Restoration potential of Asian oysters on heavily developed coastlines

Running head: Oyster restoration potential in Asia

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Author contributions: SCYL, MT, BH, BDR conceived, designed and conducted the research; SCYL performed formal analyses of the data; SCYL, BDR wrote the original draft; SCYL, MT, BH, BDR reviewed and edited the manuscript.

Abstract

Reef building oysters historically provided the main structural and ecological component of temperate and sub-tropical coastal waters globally. While the loss of oyster reefs is documented in most regions globally, assessments of the status of Asian oyster reefs are limited. The feasibility of restoration within the regional biological and societal contexts needs to be assessed before implementation. Here, we quantified the current distribution of natural oyster reefs (*Crassostrea* spp.) in the shallow coastal waters of Hong Kong, assessed the biological feasibility of re-establishing reefs using natural recruitment, and examined their current and potential water filtration capacity as a key ecosystem service provided by restoration. We found natural low relief oyster beds in the low intertidal coastal areas at a subset of the locations surveyed. These areas are, however, degraded and have sparse densities of oysters generally <2 years old. Recruitment was high in some areas (>500,000 indiv. m^{-2}) and while survival to maturity varied across sites there was adequate larval supply and survival for restoration. Filtration rates for a one-year old recruit (90 mm length, ~30 L hr^{-1} per individual) at summer temperatures (30°C) meant that even the small remnant populations are able to provide some filtration services (up to 31.7 ML h^{-1}). High natural recruitment means that oyster reef restoration can be achieved with the addition of hard substrate for recruitment, increased protection of restoration sites, and would not only increase the ecological value of reefs regionally but also serve as a model for future restoration in Asia.

Key words: Oyster reef restoration, ecosystem service, oyster recruitment, South-east Asia, coastal development

Implications for Practice

- In regions where structured oyster reefs are functionally extinct, hard substrate will need to be replaced for restoration to be based on natural recruitment
- Identifying the timing of natural oyster recruitment will help identify both prospective restoration sites and timing of deployment of hard substrate to maximise recruitment and minimize hatchery-based intervention
- In regions with ongoing intensive harvest of oysters by local communities, developing strategies to restrict harvesting will maximise the outcomes from restoration efforts
- Public education on the benefits of intact oyster reefs may be the most effective tool in generating societal and governmental support for restoration in Asia

Introduction

Coastal ecosystems are threatened globally by intense anthropogenic activities, including historical and current over exploitation, habitat destruction, pollution and altered riverine input (Lotze et al. 2006). Compounding these threats, historical ecosystem ‘management’ was primarily focused on transforming the natural environment to provide for human populations, thus enhancing the rapid loss of natural ecosystems and associated functions (Crain et al. 2009). Ecosystem loss is particularly problematic in tropical and sub-tropical cities in East and Southeast Asia since these areas tend to be of high biodiversity (Tittensor et al. 2010). These cities are also characterised by extremely large and rapidly increasing human populations, and often accompanied by unsustainable infrastructure development (Yeung 2001). Preventing further degradation of the existing ecosystems in these tropical, urbanized areas would ensure ecosystem services are maintained, biodiversity is protected, and also highlight values of sustainability and urban ecology (McDonnel & MacGregor-Fors 2016).

As ecosystem engineers, reef building oysters were historically a major structural and ecological component of sub-tropical and temperate estuarine waters. Oyster reefs have experienced ~85% loss worldwide due to over-harvesting, combined with habitat destruction, pollution and hydrological changes (Beck et al. 2011) – the greatest global loss yet documented for any coastal ecosystem (Grabowski et al. 2012). A functional, highly structured reef is estimated to provide ecosystem services up to US$162,000 ha^{-1} annually (Grabowski et al. 2012; Knoche et al. 2018), including water filtration (zu Ermgassen et al. 2013), denitrification (Kellogg et al. 2013), shoreline protection (Ysebaert et al. 2018), and production of fisheries species (zu Ermgassen et al. 2016). It is now recognised that restoring oyster reefs along urbanised coastlines can mitigate some of the environmental problems typical of coastal development, such as eutrophication (Cerco & Noel 2007), damage from storm surges (Rodriguez et al. 2014), and biodiversity declines (Lenihan 1999).

While economic factors historically account for coastal habitat loss in Asia (Williams et al. 2016), ongoing loss and lack of protection or restoration is driven by sociocultural factors. The perception that the value of ecosystems is in their use for local benefits is often encountered in conservation efforts in regional Asia, generally as continued “traditional” harvesting, with adequate financial compensation and support for communities required to stop exploitation (Bennett & Dearden 2014). Compounding this, Asian coastal cities have experienced dramatic landscape changes over several hundred years, meaning that memory of the historical condition of ecosystems and habitats seems to have been entirely forgotten (Turvey et al. 2010). There is, therefore, an urgent need to document the current habitat status as a baseline from which to assess the potential for future restorative conservation from scientific and sociocultural perspectives, as well as to document the value of ecosystem services they represent as an incentive to conserve existing habitats and implement restoration efforts.

The limited data available on the status of natural oyster reefs in Asia suggest that estimates of global oyster reef loss could be an underestimate for the region (Beck et al. 2011). However, multiple lines of evidence suggest that oyster reefs were historically extensive along Asian coasts (Fujiya 1970; Brohmanonda et al. 1988; Quan et al. 2017). If restoration of these habitat is to be successful, it is first necessary to understand the current status of extant oyster populations and capacity for natural recruitment to support reef development. In addition, understanding the current provision of ecosystem services (e.g. water filtration) is essential to provide socioeconomic and political justification for restoration efforts. Here, we take the first step in describing the current status of oyster reefs in the nearshore waters of Hong Kong, a coastal megacity in China, and identify the potential for conservation and restoration. Hong Kong serves as a model location for understanding oyster ecology in Asia as it exhibits the typical conservation challenges and potential of coastal areas within the region. Its natural shoreline has been heavily transformed with over 20% reclaimed for development and plans for major ongoing reclamation. Hong Kong has also been recognised as a marine biodiversity hotspot, hosting ~26% of the marine species recorded in China despite accounting for only ~0.03% of Chinese coastal waters (Ng et al. 2017). While natural oyster reefs have never been characterised in Hong Kong, the occurrence of reef building oysters, including

Crassostrea spp., is the basis for one of the oldest oyster aquaculture industries in Asia (Lam and Morton 2003), suggesting reefs were likely extensive in the past. Multiple species of *Crassostrea* spp. have been observed in the waters of Hong Kong, including *C. hongkongensis*, *C. bilineata*, *C. angulata* and *C. ariakensis* (Lam & Morton 2003), but their regional distributions and abundance have not been reported in the scientific literature. Here, we present; 1) the current status of natural oyster (*Crassostrea* spp.) populations in estuarine areas around Hong Kong; 2) seasonal recruitment of *Crassostrea* spp. to understand natural restoration potential; and 3) water filtration rates of the two dominant native oyster species (*C. hongkongensis* and *C. bilineata*) at a range of environmentally relevant temperatures. Overall, we provide the context for the potential of oyster reef restoration in Asia, using Hong Kong as a regional exemplar, based on understanding their current status and natural recruitment potential.

