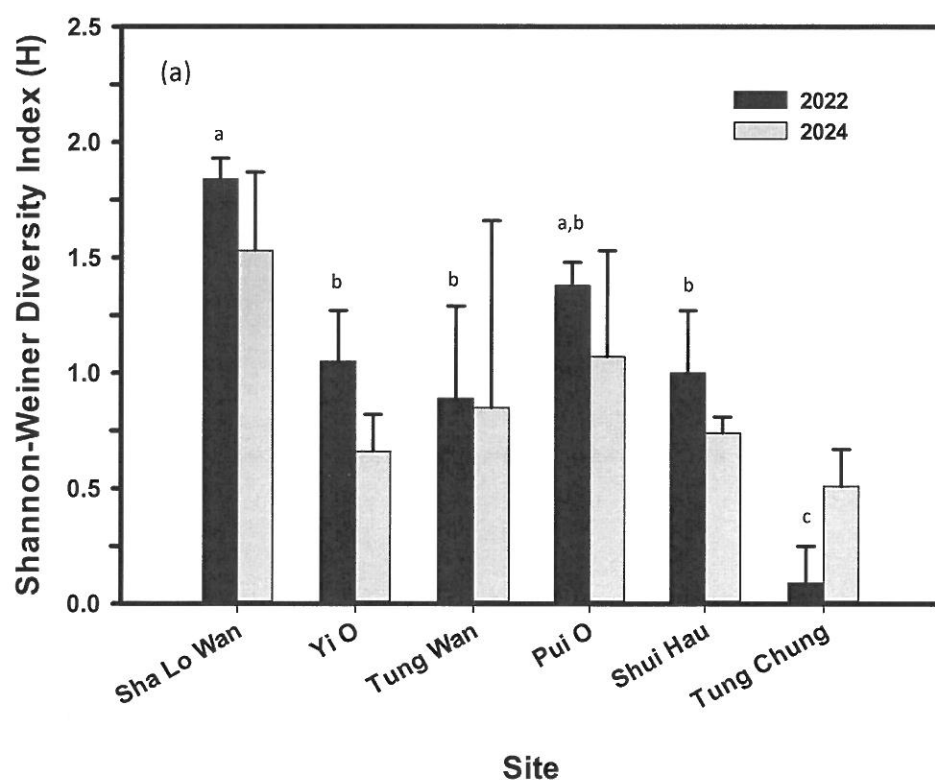
Patterns in species evenness mirrored those of species diversity (Fig. 5b). In 2022, Sha Lo Wan again had the highest evenness, significantly exceeding all other sites ($F = 16.92$, $df = 5,14$, $p < 0.001$). Evenness also varied significantly among sites in 2024 ($F = 3.40$, $df = 5,14$, $p < 0.05$), but pairwise differences were not detected using the Holm-Sidak method. Nevertheless,

Sha Lo Wan maintained the highest evenness in 2024, followed by Tung Wan, and both are non-clam digging sites.

H' and J were compared between the two surveys for each site. All comparisons were statistically non-significant ($p > 0.05$) (Table 6), except at Pui O, where species evenness was significantly lower in 2024.

Table 5. Shannon-Weiner diversity index (H') ($\pm$ SD) and species evenness (J) ($\pm$ SD) for each site in 2022 and 2024.

Site	2022		2024	
	H'	J	H'	J
Pui O	1.38 (0.10)	0.39 (0.05)	1.07 (0.46)	0.24 (0.10)
Sha Lo Wan	1.84 (0.09)	0.66 (0.07)	1.53 (0.34)	0.53 (0.16)
Shui Hau	1.00 (0.27)	0.21 (0.05)	0.74 (0.07)	0.16 (0.02)
Tung Chung	0.09 (0.16)	0.04 (0.06)	0.51 (0.16)	0.17 (0.07)
Tung Wan	0.89 (0.40)	0.38 (0.20)	0.85 (0.81)	0.39 (0.33)
Yi O	1.05 (0.22)	0.21 (0.04)	0.66 (0.16)	0.13 (0.04)



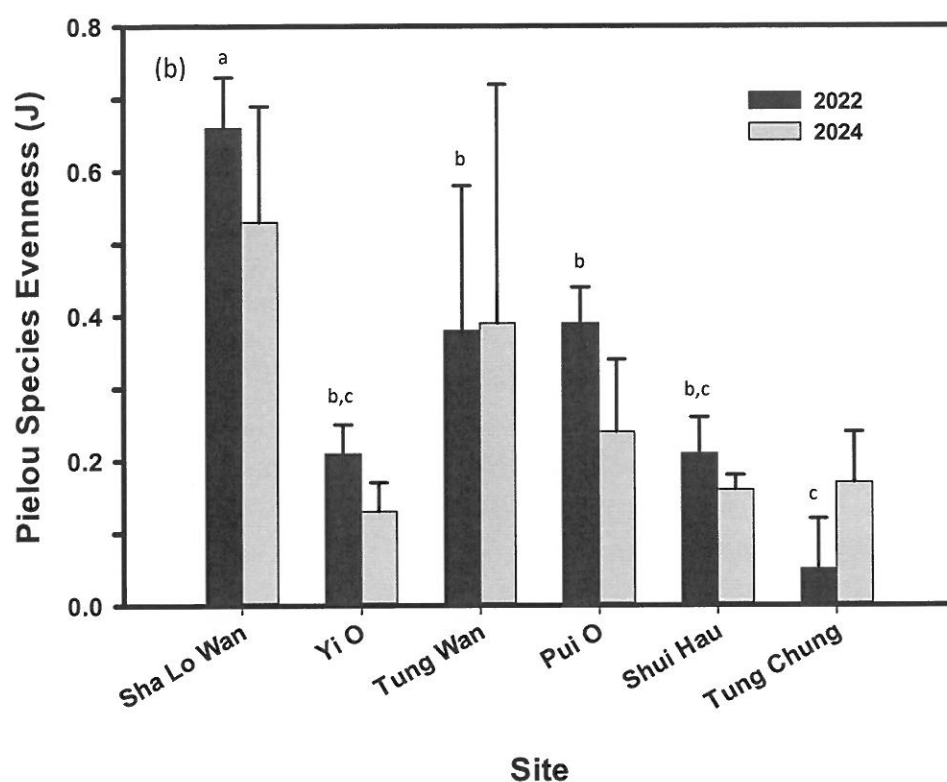


Fig. 5. (a) Shannon-Weiner diversity index and (b) Pielou's species evenness for individual sites in 2022 and 2024. Different letters indicate significant differences among sites within the same survey year.

Table 6. Species diversity (H') and species evenness (J) were compared between the two survey years (2022 and 2024) for each site. Tung Chung was excluded from the comparison because the study locations differed between the two surveys. *Probability level is < 0.05 , indicating that the comparison is statistically significant.

	Site	t-value	DF	Prob level
H'	Pui O	1.291	6	0.244
	Sha Lo Wan	1.574	4	0.191
	Shui Hau	1.860	6	0.112
	Tung Wan	0.064	4	0.952
	Yi O	2.448	4	0.071
J	Pui O	2.889	6	0.028*
	Sha Lo Wan	1.193	4	0.299
	Shui Hau	1.578	6	0.166
	Tung Wan	-0.015	4	0.989
	Yi O	2.621	4	0.059

2.2.3 *Comparisons of species composition among sites and their relationships with sediment characteristics*

Species composition and the abundance of individual clam species were analyzed using NMDS (Fig. 6). The NMDS ordination based on Bray-Curtis distances showed a moderate representation of community dissimilarities (stress = 0.174). At most sites, points representing the two survey years clustered more closely with each other than those from other sites, indicating that species composition was largely site-specific. However, this pattern was not evident at Tung Wan and Tung Chung.

Tung Wan is a highly exposed sandy beach where the shore profile undergoes substantial changes following extreme weather events such as rainstorms and typhoons, likely obscuring temporal similarity. At Tung Chung, the two surveys sampled different habitats: the 2022 site was a sandy beach, whereas the 2024 site consisted of sand interspersed with high densities of oysters and pebbles. These site differences likely account for the distinct species compositions observed between survey years.

Among the measured environmental variables, only sediment grain size was significantly correlated with community composition ($P < 0.05$), suggesting that it was the dominant environmental factor structuring community patterns across sites and years. In contrast, CaCO_3 content ($P = 0.893$), total organic carbon ($P = 0.651$), and beach slope ($P = 0.349$) were not significantly associated with the ordination, indicating that these variables did not exert detectable influences on species composition.

No clustering of clam digging sites relative to their corresponding control sites was observed, suggesting that clam digging did not measurably affect the species composition of clams.

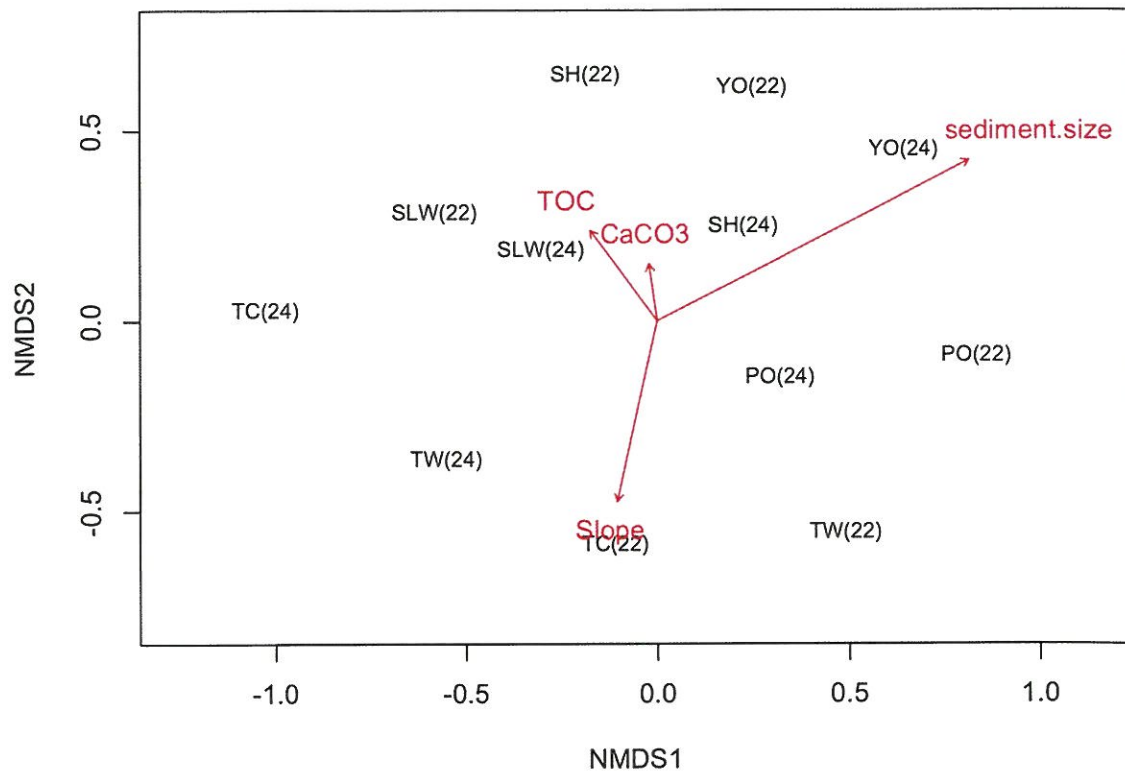


Fig. 6. NMDS ordination of species composition from stock assessments conducted at six sites (Pui O, Sha Lo Wan, Shui Hau, Tung Chung, Tung Wan, Yi O) in 2022 and 2024.

2.2.4 Mean density of target clam species

When all *Meretrix* species were pooled, clam density varied significantly among sites in 2022 ($F = 7.63$, $df = 5, 14$, $p < 0.001$; Fig. 7). Pui O had significantly higher densities than Tung Chung ($t = 5.51$, $p < 0.001$), Sha Lo Wan ($t = 4.32$, $p < 0.05$), and Tung Wan ($t = 4.22$, $p < 0.05$). However, densities at Pui O did not differ significantly from those at Shui Hau ($t = 3.33$, $p = 0.06$) or Yi O ($t = 2.44$, $p = 0.25$). No significant differences were detected among the remaining sites.

A similar pattern was observed in 2024 (Fig. 7). Clam density again differed significantly among sites ($F = 7.20$, $df = 4, 12$, $p < 0.005$), with Pui O showing significantly higher densities than Tung Wan ($t = 5.15$, $p < 0.005$), Sha Lo Wan ($t = 3.42$, $p < 0.05$) and Shui Hau ($t = 3.35$, $p < 0.05$). Density at Pui O did not significantly differ from Yi O ($t = 2.91$, $p = 0.09$). As in 2022, differences among the other sites were statistically insignificant.

Meretrix spp.

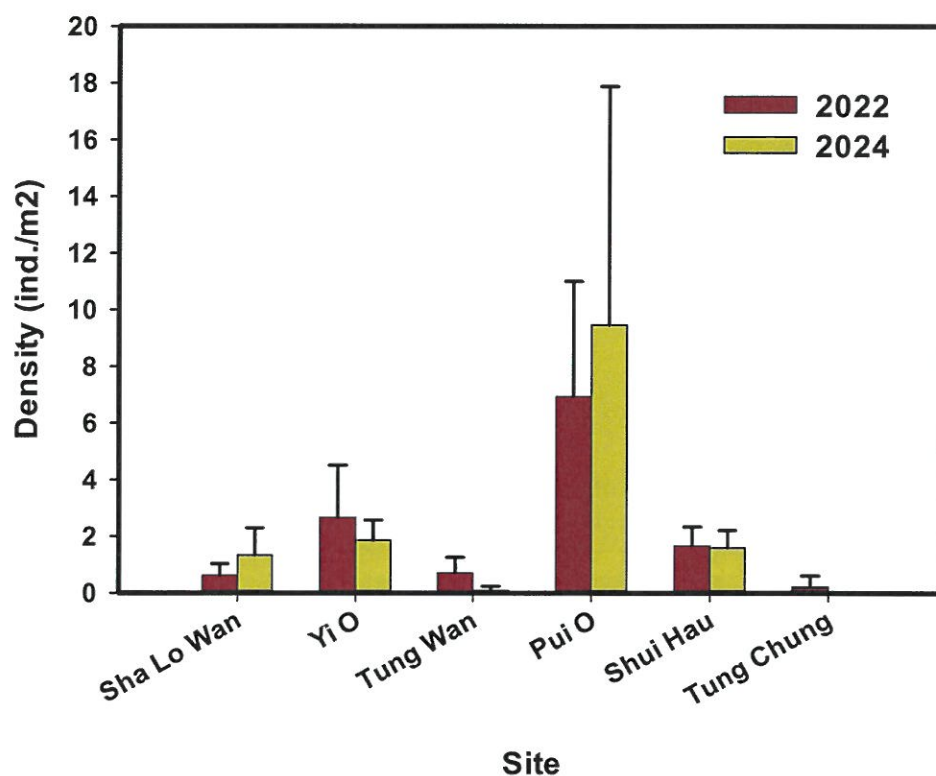


Fig. 7. Population density of all *Meretrix* species recorded at each site in 2022 and 2024.

For *Meretrix petechialis*, population density ranged from 0.18 ind. m⁻² at Sha Lo Wan and Tung Wan to 2.58 ind. m⁻² at Yi O in 2022, and from 0.44 ind. m⁻² at Sha Lo Wan to 2.53 ind. m⁻² at Yi O in 2024 (Fig. 8a). There were no significant differences in density between the two survey years at any site (t-test, $p > 0.05$). Inter-site differences in density were not statistically significant in 2024 ($F = 1.877$, $df = 3,16$, $p = 0.174$). However, in 2022, Yi O had a significantly higher density than Sha Lo Wan, Tung Wan and Shui Hau ($F = 5.706$, $df = 4, 20$, $p < 0.005$).

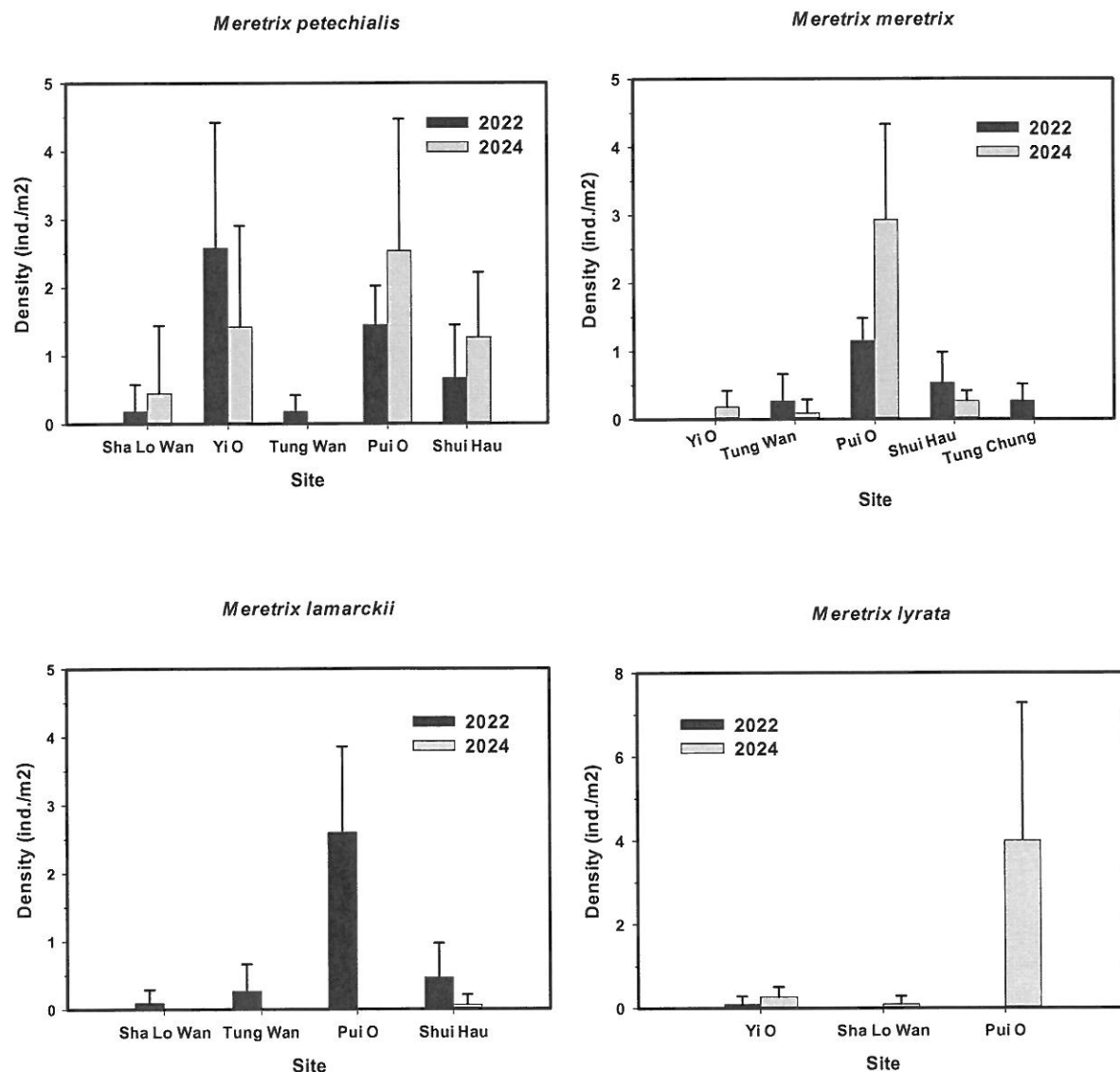
For *Meretrix meretrix*, population density varied significantly among sites in both survey years (2022: $F = 6.55$, $df = 3,16$, $p < 0.005$; 2024: $F = 18.24$, $df = 3,16$, $p < 0.001$) (Fig. 8b). In 2022, Pui O had the highest density (1.15 ind. m⁻²), which was significantly greater than densities at Tung Wan and Tung Chung. Pui O also had the highest density in 2024 (2.93 ind. m⁻²), with values significantly higher than those at Tung Wan, Yi O and Shui Hau. Between-year comparisons showed no significant differences in density at Shui Hau ($t = 1.27$, $n = 6$, $P = 0.242$) or Tung Wan ($t = 0.89$, $n = 6$, $P = 0.397$). In contrast, density at Pui O was significantly higher in 2024 than in 2022 ($t = -2.77$, $n = 6$, $p < 0.05$).

For *Meretrix lamarckii*, population density ranged from 0.09 ind. m⁻² at Sha Lo Wan to 1.15 ind. m⁻² at Pui O in 2022 (Fig. 8c). The density at Pui O was significantly higher than at all other sites (Sha Lo Wan, Tung Wan, Shui Hau) ($F = 13.53$, $df = 3,16$, $p < 0.001$). In 2024, *M. lamarckii*

was recorded only at Shui Hau, with a mean density of 0.07 ind. m⁻², and there was no significant difference in density between the two survey years ($t = 1.70$, $n = 5$, $p = 0.128$).

For *Meretrix lyrata*, population density in 2024 ranged from 0.09 ind m⁻² at Sha Lo Wan to 4.0 ind. m⁻² at Pui O (Fig. 8d). The density at Pui O was significantly higher than that at Sha Lo Wan and Yi O ($F = 6.73$, $df = 2,12$, $p < 0.05$). In 2022, *M. lyrata* was recorded only at Yi O, with a mean density of 0.09 ind. m⁻², which did not differ significantly from the 2024 value ($t = -1.27$, $n = 5$, $p = 0.242$).

In 2022, *Ruditapes philippinarum* was recorded at Shui Hau and Sha Lo Wan, with mean densities of 0.20 and 0.53 ind. m⁻², respectively (Fig. 8e). The difference between the two sites was not statistically significant ($t = -1.56$, $n = 5$, $p = 0.156$). In 2024, mean density ranged from 0.36 ind. m⁻² at Sha Lo Wan to 7.22 ind. m⁻² at Tung Chung. Density varied significantly among sites ($F = 5.91$, $df = 2,11$, $p < 0.05$), with Tung Chung showing significantly higher densities than Sha Lo Wan ($t = 3.18$, $p < 0.05$) and Tung Wan ($t = 2.85$, $p < 0.05$). The difference between Tung Wan and Sha Lo Wan was not significant ($t = 0.35$, $p = 0.73$).



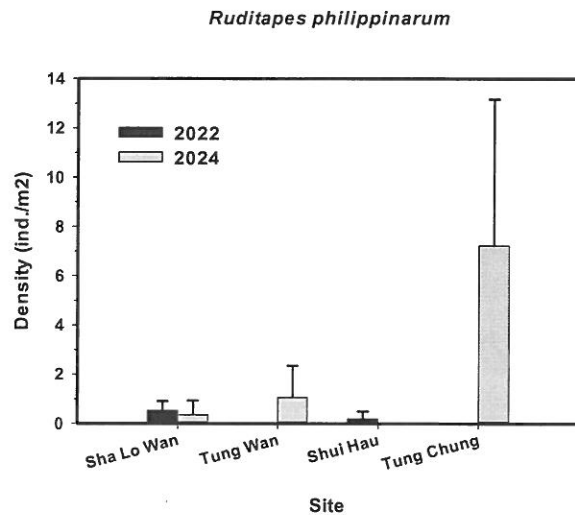


Fig. 8. Population density of (a) *M. petechialis*, (b) *M. meretrix*, (c) *M. lamarckii*, (d) *M. lyrata*, and (e) *R. philippinarum* recorded at each site in 2022 and 2024.

2.2.5 Mean size of target clam species

In 2022, the mean shell length of *Meretrix petechialis* varied significantly among sites ($F = 15.71$, $df = 4,74$), $p < 0.001$) (Fig. 9a). Individuals from Pui O were significantly smaller than those from all other sites (Shui Hau: $t = 6.57$, $p < 0.001$; Yi O: $t = 0.49$, $p < 0.001$; Sha Lo Wan: $t = 0.70$, $p < 0.05$; Tung Wan: $t = 3.00$, $p < 0.05$). No significant differences were detected among the remaining sites. The mean shell length of *Meretrix meretrix* also differed significantly among sites ($F = 6.14$, $df = 3,36$, $P < 0.005$) (Fig. 9b), with individuals from Pui O being significantly smaller than those from Tung Chung ($t = 3.57$, $p < 0.01$) and Shui Hau ($t = 18.34$, $p < 0.05$). The mean shell length of *Meretrix lamarckii* varied significantly among sites ($F = 31.58$, $df = 2,62$, $p < 0.001$) (Fig. 9c). Individuals from Tung Wan were significantly larger than those from Shui Hau ($t = 0.54$, $p < 0.001$) and Pui O ($t = 0.88$, $p < 0.001$), and individuals from Shui Hau were also significantly larger than those from Pui O ($t = 4.53$, $p < 0.001$). Comparisons of shell length for *M. lyrata* and *R. philippinarum* among sites were not conducted due to their absence or low abundance at some sites.

In 2024, the shell length of *M. petechialis* varied significantly among sites ($H = 31.20$, $df = 3$, $p < 0.001$) (Fig. 9a). Individuals from Pui O were significantly smaller than those from all other sites (Shui Hau: $Q = 5.14$, $p < 0.05$; Sha Lo Wan: $Q = 2.90$, $p < 0.05$; Yi O: $Q = 3.97$, $p < 0.05$). The shell length of *M. meretrix* varied significantly among sites ($H = 10.66$, $df = 2$, $p = 0.005$) (Fig. 9b). Individuals from Shui Hau were significantly larger than those from Pui O ($Q = 2.96$, $p < 0.05$). However, no significant differences were detected between Shui Hau and Yi O ($Q = 0.55$, $p > 0.05$), or between Yi O and Pui O ($Q = 1.49$, $p > 0.05$). These results should be interpreted with caution due to the small numbers of *M. meretrix* collected from Shui Hau (4 individuals) and Yi O (2 individuals), compared with 44 individuals from Pui O. For *M. lyrata*, shell length did not differ significantly between Pui O and Yi O (M-W U = 53, $p = 0.28$) (Fig. 9d). For *R. philippinarum*, no significant differences in shell length were detected among sites ($H = 1.44$, $P = 0.49$) (Fig. 9e).

The size ranges of the targeted clam species collected from each site in 2022 and 2024 are presented in Table 7. The largest specimens recorded in 2022 were as follows:

M. petechialis: 82 mm (Yi O), 76 mm (Pui O), 75 mm (Shui Hau), 74 mm (Sha Lo Wan), 63 mm (Tung Wan).

M. meretrix: 83 mm (Tung Chung), 63 mm (Shui Hau), 53 mm (Pui O), 45 mm (Tung Wan).

M. lamarckii: 80 mm (Tung Wan), 70 mm (Shui Hau), 56 mm (Pui O), 34 mm (Sha Lo Wan).

M. lyrata: one individual collected at Yi O with a shell length of 65 mm.

R. philippinarum: 18 mm (Shui Hau) and 42 mm (Sha Lo Wan).

The largest specimens recorded in 2024 were as follows:

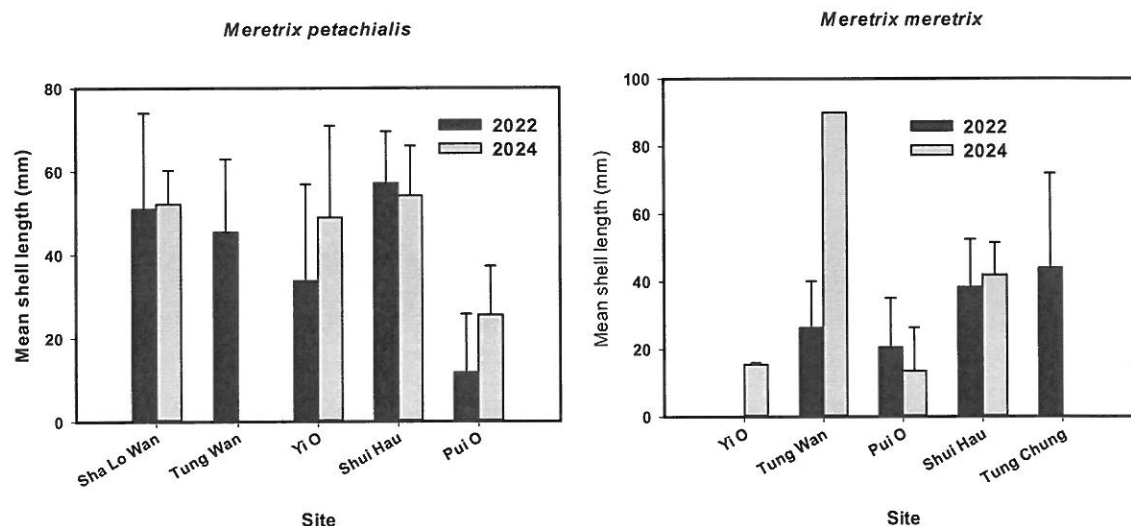
M. petechialis: 78 mm (Shui Hau), 71 mm (Yi O), 64 mm (Sha Lo Wan), 49 mm (Pui O).

M. meretrix: 70 mm (Pui O), 53 mm (Shui Hau), 16 mm (Yi O).

M. lamarckii: one specimen from Shui Hau (52 mm).

M. lyrata: 74 mm (Yi O), 70 mm (Pui O), 19 mm (Sha Lo Wan).

R. philippinarum: 37 mm (Tung Chung), 30 m (Tung Wan), 23 mm (Sha Lo Wan).



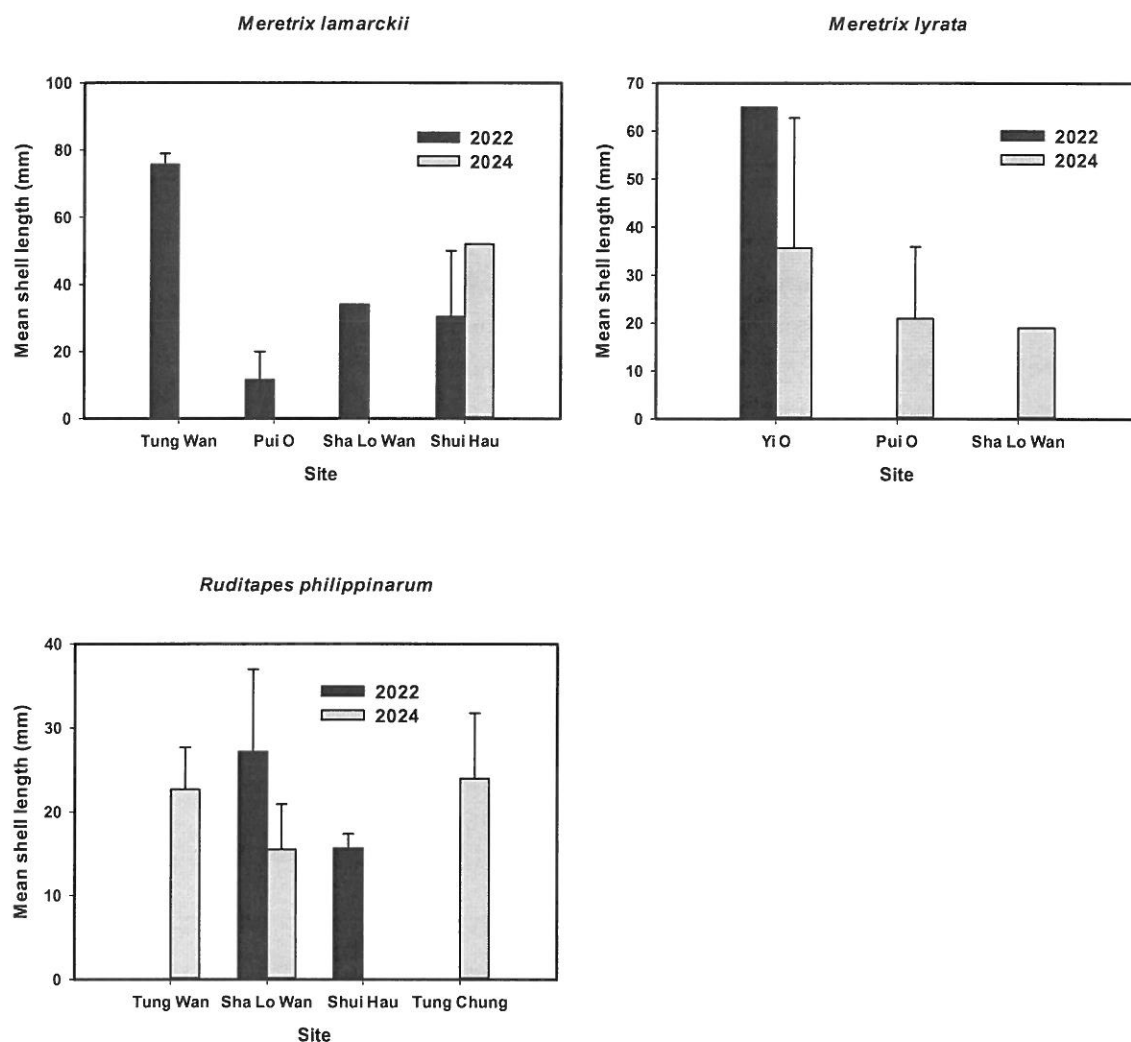


Fig. 9. Comparisons of mean shell length (mm) ($\pm$ SD) of (a) *M. petechialis*, (b) *M. meretrix*, (c) *M. lamarckii*, (d) *M. lyrata*, and (e) *R. philippinarum* collected from each site in 2022 and 2024.

Table 7. Size ranges of targeted clam species collected from each site in 2022 and 2024. Numbers in parentheses indicate the number of specimens collected.

Species	Site	Shell length (mm)	
		2022	2024
<i>M. lamarckii</i>	Shui Hau	5 – 70 (10)	52 (1)
	Sha Lo Wan	34 (1)	
	Pui O	6 – 56 (52)	
	Tung Wan	72 – 80 (3)	
<i>M. lyrata</i>	Pui O		5 – 70 (60)
	Sha Lo Wan		19 (1)
	Yi O	65 (1)	16 – 74 (3)
<i>M. meretrix</i>	Pui O	6 – 53 (23)	6 – 70 (44)
	Shui Hau	15 – 63 (11)	29 – 53 (4)
	Tung Chung	16 – 83 (3)	
	Tung Wan	12 – 45 (3)	

	Yi O		15 – 16 (2)
<i>M. petechialis</i>	Pui O	5 – 76 (29)	9 – 49 (38)
	Shui Hau	9 – 75 (15)	35 – 78 (19)
	Sha Lo Wan	28 – 74 (2)	45 – 64 (5)
	Tung Wan	28 – 63 (2)	
	Yi O	5 – 82 (31)	10 – 71 (16)
<i>R. philippinarum</i>	Shui Hau	14 – 18 (3)	
	Sha Lo Wan	15 – 42 (6)	14 – 23 (2)
	Tung Chung		10 – 37 (65)
	Tung Wan		14 – 30 (12)

3 Study 2: Census and dynamics of clam diggers

3.1 Methodology

The number of clam diggers was recorded during low tide between June 2022 and February 2023. At each site, censuses were conducted twice in both summer and winter—once on a public holiday and once on a weekday. During each low tide period when digging activity occurred, the number of professional and recreational clam diggers was counted hourly. In addition, interviews were conducted, and the number and species of clams collected by diggers were documented. Since the censuses were conducted only once on a public holiday and once on a weekday, the estimates of the number of clam diggers, and consequently the estimated number and species of clams removed, are subject to a relatively high degree of uncertainty. Nevertheless, the surveys were conducted on days with favourable weather conditions and exceptionally low tides, which are expected to reflect periods of peak clam-digging activity. Therefore, despite the limited sampling frequency, the data are considered to provide a reasonably representative snapshot of clam-digging pressure at the study sites.

3.2 Results and Discussion

The number of clam diggers recorded per hour is summarized in Table 8. Because the survey at each site was conducted only once, on both weekdays and public holidays, no statistical comparisons were performed. No clam diggers were observed during winter on either weekdays or holidays. In summer, the number of clam diggers per hour at clam digging sites ranged from 11.2 at Shui Hau to 70.0 at Pui O on weekdays, and from 8.0 at Tung Chung to 357.6 at Shui Hau during holidays (Table 8). In contrast, the numbers recorded at control sites were much lower, ranging from 0 at Sha Lo Wan to 3.5 at Yi O on weekdays, and from 0 at Yi O to 2.7 at Tung Wan on holidays. Overall, recreational clam diggers outnumbered professional diggers at all sites, with the highest ratio of professional to recreational clam diggers (1:25) recorded at Shui Hau during the holiday survey (Table 8).

The number of clam diggers per 100 m² per hour showed a pattern similar to that observed for the number of clam diggers per hour (Fig. 10), with higher values consistently recorded at the clam digging sites than at the control sites, except for Tung Wan. At clam digging sites in summer, the values ranged from 0.003 at Shui Hau to 0.052 at Pui O on weekdays, and from 0.010 at Tung Chung to 0.099 at Shui Hau on holidays. At the control sites, the values ranged from 0 at Sha Lo Wan to 0.025 at Tung Wan on weekdays, and from 0 at Yi O to 0.079 at Tung Wan on holidays. The relatively high values recorded at Tung Wan were likely due to the very small size of the beach, as only 0.8 and 2.7 clam diggers per hour were observed there during the weekday and holiday surveys, respectively.

Table 8. Number of clam diggers recorded during low tides in summer and winter, on both weekdays and holidays.

Site	Season	Date	Weekday/ Holiday	Time	Mean no. of professional diggers per hr (1SD)	Mean no. of recreational diggers per hr (1SD)	Mean no. of diggers per hr (1SD)
Tung Chung	Summer	12/09/2022	Weekday	1500 - 1900	2.4 (2.6)	9.8 (9.4)	12.2 (10.1)
		30/06/2022	Holiday	1500 - 1800	5.8 (3.6)	2.3 (2.2)	8 (2.9)
	Winter	19/02/2023	Weekday	0500 - 0800	0	0	0
		27/12/2022	Holiday	0400 - 1100	0	0	0
Pui O	Summer	14/08/2022	Weekday	1400 - 1700	9.8 (7.6)	60.3 (10.1)	70 (15.3)
		23/09/2022	Holiday	1300 - 1700	4.2 (2.2)	19.8 (2.3)	24 (2.2)
	Winter	29/12/2022	Weekday	0700 - 1100	0	0	0
		25/01/2023	Holiday	0600 - 1100	0	0	0
Shui Hau	Summer	25/07/2022	Weekday	1200 - 1700	4.2 (2.5)	7 (3.5)	11.2 (5.6)
		11/09/2022	Holiday	1300 - 1800	13.8 (8.8)	343.8 (141.7)	357.6 (143)
	Winter	19/02/2023	Weekday	0200 - 0700	0	0	0
		26/12/2022	Holiday	0600 - 1000	0	0	0
Sha Lo Wan	Summer	12/07/2022	Weekday	1300 - 1800	0	0	0
		11/09/2022	Holiday	1400 - 1800	0	2.0 (3.5)	2 (3.5)
	Winter	29/12/2022	Weekday	0700 - 1100	0	0	0
		25/01/2023	Holiday	0600 - 1100	0	0	0
Yi O	Summer	27/07/2022	Weekday	1300 - 1600	2.8 (1.9)	0.8 (0.9)	3.5 (2.4)
		24/09/2022	Holiday	1300 1700	0	0	0
	Winter	19/02/2023	Weekday	0400 - 0800	0	0	0
		25/01/2023	Holiday	0700 - 1100	0	0	0
Tung Wan	Summer	26/07/2022	Weekday	1500 - 1800	0	4 (3.7)	4 (3.7)
		16/07/2022	Holiday	1230 - 1700	0	0.8 (1.2)	0.8 (1.2)
	Winter	27/12/2022	Weekday	0200 - 0700	0	0	0
		19/02/2023	Holiday	0600 - 1100	0	0	0

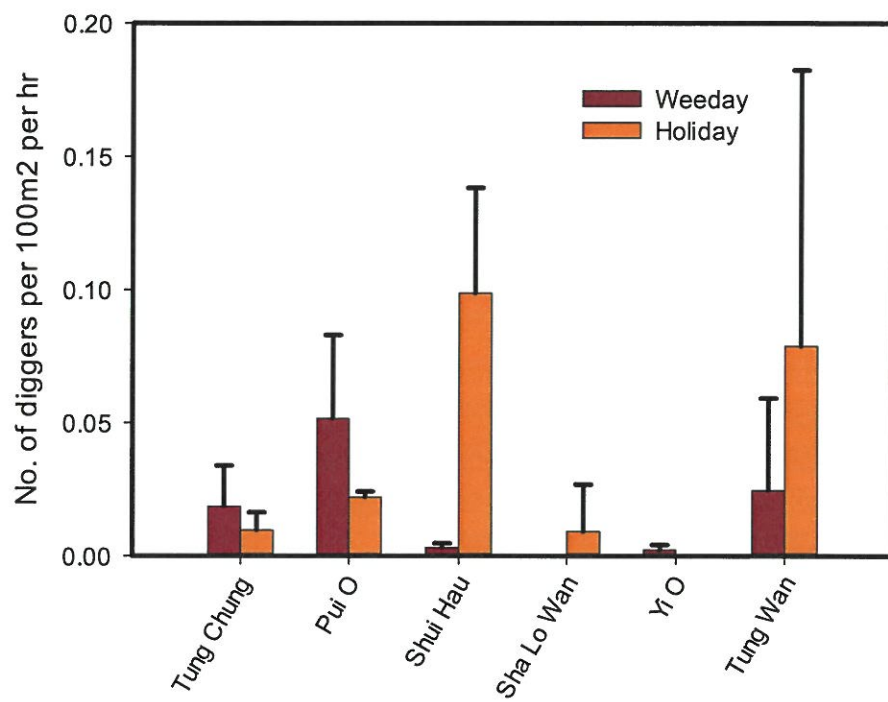


Fig. 10. Number of clam diggers per 100 m² per hour recorded at each site during weekdays and public holidays.

Table 9. Summary of the number of clam diggers interviewed and the corresponding clam species harvested. Values in brackets represent the number of clams harvested per digger.

Site	Number of diggers interviewed	Clam species				
		<i>Ruditapes philippinarum</i>	<i>Meretrix</i> sp.	<i>Cyclina sinensis</i>	<i>Marcia</i> sp.	<i>Anomalocardia flexuosa</i> / <i>Anomalodiscus squamosa</i>
Tung Chung	Weekday	17	1 (0.06)	28 (1.6)	12 (0.7)	
	Holiday	12				
Pui O	Weekday	44	173 (3.9)			3 (0.07)
	Holiday	12	46 (3.8)			
Shui Hau	Weekday	12	112 (9.3)			2 (0.17)
	Holiday	53	90 (1.7)	1 (0.02)		578 (10.9)
Sha Lo Wan	Weekday	0				
	Holiday	0				
Yi O	Weekday	4	54 (13.5)			
	Holiday	0				
Tung Wan	Weekday	5	4 (0.8)			
	Holiday	2	55 (27.5)			

Interviews were conducted with selected clam diggers to estimate the time spent at each site and the number of individuals of each clam species harvested (Table 9). The species harvested in the highest numbers were *Ruditapes philippinarum* and *Anomalocardia flexuosa*/*Anomalodiscus squamosa*. Among all species, *R. philippinarum* (27.3 individuals per digger) and *Meretrix* spp. (27.5 individuals per digger) had the highest mean harvest per digger. To minimize disturbance during interviews, data for *A. flexuosa* and *A. squamosa* were pooled, as distinguishing between the two species required additional time.

The estimated total number of diggers ranged from 0 in Sha Lo Wan (on both weekdays and holidays) to 725 in Shu Hau during the holiday period (Table 10). Using the total number of diggers at each site and the number of clams harvested per digger, we estimated the total number of individuals of each clam species harvested by all diggers on weekdays and holidays (Table 11). The most heavily harvested species were *Anomalocardia flexuosa*/*Anomalodiscus squamosa*, with 7903 individuals collected in Shui Hau during the holiday. This was followed by *Meretrix* spp. (1233 individuals) and *Hiatula acuta* (943 individuals), also in Shui Hau during the holiday. A comparable number of *Ruditapes philippinarum* (924 individuals) was harvested from Tung Chung on a weekday.

To estimate the proportion of clams removed relative to the total population at each site, the area within the tidal height of 0.5 m to 1.3 m where clam digging occurred was first estimated. Using clam density estimates from Study 1, together with the number of clam diggers and the average number of each clam species removed per digger obtained in Study 2, the monthly percentage of the total population of each clam species harvested by all diggers was calculated (Table 12). The highest monthly removal rate was recorded for *Cyclina sinensis* (49%), followed by *Hiatula acuta* (21.28%) at Shui Hau and *Ruditapes philippinarum* (16.19%) at Tung Chung. The removal of nearly half of the *Cyclina sinensis* population within a single month indicates that the species was experiencing extremely high harvesting pressure.

There are several potential sources of errors in estimating the number of clams harvested. First, the visitor survey was conducted only once, on both weekdays and holidays, at each site, leading to high uncertainty in the estimated number of diggers. Second, we interviewed a subset of diggers, counted the clams they harvested, and extrapolated these data to estimate the total number harvested by all diggers. However, some diggers may not take all the clams they collect, or may take only a portion, leading to an overestimation of the total number harvested. Third, the time each digger spent on the beach was obtained through interviews. Longer stay times result in a smaller estimated number of diggers and, therefore, a lower estimated number of clams harvested. Since the interviewed diggers were selected because they were observed taking clams away, they may have been more successful harvesters who tended to stay longer on the beach. As a result, the average time spent per digger may have been overestimated, potentially leading to an underestimation of the total number of clams harvested. Fourth, many diggers were young family members, who typically harvest fewer clams. Consequently, the number of clams harvested per digger may have been overestimated.

Table 10. The estimated total number of clam diggers at each site was calculated based on the duration of the observation period, the average number of clam diggers observed per hour, and the average time each digger spent at the site.

Site		Time	No. of hrs	Average no. of diggers per hr	Average time spent per digger (min)	Estimated total no. of diggers
Tung	Weekday	1500 - 1900	4	12.2	47	62
Chung	Holiday	1500 - 1800	3	8	106	14
Pui O	Weekday	1400 - 1700	3	70	154	82
	Holiday	1300 - 1700	4	24	85	68
Shui Hau	Weekday	1200 - 1700	5	11.2	80	42
	Holiday	1300 - 1800	5	357.6	148	725
Sha Lo	Weekday	1300 - 1800	5	0	0	0
Wan	Holiday	1400 - 1800	4	0	0	0
Yi O	Weekday	1300 - 1600	3	3.5	128	5
	Holiday	1300 1700	4	0	0	0
Tung	Weekday	1500 - 1800	3	4	80	9
Wan	Holiday	1230 - 1700	4.5	0.8	120	2

Table 11. The total number of individuals of each clam species harvested per day was estimated using the number of clam diggers at each site and the number of individuals of each clam species harvested per digger.

