

# Species composition and genetic diversity of habitat-forming oysters in Hong Kong's intertidal mudflats

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## ABSTRACT

Oysters are one of the most important foundation species in intertidal habitats, yet decay of oyster-related ecosystems has been observed globally. To facilitate efforts in oyster conservation, it is imperative to gain solid baseline knowledge on the species composition of oysters in populations of conservation interest. In this study, we present a thorough investigation of the species diversity of oysters in ten of Hong Kong's intertidal mudflats, together with information on their demographics and population genetics. We also examined the species composition of oysters that were farmed commercially in Hong Kong to identify if aquaculture could be a source of larval recruitment for restoration efforts. All oyster habitats surveyed were comprised of multiple oyster species, and a total of nine species of oysters from the genus *Magallana* and *Saccostrea* were encountered. *Magallana sikamea* was the most prominent oyster species in Hong Kong's western waters, while *M. angulata* and *M. bilineata* were both commonly found in the eastern waters of Hong Kong. To our surprise, *M. hongkongensis*, which is the dominant species in the aquaculture population (and is farmed in diploid), was not found in the natural intertidal habitats. In nine out of ten sites surveyed, only one cohort of oysters was present, indicating high mortality of the oysters. Importantly, this lack of large, older individuals in natural habitats could undermine both the role of oysters as ecosystem engineers and limit natural recruitment as a source of juveniles for restoration efforts.

## 1. Introduction

Oysters were historically one of the most important foundation species in estuaries around the world, providing diverse ecosystem functions such as habitat provisioning, nutrient removal, and water filtering (Piehler and Smyth, 2011; Grabowski et al., 2012). However, oyster habitats worldwide are in decline. There are estimates that over 85% of oyster habitats have been removed globally through overharvest and coastal development (Beck et al., 2011), though in some regions this may be an underestimate (e.g., east and southeast Asia; (Williams et al., 2024)). This loss has led to a deterioration in the local biodiversity, ecosystem functions, and services they provide (Smith et al., 2023; Smith and Pruett, 2025). In response, oyster restoration efforts have

been gaining traction worldwide in recent decades (Pogoda et al., 2020; Howie and Bishop, 2021).

Apart from being an important foundation to ecosystems, oysters are also the most commonly farmed shellfish, accounting for 37.4% of the world's total mollusc production (FAO, 2024). To satisfy both economic and ecological needs, oyster aquaculture has been proposed as an effective method to simultaneously promote both aquaculture productivity and oyster habitat restoration (Brumbaugh et al., 2000; Overton et al., 2024). By stocking oysters at high densities, the recruitment of oysters in adjacent areas can be enhanced by the increased larval production. The scheme has been put to the test, and oyster farming has been shown to be an effective supplement to other oyster reef restoration methods (Wasson et al., 2020). However, using aquaculture as a tool for

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oyster reef restoration still has its own risks and limitations. Aquaculture has been attributed as one of the main causes of the introduction of non-native oyster species (Ruesink et al., 2005; Cognie et al., 2006; Wrangé et al., 2010; Moehler et al., 2011), potentially compromising the ecosystem services provided by the local oyster populations (Alvarez-Filip et al., 2013; Herbert et al., 2016; Muthukrishnan et al., 2020; Mundra et al., 2022). Furthermore, oysters could serve as a vector for pathogens (Pernet et al., 2018) and fouling species (Haupt et al., 2012), thus the act of translocating oysters for aquaculture could aid the spread of invasive species or pathogens (Murray et al., 2020). Even when local species are used, oyster aquaculture might still lead to genetic introgression between wild and farmed populations, potentially influencing the evolutionary trajectories of the wild populations (Jarvis et al., 2019). Moreover, oyster reefs in the tropics are usually formed by multiple oyster species (Richardson et al., 2022), while aquaculture populations are often monospecific (Botta et al., 2020). Therefore, to maximize the effectiveness of oyster restoration by aquaculture, it is first essential to have solid baseline knowledge on the species compositions of the local oyster populations.

China has the highest oyster aquaculture production globally, accounting for 86% of the world's total oyster production (Botta et al., 2020); at the same time, more than 90% of the oyster reefs in China are severely degraded (Yang et al., 2023) or completely lost (Williams et al., 2024). Given the scale of the oyster farming industry in China, conservation aquaculture is a framework that could be an immensely valuable tool in facilitating the restoration of China's oyster reefs. Due to the high demand for oyster seed, most of the seeds used by Chinese oyster farmers are produced in hatcheries (Mao et al., 2019). The broodstocks used in oyster hatcheries are often chosen to maximize growth performance, with little consideration of the local oyster species composition (Mao et al., 2019). For instance, *Magallana gigas*, one of the most commonly farmed oysters in Northern China, was introduced to China from Japan in 1979 (Li et al., 2006). From the perspective of assisting habitat restoration, stocking with an introduced species could potentially have longer-term negative effects on the ecosystems. *Magallana gigas* was repeatedly introduced to Europe as an aquaculture species, and populations of the oyster eventually established in the wild, displacing species indigenous to the ecosystems (Laugen et al., 2015; Herbert et al., 2016; Reise et al., 2017). Here, we use Hong Kong in Southern China to investigate the potential for facilitating oyster conservation through aquaculture because: (1) Hong Kong has a long history of oyster aquaculture (Morton and Wong, 1975); (2) oyster aquaculture in Hong Kong relies extensively on naturally collected spat instead of triploid strains (Morton and Wong, 1975; Chan et al., 2022), thus the aquaculture population could contribute to the local larvae pool; (3) natural oyster reefs in Hong Kong have experienced substantial degradation and overharvesting to the point of near extirpation (Lau et al., 2020; Williams et al., 2024); and, (4) Hong Kong has a tradition of combining aquaculture with biological conservation (Lai et al., 2006), so the idea of synergy between industry and conservation is not foreign to the local communities.