Methods

Study sites

The west of Hong Kong is situated in the Pearl River Delta (PRD; total area = 42,800 km^2), a low-lying flood plain of the Pearl River, one of the largest estuaries in East and Southeast Asia (Wang et al. 2011) (Fig. 1). In the northeast of Hong Kong, Tolo Channel forms a long tidal inlet with multiple local freshwater inputs (total area = 80 km^2) and is not part of the PRD (Fig. 1). The field assessments of oyster populations and recruitment were done at ten intertidal mudflats; seven around Lantau Island and three in Tolo Channel (Fig. 1). Of these locations, eight are open to the public and were under intense shellfish harvesting pressure (e.g. oyster, clam) and recreational activities (e.g. tourism). Two of the locations (Tai Ho Wan outer and Tai Ho Wan inner, northern Lantau Island) are part of indigenous village lands and protected from harvesting or other public activities. We expect the oyster populations in Tai Ho Wan outer and Tai Ho Wan inner do not experience intense harvesting pressure and recreational activities due to limited site access and protection by the local villagers.

Current distribution and population demographics of reef-forming oysters

The current distribution of oyster habitat was mapped using the genus level (*Crassostrea* spp.) as a functional group (hereafter 'oyster'). We use the term 'bed' to refer to oyster habitat of low structural relief and complexity and "reef" as habitat which is highly structured and complex. In our study sites, we only found evidence of oyster beds with low structural relief. Oyster beds were defined as the percentage surface cover of living and/or non-living oyster shell substrate being ≥ 25%, the universal metric developed for monitoring oyster habitats (Baggett et al. 2014). Preliminary surveys of the sites by free diving and use of long tongs to take substrate grabs in June 2017 confirmed that no subtidal oyster habitat was present at any of the selected studied sties. Therefore, oyster bed contours were recorded by walking around the habitat margin using the tracking function embedded within hand-held GPS (Garmin GPSMAP78SC or Montana 680) during summer negative low tides (July 2017). The area of oyster bed was calculated by importing the mapped area as polygons into Google Earth Pro (version 7.3.1.4507).

Oyster density and shell length-size frequency surveys were conducted at all sites during low tide in August and September 2017 using a sampling protocol adapted from the oyster reef monitoring criterion outlined in Baggett et al. (2014). The mapped oyster beds were divided into 1° grids using the polygons projected on Google Earth Pro as reference, with each grid assigned an individual ID. A random number generator was then used to randomly select ten grids for oyster sampling per site. Ten quadrats were placed on the selected numbered grids over the mapped oyster areas at each site, with the random coordinate defining the central point in the quadrat. Within each quadrat, live oysters were counted and shell length (i.e. the longest length from umbo to shell growth margin) measured using callipers with 0.1 mm graduations. The size of the quadrat used was determined by oyster density. Quadrats of 1 m^2 and 0.5 m^2 were used when density was ≤ 100 and between 100 and 500 indiv. m^{-2}, respectively.

Larval recruitment and recruit survival to size at maturity

To quantify monthly patterns of oyster spat settlement in Hong Kong, six ceramic plates (unglazed red clay, 19.2 x 19.2 cm, coarse surface on the underside) were deployed at each study site at the beginning of the wet season (April 2017) at approximately the 0-datum tide level. Plates were attached horizontally to metal frames 0.25 m above the substrate (mud). Replicate tiles (n = 6 per site) were separated by 1 – 5 m. Plates were retrieved monthly and replaced with clean plates throughout the wet season until October 2017. We also assessed the potential of recruit to reach sexual maturity throughout the wet season. To assess survival, nine additional plates per site were also deployed in April 2017 and were left *in situ* until October 2017.

After collection, plates were transported to the laboratory on ice and kept at -20°C until processing. Each plate was photographed using a digital camera (Olympus TG-5). As the coarse underside of the plates provided structural surface for larvae to settle, only the underside of each plate was examined for oyster recruit density under a light microscope. When the recruit density per plate appeared to exceed 1000 indiv. m^{-2}, the plate was sub-sectioned into a grid containing 25 squares. Recruits were counted within five randomly selected squares (each measuring 3.84 x 3.84 cm, together making up 20% of the total plate area). When the recruit density appeared to exceed 10,000 indiv. m^{-2}, only one quarter of each of the five randomly selected squares was counted for oyster recruits (= 5% of total plate area). Each quarter within each square was randomly chosen using a random number generator. One-way ANOVA followed by a post hoc Tukey HSD analysis was used to test for the effect of location on the recruit density on settlement plates surviving to sexual maturity (SL ≥ 30 mm). Unpaired two-sample t-tests were also used to test for differences in the densities of sexually mature oysters found attached to settlement tiles (after nine months) and contemporary populations surveyed at each field site; Bonferroni adjustments were performed to reduce the chance of Type I error between multiple comparisons (i.e. the adjusted significance level of $p < 0.0025$).

Water filtration rates of *Crassostrea* spp.

Adult *Crassostrea hongkongensis* (*n* = 27) and *C. bilineata* (*n* = 33) which were able to be accurately identified using morphological features were collected from the intertidal mudflat of Tai Ho Wan outer (northern Lantau Island) and Yung Shue O (Tolo Channel), respectively, in August 2017. Oysters were immediately relocated to re-circulating aquaria connected to a biofiltration system. Salinity and temperature were maintained at 15-18 ‰ and 30°C, respectively, to replicate the field conditions at the time of collection, with ~50% water exchange twice per week. Aquaria were supplied with constant aeration and siphoned daily to remove faecal waste. Oysters were batch fed twice per day with laboratory cultured microalgae (50% *Isochrysis galbana* and 50% *Chaetoceros gracilis*). Eight days before the experiment, oysters were switched to a monoalgal diet of *I. galbana* for acclimation to experimental conditions (as per Thompson et al. 2012). After the acclimation period, water temperature in the aquaria were reduced by 1°C per day until 15°C was reached. Water filtration measurements were run on each oyster when the aquaria reached the target temperatures (30, 25, 20 and 15°C), being representative of the surface water temperatures for summer (July – September), late spring/early autumn (May – June/October – November), early spring/late autumn (April / December) and winter (January – March) around Hong Kong, respectively (EPD, 2018).

The water filtration rate of individual oysters was calculated from the change in food concentration (cell density of *I. galbana*) in a closed experimental chambers per unit time. Preliminary trials indicated that filtration rates of *C. hongkongenesis* and *C. bilineata* changed substantially with shell length and temperature, meaning that a single standard sized experimental chamber could not be used to accurately calculate water filtration rates. Therefore, filtration rates of individual oysters were measured using 10 and 5 L glass chambers at 30 and 25°C, and these were reduced to 5 and 1 L glass chambers at 20 and 15°C. All experimental chambers were placed inside water baths maintained within 0.5°C of the desired temperature. Prior to measurement, oysters were gently relocated from holding aquaria to experimental chambers and allowed at least 15 minutes rest to minimise handling disturbance. At the start of trials, *I. galbana* were added at the density of 70 cells μl^{-1}, which was found to be below the threshold for pseudofaeces production for *C. hongkongensis* and *C. bilineata* (75 – 80 cells μl^{-1}; SCY Lau pers. obs.). Filtration measurements were done in the dark to avoid behavioural response to acute light changes. Algae were kept suspended by magnetic stirrers with gentle stirring, with oysters positioned away from the water current vortex created by the magnetic stirrers (Sylvester et al. 2005). Water samples (1 ml) were taken from each experimental chamber at 5 min intervals for 40 min, preserved in 10% Lugol's solution and kept at 4°C until processing.