Site	Estimated total no. of diggers	Clam species					
		<i>Ruditapes philippinarum</i>	<i>Meretrix</i> sp.	<i>Cyclina sinensis</i>	<i>Marcia</i> sp.	<i>Anomalocardia flexuosa</i> / <i>Anomalodiscus squamosa</i>	<i>Hiatula acuta</i>
Tung Chung	Weekday	62	924	3.7	99	43	
	Holiday	14	382				
Pui O	Weekday	82		320			6
	Holiday	68		258			
Shui Hau	Weekday	42		391			7
	Holiday	725		1233	14.5		7903
Sha Lo Wan	Weekday	0					
	Holiday	0					
Yi O	Weekday	5		68			
	Holiday	0					
Tung Wan	Weekday	9		7.2			
	Holiday	2		55			

Table 12. Percentage of clams from the total population harvested per month by all diggers, estimated using clam density data from the stock assessment (Study 1).

Site	Area of study ¹ (m ²)	Estimated total no. of diggers	Clam species	No. of clams removed per day	Total no. of clams removed per month ²	Density of clams ³ (no. of clams m ⁻²)	Total no. of clams in the area of study	% of clams taken from the total population at each site per month
Tung Chung	10000	Weekday	<i>Ruditapes philippinarum</i>	924	11692	7.22	72222	16.19
		Holiday		382				
		Weekday	<i>Cyclina sinensis</i>	99	1089	0.22	2222	49.01
		Holiday		0				
Pui O	42000	Weekday	<i>Meretrix</i> sp.	3.7	40.7	0.22	2222	1.83
		Holiday		0				
		Weekday	<i>Meretrix</i> sp.	320	4552	6.93	291200	1.56
		Holiday		258				
Shui Hau	65000	Weekday	<i>Meretrix</i> sp.	391	9233	1.67	108333	8.52
		Holiday		1233				
		Weekday	<i>Anomalocardia flexuosa</i> / <i>Anomalodiscus squamosa</i>	7	31689	26.07	1694333	1.87
		Holiday		7903				
Sha Lo Wan	24000	Weekday	<i>Hiatula acuta</i>	244	6456	0.47	30333	21.28
		Holiday		943				
		Weekday	<i>Meretrix</i> sp.	68	748	2.67	120000	0.62
		Holiday		0				
Tung Wan	12000	Weekday	<i>Meretrix</i> sp.	7.2	299.2	0.71	8533	3.51
		Holiday		55				

¹The study area covered only the portion of each beach between the tidal heights of 0.5 m and 1.3 m, except at Tung Chung, where only the 0.7-1.3 m zone was included. The 0.5 m tidal zone at Tung Chung was excluded because it remained submerged during most of the periods when clam digging occurred.

²During the summer period, the peak low tide conditions suitable for clam digging occurred on roughly 15 days per month (about half a month), of which 11 were weekdays, and 4 were holidays.

³ For *Ruditapes philippinarum* in Tung Chung, density data from 2024 were used because there was no data in 2022. Densities of other species were obtained from the 2022 survey, which included the visitor surveys.

4. Study 3: Size at maturity, growth, mortality, and production of individual clam species

4.1 Methodology

The population dynamics of the clam species targeted by clam diggers—*Meretrix* spp., *Anomalocardia flexuosa*, and *Ruditapes philippinarum*—were investigated over a one-year period. *Anomalocardia flexuosa* was studied in Shui Hau, *Macridiscus aequilatera* in Tung Wan, and *Ruditapes philippinarum* in Tung Chung. For *Meretrix* spp., only a small number of individuals were collected; therefore, specimens from all sites were pooled for the construction of size-frequency histograms. As in Study 1, at each beach, three or four transect lines were established from the backshore to the waterfront, with the number determined by beach size. Four transects were set at Shui Hau and Pui O, whereas three transects were used at the other sites. Along each transect, quadrats measuring 0.5 m × 0.5 m were placed adjacent to the transect line at elevations of 0.5, 0.7, 0.9, 1.1, and 1.3 m above Chart Datum (CD). This resulted in 12 quadrat samples per tidal height at sites with four transects and nine samples per tidal height at sites with three transects.

Monthly size-frequency histograms were generated, and growth parameters were estimated using the NOREMSEP routine in the FISAT program based on all collected individuals, irrespective of the tidal height at which they were sampled on the beach. The theoretical life span was calculated using the inverse of the von Bertalanffy growth equation, and mortality rates were estimated using a length-converted catch curve.

Clams of varying sizes were collected, and size at sexual maturity was determined through gonadal smear analysis using fresh gonadal tissue. Each specimen was sexed and examined monthly to identify the presence or absence of macroscopically mature gametes. The smallest individual exhibiting a fully developed gonad was recorded as the size at maturity.

For each clam species, regressions between shell length and tissue dry mass, as well as ash-free dry mass, were developed and used to estimate the monthly dry mass and ash-free dry mass of the population based on shell length data obtained from the size-frequency histograms. Tissue dry mass was determined by drying soft tissue at 80°C to constant weight, while ash-free dry mass was obtained by combusting the dried tissue at 550°C for 5 hours.

4.2 Results and Discussion

4.2.1 Gonad maturity as revealed by gonad smears

For *A. flexuosa* in Shui Hau, mature gonads containing sperm or eggs were observed almost year-round, although a slightly higher percentage of unidentified gonads occurred between November and February (Fig. 11a). This suggests that reproduction is potentially continuous throughout the year, as even during the November-February period, the proportion of unidentified gonads remained relatively low (approximately 20%).

Similarly, *R. philippinarum* in Tung Chung exhibited mature gonads in most months of the year (Fig. 11b). However, a notably high percentage (~80%) of unidentified gonads was recorded between May and June, with an additional increase to around 25% in April.

Since the different *Meretrix* species could not be reliably identified in the field and only a small number of individuals were collected, reproductive cyclicity was assessed by pooling *Meretrix* specimens from all the study sites. Very low percentages (< 10%) of unidentified gonads were recorded in April and between June and September (Fig. 11c). No mature sperm or eggs were observed between November and February.

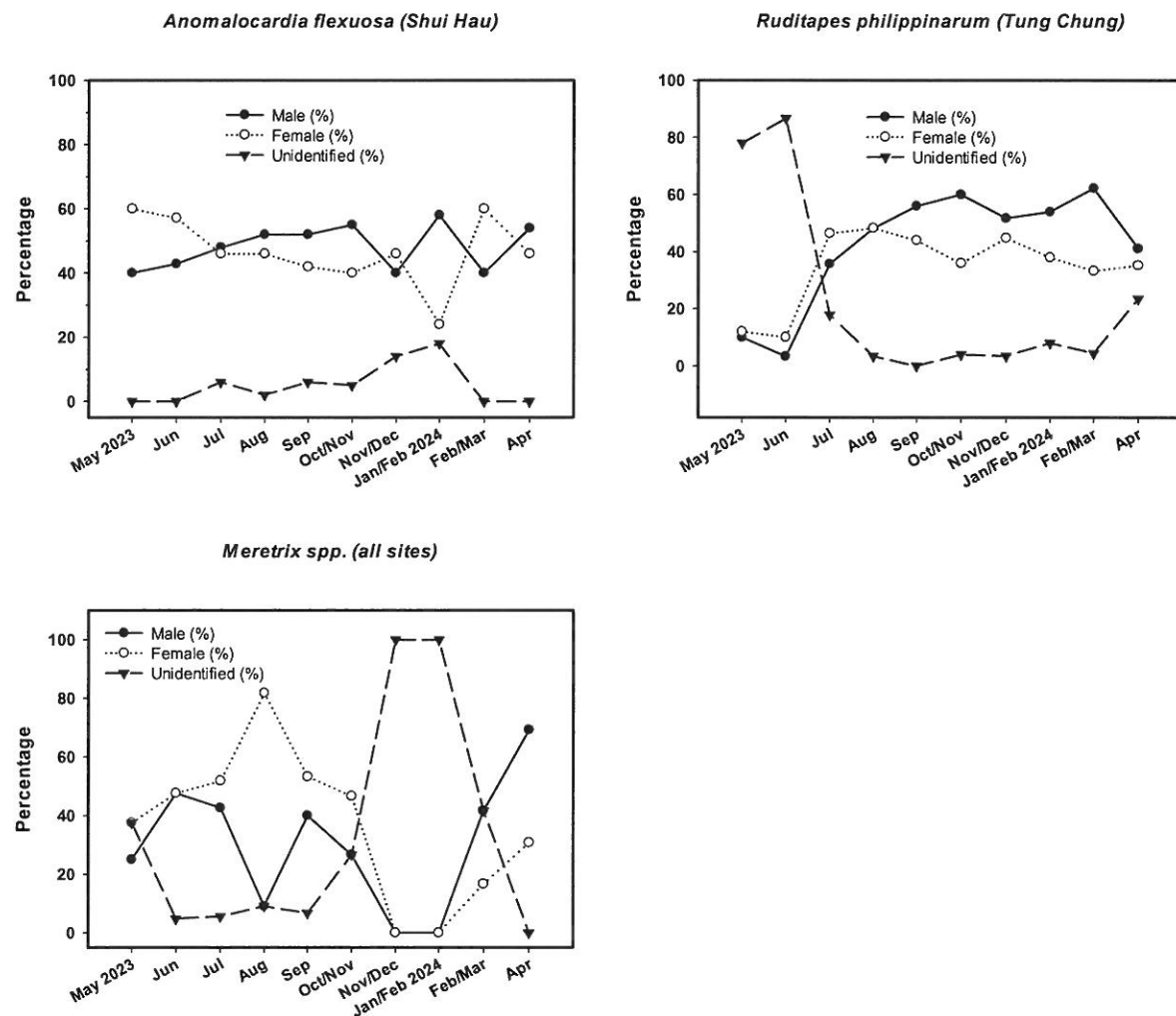


Fig. 11. Monthly changes in the percentages of male, female and unidentified individuals, as determined by gonad smear analysis, for (a) *A. flexuosa*, (b) *R. philippinarum*, and (c) *Meretrix* spp. Because only small numbers of *Meretrix* spp. were collected at each site, gonad smear data from all sites were pooled for analysis.

4.2.2 Smallest individuals with a mature gonad

Table 13 presents the number and size range of *A. flexuosa* specimens from Shui Hau examined using gonad smears. The smallest male with a mature gonad measured 25.5 mm

and was collected in February/March 2024, while the smallest mature female measured 20.6 mm and was collected in June 2023.

For *R. philippinarum* in Tung Chung, the smallest male with a mature gonad measured 23.2 mm and was collected in October/November 2023; the smallest mature female measured 19.8 mm and was collected during the same period (Table 14).

For *Meretrix spp.* pooled from all sites, the smallest male with a mature gonad measured 33.9 mm and the smallest mature female measured 32.6 mm, both were collected in July 2023 (Table 15).

Table 13. Smallest males and females of *A. flexuosa* with mature gonads recorded each month at Shui Hau. Numbers shown in red indicate the smallest individuals with mature gonads.

Month	Number examined	Size range (mm)	Smallest male with a mature gonad (mm)	Smallest female with a mature gonad (mm)
May 2023	50	27.1 - 37.8	27.8	27.1
Jun	42	20.6 - 35.1	27.8	20.6
Jul	50	28.9 - 37.1	29	28.9
Aug	50	27.8 - 33.9	28.7	27.8
Sep	50	28.2 - 34.9	28.2	28.7
Oct/Nov	40	26.8 - 36.5	26.8	29.4
Nov/Dec	50	26.4 - 36.9	27.3	26.4
Jan/Feb 2024	50	26.9 - 37.1	27.1	26.9
Feb/Mar	50	25.5 - 36.1	25.5	27.1
Apr	50	27.6 - 36.0	28.1	27.6

Table 14. Smallest males and females of *R. philippinarum* with mature gonads recorded each month at Tung Chung. Numbers shown in red indicate the smallest individuals with mature gonads.

Month	Number examined	Size range (mm)	Smallest male with a mature gonad	Smallest female with a mature gonad
May 2023	50	32.6 - 40.2	33.0	34.1
Jun	30	32.0 - 45.9	40.0	38.0
Jul	28	33.6 - 52.1	36.9	33.6
Aug	29	31.1 - 44.2	31.1	31.3
Sep	50	27.6 - 43.3	27.6	28.5
Oct/Nov	25	19.8 - 43.4	23.2	19.8
Nov/Dec	29	30.3 - 42.6	30.3	31.7
Jan/Feb 2024	50	26.5 - 47.7	27.5	26.5
Feb/Mar	45	25.6 - 46.3	25.6	26.1
Apr	34	26.3 - 46.1	27.0	26.3

Table 15. Smallest males and females of *Meretrix* spp. with mature gonads recorded each month from all sites. Numbers shown in red indicate the smallest individuals with mature gonads.

Month	Number examined	Size range (mm)	Smallest male with a mature gonad	Smallest female with a mature gonad
May 2023	8	36.6 - 93.0	48.7	70.7
Jun	21	39.8 - 76.5	39.8	41.8
Jul	54	31.7 - 99.4	33.9	32.6
Aug	11	68.4 - 88.4	71.5	68.4
Sep	15	48.5 - 80.7	48.5	56.5
Oct/Nov	15	39.6 - 81.4	67.2	58.5
Nov/Dec	9	11.5 - 68.8		
Jan/Feb 2024	13	30.8 - 85.3		
Feb/Mar	12	34.4 - 69.7	53.5	58.5
Apr	13	42.6 - 74.6	42.6	43.9

4.2.3 Temporal variations in the population density of each clam species

In Shui Hau, the mean density of *Anomalocardia flexuosa* declined over time (Fig. 12). Densities ranged from 19.4 ind m⁻² to 37.6 ind m⁻², and the temporal variation was statistically significant (one-way ANOVA: $F = 3.02$; $df = 9,20$; $p < 0.05$). However, pairwise comparisons using the Holm-Sidak procedure indicated that differences between individual months were not statistically significant.

The mean density of *Meretrix* spp. in Shui Hau remained low throughout the year, ranging from 0.59 ind m⁻² to 1.04 ind m⁻² (Fig. 12) and showed no significant temporal variation (one-way ANOVA: $F = 0.22$; $df = 9,20$; $p = 0.988$). In Yi O, mean densities ranged from 0.74 ind m⁻² to 4.0 ind m⁻² (Fig. 12), but temporal variations were likewise statistically insignificant ($F = 2.03$; $df = 9,20$; $p = 0.09$). Similarly, in Tung Wan, densities varied between 0.67 ind m⁻² and 4.0 ind m⁻² (Fig. 12), with no statistically significant variation ($F = 2.43$; $df = 9,10$; $p = 0.09$).

The mean density of *Ruditapes philippinarum* in Tung Chung ranged from 12.4 ind m⁻² to 46.7 ind m⁻² (Fig. 12), and the temporal variation was marginally non-significant (one-way ANOVA: $F = 2.94$; $df = 9,10$; $p = 0.054$).

The mean density of *Macridiscus aequilatera* in Tung Wan ranged from 0.89 ind m⁻² to 7.11 ind m⁻² (Fig. 12), and the temporal variation was marginally non-significant ($F = 2.94$; $df = 9,10$; $p = 0.054$).

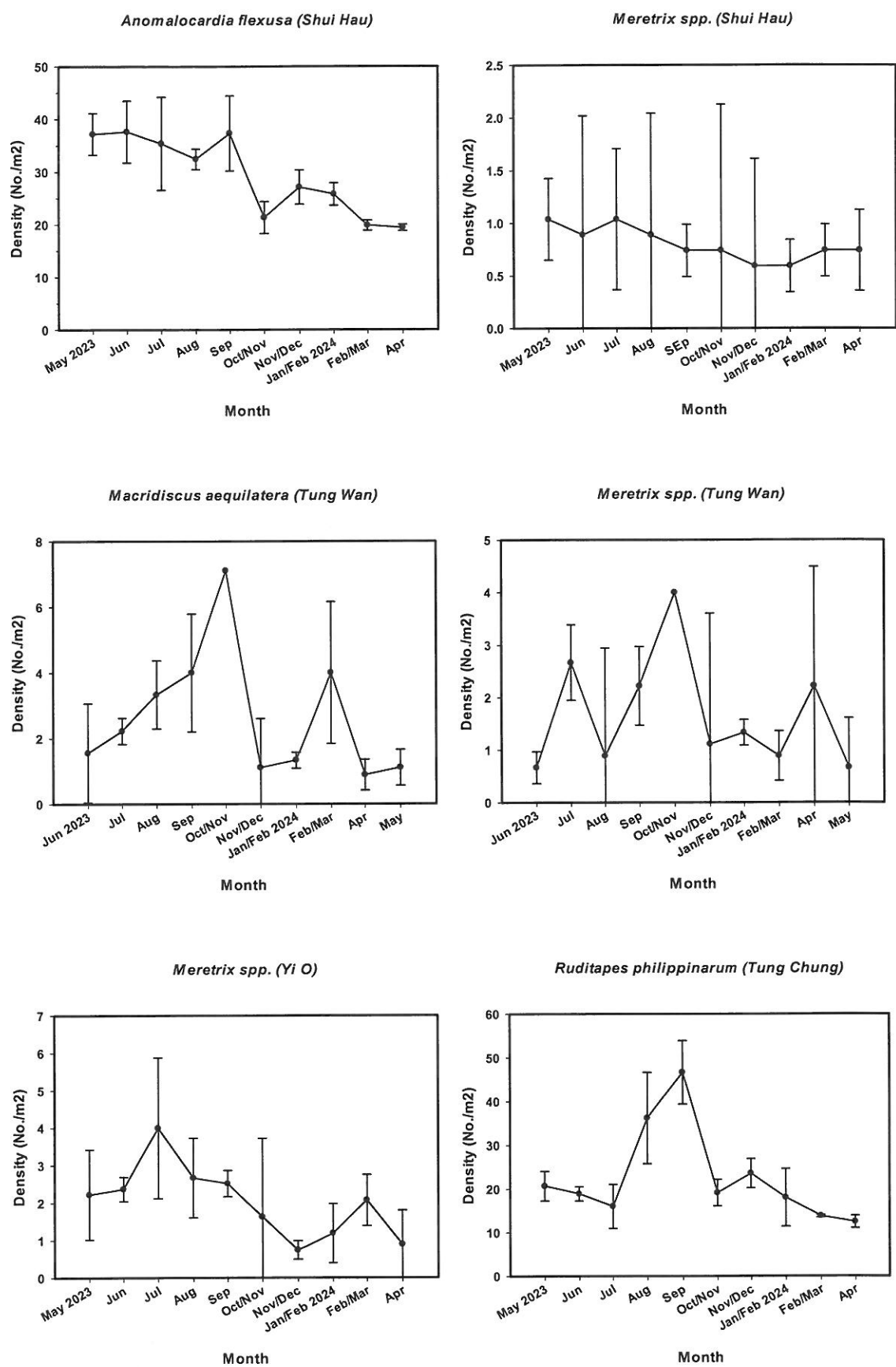


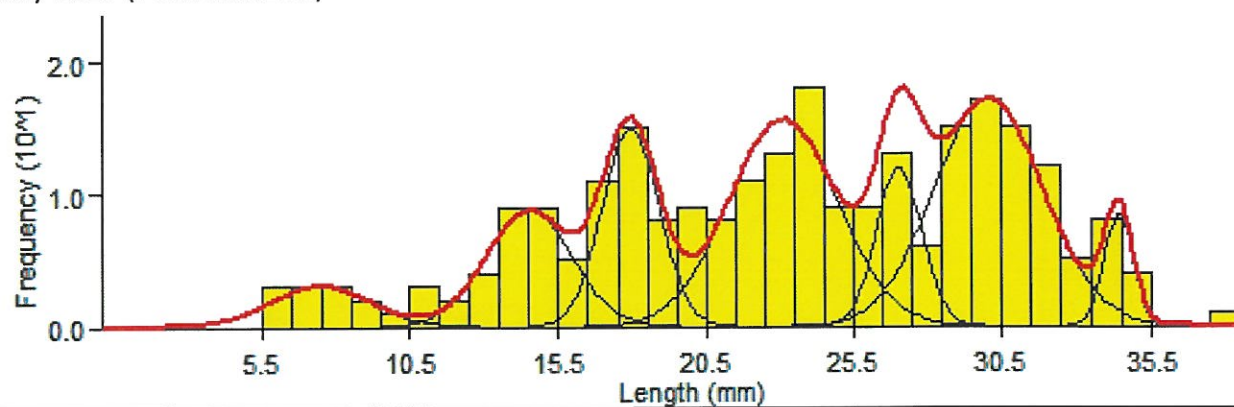
Fig. 12. Temporal variations in the population density of each clam species at the different study sites.

4.2.4 Population dynamics of individual clam species

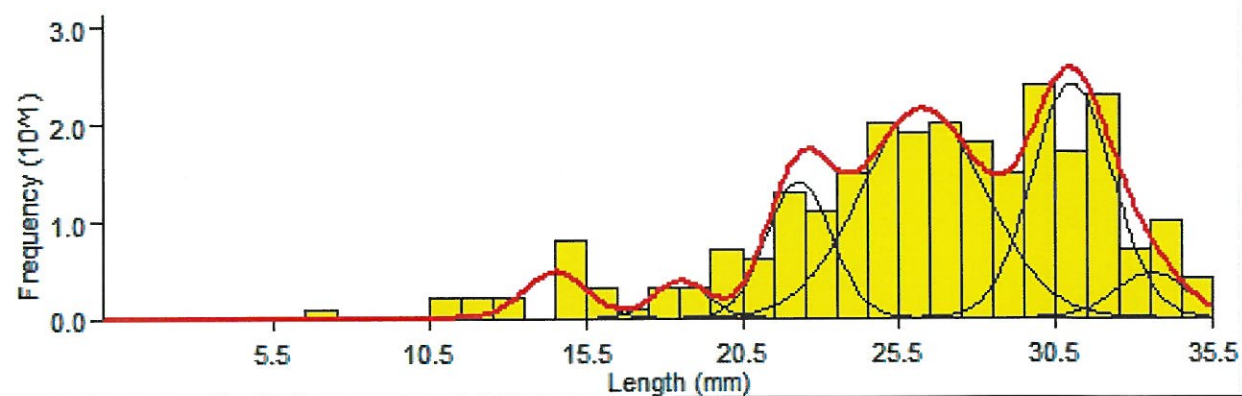
The length frequency histograms for each clam species are shown below. Because the density of *Meretrix* spp. was very low across all study sites, the number of individuals collected was insufficient for separate analyses in both Study 3 and Study 5. To enable an examination of population dynamics, all *Meretrix* spp. specimens collected from Shui Hau, Yi O and Tung Wan were therefore pooled.

The asymptotic length (L_{∞}), the theoretical maximum average length, was estimated from the von Bertalanffy growth function, and the growth rate (K), the rate at which a species approaches its asymptotic length, was estimated. The total mortality rate (Z) was estimated from the length-converted catch curve. This is a statistical estimate of how quickly a species is removed from a population due to all causes combined. For clams, these causes include natural mortality, harvesting mortality and predation. The higher the Z value, the faster the population disappears.

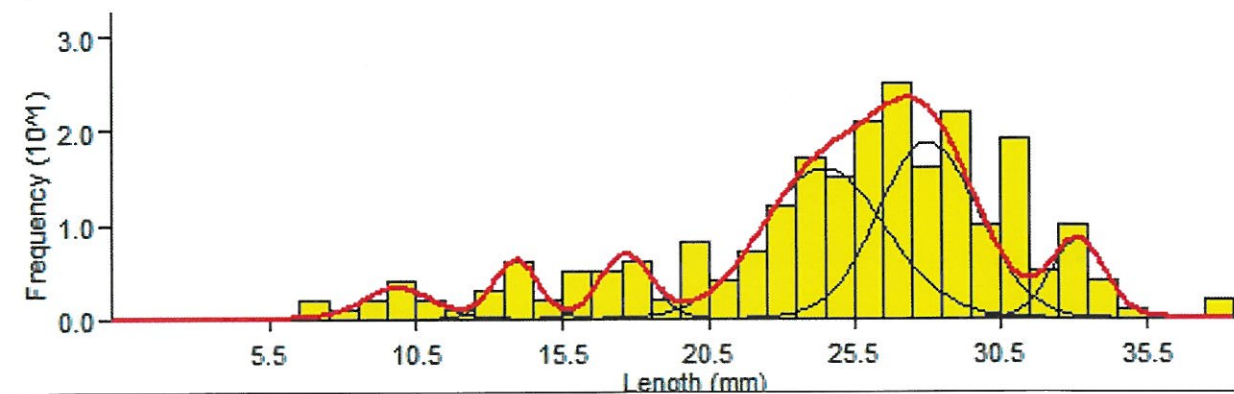
May 2023 (Total no.: 251)



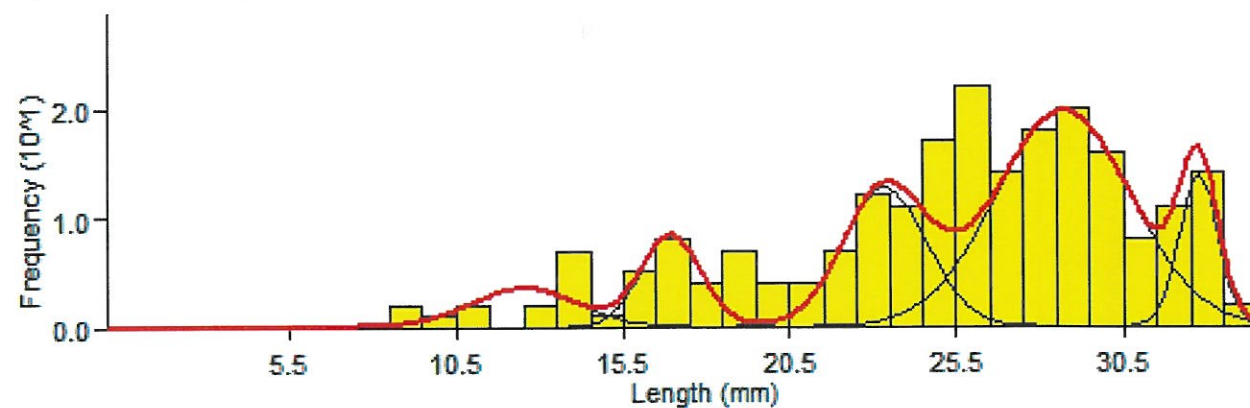
June (Total no.: 254)



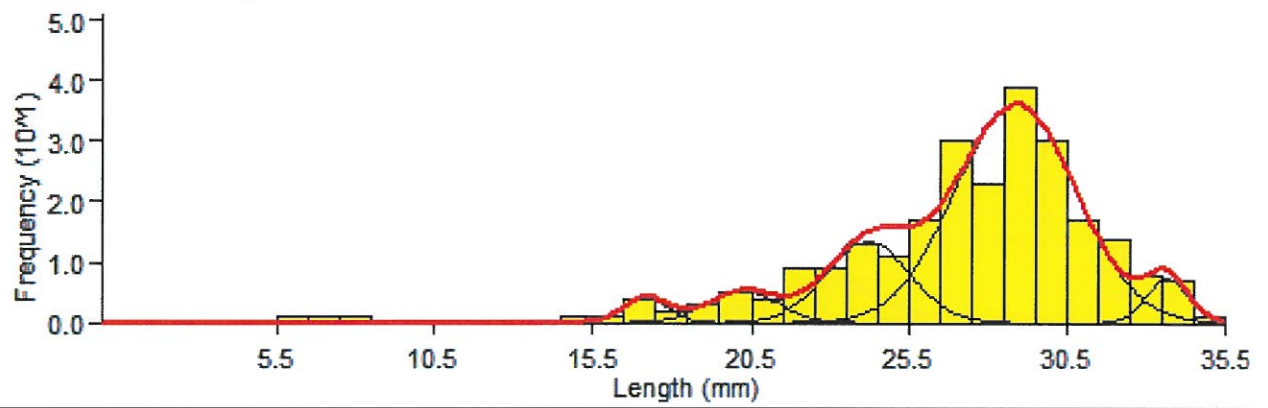
July (Total no.: 239)



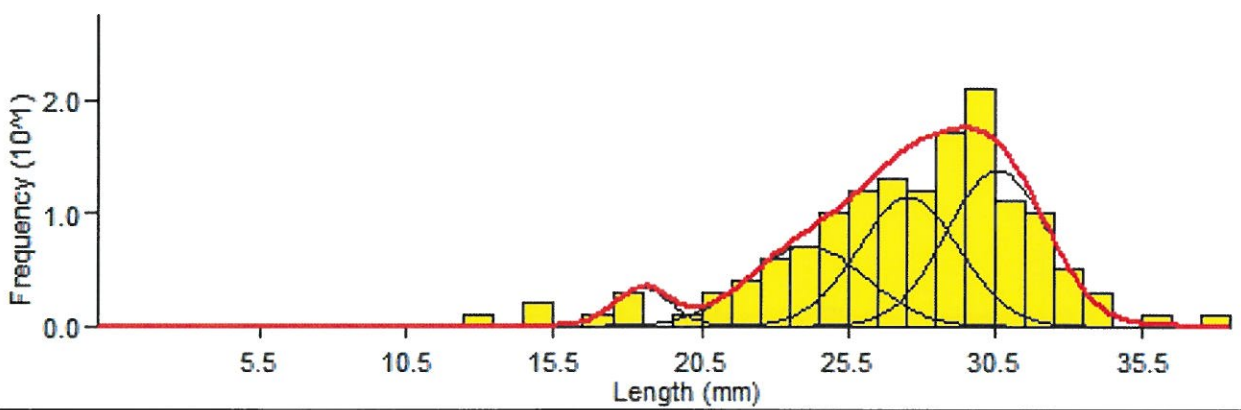
Aug (Total no.: 219)



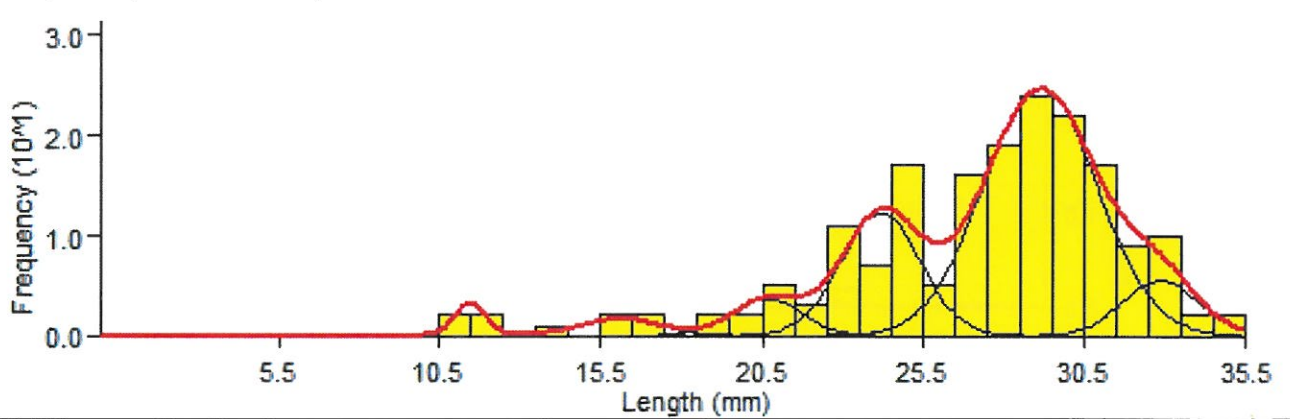
Sept (Total no.: 251)



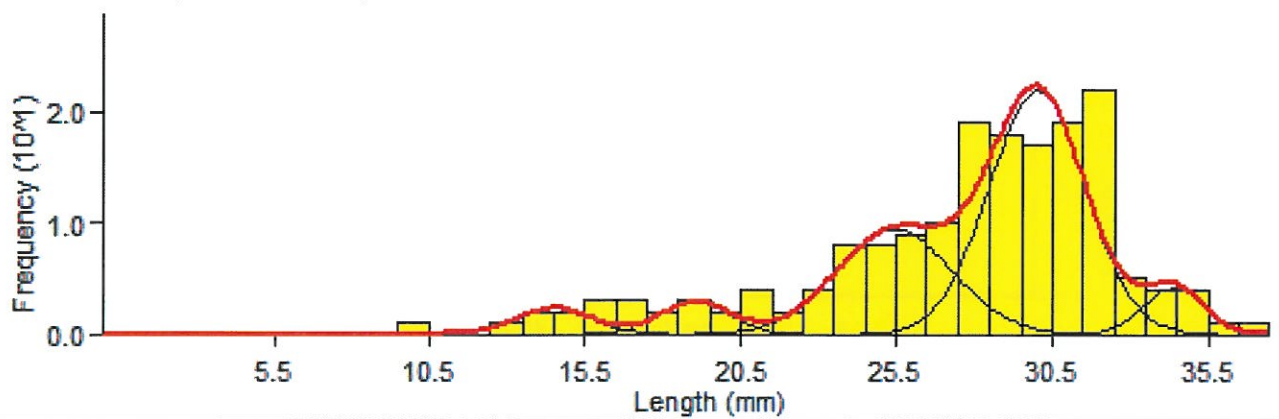
Oct/ Nov (Total no.: 144)



Nov/ Dec (Total no.: 182)



Jan/ Feb 2024 (Total no.: 174)



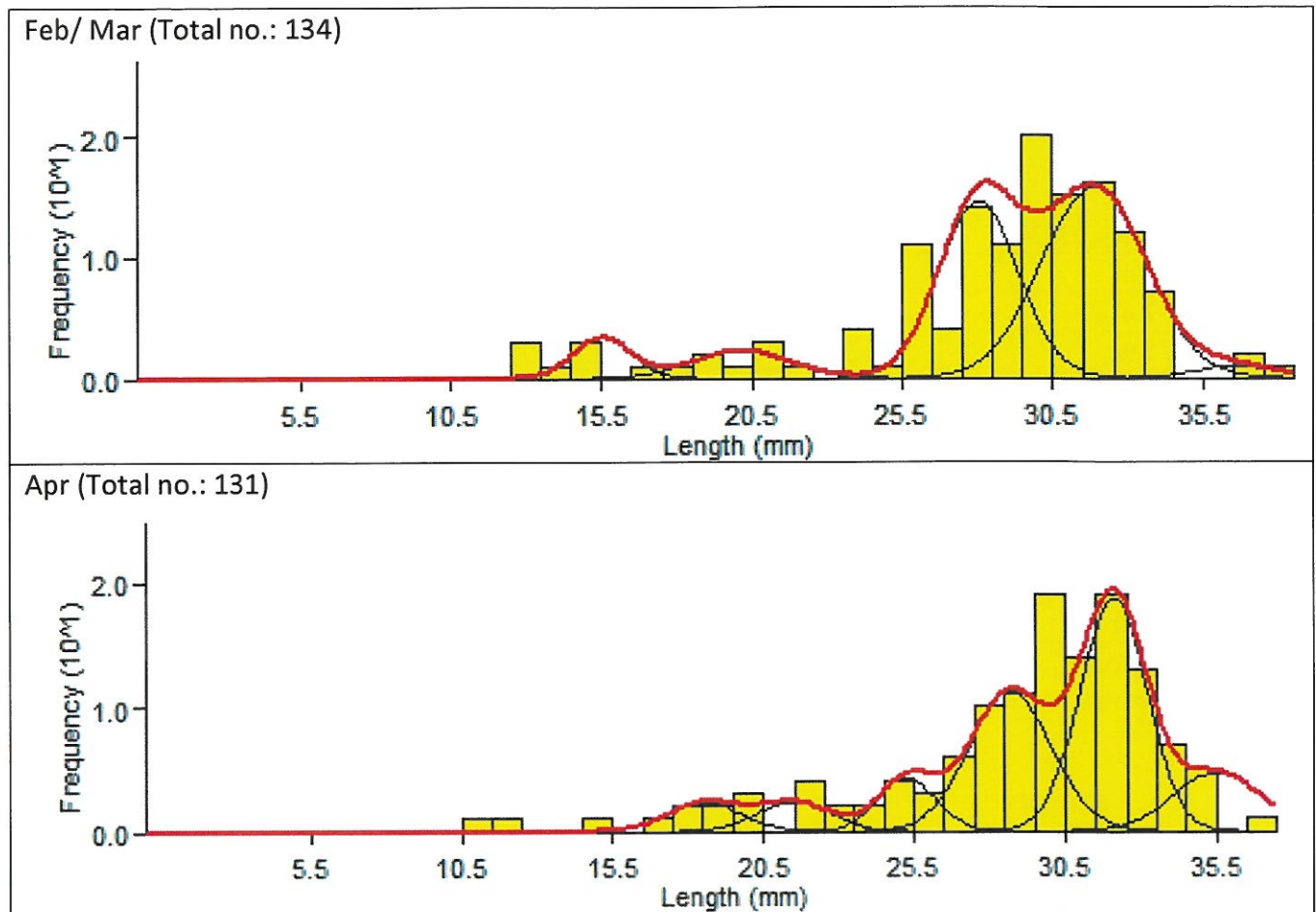


Fig. 13. Size frequency histograms of *A. flexuosa* with growth parameters estimated using the NORMSEP method in FISAT program.

Table 16. Number of *A. flexuosa* individuals in each cohort estimated using the NORMSEP method in the FISAT program. (* indicates a cohort not identified by the FISAT program due to low sample size.)

No. of individuals	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort	Total
May 2023		13	32	36	72	23	78	10	1*	265
Jun		1*	12	18	36	107	76	13		263
Jul		11		26	77	85		19	1*	219
Aug		14	19		40	100	20			193
Sep	3*		7	15	45	172	12			254
Oct/Nov		1*	8		35	49	59		1*	153
Nov/Dec		4	5	10	38	109	16			182
Jan/Feb 2024	1*	7		8	44	85	10			155
Feb/Mar		8		9	48	67	3			135
Apr	2*	7	7	10	38	51	17			132

Table 17. Average size (mm) of *A. flexuosa* cohorts estimated using the NORMSEP method in the FISAT program. (* indicates a cohort not identified by the FISAT program due to low sample size.)

Size (mm)	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort
May 2023		7.44	14.5	17.95	23.12	27.07	30.09	34.37	37.9*
Jun		6.9*	14.5	18.5	22.32	26.28	31.02	33.5	
Jul		10		17.5	24.37	28		33.13	38*
Aug		12.5	16.93		23.36	28.7	32.75		
Sep	6.43*		17.17	20.22	24.21	28.88	33.63		
Oct/Nov		13.67*	18.5		24.11	27.57	30.58		37.1*
Nov/Dec		11.5	16.08	20.64	24.19	29.14	32.84		
Jan/Feb 2024	9.5*	14.5		19.01	25.44	30.03	34.4		
Feb/Mar		15.5		20.09	28.06	31.85	36.5		
Apr	10.85*	18.5	21.5	25.25	28.69	32.08	35.5		
Annual growth		11.06	7.0	7.3	5.57	5.01	5.41		

It appears that *A. flexuosa* produced two cohorts in 2023: a major cohort between May and July and a minor cohort in September (Fig. 13, Table 16). Annual growth was calculated for each cohort using shell length measurements collected from May 2023 to Apr 2024 (Table 17). The annual growth of *A. flexuosa* declined with age, ranging from 11.06 mm in the first-year cohort (2023 first cohort) to 5.01 mm in the third-year cohort (2021 first cohort).

The asymptotic length (L_{∞}) of *A. flexuosa* estimated from the von Bertalanffy growth function was 49.8 mm, and the instantaneous growth rate constant (K) estimated was 0.28 yr^{-1} (Fig. 14) The total mortality rate (Z) was 2.68, corresponding to an annual survival rate of 6.86% (Fig. 15).

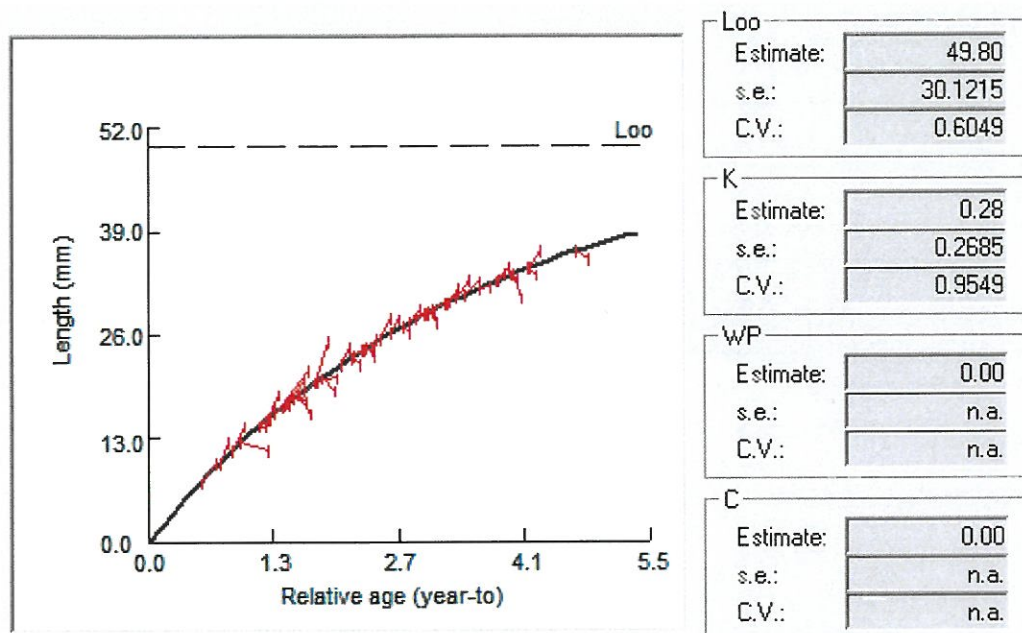


Fig. 14. Von Bertalanffy growth function for *A. flexuosa* estimated using Appeldoorn's method in the FISAT program.

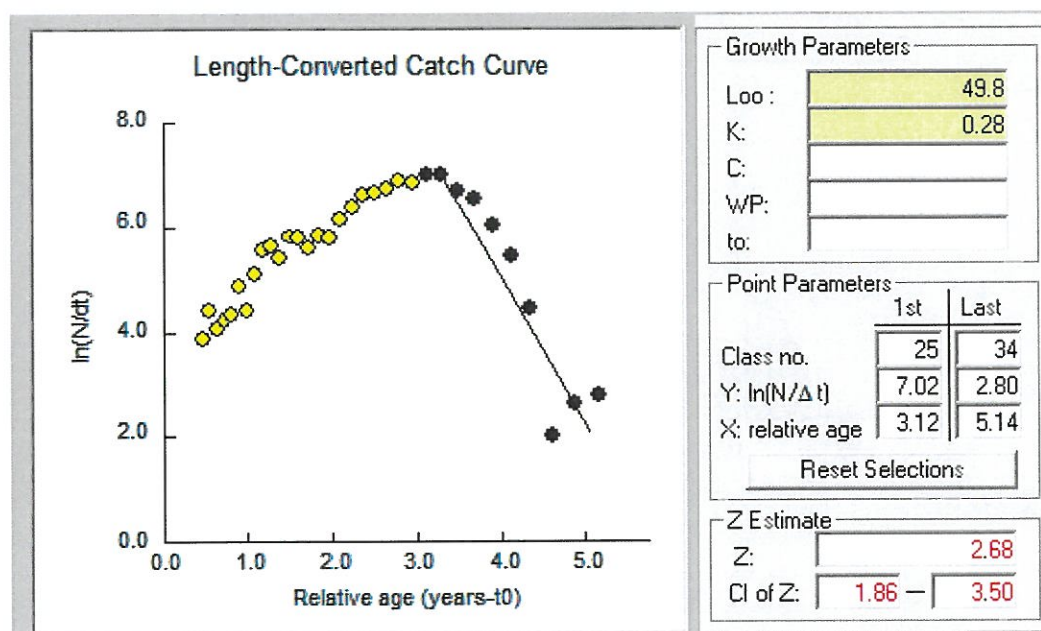
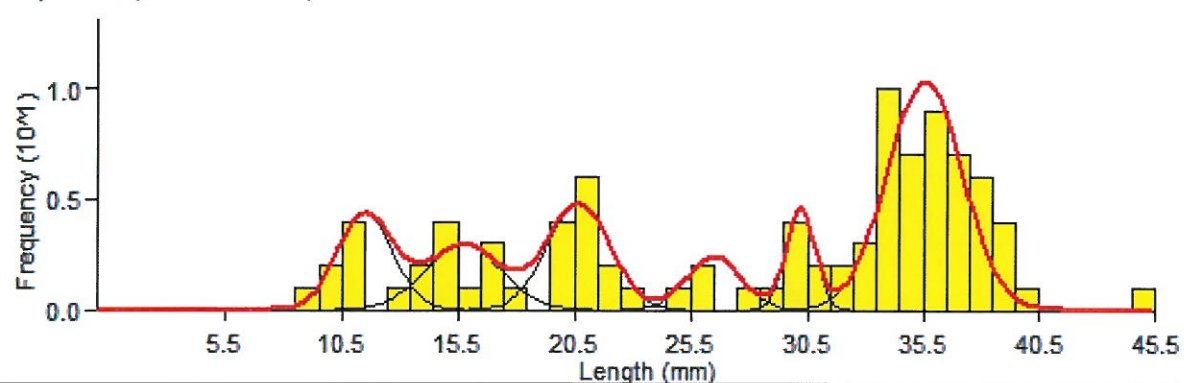
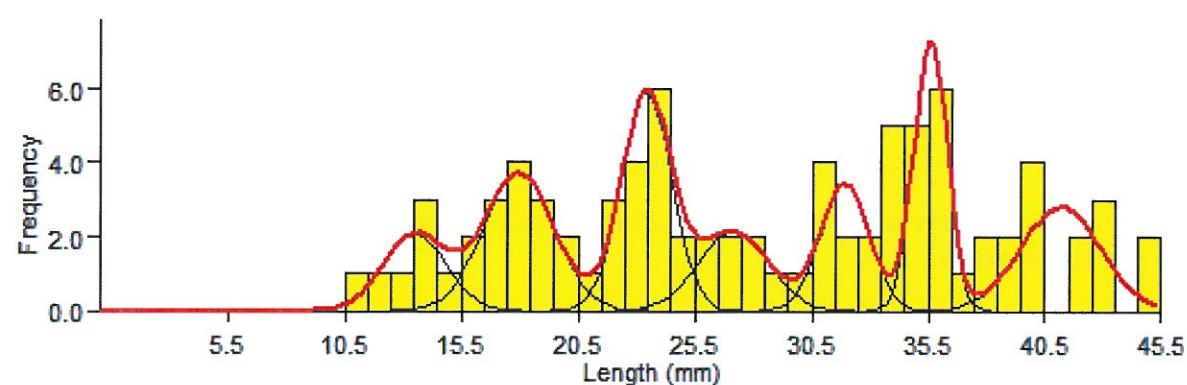


Fig. 15. Length-converted catch curve of *A. flexuosa* estimated using the FISAT program.