Hong Kong is a coastal city located on the South Chinese coastline at the outlet of the Pearl River (Lai et al., 2016). Despite its small marine area, Hong Kong is a hotspot for marine biodiversity for several reasons (Ng et al., 2017). First, although Hong Kong is located in the tropical region, it's influenced by both the northeast and southeast monsoon, leading to strong seasonality with hot, wet summers and cold, dry winters (Morton, 1996). Second, Hong Kong is under the influence of three different oceanic currents: the Hainan Current which is dominant during summer, and the Kuroshio current and Taiwan current which are dominant during winter (Morton and Morton, 1983). Third, the western waters of Hong Kong are under heavy influence of the freshwater discharge from the Pearl River and hence is estuarine; on the other hand, the eastern waters of Hong Kong are unaffected by the freshwater discharge, therefore the conditions are more oceanic (Morton and Wu, 1975). The interplay of these factors contributes to high habitat

diversity in Hong Kong's marine environments, which in turn supports a high diversity of marine organisms. Like many other coastal cities in southeast Asia, coastal ecosystems in Hong Kong were under threat of habitat degradation or destruction (Williams et al., 2016), and oyster reefs were no exception (Williams et al., 2024). Instead of forming reefs that provide high structural relief, most oyster habitats in Hong Kong exist in the form of oyster beds, where clusters of oysters are scattered on the shore (Lau et al., 2020). Besides natural oyster assemblages, cultured oysters are also an important constituent of the oyster populations in Hong Kong. Oyster aquaculture is concentrated in Deep Bay located at the northwest of Hong Kong (Fig. 1), where oyster farmers grow oysters in baskets which are suspended on floating rafts (Morton and Wong, 1975; AFCD, 2025). Most oyster habitats in Hong Kong were formed by multiple oyster species, usually by a *Magallana* species and a *Saccostrea* species (Lam and Morton, 2004). Although *Magallana* and *Saccostrea* oysters occupy similar ecological niches, the two genera of oysters show very different growth forms (Lam and Morton, 2004). Hence, the coexistence of multiple oyster species increases the heterogeneity in habitat morphology, should thus be beneficial to the biodiversity of the habitat (Thomsen et al., 2022). To accurately describe the relationship between oyster species diversity and the ecosystem services they provide, it is imperative to have solid knowledge of the composition of oyster species in oyster reefs. However, oyster species identification has always been notoriously challenging due to the high plasticity in shell morphology (Wang and Guo, 2008). Along the Chinese coastline, where large numbers of oyster species co-occur (Zhou et al., 2025), it would be virtually impossible to reliably identify oyster species by morphological examination. Such taxonomical ambiguity in the diversity of reef-forming oyster species could pose a serious hurdle to successful oyster reef restoration efforts, especially in the tropics, where oyster reefs are commonly formed by multiple oyster species (Richardson et al., 2022).

Here, we aimed to lay the groundwork for oyster conservation efforts in Hong Kong by (1) describing the diversity of oysters in the intertidal mudflats of Hong Kong; (2) documenting the population structure and genetic diversity of oyster populations in Hong Kong; and, (3) investigating if the aquaculture populations of oysters could serve as a valuable larval source for Hong Kong's natural oyster populations. To our knowledge, this study presents the first comprehensive survey of the diversity of oyster species in natural habitats and aquaculture in Hong Kong using species identification verified with molecular approaches. Therefore, the findings presented here underpin the formulation of any plan for oyster reef restoration in Hong Kong.

## 2. Methodology

### 2.1. Study sites

To gain a comprehensive view on the diversity of oysters in Hong Kong's intertidal mudflat habitats, ten intertidal oyster habitats were sampled in this study. To capture the diversity of oysters across Hong Kong's oceanographic zones, samples were collected from both the western and eastern waters of Hong Kong (Fig. 1). Pak Nai (PN), Shui Hau (SH), Sham Wat (SW), Tung Chung (TC) and Tai Ho Wan (THW) represent the western estuarine zone, while Kai Kuk Shue Ha (KKSH), Kau Sai (KS), Tai Mong Tsai (TMT), Tai Tam (TT) and Yung Shue O (YSO) represent the eastern oceanic zone (Table S1). All sampling took place in Summer 2021.