Calculation of water filtration rates

Water samples were only analysed from oysters that demonstrated gaping behaviour during the first 5 min of the experiment so that the filtration rate calculations were not biased. Algal concentration of water samples was calculated using a haemocytometer under an inverted microscope, with samples taken after the cell concentrations fell below 500 cells ml^{-1} excluded from analysis to avoid declining filtration efficiency. Control experimental chambers (10, 5, 1 L glass chambers with current vortex created by the magnetic stirrers included) with no oyster demonstrated no reduction in algal concentration during filtration trials at any temperature (one-way ANOVA, $p>0.05$).

The water filtration rate (FR; L hr^{-1}) of individual oyster was determined from the exponential decrease in algal concentration per unit time using the equation:

$$FR = Va$$

where V = volume of water (L) and a = slope of the regression line derived from the algal concentration decline over time (hr^{-1}) after natural log (ln) transformation (from Riisgård & Seerup, 2003).

A linear mixed effects (lme) model was used to examine the effects of species, shell length and temperature on water filtration rate, using the R package ‘lme4’ (Bates et al. 2019) using type III ANOVA with Satterthwaite’s method. We also incorporated individual ID (nested within species) as a random factor in the lme model due to repeated experiments on the same individuals at different temperatures. Prior to the linear mixed effects model analysis, a log transformation on filtration rates was performed in order to meet the assumption of normality, confirmed using QQ plot. Since we were particularly interested in the effects of temperature on filtration rates, a post hoc comparison of estimated marginal means (EMMs) with Tukey HSD adjustment was performed using the R package ‘emmeans’ (Lenth et al. 2019), to evaluate the influence of different temperature on filtration rate.

The water filtration rate of current oyster populations at field sites was calculated using laboratory derived filtration rates at summer temperature (30°C). Filtration rates were calculated per hour per m^2 for each site using mapped density of individuals in 5 cm size-classes. Then, the total hourly filtration per site was calculated by multiplying the filtration rate m^{-2} by the total area of oyster habitat mapped at each site.

Results

The spatial coverage of *Crassostrea* spp. was variable across study sites, ranging from 50% to less than 0.1% of the total mudflat area (Table S1). The total area of oyster bed mapped in this study was limited relative to total mudflat area, with a total of 9.1 hectares (4.5 hectares on Lantau Island and 4.6 hectares in Tolo Channel) of oyster beds found in our study. No accumulation of *Crassostrea* spp. shell was observed at any site, indicating a lack of high relief structure (vertically or laterally) to serve as reef; instead all *Crassostrea* spp. habitats across the surveyed areas are characterised as low relief, sparse (< 50% cover with interspersed mudflat) oyster beds.

Current population demographics

Crassostrea spp. reach sexual maturity at a shell length ≥ 30 mm (based on the sexual maturation rate of *C. bilineata*, Mohan Joseph & Madhyastha 1984; and other *Crassostrea* species, Harding & Mann 2000; Menzel & Nascimento 1991). The current population demographics of *Crassostrea* spp. indicated the most frequent age-class of Hong Kong oysters had just reached sexual maturity (mean shell length = 33.6 mm), regardless of whether they were located in restricted or publicly accessible sites (Fig. S1). Oysters with shell length above 100 mm (presumably to have lived in the field for at more than one spawning season) were only observed at sites with restricted access, suggesting oyster survivorship does not extend much beyond sexual maturation in publicly accessible mudflats in Hong Kong (Fig. S1).

Density of the current oyster populations was highly heterogeneous irrespective of site (high variance relative to mean oyster density). On Lantau Island, mean oyster densities between 1.1 indiv. m^{-2} (0.4) and 14.1 indiv. m^{-2} (4.5) (mean (SE)) were found on publicly accessible mudflats, whereas oyster densities between 28.2 indiv. m^{-2} (9.9) and 92.1 indiv. m^{-2} (18.1) were found at sites with restricted access (Table 1). In Tolo Channel, the overall oyster density in Yung Shue O (61.6 indiv. m^{-2} (10.6)) was less than Kei Ling Ha (90.5 indiv. m^{-2} (27.9) and Ting Kok (100.6 indiv. m^{-2} (31.8)) (Table 1). For the density of sexually mature oysters on Lantau Island, the density on publicly accessible mudflats was lower than the density in restricted areas (8.4 indiv. m^{-2} (2.1) and 44.3 indiv.

m^{-2} (9.8), respectively) (Fig S2). In comparison, the overall density of sexually mature oyster in Tolo Channel was relatively high (38.4 indiv. m^{-2} (7.2)) (Fig S2).

Recruitment rates and seasonal recruit survival

Monthly oyster recruitment during the wet season (April – October 2017) indicated open bays in North and West Lantau Island experienced one peak of spat fall in August (Fig. 2) with the highest recruit density of 197,550 m^{-2} (SE 47,980) on Northwest Lantau Island (Sham Wat). Peak recruit densities were two orders of magnitude lower in more enclosed bays on North and South Lantau (<7,000 recruits m^{-2}; Tai Ho Wan inner, outer and Shui Hau). In contrast, two peaks in recruitment were detected in south Lantau during the wet season, with a major peak in May and a minor peak in August (Fig. 2).

In Tolo Channel, the monthly oyster recruitment over the wet season indicated a large peak in May (Fig. 2), with a mean density of 850,807 indiv. m^{-2} (SE 87,334). Recruit density then sharply declined 273 to 14,454 indiv. m^{-2} (4,998) in July and remained relatively steady throughout the rest of the wet 274 season, with another moderate peak in recruitment in October (26,143 indiv. m^{-2} (4,162); Fig. 2).

The recruit density surviving to reach sexual maturity (SL ≥ 30 mm) on the long-term settlement plates (9-month exposure) indicated substantial variation in the survival of recruits among sites (one-way ANOVA, $F_{9,76} = 18.26$, $p < 0.0001$). The greatest survival to sexual maturity was at the northern Lantau Island sites (Fig. S2). At three sites on north Lantau Island (Tai Ho Wan Inner, Tung Chung and Hau Hok), the density of recruits surviving to maturity was significantly higher than the density of sexually mature individuals in the current population (Tai Ho Wan Inner, unpaired t-test, t=6.57, df = 14.91, $p < 0.0001$; Tung Chung, t = 8.30, df = 8.00, $p < 0.0001$; Hau Hok, t = 4.92, df = 8.00, $p = 0.001$). No recruits were found to have survived to sexual maturity at Shui Hau where the current population of mature oysters was 30 indiv. m^{-2} (SE 4.1).