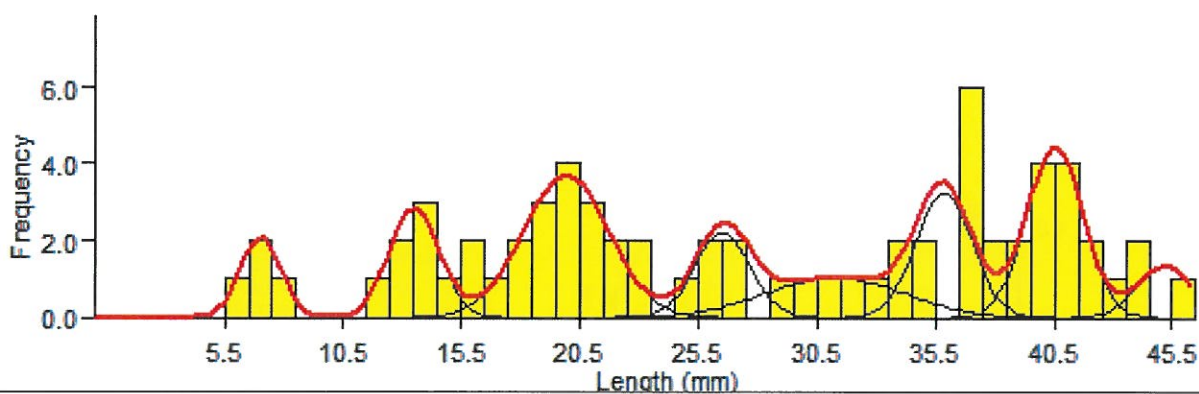
May 2023 (Total no.: 93)



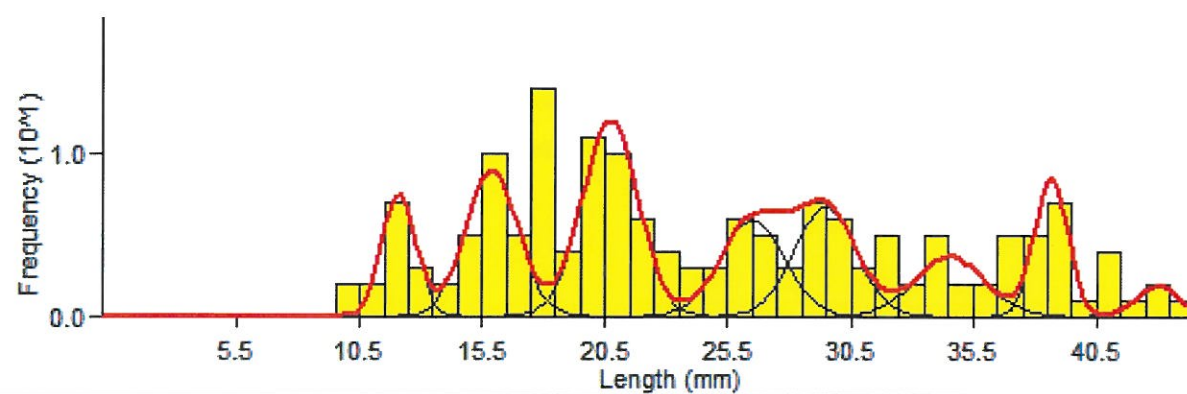
June (Total no.: 85)



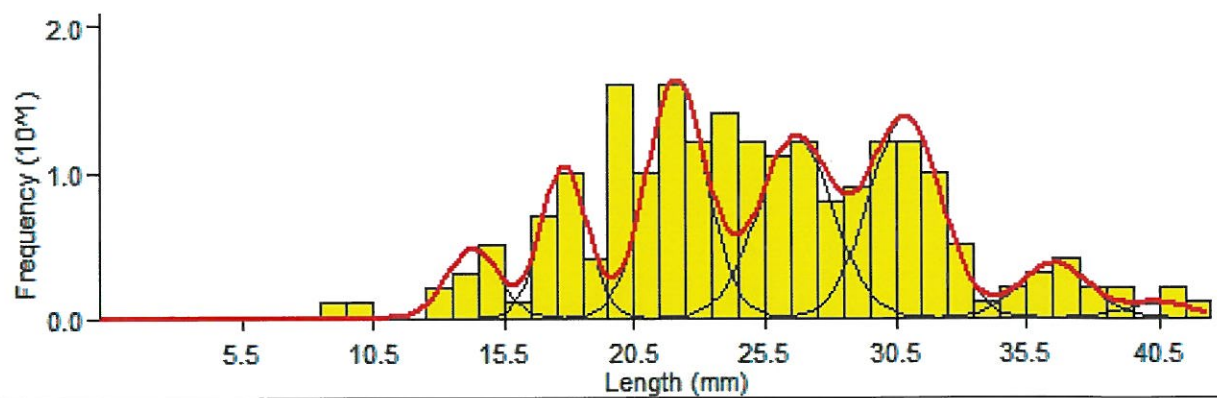
July (Total no.: 68)



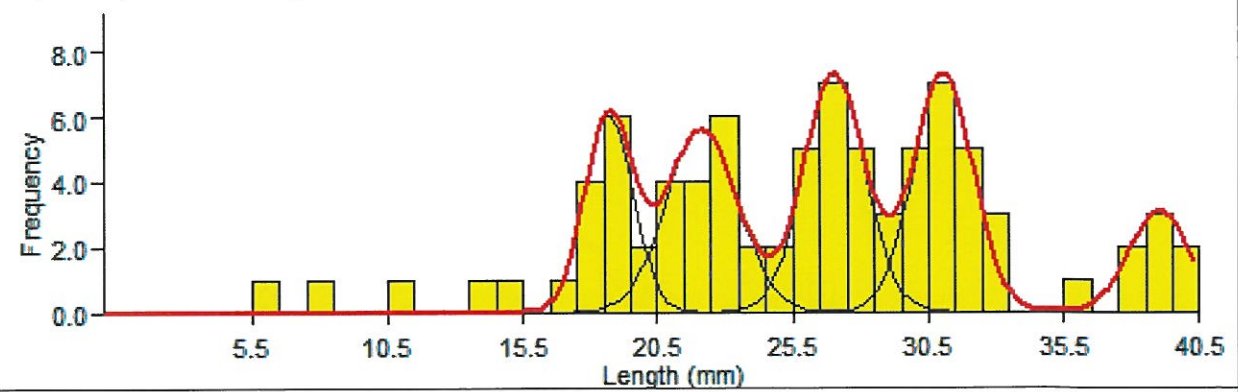
Aug (Total no.: 163)



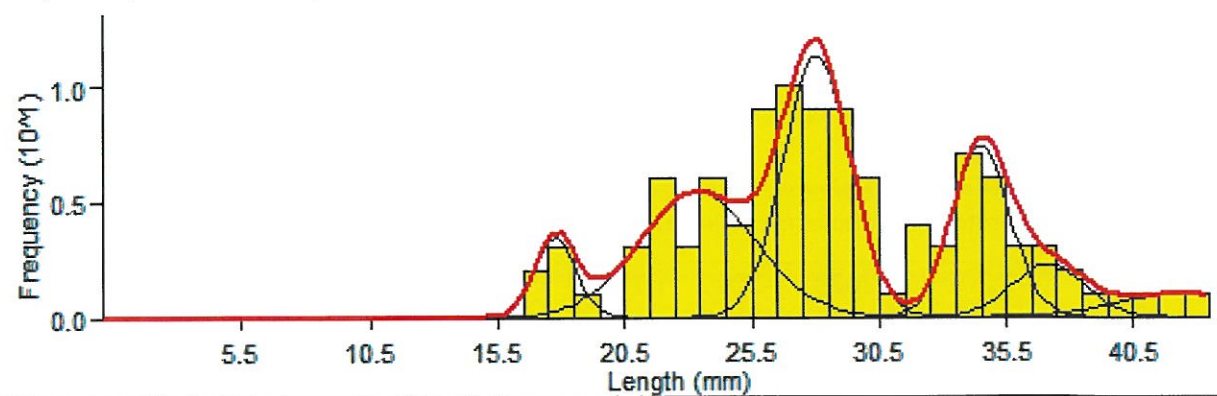
Sept (Total no.: 210)



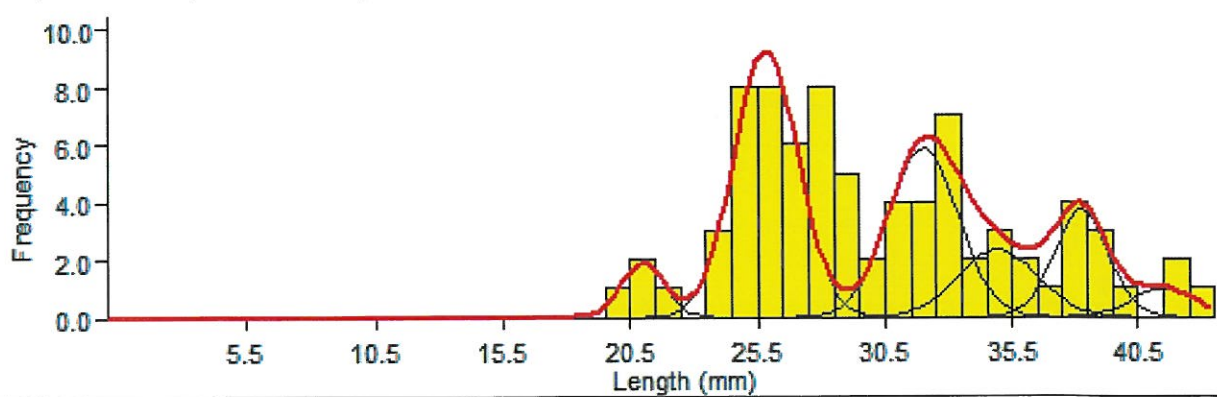
Oct/ Nov (Total no.: 84)



Nov/ Dec (Total no.: 105)



Jan/ Feb 2024 (Total no.: 78)



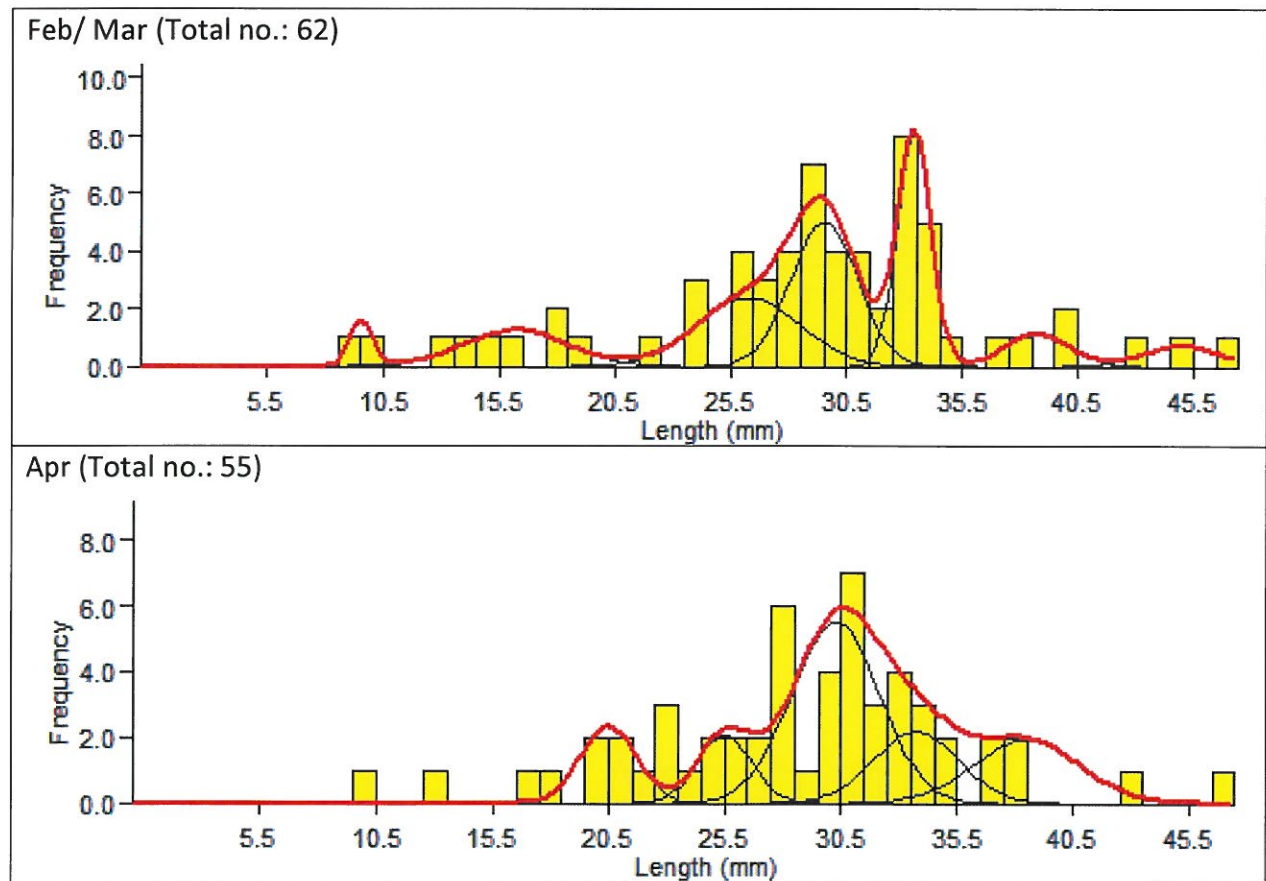


Fig. 16. Size frequency histograms of *R. philippinarum* with growth parameters estimated using the NORMSEP method in FISAT program.

Table 18. Number of *R. philippinarum* individuals in each cohort estimated using the NORMSEP method in the FISAT program. (* indicates a cohort not identified by the FISAT program due to low sample size.)

No. of individual	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort	Total
May 2023			13	12	16	7	7	42	1*	98
Jun			7	14	16	8	9	13	12	79
Jul		4	8	17	6	7	10	13	4	69
Aug		13	24	34	19	21	13	14	4	142
Sep	2*	12	23	47	44	47	12	3		190
Oct/Nov	3*	2*	14	18	21	20		9		87
Nov/Dec		7		31	37	21	8	6		110
Jan/Feb 2024			4	29	20	9	10	3		75
Feb/Mar	2	7		13	18	15	4	3		63
Apr	2*		7	6	26	10	11	1*		62

Table 19. Average size (mm) of *R. philippinarum* cohorts estimated using the NORMSEP method in the FISAT program. (* indicates a cohort not identified by the FISAT program due to low sample size.)

Size (mm)	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort
May 2023			11.5	15.76	20.69	26.5	30.2	35.56	44.5*
Jun			13.5	17.97	23.42	27.15	31.92	35.6	41.17
Jul		7	13.5	19.5	26.51	31.25	35.88	40.7	45.17
Aug		12.1	15.9	20.69	26.5	29.45	34.55	38.66	43
Sep	8.7*	14.27	17.79	22.12	26.69	30.86	36.55	40.5	
Oct/Nov	7.8*	14.5*	18.69	22.15	27.03	31.05		39	
Nov/Dec		17.77		23.38	28.07	34.5	37.16	42.33	
Jan/Feb 2024			21	25.86	32.01	34.93	38.42	41.5	
Feb/Mar	9.49	16.19		26.24	29.52	33.39	38.73	44.98	
Apr	11.25*		20.5	25.5	30.27	33.73	38.5	46.1*	
Annual growth			9.0	9.74	9.58	7.23	8.30	10.54	

R. philippinarum also produced two cohorts a year, with a major cohort appearing in July and a minor one in October/November 2023 (Fig. 16, Table 18). In contrast to *A. flexuosa*, the annual growth of *R. philippinarum* did not exhibit a clear age-related trend, although smaller cohorts generally grew faster than older ones. Annual growth ranged from 7.23 mm in the 2021 first cohort to 10.54 mm in the 2020 first cohort (Table 19). The relatively high growth estimate for the 2020 first cohort was likely influenced by a few exceptionally large individuals that had probably escaped harvest by clam diggers.

The asymptotic length (L_{∞}) estimated from the von Bertalanffy growth function was 64.3 mm, and the corresponding instantaneous growth rate constant (K) estimated was 0.32 yr^{-1} . (Fig. 17). The total mortality rate (Z) was 1.73, corresponding to an annual survival rate of 17.73% (Fig. 18).

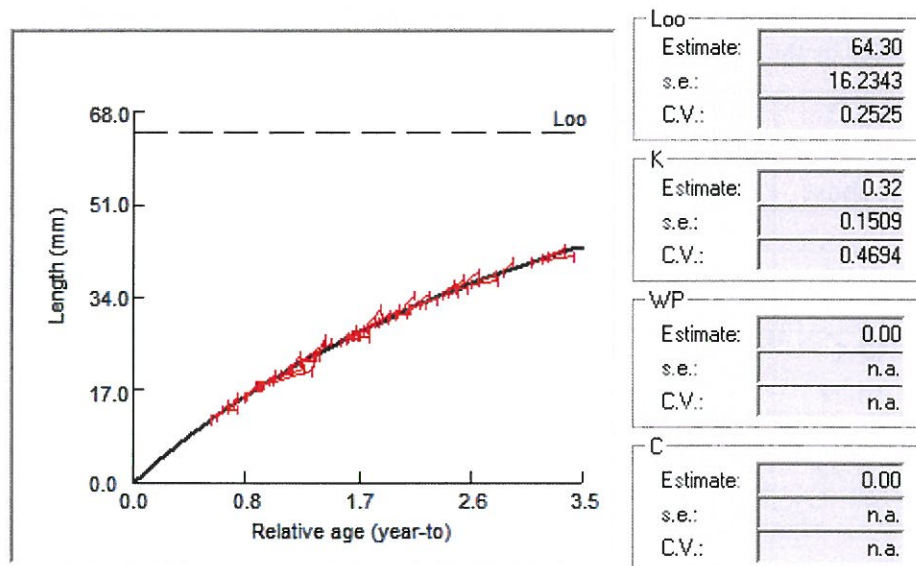


Fig. 17. Von Bertalanffy growth function for *R. philippinarum* estimated using the Appeldoorn's method in the FISAT program.

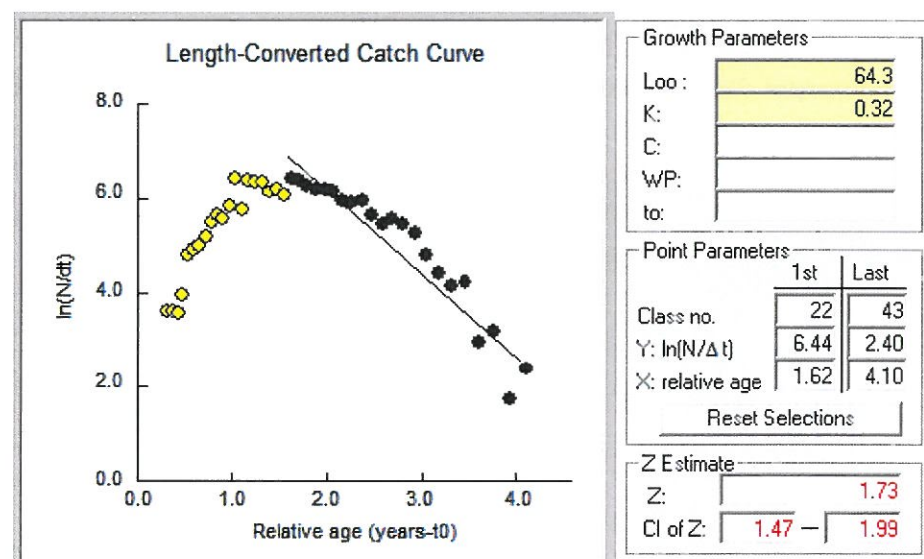
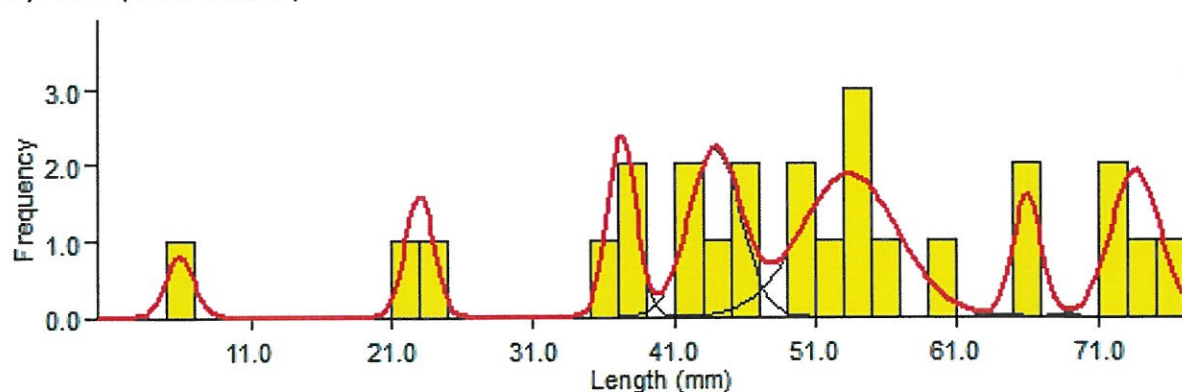
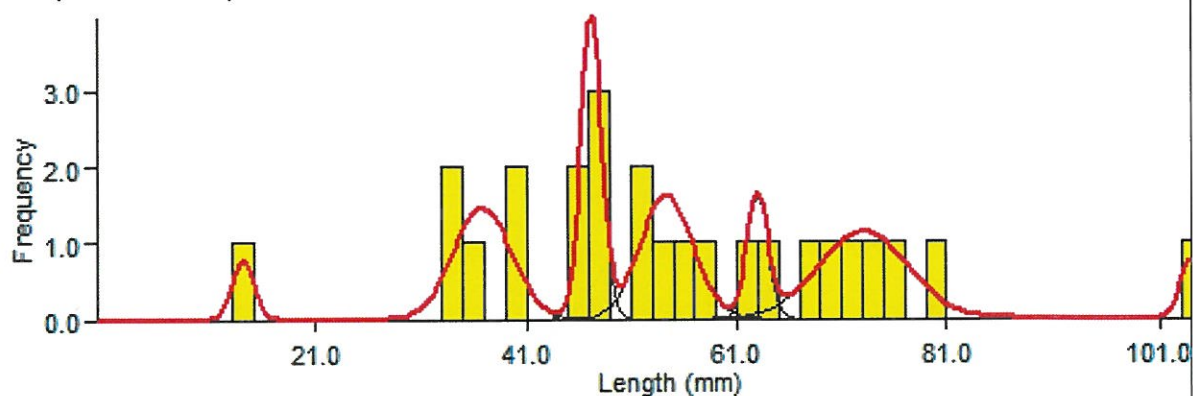


Fig. 18. Mortality rate of *R. philippinarum* estimated using the length-converted catch curve in the FISAT program.

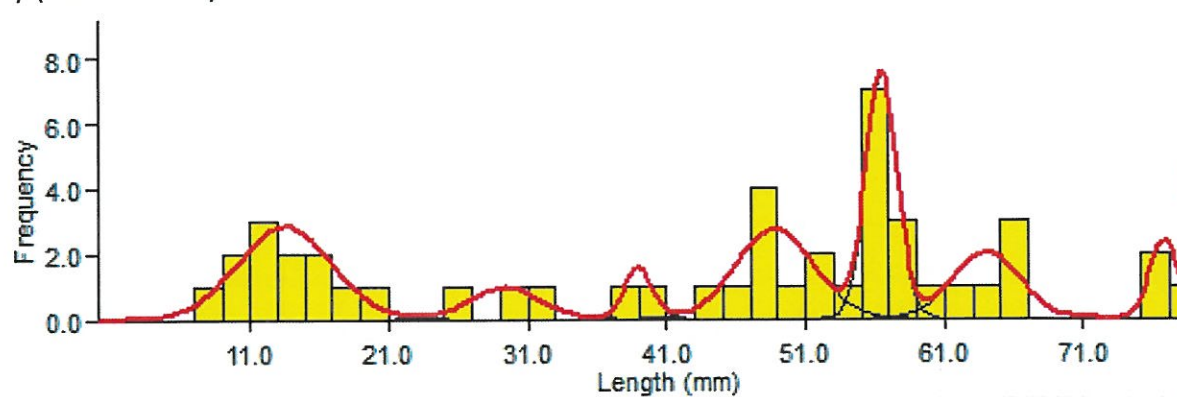
May 2023 (Total no.: 25)



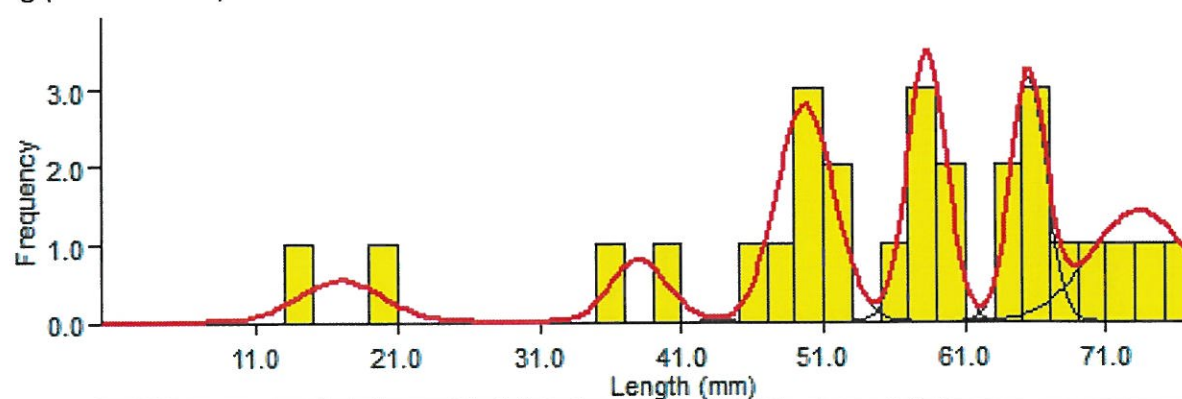
June (Total no.: 25)



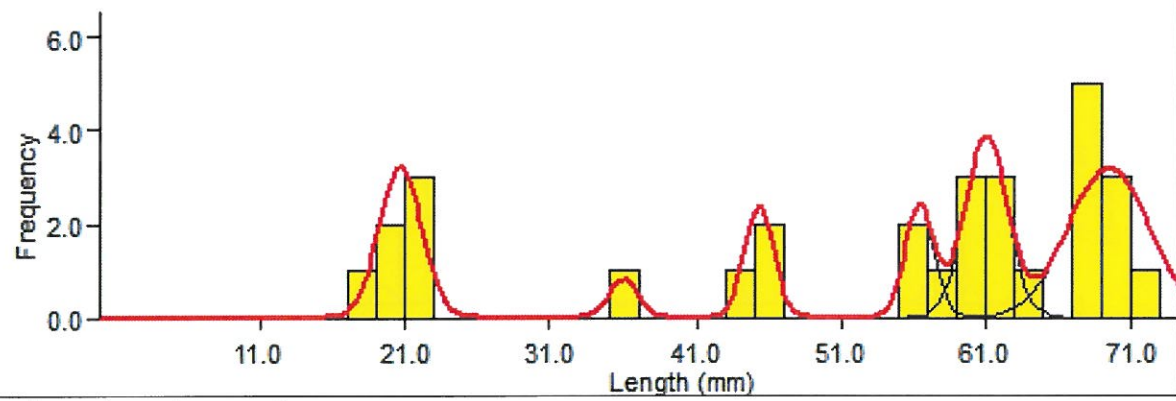
July (Total no.: 46)



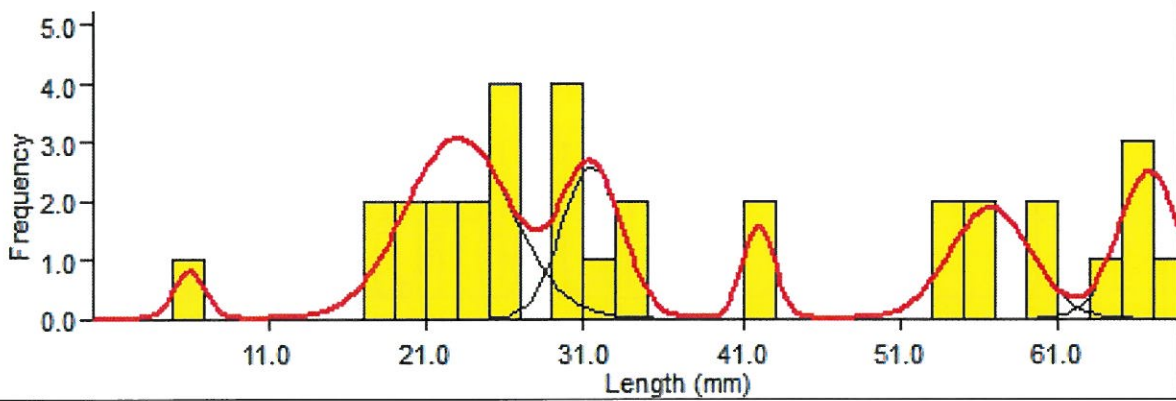
Aug (Total no.: 28)



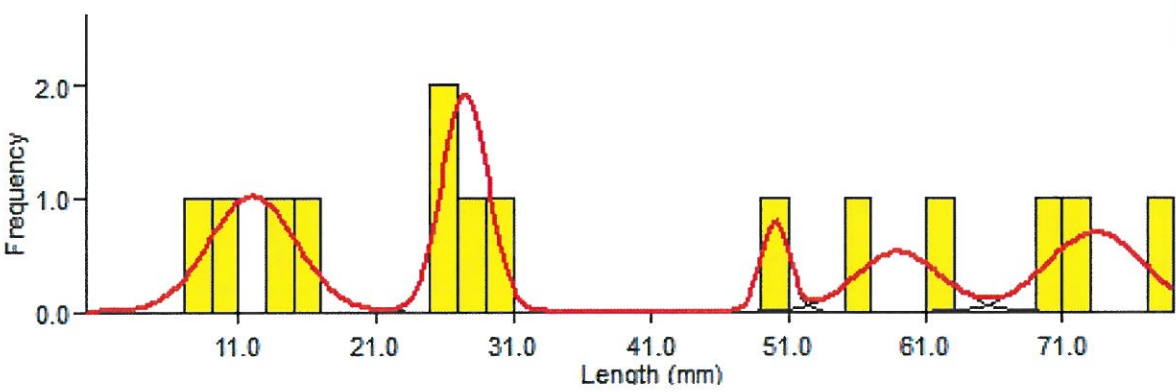
Sept (Total no.: 30)



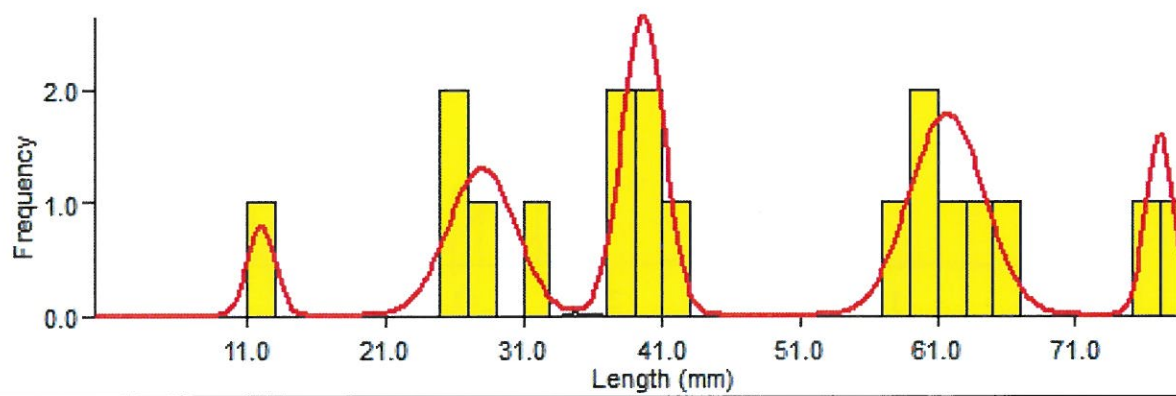
Oct/ Nov (Total no.: 34)



Nov/ Dec (Total no.: 14)



Jan/ Feb 2024 (Total no.: 18)



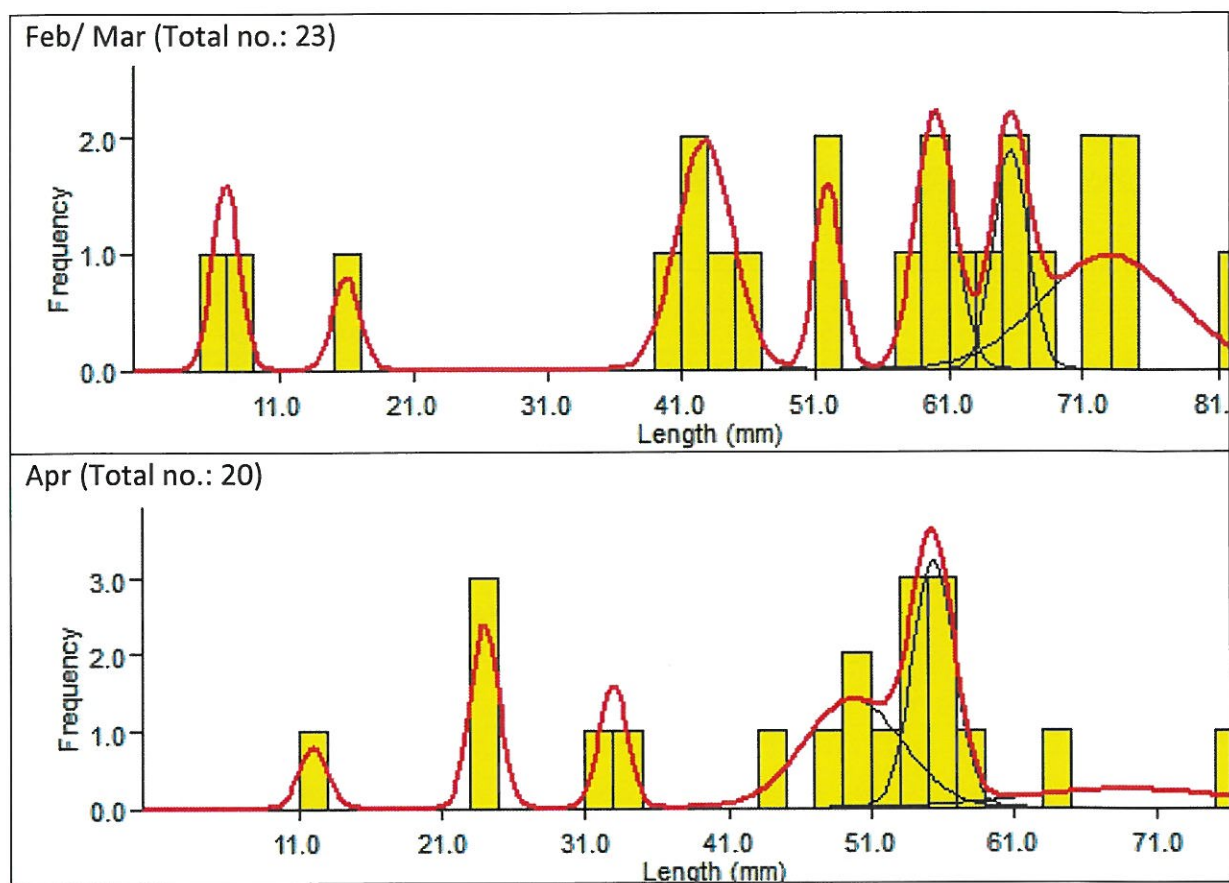


Fig. 19. Size frequency histograms of *Merertrix* sp. with growth parameters estimated using the NORMSEP method in the FISAT program.

Table 20. Number of *Merertrix* sp. individuals in each cohort estimated using the NORMSEP method in the FISAT program.

No. of individual	2024 1 st cohort	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort	Total
May 2023			1	2	3	5	8	2	4		25
June			1		5	5	5	2	6	1	25
July			12	3	2	10	10	6	3		46
Aug.			2		2	7	6	5	6		28
Sept.			6	1	3	3	7	11			31
Oct/Nov.		1	13	6	2	6	6				34
Nov/Dec.		4	4		1	2		3			14
Jan/Feb. 2024		1	4	5		6			2		18
Feb/Mar.	2	1		5	2	4	3	6			23
Apr.	1	3	2	6	6		2				20

Table 21. Average size (mm) of *Merertrix* sp. cohorts estimated using the NORMSEP method in the FISAT program.

Size (mm)	2024 1 st cohort	2023 2 nd cohort	2023 1 st cohort	2022 2 nd cohort	2022 1 st cohort	2021 2 nd cohort	2021 1 st cohort	2020 2 nd cohort	2020 1 st cohort	2019 2 nd cohort
May 2023			6	23	37.32	43.88	53.42	65.99	73.5	
Jun			14		36.81	47.19	54.34	62.96	73.07	104
Jul			13.51	29.34	38.99	48.76	56.48	63.97	76.67	
Aug			17		38	49.74	58.34	65.47	73.26	
Sep			20.67	36	45.34	56.46	61.02	69.57		
Oct/Nov		6.01	23.06	31.5	42	56.71	66.67			
Nov/Dec		12	27.5		50	58.95		73.3		
Jan/Feb 2024		12	28	39.6		61.67			77	
Feb/Mar	7	16		42.8	52	59.88	65.65	72.9		
Apr	12	24	33	49.74	55.39		68.78			
Annual growth			27.0	26.74	18.07		15.36			

Merertrix spp. exhibited two recruitment events per year, with the first occurring between May and August 2023 and the second between October/November 2023 and February/March 2024 (Fig. 19, Table 20). Although annual shell growth could be obtained for only four cohorts, an age-related decline in growth was evident, ranging from 27.0 mm in the youngest cohort (2023 first cohort) to 15.36 mm in the 2021 second cohort (Table 21).

The asymptotic length (L_{∞}) of *Merertrix* sp., estimated from the von Bertalanffy growth function, was 104 mm, and the instantaneous growth rate constant (K) was 0.36 yr^{-1} (Fig. 20). The total mortality rate (Z) was 1.47, corresponding to an annual survival rate of 22.99% (Fig. 21).

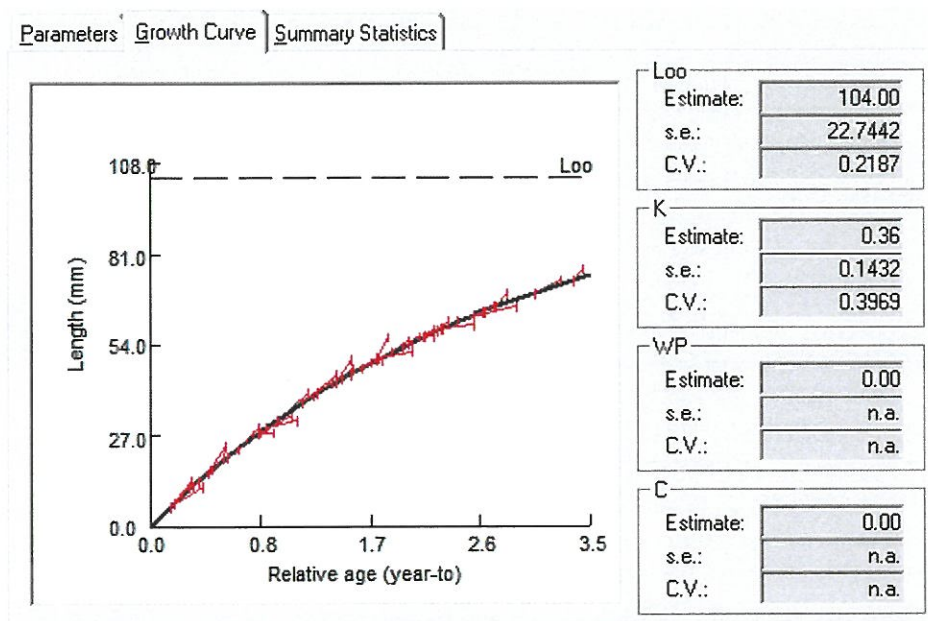


Fig. 20. Von Bertalanffy growth function for *Merertrix* sp. estimated using Appeldoorn's method in the FISAT program.

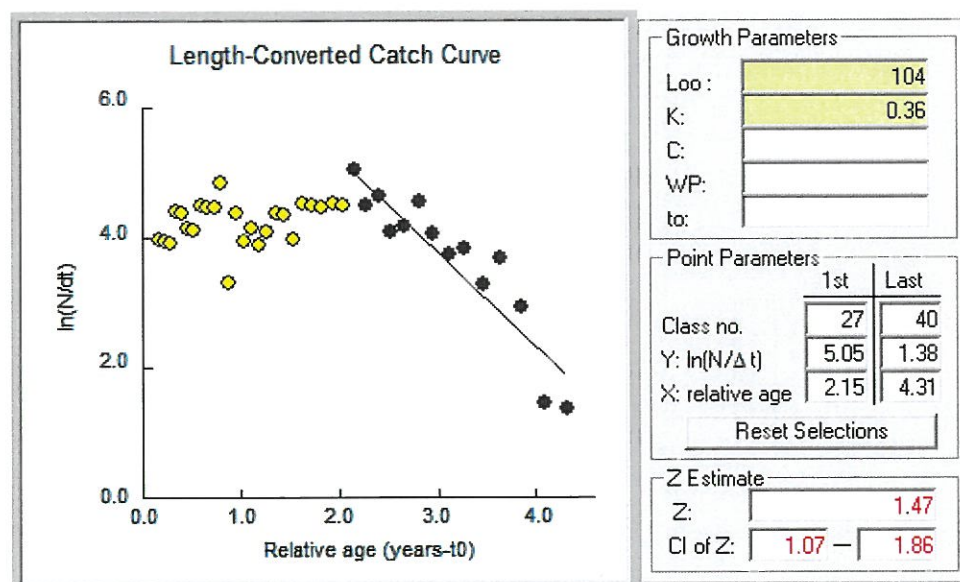
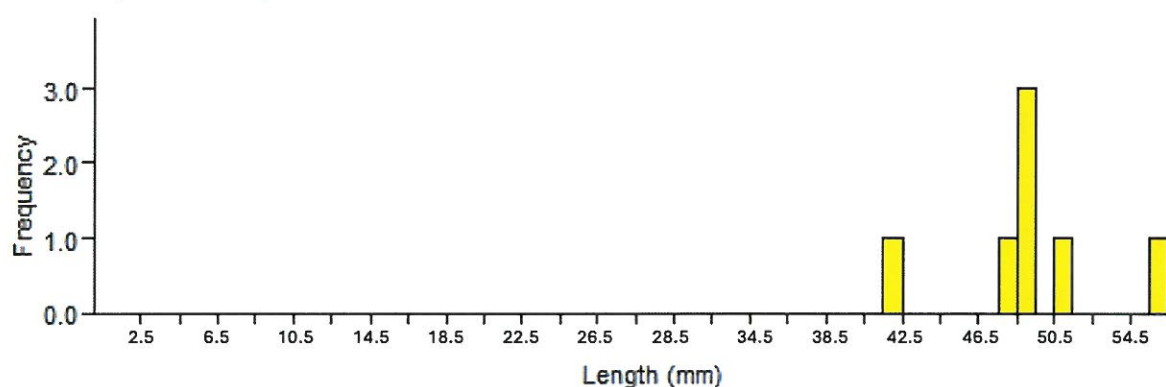
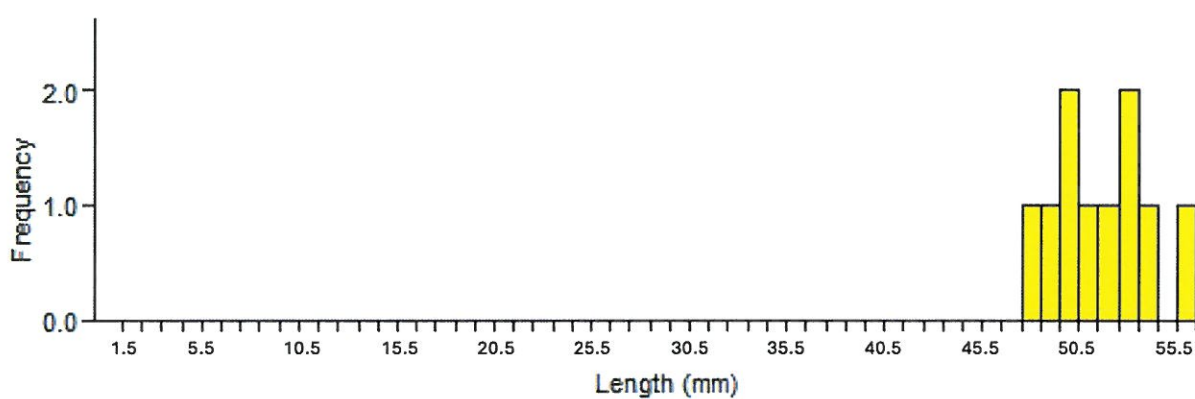


Fig. 21. Mortality rate of *Merertrix* sp. estimated using the length-converted catch curve in the FISAT program.