### 2.2. Oyster demographics

Oyster density and shell length measurements were conducted at the ten sampling sites during low tide. At each site, 10 quadrats (50 cm×50 cm) were located on the oyster bed using a stratified haphazard method, and the number of live and dead oysters was enumerated separately. After counting the number of oysters, the shell

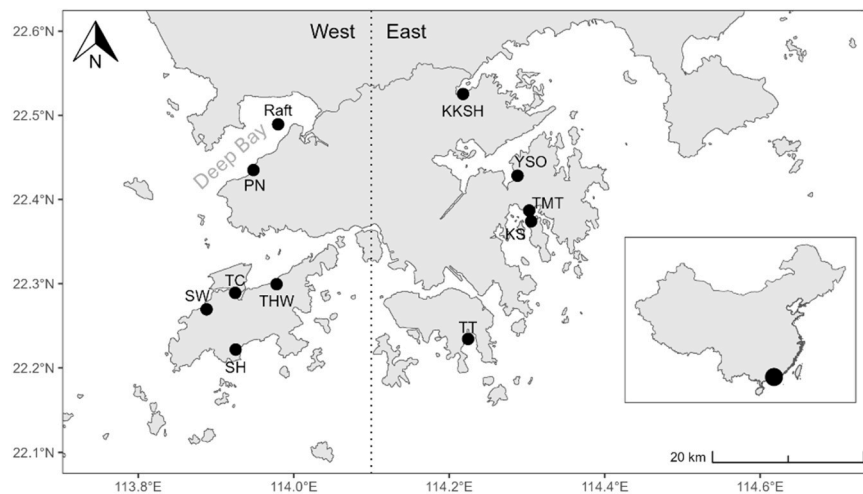


**Fig. 1.** Map of the locations of the intertidal oyster habitats surveyed in the study; the location of Hong Kong in relation to mainland China is shown in the inset map. KKSH = Kai Kuk Shue Ha, KS = Kau Sai, PN = Pak Nai, SH = Shui Hau, SW = Sham Wat, TC = Tung Chung, THW = Tai Ho Wan, TMT = Tai Mong Tsai, TT = Tai Tam, YSO = Yung Shue O. The map was created using the R packages *ggplot2* v3.4.2 and *ggspatial* v1.1.10 (Gómez-Rubio, 2017; Dunnington, 2025).

length of 20 random live oysters from each quadrat was measured using callipers.

Histograms were plotted with the R package *ggplot2* v3.4.2 to aid the visual inspection of oyster size distribution patterns in the oyster habitats surveyed (Gómez-Rubio, 2017). Oyster flesh weight ( $B$ ) within each quadrat was estimated by the formula  $B = aL^2$ , where  $L$  is the shell length and  $a$  is a scalar (Powell et al., 2016). To determine the validity of this formula on Hong Kong's oysters and to determine a suitable value for  $a$ , the shell lengths and flesh weights of 489 oysters from PN were measured. The measured length and weight data was fitted to the formula with the *lm* function from base R.

Linear models were fitted for the estimated oyster flesh weight and oyster density data to investigate their distribution between sites; models were fitted with the *lm* function from base R after log transformation, and distributions were inspected with the R package *performance* (Lüdtke et al., 2021). Another linear model was fitted to test for the effect of oceanographic zone (east vs west) on the two attributes of oyster demography. Analysis of variance (ANOVA) was performed on the models with the ANOVA function from base R, and post-hoc tests were performed with functions from the R package *emmeans* (Lenth, 2017). Spearman's rank correlation coefficient between the estimated flesh weight of oysters and the density of oysters within a quadrat was calculated with the R package *Correlation* (Makowski et al., 2022).

The total oyster flesh weight within each quadrat was estimated by multiplying the oyster density within that quadrat by the geometric mean of the estimated oyster flesh weight of the oysters sampled from that quadrat. A linear model was fitted for the total oyster flesh weight within quadrat to investigate their distribution between sites; models were fitted with the *lm* function from base R after log transformation, and distributions were inspected with the R package *performance* (Lüdtke et al., 2021). ANOVA was performed on the models with the ANOVA function from base R, and post-hoc tests were performed with functions from the R package *emmeans* (Lenth, 2017).

### 2.3. Oyster species diversity

Oysters were collected from the survey sites for species identification by DNA barcoding. To avoid selection bias, specimens were collected randomly from the quadrats placed during the oyster demographics surveys. After measuring the density and sizes of the oysters, the oysters within the quadrats were chiselled off the substrate. This process was repeated until roughly 120 intact specimens were collected from each sampling site. The specimens were then transported back to the

laboratory on ice and stored in a  $-20^{\circ}\text{C}$  freezer until dissection.

Specimens were thawed under room temperature prior to dissection. For each of the ten sampling sites, 96 specimens were selected randomly for dissection. Adductor muscle tissues were excised and preserved in 98% ethanol until DNA extraction. DNA was isolated using the methods described by Arseneau et al. (2017), and redissolved in 50  $\mu\text{L}$  nuclease-free water (Invitrogen). DNA samples were subject to quality check with NanoDrop™ One Microvolume UV-Vis Spectrophotometer (Thermo Scientific) and stored at  $-20^{\circ}\text{C}$  until further analysis.

To examine the species composition of oysters from the aquaculture populations of Hong Kong, a total of 58 specimens were collected from 11 oyster rafts located in Deep Bay in 2019 (Fig. 1). DNA was isolated from the adductor muscle of the specimens with Purelink Genomic Mini Kit (Invitrogen), and samples were subjected to quality check with NanoDrop™ One Microvolume UV-Vis Spectrophotometer (Thermo Scientific). DNA samples were stored at  $-20^{\circ}\text{C}$  until further analysis.