Water filtration rates

Water filtration rates differed between *C. hongkongensis* and *C. bilineata* (lme, $F_{1, 46} = 5.22$, $p < 0.03$), among shell lengths (lme, $F_{1,68} = 51.73$, $p < 0.0001$) and temperatures (lme, $F_{3,136} = 172.01$, $p < 0.0001$) (Fig. 3). Filtration rates within each species had a positive relationship with shell length and temperature, with temperature having the strongest effect. For *C. hongkongensis*, temperature had a strong positive effect on filtration rates above 20°C (Tukey HSD, $p < 0.001$ between 15 and 25, 15 and 30, 20 and 25 and 20 and 30°C, and $p = 0.0358$ between 25 and 30°C), but the effects of temperature on filtration rates did not differ between 15 and 20°C (Tukey HSD, $p = 0.3449$). For a *C. hongkongensis* individual of 90 mm SL (approximately one to two years of age), filtration rates would reach up to 29.8 L hr^{-1} at 30°C (summer temperatures), approximately five times that at 15°C (5.2 L hr^{-1}). In contrast, an individual *C. bilineata* with 90 mm SL showed filtration rates of 32.2 L hr^{-1} at 30°C, approximately 22 times higher than at 15°C (1.5 L hr^{-1}).

Considering the current population densities, restricted access mudflats at Tai Ho Wan have the highest potential water filtration rates per unit area (1.6 kL m^{-2} h^{-1}) as the remnant habitat is comprised of larger individuals (Table 1, Fig. 4). Conversely, the current population at Ting Kok

(Tolo Channel) is comprised of smaller, more sparsely distributed oysters, but the habitat is ~4 times more extensive than Tai Ho Wan (Table S1). Ting Kok has potential total filtration rates approximately double that of Tai Ho Wan (31.7 versus 16.5 ML h^{-1}, respectively), two orders of magnitude greater than the other sites (Fig. 4).

Discussion

Over 85% of oyster reefs have been lost globally, but the documented cases tend to be in developed nations such as North America, Europe and Australia (Beck et al. 2011; Giles et al. 2018; Pogoda 2019). The degradation of natural oyster reefs in these regions was often recorded through historical fisheries data, maps, and scientific records (zu Ermgassen et al. 2012; Alleway & Connell 2015). These resources were often officially documented and are powerful in providing social motivation and scientific baselines for restoration efforts. In contrast, the historical and current condition of oyster reefs in Asia are rarely recorded (Beck et al. 2011). There are 30 recorded extant Osteridae species in Asia, including 11 species of *Crassostrea*. Although most known natural oyster populations are reported to be over-harvested and have since been maintained by aquaculture in Asia, *Crassostrea* species have been reported to form natural beds and reefs along Asian intertidal shorelines, including northern China (Quan et al. 2012), Thailand (Brohmanonda et al. 1988) and Japan (Smith et al. 2018). Given their wide range of distribution and high diversity within Asia, they have the potential to provide ecosystem services that are valuable to the health and sustainability of coastal waters. In the case of Hong Kong, the pace and scale of coastal transformation has been overwhelmingly rapid since mid-19th century (Morton 1996). Being that north-western Hong Kong served as a key oyster harvest area in Pearl River Delta for at least 700 years (Lam & Morton 2003), making it almost certain that the historical loss of oyster reefs has been extensive, the current evidence hints that any natural oyster reefs that existed in this region were possibly destroyed before documentation. Here, we provide the first assessment of the state of remnant oyster habitats in the region. While we show that there are natural oyster habitats across the coastal waters of Hong Kong, the condition of these habitats is extremely degraded; they do not form oyster reefs *per se* but rather sparsely distributed oyster beds on soft sediment shores. As these oyster populations are characterised by strong recruitment potential, and are therefore likely not recruitment-limited but have substrate limitation superimposed by ongoing heavy recreational harvesting pressures, future oyster restoration efforts should focus on both the addition of hard substrate and increasing protection levels of oyster habitats in Hong Kong.

Such extensive loss of habitats often leads to a negative feedback, where habitats cannot re-establish. Oyster reefs are built through settlement of new recruits on multiple generations of oyster shells, meaning that degraded and functionally extinct reefs often require large-scale restoration efforts to kick-start formation (Brumbaugh & Coen 2009). Such restoration efforts will, however, only be effective where the underlying drivers of degradation are removed, in most cases harvesting (Breitburg et al. 2000; Kennedy et al. 2011). It was beyond the scope of this study to determine the causes of oyster reef loss in Hong Kong, but observations in the field suggest that the current populations are still suppressed by constant recreational and subsistence shellfish harvesting pressure, especially during the extreme low summer tides which provide access to the most intertidal area. This observation is supported by the remnant oyster populations being comprised largely of individuals less than one year old, when they attain a size that the local people consider oysters of harvestable size, suggesting oyster survivorship generally does not exceed beyond the time to sexual maturation in Hong Kong. Further, in the two sites that were protected from harvest by the local village (Tai Ho Wan Inner and Outer), the oyster population is comprised of larger individuals, suggesting that for restoration to be effective additional protection measures will need to be implemented by local authorities.

An underlying prerequisite for the re-establishment of oyster reefs is an adequate supply of larvae to the restoration site. When reefs have been degraded or removed, the low density of reproductive adults can lead to low fertilisation and settlement of recruits, meaning that functionally extinct reefs often require seeding from hatchery stock, substantially magnifying the cost of restoration (Brumbaugh & Coen 2009). The northern Lantau Island Sites are, however, influenced by the discharge from the Pearl River Delta (PRD) (Chau & Jiang 2001), meaning that these sites can also receive recruitment from outside Hong Kong's waters. Indeed, the recruitment rates for northern Lantau Island, which face the flow of the Pearl River, had extremely high recruitment rates. For example, it is likely that the recruits at Sham Wat originated from the western coast of the PRD, as the low density of oysters in the bay was unlikely to be able to provide the 350,000 recruits m^{-2} that settled. Conversely, Tolo Channel is a weakly flushed system with a water resident times of ~28 days that does not have connection to the PRD (Xu et al. 2010). The overall high recruitment rate was likely contributed by the local populations alone despite evidence of degradation, suggesting that oyster habitats in Tolo Channel (*C. bilineata* dominated) are currently self-recruiting. Therefore, while the source of recruits is likely to differ in the western and eastern waters of Hong Kong, high natural recruitment levels suggest that oyster reef restoration is possible without hatchery intervention.

Survival of recruits (to nine months post-settlement) followed a pattern that could be expected from different environmental conditions. For example, populations on northern Lantau Island had high densities of individuals surviving to maturity, while on southern Lantau none of the recruits survived to nine months. This differential survival is likely because of the smaller influence of the Pearl River on the southern Lantau Island and the more oceanic salinity of these waters; the *Crassostrea* spp. reported here are naturally found in brackish waters (Lam & Morton 2003). This does not preclude restoration in these locations, however, as some species, including *C. ariakensis* which was historically reported in Hong Kong (Lam & Morton 2004), tolerate higher salinity (Calvo et al. 2001). Therefore, despite high natural recruitment, oyster habitats on west and south Lantau Island and in Tolo Channel will likely have slower development following restoration unless native species tolerant of higher salinity are re-introduced (e.g. *C. ariakensis*). While our recruitment trials are ‘proof of concept’ and outcomes might be different when restoration efforts are scaled up (Fitzsimons et al. 2020), this knowledge will provide a valuable baseline for understanding the restoration potential through natural recruitment in Hong Kong. When assessing the feasibility of restoration, the open bays on the northern Lantau Island show the greatest initial potential for restoration among the studied sites because: 1) the waters were more estuarine due to strong influence of the Pearl River Delta, suiting the biology of the dominant species; and 2) the high survival rate of recruits to sexual maturity after just one season compared to that seen in other established restoration programs overseas (Schulte et al. 2009; La Peyre et al. 2014).