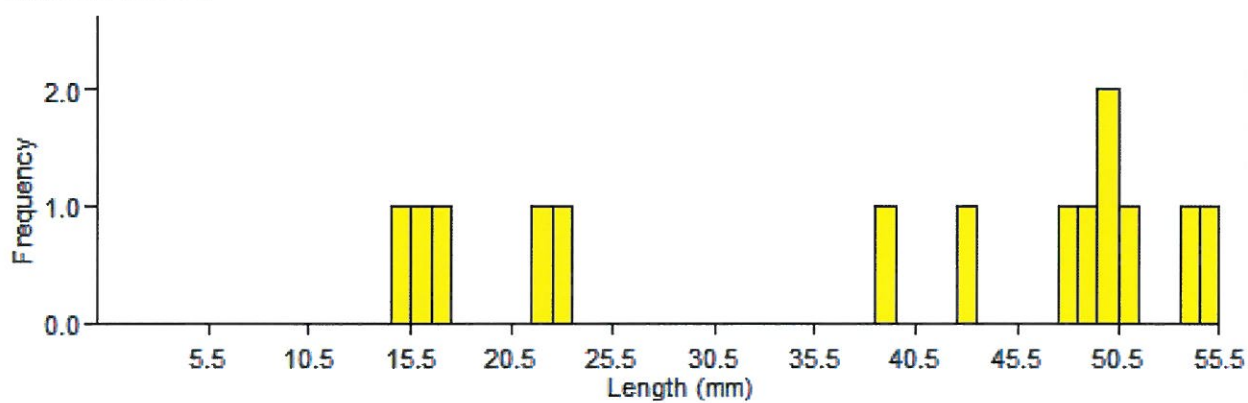
June 2023 (Total no.: 7)



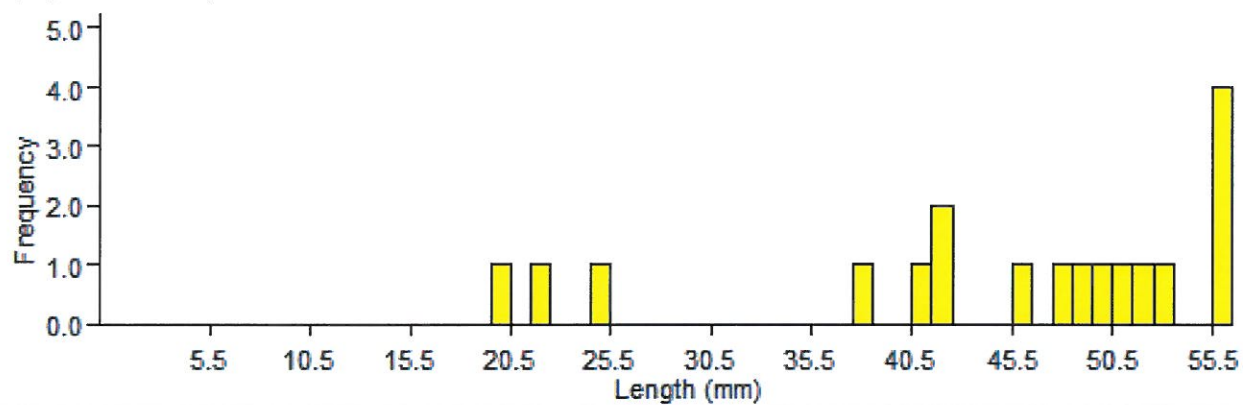
July (Total no.: 10)



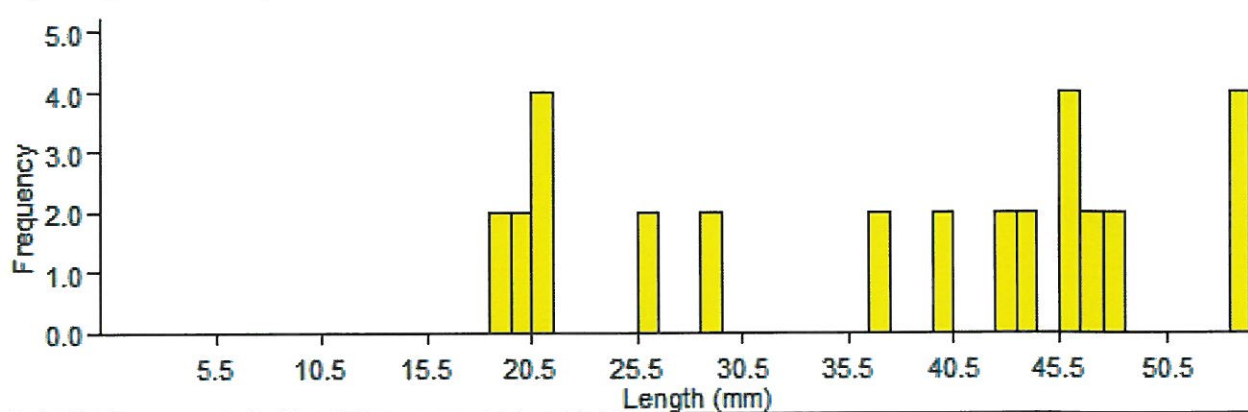
Aug (Total no.: 14)



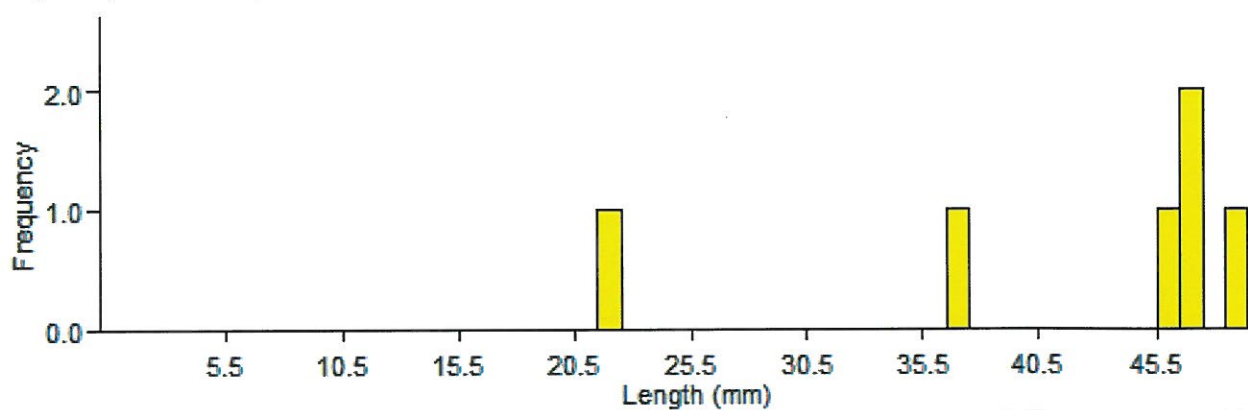
Sept (Total no.: 18)



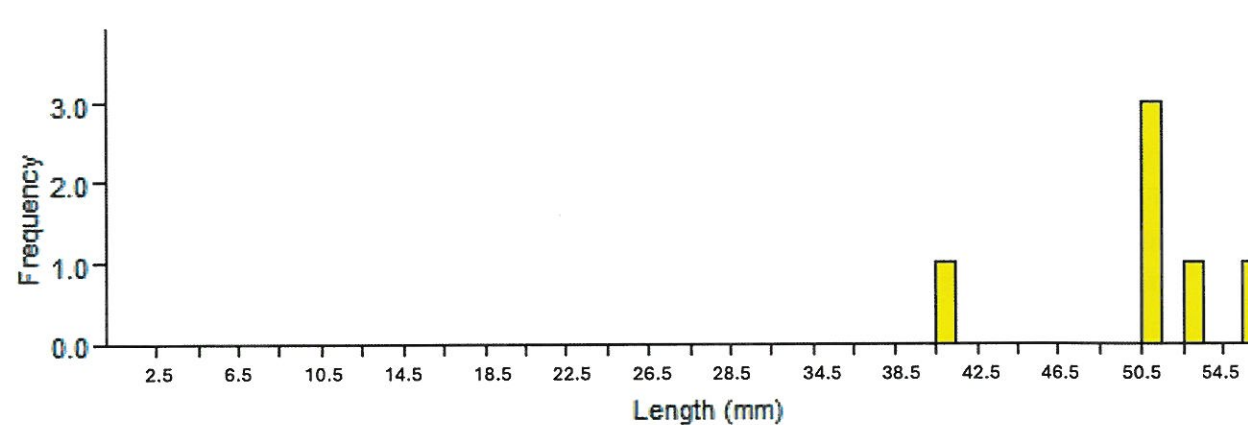
Oct/ Nov (Total no.: 32)



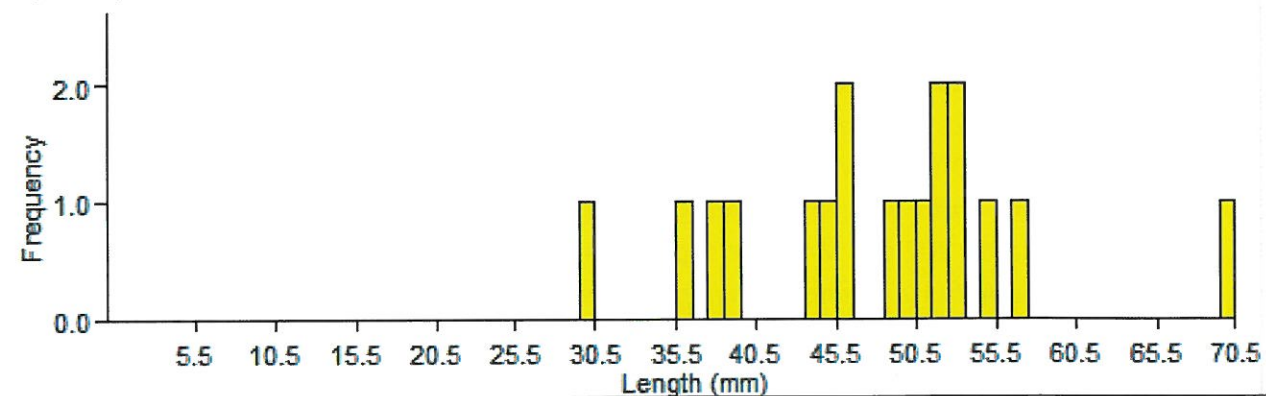
Nov/ Dec (Total no.: 6)



Jan/ Feb 2024 (Total no.: 6)



Feb/ Mar (Total no.: 18)



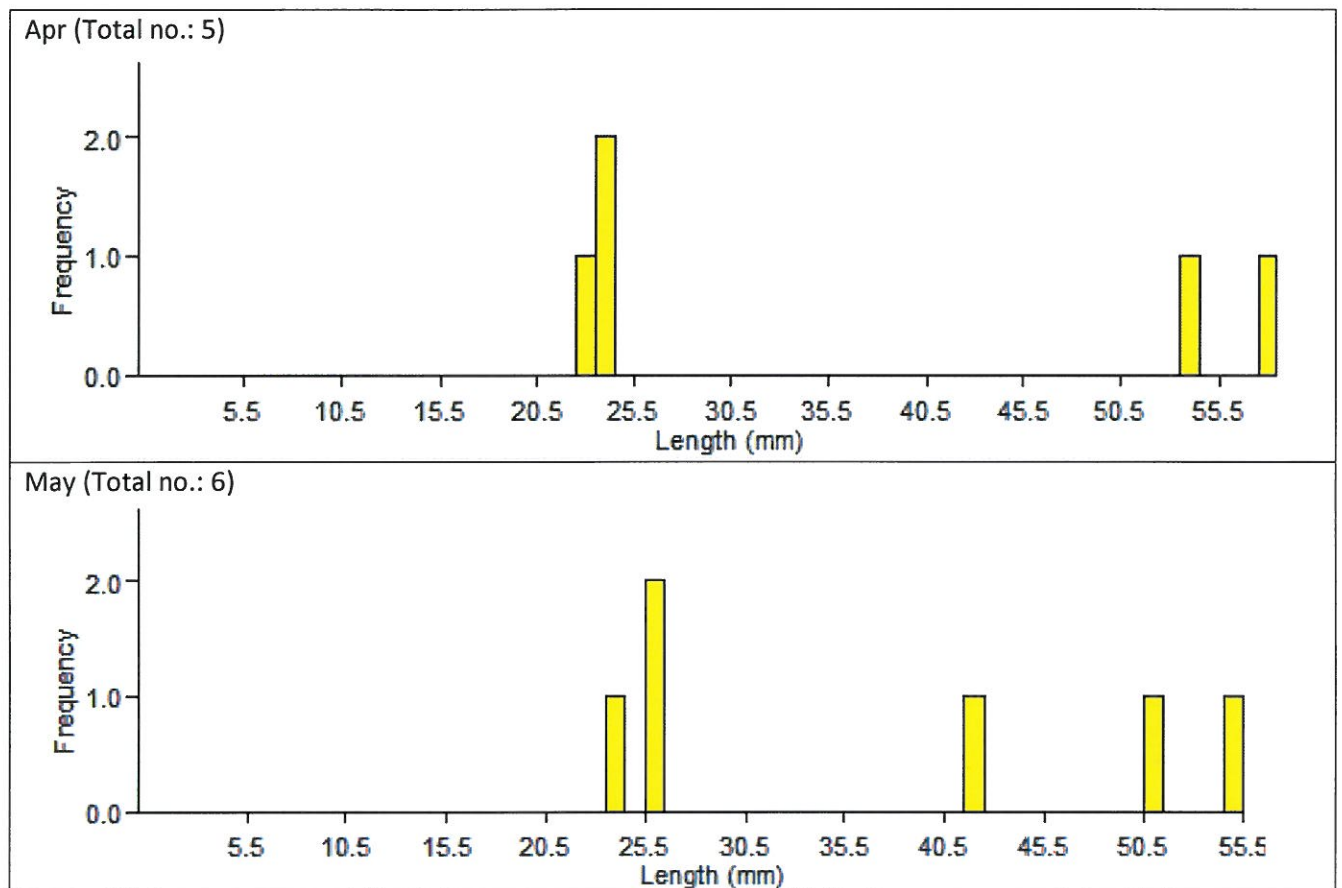


Fig. 22. Size frequency histograms of *Macridiscus aequilatera* with growth parameters estimated using the NORMSEP method in the FISAT program.

Since only a very small number of *M. aequilatera* individuals were collected in Tung Wan, cohort analysis could not be conducted (Fig. 22). Nevertheless, the length-frequency distribution suggested two recruitment events: the first between August and November/December 2023, when smaller individuals (approximately 15-20 mm) appeared in the population, and the second around April to May 2024.

4.2.5 Temporal variations of mean shell length, tissue dry mass and ash free dry mass of *A. flexuosa*, *R. philippinarum* and *Meretrix* spp.

Figures 23-25 show the mean shell length, tissue dry mass and ash free dry mass of *A. flexuosa*, *R. philippinarum* and *Meretrix* spp., respectively. The data for immature and mature individuals are shown separately. The patterns of temporal changes were similar between dry mass and ash free dry mass for all the species, but different from those for shell length. For immature individuals, the mean shell length did not vary temporally for *A. flexuosa* and *R. philippinarum*, but was significantly smaller between June and August 2023 and in February/March 202 for *Meretrix* spp. The mean shell length of mature individuals varied temporally in *A. flexuosa* and *R. philippinarum* but not for *Meretrix* spp. The mean shell length was the smallest for mature *A. flexuosa* in July and August 2023 and highest in February and April, matching the timing for the intensity of clam digging. For *R. philippinarum*, the lowest

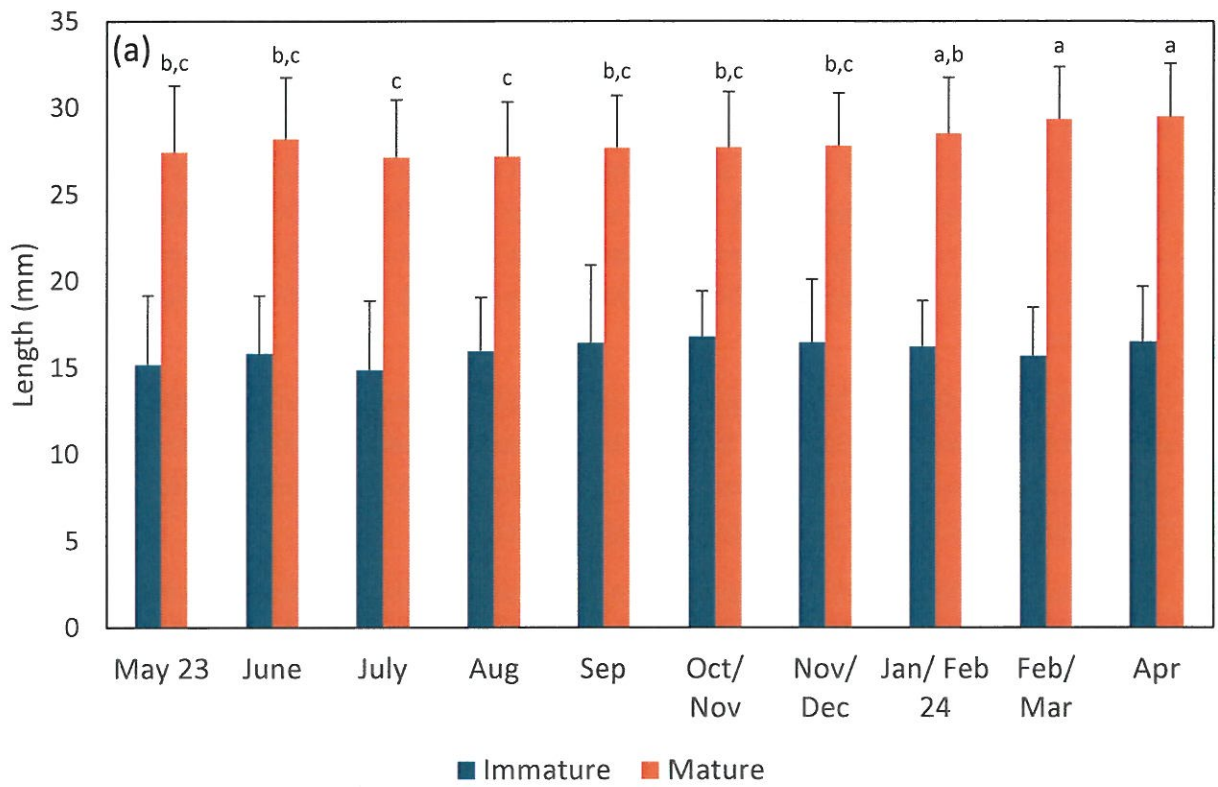
mean shell length was observed in September 2023 and the largest in July 2023, indicating that clam digging intensity was probably not a major factor responsible for the temporal differences in shell length.

For *A. flexuosa* at Shui Hau, shell length of mature individuals varied significantly over time, whereas no significant variation was observed for immature individuals (Fig. 23a). Mature individuals reached their largest shell lengths in February/March and April 2024, and their smallest in July and August 2023. Tissue dry mass (Fig. 23b) and AFDM (Fig. 23c) followed similar patterns, with higher values between January and March 2024 and lower values during the summer months (June to October/November 2023) for both mature and immature individuals.

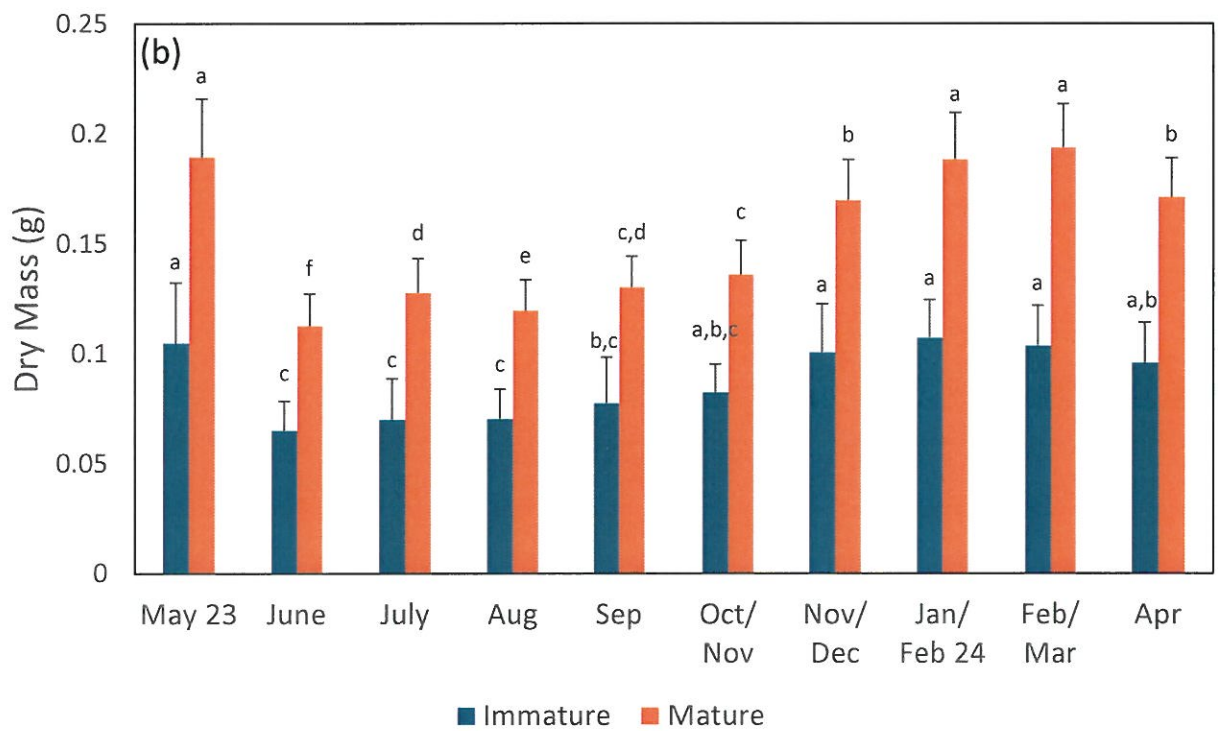
For *R. philippinarum*, the largest mature individuals were recorded in July 2023 and the smallest in September 2023 (Fig. 24a). As in *A. flexuosa*, shell length did not vary significantly over time. However, both tissue dry mass and AFDM were significantly higher between June and August 2023 than in other months (Figs. 24b–c).

Unlike *A. flexuosa* and *R. philippinarum*, the shell length of mature *Meretrix* spp. did not vary significantly over time (Fig. 25a), although immature individuals were significantly larger in October/November 2023 and January/February 2024. Tissue dry mass and AFDM varied significantly over time for both mature and immature individuals (Figs. 25b–c). For mature individuals, both metrics were highest in July 2023, whereas for immature individuals, they peaked in January/February 2024.

Anomalocardia flexuosa



Anomalocardia flexuosa



Anomalocardia flexuosa

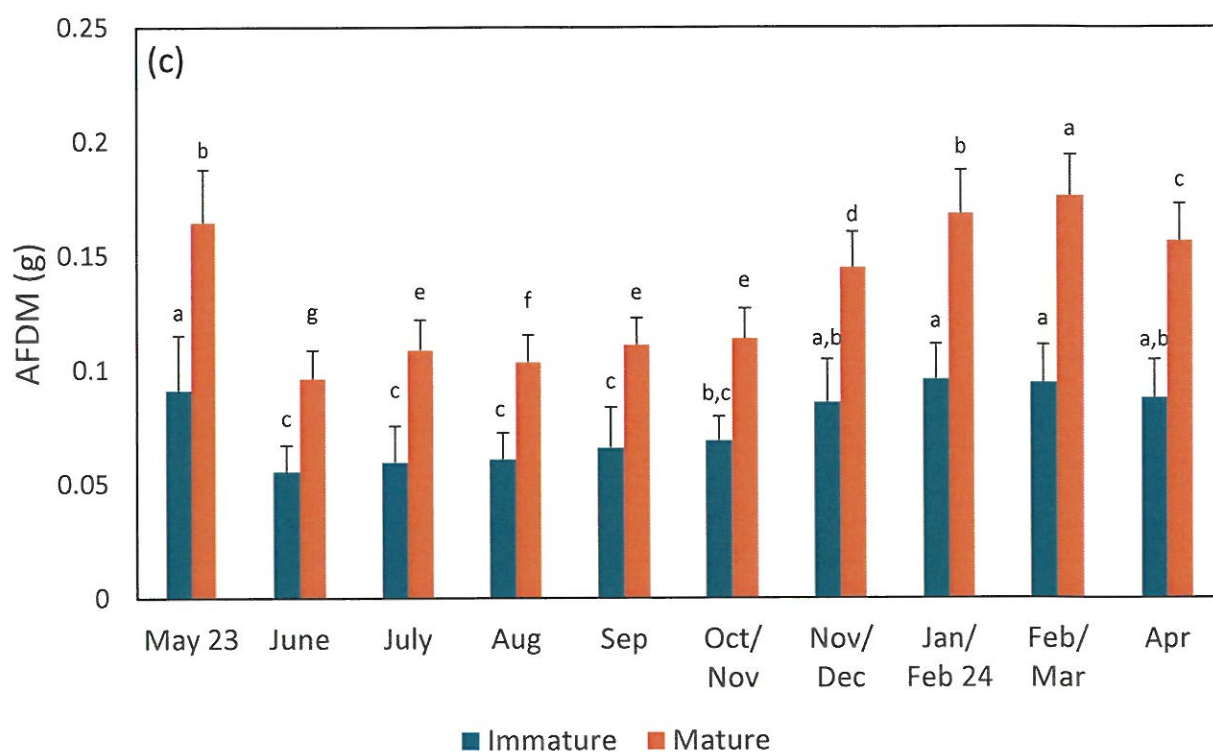
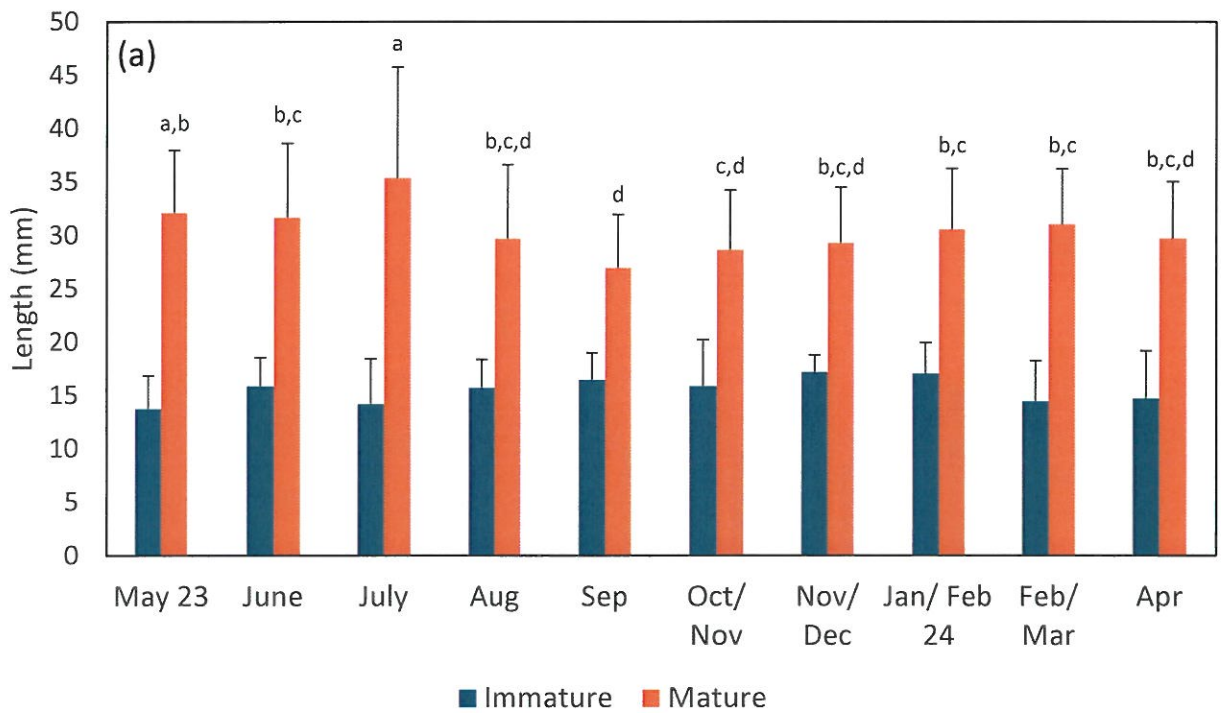
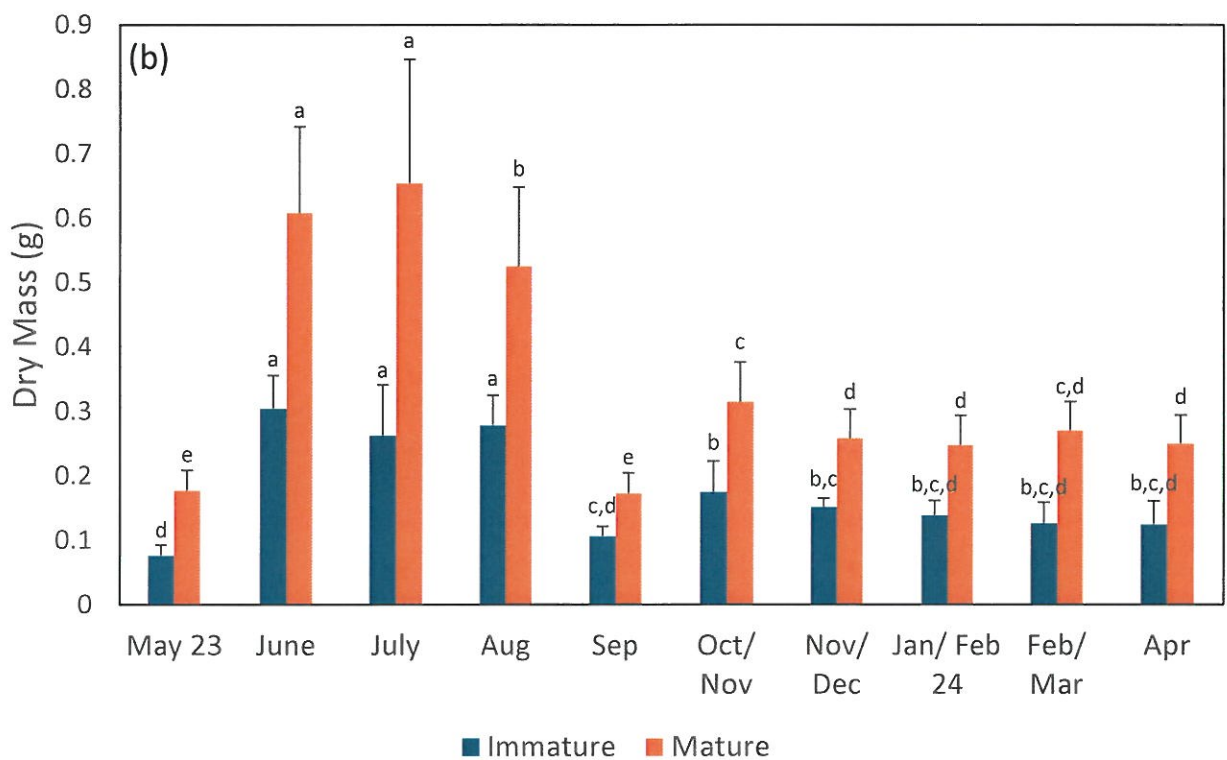


Fig. 23. Mean (a) length (mm), (b) dry mass (g), and (c) ash-free dry mass (g) of mature and immature *A. flexuosa* from May 2023 to April 2024. Different letters denote statistically significant differences among months. Data for mature and immature individuals were analyzed separately.

Ruditapes philippinarum



Ruditapes philippinarum



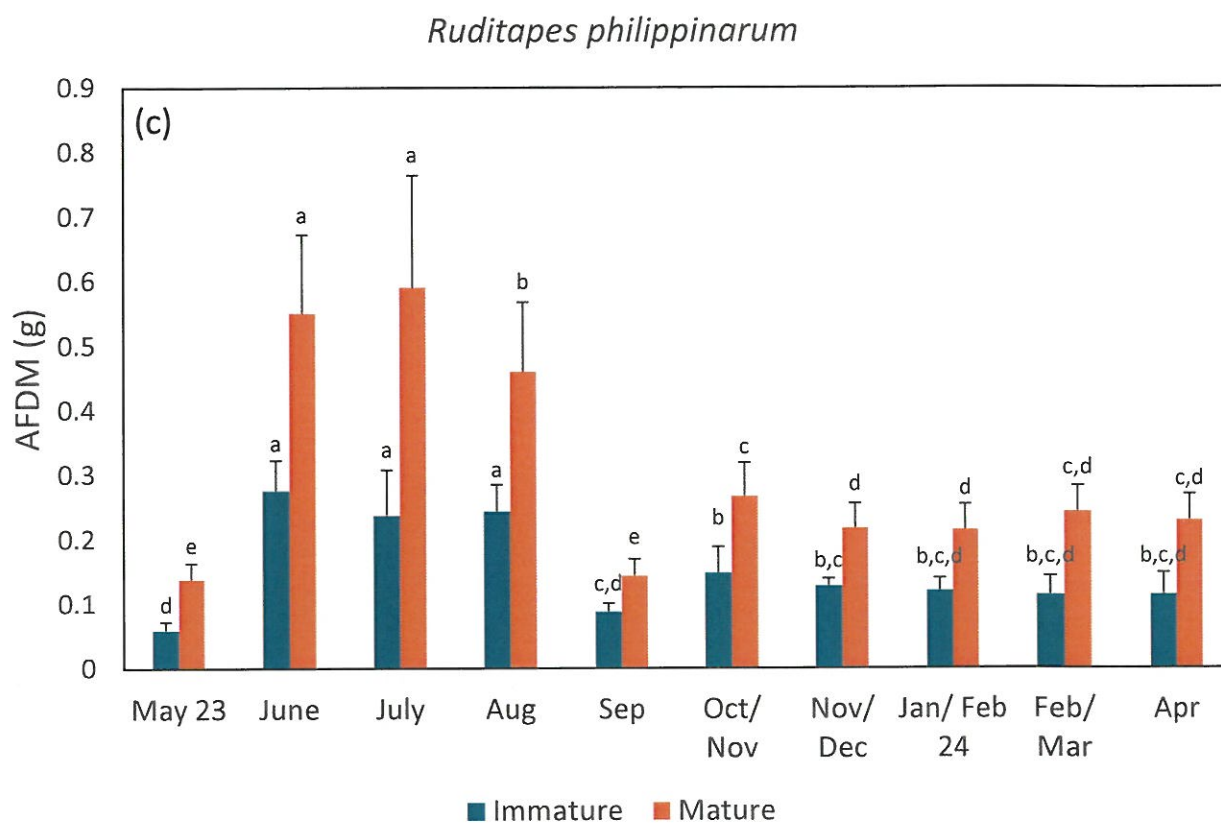
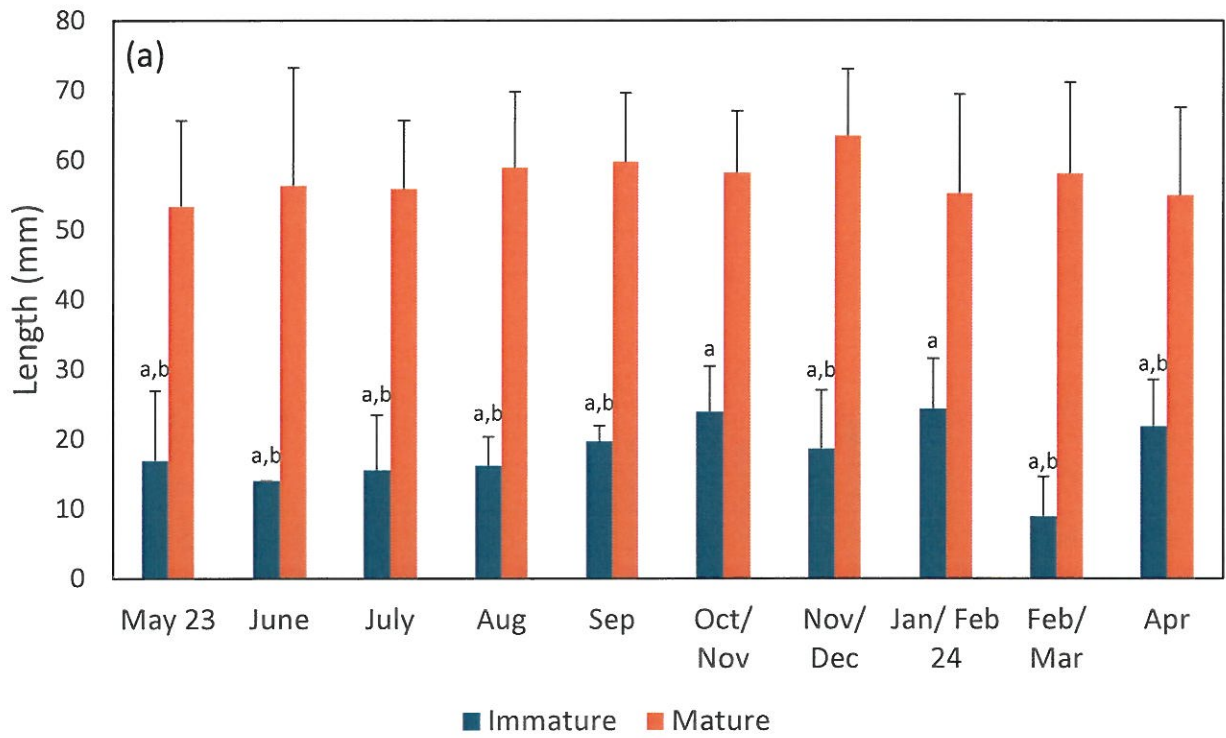
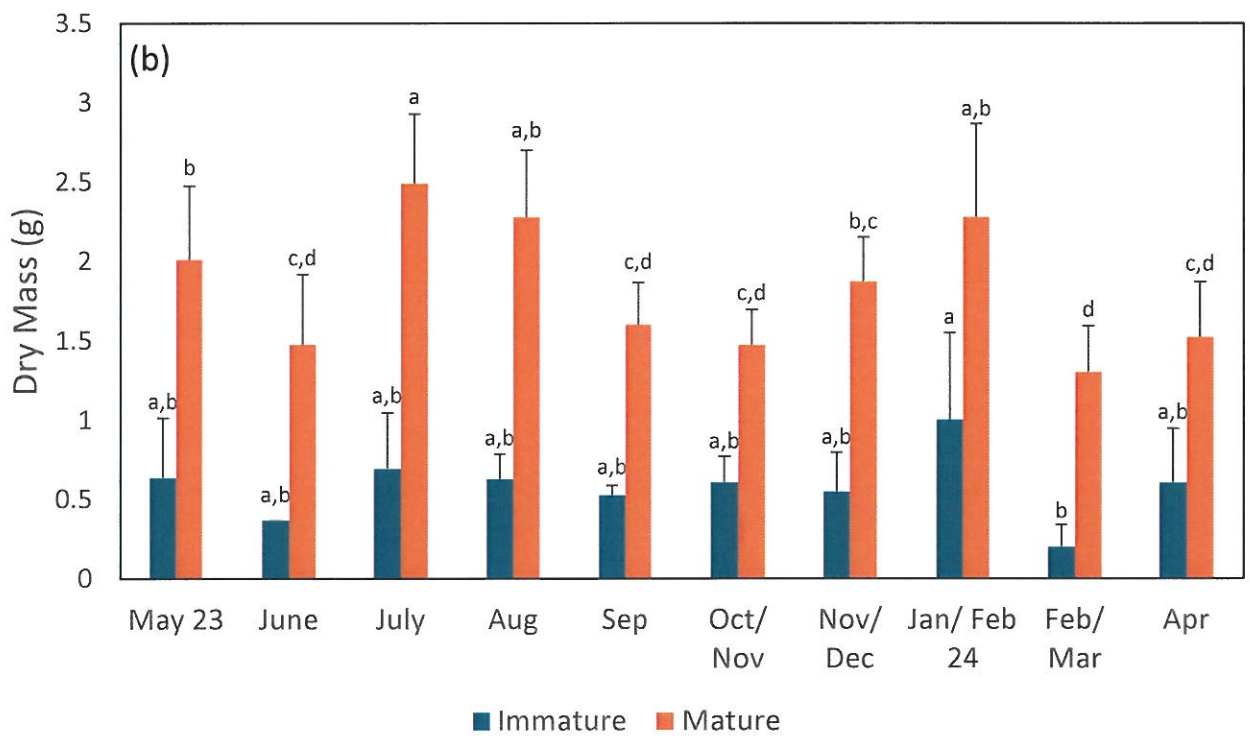


Fig. 24. Mean (a) length (mm), (b) dry mass (g) and (c) ash free dry mass (g) of both mature and immature *R. philippinarum* from May 2023 to April 2024. Different letters denote statistically significant differences among months. Data for mature and immature individuals were analyzed separately.

Meretrix spp.



Meretrix spp.



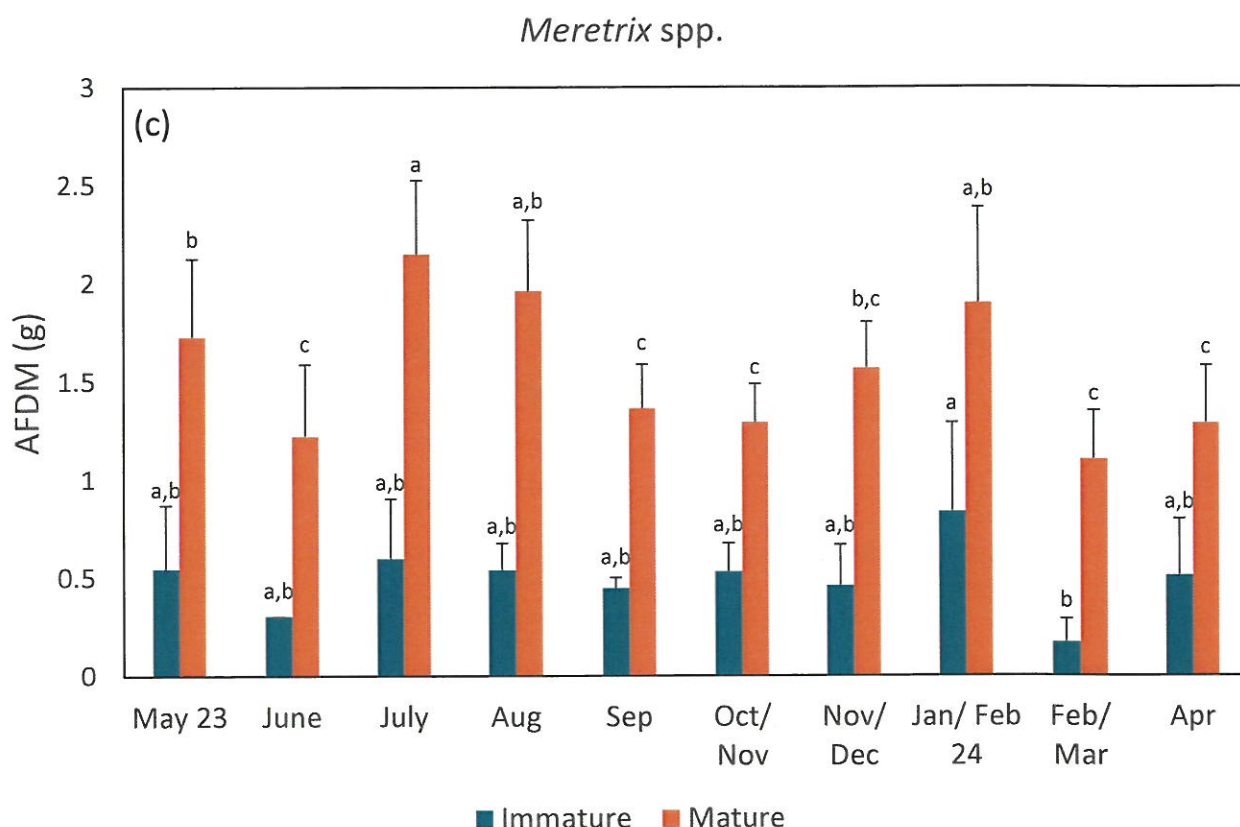


Fig. 25. Mean (a) length (mm), (b) dry mass (g) and (c) ash free dry mass (g) of both mature and immature *Meretrix* spp. from May 2023 to April 2024. Different letters denote statistically significant differences among months. Data for mature and immature individuals were analyzed separately.

4.2.6 Temporal variation in dry mass and ash free dry mass (AFDM) of standard-sized mature individuals of *Anomalocardia flexuosa*, *Ruditapes philippinarum* and *Meretrix* spp.

Figure 26 illustrates temporal changes in dry mass (DM), while Figure 27 shows ash-free dry mass (AFDM) of mature individuals of three clam species—*Anomalocardia flexuosa*, *Ruditapes philippinarum*, and *Meretrix* spp.—from May 2023 to April 2024. The standard shell lengths used were 27.85 mm, 29.85 mm, and 57.07 mm, respectively, calculated as the average size of mature clams collected in Study 3.

Temporal patterns in DM and AFDM were broadly similar across all three species, although each exhibited distinct seasonal trends. *A. flexuosa* showed an extended period of high DM and AFDM from November to May, followed by a trough between June and November. In *R. philippinarum*, a single major peak in both DM and AFDM occurred between June and August, with relatively low values during the rest of the year, particularly in May and September 2023. *Meretrix* spp. exhibited two pronounced peaks, one between July and August and another in January–February.

For clams of standard size, temporal variation in DM and AFDM primarily reflects growth and reproductive processes. Increases in body mass may result from enhanced somatic

growth associated with seasonal increases in food availability or from the accumulation of reproductive tissue prior to spawning.

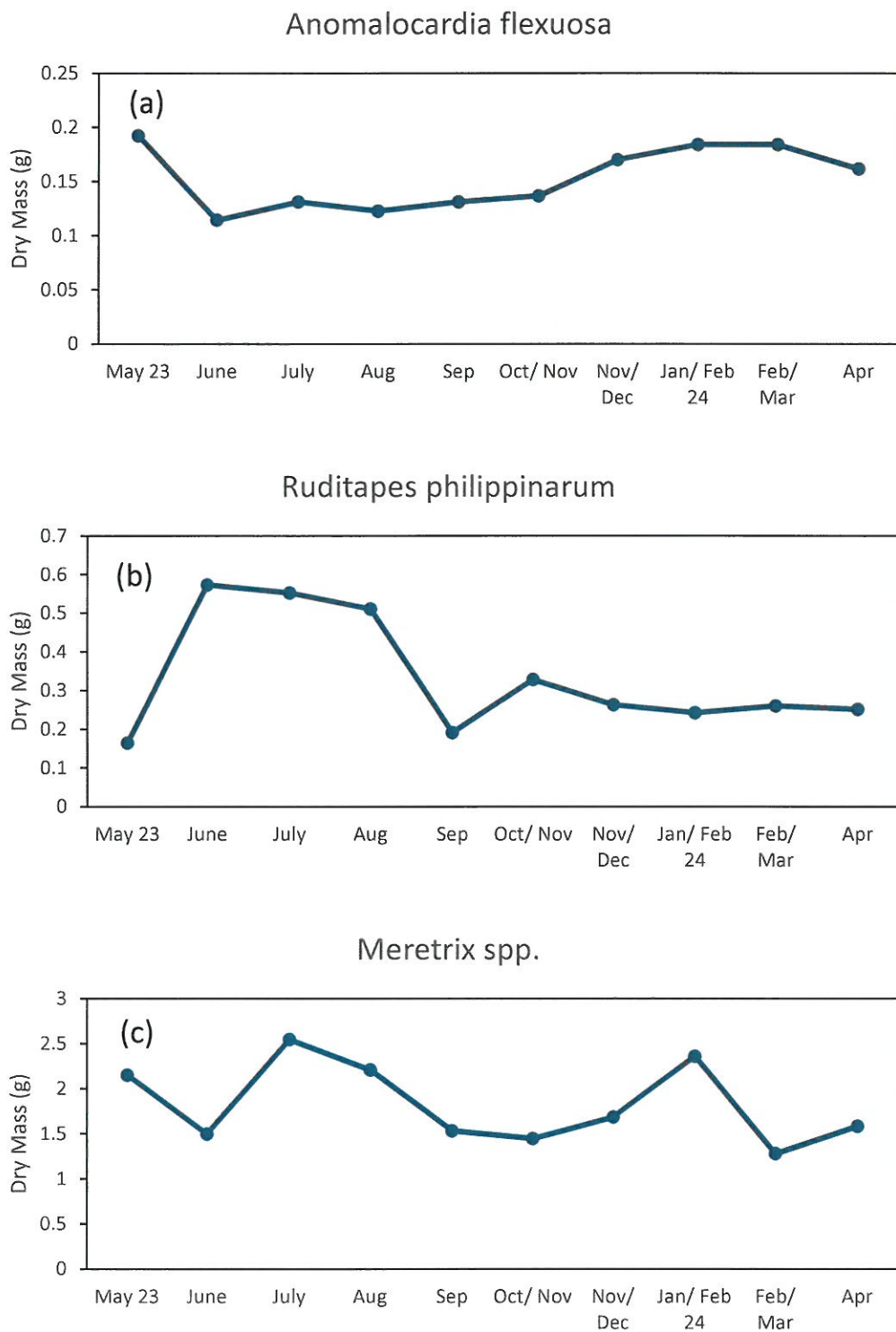


Fig. 26. Dry mass of a standard-sized mature (a) *Anomalocardia flexuosa* (27.85 mm), (b) *Ruditapes philippinarum* (29.85 mm), and (c) *Meretrix* spp. (57.07 mm) from May 2023 to April 2024.