To determine the species identity, a section of the COX1 gene was amplified with the primer pair HCO2198/LCO1490 (Folmer et al., 1994). Polymerase chain reaction (PCR) was performed with  $2 \times$  Rapid Taq Master Mix (Vazyme Biotech) in 25  $\mu\text{L}$  scale following the manufacturer's instructions. PCR protocol was as follows: an initial denaturation at  $95^{\circ}\text{C}$  for 3 min; 40 cycles of denaturation at  $94^{\circ}\text{C}$  for 15 s, annealing at  $51^{\circ}\text{C}$  at 15 s, and extension at  $72^{\circ}\text{C}$  for 15 s; plus a final extension at  $72^{\circ}\text{C}$  for 5 min. PCR products were inspected on 2% agarose gel; PCR products from reactions that yielded a single, discrete band on the agarose gel were submitted to BGI Hong Kong for Sanger sequencing.

Sanger sequencing data was processed in Python with the *Biopython* package v1.78 (Cock et al., 2009). Bases were called from the sequence trace file using the *SeqIO.AbilO* module; quality trimming was performed with the built-in implementation of Mott's algorithm, and only retaining reads longer than 600 bp for downstream analysis. Species identities were determined by aligning the DNA sequences to a local database with *BlastN* v2.11.0 (Camacho et al., 2009) using a E-value threshold of 0.001. The local BLAST database was built with COX1 DNA sequences downloaded from The Barcode of Life Data System (Ratnasingham and Herbert, 2007); to minimize the chance of false positives, only sequences originating from the family *Ostreidae* were used in the BLAST database construction. Species names returned from the BLAST search were checked on the World Register of Marine Species to ensure that the most up to date nomenclature was used (WoRMS Editorial Board, 2023). In case of multiple best hits, the specimen would be identified to the genus level.

To assess the taxonomical sampling completeness of the study, sample coverage was estimated with the *R* package *iNEXT* v3.0.0 (Hsieh et al., 2016). Chi-squared test was performed to test for the association between sampling site and oyster species composition. The Shannon diversity index for oysters in each sampling site was computed with the *estimateD* function from the *R* package *iNEXT* (Hsieh et al., 2016); sample coverage was standardized to 0.98. Student's *t*-test was performed to test for a difference in the Shannon diversity index of oyster species between eastern and western oyster habitats. To detect possible correlation between oyster diversity and (1) estimated flesh weight, (2) oyster density, and (3) total flesh weight of oysters within a quadrat, Spearman's rank correlation coefficient between the Shannon diversity of oysters and the parameters of interest was calculated with the *R* package *Correlation* (Makowski et al., 2022).

Variation in oyster species composition was assessed by principal coordinates analysis (PCoA); Bray–Curtis dissimilarities were calculated for the species abundance between the sites with the *R* package *VEGAN* v2.6–4 (Dixon, 2003). Differences in oyster species composition between the eastern and western oceanographic zones were tested with ANOSIM (Clarke, 1993); the site SW was excluded from the western group as its oyster species composition was drastically different from other sampling sites. All biodiversity computations were performed with *R* v3.0 (R Core Team, 2020) and plots were generated with *ggplot2* v3.4.2 and *ggrepel* v0.9.3 (Gómez-Rubio, 2017; Slowikowski, 2020).

#### 2.4. Population genetic structure of oyster species in Hong Kong

To analyze the intra-specific genetic diversity of the common oyster species, the number of polymorphic sites, number of haplotypes, haplotype diversity, average number of nucleotide differences, and nucleotide diversity were calculated with *DnaSP* v6.12.03 (Rozas et al., 2017). The pairwise fixation index ( $F_{ST}$ ) was calculated to determine population differentiation using *Arlequin* v3.5.2.2 (Excoffier and Lischer, 2010); populations with less than 10 individuals were not included as small sample sizes might compromise the robustness of the analysis. The significance values were assessed using 1000 permutations. To investigate the demographic history of the oyster species, Tajima's *D* (Tajima, 1989) and Fu's *F* (Fu, 1997) were calculated with *DnaSP* to test for neutrality of the mutations.

### 3. Results

#### 3.1. Oyster demographics

All sites surveyed except KKSH had a unimodal distribution of oyster

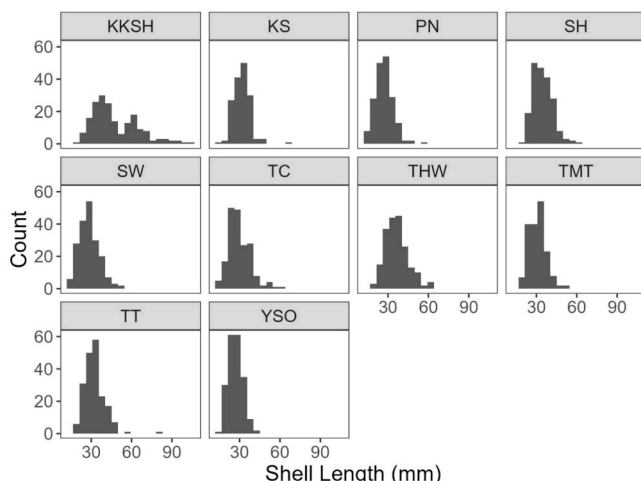


Fig. 2. Histogram showing size distribution of oysters at the survey sites.

sizes with a modal shell length of ~30 mm (Fig. 2).