Given the high densities of oysters that survived on our settlement plates in the northern Lantau Island sites, our data highlight the natural oyster habitats in Hong Kong have high natural recruitment levels but are substrate limited. As substrate limitation indicates a lack of reef structure for natural larval settlement (Brumbaugh & Coen 2009), future restoration efforts in Hong Kong should focus on the addition of hard substrate such as oyster shell, as substrate addition has shown to be effective in restoration projects in Chesapeake Bay and the Gulf Coast in the United States (Hernández et al. 2018). More importantly, however, increased supply of substrate may not be a sufficient action by itself as field observations suggest most of the current oyster populations in Hong Kong are still suppressed by ongoing recreational and harvesting pressure. Since the oyster populations protected by local village (Tai Ho Wan outer and inner) generally had larger oysters than those in sites with public access, increasing the protection level of shellfish habitats around Hong Kong would also assist in the long-term maintenance of the density and longevity of restored oyster populations. Therefore, future restoration efforts on heavily populated coastlines in Hong Kong and the broader region need to focus both on the ecology (mainly substrate addition) and the users (liaising with officials and local community groups for increased protection of restoration sites) to make restoration sustainable in the longer term.

The dominant native species of oyster that are likely to form reefs in the western and eastern waters of Hong Kong (*C. hongkongensis* and *C. bilineaeta*, respectively) showed high filtration rates at summer temperatures, amongst the highest recorded for any species of bivalve (oysters included) globally (van der Schatte Olivier et al. 2020). Given that we performed repeated filtration experiments on the same individuals across different temperatures, oysters could have experienced increased stress levels or may not have been fully acclimatised to lower temperatures, and therefore exhibited reduced filtration rates at the lower temperatures (15 and 20˚C). Despite this potential acclimation stress, however, temperature had a significant effect on filtration rates (with linear mixed effect model taking repeated experiments on the same oysters taken into account), highlighting high and low filtration rates can be linked to summer and winter temperatures, respectively. Whilst these individual rates are high in the summer, the filtration capacity of remnant populations are low because of the combined effects of the small size of individuals, sparse densities, and limited extent of habitat; the highest total filtration rates for the populations we surveyed would only be 31.7 megalitre (ML) h^{-1} in summer (based on experimental filtration rates at 30˚C), with most of the remnant populations two orders of magnitude less. If, however, local reefs were restored to a density of 500 indiv. m^{-2}, which seems achievable based on recruitment potential and survivorship (over nine months) documented here, population filtration capacities could be increased by over 100 times, or over 3 gigalitres (GL) h^{-1}, without increasing habitat coverage. Dramatic and/or noticeable difference in population filtration capacity has also been reported between the historic (non-degraded) and current (degraded) *C. virginica* reefs in the United States (zu Ermgassen et al. 2012), as well as between degraded and restored oyster reefs based on modelling (but influenced by local hydrodynamics, seasonality and species) (Gray et al. 2019). Therefore, restoring oyster reefs in Hong Kong can have a positive effect on the water quality within the vicinity of the reefs themselves, and possibly adjacent waters subject to water flows and water residence time. More importantly, oyster reef restoration in Hong Kong could be substantially achieved without expanding the areal extent of the current oyster habitat (currently <10% of habitat area). Any future broader-scale restoration efforts such as expanding the size of habitat for restoration, as seen in other parts of the world (e.g., La Peyre et al. 2014; Gillies et al. 2017; Hancock et al. 2019), could provide even greater benefits to water quality improvement in Hong Kong.

Aside from water filtration, oyster reefs can provide multiple ecosystem services including denitrification (Kellogg et al. 2013), shoreline protection (Ysebaert et al. 2018) and fish and mobile invertebrate production (zu Ermgassen et al. 2016). Given that Hong Kong is a global hotspot for marine biodiversity (Ng et al. 2016), with the waters around Lantau Island and in Tolo Channel often experiencing heavy loads of organic pollution (Yin et al. 2000; Lei et al. 2018), and that these natural estuarine ecosystems are effectively locally extinct, the benefits of restored reefs on biodiversity, water quality, sediment deposition, nutrient cycling, and production of commercially valuable species (e.g. fish, shellfish and crabs) are likely to be high. Further, demonstration of successful restoration in one of Asia's coastal mega-cities can act as an exemplar, providing evidence for the societal benefits of ecological restoration within the region. Hong Kong sits in one of the most intensively developed coastlines in Asia. This history, however, provides an opportunity as establishing effective habitat restoration would not only improve the local ecosystems and provide enhanced services; it can also demonstrate the techniques and potential for habitat restoration throughout the region. As an example, many of the most productive coastal areas for oyster aquaculture in Southern China rely on the farmers capturing natural spat by providing appropriate settlement habitat (Wang et al. 2010). This activity suggests that these areas are not recruitment-limited and that oyster reef restoration would only require habitat provision and protection, much like in Hong Kong. Yet, the benefits of oyster reefs as a functioning ecosystem, rather than a resource for exploitation, will first need to be demonstrated to local communities by effective restoration and education (McAfee et al. 2019). Ultimately, therefore, a holistic understanding of the benefits of oyster reefs in Hong Kong, to both the environment and society, will be the only way to maintain and protect them against future exploitation and encroachment of coastal development and potentially provide an example for effective ecological restoration within the region.

ACKNOWLEDGEMENTS

We thank the volunteers that helped with the field surveys and density counts on settlement panels (particularly L. Hau, A. Hung, C. Tse), Moses Ma for help with the filtration rate analysis, and G. Stokes and T. Gorman for logistical and field support. This work was funded by a grant from The Nature Conservancy Hong Kong and an *Universitas 21* Fellowship to BDR.

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Table 1. Survey locations, current extent of oyster habitats and oyster densities in Hong Kong. Total mudflat area was calculated using polygons in Google Earth and Area of mapped oyster habitat from the surveys in this study.