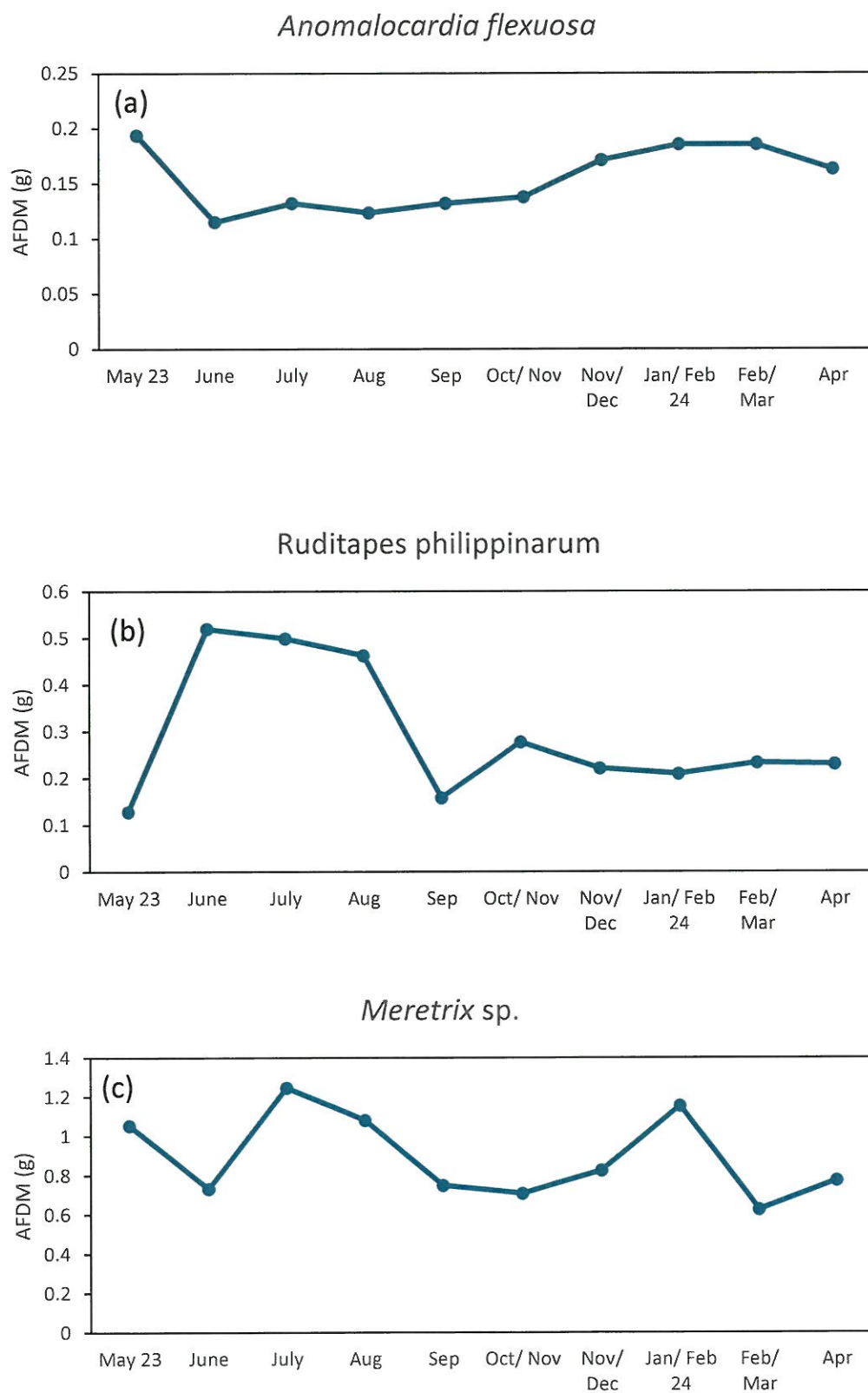


Fig. 27. Ash free dry mass of a standard-sized mature (a) *Anomalocardia flexuosa* (27.85 mm), (b) *Ruditapes philippinarum* (29.85 mm), and (c) *Meretrix* spp. (57.07 mm) from May 2023 to April 2024.

4.3 Overall Discussion

Two recruitment periods have been documented for several local bivalve species, including *Limnoperna fortunei* in fresh waters, *Brachidontes variabilis* in mangrove habitats, *Mytilopsis sallei* on hard shores and *Anomalocardia squamosa* on more open sand shores (Morton, 1977, 1978, 1988, 1989). This pattern may reflect a single breeding season divided into two phases by the onset of summer rainfall, which characteristically lowers surface water salinities throughout Hong Kong. Mid-summer rains may inhibit fertilization or spawning, restricting activity to the drier early- and late-summer periods. Alternatively, these rains may flush individuals from the habitat, creating the appearance of a bimodal recruitment pattern (Morton, 1989).

For all species surveyed in this study, the total number of new recruits collected across all quadrats was very low, with no species exceeding 20 individuals per sampling occasion. This pattern is evident in the length-frequency histograms, which illustrate the shell-length distributions of all individuals collected. While the possibility of overlooking very small individuals during sampling cannot be excluded, a more plausible explanation is the overexploitation of mature individuals, which has likely reduced overall reproductive output. This impact may have been exacerbated during the COVID-19 outbreak in 2020, when international restrictions forced many residents to remain in Hong Kong, leading to a sharp increase in local outdoor activities, including clam digging. Such intense harvesting pressure could remove large numbers of mature clams within a short time, thereby diminishing reproductive capacity. The consequences may be long-lasting, as a reduced spawning stock can lead to consistently low recruitment rates, consistent with the poor recruitment success observed in this study.

The temporal patterns of tissue dry mass and AFDW for standard-sized individuals were similar within each species. In *A. flexuosa* from Shui Hau, lower AFDW values were recorded between June and October 2023. This decline likely reflected spawning activity, consistent with the cohort-based length-frequency histograms, which showed two recruitment events: a major one between May and July 2023 and a minor one in September 2023.

R. philippinarum also exhibited two recruitment events, one in July and another in October-November 2023. However, this pattern was not clearly reflected in the temporal changes in tissue dry mass and AFDW: both metrics were high in July, when recruitment occurred. Conversely, both were low between November/December 2023 and January/February 2024, when no recruitment took place.

Similarly, *Meretrix* spp. displayed two recruitment periods each year, though with a longer duration. The first occurred between May and August 2023, and the second between October/November 2023 and February/March 2024. Although some periods of low tissue dry mass and AFDW coincided with recruitment (e.g., June 2023 and February/March 2024), AFDW also peaked during recruitment (e.g., July 2023 and January/February 2024).

Overall, changes in tissue dry mass and AFDW alone are not reliable indicators of spawning activity in these species. These metrics are influenced not only by reproductive investment but also by environmental factors such as food availability—both increase when food is abundant and decrease when food is scarce.

5. Study 4: Effect of clam digging on the macroinvertebrate community

5.1 Methodology

A field manipulation experiment was conducted at four sites to examine how clam digging affected the macroinvertebrate community. Two clam digging sites (Shui Hau, Tung Chung) were selected as impact sites, and two non-digging sites (Tung Wan, Yi O) served as controls. Four treatments were applied: Treatment A was the control without disturbance; Treatment B involved digging the sediment without removing it from the plot; Treatment C involved digging the sediment and removing the clams while leaving the sediment in place; and Treatment D involved digging the sediment up, temporarily placing it aside, and removing the clams. Three replicates were established for each treatment. At each site, three 1 m x 1 m plots were set up, with each plot containing one replicate of each of the four treatment groups. The four treatments were positioned at the four corners of each plot, with a distance of 0.5 m between treatment groups to minimize interference.

The experiment lasted for 12 weeks. Simulated clam-digging activity was carried out weekly, while sediment and associated macrobenthos were sampled every four weeks (Weeks 1, 5, 9, and 13). Sediment samples were collected using a corer (10 cm diameter) inserted to a depth of 15 cm at a randomly selected point within each plot. The extracted sediment was placed in buckets and transported to the laboratory for processing. Samples were sieved through a 1.0 mm mesh and preserved in 5% buffered formalin in seawater. Prior to sorting and identification, all specimens were transferred to 70% ethanol.

Multivariate analysis of species abundance was performed using non-metric multidimensional scaling (NMDS). Similarities in species composition among different treatments, sites and sampling times were compared using ANOSIM (analysis of similarity). Species richness and biodiversity indices were analyzed using a two-way ANOVA design.

5.2 Results and Discussion

5.2.1. Number of species and individuals collected

Seven taxonomic groups comprising 73 species were recorded throughout the study (Table 22). Polychaetes were the most dominant group at all sites, followed by gastropods and bivalves. The percentage of polychaete species was highest at Yi O (81%) and lowest in Tung Wan (55%). The total number of individuals collected varied among sites, ranging from 584 at Shui Hau to 114 in Yi O.

Table 22. Total number of species and individuals collected at each experimental site over the 12-week study period.

Taxonomic Group	Shui Hau		Tung Chung		Yi O		Tung Wan	
	No. of species	No. of individuals	No. of species	No. of individuals	No. of species	No. of individuals	No. of species	No. of individuals
Polychaetes	15	277	30	141	25	103	16	137
Gastropods	1	134	6	44	1	1	9	15
Bivalves	2	45			3	8	2	4
Hermit crabs	1	64					1	5
Amphipods	1	64					1	1
Crabs					1	1		
Barnacles			2	2				

5.2.2. NMDS ordination and dendrogram analysis of species composition and abundance

Based on the NMDS ordination and dendrogram analyses of species composition and abundance across the four sites (Shui Hau, Tung Chung, Tung Wan and Yi O), no significant similarities were observed among different treatments within each site (Figs. 28-31). In contrast, samples from the same sampling week showed higher similarity, suggesting that the effects of different clam-digging methods on the macroinvertebrate community were minimal.

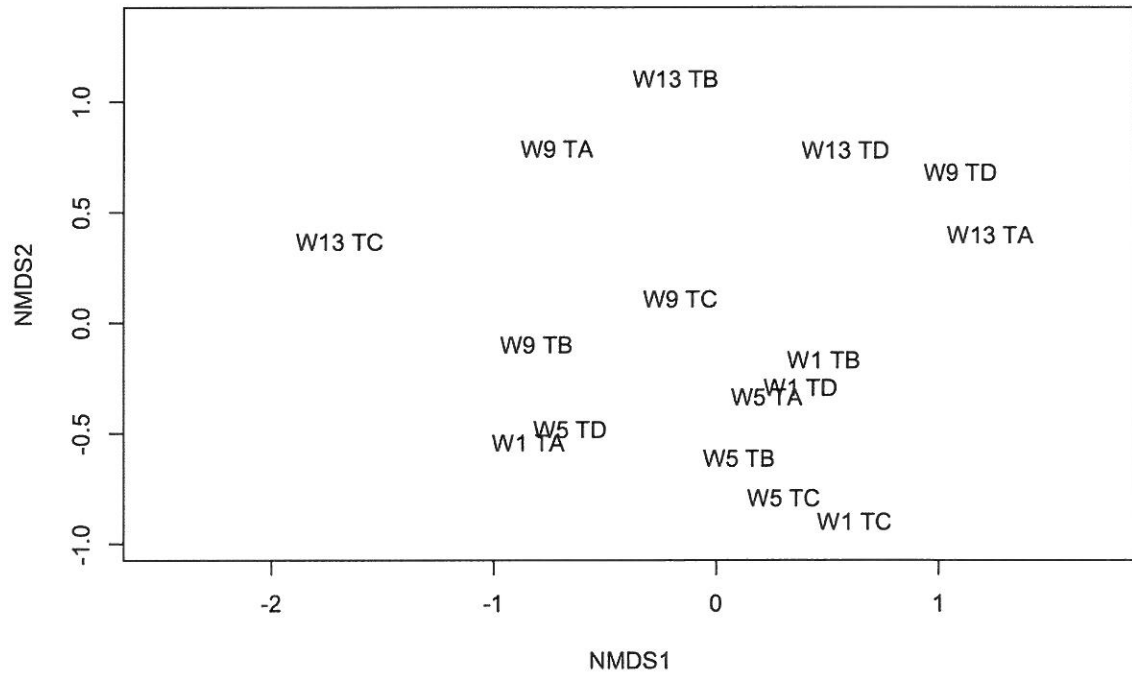
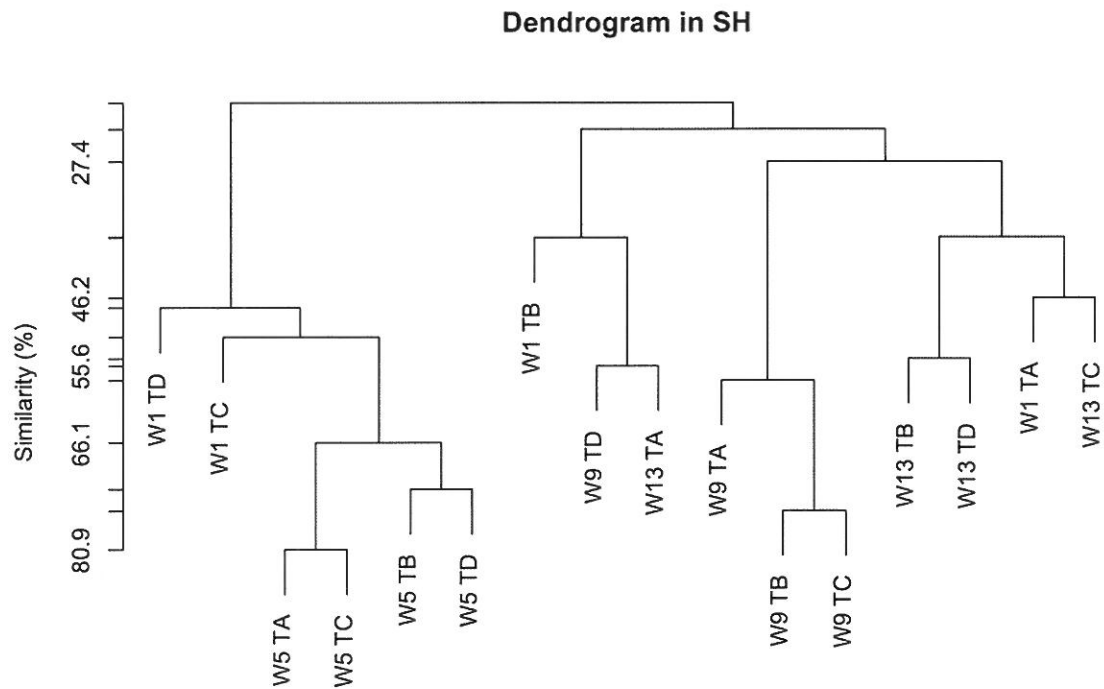


Fig. 28. NMDS ordination and dendrogram of species composition following the clam digging simulation in Shui Hau. W denotes sampling week (Week 1, 5, 9 and 13), and T denotes treatment (Treatments A, B, C and D).

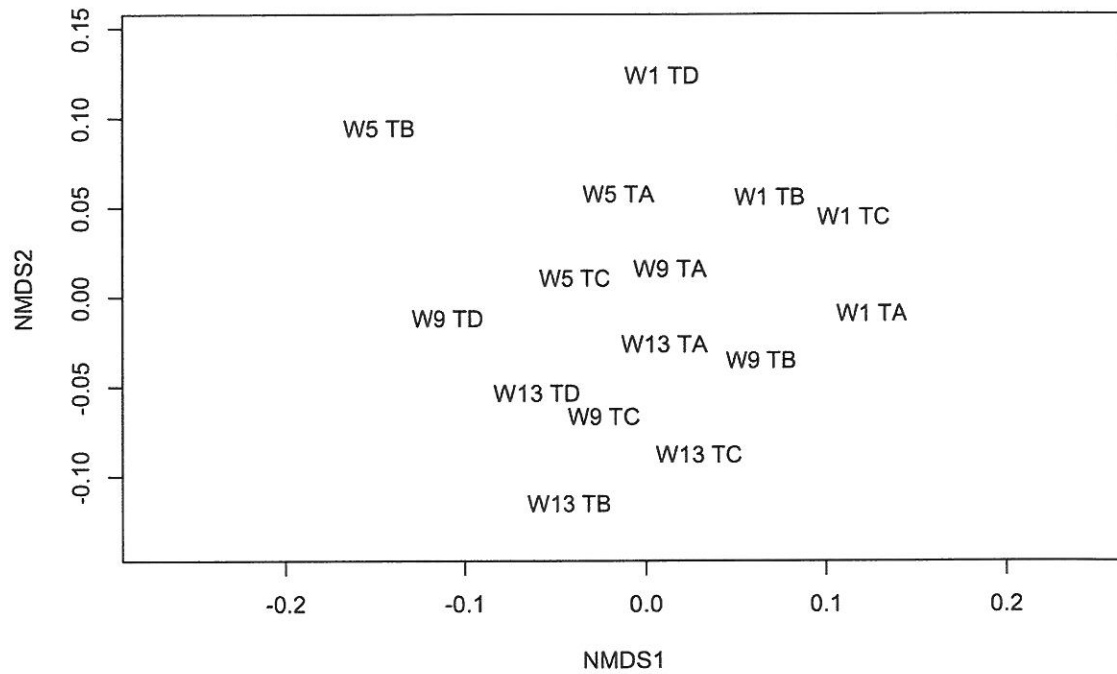
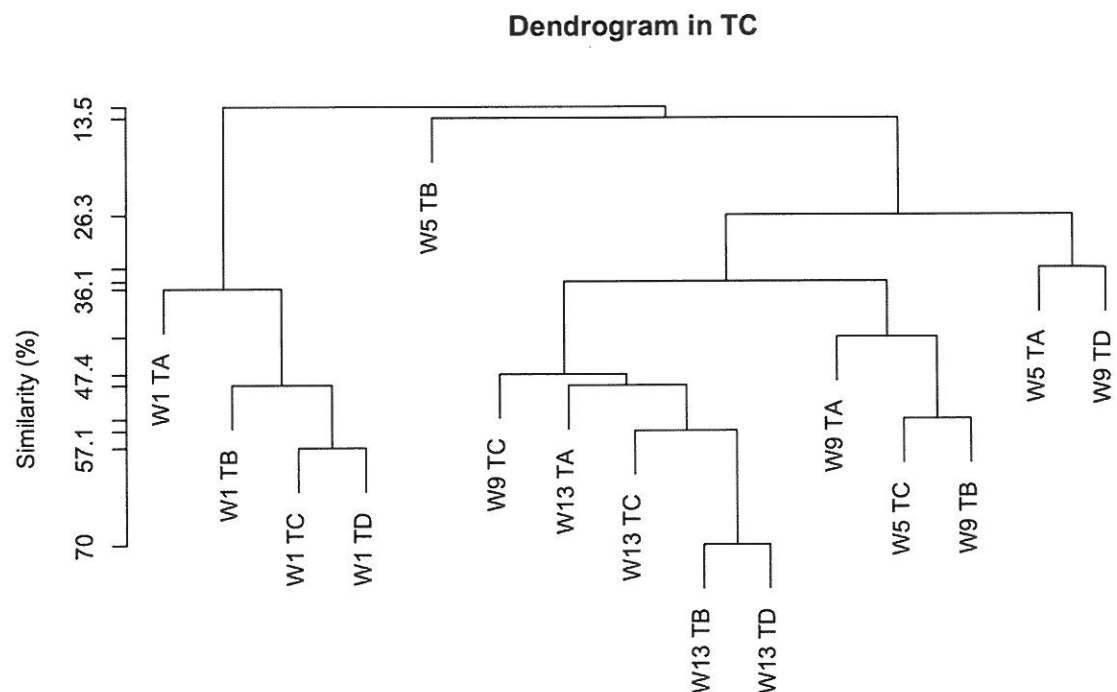


Fig. 29. NMDS ordination and dendrogram of species composition following the clam digging simulation in Tung Chung. W denotes week (Week 1, 5, 9 and 13), and T denotes treatment (Treatments A, B, C and D).

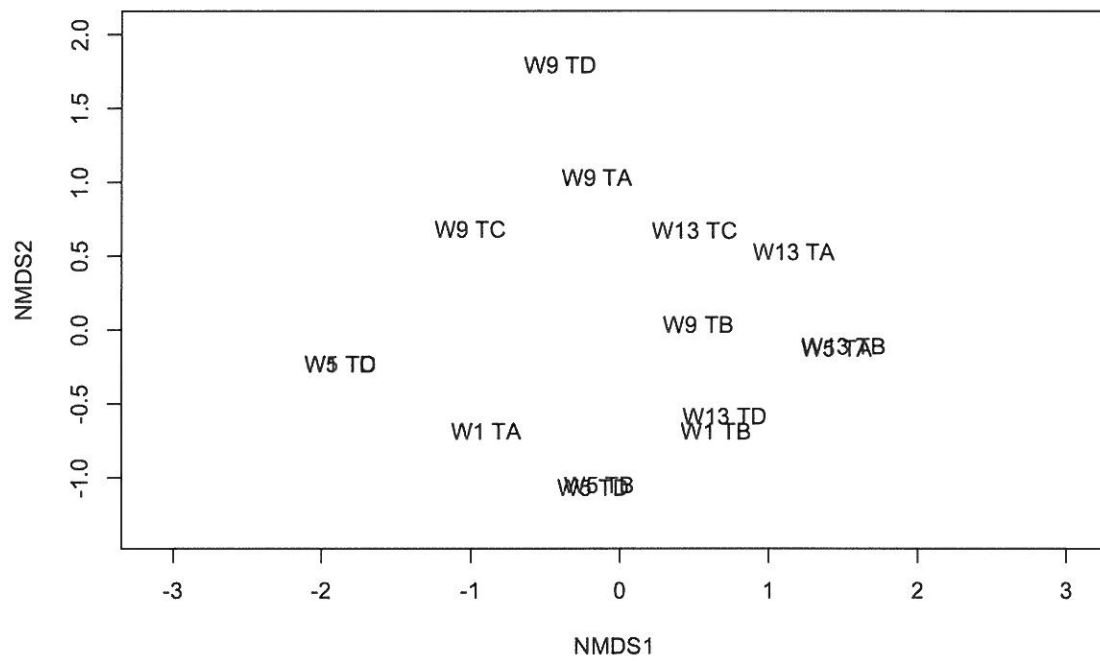
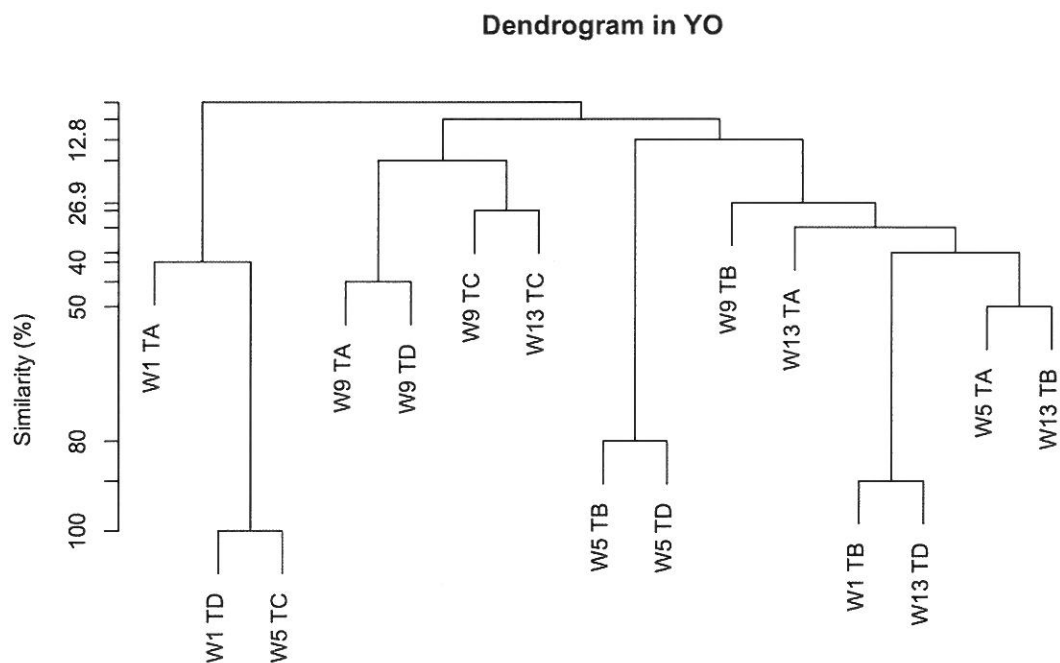


Fig. 30. (a) NMDS ordination and (b) dendrogram of species composition following the clam digging simulation in Yi O. W denotes week (Week 1, 5, 9 and 13), and T denotes treatment (Treatments A, B, C and D).

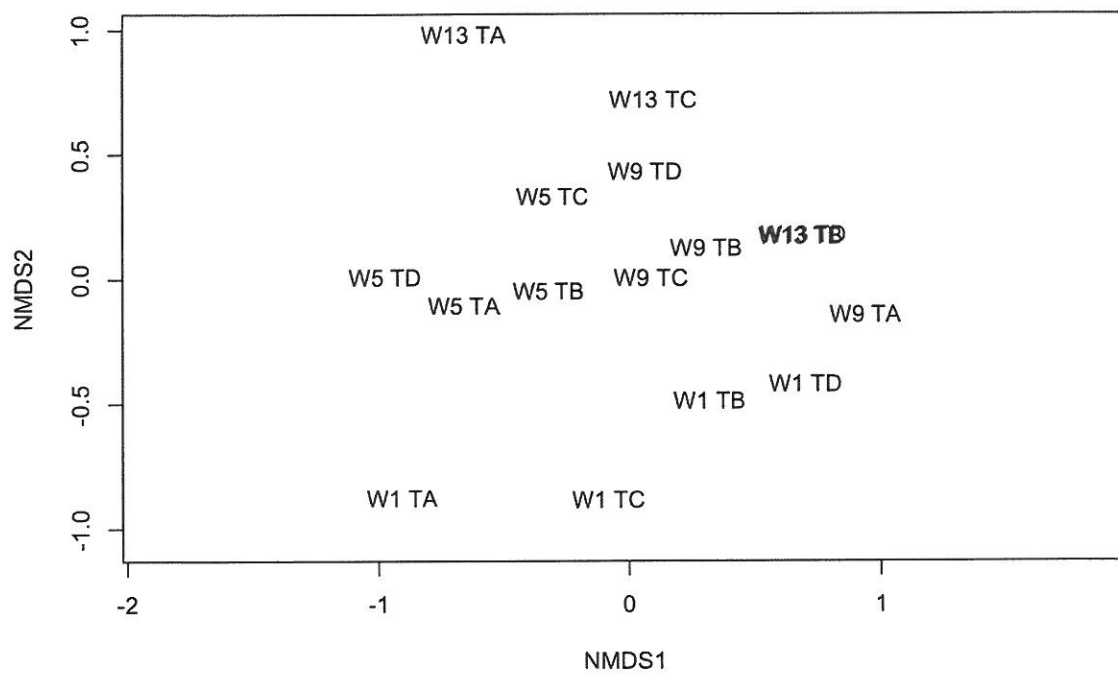
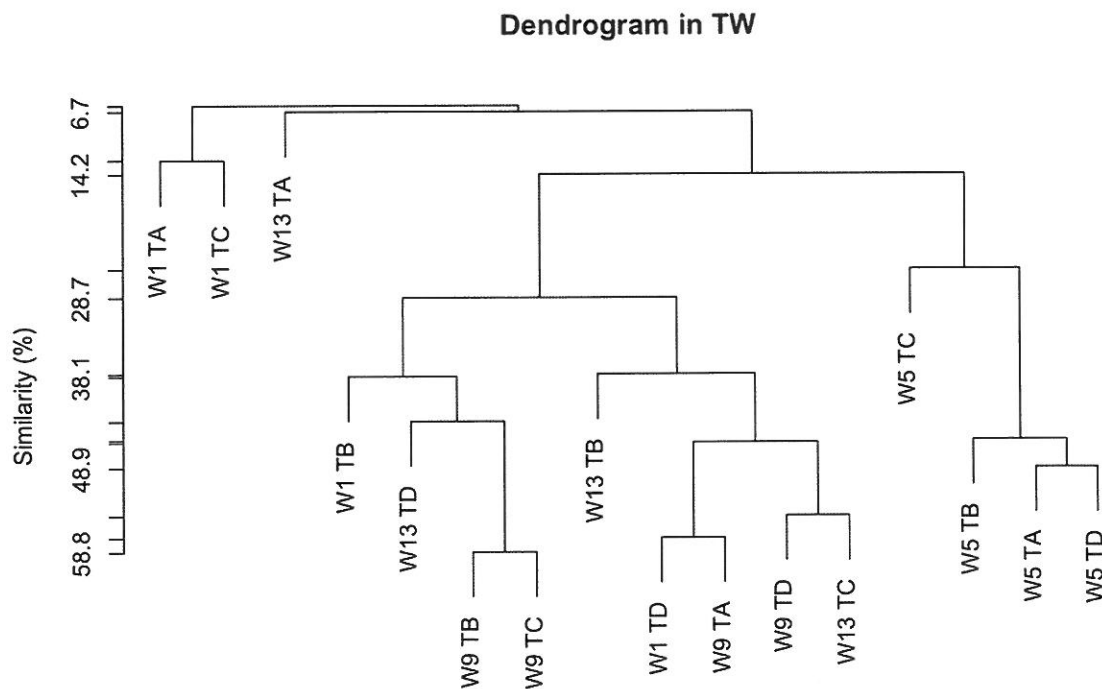


Fig. 31. (a) NMDS ordination and (b) dendrogram of species composition following the clam digging simulation in Tung Wan. W denotes week (Weeks 1, 5, 9 and 13) and T denotes treatment (Treatments A, B, C and D).

5.2.3. Species Diversity and Species Evenness

The results of the inter-site comparisons were consistent with those obtained from the NMDS analysis. At Shui Hau, mean species diversity ranged from 0.58 in Treatment D to 0.74 in Treatment B, while species evenness ranged from 0.27 in Treatment D to 0.56 in Treatment A (Fig. 32). However, neither index was significantly affected by treatment (Species Diversity Index: $F = 0.32$, $p = 0.81$; Species Evenness: $F = 1.44$, $p = 0.25$), time (Species Diversity Index: $F = 2.53$, $p = 0.08$; Species Evenness: $F = 1.14$, $p = 0.35$), or the time $\times$ treatment interaction (Species Diversity Index: $F = 1.47$, $p = 0.21$; Species Evenness: $F = 0.75$, $p = 0.66$).

At Tung Chung, mean species diversity varied significantly among treatments ($F = 2.88$, $p < 0.05$), but not over time ($F = 2.57$, $p = 0.07$) (Fig. 33a). Treatment A had significantly higher species diversity ($H' = 1.12$) than Treatment D ($H' = 0.44$) ($t = 2.80$, $p < 0.05$), whereas other pairwise comparisons among treatments were not significant ($p > 0.05$). Species evenness did not vary significantly among treatments ($F = 0.61$, $p = 0.61$) or over time ($F = 0.45$, $p = 0.61$), with mean values ranging from 0.47 in Treatment D to 0.68 in Treatment A (Fig. 33b).

At Yi O, mean species diversity did not vary significantly among treatments ($F = 1.61$, $p = 0.21$) or over time ($F = 2.73$, $p = 0.07$) (Fig. 34a), with values ranging from 0.26 in Treatment B to 0.86 in Treatment A. Similarly, species evenness did not vary significantly among treatments ($F = 0.64$, $p = 0.60$) or over time ($F = 1.02$, $p = 0.40$) (Fig. 34b), with values ranging from 0.30 in Treatment B to 0.60 in Treatment C.

At Tung Wan, mean species diversity ranged from 0.40 in Treatment A to 1.01 in Treatment C (Fig. 35a), but was not significantly affected by treatment ($F = 1.40$, $p = 0.27$), time ($F = 1.96$, $p = 0.15$), or the time $\times$ treatment interaction ($F = 0.65$, $p = 0.74$). Species evenness ranged from 0.30 in Treatment A to 0.67 in Treatment C (Fig. 35b), but likewise did not vary significantly among treatments ($F = 1.14$, $p = 0.35$), over time ($F = 1.98$, $p = 0.15$), or for the time $\times$ treatment interaction ($F = 0.52$, $p = 0.84$).

Except in Tung Chung, clam-digging activity did not significantly affect the species diversity or evenness of the macrobenthic community. In Tung Chung, clam digging affected species diversity, which was lower in the treatment where sediment was excavated, clams were removed, and the sediment was returned (Treatment D), compared with the undisturbed control (Treatment A). However, the effect of digging did not increase over time.

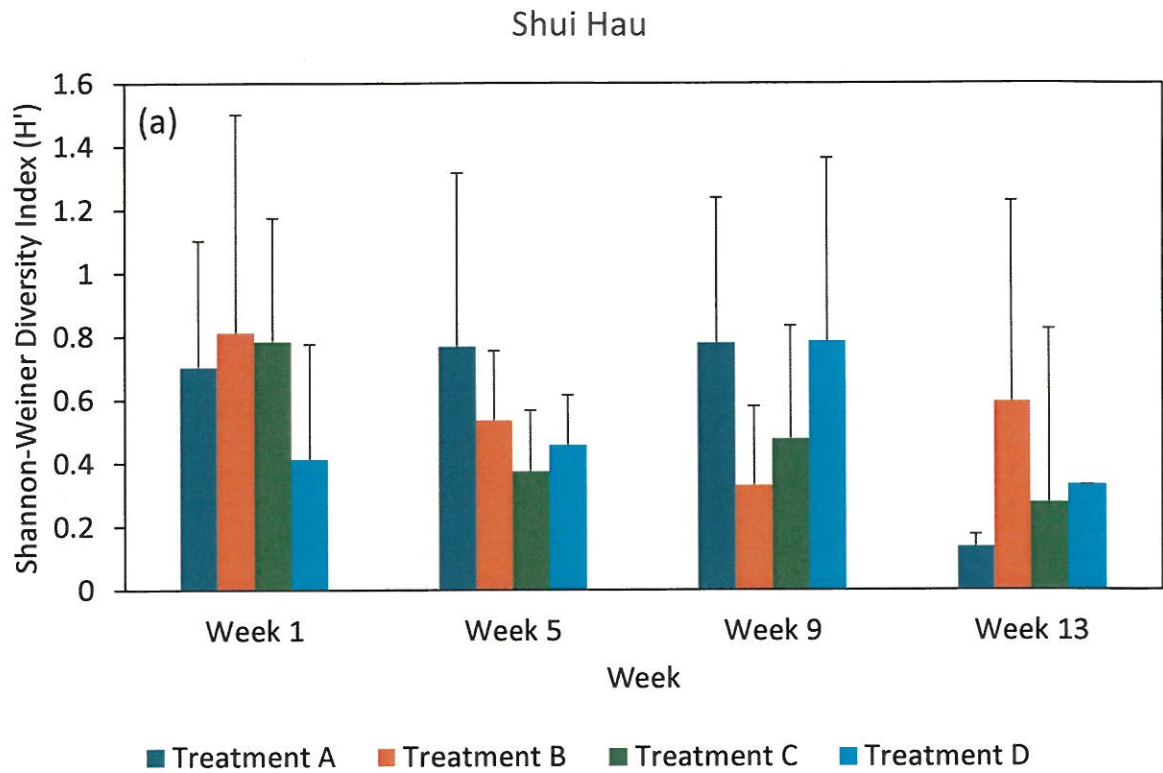
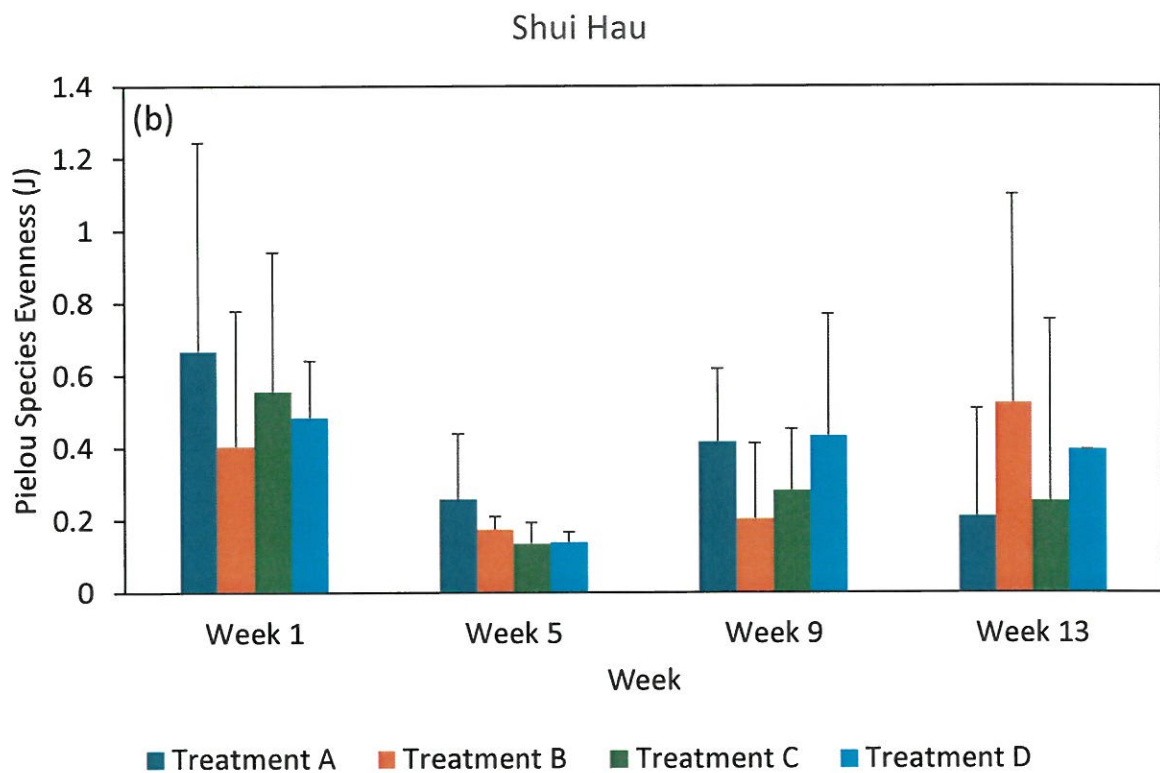


Fig. 32. (a) Shannon-Weiner Diversity Index and (b) Pielou Species Evenness in Shui Hau across different weeks of the clam digging simulation. A value of 0 indicates that only one species was present in the plot, while plots without bars indicate that no organisms were recorded.

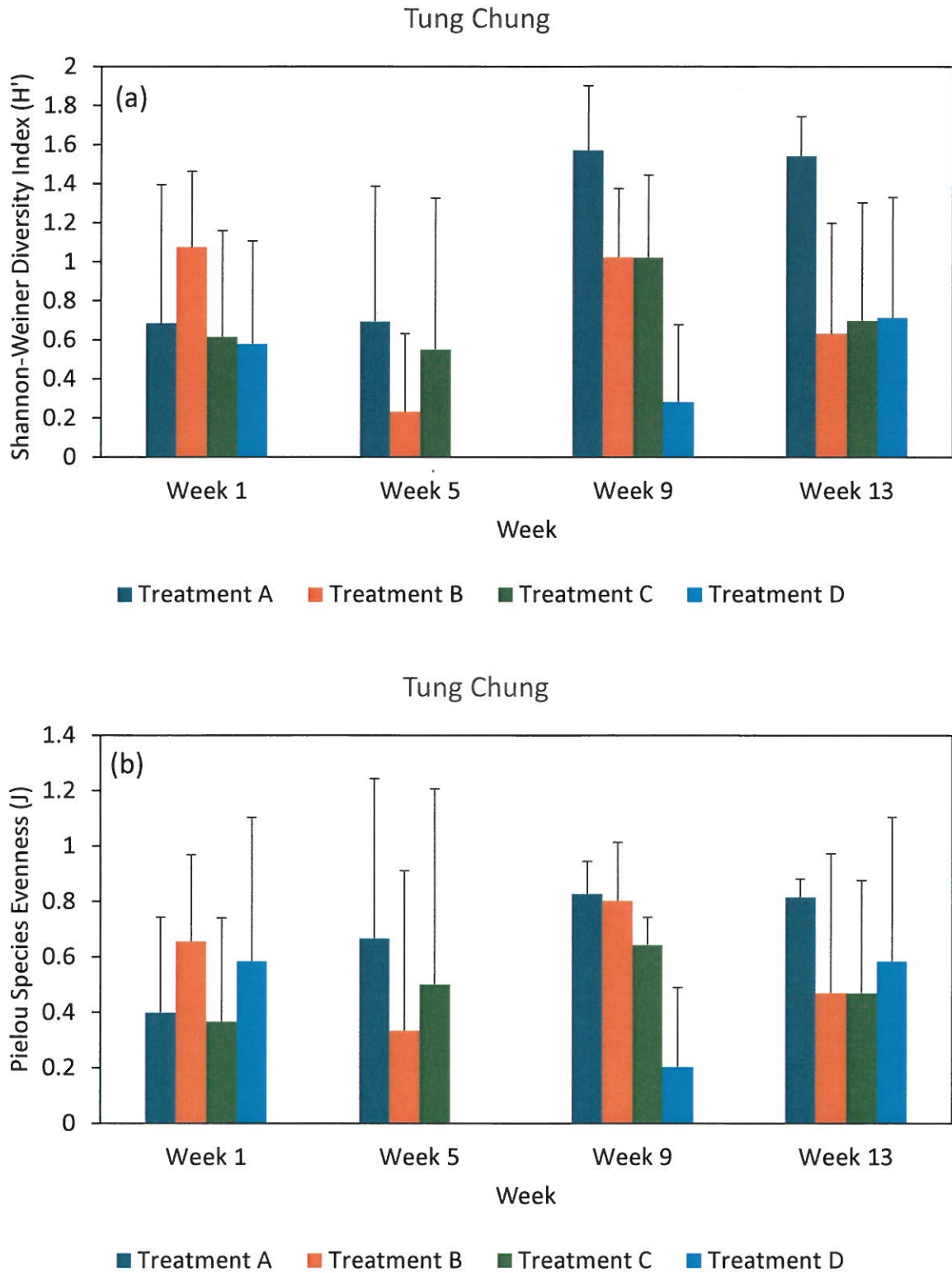


Fig. 33. (a) Shannon-Weiner Diversity Index and (b) Pielou Species Evenness in Tung Chung across different weeks of the clam digging simulation. A value of 0 indicates that only one species was present in the plot, while plots without bars indicate that no organisms were recorded.

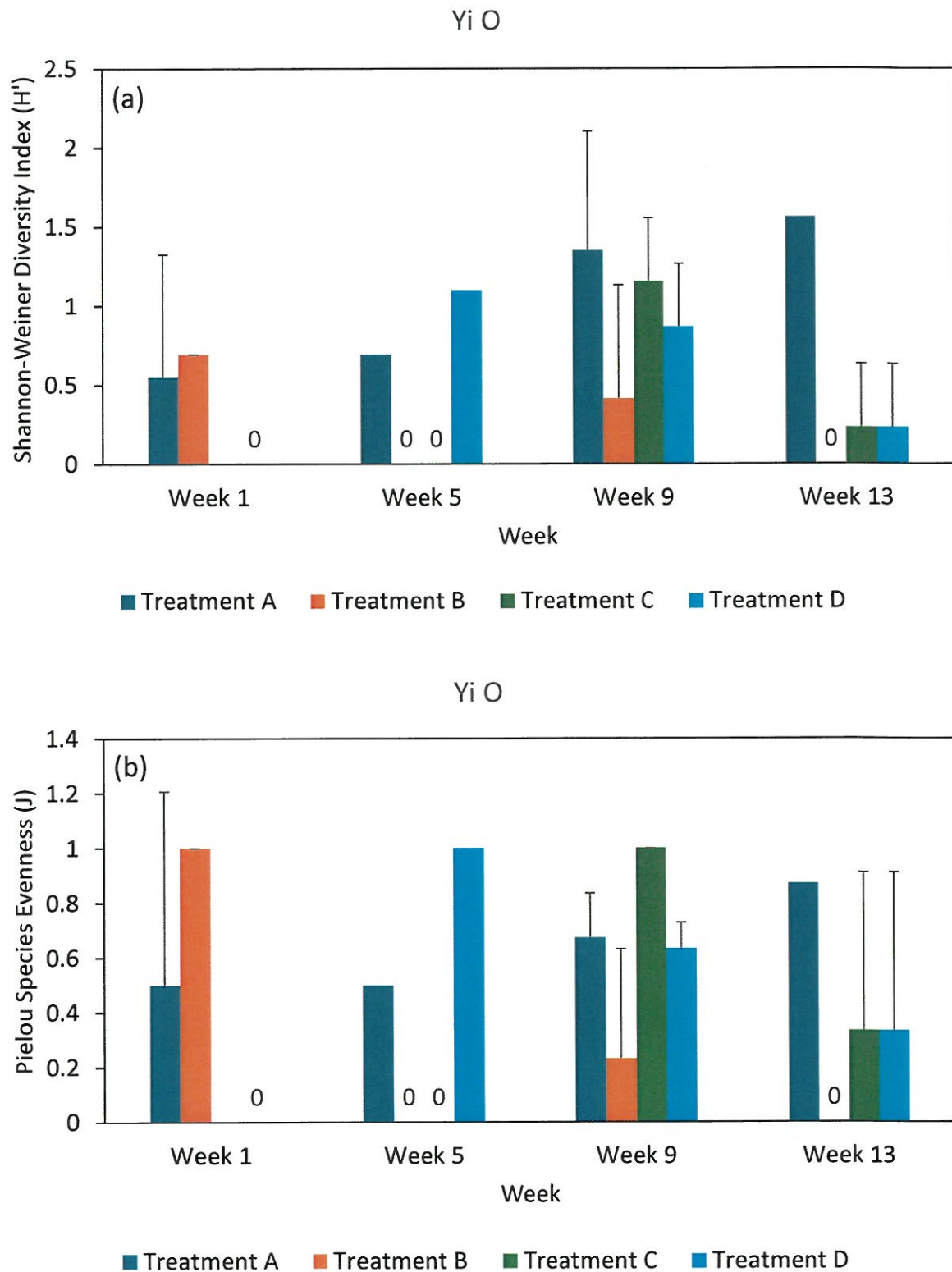


Fig. 34. (a) Shannon-Weiner Diversity Index and (b) Pielou Species Evenness in Yi O across different weeks of the clam digging simulation. A value of 0 indicates that only one species was present in the plot, while plots without bars indicate that no organisms were recorded.