A generalized linear model was fitted to predict flesh weight of oysters from shell length, and the model explained a high proportion of the variance ( $R^2 = 0.83$ ,  $p < 0.01$ ); the value of the scalar *a* was estimated to be 0.0008393 (Fig. 3 A). The flesh weights of the oysters in the survey sites were estimated from their shell lengths following the above equation, and the flesh weights of the oysters at the sampling sites exhibited log-normal distributions (Fig. 3B). The average estimated flesh weight of the oysters sampled was 0.82 g (Table S2) and differed among sites (ANOVA,  $F_{9,1874} = 89.29$ ,  $p < 0.001$ ). The estimated flesh weight of oysters from the western oyster habitats was found to be lower (ANOVA,  $F_{1,1882} = 43.79$ ,  $p < 0.001$ ), although the difference is unlikely to carry any biological significance ( $R^2 = 0.013$ ). The oyster densities at the sampling sites exhibited log-normal distribution (Fig. 3 C), with an average density of 143.5 individuals per square meter (Table S2). Difference was detected in the density of oysters in the different sites (ANOVA,  $F_{9,88} = 7.02$ ,  $p < 0.001$ ), but the difference could not be attributed to the different oceanographic zones (ANOVA,  $F_{1,96} = 1.85$ ,  $p = 0.177$ ). A negative correlation was detected between the density of oysters inside a quadrat and the estimated flesh weight of oysters inside the quadrat (Spearman's rank correlation,  $\rho = -0.15$ ,  $p < 0.001$ ).

Average oyster flesh weight density in the survey sites was 117.2 g/m<sup>2</sup> (Table S2), and the distribution of estimated total oyster flesh weights within quadrats exhibits a log-normal distribution (Fig. 3D). Although a difference was detected in the estimated oyster flesh weight densities among sites (ANOVA,  $F_{9,88} = 5.55$ ,  $p < 0.001$ ), the difference could not be attributed to the different oceanographic zones (ANOVA,  $F_{1,96} = 2.09e-3$ ,  $p = 0.964$ ).

#### 3.2. Oyster species diversity and composition

Full-length PCR products were obtained from 869 specimens, and 737 PCR products were sequenced successfully (strong signal along the length of the PCR product, low noise floor, and absence of double peaks); BLAST searches matched 696 samples to an Ostreidae entry from the Barcode of Life Database (Table S3). Five species of *Magallana* oysters and four species of *Saccostrea* oysters, namely *M. angulata*, *M. ariakensis*, *M. bilineata*, *M. hongkongensis*, *M. sikamea*, *S. cucullata*, *S. echinata*, *S. malabonensis*, and *S. palmula*, were identified from the samples (Table S4).

*iNEXT* analysis indicated a mean sampling completeness of 98.4% ( $\pm 1.86\%$ ) for the species pool of the 11 sites, suggesting that sampling effort was adequate to reveal the species diversities of the sites sampled. Oyster habitats in the eastern waters of Hong Kong have a higher diversity of oyster species than those in the west (T-test,  $t_8 = 2.90$ ,  $p = 0.020$ ). The average Shannon diversity index of oyster species in Hong Kong's eastern oyster habitats was  $3.49 \pm 0.546$ , and that for the western oyster habitats was  $2.32 \pm 0.721$ . The Shannon diversity index of oyster species in the aquaculture population was 2.12, which was within one standard deviation of the oyster species diversities in western oyster habitats.

A negative correlation was detected between oyster species diversity and oyster density in the natural oyster habitats (Spearman's rank correlation,  $\rho = -0.35$ ,  $p < 0.001$ ); on the other hand, a weak positive correlation was detected between oyster diversity and the estimated flesh weight of oysters (Spearman's rank correlation,  $\rho = 0.13$ ,  $p < 0.001$ ). Correlation between oyster species diversity and the flesh weight densities of oysters was not detected (Spearman's rank correlation,  $\rho = -0.08$ ,  $p = 0.408$ ).

A chi-squared test of independence showed an association between the site and the species composition,  $X^2(100, N = 696) = 1877.6$ ,  $p < 0.001$  (Fig. 4). The locality of the sampling site (western estuarine waters vs eastern marine waters) exerts a large influence on the species composition of oysters (ANOSIM statistic  $R = 0.8621$ ,  $p = 0.004$ , Fig. 5). Oyster habitats on the intertidal mudflats of western Hong Kong are dominated by *Magallana* spp., with the exception of Sham Wat where the