Site accessibility	Region	Study site	Total mudflat area (hectares)	Area of mapped oyster habitat (hectares)	% total mudflat area with oyster bed	Average density of oysters (indiv. m^2 (SE))
Restricted	Lantau Island	Tai Ho Wan Inner	16.93	1.04	6.1	92.1 (18.1)
		Tai Ho Wan Outer	1.44	0.59	40.6	28.2 (9.9)
Public	Lantau Island	Hau Hok	1.49	0.78	52.1	10.5 (3.1)
		Tung Chung	300.89	1.22	0.4	1.1 (0.4)
		Yi O	20.53	0.02	0.1	4.7 (2.3)
		Sham Wat	9.65	0.78	8.1	2.3 (0.9)
		Shui Hau	37.38	0.07	0.2	50.3 (4.5)
	Tolo Channel	Ting Kok	33.95	3.95	11.6	100.6 (31.8)
		Kei Ling Ha	13.85	0.33	2.4	90.5 (27.9)
		Yung Shue O	21.82	0.33	1.5	61.6 (10.6)

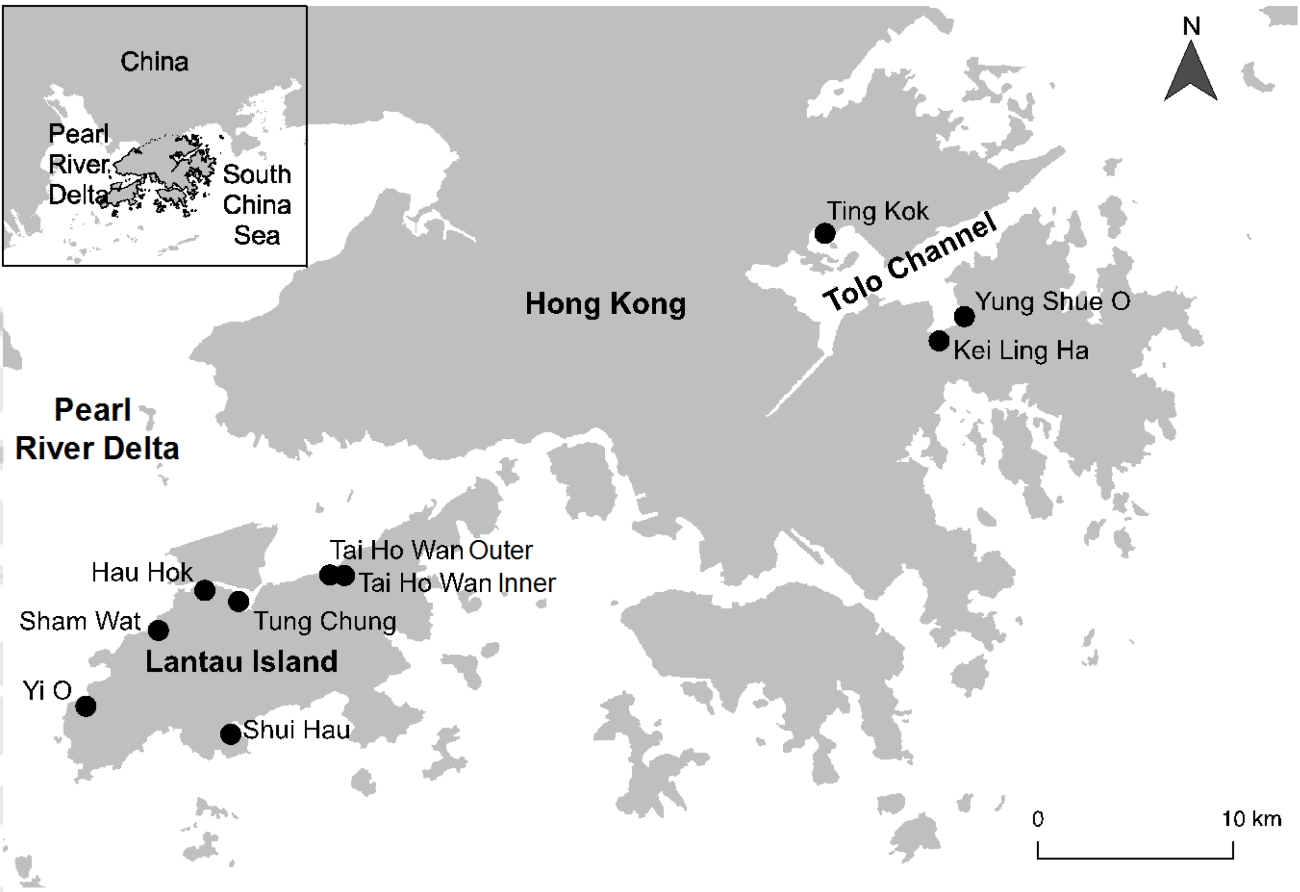

Figure 1. Map of field sites used in this study.

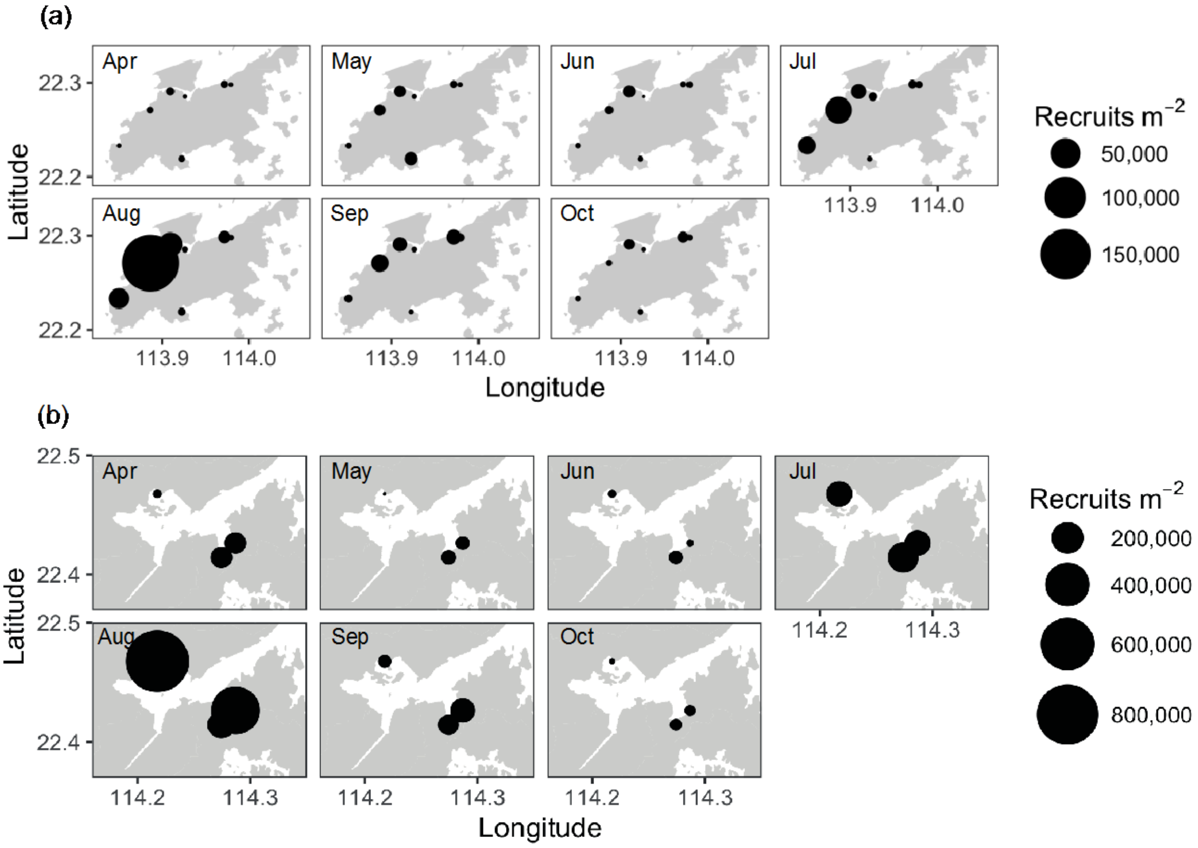

Figure 2. Average monthly recruitment of *Crassostrea* spp. over the breeding season (April – October) on (a) Lantau Island and in (b) Tolo Channel, Hong Kong. The sizes of the bubbles next to each sample site is proportional to the absolute number of average recruitment density (m^{-2}) per month, based on the scale bars on the right. For site information see Table 1.