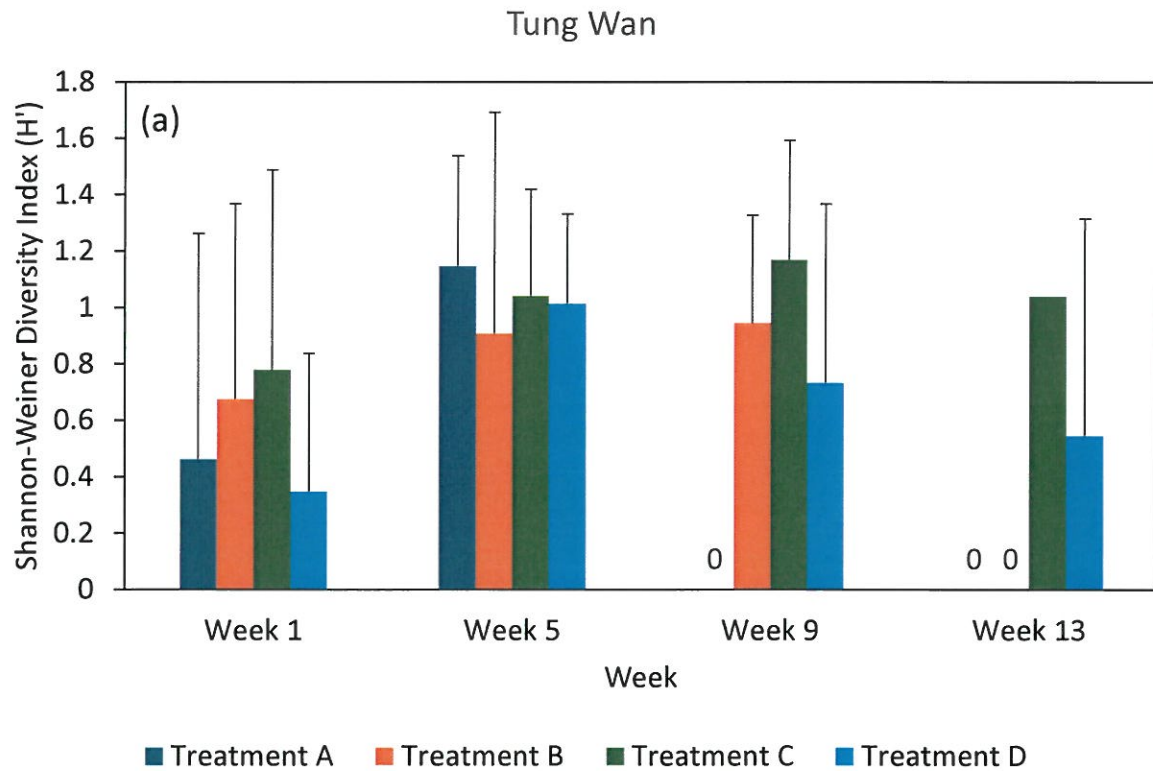
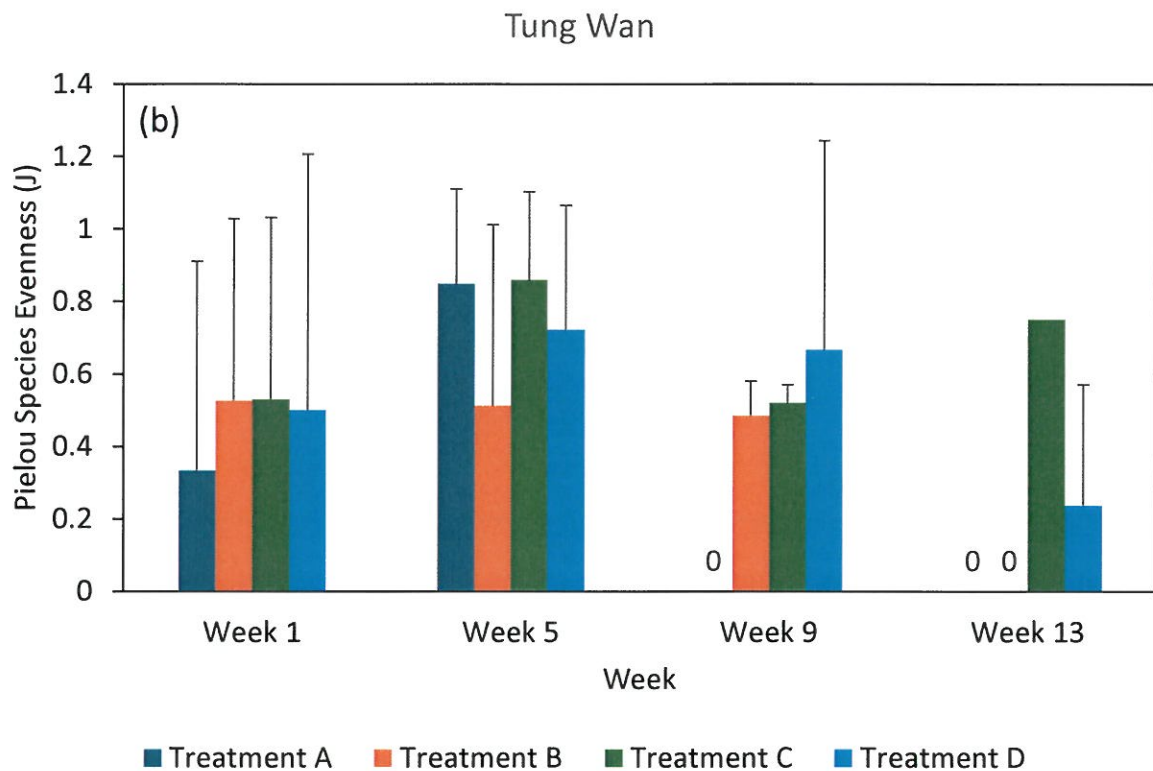


Fig. 35. (a) Shannon-Weiner Diversity Index and (b) Pielou Species Evenness in Tung Wan across different weeks of the clam digging simulation. A value of 0 indicates that only one species was present in the plot, while plots without bars indicate that no organisms were recorded.

5.2.4. Number of species and total abundance

The total number of individuals per plot in Shui Hau varied significantly over time ($F = 20.78$, $p < 0.001$), but not among treatments ($F = 0.85$, $p = 0.48$) or for the time $\times$ treatment interaction ($F = 1.02$, $p = 0.447$, Fig. 36a). Total abundance was significantly higher in Week 5 than in Week 13 ($t = 7.55$, $p < 0.001$), Week 1 ($t = 5.56$, $p < 0.001$), and Week 9 ($t = 5.22$, $p < 0.001$) (Fig. 36a).

The number of species per plot in Shui Hau did not vary significantly among treatments ($F = 0.89$, $p = 0.46$), but varied significantly over time ($p < 0.001$) and according to the time $\times$ treatment interaction ($p < 0.05$) (Fig. 36b). When data from all weeks were pooled, the mean number of species ranged from 2.25 in Treatment A to 3.00 in Treatment B. In Week 1, Treatment D supported significantly more species than Treatment A ($t = 3.21$, $p < 0.05$), while pairwise comparisons among the other treatments were not significant ($p > 0.05$). In Week 5, Treatment B had significantly more species than Treatment A ($t = 2.85$, $p < 0.05$), whereas comparisons among the remaining treatments were not significant ($p > 0.05$). No significant differences in species number among treatments were detected in Weeks 9 or 13.

The total number of individuals in Tung Chung varied significantly over time ($F = 3.67$, $p < 0.05$), but not among treatments ($F = 1.73$, $p = 0.18$) or for the time $\times$ treatment interaction ($F = 0.71$, $p = 0.69$) (Fig. 37a). Among sampling weeks, the number of individuals per plot was significantly lower in Week 5 than in Week 1 ($t = 3.27$, $p < 0.05$), whereas other pairwise comparisons among weeks were not significant ($p > 0.05$).

The number of species in Tung Chung varied significantly among treatments ($F = 7.46$, $p < 0.001$) and over time ($F = 5.42$, $p < 0.005$), but not for the time $\times$ treatment interaction ($F = 1.38$, $p = 0.24$) (Fig. 37b). Treatment A supported significantly more species than Treatment C ($t = 2.81$, $p < 0.05$) and Treatment D ($t = 4.69$, $p < 0.001$). Across sampling weeks, Week 5 had significantly fewer species than Week 1 ($t = 2.81$, $p < 0.05$), Week 9 ($t = 3.59$, $p < 0.01$), and Week 13 ($t = 3.28$, $p < 0.05$).

For Yi O, the total number of individuals per plot varied significantly over time ($F = 11.23$, $p < 0.001$), but not among treatments ($F = 2.60$, $p = 0.07$) or for the time $\times$ treatment interaction ($F = 1.11$, $p = 0.39$) (Fig. 38a). Week 9 supported significantly more individuals than all other sampling weeks, including Week 1 ($t = 4.94$, $p < 0.001$), Week 5 ($t = 4.94$, $p < 0.001$), and Week 13 ($t = 4.17$, $p < 0.001$).

The number of species in Yi O also varied significantly over time ($F = 7.50$, $p < 0.001$), but not among treatments ($F = 1.44$, $p = 0.25$) or for the time $\times$ treatment interaction ($F = 0.64$, $p = 0.76$) (Fig. 38b). Similar to the pattern observed for total abundance, Week 9 supported significantly more species than Week 1 ($t = 4.05$, $p < 0.005$), Week 5 ($t = 4.05$, $p < 0.005$), and Week 13 ($t = 3.37$, $p < 0.01$).

For Tung Wan, the total number of individuals did not vary significantly among treatments ($F = 0.40$, $p = 0.76$), over time ($F = 2.69$, $p = 0.06$), or for the time $\times$ treatment interaction ($F = 0.74$, $p = 0.67$) (Fig. 39a). In contrast, the number of species varied significantly over time ($F =$

5.32, $p < 0.005$), but not among treatments ($F = 0.47$, $p = 0.71$) or for the time $\times$ treatment interaction ($F = 0.55$, $p = 0.83$, Fig. 39b). The temporal effect was driven by a significant difference between Week 5 and Week 13, with Week 5 supporting significantly more species than Week 13 ($t = 3.99$, $p < 0.005$).

The number of individuals varied significantly over time at all sites except Tung Wan; however, no clear temporal pattern was evident, with most fluctuations occurring in the middle of the experiment (Weeks 5 and 9). Similarly, the number of species showed significant temporal variation across all sites without a consistent trend. Neither the number of individuals nor species richness differed significantly among treatments at Shui Hau, Yi O, and Tung Wan. However, at Tung Chung, Treatment A supported significantly more species than Treatments C and D.

When considering both species richness and diversity, the results suggest that clam digging negatively affected the macrofaunal community at Tung Chung, likely through direct clam removal. Sediment disturbance may also play a role: Treatment D differed from Treatment C in that sediment was returned to the excavated holes, yet both treatments supported fewer species than the control. This indicates that both clam removal and disturbance effects may be important. A similar reduction in species diversity and species richness in response to recreational clam digging was also reported by Griffiths et al. (2006).

The impact of clam digging was evident only at Tung Chung, possibly because the sandy beach area where clams were aggregated was relatively small compared with other sites. In addition, Tung Chung is the most easily accessible location, which likely resulted in higher digging pressure. Although Shui Hau is also a popular clam-digging site, the available harvesting area is much larger; consequently, digging pressure is lower and more evenly distributed, leading to a reduced impact on the macrofaunal community. In contrast, the more remote locations of Tung Wan and Yi O experience substantially lower levels of clam digging. At the control sites, the frequency and intensity of simulated digging activities were insufficient to produce detectable changes in macrofaunal communities.

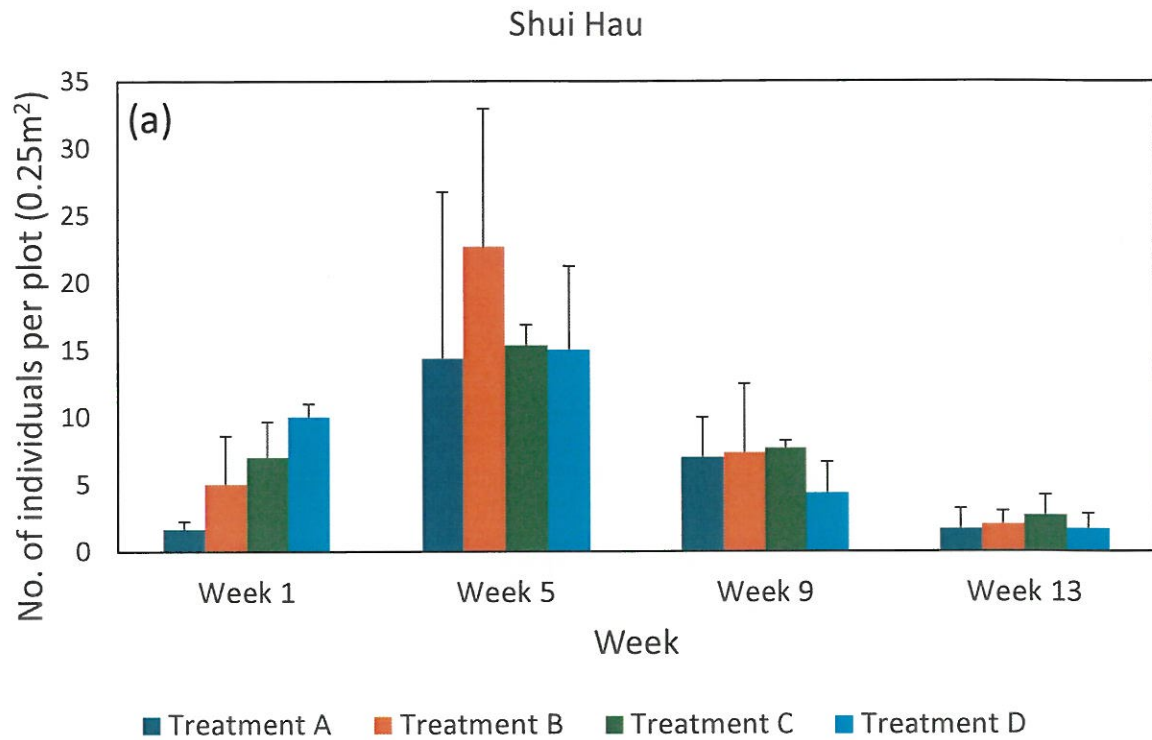
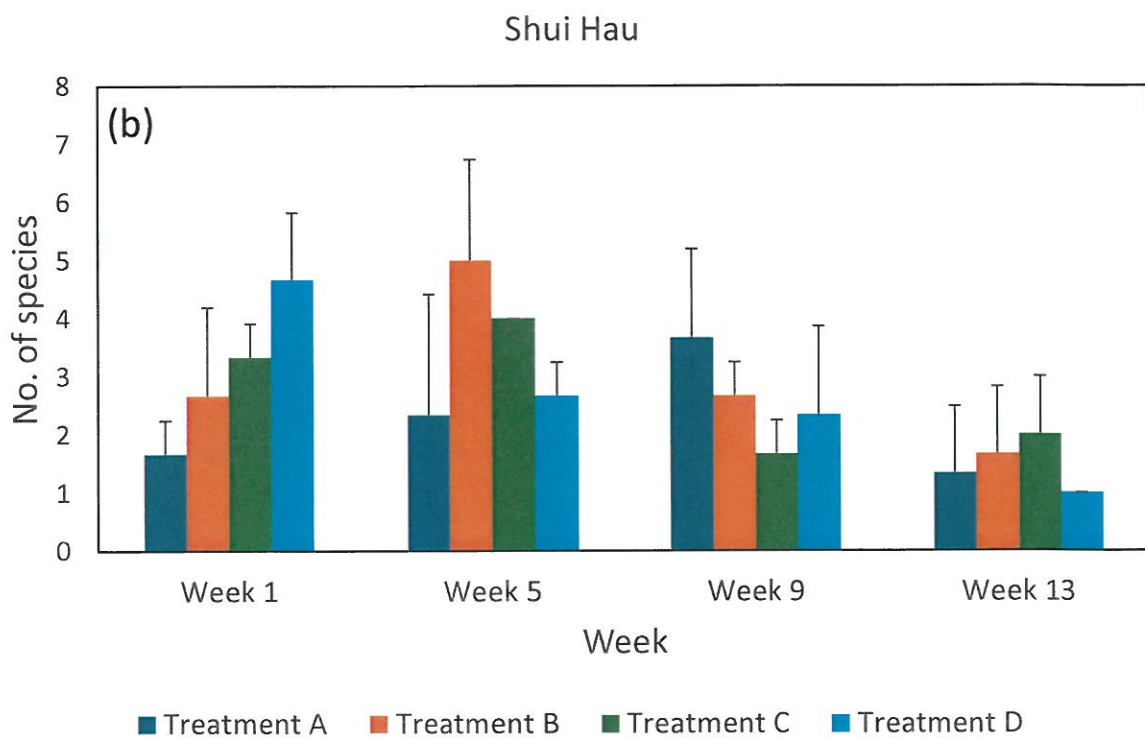


Fig. 36. (a) Total number of individuals across all species and (b) number of species in Shui Hau over different weeks during the clam digging simulation.

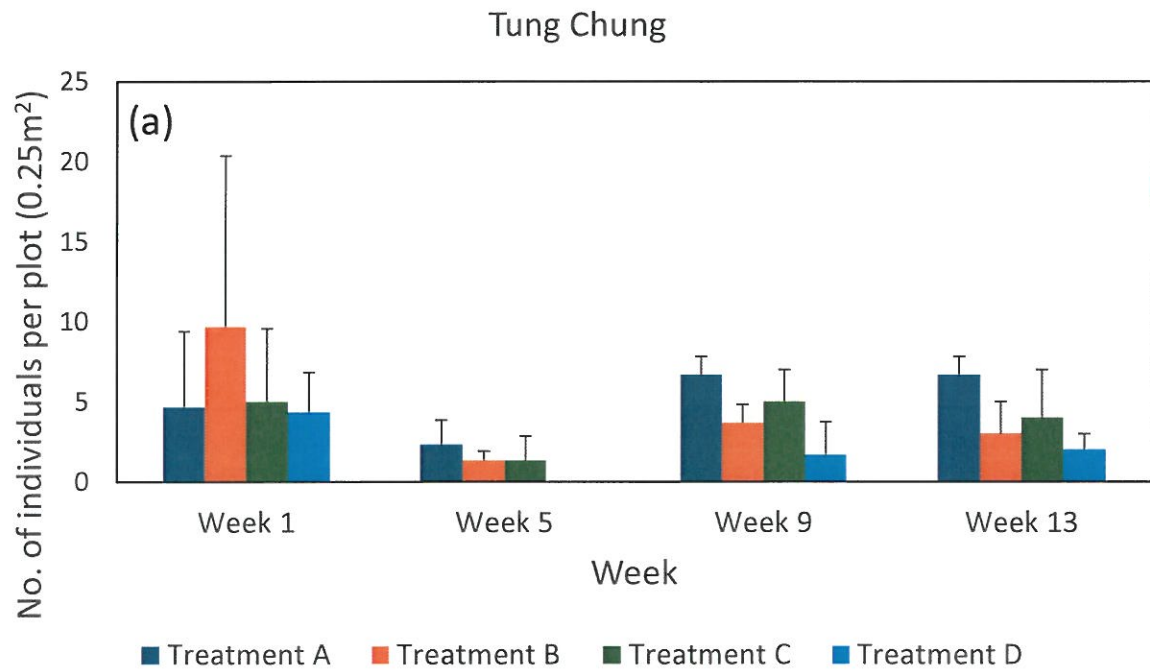
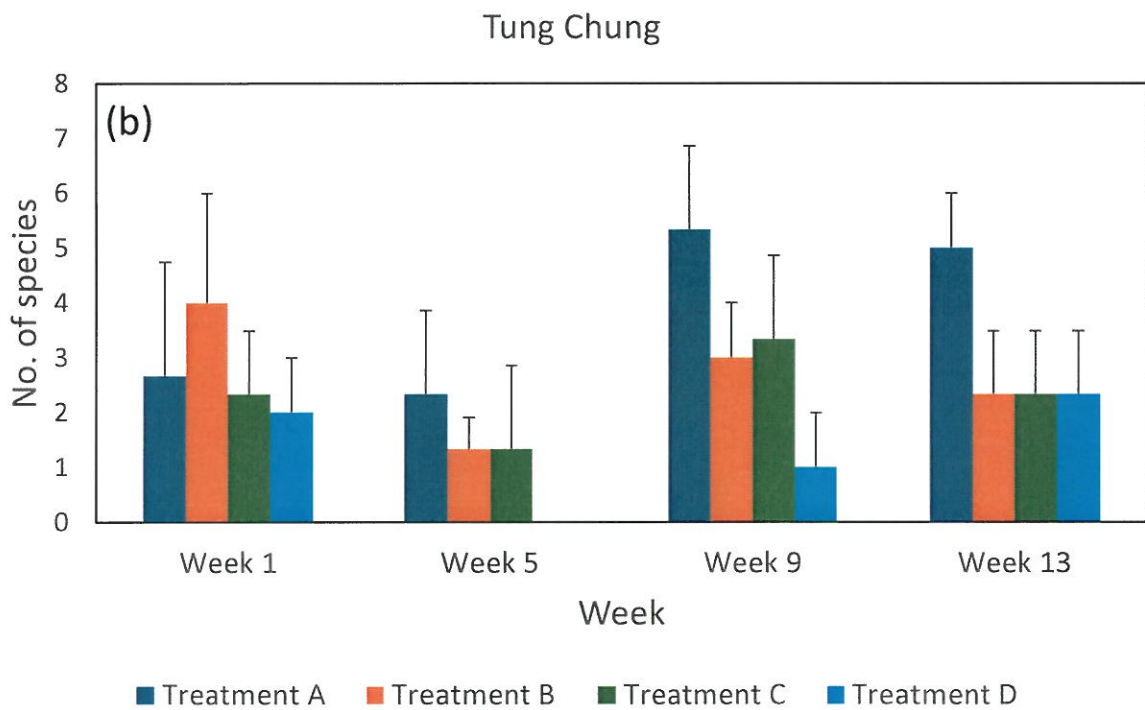


Fig. 37. (a) Total number of individuals across all species and (b) number of species in Tung Chung over different weeks during the clam digging simulation.

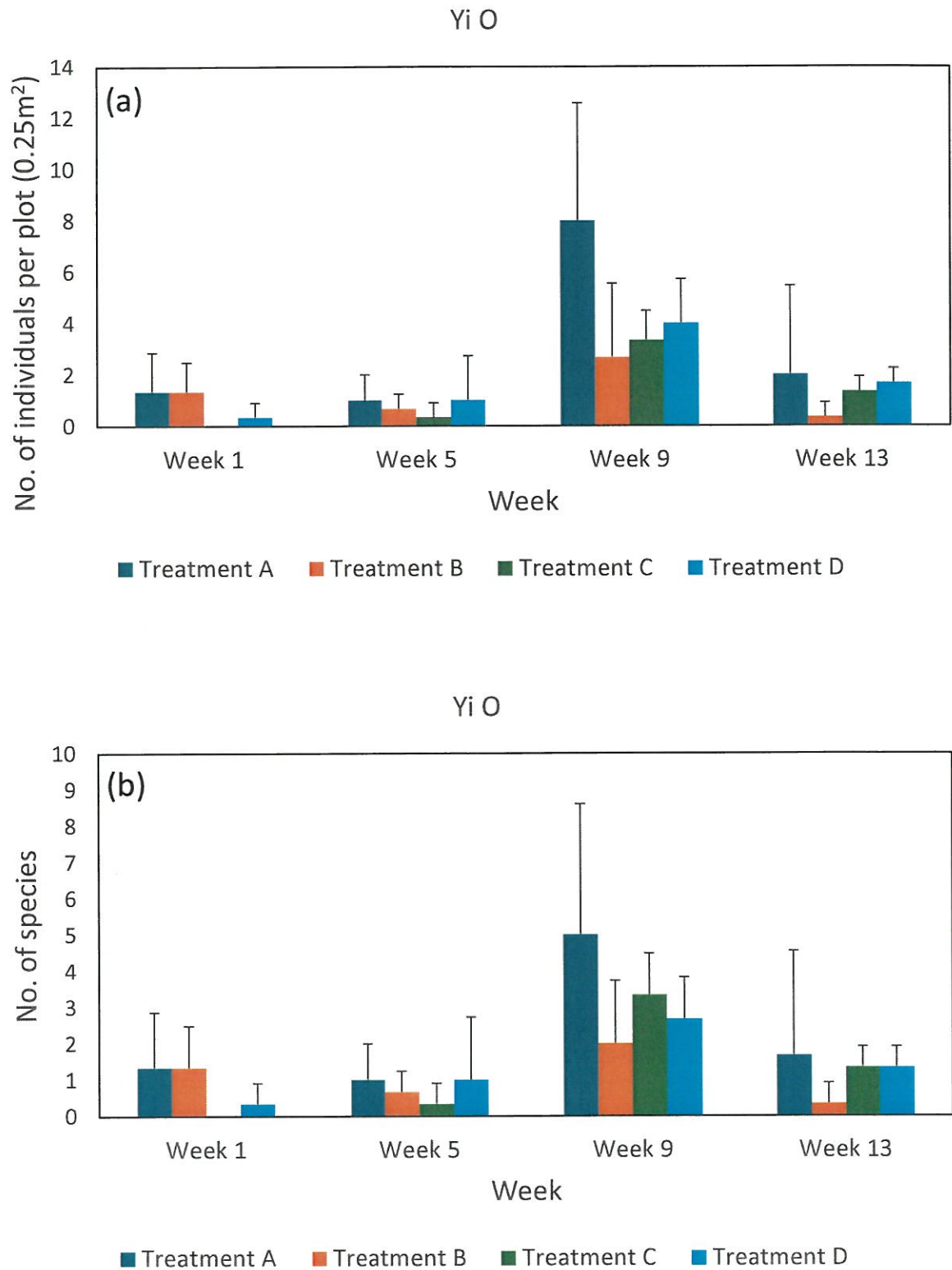


Fig. 38. (a) Total number of individuals across all species and (b) number of species in Yi O over different weeks during the clam digging simulation.

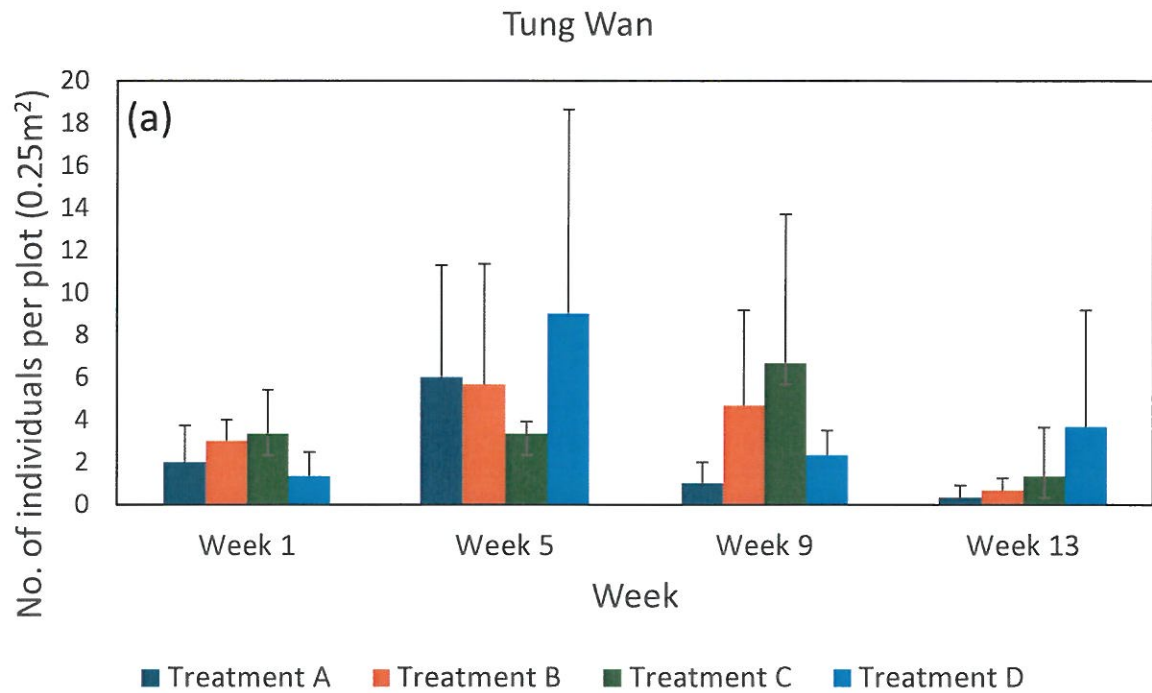
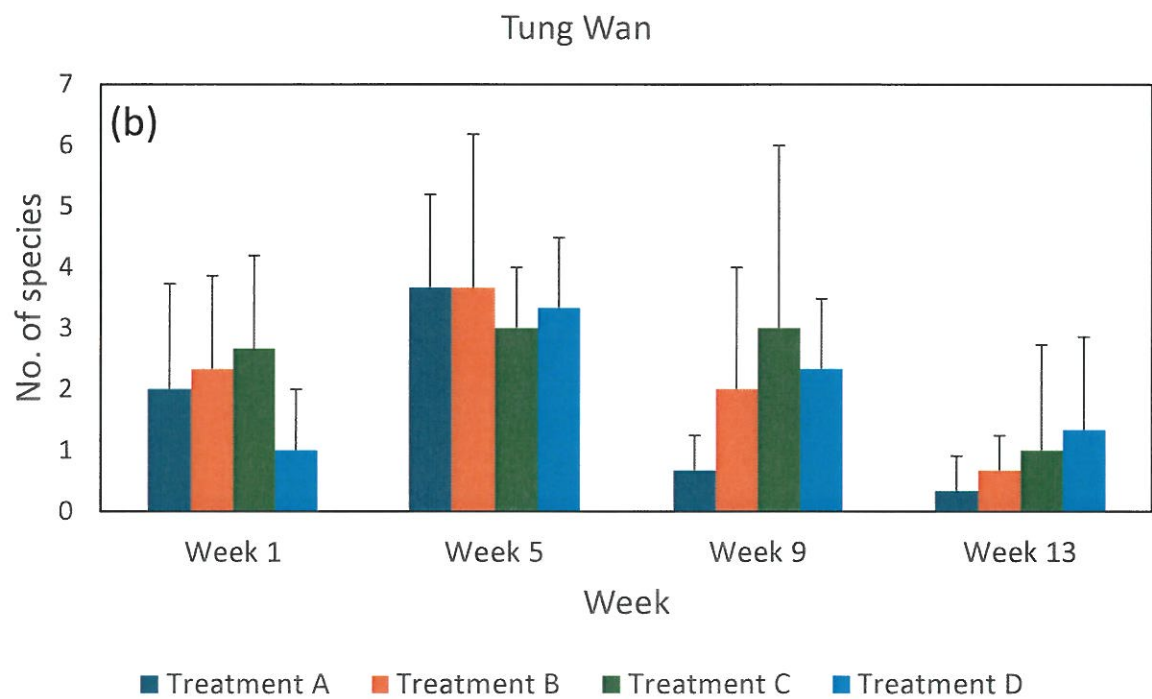


Fig. 39. (a) Total number of individuals across all species and (b) number of species in Tung Wan over different weeks during the clam digging simulation.

6. Study 5: Determining the environmental carrying capacity of clam digging

6.1 Methodology

A year-long caging experiment was conducted at two clam-digging sites (Shui Hau, Tung Chung) and two control sites (Yi O, Tung Wan), beginning in August 2022. Three metal-wire-mesh cages (mesh size: 4 mm), each measuring 50 cm length x 50 cm width x 20 cm height, were used as replicates for each clam species. The cages were buried 15 cm into the sediment. Approximately 20-25 clams were placed in each cage, and their shell lengths were measured every one to one and a half months. Dead clams were recorded and replaced with individuals collected from the same site during each visit.

Different clam species were studied at each site: *A. flexuosa* and *Meretrix* spp. at Shui Hau; *R. philippinarum* at Tung Chung; *Macridiscus aequilatera* and *Meretrix* spp. at Tung Wan; and *Meretrix* spp. at Yi O. Because individual *Meretrix* species are difficult to differentiate in the field, all *Meretrix* species were treated as a single taxonomic group for analysis.

6.2 Results and Discussion

6.2.1 Mortality rate

In Shui Hau, the annual mortality rate of *Anomalocardia flexuosa* ranged from 34.1 to 53.7% among cages, with the highest mortality occurring during summer (May and August) (Table 23). The mean annual mortality across the three replicate cages was 44.1% ($\pm 9.8\%$). *Meretrix* spp. exhibited markedly higher annual mortality rates, ranging from 69.9 to 215%, with peak mortality also occurring in summer (Table 23). The mean annual mortality across the three replicates was 129.8% ($\pm 75.8\%$). A mortality percentage greater than 100% indicates that all clams initially placed in the cage, as well as some of the replacement individuals added during the experiment, died. From a population perspective, this represents a complete failure of a cohort. Such results are likely artefactual and may be attributed to a caging effect, in which reduced water flow deteriorated sediment quality, ultimately leading to clam mortality. When comparing the two species, *A. flexuosa* appeared to be more tolerant of deteriorating sediment conditions than *Meretrix* spp.

In Tung Chung, the annual mortality of *R. philippinarum* ranged from 36.8% to 94.4% across replicates, with the highest mortality recorded in July 2024 (Table 24). The mean annual mortality across the three replicates was 71.7% ($\pm 30.7\%$).

In Tung Wan, the cumulative mortality of *M. aequilatera* from August 2023 to May 2024 ranged from 28.6% to 178.9% (mean: $121.9 \pm 81.5\%$), with a peak in September 2023 (Table 25). No data were available for June and July 2024 because the cages were lost. The cumulative mortality of *Meretrix* spp. could be determined for only one cage during the same period due to the very small number of individuals available for replacement. Mortality for this species between August 2023 and May 2024 was extremely high, reaching 336.5%. Tung

Wan is a highly exposed sandy beach with a shoreline profile that changes drastically, particularly after rainstorms and typhoons. As a result, clams experienced extreme fluctuations in environmental conditions, leading to the exceptionally high mortality observed.

In Yi O, only one cage had sufficient data to estimate the annual mortality of *Meretrix* spp., which reached 360.7% between August 2023 and July 2024 due to the very limited number of clams available for replacement (Table 26).

Table 23. Monthly mortality of *A. flexuosa* and *Meretrix* spp. kept in cages in Shui Hau from August 2023 to July 2024. A mortality percentage exceeding 100% indicates that all clams initially placed in the cage, as well as some replacement individuals added during the experiment, died.

Shui Hau	<i>A. flexuosa</i>	Aug 2023	Sep	Oct/ Nov	Nov/ Dec	Jan/ Feb 2024	Feb/ Mar	Apr	May	June	July	Cumulative Mortality (%)
	Cage A	25	25	25	25	25	25	25	25	22	22	
	No. of clams											
	No. of dead clams	3	2	1	0	0	0	1	3	0	1	
	Death rate (%)	12	8	4	0	0	0	4	12	0	4.5	44.5
	Cage B	25	25	25	25	25	25	25	25	23	23	
	No. of clams											
	No. of dead clams	0	0	0	0	1	0	0	1	0	6	
	Death rate (%)	0	0	0	0	4	0	0	4	0	26.1	34.1
	Cage C	25	25	25	25	25	25	25	25	23	19	
	No. of clams											
	No. of dead clams	1	1	2	3	0	0	0	1	5	0	
	Death rate (%)	4	4	8	12	0	0	0	4	21.7	0	53.7
	<i>Meretrix</i> spp.	20	19	14	15	15	15	15	14	14	13	
	Cage A	1	7	2	0	0	0	1	0	1	0	
	No. of dead clams											
	Death rate (%)	5	36.8	14.3	0	0	0	6.7	0	7.1	0	69.9

Cage B	No. of clams	20	20	19	18	16	15	15	14	15	15	
	No. of dead clams	1	1	1	2	6	0	0	1	0	5	
	Dead rate (%)	5	5	5.3	11.1	37.5	0	0	7.1	0	33.3	104.4
Cage C	No. of clams	20	18	15	6	12	12	12	10	10	10	
	No. of dead clams	3	12	10	2	2	0	2	0	0	0	
	Dead rate (%)	15	66.7	66.7	33.3	16.7	0	16.7	0	0	0	21.5

Table 24. Monthly mortality of *R. philippinarum* kept in cages in Tung Chung from August 2023 to July 2024. A mortality percentage exceeding 100% indicates that all clams initially placed in the cage, as well as some replacement individuals added during the experiment, died.

Tung Chung	<i>R. philippinarum</i>		Aug 2023	Sep	Oct/ Nov	Nov/ Dec	Jan/ Feb 2024	Feb/ Mar	Apr	May	Jun	Jul	Cumulative mortality (%)
	Cage A	No. of clams	21	23	24	22	23	24	24	24	21	20	
		No. of dead clams	0	0	0	1	0	0	0	3	1	3	
		Dead rate (%)	0	0	0	4.5	0	0	0	12.5	4.8	15	36.8
	Cage B	No. of clams	23	23	24	25	26	26	27	27	25	17	
		No. of dead clams	0	1	4	0	0	0	0	2	8	4	
		Dead rate (%)	0	4.3	16.7	0	0	0	0	7.4	32	23.5	84.0
	Cage C	No. of clams	25	25	25	25	22	26	25	23	22	18	
		No. of dead clams	1	0	1	1	2	1	2	1	4	7	
		Dead rate (%)	4	0	4	4	9.1	3.8	8	4.3	18.2	38.9	94.4

Table 25. Monthly mortality of *M. aequilatera* and *Meretrix* spp. kept in cages in Tung Wan from August 2023 to July 2024. A mortality percentage exceeding 100% indicates that all clams initially placed in the cage, as well as some replacement individuals added during the experiment, died.

Tung Wan	<i>Macridiscus aequilatera</i>		Aug 2023	Sep	Oct/ Nov	Nov/ Dec	Jan/ Feb 2024	Feb/ Mar	Apr	May	Jun	Jul	Cumulative mortality (%)
	Cage A	No. of clams	7	18	15	20	20	13	14	12			
		No. of dead clams	1	0	0	0	0	0	2	0			
		Dead rate (%)	14.3	0	0	0	0	0	14.3	0			28.6
	Cage B	No. of clams	21	20	19	19	20	18	19	18			
		No. of dead clams	4	18	7	0	0	0	1	5			
		Dead rate (%)	19.0	90	36.8	0	0	0	5.3	27.8			178.9
	Cage C	No. of clams	19	20		13	18	20	17				
		No. of dead clams	6	20		0	0	3	2				
		Dead rate (%)	31.6	100		0	0	15	11.8				158.3
	<i>Meretrix</i> spp.		Aug 2023	Sep	Oct/ Nov	Nov/ Dec	Jan/ Feb 2024	Feb/ Mar	Apr	May	Jun	Jul	

Cage A	No. of clams	2	13	17	20	20	4	1			
	No. of dead clams	2	8	0	0	20	3	0			
	Dead rate (%)	100	61.5	0	0	100	75	0			336.5

Table 26. Monthly mortality of *Meretrix* spp. kept in cages in Yi O from August 2023 to July 2024. A mortality percentage exceeding 100% indicates that all clams initially placed in the cage, as well as some replacement individuals added during the experiment, died.

Yi O	<i>Meretrix</i> spp.		Aug 2023	Sep	Oct/ Nov	Nov/ Dec	Jan/ Feb 2024	Feb/ Mar	Apr	May	Jun	Jul	Cumulative mortality (%)
	Cage A	No. of clams	9	6	14								
		No. of dead clams	5	3	0								
		Dead rate (%)	55.6	50	0								105.6
	Cage B	No. of clams	11										
		No. of dead clams	5										
		Dead rate (%)	45.5										45.5
	Cage C	No. of clams	20		18	8	10	21	19	15	13	7	
		No. of dead clams	1		15	4	9	10	4	2	6	1	
		Dead rate (%)	5		83.3	50	90	47.6	21.1	13.3	46.1	14.3	360.7

6.2.2 Organic content and median particle diameter

The mean organic content (%) inside and outside the cages in 2023 and 2024 is shown in Table. A substantial increase in organic content was observed at all sites in 2024 compared with 2023. This suggests that the 4-mm mesh size of the cages restricted water flow, reducing flushing and causing organic matter to accumulate. The resulting increase in decomposition and decline in oxygen levels likely led to deterioration of sediment quality, contributing to the high clam mortalities recorded inside the cages. Although the mesh size was increased from the originally proposed 2 mm to 4 mm, it still appears inadequate for maintaining sufficient water movement. For future caging studies, a larger mesh size, approximately 1 cm, is recommended to improve water circulation and minimize sediment degradation.

Table 27. Organic content (%) of sediment collected inside and outside the cages in 2023 and 2024.

Site	Type		Organic content (%)		
			2024	2023	% change
Shui Hau	Outside cage		2.93	2.56	-14.15
	<i>Meretrix</i> sp.	Cage A	2.54		-1.02
		Cage B	3.95		53.95
		Cage C	3.45		34.48
	<i>Anomalocardia flexuosa</i>	Cage A	3.64		42.11
		Cage B	3.10		20.93
		Cage C	3.02		17.59
Yi O	Outside cage		1.83	1.89	3.20
	<i>Meretrix</i> sp.	Cage A	2.25		93.12
Tung Chung	Outside cage		1.19	2.88	58.97
	<i>Ruditapes philippinarum</i>	Cage A	4.04		39.91
		Cage B	3.09		7.22
		Cage C	5.52		91.41

6.2.3 Growth in shell length

The growth of the clams in cages is shown in Figures 40-43. Because dead clams were replaced with new individuals during each visit, the mean length calculated directly from all clams (survivors + replacements) produced discontinuous growth lines. To illustrate continuous growth, adjusted growth curves were constructed by assuming that the mean length of all clams in cages was equivalent to that of the surviving clams at each sampling time.

For *A. flexuosa* in Shui Hau, the caging experiment was conducted between August 2023 and August 2024. During this period, the mean shell lengths of the three replicates increased from 24.0 mm to 28.7 mm, from 23.5 to 29.3 mm, and from 21.3 to 28.2 mm (Fig. 40). These increases correspond to annual growth increments of 4.7 mm, 5.8 mm and 6.9 mm, respectively, giving a mean annual growth of 5.8 mm. Individuals of comparable shell length in the cohort analysis were those in the 2021 2nd cohort, which had an initial shell length of 23.2 mm in May 2023, and an annual mean growth rate of 5.57 mm. Another comparable cohort (2021 1st cohort), with an initial shell length of 27.07 mm, had an annual mean growth rate of 5.01 mm. Thus, the annual growth rates estimated from the caging experiment were slightly higher than those derived from the cohort analysis.

For *R. philippinarum* in Tung Chung, the caging experiment was conducted between August 2023 and August 2024. Over this period, the mean shell length of the three replicates increased from 25.5 mm to 34.0 mm, from 30.0 to 37.6 mm, and from 24.8 to 33.0 mm (Fig. 41). These values correspond to annual growth increments of 8.5 mm, 7.6 mm and 8.1 mm, respectively, giving a mean annual growth rate of 8.1 mm. Comparing with the annual growth of similar sized individuals in Study 3 (population dynamics), the 2021 1st cohort, with a mean initial shell length of 26.5 mm in May 2023, exhibited an annual growth of 7.23 mm, while the 2020 2nd cohort, with a mean shell length of 30.2 mm, showed an annual growth of 8.3 mm. Thus, the annual growth rates estimated from the caging experiment were very similar to those derived from the cohort analysis.

For *Meretrix* spp. in Shui Hau, the caging experiment covered the same period. Over this time, the mean shell length of the three replicates increased from 44.7 mm to 57.7 mm, from 39.8 to 53.9 mm, and from 43.2 to 51.7 mm (Fig. 42). These increases correspond to annual growth increments of 13.0 mm, 14.1 mm and 8.5 mm, respectively, yielding a mean annual growth of 11.87 mm. When compared with the annual growth of similarly sized individuals in Study 3 (population dynamics), the 2022 1st cohort, which had a mean initial shell length of 37.32 mm in May 2023, exhibited an annual growth of 18.07 mm. Another slightly larger cohort (2021 1st cohort), with an initial shell length of 53.42 mm, showed an annual growth of 15.36 mm. Thus, the annual growth rates estimated from the cohort analysis were clearly higher than those from the caging experiment.

Two factors may explain this discrepancy. First, growth in the caging experiment may have been underestimated due to restricted water movement caused by the small cage mesh size. This issue appears to affect *Meretrix* spp. the most, whereas *R. philippinarum* and *A. flexuosa* were only slightly or not affected at all. Second, inherent growth rates at Shui Hau may simply be slower than at the other sites, as the cohort-based estimates were derived from pooled

samples collected across all four locations (Shui Hau, Tung Wan, Yi O and Tung Chung). This limitation can be addressed in future by conducting caging experiments at all four sites for direct comparison.

Since very few *Meretrix* spp. were found in Yi O, no annual growth could be computed. Only one cage contained enough individuals to monitor growth between October/November 2023 and August 2024, during which mean shell length increased from 66.4 mm to 70.8 mm, an increment of 4.4 mm over 10 months (Fig. 43). A comparable assessment can be made using the cohort-based estimate of growth: for the 2020 2nd cohort, mean shell length increased from 65.99 mm in May 2023 to 72.9 mm in February/March 2024, representing a 6.91 mm increase over the same duration. As observed for *Meretrix* spp. in Shui Hau, individuals kept in cages grew more slowly. No growth estimate could be computed for *Meretrix* spp. in Tung Wan because two cages were lost during the experiment, and the remaining cage contained very few individuals for several months.

For *Macridiscus aquilatera* in Tung Wan, only two cages retained sufficient individuals for continuous growth estimation between August 2023 and June 2024, as the remaining cages were lost. In one cage, the mean shell length increased from 41.6 to 47.4 mm, while in the other it increased from 40.8 to 45.9 mm (Fig. 44). These correspond to growth increments of 5.8 mm and 5.1 mm over a 10-month period, respectively, with a mean growth of 5.45 mm.

For *Meretrix* spp. in Tung Wan, data are presented for only one cage (Cage A) because the other two cages were lost during typhoons or heavy rainstorms. In Cage A, mean shell length increased from 40.7 mm in October/November 2023 to 55.0 mm in June 2024, representing a growth increment of 14.3 mm over seven months (Fig. 45).

Clams in cages exhibited a broadly similar growth pattern across sites and species, characterized by rapid growth during the first three months followed by a pronounced slowdown. This pattern is likely a caging effect. Although the mesh size was increased from 2 mm specified in the proposal to 4 mm, the openings remained too small to allow adequate water circulation. Restricted flow may also account for the high mortality observed and the elevated organic content in the sediments within the cages. This caging effect appeared to affect *Meretrix* spp. more than *A. flexuosa* and *R. philippinarum*, probably due to the latter species being more adaptive to habitats with finer sediments and lower oxygen content.

Due to the caging effect, however, the results were not entirely satisfactory, particularly for *Meretrix* spp. The observed mortality rate exceeded 100%, indicating that all individuals died during the experiment despite monthly clam replacement. This suggests that the experimental conditions had a substantial negative impact on the survival of *Meretrix* spp.