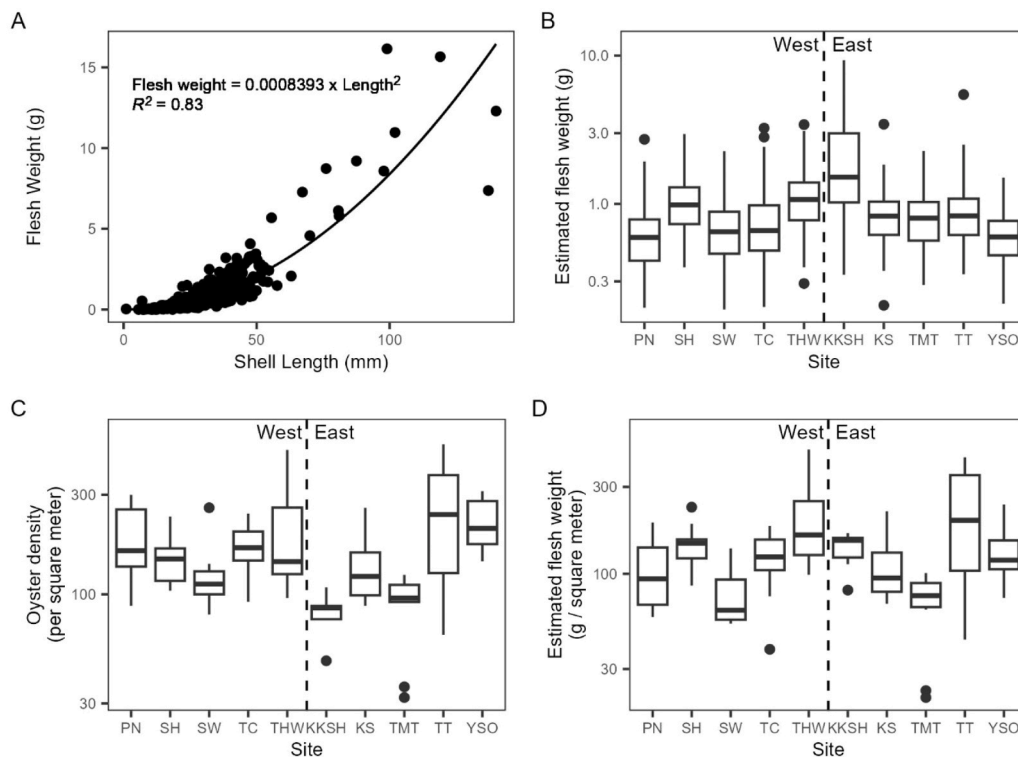


Fig. 3. (A) Correlation between the shell length of oysters and their flesh weight; (B) Estimated flesh weight of oysters in the survey sites; (C) Density of oysters in the survey sites; (D) Estimated per meter-square flesh weight of oysters in the survey sites.

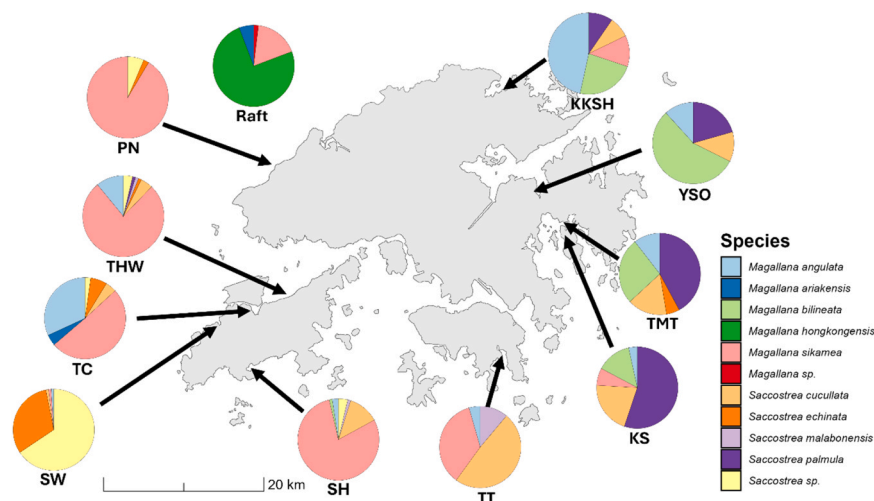


Fig. 4. Species composition of oysters in the survey sites.

oyster community was dominated by *Saccostrea* spp. *Magallana sikamea* is by far the most abundant *Magallana* species in the west, followed by *M. angulata*. On the east of Hong Kong, both *M. angulata* and *M. bilineata* were commonly found. *Saccostrea palmula*, which was not encountered on the west, was the most abundant *Saccostrea* sp. on the intertidal mud flats on the east of Hong Kong. The oyster species composition in the aquaculture population was distinct from the wild populations in Hong Kong. While absent from wild populations, *M. hongkongensis* was the dominant species in the aquaculture oyster population; some *M. ariakensis* and *M. sikamea* were also encountered on the oyster rafts.

### 3.3. Population genetics analysis of natural oyster populations in Hong Kong

*Magallana angulata*, *M. bilineata*, *M. sikamea*, *S. cucullata*, and *S. echinata* in Hong Kong had moderate to high haplotype diversities (Table S5). On the other hand, the *S. palmula* population of Hong Kong demonstrated a much lower level of haplotype diversity. The level of nucleotide diversity was low in all sampled oyster species (from 0.0016 to 0.00978) except *S. cucullata*, which had a nucleotide diversity of 0.0603. Tajima's D and Fu's F statistics were non-positive in all the populations tested, suggesting that the oyster populations of Hong Kong have not experienced any recent population bottleneck. Furthermore, Tajima's D in *M. sikamea* and Fu's F in *M. angulata* and *M. sikamea* were