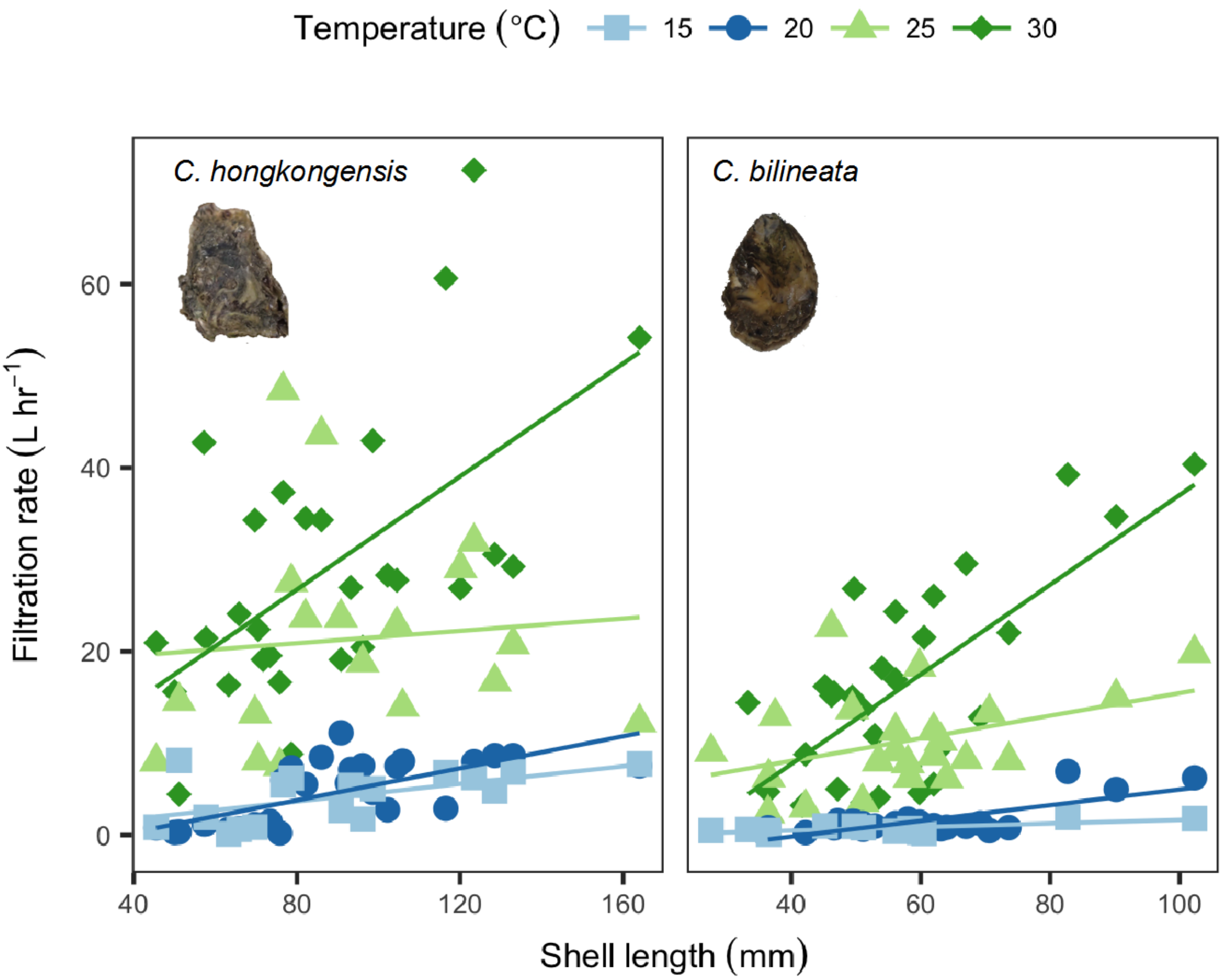

Figure 3. Filtration rates of *Crassostrea hongkongensis* and *C. bilineata* at different shell lengths and temperatures. Filtration rates were calculated in laboratory trials at the four different temperatures by quantifying the change in cell concentration of *Isochrysis galbana* in aquaria of known volume over 40 minutes. Filtration rates had a positive relationship with size for both species ($p < 0.03$), with temperature having a positive effect on filtration rates above 20˚C ($p < 0.0001$).