Nevertheless, the caging effect did not appear to significantly influence the growth and mortality estimates for *A. flexuosa* and *R. philippinarum*. Growth rates obtained from the caging experiment were comparable to those derived from the cohort analysis in Study 3. Furthermore, the mean mortality rates recorded in the caging experiment were approximately 44% for *A. flexuosa* and 71% for *R. philippinarum*, both substantially lower than the corresponding estimates from Study 3 (93% for *A. flexuosa* and 83% for *R. philippinarum*). The

higher mortality rates observed in Study 3 were likely attributable, at least in part, to harvesting pressure from clam digging

Therefore, the objectives of Study 5 were partially achieved, particularly for *A. flexuosa* and *R. philippinarum*. In contrast, the caging experiment was unsuccessful for *Meretrix* spp., highlighting the need for further refinement of the experimental design. For future caging studies, a larger mesh size, for example, approximately 1 cm, is recommended to enhance water exchange and reduce caging artefacts.

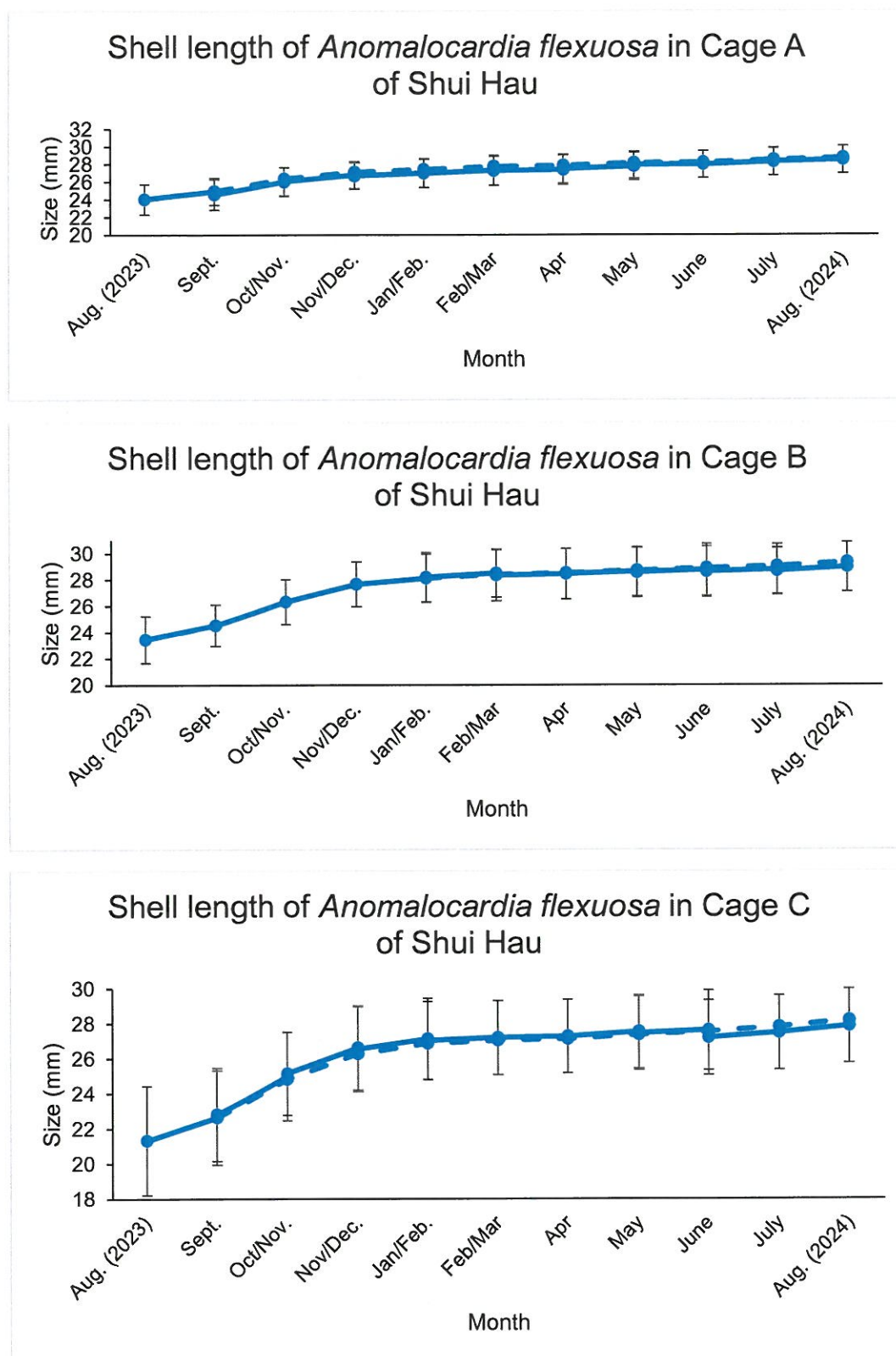


Fig. 40. Mean monthly growth of *A. flexuosa* in Shui Hau, maintained in three cages (A, B, C) between August 2023 and August 2024. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas dotted lines indicate the adjusted growth, assuming that the mean shell length of all clams in each cage was equivalent to that of the surviving individuals at each sampling time.

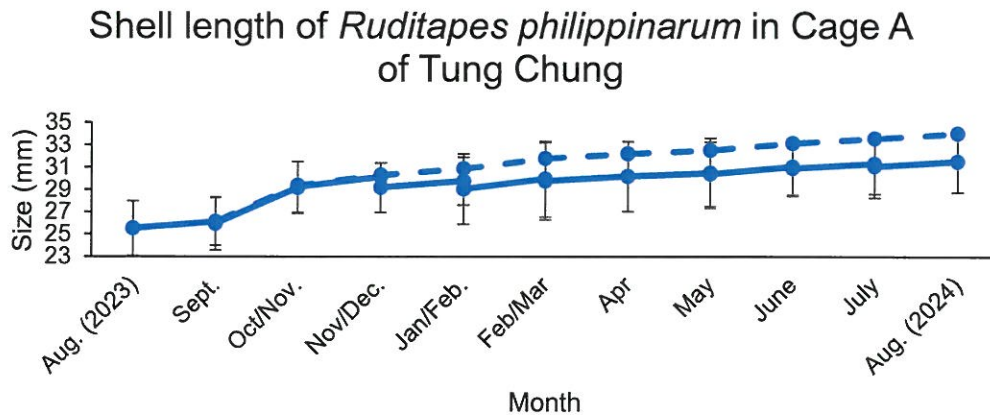
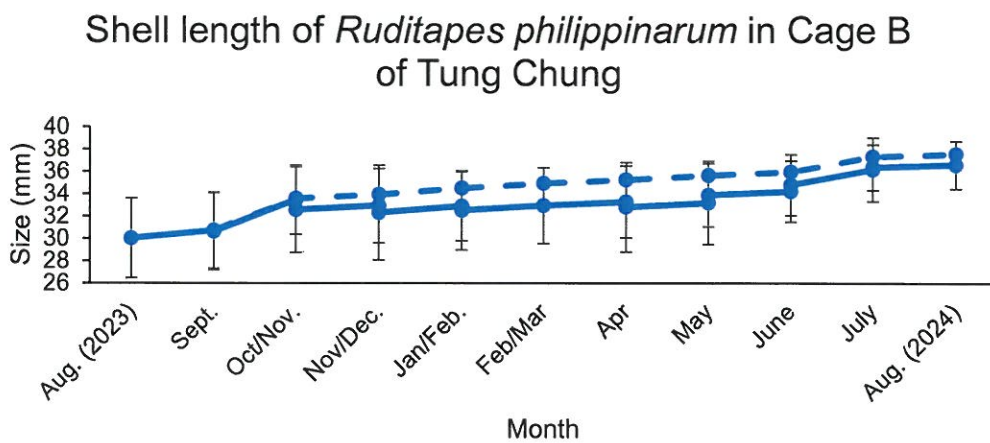
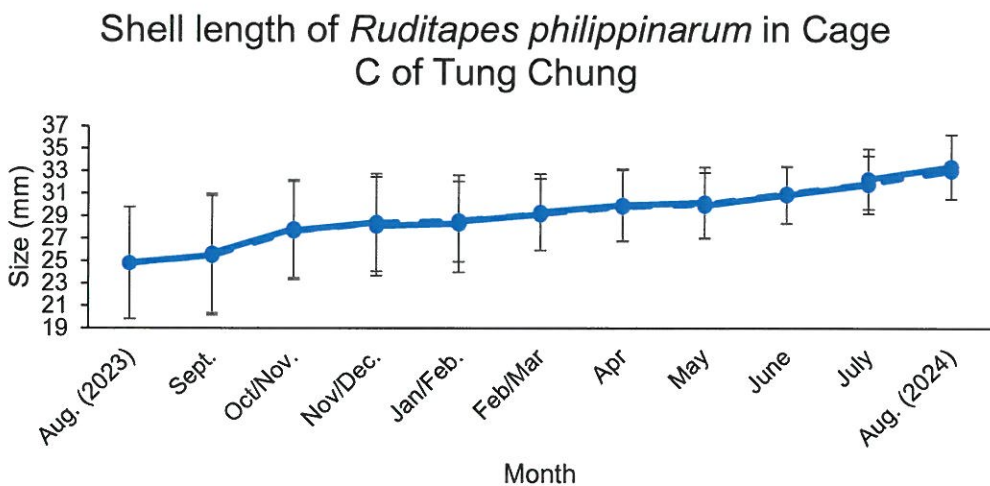


Fig. 41. Mean monthly growth of *R. philippinarum* in Tung Chung, maintained in three cages (A, B, C) between August 2023 and August 2024. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas dotted lines indicate the adjusted growth, assuming that the mean shell length of all clams in each cage was equivalent to that of the surviving individuals at each sampling time.

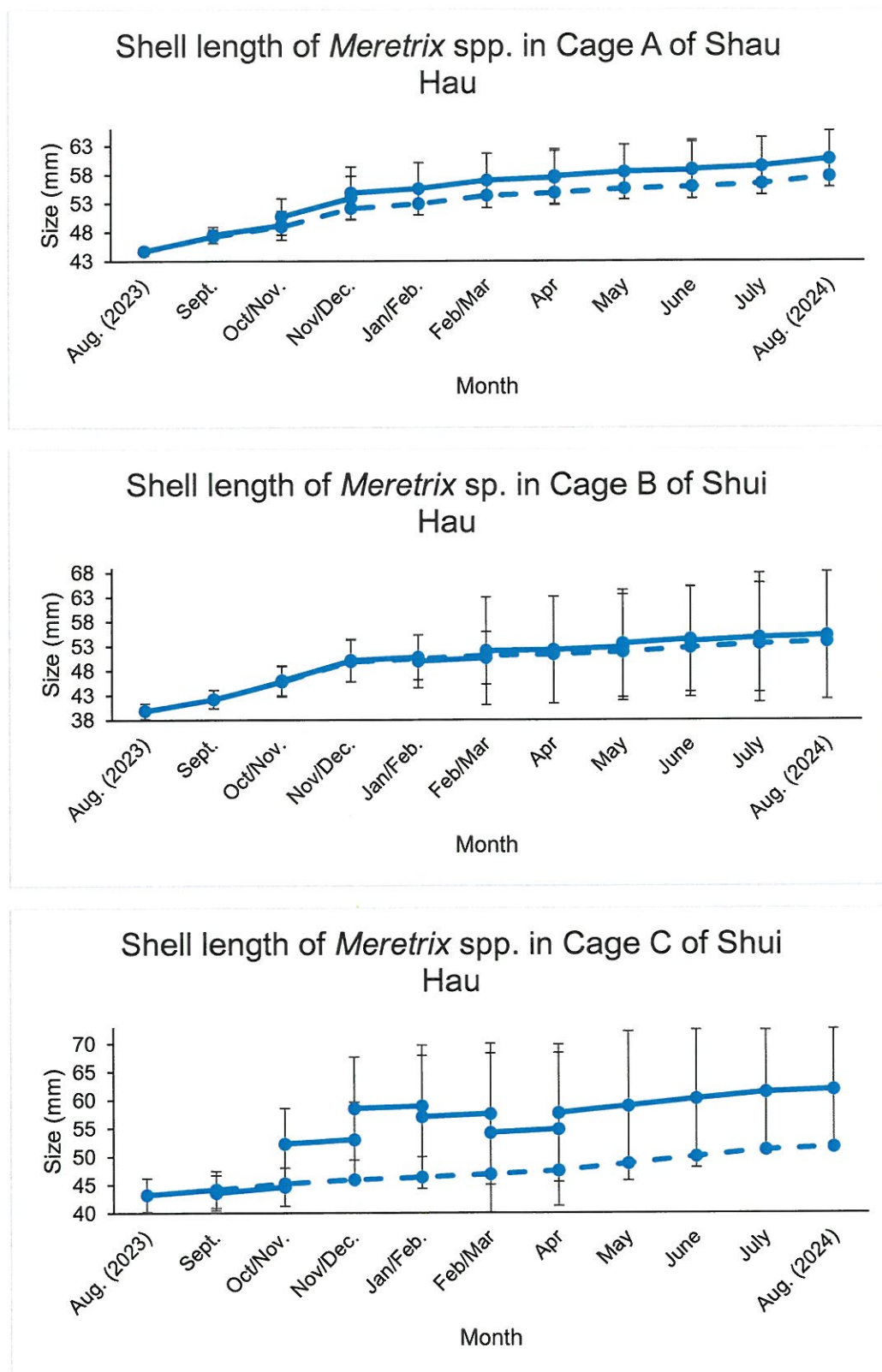


Fig. 42. Mean monthly growth of *Meretrix* spp. in Shui Hau, maintained in three cages (A, B, C) between August 2023 and August 2024. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas the dotted lines indicate the adjusted growth, assuming that the mean shell length of all clams in each cage was equivalent to that of the surviving individuals at each sampling time.

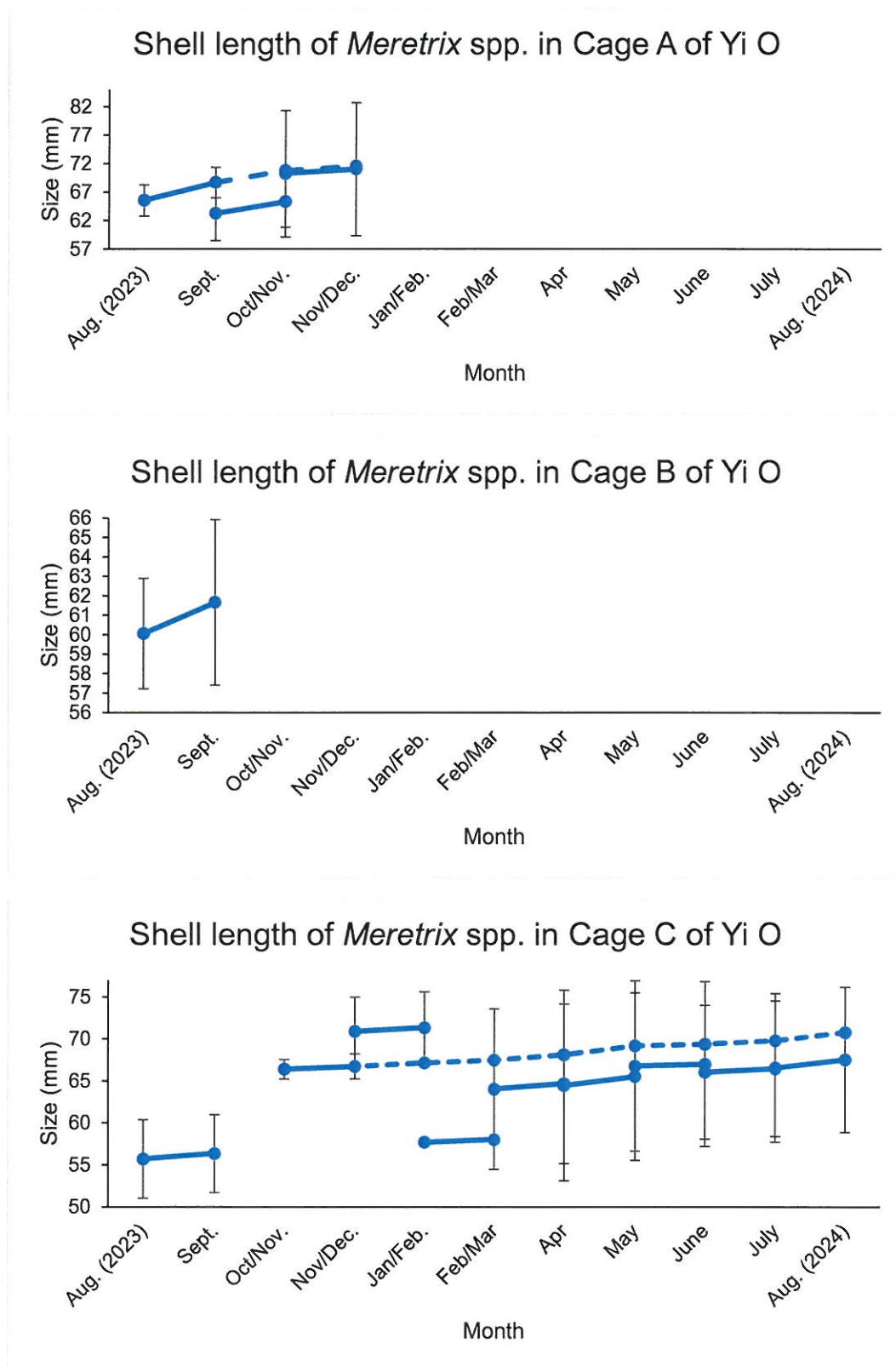


Fig. 43. Mean monthly growth of *Meretrix* spp. in Yi O, maintained in three cages (A, B, C) between August 2023 and August 2024. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas dotted lines indicate the adjusted growth, assuming that the mean shell length of all clams in each cage was equivalent to that of the surviving individuals at each sampling time. Due to the

very limited number of *Meretrix* spp. available for replacement, the experiment was terminated once all individuals in the cages had died and no further replacements could be obtained.

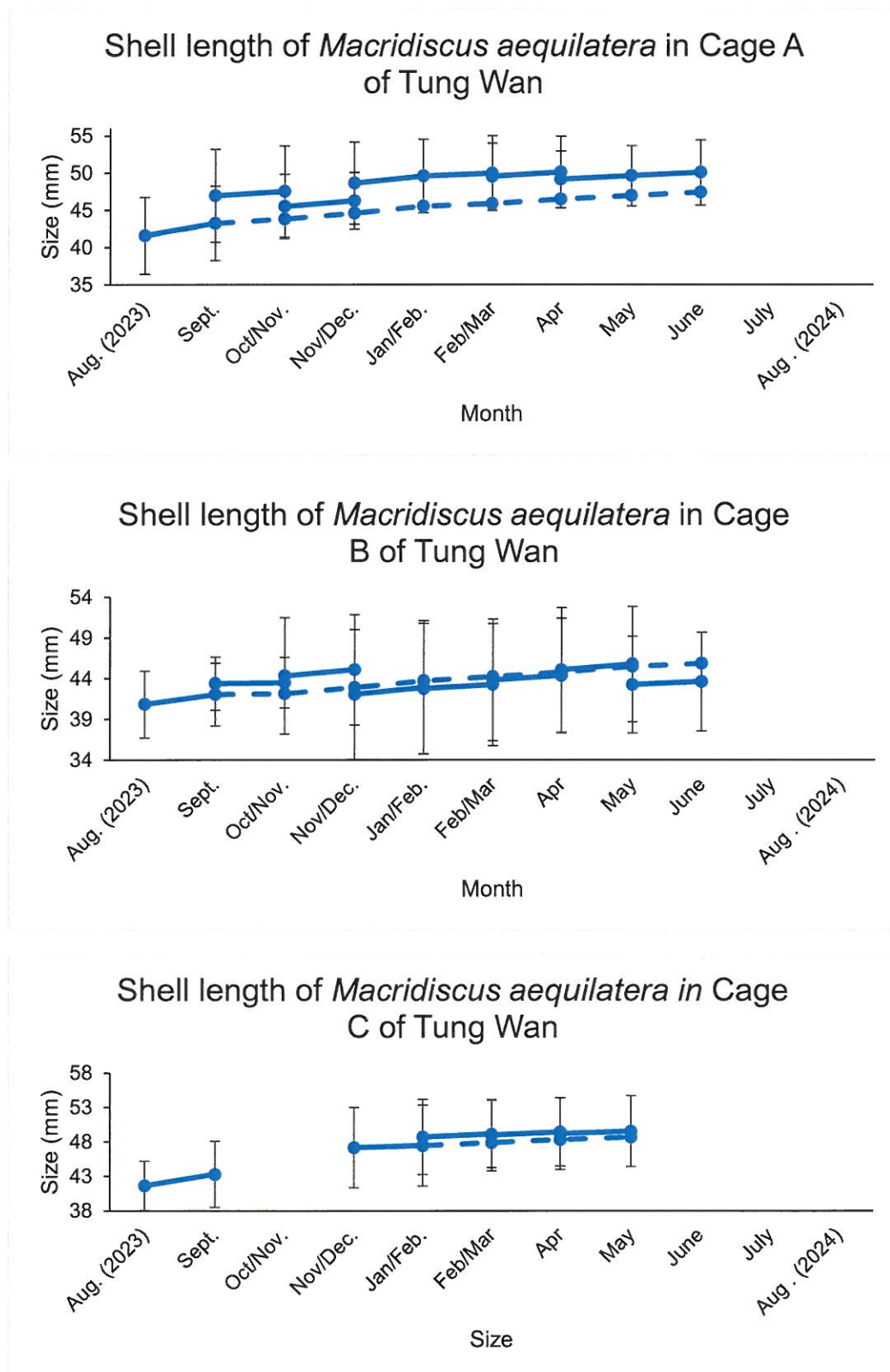


Fig. 44. Mean monthly growth of *Macridiscus aequilatera* in Tung Wan, maintained in three cages (A, B, C) between August 2023 and June 2024. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas dotted lines indicate the adjusted growth, assuming that the mean shell length of all clams in each cage was equivalent to that of the surviving individuals at each

sampling time. The results were obtained until May or June 2024 because the cages were lost during typhoons or rainstorms.

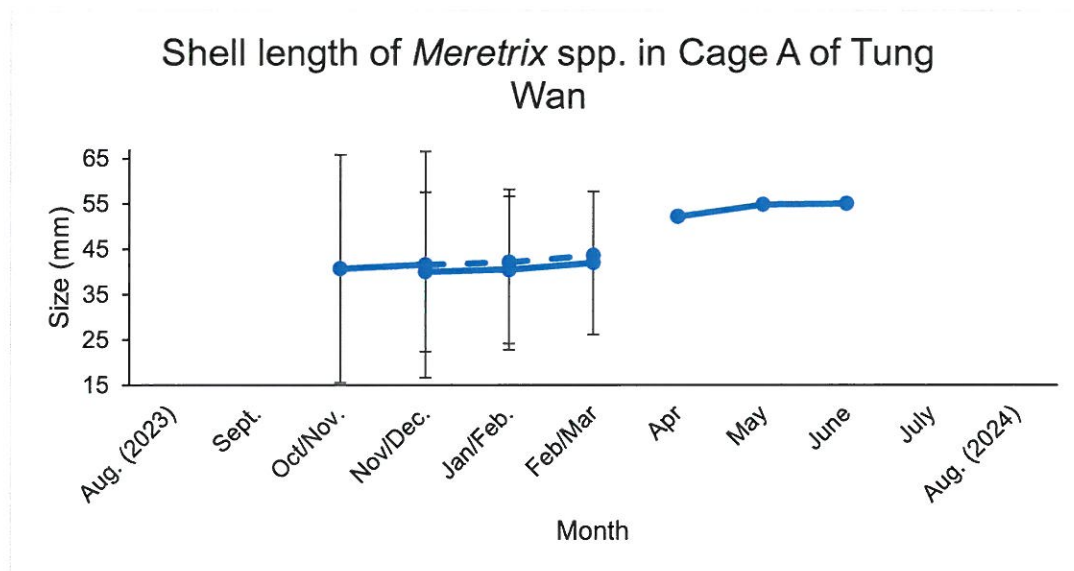


Fig. 45. Mean monthly growth of *Meretrix* spp. in Tung Wan, maintained in a cage (A) between October/November 2023 and June 2024. Only one cage is shown because the other two were lost during typhoons or rainstorms. Dead clams were replaced with similar-sized individuals collected from the site during each visit. Solid lines represent the actual growth of the surviving individuals, whereas dotted lines represent the adjusted growth, assuming that the mean shell length of all clams in the cage was equivalent to that of the surviving clams at each sampling time.

7. Study 6. Investigating the genetic connectivity of individual clam species on Lantau Island

In this study, four high-quality chromosome-level genomes were generated for *Anomalocardia flexuosa*, *Meretrix petechialis*, *Meretrix meretrix*, and *Meretrix lamarckii*. Population genomic analyses were also conducted for *M. petechialis*, *M. meretrix*, and *M. lamarckii*. Two papers arising from this work were published in Scientific Data (Law et al., 2025; 2026).

Meretrix species are among the most preferred clam species targeted by recreational clam diggers; however, the four *Meretrix* species are morphologically very similar. This necessitated the use of genomic analyses, rather than morphological traits, to reliably determine their distribution across the study sites. *Meretrix lyrata* was not included in the study because it was rare or absent at most of the sites.

7.1 Methodology

7.1.1 DNA extraction, genome sequencing and genome assembly

A. flexuosa and *M. petechialis* samples were collected at Shui Hau on 6th July, 2023 and Yi O on 28th August, 2022, respectively, while *M. meretrix* and *M. lamarckii* samples were collected in Tung Wan on 13th August, 2022. Genomic DNA was extracted from ~300 mg of adductor muscle from each sample. Tissue samples were first ground into fine powder using liquid nitrogen, followed by high-molecular-weight DNA isolation using the NucleoBond HMW DNA kit (Macherey-Nagel) for *A. flexuosa*, *M. meretrix*, and *M. lamarckii*, and the MagAttract HMW DNA Kit (Qiagen) for *M. petechialis*, in accordance with the manufacturers' instructions. DNA quality and quantity were assessed using a Qubit Fluorometer, a NanoDrop One spectrophotometer, and overnight pulsed-field gel electrophoresis.

A SMRTbell library was constructed for each sample using the SMRTbell Prep Kit 3.0, following the manufacturer's instructions. For *A. flexuosa* and *M. petechialis*, the SMRTbell libraries were sequenced on the PacBio Sequel IIe system, generating 21.83 Gb and 30.58 Gb of HiFi reads, respectively. For *M. meretrix* and *M. lamarckii*, the SMRTbell libraries were sequenced on the PacBio Revio system, yielding 62.87 Gb and 57.89 Gb HiFi reads, respectively.

In addition, an Omni-C library was prepared for each sample using the Dovetail Omni-C Library Preparation Kit according to the manufacturer's instructions. The resulting Omni-C libraries were sequenced on the Illumina HiSeq-PE150 or NovaSeq 6000 platforms, generating 60.4 Gb, 56.6 Gb, 3.55 Gb, and 3.36 Gb Omni-C data for *A. flexuosa*, *M. petechialis*, *M. meretrix* and *M. lamarckii*, respectively.

De novo genome assemblies for each sample were generated from PacBio HiFi reads using Hifiasm (Cheng et al., 2021). Haplotypic duplications were subsequently removed from HiFi read depth data using purge_dups (Guan et al., 2020). Omni-C data were then used for scaffolding with YaHS (Zhou et al., 2023) to produce the final chromosome-level assemblies.

Assembly completeness was assessed using Benchmarking Universal Single-Copy Orthologs (BUSCO) with the *metazoa_odb12* dataset (Manni et al., 2021).

7.1.2 RNA sequencing and genome annotation

Total RNA was extracted using TRIzol™ from the foot and adductor muscle, mantle, digestive gland, gill and gonad tissues of *A. flexuosa*, and from the foot, digestive gland, gill and gonad tissues of *M. petechialis*. The RNA samples were sequenced on the Illumina NovaSeq 6000 platform, generating 31.7 Gb and 23.1 Gb of transcriptome data for *A. flexuosa* and *M. petechialis*, respectively.

For gene model prediction, RNA-sequencing data from *A. flexuosa* and *M. petechialis* were processed using Trimmomatic (v0.39; Bolger, Lohse & Usadel, 2014) and Kraken2 (v2.0.8; Wood et al., 2019) to remove low-quality and contaminated reads. Clean reads were then aligned to the repeat-soft-masked genome assemblies using HISAT2 (Kim et al., 2019). In addition, a total of 389,399 molluscan reference protein sequences were retrieved from NCBI on 25 March 2024 and used as protein evidence. Genome annotation was performed using BRAKER (v3.0.8) (Hoff et al., 2019) in GeneMark-ETP mode.

For *M. meretrix* and *M. lamarckii*, molluscan reference protein sequences were used to train GeneMark-EP via BRAKER (v3.0.8) for gene model prediction. The longest transcript of each predicted gene model was subsequently evaluated for completeness using Benchmarking Universal Single-Copy Orthologs (BUSCO) with the *metazoa_odb12* dataset (Manni et al., 2021).

7.1.3 Sample collection, DNA extraction and whole-genome resequencing

Meretrix specimens were collected from five sampling sites, namely Pui O, Sha Lo Wan, Shui Hau, Tung Wan and Yi O, on Lantau Island between 1 June 2022 and 13 March 2024 (Fig. 46). Genomic DNA was extracted from the adductor muscle using the Purelink Genomic Mini Kit (Invitrogen), following the manufacturer's instructions. DNA quality and quantity were assessed by agarose gel electrophoresis and a NanoDrop spectrophotometer (Thermo Scientific).

Species identity was determined by amplifying the mitochondrial cytochrome c oxidase subunit I (COI) gene using the universal primers LCO1490 and HCO2198 (Folmer et al., 1994). PCR amplification was performed on a T100™ thermo cycler (Bio-Rad) with the following conditions: an initial denaturation at 95 °C for 3 min; 39 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 45 s; and a final extension at 72 °C for 5 min. The size of the amplified products was verified by gel electrophoresis, and the PCR products were then sent to BGI Hong Kong for Sanger sequencing. Sequence chromatograms were inspected for quality using Chromas v2.6.6 (<https://technelysium.com.au/wp/chromas/>). The resulting sequences were searched against the NCBI *nr* database using BLASTn and aligned with reference COI sequences from previous

studies (Chen et al., 2011; Wang et al., 2017; Zhang et al., 2012) using MAFFT (Katoh and Stanley, 2013). A maximum-likelihood phylogenetic tree was constructed using FastTree (Price et al., 2010).

For population genomic analysis, genomic DNA from 5, 8, and 14 individuals of *M. lamarckii*, *M. meretrix*, and *M. petechialis*, respectively, collected from 1, 2, and 5 sampling sites, was submitted to Novogene for library preparation and whole-genome resequencing on the Illumina PE150 platform at $\sim 10 \times$ coverage. Adapter sequences in raw reads were trimmed using Trimmomatic (Bolger et al., 2014), followed by contaminant removal with Kraken2 (v2.0.8) (Wood et al., 2019).

Single nucleotide polymorphisms (SNPs) were called separately for interspecific and intraspecific analyses. For interspecific analyses, reads were mapped to the *M. petechialis* reference genome, whereas for intraspecific analyses, reads were mapped to their respective species-specific reference genomes. Cleaned reads were aligned using BWA-MEM (Li, 2013), and genotypes were called using the Genome Analysis Toolkit (GATK) (DePristo et al., 2011) with the *HaplotypeCaller* and *GenotypeGVCFs* workflows. Hard filtering was applied following GATK best-practice recommendations (Van der Auwera et al., 2013) to remove variants with mapping quality (MQ) < 40.0, Fisher strand bias (FS) > 60.0, quality by depth (QD) < 2.0, mapping quality rank sum (MQRankSum) < -12.5, and read position rank sum (ReadPosRankSum) < -8.0. SNPs were further filtered using VCFtools (Danecek et al., 2011) to retain biallelic sites with no missing data, a maximum depth of 500, and exclusion of repetitive regions, generating SNP subset 0.

For interspecific analyses, SNPs at 4-fold degenerate sites were extracted using *degenotate* (<https://github.com/harvardinformatics/degenotate>) (Mirchandani et al., 2024), followed by linkage disequilibrium (LD) pruning and restriction to gene regions corresponding to single-copy orthologs among the three *Meretrix* species identified using OrthoFinder (Emms and Kelly, 2019). A minor allele frequency (MAF) threshold of 5% was then applied using PLINK v1.90b6.10 (Purcell et al., 2007) to generate the final SNP subset for interspecific analyses. For intraspecific analyses, putatively neutral SNP sets for each *Meretrix* species were obtained by further filtering SNP subset 0 through LD pruning and applying a MAF threshold of 5% using PLINK v1.90b6.10.

7.1.4 Population genomic analyses

Population genomic analyses were performed using both intraspecific and interspecific SNP subsets. Principal component analysis (PCA) was conducted in PLINK (Purcell et al., 2007) to generate eigenvalues and eigenvectors, and the first two principal components were visualized in R using the ggplot2 package (Wickham, 2016). Population structure was further inferred using ADMIXTURE (v1.3.0; Alexander, 2009), with the optimal number of genetic clusters (K) determined by the lowest cross-validation (CV) error across K values from 1 to 10.

In addition, a neighbour-joining phylogenetic tree was constructed with 1,000 bootstrap replicates in R using the adegenet (Jombart et al., 2008), ape (Paradis and Schliep, 2019),

poppr (Kamvar et al., 2014) and vcfr (Knaus and Grünwald, 2017) packages. The resulting phylogenetic tree was visualized using Evolvview v3 (Subramanian et al., 2019).

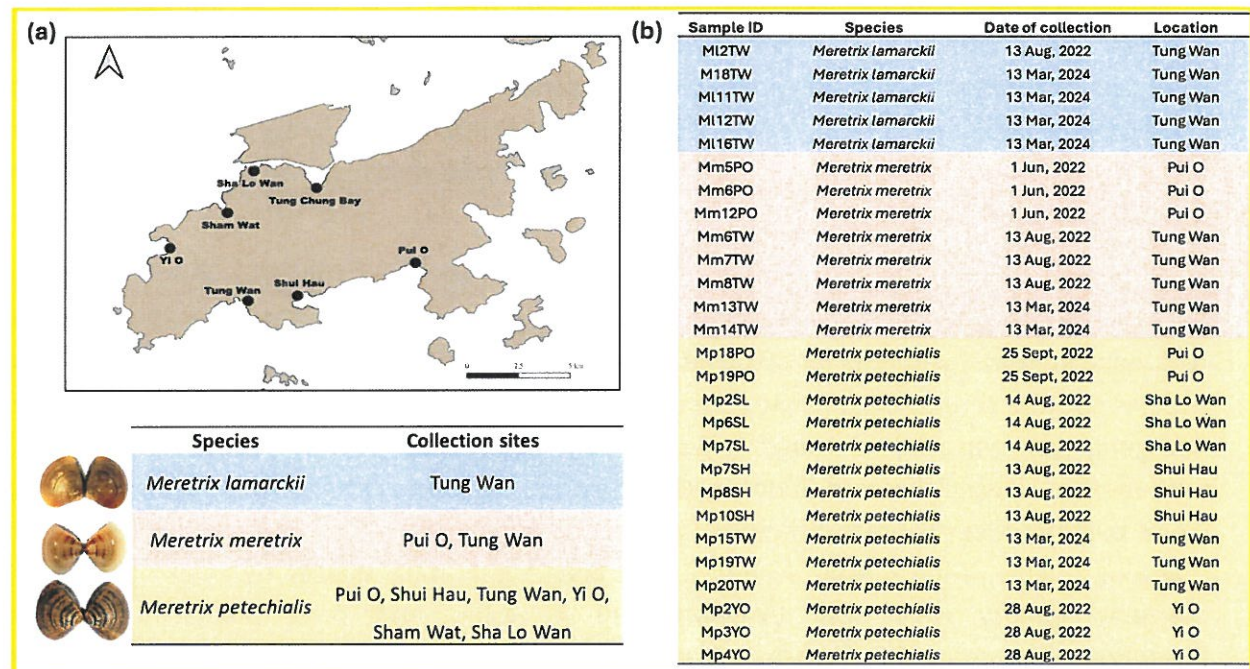


Figure 46. Summary of sample collection. (a) Geographical map of the collection sites and a tabulated summary of species identified at each site; (b) Sample information for collected individuals of *Meretrix lamarckii*, *Meretrix meretrix*, and *Meretrix petechialis*.

7.2 Results and Discussion

7.2.1 Chromosome-level genome assemblies

We generated four high-quality chromosome-level genome assemblies for *A. flexuosa*, *M. petechialis*, *M. meretrix*, and *M. lamarckii*. Each assembly anchored 19 chromosomes, with genome sizes of 1,090.7 Mb, 1,045.8 Mb, 835.1 Mb and 890.5 Mb, respectively (Figure 47). The assemblies exhibit high contiguity, with scaffold N50 values of 58.4 Mb, 53.5 Mb, 46.1 Mb, and 46.2 Mb, represented by 9 scaffolds for *A. flexuosa*, *M. petechialis*, *M. meretrix*, and *M. lamarckii*, respectively. Completeness was also high, with BUSCO scores ranging from 97.3% to 98.4%. (Figure 47).

Gene prediction identified 26,853, 25,196, 28,699 and 33,346 gene models in *A. flexuosa*, *M. petechialis*, *M. meretrix*, and *M. lamarckii*, respectively. The annotation quality was supported by BUSCO scores ranging from 93.0% to 97.6%, indicating high completeness of the predicted gene sets.

7.2.2 Population analyses

For the interspecific analysis, a subset of 115,503 neutrally evolving SNPs at 4-fold degenerate sites in single-copy orthologous genes was identified by mapping all *Meretrix* samples to the *M. petechialis* reference genome (Figure 48a). PCA analysis and phylogenetic reconstruction revealed three distinct clusters, while ADMIXTURE analysis identified the lowest cross-validation (CV) error at $K = 3$, indicating that each *Meretrix* species corresponds to a separate population (Figure 48b-d).

Within-species analyses yielded neutrally evolving SNP subsets of 1,052,921 in *M. lamarckii*, 1,977,821 in *M. meretrix*, and 8,925,093 in *M. petechialis* (Figure 49a). PCA plots for each species showed principal components with low eigenvalues, reflecting limited variance among sampled individuals (Figure 49b). ADMIXTURE analysis revealed no decline in CV error between $K = 1$ and $K = 2$, suggesting the absence of subpopulation structure within each species (Figure 49d). Consistently, the SNP-based phylogenetic trees displayed deep internodes and long-branch attraction, further supporting low genetic differentiation among individuals.

Taken together, these results indicate that genetic diversity in the clams studied here is structured at the species level rather than the population level on Lantau Island.

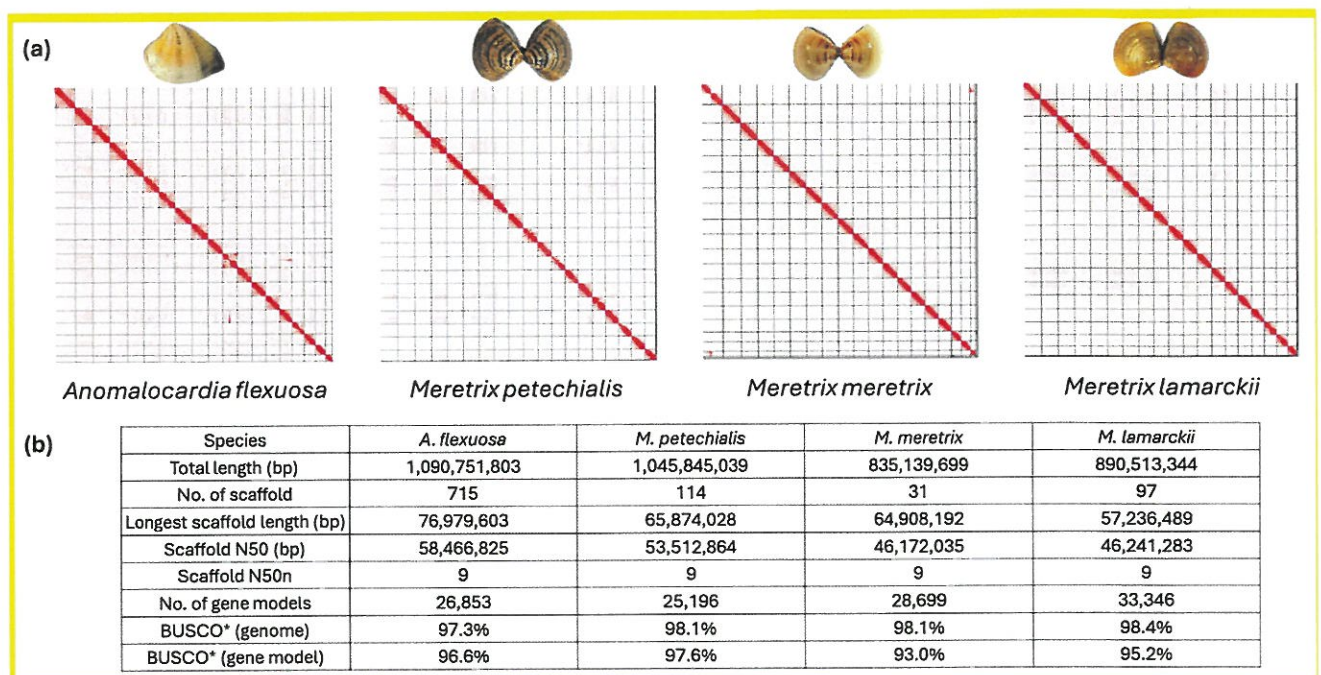


Figure 47. Summary of genome assemblies generated in this study for *Anomalocardia flexuosa*, *Meretrix petechialis*, *Meretrix meretrix*, and *Meretrix lamarckii*. (a) Omni-C contact maps of the assembled chromosomes for each species; (b) Summary statistics of the genome assemblies. Genome completeness was assessed using Benchmarking Universal Single-Copy Orthologs (BUSCO) with the *metazoa_odb12* dataset.

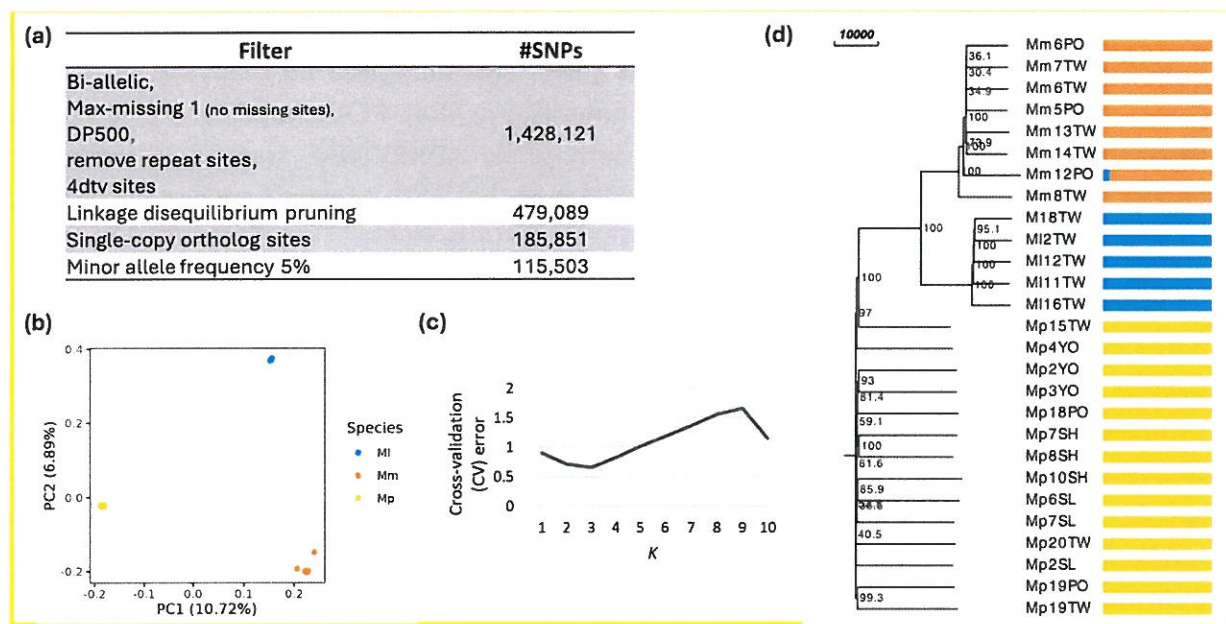


Figure 48. Interspecific population genomic analyses of *M. lamarckii*, *M. meretrix*, and *M. petechialis*. (a) Results of SNP filtering for the SNP subset used in interspecific analyses; (b) Principal component analysis (PCA) plot with *M. lamarckii*, *M. meretrix*, and *M. petechialis* samples shown in blue, orange and yellow, respectively; (c) Cross-validation (CV) error from ADMIXTURE analyses across values of *K* from 1 to 10; (d) Neighbor-joining phylogenetic tree with 1,000 bootstrap replicates (bootstrap values shown as percentages at nodes; left) and the corresponding ADMIXTURE bar plot (right). In the ADMIXTURE analysis, *M. lamarckii*, *M. meretrix*, and *M. petechialis* are represented in blue, orange and yellow, respectively.

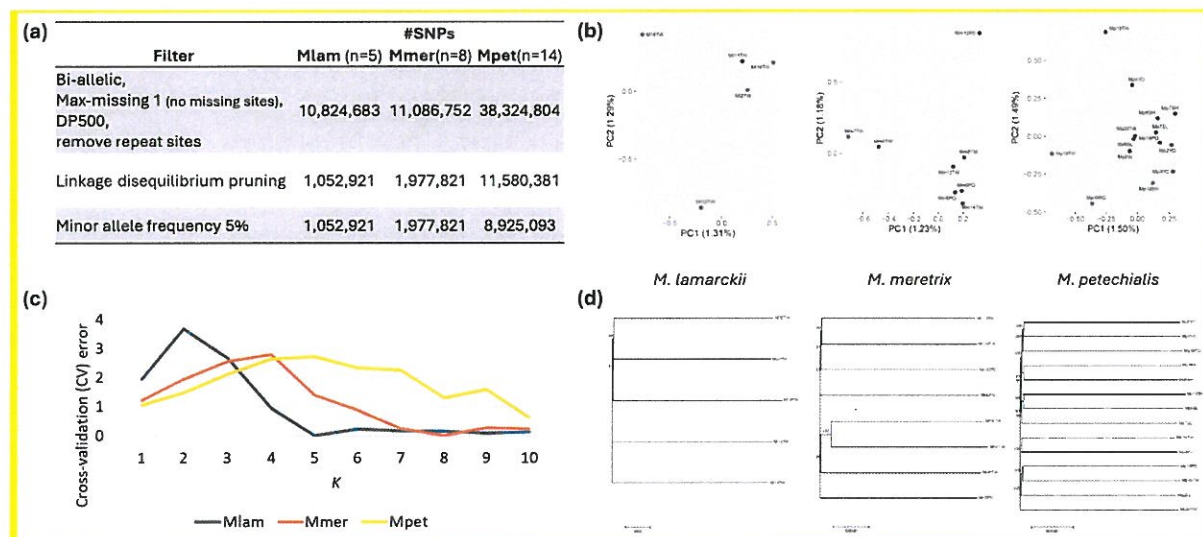


Figure 49. Intraspecific population genomic analyses of *M. lamarckii*, *M. meretrix*, and *M. petechialis*. (a) Results of SNP filtering for the intraspecific SNP subsets (Mlam, *M. lamarckii*; Mmer, *M. meretrix*; Mpet, *M. petechialis*); (b) Principal component analysis (PCA) plots for *M. lamarckii*, *M. meretrix*, and *M. petechialis*, shown from left to right; (c) Cross-validation (CV) error from ADMIXTURE analyses across values of *K* from 1 to 10 for *M. lamarckii* (blue), *M. meretrix* (orange), and *M. petechialis* (yellow); (d) Neighbor-joining phylogenetic trees with 1,000 bootstrap replicates (bootstrap values shown as percentages at nodes) for *M. lamarckii*, *M. meretrix*, and *M. petechialis*, shown from left to right.