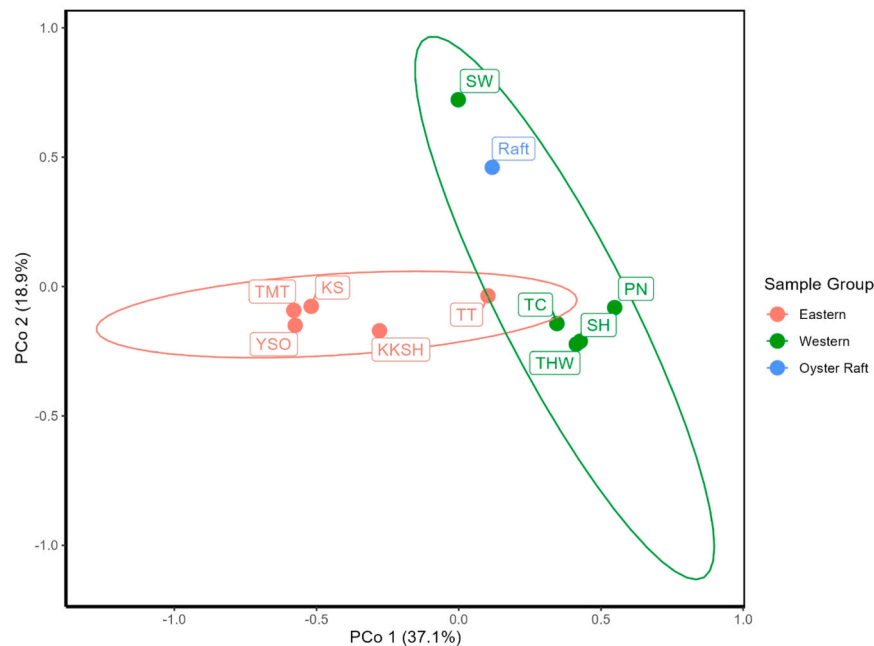


Fig. 5. PCoA plot of the Bray-Curtis dissimilarity in oyster species composition in the survey sites.

significantly negative, indicating a recent expansion in population sizes. The oyster populations in Hong Kong does not demonstrate any strong population genetics structure, as exemplified by the low  $F_{ST}$  values of  $< 0.05$  (Table S6).

#### 4. Discussion

Hong Kong is a hotspot for marine biodiversity (Ng et al., 2017), and this is reflected in the high species diversity of reef-forming oysters encountered in the intertidal mudflats of Hong Kong. Like many other tropical oyster reefs, oyster habitats in Hong Kong were found to be formed by three or more species of oysters; this is very different from temperate oyster reefs, which are mostly formed by a single species of oyster (Richardson et al., 2022). Although oysters are generally regarded as euryhaline, intertidal oyster habitats in both the eastern and western sides of Hong Kong had a different oyster species composition, likely due to the heavy influence of freshwater discharge from the Pearl River in the west. *Magallana sikamea*, which was the dominant oyster species in the western waters, has an optimal salinity of 16 ppt (Liu et al., 2024). On the other hand, *M. angulata* and *M. bilineata*, which are the two most abundant *Magallana* species in the eastern waters, have an optimal salinity range of 28–35 ppt (Moreira et al., 2018) and 25 ppt, respectively (Ng et al., 2016). Differences were also observed in the composition of *Saccostrea* species between the oyster habitats sampled; however, we were unable to attribute such differences to different salinities due to the presence of an unidentified *Saccostrea* species and the absence of information on the optimal salinity of *S. palmula*. The composition of oysters in Hong Kong's intertidal habitats was similar to other localities along the South Chinese coastline (Lu et al., 2024; Heng et al., 2025; Zhou et al., 2025). Population genetics analysis reveals that oyster populations in Hong Kong had low nucleotide diversities and moderate to high haplotype diversities, which is commonly observed in other oyster populations (Li et al., 2013, 2015; Kim et al., 2014; Hsiao et al., 2016; Hu et al., 2018; Zhou et al., 2025).

The oyster populations sampled across Hong Kong differed in average sizes (of individuals) and densities in a way that was not attributable to any geographic patterns (e.g., western estuarine, eastern oceanic influence). However, there was a negative correlation between density and size of individual, suggesting the presence of a continuum of

oyster habitat morphologies from habitats formed by few large oysters at lower densities to those formed by higher densities of smaller oysters. One of the main ecosystem services that oysters provide is habitat provisioning (Smith et al., 2023), and the morphology of the shellfish aggregate is thought to influence the macroinvertebrate community compositions due to the different structural complexity and components they provide (Trigg et al., 2011; De Smet et al., 2015; Loke and Todd, 2016; Chan et al., 2022; Fariñas-Franco et al., 2023). In this study, we found that oyster habitats formed by a more diverse group of oyster species were usually characterized by the presence of many smaller oysters. Given that in the more degraded, sparse oyster habitats seen in Hong Kong, hard substrate is a limiting factor (Lau et al., 2020, 2026), it is possible that the smaller oyster size in more dense populations is a function of competition for space. However, it is also possible that this smaller size could be a function of species identities; *Saccostrea* species tend to be smaller than *Magallana* species (Lam and Morton, 2004). Ultimately, more research is needed to derive a mechanistic explanation of the observed size-density relationship.

Oysters of the genus *Magallana* are considered to have natural lifespans of five or more years (Morton, 1975; Harding and Mann, 2006; Moore et al., 2016). However, in all but one of the oyster habitats sampled, the shell length of the oysters demonstrated a unimodal distribution, suggesting the presence of only one cohort of oysters in the populations, indicative of high post-settlement mortality rates. The high mortality rates of Hong Kong's oysters could be attributed to both natural and artificial causes. The oysters of Hong Kong typically spawn in summer, and mass mortalities are routinely observed in oyster populations following spawning due to their depleted energy reserves (Li et al., 2007). Compounding this issue, heatwaves are becoming more common in Hong Kong (Li et al., 2025), potentially amplifying the magnitude of the summer mortalities. Mass mortalities have also been observed in Hong Kong's oyster populations during winter, although the cause remains unknown (Lee et al., 2024). At the same time, recreational harvesting is also posing a strong pressure on the natural oyster populations of Hong Kong. Clam and oyster harvesting are popular recreational activities in Hong Kong (Lau et al., 2020; So et al., 2021); such activities often take place in sites with high ecological values and often exceed sustainable levels of the habitats (Cheung et al., 2003). Yet, it should also be noted that the identification of drivers of mass mortalities