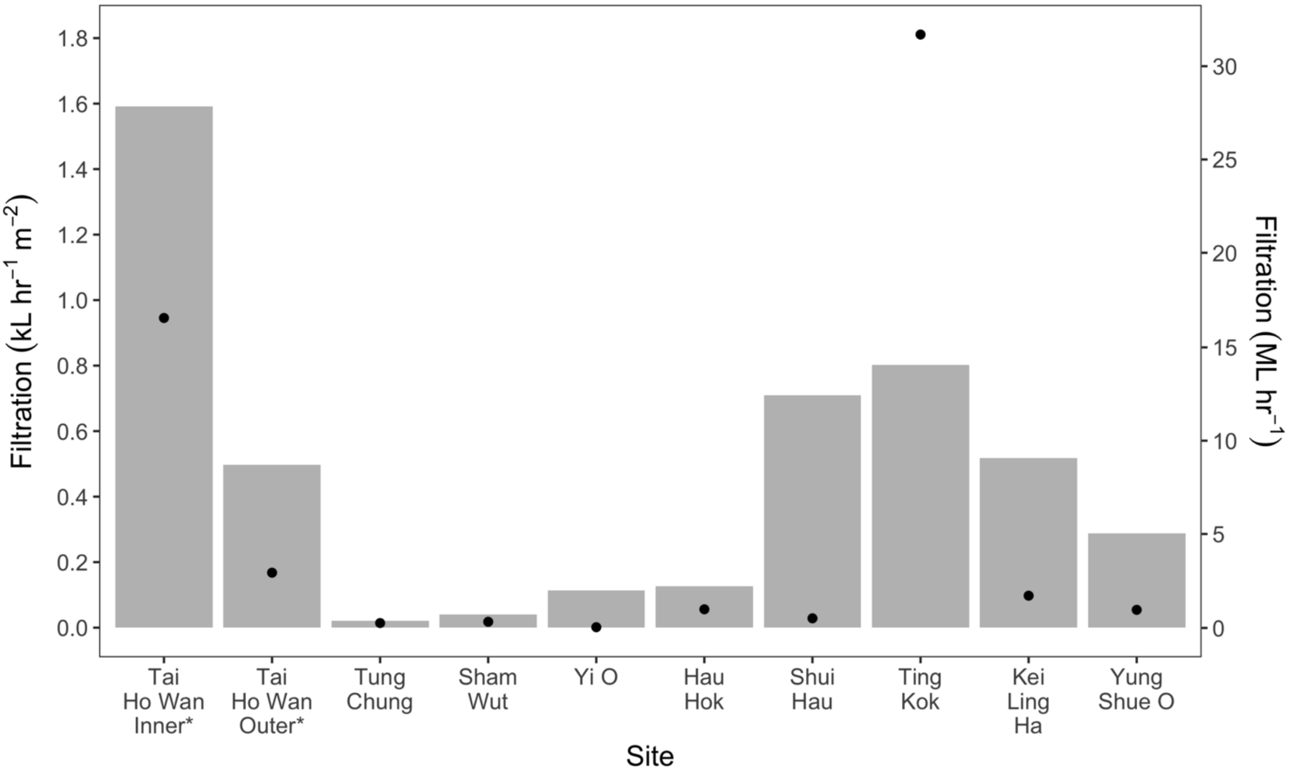

Figure 4. Water filtration of the oyster populations at the study sites expressed for both standardized area (m^{-2}; left axis, bars) and for the total population (right axis, dots). Population filtration rates were calculated using length-specific filtration rates from laboratory trials at 30°C (mean high summer temperature in August/September) for each population's density, size frequency distribution and area of coverage. Summer temperatures were chosen to identify the maximum potential filtration rates that could be provided by current oyster populations.

Supporting Information

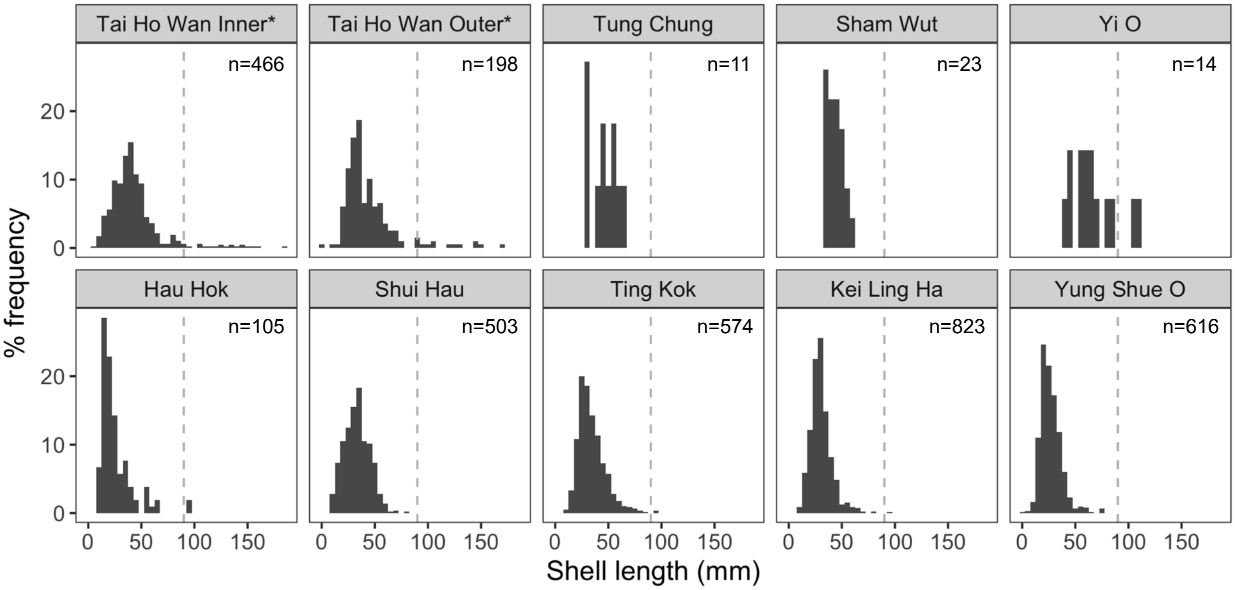

Figure S1. Shell length-frequency distribution of Crassostrea spp. in 5 mm shell length size categories on Lantau Island and Tolo Channel. *survey sites that are protected from public access by a local village. Dash lines = individuals with shell length of 90 mm, approximately one year old.

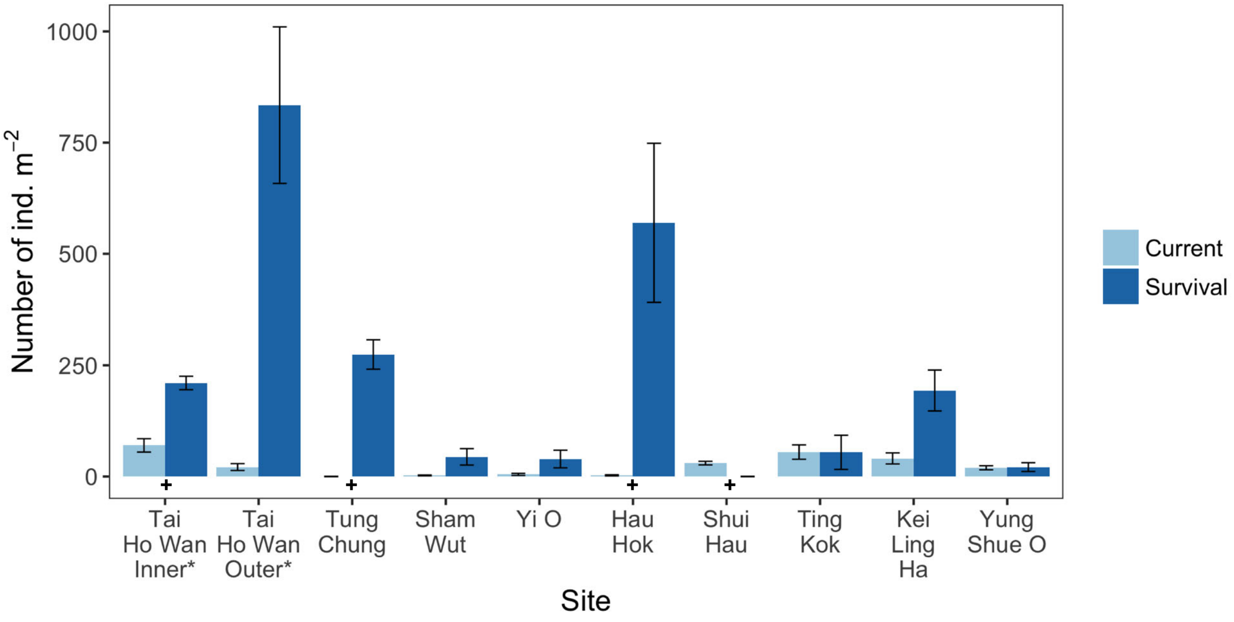

Figure S2. Density of individuals for the current population (light blue bars) and recruit survival after nine months (dark blue bars) of sexually mature *Crassostrea* spp. (shell length ≥ 30 mm) on Lantau Island and Tolo Channel, Hong Kong. Error bars ± SE. For site information see Table S1. *survey sites that are protected from public access by a local village. +bars that are significantly different from each other (unpaired t test) after Bonferroni adjustment (significance level = 0.0025).