8. General Discussion and Recommendations:

8.1 Discussion

A total of 41 clam species were recorded across six sampling sites during the 2022 and 2024 surveys. Clam species diversity varied among sites and generally increased with site size. However, among sites of comparable size, popular clam digging sites exhibited lower Shannon-Wiener species diversity and Pielou's species evenness than sites subject to low clam digging pressure. The total number of clam species recorded was similar between the two surveys, except at Shui Hau and Yi O, where declines of 57% and 25%, respectively, were observed. These observations suggest that clam digging pressure may negatively affect clam species diversity and evenness. One possible reason is that sediment disturbance caused by clam digging degrades habitat quality for some sensitive species; however, further investigation is required to substantiate this mechanism.

Clam species composition varied among sites but showed no clear differences between the two surveys. Clam digging pressure did not appear to influence species composition directly. Instead, sediment particle size emerged as the primary determining factor, as indicated by NMDS and SIMPER analyses. This conclusion is supported by the lack of clustering among clam digging sites and among control sites.

Most clam digging activity occurs during the summer months, when low tides typically occur in the afternoon. Popular digging sites are generally those with easy public transport access, such as Shui Hau and Tung Chung, whereas more remote sites, such as Sha Lo Wan and Yi O, are rarely visited. Owing to its large beach area, Shui Hau recorded the highest number of clam diggers during low tide, with more than 350 diggers per hour. In comparison, approximately 12 and 70 diggers per hour were recorded at the other two popular sites, Tung Chung and Pui O, respectively.

The most heavily harvested clam species include *Anomalocardia flexuosa*, which is restricted to Shui Hau, and *Ruditapes philippinarum* at Tung Chung. Various *Meretrix* species were among the most frequently harvested at all clam digging sites, owing to their large size and high flesh yield. On particularly crowded days, approximately 8000 individuals of *Anomalocardia flexuosa*/*Anomalodiscus squamosa* were harvested at Shui Hau, along with around 1200 individuals of *Meretrix* spp. In Tung Chung, approximately 1000 individuals of *R. philippinarum* were harvested in a single day.

Although environmental carrying capacity could not be estimated, multiple indicators suggest that populations of targeted clam species are overexploited by clam digging activities. For instance, a one-year population survey of *A. flexuosa* at Shui Hau showed a continuous decline, with population density decreasing to approximately half its initial level after one year. Similarly, *Meretrix* spp. exhibited extremely low densities across all sites, ranging from 1 to 2 individuals m⁻². Comparable densities were reported by So et al. (2021) for *M. meretrix* in Shui Hau, with 1.59 individuals m⁻² in the wet season and 0.95 individuals m⁻² during the dry season in 2018-2019.

Although Pui O exhibited a slightly higher density of approximately 7 individuals m⁻² in the present study, individuals at this site were the smallest among all surveyed sites, which is likely another consequence of human exploitation. Clam digging pressure at Pui O is probably lower than at other sites, as it is primarily a swimming beach and clam digging constitutes only part of visitors' activities. In contrast, the *R. philippinarum* population appeared less affected by harvesting pressure, with density remaining relatively stable between the start and end of the one-year survey.

The population dynamics of targeted species, *Anomalocardia flexuosa* at Shui Hau, *Ruditapes philippinarum* at Tung Chung, *Macridiscus aequilatera* at Tung Wan, and *Meretrix* spp. across Shui Hau, Pui O, Tung Wan and Yi O, were monitored over a one-year period. All species exhibited two recruitment events per year. This pattern may reflect a single breeding season temporally divided by summer rainfall, which characteristically reduces surface water salinity across Hong Kong. Mid-summer rainfall may constrain fertilization or spawning, thereby limiting successful recruitment to the earlier and later, relatively drier periods of the season. Alternatively, intense summer rainfall may flush juvenile clams from intertidal habitats, creating the appearance of a bimodal recruitment pattern (Morton, 1989). In contrast to *A. flexuosa* and *R. philippinarum*, *Meretrix* spp. displayed a longer recruitment period, extending beyond summer into winter.

For all species in this study, the total number of new recruits collected across all quadrats was very small, with no species exceeding 20 new recruits in a visit. While the possibility of overlooking very small individuals during sampling cannot be excluded, a more plausible explanation is the overexploitation of mature individuals, which has likely reduced overall reproductive output. This impact may have been exacerbated during the COVID-19 outbreak in 2020, when international restrictions forced many residents to remain in Hong Kong, leading to a sharp increase in local outdoor activities, including clam digging. Such intense harvesting pressure could remove large numbers of mature clams within a short time, thereby diminishing reproductive capacity. The consequences may be long-lasting, as a reduced spawning stock can lead to consistently low recruitment rates, consistent with the poor recruitment success observed in this study. If this hypothesis is correct, following the decrease in the number of clam diggers after COVID-19 was controlled, more clams can reach the size at maturity and increase the reproductive output, hence the densities of clams are expected to increase, unless the clam harvesting pressure continues to increase due to improved accessibility of these popular clam digging sites.

Based on cohort analysis in Study 3, all examined species have an estimated life span of approximately four to five years. Comparable results have been reported in previous studies. For example, *Anomalocardia flexuosa* is considered a short-lived clam characterized by rapid growth and high population turnover in tropical intertidal habitats, with a reported life span of approximately 3-4 years (Silva-Cavalcanti et al., 2018). *Ruditapes philippinarum* typically exhibits an effective lifespan of 4–6 years under fishing pressure (Sugiura and Kikuya, 2017), but individuals may live considerably longer (13 years) in protected or optimal habitats (Small and Birchenough, 2021).

Meretrix meretrix is generally longer-lived than many small venerid clams. Most population studies report a life span of 6-8 years, although these estimates are often influenced by overexploitation (Admodisastro et al., 2021). Reviews and regional biological profiles from India similarly indicate a life span of approximately 7–8 years based on growth and size-structure data. In contrast, the present study estimated a life span of only about 4 years for *Meretrix meretrix*, comparable to those of *A. flexuosa* and *R. philippinarum*. Coupled with its much lower population density relative to the other target clam species at the study sites, these findings suggest that *Meretrix* spp. is experiencing a more severe level of over-exploitation than the other two species.

Annual shell length growth declined with age in all three clam species—*Anomalocardia flexuosa*, *Ruditapes philippinarum*, and *Meretrix* spp. First-year growth was approximately 10 mm in *A. flexuosa* and *R. philippinarum*, whereas substantially faster first-year growth (approximately 27 mm) was observed in *Meretrix* spp. This higher annual growth rate in *Meretrix* spp. is expected, as mature individuals commonly attain shell lengths exceeding 70 mm, compared with approximately 35 mm in *A. flexuosa* and 45 mm in *R. philippinarum*.

Direct measurements of annual growth are unavailable for these three species; therefore, yearly growth increments were derived by Copilot using local size-at-age information, size at sexual maturity, and cohort progression data. The best estimate for *A. flexuosa* is ~10 mm in year 1, declining to $\leq 5 \text{ mm yr}^{-1}$ thereafter. For *R. philippinarum*, the best estimate is ~25 mm in year 1, followed by $\sim 10 \text{ mm yr}^{-1}$ in subsequent years. For *Meretrix meretrix*, first-year growth is estimated at approximately 20 mm, with an average growth rate of $\sim 12 \text{ mm} \cdot \text{yr}^{-1}$ over the lifespan.

The growth rates estimated by Copilot for both the first year and older cohorts of all three clam species match those derived in this study using cohort analysis (Tables 17, 19 and 21). However, direct comparisons for first-year growth in *R. philippinarum* was not possible because, during the one-year survey (May 2023 – Apr 2024), the first-year cohort had been present for only nine months. At the completion of the survey, this cohort had reached a shell length of 16.19 mm, representing approximately half of the first-year growth estimated by Copilot.

The instantaneous growth rate constant (K) in the von Bertalanffy growth model also reflects the overall growth rate; higher K values indicate faster growth. The estimated K values for *A. flexuosa*, *R. philippinarum* and *Meretrix* spp. were 0.28, 0.32 and 0.36 yr^{-1} , respectively. Reported K values for fast-growing bivalves typically ranged from 0.6 to 1.5 yr^{-1} , for moderate-growing clams from 0.3 to 0.8 yr^{-1} , and for slow-growing, long-lived species are $< 0.3 \text{ yr}^{-1}$ (Moss et al. 2016; Reed et al., 2020). Accordingly, the K values obtained in this study are consistent with existing data and indicate that all three species can be classified as moderate-growing clams, with *A. flexuosa* exhibiting the slowest growth and *Meretrix* spp. the fastest growth among them.

The total mortality rate (Z) estimated from growth parameters derived from the Von Bertalanffy Growth Function represents the instantaneous rate at which individuals are removed from a population per unit time due to all causes, including natural mortality (e.g.,

predation, disease, senescence, and environmental stress) as well as fishing or harvesting mortality. In the present study, the estimated Z for *A. flexuosa* was 2.68, corresponding to an annual survival rate of 6.86%. For *R. philippinarum*, Z was 1.73, corresponding to an annual survival rate of 17.73%, whereas for *Meretrix* spp., Z was estimated at 1.47, corresponding to an annual survival rate of 22.99%.

The ratio of total mortality (Z) to the von Bertalanffy Growth Function (VBGF) growth coefficient (K) provides a widely used index of exploitation pressure and population sustainability. If Z/K is low, clams are living long enough to reach a significant portion of their maximum size and, crucially, are likely participating in multiple spawning cycles. If Z/K is high, it suggests that mortality is outstripping growth. Individuals are being removed long before they reach their full reproductive potential (Beverton and Holt, 1957; Pauly, 1980; Sparre and Venema, 1998). Estimates of Z derived from the VBGF are particularly useful for marine clams because (1) individuals cannot be reliably aged using hard structures, (2) harvesting is strongly size-selective, and (3) clam fisheries are frequently data-poor. Application of the VBGF allows (1) indirect estimation of age from shell length, (2) cohort tracking using size-frequency data, and (3) estimation of mortality without direct ageing. Consequently, VBGF-derived Z provides one of the few practical approaches for assessing population sustainability in clam fisheries.

The sustainability of a clam harvest depends on the following ecological shifts driven by the Z/K ratio:

Growth overfishing: If Z/K is too high, clams are harvested before they have had a chance to build substantial biomass. This leads to a lower yield-per-recruit because the clams are "taken too soon" relative to their growth capacity.

Recruitment overfishing: Clams are often sedentary and rely on high-density spawning. If a high Z/K ratio means few individuals reach the larger, more fecund size classes, the total larval output of the bed may drop below a critical threshold, leading to population collapse.

Size at First Capture: For sustainable management, the Z/K ratio helps determine the "optimal" size at first capture. If K is small (slow growth), the population is extremely sensitive to increases in Z . In such cases, even moderate harvesting pressure can lead to an unsustainable Z/K ratio.

Summary Table: Ecological Outlook

Z/K Ratio	Population Status	Sustainability Outlook
Low (< 1.5)	Growth-dominated; many large adults.	High potential for increased harvest or stable conservation.
Moderate (~ 2.0)	Balanced; typical of steady-state populations.	Generally sustainable under current pressure.

Z/K Ratio	Population Status	Sustainability Outlook
High (> 3.0)	Mortality-dominated; population is skewed young.	High risk of collapse; likely experiencing overfishing.

In marine clams, a **Z/K ratio greater than 3** is commonly interpreted as evidence of a truncated size structure, juvenile-dominated populations, and insufficient spawning biomass (Admodisastro et al., 2021). In the present study, estimated total mortality (Z) and the von Bertalanffy coefficients (K) were 2.68 and 0.28 for *A. flexuosa*, 1.73 and 0.32 for *R. philippinarum*, and 1.47 and 0.36 for *Meretrix* spp., yielding Z/K ratios of 9.57, 5.40 and 4.08, respectively. All values greatly exceed the commonly applied reference threshold of $Z/K = 2$, indicating that none of the three clam populations is at or near equilibrium conditions. Instead, the results strongly suggest severe overexploitation in the study area.

Monthly population dynamic analyses were conducted only for clam species actively targeted by clam diggers at four sites: Shui Hau, Tung Chung, Yi O, and Tung Wan. Results for *A. flexuosa* pertained exclusively to Shui Hau, as this was the only study site where the species was encountered. Similarly, results for *R. philippinarum* reflect conditions at Tung Chung only, owing to the very low abundance of this species at the remaining sites. For *Meretrix* spp., analyses were based on pooled data from all sites, as densities at individual sites were too low to permit site-specific assessment.

Clam digging also reduced species richness and overall diversity of the macrofaunal community in Tung Chung. Similar patterns have been reported in other studies (Griffiths et al., 2006; Mosbahi et al., 2016). These impacts can arise through multiple mechanisms. During digging, sediments are turned over, loosened, and redeposited, altering grain structure and reducing sediment stability. This process can destroy or collapse the burrows of infaunal organisms, thereby reducing habitat suitability for many macrofaunal species, particularly those that depend on stable substrates, such as tube-building polychaetes (Griffiths et al., 2006).

In addition, many non-target species are injured, dislodged, or exposed on the sediment surface, increasing their risk of mortality. Taxa with low mobility, fragile body structures, and longer life cycles—such as polychaetes, crustaceans, and juvenile bivalves—are especially vulnerable to such disturbances (Clarke et al., 2017). Digging activities can also disturb newly settled juveniles and larvae in surface sediments, thereby reducing population replenishment for both target and non-target species (Toupoint et al., 2016).

Furthermore, clam harvesting may reduce prey availability for higher trophic levels, leading to cascading food-web effects with potential consequences for shorebird populations and overall coastal ecosystem functioning (Clarke, 2018).

8.2 Recommendations and Future Studies:

This study revealed significant sustainability issues associated with clam digging on Lantau Island. All three target clam species, i.e., *A. flexuosa*, *R. philippinarum*, and *Meretrix* spp. were found to be severely over-exploited, as indicated by high values of the Z/K ratio, the ratio between the total mortality rate (Z, natural mortality + fishing mortality) and the von Bertalanffy growth coefficient (K). Evidence of over-exploitation was further supported by low population densities and recruitment intensities, reduced annual survival rates, shortened life spans, and smaller sizes of mature individuals. The problem was particularly acute for *Meretrix* spp., where reproductive potential was most compromised.

The situation may have been exacerbated during the COVID-19 pandemic, when harvesting pressure was unusually high. If large numbers of mature clams were removed in 2020-2021, when citizens were confined to Hong Kong, recruitment in subsequent years would have declined sharply, leading to very low numbers of mature individuals after the pandemic subsided. Although some green groups have recently observed a decrease in clam diggers compared with 2020-2021, the one-year census conducted between 2023-2024 was too short to provide definitive conclusions. To properly assess the sustainability of these species under current harvesting pressure, a long-term population monitoring program at popular clam-digging sites is strongly recommended.

Effects of clam digging were not limited to individual clam species. Preliminary observations indicate that both clam diversity and evenness were lower at heavily exploited sites than at control sites subjected to minimal harvesting pressure, even after accounting for differences in site size. This is notable because larger sites typically support higher clam diversity. In addition, intensive clam digging was associated with reductions in overall species diversity and species richness of the broader macrofaunal community.

Clam digging may also adversely affect other ecologically sensitive species, such as the endangered horseshoe crabs found in Shui Hau. Although the spatial overlap between commonly used clam-digging areas and horseshoe crab habitats is limited, it is important to inform clam diggers to avoid these habitats in order to minimize disturbance. **Warning signage could be installed around sensitive horseshoe crab areas to alert both clam diggers and other visitors.**

In view of the ecological impact of clam digging, various regulations are implemented in different countries to maintain the population sustainability of specific clam species.

(1) United States

Clamming rules and regulations vary among states (<https://killerclamrakes.com/clamming-laws-crabbing-laws/>). Recreational clam digging is limited to approved areas, and a local license may be required in Connecticut and South Carolina. In Delaware, hard clams smaller than 3.8 cm are not allowed to be harvested. In Florida, allowable clam harvesting areas are established and managed for public health purposes. In New Jersey, timing is regulated: no clamming on Sundays, except for a few selected areas. In New York, there is a harvesting limit of no more than one bushel of clams, oysters and mussels per day.

(2) Canada

Recreational fisheries implement minimum size limits for certain clam species, such as Littleneck and Manila clams. The 35 mm minimum size limit ensures clams spawn at least once before harvest, which is crucial for population sustainability (<https://www.canada.ca/en/fisheries-oceans/news/2025/03/two-recreational-shellfish-harvesters-receive-fines-and-fishing-bans.html>).

(3) Japan

Local cooperatives set detailed rules to protect clam stocks such as the oriental hard clam. Regulations include:

- Designated beaches for clam digging.
- Catch limit of maximum 1 kg per person per day.
- Size restrictions: hard clams must be ≥ 3 cm, surf clams must be ≥ 7 cm.
- Tool restrictions: only simple hand tools are allowed; wire mesh or “joren” rakes are banned.

(https://www.pref.ibaraki.jp/nourinsuisan/gyosei/chosei/leasure/shiohigari201804.html?utm_source=copilot.com)

Clam digging and harvesting can be enjoyable due to their exploratory nature. However, clam diggers should be aware of the potential negative ecological impacts of these activities, including reductions in clam population density, fecundity, and species diversity, as well as disturbances to the sediment environment. Therefore, it is important to introduce guiding principles for responsible clam digging.

Clam digging can also serve an important **educational purpose by helping people understand the diversity and ecology of clams in Hong Kong without removing them from their natural habitat**. Such non-extractive activities have minimal impact on the ecosystem and should be encouraged. They involve gently retrieving clams from the sediment for close observation, learning about their biology, and appreciating their natural beauty before carefully returning them to the beach.

If some diggers choose to consume clams, it is advisable to **harvest only a minimum number for tasting**, given the existing problem of overexploitation. **Using clam gauges designed by WWF-HK and following the associated codes of conduct can help** determine the minimum harvestable size for each clam species and minimize disturbance to the habitat.

To improve the efficiency of clam harvesting, some diggers use specialized devices such as chi hau pa (rake), a toothed metal rake used to dig or scrape clams from sandy or muddy beaches. However, the toothed design disturbs large areas of sediment, damaging the physical structure of beaches and sandflats, harming non-target organisms living in or on the sediment, and leaving visible raked scars that can accelerate erosion and habitat degradation. The use of such devices should therefore be discouraged and abandoned in clam harvesting.

Reducing harvesting pressure is crucial for promoting the recovery of clam populations. One possible management option on large beaches, such as Shui Hau, is to temporarily close certain areas to allow clam populations to recover. For instance, the clam digging area could be divided into four sections, with **one section closed each year** to prohibit clam digging during the summer, when harvesting activity is most intense. However, this approach may have an unintended drawback: **harvesting pressure in the remaining three sections could increase** as

all clam diggers are concentrated in fewer areas. Consequently, the overall harvesting pressure may not decrease and could even increase, resulting in no net reduction—or even an increase—in the total number of clams removed from the beach. This outcome would undermine the effectiveness of the management strategy.

Following the implementation of the above management strategies, their effectiveness should be evaluated through regular population monitoring to assess whether the status of individual clam species has improved. If no improvement is observed or conditions deteriorate, more stringent management measures may be required. Such measures could include limiting the number or total biomass of clams harvested, restricting the periods during which clam harvesting is permitted, or temporarily closing certain beaches to allow populations to recover.

The present genomic study of *Meretrix* spp. indicates that genetic diversity is structured at the species level rather than at the population level on Lantau Island. Individuals collected from the same beach did not exhibit higher genetic similarity than those from different beaches. Consistent with this, samples collected from the same beach did not form distinct clusters in the PCA plot. Furthermore, species-specific phylogenetic (SNP) trees show that individuals from the same beach did not form monophyletic groups but were interspersed, or "shuffled," among samples from other sites.

These results suggest that the observed genetic variation is not associated with sampling location, but is instead more randomly distributed across beaches. One possible interpretation is that populations from different beaches share a common larval stock. This is plausible because clams undergo external fertilisation, and their embryos develop into free-swimming larvae that can be transported among beaches by ocean currents. Alternatively, the observed pattern may reflect the presence of multiple, distinct larval stocks with similar genetic compositions. Population genetic analyses alone are insufficient to distinguish between these scenarios.

If a species occurring on different beaches indeed shares a common larval stock, this would imply that overharvested beaches could be at least partially replenished by larval input from beaches experiencing low harvesting pressure. To assess this possibility, it is necessary to extend population surveys to additional beaches on Lantau Island in order to better understand the spatial patterns of diversity and abundance of clam species targeted by clam diggers.

At present, it is unclear whether overharvesting of clams is also occurring on beaches outside Lantau Island, such as those in the New Territories. Several of these beaches, including Lok Wo Sha in Ma On Shan and Ting Kok in Tai Po, are also popular clam digging sites. We therefore recommend conducting similar population assessments on these beaches to determine whether comparable pressures are affecting their clam populations.

Clams inhabiting soft shore environments play vital ecological roles and provide diverse ecosystem services. They contribute to nutrient cycling, sediment stabilization, and serve as food resources for other marine organisms. Maintaining their diversity and population sustainability is essential for the health of intertidal habitats.

Success in sustaining clam populations relies on a multi-pronged approach with strategies introduced at different stages. The first stage integrates public environmental education to raise awareness among recreational harvesters about ecological impacts and responsible practices, alongside scientific investigations to monitor clam stocks, reproductive cycles, and habitat conditions for adaptive management. If the overharvesting problem does not improve, more stringent management strategies such as catch limits, size restrictions, seasonal closures, and designated harvesting areas, together with law enforcement through licensing, inspections, and penalties, can be considered to ensure compliance and address this long-term problem.

9. References

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Appendices:

Appendix 1. Total number of bivalves recorded at six sites (Pui O, Sha Lo Wan, Shui Hau, Tung Chung, Tung Wan, Yi O) from all surveyed plots in the stock assessments conducted in 2022 and 2024 (Study 1).

No. of individuals	2022						2024					
	PO	SLW	SH	TC	TW	YO	PO	SLW	SH	TC	TW	YO
<i>Anomalocardia flexuosa</i>			376						335			
<i>Anomalodiscus squamosus</i>		4	15					9	25	2		
<i>Arcuatula senhousia</i>		2					3	4			5	
<i>Atactodea striata</i>	1						3					
<i>Borniopsis sagamiensis</i>			1			4						
<i>Cyclina sinensis</i>			3	2		1		3				
<i>Dosinia japonica</i>		2										
<i>Exolaternula spengleri</i>		2						1	1			
<i>Gafrarium tumidum</i>			1									
<i>Geloina expansa</i>						1		8				3
<i>Gonimyrtea sp.</i>			3			85						35
<i>Hiatula acuta</i>		3	7					1	7			
<i>Hiatula diphos</i>			1									
<i>Hiatula sp.</i>			2									
<i>Jactellina clathrata</i>									3			3
<i>Jitlada culter</i>			6			42						9
<i>Jitlada philippinarum</i>			20			262			5			366
<i>Joannisiella cumingii</i>		15	2	3		4		23		2	2	
<i>Kellia porculus</i>		4						3				
<i>Latona cuneata</i>					1						1	
<i>Latona faba</i>					1							
<i>Latona semisulcata semigranosa</i>	37						21					
<i>Macridiscus aequilatera</i>					26							
<i>Mactra dissimilis</i>	3		1									
<i>Marcia hiantina</i>		2	1									
<i>Meretrix lamarckii</i>	52	1	7		3		60		1			
<i>Meretrix lyrata</i>						1		1				3
<i>Meretrix meretrix</i>	23		8	2	3		44		4		1	2
<i>Meretrix petechialis</i>	29	2	10		2	29	38	5	19			16
<i>Nitidotellina soyoae</i>						1		2			4	
<i>Ruditapes philippinarum</i>		6	3					4		65	12	
<i>Rugalucina vietnamica</i>			1									
<i>Solen grandis</i>			2									
<i>Solen strictus</i>			6			2	230		9			1
<i>Strigilla tomlini</i>	1											
<i>Tapes conspersus</i>			2									
<i>Tapes literatus</i>										6	1	
<i>Tapes sp.</i>		9										
<i>Tellinella cruciata</i>						1						
<i>Tellinides timorensis</i>			1									
Unknown 1								1				
Total:	146	52	479	7	36	433	399	65	409	75	26	438

Appendix 2. Average shell length ($\pm$ SD) (mm) and density ($\pm$ SD) (m^{-2}) of bivalves recorded at six sites (Pui O, Sha Lo Wan, Shui Hau, Tung Chung, Tung Wan, Yi O) from all the surveyed plots in the stock assessments conducted in 2022 and 2024 (Study 1).

Species (Pui O)	2022	2024	2022	2024
	shell length ($\pm$ SD)	shell length ($\pm$ SD)	Density ($\pm$ SD)	Density ($\pm$ SD)
<i>Arcuatula senhousia</i>		17 (1.63)		0.2 (0.4)
<i>Atactodea striata</i>	27 (0)	15.67 (1.89)	0.07 (0.13)	0.2 (0.13)
<i>Latona semisulcata semigranosa</i>	9.62 (3.24)	12 (1.6)	2.47 (0.77)	1.4 (2.12)
<i>Mactra dissimilis</i>	9.33 (3.4)		0.2 (0.26)	
<i>Meretrix lamarckii</i>	11.52 (8.42)		3.47 (2.6)	
<i>Meretrix meretrix</i>	20.57 (14.54)	13.59 (12.84)	1.53 (0.46)	2.93 (4.45)
<i>Meretrix petechialis</i>	11.76 (14.04)	25.55 (11.71)	1.93 (1.16)	2.53 (1.03)
<i>Solen strictus</i>		24.55 (3.76)		15.33 (10.5)
<i>Strigilla tomlini</i>	17 (0)		0.07 (0.13)	

Species (Sha Lo Wan)	2022	2024	2022	2024
	shell length ($\pm$ SD)	shell length ($\pm$ SD)	Density ($\pm$ SD)	Density ($\pm$ SD)
<i>Anomalodiscus squamosus</i>	26 (2.24)	21.11 (2.28)	0.36 (0.41)	0.8 (0.46)
<i>Arcuatula senhousia</i>	19.5 (1.5)	12 (1.87)	0.18 (0.31)	0.36 (0.62)
<i>Cyclina sinensis</i>		40 (3.74)		0.27 (0.46)
<i>Dosinia japonica</i>	18.5 (1.5)		0.18 (0.31)	
<i>Exolaternula spengleri</i>	38.5 (10.5)	57 (0)	0.18 (0.15)	0.09 (0.15)
<i>Geloina expansa</i>		37.13 (11.11)		0.71 (0.56)
<i>Hiatula acuta</i>	14.67 (0.94)		0.27 (0.46)	
<i>Joannisiella cumingii</i>	14.33 (2.55)	11.78 (1.98)	1.33 (0.71)	2.04 (3.54)
<i>Kellia porculus</i>	11.25 (2.86)	13 (1.41)	0.36 (0.15)	0.27 (0.46)
<i>Marcia hiantina</i>	29.5 (0.5)		0.18 (0.31)	
<i>Meretrix lamarckii</i>	34 (0)		0.09 (0.15)	
<i>Meretrix lyrata</i>		19 (0)		0.09 (0.15)
<i>Meretrix petechialis</i>	51 (23)	52.2 (8.11)	0.18 (0.15)	0.44 (0.41)
<i>Nitidotellina soyoae</i>		16.5 (1.5)		0.18 (0.31)
<i>Ruditapes philippinarum</i>	27.17 (9.82)	15.5 (5.41)	0.53 (0.27)	0.36 (0.15)
<i>Tapes sp.</i>	28.44 (7.23)		0.8 (0.46)	
Unknown 1		11 (0)		0.09 (0.15)

Species (Shui Hau)	2022	2024	2022	2024
	shell length ($\pm$ SD)	shell length ($\pm$ SD)	Density ($\pm$ SD)	Density ($\pm$ SD)
<i>Anomalocardia flexuosa</i>	24.46 (20.96)	28.4 (4.76)	25.07 (3.34)	22.33 (5.75)
<i>Anomalodiscus squamosus</i>	21.67 (3.13)	24.2 (3.92)	1 (0.13)	1.67 (0.8)
<i>Borniopsis sagamiensis</i>	8 (0)		0.07 (0.13)	
<i>Cyclina sinensis</i>	41 (5.72)		0.2 (0.26)	
<i>Exolaternula spengleri</i>		36 (0)		0.07 (0.13)
<i>Gafrarium tumidum</i>	38 (0)		0.07 (0.13)	
<i>Gonimyrtea sp.</i>	7 (0)		0.2 (0.4)	

<i>Hiatula acuta</i>	12.43 (2.77)		0.47 (0.13)	
<i>Hiatula diphos</i>	13 (0)		0.07 (0.13)	
<i>Hiatula sp.</i>	13.5 (1.5)		0.13 (0.15)	
<i>Jactellina clathrata</i>		20 (1.63)		0.2 (0.4)
<i>Jitlada culter</i>	10.5 (0.96)		0.4 (0.46)	
<i>Jitlada philippinarum</i>	12.45 (5.5)	14.4 (1.5)	1.33 (1.04)	0.33 (0.5)
<i>Joannisiella cumingii</i>	11.5 (1.5)		0.13 (0.15)	
<i>Mactra dissimilis</i>	11 (0)		0.07 (0.13)	
<i>Marcia hiantina</i>	37 (0)		0.07 (0.13)	
<i>Meretrix lamarckii</i>	30.43 (19.58)	52 (0)	0.47 (0.26)	0.07 (0.13)
<i>Meretrix meretrix</i>	38.38 (14.16)	42 (9.54)	0.53 (0.38)	0.27 (0.38)
<i>Meretrix petechialis</i>	57.2 (12.37)	54.16 (12.01)	0.67 (0.34)	1.27 (0.67)
<i>Ruditapes philippinarum</i>	15.67 (1.7)		0.2 (0.26)	
<i>Rugalucina vietnamica</i>	8 (0)		0.07 (0.13)	
<i>Solen grandis</i>	42 (12)		0.13 (0.15)	
<i>Solen strictus</i>	21.83 (7.69)	34 (14.31)	0.4 (0.34)	0.6 (0.55)
<i>Tapes conspersus</i>	16.5 (8.5)		0.13 (0.27)	
<i>Tellinides timorensis</i>	50 (0)		0.07 (0.13)	

Species (Tung Chung)	2022	2024	2022	2024
	shell length (±SD)	shell length (±SD)	Density (±SD)	Density (±SD)
<i>Anomalodiscus squamosus</i>		18 (2)		0.22 (0.19)
<i>Cyclina sinensis</i>	43.5 (1.5)		0.22 (0.38)	
<i>Joannisiella cumingii</i>	13 (1.63)	9.5 (0.5)	0.33 (0.58)	0.22 (0.19)
<i>Meretrix meretrix</i>	44 (28)		0.22 (0.38)	
<i>Ruditapes philippinarum</i>		23.97 (7.81)		7.22 (2.52)
<i>Tapes literatus</i>		26 (3.79)		0.67 (0.58)

Species (Tung Wan)	2022	2024	2022	2024
	shell length (±SD)	shell length (±SD)	Density (±SD)	Density (±SD)
<i>Arcuatula senhousia</i>		16.4 (2.42)		0.44 (0.77)
<i>Joannisiella cumingii</i>		10.5 (0.5)		0.18 (0.31)
<i>Latona cuneata</i>	14 (0)	16 (0)	0.09 (0.15)	0.09 (0.15)
<i>Latona faba</i>	18 (0)		0.09 (0.15)	
<i>Macridiscus aequilatera</i>	46.5 (7.25)		2.31 (1.47)	
<i>Meretrix lamarckii</i>	75.67 (3.3)		0.27 (0.27)	
<i>Meretrix meretrix</i>	26.33 (13.82)	90 (0)	0.27 (0.27)	0.09 (0.15)
<i>Meretrix petechialis</i>	45.5 (17.5)		0.18 (0.15)	
<i>Nitidotellina soyoae</i>		27.5 (2.29)		0.36 (0.41)
<i>Ruditapes philippinarum</i>		22.67 (5.02)		1.07 (0.27)
<i>Tapes literatus</i>		26 (0)		0.09 (0.15)

Species (Yi O)	2022	2024	2022	2024
	shell length (±SD)	shell length (±SD)	Density (±SD)	Density (±SD)
<i>Borniopsis sagamiensis</i>	9.25 (6.26)		0.36 (0.41)	
<i>Cyclina sinensis</i>	59 (0)		0.09 (0.15)	
<i>Geloina expansa</i>	40 (0)	51.67 (1.25)	0.09 (0.15)	0.27 (0.46)

<i>Gonimyrtea sp.</i>	6.62 (1.41)		7.56 (8.18)	
<i>Jactellina clathrata</i>		13 (4.97)		0.27 (0.27)
<i>Jitlada culter</i>	10.81 (3.3)	9.56 (1.64)	3.73 (0.53)	0.8 (0.53)
<i>Jitlada philippinarum</i>	15.27 (2.59)	15.51 (2.61)	23.29 (10.69)	32.53 (6.2)
<i>Joannisiella cumingii</i>	10.75 (1.3)		0.36 (0.62)	
<i>Meretrix lyrata</i>	65 (0)	35.67 (27.11)	0.09 (0.15)	0.27 (0)
<i>Meretrix meretrix</i>		15.5 (0.5)		0.18 (0.15)
<i>Meretrix petechialis</i>	33.76 (23.2)	49 (21.94)	2.58 (1.78)	1.42 (0.56)
<i>Nitidotellina soyoae</i>	21 (0)		0.09 (0.15)	
<i>Solen strictus</i>	17.5 (2.5)	20 (0)	0.18 (0.31)	0.09 (0.15)
<i>Tellinella cruciata</i>	45 (0)		0.09 (0.15)	

Appendix 3. List of the total number of species by taxonomic group recorded at four sites (Shui Hau, Tung Chung, Tung Wan, Yi O) from all the plots across all sampling weeks following clam digging simulation in 2023 (Study 4).

Polychaetes	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
<i>Anoides oxycephala</i>	0	1	6	1	8
<i>Aricidea fragilis</i>	0	0	0	2	2
<i>Armandia intermedia</i>	167	0	20	0	187
<i>Cabira pilargiformis</i>	0	1	0	1	2
<i>Capitella capitata</i>	15	3	10	0	28
<i>Ceratonereis mirabilis</i>	0	2	0	0	2
<i>Chone infundibuliformis</i>	0	1	0	0	1
<i>Ehlersia cornuta</i>	0	2	0	0	2
<i>Eteone longa</i>	0	0	2	0	2
<i>Euclymene annandalei</i>	0	2	0	0	2
<i>Eunice aphroditoic</i>	0	1	0	0	1
<i>Eunice indica</i>	0	10	1	0	11
<i>Glycera alba</i>	1	0	0	0	1
<i>Glycera capitata</i>	0	0	6	0	6
<i>Glycera convoluta</i>	3	1	0	0	4
<i>Glycera onomichiensis</i>	1	2	0	2	5
Glyceridae sp.	0	0	1	0	1
<i>Glycinde gurjanovae</i>	0	0	4	3	7
<i>Heteromastus filiformis</i>	0	0	0	1	1
<i>Inermonephtys cf. inermis</i>	0	0	3	0	3
<i>Levinsenia gracilis japonica</i>	0	0	0	7	7
<i>Loimia medusa</i>	0	1	0	0	1
<i>Lumbrineris longifolia</i>	0	0	1	0	1
<i>Magelona pacifica</i>	13	0	0	5	18
<i>Mediomastus californiensis</i>	2	2	0	5	9
<i>Melinna cristata</i>	0	1	0	0	1
<i>Nectoneanthes oxypoda</i>	0	1	0	0	1
<i>Nephtys oligobranchia</i>	0	2	0	3	5
Nereididae sp.	0	34	0	7	41
<i>Notomastus aberans</i>	0	1	0	0	1
<i>Notomastus latericeus</i>	0	4	0	0	4
<i>Onuphis eremita</i>	2	9	0	1	12
<i>Owenia fusiformis</i>	1	1	0	0	2
<i>Paralacydonia paradoxa</i>	0	2	0	1	3
<i>Paraprionospio pinnata</i>	0	0	0	2	2
<i>Phyllodoce papillosa</i>	0	1	0	0	1
<i>Pionosyllis compacta</i>	0	5	14	0	19
<i>Poecilochaetus serpens</i>	0	20	0	8	28
<i>Poecilochaetus tropicus</i>	0	0	0	1	1
<i>Polydora cf. pilikia</i>	0	9	2	4	15
<i>Praxillella cf. affinis</i>	1	19	0	3	23
<i>Prionospio queenslandica</i>	4	1	9	6	20
<i>Pseudopolydora kemp</i>	7	1	24	3	35
<i>Rhynchospio glutaea</i>	3	0	0	2	5
<i>Scolecopsis squamata</i>	1	0	2	3	6

<i>Scoloplos armiger</i>	2	0	32	10	44
<i>Thelepus plagiostoma</i>	0	1	0	0	1
Polychaeta Total	223	141	137	81	582
Barnacles	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
<i>Amphibalanus amphitrite</i>	0	1	0	0	1
<i>Amphibalanus reticulatus</i>	0	1	0	0	1
Barnacle Total	0	2	0	0	2
Bivalves	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
Bivalva larva	37	0	0	0	37
<i>Donax semigranosus</i>	0	0	3	0	3
<i>Jitlada philippinarum</i>	0	0	0	5	5
<i>Meretrix lamarckii</i>	0	0	0	1	1
<i>Meretrix petechialis</i>	1	0	0	0	1
<i>Meretrix sp.</i>	0	0	1	0	1
Bivalva Total	38	0	4	6	48
Gastropods	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
<i>Anodontia edentula</i>	0	38	0	1	39
<i>Anomalodiscus squamosus</i>	0	1	0	0	1
<i>Batillaria zonalis</i>	0	2	0	0	2
<i>Clithon oualaniense</i>	0	1	0	0	1
<i>Crepidula sp.</i>	0	0	1	0	1
<i>Dosinia aspera</i>	0	1	0	0	1
<i>Ergalatax contractus</i>	0	0	1	0	1
<i>Littoraria articulata</i>	0	0	1	0	1
<i>Monodonta labio</i>	0	0	3	0	3
<i>Nassarius pullus</i>	0	1	0	0	1
<i>Reishia clavigera</i>	0	0	1	0	1
<i>Terebra pretiosa</i>	0	0	1	0	1
<i>Terebra sp.</i>	0	0	1	0	1
<i>Umbonium vestiarium</i>	57	0	5	0	62
<i>Zafra troglodytes</i>	0	0	1	0	1
Gastropoda Total	57	44	15	1	117
Hermit crab	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
<i>Diogenes edwardsii</i>	62	0	5	0	67
Others	Shui Hau	Tung Chung	Tung Wan	Yi O	Total
Amphipod	0	0	1	0	1
Unknown arthropod	1	0	0	0	1
All Total	381	187	162	88	818

Appendix 4. Average density ($\pm$ SD) (m^{-2}) of species recorded at four sites (Shui Hau, Tung Chung, Tung Wan, Yi O) from all plots across all sampling weeks following the clam digging simulation in 2023 (Study 4).

Shui Hau	Density ($\pm$SD) (m^{-2})
<i>Armandia intermedia</i>	55.67 (16.86)
Arthropod	0.33 (0.58)
Bivalva larva	12.33 (5.51)
<i>Capitella capitata</i>	5 (1.73)
<i>Diogenes edwardsii</i>	20.67 (10.12)
<i>Glycera alba</i>	0.33 (0.58)
<i>Glycera convoluta</i>	1 (1)
<i>Glycera onomichiensis</i>	0.33 (0.58)
<i>Magelona pacifica</i>	4.33 (1.53)
<i>Mediomastus californiensis</i>	0.67 (0.58)
<i>Meretrix petechialis</i>	0.33 (0.58)
<i>Onuphis eremita</i>	0.67 (1.15)
<i>Owenia fusiformis</i>	0.33 (0.58)
<i>Praxillella</i> cf. <i>affinis</i>	0.33 (0.58)
<i>Prionospio queenslandica</i>	1.33 (1.53)
<i>Pseudopolydora kemp</i>	2.33 (2.31)
<i>Rhynchospio glutaea</i>	1 (0)
<i>Scolecopsis squamata</i>	0.33 (0.58)
<i>Scoloplos armiger</i>	0.67 (0.58)
<i>Umbonium vestiarium</i>	19 (5.57)

Tung Chung	Density ($\pm$SD) (m^{-2})
<i>Amphibalanus amphitrite</i>	0.33 (0.58)
<i>Amphibalanus reticulatus</i>	0.33 (0.58)
<i>Anodontia edentula</i>	12.67 (17.79)
<i>Anoides oxycephala</i>	0.33 (0.58)
<i>Anomalodiscus squamosus</i>	0.33 (0.58)
<i>Batillaria zonalis</i>	0.67 (1.15)
<i>Cabira pilargiformis</i>	0.33 (0.58)
<i>Capitella capitata</i>	1 (1)
<i>Ceratonereis mirabilis</i>	0.67 (1.15)
<i>Chone infundibuliformis</i>	0.33 (0.58)
<i>Clithon oualaniense</i>	0.33 (0.58)
<i>Dosinia aspera</i>	0.33 (0.58)
<i>Ehlersia cornuta</i>	0.67 (1.15)
<i>Euclymene annandalei</i>	0.67 (0.58)
<i>Eunice aphroditoic</i>	0.33 (0.58)
<i>Eunice indica</i>	3.33 (4.16)
<i>Glycera convoluta</i>	0.33 (0.58)
<i>Glycera onomichiensis</i>	0.67 (0.58)
<i>Loimia medusa</i>	0.33 (0.58)

<i>Mediomastus californiensis</i>	0.67 (1.15)
<i>Melinna cristata</i>	0.33 (0.58)
<i>Nassarius pullus</i>	0.33 (0.58)
<i>Nectoneanthes oxypoda</i>	0.33 (0.58)
<i>Nephtys oligobranchia</i>	0.67 (0.58)
Nereididae sp.	11.33 (5.77)
<i>Notomastus aberans</i>	0.33 (0.58)
<i>Notomastus latericeus</i>	1.33 (0.58)
<i>Onuphis eremita</i>	3 (2)
<i>Owenia fusiformis</i>	0.33 (0.58)
<i>Paralacydonia paradoxa</i>	0.67 (1.15)
<i>Phyllodoce papillosa</i>	0.33 (0.58)
<i>Pionosyllis compacta</i>	1.67 (0.58)
<i>Poecilochaetus serpens</i>	6.67 (2.31)
<i>Polydora</i> cf. <i>pilikia</i>	3 (1.73)
<i>Praxillella</i> cf. <i>affinis</i>	6.33 (2.08)
<i>Prionospio queenslandica</i>	0.33 (0.58)
<i>Pseudopolydora kempi</i>	0.33 (0.58)
<i>Thelepus plagiostoma</i>	0.33 (0.58)

Tung Wan	Density ($\pm$SD) (m⁻²)
amphipod	0.33 (0.58)
<i>Anoides oxycephala</i>	2 (0)
<i>Armandia intermedia</i>	6.67 (1.53)
<i>Capitella capitata</i>	3.33 (3.51)
<i>Crepidula</i> sp.	0.33 (0.58)
<i>Diogenes edwardsii</i>	1.67 (0.58)
<i>Donax semigranosus</i>	1 (1)
<i>Ergalatax contractus</i>	0.33 (0.58)
<i>Eteone longa</i>	0.67 (0.58)
<i>Eunice indica</i>	0.33 (0.58)
<i>Glycera capitata</i>	2 (2)
Glyceridae sp.	0.33 (0.58)
<i>Glycinde gurjanovae</i>	1.33 (0.58)
<i>Inermonephtys</i> cf. <i>inermis</i>	1 (1.73)
<i>Littoraria articulata</i>	0.33 (0.58)
<i>Lumbrineris longifolia</i>	0.33 (0.58)
<i>Meretrix</i> sp.	0.33 (0.58)
<i>Monodonta labio</i>	1 (1)
<i>Pionosyllis compacta</i>	4.67 (7.23)
<i>Polydora</i> cf. <i>pilikia</i>	0.67 (0.58)
<i>Prionospio queenslandica</i>	3 (2)
<i>Pseudopolydora kempi</i>	8 (10.44)
<i>Reishia clavigera</i>	0.33 (0.58)
<i>Scoelepis squamata</i>	0.67 (1.15)

<i>Scoloplos armiger</i>	10.67 (4.16)
<i>Terebra pretiosa</i>	0.33 (0.58)
<i>Terebra</i> sp.	0.33 (0.58)
<i>Umbonium vestiarium</i>	1.67 (1.15)
<i>Zafra troglodytes</i>	0.33 (0.58)

Yi O	Density ($\pm$ SD) (m ⁻²)
<i>Anodontia edentula</i>	0.33 (0.58)
<i>Anoides oxycephala</i>	0.33 (0.58)
<i>Aricidea fragilis</i>	0.67 (0.58)
<i>Cabira pilargiformis</i>	0.33 (0.58)
<i>Glycera onomichiensis</i>	0.67 (0.58)
<i>Glycinde gurjanovae</i>	1 (1)
<i>Heteromastus filiformis</i>	0.33 (0.58)
<i>Jitlada philippinarum</i>	1.67 (0.58)
<i>Levinsenia gracilis japonica</i>	2.33 (2.08)
<i>Magelona pacifica</i>	1.67 (0.58)
<i>Mediomastus californiensis</i>	1.67 (0.58)
<i>Meretrix lamarckii</i>	0.33 (0.58)
<i>Nephtys oligobranchia</i>	1 (0)
<i>Nereididae</i> sp.	2.33 (2.08)
<i>Onuphis eremita</i>	0.33 (0.58)
<i>Paralacydonia paradoxa</i>	0.33 (0.58)
<i>Paraprionospio pinnata</i>	0.67 (1.15)
<i>Poecilochaetus serpens</i>	2.67 (2.52)
<i>Poecilochaetus tropicus</i>	0.33 (0.58)
<i>Polydora</i> cf. <i>pilikia</i>	1.33 (1.15)
<i>Praxillella</i> cf. <i>affinis</i>	1 (1)
<i>Prionospio queenslandica</i>	2 (1.73)
<i>Pseudopolydora kemp</i>	1 (0)
<i>Rhynchospio glutaea</i>	0.67 (1.15)
<i>Scolecopsis squamata</i>	1 (0)
<i>Scoloplos armiger</i>	3.33 (1.15)

Any opinions, findings, conclusions, or recommendations expressed in this publication/event do not necessarily reflect the views of the Government of the Hong Kong Special Administrative Region or the Lantau Conservation Fund Advisory Committee.