in wild bivalve populations is often not a straight forward endeavor. Mass mortalities are often caused by the synergistic effect of multiple stressors (Soon and Ransangan, 2019); in many cases, drivers of mass mortality events could only be partly explained (Burdon et al., 2014). High post-settlement mortality could pose a major hurdle to the restoration of Hong Kong's oyster habitats. On one hand, there is a strong positive correlation between the size of an oyster and its fecundity (Royer et al., 2008; Mroch et al., 2012). On the other hand, the sex ratio of oysters is correlated to their sizes, with a higher proportion of female in larger individuals (Harding et al., 2013; Yasuoka and Yusa, 2016; Broquard et al., 2020). Therefore, a lack of large individuals could lead to a shortage in the abundance of reproductive female, which would ultimately affect local larval supply.

Oysters have been commercially farmed in Hong Kong for more than 700 years (Morton and Wong, 1975; Williams et al., 2024) but the identity of the species being farmed remained enigmatic until recent decades. Lam and Morton (2003) found the species of oyster in farmed in Hong Kong to be genetically distinct from other oyster species in intertidal habitats, subsequently naming it *Crassostrea hongkongensis* (now revised to *Magallana hongkongensis*) (Salvi et al., 2014). In this study, we confirmed that *M. hongkongensis* is the main species of oyster farmed in Hong Kong. Now broadly considered as native to the region and having likely been farmed for centuries (Williams et al., 2024; Lau et al., 2026), to our surprise, we did not encounter any *M. hongkongensis* in the natural intertidal oyster habitats of Hong Kong, even in Pak Nai (PN), which is immediately adjacent to the oyster aquaculture area. Given the high sampling effort of this study, we conclude that, as of the time of sampling, *M. hongkongensis* is not a common oyster species in the mid- to upper intertidal areas based on natural recruitment. Traditionally, oyster farmers in Hong Kong relied on spat collected naturally from the Deep Bay area, where Pak Nai is located (Lam and Morton, 2003). In recent decades, however, there has been a shift towards the use of oyster spat purchased from other parts of the Pearl River Delta (AFCD, 2025). Based on our data, we speculate that *M. hongkongensis* may not have large wild reproductive populations in Hong Kong; instead, the major population in Hong Kong is from aquaculture imports. Moreover, the lack of any significant *M. hongkongensis* population in Hong Kong's natural oyster habitats, despite repeated introductions, is suggestive of a mismatch between the species' niche and the environments in Hong Kong's intertidal mudflats. It should be noted, however, that we did not survey the very low intertidal (e.g., approaching 0 m chart datum) or subtidal habitats in this study, so it is possible that there are *M. hongkongensis* in these areas where temperatures and salinity are more stable (Lam and Morton, 2004). If *M. hongkongensis* is not adapted to the intertidal environments in Hong Kong, it would be advantageous for the oyster farmers in Hong Kong to consider using a commercially viable species that is more commonly found in the wild in Hong Kong (e.g. *M. sikamea* or *M. angulata*). The benefits of this are twofold: first, using oyster species that are adapted to the environments of Hong Kong could potentially improve the yields of the aquaculture industry; second, larvae derived from the diploid aquaculture population could potentially contribute to the local larval pool, thus fully utilizing the potential of oyster aquaculture as a tool to facilitate oyster restoration.

In conclusion, this study provides baseline knowledge on the diversity, distribution and demography of oyster species in Hong Kong's intertidal mudflat habitats. Nine species of oysters from two genera were recorded, and we found a distinct community composition between the western estuarine zone and eastern marine zone of Hong Kong. Furthermore, the dominant oyster species in the aquaculture population, *M. hongkongensis*, was not found in natural intertidal habitats. It should be noted, however, that this study covered the intertidal mudflats of Hong Kong and to develop a comprehensive distribution of the species it would be necessary to survey low intertidal and subtidal populations. Importantly, based on the population demographics, post-settlement mortality is high in the natural oyster populations in Hong Kong (also noted in Lau et al., 2020). While there are some indicators that high

harvest pressure may be a large cause of mortality (Lau et al., 2020), there is also anecdotal evidence of mass mortality from summer heat-waves. Therefore, to ensure the long-term viability of oyster natural populations in Hong Kong, further investigations would be needed to clarify the causes of such high mortality rates and mitigation strategies incorporated into any restoration activities.

## CRediT authorship contribution statement

**Huang Elaine Y. Y.:** Writing – review & editing, Methodology, Investigation. **Ho Tin Wong:** Writing – review & editing, Investigation. **Bayden D. Russell:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Juan Diego Gaitán-Espitia:** Writing – review & editing, Supervision, Formal analysis. **Jerome H.L. Hui:** Writing – review & editing, Supervision, Investigation. **Khan Cheung:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Jay Joan Minuti:** Writing – review & editing, Supervision, Investigation, Conceptualization.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2026.105235.

## Data availability

Research Link Provided.

Supporting data for "Species composition and genetic diversity of habitat forming oysters in Hong Kong's intertidal mudflats" (HKU data repository)

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